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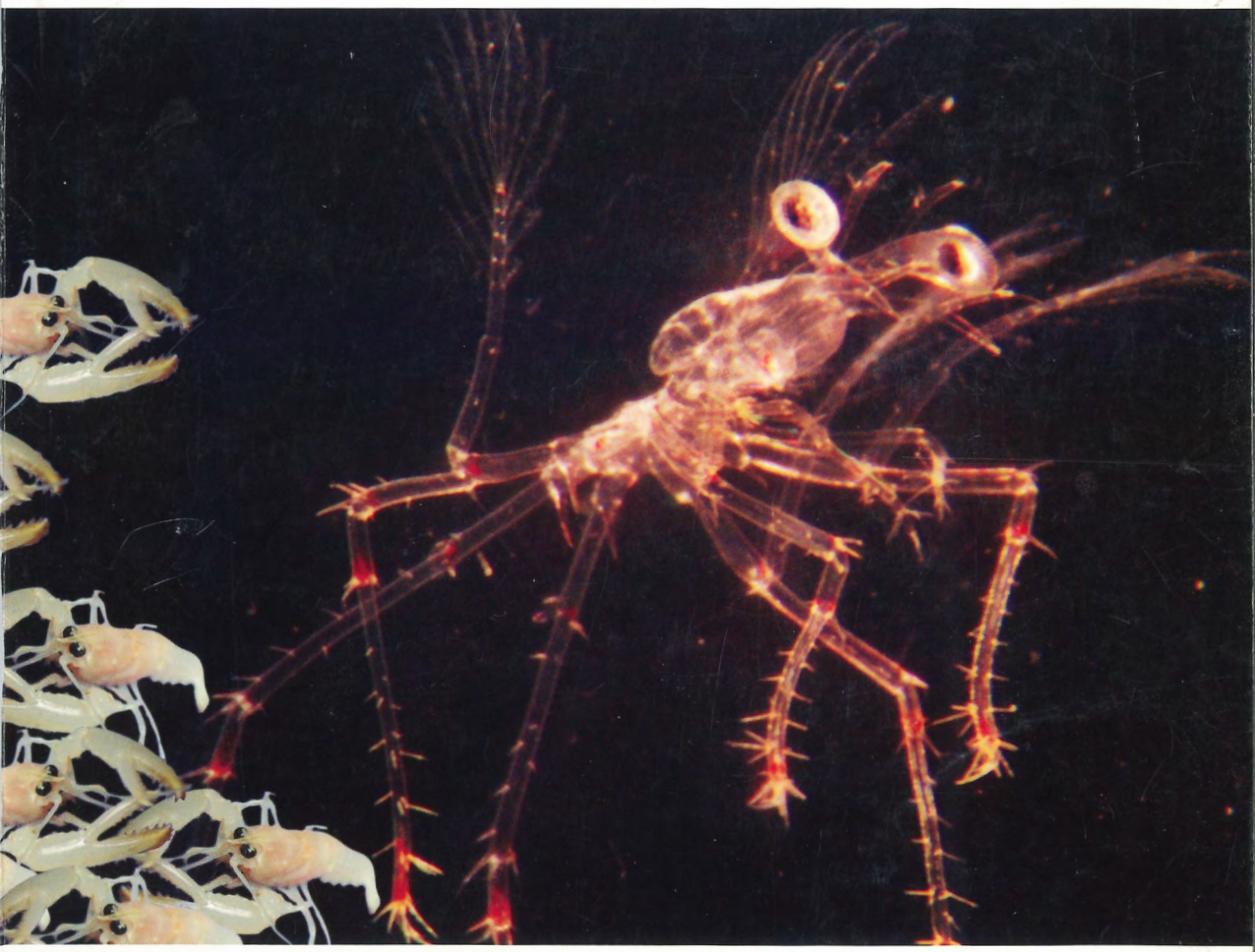

Special issue 1: Lobster biology and management

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Cover: In full flight; a stage-I southern rock lobster (*Jasus edwardsii*) phyllosoma psyching up for an imminent shift in salinity. Photo: Michel Bermudes. (See Bermudes & Ritar pp. 243–249.) White hatchery-reared American lobsters (*Homarus americanus*). Photo: M. Tlusty. (See Tlusty pp. 571–580.)

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Special issue 1: Lobster biology and management

Proceedings of the 7th International Conference and Workshop on Lobster Biology and Management, 8–13 February 2004, Hotel Grand Chancellor, Hobart, Tasmania, Australia

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Foreword

The 7th International Conference and Workshop on Lobster Biology and Management: an introduction

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The 7th International Conference and Workshop on Lobster Biology and Management (ICWL) marked 27 years since the inaugural conference in 1977 held in Perth, Australia. It was also the first time that the conference had returned to Australia. In 1977, 34 scientists and managers from 6 countries met to discuss common issues and themes. Since this time, the ICWL has met in St Andrews, Canada in 1985, Havana, Cuba in 1990, Sanriku, Japan in 1993, Queenstown, New Zealand in 1997, and Key West, United States in 2000. At each meeting the number of delegates, oral presentations and poster presentations continues to grow. Over 150 oral and 48 poster presentations were made from delegates from 19 countries at this conference.

Lobsters are one of the world's premier seafoods. They are found throughout the world's temperate and tropical oceans, in developed and developing countries and the demand for lobsters has resulted in major fisheries around the globe. These fisheries are based on three families: Nephropidae, the clawed lobsters; Palinuridae, the spiny lobsters; and Scyllaridae, the slipper lobsters.

The global distribution of over 50 different species of lobsters has resulted in science and management occurring at different scales and the ICWL provides a focal point for scientists, managers, and industry members to discuss and learn from their different experiences.

With such a broad distribution and commercial importance it is not surprising that lobsters have attracted considerable scientific research. Research needs are broad, including fisheries, management, conservation, and more recently investigations of aquaculture. An indication of the extensive research activity around lobsters is the number of scientific publications—over 1000 have been produced in the last 5 years. Clearly lobsters are an important group of animals for investigation in the field of marine science.

Encouragingly, the quality of presentations and posters from students demonstrated that lobster research will continue to be both innovative and relevant for ensuring optimal allocation of lobster resources whether it be for commercial or recreational fishing, aquaculture, or conservation uses.

The conference was opened by His Excellency Mr Richard Butler, the Governor of Tasmania. In welcoming delegates Mr Butler noted the global distribution of resources and encouraged scientists to pursue a truly global network, particularly in supporting those countries where scientific research and management support and infrastructure was limited. Both recreational and commercial fishing provide important social and economic benefits to rural coastal populations throughout the world. Understanding the biology and ecology of lobsters including their role in the ecosystem and the impact of harvesting was necessary for sustainable management.

Over the last few years new challenges have emerged for scientists, managers, and industry. Co-management and cooperative research is seen as the future model for managing the world's marine resources. Ecosystem based management has refocused research into metapopulation studies including marine protected areas (MPAs) and ecosystem modelling. High prices have also attracted interest in aquaculture and enhancement. Meeting these challenges has resulted in significant advances in the methods used to study lobster resources. These challenges were reflected in the presentations that covered themes of reproduction, disease, modelling and analysis, larval transport and recruitment, spatial patterns, environment and ecosystem interactions, behaviour, assessment methodology, tagging and growth, physiology, management and assessment,

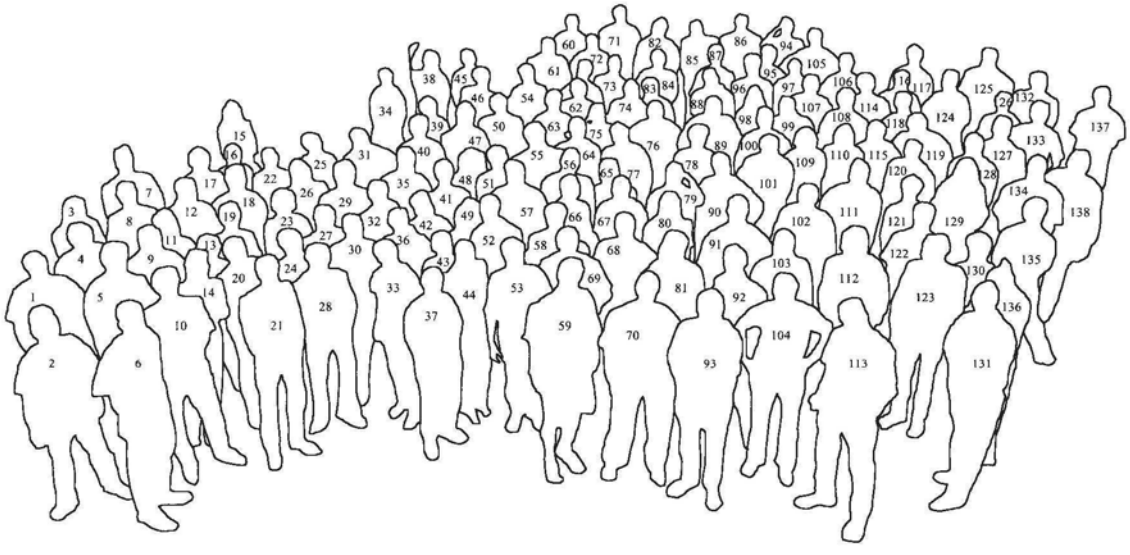
enhancement, aquaculture and husbandry, and post-harvest.

It is not possible to capture the breadth of topics covered but there were several new highlights that are of interest to the Fishing Community. As noted by Dr Jim Penn (WA Fisheries) when introducing the management sessions: "allocation of marine resources is one of the 'burning' issues". The three sectors currently seeking allocation are the commercial and recreational fisheries and the environmental lobby, the later being primarily through MPAs at present. Research identified that managing displaced fishing effort is one of the core requirements when declaring MPAs. Taking the same catch or focusing the same effort on the reduced resource can have catastrophic impacts. Results from both Tasmanian and Spanish research organisations also demonstrated the need to understand the inter-specific interactions, particularly predator-prey relationships. While some fisheries did benefit from the "spillover" effect of lobster moving out of the reserve and into the adjacent fishery, others had decreased lobster abundance through increased predation on juvenile lobsters. The emergence of social and ecosystem science in the conference to address the ESD agenda was also apparent with several papers aimed at broadening management decision making to include these interactions.

GIS studies had increased prominence including the combination of detailed habitat maps with developments in underwater video systems. Habitat mapping techniques are being combined with accurate positioning of fishing gear and tagging studies to provide improved information on population sizes. Other talks related to population estimation highlighted the need for careful consideration of potential biases including growth rate estimates from tagging, catch composition from traps, and catch rate data from fishers.

Larval transport and recruitment processes formed a significant part of the program confirming the importance and strategic significance of this research to managing lobster resources. Lobsters have a complicated and relatively long larval component of their life cycle that is mostly spent in oceanic waters. Substantial advances are being made in modelling transport and recruitment processes based on the collaboration between biologists and physical oceanographers. Subsequent discussions centred on incorporating further biological data into the modelling process. The forum provided an ideal opportunity for groups working in different parts of the world to foster connections and compare modelling techniques.

The aquaculture segment was the largest ever with 30 presentations, indicating its growing importance in countries as diverse as India, Mexico, Japan, United States, and Australia. A highlight was the Japanese study in which phyllosoma larvae cultured from hatch had survival rates greater than 20%, much higher than any previous results, indicating that commercialisation of rock lobster aquaculture



Conference participants: 1, Rod Pearn; 2, Matt Sheehy; 4, Knut Jørstad; 5, Nokome Bentley; 7, David Hall; 8, Juan M. Posada; 9, Ron Brady; 11, Ali's student; 12, David Diaz; 14, Raquel Goni; 15, Verónica Castañeda-Fernández-de-Lara; 16, Cass Hunter; 17, Robert Kilpatrick; 20, M. Vijayakumaran; 21, Sean Sloan; 22, Katherine Tattersall; 23, Barbara Sommers; 24, John Booth; 25, Margaret Barclay; 26, Alison MacDiarmid; 27, Peter Lawton; 28, Adrian Linnane; 29, Julian Addison; 30, Jason Goldstein; 31, Simon Irvine; 32, Mike Dunnington; 33, Louise Gendron; 34, Paul Burch; 35, Tom Idhe; 36, Kathleen Castro; 37, Mike Hall; 38, Malcolm Haddon; 39, Michel Bermudes; 40, Matthew Nelson; 41, Rom Lipcius; 42, Richard Wahle; 43, Gro van der Meeren; 44, Louise Ward; 45, Megan Oliver; 46, Jan Factor; 47, Malcolm Lawson; 48 Natelie Rathke; 49, Rochelle Seitz; 50, Kevin Sullivan; 51, Bill Herrnkind; 53, David Banks; 54, Michael Roberts; 55, Peter Bouwma; 56, Enrique Lozano-Álvarez; 57, Ian Wright; 60, Paul Breen; 62, Richard Musgrove; 63, Andy Cockroft; 65, Patricia Briones-Fourzán; 67, Jean Lavallee; 68, Michael Tlusty; 69, Jeremy Lyle; 70, Alistair Dove; 71, Philippe Lallemande; 72, Simon Anderson; 74, Robert van Barnveld; 75, Raymond George; 76, Kirubagran Ramalingam; 77, Nic Caputi; 78, Dawn Jordan; 79, John Tremblay; 80, Danielle Johnson; 81, Matthew Iacchei; 82, Daryl Sykes; 83, Hilary Revill; 84, William Sharp; 85, Tony Harrison; 86, Abdirahman Kulmiye; 88, John Carragher; 89, Rodney Treloggen; 91, Peter Nichols; 92, Ed Smith; 93, Connor Thomas; 94, Roy Melville-Smith; 95, Caleb Gardner; 96, Hannah Williams; 97, Stewart Frusher; 99, Neil Stump; 100, David Hobday; 101, Neville Perryman; 102, Gerard DiNardo; 103, Serena Gillott; 105, Dave Molloy; 107, Johann Groenveldt; 108, E. V. Radhakrishnan; 109, Rhonda Flint; 110, Irma Laura Peralta Navarro; 112, David Lucas; 114, David Mills; 115, Raúl Pérez-González; 117, Phillipe Ziegler; 118, Arthur Ritar; 120, Indra Jasmine; 121, Richard Campbell; 122, Craig Thomas; 123, Steve Chiswell; 124, Barre Kare; 126, Anthony Tolomei; 128, David Smith; 130, Jiro Kittaka; 131, Steve Montgomery; 132, Mike Geddes; 133, Greg Smith; 134, Joseph O'Malley; 138, Larnce Wichman. *Missing*: Russ Bradford, Barry Bruce, Andew Levings, Bob Steneck, Eric Annis, Tim Ward, Kevin Williams, Brian Patterson, Bruce Phillips, Craig Mackinnon.

may be possible. The business of farming the Bay Lobster (Moreton Bay bug), which also has phyllosoma larvae, is now a reality in Queensland and a paper was presented on culturing of "soft-shell" Bay Lobsters for the United States market.

A special part of the dinner proceedings was an award, and standing ovation, to Professor Jiro Kittaka in recognition of his unparalleled contribution to the development of techniques for palinurid larval culture. John Booth described how Jiro's success with *Jasus lalandii*, the first palinurid to be cultured to the puerulus stage, was followed by several other species being cultured to metamorphosis, and how these accomplishments had led to a greatly improved understanding of palinurid larval biology. Professor Kittaka was presented with the framed original illustration of the final-stage phyllosoma larva of *Jasus edwardsii* (see his paper in these proceedings), drawn by Rick Webber of Museum of New Zealand Te Papa Tongarewa.

Naturally a conference of this magnitude could not be achieved without the generous support of sponsors. We thank the principal sponsor The Australian Government's Fisheries Research and Development Corporation. Other major sponsors included The Tasmanian Aquaculture and Fisheries Institute, The Australian Department of Environment and Heritage, the South Australian Research and Development Institute, Primary Industries and Resources South Australia, Western Australian Fisheries, The National Institute of Water and Atmosphere in New Zealand, The New Zealand Rock Lobster Industry, CSIRO, The Tasmanian Rock Lobster Fishermen's Association, the Department of Primary Industries Victoria, New South Wales Fisheries, the Department of Agriculture, Forestry and Fisheries Australia. Additional sponsorship was provided The Australian Institute of Marine Science, SANTOS, and Darden Restaurants.

Finally we thank Conference Design for their management and planning of the Conference and the staff of the Tasmanian Aquaculture and Fisheries Institute's Crustacean Section who handled all the "behind the scenes" activities to ensure the smooth running of this conference.

We hope that the contacts and networks that were established at this conference will further contribute to high publication rates and quality scientific research on lobsters. We look forward to meeting in Charlottetown, Prince Edward Island, Canada in September 2008 for the 8th International Conference on Lobster Biology and Management.

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Invited review

Lobsters: the search for knowledge continues (and why we need to know!)

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Abstract Lobsters are the focus of very valuable fisheries, and mainly because of this are among the most researched animals on earth. There is a continuing and expanding need for their further study because of changing areas of public interest in their biology and management. They are used as animals for teaching students in a wide range of disciplines, and are species of considerable community interest. The range of scientific studies of lobsters includes: larval ecology, juveniles, behaviour, genetics, stocks, fishing gear and effects of fishing, recreational fishing, disease, post-harvest practices, economics, triple bottom line reporting, aquaculture and enhancement, eco-labelling and certification, ecosystem management, and marine protected areas. Examination of important research questions identified at workshops held at previous lobster conferences indicates that some of these questions are being addressed, but in many instances new priorities for research have occurred because of developing technology in the fishery, increasing recreational fishing, disease, changing catch levels; as well as political developments such as marine protected areas, and changing and continuous demand for new or expanded data sets to address new issues such as eco-labelling. Dissemination of information about lobsters to a wide audience has resulted in a range of methods to achieve better communication including scientific papers, popular magazine articles, fishing magazine articles, and scientific and popular books and films.

Keywords lobsters; knowledge; dissemination of information

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INTRODUCTION

Lobsters, both clawed and spiny, are amongst the most studied animals on the planet. Those of us who study them are commonly asked questions such as "Surely you know everything that it is possible to know about lobsters?"; or "What else could you possibly need to know about lobsters?"

Our replies to such questions tend to be a mixture of laughter and denial, as we attempt to explain to a non-technical audience why we study lobsters at all. We usually retreat into declarations about the size and value of the catch being many 1000s of metric tonnes and worth 100s of millions of dollars, and perhaps point out that the aim of our research is to maintain the sustainability of the stocks and the fishery. At that point we tend to change the subject.

After being asked to give this opening talk, I decided that the questions being asked really do deserve sensible and more comprehensive answers; and so I take this opportunity to suggest what they might be. As a marine biologist I will stick fairly closely to my field of expertise, but I make no apology if I digress slightly into other areas that have become popular in recent years. There are many genera of lobsters but I will try to concentrate on *Homarus* (Fig. 1) and some of the spiny (rock) lobsters, because it was probably familiarity with these species that generated the original questions.

DEFINING KNOWLEDGE

For about 25 years I have subscribed to an abstracting service to provide me with the most up-to-date published material on lobsters. The number of references is astounding. My own restricted

Fig. 1 *Homarus americanus* (from Herrick 1895).

database has over 7500 references. In addition, they cover a huge range of topics, from biology to economics and shipping, and from management to disease and social issues. They are still growing at a phenomenal rate and include new techniques of assessment and analysis, which enable better and different interpretations to be made of existing biological data.

When I started studying rock lobsters with Graham Chittelborough in the 1960s it was probably possible to read all of the papers published annually on lobsters. Now we have all become specialists in one or more disciplines of lobster research and it is impossible to read more than a reduced percentage of the total literature that is produced.

TEACHING

Lobsters of all kinds are useful as animals that can be used as research organisms for teaching students, particularly at university level. Part of the reason for this is that they are tough animals and easily kept alive under aquarium type conditions.

There are studies of vision, sound or vibration reception; biochemical responses to stimuli such as food or chemical odours; the mechanics or development of various parts of the body, including both external morphology and internal musculature; growth studies under various environmental conditions; behaviour of larvae, juveniles and adults; etc.

Not all of these studies would fall under my category of "the search for knowledge continues", although they do add to the pool of knowledge.

Fig. 2 **A**, Phyllosoma larvae and **B**, puerulus stage of *Panulirus cygnus*.

Fig. 3 Early juveniles of *Panulirus cygnus*.

Fig. 4 "White" and "red" phases of *Panulirus cygnus*.

POPULAR PUBLICATIONS AND FILMS

The knowledge gap first seriously came to my attention when my colleague Roy Melville Smith and I were asked to contribute a chapter on western rock lobsters to a popular book "Under Southern Seas: the ecology of Australia's rocky reefs" (Phillips & Melville Smith 1999).

The editor, partly to provide some conformity in the coverage of the chapters, but also to ensure that we did not leave out salient points, provided us with a list of topics. It was an illuminating list. We were amazed how many of the topics we could not provide answers to. For example, what was the maximum age of males and females? How many females can a male fertilise? Does the western rock lobster walk in lines during its offshore migration? What do the phyllosoma larvae eat?

Not only did we not know the answers to these types of questions, but it was also apparent that it was assumed that we would have this basic knowledge of our species. Part of the reason for this assumption

is the number of nature programmes on television. These are extremely popular and dispense vast amounts of information in an authoritative way, although it is not all accurate, sometimes because of the language that is used.

About a year ago, the BBC sent a film crew and a journalist to Western Australia for 6 months to make a film for television about rock lobsters. It was very successful, but this only increased the demand for information.

SCIENTIFIC INFORMATION

The usual basis for the acquisition of additional knowledge about lobsters falls under three objectives. These are: (1) the management of the fisheries; (2) to ensure the sustainability of the stocks; and (3) the continued/and or increased profitability of the fisheries.

These objectives are hard to argue with, as they are motherhood statements familiar to all of us. The lobster fisheries are very valuable industries that, in addition to yielding finance to the industry and the country in which they occur, also provide employment in the catching, processing, and marketing sectors and are integrated in the culture of the societies in the countries in which they are located. Lobsters in Japan are referred to as the "food of the gods".

Every document that I have read concerning good management of a lobster species comments on the depth or lack thereof of the biological information available on the species comprising the fishery. The greater the depth of knowledge, the better the management system that can be devised and the more successfully it can be operated. The western rock lobster is one of the best researched spiny lobster fisheries in the world and it is claimed to be the best managed fishery in the world (Phillips & Brown 1989) and yet there are a lot of topics on which we still do not have adequate data (Phillips & Melville Smith 2003, 2004).

Larval ecology

Our knowledge of the larval cycles of most species is minimal. The western rock lobster *Panulirus cygnus* is a species on which much research into the oceanic cycle of the phyllosoma larvae and puerulus stage (Fig. 2) has taken place (see review by Pearce & Phillips 1994).

Despite descriptions of the diurnal vertical behaviour, which changes with development of the larvae, and an understanding of both the offshore and eventual return transport of the larvae back to the edge of the continental shelf, there are many questions which remain unanswered. As already mentioned, we do not even know what the phyllosoma larvae eat. More importantly, although we know the larvae travel at least 1500 km offshore and are distributed far to the north and the south, we have no idea which of the larvae complete the cycle by returning to the coast of Western Australia, metamorphosing into a pueruli, swimming to the costal reefs, and settling. We also have no idea of the source of the larvae that return. Both coastal and island populations are monitored for breeding stock size but for all we know all of the successful larvae could come from just a few of the breeding stock.

One of the problems of obtaining additional information on lobster larval ecology is the enormous cost of ship time and the other resources needed to undertake sampling in the ocean.

Juveniles

There have been many studies of juvenile lobsters (Fig. 3). The juvenile phase in many species is identified as a "bottleneck" because of density-dependent mortality caused by shortages of shelter and/or food or both. This is seen as an area of opportunity for understanding the recruitment process, and perhaps intervention, and there are many studies in this research area (e.g., Incze et al. 1997 on *Homarus americanus*; Skews et al. 1997 on *Panulirus ornatus*).

Behaviour

There are all sorts of behavioural studies including effect of environmental variables on movements of different phases (Fig. 4), mating, capture by fishing gear, responses to pollution, etc. A number of these have provided valuable information. However, I must profess to have a biased view as to the usefulness of most behavioural studies of lobsters carried out solely in the laboratory. This is based on my observation that in the wild, small juvenile lobsters (carapace 10–20 mm) are nocturnal, non-gregarious, and extremely difficult to find. The occasional specimens that are located and captured, once they have been placed in an aquarium system, run about in daylight after one or two days and will take food from the hand of the person feeding them!

Genetics

The genetic questions still to be answered are almost too numerous to mention! However, Roy Melville Smith (Department of Fisheries pers. comm.) has raised some interesting points about the effects of fishing on the genetic structure of the western rock

lobster population which, through its complex management arrangements comprising minimum sizes for both sexes, maximum sizes for females, protection of spawners (setose-bearing females), and different legal sizes within the season and for different localities, may be encouraging the selection for early maturing, slow growing, individuals. Time and a lot more data analysis will be needed to confirm or reject these ideas.

Stocks

Identity

This is a crucial question for all fisheries management. In some instances it is clear-cut, but in others it is by no means certain.

In its simplest form we have the example of the *Jasus edwardsii* populations in both Australia and New Zealand and discussion about whether the Australian stocks contribute to the New Zealand fishery, and if so, at what level. It was really simple at one stage when we identified the Australian stock by a different name (*Jasus novaehollandiae*), but Smith et al. (1980) produced new data that showed that it was the same species in both countries. The question is, "Is Australia the source for New Zealand rock lobster?" (Chiswell et al. 2003).

The Caribbean *P. argus* populations are a more serious situation. There are fisheries in many countries in the Caribbean, but it is still not possible to identify with certainty the source of the settling pueruli which supply the fisheries. In fact there may be several sources, and these sources may contribute to different populations in different months or years (Silberman et al. 1994).

Stock size

One of the most interesting occurrences in the lobster world has been the nearly doubling of the catch of *H. americanus* between 1992 and 1999 (ASMFC 2000). There are many theories about the reason for this increase, and it has generated extensive review of the data on the fishery (Steneck & Wilson 2001) but as pointed out by Fogarty (1995), "long-term monitoring of critical life history phases must be undertaken if we are to understand the regulatory mechanisms controlling these populations".

An equally interesting question that has yet to be fully explained is the sudden decrease in the growth rates of the South African *Jasus lalandii* lobsters that occurred in the late 1980s, and which is still apparent today.

This change in productivity has been responsible for decreasing Total Allowable Catches from 4000 t in the 1980s to around half of that tonnage in the last decade (Pollock et al. 2000).

Spatially explicit models estimating population size have now called for much more accurate data on the position of the catch and habitat locations. Although not available in the past, modern technology is now providing this type of data on many different scales.

Spawning stock size

The size of the spawning stock needed to maintain the reproductive capacity of a species has been widely debated within the scientific community (Frank & Brickman 2001). The *P. cygnus* fishery use spawning stock size as a major factor in managing the fishery. The *P. cygnus* level is targeted at c. 20% (Hall & Chubb 2001). Hall & Chubb have also described how management controls can be used to increase egg production, but the basic question of the minimum stock size remains unanswered. A 5% level is used as a medium-term target level for *H. americanus* (see Ennis & Fogarty 1997). The correct level is in doubt, but in view of the doubling of the catch in *H. americanus* over the last decade the answer is probably of little interest at the moment.

Fishing gear and effects of fishing

We live in a world of technological improvements. Continual changes are being made to boats, ropes, floats, communication equipment, training of crews and, in some fisheries, pot (trap) design. All such changes affect fishing effort and there are many studies monitoring or measuring this effort, e.g., Frusher et al. (2003) measuring pot selectivity in *J. edwardsii*.

Recreational fishing

Not all countries allow fishing of lobsters for recreational purposes but it is permitted in Australia, New Zealand, South Africa, the United States, and Namibia. These countries are finding that the recreational fishers are taking an increasing proportion of the total catch. This is certainly so in Australia—especially in Western Australia, South Australia, and Tasmania, and in New Zealand and Florida in the United States. What to do about it is another unanswered question (Melville Smith et al. 2000). Commercial fishers want the recreational catches contained, but recreational fishers want to further increase their catch share. The politicians have perhaps noted that there are more votes to be gained from the large numbers of recreational fishers than the smaller number of commercial fishers!

Fig. 5 *Homarus americanus* showing brown shell disease. (Photo: Laura Skrobe, University of Rhode Island, United States.)

Disease

Diseases are not common in wild caught lobsters but a recent outbreak in *H. americanus* is of importance. A wasting disease, Brown Shell (Fig. 5), is affecting lobsters in Long Island Sound (New York and Connecticut), and fishers are concerned that it is a result of the effects of insecticides. It occurs at a significant incidence and is affecting population dynamics by changing natural mortality rates (Stan Cobb pers. comm.).

Post-harvest practices

It is one thing to catch lobsters; it is another to sell them. I am the leader of the FRDC Rock Lobster Post-Harvest Subprogram. It directs studies to assist the rock lobster industry to make profits for Australia. Studies to reduce leg loss, improve cooking practices, improve health and safety, and increase the value of large lobsters are all generating information to assist fishers, processors, and marketers. The list of possible topics is endless because the markets and the products they desire change continually.

Economics

I am not an economist so this will not be a technical comment. However, the point I wish to make is that the collection of this type of data for fisheries management purposes is of fairly recent origin in Australia.

It was the formation of the Australian Fisheries Management Authority in 1992 that established the need for economic data. One of its objectives was the achievement of maximum economic efficiency, whatever that is! Suddenly we were in the economic management business.

Naturally this has called for a whole range of data and its integration with other assessment methods on the fisheries.

Triple bottom line reporting

The method of reporting to the minister, the parliament, and hence the community has changed. As well as stock and catch type information, reports on each fishery now include additional data on Ecosystem Effects, Social Effects, and Economic Effects (Department of Fisheries 2004). All of these now require information which was never necessary in the past. The type of data being collected will also change as more professionals from these additional research areas become involved. We will also have to learn a new language. I certainly do not know what is meant by "social capital".

Aquaculture and enhancement

Lobster aquaculture has been a dream of many people for a long time. Studies on *Homarus gammarus* have resulted in the production of a detailed CD of data needed for the process (Goldstein & Bartko 1999). However, spiny lobster aquaculture is in the developmental stage and it is a fertile area for research activity.

The number of species being examined for suitability for culture or enhancement is large. At the last workshop, which was held in Key West, Florida, there were papers on *Jasus edwardsii*, *J. verreauxi*, *Panulirus ornatus*, *H. gammarus*, *P. argus*, *P. japonicus*, *P. cygnus*, and *P. elephas*; and this workshop will add *P. interruptus* and *P. homarus*, but there are others (Phillips & Liddy 2003).

It is when we enter this research area that we find again the same life cycle questions being asked of

us as we were asked when preparing the book "Under Southern Seas", e.g., how many females can a male fertilise?

Our knowledge of lobsters mating in the wild is minimal. As the activity occurs in deep water and probably at night, this is not surprising. Studies of mating in tanks have been made (Atema & Cobb 1980), particularly in microcosm type tanks, but it is impossible to say how well the results of these studies mirror the situation in the wild. This is irrelevant, or of less importance to research in the wild population, but critical for aquaculture.

Commercial aquaculture of spiny lobsters is many years away, and the questions that need to be answered are numerous including larval rearing conditions, grow out of juveniles, increasing the frequency of moulting and the intermoult duration, suitable diets, and holding conditions. Many are already being tackled, such as the best type of shelters to eliminate or at least reduce cannibalism (Jones et al. 2001), but some have not yet been identified.

Studies with *P. argus* that I observed in Mexico in 1998, showed that on several occasions, juveniles held in captivity developed aggressive behaviour between individuals after c. 6 weeks in captivity. This could not be related to any known factor. There is much to learn if aquaculture is to be successful.

Calls for enhancement of stocks are also with us. Roy Melville Smith and I are involved in a study of the possibilities for *P. cygnus*. After having spent more than a year conducting behavioural studies of pueruli and very early juveniles I am truly aware how little I know about the behaviour of lobsters. The same lobsters that we observe occupying holes or crevices during the day, become extremely active and aggressive to each other during the night. I presume this is what we are calling "normal behaviour", but it seems to me that it is a bit like measuring normal human behaviour from studying an episode of "Big Brother" on television.

Eco-labelling and certification

The Western Rock Lobster Fishery has become the first fishery in the world to be awarded Marine Stewardship Council certification as a well-managed fishery. However, a small number of conditions were imposed on the fishery to ensure that it fully complied with the Principles and Criteria for Sustainable Fishing.

As an example, one of the conditions was:
"Data on Bycatch of Icon Species—Within 12 months of certification, formal monitoring systems in the fishery will have improved arrangements for recording data on the bycatch of, or any other interactions of the fishery with, mammals, seabirds, manta rays, dolphins, or whales."

This has led to a whole new research area including the testing for possible introduction of sea lion exclusion devices in pots.

Another condition was:
"Environmental Management Strategy—Within 24 months of certification, an Environmental Management Strategy (EMS) for the fishery will be prepared and distributed for public comment and input. The EMS will address impacts of the fishery on the environment, and will include proposed objectives, strategies, indicators, and performance measures. The EMS will specify an operational plan, including implementation actions and a supporting program of research. Future research should aim to provide information on the impacts of the fishery on the ecosystem that is at least as scientifically valid as that produced by studies of fished versus unfished areas."

We are therefore talking about ecosystem assessment, so I will move to this as a topic.

Ecosystem management

We have been through a couple of decades with people using words like sustainability and biodiversity and recently there has been an emerging enthusiasm for what is being called ecosystem management. Definitions of what it is vary, but I have chosen that of Link et al. (2002):

"Involves management decisions, which involve a broad awareness of the consequences of fishing or other human actions to an ecosystem.

"Used to infer the necessity of understanding multi-species interactions and questions of altered structure of the biological community (ecosystem stability).

"Presumes a reasonable understanding of the physico-chemical environment and the biological species which describe an ecosystem, plus an understanding of the interactions among and between the species complex and the environment."

All of these call for a lot more information to be considered if we are to provide advice on which confident management decisions can be made in the future.

Marine protected areas

These are definitely flavour of the month and there are numerous discussions taking place as to their suitable size, location, purpose, monitoring of effectiveness, etc. This includes areas which have lobsters and therefore by definition generally excludes fishing, either commercial, recreational, or

both. We have then a direct interest in marine protected areas. But before we can make a decision in support or rejection of a particular area for a reserve we need a lot of information.

An excellent study by Lipcius et al. (2001) showed that for *P. argus*, random selection of a reserve site from four that were studied would yield only a 50% chance of increasing recruitment. They further showed that selection based on habitat quality, the "pristine" nature of the site, or adult density would, in this instance, provide no greater likelihood of success than would random selection—50%. The only strategy that increased the likelihood of selecting a marine reserve that was effective in increasing recruitment was one that incorporated transport processes of the larvae. Clearly a considerable amount of data and modelling was needed to provide the necessary information to select the best area.

Many questions about marine reserves and their effectiveness for lobsters were reported by Childress (1997) from the workshop held in New Zealand in 1997. An attempt at the same time to produce a "position statement" about the utility of lobster reserves ran into difficulties, essentially because of a lack of agreed knowledge.

Subsea pipeline

Just when you think you have heard of everything, along comes another topic. A company is proposing the construction and operation of subsea gas pipelines off the north-east coast of the United States and Canada. Questions being asked are: (1) Could the pipelines act as physical barriers to lobster movement and migration and, in turn, affect lobster survival, reproduction, or catchability?; and (2) Could noise, vibration, or increased water temperatures associated with the pipeline influence movements by attracting or repelling the animals? (Blue Atlantic Transmission System 2003).

A series of short-term experimental research investigations to provide information on lobster behaviour relative to the natural gas pipeline are to be commissioned.

QUESTIONS RAISED AT PREVIOUS WORKSHOPS

As this is one of a series of Conferences and Workshops, it might be interesting to examine if knowledge gaps identified at previous workshops are being filled.

I chose the fifth conference, which was held in New Zealand, because the outcomes of workshops held as part of the meeting were published in Marine and Freshwater Research.

There were a number of reports but I chose only two to consider. First, the oceanic processes report contained recommendations under three headings: (1) data, including molecular tools, and the need for funding of internationally collaborative research; (2) research on distributions, vertical migration, cues that trigger metamorphosis, length of phyllosoma period; and (3) the continuing discovery of new species and unfished populations should be exploited to determine, by molecular techniques, the genetic structure of a population before and after fishing (Cobb 1997).

This is only a summary of a huge list of needs, which Cobb pointed out was not markedly different from a summary of the status of larval dynamics at the time of the 1985 Lobster Workshop (Phillips 1986)! So perhaps the answer is no. However, the modelling studies by David Griffin and colleagues on the possible larval sources and paths for *P. cygnus* in Western Australia would appear to be providing indications of how to proceed to find the answers (Griffin et al. 2001).

Second, the benthic processes in lobster ecology report noted that three of the four themes that dominated the papers in this section of the workshop were new, in the sense that they had not been the explicit focus of attention at previous workshops (Butler 1997).

The fourth theme was not new but revised and expanded on a previous workshop subject. Cobb (1986) commented, "substrate type is a prime factor in determining the geographic distribution of lobsters". He went on to suggest that, "... we should prepare more finely detailed charts of our areas in which we do not simply identify 'good lobster ground' and 'bad lobster ground' but 'good ground for small lobsters'". These points were emphasised at the 1997 workshop, and extended to include other elements of the environment besides substratum temperature, dissolved oxygen, and conspecifics), that vary spatially in concentration and affect the local ecology of lobsters.

This latter example suggests perhaps yes, but that there is a changing and continuous demand for new or expanded data sets.

CLOSING THOUGHTS ON DISSEMINATION OF INFORMATION

Managing fisheries sustainably is a dynamic process. Although some future questions in most fisheries can be identified from the topics I have discussed, it is

inevitable that other unforeseen ones will arise. The challenge for fisheries researchers, managers, and industry, is to have the foresight to identify these potential problems and to have the continued means and ability to address them.

I am sure that you are now more than adequately informed to answer the original questions, but I also gained some other insights during the preparation of this talk.

It is of no value to collect knowledge unless it is disseminated to the people who can use it. With regard to lobsters this is a wide audience including students, scientists, managers, administrators, etc.

When you look at the way we currently tend to prepare material for these workshops it is clear that mostly it is with a view to publication in the journal chosen by the organisers, or we have some other journal in mind. Most papers cover a single species and very focused topics, because this is normal journal style.

This is different to how this series of workshops began. The original workshop was essentially a presentation for review of information on different species, and the main participants were from the United States and Australia. The meeting concentrated on finding ways that the participants could work collaboratively to find solutions to research questions discussed at the meeting. Publication of the review of this material became the two volume books "The biology and management of lobsters" (Cobb & Phillips 1980a,b).

Since that time two other spiny lobster books—"Spiny lobster management" (Phillips et al. 1994) and "Spiny lobsters: fisheries and culture" (Phillips & Kittaka 2000)—have been published, which continued the theme of presenting reviews of updated information and an expanded range of topics to include aquaculture and recreational fishing. In addition, a major synthesis of knowledge on *H. americanus* was published (Factor 1995).

These books have made available a vast amount of material to those who do not have access to the past-published material on lobsters. They also present the most updated material on a topic for those who are not privileged, as we are, to attend these workshops and conferences on lobsters.

Reviews are a good idea, but I think it would be useful to commission them differently. I was impressed by the paper of Richard Wahle (2003) examining stock-recruitment relationships in several important species of lobsters (both spiny and clawed) and crabs. It is time we had more of these types of papers. Comparative studies of the biology of spiny lobsters and *Homarus* are rare. In fact in some research areas, comparative studies of different species of spiny lobsters are rare!

We intend to not just talk about this but to take action to remedy the situation. A new book on lobsters has just been commissioned, and it has a different format to the previous books I have mentioned. The authors will synthesise the latest information on a genera rather than a species basis and in so doing compare and contrast species to draw out important conclusions and identify gaps in our knowledge. This leaves the genera-to-genera comparisons open for an enthusiastic author and I hope I am addressing some of those in the audience today.

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REFERENCES

ASMFC (Atlantic States Marine Fisheries Commission) 2000: American Lobster Stock Assessment Report. Washington DC, Atlantic States Marine Fisheries Commission. 350 p.

Atema, J.; Cobb, J. S. 1980: Social behavior. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. Vol. 1: Physiology and behaviour. New York, Academic Press. Pp. 409–450.

Blue Atlantic Transmission System 2003: Proceedings of a workshop on the potential effects of the construction and operation of subsea pipelines on lobster movement and behavior. Canada, Nova Scotia. P. 152

Butler, M. J. 1997: Benthic processes in lobster ecology: report from a workshop. *Marine and Freshwater Research 48*: 659–662.

Childress, M. J. 1997: Marine reserves and their effects on lobster populations: report from a workshop. *Marine and Freshwater Research 48*: 1111–1114.

Chiswell, S.; Wilkin, J.; Booth, J. D.; Stanton, B. 2003: Trans-Tasman Sea larval transport: is Australia a source for New Zealand rock lobsters? *Marine Ecology Progress Series 247*: 173–182.

Cobb, J. S. 1986: Summary of session 6: ecology of population structure. *Canadian Journal of Fisheries and Aquatic Sciences 43*: 2389–2390.

Cobb, J. S. 1997: Oceanic processes affecting lobster larvae: report from a workshop. *Marine and Freshwater Research 48*: 771–775.

Cobb, J. S.; Phillips, B. F. 1980a: The biology and management of lobsters. Vol. 1: Physiology and behaviour. New York, Academic Press. P. 463.

Cobb, J. S.; Phillips, B. F. 1980b: The biology and management of lobsters. Vol. II. Ecology and management. New York, Academic Press. P. 390.

Department of Fisheries 2004: State of the Fisheries Report 2002/2003. Western Australia. P. 235.

Ennis, G. P.; Fogarty, M. J. 1997: Recruitment overfishing reference point for the American lobster, *Homarus americanus*. *Marine and Freshwater Research 48*: 1029–1034.

Factor, J. F. 1995: Biology of the lobster *Homarus americanus*. San Diego, Academic Press. P. 528.

Fogarty, M. J. 1995: Populations, fisheries and management. *In*: Factor, J. F. *ed.* Biology of the lobster *Homarus americanus*. San Diego, Academic Press. Pp. 111–137.

Frank, K. T.; Brickman, D. 2001: Contemporary management issues confronting fisheries science. *Journal of Sea Research 45*: 173–187.

Frusher, S. D.; Hoenig, J. M.; Gardner, C. 2004: Have changes in selectivity masked recruitment declines in crustacean trap fisheries? *Fisheries Research 65*: 467–474.

Goldstein, J. S.; Bartko, S. 1999: Laboratory culture for the American lobster. Boston, New England Aquarium. P. 56.

Griffen, D. A.; Wilkin, J. L.; Chubb, C. F.; Pearce, A. F.; Caputi, N. 2001: Mesoscale oceanographic data analysis and data assimilative modelling with application to Western Australian fisheries. Hobart, CSIRO Marine Research. P. 52.

Hall, N.; Chubb, C. F. 2001: The status of the western rock lobster, *Panulirus cygnus*, fishery and the effectiveness of management controls in increasing egg production of the stock. *Marine and Freshwater Research 52*: 1657–1668.

Herrick, F. H. 1895: The American lobster: a study of its habits and development. *Bulletin of United States Fisheries Commission 15*: 1–252.

Incze, L. S.; Whale, R. A.; Cobb, J. S. 1997: Quantitative relationships between postlarval production and benthic recruitment in lobster, *Homarus americanus*. *Marine and Freshwater Research 48*: 729–744.

Jones, C. M.; Linton, L.; Horton, D.; Bowman, W. 2001: Effect of density on growth and survival of ornate rock lobster, *Panulirus ornatus* (Fabricius, 1798), in a flow-through raceway system. *Marine and Freshwater Research 52*: 1425–1429.

Link, J. S.; Brodziak, J. K. T.; Edwards, S. F.; Overholtz, D. M.; Jossi, J. W.; Smith, T. D.; Fogarty, M. J. 2002: Marine ecosystem assessment in a fisheries management context. *Canadian Journal of Fisheries and Aquatic Science 59*: 1429–1440.

Lipcius, R. N.; Stockhausen, W. T.; Eggleston, D. B. 2001: Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. *Marine and Freshwater Research 52*: 1589–98.

Melville-Smith, R.; Phillips, B. F.; Penn, J. 2000: Recreational spiny lobster fisheries-research and management. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. Oxford, Fishing News Books. Pp. 447–462.

Pearce, A. F.; Phillips, B. F. 1994: Oceanic processes, puerulus settlement and recruitment of the western rock lobster *Panulirus cygnus*. *In*: Sammarco, P.; Heron, M. *ed.* The bio-physics of marine larval dispersal. Washington DC, American Geophysical Union. Pp. 279–303.

Phillips, B. F. 1986: Summary of session 3: larval dynamics. *Canadian Journal of Fisheries and Aquatic Sciences 43*: 2380–2382.

Phillips, B. F.; Brown, R. S. 1989: The west Australian rock lobster fishery: research for management. *In*: Caddy, J. F. *ed.* Marine invertebrate fisheries: their assessment and management. New York, John Wiley & Sons. Pp. 159–181.

Phillips, B. F.; Kittaka, J. *ed.* 2000: Spiny lobsters: fisheries and culture. Oxford, Fishing News Books. P. 679.

Phillips, B. F.; Liddy, G. C. 2003: Recent developments in spiny lobster aquaculture. *In*: Phillips, B. F.; Magrey, B.; Zhou, Y. *ed.* Proceedings of third World Fisheries Congress, American Fisheries Society. Pp. 43–57.

Phillips, B. F.; Melville-Smith, R. 1999: Western rock lobsters. *In*: Andrew, N. *ed.* Under southern seas. Sydney, University of New South Wales Press. Pp. 118–125.

Phillips, B. F.; Melville-Smith, R. S. 2003: Sustainability of the western rock lobster fishery: past progress and future challenges. Perth, Australia, Curtin University of Technology. *Department of Biology Bulletin No. 25*: 24.

Phillips, B. F.; Melville-Smith, R. S. 2004: Sustainability of the western rock lobster fishery: a review of past progress and future. *Biological Bulletin* (In press).

Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* 1994: Spiny lobster management. London, Fishing News Books. P. 550.

Pollock, P. E.; Crockroft, A. C.; Groeneveld, J. C.; Schoeman, D. S. 2000: The commercial fisheries for *Jasus* and *Palinurus* species in the south-east Atlantic and south-east Indian Oceans. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. Oxford, Fishing News Books. Pp. 105–120.

Silberman, J. D.; Sarver, S. K.; Walsh, P. J. 1994: Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus*. *Marine Biology 120*: 601–608.

Smith, P. J.; McKoy, J. L.; Machin, P. J. 1980: Genetic variation in the rock lobsters *Jasus edwardsii* and *Jasus novaehollandiae*. *New Zealand Journal of Marine and Freshwater Research 14*: 55–63.

Skews, T. D.; Dennis, D. M.; Pitcher, C. R.; Long, B. G. 1997: Age structure of *Panulirus ornatus* in two habitats in Torres Strait, Australia. *Marine and Freshwater Research 48*: 745–750.

Steneck, R. S.; Wilson, C. J. 2001: Large scale and long term, spatial and temporal patterns in demography and landings of the American Lobster, *Homarus americanus*, in Maine. *Marine and Freshwater Research 52*: 1303–1319.

Wahle, R. A. 2003: Revealing stock-recruitment relationships in lobsters and crabs: is experimental ecology the key? *Fisheries Research 65*: 3–32.

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Development and metabolic rate of stage I spiny lobster (*Jasus edwardsii*) larvae under constant and fluctuating salinities

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Abstract The effects of fluctuating salinity on the development and metabolic rate of stage I *Jasus edwardsii* larvae were investigated. *J. edwardsii* larvae were reared from hatching through to stage II under continuous salinity regimes at 28, 31, 34, and 37 psu, and under repeated exposure to 28, 31, and 37 psu from a salinity of 34 psu. Continuous exposure to salinities between 28 and 37 psu did not affect the duration of larval development. In the repeated exposure treatments, only larvae subjected to 28 psu developed slower than those in the 34 psu continuous exposure group. Although post-moult growth to stage II was not suppressed by fluctuating salinity in the 31 and 37 psu groups, larvae repeatedly exposed to 28 psu and larvae under continuous salinities of 28, 31, and 37 psu were significantly smaller than those from the 34 psu continuous treatment. The effect of salinity acclimation on the respiratory response of mid-stage I larvae was examined in a second experiment. The reduced oxygen consumption of acclimated larvae at subnormal salinities (i.e., 28 psu) was characteristic of stenohaline organisms, and overall there was little relationship between metabolic rate and larval growth performance. From the results obtained in this study we recommend the monitoring and control of environmental salinity for the propagation of *J. edwardsii* larvae to prevent prolonged exposure to suboptimal salinities.

Keywords *Jasus edwardsii*; larvae; salinity; growth; oxygen consumption

INTRODUCTION

The propagation of the southern rock lobster (*Jasus edwardsii* Hutton) is one of the current priorities of aquaculture research and development in Tasmania, Australia. Southern rock lobster post-larvae (i.e., pueruli) have been produced in small numbers (Kittaka 1994; Booth 1996). However, high mortalities experienced during larval development highlight the need for further research that addresses culture parameters and to extend our knowledge of the tolerance of phyllosomas to hatchery conditions. In the wild, the early life history of *J. edwardsii* is characterised by a pelagic larval phase occurring in oceanic waters (Booth 1994; Bruce et al. 2000). Keys to the success of the mass production of pueruli may lie either in our ability to mimic these oceanic conditions or in the capacity of phyllosomas to adapt to a hatchery environment. Although not a general rule, many marine hatcheries experience occasional and/or seasonal changes in the quality of the sea water they use to produce seed stock, and these shifts may be detrimental to larval development and survival. At this early stage of the research into the propagation of *J. edwardsii*, it is therefore essential to determine the tolerance of phyllosomas to shifts in water quality variables such as salinity, so as to design suitable culture systems that maximise larval survival. The study of salinity fluctuation tolerance

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in *J. edwardsii* larvae was further prompted by sudden changes in the salinity of the water at the Marine Research Laboratories of the Tasmanian Aquaculture and Fisheries Research Institute (TAFI MRL), situated on the Derwent River estuary, where research in the propagation of *J. edwardsii* is currently underway. For instance, salinities ranging from 29.5 to 34.5 psu have been recorded (Chamchang 1997). Importantly, though, the estuarine water is drawn from the immediate vicinity of a large naturally-breeding population of *J. edwardsii*, which hatches larvae during a period of likely salinity fluctuations caused by spring rains.

The effects of salinity on marine invertebrates is well documented and ranges from sublethal to lethal according to the magnitude of the change in salinity and the tolerance of the species. Estuarine and coastal crustaceans are often euryhaline and can withstand large shifts in environmental salinity as opposed to their stenohaline oceanic counterparts that live in or actively select isohaline waters (Willmer et al. 2000). In a euryhaline species such as *Carcinus maenas* for instance, larval development is not affected by salinities ranging from 25 to 32 psu (Anger et al. 1998). In contrast, the stenohaline *Pandalus borealis*, known to have an optimal salinity c. 31 psu, does not complete larval development at 25 psu (Wienberg 1982). In culture, sublethal salinities may result in delayed development and reduced growth (Anger et al. 1998; Hereu & Calazans 2000; Pechenik et al. 2000; Kumlu et al. 2001).

The present work was carried out to examine the effect of salinity, either continuous or fluctuating, on the survival, growth, and oxygen consumption of the first stage of the spiny lobster, *J. edwardsii*. The experimental salinities cover the range of salinities occurring at TAFI MRL. Hypersaline conditions were also tested since they may occur in hatcheries working with a recirculation system.

MATERIAL AND METHODS

Origin of larvae

Larvae were sourced from ovigerous females caught off the east coast of Tasmania, Australia from June to October in 1999 and 2000, and brought to TAFI MRL. Newly-hatched larvae were collected from hatching tanks from September to December of both years. The ambient temperature and salinity at the time of hatching ranged from 12.0 to 17.1°C and from 31.2 to 35.3 psu, respectively.

Rearing under constant and fluctuating salinities

To examine the effect of frequent changes in salinity (28, 31, 34, and 37 psu) on the survival and growth of stage I larvae, newly-hatched animals were placed under two salinity regimes: continuous exposure and repeated exposure from a salinity level of 34 psu. In the repeated exposure group, larvae were exposed to their respective treatment salinity (28, 31, or 37 psu) at the start of the trial. After 24 h of exposure to these conditions, larvae were returned to 34 psu for 24 h before a further 24 h exposure to treatment salinity, and so on. The 34 psu continuous exposure treatment was used as a control for repeated exposure. In both continuous and repeated exposure groups, larvae were returned to 34 psu from day 9 after hatching and until moulting to stage II occurred, so that larvae in all treatments would moult under the same conditions. Throughout stage I, larvae in the repeated exposure group were placed 5 times for 24 h each under treatment salinities. Larvae were reared in 60 ml plastic jars with 50 ml water and 25 ppm oxytetracycline. There were 12 larvae per jar (four from each of three broods) and five replicated jars per treatment. Feeding of live *Artemia* (1–2 mm in length), complete water exchange (+25 ppm oxytetracycline), and removal of dead larvae were carried out daily. All larvae that moulted to stage II were measured for total body length (from the anterior of the cephalic shield to the end of the telson) on a Nikon Profile Projector Model 6C to the nearest 25 μm. Minimum (after water exchange) and maximum (before water exchange) salinities were recorded daily and averaged to obtain a salinity measurement for each day. Mean (±SD, n = duration of experiment in days) salinity levels were 28.05 ± 0.14, 31.06 ± 0.08, 34.09 ± 0.15, and 37.08 ± 0.17 psu and are rounded down to the nearest integer in the text. The pH at each salinity was initially adjusted to 8.2 with a few drops of a sodium bicarbonate solution (pH 9). The mean (±SD, n = duration of experiment in days) pH in culture media from daily measurements of initial (after water exchange) and final pH (before water exchange) were 8.01 ± 0.04, 8.02 ± 0.04, 8.04 ± 0.05, and 8.07 ± 0.05 at 28, 31, 34, and 37 psu, respectively. The pH was not significantly different between salinity treatments (ANOVA, $P > 0.05$). Mean (±SD; n = duration of experiment in days) rearing temperature was 18.5 ± 0.2°C.

Routine metabolic rate in acclimated and non-acclimated larvae

The effect of acclimation to different salinities (28, 31, 34, and 37 psu) on the routine metabolic rate (oxygen consumption in unrestrained animals) of

stage I larvae was assessed from measurements of oxygen consumption (VO_2) in acclimated and non-acclimated larvae. Acclimated phyllosomas were 4 days old and reared from hatching at constant salinities (mean ±SD, $n = 3$ days) of 28.6 ± 0.5, 31.7 ± 0.6, and 37.6 ± 0.2 psu. Non-acclimated larvae of the same age had been cultured at the control salinity (mean ±SD, $n = 3$ days) of 34.7 ± 0.4 psu. Larvae from three broods were reared, fed, and water was exchanged as described above. Food was withheld 18 h before the start of the experiment. Mean ±SD ($n = 3$ days) temperature during acclimation was 17.9 ± 0.2°C. There were 10 larvae per jar and animals from each jar were placed in a respirometer (12 ml plastic syringe). In each salinity treatment there were six replicate respirometers (two for each brood) and two control respirometers without larvae. The syringe respirometers were filled with UV-sterilised, 0.2 µm filtered sea water treated with oxytetracycline (25 ppm) to minimise background microbial respiration. Larvae were left to recover from handling stress while acclimating to the respirometers for 1–2 h before a first water sample (0.75 ml) was drawn to determine the initial oxygen saturation level. The oxygen content was left to decline in the respirometer for 4–6 h at an incubation temperature of 17.9°C, and a second water sample was obtained to determine final oxygen tension. Percentage oxygen saturation of initial and final samples was measured with a polarographic electrode connected to a digital controller (Rank Brothers Ltd, United Kingdom). The dry mass (DM) of test animals was determined from three samples of larvae rinsed in 0.9% ammonium formate and dried for 24 h at 60°C (Lovegrove 1962). The mass of each sample was measured to the nearest 10 µg on a precision balance (Mettler AT261 DeltaRange, Mettler-Toledo AG, Switzerland). Oxygen consumption was expressed in µl O_2 mg DM^{-1} h^{-1} after background respiration obtained from the control respirometers was subtracted. Throughout these trials, oxygen saturation in the respirometers was kept above 80% as recommended by Ikeda et al. (2000).

Statistical analysis

All data were tested for normality (Shapiro-Wilk W test) and for homoscedasticity (Levene's test) or for the independence of standard deviation of the magnitude of the means (regression analysis). The effects of salinity on survival, duration of stage I, and growth under continuous and repeated exposure, and the effect of salinity on oxygen consumption in the acclimated and non-acclimated groups were tested with analysis of variance (ANOVA). In the event of significant treatment effect among the repeated exposure groups or non-acclimated groups, comparisons with control (34 psu continuous exposure or 34 psu acclimated group, respectively) were carried out using the Dunnett's test. Tukey's honestly significant difference test (Tukey-HSD) was used for multiple means comparisons among continuous and acclimated groups. Differences in the patterns of response (survival, duration of stage I, growth, and oxygen consumption) between groups (continuous exposure versus repeated and acclimated versus non-acclimated) as well as interaction between the effects of salinity and exposure or acclimation were tested with two-way ANOVA excluding respective 34 psu groups. Linear regression and t-test analyses were used to further highlight specific trends and differences between groups or treatments. Survival data were arcsine square-root transformed before analysis. All computations were carried out with Microsoft Excel 2000 and JMP 3.1 statistical software.

RESULTS

Rearing under constant and fluctuating salinities

Overall mean (±SD) survival of stage I larvae to stage II was 75.0 ± 15.6%. Survival was not affected by salinity in both continuous (ANOVA, $P = 0.665$) and repeated (ANOVA, $P = 0.243$) exposure groups (Table 1). Additionally, the form of exposure to salinity (continuous or repeated) did not influence survival (2-ANOVA, $P = 0.255$).

Overall, there was no significant difference in developmental time between larvae in the continuous and repeated exposure groups (2-ANOVA, $P = 0.690$). However, the pattern of response to salinity was different between the two exposure groups (2-ANOVA, $P < 0.01$). Although continuous exposure

Table 1 Percentage survival (mean ±SD) to stage II in stage I *Jasus edwardsii* larvae reared either under continuous or repeated exposure to different salinities.

	Exposure	
Salinity (psu)	Continuous	Repeated
28	78.00 ± 10.95	68.00 ± 21.68
31	56.00 ± 26.08	80.00 ± 7.07
34	74.00 ± 15.17	–
37	70.00 ± 7.07	76.00 ± 5.48

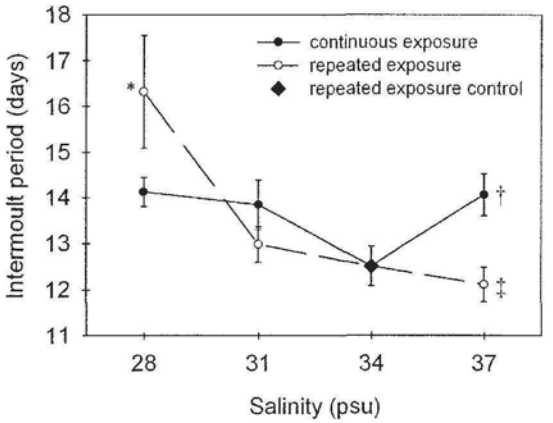

Fig. 1 Mean (±SE) duration of the intermoult period of stage I *Jasus edwardsii* larvae exposed continuously or repeatedly to different salinities. Treatments with different symbols differed significantly (*t* test, $P < 0.05$). (*, significantly different from control (Dunnett's, $P < 0.05$).)

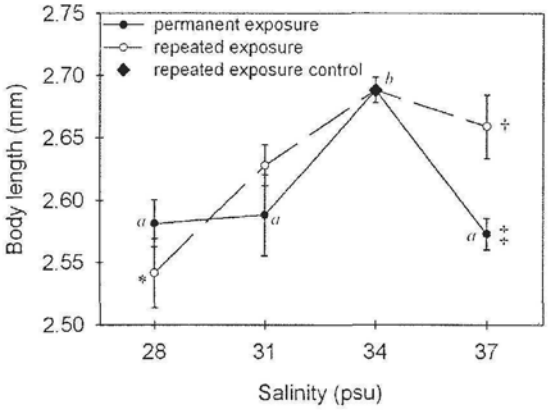

Fig. 2 Mean (±SE) body length at stage II in *Jasus edwardsii* larvae exposed continuously or repeatedly to different salinities during stage I. Treatments with different letters differed significantly (Tukey-HSD, $P < 0.05$). Treatments with different symbols differed significantly (*t* test, $P < 0.05$). (*, significantly different from control (Dunnett's, $P < 0.05$).)

to salinities ranging from 28 to 37 psu had no significant effect on the duration of stage I (ANOVA, $P = 0.067$), repeated exposure within the same range of salinities significantly affected development (ANOVA, $P < 0.01$). Indeed, larval development was significantly slower in the 28 psu repeated exposure group than in the 34 psu continuous regime control (Dunnett's, $P < 0.05$; Fig. 1). The difference in response pattern between continuous and repeated exposure groups was particularly marked at 37 psu (*t* test, $P < 0.05$).

Salinity affected body length growth in both continuous exposure (ANOVA, $P < 0.01$) and repeated exposure (ANOVA, $P < 0.05$) groups (Fig. 2). Overall, the form of exposure to salinity (repeated and continuous) had no significant effect on the body growth of larvae throughout stage I (2-ANOVA, $P = 0.143$). However, the pattern of body growth response to salinity was significantly different between the two groups (2-ANOVA, $P < 0.05$). The continuous exposure to 28, 31, and 37 psu during stage I resulted in significantly reduced post-moult size compared with larvae cultured at 34 psu (Tukey-HSD, $P < 0.05$). In contrast, in the repeated exposure group, only larvae reared at 28 psu moulted to a significantly smaller size (Dunnett's, $P < 0.05$) than larvae in the control group (34 psu continuous exposure). The difference in growth response between repeated and continuous exposure groups was particularly marked at 37 psu (*t* test, $P < 0.05$; Fig. 2).

Routine metabolic rate in acclimated and non-acclimated larvae

A two-way ANOVA excluding the 34 psu acclimated group indicated a significant effect of salinity on the oxygen consumption of stage I larvae ($P < 0.05$; Fig. 3). Additionally, respiratory rates were higher overall in non-acclimated larvae than in acclimated animals (2–ANOVA, $P < 0.01$). Although the influence of salinity on VO_2 was significant in both acclimated (ANOVA, $P < 0.05$) and non-acclimated larvae (ANOVA, $P < 0.05$), the pattern of response to salinity was different between the two groups (2–ANOVA, $P < 0.01$). In acclimated larvae, oxygen consumption was significantly lower at 28 psu than at 31 and 34 psu, and uniform between 31 and 37 psu (Tukey-HSD, $P < 0.05$), whereas in non-acclimated larvae, VO_2 steadily declined from 28 to 37 psu (linear regression, $P < 0.01$). At 28 psu, this difference in response between the two groups was highlighted by a significantly lower VO_2 in non-acclimated phyllosomas than in acclimated larvae (*t* test, $P < 0.0001$).

DISCUSSION

During larval rearing, the survival of stage I *J. edwardsii* larvae was uniformly high over the range of salinities tested (i.e., 28–37 psu), whether in a continuous or repeated exposure environment.

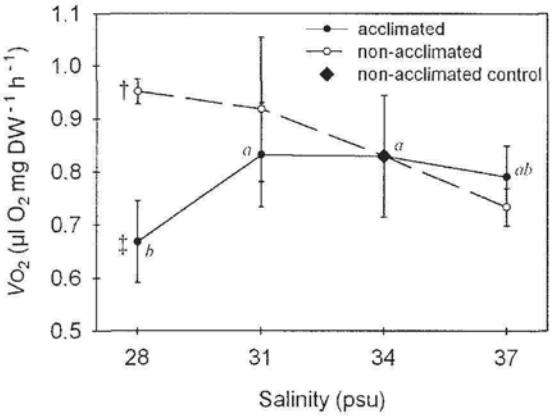

Fig. 3 Mean (±SD) oxygen consumption by stage I *Jasus edwardsii* larvae following a sudden change in salinity from the control condition (34 psu) and at different acclimation salinities. Treatments with different letters differed significantly (Tukey-HSD, $P < 0.05$). Treatments with different symbols differed significantly (t test, $P < 0.05$).

Larvae were exposed to sub and supranormal salinities for a maximum of 9 days, which is only a short period within a larval cycle that may last between 212 and 416 days in hatchery conditions (Kittaka 1994; Booth 1996). Therefore, the uniform survival across treatments observed in the present work does not preclude mortality under longer-term exposure to suboptimal salinities, as with *P. borealis* larvae (Wienberg 1982), *Metapenaeus monoceros* larvae (Kumlu et al. 2001), and *Farfantepenaeus californiensis* juveniles (Villarreal et al. 2003).

Continuous exposure to suboptimal salinities reduced post-moult larval size at 28, 31, and 37 psu. Similarly, slight shifts from optimal salinity (≤ 5 psu) were reported to impair growth in larval marine crustaceans such as *P. borealis* (Wienberg 1982) and in *M. monoceros* (Kumlu et al. 2001). Interestingly, the repeated exposure of *J. edwardsii* larvae to subnormal concentrations during stage I did not suppress development at 31 and 37 psu. However, larvae repeatedly subjected to wider shifts in salinity of larger amplitude (i.e., between 28 and 34 psu) were delayed in their development and moulted to a smaller size than larvae in the control group. This suggests that *J. edwardsii* larvae are not able to adapt to long-term changes in salinity but that they tolerate repeated shifts in salinities of 3 psu of magnitude, whereas exposure to shifts of larger magnitude (i.e., 6 psu) would affect their development. Additionally, growth data indicated that stage I *J. edwardsii* larvae have a greater tolerance for short-term shifts in salinity than for continuous acclimation within the 31–37 psu range. However, this pattern did not hold true for larvae reared at 28 psu. In fact, at 28 psu, development was faster and larvae tended to be larger under continuous exposure than in a fluctuating salinity environment. Frequent shifts in salinity between 28 and 34 psu may have repeatedly altered the concentration of moulting hormones in the body fluid as was reported in fish (Woo et al. 1997) and interfered with the ecdysial processes of phyllosomas. Additionally, larvae repeatedly exposed to 28 psu may have faced significant energetic losses in the repeated accumulation and loss of endogenous proteins, known to occur in the regulation of cell volume in invertebrates during hyper- and hyposaline adjustments (Pierce 1971; Hawkins & Hilbish 1992; McAllen 2003).

The oxygen consumption response to declining salinity (i.e., a steady decline of VO_2 between 28 and 37 psu) observed in non-acclimated *J. edwardsii* larvae was similar to the increase in oxygen consumption at lower salinities reported in adult *Neomysis intermedia* (Simmons & Knight 1975) and adult *Trigriopus bervicornis* (McAllen & Taylor 2001), and to the salinity stress observed in *Cancer magister* megalopas (Brown & Terwilliger 1999). In contrast, the oxygen consumption of salinity acclimated *J. edwardsii* larvae increased above 28 psu before reaching a steady level between 31 and 37 psu. A decline in oxygen consumption at low salinity was also reported in acclimated *F. californiensis* juveniles (Villarreal et al. 2003). According to Kinne (1971), reduced oxygen consumption at subnormal acclimation salinities is characteristic of stenohaline organisms, which suffer from osmotic damage whenever the salinity deviates significantly from normal (i.e., from 34 to 28 psu in *J. edwardsii* larvae).

Previous investigations attempted to relate the metabolic rate of aquatic organisms with their growth performances under different salinities (Anger et al. 1998; Pechenik et al. 2000; Villareal et al. 2003). In the present study, respiratory data in non-acclimated larvae indicated increased energy loss through metabolism under hyposmotic stress (i.e., 28 psu). This may explain the reduced growth recorded in the larvae repeatedly exposed to 28 psu. However, the respirometry results obtained for stage I larvae acclimated at different salinities did not provide convincing physiological evidence for the marked effect of suboptimal salinities on larval development in the continuous exposure group. For

instance, groups of larvae acclimated to 31 and 37 psu had similar oxygen consumption to larvae in the control group (34 psu), which contrast with the reduced growth observed at 31 and 37 psu under continuous exposure. Pechenik et al. (2000) also reported a poor relationship between growth rate and energy expenditure in the euryhaline polychaete (*Capitella* sp. I). Working on *Carcinus maenas* larvae, Anger et al. (1998) concluded that from measurements of oxygen consumption and food assimilation, only the decline in assimilation could provide a sensible explanation for the decrease in larval growth observed under reduced salinities. However, this cannot be confirmed for the present study because food assimilation was not determined.

As for most marine invertebrates, *J. edwardsii* larvae are stenohaline with a weak tolerance for hypo- and hypersaline conditions between 31 and 37 psu. Although we should stress that these findings apply to stage I only, the oceanic habitat of the more advanced larval stages suggest that they would also be stenohaline. Although the survival of stage I larvae was not affected by salinities ranging from 28 to 37 psu, their long-term tolerance may be diminished from the constant exposure to waters shifting only slightly from normal salinity (i.e., c. 34–35 psu) as larval growth was reduced at 31 and 37 psu. However, repeated shifts from normal salinity within the range of 31–37 psu did not appear to affect development during stage I. From these results, we therefore recommend the monitoring and control of ambient salinity during the larval rearing of *J. edwardsii* to avoid prolonged exposure to suboptimal salinities. Measurement of oxygen consumption alone was not sufficient to explain the effects of suboptimal salinities on larval growth. Therefore, a next step in understanding the long-term effects of changes in salinity in phyllosoma should be an integrated physiological approach including the studies of body fluid osmosis, respiration, excretion, feeding, and behaviour. Such detailed investigation would possibly provide the necessary data to assess the effects of constant and fluctuating salinities on a scale beyond the scope of the present study.

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REFERENCES

Anger, K.; Spivak, E.; Luppi, T. 1998: Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. *Journal of Experimental Marine Biology and Ecology 220*: 287–304.

Booth, J. D. 1994: *Jasus edwardsii* larval recruitment off the east coast of New Zealand. *Crustaceana 66*: 295–317.

Booth, J. 1996: Phyllosoma reared to settlement. *The Lobster Newsletter 8(2)*: 1 and 12.

Brown, A. C.; Terwilliger, N. B. 1999: Developmental changes in oxygen uptake in *Cancer magister* (Dana) in response to changes in salinity and temperature. *Journal of Experimental Marine Biology and Ecology 241*: 179–192.

Bruce, B.; Bradford, R.; Griffin, D.; Gardner, C.; Young, J. 2000: A synthesis of existing data on larval rock lobster distribution in southern Australia. Final Report, Project No. 96/107, Fisheries Research & Development Corporation, Australia.

Chamchang, C. K. 1997: Ecology of fish larvae. Unpublished PhD thesis, University of Tasmania, Hobart, Tasmania.

Charmantier, G. 1998: Ontogeny of osmoregulation in crustaceans: a review. *Invertebrate Reproduction and Development 33*: 177–190.

Hawkins, A. J. S.; Hilbish, T. J. 1992: The costs of cell volume regulation: protein metabolism during hyperosmosis adjustment. *Journal of the Marine Biological Association of the United Kingdom 72*: 569–578.

Hereu, C. M.; Calazans, D. 2000: The effect of salinity on larval development of the spider crab *Libinia spinosa* (Brachyura, Majidae) reared in the laboratory. *In*: Shram, F. R. *ed.* Crustacean issues. Vol. 12. The biodiversity crisis and crustacean. Rotterdam, A. A. Balkema. Pp. 605–608.

Ikeda, T.; Torres, J. J.; Hernandez-Leon, S.; Geiger, S. P. 2000: Metabolism. *In*: Harris, R.; Wiebe, P.; Lenz, J.; Skoldal, H. R.; Huntley, M. *ed.* ICES Zooplankton methodology manual. New York, Academic Press. Pp. 455–532.

Kinne, O. 1971: Salinity—Invertebrates. *In*: Kinne, O. *ed.* Marine ecology: a comprehensive, integrated treatise on life in oceans and coastal waters. Vol. 1. London, Wiley & Sons. Pp. 683–1244.

Kittaka, J. 1994: Larval rearing. *In*: Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* Spiny lobster management. London, Blackwell Scientific Publications. Pp. 402–423.

Kumlu, M.; Eroldogan, O. T.; Aktas, M.; Sağlamtimur, B. 2001: Larval growth, survival and development of *Metapenaeus monoceros* (Fabricius) cultured in different salinities. *Aquaculture Research 32*: 81–86.

Lovegrove, T. 1962: The effect of various factors on dry weight values. *Rapports et proces-verbaux des reunions, Conseil Permanent International pour l'Exploration de la Mer 153*: 86–91.

McAllen, R. 2003: Variation in the free amino acid concentrations of the supralittoral rockpool copepod crustacean *Tigriopus brevicornis* during osmotic stress. *Journal of the Marine Biological Association of the United Kingdom 83*: 921–922.

McAllen, R.; Taylor, A. 2001: The effect of salinity change on the oxygen consumption and swimming activity of the high-shore rockpool copepod *Tigriopus brevicornis*. *Journal of Experimental Marine Biology and Ecology 263*: 227–240.

Pechenik, J. A.; Berard, R.; Kerr, L. 2000: Effects of reduced salinity on survival, growth, reproductive success, and energetics of the euryhaline polychaete *Capitella* sp. I. *Journal of Experimental Marine Biology and Ecology 254*: 19–35.

Pierce, S. K. Jr. 1971: A source of solute for volume regulation in marine mussels. *Comparative Biochemistry and Physiology 38A*: 619–635.

Simmons, M. A.; Knight, A. W. 1975: Respiratory response of *Neomysis intermedia* (Crustacea: Mysidacea) to changes in salinity, temperature and season. *Comparative Biochemistry and Physiology 50A*: 181–193.

Sokal, R. R.; Rohlf, F. J. 1995: Biometry. New York, W. H. Freeman & Company.

Villarreal, H.; Hernandez-Llamas, A.; Hewitt, R. 2003: Effects of salinity on growth, survival and oxygen consumption of juvenile brown shrimp, *Farfantepenaeus californiensis* (Holmes). *Aquaculture Research 34*: 187–193.

Wienberg, R. 1982: Studies on the influence of temperature, salinity, light, and feeding rate on laboratory reared larvae of deep sea shrimp, *Pandalus borealis* Krøyer 1838. *Meeresforschung Reports on Marine Research 29*: 136–153.

Willmer, P.; Stone, G.; Johnston, I. 2000: Environmental physiology of animals. London, Blackwell Science.

Woo, N. Y. S.; Leung, T. B.; Chow, C. Y. 1997: Enhancement of growth in tilapia *Oreochromis niloticus* in iso-osmotic medium. *Journal of Applied Ichthyology 13*: 67–71.

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Effects of diet on the growth, survival, and condition of sea-caged adult southern rock lobster, *Jasus edwardsii*

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Abstract Live-holding of fisheries-caught adult southern rock lobster (*Jasus edwardsii*) presents a means of value-adding to the South Australian commercial catch through strategic marketing and product enhancement. This study investigated the effects of live mussel and three manufactured diets on the survival, growth, and condition of sea-caged adult *J. edwardsii* held for an extended period of 29–30 weeks during the closed fishing season. Two trials were conducted in existing industry cage systems. All four diets tested were successful in keeping lobsters alive, promoting growth at moult, and maintaining/improving the condition of lobsters. Unfed lobsters had lowered survival, negative or zero growth at moult, and lowered condition. All lobsters moulted during the trials. Addition of 1% mussel mince to pellets as a feeding stimulant did not increase survival or growth. Males showed substantially greater weight gain at moult than females (means of 8% for females and 17% for males). Biomass of male lobsters increased by up to 16% in one trial treatment, where growth of individual lobsters more than compensated for weight loss caused by mortality. Two different levels of carotenoid (0.15% and 0.25%) proved sufficient to maintain and/or improve colour. Where females were held separate from, but adjacent to, males there was some spawning activity (up to 14%). The one negative outcome of the study was that tail fan damage was found to be a major problem, occurring in both trials and across all diets without apparent pattern. The causes and management of tail fan damage need to be addressed before a long-term live-holding industry can be developed. However, in terms of survival and weight gain, results were very encouraging as improvements in pellet formulation, pellet production, and food delivery can be expected.

Keywords aquaculture; *Jasus edwardsii*; live-holding; moulting; growth; survival; condition

INTRODUCTION

The southern rock lobster, *Jasus edwardsii* (Hutton), fishery is South Australia's most valuable, landing c. 2600 t annually worth an estimated AU$100 million in export revenue. About 95% of the commercial catch is exported live to Asian markets. The fishery is harvested sustainably and there is limited scope for improvement of returns through higher catches. Live-holding of fisheries-caught lobster represents a means of value-adding to the commercial catch through strategic marketing during the closed fishing season from June to October. In addition, live-holding may also enable product enhancement through weight gain, damage repair, and the improvement of condition and colour.

Weight gain and repair of damaged limbs in a live-holding system can only be achieved if lobsters are held through a moult. Moulting shows a seasonal pattern in South Australia that is not yet fully understood. Prescott et al. (1997) found two peaks in moulting activity per year in males of <120 mm carapace length (CL), with one in "summer" (between October and March) and a second in "winter" (between March and October). Larger males of >120 mm CL generally moult only once per year either in summer or winter. Small females of <90 mm CL may moult twice per year, females up to 110 mm CL moult once per year, and females

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>120 mm CL may moult once per year but show only very small moult increments. Thus small female and small and medium sized male lobsters offer the best prospects for growth in live-holding systems. The likely moult increments and seasonality of moulting were taken into account in the present project.

The colour of lobsters in South Australia is related to the depth from which they are caught, with "red" lobsters occurring in the shallower waters, "speckled" lobsters in deep waters, and pale "white" lobsters in the deepest waters (McGarvey et al. 1999). The white lobsters are generally in poorer "condition" than red lobsters and do not handle live export as well as red lobsters. Condition refers here to the physiological state of a lobster as measured by the size and moisture content of the hepatopancreas and abdomen, with a relatively large hepatopancreas and/or abdomen with low moisture content being indicative of an animal in good condition (Dall 1974; Trendall & Prescott 1989; McClain 1995; Musgrove 1998). In addition to good physiological condition, a red coloration is preferred in the Asian markets. Consequently, white lobsters are generally lower priced than red lobsters. Therefore, the ability to improve both the physiological and external condition of white lobsters represents a means of product enhancement through live-holding, an issue that is addressed in the present study.

Growth at moult depends upon the extent of energy and tissue accumulation during the intermoult period, i.e., the condition of the lobster before moult. Maintaining and/or improving condition and accumulating tissue and energy for growth in live-held *J. edwardsii* requires feeding, and a key component of this study was to evaluate alternative feeds. Although there have been several studies in which rock lobsters were fed a natural diet (especially mussels; James & Tong 1997, 1998; Lorkin et al. 1999), very few studies have used a manufactured diet. The present study tested both natural and manufactured diets.

Previous studies by Aquasearch (1996) and Lorkin et al. (1999) have explored the potential for long-term sea-based live-holding of adult *J. edwardsii*. However, although the results from these studies were encouraging, the Aquasearch (1996) study was inconclusive and the Lorkin et al. (1999) study was conducted on a pilot scale. The present study therefore aimed to build on the results of these two studies and to investigate the effects of different feeds on the survival, growth, and condition of red and white male and female lobsters over the winter moult period.

MATERIALS AND METHODS

Two field trials were conducted within South Australia; one in Boston Bay adjacent to the township of Port Lincoln (PL) on Eyre Peninsula, and one in Nepean Bay adjacent to the township of Kingscote on Kangaroo Island (KI). The PL trial ran for 29 weeks from 16 April 1999 to 2 November 1999 and was used to test different diets for their ability to maintain condition and promote growth over the winter moult in red male lobsters. The KI trial ran for 30 weeks from 21–22 April 1999 to 17 November 1999 and was used to test different diets for their ability to improve condition and colour and to promote growth over the winter moult in white male and female lobsters.

Pelleted diets (Table 1) were formulated and manufactured according to advice from Williams et al. (2000). Diet "Dry Pellet + M" (Table 1) was formulated to investigate the effects of mussel flesh inclusion on the survival, growth, and condition of lobsters. Diet "Dry Pellet + C" (Table 1) was formulated to investigate the effectiveness of elevated Carophyll Pink (i.e., carotenoid; Skretting Australia, Cambridge, Tasmania) levels in improving the colour of white lobsters. Dry pellets of 10–20 mm length were produced in a commercial steam pelleting machine after extrusion through a 4-mm diameter die.

For the PL Trial, four feed treatments (No Feed, Dry Pellet, Dry Pellet + M, and Live Mussels) were stocked with 40 red male lobsters per treatment. Each of the four treatments comprised two replicate compartments containing 20 lobsters per compartment. For the KI trial, five treatments were compared. Three of the treatments were stocked with speckled/white female lobsters, and the other two treatments with speckled/white male lobsters. Each of the female and male "fed" treatments (Female—Dry Pellet, Female—Dry Pellet + C, Male—Dry Pellet, and Male—Dry Pellet + C) comprised two replicate compartments containing 15 lobsters per compartment. The Female No Feed treatment comprised a single compartment containing 15 female lobsters. Group stocking of individual compartments was deemed necessary to mimic industry practices.

Trials were conducted in existing industry sea-cage systems comprising a steel floating pontoon with holding bays for lobster cages and a gantry/winch

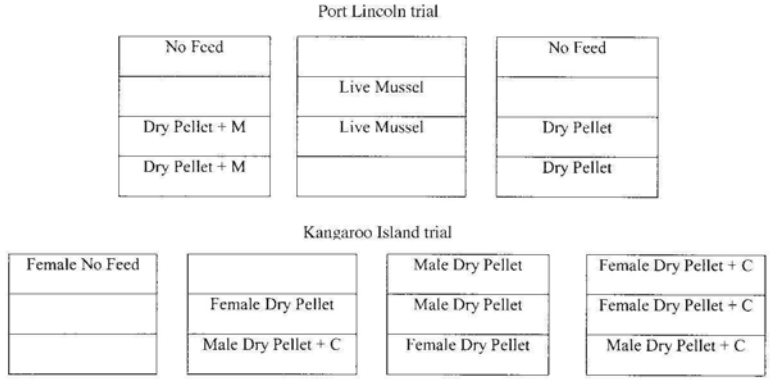

Fig. 1 Spatial arrangement of feed treatments in different compartments across separate industry cages for adult *Jasus edwardsii* held during the Port Lincoln and Kangaroo Island trials conducted in Boston Bay and Nepean Bay, respectively, in South Australia. See Materials and Methods section for descriptions of cage designs.

Table 1 Formulations for the three manufactured pellet diets tested in the Port Lincoln and Kangaroo Island trials conducted in Boston Bay and Nepean Bay, South Australia. Values are % inclusion. Numbers in bold highlight significant formulation differences between diets.

	Diet		
Ingredient	Dry Pellet	Dry Pellet + M	Dry Pellet + C
Fish meal	43.40	43.40	43.40
Wheat gluten	6.00	6.00	6.00
Wheat flour	25.10	24.10	25.00
Mussel mince	0	**1.00**	0
Crustacean meal	20.00	20.00	20.00
Aquabind	3.00	3.00	3.00
Banox E	0.01	0.01	0.01
Vitamin pre-mix	0.20	0.20	0.20
Vitamin C	0.10	0.10	0.10
Carophyll Pink	0.15	0.15	**0.25**
Cholesterol	0.20	0.20	0.20
Lecithin	1.20	1.20	1.20
Fish oil	0.60	0.60	0.60

system for manoeuvring the cages. Lobsters were held within cages consisting of four tiered compartments of 1 m × 1.7 m × 0.3 m at PL, and three tiered compartments of 1.5 m × 1.5 m × 0.5 m at KI. All cages were constructed of polyethylene tubular framing and lined with 12 mm × 12 mm polyethylene oyster mesh. The interior bottom and lower 100 mm of all experimental cage compartments were lined with 3 mm plastic mesh to prevent immediate loss of pellet feeds. Each compartment was fitted with a vertically-oriented PVC feeding chute. All holding bays were covered with shadecloth-lined lids. Stocking densities equated to 11.8 and 6.7 lobsters m^{-2} of bottom compartment surface and 4.0 and 2.0 lobsters m^{-2} of total compartment surface (lobsters can utilise all surfaces) in the PL and KI Trials, respectively.

In an attempt to minimise potential effects of uneaten feed falling onto adjacent lower compartments (and with a limited number of industry cages available), the eight compartments from the four treatments in the PL trial were spread across three separate cages (Fig. 1), whereas the nine compartments from the five treatments in the KI trial were spread across four separate cages (Fig. 1). In each trial, all cages were held within a single holding bay. Thus, physical conditions were the same between cages, but were slightly different within cages because of minor decreases in light intensity from upper to lower compartments. Overall, because of logistical constraints on the numbers of cages/compartments/lobsters, and the need for group stocking, there were some limitations with the

experimental designs and subsequent statistical analyses (see later). However, these limitations did not prevent successful completion of the aims of the study.

Lobsters were fed at a set rate of 2% (dry weight feed) and 2% (wet weight feed) per wet weight of lobster per day for manufactured pellets and live mussels, respectively. Values of 36% wet mussel flesh per whole mussel and 13.7 g for the average weight of a whole mussel were used when calculating the number of live mussels required to maintain a 2% feeding rate. As mussels were fed to lobsters live and unopened, the feeding rate for live mussels actually equated to *ad libitum*. Lobsters on manufactured pellets were fed twice weekly during the daytime, i.e., 7% per feed time.

Lobsters were obtained from commercial lobster fishers and held in processor tanks or sea-cage systems before use in trials. Most lobsters used in the trials were close to the Northern Zone minimum legal size of 102 mm CL and weighed between 450 and 650 g. Twenty lobsters were randomly selected as an initial sacrificial "fishery" sample. At the start of a trial, each lobster from within a compartment was individually marked by pleopod clipping after Lorkin et al. (1999). All lobsters were assessed using the following standard procedure: CL (measured to the nearest 0.1 mm from the antennal platform to the posterior dorsal mid-margin of the carapace); wet weight (measured to the nearest 1 or 5 g); colour (determined by visual assessment of the carapace and classified as red, speckled, or white against standardised photographs); carapace hardness (determined by physical examination and classified as hard or soft); carapace fouling (described by the visual presence of bio-fouling); leg loss (described by the absence of legs and whether the leg loss was old or new); and tail fan damage (described by the presence of raggedness, blistering, and/or erosion after Lorkin et al. (1999) on each of the five tail fans). Raggedness is the breakage and loss of small sections of exoskeleton along the posterior margins of the tail fan. Blistering is the appearance of swollen areas of tissue under the surface of the tail fan. Erosion is the loss of relatively large sections of exoskeleton and tissue from the tail fan and has lately been termed tail fan necrosis (Musgrove et al. 2005).

After initial assessment, sacrificial fishery samples were frozen whole for later condition analyses. Within 2 weeks of commencement, trials were checked for mortalities and these were replaced with live lobsters. Experimental lobsters (including replacements) were then assessed using the standard procedure approximately bi-monthly during the trials. The presence of regrowth on clipped pleopods was also noted, as this is an excellent indicator that a lobster has moulted (Lorkin et al. 1999). Lobsters that had pleopod regrowth were re-clipped so that further moults could be detected. At the completion of each trial, the standard assessment was undertaken. All lobsters were then frozen whole for later condition analyses. Water temperature was recorded in cages every 2 h during trials with Tinytag Plus temperature dataloggers (Gemini Data Loggers, United Kingdom).

Growth increments in CL or wet weight were calculated only for those lobsters that had survived the entire duration of a trial, moulted during the trial, and were hard-shelled at the final assessment. A lobster was deemed to have moulted if it displayed one or more of the following features: pleopod regrowth, leg regrowth, the disappearance of fouling on the carapace, a change in CL of >2 mm, or a substantial change in weight. Pleopod regrowth was generally the most reliable indicator of moulting except in lobsters that had moulted early in a trial; these lobsters generally showed no pleopod regrowth. As the lobsters moulted only once during the trials, the moult increment was taken as the difference in CL or weight between the initial assessment and the final assessment. CL and weight increments were also calculated as percentage changes from the initial measurement. Because of logistical difficulties in collecting uneaten feed, a true feed conversion ratio (FCR) could not be calculated. Rather a "feed supplied conversion ratio" (FSCR) was calculated for those treatments where there was an increase in total treatment biomass over the duration of a trial, where FSCR = dry weight of feed supplied (kg)/biomass gain (kg).

To assess physiological condition, frozen whole lobsters from the fishery and experimental groups were thawed in warm water and then dissected to remove the entire hepatopancreas organ and entire abdominal muscle tissue (including muscle that extended into the carapace). Tissues were weighed wet, dried in an oven for 96 h at 60°C, and then re-weighed to obtain the dry weight. Moisture content (%) and dry weight index (%) for both the hepatopancreas and the abdomen were calculated as 100—((tissue dry weight/tissue wet weight) × 100) and (tissue dry weight/lobster wet weight) × 100, respectively. External condition of lobsters was measured as shell colour and tail fan damage (see earlier).

Statistical tests were used to compare CL and wet weight growth increment measures between the

different feed treatments in each of the trials, and also to compare the four physiological condition measures between the different feed treatments and the sacrificial (fishery) sample in each of the trials. In all tests, data from replicate compartments within treatments were pooled. Pooling of data was considered appropriate because: (1) the assignment of treatments across compartments and cages was non-random and the array of compartments/cages/treatments/fishery samples was unbalanced, thus preventing meaningful use of a randomised-block, nested, or factorial ANOVA, and (2) initial comparisons (using one-way ANOVAs at $\alpha = 0.05$ level) of all compartments/fishery samples indicated only a few marginally significant differences between replicate compartments out of all possible comparisons in the two trials (i.e., six growth and condition measures by eight treatments containing replicate compartments = 48 comparisons). Although comparisons using inferential statistics on both the individual compartment and pooled treatment data constitute pseudoreplication (Hurlbert 1984), it was decided that statistical testing of these data sets was still useful.

Pooled data were tested for normality using the Shapiro-Wilk test and for homogeneity of variances using the Levene test. If data conformed to the assumptions of normality and homogeneity of variances then a parametric one-way ANOVA was performed to detect differences between group means. If the data did not meet the assumptions for parametric testing then a non-parametric Kruskal-Wallis test was used to detect differences between groups. The significance level was set at $\alpha = 0.05$. Differences between groups were detected using Tukey's HSD test after an ANOVA, and using a multiple comparison testing procedure described by Zar (1984) after a Kruskal-Wallis test. All statistical tests (except for the multiple comparison test) were performed using the software package JMP IN Version 3.2 for Windows (SAS Institute Inc.).

RESULTS

Port Lincoln trial

Temperature showed a gradual decrease and then increase over the duration of the trial, reflecting the winter trial period. Temperature averaged 15.2°C, with a minimum of 12.9°C on 13 August and a maximum of 19.0°C on 18 April.

Survival was very high in the Dry Pellet (95%) and Dry Pellet + M (98%) treatments, slightly lower in the Live Mussel treatment (83%), and lowest in the No Feed treatment (65%; Table 2). All surviving lobsters in each treatment moulted once during the trial (Table 2). Relatively few lobsters moulted during the early part of the trial (2% between 16 April and 16 June), with the majority moulting during the middle (53% between 16 June and 25 August) and latter (45% between 25 August and 2 November) stages of the trial. All three of the fed treatments had significantly greater CL and weight percentage increments than the No Feed treatment (Table 2). The Live Mussel treatment had the largest

Table 2 Survival and growth data for adult *Jasus edwardsii* fed on different diets during the Port Lincoln trial conducted in Boston Bay, South Australia. Moulters (%) are surviving lobsters that had moulted during the trial. Carapace length (CL) and weight data are means ± standard errors and were calculated from surviving lobsters that had moulted and were hard-shelled at the completion of the trial. Different superscripts within the same row indicate statistically significant differences ($P < 0.05$).

	No Feed	Dry Pellet	Dry Pellet + M	Live Mussel
Initial no. lobsters	40	40	40	40
Final no. lobsters	26	38	39	33
Survival (%)	65	95	98	83
Initial CL (mm)	104.35 ± 0.34	105.32 ± 0.39	105.49 ± 0.44	104.21 ± 0.42
CL increment (mm)	1.92 ± 0.24	4.45 ± 0.29	4.40 ± 0.28	5.35 ± 0.26
CL increment (%)	1.84 ± 0.23 ^{a}	4.21 ± 0.26 ^{bc}	4.17 ± 0.26 ^{b}	5.14 ± 0.25 ^{c}
n	26	38	39	32
Initial weight (g)	538.2 ± 6.0	551.9 ± 6.5	561.6 ± 6.8	535.5 ± 6.8
Weight increment (g)	17.8 ± 5.0	87.2 ± 5.1	82.8 ± 5.3	98.3 ± 5.3
Weight increment (%)	3.32 ± 0.96 ^{a}	15.75 ± 0.83 ^{bc}	14.80 ± 0.94 ^{b}	18.49 ± 1.02 ^{c}
n	26	38	39	32

mean CL and mean weight increments (5.14% and 18.49%, respectively) and these were significantly greater than those of the Dry Pellet + M treatment but not the Dry Pellet treatment (Table 2).

The No Feed treatment had a large loss of biomass (33.1%) whereas the Live Mussel treatment had a small loss of biomass (3.7%; Table 3). The Dry Pellet and Dry Pellet + M treatments had biomass gains of 10 and 12%, respectively (Table 3). Large amounts of feed were used in each of the three fed treatments (Table 3). Consequently, the FSCRs for the two pellet treatments were very high (Table 3). Hepatopancreas and abdomen dry weight index and moisture content values all indicate that the No Feed lobsters had a significant decline in condition whereas the three fed treatments all maintained condition in comparison to the Fishery sample (Table 4).

The majority of lobsters (c. 70%) in each of the four treatments maintained coloration during the trial. The remainder of these darkened in coloration. There was a high incidence of tail fan damage in each of the four treatments with between 36% and 51% of lobsters developing damage during the trial. Between 16% and 38% developed advanced tail fan damage, i.e., tail fan erosion. There were no apparent patterns of damage that could be related to the feeding treatments.

Kangaroo Island trial

Temperature fluctuated considerably but showed a marked seasonal pattern with lowest temperatures during winter and maximum temperatures during October/November at the end of the trial. Temperature averaged 15.4°C, with a minimum of 12.3°C on 15 May and a maximum of 19.8°C on several days during October.

Survival was very high (93–100%) in all four of the fed treatments (Female Dry Pellet, Female Dry Pellet + C, Male Dry Pellet, and Male Dry Pellet + C) and lowest in the Female No Feed treatment at 80% (Table 5). All surviving lobsters in each treatment moulted once during the trial (Table 5). Relatively few lobsters moulted during the early part of the trial (1% between 20 April and 9 June), with the majority moulting during the middle (49%

Table 3 Biomass returns, feed usage, and feed supplied conversion ratios for adult *Jasus edwardsii* fed on different diets during the Port Lincoln trial conducted in Boston Bay, South Australia. (–, indicates not calculated or not applicable.)

	No Feed	Dry Pellet	Dry Pellet + M	Live Mussel
Initial biomass (kg)	21.614	22.076	22.441	21.611
Final biomass (kg)	14.455	24.288	25.131	20.808
Change in biomass (kg)	–7.159	2.212	2.690	–0.803
Change in biomass (%)	–33.1	10.0	12.0	–3.7
Wet weight of feed used (kg)	–	89.3	92.7	76.8
Dry weight of feed used (kg)	–	84.0	86.2	11.3
Whole wet weight mussels (kg)	–	–	–	263.0
Feed supplied conversion ratio	–	38.0	32.0	–

Table 4 Physiological condition measures for fishery-caught adult *Jasus edwardsii* and live-held adult *J. edwardsii* fed on different diets during the Port Lincoln trial conducted in Boston Bay, South Australia. Values are means ± standard errors. Different superscripts within the same row indicate statistically significant differences ($P < 0.05$). (HDWI, hepatopancreas dry weight index; HMC, hepatopancreas moisture content; ADWI, abdomen dry weight index; AMC, abdomen moisture content.)

	Feed treatment				
	No Feed	Dry Pellet	Dry Pellet +M	Live Mussel	Fishery
HDWI (%)	0.31 ± 0.02^{a}	1.25 ± 0.06^{b}	1.45 ± 0.06^{b}	1.47 ± 0.08^{b}	1.17 ± 0.10^{b}
HMC (%)	84.83 ± 0.55^{a}	66.04 ± 1.24^{b}	63.68 ± 1.21^{b}	60.28 ± 1.46^{b}	66.43 ± 2.11^{b}
ADWI (%)	7.10 ± 0.11^{a}	8.31 ± 0.09^{b}	8.34 ± 0.09^{bc}	8.72 ± 0.13^{c}	8.56 ± 0.15^{bc}
AMC (%)	77.31 ± 0.25^{a}	73.80 ± 0.19^{b}	73.78 ± 0.19^{b}	72.54 ± 0.35^{c}	73.81 ± 0.36^{b}
n	26	33	39	28	20

between 9 June and 1 September) and latter (50% between 1 September and 18 November) stages of the trial. CL and weight increments were smallest in the Female No Feed treatment and largest in the two male treatments (Table 5). In fact the No Feed treatment had a negative value for mean percentage weight increment (Table 5). The two fed female treatments had significantly larger percentage weight increments than the No Feed female treatment (Table 5). The two male treatments had significantly larger CL and weight percentage increments than all three of the Female treatments (Table 5).

The Female No Feed treatment had a substantial loss of biomass whereas the two Female Pellet treatments more-or-less maintained biomass (Table 6). The two Male Pellet treatments had substantial increases in biomass (Table 6). Large amounts of feed were used in each of the Pellet treatments and as such the FSCRs for the two male treatments were high (Table 6).

The physiological condition of the female and male treatments was analysed separately (Tables 7 and 8). For the female lobsters, the condition measures indicate that the No Feed animals significantly declined in condition whereas the Dry Pellet and Dry Pellet + C lobsters significantly improved in condition (Table 7). For the male lobsters, the condition measures indicate that the Dry Pellet and Dry Pellet + C lobsters significantly improved in condition (Table 8). In one instance there was also a significant difference between the two male pellet treatments (Table 8).

Lobsters in all five treatments showed enhanced coloration with only five from a total of 118 lobsters not improving colour. These few showed no pattern among the five feed treatments. There was a very

Table 5 Survival and growth data for adult *Jasus edwardsii* fed on different diets during the Kangaroo Island trial conducted in Nepean Bay, South Australia. Details as for Table 2. (CL, carapace length.)

	Female			Male	
	No Feed	Dry Pellet	Dry Pellet + C	Dry Pellet	Dry Pellet + C
Initial no. lobsters	15	29*	30	30	30
Final no. lobsters	12	27	29	30	30
Survival (%)	80	93	97	100	100
Initial CL (mm)	98.04 ± 0.47	106.89 ± 1.30	104.16 ± 1.01	104.62 ± 0.94	104.87 ± 0.61
CL increment (mm)	0.84 ± 0.25	2.41 ± 0.23	2.34 ± 0.32	4.52 ± 0.40	5.60 ± 0.39
CL increment (%)	0.87 ± 0.26 [a]	2.31 ± 0.24 [a]	2.27 ± 0.31 [a]	4.36 ± 0.40 [b]	5.35 ± 0.38 [b]
n	12	27	29	30	30
Initial weight (g)	489.7 ± 8.1	621.3 ± 20.4	573.0 ± 16.9	546.9 ± 16.6	552.9 ± 10.8
Weight increment (g)	–6.1 ± 6.9	43.9 ± 5.6	42.2 ± 6.1	83.8 ± 6.9	93.7 ± 7.1
Weight increment (%)	–1.08 ± 1.40 [a]	7.67 ± 1.01 [b]	7.78 ± 1.13 [b]	15.82 ± 1.33 [c]	17.11 ± 1.35 [c]
n	12	27	29	30	30

*One lobster from this treatment was lost during transfer to the holding system and was not replaced.

Table 6 Biomass returns, feed usage, and feed supplied conversion ratios for adult *Jasus edwardsii* fed on different diets during the Kangaroo Island trial conducted in Nepean Bay, South Australia. (–, indicates not calculated or not applicable.)

	Female			Male	
	No Feed	Dry Pellet	Dry Pellet + C	Dry Pellet	Dry Pellet + C
Initial biomass (kg)	7.375	17.950	17.131	16.408	16.588
Final biomass (kg)	5.803	17.961	17.841	18.923	19.399
Change in biomass (kg)	–1.572	0.011	0.710	2.515	2.811
Change in biomass (%)	–21.3	0.1	4.1	15.3	16.9
Wet weight of feed used (kg)	–	74.1	71.0	70.7	70.2
Dry weight of feed used (kg)	–	69.6	66.8	66.4	65.9
Feed supplied conversion ratio	–	–	–	26.4	23.4

Table 7 Physiological condition measures for female fishery-caught adult *Jasus edwardsii* and female live-held adult *J. edwardsii* fed on different diets during the Kangaroo Island trial conducted in Nepean Bay, South Australia. Details as for Table 4.

	Feed treatment			
	No Feed	Dry Pellet	Dry Pellet + C	Fishery
HDWI (%)	0.41 ± 0.03 [a]	1.86 ± 0.07 [b]	2.00 ± 0.09 [b]	1.28 ± 0.05 [c]
HMC (%)	82.15 ± 0.74 [a]	54.89 ± 1.18 [b]	55.05 ± 1.42 [b]	62.26 ± 1.14 [c]
ADWI (%)	7.00 ± 0.13 [a]	9.33 ± 0.09 [b]	9.21 ± 0.11 [b]	9.37 ± 0.12 [b]
AMC (%)	76.91 ± 0.27 [a]	71.83 ± 0.20 [b]	72.03 ± 0.26 [b]	72.88 ± 0.22 [c]
n	12	27	29	20

Table 8 Physiological condition measures for male fishery-caught adult *Jasus edwardsii* and male live-held adult *J. edwardsii* fed on different diets during the Kangaroo Island trial conducted in Nepean Bay, South Australia. Details as for Table 4. Fishery sample was the same as that used in the Port Lincoln trial.

	Feed treatment		
	Dry Pellet	Dry Pellet + C	Fishery
HDWI (%)	1.70 ± 0.09 [a]	2.04 ± 0.08 [b]	1.17 ± 0.10 [c]
HMC (%)	59.61 ± 1.50 [a]	57.24 ± 1.10 [a]	66.43 ± 2.11 [b]
ADWI (%)	8.67 ± 0.13 [a]	8.86 ± 0.08 [a]	8.56 ± 0.15 [a]
AMC (%)	72.34 ± 0.25 [a]	72.40 ± 0.19 [a]	73.81 ± 0.36 [b]
n	30	30	20

high incidence of tail fan damage in each of the treatments at the end of the trial (90–100%). Of these lobsters, 41–47% developed the damage during the trial, i.e., around half of the lobsters already had damaged tails at the start of the trial. However, of the 33–43% of lobsters that had tail fan erosion at the end of the trial, almost all had developed it during the trial. There were no apparent patterns of damage that could be related to the feed treatments. Some females in the Dry Pellet (11%) and Dry Pellet + C (14%) treatments had small egg masses at the end of the trial.

DISCUSSION

Survival

Survival of lobsters during the trials could have been affected by a number of factors including their handling before the trials, and environmental conditions, nutrition, and cannibalism during the trials. A general trend across the two trials was that survival was always lower in the unfed (No Feed) treatments than in the fed (Pellet and Live Mussel) treatments. Unfed lobsters may have died directly from a depletion of energy reserves (i.e., starvation) or through cannibalism by other hungry lobsters (see Lorkin et al. 1999), especially when soft-shelled after moulting. Lorkin et al. (1999) also found that survival was lower in unfed lobsters than in fed lobsters. Nonetheless, in the present study the survival of >60% of lobsters in each of the No Feed treatments after extended periods of not being directly fed, demonstrates the incredible tolerance of adult *J. edwardsii* to conditions of poor nutrition. In the fed treatments, survival was high with all 60 male lobsters in the KI trial surviving and only 3 of 80 pellet fed lobsters dying in the PL trial. This high survival was observed at high holding density (with no refuges supplied) and over a period when all lobsters moulted.

Moulting activity

A natural seasonal pattern which synchronises moulting during late winter/early spring (see Prescott et al. 1997) probably affected the timing of moulting in the present study, as almost all surviving lobsters moulted between June and November. Aquasearch (1996) also recorded high levels of moulting activity during winter for *J. edwardsii* held in sea-cages in Boston Bay. All male and female lobsters in the No Feed treatments of both trials also moulted in the

present study, thus demonstrating the strength of the winter seasonal pattern of moulting in lobsters around the legal size.

Growth at moult

Growth of lobsters at moult during the trials could have been affected by a number of factors including their prior handling, their moult stage and nutritional status upon entry, and environmental conditions and nutrition during the trials. Several general trends in growth at moult are evident. Growth at moult was far lower in the No Feed treatments than the feed treatments. Lobsters in the No Feed treatments could have gained some nutrition by consuming the abundant bio-fouling organisms from the holding cage surfaces. It was noted that the mesh surrounding the unfed compartments was always cleaner than that surrounding the fed compartments. Similar behaviour has also been documented for unfed *J. lalandii* kept in sea cages (Barkai & Branch 1988). Although partially devoured lobsters were not noted during assessment times in the present study, it is possible that unfed lobsters could also have gained some nutrition through cannibalism, particularly when lobsters were soft-shelled and vulnerable post-moult.

Mussels have been shown to be superior to prepared pellet feeds in growth trials of juvenile *J. edwardsii* (Crear et al. 1999). In the present study there were no consistent differences in growth at moult between the mussel treatment and pellet treatments in the PL trial. However, the adult lobsters in our trials moulted only once and growth differences related to diet may only become apparent over two or more moults. Furthermore, lobsters in sea cages have access to some drift and fouling organisms as dietary supplements. The effects of pellet formulation and nutrition are more likely to be observed in juvenile grow-out where a complete diet is needed and animals are moulting regularly.

Growth at moult for the pellet treatments in the KI trial was far greater in males than females. The majority of females used in the KI trial were sexually mature. Growth rate declines in *J. edwardsii* females when they become sexually mature (Prescott et al. 1997). Furthermore, some of the females in the present study diverted energy reserves away from growth and into egg production. Thus it is possible that immature females might attain similar moult increments to males of a similar size.

Prescott et al. (1997) recorded an average CL moult increment of c. 8 mm for wild male *J. edwardsii* in the CL size classes of 80–89.9 and 120–129.9 mm. In the present study the maximum average CL moult increment for males c. 100–110 mm CL was c. 4–5 mm. Thus the full growth potential of *J. edwardsii* was not achieved in the live-holding trials of the present study. Based upon regression estimates from the present study, if 8 mm CL moult increments were achieved, this would add a further 50 g (or 10%) in weight gain at moult for 500 g lobsters. This would be a substantial improvement in growth beyond that achieved in our trials. Possible ways of improving weight gain at moult include increasing feeding frequency (Robertson et al. 1993), feeding at dusk (Thomas et al. 2003), decreasing holding density (James et al. 2001), and advancements in feed formulation and stability (see later).

Growth of 100 mm CL *J. edwardsii* has been found to be lower for speckled/white lobsters captured from deep waters than for red lobsters taken from shallower waters (McGarvey et al. 1999). Nonetheless, growth at moult of speckled/white male lobsters in the KI trial was equivalent to that of the red male lobsters in the PL trial of the present study, thus supporting the view of McGarvey et al. (1999) that differences in growth between white and red lobsters are related to diet/nutrition associated with depth. However, it must be acknowledged that the two-fold difference in holding density between the KI and PL trials may also have contributed to the observed differences in growth (see James et al. 2001).

Biomass returns and FSCRs

Biomass returns reflected survival, moulting activity, and weight gain at moult. Biomass returns were negative in the No Feed treatments as a result of lowered survival and growth at moult. Biomass returns for the male pellet treatments in the PL and KI trials were positive. The two pellet treatments using speckled/white male lobsters in the KI trial had the highest biomass returns of 15.3 and 16.9%. These two treatments had 100% survival, 100% moulting activity, and substantial growth at moult. Despite the high growth at moult in the Live Mussel treatment of the PL trial, this treatment had a negative biomass return because of the lowered (but inexplicable) survival in this treatment. This result emphasises the need for a high survival rate in a live-holding operation based on weight gain for profit.

Feed supplied conversion ratios were extremely high for the pellet-fed treatments in the trials. The main reasons for this were the high feeding rates and the breakdown and loss of pellets from the cages

after feeding. Experimental laboratory work found that adult *J. edwardsii* of c. 470 g consumed only c. 2–3 g dry weight of feed per day, representing only 0.4–0.6% of their body weight per day (Geddes et al. 2001). The results of that work also demonstrated a cyclical nature of daily feed intake. In the present study, lobsters were fed at a rate of 2% of their body weight per day, given as two feeds per week of 7% of their body weight. This rate was far in excess of what the lobsters could have eaten in one day and a large amount of uneaten food would have fallen through the cage mesh as waste. To improve FSCRs (and thus FCRs) for lobsters being fed on pellets in sea-cage systems, the feeding rate, feeding frequency, and size of pellet all need to be optimised.

Condition of lobsters

One function of the hepatopancreas is to store energy that can be utilised by lobsters in times of starvation, poor nutrition, and high metabolic demand. Studies have shown that the size and moisture content of the hepatopancreas, and also the abdomen, can change markedly during times of starvation and poor nutrition (Stewart et al. 1967; Dall 1974; Trendall & Prescott 1989; McClain 1995; Musgrove 1998). Our observations agree with these other studies as unfed lobsters showed significant reductions in dry matter and significant increases in moisture content of both the hepatopancreas and abdomen. Although the size and moisture content of the hepatopancreas and abdomen do change through the moult cycle in *J. edwardsii* (Musgrove 1998, 2001), this did not compromise results of the present study, as the majority of lobsters analysed for condition were in the inter-moult stage. Based upon the results of the present study, it can be concluded that in a live-holding situation, the physiological condition of lobsters declines markedly without feeding, but that it can be maintained and/or improved through feeding with natural or manufactured diets.

The ability to maintain coloration in red lobsters and to improve coloration in speckled/white lobsters is an important consideration in live-holding. Colour maintenance of red lobsters was achieved in mussel-fed, pellet-fed, and unfed treatments. Colour improvement of speckled/white lobsters was achieved in pellet-fed, and unfed treatments. Colour change over time in the exoskeleton of captive decapod crustaceans has been reported on several occasions (e.g., D'Abramo et al. 1983; Howell & Matthews 1991; Menasveta et al. 1993; James & Tong 1997; Lim et al. 1997). These changes can usually be attributed to the level of carotenoids in the diet as carotenoids are essential for the pigmentation of the exoskeleton. In the present study, unfed speckled/white lobsters also changed in coloration, possibly deriving carotenoids through consumption of biofouling organisms from the cage surfaces.

The greatest problem with the external condition of lobsters in the present study was that of tail fan damage. In many instances the damage was so extreme that it made the lobsters very unsightly and probably unmarketable. Tail fan damage (raggedness, blistering, and erosion) was also a major problem in the pilot study of sea-based live-holding of *J. edwardsii* conducted by Lorkin et al. (1999). Further investigation of tail fan damage has been undertaken and results reported in other papers in this volume (see Musgrove et al. 2005).

The present study has provided biological and husbandry information on potential survival rates, growth at moult, and conditioning and feeding of live-held lobsters. Diets of live mussel and three different manufactured pellets were all successful in keeping lobsters alive, promoting growth at moult, and in maintaining/improving the physiological condition of lobsters. Speckled/white lobsters fed on manufactured pellets improved in colour. Although results from the study were generally very encouraging, tail fan damage was found to be a major problem with long-term live-held lobsters. Such information is useful for industry to make informed decisions and it has demonstrated that long-term live-holding of adult *J. edwardsii* is technically feasible. In live-holding, the timing of moult and extent of growth at moult needs to be considered, as does the different growth increments of the sexes. Although the diet formulated for this study proved nutritionally adequate, husbandry could be improved through better pellet feeds and feeding regimes.

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REFERENCES

Aquasearch 1996: The bio-economic development of long-term holding and aquaculture of southern rock lobster (*Jasus edwardsii*). Final Report for Fisheries Research and Development Corporation Project 94/134.05. 22 p.

Barkai, A.; Branch, G. M. 1988: Energy requirements for a dense population of rock lobsters *Jasus lalandii*: novel importance of unorthodox food sources. *Marine Ecology Progress Series 50*: 83–96.

Crear, B.; Thomas, C.; Hart, P. 1999: An evaluation of the suitability of artificial prawn diets for the southern rock lobster, *Jasus edwardsii*. *In*: World Aquaculture '99. Book of Abstracts. The Annual International Conference and Exposition of the World Aquaculture Society, 26 April–2 May 1999, Sydney, Australia, World Aquaculture Society. P. 183.

D'Abramo, L. R.; Baum, N. A.; Bordner, C. E.; Conklin, D. E. 1983: Carotenoids as a source of pigmentation in juvenile lobsters fed a purified diet. *Canadian Journal of Fisheries and Aquatic Sciences 40*: 699–704.

Dall, W. 1974: Indices of nutritional state in the western rock lobster, *Panulirus longipes** (Milne-Edwards). I. Blood and tissue constituents and water content. *Journal of Experimental Marine Biology and Ecology 16*: 167–180.

Geddes, M. C.; Bryars, S. R.; Jones, C. M.; Crear, B. J.; Hart, P. R.; Thomas, C.; Linton, L.; Jeffs, A. G. 2001: Rock Lobster Enhancement and Aquaculture Subprogram Project 5: determination of the optimum environmental and system requirements for juvenile and adult rock lobster holding and grow-out. Final Report of Project 1998/305 to Fisheries Research and Development Corporation. 177 p.

Howell, B. K.; Matthews, A. D. 1991: The carotenoids of wild and blue disease affected farmed tiger shrimp (*Penaeus monodon*, Fabricus). *Comparative Biochemistry and Physiology 98B(2/3)*: 375–379.

Hurlbert, S. H. 1984: Pseudoreplication and the design of ecological field experiments. *Ecological Monographs 54(2)*: 187–211.

James, P. J.; Tong, L. J. 1997: Differences in growth and moult frequency among post-pueruli of *Jasus edwardsii* fed fresh, aged or frozen mussels. *Marine and Freshwater Research 48*: 931–934.

James, P. J.; Tong, L. J. 1998: Feeding technique, critical size and size preference of *Jasus edwardsii* fed cultured and wild mussels. *Marine and Freshwater Research 49*: 151–156.

James, P. J.; Tong, L.; Paewai, M. 2001: The effect of stocking density and shelter on growth and mortality of early juvenile *Jasus edwardsii*. *Marine and Freshwater Research 52(8)*: 1413–1417.

Lim, B. K.; Sakurai, N.; Sugihara, T.; Kittaka, J. 1997: Survival and growth of the American lobster *Homarus americanus* fed formulated feeds. *Bulletin of Marine Science 61(1)*: 159–163.

Lorkin, M.; Geddes, M.; Bryars, S.; Leech, M.; Musgrove, R.; Reuter, R.; Clarke, S. 1999: Sea-based live holding of the southern rock lobster, *Jasus edwardsii*: a pilot study on long term holding feeding. SARDI Research Report Series No 46, December 1999. 22 p.

McClain, W. R. 1995: Effects of population density and feeding rate on growth and feed consumption of red swamp crawfish *Procambarus clarkii*. *Journal of the World Aquaculture Society 26(1)*: 14–23.

McGarvey, R.; Ferguson, G. J.; Prescott, J. H. 1999: Spatial variation in mean growth rates at size of southern rock lobster, *Jasus edwardsii*, in South Australian waters. *Marine and Freshwater Research 50*: 333–342.

Menasveta, P.; Worawattanamateekul, W.; Latscha, T.; Clark, J. S. 1993: Correction of black tiger prawn (*Penaeus monodon* Fabricius) coloration by astaxanthin. *Aquacultural Engineering 12*: 203–213.

Musgrove, R. J. B. 1998: Condition and its assessment in the southern rock lobster *Jasus edwardsii*. i. Assessment of condition indices and moult staging techniques. Final Report for Fisheries Research and Development Corporation Project 95/017.

Musgrove, R. J. B. 2001: Interactions between haemolymph chemistry and condition in the southern rock lobster, *Jasus edwardsii*. *Marine Biology 139*: 891–899.

Musgrove, R. J.; Geddes, M. C.; Thomas, C. 2005: Causes of tail fan necrosis in the southern rock lobster, *Jasus edwardsii*. *New Zealand Journal of Marine and Freshwater Research 39*: 293–304.

Prescott, J.; McGarvey, R.; Ferguson, G.; Lorkin, M. 1997: Population dynamics of southern rock lobster in South Australian waters. Final Report for Fisheries Research and Development Corporation Project 93/086 & 93/087.

Robertson, L.; Lawrence, A. L.; Castille, F. L. 1993: Effect of feeding frequency and feeding time on growth of *Penaeus vannamei* (Boone). *Aquaculture and Fisheries Management 24*: 1–6.

Stewart, J. E.; Cornick, J. W.; Foley, D. M.; Li, M. F.; Bishop, C. M. 1967: Muscle weight relationship to serum proteins, hemocytes, and hepatopancreas in the lobster, *Homarus americanus*. *Journal of the Fisheries Research Board of Canada 24(11)*: 2339–2354.

Thomas, C. W.; Carter, C. G.; Crear, B. J. 2003: Feed availability and its relationship to survival, growth, dominance and the agonistic behaviour of the southern rock lobster, *Jasus edwardsii* in captivity. *Aquaculture 215*: 45–65.

Trendall, J. T.; Prescott, J. 1989: Severe physiological stress associated with the annual breeding emigration of *Panulirus ornatus* in the Torres Strait. *Marine Ecology Progress Series 58*: 29–39.

Williams, K.; Smith, D.; Crear, B.; Glencross, B.; Evans, L. 2000: Rock Lobster Enhancement and Aquaculture Subprogram Project 3: feed development for rock lobster aquaculture. Final Report of Project 1998/303 to Fisheries Research and Development Corporation.

Zar, J. H. 1984: Biostatistical Analysis. 2nd ed. New Jersey, Prentice-Hall Inc.

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Development of the red rock lobster, *Jasus edwardsii*, from egg to juvenile

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Abstract Mature red rock lobster, *Jasus edwardsii* were air freighted from the North Island, New Zealand to Japan in 1985. During most years since, egg extrusion has taken place during November and December and egg hatching from February to April. In the main experiment, phyllosomas were cultured in 100-litre containers. Each container had an upwelling system, connected either to a *Nannochloropsis* culture tank (Experiment 1) or to a coral sand filter tank (Experiment 2). *Artemia* nauplii and mussel gonad were the main foods provided. The numbers of 1st, 5th, and 15th instars were 12 000, 1500, and 137 respectively in Experiment 1, and 1500, 99, and 67 in Experiment 2. The intervals between Instars 1–4 and 4–14 were 43 and 175 days respectively for Experiment 1, and 43 and 169 days for Experiment 2. In Experiment 1, nine phyllosomas (13–15th instar) died during metamorphosis to the puerulus and a single 17th instar metamorphosed 303 days after hatching, 19 days later moulting into the juvenile. In Experiment 2, six 17th instar larvae metamorphosed 293 days and more after hatching, with all dying over the following 3 days. In an ancillary experiment, 30 phyllosomas were cultured in each of two 30-litre tanks containing microalgae: survival was higher, 20% and 43% reaching Instars 14/15 and six metamorphosing after 212–274 days. In all experiments, the developmental sequence was generally consistent with that for larvae from the field. Gill buds appeared at the 13th instar and gills were complete at the 17th instar. Improved culture methods are required to reduce late-stage mortalities.

Keywords Palinuridae; rock lobster; spiny lobster; *Jasus edwardsii*; phyllosoma; instar; larval development; metamorphosis; puerulus

INTRODUCTION

Jasus edwardsii (Hutton, 1875) (Decapoda: Palinuridae) is one of six species of *Jasus*, all of which live in temperate waters at mid-south latitudes. *J. edwardsii* is found in New Zealand and Australia where it is the basis of important fisheries (Booth 2000; Phillips et al. 2000).

Jasus spp. hatch as naupliosoma larvae and then pass through several phyllosoma instars before metamorphosing to the puerulus (Lesser 1974, 1978). For *J. edwardsii*, Thomson (1907), Archey (1916), Dakin & Colefax (1940, as *J. novaehollandiae*), Wear (1965), Batham (1967), Lesser (1974), and McWilliam & Phillips (1987, as *J. novaehollandiae*) provided illustrations and/or brief descriptions of mainly early phyllosoma stages, and Archey (1916) of the puerulus stage. A more comprehensive description of larval development was given by Lesser (1978) based on field-caught larvae. Kittaka et al. (1988) achieved full larval development to the puerulus stage of a "cross" between *J. novaehollandiae* and *J. edwardsii* at a time when the former was still considered to be a

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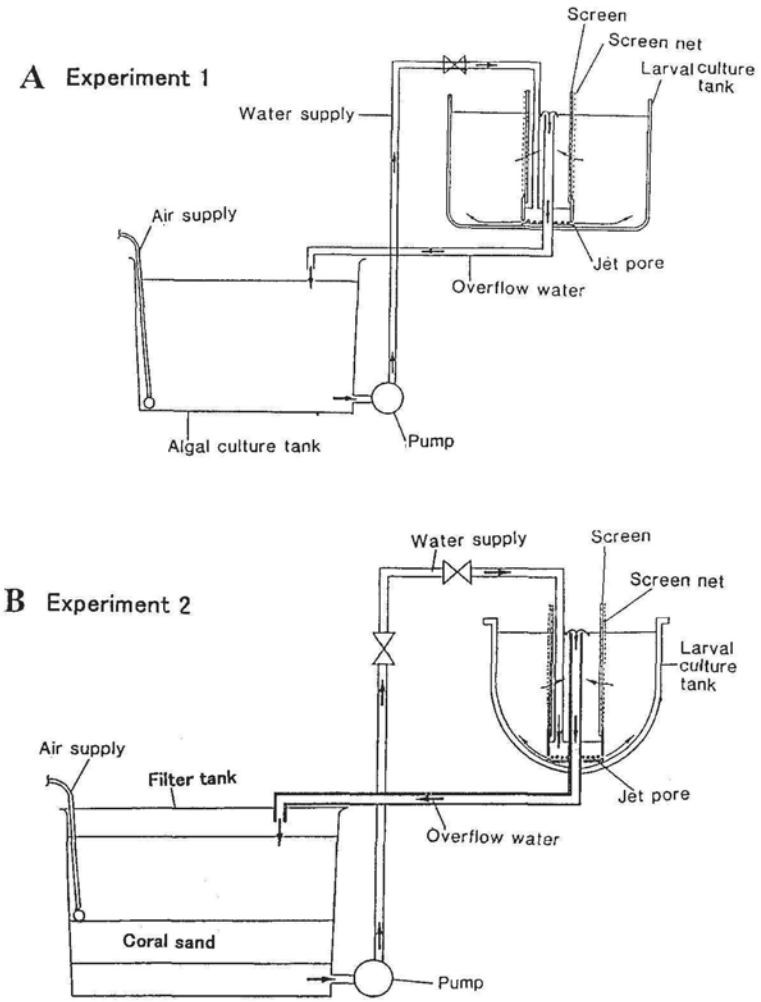

Fig. 1 *Jasus edwardsii* phyllosoma culture system. **A**, a 100-litre phyllosoma culture container with flat bottom connected to a 300-litre reservoir. Microalgae *Nannochloropsis oculata* and *Tetraselmis tetrathele* cultured in the reservoir were recirculated through the system (Sanriku, 1989–90, Experiment 1). **B**, a 100-litre phyllosoma culture container with semi-spherical bottom connected to a 300-litre reservoir with a built-in coral sand filter (no microalgae, Nemuro, 1998–99, Experiment 2).

distinct species. Other palinurids cultured to settlement have been *Jasus lalandii* (Kittaka 1988), *Sagmariasus* (formerly *Jasus*) *verreauxi* (Kittaka et al. 1997), *Palinurus elephas* (Kittaka & Ikegami 1988; Kittaka et al. 2001), *P. japonicus* (Kittaka & Kimura 1989; Yamakawa et al. 1989), and *P. longipes bispinosus* (as *P. longipes*) (Matsuda & Yamakawa 2000).

Larval culture can help clarify the early life histories of species and allow, or confirm, identification of larvae caught at sea. It can also verify the number of instars—which in *J. edwardsii*, as in other palinurids, has been arbitrarily grouped into stages (Lesser 1978). Behaviour of larvae in the laboratory, including at metamorphosis, can help explain field observations and assist in understanding larval recruitment mechanisms. Culture of larvae can also lead to methods for producing juveniles for aquaculture or for restocking.

In this paper we describe the culture conditions for, and larval development of, *J. edwardsii* from New Zealand, and compare this development with that inferred from the field.

MATERIALS AND METHODS

Source of breeding stock

Five female and three male *J. edwardsii* were transported to Sanriku, Iwate Prefecture, Japan from Gisborne, North Island, New Zealand by air on 8 December 1984. Two females and one male died during transport. The survivors were held in a breeding tank (2.5 m × 1.2 m × 0.7 m high) at water

temperatures ranging from 10–12°C in winter to 18–20°C in summer and fed mainly the mussel, *Mytilus edulis*. The numbers of breeders were augmented by later shipments, resulting in eight females and six males being present in 1989 and a total of 24 females and males being transported from Sanriku to Nemuro, northern Japan in 1994, where the experiments continued.

Phyllosoma culture experiments

Phyllosomas hatched on 20 December 1989 were used for Experiment 1 at Sanriku, and those on 7 February 1998 for Experiment 2 in Nemuro. First-instar phyllosomas which gathered at the surface of the tanks under light were scooped up with a 1-litre beaker. Approximately 12 000 and 1500 larvae were used for Experiments 1 and 2 respectively. In each experiment, the phyllosoma culture tank was connected to a 300-litre reservoir tank containing sea water that had been filtered through a 5 µm cartridge filter and irradiated with an ultraviolet steriliser. Water quality in the reservoir was maintained either by cultured microalgae or by a coral sand filter. In Experiment 1, cultured microalgae *Nannochloropsis oculata* and *Tetraselmis tetrathele* were added to the reservoir and recirculated in the culture system (Fig. 1A). In Experiment 2, a coral sand filter was built into the reservoir of the culture system (Fig. 1B).

Two groups of 30 phyllosomas from Experiment 1 were transferred separately into small tanks about 30 days after hatching to become Experiments 11a and 11b using *N. oculata* and *T. tetrathele* respectively.

The phyllosoma culture systems were as follows. A 100-litre round tank with a flat bottom set up in a greenhouse was used for Experiment 1, and 30-litre tanks of similar type in a controlled environment room indoors for Experiment 11. For Experiment 2 in Nemuro, a 100-litre round tank with a semi-spherical bottom was set up indoors. Water was supplied at the bottom of each culture tank through an upwelling system which created currents in the tank that kept the larvae off the bottom.

Newly hatched nauplii of *Artemia salina* were fed to the early phyllosoma instars at a rate of c. 5000–20 000 per day for each 100-litre tank. Small pieces (2 mm cubes) of mussel gonad were the main food for advanced phyllosomas (Table 1). For Experiment 2, phyllosomas were fed *A. salina* and mussel gonad for the initial 70 days, and later from time to time fed fish larvae in combination with mussel: red sea bream *Pagrus major* were fed 71–75, 81–84, and 99–100 days after phyllosoma hatching; goldstriped amberjack *Seriola lalandi* after 109–113 days; tidepool gunnel *Pholis nebulosa* after 114–147 days; and sailfin sandfish *Arctoscopus japonicus* were fed to late-stage phyllosomas 317–387 days after hatching.

The culture water was changed every 2 weeks in Experiments 1 and 11, and about every 40 days in Experiment 2. Water temperature, salinity, pH, concentration of *N. oculata* and *T. tetrathele*, rate of

Table 1 Environmental and feeding conditions during phyllosoma culture. See text for descriptions of each experiment.

Water control method:	Experiment 1 Microalgae	Experiment 2 Coral sand filter	Experiment 11a *Nannochloropsis*	Experiment 11b *Tetraselmis*
Mean temp. (range) (°C)	19.4 (18.8–20.0)	17.5 (16.7–19.2)	20.9 (20.5–21.3)	20.8 (19.7–21.6)
Mean salinity (range)	34.75 (33.04–35.40)	36.06 (36.0–39.0)	35.22 (35.07–35.27)	35.19 (35.06–35.64)
Mean pH (range)	8.22 (8.06–8.36)	8.06 (7.69–8.29)	8.20 (8.09–8.31)	8.22 (8.09–8.32)
Nannochloropsis ($\times 10^3$)	1420	0	1860	
Tetraselmis ($\times 10^3$)	4.7	0		3.9
Water change (%/month)	174	121	180	175
Feeding				
Artenia nauplii (total)	166 000	198 000		
Mussel (pieces/day)	73	58	38	46
Fish larvae* (total)	0	2350		
Fish larvae† (total)	0	1700		
Fish larvae‡ (total)	0	1150		

*Red sea bream (*Pagrus major*) and goldstriped amberjack (*Seriola lalandi*).
†Tidepool gunnel (*Pholis nebulosa*).
‡Sailfin sandfish (*Arctoscopus japonicus*).

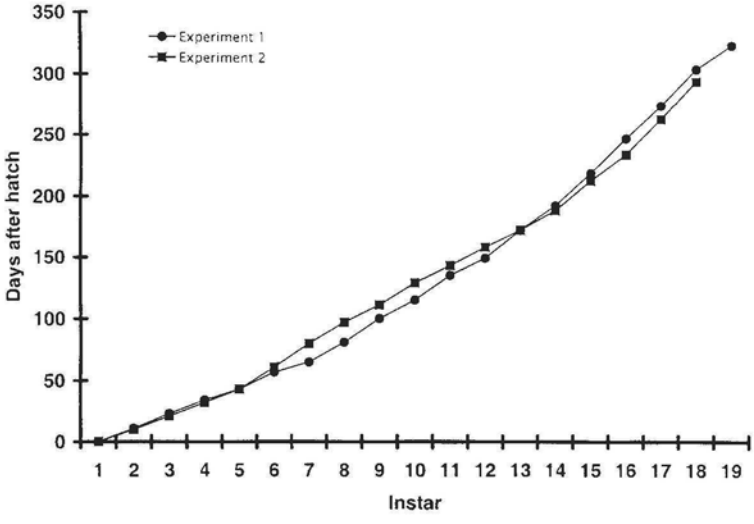

Fig. 2 Instar advancement of *Jasus edwardsii* phyllosomas and pueruli. 12 000 Instar 1 larvae were cultured in a 100-litre container with the microalga *Nannochloropsis oculata* at Sanriku (Experiment 1). 1500 Instar 1 larvae were cultured in a 100-litre container with coral sand filter in Nemuro (Experiment 2).

water change, and amount of food given were measured daily. These parameters were averaged over 10-day periods. Dead larvae and larval moults were removed daily and examined for morphological development. Larval descriptions were based on distinguishing features in successive instars. For each instar, the anterior portion of the cephalothorax with antennule and antenna and/or the posterior portion with pereopods and abdomen were drawn. Total length (TL) was the linear distance between the base of the eyestalks and the posterior margin of the telson. After metamorphosis, the pueruli were transferred to individual cages which were placed in a separate culture tank with running sea water.

RESULTS

Reproduction

For the first shipment of adults to Sanriku, one male moulted on 5 April 1985 and two females moulted on 2 and 7 May 1985. The first spawning occurred on 2 May 1985. The other two females were found to be carrying eggs in the middle of May 1985. The first hatching of phyllosomas occurred on 10 August 1985. Thereafter, spawning occurred in November and December every year. Hatching occurred from February to April with a peak in March. The reproduction schedule in Nemuro was similar to that at Sanriku: moulting occurred mainly in January–April and occasionally in October–December, spawning in November and December, and hatching mainly in February and March.

Larval rearing

Water temperature, salinity, pH, microalgae (*N. oculata* and *T. tetrathele*) concentration, water change rate, and feeding amount (*A. salina* nauplii, mussel gonad, and fish larvae) in the culture experiments are shown in Table 1.

Water temperatures were higher in Experiments 11a and 11b than in Experiment 1 because of higher air temperatures indoors than within the greenhouse, and were lower in Experiment 2 because of the cooler Nemuro climate. Salinity ranged between 33 and 35 ppt in tanks with the microalgae reservoir and were higher (mean 36 ppt) in the coral sand filter tank. The value of pH ranged between 8.1 and 8.4 in the microalga tank and was lower, between 7.7 and 8.3, in the coral sand filter tank. The *N. oculata* concentration was 1.4–1.9 million cells ml^{-1} and the *T. tetrathele* concentration 4000–5000 cells ml^{-1}. The monthly water change rate was 170–180% in the microalga method and 120% in the coral sand filter method.

Instar advancement

The advancement of instars in Experiments 1 and 2 is shown in Fig. 2. In Experiment 1 (Sanriku), first instar phyllosomas moulted into 2nd, 3rd, 4th instars and so on to the 17th instar, then the puerulus, on average 11, 23, 34, 43, 57, 65, 81, 100, 115, 135, 149, 172, 192, 218, 246, 273, and 303 days after hatching respectively. In Experiment 2 (Nemuro), first instar phyllosomas moulted into the succeeding phyllosoma instars and the puerulus on average 10, 21, 32, 43, 61, 80, 97, 111, 129, 143, 158, 172, 188, 212,

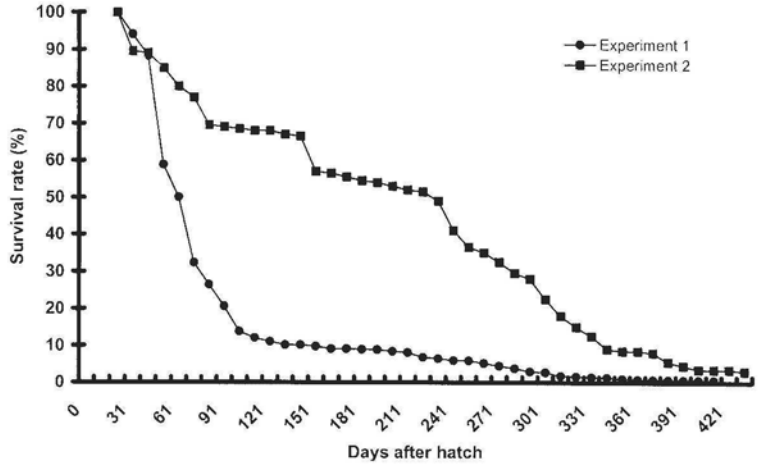

Fig. 3 Survival rate of the *Jasus edwardsii* phyllosomas referred to in Fig. 2.

233, 262, and 293 days after hatching respectively. Development times from Instar 1 to Instar 5 were similar between Experiments 1 and 2, but for Instars 6–12 the larvae advanced more rapidly in Experiment 1. After Instar 13, progression was slower in Experiment 1 than in Experiment 2.

In Experiment 2, phyllosomas were cultured with the standard feeds (*Artemia* nauplii and mussel gonad) for the first 70 days, the average intermoult period between Instars 1 and 5 being 12.2 days. Then, red sea bream and goldstriped amberjack larvae were intermittently given for a total of 16 days to Instars 6–8 (duration 50 days), and tidepool gunnel larvae for 34 days to Instars 9–12 (duration 61 days). The average intermoult periods were 16.6 and 15.2 days respectively. In contrast, when using the standard feeds in Experiment 1 the average intermoult periods were 11.4, 14.7, and 18.0 days for Instars 1–5, 6–8, and 9–12 respectively. Feeding with tidepool gunnel larvae in particular, appeared to shorten the intermoult period.

Survival rate

Survival was lower in Experiment 1 than in Experiment 2 (Fig. 3). About 12 000 and 1500 1st instars were used in Experiments 1 and 2 respectively. Initial mortality was very high in both, with c. 1700 and 202 phyllosomas surviving to the 3rd instar in Experiments 1 and 2 respectively. Based on the numbers alive at the 3rd instar, the percentage surviving at the 3rd, 4th, 5th, and so on to the 13th instars were estimated to be c. 100, 94.1, 88.2, 50.0, 26.5, 20.6, 13.8, 12.0, 10.1, 10.1, and 9.1 respectively for Experiment 1. Equivalent percentage values for Experiment 2 were 100, 89.5, 89.0, 85.0, 69.5, 68.5, 68.0, 67.0, 66.5, 56.5, and 55.5 respectively. Thus, mortality was seen to increase markedly after the 13th instar in both Experiments 1 and 2. Ten late-stage instars (one 13th, two 14th, six 15th, and one 17th) metamorphosed into the puerulus stage in Experiment 1 and six 17th instars in Experiment 2 (Table 2). The rate of metamorphosis from the 3rd instar was therefore 0.6% and 3.0% for Experiments 1 and 2 respectively.

Survival rates for Experiments 11a and 11b are shown in Table 3. Survival from 3rd to 14th/15th instar was 20.0% and 43.3% for Experiments 11a and 11b respectively. Survival fell markedly from about the 9th instar, and the intermoult days extended after Instars 11/12. Both better survival and shorter intermoult periods were seen in Experiment 11b (cultured with *T. tetrathele*) than Experiment 11a (cultured with *N. oculata*). The rate of metamorphosis based on the numbers of 3rd instars was 6.7% and 13.3% for Experiments 11a and 11b respectively.

Metamorphosis

Phyllosomas metamorphosed at Instars 13–17, as shown in Table 2. Those that metamorphosed at an earlier stage (Instars 13–15) all died during or soon after metamorphosis. Three of seven 17th instars survived metamorphosis. One moulted to the first-instar juvenile after 19 days but the other two died 3 days after metamorphosing.

Morphological features of the phyllosomas

The naupliosoma could not be distinguished from that described by Archey (1916) and Batham (1967). Distinguishing features of the phyllosomas, described as they appeared, were as follows and are also summarised in Tables 4 and 5.

Table 2 Days after hatching and the instar for *Jasus edwardsii* phyllosomas that metamorphosed to pueruli. See text for details concerning Experiments 1, 11, and 2.

Experiment	Days after hatch	Instar at metamorphosis (intermoult period)	
1 (Sanriku)	243	13	Died during metamorphosis
	225	14	Died during metamorphosis
	256	14	Died during metamorphosis
	246	15	Died during metamorphosis
	251	15	Died during metamorphosis
	252	15	Died during metamorphosis
	258	15	Died during metamorphosis
	270	15	Died during metamorphosis
	287	15	Died during/just after metamorphosis
	303	17	Survived for 19 days before moulting into juvenile
11 (Sanriku)	212	13	Died during metamorphosis
	232	13	Died during metamorphosis
	221	14	Died during metamorphosis
	226	14	Died during metamorphosis
	275	14	Died during metamorphosis
	274	15	Died during metamorphosis
2 (Nemuro)	293	17 (31 days)	Died just after metamorphosis
	321	17 (41 days)	Died on day of metamorphosis
	394	17 (29 days)	Died 3 days after metamorphosis
	396	17	Died during metamorphosis
	412	17	Survived for 3 days after metamorphosis
	435	17	Died on day of metamorphosis

Table 3 Days from hatching, number of intermoult days, and % survival from Instar 3 for *Jasus edwardsii* phyllosomas cultured indoors in a controlled environment (Experiment 11a using *Nannochloropsis oculata*, left; Experiment 11b using *Tetraselmis tetrathele*, right). For further details, see text.

Microalga:	*Nannochloropsis*			*Tetraselmis*		
Instar	Days after hatch	Intermoult days	Survival rate (%)	Days after hatch	Intermoult days	Survival rate (%)
3	31		100	24		100
4	38	13	100	33	11	100
5	51	10	97	44	13	100
6	61	16	97	57	15	100
7	77	17	97	72	16	83
8	94	14	83	88	18	73
9	108	16	46	106	18	60
10	124	20	33	124	18	53
11	144	25	33	142	16	47
12	169	18	33	158	21	47
13	187	32	27	179	20	47
14	219	16	27	199	22	43
15	235	39	20			
16	274					
17						
Puerulus	274			212		
	275		6.7	221		
				226		
				232		13.3

Instar 1 (Fig. 4, 1): TL 1.9 mm. Cephalic shield broadly pear-shaped, longer than wide, slightly more than 50% TL (remains so throughout larval development); posterior margin convex. Eyestalk similar length to antenna, unsegmented. Antennule unsegmented, with three long aesthetascs apically. Antenna similar length to antennule, unsegmented, biramous 33% length from tip (outer ramus gradually diminishes in subsequent instars and disappears at Instar 9). First maxilla biramous, coxal endite with two setae, basal endite with two setae. Second maxilla uniramous, elongated basal endite bearing three very long plumose setae. First maxilliped small bud with single spine. Second maxilliped five-segmented; fused ischium-merus with a single spine at mid-length, without exopod (appears at Instar 16). Third maxilliped five-segmented; fused coxa-basis, fused ischium-merus, carpus, propodus, and dactyl. Pereopods (Pr) 1 and 2, complete, five-segmented; two-segmented exopod arising at mid-length of fused ischium-merus bearing six pairs of plumose natatory setae. Pr 3, incomplete, five-segmented; exopod a small, unarmed bud. Pr 4, indistinct, unarmed bud. Pr 5, absent. Ventral spine on fused coxa-basis of third maxilliped and Pr 1–Pr 3 (ventral coxa-basis spines appear on Pr 4 at Instar 5 and on Pr 5 at Instar 6). Abdomen small, tapering, unsegmented, without pleopods, terminating in two posterolateral, unarmed bud-like processes. Distal margin concave (remains so through Instar 10).

Instar 2 (Fig. 4, 2): TL 3.0 mm. Eyestalk segmented. Pr 3, exopod bud with two small terminal setae. Pr 4, five-segmented with exopod a rudimentary bud.

Instar 3 (Fig. 4, 3): TL 4.1 mm. Antennule segmented basally. Pr 3, exopod fully developed with five pairs natatory setae. Pr 4, elongate, about three times length of abdomen; exopod bud almost 40% length. Pr 5, an undifferentiated bud 75% length of abdomen.

Instar 4 (Fig. 4, 4): TL 5.7 mm. Antennule with incipient inner ramus 65% along length. Antenna jointed midway along length, distal to outer ramus. Pr 4, with full complement of five segments; exopod an elongate unarmed bud. Pr 5, bud now 1.5 times length of abdomen.

Instar 5 (Fig. 4, 5): TL 6.3 mm. Antenna now equal in length to antennule. Pr 4, exopod bud armed with five pairs natatory setae. Pr 5, fused coxa-basis now differentiated; distal unarmed portion (with unclear joint) now three times length of abdomen.

Instar 6 (Fig. 4, 6): TL 7.2 mm. Antennule now two segments of similar length; inner ramus 33% length of distal segment, now a distinct bud. Antenna

Table 4 Summary table of relationships between phyllosoma instar (this paper) and stage (based on Lesser 1978) for *Jasus edwardsii*, and the average duration of each instar in Experiments 1 and 2. (Pr, pereopod; Urpd, uropod; Pl, pleopod; complete, pereopods with 5-segmented endopod plus, for pereopods 1–4, a segmented exopod with at least some natatory setae present.)

Instar	Days		Stage	Note
	Experiment 1	Experiment 2		
1	11	10	I	Pr 1,2 complete
2	12	11	II	
3	11	11	III	Pr 3 complete
4	9	11	IV	Pr 4 complete (Lesser)
5	14	18		Pr 4 complete (this study)
6	8	19	V	Urpd buds
7	16	17	VI	Pr 5 complete (Lesser)
8	19	14	VII	Pr 5 complete (this study)
9	15	18	VIII	Pl buds
10	20	14		Urpd 25% cleft
11	14	15		Urpd 33% cleft
12	23	14		Urpd 50% cleft
13	20	16	IX	Urpd 75% cleft; Pl 33% cleft, minute gill buds
14	26	24	X	Pl 50% cleft, gill buds
15	28	21		Gills elongated
16	27	29		Gills elongated
17	30	31	XI	Gills fully developed
Total	303	293		

Table 5 Details of progression of phyllosoma instars (from this study) compared with Stage I–XI (based on Lesser 1978 and indicated by *) for *Jasus edwardsii*. (segs, segments; prs, pairs; Seg., segmented; Elong., elongated bud without segmentation; a.i, appendix interna; l.s, lateral spine; l.ss, lateral spines; Segtn., segmentation; ‡ ,this may be a difference in interpretation: Lesser probably interpreted the presence of the appendage as equivalent to a segment whereas in this paper a segment requires segmentation; Complete refers to pereopods with 5–segmented endopod plus a segmented exopod with at least some natatory setae present – except for pereopod 5 which has no exopod; Incomplete, without natatory setae, and without exopodal segmentation in some cases. Where no data are given for a character, this indicates no change in that character from the previous instar, except in the case of the exopodal setae in Instars 1–11, for which setae were not counted and only the data of Lesser are given.)

Stage (Lesser 1978):	I	II	III	IV		V	VI	VII	VIII				IX	X			XI
Instar (this study):	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Eye	Not stalked	Stalked															
Antennule (segs)	0,*1‡		1,*1	1,*1–2		2,*2	3,*2–3	4,*2–3	4,*3‡								
Antenna (segs)	0,*1‡			1,*1			1.*1–2	2	3,*2–3		4(1 unclear)	4	4,*3‡				
1st pereopod	Complete																
Natatory setae (prs)	*6	*7–8	*9–10	*11–12		*14–15	*17	*18–20	*21–24			22–24	26–27,*25–28	28–31,*29	31		34–35,*30–32
2nd pereopod	Complete																
Natatory setae (prs)	*6	*7–8	*9–10	*11–12		*13–15	*16–17	*18–20	*21–24			21	25,*25–27	27–30,*28	31		31–35,*29–32
3rd pereopod	Incomplete		Complete														
Exopod	Bud	Elong.,*1 seg.‡	Seg.														
Natatory setae (prs)	*0	1,*0–2	5,*3–5	*7–9		*10–12	*13–14	*17–18	*19–22			20–21	21–24,*23–25	25–27,*27	29		30–32,*28–32
4th pereopod	Bud	Incomplete		*Complete	Complete												
No. of segs		1		5													
Exopod		Absent, *Scale	Bud,*Elong	Elong.	Seg.												
Natatory setae (prs)				0,*0–5	5	9,*7–9	11,*11–12	15,*14–16	*17–21			17–20	21–22,*21–24	24–26,*25–26	26	28	26–31,*26–30
5th pereopod	Absent	Bud,*Low bud	Bud, *Bud	Elong.	Incomplete		*Complete	Complete									
No. of segs				*1	3(2 unclear)	4,*3		5									
Pleopod	Absent						*Low buds		Buds, *Buds			Elong.	Bifid				
Cleft (%)												*<25	33,*<50	50,*50			
Outer ramus															Seg.		
Inner ramus														* a.i (buds)	a.i buds	Segtn. unclear a.i elong.	Seg., a.i seg.
Uropod	Absent					Buds, *Buds				Bifid		Elong.					
Cleft (%)								*<25	*25–50	25	33	50	75,*50–66				
Outer ramus														Seg. with 1 l.s, *trace of l.ss			Many l. ss, *many l. ss
Inner ramus																2 l.ss	
														Segtn. unclear		Seg.	Many l. ss, *many l. ss
Abdomen																	
Segmentation	Unsegmented												Unclear,*Slightly	Seg.,*Seg.			
Gills	Absent																
													Minute buds	Buds,*Absent	Elong.		Further elong., *Present

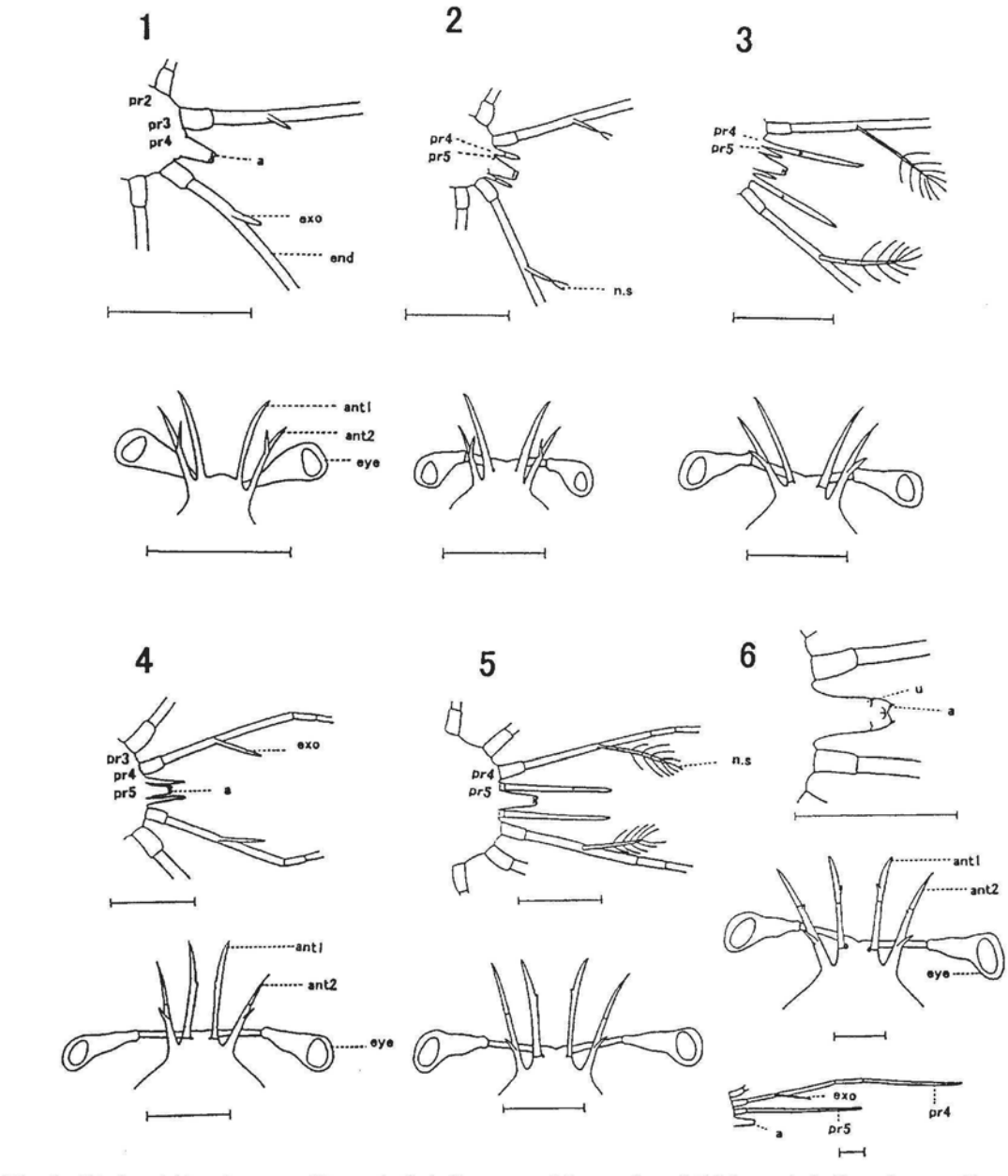

Fig. 4 Distinguishing features of Instar 1–6 phyllosomas of *Jasus edwardsii*. Numerals indicate instars. (Bars indicate 1 mm; ant 1, antennule; ant 2, antenna; pr 2–5, 2nd to 5th pereopods; end, endopod; exo, exopod; u, uropod; a, anus.)

also with inner ramus bud immediately proximal to joint; joint now at 65% length of antenna. Pr 5, 50–60% length of Pr 4; four-segmented. Abdomen armed with single pair uropod buds; each posterolateral corner with a single small spine (spines remain through Instar 11).

Instar 7 (Fig. 5, 7): TL 8.7 mm. Antennule now of three segments; inner ramus now more elongate. Antenna now somewhat longer than antennule. Pr 5, now c. 85% length of Pr 4.

Instar 8 (Fig. 5, 8): TL 10.2 mm. Antennule now of four segments; inner ramus now more elongate.

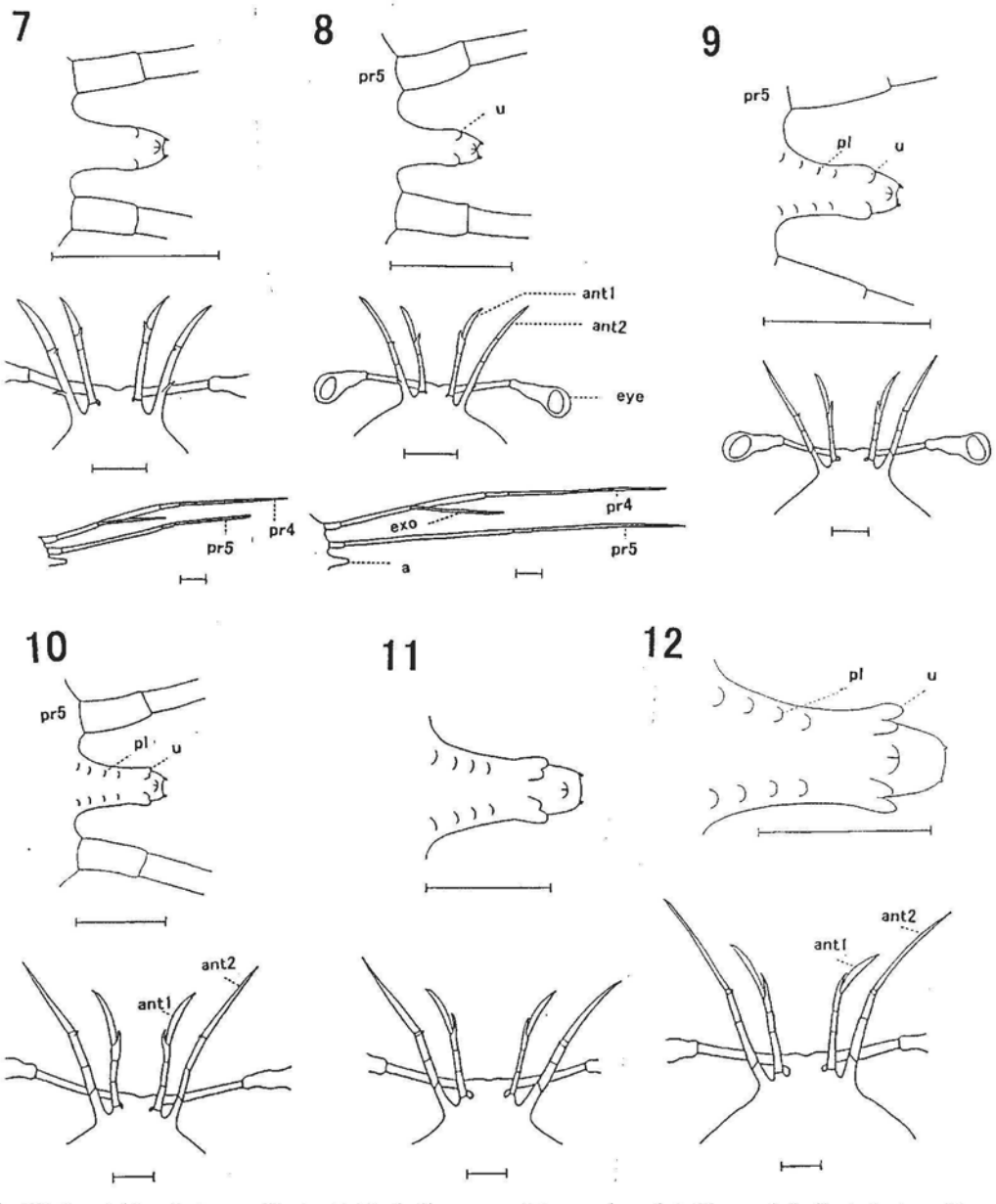

Fig. 5 Distinguishing features of Instar 7–12 phyllosomas of *Jasus edwardsii*. Numerals indicate instars. (Bars indicate 1 mm; ant 1, antennule; ant 2, antenna; pr 4, 5, 4th and 5th pereopods; end, endopod; exo, exopod; pl, pleopod; u, uropod; a, anus.)

Antenna now distinctly longer than antennule; now with two joints, at c. 45% and 65% of length. Pr 5, now five-segmented and marginally longer than Pr 4. Abdomen now with a narrowing anterior to uropod buds.

Instar 9 (Fig. 5, 9): TL 11.1 mm. Antenna now with three joints, at c. 25%, 40%, and 50% of length; outer ramus of early instars now absent; ramus on penultimate segment no further developed than Instar 6. Abdomen with four pairs of incipient pleopod buds.

Instar 10 (Fig. 5, 10): TL 12.7 mm. Antennule outer ramus more characteristically sickle-shaped. Antenna 30% longer than antennule. Abdomen uropod buds indistinctly biramous.

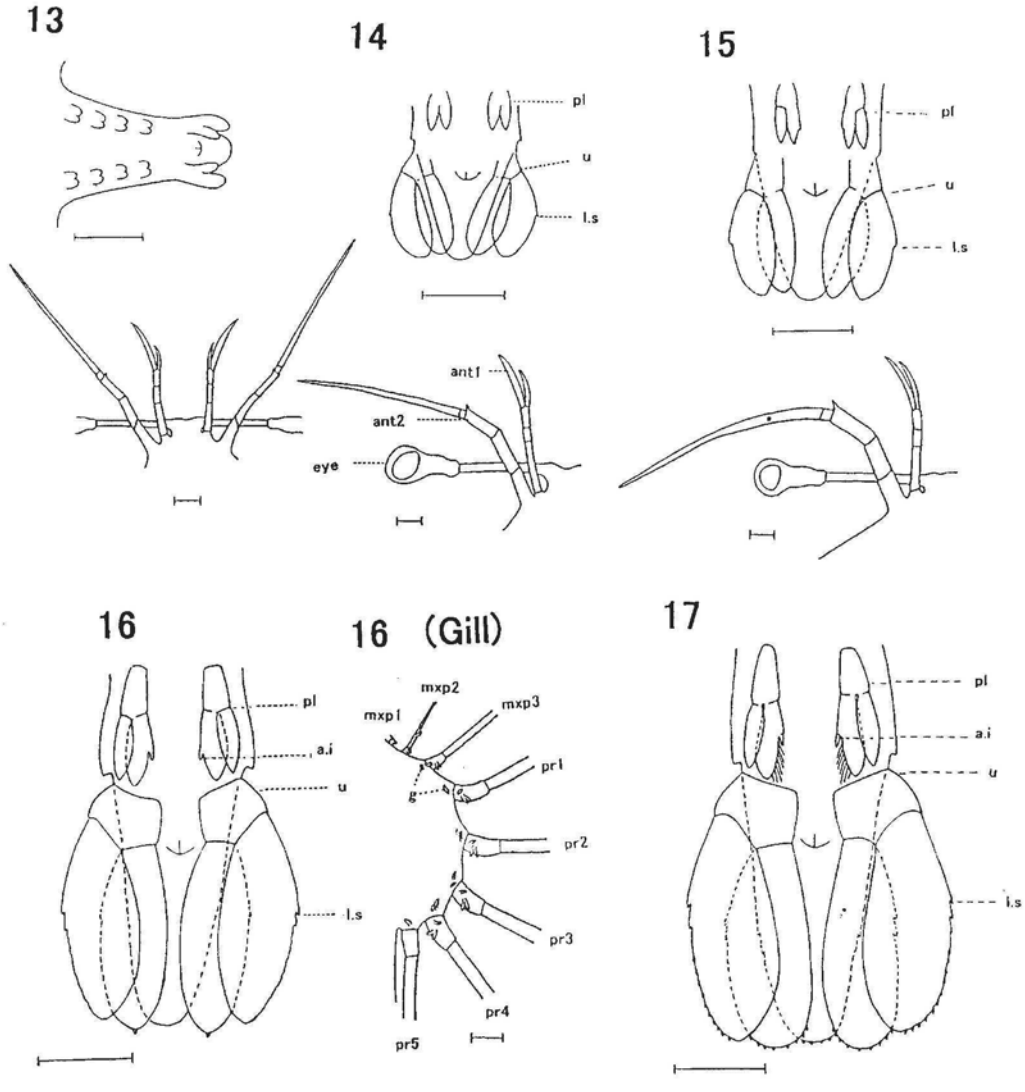

Fig. 6 Distinguishing features of Instar 13–17 phyllosomas of *Jasus edwardsii*. Numerals indicate instars. (Bars indicate 1 mm; ant 1, antennule; ant 2, antenna; mxp 1–3, 1st to 3rd maxillipeds; pr 1–5, 1st to 5th pereopods; end, endopod; exo, exopod; pl, pleopod; u, uropod; a.i, appendix interna; l.s; lateral spine; g, gills.)

Instar 11 (Fig. 5, 11): TL 14.7 mm. Antennule inner ramus c. 30% length of outer ramus. Antenna now with a small flagellum basal segment, distal to three-part peduncle. Abdomen posterior margin slightly convex; uropod buds larger and more distinctly biramous.

Instar 12 (Fig. 5, 12): TL 17.6 mm. Antennule inner ramus c. 40% length of outer ramus. Pleopod buds larger; uropod buds elongate, to level of anus.

Instar 13 (Fig. 6, 13): TL 20.9 mm. Antennule inner ramus c. 50% length of outer ramus. Antenna with flagellum greatly extended, now twice length of antennule. Pleopod buds now biramous; uropod rami subequal with posterior margin of abdomen, unarmed. Rudimentary gills now present. Abdomen corner spines present but not visible in figure.

Instar 14 (Fig. 6, 14): TL 27.2 mm. Antennule inner ramus 65% length of outer ramus. Pleopod rami now recognisable as exopod and endopod. Uropods fully developed and differentiated into exopod and endopod; exopods subequal with abdomen tip, endopods somewhat shorter; exopod

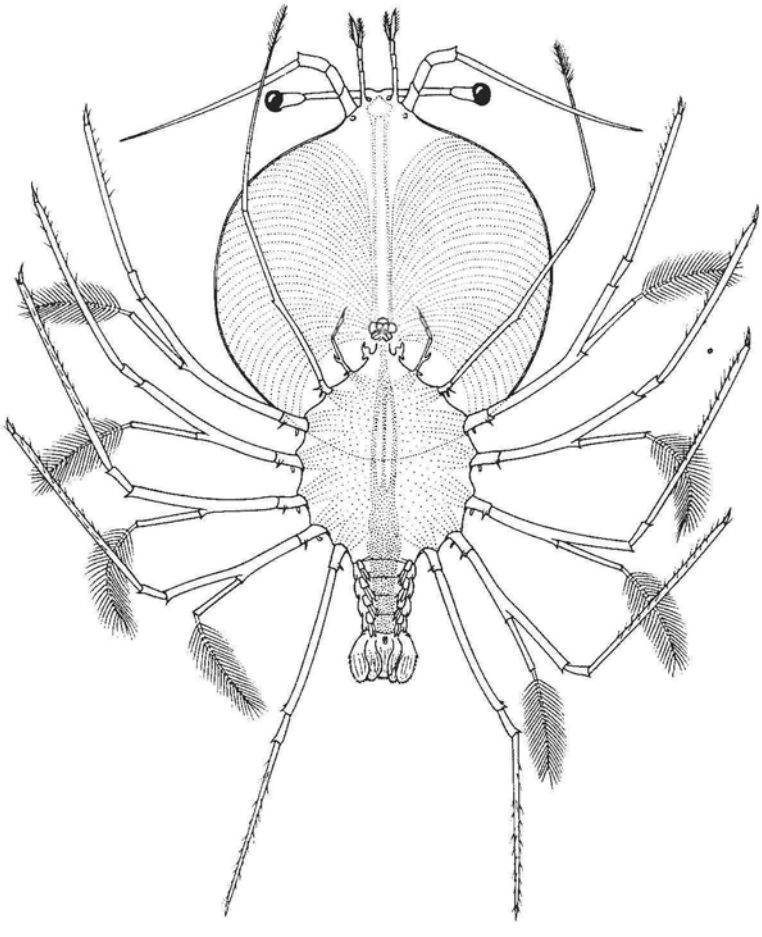

Fig. 7 Final (17th) instar of phyllosoma of *Jasus edwardsii* (gills not shown). Total length = 43.5 mm.

with small lateral spine c. 50% length. Abdomen corner spines no longer present. Posterior of abdomen more elongate but not differentiated into telson.

Instar 15 (Fig. 6, 15): TL 32.0 mm. Uropod lateral spine distinctly stronger. Pleopods with basipod now differentiated from abdomen; exopod also differentiated; endopod with distinct bud of appendix interna; unarmed. Gill buds elongate.

Instar 16 (Fig. 6, 16): TL 36.6 mm. Antennule inner ramus 80% length of outer ramus. Antennal peduncle subequal with antennule; antenna three times longer than antennule. Uropod endopod distinctly outreaching exopod and telson; exopod with two lateral spines; basipod differentiated from abdomen. Pleopods 50% longer. Gill buds cleft.

Instar 17 (Fig. 6, 17; 7): TL 44.2 mm. Uropods and pleopods fringed with setae. Appendix interna differentiated. Buds of gills further elongate and cleft.

DISCUSSION

This is the first description of the complete larval development of *Jasus edwardsii* based on cultured material. Earlier descriptions were of the nauplio-soma and the first three phyllosoma stages from the laboratory (Thomson 1907; Batham 1967; Lesser 1974), and of a few (Dakin & Colefax 1940; McWilliam & Phillips 1987) or all (Lesser 1978) phyllosoma stages from the field. The results from this paper allow the developmental sequence of particular features in cultured larvae to be compared with that in the wild, and to be specific about the number of instars.

Stage I–III larvae of *J. edwardsii* described from laboratory culture by the above authors were inseparable from the first three instars described here. The same was true for the field-caught larvae described by Lesser (1978) (all stages) and McWilliam & Phillips (1987) (Stages X and XI, referred to as *J.*

novaehollandiae), with the exception that there was no hint of an exopod on the fifth pereopod in Stage III (see McWilliam & Phillips 1987, p. 23). Based on the development of particular features, cultured Instars 1–15 were smaller than those reported for *J. edwardsii* from the field (Lesser 1978; Booth 1994). Smaller larvae for cultured versus wild-caught specimens for any particular stage of development have also been reported for other palinurids. But our final (gilled) instar phyllosomas achieved 44 mm TL in culture, which is similar to the means of 40–46 mm TL for those from the field (Booth 1994). Our results suggest that the food given to the late-stage larvae was nutritionally satisfactory, at least in terms of achievement of body size.

Cultured *J. edwardsii* had 17 instars, which is believed to be about the same as in the field, although there is the possibility of mark-time moulting (Booth 1994). Using Lesser's (1978) 11-stage categorisation as the comparison, there is a high overall level of consistency between the laboratory and field developmental sequences (Tables 4 and 5); the developmental sequence and times reported for the phyllosomas cultured to final stage/metamorphosis by Kittaka et al. (1988) were also in close agreement but comparisons cannot be taken further because only two larvae were cultured beyond early stage. There are single instars for the first three stages and then 1–4 instars for later stages. Instars 1–3 correspond with Stages I–III respectively, Instars 4 and 5 with Stage IV, Instars 6–8 with Stages V–VII respectively, and Instars 9–12 with Stage VIII. Stage VIII is when the uropods and pleopods show extensive development following the completion of pereopod development (Booth 1994). (Similar changes were found in Stage VIII phyllosomas of *Panulirus japonicus*, in which there were 8 instars—Kittaka & Kimura 1989.) Pereopods develop into functional appendages—with segmentation, appearance of an exopod, and relatively regular increase in number of natatory setae—earlier than the uropods or pleopods, which develop more gradually between the instars after Instar 6. Only at Instar 17 are the uropods and pleopods fully segmented and setose. Instar 13 corresponds with Stage IX, Instars 14–16 with Stage X, and Instar 17 with Stage XI.

The larval development of *J. edwardsii* is therefore very similar to that reported for *S. verreauxi* by Kittaka et al. (1997), including the development of the gills over several instars. The main differences were the development of exopods on the third maxilliped and the fifth pereopod, which are not present on *J. edwardsii*.

The *J. edwardsii* larvae at all stages of development showed the same looping swimming pattern illustrated by Kittaka (1994). Feeding behaviour was also similar to that reported for other species, with prey items usually being fixed on the point of a pereopod before being transferred to the mouthparts.

Metamorphosis to pueruli took place without any particular stimulation being provided and so was thought to be a product of stage of development, time, and energy accumulation. However, laboratory culture conditions appear to have led to a level of premature metamorphosis, those metamorphosing at Instars 13–15 failing to survive. Metamorphosis always occurred in the same general sequence. Two to three days before it, the phyllosomas stopped feeding. The abdomen increased in thickness and on the day of metamorphosis the body appeared whitish and turbid. Several hours before moulting the eyestalks became flaccid. Such body changes were common between species (e.g., Kittaka 1997). Newly metamorphosed pueruli were almost colourless and transparent. The pueruli swam forward, generally in large circles, with the second antennae extended anteriorly, using vigorous beating of the pleopods. Sometimes a puerulus would lie on its back and bury in the silt that had accumulated on the bottom of the culture vessel. A few days after metamorphosis, the puerulus began to display shelter-seeking behaviour and to cling to rocks. Pigmentation began to develop around the eyes and antennae. The 19 days duration of the puerulus stage here is less than that estimated for this species in the wild, but whereas time from metamorphosis to moulting to the juvenile can be observed, there is no way of knowing in wild-caught pueruli when metamorphosis actually took place. Field estimates of puerulus duration are therefore very imprecise.

The survival rate was much higher in the small-scale indoor culture room (initial phyllosoma density of a single Instar 3 phyllosoma per litre of water in Experiments 11a and 11b, using 30-litre containers) compared with the larger-scale culture in the greenhouse (initial phyllosoma densities of 17 and 2 Instar 3 phyllosomas per litre in Experiments 1 and 2 respectively, using 100-litre containers) (Table 2). For the larger-scale systems, phyllosoma culture using the coral sand filter method (Experiment 2) showed better larval survival than did the microalgae method (Experiment 1). This implies that the coral sand filter may be better at maintaining essential water quality than the use of microalgae such as *N. oculata*. Recently, Matsuda & Takenouchi (2005) achieved high survival of late-stage phyllosomas and

pueruli of *P. japonicus* using a relatively shallow elliptical tank in a flow-through system of clean water, again suggesting that the supply of sufficiently clean sea water can improve survival rates. Ritar (2001) also cultured phyllosomas (*J. edwardsii*) to mid-stage with good survival using a similar method. However, because of the need for large volumes of filter material and clean water in such systems, scaling-up should be easier with the microalgae method—but the causes of mortality in the late-stage phyllosomas and pueruli need to be investigated more thoroughly to establish the optimum large-scale culture method.

Annual breeding with seasonal consistency occurred in captive *J. edwardsii* from 1986, 2 years after their arrival in Japan. Our observations are consistent with others regarding breeding frequency (once per year), and egg-bearing and hatching seasons (late autumn to spring, and spring, respectively) in New Zealand (MacDiarmid & Kittaka 2000) and Australia (Frusher et al. 1999).

Although complete larval development has been achieved for several species of rock (spiny) lobster, larval survival has generally been low and few pueruli have been produced. This was also so for *J. edwardsii* in this study. More success was achieved with *S. verreauxi*, in which 168 pueruli (c. 10% of hatched phyllosomas) were produced (Kittaka et al. 1997). The key to success in attaining higher survival through the larval stage with *J. edwardsii* is believed to depend on providing more appropriate food and better quality water. Feeding with fish larvae may shorten the intermoult period, and therefore accelerate growth rates, of *J. edwardsii* phyllosomas. In Experiment 2, sailfin sandfish larvae were fed to late-stage phyllosomas 317–387 days after hatching, with a high proportion (four out of six) metamorphosing after 394–435 days. This suggests that sailfin sandfish larvae have particularly high nutritional value for *J. edwardsii*. (Sailfin sandfish larvae were also effective food for the European spiny lobster *Palinurus elephas*—Kittaka et al. 2001). But studies of biochemical changes with development of larvae, such as those of Ritar et al. (2003) on early-stage phyllosomas of *J. edwardsii*, are needed to develop nutritionally complete diets for the late-stage phyllosomas.

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REFERENCES

Archey, G. 1916: Notes on the marine crayfish of New Zealand. *Transactions and Proceedings of the New Zealand Institute 48*: 396–406.

Batham, E. J. 1967: The first three larval stages and feeding behaviour of phyllosoma of the New Zealand palinurid crayfish *Jasus edwardsii* (Hutton 1875). *Transactions of the Royal Society of New Zealand 9*: 53–64.

Booth, J. D. 1994: *Jasus edwardsii* larval recruitment off the east coast of New Zealand. *Crustaceana 66*: 295–317.

Booth, J. D. 2000: New Zealand's rock lobster fisheries. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. Oxford, Blackwells. Pp. 78–89.

Dakin, W. J.; Colefax, A. N. 1940: The plankton of the Australian coastal water off New South Wales. *Publications of the University of Sydney, Department of Zoology, 1*: 1–215.

Frusher, S.; Prescott, J.; Edmunds, M. 1999: Southern rock lobsters. *In*: Andrew, N. *ed.* Under southern seas. Sydney, University of New South Wales Press. Pp. 106–113.

Kittaka, J. 1988: Culture of the palinurid *Jasus lalandii* from egg stage to puerulus. *Nippon Suisan Gakkaishi 54*: 87–93.

Kittaka, J. 1994: Culture of phyllosomas of spiny lobster and its application to studies of larval recruitment and aquaculture. *Crustaceana 66*: 258–270.

Kittaka, J.; Ikegami, E. 1988: Culture of the palinurid *Palinurus elephas* from egg stage to puerulus. *Nippon Suisan Gakkaishi 54*: 1149–1154.

Kittaka, J.; Kimura, K. 1989: Culture of the Japanese spiny lobster *Panulirus japonicus* from egg to juvenile. *Nippon Suisan Gakkaishi 55*: 963–970.

Kittaka, J.; Iwai, M.; Yoshimura, M. 1988: Culture of a hybrid of spiny lobster genus *Jasus* from egg stage to puerulus. *Nippon Suisan Gakkaishi 54*: 413–417.

Kittaka, J.; Ono, K.; Booth, J. D. 1997: Complete development of the green rock lobster, *Jasus verreauxi* from egg to juvenile. *Bulletin of Marine Science 61*: 57–71.

Kittaka, J.; Kudo, R.; Onoda, S.; Kanemaru, K.; Mercer, J. P. 2001: Larval culture of the European spiny lobster *Palinurus elephas*. *Marine and Freshwater Research 52*: 1439–1444.

Lesser, J. H. R. 1974: Identification of early larvae of New Zealand spiny and shovel-nosed lobsters (Decapoda, Palinuridae and Scyllaridae). *Crustaceana 66*: 259–277.

Lesser, J. H. R 1978: Phyllosoma larvae of *Jasus edwardsii* (Hutton) (Crustacea: Decapoda: Palinuridae) and their distribution off the east coast of the North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research 12*: 357–370.

MacDiarmid, A. B.; Kittaka, J. 2000: Breeding. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. Oxford, Blackwells. Pp. 485–507.

McWilliam, P. S.; Phillips, B. F. 1987: Distinguishing the phyllosoma larvae of rock lobster species of the genus *Jasus* (Decapoda, Palinuridae) in the waters of Australia and New Zealand. *Crustaceana 52*: 1–24.

Matsuda, H.; Takenouchi, T. 2005: New tank design for larval culture of Japanese spiny lobster *Panulirus japonicus*. *New Zealand Journal of Marine and Freshwater Research 39*: 279–285.

Matsuda, H.; Yamakawa, T. 2000: The complete development and morphological changes of larval *Panulirus longipes* (Decapoda, Palinuridae) under laboratory conditions. *Fisheries Science 66*: 278–293.

Phillips, B. F.; Chubb, C. F.; Melville-Smith, R. 2000: The status of Australia's rock lobster fisheries. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. Oxford, Blackwells. Pp. 45–77.

Ritar, A. J. 2001: The experimental culture of phyllosoma larvae of southern rock lobster (*Jasus edwardsii*) in a flow-through system. *Aquacultural Engineering 24*: 149–156.

Ritar, A. J.; Dunstan G. A.; Crear, B. J.; Brown, M. R. 2003: Biochemical composition during growth and starvation of early larval stages of cultured spiny lobster (*Jasus edwardsii*) phyllosoma. *Comparative Biochemistry and Physiology Part A 136*: 353–370.

Thomson, G. A. 1907: Note on the development of *Palinurus edwardsii*. *In*: Anderton, T. *ed.* Observations on New Zealand fishes, etc., made at the Portobello Marine Fish-hatchery. *Transactions and Proceedings of the New Zealand Institute 39*: 484–485.

Wear, R. G. 1965: Zooplankton of Wellington Harbour, New Zealand. *Zoology Publications, Victoria University of Wellington 38*.

Yamakawa, T.; Nishimura, M.; Matsuda, H.; Tsujigado, A.; Kamiya, N. 1989: Complete larval rearing of the Japanese spiny lobster *Panulirus japonicus*. *Nippon Suisan Gakkaishi 55*: 745.

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New tank design for larval culture of Japanese spiny lobster, *Panulirus japonicus*

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Abstract Middle-stage phyllosoma of *Panulirus japonicus* (mean body length 11.5 mm) were cultured using 40-litre elliptical tanks with concave bottoms (85 cm long × 60 cm wide × 15 cm deep) in a flow-through system (24–25°C). The phyllosoma were fed with *Artemia* and mussel gonad. Survival rates to the puerulus stage were 54 ± 1%, 51 ± 0%, and 37 ± 9% at densities of 40, 60, and 90 phyllosoma/tank, respectively. The densities did not significantly affect the growth of phyllosoma. Major causes of phyllosoma mortality included moulting complications, bacterial disease, and cannibalism. The survival rates were significantly higher than in our previous studies, indicating that the new elliptical tank design may be suitable for mass culturing of phyllosoma. The survival of puerulus to the first juvenile stage was 83 ± 7% and did not differ between densities during phyllosoma rearing.

Keywords *Panulirus japonicus*; phyllosoma culture; culture tank; density; survival; growth

INTRODUCTION

The Japanese spiny lobster, *Panulirus japonicus*, has a limited distribution in the north-west Pacific region (Holthuis 1991). This lobster has a high economic value in Japan; the total catch was 1486 t in 2001, valued at c. US$50 million. Japan has a long history in research on the ecology, stock management, and aquaculture of this species (Nonaka et al. 2000). In particular, phyllosoma culture has been studied for more than 100 years with the first trial undertaken in 1898 (Hattori & Oishi 1899). The first complete larval culture from hatching to the juvenile stage was in May 1988 by Yamakawa et al. (1989); they obtained one juvenile from c. 1000 newly hatched phyllosoma in the laboratory. This was also the first successful larval culture from hatching to the juvenile stage of genus *Panulirus*. Kittaka & Kimura (1989) produced two juveniles of *P. japonicus* from newly hatched phyllosoma in July 1988. Thereafter, culturing conditions, such as temperature, quality of the sea water, and design of the tank, have been investigated (e.g., Matsuda & Yamakawa 1997; Shioda et al. 1997; Sekine et al. 2000). Survival from hatching to the juvenile stage, however, is still low (0–10%, our unpubl. data) and mass culture of phyllosoma has had difficulties in the middle and late stages.

Factors that hinder palinurid larval culture include the peculiar form of body (small mouthparts to body size and long pereiopods), excessive aggregation, a long phyllosoma phase (a few months to almost 2 years) and diseases, along with little information on the ecology. When phyllosoma are cultured communally, they aggregate in the same parts of the culture tank because of negative phototaxis, except for a few weeks after hatching, and they entangle with each other. This aggregation probably causes loss of long pereiopods and a decrease in the amount of feeding, resulting in slow growth and low survival. To establish mass culture of phyllosoma, preventing aggregation is necessary by regulating the rearing conditions, such as lighting, water current, and tank design. Inoue (1981) designed a 30-litre hemispherical tank with many tiny holes on the bottom, through which sea water was supplied at a slow water flow, which maintained phyllosoma in suspension and prevented aggregation. Using this culture tank, he successfully obtained a single gilled stage phyllosoma of *P. japonicus*. Sekine et al.

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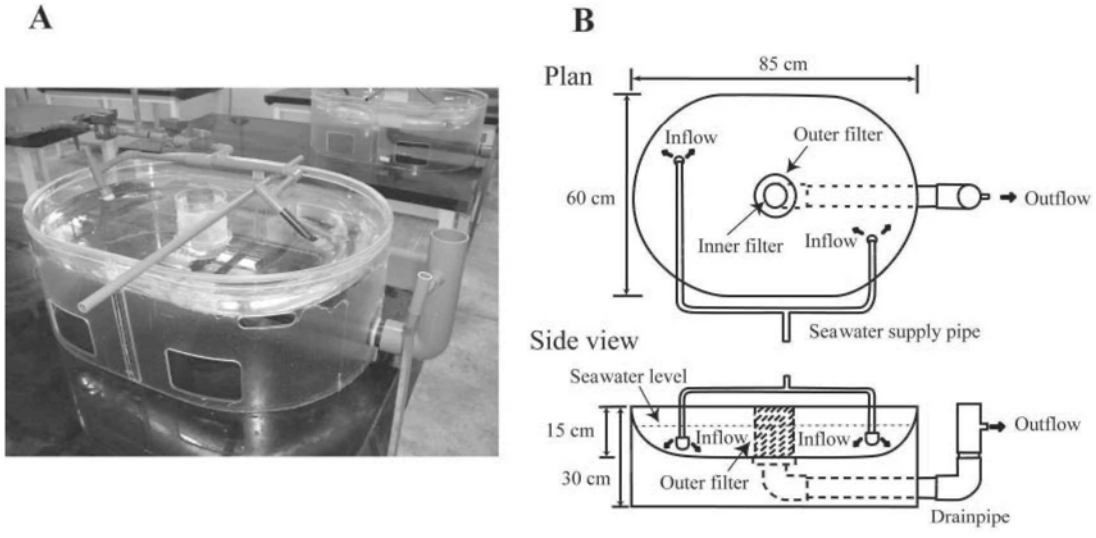

Fig. 1 **A**, photograph and **B**, schematic views of a 40-litre elliptical tank for *Panulirus japonicus* phyllosoma culture.

(2000) used similar shaped tanks without holes on the bottom and passed sea water through air-tubes fitted to air-stones, producing 178 pueruli over several years. Illingworth et al. (1997) developed a system for phyllosoma of *Jasus edwardsii* consisting of four square tanks that allowed phyllosoma to be transferred without handling. Kittaka (2000) designed an upwelling system with circular tanks modified from a plankton kreisel for larval culture of clawed lobster developed by Greve (1968). These attempts at improving culture tanks have been successful to some extent for early- and middle-stage phyllosoma, but no tank suitable for later-stage phyllosoma has been developed.

In this study, a new culture tank was designed for middle- to late-stage phyllosoma of *P. japonicus* and was used at three phyllosoma densities. We describe here the tank, its function, and the results of the phyllosoma culture.

MATERIALS AND METHODS

Culture tank design

The culture tanks, made from transparent acrylic resin, were elliptical and shallow (85 cm long, 60 cm wide, and 15 cm deep), each with a capacity of 40 litre (Fig. 1). The bottoms of the tanks were concave, having smoothly curved corners designed to prevent excessive aggregation of phyllosoma and a flat area of 1500 cm^2 at the centre. The shallow depth allowed phyllosoma to be observed well, permitting prompt removal of uneaten food and exuviae and easy transfer of phyllosoma with spoons when the dirty culture tanks were changed to clean ones.

Sea water gently entered the tanks through two 12-mm diameter polyvinyl chloride (PVC) pipes, to which faucet cups were fitted at each pipe outlet, and the water flow rate was c. 60–70 litres h^{-1}. The faucet cups assisted in creating a moderate seawater current in the tanks. Drainage was through a 50-mm diameter PVC drainpipe mounted at the centre of the tank fitted with double filters. The filters were constructed in PVC frames around which nylon screens were fixed (the outer filter with 3-mm mesh screen and the inner one with 0.2-mm mesh screen); the outer filter prevented phyllosoma from escaping and the inner one prevented the outflow of *Artemia*.

Phyllosoma culture

The 390 middle-stage phyllosoma, which had hatched on 15 July 2002, were previously cultured in six 40-litre hemispheric tanks according to Sekine et al. (2000). The phyllosoma were 123 days old at the start of experiment, with a body length of 11.5 ± 0.9 mm (mean ± SD, $n = 60$) and had a survival from hatch of over 80%. The middle-stage phyllosoma were cultured at three densities of 40, 65, and 90 phyllosoma/tank with each density in duplicate tanks.

Phyllosoma were fed with diets of live *Artemia* and fresh gonads of the mussel *Mytilus galloprovincialis*. *Artemia* were cultured on diets of the diatom *Phaedactylum tricornutum* and the green algal flagellate *Tetraselmis tetrathele* for c. 1 month to 7–9 mm body length. The density of *Artemia* added to each tank was 0.01–0.02 individuals ml^{-1}. Mussel gonads were finely minced to c. 1–4 mm^3 and were fed to phyllosoma (100–200 pieces in each tank). *Artemia* and mussel gonads were replaced daily. To wash away uneaten *Artemia*, the inner screen mounted around the drainpipe was removed for a few hours daily. Uneaten mussel gonads were removed with a siphon.

Sea water for the phyllosoma culture was filtered through a 0.2–μm mesh membrane filter, sterilised with ultraviolet light and heated to 24–25°C. Phyllosoma had a constant photoperiod of 12 h light and 12 h dark using fluorescent lights equipped with an electric timer. The light intensity during the light phase was c. 0.05 μmol m^{-2} s^{-1}, except for c. 3 h at 5 μmol m^{-2} s^{-1} to remove uneaten food and exuviae, to supply newly prepared food, and to change the culture tanks. The culture tanks were replaced every week by transferring phyllosoma with a spoon by hand, and then the antibiotics ampicillin or chloramphenicol were added to the clean tanks at a concentration of 10 mg $litre^{-1}$ for 24 h to prevent bacterial diseases.

Throughout the culture, dead phyllosoma and exuviae were removed daily. The causes of deaths were classified into 10 categories based on the appearances of dead phyllosoma (Table 1). Phyllosoma that had lost more than three pereiopods were also removed and included in the causes of mortalities because they probably could not capture sufficient food and survive until the puerulus stage. The survival rate in each tank was calculated daily from the number of phyllosoma removed from the tanks and verified when the culture tank was replaced every week. Body lengths of 20 phyllosoma randomly sampled from each tank were measured monthly during the period from the start of experiment to 5 months because metamorphoses to the puerulus stage occurred after 5 months of the experiment.

When phyllosoma were approaching metamorphosis to the puerulus stage, they were transferred to six 5-litre circular tanks, one for each larval culture tank, in which they were held until the morning after metamorphosis because newly metamorphosed pueruli have soft bodies, little activity, and are cannibalised by the remaining phyllosoma. Sea water filtered through 0.2–μm mesh filter was provided at a water flow rate of 60 litres h^{-1}.

Puerulus culture

Pueruli were cultured individually in 400-ml glass cups with a still-water system or in 500-ml plastic containers with a flow-through system at 24°C until moulting to the first juvenile stage. A small PVC pipe was placed as a shelter in each culture vessel. The pueruli were not provided with food as they do not feed (Nishida et al. 1990).

Statistics

Differences in survival of phyllosoma between treatments were analysed using repeated measures ANOVA with data at 223 and 323 days after hatching (100th and 200th days, respectively, of experiment) and at the termination of the experiment (425 days after hatching). Survivals during the

Table 1 Percentage compositions (mean ±SD) in the causes of mortalities of *Panulirus japonicus* phyllosoma cultured at densities of 40, 65, and 90 larvae/tank.

Cause of mortalities	Density (larvae/tank)		
	40	65	90
Necrosis of pereiopod	3 ± 4	6 ± 4	2 ± 0
Cloudiness of thorax	3 ± 4	2 ± 2	3 ± 2
Cloudiness of midgut gland	8 ± 4	6 ± 4	9 ± 1
Cloudiness of antenna gland	11 ± 7	9 ± 4	8 ± 2
Cloudiness of hindgut	11 ± 7	0	4 ± 1
Weakening	0	6 ± 4	2 ± 2
Moult complications	35 ± 3	41 ± 9	23 ± 3
Cannibalism	11 ± 0	5 ± 2	16 ± 5
Lost more than three pereiopods	0	13 ± 4	25 ± 1
Unknown	19 ± 20	13 ± 13	9 ± 4

puerulus stage were compared between treatments using one-way ANOVA. Percentage data were arcsine-transformed. Differences in body length of phyllosoma were tested by repeated measures ANOVA, and total numbers of culture days to the puerulus stage were compared using one-way ANOVA. The level of significance for all analyses was $P < 0.05$. All data are presented as mean ±SD.

RESULTS

Few phyllosoma mortalities were found in all tanks until c. 2 months after the start of culture and the survival was over 95% at 173 days after hatching (50th day of culture) irrespective of phyllosoma density (Fig. 2), after which the mortalities increased gradually for all tanks. Survival appeared to be lowest at 90 phyllosoma/tank but was not significantly different to the other densities ($F = 9.2888$, $P = 0.0518$) (Table 2).

Moulting complications, including deformation of body in the process of and at the end of moulting, were the major causes of phyllosoma death (Table 1), and were 23–41% of all causes of death. Bacterial diseases (cloudiness of antenna gland, midgut gland, hindgut, and thorax) were also found. Cannibalism of soft shell phyllosoma occurred in all tanks within 1 h after moulting. In treatments 65 and 90 phyllosoma/tank, 13 ± 4 and 25 ± 1%, respectively, of phyllosoma were removed because they lacked more than three pereiopods.

There were no significant differences between the three phyllosoma densities in body length ($F = 0.3406$, $P = 0.7836$) (Fig. 3), as well as in the total number of culture days to the puerulus stage ($F = 0.4013$, $P = 0.7007$) (Table 2).

Pueruli in all treatments moulted to the first juvenile stage with survival rates of 79–86% (Table 2) and there were no differences between the three phyllosoma densities ($F = 0.3188$, $P = 0.7489$). Mortalities of pueruli within 2 days after metamorphosis to the puerulus stage, probably related to metamorphosing, were 71% of all mortalities in this study.

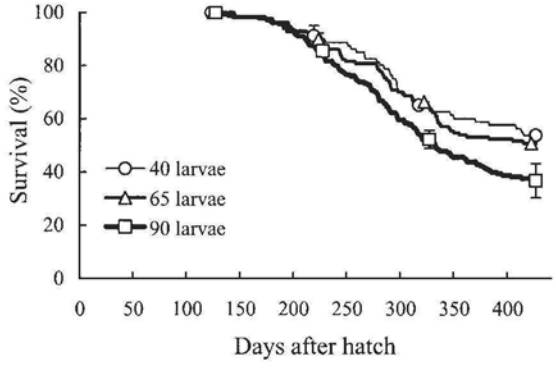

Fig. 2 Survival of *Panulirus japonicus* phyllosoma cultured at three densities (40, 65, and 90 larvae/tank) in elliptical tanks. Lines indicate daily survivals, and symbols and vertical bars indicate the mean and the standard deviation at 223 and 323 days after hatching (100th and 200th days of experiment) and at the termination of the experiment (425 days after hatching).

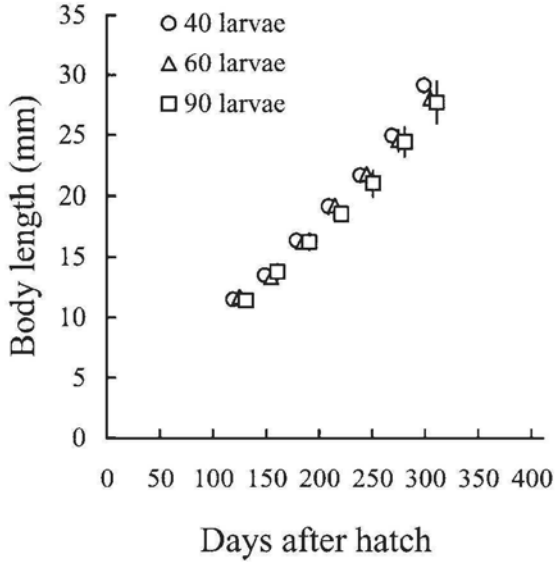

Fig. 3 Body length of *Panulirus japonicus* phyllosoma cultured at 40, 65, and 90 larvae/tank. Symbols and vertical bars indicated the mean and the standard deviation, respectively.

DISCUSSION

In this study, middle-stage phyllosoma (11.5 ± 0.9 mm body length) of *P. japonicus* cultured in elliptical tanks had survival rates to the puerulus stage of 37–54% which were much higher than for any previous results. This constitutes a significant advance in the aquaculture of this species. The preceding culture of newly-hatched phyllosoma in 40-litre hemispheric tanks achieved survival to the middle stage of over 80%. Hence, pueruli could be produced with survival of 30–43% from hatch.

Although some palinurid lobsters have been completely cultured to the puerulus stage in the laboratory, the survival was generally low (Illingworth et al. 1997; Kittaka 1997, 2000; Kittaka et al. 2001) with the highest survival at 12.6% for *Jasus verreauxi* (Kittaka et al. 1997).

The tank developed in this study has some advantages over previous designs used for palinurid phyllosoma: (1) the shallow depth allows phyllosoma to be conveniently observed and transferred by hand to clean tanks; (2) avoiding excessive aggregation of phyllosoma is possible because of the concave bottom and the central flat area of the tank; and (3) uneaten food (*Artemia* and mussel gonads) can be easily removed through a drainpipe or by a siphon.

Disease is a serious problem that typically causes low survival in palinurid phyllosoma culture (Radhakrishnan & Vijayakumaran 1995; Diggles et al. 2000; Kittaka 2000). To minimise the likelihood of gut infections and colonisation of the exoskeleton by fungi and achieve high survival, good culture tank hygiene is necessary (Lesser 1974, cited in Illingworth et al. 1997). Illingworth et al. (1997) pointed out that a culturing system is needed to regularly transfer phyllosoma to clean tanks without handling. Their system was effective for early- and middle-stage *J. edwardsii* phyllosoma which had a high survival of 74% from hatching to Stage VII. For late-stage phyllosoma, however, the survival decreased markedly, resulting in only one puerulus. In this study, we transferred phyllosoma to the clean shallow tanks every week by hand, which only took 10 min for the 65 larvae. We believe that this tank can be useful to culture up to 100 late-stage phyllosoma, but scaling up may be difficult.

Culture density affects the survival and growth of decapod larvae (Ennis 1995). This study appeared to show that survival at a density of 90 phyllosoma/tank was lower than at 40 and 65 phyllosoma/tank. The number of pueruli obtained at 40 phyllosoma/tank was lower than at 65 and 90 phyllosoma/tank and there was no significant difference between 65 and 90 phyllosoma/tank. Therefore, 65 phyllosoma/tank may be most suitable to enhance survival and to produce as many pueruli as possible. However, the culture density did not affect the growth, in terms of body length and duration to puerulus.

Phyllosoma of spiny lobsters are not thought to be cannibalistic (Kittaka 2000). In this study, however, many mortalities were caused by cannibalism at the moult. Moreover, phyllosoma (13–25%) cultured at densities 65 and 90 phyllosoma/tank were removed from the tanks because they lacked more than three pereiopods. The lack of pereiopods seemed to be primarily caused by other phyllosoma grasping them immediately after the moult. This suggests that the phyllosoma were more vigorous and aggressive than in previous studies, reflecting better culture conditions. Cannibalism and damage to newly moulted phyllosoma are problems to be resolved to increase the production of pueruli, and further improvement of larval culture method is necessary.

For early- and middle-stage phyllosoma, optimal feeding conditions, in terms of food density and size, were determined by Inoue (1981), Tong et al. (1997), and Moss et al. (1999), but for late-stage phyllosoma, these parameters have not yet been investigated. In addition to tank design, the size and nutritional profile of foods are important for the high survival and rapid growth of *J. edwardsii* phyllosoma to Stage VIII (Illingworth et al. 1997). The phyllosoma of this study were fed with larger *Artemia* (7–9 mm) than in previous studies in *P. japonicus* (e.g., 4 mm body length, Matsuda & Yamakawa 1997; 3 mm body length, Sekine et al. 2000), and the larvae appeared to take the large *Artemia* more easily than smaller ones. This suggests that feeding with large *Artemia*, as well as the new tank design, resulted in the high survival to puerulus and juvenile.

Pueruli produced in the laboratory generally have poor survival to juvenile: 17% for *J. verreauxi* (Kittaka et al. 1997) and 42% for *P. japonicus*

Table 2 Survival (mean ±SD) of phyllosoma to the puerulus and 1st juvenile stage and time taken to reach the puerulus stage after the start of experiment when cultured at densities of 40, 65, and 90 larvae per tank. Experiment commenced with mid-stage phyllosoma that were 123 days old.

Density (larvae/tank)	Survival to puerulus stage (%)	No. of pueruli metamorphosed	Survival to 1st juvenile stage from metamorphosis (%)	No. of days to puerulus stage
40	54 ± 1	21 ± 1	86 ± 0	212 ± 13
65	51 ± 0	33 ± 0	79 ± 13	219 ± 5
90	37 ± 9	33 ± 8	83 ± 6	215 ± 5

(Sekine et al. 2000). The survival of pueruli in this study was much higher at 79–86%. Mortalities are thought to be related to insufficient nutritional storage during the phyllosoma stage to support energy consumption and development during the non-feeding puerulus stage (Kittaka 2000). Many mortalities during the puerulus stage occur within 2 days after metamorphoses (Kittaka 2000; this study), suggesting that they are not a result of insufficient nutritional storage. The high survival at pueruli was probably related to the high survival during the phyllosoma stage.

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REFERENCES

Diggles, B. K.; Moss, G. A.; Carson, J.; Anderson, C. D. 2000: Luminous vibriosis in rock lobster *Jasus verreauxi* (Decapoda: Palinuridae) phyllosoma larvae associated with infection by *Vibrio harveyi*. *Diseases of Aquatic Organisms 43*: 127–137.

Ennis, G. P. 1995: Larval and postlarval ecology. *In*: Factor, J. R. *ed.* Biology of the lobster *Homarus americanus*. San Diego, Academic Press. Pp. 23–46.

Greve, W. 1968: The 'planktokreisel', a new device for culturing zooplankton. *Marine Biology 1*: 201–203.

Hattori, T.; Oishi, Y. 1899: Hatching experiment on Ise lobster I. *Report of Imperial Fisheries Institute 1*: 76–132. (In Japanese.)

Holthuis, L. B. 1991 : Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date. *FAO Fisheries Synopsis No. 125, Vol 13*.

Illingworth, J.; Tong, L. J.; Moss, G. A.; Pickering, T. D. 1997: Upwelling tank for culturing rock lobster (*Jasus edwardsii*) phyllosomas. *Marine and Freshwater Research 48*: 911–914.

Inoue, M. 1981: Studies on the cultured phyllosoma larvae of the Japanese spiny lobster *Panulirus japonicus* (von Siebold). *Special Report of Kanagawa Prefectural Fisheries Experimental Station 1*: 1–91. (In Japanese.)

Kittaka, J. 1997: Culture of larval spiny lobster: a review of work done in northern Japan. *Marine and Freshwater Research 48*: 923–930.

Kittaka, J. 2000: Culture of larval spiny lobster. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. 2nd ed. Oxford, Blackwell Scientific Publications. Pp. 508–532.

Kittaka, J.; Kimura, K. 1989: Culture of the Japanese spiny lobster *Panulirus japonicus* from egg to juvenile stage. *Nippon Suisan Gakkaishi 55*: 963–970.

Kittaka, J.; Ono, K.; Booth, J. D. 1997: Complete development of the green rock lobster, *Jasus verreauxi* from egg to juvenile. *Bulletin of Marine Science 61*: 57–71.

Kittaka, J.; Kudo, R.; Onda, S.; Kanemaru, K.; Mercer, J. 2001: Larval culture of the European spiny lobster *Palinurus elephas*. *Marine and Freshwater Research 52*: 1439–1444.

Lesser, J. H. R. 1974: Identification of early larvae of New Zealand spiny and shovel-nosed lobster (Decapoda, Palinuridae and Scyllaridae). *Crustaceana 27*: 259–277.

Matsuda, H.; Yamakawa, T. 1997: Effects of temperature on growth of the Japanese spiny lobster, *Panulirus japonicus* (V. Siebold) phyllosomas under laboratory conditions. *Marine and Freshwater Research 48*: 791–796.

Moss, G. A.; Tong, L. J.; Illingworth, J. 1999: Effects of light intensity and food density on the growth and survival of early-stage phyllosoma larvae of the rock lobster *Jasus edwardsii*. *Marine and Freshwater Research 50*: 129–134.

Nishida, S.; Quigley, B. D.; Booth, J. D.; Nemoto, T.; Kittaka, J. 1990: Comparative morphology of the mouthparts and foregut of the final stage phyllosoma, puerulus, and postpuerulus of the rock lobster *Jasus edwardsii* (Decapoda, Palinuridae). *Journal of Crustacean Biology 10*: 293–303.

Nonaka, M.; Fushimi, H.; Yamakawa, T. 2000: The spiny lobster fishery in Japan and restocking. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. 2nd ed. Oxford, Blackwell Scientific Publications. Pp. 221–242.

Radhakrishnan, E. V.; Vijayakumaran, M. 1995: Early development of the spiny lobster *Panulirus homarus* (Linnaeus, 1758) reared in the laboratory. *Crustaceana 68*: 151–159.

Sekine, S.; Shima, Y.; Fushimi, H.; Nonaka, M. 2000: Larval period and molting in the Japanese spiny lobster *Panulirus japonicus* under laboratory conditions. *Fisheries Science 66*: 19–24.

Shioda, K.; Igarashi, M. A.; Kittaka, J. 1997: Control of water quality in the culture of early-stage phyllosomas of *Panulirus japonicus*. *Bulletin of Marine Science 61*: 177–189.

Tong, L. J.; Moss, G. A.; Paewai, M. M.; Pickering, T. D. 1997: Effect of brine-shrimp numbers on growth and survival of early-stage phyllosoma larvae of the rock lobster *Jasus edwardsii*. *Marine and Freshwater Research 48*: 935–940.

Yamakawa, T.; Nishimura, M.; Matsuda, H.; Tsujigadou, A.; Kamiya, N. 1989: Complete larval rearing of the Japanese spiny lobster *Panulirus japonicus*. *Nippon Suisan Gakkaishi 55*: 745.

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Moulting behaviour responses of Bay lobster, *Thenus orientalis*, to environmental manipulation

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Abstract Bay lobster, *Thenus orientalis*, locally known as Moreton Bay bug, is being investigated for aquaculture, and controlling the moulting process is critical to success in the production of softshell animals. Identification of moult stages is possible because of the existence of exoskeleton ecdysial sutures (crack lines) on the gill chambers. The timing of moulting is synchronised and occurs around sunset when animals are under a natural day-night condition. The timing and synchrony of moulting can be manipulated by altering the day-night cycle, whereas the length of the actual moult stage can be shortened/prolonged by manipulating temperature. During the intermoult stage for juveniles (average weight 79 g), body weight increases only by 9%, whereas the majority of weight gain (an additional 44%) occurs within the short period just before and after the actual moult stage. These findings have application for the development of "softshell" products, which can be harvested at around the actual moult stage.

Keywords Bay lobster; *Thenus*; photoperiod; moult stage; moult increment

INTRODUCTION

Crustaceans moult regularly for growth to increase (or sometimes decrease) their size and to change their morphology. Moulting (or ecdysis) is a unique and complicated process. One moult cycle is set off by the shedding of the old exoskeleton, and dramatic changes to the physiology and biochemistry of animals may occur both before and after this event. Though the actual act of shedding the old exoskeleton is the most obvious phenomenon of the moult cycle (this comprises only a short period within a cycle that may take up to a year or more), the vast majority of events during the cycle occur internally. Many factors—environmental, nutritional, physiological, behavioural, and reproductive—are thought to influence the moult processes/phases, and these are regulated by combinations of hormones, such as moult-inhibiting hormone (MIH) and ecdysone (see Chang 1995). Little is known about the mechanism and regulation of hormonal activities during the moult cycle, because of the complexity of the hormone regulatory systems.

Bay lobsters, *Thenus orientalis* (Lund) and *Thenus indicus* (Lund), locally known as Moreton Bay bugs (or sand bug for *T. orientalis* and mud bug for *T. indicus*), are found along the entire northern coast of Australia from Shark Bay in Western Australia to Coffs Harbour in northern New South Wales (Kailola et al. 1993). Mass rearing techniques for these species have been established, and commercialisation of aquaculture development is currently being undertaken (AFFA 2001). Understanding the moult cycle is the key to improving culturing techniques. Laboratory observations on the process of moulting in *T. orientalis* were made in this study to improve the knowledge and understanding of the moult cycle.

MATERIALS AND METHODS

General rearing methods

All animals used in this study were raised in the hatchery between 1998 and 2001. Ovigerous *T. orientalis* females were caught off Hervey Bay,

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south-eastern Queensland and transported to the QDPI Bribie Island Aquaculture Research Centre in aerated sea water in a fish transporter (0.5 m^3). Berried females were kept in a 1 m^3 holding tank with running filtered (1.0 μm) sea water. Temperature was maintained at between 24 and 27°C and animals were fed once daily with fresh flesh of the bivalve *Donax deltoids*. When embryos became visibly amber-brown in colour, females were transferred to individual 0.2 m^3 hatching tanks, with 500 μm mesh covering the outlet, for larval hatching. Newly hatched phyllosomas were immediately harvested and transferred from the hatching tanks to prepared raceway larval rearing systems. These rearing systems had three major components: pre-water treatment, endless raceway (rearing vessel), and recirculation. The new incoming water was filtered through a 0.5 μm cartridge filter, and then sterilised through a 60 W UV unit at the pre-water treatment component. The treated water was pooled in a sump (0.38 m^3) of the recirculation component; ozone (O_3) was constantly injected through a snorkel equipped power head, and temperature was maintained at 27°C by a 3 kW heater. Because maintenance of O_3 level in the rearing water was extremely difficult owing to constant changes in organic matter and biomass, the maximum dose of O_3 into rearing water was preset before the start of larval rearing at 0.05 mg $litre^{-1}$, and this preset amount of O_3 was constantly injected throughout the larval rearing period. The water in the sump was sent through the 19 mm polyethylene pipe surrounding the raceway and was injected to the raceway (0.3 m width, 0.3 mm depth, 12 m length) by 4 mm injectors to create one-way circulation. The rearing water in the raceway was drained to the sump, where new water was added (1–4 litres min^{-1}) and O_3 was injected constantly, and was recirculated back to the raceway. Finely chopped fresh flesh (1–4 mm in size) of the bivalve *D. deltoids* was fed to the phyllosomas twice daily. The survival of phyllosomas to the nisto stage was generally >80%, with >1500 nistos produced from each trial. Nistos were reared in 0.38 m^3 tanks, with running 1 μm pre-filtered sea water at 25–27°C. The duration of the nisto stage was generally 7 days (>90% survival). No food was given to nistos. The juveniles of *T. orientalis* were reared either in 0.3 m wide or 1.1 m wide raceways with sea water 0.15 m deep. The rearing water was pre-filtered through 20 μm multimedia filters and was maintained at a temperature range of between 24 and 28°C. Early stage juveniles (<20 g body weight) were fed on freshly chopped *D. deltoids*, and older juveniles were fed on defrosted flesh of squid. There was no artificial illumination. The survival of juveniles (up to 45 g body weight) was generally >80%.

Identification of moult stages

Fifty post-moult juveniles (79 ± 7.1 g (mean ± SD)) of *T. orientalis* from the same batch were numbered on the surface of their carapaces by liquid paper, and then the sutures on the ventral surface of the carapace were monitored. At the same time, body weight of individual animals was monitored throughout the intermoult period. Another group of 50 juveniles (16 ± 5.7 g (mean ± SD)) were selected from the same batch of juveniles on the morning of moulting, and changes in body weight were monitored.

Diel timing of moulting

The diel timing of moulting of *T. orientalis* reared under the natural day/night period was observed. The time of daily sunset and the time of moult (when new animals are totally detached from old exoskeleton) were recorded. To understand the mechanism of moult synchrony, the photoperiod was manipulated before moulting to: (1) standard (natural day/night); (2) continuous darkness from 1 day before moulting; (3) continuous light while moulting; (4) continuous darkness from 2 days before moulting (except cleaning and feeding in the morning/evening for 10 min); (5) illuminated for 1 h during the night for 2 days before moulting; and (6) continuous light for 2 days before moulting. Also, premoult juveniles were transferred to water 4°C warmer than rearing temperature 12 h before moulting (at 0600 h).

RESULTS

Moult stages

Four moult stages were recognised in juveniles of *T. orientalis* from visual observation—(1) postmoult: soft exoskeleton, inactive, no feeding; (2) intermoult: hard exoskeleton, active feeding, no ecdysial sutures at ventral side of carapace; (3) premoult: hard exoskeleton, inactive feeding, appearance of ecdysial sutures (Fig. 1); and (4) actual moult: swallowing body under exoskeleton, shedding of old exoskeleton.

The length of each moult stage can be manipulated since the duration of the intermoult stage depends on the size of animals and rearing conditions such as nutrition and temperature, but in general it is 7% for the postmoult stage, 74% for the intermoult stage, 17% for the premoult stage, and 2% for the actual moult stage in juvenile animals (<45 g

Fig. 1 Premoult stage of *Thenus orientalis* juveniles. Arrow indicates ecdysial sutures.

body weight). Small juveniles (<16 g) started eating from 24 h after moulting, but larger juveniles (16–45 g) did not eat until at least 2 days after moulting. Ecdysial sutures on the ventral side of the carapace started appearing 7–12 days before the actual moult stage, and cracks appeared at the beginning of the actual moult stage (c. 12 h before shedding the exoskeleton).

Figure 2 shows the change in body weight through four moult stages in *T. orientalis* (79 ± 7.1 g). At this size, the average increment in body weight between two actual moult stages was 54.5% from original weight. During intermoult and premoult stages, body weight did not change much; animals only gained 8.9% of original weight, with the majority of weight gain occurring only at the actual moult stage. Fig. 3 shows the change in body weight at the actual moult stage in *T. orientalis* juveniles (16 ± 5.7 g). At this stage, the mean increment in body weight during actual moult stage was 61%. The increase in body weight started c.12 h before the shedding of the exoskeleton, gradually increasing by 16% of body weight. From 1 h before to 2 h after the moult, there was a further 45% increase in weight, with a further gradual increase by 2% over the following 10 h.

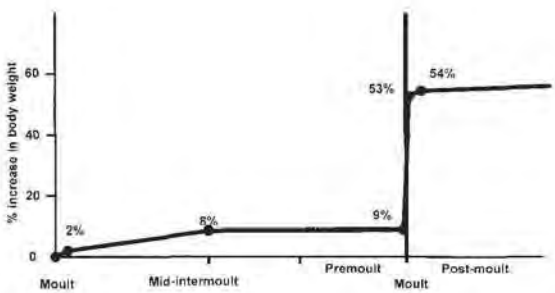

Fig. 2 Change in body weight over the moult cycle of *Thenus orientalis* juveniles (79 ± 7.1 g (mean ± SD)).

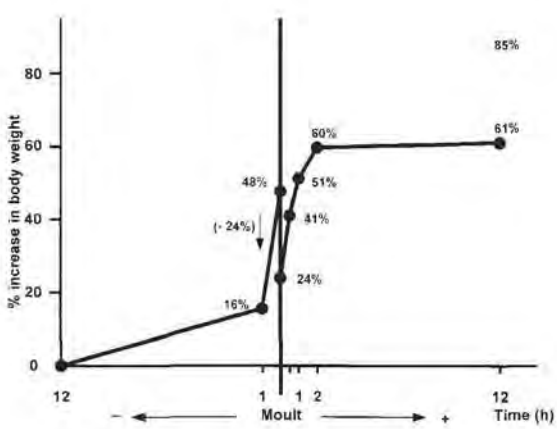

Fig. 3 Change in body weight over the moult cycle of *Thenus orientalis* juveniles (16 ± 5.7 g (mean ± SD)).

Diel timing of moult

Under the natural day/night photoperiod, all juveniles of *T. orientalis* moulted between 0.5 h and 5 h after sunset (mean 2 h 23 min). When rearing temperature of juveniles (all sizes) was increased 4°C on the morning of the expected moult day, the

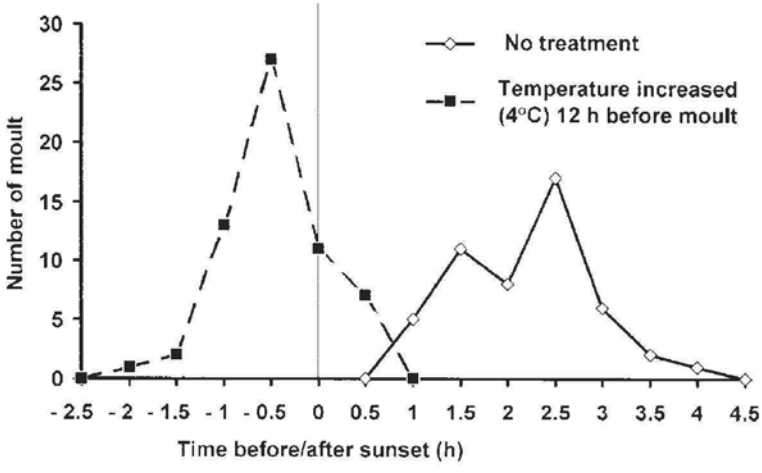

Fig. 4 Effect of temperature on diel timing of moult in *Thenus orientalis* juveniles.

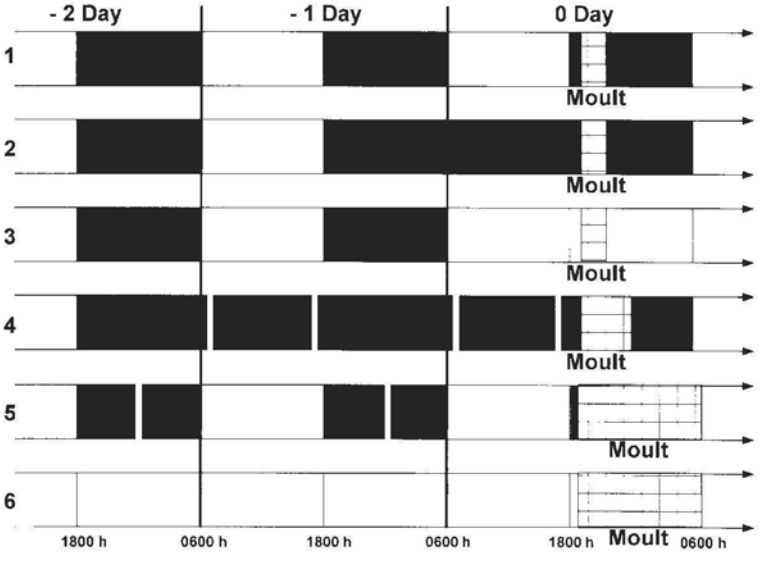

Fig. 5 Effects of changing of photoperiod on the timing of moulting in *Thenus orientalis* juveniles. (1, natural light; 2, continuous dark at the day of moult; 3, continuous light at the day of moult; 4, continuous dark from 2-day before moult (0.5 h light on at morning and evening for husbandry); 5, short illumination (0.5 h) during the dark period; and 6, continuous light from 2-day before moult.) Black area indicates dark period; white area indicates light period; mesh area indicates period animal moulted.

time of moult was advanced on average 3 h 38 min more than that of the no treatment group (Fig. 4). The diel time of moult lost synchrony when the day/night cycle was modified 24 h before the actual moult (Fig. 5). However, synchrony of moulting was not affected if the day/night cycle was changed within 24 h of the actual moult.

DISCUSSION

The characteristics of moult sequences of crustaceans have been well documented (see Phillips et al. 1980; Skinner 1985). In general there are four moult stages during one moult cycle: metecdysis (postmoult), anecdysis (intermoult), proecdysis (premoult), and ecdysis (actual moult). In addition to these four stages, further sub-stages have been reported on the basis of morphological changes (Dall et al. 1990). Rahman & Subramonian (1989) described morphological and behavioural characteristics of the moult cycle in *T. orientalis*, and this study identified four clear moult stages (postmoult, intermoult, premoult, and actual moult) based on the external morphological characteristics of *Thenus* juveniles. Previously, the separation between intermoult and premoult stages was unclear, but in *Thenus* the separation of the two stages is obvious; the premoult stage starts when ecdysial sutures appear on the abdominal surface of the carapace.

When these ecdysial sutures appear, the length of time to actual moult can be estimated according to the progression of the ecdysial sutures. Although, of course, the estimated time to the actual moult can alter depending on the environmental and nutritional condition of the animals, this method for predicting the timing of the moult is a useful tool from an aquaculture point of view, especially with respect to the harvesting of "softshell" animals. Softshells are harvested during the actual moult/postmoult period immediately after the shedding of the exoskeleton. In the United States, softshell crabs are already well known and have achieved premium prices (Oesterling 1998). Because softshell animals have to be harvested immediately after the shedding of the exoskeleton, the prediction of moult timing is crucial. Together with synchronised moult time after sunset shown in the present study, the *Thenus* species may have great softshell potential because prediction of exact harvesting time (both date and time) is both possible and easy.

It is known that crustacean species accumulate reserves such as glycogen and lipids in the haemolymph and midgut from feeds during the intermoult stage, and that morphological and physiological preparations are made for the final stage of ecdysis in the premoult stage (Dall et al. 1990). An interesting finding in this study is that there was little body weight gain in *Thenus* during the intermoult and premoult stages, even though they feed continuously throughout these stages. The majority of weight gain occurs only a few hours before and after the actual moult stage, as a result of water absorption. Animals accumulate feed reserves and reduce water content in their body during the intermoult stage. They then use these reserves to prepare for the next moult at the premoult stage. Finally, they increase their body size by absorbing water from the environment at the actual moult stage. This pattern of body weight increase agrees with the report of the moult cycle of rock lobster *Panulirus argus* (Travis, 1954), though *P. argus* also tended to increase weight during the intermoult stage.

DeCoursey (1983) reviewed the biological timing of crustaceans, describing endogenous rhythms associated with environmental factors. Light is probably the most important single factor influencing endogenous activities, affecting the time of rhythmic moulting in *Thenus* phyllosomas, nisto, and juveniles (Mikami & Greenwood 1997). In *Thenus*, synchronised moulting can be observed just before sunrise during the planktonic phyllosoma stages (Mikami & Greenwood 1997) and just after sunset in subsequent benthic juvenile/adult stages (present study). It appears that the biological timing which regulates synchronised diel moult time in *Thenus* is influenced by the circadian day/night rhythm during the moult cycle, and that the signal for moult time is set at least 24 h before the moult. The mechanism of switching moult time from sunrise (phyllosomas) to sunset (nistos/juveniles/adults) is still unknown. Synchronised moult time can be changed quickly by altering rearing temperature on the day of actual moult. This method of altering moult time can be useful since animals tend to lose synchrony of moult time when light regimes are changed.

Though the body weight does not change much during the intermoult and postmoult stages, it is obvious that the physiology and biochemistry of the animals change dramatically during the moult cycle (see reviews by Quackenbush 1986; Chang 1995). The hormonal scheme regulating the moult cycle is very complex and little is known about it. It is generally believed that ecdysteroid secretion from the Y-organs is negatively regulated by the neuropeptide MIH, secreted from the X-organ sinus gland system located in the eyestalk. The MIH inhibits activities of the Y-organ during the intermoult stage, then the Y-organ is activated when freed from the inhibitory regulation of MIH when entering the premoult stage (Chang 1995). However, the regulatory mechanism of hormonal activities is complicated by other factors; the environment, nutrition, maturation, and growth are all involved in the process of moulting. The present study may suggest two different (but related) regulatory systems of moulting hormones; one regulates commencement of moulting (length of intermoult), and the other regulates the diel time of moulting, which is also regulated by day-night cycles. The details of these regulatory systems are still unknown, and further studies in the biochemistry of moulting are necessary for a full understanding.

REFERENCES

Agriculture, Fisheries and Forestry—Australia 2001: Made in Australia. Canberra, Food Business Group, Department of Agriculture, Fisheries and Forestry—Australia.

Chang, E. S. 1995: Physiological and biochemical changes during the molt cycle in decapod crustaceans: an overview. *Journal of Experimental Marine Biology and Ecology 193*: 1–14.

Dall, W.; Hill, B. J.; Rothlisberg, P. C.; Staples, D. J. 1990: Moulting and growth. *In*: Advance in marine biology. Vol. 27. The biology of the Penaeidae. London, Academic Press. Pp. 213–250.

DeCoursey, P. J. 1983: Biological timing. *In*: Vernberg, E. J.; Vernberg, W. B. *ed*. The biology of crustacea. Vol. 7. New York, Academic Press. Pp. 106–162.

Kailola, P. J.; William, M. J.; Stewart, P. C.; Reichelt, R. E.; McNee, A.; Grieve, C. 1993: Australian fisheries resources. Canberra, Bureau of Resource Sciences, Department of Primary Industries and Energy/Fisheries Research and Development Corporation.

Mikami, S.; Greenwood, J. G. 1997: Influence of light regimes on phyllosomal growth and timing of moulting in *Thenus orientalis* (Lund) (Decapoda: Scyllaridaae). *Marine and Freshwater Research 48*: 777–782.

Oesterling, M. J. 1998: Soft crabs in closed systems: a Virginia success story. *In*: Successes and failures in commercial recirculating aquaculture. Northeast Regional Agricultural Engineering Service (NRAES) Proceedings II, Roanoke, Virginia, 19–21 July 1996. New York, NRAES Cooperative Extension. Pp. 461–466.

Phillips, B. F.; Cobb, J. S.; George, R. W. 1980: General biology. *In*: Cobb, J. S.; Phillips, B. F. *ed*. The biology and management of lobsters. Vol. 1. Pp. 1–82.

Quackenbush, L. S. 1986: Crustacean endocrinology: a review. *Canadian Journal of Fisheries and Aquatic Sciences 43*: 2271–2282.

Rahman, M. K.; Subramoniam, T. 1989: Molting and its control in the female sand lobster *Thenus orientalis* (Lund). *Journal of Experimental Biology and Ecology 128*: 105–115.

Skinner, D. M. 1985: Molting and regeneration. *In*: Bliss, D. E.; Mantel, L. H. *ed*. The biology of Crustacea. Vol. 9. New York, Academic Press. Pp. 43–146.

Travis, D. F. 1954: The moulting cycle of the spiny lobster, *Panulirus argus* Latreillle. I. Moulting and growth in laboratory-maintained individuals. *Biological Bulletin 107*: 433–450.

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Causes of tail fan necrosis in the southern rock lobster, *Jasus edwardsii*

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Abstract Tail fan necrosis (TFN) is a recognised constraint on the advancement of the South Australian rock lobster (*Jasus edwardsii*) liveholding industry because of a reduction in value of afflicted lobsters. Trials were run in the laboratory and at a shore-based experimental live-holding facility (LHF) to determine the influence of at-sea post-harvest handling, feeding frequency (LHF only), density (LHF only), and temperature (laboratory only) on the advent of the condition. Lobsters were caught during normal fishing operations and either immediately placed in protective fine-mesh nylon bags and stored in the boat's well or placed unbagged in the well. At the laboratory, the tail fans of half the bagged lobsters were deliberately damaged with sterile instruments. At the LHF the TFN level increased significantly over 4 months. The bagged treatment showed significantly less late-stage TFN than unbagged daily or weekly-fed treatments with 60% of bagged lobsters showing no TFN at 4 months. With unbagged lobsters, 50% showed erosion in the <25% category and 30% showed erosion of >25% of the tail fan. Lobster density and feeding frequency had no effect on TFN incidence. In the laboratory, bagged and bagged-damaged treatments had no advanced TFN after the 6-week period suggesting that post-harvest bagging minimises TFN and that inflicting physical damage to lobster tail fans with aseptic instruments does not lead to its development. Temperature had no effect on TFN development. The highest incidence of TFN was found in lobsters given normal post-harvest handling, that is, communal holding in boat holds and tanks (i.e., without bags). These conditions are normally associated with physical damage inflicted by conspecifics. Such damage will presumably also involve infection of wounds by the bacterial flora of the crayfish exoskeleton, leading to development of TFN.

Keywords southern rock lobster; *Jasus edwardsii*; tail rot; tail fan necrosis; liveholding; *Vibrio*

INTRODUCTION

Live-holding of wild-caught lobsters is seen as a means of value-adding to the existing commercial catch of southern rock lobsters (*Jasus edwardsii*) in South Australia (worth c. AU$100 million export revenue). This value-adding can occur in two ways: strategic marketing and product enhancement. By having access to holding facilities, fishers can strategically market their catch by holding lobsters at times of low prices and then selling them at times of higher prices. In addition, live-holding may also enable product enhancement, i.e., increases in weight through growth, and improvement in condition through feeding and growth of damaged, sick, and "white" lobsters.

Recent field trials looking at optimum environment and system requirements for adult rock lobster grow-out (Geddes et al. 2001) produced high survival rates, and improved physiological and external condition (damage and colour) were observed in live-held lobsters. These results were promising for an industry based on the long-term

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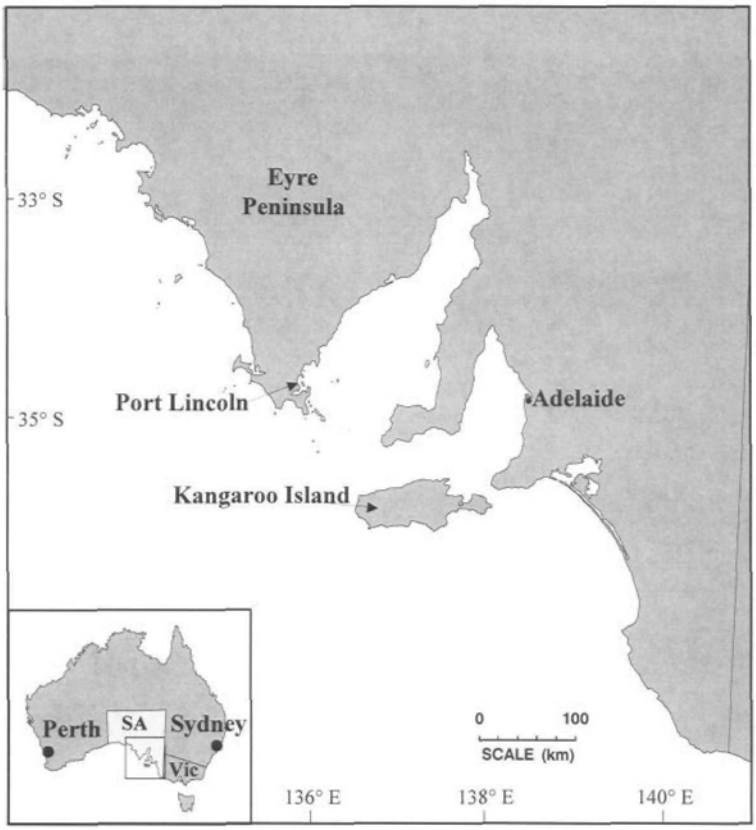


Fig. 1 South Australia showing Port Lincoln and Adelaide, the sites of the trials in this study.

live-holding of lobsters for strategic marketing alone. However, for an industry to develop, based on the live-holding of lobsters for product enhancement, improvements are required in the areas of weight gain, colour change, holding time, and feeding efficiency. In addition, tail fan damage and infections were a major problem with long-term live-held southern rock lobster. In fact the problem may be a major obstacle to the future success of the live-holding industry.

We have defined the condition as tail fan necrosis (TFN), which is characterised by loss of tissue and progressive necrosis of the tail fan with associated melanisation of the area. Despite the severity and importance of the condition, little is known about its cause or progression. Previous observations (Geddes 2001) suggest that the severity of TFN may be related to seasonal water temperatures, with summer temperatures promoting the worst damage. This apparent relationship to temperature may, in turn, be related to bacterial numbers; bacterial infections (especially *Vibrio*) have been identified from damaged tails (Geddes 2001). However, it is not known if the bacteria are incidental or causative.

This study focused on the effect of post-harvest handling, feeding and holding conditions, and temperature on TFN. Bacteria and other agents involved in the infection were also identified to provide an understanding of the microbiology of TFN.

METHODS

Two experiments were undertaken to investigate the causes of TFN. The first was based in raceways at a commercial abalone farm near Point Lincoln, South Australia (Fig. 1) and looked at the effects of post-harvest handling, holding density, and feeding regime. The second was based in the aquarium facility at the South Australian Aquatic Sciences Centre, in Adelaide, and looked at post-harvest handling, temperature, and tail fan damage.

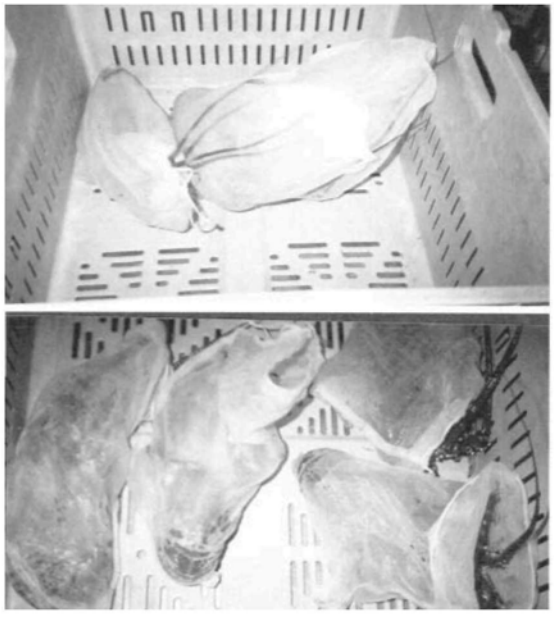


Fig. 2 Fine mesh nylon bags used to bag lobsters for the trials.

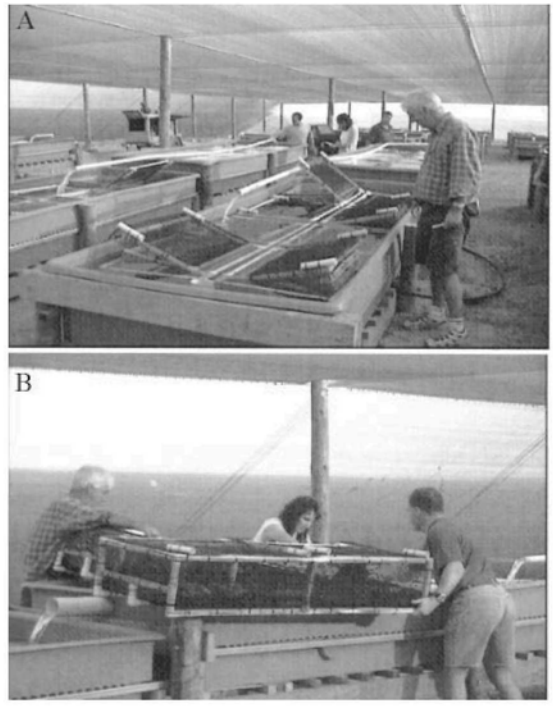


Fig. 3 Flow-through tanks and cages used for field trial. **A**, cages set up and ready for the introduction of lobsters; **B**, placing a cage into a tank.

Effects of post-harvest handling, holding density, and feeding regime on the development of TFN in a raceway holding system

In November 2000, 450 lobsters were bought from local fishers with 420 used for the experiment. The remainder were used to replace mortalities in the first 2 weeks of the experiment. At capture, 130 of the animals were put straight from the lobster pot on the fishing vessel into individual fine mesh (0.5 mm) nylon bags (Fig. 2), protecting the animals until they could be released into the experimental cages, at which point the bags were removed. This was intended to control for damage that might have occurred on the boat and during the transport, potentially leading to TFN.

The time from capture to release into onshore lobster processors tanks varied between 7 and 14 days depending on the length of time a given fisher remained out fishing. Lobsters then remained in tanks for a week before initial scoring for damage. Those in bags were left as such. This variation in time before entering the experiment applied equally to bagged and unbagged lobsters.

The experiment was run over the summer of 2000/01; it began on 27 November 2000 and was completed at the end of March 2001. It was set up in seven outside tanks at Southern Australian Seafoods near Port Lincoln (Fig. 3).

The tanks were rectangular, c. 4 m long and were continuously aerated and supplied with water (flow-through). They were situated within a shade-cloth enclosure. Temperature was monitored using data loggers. Each tank contained four PVC/oyster mesh cages (28 in total). There were three treatments of feeding frequency (daily fed, weekly fed, and starved) and two of density (10 lobsters per cage (6.3/m^2) and 20/cage (12.7/m^2)) (Fig. 4). Four replicates were used for the daily and weekly fed treatments and two for the starved treatment. In addition, a further treatment involved daily feeding of lobsters that had been bagged at capture; this was run at two holding densities and with four replicate cages. Lobsters were assigned randomly (within bagged and unbagged categories) to density and feeding treatments. Randomisation was achieved using random number tables. Lobsters were placed in the cages, which were then secured in the raceways (Fig. 3), with bags removed just before release into cages. In all fed treatments lobsters were allocated 2% body weight per day of an artificial diet formulated for the trials (Table 1).

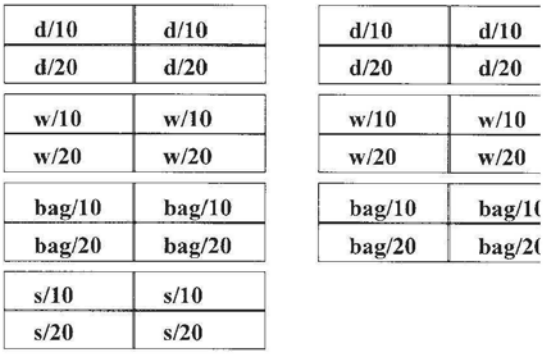


Fig. 4 Experimental design for feeding frequency density trial. (d, daily fed; w, weekly fed; bag, bagged daily feed; s, starved. Numbers refer to lobsters per cage.)

Table 1 Rock lobster, *Jasus edwardsii*, diet used in field and laboratory trials (RL35D). (Formulated by K. Williams, Queensland Department of Primary Industry, Queensland, Australia.)

Component	Percentage
Fish meal	45.7
Wheat gluten	6
Wheat flour	22.9
Crustacean meal	20
Aquabind	3
Banox E	0.01
Vitamin mix	0.2
Vitamin C	0.1
Carophyll pink	0.07
Cholesterol	0.2
Lecithin	1.2
Fish oil	0.6
Total	100.0

Tail fan state was assessed every 2 months as follows. Each of the five appendages of the tail were assessed individually for the presence of scratches, tears, blisters, holes, and erosion as follows. Each damage category was classified as either large or small and assigned a letter accordingly: T = tears ≤ or >7 mm; b or B = blisters ≤ or >5 mm; s or S = scratches ≤ or >7 mm; h or H = holes ≤ or >2 mm; e = erosion of the limb margin not extending into the limb proper, E = erosion of the limb proper.

Percentage TFN was divided into seven categories as follows: no erosion; <25% of the margin of the limb; >25% of the margin of the limb; affecting more than the entire margin but less than or equal to 25% of the whole limb; >25%–50%; >50%–75%, and >75–100%. All subdivisions were made based on previous observations of damage. Most analyses were undertaken on damage classified as TFN and, for statistical analyses, damage assessment was combined into one of three TFN erosion categories: nil, <25%, and >25% erosion of the tail fan limb.

Erosion involved the loss of tissue, necrosis, and melanisation and so is considered TFN in this study. Other damage such as scratches, tears, blisters, and holes may be the precursors of TFN. Photographs were taken of each tail fan at each assessment date, and the photos used to standardise assessment.

Microbiology and scanning electron microscopic observations

Swabs of the surface of healthy and damaged (including TFN) tail fans of randomly selected lobsters from each treatment were plated out onto Thiosulphate-Citrite-Bile-Sucrose (TCBS) agar (Oxoid) and marine agar (1% w/v Oxoid Peptone, 1% Oxoid Lab Lemco powder, 3% w/v NaCl, 1.5% w/v agar) for assessment of the microbial flora. Pure cultures of colonies of bacteria randomly selected from TCBS and marine agar were prepared and identified where possible to species level. The Gram reaction, motility status, and oxidase reaction of pure cultures of individual isolates were determined. Isolates were then characterised using Microbact 24E Identification System (Medvet Diagnostics, Adelaide, SA, Australia). The results of these phenotypic tests were used to identify each isolate, where possible, to species level. Pure cultures of identified bacterial isolates were stored at –70°C in 1 ml volumes of a solution containing glycerol (32% v/v) and Difco Bacto Peptone (0.6%).

At the completion of the field experiment three lobsters were also randomly selected from each of the daily, weekly, and bagged treatments and placed on ice and bought back to Adelaide. Discs (1 cm diam.) of tissue were removed from unaffected (i.e., no TFN) and affected uropods from each individual, homogenised and plated on marine agar and TCBS agar to quantify the bacterial flora, and for examination by scanning electron microscopy (SEM).

Fluid was also extracted from a number of intact tail fan blisters. This material was plated onto TCBS and marine agar to look for the presence of a microbial flora.

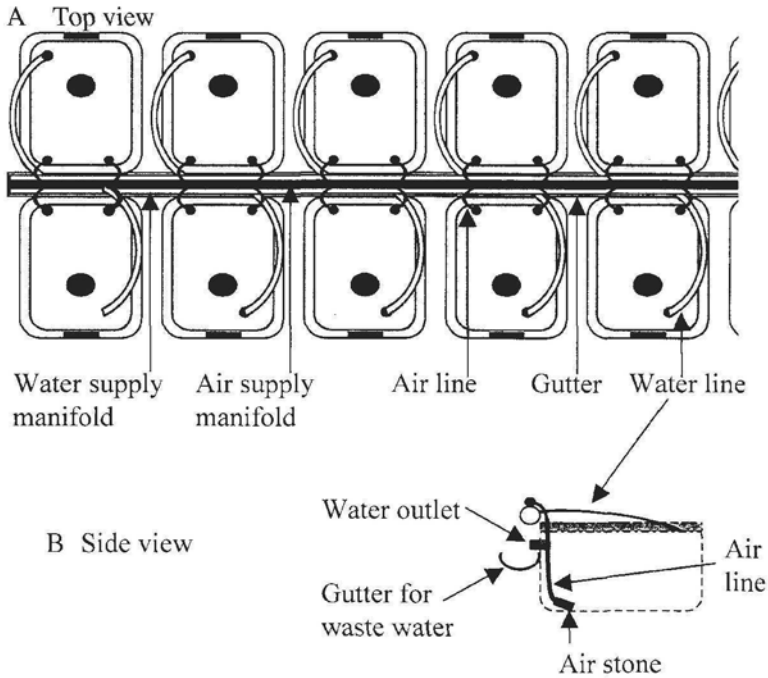


Fig. 5 Tank array used for laboratory experiment.

Effects of temperature, physical damage, and bagging on the development of TFN in laboratory trials

In February 2001, 70 lobsters were caught over a 3-day period during normal fishing operations with the assistance of a commercial lobster fisher. The pots were set in 30–50 m of water off the south coast of Kangaroo Island (Fig. 1). When pots were hauled up, males just over the legal limit (102 mm carapace length) were separated from the catch. Forty-five of these lobsters were put into mesh bags and the remainder (25) left unbagged. The same technique was used in setting up the field experiment and had shown that bagged lobsters sustained much less tail fan damage, and damage in general, than those left without bags, the standard commercial practice.

The day after the completion of the sampling period, lobsters were transferred to a processor's tanks on the mainland and, the following day, to the South Australian Aquatic Sciences Centre (SAASC) in Adelaide (Fig. 1). During the journey they were treated in the same way as commercial lobsters, that is, housed in crates covered with damp sacking in a chiller truck (10–12°C). Once at SAASC they were kept in flow-through communal tanks (15°C) for 1 week before the start of the experiment.

After the acclimation period, 60 of the harvested lobsters were assigned randomly to individual 38-litre tanks (Fig. 5) using random number tables. Lobsters were removed from bags before tank assignment. The tanks were divided into two groups of 30, kept at either 15°C or 23°C and each had its own separate flow-through water (0.4 litre/h per tank) and air supply. Water temperature was controlled through a sensor attached to a Building Automation System. Day length was set at 12:12 light:dark. Within each group, bagged lobsters were randomly assigned to tanks within either bagged or bagged-damaged treatments, 10 lobsters per treatment. Lobsters which had not been put into bags at harvest were randomly assigned to tanks within the unbagged treatment.

Bagged-damaged animals were purposely damaged before they were put into tanks. Four of the five tail fan appendages (the telson and three uropods (left to right)) out of each animal had holes (2 mm diam.) punched through them and cuts (7 mm) made at opposite ends of the distal margins. All holes and cuts were made with sterile instruments.

The tail fan states of all lobsters were assessed each fortnight as described above and photographs taken of all fans. Swabs for microbial analysis were also taken from the same 18 lobsters each fortnight (three lobsters for each of the three bagging treatments from each temperature) and plated out onto TCBS and Nutrient agar for assessment of microbial flora.

The remaining 10 animals (five bagged, five unbagged) were used to replace any mortalities

during the first week of the experiment. During acclimation and experimental periods lobsters were fed 3 times per week at 2% body weight per day. The experiment was run for 6 weeks.

Data analysis

Initial damage of lobsters entering both field and laboratory experiments was analysed using a one-tailed Mann-Whitney U test (SPSS). Treatment effects on the development of tail fan damage in both experiments, measured as erosion categories, were analysed with a Poisson Regression (Genstat) and significant differences tested using analysis of deviance (ANOD, Payne 2002).

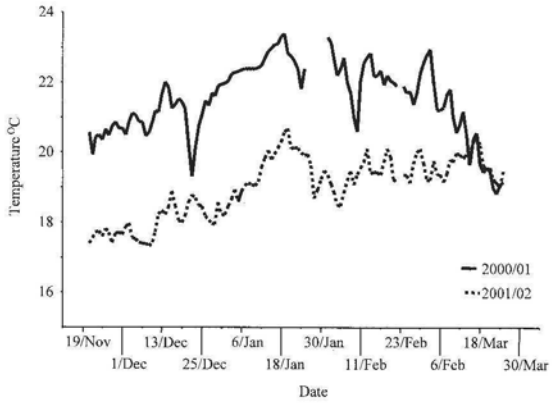


Fig. 6 Mean water temperatures at field site (Southern Australian Seafoods) 2000/01 (n = 119) and 2001/02 (n = 125).

RESULTS

Effects of holding density, feeding regime, and bagging on the development of TFN in a raceway holding system

Water temperature

Water temperatures (Fig. 6) were unusually high (mean = 21.5 + 0.10°C, N = 119) during the summer of the experiment, averaging 2.5°C warmer than the following year (18.99°C + 0.08, N = 125).

Survival

Survival was highly variable (Table 2), high water temperatures and resulting poor water quality contributing much of the mortality. An early water-flow failure in the bagged treatment resulted in a high mortality in that treatment.

Initial damage and TFN

The extent of initial damage at the start of the experiment, after lobsters had been held for varying periods from 14 to 21 days from capture, is shown in Fig. 7. Minor damage was recorded on lobsters from unbagged and bagged post-harvest handling groups, but advanced erosion (E, Fig. 7) which represents TFN was only observed on unbagged lobsters, with 10.8% of unbagged lobsters showing TFN compared with none for bagged lobsters (Fig.

Table 2 Percentage survival of lobsters in raceway system over 4 months for lobsters fed daily, weekly, bagged, and starved. Bagged lobsters were fed daily. Pooled over replicates within treatments. Four replicate cages of 10 or 20 for each of daily, weekly, and bagged treatments, two replicate cages for each starved treatment

	No. of lobsters			% survival	
	Initial	2 months	4 months	2 months	4 months
Daily 10	40	35	21	88	53
Daily 20	80	66	48	83	60
Total	120	101	69	84	58
Weekly 10	40	34	22	85	55
Weekly 20	80	69	37	86	46
Total	120	103	59	86	49
Bagged 10	40	25	20	63	50
Bagged 20	80	43	35	54	44
Total	120	68	55	57	46
Starved 10	20	16	14	80	70
Starved 20	40	38	25	95	63
Total	60	54	39	90	65

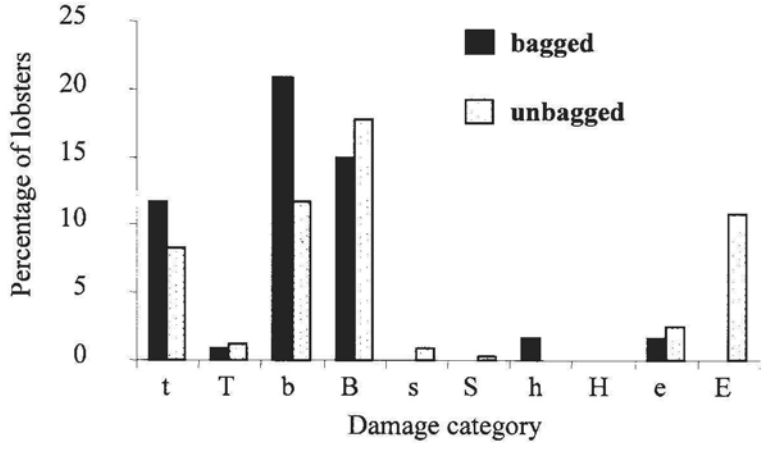


Fig. 7 Percentage of lobsters with pre-existing tail fan damage/necrosis used in the field experiment. (T, tears or >7 mm; b or B, blisters or >5 mm; s or S, scratches or >7 mm; h or H, holes or >2 mm; e, erosion of the limb margin not extending into the limb proper; E, erosion of the limb proper. $N = 420$.)

7). This suggests that post-harvest bagging minimises physical damage that may lead to TFN.

The progress of TFN has been analysed by looking at the occurrence of TFN on lobsters at the start of the experiment (Fig. 8A), after 2 months (Fig. 8B), and at the completion of the trial after 4 months (Fig. 8C). Lobster density had no effect on TFN ($P = 0.832$) so the data were pooled within feeding and bagged treatments. Data from replicates within treatments were also pooled, as there were no significant differences between replicates in any treatment ($P > 0.05$). The level of TFN (defined by erosion categories of nil, <25%, and >25% loss of tail fan tissue) increased significantly during the trial ($P < 0.001$) and showed significant two-way interactions with time and with treatment (P 0.001) (ANOD). Bagged treatments showed significantly less advanced (i.e., >25%) erosion than weekly or daily-fed treatments throughout the trial (Fig. 8) with 51% of bagged lobsters showing no TFN at the 4-month termination of the experiment ($P < 0.001$). In the unbagged treatments, 46–50% of lobsters showed erosion in the <25% category and 25–33% showed erosion of more than 25% of the tail fan, the latter being 2–3 times that recorded for bagged lobsters (11%). There were only minor differences between the groups fed daily, weekly, and starved with the starved lobsters showing slightly lower rates of advanced TFN (>25%) than the fed treatments.

Microbiology and SEM

Samples of tissue taken from TFN-affected areas and normal intact tail fan limbs, both of lobsters at the end of the experiment, were examined by SEM. Bacterial cells were only occasionally located on the surface of normal tail fan tissue. However, significant concentrations of rod shaped cells of bacterial size (c. 1 μm × 2 μm) were visible on the surface of tissue taken from lesions and tears (Fig. 9). Larger spherical structures (i.e., cocci) were often found associated with these cells.

Three lobsters, two from the daily-fed treatment and one from the bagged treatment, were studied quantitatively by plating from homogenised tail-fan tissue. Microbiological analysis showed that greater numbers of bacteria were recovered from uropods with TFN compared with those without the condition (i.e., the controls) (Table 3). Moreover, the number of isolates capable of producing acid from sucrose (i.e., sucrose fermenters) was undetectable on control tissue samples, whereas significant numbers of these bacteria were obtained from tissue samples from uropods displaying TFN.

This observation suggested that TFN lesions were associated with colonisation of tissue by *Vibrio* spp., a conclusion supported by the finding that most isolates from tail fan tissue were catalase and oxidase positive gram-negative rods, motile by polar flagellum, able to grow in the presence of 3% NaCl, and could ferment glucose.

More specifically, the following bacteria were identified from TFN-affected uropods: *Vibrio vulnificus*, *V. parahaemolyticus*, *V. alginolyticus*, and *Aeromonas caviae*. For further identification and characterisation of microbial flora, refer May (2002).

Finally, tail fan blister contents proved to be sterile, suggesting the fan infection is externally derived, not originating from a more general systemic infection.

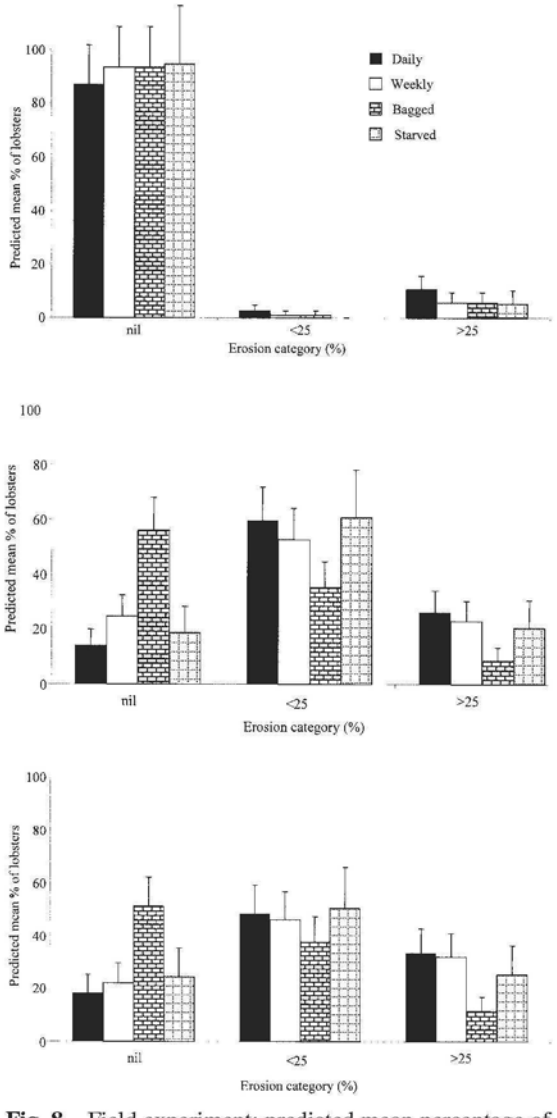


Fig. 8 Field experiment: predicted mean percentage of lobsters (±SE) expected to have each erosion category within each treatment. Data pooled across densities within feeding and bagged treatments: **A**, tail fan necrosis (TFN) at T_0 (n_{daily} = 120, n_{weekly} = 120 , n_{bagged} = 120, $n_{starved}$ = 60); **B**, 2 months (n_{daily} = 101 , n_{weekly} = 103 , n_{bagged} = 68, $n_{starved}$ = 54); and **C**, 4 months (n_{daily} = 69, n_{weekly} = 59, n_{bagged} = 55, $n_{starved}$ = 39).

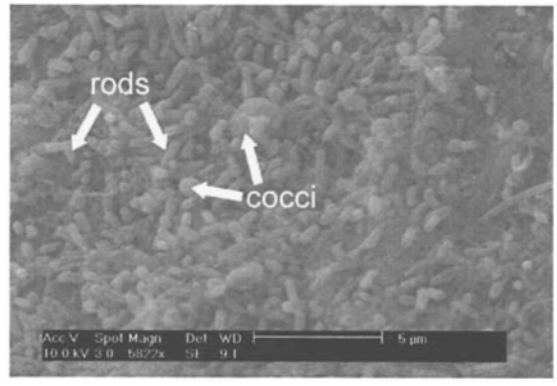


Fig. 9 Bacterial cells on the surface of tail fan necrosis (TFN) lesions observed under scanning electron microscopy. Scale bar is 5 mm.

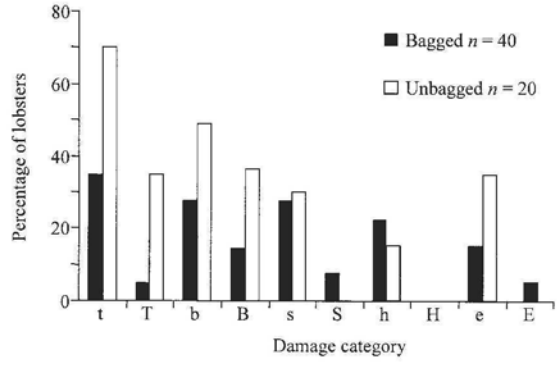


Fig. 10 Initial assessment: damage found in bagged and unbagged lobsters bought into laboratory. (T, tears ≤ or >7mm; b or B, blisters ≤ or > 5 mm; s or S, scratches ≤ or >7 mm; h or H, holes ≤ or > 2 mm; e, erosion of the limb margin not extending into the limb proper; E = erosion of the limb proper. Unbagged>Bagged, one-tailed Mann Whitney U, $P < 0.01$.)

Effect of temperature and physical damage on the development of TFN in laboratory trials

The extent of initial damage at the start of the experiment, after lobsters had been held for between 9 and 11 days, is shown in Fig. 10. Unbagged lobsters showed significantly more initial damage ($P < 0.01$, one-tailed Mann-Whitney U test—Zar 1984, p. 141) in most categories compared with those that had been transported to the facility in mesh bags (Fig. 10). A single lobster in the bagged treatment showed erosion of the margin of a tail fan limb and one lobster showed erosion of <25% of a limb. Data were pooled over all categories for the analysis.

There were marked differences in TFN between treatments over the period of experiment (6 weeks), especially between bagged and unbagged lobsters (Fig. 11). There were no mortalities. Temporal and temperature effects were analysed using Poisson Regression on Genstat. TFN data were re-categorised as either "nil", "≤25%", or ">25%". Analysis was carried out using these categories for

three bagged treatments (bagged, bagged-damaged, and unbagged) and two temperature treatments (15 and 23°C at four time intervals (T_0, T_{2weeks}, T_{4weeks}, and T_{6weeks})). ANOD showed an overall significant treatment effect ($P < 0.001$), with unbagged lobsters showing highest levels of advanced TFN, >25% tail erosion (Fig. 11A–E). There were significant interactions between bag treatment and TFN level ($P < 0.001$) and time and TFN level ($P < 0.001$). Temperature had little effect on TFN, significant only at the end of week 2 ($P < 0.001$) via an interaction with treatment (Fig. 11B,C). There were significant bag effects at each individually analysed sampling date (P 0.001); in each instance the unbagged treatment showing the highest level of advanced TFN. The TFN levels for bagged and bagged-damaged treatments were significantly different ($P = 0.05$) for the 15°C treatment at T_{2weeks}.

The highest incidence of TFN was in the lobsters given the normal post-harvest handling of communal holding in boat holds and processor trays and tanks. These conditions are associated with physical damage inflicted on the lobsters by each other. Such damage will involve both physical damage and presumably the infection of wounds by the bacterial flora of the crayfish exoskeleton. The bagged and bagged-damaged treatments had very little advanced TFN after the 6-week period.

Microbiology

Plating of swab samples of tail fan tissue on marine agar and TCBS agar indicated that there were similar numbers of bacteria present on these surfaces for bagged, bagged damaged, and unbagged treatments. There were no patterns visible with sucrose or non-sucrose fermenting bacteria with time.

The same species of bacteria were identified from TFN-affected limbs as reported for the field trial, *viz*: *V. vulnificus*, *V. parahaemolyticus*, *V. alginolyticus*, and *A. caviae*. For further identification and characterisation of microbial flora, refer May (2002).

DISCUSSION

There is little record in the literature on lobsters of what we have termed TFN. Recent studies on southern rock lobsters, *J. edwardsii*, in live-holding systems have identified TFN as the major problem in live-holding (Lorkin et al. 1999; Geddes et al. 2001) and have identified *Vibrio* and *Aeromonas* species associated with the disease. Other reviews (Evans & Bock 1994; Evans 1997) have reported that the majority of diseases observed in live-held and cultured lobsters are opportunistic infections caused by microscopic organisms, especially *Vibrio* spp., that are widely distributed in the marine environment. Overall, Australian rock lobsters have been seen to be free of serious disease threats (Evans 1997).

In the North American clawed lobster, *Homarus americanus*, three main types of disease have been identified in lobsters that are live held (Bayer et al. 1999; Cawthorn 1999). The major problem is gaffkemia, an infection of the tail muscle caused by the bacteria *Aerococcus viridans* breaching the integument through wounds. Heavy infection leads to the disease gaffkemia or "red tail". This system infection can be treated with antibiotics. The second disease involves the ciliate protist *Anophryoides haemophila* which invades lobster tissue and haemal spaces through perforations in the integument and can lead to "box car" disease. A third group of diseases are termed shell diseases, a catch-all term for lesions associated with bacteria of the genera *Vibrio*, *Aeromonas*, and *Pseudomonas*. Shell disease can occur over widespread areas of the carapace, the

Table 3 Counts of bacteria per tissue disc on marine agar and Thiosulphate-Citrite-Bile-Sucrose (TCBS) agar from unaffected tail fan limbs and those with tail fan necrosis. Counts on TCBS agar are of bacteria capable of producing acid from sucrose and counts of bacteria unable to produce acid from sucrose. (nd, none detected.)

			TCBS agar	
Animal ID	Sample	Marine agar	Acid from sucrose	No acid from sucrose
Daily 10/2	Unaffected limb	5.10E+03	nd	nd
	Limb with TFN	3.60E+05	4.00E+03	1.10E+04
Daily 10/1	Unaffected limb	2.80E+03	nd	nd
	Limb with TFN	1.33E+06	1.80E+05	5.40E+05
Bagged 10/1	Unaffected limb	1.30E+03	nd	nd
	Limb with TFN	1.62E+05	2.30E+04	8.50E+04

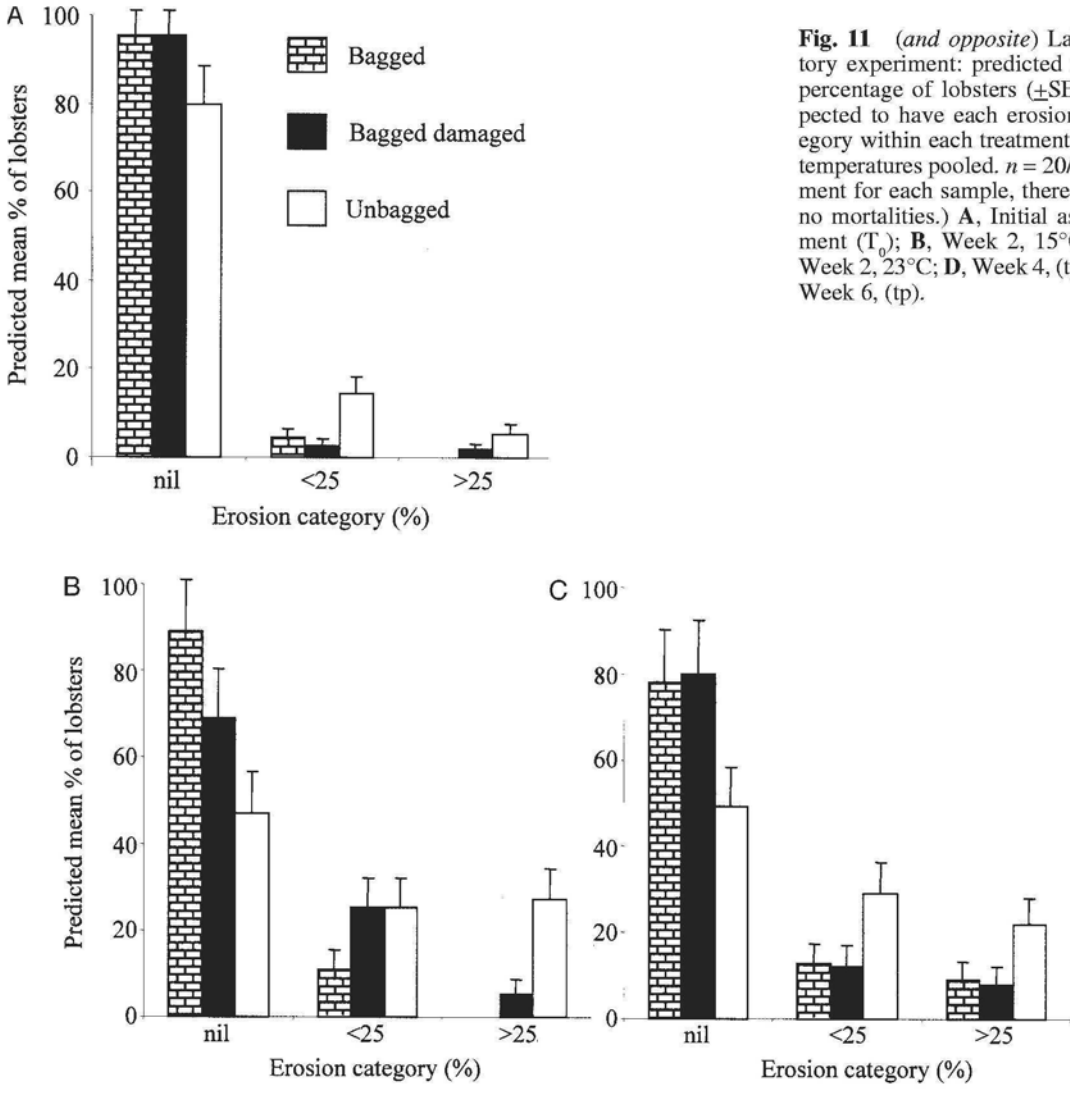
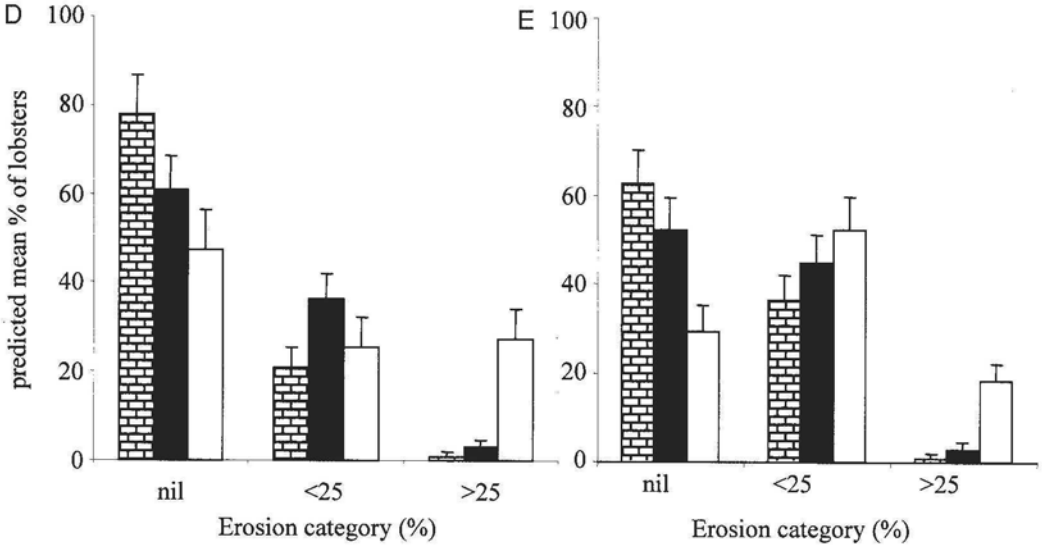


Fig. 11 (*and opposite*) Laboratory experiment: predicted mean percentage of lobsters (±SE) expected to have each erosion category within each treatment. (Tp, temperatures pooled. $n = 20$/treatment for each sample, there were no mortalities.) **A**, Initial assessment (T_0); **B**, Week 2, 15°C; **C**, Week 2, 23°C; **D**, Week 4, (tp); **E**, Week 6, (tp).

tail, and the claws (Bayer et al. 1999). Interestingly it is not noted as prevalent on the tail fan of *Homarus*.

A recent study on the Caribbean spiny lobster *Panulirus argus* identified necrotic lesions on the uropods and telson of captive lobsters (Porter et al. 2001). They studied the bacterial flora associated with the exoskeleton of the lobsters and the necrotic lesions. Microbial investigation showed that the genera *Vibrio* and *Pseudoalteromonas* were common both on the exoskeleton of healthy lobsters and in the tissue in the area of the shell disease. A tail fan disease very similar to that described here for *J. edwardsii* has been identified in the western rock lobster *Panulirus cygnus* (R. Musgrove pers. obs.). The microbiology has not been characterised. It seems that among the spiny lobsters, at lease those studies to date of *P. argus*, *P. cygnus*, and *J. edwardsii*, tail fan infections and TFN are the most common form of shell disease. There does not seem to be widespread occurrence of shell disease on general areas of the carapace as seen in *Homarus*.

The reason for the particular susceptibility of the tail fan of spiny lobsters to shell disease and necrosis, TFN, may relate to the structure of the uropods and telson. They have a thin carapace and so physical damage can be easily inflicted. Furthermore it is likely that the uropods and telson are not well perfused with haemolymph, limiting any immunological response.



Our limited microbiological studies indicated that live-holding results in gradual increases in numbers of bacteria present on the external surface of lobsters. On tail fans in particular, we observed significant increases in numbers of bacteria capable of growth on TCBS agar, a medium used for selective isolation of *Vibrio* spp. Moreover, the number of these bacteria present on surfaces of live-holding tanks was higher for groups of animals fed on a regular basis. We therefore conclude that even with adequate flow of fresh sea water, feeding increases the nutritional status of the water to an extent that supports larger populations of bacteria associated with holding-tank surfaces. This was reflected in the slightly lower rates of advanced TFN in lobsters in the starved treatment. This observation may have an important impact on development and incidence of TFN in live-holding lobster operations.

We can propose mechanisms by which TFN may be initiated and develop. One possibility is that it may be initiated via a systemic infection and a compromised immune response perhaps associated with stress of live-holding, leading to the blisters often observed in the early stage of TFN. However not all TFN starts with blisters and, more importantly, samples of fluid from the blisters showed they were sterile with no bacteria cultured from them. We conclude that TFN is initiated externally by damage to the integument, which allows the entry of common marine bacteria, especially *Vibrio* spp. These bacteria are present on the carapace of lobsters and it is likely that in most instances TFN is initiated by physical damage to the tail fan by self-damage or by another lobster. This would have the effect of breaching the integument and inoculating/injecting a mix of bacteria from the lobster carapace into the wound. Such damage is highly likely to occur in the post-harvest handling of southern rock lobsters. During transfer from the pot to the holding well lobsters flap in air and can easily inflict wounds. They are stored at high density in the well, in close proximity to other lobsters that can cause them damage. During processing they are transported in crates in air where lobsters can easily rub and scratch against each other. If lobsters are subsequently live-held at ambient temperatures there is a high probability that TFN will develop.

The bacterial infection generally elicits a melanisation response from the immune system of the lobster which results in blackening of lesion associated tissue. However the bacteria continue to multiply in the tissue. As most vibrios possess chitinase activity (Murray et al. 1984 in May 2002), it is possible that they can continue to break down the integument and spread across the tail fan. From an initial wound, more and more of the tail fan is infected and the tissue lost. As the bacteria continue to multiply, the tissue melanises and becomes necrotic. Migration of granulocytes to the site of infection probably leads to the typical swelling associated with chronic TFN. These granulocytes may act to restrict the growth of lesion-associated bacteria and limit spread of bacteria via the hemolymph to other parts of the lobster.

It might be expected that the progress of TFN would be related to temperature and the associated

activity of the bacteria. The field experiment where temperatures were 17–24°C showed rapid advancement of TFN. In the laboratory the initial progression of TFN was faster at 23°C than 15°C, but after 4 weeks TFN was well progressed at 15°C. The difference in the occurrence of TFN in laboratory and in the field, given similarities in high-level temperatures (i.e., 23°C cf. 24°C) may be accounted for by water quality differences which could be inferred from high mortalities suffered during the field trials. It is likely that lower temperatures, such as those generally maintained in southern rock lobster processor holding tanks (10–12°C), would greatly limit the progress of TFN.

The present study investigated physical methods of limiting or controlling the development of TFN in live-held rock lobsters. The mesh bags developed for the "bagging" treatments, where lobsters were placed in bags at capture, limited physical damage and resulted in lower levels of TFN in live-holding. Lobsters spent up to 20 days in bags from when they were placed in them from the pots, held in wells of fishing vessels, and then in processor's tanks before assessment at the start of experiments. Lobsters immediately became inactive in the bags, did not interact with other lobsters, and were easy to handle during processing. This post-harvest technology will increase the feasibility of live-holding by minimising TFN and is worthy of further investigation at a commercial scale.

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REFERENCES

Bayer, R. C.; Prince, D. L.; Tall, B.; Fall, S.; Crosby, M. A.; Loughlin M. B. 1999: Health Management in the American Lobster. *In*: Evans, L. H. *ed.* International Symposium on Lobster Health Management. 41 p.

Cawthorn, R. J. 1999: Coldwater lobster health: a North American perspective. *In*: Evans, L. H. *ed.* International Symposium on Lobster Health Management. Aquatic Science Research Unit, Curtin University of Technology. P. 20.

Evans, L. H.; Brock, J. A. 1994: Diseases of spiny lobsters. *In*: Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* Spiny lobster management. Oxford, Blackwell Scientific Publications. Pp. 186–187.

Geddes, M. C.; Bryars, S. R.; Jones, C. M.; Crear, B. J.; Hart, P. R; Thomas, C.; Linton, L. 2000: Determination of the optimal environmental and system requirements for juvenile and adult rock lobster holding and grow-out. Fisheries Research and Development Corporation Report 1998/305. 141 p.

Lorkin, M.; Geddes, M.; Bryars, S.; Leech, M.; Musgrove, R.; Reuter R.; Clarke S. 1999: Seabased live holding of the southern rock lobster, *Jasus edwardsii*: a pilot study on long term holding and feeding. *SARDI Research Report Series No 46*. 20 p.

May, D. G. 2002: Identification and characterization of bacteria associated with tail fan necrosis of southern rock lobsters(*Jasus edwardsii*). Unpublished BSc (Hons) thesis, Department of Microbiology and Immunology, University of Adelaide, Australia.

Payne, R. W. *ed.* 2002: The Guide to Genstat© Part 2: Statistics. VSN International Ltd, Wilkinson House, United Kingdom. P. 182.

Porter, L.; Butler, M.; Reeves, R. H. 2001: Normal bacterial flora of the spiny lobster *Panulirus argus* and its possible role in shell disease. *Marine and Freshwater Research 52*: 1401–1405.

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0028–8330/05/3902–0305

Reproductive cues in *Panulirus ornatus*

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Abstract Two experiments were performed to assess the effect of photoperiod and temperature on spawning of *Panulirus ornatus*. In experiment 1, sexually mature lobsters taken from the wild during summer were held at one of two photoperiods, winter (13 Light:11 Dark) and summer (14.5 Light:9.5 Dark). Additionally, lobsters were also exposed to either summer (29°C) or winter (24°C) average water temperatures. Spawning was significantly greater when animals were exposed to summer photoperiod than to winter photoperiod, irrespective of temperature. Although a higher percentage of lobsters spawned when placed under a higher temperature, this trend was not statistically significant. In experiment 2, sexually mature lobsters were taken from the wild during winter and exposed to the same two photoperiods as in experiment 1, at a summer equivalent temperature of 29°C. Breeding started earlier and was more successful at the summer photoperiod. Time to first breeding was 17 weeks after exposure to summer photoperiod, compared with less than 1 week in experiment 1, and did not occur until individuals had moulted. Moulting occurred in 81% of lobsters, primarily after an increase in temperature to 29°C. The time between moulting and mating was varied and there was no significant difference in moult frequency between the two experimental photoperiods. After the lobsters had moulted, breeding success was reached earlier if photoperiod was lengthened. Results suggest photoperiod is the primary cue for the onset of gonad maturity and mating activity, with temperature playing a less important role. Physiological rest and possibly a moult may be required between breeding seasons before spawning can occur. Furthermore, temperature may be an important cue for pre-reproduction moulting.

Keywords *Panulirus ornatus*; photoperiod; temperature; breeding; moulting

INTRODUCTION

In marine lobsters, the relative importance and magnitude of temperature and photoperiod that induce gonad development, differs between species according to natural environment and breeding season (Muesy & Payen 1988). For example, Chittleborough (1976) identified temperature alone as the primary stimulus for gonad development in *Panulirus cygnus* which has a distinct spring/summer breeding season. This is in contrast with *Panulirus japonicus* which depends on both photoperiod and temperature to cue the onset of gonad maturation (Matsuda et al. 2002). Although temperature was important, gonad development in *P. japonicus* was retarded at photoperiods of less than 12.5 h of light per day. Findings were similar for *Panulirus argus* for which gonad development and mating behaviours were significantly enhanced in animals held at longer day-length, irrespective of temperature (Lipcus & Herrnkind 1985). Breeding in many lobster species has been controlled in captivity through the manipulation of environmental factors, in particular photoperiod and temperature (Lipcus & Herrnkind 1985, 1987; Matsuda et al.

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2002). To be able to successfully breed *P. ornatus* in captivity it is important that the breeding cues are first properly identified for this species.

Panulirus ornatus is known to take part in a mass annual summer breeding migration from the Torres Strait, across the Gulf of Papua to Yule Island (Moore & MacFarland 1984). However, breeding populations of *P. ornatus* on the north-east Queensland coast are non-migratory (Bell et al. 1987). In both instances, breeding is nonetheless seasonal with berried females reported in summer months when photoperiod is at its annual longest and water temperature at its highest level.

This paper aims to assess the use of photoperiod and/or temperature by *P. ornatus* as cues to the onset of breeding.

METHODS

To determine the effects of photoperiod and temperature on spawning in *P. ornatus*, wild-caught mature lobsters were exposed to different combinations of these factors. As the reproductive condition of lobsters brought into captivity for experimentation would likely influence the response to controlled environmental stimuli, lobsters were exposed to winter conditions of water temperature and photoperiod (as measured from their typical natural environment), before the application of experimental conditions for a period of 4 weeks. To mimic photoperiods that *P. ornatus* would be exposed to in nature, mean summer (14.5 Light (L) : 9.5 Dark (D)) and a mean winter (13L:11D) photoperiods were used. These were chosen as they represent nautical day lengths as recorded at Cockburn Reef (11°49′E 143°21′S) on the east coast of Queensland, from where experimental animals were collected and where breeding individuals had been found (Anon. 2002b). Similarly, water temperature equivalent to summer (29 ± 0.3°C) and winter (24 ± 0.3°C) in this location were also used (http://www.auslig.gov.au/geodesy/astro/ (accessed 2002)).

To elucidate the effects of light and temperature on breeding, two photoperiod treatments (summer and winter) were applied to sexually mature and active lobsters maintained at summer or winter (24°C and 29°C) (experiment 1). To determine if time of year (i.e., season) also influenced breeding, the above photoperiod treatments were also applied to seasonally sexually inactive lobsters maintained, in winter, at a summer temperature of 29°C (experiment 2).

Both experiments were conducted in six 2000 litre round polyethylene tanks supplied with semi-recirculated sea water, within an environmentally controlled room. Three tanks were applied to each of the two treatments within a separate recirculation system. Each system was connected to a 2000 litre sump. Water in each system was recirculated continually at the rate of 330 litre/h^{-1} providing a total replacement of water in each tank 4 times per day.

Water from each tank drained to the sump through a screen to collect larger solids, and was then pumped through bead and fluidised bed filters, a protein skimmer and a heat pump before delivery back to the tanks. Water temperature for each of the two systems was controlled using Aqua hort™ heat exchange units and logged in each system by Gemini Tinyview™ temperature loggers.

Light was applied by single 20-watt halogen waterproof lights mounted on the wall of each covered tank. Maximum light levels of an intensity of 110 lux were used to simulate typical light levels found in the natural environment of *P. ornatus*. Light was remotely controlled by a Clipsal Pty Ltd C-Bus™ home automation system which ramped tank light levels up and down at specific programmed times. Sunrise and sunset were programmed to occur over 17 min each daily within each tank. Light was monitored and logged by Stowaway SLA-08™ light loggers.

Each tank was equipped with a freestanding PVC table shelter measuring 600 mm × 800 mm and standing 250 mm high. A 1 m^2 strip of plastic mesh (10 mm mesh size) was suspended from the edge of each tank and weighted so as to partially cover an area of the tank wall and floor to enable spawning females to hang vertically, as an aid for oviposition (Berry 1970).

Previous studies have shown that in wild breeding populations, females with carapace lengths (CL) of >100 mm comprise the majority of reproductive animals (MacFarlane & Moore 1986). Consequently, only females >100 mm and <130 mm CL were used in these experiments. Similarly, as mating success has been demonstrated to improve with increased male relative to females size (Berry 1970), only males >130 mm CL were used. In the wild, at recognised breeding areas for *P. ornatus*, males tend to be larger and females more abundant (ratio of males to females is 1:1.5 or greater) (MacFarlane & Moore 1986). Lobsters for the experiments were chosen accordingly. Seven adult lobsters, two male and five female were assigned to each tank (male to female ratio of 1:2.5). Animals were selected from commercial landings from Cockburn Reef (11°49′E

143°21′S), north-eastern coast of Australia in October 2002 and 2003 and April 2003.

Individual weight, CL, and sex were recorded at the time of stocking to the experimental tanks. Lobsters were identified using individually numbered tags, consisting of small round pieces of waterproof paper glued to the base of the rostrum using Locktite 454™ instant adhesive. Moulted individuals were recognised during daily tank checks as those without a tag, and based on the tagged exuvium were identified (by patterns between the frontal horns) and re-tagged.

Lobsters were stocked to the experimental tanks and then conditioned to average winter temperature and photoperiod by incrementally adjusting water temperature to 24°C ± 0.3°C and photoperiod to 13L:11D over a period of one week to stimulate them to a non-breeding condition. For experiment 1, this involved a reduction from ambient summer conditions, and for experiment 2, from ambient winter conditions. Lobsters were held in these conditions for 4 weeks. For initiating the treatment effect in both experiments, photoperiod was increased immediately from the winter (13L:11D) condition to summer (14.5L:9.5D) photoperiod in half of the experimental tanks. For experiment 1, water temperature was maintained at either 24°C ± 0.3°C or increased to 29°C ± 0.3°C overnight. For experiment 2, the water temperature in all tanks was increased overnight to 29°C ± 0.3°C at this point.

Experimental conditions (post conditioning) were maintained until a majority had spawned (3 weeks for experiment 1). In experiment 2, at 16 weeks post-conditioning, the photoperiod for the winter, short day treatment was increased to 18L:6D to impose a large photoperiodic increase in an attempt to shock the animals into breeding. Females were examined on a weekly basis to check for spawning activity.

At the end of the experiments, weights and CL were re-recorded. Animals from experiment 1 that had not spawned were dissected and the ovaries macroscopically staged from 1–4 as follows.

Stage 1: Immature. Ovaries white, flattened dorso-ventrally.
Stage 2: Developing. Ovaries pink to pale orange, noticeably enlarged.
Stage 3: Ripe. Ovaries bright orange to red, greatly enlarged.
Stage 4: Spent. Ovaries white, yellow or pale pink, often with a few enlarged ova retained from stage 3 at overall lobe extremities (often indistinguishable from stage 1).

pH, salinity, dissolved oxygen, ammonia, and nitrite were measured and recorded weekly and more frequently if outside the desirable range. Food provided to the experimental lobsters consisted of live and frozen pipis *Plebidonax deltoides*, frozen green mussels *Perna canaliculus*, and squid *Loligo opalescens* provided once per day after 1500 h. Animals were fed at the rate of 3% body weight per day consistently for all tanks (approximate maximum food intake from pilot study).

The proportion of females within each treatment that had spawned was analysed by application of a two-way ANOVA using Genstat 5th ed. (Lawes Agricultural Trust). Data was first ArcSin transformed to normalise the distribution. Additionally, ANOVA was used to asses differences in weight and CL between both sexes and tanks.

RESULTS

Experiment 1

Of the original female stock held at 24°C, 30% unexpectedly produced unfertilised eggs during the conditioning period and were excluded from the trial. As a consequence, only four of the six proposed replicates were run with unspawned animals repositioned into four tanks to maintain the initial stocking density. A similar phenomenon was observed for the 29°C trial, however more animals were conditioned which, therefore, enabled the stocking of the full six available tanks. Three weeks after the application of the two photoperiod treatments, significantly more females had spawned under the summer photoperiod (14.5L:9.5D) than at the winter photoperiod (13L:11D) ($P = 0.030$) irrespective of temperature (Fig. 1). Temperature slightly increased breeding success, however not significantly ($P = 0.380$) (Fig. 1). Dissections of the remaining animals found significantly greater ovary development in animals held under summer photoperiod ($P = 0.004$) (Fig. 2).

There was no significant difference in weight within or between tanks for each sex. Males were significantly heavier and had significantly longer CL than females within each tank ($P = 0.001$). Neither CL nor weight was found to have affected breeding ($P = 0.324$ and 0.176 respectively).

Experiment 2

Moulting rate increased dramatically 4 weeks after the conditioning period was completed, i.e., after the temperature had been increased to 29°C (Fig. 3). No

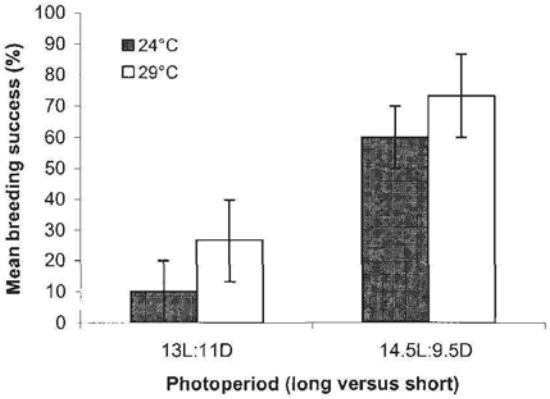

Fig. 1 Percentage of lobsters (*Panulirus ornatus*) (female) spawning in each tank under two photoperiod treatments: short day (13L:11D) and long day (14.4L:9.5D) at either summer or winter average temperature.

significant difference in frequency of moulting was evident between winter and summer photoperiod ($P = 0.505$, $n = 42$). When no spawning occurred after 16 weeks, but the bulk of lobsters moulted, it was postulated that a pre-reproduction moult was necessary before reproduction could be triggered. In an attempt to cue the onset of reproduction the winter (13L:11D) treatment was increased to 18L:6D (Fig. 3). Breeding occurred first in the animals held in the summer photoperiod treatment, 17 weeks after the end of conditioning (Fig. 3). Breeding began 2–3 weeks later for populations exposed initially to winter photoperiod.

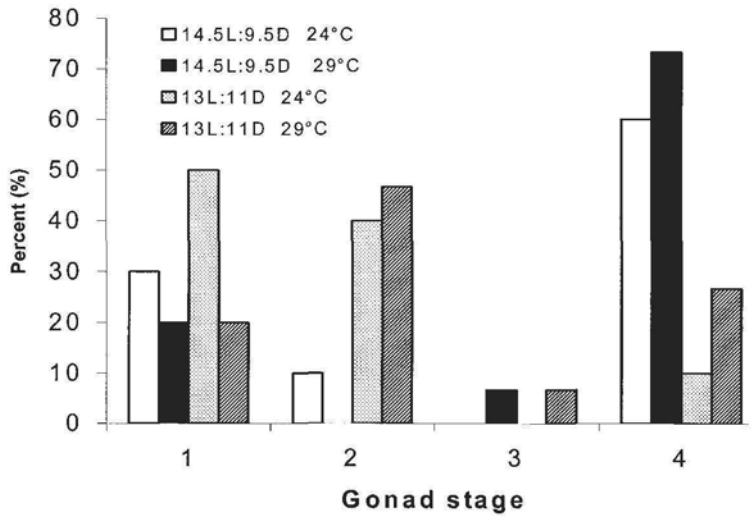

Fig. 2 Stages of ovary development from animals held under long or short day lengths at both temperatures (%). Spawned animals were assumed to be at a spent (stage 4) condition and recorded as such. Stages are described under methods.

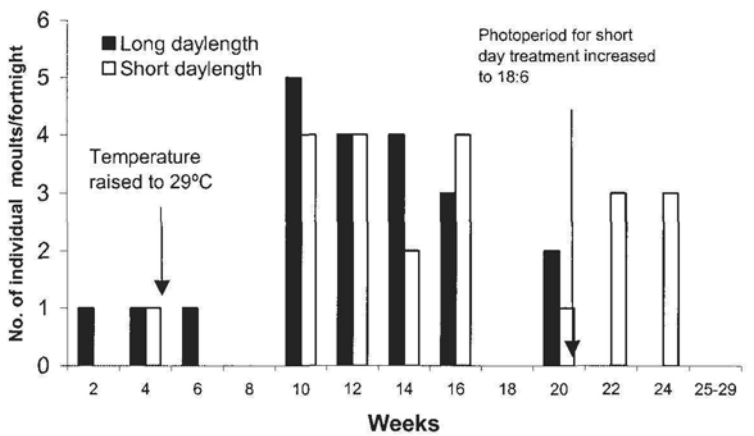

Fig. 3 Overall number of moults per fortnight through the experiment for each treatment (long and short photoperiod). Conditioning period ended after 4 weeks, at which time water temperature was raised to 29°C.

DISCUSSION

Panulirus ornatus is known to take part in migration to breeding aggregation sites during summer (Moore & MacFarlane 1984; Bell et al. 1987). Breeding is seasonal with berried females reported within summer months annually. Seasonally changing environmental parameters may be used by this species as cues to aid synchrony of migratory behaviour/breeding. However possibilities are numerous and may include, for example, seasonal changes in water temperature, photoperiod, or other abiotic stimuli (Herrnkind 1980). Temperature and photoperiod were tested in this experiment. As breeding occurs in *P. ornatus* populations when photoperiod is at its annual longest and water temperature at its highest, different combinations of these factors were assed as cues for breeding in *P. ornatus*.

Results from experiment 1 implicate photoperiod as a significant cue for breeding in *P. ornatus*. Photoperiod is used to cue processes such as diapause, hibernation, breeding, and migration in many species of animals including marine invertebrates, resulting most probably from annual reliability (Herrnkind 1980; Gwinner 1981; Olive 1995). Findings from this study compare with other similar studies which have also determined photoperiod to be an important environmental cue to breeding in other palinurid species (Lipcus & Herrnkind 1985, 1987; Matsuda et al. 2002).

Why photoperiod is used as a primary cue and not temperature may be related to the occurrence of mass migrations for spawning *P. ornatus*. General trends in water temperature, although most likely important to moulting and gonad maturation, are subject to significant variation within season or local geographic area. Although mass spawning populations of *P. ornatus* are restricted within the species distribution, local variations in water temperature across this range, especially at small isolated reefs, may not allow for synchronised timing of the migratory and spawning event. However, photoperiod as a feature of latitude would be expected to vary little over the range of this species and as such may be a more reliable cue, allowing for breeding synchrony across the population (Olive 1995).

Temperature appears to be of less significance. However, it is possible that this was shown to be non-significant because of low sample size within this trial. Spawning rates were increased (non-significantly) and dissected gonads were further advanced in animals held under high temperatures. It is likely that temperature is in some way related to the onset of breeding. However, based on the results of this study it is probably a less important breeding cue for this species.

The absence of breeding activity in experiment 2 (17 weeks exposed to the experimental treatments) was unexpected. In all respects, experiment 2 was equivalent to experiment 1 with only one major difference: the experimental lobsters were obtained from the wild during winter (in a non-breeding condition) relative to those of experiment 1 which were obtained in summer. Although the summer photoperiod cue may be appropriate to stimulate spawning, it may only work for lobsters physiologically prepared. An important part of this may be a necessity to moult before breeding. The dramatic increase in moulting of lobsters in experiment 2 after the temperature was raised suggests that the increase in temperature may be a cue for pre-reproductive moulting. Twelve weeks after the sudden increase in moulting, spawning activity was still not evident and the photoperiod of the winter photoperiod treatment (13L:11D) was increased to 18L:6D to provide a further cue to trigger onset of reproduction. This appeared to have an effect with breeding occurring in subsequent weeks. It may be possible to somewhat hasten breeding through the induction of a moult and subsequent increase in photoperiod post moult.

The speed with which these treatments have their desired effect has important implications to the establishment of management protocols for year-round breeding. Although it may be possible to shift the reproductive season, using controlled conditions, to enable breeding out of phase with wild populations, it may not be possible to significantly condense the reproductive cycle into a period less than 12 months. Additionally, condensation of the breeding season may have consequences for larval quality. Although several other tropical Palinurid species have been shown to breed year round (Macdonald 1982; Juinio 1987; Briones-Fourzan & Lozano-Alvarez 1992), continuous breeding of the same captive lobsters, many successive times, may not generate high quality eggs and larvae. For example, it is possible that lobsters forced to breed for two or more seasons in one year may hatch larvae of lesser quality than those that undergo the usual one breeding season annually. The establishment of multiple breeding populations that are out of phase with wild season is likely to be the most effective way to generate high quality larvae year round.

The necessity for a pre-reproduction moult is well documented for many crustaceans. In lobsters,

moulting provides the female with fresh ovigerous setae on the endopods of the pleopods which are critical for attachment of the freshly laid eggs (MacDiarmid & Kittaka 2000). In establishing protocols for year-round breeding, it may be necessary to stimulate a moult before the initiation of mating and spawning.

Although this preliminary work has isolated some of the cues important to breeding, further research into the endocrinology of moulting and gonad development as well as flow-on research into effects of different breeding regimes on larval quality may provide a more complete understanding of *P. ornatus* reproduction.

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REFERENCES

Bell, R. S.; Channells, P. W.; MacFarlane, J. W.; Moore R.; Phillips B. F. 1987: Movements and breeding of the ornate rock lobster (*Panulirus ornatus*), in the Torres Strait and on the north-east coast of Queensland. *Australian Journal of Marine and Freshwater Research 38*: 197–210.

Berry, P. F. 1970: Mating behaviour, oviposition and fertilization in the spiny lobster *Panulirus homarus* (Linnaeus). *South African Oceanographic Research Institute, Investigation Report No. 24*: 1–16.

Briones-Fourzan, P.; Lozano-Alvarez, E. 1992: Aspects of the reproduction of *Panulirus inflatus* and *P. gracilis*) from the Pacific coast of Mexico. *Journal of Crustacean Biology 12*: 41–50.

Chittleborough, R. G. 1976: Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Australian Journal of Marine and Freshwater Research 27*: 499–516.

Grove-Jones, R.; Kolkovski S.; van Barneveld, R. 2002: Review. Rock lobster propagation research (FRDC 2000/214 and 2000/263) within the Rock Lobster Enhancement and Aquaculture Subprogram. Australia, Fisheries Research and Development Corporation.

Gwinner, E. 1981: Annual rhythms: perspective. *In*: Ashcroft, J. *ed.* Handbook of behavioural neurobiology. Vol. 4: Biological rhythms. New York, Plenum Press. Pp. 381–389.

Herrnkind, W. F. 1980: Spiny lobsters: patterns of movement. *In*: Cobb, J. S; Phillips, B. S. *ed.* The biology and management of lobsters. Vol. 1: Physiology and behaviour. New York, Academic Press. Pp. 349–407.

Juinio, M. A. R. 1987: Some aspects of the reproduction of *Panulirus penicillatus* (Decapoda:Palinuridae). *Bulletin of Marine Science 41*: 242–252.

Lipcius, R. N.; Herrnkind, W. F. 1985: Photoperiodic regulation and daily timing of spiny lobster mating behaviour. *Journal of Experimental Marine Biology and Ecology 89*: 191–204.

Lipcius, R. N.; Herrnkind, W. F. 1987: Control and coordination of reproduction and moulting in the spiny lobster (*Panulirus argus*). *Marine Biology 96*: 207–214.

Macdonald, C. D. 1982: Catch composition and reproduction of the spiny lobster *Panulirus versicolor* in Palau. *Transactions of the American Fisheries Society 111*: 694–699.

MacDiarmid, A. B.; Kittaka, J. 2000. Breeding. *In*: Phillips, B.; Kittaka, J. *ed.* Spiny lobster: fisheries and culture. Oxford, Blackwell Science Ltd.

MacFarlane, J. W.; Moore, R. 1986: Reproduction of the ornate rock lobster (*Panulirus ornatus*) in Papua New Guinea. *Australian Journal of Marine and Freshwater Research 37*: 55–65.

Matsuda, H.; Tekenouchi, T.; Yamakawa, T. 2002: Effects of photoperiod and temperature on ovarian development and spawning of the Japanese spiny lobster *Panulirus japonicus*. *Aquaculture 205*: 385–398.

Moore, R.; MacFarlane, J. W. 1984: Migration of the ornate rock lobster, *Panulirus ornatus* (Fabricius) in Papua New Guinea. *Australian Journal of Marine and Freshwater Research 35*: 197–212.

Muesy, J. J.; Payen, G. G. 1988: Review. Female reproduction in malacostracan crustacea. *Zoological Science (Tokyo) 5*: 217–265.

Olive, P. J. W. 1995: Annual breeding cycles in marine invertebrates and environmental temperature: Probing the proximate and ultimate causes of reproductive synchrony. *Journal of Thermal Biology 20(1–2)*: 79–90.

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Short communication

Growth, repetitive breeding, and aquaculture potential of the spiny lobster, *Panulirus ornatus*

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Abstract A pair of subadult *Panulirus ornatus* was reared in the laboratory from July 2001. The female grew from 0.6 to 1.3 kg and the male from 0.5 to 1.6 kg in 2 years before the first mating in July 2003. In 6 months, from July to December 2003, the pair mated and spawned 3 times, producing 1.6 million eggs and 1.1 million phyllosoma larvae. Mating occurred 25 and 63 days after moulting. The female spawned 2–3 days after mating and the incubation time ranged from 23 to 27 days. The phyllosoma larvae were released over 2 successive days. The growth rate reduced after first mating in both the male and female and the female expended 42% of the total weight gain for egg production.

Keywords *Panulirus ornatus*; growth rate; repetitive breeding; egg production

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INTRODUCTION

Among the spiny lobsters exported live from India, *Panulirus ornatus* (Fabricius, 1798), which is termed "tiger" in the export trade, enjoys the highest value. This species is also the largest tropical lobster, growing to over 6.5 kg. Attainment of 300 g in the first year from puerulus stage (<1 g) was reported for this species by Tamn (1980). *P. ornatus* grows faster in the laboratory than other tropical lobsters such as *P. homarus*, *P. polyphagus*, and *P. versicolor* (Radhakrishnan & Vijayakumaran 1990; Vijayakumaran & Radhakrishnan 1997). Because of its faster growth rate and attainment of sexual maturity at c. 1 kg size, it is considered as the ideal species for aquaculture. About 15% of *P. ornatus* exported from India is in the size group of 300–500 g (Vijayakumaran & Radhakrishnan 1997) and a sizeable number of juvenile *P. ornatus* below 300 g size are caught on the south-east coast of India. These can be fattened for short periods in indoor tanks or in open sea cages for value addition. The National Institute of Ocean Technology, Chennai, India has initiated attempts to rear the phyllosoma larvae of *P. ornatus* from captive breeders for continuous availability of larvae for experiments.

METHODS

Two *P. ornatus* females weighing 545 and 596 g and a male weighing 510 g were collected in late July 2001. The smaller female died after 2 months and the remaining two were reared along with other species of lobsters such as *P. homarus* and *P. polyphagus* at the NIOT laboratory at Chennai. In January 2003, the pair of *P. ornatus* were transferred to a rectangular cement tank of 5.3 m^2 area without artificial shelter. The lobsters were fed with green mussel, *Perna viridis* and occasionally with the marine clam, *Donax cuneatus*. Moulting and growth of these lobsters were monitored. Moulting times were recorded and the lobsters were measured 10 days after each moult. As soon as the female spawned, she was removed and retained in an

individual broodstock tank (capacity: 700 litre). The number of eggs carried by the lobster was estimated by using counts from three weighed subsamples, each having more than 200 eggs, and the weight of the whole egg mass. The total weight of whole egg mass was calculated as the difference between the weights just after spawning and after complete release of larvae. The eggs were examined for the fertility status when first spawned and periodically until the release of larvae. Even when the female did not retain any sperm mass, it was observed for further egg deposition for one more week, after the release of the last batch of phyllosoma larvae, before it was returned to the broodstock tank. Temperature, salinity, pH, and dissolved oxygen in the broodstock tank were monitored daily.

The water quality parameters in the broodstock tank from January to December are plotted in Fig. 1. Salinity ranged from 26.9 to 35.0 psu, temperature from 24.9 to 31.2°C, pH from 7.85 to 8.40, and dissolved oxygen from 4.79 to 6.47 mg/litre from January to December in 2003 in the broodstock tank.

RESULTS

The growth of male and female lobsters is given in Fig. 2. Distinct increase in growth was observed after the lobsters were removed to the broodstock tank in January and fed *ad libitum* with green mussel. In 18 months from July 2001 to January 2003, the weight of the female increased from 596 to 1040 g, whereas that of the male increased from 510 to 990 g. However the female, which moulted twice and attained the maximum weight of 1324 g (before first mating) in May, lost weight once it mated and spawned in July 2003. It moulted once after the first release of phyllosoma larva. In the 12-month period in 2003, the weight of the female increased by 226 g. At the same time it lost 165 g in egg/larval production. In the male, extension of intermoult period and reduction in weight gain was observed after first mating. From January to July 2003, the male moulted 3 times and increased its weight by 400 g. From July to December it moulted only once and the weight increase was 199 g. Initially, when they were reared together with other species of lobsters, not all moultings were recorded and individual growth was not monitored. From January 2003, moults and growth after each moult were recorded. The intermoult period ranged from 103 to 130 days in the female and from 57 to 99 days in the male.

The chronology of repetitive breeding and temporal sequence of moulting, mating, spawning, and larval release are given in Table 1. The female lobster mated and spawned 3 times within a period of 6 months from July to December 2003, with two matings in one intermoult period. The weight of eggs and the number of phyllosoma released are given in Table 2. A total of 1 625 683 eggs were produced and 1 135 827 phyllosoma larvae were released during this period. The average hatching percentage was 70.62 with a range of 62.92–77.01. On two occasions, the larvae were released in two batches, with maximum release on the first day in the first brood and on the second day in the third brood. Remaining eggs, which were less than 1–2% of the total and were mostly unfertilised or malformed, and egg cases were shed along with the release of the second batch of larvae. When the larvae were released in one batch in the second brood, the remaining eggs and egg cases were shed 2 days after the release of the larvae. In addition, small amounts of eggs were shed on a few occasions before the release of larvae. A single spawning was observed on the second or third day after mating. Even though a sperm mass was present in the sternum, no second spawning was observed over a 12-day period after release of phyllosoma.

DISCUSSION

The growth rate of *P. ornatus* is considerably higher than that obtained for *P. homarus* (Radhakrishnan & Vijayakumaran 1990; Vijayakumaran & Radhakrishnan 1997). The weight increase for 18 months up to February 2003 was 444 g for female and 590 g for male. Higher weight increase was obtained in the subsequent months because of improvement in the rearing conditions and provision of abundant quantity of quality feed, the green mussel. Despite this, the female lost weight once it started mating and spawning. Similar observations on reduction of weight in females after breeding starts were reported in captive broodstock of *P. homarus* by Vijayakumaran et al. (2004a). The male grew faster than the female but also lost weight after it started mating. For commercial aquaculture, males and females have to be grown separately after they attain maturity to get maximum growth rate by preventing them from mating and breeding. However, this should not be a major problem in rearing *P. ornatus*, since maturity is attained at a larger size than the peak market size (<1 kg).

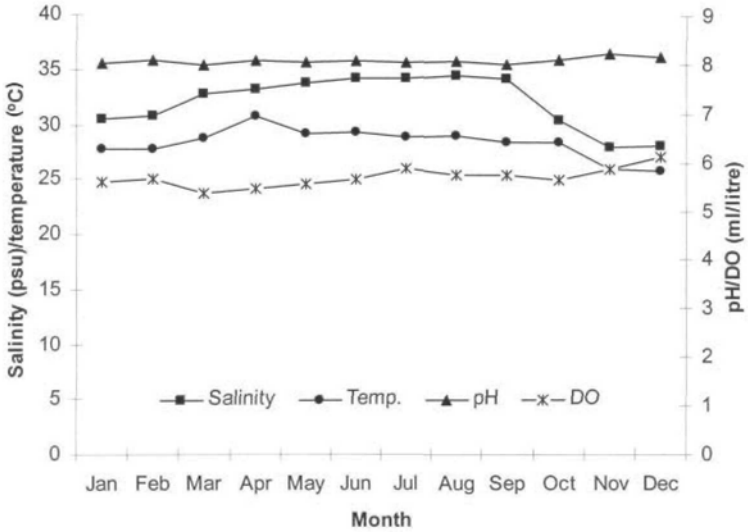

Fig. 1 Water quality parameters in the broodstock tank during 2003. (DO, Dissolved oxygen.)

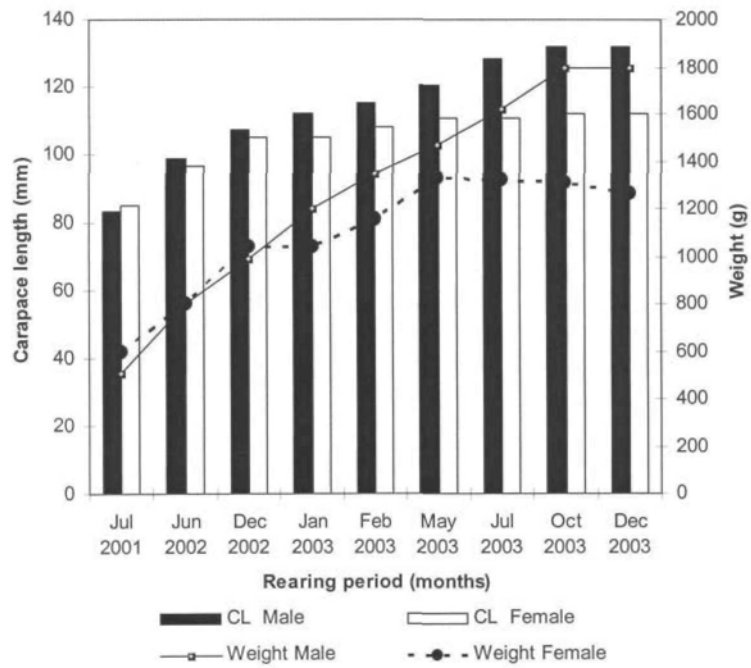

Fig.2 Growth of *Panulirus ornatus*. Female attained first maturity in July 2003.

Fast growth rate and attainment of sexual maturity above the size required for marketing, makes *P. ornatus* the most ideal species of spiny lobster for aquaculture. This study, even though involving only a pair of lobsters, indicates that *P. ornatus* can be successfully bred in captivity to produce phyllosoma throughout the year. Three spawnings in 6 months just after attaining sexual maturity confirm the view expressed by Chittleborough (1976) and Vijayakumaran et al. (2004a) that spiny lobsters can breed 6 times or more in captivity if ideal conditions and nutritionally rich feed are given. The average brood size of *P. ornatus* obtained in this study, 541 894 ± 98 755 is much lower than the average of 1 121 507 ± 576 158 reported from wild breeders by Vijayakumaran et al. (2004b). This could be because

Table 1 Chronology of repetitive spawning and temporal sequence of reproduction in *Panulirus ornatus* from July to December 2003.

	Date			
Spawning details	Mating	Spawning	Larval release	Moulting
First	19 Jul 2003	21 Jul 2003	13 and 14 Aug 2003	27 Sep 2003
Second	22 Oct 2003	25 Oct 2003	16 Nov 2003	Did not moult before next mating
Third	01 Dec 2003	03 Dec 2003	29 and 30 Dec 2003	

Table 2 Egg number and phyllosoma larvae released from one female *Panulirus ornatus*. (CL, Carapace length.)

CL (mm)	Body wt (g)	No. of brood	Egg wt (g)	Egg no.	Phyllosoma no.	Incubation period (days)
110.7	1320	First	72	654 540	411 866	22
111.0	1320	Second	46	470 220	338 250	22
111.0	1324	Third	49	500 923	385 771	26

of the small size of the breeder in its first year of egg production. It is reported that *P. polyphagus* produces fewer eggs in the first year of egg production (Kagwade 1988a,b). Considerable reduction in brood size in repeat spawnings within the same season has been reported for *Panulirus argus* (Creaser 1950), *P. japonicus* (Ino 1950), *P. inflatus* (Briones & Lozano 1992), *P. homarus* (Vijayakumaran et al. 2004a), and *P. ornatus* (Macfarlane & Moore 1986). The results in this study also indicate that the brood size was maximum in the first spawning and lower but about equal in the second and third spawning. It is noteworthy that a second spawning from one mating, as reported in *P. homarus* (Vijayakumaran et al. 2004a) was not found in *P. ornatus*.

Mating in some species of spiny lobsters occurs after the female moults, as the moult provides her with fresh ovigerous setae on the endopods of pleopods for attachment of eggs (Kittaka & MacDiarmid 1994). In *P. ornatus*, the length of the ovigerous setae increases with every moult after maturity and no shedding of the setae was recorded at moult. In some tropical species, a second mating takes place either before or after the release of larvae from the previous brood (Creaser 1950; MacFarlane & Moore 1986; Briones & Lozano 1992). In *P. ornatus*, a second mating was observed 16 days after release of phyllosoma and complete shedding of the remaining eggs. Chittleborough (1976) observed that moulting and mating in the female might be separated by 2–97 days in *Panulirus cygnus*. In *P. ornatus*, the interval between moulting and mating was 63 days for the first and 25 days for the second mating and moulting did not precede the third mating.

MacFarlane & Moore (1986) reported low levels of infertility and egg loss in *P. ornatus*. In this study the fertilisation was almost 100%, and on an average, 70.62% hatching success was achieved. It could further be improved in captive breeders as most of the egg loss was caused by handling and disturbance of lobsters while taking measurements.

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REFERENCES

Briones-Fourzan, P.; Lozano-Alvarez, E. 1992: Aspects of reproduction of *Panulirus inflatus* (Bouvier) and *P. gracilis* Streets (Decapoda: Palinuridae) from the pacific coast of Mexico. *Journal of Crustacean Biology 12*: 41–50.

Chittleborough, R. G. 1976: Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Australian Journal of Marine and Freshwater Research 27*: 499–516.

Creaser, E. P. 1950: Repetition of egg laying and number of eggs of the Bermuda spiny lobster. *Proceedings of the Gulf Caribbian Fisheries Institute 2*: 30–31.

Kagwade, P. V. 1988a: Reproduction in the spiny lobster, *Panulirus polyphagus* (Herbst). *Journal of the Maine Biological Association of India 30(1&2)*: 37–46.

Kagwade, P. V. 1988b: Fecundity in the spiny lobster, *Panulirus polyphagus* (Herbst). *Journal of the Maine Biological Association of India 30(1&2)*: 114–120.

Kittaka, J.; MacDiarmid, A. B. 1994: Breeding. *In*: Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* Spiny lobster management. Pp. 384–401.

MacFarlane, J. W.; Moore, R. 1986: Reproduction of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. *Australian Journal of Marine and Freshwater Research 37*: 55–65.

Radhakrishnan, E. V.; Vijayakumaran, M. 1990: An assessment of potential of spiny lobster culture in India. *Bulletin of Central Marine Fisheries Research Institute 44 (part 2)*: 416–427.

Tamn, G. R. 1980: Spiny lobster culture: an alternative to natural stock assessment. *Fisheries 5*: 4.

Vijayakumaran, M.; Radhakrishnan, E. V. 1997: Spiny lobster fattening and live transport. *In*: Proceedings of the Workshop, National Aquaculture Week, Aquaculture Foundation of India, Chennai. Pp. 97–103.

Vijayakumaran, M.; Senthil Murugan, T.; Remany, M. C.; Mary Leema, T.; Dilip Kumar Jha; Santhanakumar, J.; Venkatesan, R; Ravindran, M. 2004a: Captive breeding of the spiny lobster *Panulirus homarus* (Linnaeus, 1758). 7th International Conference and Workshop on Biology and Management of Lobsters, Hobart, Tasmania, 8–13 February 2004. Abstract. P. 99.

Vijayakumaran, M.; Maharajan, A.; Rajalakshmi, S.; Jayagopal, P.; Subramanian, M. S. 2004b: Fecundity and viability of eggs in wild breeders of the spiny lobsters, *Panulirus homarus* (Linnaeus, 1758), *Panulirus versicolor* (Latrielle, 1804) and *Panulirus ornatus* (Fabricius, 1798). 7th International Conference and Workshop on Biology and Management of Lobsters, Hobart, Tasmania, 8–13 February 2004. Abstract. P. 147.

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Effect of physical disturbance on reproductive performance in the spiny lobster, *Jasus edwardsii*

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Abstract A study was conducted to examine the effects of physical disturbance on *Jasus edwardsii* spiny lobster broodstock during ovarian recrudescence through to larval hatch. Undisturbed broodstock were held in relative isolation and subjected to minimal human disturbance, which contrasted with weekly air exposure and handling of the disturbed animals. Broodstock behavioural response, phyllosoma number, competency, and survival in culture were examined. A higher proportion of broodstock from the undisturbed treatment were active during daylight hours compared with those in the disturbed treatment. All ovigerous females in the undisturbed group produced phyllosoma larvae compared with 72.7% of animals in the disturbed treatment. Individual undisturbed females produced greater numbers of phyllosoma larvae, which in turn performed better in larval competency tests, were larger at hatch, and survived better in culture than those from disturbed females. This study demonstrated that physical disturbance altered reproductive performance and larval competency of *J. edwardsii*. Protocols are suggested to minimise disturbance associated with handling in crustacean broodstock.

Keywords *Jasus edwardsii*; spiny lobster; disturbance; fecundity; larval competency; reproduction

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INTRODUCTION

The spiny lobster *Jasus edwardsii* is gregarious, when fed to satiation co-habits with similar size animals without cannibalism, and is able to tolerate handling and air exposure without sustaining mortalities (pers. obs.). These are some of the culture characteristics that make it a suitable candidate for aquaculture.

The ability of marine decapod crustaceans to mature, mate, extrude eggs, and hatch larvae in captivity are important components in their domestication (Browdy 1992). Captive breeding has been achieved in many species (Templeman 1940; Hudinaga 1942; Vincete et al. 1990; Kittaka 1994). However, the impact of physical disturbance on reproductive performance is largely undefined. In general, crustaceans are sensitive to disturbance during maturation, low light levels should be maintained, and a reduction in handling enhances mating success (Vicente et al. 1990; Chen et al. 1991; Aktas et al. 2003). Information on broodstock husbandry protocols are insufficiently reported, this is in part because of commercial confidentiality (Browdy 1992).

Physical disturbance of broodstock, including routine husbandry procedures, may require air exposure of animals producing stress reactions (tail flipping in lobsters). The effects of disturbance on an animal's physiology include changes to haemolymph biochemistry resulting in decreased pH and oxygen carrying capacity, and increased lactate, glucose, and ammonia concentrations (McDonald et al. 1979; Vermeer 1987; Crear 1998). The ability to return to homeostasis is species-specific and depends upon the duration of the disturbance, post-stress environmental parameters, and general animal health (Telford 1968; Crear 1998). The haemolymph biochemistry in *J. edwardsii* normalises within 24 h of a single disturbance (Crear unpubl. data). Minimising disturbance has led to a range of protocols for the successful live handling and transport of crustaceans leading to a reduction in mortalities associated with acute stress.

Chronic stress from repeated handling is more likely to be of concern in a hatchery. Although some species demonstrate an ability to acclimate to stress (Hall & van Ham 1998), the interspecies capacity to habituate to repeated handling is unknown.

For spiny lobster aquaculture, important reproductive parameters include sexual maturation, egg extrusion, fecundity, hatchability, and larval viability (MacDiarmid & Kittaka 2000; Smith et al. 2002). The influence of diet on some of these parameters has been examined in several crustaceans (Browdy et al. 1989; Wen et al. 2002; Smith et al. 2004). However, the role of physical disturbance on reproduction has not been quantified. This study examined whether there were any impacts of disturbance on reproduction in *J. edwardsii* so as to provide guidelines for the development of suitable broodstock handling protocols.

MATERIALS AND METHODS

Broodstock collection and holding

Experimental work was carried out at the Tasmanian Aquaculture and Fisheries Institute, Marine Research Laboratories (TAFI MRL), Hobart, Australia. Broodstock were caught off Flinders Island on Tasmania's north-east coast (40°32′S, 148°16′E) and held at TAFI MRL for 7 months before their introduction to the experiment in January 2002. All broodstock were held under ambient conditions of temperature and photoperiod. Temperature gradients ranged from 18.0°C in summer to 9.5°C in winter with the associated day length spanning 14.5–8.5 h, respectively. Lobsters were exposed to a light intensity of <4 μmol m^{-2} s^{-1} at the tank floor during daylight hours.

At the start of the experiment lobsters were abdominal tagged (t-bar anchor tags, Hallprint Pty Ltd, Victor Harbour, SA, Australia) and antennae tagged (2 × 4 cm white numbered plastic tags attached to the base of the antennae with an electrical cable-tie). Abdominal tags are retained during moulting whereas antennae tags are lost at the moult but permit the individual identification of animals from the water surface.

Before the start of the study animals were weighed (mean ± SEM; 927.4 ± 45.3 g) and carapace lengths (CL) measured (males 115.3 ± 1.2 mm, females 122.9 ± 1.9 mm). Animals were stratified on CL. Similar sized females (16) and males (4) were randomly distributed to each of 4 × 4000-litre square fibreglass tanks with two replicate tanks per treatment. All replicates sustained one mortality in the first 3 weeks of the study, whereas one of the disturbed replicates sustained two. Mortalities were assumed to be associated with abdominal tagging; animals were replaced with others of similar CL. Each tank was fitted with a series of 400 × 200 × 200 mm hollow concrete blocks arranged in a semicircular coliseum structure, providing 30 separate lobster shelters. Flow-through sea water was provided to each tank at 1000 litre h^{-1}, facilitating six water exchanges per day.

Treatments

Undisturbed and disturbed treatments differed primarily on the amount of human interaction they received (Table 1). Lobsters in the undisturbed treatment were housed in tanks that were visually isolated from the facility behind black plastic screens. They were not handled except to replace antennae tags after moulting and to check ovigerous state immediately before hatch. Animals in the disturbed treatment were not visually isolated and were randomly subject to the day-to-day activities of the facility, consisting of the movement of staff in their immediate proximity, and weekly draining of tanks. Animals in this treatment were removed by hand and their health (physical damage, ovigerous status) and growth (weights and measures) examined, resulting in air exposure of 2–3 min per week, per animal. Drained tanks were scrubbed to remove biofouling, lobsters replaced, and tanks refilled over a 4 h period.

Table 1 Differences between the broodstock handling protocols in the undisturbed and disturbed treatments.

Broodstock handling protocols	Undisturbed	Disturbed
Tank screened from the facility	✓	✗
Constant water level	✓	✗
Weekly weights and measures	✗	✓
Removal from tank for cleaning	✗	✓

Both treatments had water flows, temperature, and the presence of newly ovigerous females (tail tucked beneath them when ovigerous) monitored. A dip net was used to remove exoskeletons, and to facilitate antennae tagging of freshly moulted animals. Tanks had floors sloping to a central drain to assist in the removal of lobster waste; drain valves were purged daily for 10–15 s.

Lobster dietary regime

Lobsters were fed mussels (*Mytilus edulis*), squid (*Nototodarus sloanii*), or commercial prawn pellet (Vital prawn, Higashimaru, Japan) to excess on three separate days. To counter selective consumption of individual components (Fielder 1965; Barkai et al. 1996) mussels were fed on Friday, squid on Monday and pellets on Wednesday. Lobsters were observed to feed on all dietary components. Feed was placed on 0.6 × 1.2 m mesh trays (fitted with 0.1 m sides to retain the food) in the evening, and lowered to the tank bottom with ropes attached to a float. Uneaten food generally remained within the feed tray, which was removed within 24 h of the initial feeding. Ration size was reduced from 2% of biomass per week in summer to 1.5% during winter (dry weight (DW) diet: wet weight (WW) lobster), as determined by the periodic monitoring of lobster weights, and consumption patterns in individual tanks in the disturbed treatment. Feed was provided at least 10% in excess of requirement and although intake was not quantified, weekly consumption appeared similar across all treatments and replicates.

Monitoring broodstock activity

Broodstock activity levels were monitored fortnightly over 24-h periods; 1 h after light (light, during the study ranged from 0500 to 0830 h), at 1700 h when food was presented and at 1 h after dark (dark, during the study ranged from 1800 to 2000 h). Monitoring was conducted shortly after the start of the study (February) until before phyllosoma larval hatch (October). The monitoring times encompassed the peak lobster activity during light and dark hours, and at the presentation of feed (Westbury 1999; Crear et al. 2003). Activity was noted and a score of 1 given when an animal was exposed on top of the shelter structure or on the tank floor; whereas a score of 0 was recorded for animals partially or fully located within shelters. Therefore, the range of results for any given observation was between 0 and 20, where 0 designated all animals sheltering and 20 when no animals were confined to shelters.

Monitoring the timing of moult, mating, and hatch

Individual moults were noted daily, antennae tags replaced, and animals were monitored 2–4 weeks later for characteristic ovigerous behaviour, i.e., walking with the tail retracted up to the abdomen and grooming of the pleopods. In the disturbed treatment, the ovigerous state of animals was confirmed during weekly inspections, and the relative size of egg bundles (large, medium, and small) to female size was monitored, individual egg numbers were not counted. Confirmation of egg bundle size was not obtained in undisturbed animals until their removal to the hatch container immediately before hatch.

Proximity to hatch can be identified by a change in the egg colour (from red at egg extrusion to orange and finally translucent brown at hatch) and by monitoring egg eye indices (Tong et al. 2000). In the disturbed treatment, this was noted during weekly inspections, whereas those in the undisturbed treatment were checked 4 months after egg extrusion by selectively removing individuals with a dip net.

Determination of relative viable fecundity

Before hatching (2–7 days), females were removed with a dip net and placed into individual 20-litre hatching containers fitted with a 500-μm screen to retain larvae. Larval hatch containers were supplied with isothermal water and suspended in their original tank (Smith et al. 2003a). Larvae hatched synchronously at dawn on each of 4–7 consecutive days (Smith et al. 2002) and were transferred to 10 litres of aerated 18°C sea water. Phyllosoma numbers were estimated volumetrically from triplicate 75 ml subsample counts. Relative viable fecundity (RVF) was calculated for each female by dividing the total number of Stage I phyllosoma produced by a female by the CL (mm). This did not include non-viable eggs or larvae that did not progress beyond naupliosoma stage, a brief non-feeding post-hatch stage typically lasting <1 h before the moult to Stage I phyllosoma (Tong et al. 2000).

Phyllosoma viability, and size

Phyllosoma viability was ascertained by exposing newly-hatched phyllosoma to a 1 h activity test (Smith et al. 2003b, 2004). Briefly, triplicate 200 ml plastic sample jars containing 20 larvae were exposed to stressors of warm water (21°C) and low salinity (10‰). The number of prostrate phyllosoma was recorded at 3-min intervals, and a cumulative index compiled at the completion of 1 h exposure. Low indices are indicative of better survival in culture. The total lengths (anterior tip of the cephalic

shield to the posterior point of the abdomen) of 20 Stage I and II phyllosoma from each female were measured to the nearest 0.05 mm using an overhead projection microscope (Nikon Profile Projector, model 6C, 20× magnification).

Larval rearing and survival

Phyllosoma resulting from females in the disturbed ($n = 8$ from each replicate, i.e., all ovigerous females) and undisturbed ($n = 8$ from each replicate, chosen at random over the hatch period) treatments were cultured in triplicate to Stage II (14 days) in lightly aerated 1-litre glass beakers maintained in water baths at 18°C at a density of 100 larvae litre^{-1}. Survival of phyllosoma after 14 days culture (Stage II) was noted. Phyllosoma were fed fresh 1.5 mm juvenile *Artemia* at a rate of 3 ml^{-1} daily following water exchange and flushing away of uneaten *Artemia*, and application of antibiotics (oxytetracycline hydrochloride 25 mg litre^{-1}, Intervet Engemycin 100, Melbourne, Australia) to the culture water. Before use, *Artemia* were disinfected by purging for 30 min in 10 litres of microalgae (*Chaetoceros muelleri*, 6.0×10^6 cells ml^{-1}) before rinsing on a 250-µm screen with fresh water for 20 s and resuspension in sea water (Tolemei et al. 2004).

Statistics

Statistical analyses were conducted using repeated measure analysis for time series data, ANOVA with Tukey-Kramer HSD for post-hoc comparison. Arcsine of square root transforms were performed on percentage data (Sokal & Rohlf 1995). ANCOVA was used to determine differences between the slopes and intercepts of linear regressions. Data are presented as mean ± standard error of the mean (SEM), significance level $P < 0.05$. Statistics were determined using JMP version 5.1. (SAS Institute Inc., Cary, NC, United States).

RESULTS

Broodstock activity monitoring

There was no significant difference between the daily activity patterns of animals in the undisturbed and disturbed treatments over time (repeated measure analysis, $P > 0.05$, Fig. 1). Time series were pooled into three groups that encompassed the major reproductive milestones examined; before moulting (February–April), moulting and mating (May–July), and egg-bearing to hatch (August–October). However, activity was significantly lower in animals from the disturbed group compared with the undisturbed group between times of the year and at different times of the day (ANOVA, $P < 0.05$). Lobster activity was lowest at 1700 h, increased significantly at light, and was at its maximum with the onset of dark in both treatments. The one exception was the August–October group within the undisturbed treatment where the light and the dark activity levels were not significantly different (ANOVA, $P > 0.05$).

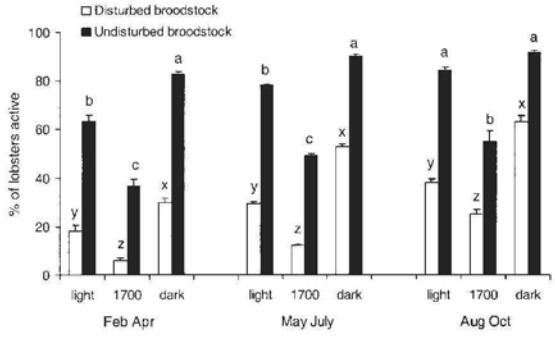

Fig. 1 Relative distribution of lobsters (*Jasus edwardsii*) from disturbed and undisturbed treatments that were active at light (1 h after light), 1700 h (feeding), and dark (1 h after dark). Observations were taken over a 9-month period and arbitrarily divided into three subgroups: February–April (before moulting); May–July (moulting and mating); and August–October (egg incubation). Animals were noted as active when they were completely outside the provided hides. Different letters denote a significant difference between activity at different times of the day within a treatment (ANOVA, $P < 0.05$). Activity differed significantly between treatments at the same time of the day (ANOVA, $P < 0.05$).

Moulting, mating, hatch, and relative viable fecundity

The moulting, mating, and hatch patterns of broodstock were similar for disturbed and undisturbed treatments (Fig. 2). The proportion of females successfully mating and extruding eggs did not differ between treatments (68.8% ± 0.0%). However, the proportion of females successfully maintaining egg bundles to hatch decreased from 22 to 16 in the disturbed treatment whereas all 22 maintained eggs in the undisturbed group. In the majority (>80%) of observations on egg bundle size (large, medium, and small) in disturbed broodstock there was a qualitative reduction in size noted from large to medium to small or even total egg loss; smaller egg bundles were most evident during the second-half of egg

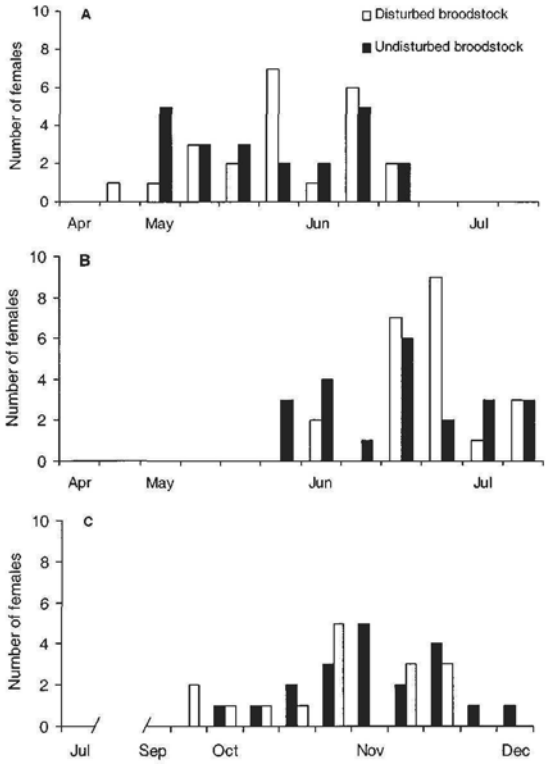

Fig. 2 Pattern of **A**, moulting; **B**, mating; and **C**, phyllosoma hatch from broodstock in disturbed and undisturbed treatments over a 9-month observation period.

incubation. Animals from the undisturbed group were only monitored at hatch, but in all instances had either large or medium egg bundles. The difference between the sizes of the egg bundles was reflected in the quantitative data for RVF. The CL of females was the same in both treatments (122.9 ± 1.9 mm) but the RVF of the undisturbed group was greater (ANOVA, $P < 0.05$) than that of the disturbed group (1190 ± 76 and 362 ± 79 phyllosoma per mm female CL, respectively), resulting in 3.2×10^6 phyllosoma from 22 females in the undisturbed group compared with 0.7×10^6 phyllosoma from 16 females in the disturbed group.

Phyllosoma viability, size, and survival

Phyllosoma hatching from the undisturbed broodstock displayed significantly smaller activity indices compared with those from disturbed broodstock (42.7 ± 11.9 and 142.0 ± 10.2, respectively). The total length of phyllosoma from undisturbed broodstock compared with those from disturbed broodstock was greater (ANOVA, $P < 0.05$) at Stages I (2.05 ± 0.02, 1.90 ± 0.02, respectively) and II (3.01 ± 0.02, 2.88 ± 0.02, respectively). Survival to Stage II was also greater in phyllosoma from undisturbed broodstock compared with those from disturbed broodstock (83.8 ± 2.4%, 46.5 ± 3.9%, respectively). Linear relationships existed between survival in culture and initial phyllosoma activity in both undisturbed and disturbed groups (Fig. 3), with no significant difference existing between the slopes of the regressions ($F_{1,35} = 0.06$, $P = 0.8384$) although the intercepts differed significantly ($F_{1,35} = 5.78$, $P = 0.0224$).

DISCUSSION

Spiny lobsters become more active at the onset of the dark phase of the photoperiod (Crear et al. 2003), a phenomenon seen in this study in both treatments. However, activity was suppressed in animals from the disturbed treatment, which we suggest was a consequence of frequent disturbance. It is interesting to note that animals did not habituate to disturbance during the experiment, contrary to *Penaeus monodon* (Hall & van Ham 1998) where disturbance resulted in normalisation of haemolymph glucose concentrations, an indication of recovery from the stress. We suggest that during our study, the frequency of the disturbance was greater than the recovery time required to attain undisturbed activity levels.

Spiny lobster reproductive patterns are highly regulated by photoperiod and temperature (Quackenbush 1994; Matsuda et al. 2002). Physical disturbance did not alter the timing of moulting or mating as seen in *Homarus americanus*, where the moult synchronicity was be altered by crowding, tagging, and handling (Telford 1968). The duration of embryonic incubation did not diverge with disturbance and is believed to be regulated by temperature in crustaceans (Perkins 1971; Silberbauer 1971; Tong et al. 2000; Smith et al. 2002).

In the disturbed treatment, there appeared to be large reductions in the sizes of egg bundles with egg loss occurring in some animals. Annala & Bycroft (1987) reported up to 20% of eggs might be lost to mid-incubation in wild New Zealand *J. edwardsii* whereas MacDiarmid & Kittaka (2000) reported significant and sometimes total loss of eggs in captivity. Perkins (1971) suggested that the amount of loss may be related to incubation duration and reported 36% egg loss in *H. americanus* during 9 months of incubation. Although some egg loss in

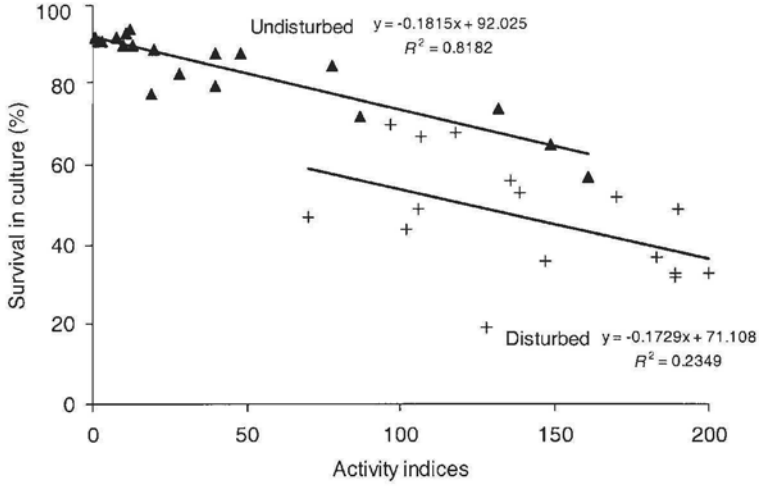

Fig. 3 Linear regressions of newly-hatched larval activity scores and survival to Stage II, larvae were from undisturbed and disturbed broodstock treatments.

crustaceans appears to be typical rather than the exception (Tuck et al. 2000), it was exacerbated in this study in disturbed animals, as evident by reduced phyllosoma number. It is suggested that initial egg losses may have been caused by poor attachment (Talbot & Harper 1984), with sequential loss during incubation in the disturbed females as a result of over-grooming of the egg bundles (MacDiarmid pers. comm.).

Exposing crustacean larvae to salinity stress is a common method to quantify competency and is based on the premise that an adverse environmental condition will elicit a response based on the animal's physiological and nutritional status (Tackaert et al. 1989; Villalón 1991; Clifford 1992; Fegan 1992; Bray & Lawrence 1992; Samocha et al. 1998), potentially indicating their ability to mobilise nutrients under duress (Racotta et al. 2003). Therefore, salinity stress tests are effective in predicting larval competence, especially in *J. edwardsii* (Smith et al. 2003b, 2004). Phyllosoma resulting from the disturbed broodstock had higher activity indices, were smaller, and performed more poorly in culture compared with larvae from undisturbed females, suggesting that disturbance produces less competent larvae. These differences between undisturbed and disturbed broodstock were possibly as a result of differences in their utilisation of food. (Kontara et al. 1997; Sampedro et al. 1997). Although food intakes were similar in both groups, the environmental stresses (disturbance, air exposure, and handling) in disturbed animals may have reduced their ability to efficiently sequester and provide nutrients during ovarian recrudescence.

CONCLUSIONS

There was a considerable range in the effects of disturbance in *J. edwardsii* broodstock. The timing of moulting, mating, and hatch were well entrained and thus did not forewarn of the susceptibility of broodstock to disturbance. However, the reduction in RVF and larval competence somewhat dispels the myth of the robust reproductive nature of this animal in captivity. A number of simple protocols can be adopted in research and maturation facilities to circumvent these problems in *J. edwardsii*, and possibly crustaceans in general. They include the visual isolation of stock, minimising air exposure and handling of animals, and the use of feed trays and central draining tanks to maintain a clean tank environment with minimal disturbance. The use of feed trays reduced fouling of the tanks and therefore reduced the need for handling and air exposure of animals during cleaning. Although the effects of various individual components of disturbance were not quantified, it is suspected that air exposure and handling were the major components that affected reproductive performance.

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REFFERENCES

Aktas, M.; Kumlu, M.; Eroldogan, O. T. 2003. Off-season maturation and spawning of *Penaeus semisulcatus* by eyestalk ablation and/or temperature-photoperiod regimes. *Aquaculture 228*: 361–370.

Annala, J. H.; Bycroft, B. L. 1987: Fecundity of the New Zealand red rock lobster *Jasus edwardsii*. *New Zealand Journal of Marine and Freshwater Research 21*: 591–597.

Barkai, A.; Davis, C. L.; Tugwell, S. 1996: Prey selection by the South African cape rock lobster *Jasus lalandii*: Ecological and physiological approaches. *Bulletin of Marine Science 58*: 1–8.

Bray, W. A.; Lawrence, A. L. 1992: Reproduction of *Penaeus species* in captivity. *In*: Fast, A. W.; Lester, J. L. *ed.* Marine shrimp culture: principles and practices. Amsterdam, Elsevier. Pp. 93–170.

Browdy, C. 1992: A review of the reproductive biology of *Penaeus* species: perspectives on controlled shrimp maturation systems for high quality nauplii production. *In*: Wyban, J. *ed.* Proceedings of the special session on shrimp farming. World Aquaculture Society, Baton Rouge, LA. United States.

Browdy, C. L.; Hadani, A.; Samocha, T. M.; Loya, Y. 1989: An evaluation of frozen *Artemia* as a dietary supplement for the stimulation of reproduction in penaeid shrimp. *In*: De Pauw, N.; Jaspers, E.; Ackefors, H.; Wilkins, N. *ed.* Aquaculture: a biotechnology in progress. European Aquaculture Society, Bredene, Belgium. Pp. 617–623.

Chen, F.; Ried, B.; Arnold, C. R. 1991: Maturing, spawning and egg collecting of the white shrimp *Penaeus vannamei* Boone in a recirculating system. *Journal of the World Aquaculture Society 22*: 167–172.

Clifford, H. C. 1992: Marine shrimp pond management: a review. *In*: Wyban, J. *ed.* Proceedings of the special session on shrimp farming. World Aquaculture Society, Baton Rouge, LA, United States. Pp. 110–137.

Crear, B. J. 1998: A physical investigation into methods of improving the post-capture survival of both the southern rock lobster, *Jasus edwardsii*, and the western rock lobster, *Panulirus cygnus*. Unpublished PhD thesis, University of Tasmania, Launceston, Australia.

Crear, B. J.; Hart, P. R.; Thomas, C. W. 2003: The effect of photoperiod on growth, survival, colour and activity of juvenile southern rock lobster, *Jasus edwardsii*. *Aquaculture Research 34*: 439–444.

Fegan, D. F. 1992: Recent developments and issues in the Penaeid shrimp hatchery industry. *In*: Wyban, J. *ed.* Proceedings of the special session on shrimp farming. Baton Rouge, LA, United States, World Aquaculture Society. Pp. 55–70.

Fielder, D. R. 1965: The spiny lobster, *Jasus lalandii* (H. Milne-Edwards), in South Australia. III. Food, feeding and locomotive activity. *Australian Journal of Marine and Freshwater Research 16*: 351–67.

Hall, M. R.; Van Ham E. H. 1998: The effects of different types of stress on blood glucose in the giant tiger prawn *Penaeus monodon*. *Journal of the World Aquaculture Society 29*: 290–299.

Hudinaga, M. 1942: Reproduction, development and rearing of *Penaeus japonicus* Bate. *Japanese Journal of Zoology 10*: 305–593.

Kittaka, J. 1994: Culture of phyllosomas of spiny lobster and its application to studies of larval recruitment and aquaculture. *Crustaceana 66*: 258–270.

Kontara, I. K.; Merchie, G.; Lavens, P.; Robles, R.; Nelis, H.; De Leenheer, A.; Sorgeloos, P. 1997: Improved production of postlarval white shrimp through supplementation of L-ascorbyl–2–polyphosphate in their diet. *Aquaculture International 5*: 127–136.

MacDiarmid, A. B.; Kittaka, J. 2000: Breeding. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture, 2nd ed. Oxford, Blackwell Scientific Publications. Pp. 485–507.

McDonald, D. G.; McMahon, B. R.; Wood, C. M. 1979: An analysis of acid-base disturbances in the haemolymph following strenuous activity in the Dungeness crab, *Cancer magister*. *Journal of Experimental Biology 79*: 47–58.

Matsuda, H.; Takenouchi, T.; Yamakawa, T. 2002: Effects of photoperiod and temperature on ovarian development and spawning of the Japanese spiny lobster *Panulirus japonicus*. *Aquaculture 205*: 385–398.

Perkins, H. C. 1971: Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). *Fisheries Bulletin 69*: 451–453.

Quakenbush, S. L. 1994: Lobster reproduction: a review. *Crustaceana 67*: 82–94.

Racotta, I. S.; Palacios, E.; Ibarra, A. M. 2003: Shrimp larval quality in relation to broodstock condition. *Aquaculture 227*: 107–130.

Samocha, T. M.; Guajardo, H.; Lawrence, A. L.; Castille, F. L.; Speed, M.; McKee, D. A.; Page, K. I. 1998: A simple stress test for *Penaeus vannamei* postlarvae. *Aquaculture 165*: 233–242.

Sampedro, M. P.; Fernandez, L.; Freire, J.; Gonzalez-Gurriaran, E. 1997: Fecundity and reproductive output of *Pisidia longicornis* (Decapoda, Anomura) in the Ria de Arousa (Galicia, NW Spain). *Crustaceana 70*: 95–110.

Silberbauer, B. E. 1971: The biology of the South African rock lobster *Jasus lalandii*. 1. Development. Republic of South Africa Division of Sea Fisheries Investigational Report 92. 73 p.

Smith, G. G.; Ritar, A. J.; Thompson, P. A.; Dunstan, G. A.; Brown, M. R. 2002: The effect of embryo incubation temperature on indicators of larval viability in Stage I phyllosoma of the spiny lobster, *Jasus edwardsii*. *Aquaculture 209*: 157–167.

Smith, E. G.; Ritar, A. J.; Carter, C. G.; Dunstan, G. A.; Brown, M. R. 2003a. Morphological and biochemical characteristics of phyllosoma after photothermal manipulation of reproduction in broodstock of the spiny lobster, *Jasus edwardsii*. *Aquaculture 220*: 299–311.

Smith, G. G.; Ritar. A. J.; Dunstan, G. A. 2003b: An activity test to evaluate larval competency in spiny lobsters (*Jasus edwardsii*) from wild and captive ovigerous broodstock held under different environmental conditions. *Aquaculture 218*: 293–307.

Smith, G. G.; Ritar, A. J.; Johnston, D.; Dunstan, G. A. 2004: Influence of diet on broodstock lipid and fatty acid composition and larval competency in the spiny lobster, *Jasus edwardsii*. *Aquaculture 233*: 451–475.

Sokal, R. R.; Rohlf, J. F. 1995: Biometry: the principles and practice of statistics in biological research. New York, Freeman. 468 p.

Tackaert, W.; Abelin, P.; Dhert, P.; Léger, P.; Grymonpré, D.; Bombeo, R.; Sorgeloos, P. 1989: Stress resistance in postlarval penaeid shrimp reared under different feeding procedures. *Journal of World Aquaculture Society 20*: 74A.

Talbot, P.; Harper, R. 1984: Abnormal eyestalk morphology is correlated with clutch attrition in laboratory maintained lobsters. *Biological Bulletin 166*: 349–356.

Telford, M. 1968: The effects of stress on blood sugar composition of the lobster, *Homarus americanus*. *Canadian Journal of Zoology 46*: 819–826.

Templeman, W. 1940: Embryonic development rates and egg-laying of Canadian lobsters. *Journal of Fisheries Resource Board of Canada 5*: 71–83.

Tolomei, A.; Burke, C.; Crear, B.; Carson, J. 2004: Bacterial decontamination of on-grown *Artemia*. *Aquaculture 232*: 357–371.

Tong, L. J.; Moss, G. A.; Pickering, T. D.; Paewai, M. P. 2000: Temperature effects on embryo and early larval development of the spiny lobster *Jasus edwardsii*, and description of a method to predict larval hatch times. *Marine and Freshwater Resources 51*: 243–248.

Tuck, I. D.; Atkinson, R. J. A.; Chapman, C. J. 2000: Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland II: fecundity and size at onset of sexual maturity. *ICES Journal of Marine Science 57*: 1227–1239.

Vermeer, G. K. 1987: Effect of air exposure on desiccation rate, hemolymph chemistry and escape behavior of the spiny lobster, *Panulirus argus*. *Fisheries Bulletin 85*: 45–51.

Villalón, J. R. 1991: Practical manual for semi-intensive commercial production of marine shrimp. Texas A&M University, Sea Grant Program, Galveston, United States. 103 p.

Vincente, H. J.; Openiano, A. E.; Openiano, P. L. Jr.; Valdez, L. S.; Pagalan, G. D. 1990: Maturation and spawning in captivity of *Penaeus indicus* H. Milne Edwards and *Penaeus mergeiensis* de Man in experimental and commercial scale. *In*: Hirano, R.; Hanyu, I. *ed*. Proceedings of the Second Asian Fisheries Forum, Tokyo, Japan. Pp. 613–616.

Wen, B. W.; Chen, L. Q.; Zhou, Z. L.; Ai, C. X.; Deng, G. Y. 2002: Reproduction response of Chinese mitten-handed crab (*Eriocheir sinensis*) fed different sources of dietary lipid. *Comparative Biochemistry and Physiology 131A*: 675–681.

Westbury, H. G. J. 1999: Agonistic behaviour and its relationship to stocking density, size and feeding regime in cultured juvenile southern rock lobsters *Jasus edwardsii*. Unpublished honours thesis, University of Tasmania, Launceston, Australia.

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Captive breeding of the spiny lobster, *Panulirus homarus*

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Abstract Captive broodstock of the spiny lobster, *Panulirus homarus*, mated successfully and produced more than 105 spawnings over 4 years. Improvements in nutrition and rearing conditions increased the number of spawnings from less than 2, to 4 per year. A single breeder mates three or more times in a year and may spawn more than once following a single mating. An average of four repetitive spawnings per year was recorded. One third of the females spawned 5 times and a single female spawned 7 times in one year. The phyllosoma were released in one or two batches on successive days. The number of phyllosoma larvae released varied from 16 000 to 529 180 with breeder weights ranging from 218 to 696 g.

Keywords *Panulirus homarus*; captive broodstock; repetitive spawning; brood size

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INTRODUCTION

Panulirus homarus (Linnaeus 1758) is recognised as having three subspecies in the Indo-west Pacific region. In India, the nominal subspecies *P. h. homarus* lives in the rocky near-shore areas of the south-west and south-east coasts. The other two subspecies are *P. h. megasculpta* of the Arabian Sea and *P. h. rubellus* of the west Indian Ocean (Holthuis 1991). Larval rearing of spiny lobsters with an intent to produce puerulii was initiated in Japan more than 50 years ago where the larval cycle of six species of temperate spiny lobsters has been completed (Kittaka 1994). In India, larval rearing to the 6th stage was achieved in the spiny lobster, *P. homarus*, by Radhakrishnan & Vijayakumaran (1986, 1995) and Vijayakumaran & Radhakrishnan (1986). Vijayakumaran et al. (2004a) reported early larval development to stage IV of three species of tropical spiny lobsters, *P. homarus*, *P. ornatus*, and *P. versicolor*.

Use of wild broodstock for larval production necessitates the location of lobster hatcheries near to the lobster landing centres as transportation is difficult and often results in bacterial infection, which causes severe egg loss and production of weak larvae (Kittaka 1994; Vijayakumaran et al. 2004b). The establishment of culture conditions in which reproduction can be controlled to produce larvae all year round is one of the requirements for successful larval rearing of spiny lobsters and the success of captive breeding of *P. homarus* is discussed in this paper.

METHODS

Larval rearing of the spiny lobster, *P. homarus*, was initially carried out by collecting wild breeders at the seafront laboratory of the National Institute of Ocean Technology, Chennai, India. The breeders, after release of larvae, as well as subadults grown in the laboratory, were reared along with other species of lobsters, *P. ornatus*, *P. versicolor*, and *P. polyphagus*

in 0.7 and 2.5 m^3 fibreglass tanks and in 5.0 m^3 rectangular cement tanks. Sea water was directly pumped from subsurface in the intertidal area without filtration. Almost continuous aeration was provided. Egg-bearing lobsters were removed, measured, and reared in 0.7 m^3 tanks until all the phyllosoma larvae were released. The breeders were weighed after the release of larvae and returned after a week to the breeding tanks. The number of phyllosoma larvae released was counted by taking 10 subsamples from the hatching tank after thoroughly mixing the water. Healthy larvae were collected from the surface by using their positively phototactic movement, and transferred to larval rearing tanks.

A filtration unit with a chlorination and dechlorination facility, slow sand filter, activated charcoal filter, and UV sterilisation unit was installed in late 2002 to improve the water quality in the laboratory. Initially, the lobsters were exposed to intense light during daytime because of the transparent sheets on the roof. To reduce the intensity of light, the transparent sheets in the roof were painted black. In late January 2003, all the *P. homarus* broodstock were removed to two rectangular cement tanks, which were also painted with black food-grade, non-toxic, epoxy paint to further reduce the light intensity. No shelter was provided to the lobsters in the tank. The broodstock were stocked at the rate of 4 per m^2 with a male:female ratio of less than one initially. Later the ratio increased to 1.4 males to 1 female resulting from breeder mortality. The lobsters were fed *ad libitum* with green mussel, *Perna viridis*, supplemented with the marine clam, *Donax cuneatus*. Live clams and mussels were always made available in the broodstock tank. Each morning 80% of the water was exchanged. To follow growth and breeding, all lobsters were individually marked by affixing numbers or letters cut from linoleum sheet and pasted to the median antero-dorsal portion of the carapace. The markings were replaced a week after each moult, after taking measurements. Weekly examinations were done to check mating/spawning, and those bearing eggs were transferred to hatching tanks. Females with fresh spermatophoric mass were examined daily to record exact date of spawning. To calculate the number of eggs in the brood, three samples of eggs, with a minimum of 200 numbers, were taken, weighed (wet weight), and counted. Since this was not done before January 2003, the values given by Vijayakumaran (1990) for eggs of *P. homarus* in different stages of development were used to calculate the number of eggs. The total wet weight of the egg mass was calculated as the

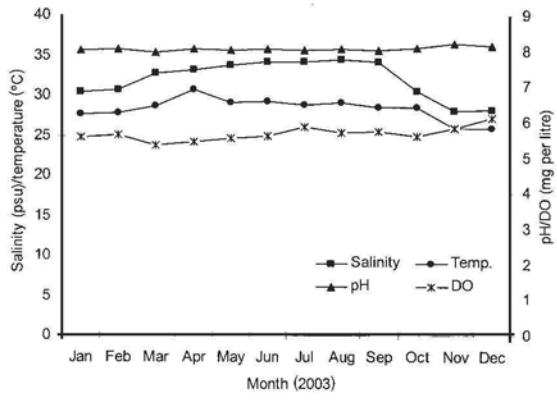

Fig. 1 Water quality parameters in the broodstock tank in 2003. (DO, dissolved oxygen.)

difference in weight between the berried and fully spent female. The water quality parameters of temperature, salinity, pH, and dissolved oxygen were monitored daily in the morning (Fig. 1). The ambient water temperature in the tanks ranged from 25.6 to 31.5°C with the minimum in November and the maximum between April and July. Salinity ranged from 26.5 psu (g $litre^{-1}$) in October–November to 35.0 psu in June–July. The pH ranged from 7.68 to 8.5 and the dissolved oxygen from 4.50 to 6.47 mg $litre^{-1}$.

Statistical analyses were carried out following Snedecor & Cochran (19 67).

RESULTS

Mating of *P. homarus*

Mating of lobsters was usually observed in the morning during water exchange when water volume was reduced to c. 20%. On one occasion, it was observed for 150 min and two copulations lasting a few seconds were witnessed. The male selected a female and chased it throughout the tank. The female appeared to avoid the male. The pair moved all over the tank bottom and other males were chased away when they approached the courting pair. The male did not approach other females in the tank, even when it came into contact with them, and returned to the same female after chasing other males. The male scratched the dorsal and ventral side of the carapace of the female and tried to grasp it with the periopods. On coming to head contact, it tried to lift the female's carapace several times. After c. 90 min, it succeeded in the frontal approach and lifted the

head of the female until both were in an upright position with the bent uropods touching the bottom of the tank. The sterna of the lobsters were in contact and the copulation lasted for c. 10 s after which the female moved away with her tail flipping. The male continued to chase the female and the second copulation was observed after c. 30 min. After failing in the frontal approach many times, the male climbed over the female from behind, grasped it with the periopods and overturned it. Both male and the female were on their backs with the male below. In a quick movement the male, still lying on its dorsal side, overturned the female again so that the sternums of both were in contact, but their heads were in opposite directions. It remained in this position for c. 20 s, which was longer than the first copulation. The male again chased the same female, but the observation could not be continued after another 30 min. No sperm deposition was noticed in the female when it was observed on the following day suggesting that the male had not been successful in sperm deposition. Another female in the same tank was observed with fresh spermatophore on its sternum indicating, probably, that the male had succeeded in mating during the night as only one of the males in the tank was found courting females at a time. The first female, which was forced to mate, moulted after 7 days. On another occasion, a male succeeded in sperm deposition after 2 days of courting a female. The female, however, did not ovulate and carried the sperm mass for 31 days and then moulted.

Only one male was observed to actively court a female, unlike the other males that tried to move away from the courting male whenever they met. The courting male chased other males just to keep them away and did not pursue and fight. No death of males was recorded as a result of fighting between the males in the broodstock tanks.

Breeding season

The number of spawnings per year considerably increased from an average of 16.6 (less than 2 per female) during 2000–02 to 45 (4 per female) in 2003 (Table 1) even though there were fewer female breeders during the latter period. No berried females were observed in January or June 2003. In January 2004, 41.7% of the females spawned and 50.0% had spawned in February 2003. The maximum spawning of 84.6% (when 11 out of 13 females spawned) was recorded in August 2003 (Fig. 2). During 2000–02, maximum spawning was recorded in April and July–August.

Brood size and hatching success

The number of repetitive broods by individual breeders, the weight of the egg mass, the number of eggs per brood, the number of phyllosoma released, and the percentage of hatching are given in Table 2. The breeders ranged in size from 52.7 to 90.0 mm carapace length (CL) with weights of 156.8–696.0 g. The average egg weight increased from 14.2 g in the smallest size group to 35.8 g in the size group with an average CL of 82.0 mm (range: 8.1–63.0 g). The

Table 1 Details of spawning of captive breeders of *Panulirus homarus*.

Month	No. of spawnings		No. of adults (2003)		% of spawned females in 2003
	2000–02 (average)	2003	Female	Male	
Jan	1.00	0	22	21	0.00
Feb	0.66	11	22	20	50.00
Mar	1.66	5	21	20	23.80
Apr	2.66	1	20	19	0.05
May	1.33	7	19	19	36.80
June	1.66	0	18	16	0.00
July	2.33	2	14	17	14.20
Aug	2.66	11	13	17	84.61
Sep	1.33	2	13	17	15.38
Oct	0.33	1	13	17	7.70
Nov	0.33	3	12	17	25.00
Dec	0.66	2	12	15	16.67
Total	16.61	45			
Jan 2004		5	12	15	41.67

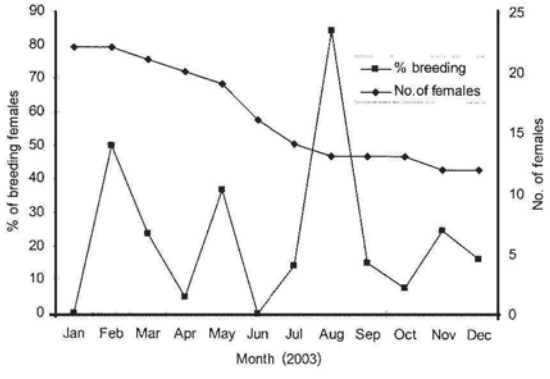

Fig. 2 Breeding sequence in captive breeders of *Panulirus homarus* in 2003.

number of phyllosoma released ranged from 0 to 529 180. In a few instances the whole egg mass was shed with 0% hatching although a maximum hatching of 99.0% was also recorded. Unlike the wild breeders, an average of 95.0% of eggs were fertilised with the minimum being 76.5% and the maximum 100%.

On average, a single female produced four broods in 2003. One of the lobsters had only one spawning which happened to be its first spawning. Another lobster completed seven spawnings within 12 months whereas four completed five spawnings (Table 3). In the female which completed seven spawnings, one batch of eggs was shed 2 days after spawning but it spawned again within 7 days. The

Table 2 Egg and phyllosoma production in different size groups of captive breeders of *Panulirus homarus*. (Mean ± SD; CL, carapace length.)

No. of spawnings	CL (mm)	Female weight (g)	Egg weight (g)	Egg no.	Phyllosoma no.	% hatching
2	55.90 ± 4.54	187.50 ± 43.42	14.20 ± 8.55	57 287.50 ± 105 050.61	39 875.00 ± 8 874.19	4.08 ± 45.25*
9	64.90 ± 0.17	311.40 ± 26.97	24.90 ± 4.95	261 440.90 ± 73 892.04	128 121.80 ± 66 426.78	51.10 ± 25.22
14	68.30 ± 1.68	338.80 ± 26.07	23.80 ± 6.86	241 852.40 ± 67 471.06	85 534.30 ± 83 176.39	31.00 ± 26.41
22	72.09 ± 1.35	390.60 ± 18.49	27.60 ± 7.49	284 088.40 ± 98 608.65	152 263.60 ± 79 693.95	56.10 ± 25.90
31	77.40 ± 1.36	447.80 ± 42.41	29.70 ± 7.86	283 848.30 ± 103 018.54	232 911.00 ± 338 243.99†	60.70 ± 34.01
6	82.00 ± 1.34	551.90 ± 33.17	35.80 ± 8.36	361 155.00 ± 97 558.33	240 628.50 ± 173 886.29	61.80 ± 31.69
9	88.10 ± 1.37	596.80 ± 51.21	35.10 ± 17.01	305 161.10 ± 147 010.49	178 223.20 ± 127 891.41	59.70 ± 37.98
Mean	70.20 ± 18.32	398.70 ± 132.04	27.10 ± 10.27	259 226.60 ± 108 637.34	164 564.30 ± 205 645.74	53.90 ± 31.49

*Of only two females in this size group, one had very few eggs and the hatching rate was very low in the female with maximum number of eggs.
†Few females shed all eggs releasing no phyllosoma.

Table 3 Number of repetitive spawnings and number of eggs/phyllosoma produced by 14 captive breeders of *Panulirus homarus*. (CL, carapace length.)

Initial CL (mm)	Length of time held in captivity (months)	No. of spawnings	No. of eggs	No. of phyllosoma	% hatching
65.0	8	3	897 860	352 000	39
65.2	11	2	566 258	20 000	3
65.9	11	1	115 300	0	0
66.5	11	2	447 160	419 206	93
69.0	10	5	1 415 155	374 134	26
70.0	10	2	576 620	320 400	55
73.8	11	5	1 321 880	674 858	51
74.0	11	4	1 559 230	616 260	39
75.0	8	5	986 580	583 500	59
76.0	13	5	1 904 937	1 556 627	81
76.0	7	3	733 230	485 839	66
76.2	10	4	624 920	396 691	63
79.2	25	7	1 917 260	1 224 000	63
79.3	14	7	1 962 151	1 581 596	80
Average					
72.66 ± 5.16	11.43 ± 4.31	3.93 ± 1.86	1 073 467 ± 606 206	614 650.79 ± 499 640.38	51.29 ± 27.62

total average egg production per female during the period was 1 073 467 ± 606 206 with a range of 115 300–1 962 151. On average, 614 651 ± 499 640 phyllosoma larvae were released (range: 0–1 556 627).

Spawning occurred during the night or early morning and on all but one occasion, fully developed phyllosoma larvae were released. On that unusual occasion, 75% of the larvae were released as "prephyllosoma". In most instances spawning occurred over two consecutive days with the maximum release of larvae on the first day. Only on one occasion were the majority of larvae released on the second day. The remaining eggs, egg cases, and stalks were released along with the second batch of phyllosoma. In a few instances, the egg cases were shed after a few more days of larval release. If sufficient of the original sperm mass remained viable after first release of eggs, the lobster spawned again within 2–3 days. About 20% of spawnings were recorded as second spawning from only a single mating. In one instance, a female with no remnants of sperm mass spawned again after release of phyllosoma larvae. All eggs were unfertilised and were shed within a few days.

The increase in body weight, the cumulative weight of eggs produced in repetitive spawning, and the percentage of egg weight in the breeding female in total increase (body weight + egg weight) in 11.40 ± 4.33 months in 2003 are recorded in Table 4. 68.60 ± 35.51% of the total increase in biomass (increase in body weight + total egg weight) was spent for egg production. In one instance, a lobster lost 22.2 g from the initial weight in a period of 7 months but produced 72.9 g of eggs in three spawnings.

Figure 3 represents the temporal sequence of moulting, mating, spawning, and hatching in 13 females over a period of 12 months. The number of spawnings was less in smaller breeders (below 69 mm CL), which completed up to three moults between successive matings. Two thirds of the bigger females (69 mm CL and above) mated after every moult and in one third of the females a second mating within an intermoult period was recorded.

Figures 4–7 represent the average number of days taken to mate after moulting, to spawn after mating, to hatch, and to moult after hatching in captive breeders during 2002–04. The average values were 19.40 ± 14.02 days between moulting and mating, with 38% mating within 10 days of moulting and another 23% within 20 days (range: 2–47 days). On average, 2.20 ± 1.13 days were taken for spawning after mating with 15% spawning in 1 day and 66% in 2 days (range: 1–7days). In two instances, the spawning was 5 and 7 days after mating. Egg development was completed in 26.00 ± 3.78 days with 49% completing in less than 25 days (range: 20–37 days). The lobsters moulted 28.50 ± 16.35 days after hatching, with 22% moulting within 10 days and another 12% within 20 days (range: 1–59 days).

Three groups of breeders, i.e., females with whole spermatophore, those with partially eroded (used)

Table 4 Growth and egg production in captive females of *Panulirus homarus*.

Time in captivity (months)	Total increase in weight (g) (including egg weight)	Egg weight (g)	% of egg weight in total increase
8	246.46	135.36	55.01
7	50.65*	72.84	143.8*
8	238.19	90.65	37.94
10	171.79	77.98	45.39
10	53.42*	67.72	126.77*
13	245.65	162.21	66.03
11	187.94	113.14	60.20
10	40.31*	42.36	105.09*
11	171.86	42.98	25.01
11	220.59	132.08	59.88
11	157.84	133.76	84.74
11	49.00	11.00	22.45
14	317.63	226.37	71.27
25	317.69	199.22	62.71

*Weight of female decreased from the initial weight.

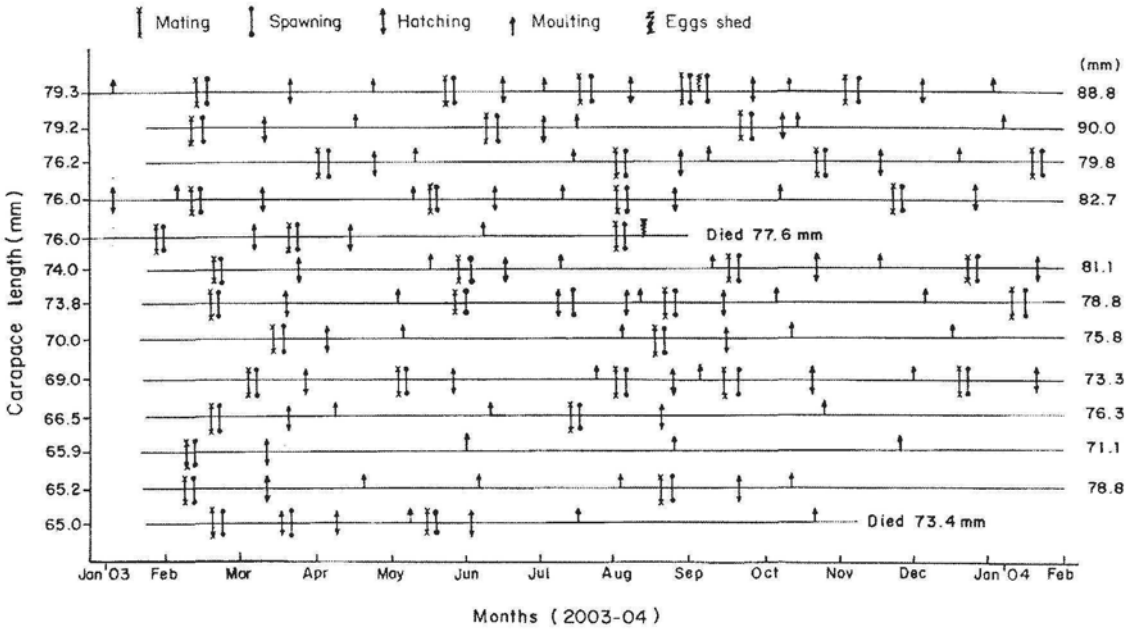

Fig. 3 Temporal sequence of mating, spawning, hatching, and moulting in 13 females of *Panulirus homarus* in 2003.

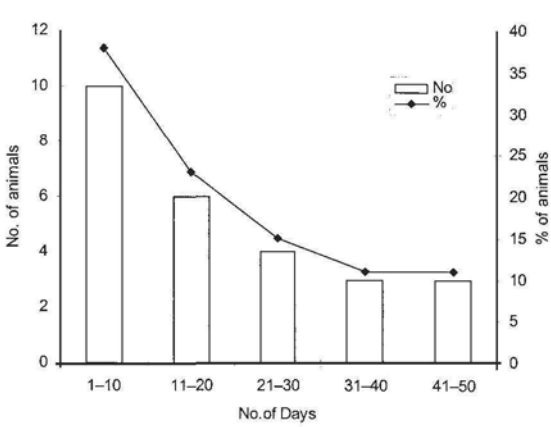

Fig. 4 Number of days taken to mate following moulting in captive breeders of *Panulirus homarus* (n = 26).

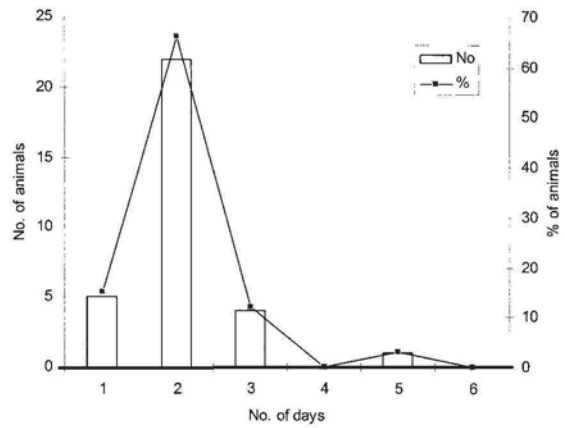

Fig. 5 Number of days taken to spawn following mating in captive breeders of *Panulirus homarus* (n = 34).

spermatophore, and those with completely eroded spermatophore (with or without eggs), were observed in *P. homarus* and most of those with partially eroded spermatophore spawned again with in 2–3 days after release of the larvae. The egg developmental period was longer during November–January, when the temperature of water was 2–3°C lower than the average during other months.

DISCUSSION

Although *P. homarus* breeds repetitively throughout the year in captivity, it breeds more frequently when optimum conditions are provided during November–January, when the breeding is otherwise minimal because of low water temperature. At ambient temperatures between November and January,

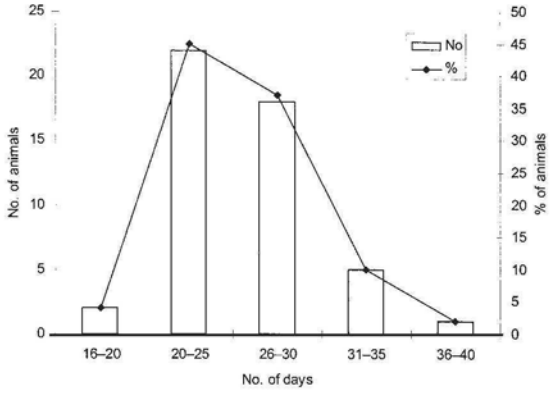

Fig. 6 Number of days taken for incubation in captive breeders of *Panulirus homarus* ($n = 51$).

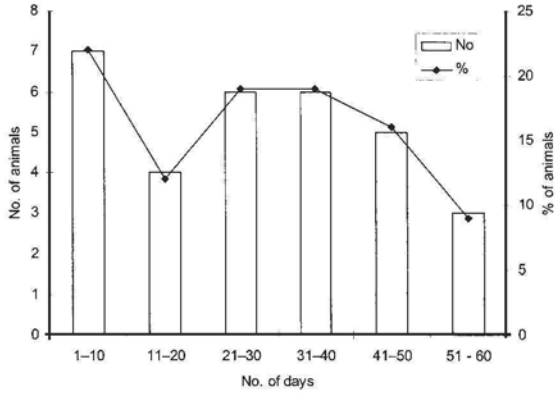

Fig. 7 Number of days taken to moult following larval release in captive breeders of *Panulirus homarus* ($n = 31$).

16.7–41.7% of the breeders spawned when abundant food and good water quality were provided. The seven spawnings that were recorded in 1 year by one female *P. homarus* is the highest recorded for any spiny lobster. An average of nearly four spawnings per year, with 33% of the breeders spawning 5 times, was recorded for *P. homarus* in this study. Chittleborough (1976) reported that the western rock lobster, *Panulirus cygnus*, which usually breeds in the wild once or twice a year, spawned 6 times in a year in the laboratory when reared under constant elevated temperature and abundant food conditions. The data obtained in captive breeding of *P. homarus* gives credence to the opinion that tropical species of *Panulirus* breed repetitively and the frequency of broods increases with age. For instance, *P. polyphagus* produces two batches of eggs in year 3, 3–5 batches in year 4, and more than five batches in subsequent years in the wild (Kagwade 1988a,b). The average total egg production in our 11.40-months study (1 073 467) is almost identical to the projected egg production of 1 137 140 (in four spawnings) for wild breeders of *P. homarus* by Vijayakumaran et al. (2004b).

The increase in spawning frequency in 2003 by *P. homarus*, and similar observations in *P. ornatus* by Senthil Murugan et al. (2004), when better water quality, habitat, and abundant food (green mussel) were provided, support the view expressed by Chittleborough (1976) that the number of spawnings, moults per year, and overall fecundity for many palinurid species are the consequence of the interaction between important ecological factors, such as temperature, food availability and quality, substrate suitability, population density, and water chemistry, etc.

Berry (1971) reported a linear relationship between CL and the number of eggs per brood in wild breeders of *P. h. rubellus*. The relationships between CL and weight of eggs/number of eggs in this study (Fig. 8 and 9) were not linear. The average brood size (weight and number of eggs) was marginally lower in captive broodstock compared with the wild *P. homarus* (Vijayakumaran et al. 2004b) and this could be because of repetitive spawning of the same breeders. The average number of eggs per g body weight (623; range: 282–840) (Fig. 10) is similar to the value reported for wild breeders of the same species (618; range: 529–899) by Vijayakumaran et al. (2004b). The number of eggs per g body weight in other species of palinurids like *P. ornatus* (716) and *P. versicolor* (737) (Vijayakumaran et al. 2004b) and *P. argus* (500–830; Bertelsen & Mathews 2001) also falls within this range. The maximum number of eggs per g body weight was recorded in the size group 61–65 mm CL and the number declined in still bigger lobsters (Fig. 10), a trend observed in many palinurids (Bertelsen & Mathews 2001; Vijayakumaran et al. 2004b). In wild breeders of the same species, lobsters with 61–65 mm CL also had the maximum number of eggs per g body weight (Vijayakumaran et al. 2004b).

Unlike wild breeders, fertilisation rate was very high in captive breeders (>95.0%) and except on a few occasions the larvae were very healthy. No stoppage of development of eggs was observed and the hatching percentage was also high with a maximum of 99%. Handling-stress because of

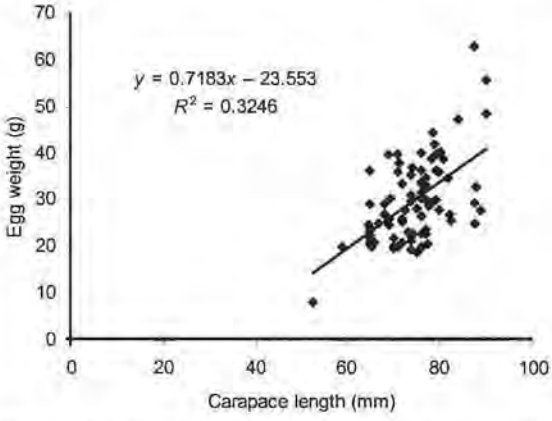

Fig. 8 Relationship between carapace length and weight of eggs in *Panulirus homarus*.

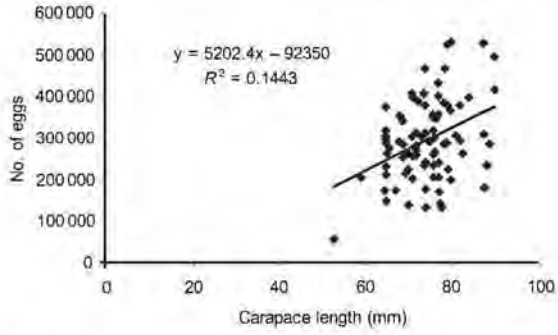

Fig. 9 Relationship between carapace length and number of eggs in *Panulirus homarus*.

measurements and periodic examination of eggs resulted in shedding of eggs in a few breeders, bringing down the hatching rate. However, almost complete shedding was observed on three occasions, which could not be attributed to handling-stress as these lobsters were left undisturbed. A brood with unfertilised eggs, deposited immediately after release of phyllosoma, carried it for few days before shedding it completely.

Ovarian maturation goes on synergistically in lobsters along with the incubation of previously spawned eggs. In rare instances, the ova development culminates in compulsory spawning, as observed in a few lobsters, even when remnants of the sperm mass were not present. The same phenomenon has been observed on a few occasions in wild breeders of *P. homarus* (Vijayakumaran unpubl. data).

Mating coincides with moulting in some species of *Jasus* (Kanciruk 1980). Evidence of premoult females evoking increased activity in males has been reported in *Jasus lalandii* (Silberbauer 1971). Mating between 2 h and 63 days after moulting has been observed in three species of *Jasus* (Kittaka & MacDiarmid 1994). Kanciruk & Hernkind (1976), using external fouling as an indicator of time since last moult in *P. argus*, determined that females do mate soon after moulting, whereas Chittleborough (1976) reported that moulting and mating may be separated by 2–97 days in *P. cygnus*. In captive broodstock of *P. homarus*, the two events were separated by 2–47 days with an average of 19.4 ± 14.0 days (Fig. 4). The interval was higher in females which spawned again immediately after hatching and in those which performed a second mating after hatching. The evidence suggests that mating need not occur immediately after moulting for successful spawning. In the bigger females above 69 mm CL which spawned more frequently, mating generally followed moulting whereas in the smaller ones, two or three moults were recorded between successive matings. Kittaka & MacDiarmid (1994) reported that breeding in spiny lobsters occurs after the female moults as the moult provides her with fresh ovigerous setae on the endopods of the pleopods for attachment of eggs. In 2003, three out of 13 females spawned again 2–4 days after hatching and a second mating in an intermoult period was recorded in another three, suggesting that new ovigerous setae are not essential for successful egg deposition. The smaller number of eggs in such second spawnings may be a combined effect of reduced ovigerous setae and the quantity of remaining viable sperm in the eroded sperm mass.

The average days taken to mate after a moult (19.4), to spawn after mating (2.2), to incubate the eggs (26.0), and to moult after hatching (28.5) adds up to 76 days to complete the whole cycle in *P. homarus*. This suggests that *P. homarus* can spawn on an average of 4 times in a year. In comparison, the cycle is completed in 96 days in *P. argus* (moulting to mating: 13–20 days; mating to spawning: 6–9 days; spawning to larval release: 20–30 days, and larval release to moulting: 38–56 days (Kanciruk & Hernkind 1976)).

Reproductive activity affects somatic growth in almost all animals. As much as 68.6% of the total increase in biomass in 11.4 months in 2003 in *P.*

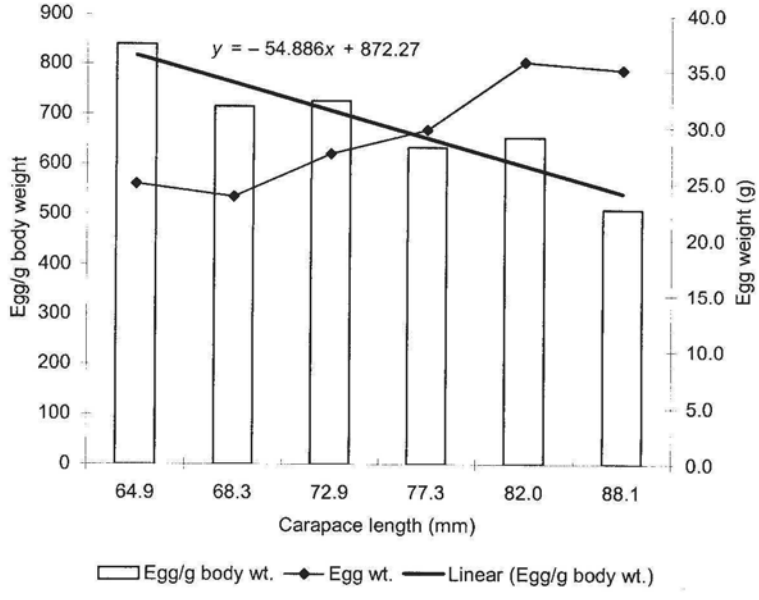

Fig. 10 Egg weight, and egg/g body weight in captive breeders of *Panulirus homarus*

homarus was utilised for egg production. The body weight decreased in 24% of the breeders, suggesting that even body reserves are utilised for egg production over and above the energy obtained from the feed.

The pre-copulatory courtship phase in *P. argus* may extend up to 50 days (Lipicus & Hernkind 1985). The frontal approach behaviour of *P. argus* is pre-mating, which allows definite recognition of imminent copulation (Lipicus et al. 1983). Both the courtship and pre-mating frontal approach were observed in *P. homarus* in this study. Confinement in laboratory tanks encourages male aggression and female submission during mating in *P. homarus* and copulation occurs with a frontal approach leading to a vertical embrace as in *P. h. rubellus* (Berry 1970) even though other rare forms of mating, such as approaching the female from behind, are also possible. Male aggression towards females is rare as evidenced in only two matings: one with unsuccessful spermatophore deposition and the other where sperm deposition was successful but spawning did not occur. Both these females moulted before further mating, clear evidence that they were not ready for egg production and mating was forced on them. Up to four copulations have been reported by a single pair in *Jasus edwarsii*, *P. argus*, and *P. japonicus* (Lipicus et al. 1983; Kittaka 1987; Deguchi 1988; Deguchi et al. 1991). Two matings within a period of 30 min in *P. homarus* indicates such a possibility in this species also. No fighting between males was found and the reported aggressive males embrace in *P. homarus* leading to loss of limbs as reported by Berry (1970) was not observed.

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REFERENCES

Bertelsen, R. D.; Mathews, T. R. 2001: Fecundity dynamics of female spiny Lobster (*Panulirus argus*) in a South Florida fishery and Dry Tortugas Park Lobster sanctuary. *Marine and Freshwater Research 52*: 1559–1565.

Berry, P. F. 1970: Mating behaviour, oviposition and fertilization in the spiny lobster, *Panulirus homarus* (Linnaeus). *South African Association for Marine Biological Research, Investigational Report 24*: 1–16.

Berry P. F. 1971: The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of southern Africa. *Investigational Report of the Oceanography Research Institute 28*: 1–75.

Chittleborough, R. G. 1976: Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Australian Journal of Marine and Freshwater Research 27*: 499–516.

Deguchi, Y. 1988: II. Copulation and spawning. 4. Spiny lobster. *In*: Hirano, R. *ed.* Seed production of decapod crustaceans. Tokyo, Koscisha-Koscikaku. Pp: 64–76. (In Japanese.)

Deguchi, Y.; Sugita, H.; Kamemoto, F. 1991: Spawning control of Japanese spiny lobster. *Memoirs of the Queensland Museum 31*: 449.

Kagwade, P. V. 1988a: Reproduction in the spiny lobster, *Panulirus polyphagus* (Herbst). *Journal of the Maine Biological Association of India 30(1&2)*: 37–46.

Kagwade, P. V. 1988b: Fecundity in the spiny lobster, *Panulirus polyphagus* (Herbst). *Journal of the Maine Biological Association of India 30(1&2)*: 114–120.

Kanciruk, P. 1980: Ecology of juvenile and adult Palinuridae (spiny lobsters). *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. Vol. 2. New York, Academic Press. Pp. 59–96.

Kanciruk, P.; Hernkind, W. F. 1976: Autumnal reproduction in *Panulirus argus* at Bimini, Bahamas. *Bulletin of Marine Science 26*: 417–32.

Kittaka, J. 1987: Ecological survey of rock lobster *Jasus* in the southern hemisphere. Ecology and distribution of *Jasus* along the coast of Australia and New Zealand. Report to the Ministry of Education, Culture and Science. Pp. 1–232.

Kittaka, J.; MacDiarmid, A. B. 1994: Breeding. *In*: Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* Spiny lobster management. Oxford, Fishing News Books, Blackwell Scientific Company. Pp. 384–401.

Kittaka, J. 1994: Larval rearing. *In*: Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* Spiny lobster management. Oxford, Fishing News Books, Blackwell Scientific Company. Pp. 402–403.

Lipicus, R. N.; Hernkind, W. F. 1985: Photoperiodic regulation and daily timing of Spiny lobster mating behaviour. *Journal of Experimental Marine Biology and Ecology 89*: 191–204.

Lipicus, R. N.; Edwards, M. L.; Hernkind, W. F.; Watterman, S. A. 1983: *In situ* mating behaviour of the spiny lobster *Panulirus argus. Journal of Crustacean Biology 3*: 217–222.

Radhakrishnan, E. V.; Vijayakumaran, M. 1986: Observations on the feeding and moulting of laboratory reared phyllosoma larvae of the spiny lobster, *Panulirus homarus* (Linnaeus) under different light regimes. Proceedings of the Symposium on Coastal Aquaculture (Marine Biological Association of India). Vol. 4. Pp. 1261–1266.

Radhakrishnan, E. V.; Vijayakumaran, M. 1995: Early larval development of the spiny lobster, Panulirus *homarus* (Linnaeus 1758). *Crustaceana 68(2)*: 151–159.

Rudd, S.; Warren, F. L. 1976: Evidence for a pheromone in the South African rock lobster *Jasus lalandi. Transactions of Royal Society of South Africa 42(1)*: 103–105.

Senthil Murugan, T.; Remany, M. C.; Mary Leema, T.; Dilip Kumar, J.; Santhanakumar, J.; Vijayakumaran, M.; Venkatesan, R.; Ravindran, M. 2004: Growth and breeding of the spiny lobster, *Panulirus ornatus* (Fabricius 1798). Abstract. Programme and abstracts, 7th International conference and workshop on biology and management of lobsters, Hobart, Tasmania, 8–13 February 2004. Pp. 146.

Silberbauer, B. I. 1971: The biology of the South African rock lobster *Jasus lalandi* (H. Milne Edwards) 1. Development. *South African Division of Sea Fisheries Investigational Report 93*.

Vijayakumaran, M. 1990: Energetics of a few marine crustaceans. Unpublished PhD thesis, Cochin University of Science and Technology, Kochi, India. 138 p.

Vijayakumaran, M.; Radhakrishnan, E. V. 1986: Effect of food density and feeding on moulting of phyllosoma larvae of the spiny lobster, *Panulirus homarus* (Linnaeus). Proceedings of the Symposium on Coastal Aquaculture (Marine Biological Association of India). Vol. 4. Pp. 1281–1285.

Vijayakumaran, M.; Maharajan, A.; Rajalakshmi, S.; Jayagopal, P.; Subramanian, M. S. 2004a: Early larval developmental stages of the spiny lobsters, *Panulirus ornatus* (Fabricius, 1798), *Panulirus versicolor* (Latrielle, 1804) and *Panulirus homarus* (Linnaeus, 1758). Abstract. Programme and abstracts, 7th International conference and workshop on biology and management of lobsters, Hobart, Tasmania, 8–13 February 2004. Pp. 146.

Vijayakumaran, M.; Maharajan, A.; Rajalakshmi, S.; Jayagopal, P.; Subramanian, M. S. 2004b: Fecundity and viability of eggs in wild breeders of spiny lobsters, *Panulirus homarus* (Linnaeus, 1758), *Panulirus versicolor* (Latrielle, 1804) and *Panulirus ornatus* (Fabricius, 1798). Abstract. Programme and abstracts, 7th International conference and workshop on biology and management of lobsters, Hobart, Tasmania, 8–13 February 2004. Pp. 147.

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Movement patterns of the southern rock lobster, *Jasus edwardsii*, off South Australia

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Abstract Movement patterns of the southern rock lobster *Jasus edwardsii* were determined from 14 280 tag-recapture events across South Australia between 1993 and 2003. In total, 68% of lobsters were recaptured within 1 km of their release site and 85% within 5 km. The proportion of lobsters moving >1 km in marine fishing areas (MFAs) ranged from 13% to 51%. Movement rates were noticeably high in the south-east and at Gleesons Landing lobster sanctuary off the Yorke Peninsula but patterns of movement differed spatially. In the south-east, lobsters moved distances of <20 km from inshore waters to nearby offshore reefs whereas at the Yorke Peninsula, individuals moved distances >100 km from within the sanctuary to sites located on the north-western coast of Kangaroo Island and the southern end of Eyre Peninsula. In total, 85% of all lobsters released inside the sanctuary moved distances >1 km. Movement was highest in immature females within most MFAs. Females also remained at large an average of 124 days longer than males. The high variation in lobster movement observed across South Australia highlights the need for locally derived, regionally specific data when assessing the proposed location and subsequent modelling of marine protected areas. This is of particular importance to inshore areas, where movement rates of lobsters were highest.

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Keywords lobster; *Jasus edwardsii*; movement; South Australia; marine fishing area; marine protected area

INTRODUCTION

The southern rock lobster *Jasus edwardsii* (Hutton, 1875) is widely distributed around southern mainland Australia, Tasmania, and New Zealand. It is South Australia's most valuable fisheries resource, with an export value of AU$110 million in the 2002/03 season. The fishery is divided into two zones for management purposes: a southern zone (SZ) that extends from the Victorian border to the mouth of the Murray River and a northern zone (NZ), from the mouth of the Murray River to the Western Australian border (Fig. 1). Since the 1960s, both fisheries have shared a range of input controls including limited entry, pot restrictions, minimum landing size, and seasonal closures. In 1993 and 2003, output controls in the form of total allowable catches (TACs) and individual transferable quotas (ITQs) were implemented into the SZ and NZ respectively (Copes 1978; Zacharin 1997). Fishing is undertaken from October to May, the majority of the catch being taken in the first 4 months of the season (Ward et al. 2004a,b). Fishers use baited pots that are generally set over night and hauled at first light, with over 90% of the catch in both zones landed in depths of <60 m. There are four lobster sanctuaries in South Australia in which lobster fishing is prohibited, one of which is Gleesons Landing located off the Yorke Peninsula in the NZ (Fig. 1).

Reproduction and moulting in *J. edwardsii* are highly seasonal with male and female cycles differing by c. 6 months (Annala & Bycroft 1988; MacDiarmid 1989). Mature males moult in spring between October and November to ensure being in intermoult during mating. Females generally moult from April to June but the timing of ecdysis can vary spatially (McKoy & Esterman 1981). Mating occurs shortly after the female moult with eggs brooded externally for 3–4 months over the winter period.

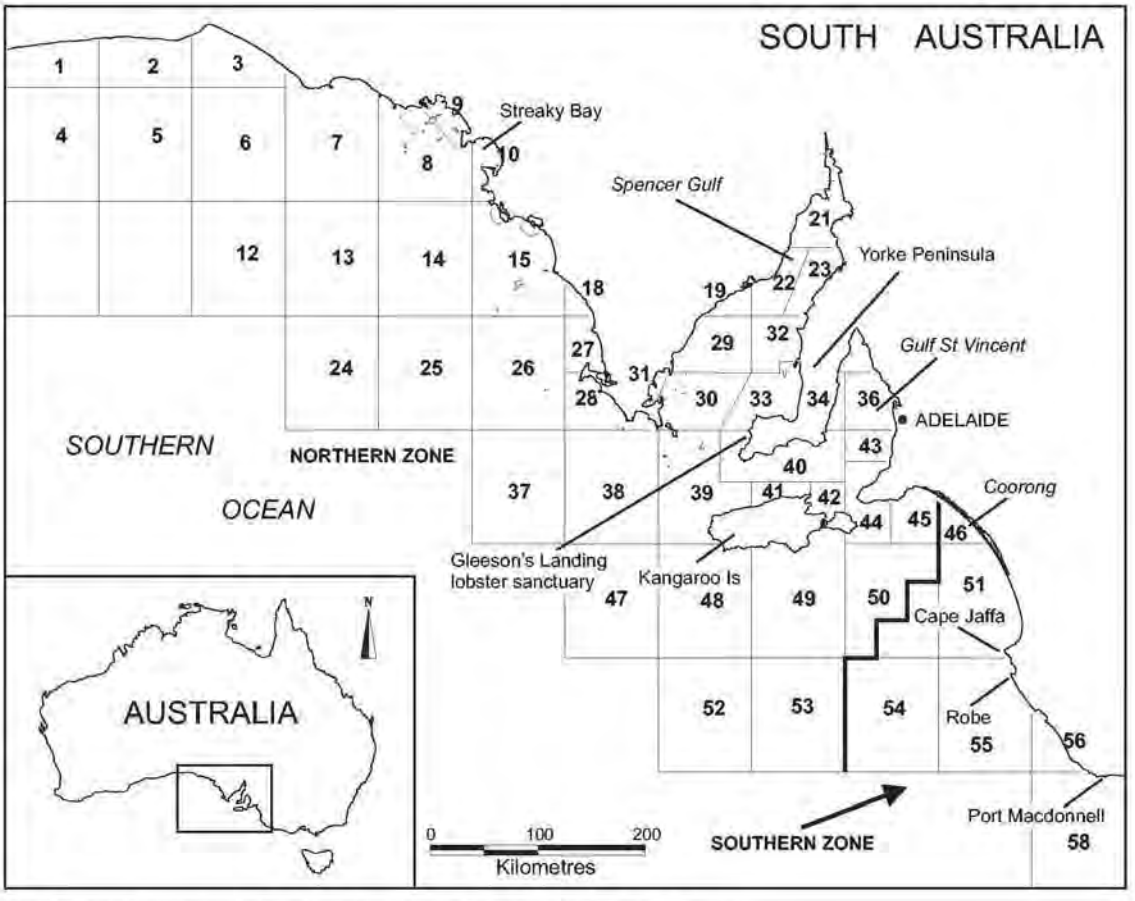

Fig. 1 Study range with location of marine fishing areas in South Australia.

Larvae hatch in early spring c. September–October (MacDiarmid 1989, 1991). Patterns of food consumption appear closely related to reproductive and moult cycles (Kelly et al. 1999). Peak food consumption by both sexes is observed on the resumption of feeding c. 2–4 weeks after ecdysis. Males also cease feeding during the autumn mating season.

Herrnkind (1980) categorised patterns of lobster movement into: homing, nomadism, and migration. "Homing", describes periodic excursions from a shelter to a nearby area with subsequent return, often within a 24-h period. The behaviour has been detailed for both *Panulirus argus* (Herrnkind & McLean 1971) and *P. cygnus* (Chittleborough 1974) where individuals are known to emerge at dusk and spend the night on foraging excursions, before returning to the home den at dawn from distances of up to 300 m. A range of visual and chemical cues that provide a cognitive map for individuals is believed to underpin decapod homing behaviour (Vannini & Cannicci 1995).

"Nomadism" describes the wandering of individuals over a large area without clear-cut start and endpoints. In *P. argus*, it is particularly common in immature individuals where both habitat and food supply are widely dispersed or where density is high relative to localised cover (Little 1972; Davis 1977). Nomadic behaviour has also been described for the Scyllarid lobster *Ibacus peroni* (Stewart & Kennelly 1998) and *Thenus* spp. (Jones 1988).

"Migration" describes the movement of a population or individual within a confined time period over relatively long distances. It is distinguished from nomadism by incorporating directedness, periodicity, and temporal confinement. Migrations are usually linked to specific periods in the life cycle, namely, pre-adult, moulting, and reproductive stages

(Herrnkind 1980). They are therefore generally seasonal, but can be highly variable in distance between regions. One of the most notable examples documented is the mass migration of the ornate rock lobster *Panulirus ornatus* from nursery grounds in northern Torres Strait to the spawning grounds in the east of the Gulf of Papua, a distance of up to 511 km (Moore & MacFarlane 1984). Mass movement of lobsters to distinct breeding grounds have also been recorded for *P. argus* (Herrnkind 1980), *P. cygnus* (Phillips 1983), and *Jasus verreauxi* (Booth 1984, 1997). Migration in a counter-current direction, presumed to be a behavioural mechanism to redress downstream larval dispersal, is evident in a number of species, namely *Palinurus delagoae* (Groeneveld 2002), *Palinurus gilchristi* (Groeneveld & Branch 2002), and *J. verreauxi* (Booth 1997).

Movement patterns of *J. edwardsii* are typically migrational and in New Zealand appear closely linked to reproductive, moulting, and feeding cycles. Aggregations of lobsters on offshore sites are highly seasonal and directional movement to these areas appear strongly correlated to the timing of these events (McKoy 1983; Annala & Bycroft 1993; Kelly et al. 1999; Kelly 2001). Specifically, aggregations of male lobsters peak offshore at times of elevated feeding rates in July (after mating), whereas ovigerous female numbers are highest in August before larval release in September/October.

In Australia, evidence of mass directional migration by *J. edwardsii* has not been largely evident to date. An initial tagging study in South Australia in the 1970s revealed that recaptured lobsters had moved relatively short distances (<5 km) and exhibited strong site fidelity (Lewis 1981). A small proportion of animals, however, did exhibit long-distance directional migration (up to 28 km) from inshore to offshore sites in the Cape Jaffa region (Fig. 1). Similarly, a study of 39 000 tag-recapture events in sites around Tasmania between 1973 and 2001 indicated that in most areas, more than 90% of animals moved <5 km (Gardner et al. 2003). Directional movement was only evident in a single site where animals moved distances greater than 8 km to deeper water in Tasmania's north-west (Pearn 1994).

Movement patterns of lobster species have particular relevance for Marine Protected Areas (MPAs). Specifically, the implications of lobster "spillover" from MPAs arising from density-dependant factors (Childress 1997) warrant information on spatial distribution and movement when assessing their proposed location. Current management arrangements in South Australia include closed areas, but lack of information about lobster migration limits assessment of effectiveness and potential effect of closure sites. Recent proposals for the development of additional MPAs across the range of *J. edwardsii* in South Australia have highlighted the requirement for accurate and dependable data on its movement patterns.

The aim of the study was to investigate the movement patterns of *J. edwardsii* in South Australia by means of a large-scale tag and recapture programme. Movement was analysed in relation to lobster size, sex, marine fishing area (MFA), and sexual maturity. A particular focus of the study was the movement patterns of tagged animals released within the lobster sanctuary located at Gleesons Landing (Fig. 1) in the Yorke Peninsula.

METHODS

Tagging and recapture

Between August 1993 and May 1996, 64 475 lobsters were tagged between Streaky Bay in the NZ and Port Macdonnell in the SZ of South Australia (Fig. 1). All lobsters were caught using standard baited traps as required by the commercial lobster fishing industry of South Australia (Zacharin 1997). The size range of males (N = 25 520) and females (N = 38 955) was 22–215 mm carapace length (CL) (mean 101.6 ± 21.6 SD) and 21–185 mm CL (mean 98.08 ± 14.87 SD) respectively.

Lobsters were tagged using Hallprint T-anchor tags. The tags were 55 mm long with a 30 mm shaft length and 10 mm T-bar length. Each was identified with the title "SA FISH" and a unique 6-digit number. All tags were inserted ventrally, using a Dennison tag-fast® III tag applicator, into the anterior oblique muscle between the first and second abdominal sterna.

Scientists from the South Australian Research and Development Institute (SARDI) executed the tagging programme in conjunction with volunteer commercial fishers. It was conducted using chartered vessels and by fishers during routine fishing operations. On chartered vessels, all lobsters captured were tagged and released, whereas sublegal lobsters and spawning females were tagged only during commercial fishing operations.

Data recorded upon initial tagging and subsequent recapture included location, sex, CL, depth, and sexual maturity based on setal development (Musgrove 2000). Lobsters were released as close

to the point of capture as possible using the vessels' global positioning system (GPS). Recaptures were made during the commercial fishing season, i.e., from 1 October to 30 April in the SZ and from 1 November to 31 May in the NZ. Fishers voluntarily recorded recapture information in conjunction with periodic observation trips by SARDI scientists.

Data analysis

Distance moved was calculated as the straight-line distance between release and most recent recapture. Movement was deemed to have occurred when this exceeded 1 km. Linear regression analysis of log-transformed data analysed the relationship between distances moved and days-at-large (DAL), and a chi-square test of homogeneity was used to test if movement was significantly different between MFAs.

To determine whether lobster movement was size-dependant, distance moved by lobsters in three size categories—small (CL <100 mm), medium (100 CL 130 mm), and large (CL >130 mm)—was compared in MFAs where the proportion of lobsters moving >1 km exceeded 30%. Data were logged to meet the assumptions of normality, with distance moved by lobsters in each size category compared by means of ANOVA. Where significant, differences within categories were compared using a multiple-comparison Tukey test (Zar 1984).

RESULTS

Distance and direction of movement

From the 64 475 individuals tagged, a total of 14 280 (22%) have been recaptured to date. Based on most recent recapture location, 68% of lobsters had moved <1 km from their original capture position (Fig. 2). Of the migrants, 16.5% moved distances of 1–5 km, 11.5% moved 5–20 km, and 4% moved >20 km. The observed direction of movement during the study tended to be from inshore to offshore sites (Fig. 3). This was evident in both sexes and in various reproductive states. This result may, in part, be a function of the spatial distribution of tagged releases. About 70% of lobsters were initially captured and tagged in depths of 0–30 m, but most recaptures were in depths of 31–60 m, reflecting the depths at which over 50% of the commercial catch was taken during the study period (Fig. 4). However, across all areas a strong pattern emerged in which nearly all movement occurred in lobsters tagged inshore, whereas all lobsters tagged offshore remained resident. In total, 92% of the 580 lobsters moving >20 km (Fig. 2) were originally tagged in depths of <50 m whereas none of the 1960 recaptured lobsters originally tagged on offshore reefs in depths >50 m moved >20 km.

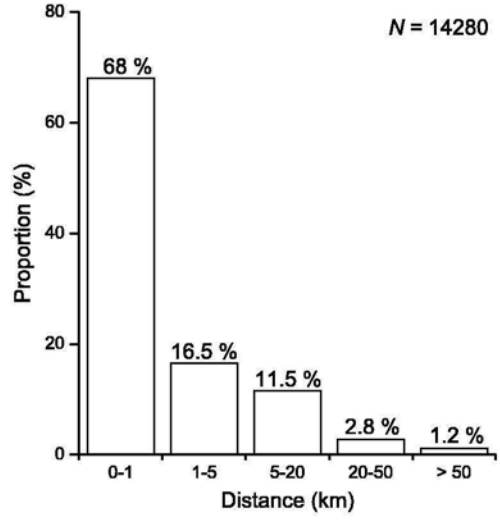

Fig. 2 Percentage of lobsters that moved within a range of distance categories based on distance from initial tagging to final resight locations across all marine fishing areas in South Australia.

Spatial analyses and pattern of movement

The proportion of lobsters moving >1 km, 1–5 km, and >5 km in each MFA is presented in Fig. 5A–C. The proportion moving >1 km (Fig. 5A) ranged from 13% to 51%. Highest levels (>30%) were recorded in the south-east of the SZ within MFAs 51, 55, 56, and 58 (Fig. 1). Notably, these MFAs commonly have the highest catch-per-unit-effort (CPUE) in the fishery, indicating that lobster density in these areas is also high (Fig. 5A).

The majority of movement patterns in the south-east tended to be longshore or inshore-offshore migrations of <20 km (Fig. 6A). However, long-distance movement was observed in a cohort of lobsters released within inshore sites of the Coorong, west of Kingston. Here, lobsters moved distances >50 km in a highly directional pattern to sites located in offshore waters, west of Cape Jaffa. Movement by these individuals was the only evidence of long-distance migration to be observed in the SZ.

In the NZ, elevated levels of movement were observed in MFAs 33 and 40 (Fig. 5A). Both MFAs are located at the Yorke Peninsula with Gleesons

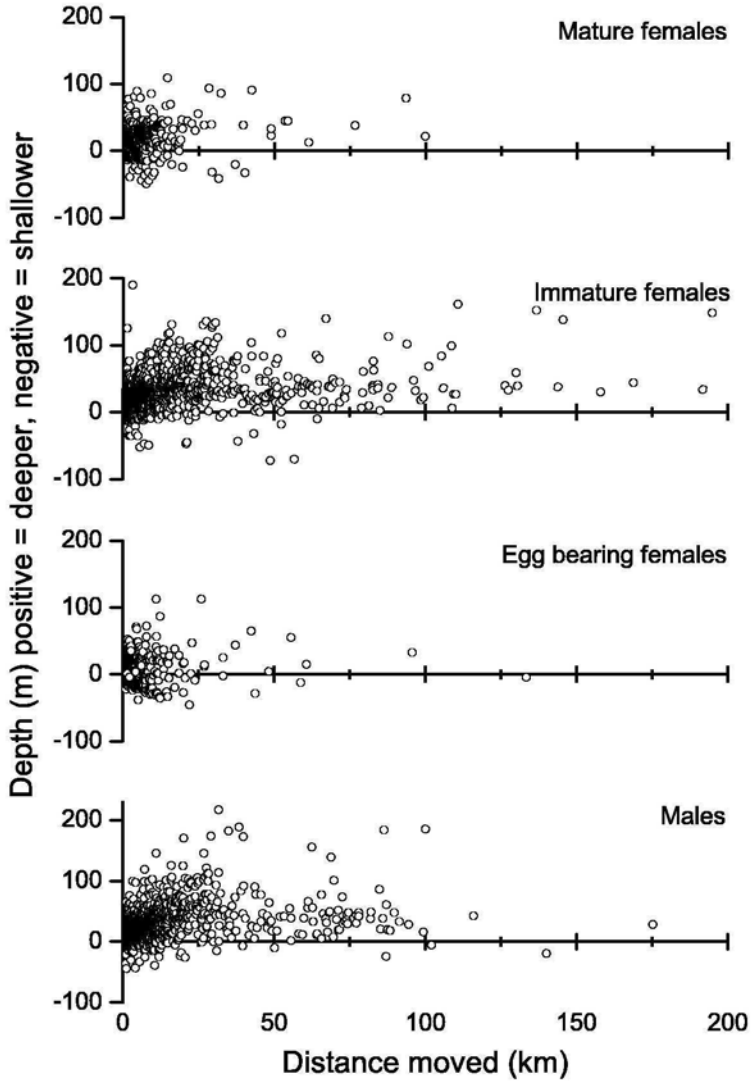

Fig. 3 Changes in depth made by lobsters moving distances >1 km presented by sex and reproductive status.

Landing lobster sanctuary in MFA 33 (Fig. 1). The movement pattern in these areas was evidently different to that of the SZ sites (Fig. 6B). MFA 33 had the highest proportion of lobsters moving long-distance, with 68 of the 171 lobsters released observed to move >5 km. Movement was highly directional to the north-western coast of Kangaroo Island and to sites located at the southern end of Eyre Peninsula. Movement tended to be in a south-west direction with distances exceeding 100 km. The maximum distance moved was 127 km. This pattern appeared specific to the Yorke Peninsula and was not highly evident in lobsters moving from other parts of the Eyre Peninsula within the NZ fishery (Fig. 6C).

Mean rate of movement ranged between 0.02 km day^{-1} (SE = ±0.001) and 0.07 km day^{-1} (SE = ±0.02) and was highest in MFA 40 (Table 1). There was no significant difference in movement among MFAs (chi-square; $P > 0.05$).

Movement at Gleesons Landing

In total, 422 lobsters were tagged and released inside Gleesons Landing lobster sanctuary in MFA 33, off the Yorke Peninsula (Fig. 1). Of the 66 subsequent recaptures, 56 (85%) moved distances >1 km

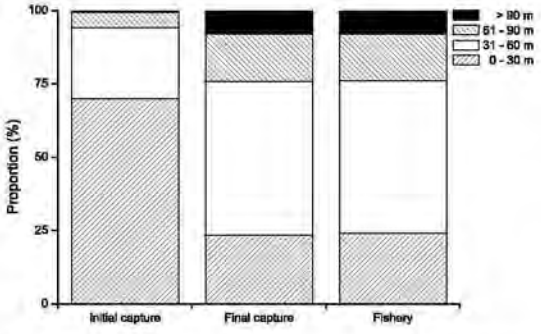

Fig. 4 Depth ranges of initial tagging and final recapture compared to depths where commercial fishing was primarily undertaken from 1991 to 2000.

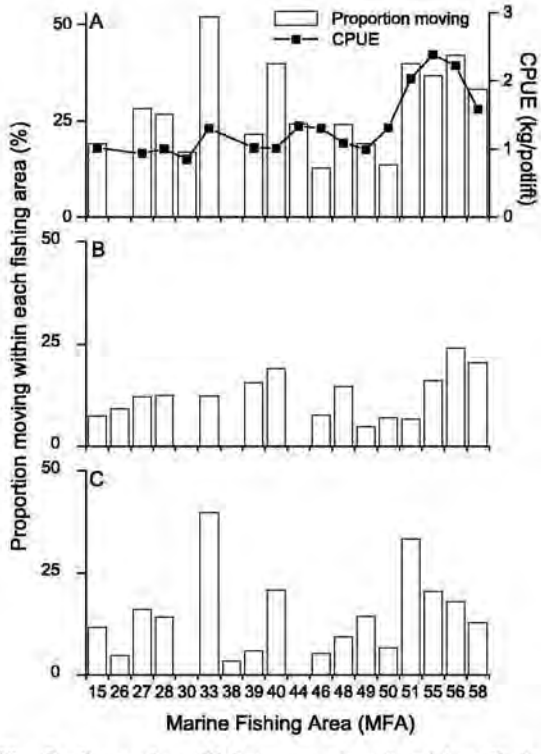

Fig. 5 Proportion of lobsters moving: **A**, >1 km; **B**, 1–5 km; and **C**, >5 km in various marine fishing areas (MFAs) in South Australia. Catch rates from each MFA from the 2002/03 commercial fishing season are provided in 5A (source: Ward et al. 2004a). (CPUE, catch-per-unit-effort.)

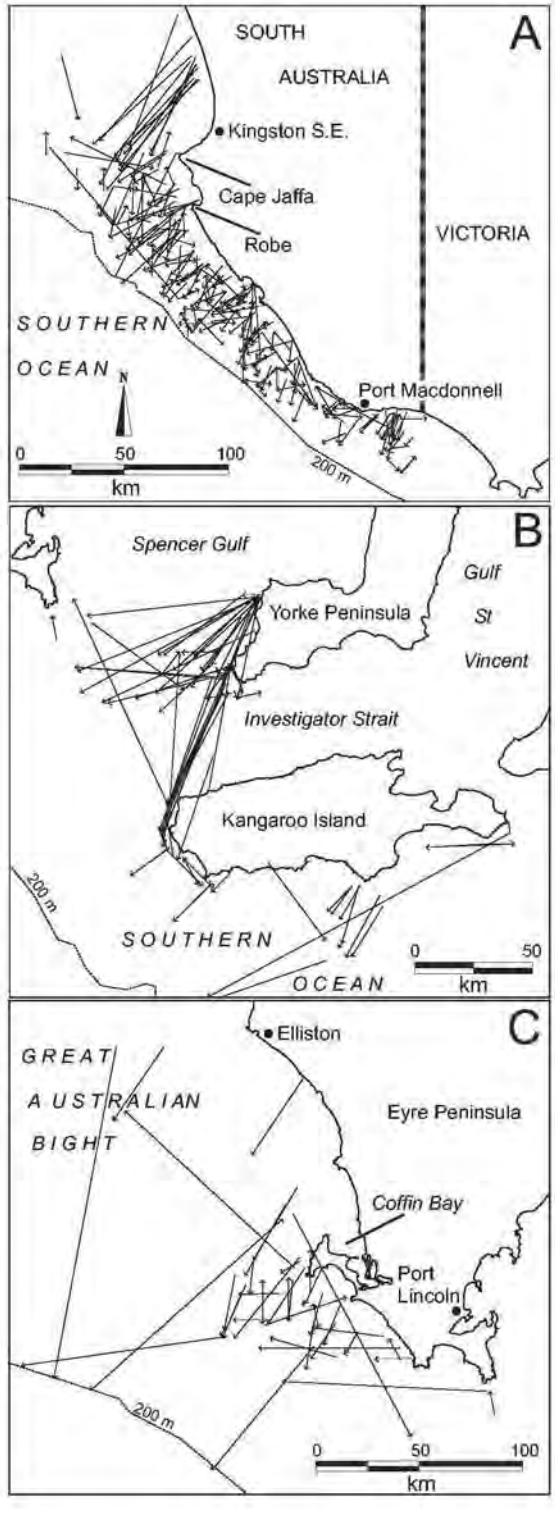

Fig. 6 (*right*) Movement patterns of southern rock lobster *Jasus edwardsii* in three areas of South Australia: **A**, the south-east; **B**, Yorke Peninsula; and **C**, Eyre Peninsula.

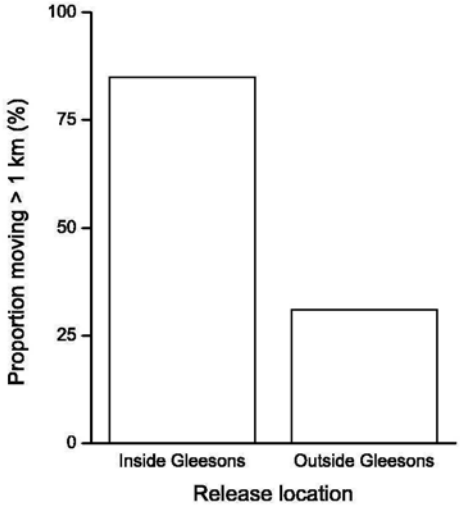

Fig. 7 Proportion of lobsters moving >1 km in marine fishing area 33 based on release location.

(Fig. 7). A total of 311 lobsters were released in waters outside the lobster sanctuary but within MFA 33. Of these, 105 were recaptured with 33 (31%) observed to move >1 km. All of the lobsters exhibiting long-distance directional migration from MFA 33 (Fig. 6B), originated from within the sanctuary.

Days-at-large

Days-at-large (DAL) was defined as the period between initial tagging and final capture. Lobsters remained at large for periods ranging from 1 to 3364 days (mean DAL = 563.5 days). Most lobsters (72.6%) were recaptured within 730 days (2 years) of being released, and 27.4% remained at large for longer periods. The lobster at large for the longest period to date is a 122 mm CL female released in November 1993 and last recaptured in January 2003. During this period it was recaptured 13 times. On average, females (mean DAL = 609 days) remained at large for 124 days more than males (mean DAL = 485 days). Linear regression analysis of log-transformed data confirmed that distance moved was not related to DAL ($y = 0.0002+0.6193$, $R^2 = 0.03$).

Size and female reproductive status

The distance moved by various size classes across all MFAs is presented in Fig. 8. In total, 65% and 66% of all males and females respectively that moved >1 km, were in the 75–100 mm CL size class. To determine whether lobster movement was size-dependant, distances moved by small (<100 mm CL), medium (100 CL 130 mm), and large (>130 mm CL) lobsters were compared in MFAs where the proportion of lobsters moving >1 km exceeded 30%, i.e., MFAs 40, 55, 56, and 58 (Table 1). There was no significant difference in the distance moved by any size class of male lobster in any of the MFAs analysed. However, small females (<100 mm CL) moved significantly more than any other size class of males or females in three (40, 55, and 56) of the four MFAs compared.

In MFA 33, 89% of females moving >1 km were sexually immature (Fig. 9). In all other MFAs, immature females accounted for 40–60% of female movers. In total, 59% of all spawning females recaptured had initially been tagged as either sexually immature or sexually mature but without eggs, thus suggesting that the tagging and handling process had not unduly influenced the reproductive biology of females.

Table 1 Comparison of distance moved by three size-classes of male and female *Jasus edwardsii* in marine fishing areas (MFAs) where proportion of lobsters moving >1 km exceeded 30%. (NS, not significant; CL, carapace length.)

					Tukey test		
MFA	Rate (km/day ± SE)	*N*	Sex	ANOVA	Small (<100 mm CL)	Medium (100 CL 130 mm)	Large (>130 mm CL)
40	0.07 ± 0.02	150	F	$F = 8.192, P < 0.05$	$P < 0.05$	NS	NS
		87	M	$F = 0.889, P > 0.05$	NS	NS	NS
55	0.05 ± 0.007	950	F	$F = 7.882, P < 0.05$	$P < 0.05$	NS	NS
		453	M	$F = 2.6, P > 0.05$	NS	NS	NS
56	0.02 ± 0.001	838	F	$F = 37.6, P < 0.05$	$P < 0.05$	NS	NS
		387	M	$F = 1.03, P > 0.05$	NS	NS	NS
58	0.03 ± 0.01	446	F	$F = 0.155, P > 0.05$	NS	NS	NS
		235	M	$F = 0.618, P > 0.05$	NS	NS	NS

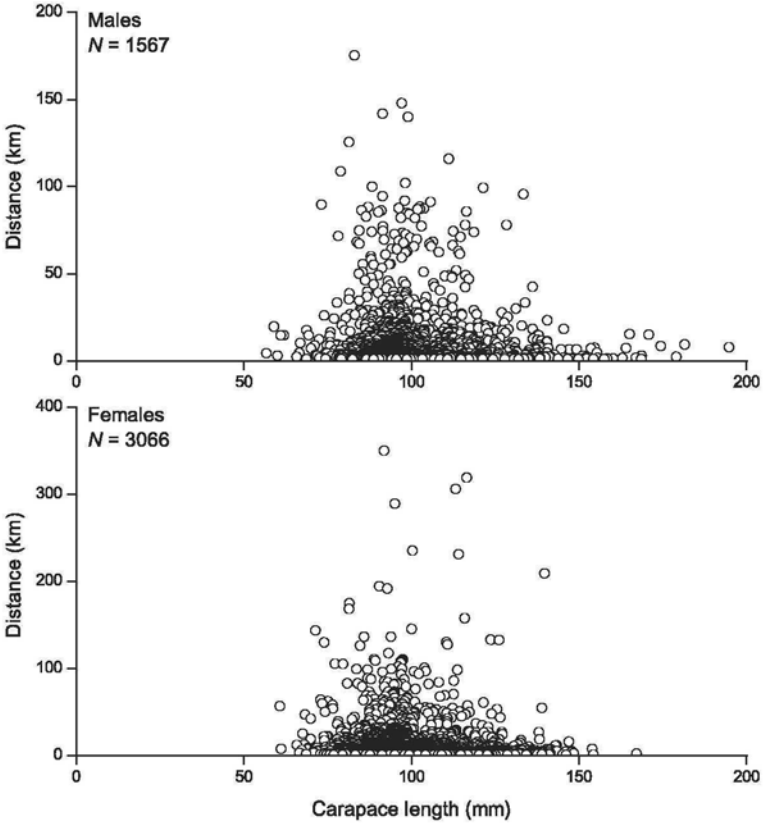

Fig. 8 Distance moved by size class of male and female *Jasus edwardsii* in South Australia.

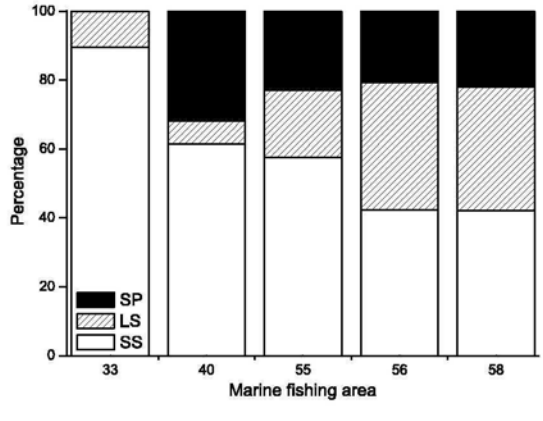

Fig. 9 Reproductive condition of females moving >1 km in five main marine fishing areas (MFAs) of South Australia where high movement was observed. $N = 2339$. (SS, short setae (sexually immature); LS, long setae (sexually mature but not spawning); SP, spawning.)

DISCUSSION

The underlying assumptions associated with the tag and recapture programme used in the study must be addressed before a complete interpretation of the observed movement patterns by *J. edwardsii* can be considered. The associated bias and problems of interpretation with commercial fishery tag returns have been discussed by Herrnkind (1980). He highlighted that the greatest number of returns will occur where commercial fishing effort is highest and that certain cohorts of the population will not be sampled because of biased catch effectiveness or because certain grounds are unfished. In addition, smaller-sized lobsters (<70 mm CL) are not generally landed and therefore size-dependent movement is disproportionate. The result is that migratory pathways can be missed and the direction of migration cannot be determined. The assumptions

that migration occurs along a straight line and that lobsters are tagged at the onset of migration and recaptured at their final destination are also highly unlikely, thus biasing estimates of distances moved, direction taken, and movement rates.

The effects of capture, handling, and tagging on the survival and behaviour remain unknown for many lobster species. However, tagging mortality and tag retention is largely size dependent (Linnane & Mercer 1998). The fact that many female lobsters in the South Australian population continued to mature sexually after tagging indicated that the tagging process in this study did not affect the reproductive behaviour at least, of *J. edwardsii*. In addition, many individuals retained their tags over several years, with a single individual at large for almost 10 years. Given that moulting is annual in all but the larger size ranges (Hobday & Ryan 1997), this indicates that tag loss by individuals was minimal.

Regional differences were apparent in the movement patterns of lobsters between northern and southern zones of South Australia. More animals undertook migrations in the south-east but these tended to be predominantly small-scale in nature (<20 km). The apparent direction was from inshore to offshore sites, with some long-shore movements. In New Zealand, similar movements to offshore reefs by *J. edwardsii* are highly seasonal and strongly linked to reproductive cycles (McKoy & Leachman 1982; Kelly et al. 1999; Kelly 2001). Specifically, spawning females aggregate in large numbers offshore during the summer months for larval release before migrating back inshore to mate in April–June. The continuous limestone reef system and narrow shelf (<30 nm) in the south-east of South Australia (Lewis 1981) would clearly benefit migrants, in that protective cover to offshore sites is largely available. Despite this, evidence for a return movement to inshore waters later in the season was not observed in the south-east. Given that tag returns were primarily obtained through the commercial fishery where effort is greatest from October to January (Ward et al. 2004a,b), the return migration, if present, may not be clearly obvious. However, a breakdown of movement data by month did not indicate that such a trend existed.

The long-distance migrations by lobsters originating from the Coorong support the findings of a small-scale study in the region by Lewis (1981). The Coorong is noted for its unusual habitat features consisting of narrow bands of limestone reef that run parallel to an expansive beach. The reef system is not continuous however, with reef patches separated by sandy stretches. As a result, movement to more continuous reef habitat west of Cape Jaffa would appear to be the plausible explanation for the observed migration from the area. Long-shore movement by individuals also featured in the south-east, but without any clear direction. Booth (1997) suggested that such movement best fits nomadism, most likely caused by the displacement of the individual from its home reef because of potting. Catch rate data indicates that densities in the south-east are the highest in the fishery (Ward et al. 2004a), which could force displaced individuals to travel considerable distances before obtaining suitable habitat.

The highly directional long-distance movement by immature females observed in the NZ off the Yorke Peninsula is consistent with recorded movements of *J. edwardsii* in southern New Zealand. Street (1969, 1971) first reported this movement pattern in tagged lobsters released in Otago, Foveaux Strait, and Fiordland between 1957 and 1970. The majority of lobsters were recaptured within 16 km of their release points but some moved greater distances to specific sites in southern Fiordland over a 2-year period. In all instances, lobsters which moved long distances were sexually immature females ranging from 90 to 105 mm CL. Working from Stewart Island off the south coast, McKoy (1983) reported that 87% of tagged recaptures were within 5 km, but the remainder moved in a highly directional pattern to specific sites on the coast of the South Island. The maximum distance moved was 350 km, with migrations largely made by immature females. Similarly, Annala & Bycroft (1993) reported that the largest proportion of lobsters observed to migrate in Fiordland were immature females that moved in a northerly direction.

Why lobsters moved specifically to the north-west coast of Kangaroo Island is unclear, but habitat limitation must also be considered as a possible driver. Unlike the south-east, which is dominated by continuous limestone reefs (Lewis 1981), habitat in the NZ is not spatially widespread and mainly consists of igneous rock intrusions, particularly granites. As a result, lobsters moving from the Yorke Peninsula could feasibly travel considerable distances before finding a suitable reef location.

Long-distance directional migration by immature females has also been recorded in Victoria (Treble 1996) and Tasmania (Pearn 1994). Booth (1997) suggested that higher levels of migration by immature females might facilitate larval release on

maturity in areas more favourable to larval survival. Specifically, the mechanism allows for the dispersal of larvae away from inshore reef-dwelling planktivores. Other potential benefits of movement, particularly to offshore sites, include access to new feeding grounds (Kelly et al. 1999) and avoidance of seasonal changes in inshore salinity (Watson et al. 1999). Similar size-related characteristics of movement by immature individuals have also been reported for other spiny lobster species, *P. cygnus* (Phillips 1983), *P. argus* (Davis & Dodrill 1989), *P. gilchristi* (Groeneveld & Branch 2002), and *P. delagoae* (Cockcroft et al. 1995; Groeneveld 2002).

On average, females remained at large for longer periods throughout the study. The spatially distinct nature of commercial fishing in South Australia may be a confounding factor. In the study, some spatial differences did exist between release sites and areas subsequently fished. Fishing effort and subsequent catch rates are highest in depths of 30–60 m (Ward et al. 2004a,b), whereas the majority of tagged lobsters were initially captured and released in depths of 0–30 m. Consequently, tagged females may have been resident in or moved to, specific locations that were not fished during certain times of the season. Homing behaviour could explain the lack of a relationship between DAL and distance moved.

The mechanisms underlying the high levels of movement from MFA 33 and specifically from the lobster sanctuary at Gleesons Landing warrant particular focus, given that all lobsters expressing long-distance movement from the Yorke Peninsula originated from within the sanctuary. Research in New Zealand has shown that lobsters inside MPAs tend to increase in biomass relative to adjacent fished sites (Kelly et al. 2000; Davidson et al. 2002; Kelly & MacDiarmid 2003). Movement from MPAs is therefore important as it effects biomass rebuilding within the MPA and contributes to the issue of biomass spillover from it. Using the same dataset as the current study, McGarvey (2003) estimated that the yearly emigration rate of rock lobsters moving >3 km from Gleesons Landing was 62%. Movement patterns differed between fished and unfished sites; sanctuary lobsters moved further distances and had a higher overall tendency to migrate. These results confirm our findings that in MFA 33, proportionally more lobsters migrated from within the sanctuary compared with those outside it. The mechanisms underlying this movement are speculative. In the absence of fishing, it is reasonable to suggest that density-dependant forces were stronger inside the sanctuary owing to lower rates of removal. This is supported by catch-rate data from the south-east, which showed that movement was highest in MFAs with the highest CPUE. However, a similar tag-recapture study with *J. edwardsii* in Tasmania indicated that high lobster density does not necessarily stimulate large-scale movement. In particular, the fishing blocks that had the highest abundance had the lowest levels of movement (Gardner et al. 2003).

Overall, given the variation in lobster movement observed across South Australia, the results highlight the need for locally derived, regionally specific data when assessing the proposed location and subsequent modelling of MPA effects. This is of particular importance in areas where MPAs are proposed for inshore locations, given that the observed direction of movement in the study was from inshore to offshore sites. Finally, the results confirm the findings of Gardner et al. (2003) that spatial variation in movement by *J. edwardsii* may contribute to the variable performance of marine reserves (Edger & Barrett 1999) in increasing lobster biomass.

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REFERENCES

Annala, J. H.; Bycroft, B. 1988: Growth of rock lobsters (*Jasus edwardsii*) in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research 22*: 29–41.

Annala, J. H.; Bycroft, B. 1993: Movement of rock lobsters (*Jasus edwardsii*) tagged in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research 27*: 183–190.

Booth, J. D. 1984: Movement of packhorse rock lobsters (*Jasus verreauxi*) tagged along the eastern coast of the North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research 18*: 275–281.

Booth, J. D. 1997: Long-distance movements in *Jasus* spp. and their role in larval recruitment. *Bulletin of Marine Science 61*: 111–128.

Childress, M. J. 1997: Marine reserves and their effects on lobster populations: report from a workshop. *Marine and Freshwater Research 48*: 1111–1114.

Chittleborough, R. G. 1974: Developments of a tag for the western rock lobster. *CSIRO Division of Fisheries and Oceanography Report 56*.

Cockcroft, A. C.; Groeneveld, J. C.; Cruywagen, G. C. 1995: The influence of depth, latitude and width of the continental slope on the size distribution and availability of spiny lobster *Palinurus delagoae* off the east coast of South Africa. *South African Journal of Marine Science 16*: 149–160.

Copes, P. 1978: Resource management of the rock lobster fisheries of South Australia. A report commissioned by the Steering Committee for the Review of Fisheries of the South Australian Government.

Davis, G. E. 1977: Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. *Bulletin of Marine Science 27*: 223–236.

Davis, R. J.; Dodrill, J. W. 1989: Recreational fishery and population dynamics of spiny lobsters, *Panulirus argus*, in Florida Bay, Everglades National Park, 1977–1980. *Bulletin of Marine Science 44*: 78–88.

Davidson, R. J.; Villouta, E.; Cole, R. G.; Barrier, R. G. F. 2002: Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems 12*: 213–227.

Edgar, G. J.; Barrett, N. S. 1999: Short term monitoring of biotic change in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology 213*: 261–279.

Gardner, C.; Frusher, S. D.; Buxton, C.; Haddon, M. 2003: Movements of southern rock lobster, *Jasus edwardsii*, in Tasmania, Australia. *Bulletin of Marine Science 73*: 653–671.

Groeneveld, J. C. 2002: Long-distance migration of the rock lobster *Palinurus delagoae* off South Africa and Mozambique. *South African Journal of Marine Science 24*: 395–400.

Groeneveld, J. C.; Branch, G. M. 2002: Long-distance migration of South African deep-water rock lobster *Palinurus gilchristi*. *Marine Ecology Progress Series 232*: 225–238.

Herrnkind, W. F. 1980: Spiny lobsters: patterns of movement. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters, Vol. 1. Physiology and behaviour. New York, Academic Press. 463 p.

Herrnkind, W. F.; McLean, R. B. 1971: Field studies of homing, mass emigration and orientation in the spiny lobster, *Panulirus argus*. *Annals of the New York Academy of Science 188*: 359–377.

Hobday, D. K.; Ryan, T. J. 1997: Contrasting sizes at sexual maturity of southern rock lobster (*Jasus edwardsii*) in the two Victorian fishing zones: implications for total egg production and management. *Marine and Freshwater Research 48*: 1009–1014.

Jones, C. 1988: The biology and behaviour of Bay Lobsters, *Thenus* spp. (Decapoda Scyllaridae) in Northern Queensland, Australia. Unpublished PhD thesis, University of Queensland, Brisbane, Australia.

Kelly, S. 2001: Temporal variation in the movement of spiny lobster, *Jasus edwardsii*. *Marine and Freshwater Research 52*: 323–331.

Kelly, S.; MacDiarmid, A. B. 2003: Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *New Zealand Journal of Marine and Freshwater Research 37*: 149–158.

Kelly, S.; MacDiarmid, A. B.; Babcock, R. C. 1999: Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed and sandy areas. *Marine and Freshwater Research 50*: 409–416.

Kelly, S.; Scott, D.; MacDiarmid, A. B.; Babcock, R. C. 2000: Spiny lobster, *Jasus edwardsii*, recovery in New Zealand Marine Reserves. *Biological Conservation 92*: 359–369.

Lewis, R. K. 1981: Southern Rock Lobster *Jasus novaehollandiae*: Zone S Review. *South Australian Department of Fisheries Internal Report 88*: 1–12.

Linnane, A.; Mercer, J. P. 1998: A comparison of methods for tagging juvenile lobster (*Homarus gammarus* L.) reared for stock enhancement. *Aquaculture 163*: 195–202.

Little, E. J. 1972: Tagging of spiny lobsters (*Panulirus argus*) in the Florida Keys, 1967–1969. *Florida Department of Natural Resources, Marine Laboratory Special Scientific Report 31*.

MacDiarmid, A. B. 1989: Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda: Palinuridae) in northern New Zealand. *Marine Biology 103*: 303–310.

MacDiarmid, A. B. 1991: Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus edwardsii* on a coastal reef in northern New Zealand. *Coastal Management 30*: 155–166.

McGarvey, R. 2003: Assessing the impact of proposed Marine Protected Areas on South Australian rock lobster catches. *Final Report for the Fisheries Research and Development Corporation*. Project No. 2000/195.

McKoy, J. L. 1983: Movements of rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae), tagged near Stewart Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research 17*: 357–366.

McKoy, J. L.; Esterman, D. B. 1981: Growth of rock lobsters (*Jasus edwardsii*) in the Gisborne region, New Zealand. *New Zealand Journal of Marine and Freshwater Research 15*: 121–136.

McKoy, J. L.; Leachman, A. 1982: Aggregations of ovigerous female rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae). *New Zealand Journal of Marine and Freshwater Research 16*: 141–146.

Moore, R.; McFarlane, J. W. 1984: Migration of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. *Australian Journal of Marine and Freshwater Research 35*: 197–212.

Musgrove, R. J. B. 2000: Molt staging in the southern rock lobster *Jasus edwardsii*. *Journal of Crustacean Biology 20*: 44–53.

Pearn, R. 1994: Rock lobster tagging shows movement occurs. *Fishing Today (Tasmania) 7*: 27–29.

Phillips, B. F. 1983: Migrations of pre-adult western rock lobsters, *Panulirus cygnus*, in Western Australia. *Marine Biology 76*: 311–318.

Stewart, J.; Kennelly, S. J. 1998: Contrasting movements of two exploited Scyllarid lobsters of the genus *Ibacus* off the east coast of Australia. *Fisheries Research 36*: 127–132.

Street, R. J. 1969: The New Zealand crayfish, *Jasus edwardsii* (Hutton 1875). *New Zealand Marine Department Fisheries Technical Report 30*. 29 p.

Street, R. J. 1971: Rock lobster migration off Otago. *Commercial Fishing 10*: 16–17.

Treble, R. J. 1996: The southern rock lobster (*Jasus edwardsii*): fisheries biology and abundance estimation. Unpublished PhD thesis, Department of Zoology, University of Melbourne, Australia.

Vannini, M.; Cannicci, S. 1995: Homing behaviour and possible cognitive maps in crustacean decapods. *Journal of Experimental Marine Biology and Ecology 193*: 67–91.

Ward, T. M.; McGarvey R.; Xiao, Y.; Ferguson, G.; Linnane, A. 2004a: Southern Zone Rock Lobster (*Jasus edwardsii*) Fishery 2002/03. *South Australian Fisheries Assessment Series RD03/0153*. 81 p.

Ward, T. M.; McGarvey, R.; Xiao, Y.; Ferguson, G.; Linnane, A. 2004b: Northern Zone Rock Lobster (*Jasus edwardsii*) Fishery 2002/03. *South Australian Fisheries Assessment Series RD03/0142*. 86 p.

Watson, W. H.; Vetrovs, A.; Howell, W. H. 1999: Lobster movements in an estuary. *Marine Biology 134*: 65–75.

Zacharin, W. 1997: Management Plan for the South Australian Southern Zone Rock Lobster Fishery. *South Australian Fisheries Management Series No. 29*.

Zar, J. H. 1984: Biostatistical analysis, 2nd ed. Englewood Cliffs, New Jersey, Prentice-Hall Inc. 620 p.

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Short communication

Remote multi-camera system for *in situ* observations of behaviour and predator/prey interactions of marine benthic macrofauna

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Abstract There are few options for obtaining information on intra- and inter-species behavioural interactions between marine animals other than direct observation. Underwater video and infrared lighting can be used to overcome some of the biases and limitations associated with diver observations. We outline the assembly and application of a multi-camera underwater video system consisting largely of moderately priced components produced for the security surveillance industry. Signals from up to eight cameras on the seafloor are processed on a floating pontoon into a single video stream and transmitted to a remote monitoring station for viewing or recording. High-red and infrared lights are used for night viewing to minimise disturbance. Experiments incorporating this system have provided high-quality data on predation and behaviour of lobsters.

Keywords underwater video; animal behaviour; predator/prey interactions

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INTRODUCTION

With the building emphasis on multi-species and ecosystem-based management of fisheries (Constable 2001), behaviour and interactions at the level of individuals have been increasingly recognised as key issues in understanding ecosystem function, organisation, and response to perturbation (Piraino et al. 2002; Butler 2003). Models capable of capturing the dynamics of individuals within a system (e.g., Werner et al. 2001; Butler 2003) depend on data collected at a resolution only attainable through direct observation.

Direct observations of marine animal behaviour are restricted to varying degrees by the harsh operating environment. Physiological limits to dive duration and physical limits to range of visibility complicate such studies under water. Behaviour of animals being observed is likely to be altered by the close proximity of divers (e.g., Rutecki et al. 1983). These difficulties are compounded when observing animals such as lobsters that are most active at night (Mills et al. 2004). Not only does diving become more hazardous, animals are also likely to respond to the presence of visible light required for observation.

Underwater video, time-lapse recording technology, and lighting at wavelengths invisible to animals have been adopted to overcome these problems. The use of single camera, fixed video systems has enabled constant monitoring of a limited area for periods of hours to days (Chapman & Howard 1979; Burrows et al. 1999; Jury et al. 2001). Although the use of video overcomes many of the problems and biases associated with diver observations, a single, fixed camera has a limited field of view. This problem is compounded at night when field of view is further limited by lighting. Possibilities to overcome this limitation include the use of remotely controlled cameras with zoom, pan and tilt functions, or the use of multiple cameras. We chose to adopt the latter as we believe it offers a simple, robust system with greater versatility. This paper provides details of a multi-camera system

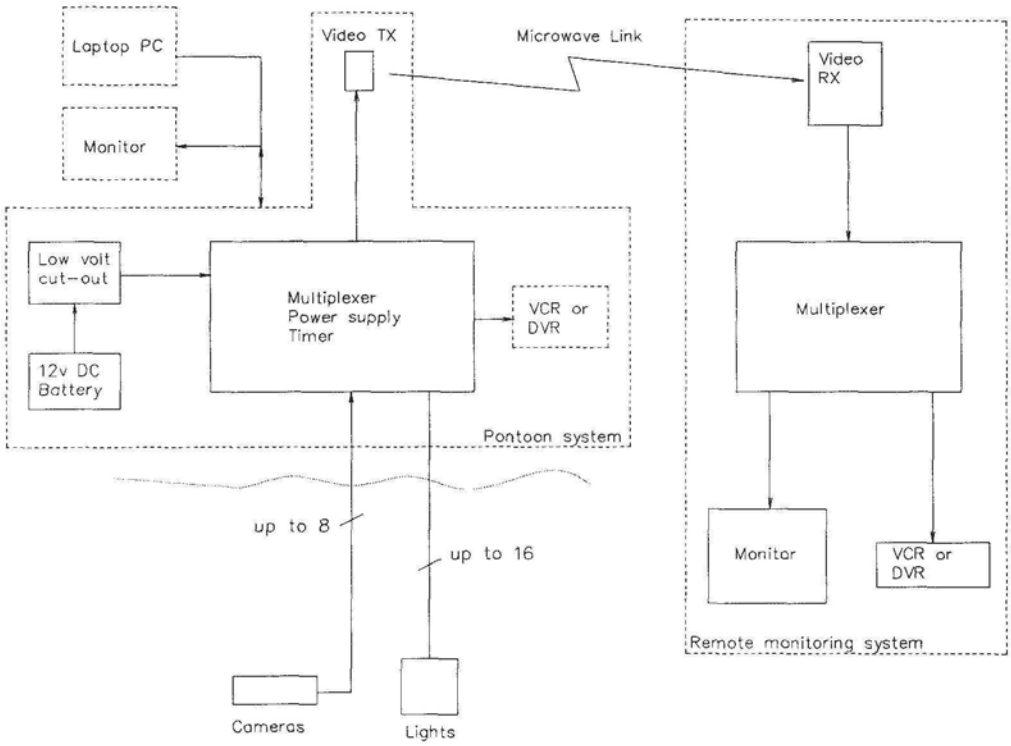

Fig. 1 Schematic representation of camera system. Pontoon system provides power to lights and cameras, and receives the signals from up to eight cameras. These are processed into a single data stream, and transmitted (TX) to the remote video receiver (RX). Camera settings and frame rates can be altered using a computer via a physical connection to the multiplexer unit. Multiplexed video signal can be recorded to a single storage medium (e.g., video cassette) at a remote station or on the pontoon.

constructed predominantly using off-the-shelf items designed for the security surveillance industry.

System assembly

The camera system has three main component types: an underwater system consisting of cameras and lights; a surface pontoon system including power supply, video processor and transmitter; and a remote monitoring system including video receiver, decoder, and recording device (Fig. 1).

Cameras were low light (0.05 lux) black and white 1/3″ CCD (charge couple device) image sensors with a 3.6 mm lens (GoVideo 3619 modules) providing a 42° viewing angle in water. Black and white CCDs were used as they have a broader wavelength detection capability than colour modules, enabling viewing with infrared light. Camera modules were protected in waterproof housings, and linked to the surface system by 30 m polyurethane-sheathed copper cables. To guarantee a clean power supply for the cameras, a switch-mode DC-DC converter (Cosel ZUS151212) was fitted providing regulated 12 V DC.

We constructed high-red lights emitting a wavelength of 680 nm and infrared lights with wavelength of 845 nm for use in different circumstances. Choice of wavelength of lighting sources is critical. Absorption of light in water increases dramatically as wavelength increases into the red region of the visible spectrum, and then increases exponentially at infrared wavelengths. Increases are particularly marked at c. 700 nm for red light and 850 nm for infrared light (Kirk 1994). Applying formulae presented in Kirk (1994) we find that in water 72% of 680 nm high-red light is transmitted at a distance of 1 m and this reduces to 14% at infrared wavelengths of 845 nm.

All lights consisted of an array of 40 high intensity light emitting diodes (max. radiant intensity c. 120 mW/sr @ 100 mA) encapsulated in resin for

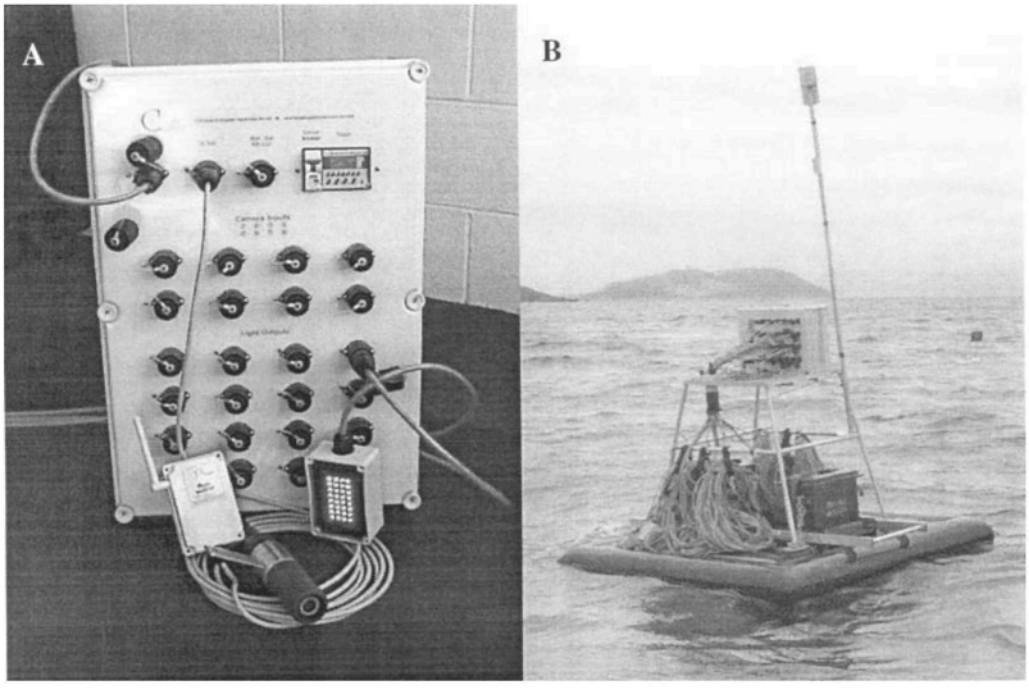

Fig. 2 **A**, Main multiplexer, power supply and timer unit with weatherproof connectors for camera inputs (eight connectors) power supply to lights (16 connectors) and multiplexer control, transmitter out and power in from batteries (one connector each). Also shown are a camera (lower centre) transmitter (lower left) and high-red light (lower right). **B**, Pontoon with light and camera cables coiled on frame ready for deployment. A moulded plastic hood covers the top of the system once deployment is complete.

protection and waterproofing, and connected to the pontoon system via a 30 m polyurethane-sheathed cable. Two of these lights were deployed with each camera and together are capable of effectively illuminating an area of seafloor not greater than 0.8 × 0.8 m from a distance of c. 0.8 m.

Camera and light cables are connected on the surface pontoon to a weatherproof housing (Fig. 2A) containing the camera power supply, a timer to allow lights to be switched on and off when appropriate, and a multiplexer. A duplex time-division multiplexer (AND MPC8DX) is central to the functioning of this system. The multiplexer receives the signals from up to eight cameras simultaneously, samples the video inputs from each camera sequentially, and interleaves sampled frames into one composite video signal. This coded signal from all cameras can then be recorded directly on a single recording medium, or transmitted to a remote monitoring station. To view the signal, whether live or from videotape, a decoding multiplexer reassembles the frames into single camera video streams. Images can be viewed with several cameras displayed on a split screen, or a single camera can be viewed in full-screen resolution. The penalty for using a multiplexed signal is that the frame rate from each camera is reduced to a degree defined by the number of cameras being monitored. For example, when recording 24 h of footage to a 3 h videotape with eight cameras connected, a frame is captured from each camera at c. 1 s intervals. Multiplexer settings, including individual camera brightness and contrast, frame capture rate, and on-screen displays can be adjusted using a laptop computer interfaced to the multiplexer via a weatherproof connector on the housing.

Power is provided to the system by 2 × 165 amp-h deep-cycle lead acid batteries (Trojan 5SHP) housed in waterproof boxes on the pontoon (Fig. 2B) connected in parallel. Batteries must be exchanged at intervals of 24 h. Solar panels could be used to extend time between battery changes although they would be susceptible to damage during system deployment. A low-voltage cutout unit is connected in series after the batteries. If circumstances such as poor weather do not allow for battery changes, this

prevents over-discharge and subsequent damage to the batteries.

The camera signals are transmitted to a remote monitoring station using a microwave video link operating in the 2.4 GHz license-free band. Output power is low (10 mW) and transmission range varies greatly depending on weather, location, and antenna type. With a directional parabolic antenna on the receiver, range may be up to 1.6 km. Although this short transmission range was suited to our application, a system with a range of in excess of 10 km could be built using a video server coupled with a wireless network hub. The remote monitoring station may be set up on a boat or on land, and consists of a video receiver, multiplexer to decode video signals, a monitor, and a recording device. Camera signals can be recorded using a 12 V time-lapse VCR (e.g., Mitsubishi HS-7424EDC) or similar digital device. Where there is no convenient site to establish a remote station, the signal can be recorded on the pontoon. This system has the disadvantage that access to the pontoon is required to change recording media.

The pontoon base was constructed from three squares, one inside another, of welded polyethylene tubing (250 mm diam., 12 mm wall thickness). The outer square has sides of 1.7 m. This provides sufficient buoyancy and stability to support the camera system and up to two people during battery changes and deployment. Cameras and lights are deployed by lowering them to the seafloor through a 0.3 × 0.3 m hole in the centre of the pontoon. An aluminium frame supports the weatherproof housing (and recording device if used) c. 1 m above the water surface. A plastic hood (not shown in Fig. 2B) is placed over the housing once the system is deployed. The pontoon is held in place and stabilised by three anchors connected by chain and rope to the sides of the pontoon. This prevents the pontoon from turning and tangling camera and light cables. The system can be deployed by three operators in a vessel as small as 7 m. Operators should consider the potential navigational hazard presented by the pontoon, and provide navigation lighting as prescribed by local regulations.

This system has the capacity to generate immense quantities of video data. For review purposes, a video signal splitter was built that enabled the signal to be fed to two multiplexers, and thus up to eight cameras could be viewed simultaneously on two split screens. When an event of interest occurred, single cameras were brought up in full screen view for detailed observation. Signals recorded in 24 h time-lapse were reviewed at standard video speed, thus taking a minimum of 3 h to review 24 h of footage from up to eight cameras.

System applications

Using this system we have observed and quantified behaviours and interactions between lobsters and predators that were previously unknown and difficult to observe by other methods. Oliver et al. (2005) monitored the fate of tethered lobsters, identifying major predators (Fig. 3A) and determining survival time and diel variations in predation rates. These same data were used to test the validity of tethering trials in determining spatial variability in survival rates (Gardner et al. 2004), and showed that without detailed information on predator suite composition, tethering results could be very misleading. Lobster catch rates in traps are routinely used as a measure of abundance for stock assessment purposes, and a simple linear relationship between catch and abundance is assumed. Green (2002) used this camera system to observe behaviour of lobsters in and around traps (Fig. 3B), and demonstrated that the trap catch was influenced by a complex mosaic of interactions before, during, and after entering a trap, with only 13% of the observed lobsters being caught. These experiments illustrate the versatility of the multi-camera approach, using the cameras to observe simultaneous experimental replicates (Oliver et al. 2005), or to build a composite picture of a larger area with images from several perspectives (Green 2002).

Different lighting sources were used in the two experiments. Green (2002) was interested in lobster behaviour and interactions between lobsters. The anatomy of *Jasus edwardsii* eyes is such that they are incapable of perceiving red light of wavelength greater than 600 nm (Meyer-Rochow & Tiang 1984). Accordingly, high-red lights were used without concerns about influencing behaviour. As the extinction of high-red light in water is substantially lower than that of infrared light (Kirk 1994), high-red lights provide brighter illumination than infrared lights for the same power consumption. Oliver et al. (2005) were interested in the behaviour of lobster predators including fish and octopus. The complex eyes of these predators can likely perceive high-red light, so infrared lights were used.

The versatility of this system will see it used in the near future in diverse projects observing octopus behaviour around lobster pots, predation on invading sea urchins, comparative behaviour of lobsters on natural and artificial reefs, and spawning behaviour in reef fishes. We believe that the use of video

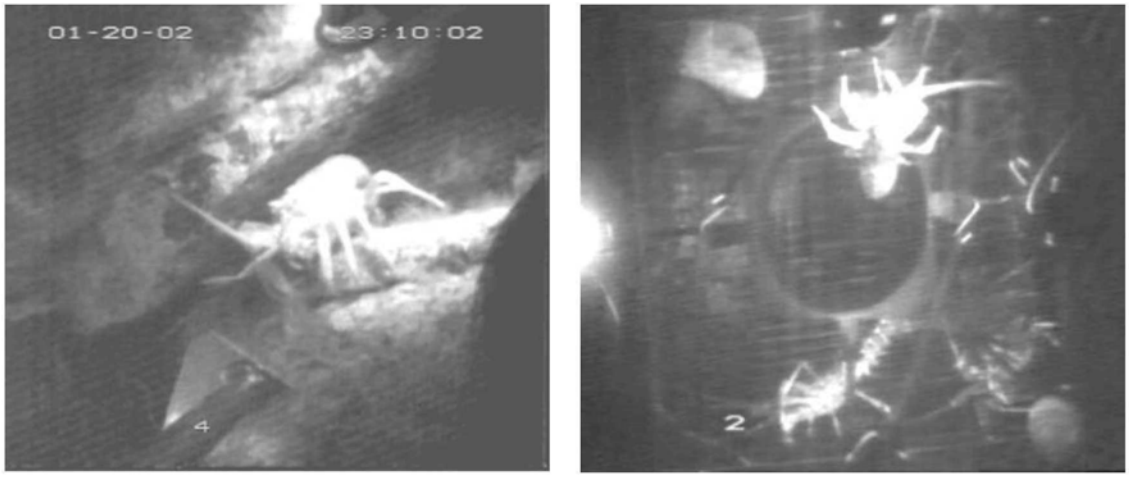

Fig. 3 **A**, Adult wild lobster observed at night under infrared light just after capturing a small tethered lobster. **B**, Lobster trap viewed from above at night using high-red light. One lobster is exiting the pot, while several other lobsters can be seen within the pot.

systems as described in this paper will become an integral component of research to address questions relating to ecosystem-based management and the effects of fishing on the marine environment.

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REFERENCES

Burrows, M. T.; Kawai, K.; Hughes, R. N. 1999: Foraging by mobile predators on a rocky shore: underwater TV observations of movement of blennies *Lipophrys pholis* and crabs *Carcinus maenas*. *Marine Ecology Progress Series 187*: 237–250.

Butler, M. J. 2003: Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit, individual-based approach. *Fisheries Research 65*: 63–79.

Chapman, C. J.; Howard, F. G. 1979: Field observations of the emergence rhythm of the Norway Lobster *Nephrops norvegicus*, using different methods. *Marine Biology 51*: 157–165.

Constable, A. 2001: The ecosystem approach to managing fisheries: achieving conservation objectives for predators of fished species. *CCAMLR Science 8*: 37–64.

Gardner, C.; MacDiarmid, A. B.; Mills, D. J.; Oliver, M. D.; Stewart, R. 2004: Evaluating the release and survival of juvenile rock lobsters released for enhancement purposes. Final report (FRDC 2000/185) to the Fisheries Research and Development Corporation, Australia. 145 p. (available from http://www.utas.edu.au/tafi/TAFI_Download.htm)

Green, N. 2002: Video analysis of the behaviour of the southern rock lobster *Jasus edwardsii* to traps. Unpublished Honours thesis, University of Tasmania, Australia. 112 p.

Jury, S. H.; Howell, H; O'Grady, D. F.; Watson, W. H. 2001: Lobster trap video: *in situ* video surveillance of the behaviour of *Homarus americanus* in and around traps. *Marine and Freshwater Research 52*: 1125–1132.

Kirk, J. T. O. 1994: Light and photosynthesis in aquatic ecosystems. England, Cambridge University Press. 509 p.

Meyer-Rochow, V. B.; Tiang, K. M. 1984: The eye of *Jasus edwardsii* (Crustacea, Decapoda, Palinuridae): electrophysiology, histology, and visual behavior. *Zoologica 45*: 1–85.

Mills, D. J.; Gardner, C.; Ibbott, S. 2004: Behaviour of ongrown juvenile spiny lobsters, *Jasus edwardsii* after reseeding to coastal reef in Tasmania, Australia. *In*: Leber, K. M.; Kitada, J.; Blackenship, H. L.; Svåsand, T. *ed.* Stock enhancement and sea ranching: developments, pitfalls and opportunities. London, Blackwell Scientific. Pp. 168–180.

Oliver, M. D.; Stewart, R.; Mills, D. J.; MacDiarmid, A. B.; Gardner, C. 2005: Stock enhancement of rock lobsters (*Jasus edwardsii*): timing of predation on naïve juvenile lobsters immediately after release. *New Zealand Journal of Marine and Freshwater Research 39*: 391–397.

Piraino, S.; Fanelli, G.; Boero, F. 2002: Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology 140*: 1067–1074.

Rutecki, T. L.; Schneeberger, P. J.; Jude, D. J. 1983: Diver and underwater television observations of fish behaviour in a Great Lakes commercial trap net. *Journal of Great Lakes Research 9*: 359–364.

Werner, F. E.; Quinlan, J. A.; Lough, R. G.; Lynch D. R. 2001: Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. *Sarsia 86*: 411–421.

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Effects of trap-shape, bait, and soak-time on sampling the eastern rock lobster, *Jasus verreauxi*

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Abstract It is important when analysing catch and effort information from either fishery-dependent or fishery-independent sources, to understand how external factors influence catches so that data can be standardised to be more representative of the abundance of the target species. In New South Wales, Australia, commercial fishers primarily use trapping as the method to capture the eastern rock (spiny) lobster (*Jasus verreauxi*) and consider trap-shape, bait-type, and soak-time to be the most important factors affecting their catches. Two experiments were done to test hypotheses about the influence of these factors upon catches of lobsters on inshore grounds (<15 m depth). There were no differences in mean numbers caught between bait-types (flathead, redfish, or blackfish) and soak-times (1–3 days), but trap-shape (beehive, rectangular, or "D"-shaped) affected catches. D-shaped and rectangular traps caught more lobsters than beehive traps. There were no differences in the sizes of lobsters caught between trap-shapes and the sex ratios did not differ from unity, suggesting that there were no differences in selectivity between trap-shapes. It is recommended that the compulsory daily log sheets in place in the fishery require commercial fishers to provide information about the shape of the traps they use. When designing fishery-independent surveys to sample juvenile *J. verreauxi*, it is recommended that: (1) groups of rectangular traps be set as a single replicate to saturate a defined area; (2) as many replicates as practically possible be included; (3) any of the bait-types described in this paper be used; and (4) the soak-time for the gear be one day.

Keywords trap-shape; bait; soak-time

INTRODUCTION

Catch and effort information are used to calculate indices of relative abundance (catch-per-unit-effort, CPUE) and as such are fundamental to the assessment of populations in which the numbers of individuals cannot be directly counted (e.g., Pennington 1986; Richards & Schnute 1992). It is important that the index of relative abundance be standardised so that differences in fishing methods do not bias the time series of information and that this series remains as consistent in proportion to the abundance of the target species in the wild as is possible (e.g., Kimura 1981). Although quantifying and standardising catch is usually straightforward, methods to standardise effort are not. The efficiency of a unit of effort to take catch may depend upon factors relating to the fishing strategy, the environment, the behaviour of the target species, or any combination of these (e.g., Kennelly & Craig 1989; Godo & Sunnana 1992; Otway et al. 1996). Ideally, fishing effort used for stock assessment purposes should be uniform, unbiased, optimal with respect to catch, and replicated in space and time so as to consider the above variables.

Studies to assess methods which are used to catch commercially important marine species have been completed in many fisheries (see reviews by: Sissenwine 1983; Gunderson 1993). Although several papers have assessed the effect of external factors on catches of various species of decapods in

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traps (e.g., Krouse 1989; Miller 1990), few have been published about the effect of such factors upon catches of spiny lobsters. Literature regarding trapping decapods identifies several factors that may influence catches, including trap-shape and size, bait-type, competition between traps, and the soak-time of traps (duration of time between setting and hauling a trap).

There is little information about the effect of trap-shape on catches of marine species, perhaps because this effect is often confounded with that of factors such as the position of the trap entrance. Trap size can affect catch rates by influencing the density of animals in the trap (Munro 1974; Crossland 1976; Miller 1978; Sheaves 1995). The size of traps used in the experiments described in this paper was restricted by the requirement that traps be small enough to be wedged between rocks and crevices on shallow vegetated reefs and be able to withstand sea swell. Bait type may affect catches as target species are attracted to the odours of some species more than others (e.g., Krouse 1989; Whitelaw et al. 1991; Furevik & Lokkeborg 1994). Generally, the relationship between catch and soak-time for traps is curvilinear. The numbers of individuals caught in a trap increases with soak-time to a maximum; at longer soak-times numbers either remain around the maximum or decline (e.g., Munro 1974; Austin 1977; Miller 1978, 1983b, 1990; Kennelly 1989; Whitelaw et al. 1991; Sheaves 1995).

The eastern rock (spiny) lobster, *Jasus verreauxi* (Milne-Edwards 1851), occurs in waters off the east coast of Australia from Tweed Heads (28°S) to Tasmania (42°S), and as far west into Bass Strait as Port MacDonnell (140°E) (Fig. 1 insert). It is also found in New Zealand waters, principally off the North Island. The commercial fishery for this species in waters off New South Wales, Australia, is small by international standards with landings of c. 150 t per annum, but it is one that targets a highly priced species (c. AU$45 per kg) that is considered a "boutique" seafood. The fishery extends from the shoreline to waters of c. 220 m depth and can be partitioned into inshore (0.5–15 m), mid shelf (16–100 m), and deep grounds (>100 m) (Montgomery 1998). There is no published information about the effects of external factors upon catches of *J. verreauxi* in traps. This paper considers only the gear used on inshore grounds. The inshore fishery operates year round on shallow, vegetated reef habitat. Fishers use traps of various designs (Fig. 2) with top or side entrances and which are restricted by regulations to having a base with a length or diameter no longer than 1.2 m. They use fresh bait and fish the gear with soak-times of usually less than 3 days.

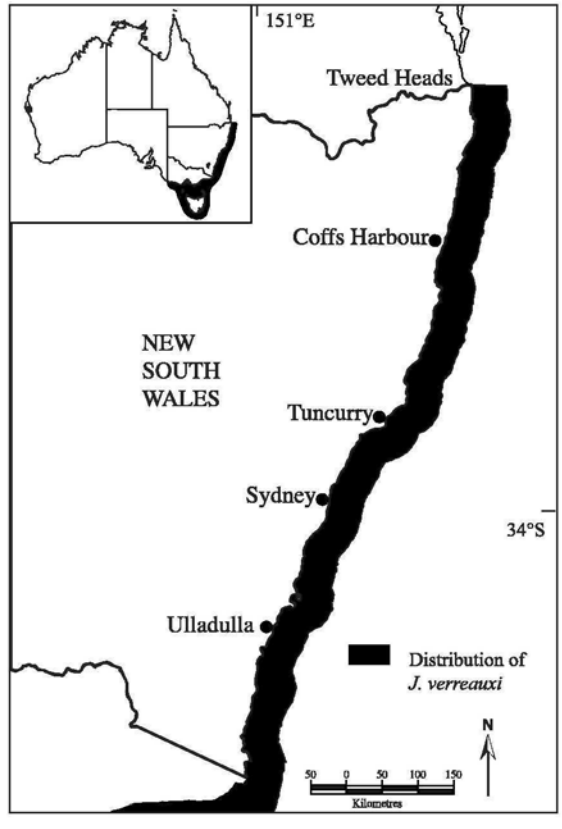


Fig. 1 Distribution of *Jasus verreauxi* off Australia (insert) and New South Wales. Map of New South Wales shows the locations of experiments to investigate the effects of external factors on catches of juvenile *J. verreauxi* in traps on inshore grounds.

This paper describes manipulative experiments done to assess the effects of trap-shape, bait-type, and soak-time upon catches of *J. verreauxi* in traps on inshore grounds. Results from these experiments were used in designing a full-scale sampling strategy to do fishery-independent surveys of juvenile *J. verreauxi* and also provided valuable information for interpreting and standardising fishery-dependent catch and effort information.

MATERIALS AND METHODS

The only trap-shapes, soak-times, and bait-types assessed in experiments were those most commonly used by the commercial fishers in the fishery. This

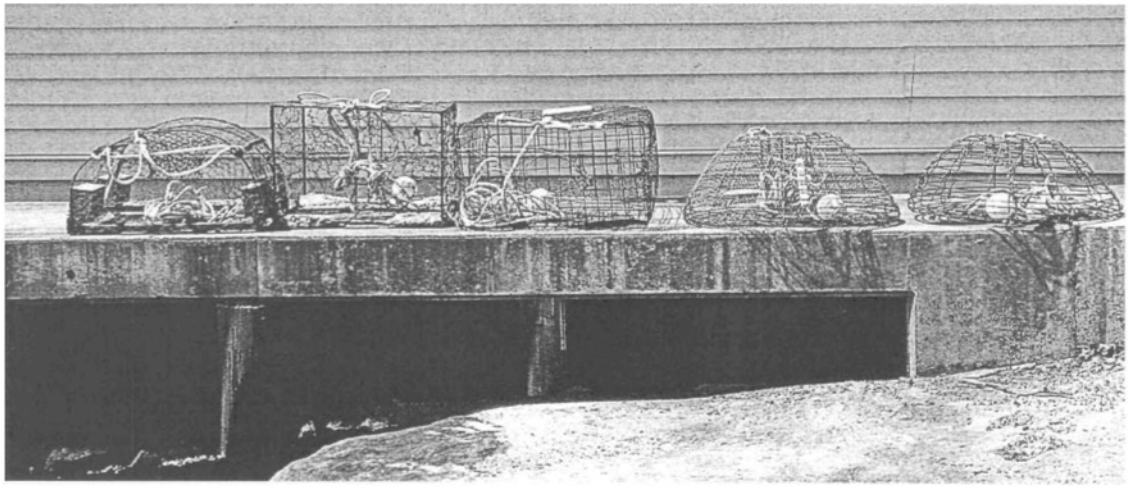


Fig. 2 Examples of D-shaped (left), rectangular (centre), and beehive traps (right) used by commercial fishers and in experiments described in this study.

approach meant that the results would have relevance when interpreting catch and effort data from the fishery. Experiments were done on grounds in waters less than 15 m deep to test the general hypothesis that catches of lobsters differed between trap-shapes, bait-types, and soak-times.

Experiment 1

The experiment was done off Port Hacking on the coast of New South Wales (Fig. 1). Fixed factors were Trap-Shape (beehive or D-shaped traps), Bait-Type (flathead, *Neoplatycephalus* sp. or redfish, *Centroberyx affinis*), and Soak-Time (1, 2, or 3 days). Beehive traps had a base with a diameter 750 mm from which 27 equally spaced semicircular ribs rose. Wire bands were woven between the ribs so that there was a gap of c. 37 mm between each band. The height from the base to the top of the trap was 280 mm. The D-shaped traps consisted of a frame made up of three semicircular hoops that were attached to a base of 800 mm by 700 mm with a covering of 35 mm wire mesh. A round entrance of 184 mm internal diameter was set in the top of each beehive and D-shaped trap. D-shaped traps were weighted by a (5 kg) house brick in each of the four corners of the base of the trap, whereas beehive traps had a 5 kg piece of iron attached to the centre of the base inside the trap. Each trap in the experiment had 6 m of 4 mm diameter rope with a float of 100 mm diameter to mark its position at the surface.

Fresh pieces of bait of either species were packed into 23 cm × 19 cm bait bags made of 10 mm wire mesh. A bait bag was secured inside each trap so that it lay against the inside of the neck of traps. Three replicates of each treatment (a total of 36 traps) were set in a random order by a chartered commercial fisher and then were hauled aboard the commercial fishing vessel at the assigned Soak-Time. Each lobster caught in a trap had its gender determined and carapace length (CL) measured. The experiment was repeated to give a total of 6 replicates for each treatment.

Experiment 2

The hypothesis that trap-shape affects catches of lobsters was tested at three locations: Coffs Harbour, Tuncurry, and Ulladulla (Fig. 1). D-shaped traps were replaced with rectangular traps because the former lost shape during heavy sea-swells and so could not be relied upon as a standard unit of sampling for the purposes of fishery-independent surveys. Ten replicate groups of four beehive and four rectangular traps were set on each of three occasions between August and November at each location. Beehive traps were the same as used in Experiment 1 whereas the rectangular traps were made of a 6 mm rio-steel frame of 800 × 700 × 400 mm and covered with 50 mm wire mesh. All rectangular traps had an entrance of 179 mm internal diameter on each of three sides and were weighted by attaching a house brick in each of the four corners of the base of each trap. Each trap contained a bait bag filled with pieces of blackfish (*Girella tricuspidata*) and was connected to a 100 mm diameter

polystyrene float at the surface by 6 mm diameter polyethylene rope.

The gear was set by a chartered commercial fisher at each location and in an attempt to overcome the patchy distribution of *J. verreauxi*, replicate groups of traps were set so that neighbouring traps in a group were no closer to one another than 5 m and all traps in the group were within a 1000 m^2 area. The gear was set one day, left overnight, and then lifted the next day (defined as a day for the purposes of this paper). Results from Experiment 1 suggested that there were no significant increases in catch for longer soak-times. There was also a risk of lobsters being pilfered if traps were left unattended for more than one night on inshore grounds.

Each lobster caught had its gender determined and length measured (CL in mm). The numbers of lobsters caught in a group of gear were then summed for each trap type to create a total of 20 replicate observations for each treatment.

Data analyses

Experiment 1 was used to evaluate the effects of trap-shape, bait, and soak-time upon catches whereas Experiment 2 examined only trap-shape. For both experiments, homogeneity of variance was evaluated with Cochran's test and then analysis of variance was used to test for differences in mean numbers. Patterns in mean numbers between treatments were detected by using the Student Newman Keul's test (SNK test; Underwood 1997). A chi-square test was used to detect deviations from unity in the sex ratio in each treatment. Lengths of lobsters were compared between treatments by using one-way analysis of variance to test for differences in means and by using the Kolmogorov-Smirnov Two-Sample Test (Siegel & Castellan 1988) to test for differences in the shape of the length distributions.

RESULTS

Experiment 1

A total of 439 lobsters were caught during the experiment. More lobsters were caught in D-shaped traps than in beehive traps (SNK tests, Table 1; Fig. 3A), and neither Bait-Type nor Soak-Time affected the mean numbers of lobsters caught in traps (Table 1; Fig. 3B,C).

The sex ratio of lobsters in traps did not vary from 1:1 ($\chi^2_1 = 1.20$ $P < 0.25$ for beehives and $\chi^2_1 = 0.18$ $P < 0.5$ for D-shaped traps, respectively). Neither the mean length of lobsters nor the shape of the length

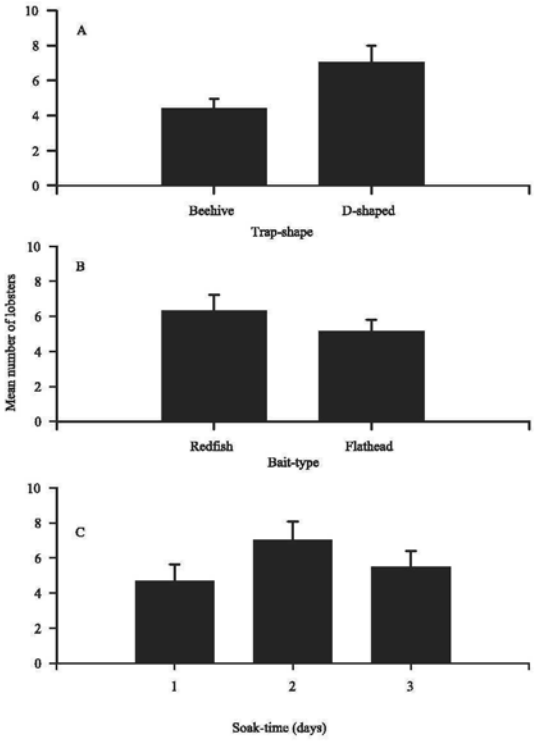


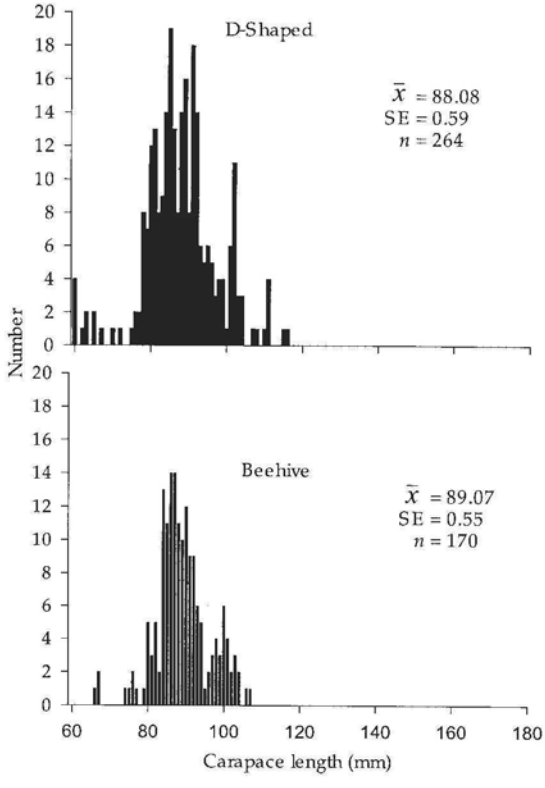
Fig. 3 Comparison of mean catches (+SE) of *Jasus verreauxi* per trap lift on inshore grounds between: **A**, Trap-Shape; **B**, Bait-Type; and **C**, Soak-Time used in Experiment 1.

Table 1 Analyses of catches of *Jasus verreauxi* on inshore grounds in Experiment 1. Residual degrees of freedom have been reduced by 2 to account for missing values. (NS, not significant ($P > 0.05$); Cochran's test, $C = 0.18$ NS.)

Source of variation	d.f.	MS	*F*	*P*
Trap-Shape = T	1	127.86	5.04	$P < 0.05$
Bait-Type = B	1	0.90	0.04	NS
Soak-Time = S	2	33.59	1.32	NS
T×B	1	5.12	0.20	NS
T×S	2	2.36	0.09	NS
B×S	2	7.13	0.28	NS
T×B×S	2	8.76	0.35	NS
Residual	58	25.39		

SNK Comparisons of mean (SE) of significant sources of variation ($P = 0.05$) (=, equal; >, greater than; <, less than.)

	Beehive		D-shaped
Trap-Shape:	4.38 (0.59)	<	7.04 (0.95)



distributions differed between treatments (Tables 2 and 3; Fig. 4).

Experiment 2

A total of 266 lobsters were caught across all treatments. There was no interaction between Trap Shape and Location suggesting that the same patterns in catches between trap-shapes occurred at each location (Table 4). Rectangular traps caught more lobsters than did beehive traps (Fig. 5; Table 4) and more lobsters were caught off Coffs Harbour and Tuncurry than off Ulladulla.

The sex ratio of lobsters in traps did not vary from 1:1 ($\chi^2_1 = 0.87$ $P < 0.5$ and 1.79 $P < 0.1$ for beehive and rectangular traps off Coffs Harbour; $\chi^2_1 = 0.22$ $P < 0.5$ and 1.42 $P < 0.1$ for beehive and rectangular traps off Tuncurry; $\chi^2_1 = 0.1$ $P < 0.25$ and 0.4 $P < 0.5$ for beehive and rectangular traps off Ulladulla). Mean length did not differ between trap-shapes at any location but there were differences in the shape of the length distributions at Coffs Harbour and

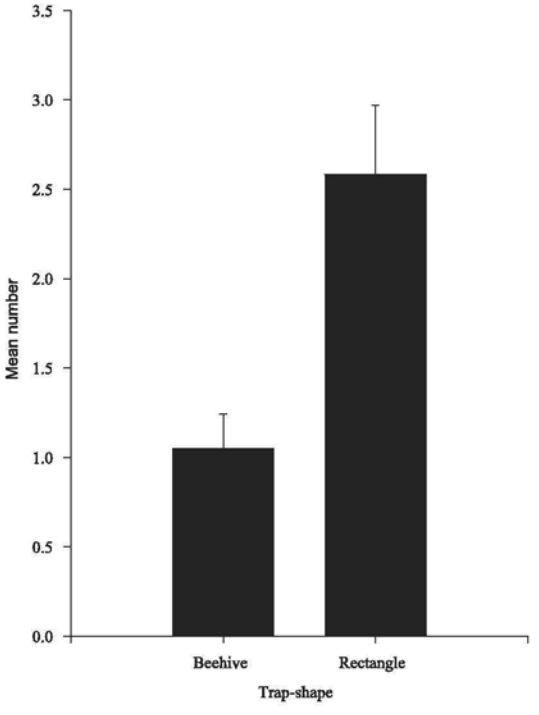
Fig. 4 Length distributions of *Jasus verreauxi* caught on inshore grounds in each Trap-Shape used in Experiment 1. Mean ($\bar{x}$), standard error (SE), and sample size (n) are shown.

Table 2 Analysis of variance of mean lengths of *Jasus verreauxi* on inshore grounds between treatments in Experiments 1. (NS, not significant ($P > 0.05$); Cochran's test, $C = 0.34$ NS.)

Source of variation	d.f.	MS	F	P
Trap-Shape = T	4	100.65	1.49	NS
Residual	318	67.77		

Table 3 Kolmogorov-Smirnov tests to compare distributions of lengths of *Jasus verreauxi* between treatments in Experiment 1. Shown are the calculated $D_{max.}$ values and the sample sizes for m and n. Critical P values have been bonferronised to allow for 6 pair-wise comparisons at a nominal probability of Type I error, $p < 0.05$ (Miller 1966). (b, beehive trap; d, D-shaped trap; f, flathead bait; r, redfish bait. NS, Not significant ($P > 0.05$).)

	b,f versus d,f	b,f versus b,r	d,f versus b,r	b,f versus d,r	d,f versus d,r	b,r versus d,r
m,n	90,151	90,80	151,80	90,112	151,112	80,112
$D_{m,n}$	0.13	0.09	0.10	0.20	0.07	0.16
	NS	NS	NS	NS	NS	NS



Ulladulla (Tables 5 and 6; Fig. 6). At these locations, rectangular traps contained more lobsters in the longer length classes than did beehive traps (Table 6). When data were pooled across trap-shapes to compare lengths of lobsters between locations, there were differences in the shape of the length distributions between all locations (Table 8) and the mean length was shorter off Ulladulla than at the other locations (Table 7). There were no differences in mean length between Coffs Harbour and Tuncurry.

Fig. 5 Comparisons of mean numbers (+SE) of *Jasus verreauxi* per trap lift on inshore grounds between Trap-Shapes in Experiment 2. Data are for a balanced subset of catches from each type of gear ($n = 20$).

Table 4 Analysis of catches of *Jasus verreauxi* between Trap-Shapes on inshore grounds in Experiment 2 at Coffs Harbour (CH), Tuncurry (T), and Ulladulla (U), Australia. Data were transformed ($\sqrt{(x+1)}$) to stabilise variances. (NS, not significant ($P > 0.05$); Cochran's test, $C = 0.24$ NS.)

Source of variation	d.f.	MS	*F*	*P*
Trap-Shape = T	1	6.55	15.57	$P < 0.01$
Location = L	2	1.96	4.67	$P < 0.05$
T×L	2	0.93	2.21	NS
Residual	114	0.42		

SNK comparisons of mean numbers (SE) for Locations and Trap-Shape. (=, equal; >, greater than; <, less than.)

	Rectangle				Beehive
Trap-Shape:	2.58 (0.39)			>	1.05 (0.19)
	CH		T		U
Location	1.78 (0.41)	=	2.58 (0.45)	>	1.10 (0.27)

Table 5 Analysis of variance of mean lengths of *Jasus verreauxi* on inshore grounds between Trap-Shapes in Experiment 2. (NS, not significant ($P > 0.05$); Cochran's test, $C = 0.64$ NS.)

Source of variation	d.f.	MS	*F*	*P*
Trap-Shape = T	1	393.75	1.63	NS
Residual	26	241.24		

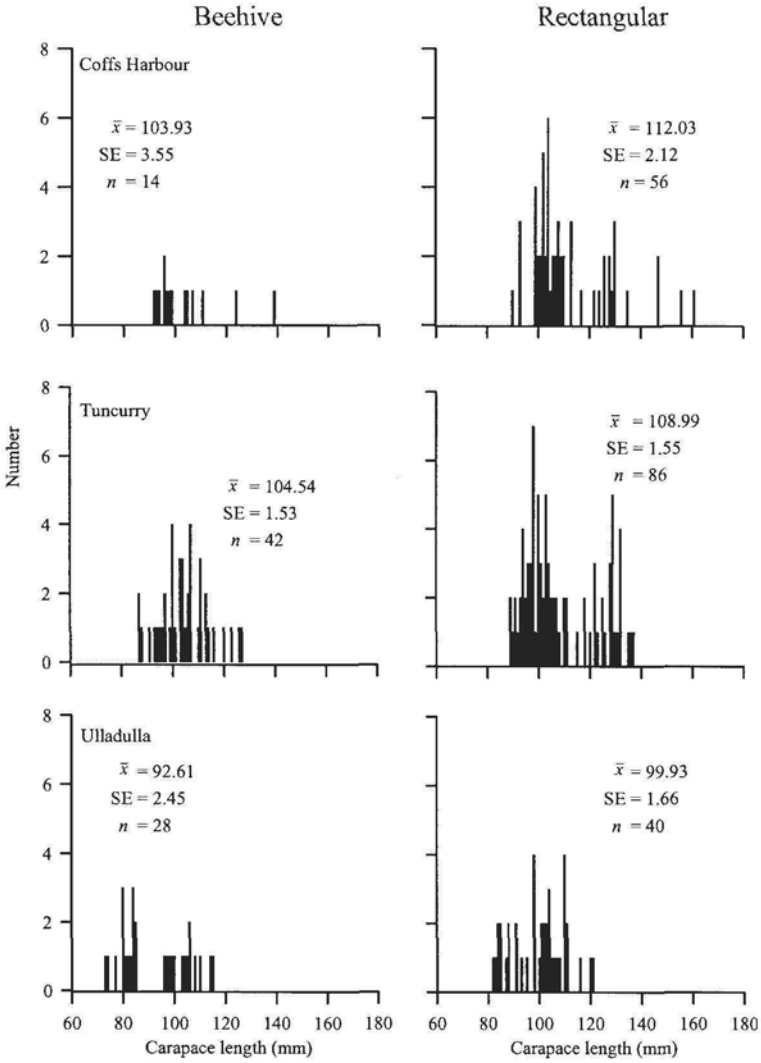


Fig. 6 Length distributions of *Jasus verreauxi* caught on inshore grounds in each Trap-Shape used in Experiment 2. The mean ($\bar{x}$), standard error (SE), and sample size (n) are shown.

Table 6 Kolmogorov-Smirnov tests to compare distributions of lengths of *Jasus verreauxi* between treatments in Experiment 2. Shown are the calculated $D_{max.}$ values, the sample sizes for m and n, and the critical P values. (NS, not significant $P > 0.05$.)

	Coffs Harbour b versus r	Tuncurry b versus r	Ulladulla b versus r
m,n	14,56	42,86	28,40
$D_{m,n}$	0.43	0.23	0.35
	$P > 0.01$	NS	$P > 0.01$

Table 7 Analysis of variance of mean lengths of *Jasus verreauxi* on inshore grounds between locations in Experiment 2. (Cochran's test, $C = 0.24$ not significant.)

Source of variation	d.f.	MS	F	P
Location = L	2	3669.12	18.99	$P < 0.05$
Residual	201	193.21		

SNK comparisons of mean lengths (SE) for Locations. (=, equal; >, greater than; <, less than.)

	CH		T		U
Location	110.75 (1.91)	=	108.10 (1.66)	>	96.91 (1.46)

Table 8 Kolmogorov-Smirnov tests to compare distributions of lengths of *Jasus verreauxi* between locations in Experiment 2. Shown are the calculated $D_{max.}$ values and the sample sizes for m and n. Critical P values have been bonferronised to allow for 6 pair-wise comparisons at a nominal probability of Type I error, $P < 0.05$ (Miller 1966).

	T versus U	T versus C	U versus C
m,n	149,111	149, 107	111, 107
$D_{m,n}$	0.23	0.24	0.22
	< 0.05	$P < 0.05$	$P < 0.05$

DISCUSSION

Results in this study showed that catches of *J. verreauxi* in traps were unaffected by bait-type and soak-times up to 3 days, but were influenced by trap-shape. This information shall contribute towards the designing of an optimal sampling strategy for doing fishery-independent surveys of juvenile *J. verreauxi* on inshore grounds and interpreting catch and effort information from the fishery.

Experiments showed that lobsters entered traps with either top (beehive or D-shaped traps) or side (rectangular) entrances. The results suggested that trap-shape should be considered when interpreting catch and effort data from fishery-dependent sources. Beehive traps caught fewer lobsters than either D-shaped or rectangular traps. It is recommended for fishery-independent surveys that rectangular traps be used. Rectangular traps caught more lobsters at each location than beehives, did not change shape during heavy seas like the other gears and so can be considered the most consistent trap gear available.

Although professional fishers have vast knowledge about how best to catch target species, their personal preferences toward certain pieces of gear may not always be the most appropriate for use in fishery-independent surveys. For example in this study, commercial fishers at some ports preferred to use beehive traps, claiming they caught more lobsters than other trap-shapes and were easy to handle. Whereas rectangular traps may have been slightly more difficult to handle, they caught more lobsters, even in areas where commercial fishers thought that beehive traps would catch best.

Results suggested that soak-times of between 1 and 3 days did not affect catches. The pattern in Fig. 3C suggests that the traps become saturated between 1 and 2 days and this is supported by preliminary experiments when soak-times of up to 5 days were tested (Montgomery 1998). Studies on trapping marine decapods have suggested optimal soak-times of 1 h for *Ranina ranina* (Kennelly 1989), 1 day or less for *Homarus gammarus* and *H. americanus* (Bennett 1974; Miller & Rodger 1996), and up to 4 days for *Chionoecetes opilio* (Miller 1983a). A soak-time of 1 day is recommended for fishery-independent surveys of *J. verreauxi* on inshore grounds for cost benefit reasons and to reduce the risk of theft.

The patchy distribution of *J. verreauxi* is typical of palinurids and of many other populations in the

wild (e.g., Polacheck & Volstad 1993; Rosenberg et al. 1995). To address such distributions when doing manipulative experiments such as those in this study, it is advisable to do preliminary work to find grounds with sufficient uniformity in the distribution of lobsters so as to minimise variability between replicates. This was done before the experiments described in this study were completed. Successful attempts were made in these experiments to further minimise the variability between replicates by repeating experiments (Experiments 1 and 2) and by saturating areas with traps (Experiment 2).

In each experiment the sex ratio of trapped *J. verreauxi* remained around unity but sizes differed between trap-shapes in Experiment 2. At two locations, rectangular traps caught more longer lobsters than beehive traps suggesting that size selectivity is affected by trap-shape. Confounding this however, is the fact that the entrance position and number were not considered in this study as factors that affect catch. Further research would be needed to determine whether the differences in size selectivity are caused by entrance position and number, or trap-shape. The ratio of genders in juvenile palinurids in traps typically remains around unity until sexual maturity is reached, after which growth and behavioural patterns can affect the sex ratio and sizes of lobsters in catches (Cobb & Wang 1985).

Differences in the sizes of *J. verreauxi* between locations are also typical of palinurids (e.g., Aiken 1980; Pollock 1991). The differences in sizes between locations found in this study are consistent with the patterns in sizes of *J. verreauxi* recruits (puerulus stage to early juvenile stages, Montgomery 2000, 2005). Possible explanations for these spatial differences in lengths are differences in rates of growth, rates of survival, or patterns of behaviour. Growth and survival of other species of palinurids are affected by changes in environmental conditions and the supply of food. Generally, rates of growth are faster in warmer than in cooler waters (Chittleborough 1975; Lipcius & Herrnkind 1986). Certainly, the oceanic water is warmer in the north off New South Wales (Cresswell & Legeckis 1986) where the largest lobsters were found. Warmer waters may induce faster growth resulting in lobsters of the same age being longer in northern than southern waters. Hence, although lobsters may first enter traps at around the same age, those in northern waters will be longer than those in southern waters.

These experiments provided some of the information necessary to design a standardised sampling strategy for fishery-independent surveys to estimate abundances of juvenile *J. verreauxi* on shallow grounds. When designing these surveys, consideration needs to be given to addressing the patchy distribution of *J. verreauxi*. This consideration should include the approaches of high levels of replication; adjusting the number of replicates in an area to the variance between replicates (e.g., Gunderson 1993) or to the density of lobsters (e.g., Jolly & Hampton 1990); saturating defined areas with traps as a single replicate and the use of adaptive cluster sampling (Thompson & Seber 1996). The design of fishery-independent surveys for juvenile *J. verreauxi* should include grouping rectangular traps as a single replicate, and although it is preferable to keep bait-type and soak-time standard, changes in bait between the types used in this study and changes in soak-time between 1 and 3 days should not appreciatively change the standardisation of the sampling. Furthermore, when fishery-dependent data are being interpreted, data need to be standardised for differences in efficiency between trap-shapes.

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REFERENCES

Aiken, D. E. 1980: Molting and growth. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. Vol I. New York, Academic Press. Pp. 91–163.

Austin, C. B. 1977: Incorporating soak-time into measurement of fishing effort into trap fisheries. *Fisheries Bulletin (US) 75*: 213–218.

Bennett, D. B. 1974: The effects of pot immersion time on catches of crabs, *Cancer pagurus* L. and lobsters, *Homarus gammarus* (L.). *Journal du Conseil International pour l'Exploration de la Mer 35*: 332–336.

Chittleborough, R. G. 1975: Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). *Australian Journal of Marine and Freshwater Research 26*: 177–196.

Cobb, J. S.; Wang, D. 1985: Fisheries biology of lobsters and crayfishes. *In*: Bliss, D. E *ed.* The biology of Crustacea. Vol 10. Orlando, Academic Press Inc. Pp. 167–247.

Cresswell, G. R.; Legeckis, R. 1986: Eddies of southeastern Australia. *Deep-Sea Research 33*: 1527–1562.

Crossland, J. 1976: Fish trapping experiments in northern New Zealand waters. *New Zealand Journal of Marine and Freshwater Research 10*: 511–516.

Furevik, D. M.; Lokkeborg, S. 1994: Fishing trials in Norway for Torsk (*Brosme brosme*) and cod (*Gadus morhua*) using baited traps. *Fisheries Research 19*: 219–229.

Godo, O. R.; Sunnana, K. 1992: Size selection during trawl sampling of cod and haddock and its effect on abundance indices at age. *Fisheries Research 13*: 293–310.

Gunderson, D. R. 1993: Surveys of fisheries resources. New York, John Wiley & Sons. 232 p.

Jolly, C. M.; Hampton, I. 1990: A stratified random transect design for acoustic surveys of fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences 47*: 1282–1291.

Kennelly, S. J. 1989: Effects of soak-time and spatial heterogeneity on sampling populations of spanner crabs *Ranina ranina*. *Marine Ecology Progress Series 55*: 141–147.

Kennelly, S. J.; Craig, J. R. 1989: Effects of trap design, independence of traps and bait on sampling populations of spanner crabs *Ranina ranina*. *Marine Ecology Progress Series 51*: 49–56.

Kimura, D. K. 1981: Standardised measures of relative abundance based upon modelling log (c.p.u.e.), and their application to Pacific ocean perch (*Sebastes alutus*). *Journal du Conseil International pour l'Exploration de la Mer 39*: 211–218.

Krouse, J. S. 1989: Performance and selectivity of trap fisheries for crustaceans. *In*: Caddy, J. F. *ed.* Marine invertebrate fisheries: their assessment and management. New York, John Wiley & Sons. Pp. 307–325.

Miller, R. J. 1978: Saturation of crab traps: reduced entry and escapement. *Journal du Conseil International pour l'Exploration de la Mer 38*: 338–345.

Miller, R. J. 1983a: How many traps should a crab fisherman fish? *North American Journal of Fisheries Management 3*: 1–8.

Miller, R. J. 1983b. Considerations for conducting field experiments with baited traps. *Fisheries 8*: 14–17.

Miller, R. J. 1990. Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences 47*: 1228–1251.

Miller R. J.; Rodger, R. S. 1996: Soak times and fishing strategy for American lobster. *Fisheries Research 26*: 199–205.

Montgomery, S. S. 1998: Relative abundance of the eastern rock lobster, *Jasus verreauxi*. Unpublished PhD thesis, University of Sydney, Australia.

Montgomery, S. S. 2000: Effects of nearness to reef and exposure to sea-swell on estimates of relative abundance of *Jasus verreauxi* (H. Milne-Edwards, 1851), recruits on collectors. *Journal of Experimental Marine Biology and Ecology 225*: 175–186.

Montgomery, S. S.; Craig, J. R. 2005: Distribution and abundance of recruits of the eastern rock lobster *Jasus verreauxi* along the coast of New South Wales, Australia. *New Zealand Journal Marine and Freshwater Research 39*: 619–628.

Munro, J. L. 1974: The mode of operation of antillean fish traps and the relationships between ingress, escapement, catch and soak. *Journal du Conseil International pour l' Exploration de la Mer 35*: 337–350.

Otway, N. M.; Craig, J. R.; Upston, J. M. 1996: Gear-dependent size selection of snapper, *Pagrus auratus*. *Fisheries Research 28*: 119–132.

Pennington, M. 1986: Some statistical techniques for estimating abundance indices from trawl surveys. *Fishery Bulletin 84*: 519–525.

Polacheck, T.; Volstad, J. H. 1993: Analysis of spatial variability of Georges Bank haddock (*Melanogrammus aeglefinus*) from trawl survey data using a linear regression model with spacial interaction. *ICES Journal of Marine Science 50*: 1–8.

Pollock, D. E. 1991: Spiny lobsters at Tristan Da Cunha, South Atlantic: inter-island variations in growth and population structure. *South African Journal of Marine Science 10*: 1–12.

Richards, L. J.; Schnute, J. T. 1992: Statistical models for estimating CPUE from catch and effort data. *Canadian Journal of Fisheries and Aquatic Sciences 49*: 1315–1327.

Rosenberg, D. K.; Overton, S. W.; Anthony, R. G. 1995: Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management 59*: 252–261.

Sheaves, M. J. 1995: Effect of design modifications and soak-time variations on antllean-Z fish trap performance in a tropical estuary. *Bulletin of Marine Science 56*: 475–489.

Siegel, S.; Castellan, N. J. 1988: Non parametric statistics for behavioural sciences. New York, McGraw-Hill. 399 p.

Sissenwine, M. P.; Azarovitz, T. R.; Suomala, J. B. 1983: Determining the abundance of fish. *In*: MacDonald, A. G.; Priede, I. G. *ed.* Experimental biology at sea. New York, Academic Press. Pp. 51–101.

Thompson, S. K.; Seber, G. A. F. 1996: Adaptive sampling. New York, John Wiley & Sons. 265p.

Underwood, A. J. 1997: Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge, Cambridge University Press. 504 p.

Whitelaw, A. W.; Sainsbury, K. J.; Dews, G. J.; Campbell, R. A. 1991: Catching characteristics of four fish-trap types on the north west shelf of Australia. *Australian Journal of Marine and Freshwater Research 42*: 369–382.

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Effect of reproductive state and sex on movement and food consumption of western rock lobster (*Panulirus cygnus*) in a tank environment

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Abstract The catchability of western rock lobsters (*Panulirus cygnus*) during the spawning season (October and November) may be affected by their reproductive state. In this study, movement and food consumption of males and females of different reproductive states held in laboratory tanks were measured as proxies for catchability. Density of lobsters was found to influence both movement and food consumption. Solitary animals and, to a lesser extent, two lobsters per tank, were more sedentary and consumed significantly less food than animals at a density of three or four specimens per tank. Tests using three animals per tank confirmed that mature, unmated, and ovigerous females carrying early stage eggs moved more frequently away from their shelters than males or females carrying late stage eggs ($P < 0.0001$, d.f. = 3). Further, unmated females and females with early stage eggs recorded significantly higher food consumption ($P < 0.0061$, d.f. = 3) compared with males or females carrying late stage eggs. The greater time spent away from shelter and also food consumption make unmated females and females with early stage eggs likely to be more catchable than males or females with late stage eggs. As catchability is commonly used to obtain population estimates from survey data, these results have implications for surveys which use catch rates of breeding animals as indicators of egg production.

Keywords *Panulirus cygnus*; western rock lobster; movement; food consumption; reproductive state; density; catchability

INTRODUCTION

Catchability is an important parameter used to measure stock length structure and/or biomass from catch data (Bowen & Chittleborough 1966), the assumption being that the probability of an animal being caught by an applied unit of effort remains constant over time (Morgan 1974). Changes in catch rates of animals may result from either: (1) changes in abundance of the animals; (2) changes in the way animals respond to the unit of effort; or (3) changes in the effectiveness of the effort (Morgan 1974). Knowing the changes in behaviour of the lobsters and how these changes affect their catchability is important in predicting changes in population abundance of the species.

Breeding of western rock lobsters (*Panulirus cygnus* George) occurs during the spring and summer (September–December) (Chittleborough 1976). Mature, adult females moult in June/July just before mating. During this moult, females develop setae on the endopodites of their pleopods (Chittleborough 1976). These setae hold the fertilised eggs to the underside of the female's abdomen. The presence of these setae indicate a female that is sexually mature (Chittleborough 1976). Frequency of spawning in *P. cygnus* is size dependent, with larger mature females

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commonly spawning twice in a season, compared with one spawning per season common amongst smaller, mature females (Chittleborough 1976). Following spawning, females moult again in January/February (Gray 1992). It is during this moult that setae are lost from the pleopods (Gray 1992). As females do not moult following male deposition of the spermatophore on their sternal plate, one spermatophore may be used to fertilise eggs from successive broods released in one breeding season.

In *P. cygnus*, there is particular relevance in having knowledge of female catchability in different breeding states because indices which are used to monitor the state of egg production in the fishery are based on the catch rates of mature, often ovigerous, animals (Chubb 1991; Phillips & Melville-Smith 2003). Changes in catchability with reproductive state would have the potential to distort the number of mature females in the population, leading to an incorrect estimation of egg production in the population.

Catchability of a lobster presumably is related to the probability of a lobster encountering a trap, followed by its entry and retention within the trap. This study used movement and food consumption of lobsters in a tank environment to estimate foraging activity hence the possible impact on catchability of lobsters in the wild. Traps in the *P. cygnus* fishery are set amongst the reefs and seagrass beds where lobsters are known to forage (Jernakoff & Phillips 1988). Foraging activity is closely related to catchability of *P. cygnus* as it is during the times a lobster is foraging that it is caught in a lobster trap. Movement is related to foraging activity, as those lobsters with greater movement in the tank environment will presumably display greater movement in the wild, hence their foraging activity and chance of encountering a lobster trap will increase. Food consumption is related to the lobsters desire for food (Branford 1979). Those lobsters with a greater desire for food will forage more in the wild to satisfy their greater desire for food.

Factors which affect the lobster's catchability fall into two categories—physical and biological. Physical factors such as water temperature, swell, and light intensity all affect the catchability of western rock lobsters (Chittleborough 1970, 1975; Morgan 1974, 1978, 1979; Jernakoff 1987; Srisurichan 2001). By their very nature, physical factors are likely to induce quite rapid changes in catchability and are usually of very short duration. Biological factors include moult state, size, and sex (Chittleborough 1970; Morgan 1974, 1979; Jernakoff 1987; Hall et al. 2000). Reproductive state has not been recorded previously as affecting western rock lobster catchability, although it has been noted as a factor influencing the catchability of spiny lobster, *Panulirus argus* (Kanciruk 1980; Morgan 1980). The present study was designed to determine whether reproductive state affects the behaviour of western rock lobster (*P. cygnus*), particularly their movement and food consumption measured as proxies for catchability.

MATERIALS AND METHODS

All experimental lobsters were collected from Lancelin, Western Australia (31°01′S: 115°20′E) during October 2003 using baited traps. The lobsters were transported to the laboratory in aerated tanks where they were held in raceways, with food supplied to excess, before the start of the experiment.

Four tanks, 1 m in diameter and 80 cm deep were used in all trials. Bricks and PVC sheets were placed over half the bottom of an experimental tank, providing shelter to the lobsters. Lobsters were randomly allocated to the experimental tanks to reduce any effect associated with the tank or its position in the laboratory on their behaviour. Lighting in the laboratory was on a 12 h fluorescent light/12 h red light cycle.

All lobsters used in the experiment were in C stage of intermoult according to the criteria of Dall & Barclay (1976). As moult state has been shown to affect food consumption of *P. cygnus* (Chittleborough 1970, Morgan 1974), it was important that it was standardised in this study so as not to influence the results. Water temperature, light intensity, and moon phase were controlled during the experiment. While light intensity was constant across all tanks in the laboratory, the effect of other factors (water temperature and moon phase) was minimised by acclimating lobsters in the laboratory for three weeks before trials began.

In the first experiment, to test whether number of animals per tank influenced the movement and food consumption, male animals 77–85 mm carapace length (CL) in size that had been held for at least 7 days before experimentation were stocked at densities of 1, 2, 3, and 4 lobsters per tank. Three trials were performed for each of the four categories. The animals were stocked 24 h before trials started during which time they were fed to excess. Measurement of movement and food consumption was carried out for 5 days and 5 nights.

A second series of experiments was carried out to measure whether reproductive state influences movement and food consumption. Five trials were performed in which four tanks were stocked with animals 80–95 mm CL in size that had been held for at least 3 weeks before trials began. Each tank was stocked with three animals of one of the following reproductive states: (1) males; (2) mature, unmated females (with ovigerous setae); (3) females with stage one eggs; and (4) females with late stage eggs.

Criteria for determining egg stages corresponded to those described by Silberbauer (1971); early stage eggs were consistent with stages 1, late stage eggs with stage 4 in Silberbauer (1971).

Lobsters fed to excess in experimental tanks for 24 h before trials began. Measurement of movement and food consumption occurred for 7 days and 7 nights to complete each trial. Where possible, lobsters were only used once in an experiment, however because most of the experimental animals had either none or only early stage eggs at capture, it was necessary to re-use most of these animals in the same series of experiments for later stages of egg development. It is recognised that this had the potential for pseudoreplication, however the same lobsters were not used in consecutive experiments, and the experiments were of an observational rather than a manipulative nature.

Red light of a wavelength of 660 nm was used during darkness to allow movement of the lobsters to be observed using video cameras. Red light of this wavelength is outside the spectral range of spiny lobsters including *P. cygnus* (Cummins et al. 1984) but allowed movement to be recorded.

The movement of lobsters was recorded using two video cameras mounted above the experimental tanks, each camera monitoring the movement in two tanks. Video cameras were connected to long play VHS recorders. Movement was recorded continuously for the duration of the trial. When analysing the recordings, the tapes were stopped every 5 min and the number of lobsters present outside the shelter were recorded. A lobster was recorded as being outside its shelter only if at least 50% of its body was visible outside the shelter. The total number of lobster sightings for a 12-h red light/white light period was divided by the density of animals in the tank to give a measure of movement which was then expressed as the number of sightings outside shelter per lobster.

A relationship between the total length mussel shell (*Mytilus edulis*) and dry weight of organic matter contained within was determined, which allowed the food consumption of the lobsters to be monitored. At the start of the trials, 10 unopened mussels were placed at the end of the tank furthest away from the lobsters' shelter. The weight of mussels consumed by the experimental lobsters was assessed each morning and fresh mussels were added to the tank as required over a 7-day period. Food consumption for each tank was expressed as g of mussel consumed per lobster over the duration of the trial.

Data were checked and found to be normal using residual plots. Data were analysed using ANOVA to determine any effect of density, reproductive state, and trial on the movement of lobsters. Where significant differences were found, post-hoc Tukey tests were used to determine which groups differed.

RESULTS

Lobsters displayed more movement during the night than during the day. Analysis using one-way ANOVA indicated that lobster movement was influenced by the density at which they were kept, with male lobsters held at densities of 3 and 4 animals per tank having significantly greater movement than those held at densities of 1 and 2 animals per tank (Fig. 1, 2).

Following analysis using one-way ANOVA, post-hoc Tukey tests were performed on the data to determine which densities significantly differed. Significant differences were more commonly detected within trials between densities of 3 and 4 lobsters per tank when compared with 1 and 2 lobsters per tank ($P < 0.05$, d.f = 3).

Food consumption also differed depending on the density of lobsters in the experimental tanks. Male lobsters held at densities of 3 or 4 lobsters per tank had higher food consumption than male lobsters held at densities of 1 or 2 lobsters per tank. Analysis using two-way ANOVA indicated that the effect of trials was not affecting the food consumption of lobsters during the density trials ($P = 0.57$, d.f. = 2). This implies that food consumption data from all trials could be pooled for the analysis, as factors associated with the trials were not changing the food consumption of the lobsters.

Food consumption data were pooled and analysed using one-way ANOVA. The result showed there to be significant differences in food consumption with varying densities ($P = 0.02$, d.f. = 3) (Fig. 3). Further analysis using Tukey tests indicated that lobsters held at densities of 3 and 4 lobsters per tank had

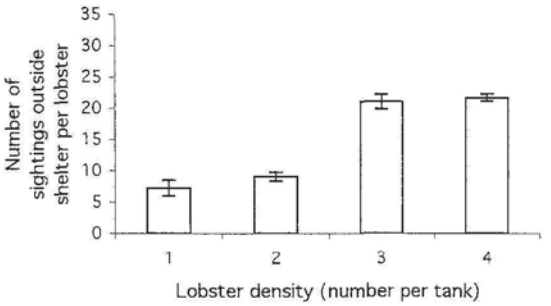

Fig. 1 Example of one replicate showing daytime movement of male western rock lobsters (*Panulirus cygnus*) held at different densities in the experimental tanks ($n = 5$ days) (mean ± SE).

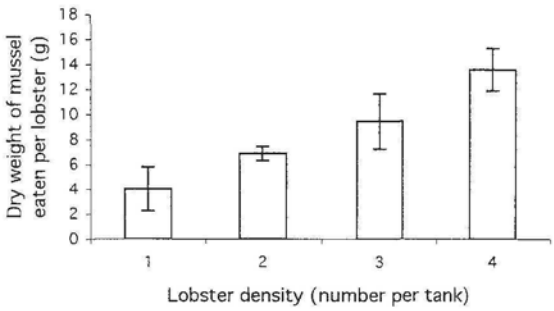

Fig. 3 Food consumption of male western rock lobsters (*Panulirus cygnus*) held at four different densities ($n = 3$ trials) (mean ± SE).

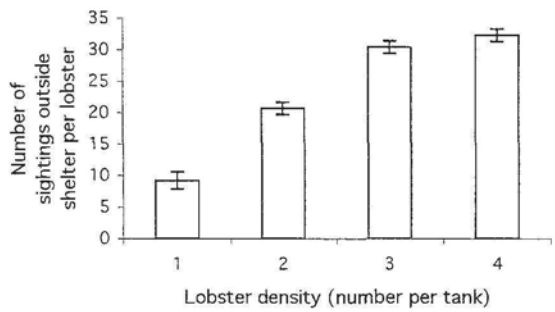

Fig. 2 Example of one replicate showing night-time movement of male western rock lobsters (*Panulirus cygnus*) held at different densities in the experimental tanks ($n = 5$ days) (mean ± SE).

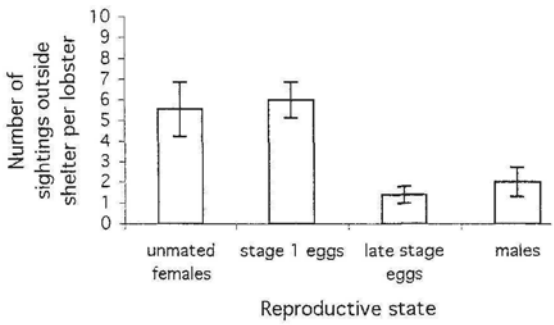

Fig. 4 Example of one replicate showing daytime movement of western rock lobsters (*Panulirus cygnus*) in different reproductive stages of development ($n = 7$ days) (mean ± SE).

significantly higher food consumption per individual than those held at 1 and 2 per tank.

On the basis of the above movement and food consumption data, it was concluded that further experimental work required at least 3 animals per tank to show optimally the effects of reproductive state on movement and food consumption.

Comparisons of average daytime and night-time movement were made between unmated females, females with stage one eggs, females with late stage eggs, and males (Fig. 4, 5). Typically, the amount of movement during day (Fig. 4) was less than during night (Fig. 5). Movement by unmated females and females carrying stage one eggs was similar and exceeded the movement displayed by females with late stage eggs, and males (e.g., Fig. 4, 5).

Analysis using two-way ANOVA indicated that lobster movement was significantly influenced by reproductive state ($P < 0.0001$, d.f. = 3), density ($P = 0.002$, d.f. = 3) and trial ($P < 0.0001$ d.f. = 4). Lobster movement appeared to be significantly influenced by trial, suggesting that exogenous factors such as moon phase, or temperature, that were unable to be controlled in the experiment, could have affected lobster movement. For this reason movement data were analysed using one-way ANOVA. Analysis using one-way ANOVA allowed these factors to be discounted by comparing movement within each trial.

Food consumption also differed depending on the reproductive state of lobsters in the experimental tanks. Unmated females and females carrying stage one eggs had higher food consumption than females carrying late stage eggs, and males. Analysis using two-way ANOVA indicated that the effect of trials was not affecting the food consumption of lobsters during the reproductive state trials ($P = 0.58$, d.f. = 4). This implies that food consumption data from all

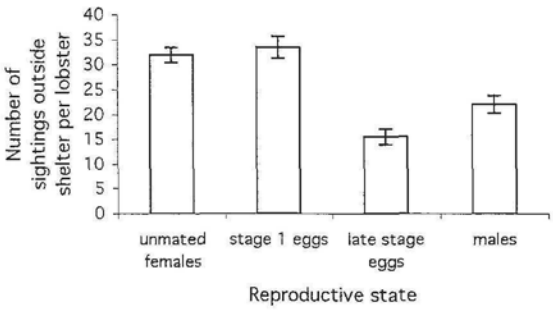

Fig. 5 Example of one replicate showing night-time movement of western rock lobsters (*Panulirus cygnus*) in different reproductive stages of development ($n = 7$ days) (mean ± SE).

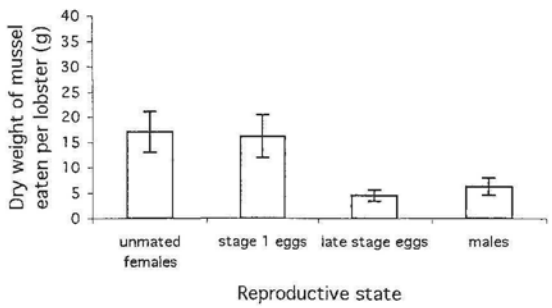

Fig. 6 Food consumption for western rock lobsters (*Panulirus cygnus*) in different reproductive stages of development ($n = 5$ trials) (mean ± SE).

trials could be pooled for the analysis, as factors associated with the trials were not changing the food consumption of the lobsters.

There were significant differences in food consumption of reproductively different lobsters ($P = 0.0061$, d.f. = 3). These data were plotted (Fig. 6) and differences analysed using post-hoc Tukey tests. Tukey tests indicated that unmated females and females carrying stage one eggs consumed significantly more food than females carrying late stage eggs, and males ($P < 0.05$, d.f. = 3).

DISCUSSION

Reproductive state of female lobsters was found to affect their movement and food consumption, with unmated females and females carrying stage one eggs having significantly greater movement and food consumption than females carrying late stage eggs and males. This implies that unmated females and females carrying stage one eggs would be likely to forage more and therefore be more catchable in the wild, than females carrying late stage eggs, and males. This is in contrast to the findings of Jernakoff (1987) where males were observed to forage more actively than females. However seasonal changes in foraging activity have also been observed in spiny lobsters (Jernakoff 1987, Ziegler et al. 2002), meaning that direct comparison of studies is not possible. Greater movement and food consumption by females in this study may be because they need to forage more than males during the breeding season, to satisfy their greater metabolic energy requirements associated with reproduction. Zoutendyk (1990) found that the costs to females in terms of mating is approximately two orders of magnitude higher than that of males, whereas Buesa (1979) found that berried females have a metabolic rate 1.6 times higher than an equivalent unberried female. This increase in energy expenditure by berried females is related to egg ventilation and maintenance during the incubation period (Zoutendyk 1990).

Spiny lobsters are gregarious animals and their behaviour varies depending on the number of individuals of the same species around them (Atema & Cobb 1980; Turner & Pitcher 1986; Zimmer-Faust & Spanier 1987; Lima & Dill 1990; Childress & Herrnkind 2001). Lobsters kept at densities of 3 and 4 per tank were found to have greater movement and food consumption than those kept at lower densities of 1 and 2 per tank. Consequently, 3 lobsters per tank was selected as the density for experiments on reproductive state. Because of the availability of lobsters during the density trials, male lobsters were used to determine a suitable density of lobsters in the experimental tanks. The assumption was then made that the behavioural response of male lobsters to density in terms of variation in movement and food consumption is representative of behavioural responses displayed by females of different reproductive states used in this study.

The results of this study suggest that both reproductive state and density have a significant effect on the movement and food consumption of *P. cygnus* in a tank environment. Food consumption of lobsters did not change significantly across the trials carried out during either the experiment to establish the effects of density or the effect of reproductive state. By comparison, there were significant differences in the amount of movement between the same trials. These differences may relate to either the biology of the species or the experimental design.

A significant increase in the movement of the lobsters over the course of the trials may have been indicative of a progressive behavioural response over the course of the experiment. The absence of predators in the tanks may have led the lobsters into becoming more ready to move outside their shelter. An alternative explanation for the increase in movement over the course of the experiment may be related to an increase in water temperature of 1.5°C over 5 weeks in the experimental tanks. A positive relationship between walking rate and temperature has been previously found for *P. cygnus* (Morgan 1974) and the American lobster *Homarus americanus* (McLeese & Wilder 1958).

Catchability of lobsters in the field would be expected to be related to movement, as the more a lobster moves around, the greater the chance it could be expected to have of arriving in a position from where bait may be detected. This poses difficulties in laboratory simulations of catchability, in that the experimental set-up (small size of tank and lack of surge for example) generally dictates that bait will usually be detectable to the lobsters from all localities in the tank. Observed movement of lobsters in the tanks will therefore usually be of two types: (1) movement to and from food when eating; and (2) general movement performed outside the lobster's shelter, unrelated to feeding.

Movement to food when eating by the lobsters will be the more reliable measure of catchability. General movement performed outside the shelter may occur for other reasons besides foraging, but if food is detected in the course of this movement the lobsters will seek out the food source as food is usually limited in the lobster's natural environment (Chittleborough 1975). Thus, differences in both direct and general movement of lobsters of different reproductive states might be expected to be suitable indicators of catchability in the field.

This study used movement and food consumption in experimental tanks to estimate foraging activity and subsequent catchability of lobsters in the wild. Because of limitations associated with making inferences about foraging activity and catchability of lobsters in the wild using tank data, survey data from a field situation was compared with results from this study.

The *P. cygnus* population is sampled annually during the height of the egg bearing season, to estimate egg production of the fishery (Phillips & Melville-Smith 2003). Unmated females (33–62%) and females carrying stage one eggs (37–67%) comprise most of the catch across the fishing grounds in the three most recent seasons for which comprehensive data exist. In contrast, the proportion of females caught carrying late stage eggs in those same years was low across all sites (0.1–5%) (Waddington 2004). Patterns identified in the data were not considered to be attributable to either time of year, or the amount of time female *P. cygnus* carry stage one eggs compared to late stage eggs (Waddington 2004). The implication, therefore, is that the patterns seen in the wild fishery survey data are catchability effects caused by the same differences in foraging activity and food consumption that were measured for female western rock lobsters of different reproductive states in the laboratory experiments described in this study.

This study found that the movement and food consumption of *P. cygnus* depends on reproductive state, with unmated females and females carrying stage one eggs sighted outside shelter more frequently, and consuming significantly more food, than females carrying late stage eggs, and males. As movement and food consumption are used to estimate foraging activity and catchability of *P. cygnus* in this study, unmated females and females carrying stage one eggs will be more catchable in the wild than females carrying late stage eggs, and males. As egg production of the fishery is based on catch data of berried females, the results of this study have implications for surveys which use catch rates of berried females to estimate egg production.

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REFERENCES

Atema, J.; Cobb, J. S. 1980: Social behaviour. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. New York, Academic Press. Pp. 409–450.

Bowen, B. K.; Chittleborough, R. G. 1966: Preliminary assessments of stocks of the West Australian crayfish, *Panulirus cygnus* George. *Australian Journal of Marine and Freshwater Research 17*: 93–121.

Branford, J. R. 1978: The influence of daylength, temperature and season on the hatching rhythm of *Homarus gammarus*. *Journal of the Marine Biological Association of the United Kingdom 58*: 639–658.

Buesa, R. J. 1979: Oxygen consumption of two tropical spiny lobsters, *Panulirus argus* (Latreille) and *P. guttatus* (Latreille) (Decapoda, Palinuridae). *Crustaceana 36*: 99–107.

Childress, M. J.; Herrnkind, W. F. 2001: The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behaviour 62*: 465–472.

Chittleborough, R. G. 1970: Studies on recruitment in the Western Australian rock lobster, *Panulirus longipes cygnus* George: density and natural mortality of juveniles. *Australian Journal of Marine and Freshwater Research 21*: 131–148.

Chittleborough, R. G. 1975: Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). *Australian Journal of Marine and Freshwater Research 26*: 177–196.

Chittleborough, R. G. 1976: Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Australian Journal of Marine and Freshwater Research 27*: 499–516.

Chubb, C. F. 1991: Measurement of spawning stock levels for the western rock lobster, *Panulirus cygnus*. *Revista Investigaciones Marinas 12*: 223–233.

Cummins, D. R.; Chen, D.; Goldsmith, T. H. 1984: Spectral sensitivity of the spiny lobster, *Panulirus argus*. *Biological Bulletin 166*: 269–276.

Dall, W.; Barclay, M. C. 1976: Induction of viable ecdysis in the western rock lobster by 20–hydroxyecdysone. *General and Comparative Endocrinology 30*: 323–334.

Gray, H. 1992: The western rock lobster. Book 1: A natural history. Geraldton, Westralian Books.

Hall, N.; Cao, L.; Chubb, C.; Caputi, N.; Cheng, H.; Melville-Smith, R.; Shanks, S. 2000: Modelling to explore management strategies to optimise the value of the rock lobster fishery of Western Australia. Fisheries Research Development Corporation, Report 97/104.

Jernakoff, P. 1987: Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology 113*: 125–144.

Jernakoff, P.; Phillips, B. F. 1988: Effect of a baited trap on the foraging movements of juvenile western rock lobsters, *Panulirus cygnus* George. *Australian Journal of Marine and Freshwater Research 39*: 185–192.

Jernakoff, P.; Phillips, B. F.; Maller, R. A. 1987: A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology 113*: 9–21.

Kanciruk, P. 1980: Ecology of juvenile and adult Panuliridae (spiny lobsters). *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. New York, Academic Press. Pp. 59–96.

Lima, S. L.; Dill, L. M. 1990: Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology 68*: 619–640.

McLeese, D. W.; Wilder, D. G. 1958: The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *Journal of the Fisheries Research Board of Canada 5*: 1345–1354.

Morgan, G. R. 1974: Aspects of the population dynamics of the western rock lobster, *Panulirus cygnus*. II. Seasonal changes in the catchability coefficient. *Australian Journal of Marine and Freshwater Research 25*: 249–259.

Morgan, G. R. 1978: Locomotor activity in the western rock lobster, *Panulirus longipes cygnus*. *Australian Journal of Marine and Freshwater Research 29*: 169–174.

Morgan, G. R. 1979: Trap response and the measurement of effort in the fishery for the western rock lobster. *Rapports et procés-verbaux des réunions/ Conseil Permanent International pour L'exploration de la Mer 175*: 197–203.

Morgan, G. R. 1980: Population dynamics of spiny lobsters. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. New York, Academic Press. Pp. 189–217.

Phillips, B. F.; Melville-Smith, R. 2003: Sustainability of the western rock lobster fishery: past progress and future challenges. Curtin University of Technology. *Department of Environmental Biology Bulletin No. 25*. Perth, Australia.

Silberbauer, B. I. 1971: The biology of the South African rock lobster *Jasus lalandii*. 1. Development. *Division of Sea Fisheries Investigational Report 92*. 70 p.

Srisurichan, S. 2001: Time series modelling of the environmental factors affecting the daily catch rates of the western rock lobster. Unpublished PhD thesis, Edith Cowan University, Perth, Western Australia.

Turner, G. F.; Pitcher, T. J. 1986: Attack abatement: a model for group protection by combined avoidance and dilution. *American Naturalist 128*: 228–240.

Waddington, K. 2004: Effect of reproductive state on movement and food consumption of western rock lobsters, *Panulirus cygnus*. Unpublished honours thesis, School of Plant Biology, The University of Western Australia, Perth, Western Australia.

Ziegler, P. E.; Frusher, S. D.; Johnson, C. R.; Gardner, C: Catchability of the southern rock lobster *Jasus edwardsii*. I. Effects of sex, season and catch history. *Marine and Freshwater Research 53*: 1143–1148.

Zimmer-Faust, R. K.; Spanier, E. 1987: Gregariousness and sociality in spiny lobsters: implications for den habitation. *Journal of Experimental Marine Biology and Ecology 105*: 57–71.

Zoutendyk, P. 1990: Gonad output in terms of carbon and nitrogen by the cape rock lobster *Jasus lalandii* (H. Milne Edwards, 1837) (Decapoda, Palinuridea). *Crustaceana 59*: 180–192.

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Characterising shelter preferences in captive juvenile *Jasus edwardsii* (Palinuridae)

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Abstract Any attempt to enhance rock lobster production by increasing survival after settlement, or by ongrowing or outplanting young juveniles, requires knowledge of the shelter preferences of young juveniles. For juvenile *Jasus edwardsii* in the wild these are not well known. Information available suggests that juveniles up to c. 35 mm carapace length (CL) occupy shelters that generally conform closely to their body dimensions but that larger juveniles use shelters of more variable dimension, often much larger than their body size. We investigated mainly physical factors important in shelter choice by 15–59 mm CL (c. 2–24-month-old juveniles) in laboratory tank experiments. In overnight tests, all sizes of juvenile lobster chose to occupy holes (shelters with sides) over open horizontal gaps. Preference for open horizontal gaps versus horizontal crevices (where the height reduces from a maximum at the mouth to zero at the opposite end) was much less clear-cut; choice varied according to lobster size. For the number of entrances into holes, there was evidence for an ontogenetic shift in preference, small lobsters preferring two openings over one, whereas those >30 mm CL (c. 9 months old) preferred one over two. For lobsters <40 mm CL, the hole size and gap size preferences revealed were generally consistent with the field evidence for *J. edwardsii* in that there was a close and proportional relationship between lobster size and shelter size; what differed was that the open gaps chosen in the tanks by the smallest lobsters (15–19 mm CL) were larger than the holes used in the tank experiments and 30–50% larger than those reportedly used in the field. For lobsters >40 mm CL, the holes and gaps chosen in the tanks were generally larger and more variable in size, as in the field.

Keywords palinurid; rock lobster; *Jasus edwardsii*; juvenile; habitat preference; enhancement

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INTRODUCTION

The red (spiny) rock lobster *Jasus edwardsii* (Hutton, 1875) (family Palinuridae) is an important commercial and recreational seafood in Australasia, the New Zealand wild stocks of which are fully exploited (Sullivan & O'Brien 2002). Potential means of increasing production include: (1) catching or culturing pueruli or juveniles to later ongrow or outplant; and (2) increasing juvenile survival and abundance in the wild by moderating the impact of any survival bottlenecks in the early benthic life history. Knowing the form of shelter preferred by young juvenile lobsters can facilitate these. The focus of this work was juveniles 15–59 mm carapace length (CL) (c. 2–24 months post-settlement).

Little is known of the ecology of juvenile palinurids (Herrnkind et al. 1994), mainly because their cryptic colour and behaviour mean that they are difficult to locate and study. For shallow-water palinurids, including *J. edwardsii*, most settlement appears to take place inshore, in waters a few metres deep. It is common for the juveniles first to be asocial, and then to become communal at c. 1 year of age (Lipcius & Eggleston 2000). The evidence for *J. edwardsii* is that first instar juveniles are not attracted to conspecifics (Butler et al. 1999; Booth 2001) and, based mainly on tank studies, they remain asocial and mainly solitary until they reach c. 35 cm CL (c. 1 year) (Butler et al. 1999; Frusher et al. 1999). However, the field evidence concerning gregariousness is not unequivocal. In probably the most comprehensive field observation of shelter

occupancy by young *J. edwardsii*, Edmunds (1995) found that most small juveniles (<35 mm CL) were solitary, yet MacDiarmid (1994) reported that only 15–16% of juveniles <30 mm CL in the field resided solitarily. Cohabitation with conspecifics is widespread for lobsters >35 mm CL (MacDiarmid 1994; Edmunds 1995).

There is little field information on the characteristics of shelters used by young juveniles of any palinurid, including *J. edwardsii*, compared with that available for late juveniles and adults. Virtually all 15–60 mm CL *J. edwardsii* in both New Zealand and Australia have been found on hard substrates in shelters with low levels of ambient light and into which the lobsters can withdraw (Lewis 1977; Gabites 1990; Booth & Forman 1995; Edmunds 1995; Frusher et al. 1999; NIWA divers). The smaller lobsters have been most commonly reported to occupy holes not much larger than themselves (Lewis 1977; Edmunds 1995; Frusher et al. 1999). For example, pholad (bivalve) holes containing first instar juveniles (mainly 12–15 mm CL) in Port Gisborne, on the south-east coast of the North Island of New Zealand, averaged 17.5 mm diameter (SD 4.38 mm), holes available being 6–26 mm in diameter (Booth & Forman 1995). Broadly consistent with this, catch rates of pueruli and first instar juveniles combined were significantly lower when the crevice openings of the crevice collector (Booth & Tarring 1986) used to monitor levels of *J. edwardsii* settlement in Australasia were smaller (12 mm high) or larger (60 mm high) than the standard 25 mm (Booth & Forman 1995). Edmunds (1995) found that juveniles up to 35 mm CL displayed a strong relationship between shelter size and body size, the lobsters occupying shelters that generally conformed to their body dimensions and the holes used being relatively deep compared with the width or height of the entrance. Typically a 17 mm CL juvenile occupied a hole with an opening c. 25 mm high, a 25 mm CL juvenile a hole c. 45 mm high, and a 35 mm CL lobster a 55 mm high hole.

For juveniles larger than 35 mm CL, Edmunds (1995) found that the dimensions of the shelters occupied were more variable, the lobsters often being present in shelters much larger than their body size, and usually with more than one opening to the rear or sides. The shelters were often quite expansive, such as open ledges and boulder junctions. Edmunds (1995) found that 40 mm CL juveniles used shelters averaging c. 70 mm in height; 50 mm CL juveniles used 100 mm high shelters; and 60 mm CL juveniles used 130 mm high shelters. Gabites (1990) also found that larger juveniles occupied a wide range of shelter sizes, the lobsters most often dwelling in wide, horizontal shelters with a roof. Although most shelters had only one opening, fewer lobsters than expected were found in those shelters than in ones with two or more openings. Consistent with these observations, NIWA divers report juveniles frequently occupying crevices such as those that exist among small boulders and between stones and the sea floor, and also flat, more or less horizontal spaces, such as those that occur beneath large flat boulders that are not sitting flush with the sea floor.

In all such field observations it is not possible to separate choice of shelter from occupancy patterns that result from other factors, including predation pressure—something which is possible in laboratory experiments. In tank studies, first instar *J. edwardsii* juveniles preferred conditioned refuges over those unconditioned, horizontal apertures over vertical ones, and rough surfaces over smooth (Booth 2001). The preferred number of openings (entrances) for first instar juveniles was unclear, although field experiments using pipes open at both ends or one end suggested that there was either no preference or possibly preference for one opening (A. Jeffs & S. Hooker, NIWA pers. comm.). There have been no similar tank studies of shelter choice for larger juvenile *J. edwardsii*.

These observations of shelter choice/occupancy for *J. edwardsii* seem to be generally consistent with those available for other palinurids. Species being solitary and occupying body-scaled shelter as newly settled juveniles and becoming gregarious and occupying much larger holes when reaching c. 1 year of age include *Panulirus argus* (Marx & Herrnkind 1985), *P. japonicus* (Chen et al. 1987; Yoshimura & Yamakawa 1988; Norman et al. 1994; Yoshimura et al. 1994), *P. cygnus* (Jernakoff 1990), and *P. ornatus* (Dennis et al. 1997).

In this study we investigated mainly the physical features of the shelters chosen and occupied by *J. edwardsii* juvenile lobsters up to c. 60 mm CL in tank experiments. The features of the basic experimental units, concrete blocks, were purposely constrained by the commercial product readily available—these are more likely to be used in any attempt to improve lobster survival in field enhancement initiatives and in ongrowing facilities than custom-made structures. We were particularly interested in changes, including any ontogenetic, in shelter choice regarding hole size and shape, and in the number of openings (entrances).

METHODS

Source and size of experimental animals

Lobsters were collected within or near Port Gisborne, New Zealand (38°41′S, 178°02′E) and the experiments conducted in sea-water tanks set up in a live lobster holding plant in Gisborne. Lobsters were grouped into the following size categories (or composites thereof) for study: 15–19, 20–29, 30–39, 40–49, and 50–59 mm CL juveniles. The very small juveniles (15–24 mm CL, c. 2–6 months old) were taken mainly on crevice collectors. Larger juveniles (c. 6–24 months old and 25–59 mm CL) were caught by hand by divers. (*J. edwardsii* is rarely taken smaller than 70 mm CL in traps—see Gardner et al. 2001.) The lobsters were held for up to 8 days (but usually less than 5 days) without feeding as they were used in the experiments—which were conducted about monthly over the course of more than 1 year—and then returned into the wild near to where they had been captured. Because lobsters had to be obtained afresh each month, there was little control possible over the numbers available for each size group, which were sometimes very variable.

Experimental procedures

Tank experiments in still but aerated sea water were used to determine the occupancy by the juvenile lobsters of particular shelter types. Tanks were stocked to a level approaching the realistic maximum when the lobster and tank sizes were considered. Overall sample numbers for each experiment were increased through replication, but in the analyses of results, replicates were combined. Simultaneous field and tank approaches in shelter testing, where any differences in shelter occupation observed would be at least in part a result of predator pressure, would have been preferable but were not possible. The difficulty in locating sufficient small juveniles in the field, and the logistics and experimental implications of restraining them in the study sites so they could be repeatedly censused, meant that only tank experiments took place. These tank experiments allowed shelter choice to be expressed in a predation- and predator-free environment. Because *J. edwardsii* are active at night and take cover during the day, it was assumed that overnight was a reasonable interval for any choice of refuge to be established. Lobsters were released into the centre of the tank in the early evening and their positions noted, without disturbance, early the next morning. Usually, any individual lobster was used only once for any particular experiment. Although they were held for several days in any one session of experiments, we assumed they retained their instinctual predator-avoiding behaviour and hence all their natural preferences for shelter characteristics.

For most experiments, the tanks used were round, flat-bottomed, just under 1 m in diameter, and filled with sea water to a height of c. 15 cm. However, in tests of open horizontal gap height preferences (see later), particularly for lobsters >40 mm CL, a larger tank was necessary; this was 58 × 115 cm, filled to c. 20 cm with sea water. The facilities and tanks available meant that no more than one pair of options (e.g., one pair of hole sizes) could be tested at any one time in any one tank. The numbers of lobsters in the tank that became associated with a shelter type after being left undisturbed overnight was interpreted to be a measure of how much the lobster was attracted to or preferred that shelter type.

For many of the experiments we used commercial, hollow construction blocks (Firth Industries Ltd, P.O. Box 30 102, Lower Hutt, New Zealand) of two types: 10.01 (39 cm long × 19 cm wide × 9 cm high, with three equally spaced 9.5 cm long × 3.8 cm high holes through the width) and 15.01 (39 × 19 × 14 cm, with two 13.0 × 8.2 cm holes through the width). Concrete blocks such as these are useful because they are rough textured and so readily accumulate biofilm, they are standard in size and form, readily available and inexpensive, they can be built into a myriad of forms, and they are dense, durable, and resilient in sea water. Smaller holes were required for the small lobsters; these were created by inserting lengths of 18 mm (4 pieces), 25 mm (3), or 32 mm (2) internal diameter alcathene pipe into each hole in the 10.01 blocks. No blocks were available with hole sizes intermediate between those of the 10.01 and 15.01 blocks, nor were inserts placed in the 15.01 blocks. In all experiments, the blocks were placed so that the holes were horizontal.

Level of conditioning

The level of conditioning (seasoning) of shelters can strongly influence invertebrate occupancy. Conditioning here means the development of a biofilm layer and, when conditioned for long enough, the growth of larger items, both invertebrate and plant. Levels of conditioning tested by lobster size group ranged from none to 12 months for blocks that contained what was estimated to be about the optimal hole size for that size group of lobster (25 mm diam. inserts for 15–19 mm and 20–29 mm CL lobsters, 10.01 bricks without inserts for larger lobsters), but with any large growth scraped off. Blocks with their

alcathene pipes in place were conditioned by being immersed within Port Gisborne, from which the water for the experiments was also drawn. For all size groups tested (15–19, 20–29, 30–49, and 50–59 mm CL), the occupancy preference order was 12 months conditioned = 3.5 months conditioned = 2.5 months conditioned > 1 month conditioned > well soaked > new. The results showed that several months of conditioning was preferred so all shelter choice experiments used materials that had been conditioned in Port Gisborne for at least 3 months.

Shelter choice experiments

Different shelter shapes were compared for each lobster size group: (1) horizontal holes (a more-or-less round space with firm walls in which the depth far exceeds the diameter); (2) horizontal open gaps (a flat space where the firm floor and roof are parallel and there are no sides); and (3) horizontal closed crevices (a flat space with firm floor and roof but no sides and where the height reduces from a maximum at the mouth to zero at the opposite end). We assumed that lobsters up to at least 40 mm CL (a little over 1 year) were asocial and therefore acted independently—that the presence of one lobster in the tank did not influence the search for and occupancy of a refuge by another lobster. Previous work (e.g., Edmunds 1995; Butler et al. 1999) suggested that such an assumption would not necessarily hold for juveniles between 1 and 2 years (c. 40 and 60 mm CL), but many of the experiments used shelters in which only one animal could fit and so to that extent lobsters would have behaved independently. Ideally, so as to account for any lack of independence in shelter choice and for any chemical cue that might have remained within previously occupied shelters, every experiment would have been conducted with a single lobster and previously unoccupied (but nevertheless conditioned) blocks—something not logistically possible. The holes tested were those provided by the blocks, with lengths of alcathene pipe inserted for the smaller lobsters—all well conditioned—as described above. The gaps and crevices were created by using well-conditioned sheets of 5 mm thick cement sheet supported above the tank floor by thin spacers. When occupancy of gaps was compared with that of holes, the cement sheets had about the same surface area as the block (39 × 19 cm). Gap and crevice occupancy was tested using these same sheets for most of the experiments involving small lobsters, but using 40 × 40 cm sheets for others and for the larger lobsters.

When comparing hole size preferences, hole sizes thought appropriate to the size class of the lobster were tested first, and then the range broadened, lobster numbers being kept appropriate to the lobster and tank sizes. (A similar approach was taken when determining open gap size choice.) Also, there were always enough holes of each of the two hole sizes being compared to house all lobsters, and usually there were equal numbers of holes of each of the two sizes. The exception was for small lobsters when the number of the smaller holes exceeded that of the larger ones. Results in which the lobsters mostly occupied the hole size that was more numerous must be treated with caution; conversely, where the hole size chosen was the one least abundant, the result was particularly compelling.

The preference for number of openings (entrances) into horizontal holes was determined for each size group of lobster, with equal numbers of holes with one or two openings being available. For example, three 10.01 bricks were used in a tank, two of which had their holes blocked at one end whereas in the third brick the holes were unblocked.

Statistical analyses

The null hypothesis was that there was no difference in level of association of the lobsters with the different options being tested, so the counts would be the same. For the experiments investigating hole versus crevice and crevice versus open gap preferences, the preferred number of openings, and for the hole size and open gap size experiments where there was the choice of only two refuge sizes, the chi-square test for goodness of fit of the observed numbers of animals to the expected number was used.

For the hole size and open gap size experiments where there were three or more choices tested, the data were analysed using a Bradley-Terry model (Bradley & Terry 1952; Agresti 1990).

$$P(\text{hole } i \text{ preferred to hole } j) = \gamma_i / (\gamma_i + \gamma_j)$$

where γ_i is a positive-valued parameter associated with hole i—a measure of the "desirability" of hole i. Thus the odds of hole i being selected over hole j are γ_i/γ_j.

The model was implemented in R version 1.81 (R Development Core Team 2003), which uses an alternative parameterisation:

$$\text{logit}[P(\text{hole } i \text{ preferred to hole } j)] = \lambda_i - \lambda_j$$

where $\lambda_i = \log \gamma_i$ for all i, and the parameters λ are estimated by maximum likelihood.

Analyses were carried out separately for each different size group of lobsters for ease of implementation and interpretation. For each size group, the theoretical probability of a particular hole size being selected, given a choice of all possible hole sizes, was obtained by examining each preference parameter against all others:

$P_{select} = \gamma_i / \Sigma_i \gamma_i$ for all hole sizes i.

RESULTS

Hole versus open gap

Where occupancy of more-or-less round holes was compared with open gaps, all size groups used the holes more than the gaps (Table 1). In all but one size group, the difference was significant; for 30–39 mm CL juveniles, it was nearly so at $P = 0.067$.

Open gap versus crevice

When an open gap was tested against a crevice, only the larger lobsters showed any preference: 30–39 mm CL lobsters preferred gaps and those 40–49 mm CL preferred crevices (Table 2).

Hole size

Juveniles up to 39 mm CL (c. 1 year) generally preferred small holes. The holes most used by 15–19 mm CL lobsters were 25 mm diameter, 38 mm diameter for 20–29 mm lobsters, and 38/82 mm for 30–39 mm CL lobsters (Tables 3–5). The larger lobsters (40–59 mm CL) preferred much larger holes (82 mm, Table 6), but size preferences were not further narrowed down.

Open gaps

Juveniles 15–19 mm CL occupied comparatively large (32 and 38 mm high) gaps (Tables 7–9). The results for larger juveniles were more similar to those found for hole use: 20–29 mm CL juveniles preferred 38 and 32 mm holes; 30–39 (38 and 82 mm); 40–49 (82 and 100 mm); and 50–59 mm (100 mm).

Number of entrances

When testing the preferred number of openings, one versus two, and using holes near the optimal size for each size group, there was a change in choice with size. There was preference (compelling but not

Table 1 Use by juvenile *Jasus edwardsii* lobsters of holes versus open gaps. (d.f. = 1 for each size group; CL, carapace length; *N*, number of lobsters; χ^2, chi-squared; *P*, p value; NS, not significant.)

Size group (mm CL)	Aperture size (mm)	*N*	χ^2	*P*	Choice and significance
15–19	25	24	24.00	<0.001	Hole $P < 0.001$
	32	24	6.00	0.014	Hole $P < 0.05$
20–29	38	20	20.00	<0.001	Hole $P < 0.001$
30–39	38	30	3.33	0.067	Hole NS
40–49	38	12	5.33	0.021	Hole $P < 0.05$
50–59	80	12	12.00	<0.001	Hole $P < 0.001$

Table 2 Use by juvenile *Jasus edwardsii* lobsters of open gaps versus crevices. Gap and crevice dimensions in mm. (d.f. = 1 for each size group; CL, carapace length; *N*, number of lobsters; χ^2, chi-squared; *P*, p value; NS, not significant.)

Size group (mm CL)	Gap height	Crevice opening height	*N*	χ^2	*P*	Choice and significance
15–19	32	40	39	2.08	0.150	Crevice NS
20–29	38	50	24	0.17	0.683	Gap NS
30–39	38	50	14	10.29	0.001	Gap $P < 0.001$
40–49	38	50	26	9.85	0.002	Crevice $P < 0.01$

Table 3 Experiments undertaken to quantify hole size (diameter) preference in juvenile *Jasus edwardsii* lobsters, 15–39 mm carapace length, in three size groups. (*N*, number of lobsters.)

Size group	Hole sizes (mm)	*N*	Size group	Hole sizes (mm)	*N*
15–19	18 versus 25	51	20–29	25 versus 32	22
	18 versus 32	18		25 versus 38	18
	18 versus 38	18		25 versus 82	16
	25 versus 32	19		32 versus 38	20
	25 versus 38	20		32 versus 82	31
	32 versus 38	20		38 versus 82	19
			30–39	32 versus 38	23
				32 versus 82	18
				38 versus 82	46

Table 4 Parameter estimates for 15–39 mm carapace length (CL) lobsters, in three size groups, using holes of different diameter (in mm, indicated by the λ subscript). Lobster size groups in mm CL. (SE, standard error.)

		Desirability			
Size group		Estimate	SE	*z* value	*P*
15–19	λ_{18}	0	–	–	–
	λ_{25}	1.8108	0.2855	6.344	< 0.001
	λ_{32}	1.1275	0.3522	3.202	0.001
	λ_{38}	–0.2675	0.3566	–0.750	0.453
20–29	λ_{25}	0	–	–	–
	λ_{32}	2.0401	0.4444	4.591	< 0.001
	λ_{38}	2.9990	0.5330	5.627	< 0.001
	λ_{82}	0.6151	0.4188	1.469	0.142
30–39	λ_{32}	0	–	–	–
	λ_{38}	1.5034	0.4152	3.621	< 0.001
	λ_{82}	1.3129	0.4211	3.118	0.002

Table 5 Overall selection probabilities (P_{select}) and pairwise significance tests (*P*) for hole use by juvenile *Jasus edwardsii* lobsters, 15–39 mm carapace length, in three size groups. Hole sizes (mm diam.) are presented in order of highest selection probability to lowest. *P* values refer to adjacent pairings.

Size group	Overall hole size selection probability (P_{select})	Significance tests of overall hole sizes with adjacent categories (*P*)
15–19	25(0.558) > 32(0.282) > 18(0.091) > 38(0.070)	25 (0.051) > 32(0.001) > 18(<0.001) > 38
20–29	38(0.656) > 32(0.251) > 82(0.060) > 25(0.033)	38(0.022) > 32(<0.001) > 82(0.142) > 25
30–39	38(0.488) > 82(0.403) > 32 (0.109)	38(0.492) > 82(0.002) > 32

Table 6 Use of holes by juvenile *Jasus edwardsii* lobsters, 40–59 mm carapace length, in two size groups. (d.f. = 1 for each size group; *N*, number of lobsters; χ^2, chi-squared; NS, not significant.)

Size group	Hole sizes tested (mm)	*N*	χ^2	*P*	Choice and significance
40–49	38 versus 82	17	0.53	0.467	82 > 38 NS
50–59	38 versus 82	12	8.33	0.004	82 > 38 *P* < 0.01

Table 7 Experiments undertaken to quantify open horizontal gap size preferences by juvenile *Jasus edwardsii* lobsters, 15–59 mm carapace length, in five size groups. (*N*, number of lobsters.)

Size group	Gap heights (mm)	*N*	Size group	Gap heights (mm)	*N*
15–19	18 versus 32	67	30–39	32 versus 38	10
	25 versus 32	75		32 versus 80	12
	32 versus 38	44		32 versus 100	6
	32 versus 45	9		38 versus 80	6
	32 versus 52	15		38 versus 100	6
	32 versus 59	15		80 versus 100	6
	38 versus 45	36	40–49	32 versus 38	8
	38 versus 52	17		38 versus 80	8
	38 versus 59	15		38 versus 100	15
	45 versus 52	36		38 versus 120	15
	45 versus 59	15		80 versus 100	8
	52 versus 59	19		80 versus 120	15
20–29	25 versus 32	6		100 versus 120	7
	32 versus 38	44	50–59	60 versus 80	8
	32 versus 50	17		60 versus 100	10
	32 versus 60	10		60 versus 120	19
	32 versus 80	10		80 versus 100	8
	38 versus 50	17		80 versus 120	10
	38 versus 60	12		100 versus 120	10
	38 versus 80	12			
	50 versus 60	16			
	50 versus 80	10			
	60 versus 80	12			

Table 8 Parameter estimates for 15–59 mm carapace length *Jasus edwardsii* lobsters, in five size groups using open horizontal gaps of different height (in mm, indicated by the λ subscript). Lobster size groups in mm. (SE, standard error.)

		Desirability			
Size group		Estimate	SE	*z* value	*P*
15–19	λ_{18}	0	–	–	–
	λ_{25}	0.1504	0.3581	0.420	0.674
	λ_{32}	0.7841	0.2634	2.977	0.003
	λ_{38}	0.7638	0.3711	2.058	0.040
	λ_{45}	0.2457	0.4183	0.587	0.557
	λ_{52}	–0.7423	0.4394	–1.689	0.091
	λ_{59}	–1.6325	0.5072	–3.218	0.001
20–29	λ_{32}	0	–	–	–
	λ_{38}	0.4122	0.2624	1.571	0.116
	λ_{50}	–0.7638	0.3328	–2.295	0.022
	λ_{60}	–0.3537	0.3552	–0.996	0.319
	λ_{80}	–0.8465	0.3801	–2.227	0.026
30–39	λ_{32}	0	–	–	–
	λ_{38}	0.45304	0.49291	0.919	0.358
	λ_{80}	0.28659	0.46587	0.615	0.538
	λ_{100}	0.02162	0.5442	0.040	0.968
40–49	λ_{32}	0	–	–	–
	λ_{38}	1.0986	0.8165	1.346	0.179
	λ_{80}	2.2887	0.9987	2.292	0.022
	λ_{100}	1.5181	0.9352	1.623	0.105
	λ_{120}	–0.8839	1.0335	–0.855	0.392
50–59	λ_{60}	0	–	–	–
	λ_{80}	0.2974	0.4917	0.605	0.545
	λ_{100}	1.9684	0.5985	3.289	0.001
	λ_{120}	0.2401	0.3964	0.606	0.545

Table 9 Overall selection probabilities (P_{select}) and pairwise significance tests (P) for open horizontal gap use by juvenile *Jasus edwardsii* lobsters, 15–59 mm carapace length, in five size groups. Gap sizes (mm) are presented in order of highest selection probability to lowest. P values refer to adjacent pairings.

Size group	Overall gap height selection probability (P_{select})	Significance tests of overall gap size with adjacent categories (P)
15–19	32(0.259) > 38(0.254) > 45(0.151) > 25(0.138) > 18(0.118) > 52(0.056) > 59(0.023)	32(0.938) > 38(0.058) > 45(0.814) > 25(0.674) > 18(0.091) > 52(0.019) > 59
20–29	38(0.368) > 32(0.244) > 60(0.171) > 50(0.113) > 80(0.104)	38(0.116) > 32(0.319) > 60(0.244) > 50(0.830) > 80
30–39	38(0.319) > 80(0.270) > 100(0.207) > 32(0.203) > 25(0)	38(0.754) > 80(0.634) > 100(0.968) > 32(*) > 25
40–49	80(0.524) > 100(0.242) > 38(0.159) > 32(0.053) > 120(0.022)	80(0.178) > 100(0.358) > 38(0.178) > 32(0.392) > 120
50–59	100(0.664) > 80(0.125) > 120(0.118) > 60(0.093)	100(0.007) > 80(0.904) > 120(0.545) > 60

*There was one trial where lobsters were offered a choice between 32 and 25 mm gaps. Always the 32 mm gap was chosen, which precluded the inclusion of the 25 mm data in the statistical analyses. The 25 mm gap was subjectively placed at the bottom of the preference listing.

Table 10 Use by juvenile *Jasus edwardsii* lobsters of refuges (blocks) with one or two openings. (d.f. = 1 for each size group; CL, carapace length; N, number of lobsters; χ^2, chi-squared; NS, not significant.)

Size group (mm CL)	N	χ^2	P	Choice and significance
15–19	55	3.07	0.080	2 > 1 NS
20–29	48	0	1.00	1 = 2
30–49	27	1.81	0.178	1 > 2 NS
50–59	20	9.80	0.002	1 > 2 $P < 0.01$

significant) for two holes by 15–19 mm CL lobsters (almost significant at $P = 0.080$), to no detectable preference for those 20–29 mm CL, to one opening preferred by all the larger lobsters (Table 10).

DISCUSSION

The results from these experiments indicate that for all sizes of lobster, 15–59 mm CL, horizontal holes are preferred over open horizontal gaps. For 15–19 mm CL lobsters, the optimal hole diameter of those tested was 25 mm and two openings were preferred; the optimum gap height was larger, 32/38 mm. For 20–29 mm CL lobsters, the optimal hole diameter of those tested was 38 mm with either one or two openings; the optimum gap height was 38 mm. For 30–39 mm CL lobsters, the optimal hole diameter of those tested was large, in the range 38–82 mm, and one opening was preferred; the optimum gap height was also 38–82 mm. For 40–49 mm CL lobsters, the optimal hole diameter of those tested was 82 mm, and one opening was preferred; the optimum gap was 82/100 mm. For 50–59 mm CL lobsters, the optimal hole diameter between those tested was 82 mm and one opening was preferred; the optimum gap height was 100 mm. Although all holes <38 mm diameter were of alcathene, and all those ≥38 mm were of brick, all surfaces were well conditioned with natural marine growth and at least to that extent were similar.

The difficulty in locating sufficient juveniles for experiments to be conducted *in situ* in the wild, and other logistic constraints, meant that the investigations were confined to captive lobsters. The choices of shelter size by each of the different size groups found in the tanks are generally consistent with records from the field except that the smallest lobsters (15–19 mm CL) generally chose much larger gaps (but not holes) than expected. For

example, Edmunds (1995) found 17 mm CL lobsters in holes c. 25 mm high, but we found them choosing much larger gaps (32 and 38 mm high).

As discussed by Edmunds (1995), for lobsters <35 mm CL small holes closely fitting the body size of the lobster provide a high degree of protection from both predators and environmental forces. The close association of the lobster's size and hole dimensions is likely to restrict the entry of larger predators and enable the lobster to wedge itself in the hole to resist extraction and displacement. In contrast, the relatively spacious shelters frequently inhabited by >35 lobsters mm CL provide access for larger predators and provide fewer opportunities for wedging. However, these shelters frequently provide more opportunities for escape through additional openings or the enlarged opening, and for cohabitation with conspecifics which may facilitate protection through communal defence behaviour, increased prey vigilance, and concealment among conspecifics (Edmunds 1995). It is possible that the unexpectedly large open gaps selected by the 15–19 mm CL lobsters in the tank experiments above reflected some such joint defence behavioural choice elicited among these juveniles when placed in the most unnatural situation of having many small conspecifics in close proximity. The absence of direct predatory pressure may also have contributed, although because the lobsters were held for short periods (only a few days) it is not expected they had acclimatised to the conditions.

The choice of holes over gaps by all lobster size groups may indicate that holes are likely to be more effective than crevices in the construction of puerulus collectors. Indeed holes can be equally or even more effectual for *J. edwardsii* (A. Jeffs & S. Hooker, NIWA pers. comm.), but holes often fill with marine growth and silt and so are more difficult to maintain in a standard sampling condition than are crevices.

The preference exhibited toward the number of openings (entrances) in hole shelters (two for the smallest lobsters, with evidence for an ontogenetic shift in preference to one for the larger ones) was unexpected. In nature, the solitary and cryptic smaller lobsters (Butler et al. 1999) are most often observed in simple, single-opening holes such as pholad shafts; yet in the tanks, holes with two openings were chosen over those with one. One explanation might be that, although two openings are preferred—perhaps because of the additional escape route available—small holes with two openings are rare in nature. For the larger size groups of experimental lobsters, holes with one opening were used significantly more often than those with two, which is also at odds with the field observations for *J. edwardsii* summarised earlier. Again, part of the explanation may lie in there being few large holes with only one opening, the larger recesses more likely being crevices than holes.

Reservations associated with these laboratory studies include: (1) the small size of the tanks (see Rodriguez et al. 1993 for discussion of the implications of experimental scale); (2) most of the experiments were in static water that did not reflect the physical and chemical complexity of the natural benthic environment; (3) the lobsters may not have behaved naturally because they were contained, perceiving greater and more prolonged threat than in the wild; (4) any density-dependence of association was not addressed, although tank numbers were generally low; and (5) some results were inconclusive because of the necessarily low numbers of animals used. Nevertheless, laboratory experiments, in which certain components of the environment are controlled for, are well established and widely used in behavioural studies. They have potential to discern the effects of predator and prey pressure on habitation patterns in the field because these can be specifically excluded. When tank results are consistent with field observations, the conclusions are particularly compelling.

Recommendations for the design of ongrowing tanks and of artificial reefs aimed at enhancing juvenile survival in the wild can be made from this work. For all juvenile size groups up to at least 60 mm CL, but ignoring any practical issues associated with ongrowing such as tank cleaning and removal of excess food, and the economic need to maintain high lobster densities, horizontal holes should be provided over open horizontal gaps. The holes should have two openings for the smallest size groups but only one opening for the larger ones, and the shelters provided should have been conditioned for several months. Presumably provision of shelters with the optimal characteristics indicated by these experiments can result in less stressed lobsters that are more likely to thrive.

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REFERENCES

Agresti, A. 1990: Categorical data analysis. New York, John Wiley & Sons. 558 p.

Booth, J. D. 2001: Habitat preferences and behaviour of newly settled *Jasus edwardsii* (Palinuridae). *Marine and Freshwater Research 52*: 1055–1065.

Booth, J. D.; Forman, J. S. 1995: Larval recruitment in the red rock lobster, *Jasus edwardsii*. *New Zealand Fisheries Assessment Research Document 95/7*.

Booth, J. D.; Tarring, S. C. 1986: Settlement of the red rock lobster, *Jasus edwardsii*, near Gisborne, New Zealand. *New Zealand Journal of Marine and Freshwater Research 20*: 291–297.

Bradley, R. A.; Terry, M. E. 1952: Rank analysis of incomplete block designs I: the method of paired comparisons. *Biometrika 39*: 324–345.

Butler, M. J.; MacDiarmid, A. B.; Booth, J. D. 1999: The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Marine Ecology Progress Series 188*: 179–191.

Chen, S-B.; Watanabe, S.; Koike, Y.; Takagi, K. 1987: Biologically effective space in the artificial reef for the spiny lobster. *La Mer 25*: 109–118.

Dennis, D. M.; Skewes, T. D.; Pitcher, C. R. 1997: Habitat use and growth of juvenile ornate rock lobsters, *Panulirus ornatus* (Fabricius, 1798), in Torres Strait, Australia. *Marine and Freshwater Research 48*: 663–670.

Edmunds, M. 1995: The ecology of the juvenile southern rock lobster, *Jasus edwardsii* (Palinuridae: Hutton 1875). Unpublished PhD thesis, University of Tasmania, Australia.

Frusher, S.; Prescott, J.; Edmunds, M. 1999: Southern rock lobsters. *In*: Andrew, N. *ed.* Under southern seas. Sydney, University of New South Wales Press. Pp. 106–113.

Gabites, B. P. 1990: Shelter related distribution of the lobster *Jasus edwardsii*. Unpublished MSc thesis, University of Auckland, New Zealand.

Gardner, C.; Mills, D.; Ibbott, S.; Wilcox, S.; Crear, B. 2001: Preliminary investigation towards ongrowing puerulus to enhance rock lobster stocks while providing animals for commercial culture. Final Report (FRDC Project 1999/314) to the Fisheries Research and Development Corporation, Australia.

Herrnkind, W. F.; Jernakoff, P.; Butler, M. J. 1994: Puerulus and post-puerulus ecology. *In*: Phillips, B. F.; Cobb, J. S.; Kittaka, J. *ed.* Spiny lobster management. Oxford, Blackwell Scientific. Pp. 213–229.

Jernakoff, P. 1990: Distribution of newly settled western rock lobsters *Panulirus cygnus*. *Marine Ecology Progress Series 66*: 63–74.

Lewis, R. K. 1977: Rock lobster puerulus settlement in the south east. *South Australian Fishing Industry Council 13*: 9–11.

Lipcius, R. N.; Eggleston, D. B. 2000: Introduction: ecology and fishery biology of spiny lobsters. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fisheries and culture. Oxford, Blackwell Scientific. Pp. 1–41.

MacDiarmid, A. B. 1994: Cohabitation in the spiny lobster *Jasus edwardsii* (Hutton, 1875). *Crustaceana 66*: 341–355.

Marx, J. M.; Herrnkind, W. F. 1985: Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. *Bulletin of Marine Science 36*: 423–431.

Norman, C. P.; Yamakawa, H.; Yoshimura, T. 1994: Habitat selection, growth rate and density of juvenile *Panulirus japonicus* (von Siebold, 1824) (Decapoda, Palinuridae) at Banda, Chiba Prefecture, Japan. *Crustaceana 66*: 366–383.

R Development Core Team 2003: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (see: http://www.R-project.org)

Rodriguez, S. R.; Ojeda, F. P.; Inestrosa, N. C. 1993: Settlement of benthic marine invertebrates. *Marine Ecology Progress Series 97*: 193–207.

Sullivan, K. J.; O'Brien, C. J. 2002: Report from the Mid-Year Fishery Assessment Plenary, November 2002: stock assessments and yield estimates. Wellington, New Zealand, Ministry of Fisheries.

Yoshimura, T.; Yamakawa, H. 1988: Microhabitat and behavior of settled pueruli and juveniles of the Japanese spiny lobster *Panulirus japonicus* at Kominato, Japan. *Journal of Crustacean Biology 8*: 524–531.

Yoshimura, T.; Yamakawa, H.; Norman, C. P. 1994: Comparison of hole and seaweed habitats of post-settled pueruli and early benthic juvenile lobsters, *Panulirus japonicus* (von Siebold, 1824). *Crustaceana 66*: 356–365.

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Seasonal variations in chemical response to conspecific scents in the spotted spiny lobster, *Panulirus guttatus*

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Abstract Chemical response to conspecific scents mediate aggregations in some species of spiny lobsters, but patterns of co-denning of adult lobsters in their natural habitats vary widely. This is so for *Panulirus guttatus*, a small, sedentary, obligate reef-dwelling species with a protracted, almost year-round reproductive season. We hypothesised that changes in patterns of aggregation may vary with the intensity of reproductive activity in the population, which in turn may cause changes in responses to conspecific scents. To test this hypothesis, we conducted three laboratory experiments with Y-mazes to test for seasonal variations in gender-related and size-related response to conspecific scents in mature *P. guttatus*. When reproductive activity (RA) was high (experiment High-RA, 67.4% reproductive females), males responded significantly to scents of conspecifics of both genders, but females only to the scent of females. When reproductive activity had not yet reached its yearly lowest point (experiment Medium-RA, 50.0% reproductive females), only females responded significantly to scents of other females, and when reproductive activity was at its lowest (experiment Low-RA, 4.8% reproductive females) no treatment yielded significant responses. However, results of the size-related treatments showed that only large individuals responded significantly to scents of other large lobsters during the High-RA experiment, whereas during the Medium-RA only small individuals responded to scents of both small and large lobsters. These results are in accordance with previously observed size-dependent reproduction in *P. guttatus* over the protracted reproductive season. Therefore, chemical response to conspecific scents in *P. guttatus* vary with season, gender, and size and may influence co-denning patterns of mature individuals in the reef habitat.

Keywords chemical cues; *Panulirus guttatus*; reproductive activity; spiny lobster

INTRODUCTION

Conspecific chemical cues play an important role in the social behaviour of many decapods, including spiny lobsters (family Palinuridae) (Dunham 1978; Zimmer-Faust & Spanier 1987; Karavanich & Atema 1998). For example, chemical communication appears to mediate aggregation of conspecifics in *Panulirus interruptus* (Zimmer-Faust et al. 1985), *P. argus* (Ratchford & Eggleston 1998, 2000; Nevitt et al. 2000), and *Jasus edwardsii* (Butler et al. 1999). The influence of chemical cues in the aggregation of conspecifics is consequential because variations in gregariousness may cause marked differences in the patterns of distribution and hence in the susceptibility to the fishery of spiny lobsters (MacDiarmid 1994).

Experiments testing gregarious behaviour and the response of spiny lobsters to conspecific chemical scents (e.g., Childress & Herrnkind 1996; Ratchford & Eggleston 1998, 2000; Butler et al. 1999; Nevitt et al. 2000) have generally used immature individuals as experimental subjects because juveniles of spiny lobsters are highly gregarious (Atema & Cobb 1980). In contrast, aggregations of adult spiny lobsters in their natural habitats vary widely. For example, in California, United States, the distribution of individuals of *P. interruptus* in natural dens was random in the winter but aggregated in the spring, with no relationship between cohabitation

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and lobster gender (Zimmer-Faust & Spanier 1987). In *P. argus*, cohabitation varied greatly among coral reef sites in St. John, United States Virgin Islands, with cohabiting individuals often of the same gender (Herrnkind et al. 1975), whereas aggregations of adult *J. edwardsii* showed clear seasonal trends, which differed between mature males and females (MacDiarmid 1994).

Aggregations of adult *Panulirus guttatus* (Latreille, 1804), a small tropical spiny lobster that occurs throughout the Caribbean Sea, appear similarly variable both in the field and in the laboratory (Sharp et al. 1997; Lozano-Álvarez & Briones-Fourzán 2001; Segura-García et al. 2004; Lozano-Álvarez et al. unpubl. data). Individuals of *P. guttatus* are obligate crevice-dwellers and live in the reef habitat throughout their benthic life. Small juveniles are highly cryptic, but mature individuals are sedentary and have a limited home range (Sharp et al. 1997; Lozano-Álvarez et al. 2002; Negrete-Soto et al. 2002). Reproduction occurs almost year-round and large females breed more often through the protracted reproductive period than small mature females. A period of minimal reproduction occurs around late summer–early autumn, but the onset of this period varies from year to year (Chitty 1973; Briones-Fourzán & Contreras-Ortiz 1999; Negrete-Soto et al. 2002).

During field research into the patterns of den use of individuals of *P. guttatus* in fore-reef habitats in the Mexican Caribbean, we recorded more aggregations of individuals during winter–spring than during summer–autumn (Lozano-Álvarez et al. unpubl. data). We hypothesised that this pattern could be related to changes in the response to conspecific chemical cues in adult *P. guttatus* related to changes in the general reproductive activity of the population. We herein present results on laboratory experiments to test this hypothesis.

METHODS

The experiments were conducted in the Unidad Académica Puerto Morelos, Universidad Nacional Autónoma de México, located at Puerto Morelos on the Caribbean coast of Mexico (20°54′N, 86°54′W). Lobsters were collected by hand from the coral reef habitat, using nocturnal SCUBA diving. A few additional individuals were caught in traps (Segura-García et al. 2004). Lobsters were transported to the laboratory within 1 h of their collection and kept in acclimatisation tanks, 2 m in diameter and 1 m in

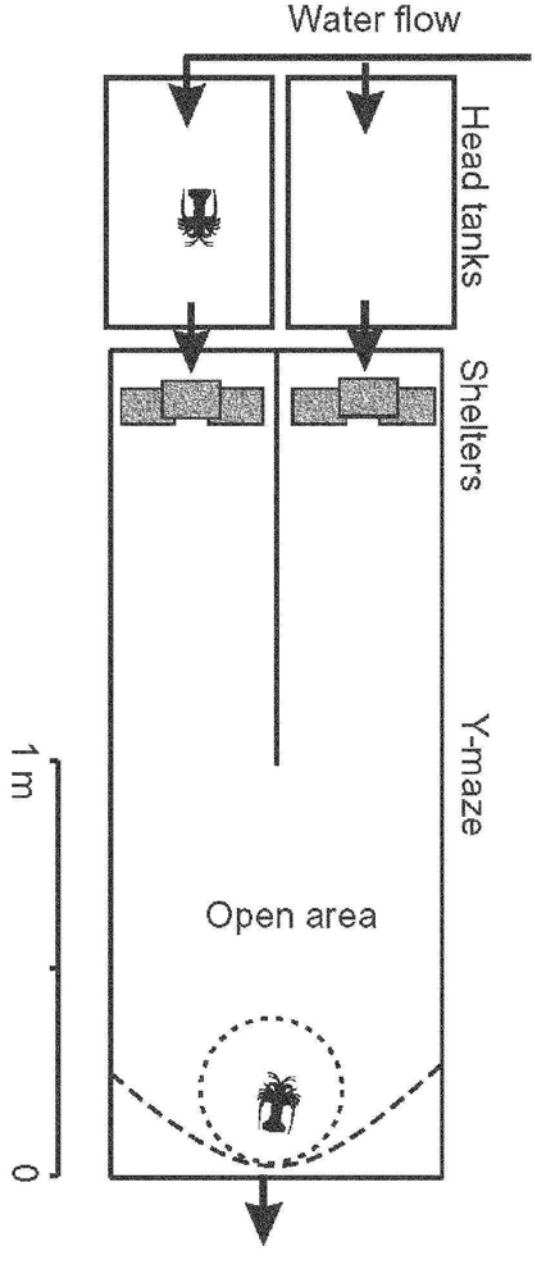

Fig. 1 Schematic representation of an experimental unit to test for response to conspecific scents in *Panulirus guttatus*. Sea water flowed through two head tanks, one of which contained a conspecific (scent producer), then into the arms of the Y-maze, just above two equal shelters made with concrete blocks. Water from both arms mixed in the open area of the Y-maze. One test lobster was placed at the start area of the Y-maze in the early evening and allowed to acclimatise in a wire mesh cylinder, which was removed after 2 h. Test lobster made a shelter choice by the following morning.

height, for 2 weeks. The acclimatisation tanks and the experimental units (see below) were kept under shade. A continuous seawater flow maintained ambient temperature in the tanks. Shelter for lobsters in the acclimatisation tanks was provided in the form of multiple segments of dark PVC pipes, 7.3 cm in diameter, sealed on one end and scattered over the floor of the tanks. During the acclimatisation period, lobsters were fed every other day with clams and mussels, but they were not fed during the experiments. Lobsters that moulted during the acclimatisation period were not used in the experiments. At the end of each experiment, lobsters were tagged and released in their natural habitat. Tags were applied to avoid collecting these lobsters again and using them in subsequent experiments.

Experimental set-up

We used four experimental units, each consisting of a Y-maze and two head tanks, to test for chemical response of individuals of *P. guttatus* to conspecific scents (Bushmann & Atema 1997; Ratchford & Eggleston 1998, 2000). The head tanks measured 0.6 × 0.5 × 0.5 m and each held c. 90 litres of water when filled to a standpipe height of 0.3 m. The Y-maze measured 2.0 × 0.8 × 0.6 m, and contained c. 500 litres when filled to a standpipe height of 0.3 m. A panel measuring 1.0 × 0.6 m divided half the length of the Y-maze into two equal arms (Fig. 1). Sea water from a continuous, open system flowed into the head tanks and from each head tank to an arm of the Y-maze. The water then mixed in an open area at the end of the two arms and later flowed out a standpipe at the opposite extreme of the tank, called the "start area" of the maze. The fibreglass head tanks and Y-mazes were completely opaque to preclude visual contact between lobsters and were mounted on different surfaces to eliminate the transference of vibrations. Also, to prevent the transference of acoustic cues through water, the water from the head tanks fell from a height of 5 cm above the water surface of the Y-maze.

Two identical shelters were placed, one in each arm. One of the shelters received water that had flowed through a head tank containing a conspecific whereas the other received water that had flowed through a head tank that held no lobster. The two shelters in each Y-maze were built with three concrete blocks forming a pyramid with a central den and were located 1.8 m from the start area, near the extremes of the Y arms (Fig. 1). Water flow into the head tanks was 1.5–2.0 litre min^{-1}. To prevent the possibility of lobsters using the corners in the start area of the Y-maze as refuges (Ratchford & Eggleston 1998), a semicircular wire-mesh screen was positioned at the start area (Fig. 1).

Trials were conducted at night. Lobsters were randomly assigned to specific treatments and to the left or right head tanks. The lobsters that were held in the head tanks were designated "scent producers" and those tested in the Y-maze "test lobsters". The scent producer was placed in the head tank 30 min before dark, and the test lobster was then placed in the start position of the Y-maze, where it was allowed to acclimatise within a mesh cylinder (0.45 m diam., 0.4 m height). After 2 h, the cylinder was removed and the test lobster was free to roam the Y-maze. Between 0900 and 1000 h the following morning, we recorded the position of the test lobster in the Y-maze as well as the flow rate into the head tanks. All lobsters were then removed and measured (carapace length (CL) from between the rostral horns to the posterior margin of the carapace, ± 0.1 mm). Lobsters were measured at the end of each trial to minimise stress from handling before the trials. To ensure that no scents remained after each trial, the head tanks and Y-mazes were drained and thoroughly brushed. Water was then allowed to flow at a high rate until the beginning of the next trial. No lobster was used more than once as scent producer and no lobster was used more than once as test lobster.

Experimental trials

Our main objective was to explore whether: (1) mature lobsters responded to conspecific scents; (2) this response was gender-related; and (3) the response was related to reproductive activities. Therefore, we used only sexually mature individuals (i.e., females 35 mm CL; males 45 mm CL, Sharp et al. 1997; Briones-Fourzán & Contreras-Ortiz 1999; Robertson & Butler 2003) and conducted three experiments at different seasons reflecting different intensities in reproductive activity in the general population, as indicated by the percentage of all females collected that were carrying egg-masses, new spermatophores, or remnants of egg capsules in their pleopods (reproductive females). We designated these experiments as High-RA (high reproductive activity, 67.4% reproductive females, February–April 2002), Medium-RA (medium reproductive activity, 50.0% reproductive females, July–September 2003), and Low-RA (low reproductive activity, 4.8% reproductive females, July–September 2002). The proportion of reproductive females was significantly different between

experiments High-RA and Medium-RA ($\chi^2 = 4.97$, d.f. = 1, $P = 0.025$). Although experiments Medium-RA and Low-RA were conducted over the same period in consecutive years, the different percentages of reproductive females were a result of the annual variation in the onset of the period of minimal reproductive activity.

Each experiment consisted of four treatments in which the paired combinations of scent producers:test lobsters were, respectively, males:males (M:M), females:females (F:F), males:females (M:F), and females:males (F:M). At least 18 replicates were run for each treatment. The result of each treatment was analysed as a one-tailed binomial test (Zar 1999). The null hypothesis was that choosing the shelter having the conspecific scent would have a probability of 0.5.

However, the possibility existed that the release of scent was size-related rather than gender-related (Ratchford & Eggleston 1998); therefore, we reanalysed the results by categorising lobsters into small and large individuals, based on the median size of all our experimental females and males. Thus, small lobsters comprised females 35.0–54.0 mm CL and males 45.0–62.0 mm CL, whereas large lobsters included females 54.1–66.8 mm CL and males 62.1–79.0 mm CL. This procedure yielded four paired combinations of scent producers:test lobsters—small:small (S:S), small:large (S:L), large:small (L:S), and large:large (L:L). The result of each size-related treatment was also analysed as a one-tailed binomial test.

In 55 trials during experiment High-RA, we observed the movement of test lobsters every 30 min during the first 1.5 h after the removal of the mesh cylinders, and recorded their position at the end of this period to assess whether lobsters explored both arms of the Y-maze or whether they chose one arm from the beginning of the experiment.

RESULTS

The movements of the 55 test lobsters observed during experiment High-RA for 1.5 h following the removal of the mesh cylinders were very variable. During this period, most lobsters explored one or both arms of the Y-maze but some remained in the start position or in the open area of the Y-maze. The arm of the Y-maze that the test lobsters first explored did not correspond to the arm containing the conspecific scent (26 of 55 trials) or to the arm containing the shelters chosen by the following morning (26 of 55 trials). Therefore, response of a test lobster to the scent of conspecifics was not immediate.

Significant differences in the mean size of lobsters occurred among experiments (one-way ANOVA on log-transformed data: $F = 18.078$, d.f. = 2, 533; $P < 0.0001$). Lobsters used in experiment High-RA were overall larger (mean ± SD: 59.4 ± 8.3 mm CL) than those used in experiments Medium-RA (54.3 ± 8.4 mm CL) and Low-RA (56.8 ± 7.4 mm CL).

Results of the gender- and size-related treatments are shown in Table 1. Over experiment High-RA, males responded significantly to male and female scents, whereas females only responded significantly to female scents. However, the only size-related treatment with a significant result was that of large individuals responding to scents of other large individuals (Table 1). In experiment Medium-RA, only females responded significantly to female scents, and only small individuals responded significantly to scents of both small and large conspecifics (Table 1). None of the trials conducted during experiment Low-RA yielded significant results (Table 1).

These results suggested that variations in the response to conspecific scents were related to the intensity of reproductive activity, but also that the response was highly influenced by the interaction of gender and size of individuals at different seasons. To fully test this interaction, it would have been necessary to break down the results of each experiment into four combinations of scent producers (SF, LF, SM, LM), each tested against the same four combinations of test lobsters. However, this procedure would have yielded too few replicates in most trial combinations to be of statistical consequence. As an alternative approach, we rearranged the data to test separately the joint effect of gender and size of scent producers on the response of test lobsters of either gender regardless of their size, and the joint effect of gender and size of test lobsters on their response to scent producers of either gender, also irrespective of size. This procedure yielded few replicates in about one third of the "new" treatments, but provided some insight into partial interaction effects (Table 2).

During experiment High-RA, the only new treatments with significant results were those of females responding to scents of large females, and of males responding to scents of large females and large males (Table 2, upper part). However, only the large males and females displayed significant responses (Table 2, lower part). In contrast, during experiment Medium-RA, the only new treatments

with significant results were those of females responding to scents of large females, small females, and small males (Table 2, upper part), and of small females responding to female and male scents (Table 2, lower part). No new treatments yielded significant results during experiment Low-RA (Table 2).

Table 1 Results of experiments exploring the response to conspecific scents in *Panulirus guttatus*. Experiment High-RA was conducted during a period of high reproductive activity in the population (February–April 2002); experiment Medium-RA during a period of medium reproductive activity (July–September 2003); experiment Low-RA during a period of minimal reproductive activity (July–September 2002). Four treatments were conducted in each experiment to test for different combinations of gender of scent producers and test lobsters (upper part of table; F, female; M, male). Data were then reanalysed to test for different combinations of size (lower part of table; S, small individuals, females 35.0–54.0 mm carapace length (CL) and males 45.0–62.0 mm CL; L, large individuals, females 54.1–66.8 mm CL and males 62.1–79.0 mm CL). (*N*, number of trials; *N* Yes, trials where test lobsters chose the shelter with the conspecific scent. *P* values were based on one-tailed binomial tests (Zar 1999), where the probability of choosing a shelter having the conspecific scent was 0.5.)

		Experiment conducted during:								
Scent	Test	High-RA			Medium-RA			Low-RA		
producers	lobsters	*N*	*N* Yes	*P*	*N*	*N* Yes	*P*	*N*	*N* Yes	*P*
F	F	23	16	0.046	18	15	0.004	23	13	0.339
F	M	23	18	0.005	17	8	0.500	20	13	0.132
M	F	23	15	0.105	20	14	0.058	20	13	0.132
M	M	38	26	0.017	20	13	0.132	27	16	0.221
S	S	19	10	0.500	29	20	0.031	23	14	0.202
S	L	25	16	0.115	21	12	0.332	26	16	0.163
L	S	24	16	0.076	15	12	0.018	23	15	0.105
L	L	39	33	0.000	10	6	0.377	18	10	0.407

Table 2 Breakdown of results to test the combined effect of gender and size of scent producers on the response of test lobsters (*Panulirus guttatus*) of either gender regardless of their size (upper part of table), and the joint effect of gender and size of test lobsters on their response to scent producers of either gender, also irrespective of size (lower part of table). Statistical analyses and labels as in Table 1.

		Experiment conducted during:								
Scent	Test	High-RA			Medium-RA			Low-RA		
producers	lobsters	*N*	*N* Yes	*P*	*N*	*N* Yes	*P*	*N*	*N* Yes	*P*
SF	F	9	4	0.500	13	10	0.046	12	8	0.194
SF	M	8	6	0.144	12	4	0.194	12	7	0.387
LF	F	14	12	0.006	5	5	0.031	11	5	0.500
LF	M	15	12	0.018	5	3	0.500	8	6	0.144
SM	F	10	6	0.377	14	11	0.029	12	7	0.387
SM	M	15	9	0.304	10	5	0.623	13	8	0.291
LM	F	13	9	0.133	6	4	0.344	8	6	0.145
LM	M	23	17	0.017	10	8	0.055	14	8	0.395
F	SF	9	5	0.500	12	10	0.019	11	8	0.113
F	LF	14	11	0.029	6	5	0.109	12	5	0.387
F	SM	10	7	0.172	7	3	0.500	11	7	0.274
F	LM	13	11	0.011	10	5	0.623	9	6	0.254
M	SF	10	7	0.172	13	10	0.046	14	9	0.212
M	LF	13	8	0.291	7	4	0.500	6	4	0.344
M	SM	15	8	0.500	11	8	0.113	10	5	0.623
M	LM	23	18	0.005	9	5	0.500	17	11	0.166

DISCUSSION

Identifying potential mating partners and competitors is an important aspect of social behaviour in resident lobster populations and conspecific, waterborne odours are likely to convey this information (Atema & Cowan 1986; Karavanich & Atema 1998; MacDiarmid & Butler 1999). Locating appropriate shelters is important to spiny lobsters, and conspecific odours may provide individuals with a means of assessing the quality of a potential shelter (Nevitt et al. 2000).

Therefore, lobsters may respond to scents of conspecifics of both genders and tend, in general, to do so. Without any considerations to gender or size, response to conspecific scents would have been significant in our three experiments (experiment High-RA: N trials = 107, 75 responded, $P < 0.0001$; Medium-RA: $N = 75$, 50 responded, $P = 0.003$; Low-RA: $N = 90$, 55 responded, $P = 0.022$). However, specific treatments in which lobsters significantly chose shelters with conspecific scents occurred only during experiments High-RA and Medium-RA, and significant responses varied also with gender and size.

We do not know if what changed in time was the scent production, the receptivity to the scent, or both. Ratchford & Eggleston (2000) found that in *P. argus* it was the scent production, not the receptivity to the scent that varied in time, but their experimental individuals were sexually immature. Because all our experimental individuals were adults, our results suggest that changes in chemical responses were related to the time within the protracted reproductive period, the size of individuals involved in reproductive activities, and probably the physiological state of individuals. For example, physiological changes before and during the moult may change the general body odour of individuals (Atema & Cowan 1986). Thus, interpretation of these results should be set in the context of the reproductive and moult cycles of *P. guttatus*.

In the Mexican Caribbean, large females of *P. guttatus* start breeding early and produce several broods during the prolonged reproductive period. In contrast, the onset of both the beginning and the end of reproductive activity in small females varies more widely from year to year, but spring is an important reproductive season for both small and large females (Briones-Fourzán & Contreras-Ortiz 1999). Thus, as expected, significantly more females were reproductive during experiment High-RA than during experiment Medium-RA. However, the percentage of small reproductive females was similar in both experiments (68.6 and 55.3% respectively, $\chi^2 = 1.48$, d.f. = 1, $P = 0.224$), whereas the percentage of large reproductive females was greater in experiment High-RA (66.7%) than in experiment Medium-RA (39.1%) ($\chi^2 = 5.13$, d.f. = 1, $P = 0.024$). This suggests that at the time of experiment Medium-RA, large lobsters were nearer their yearly period of minimal reproductive activity than small lobsters.

We did not moult-stage our experimental lobsters, but most adult *P. guttatus* moult at the end of the reproductive period (Chitty 1973; Robertson & Butler 2003). Moreover, spiny lobsters usually remain secluded during the vulnerable pre- to post-moult stages. If large *P. guttatus* in the population end their reproductive activities and start moulting before small individuals, this could explain the smaller mean size of our experimental lobsters during experiments Medium-RA and Low-RA. This is in accordance with Negrete-Soto et al. (2002), who found that the mean size of trap-caught *P. guttatus* in the reef habitat at Puerto Morelos decreased during June–October.

Inter-gender responses differed between experiments High-RA and Medium-RA. In experiment High-RA, males responded significantly to the scents of large females, but the response of females to male scents was not significant. However, only large males displayed significant responses. Experiment High-RA was conducted at the peak of the reproductive period during which, as noted before, large females of *P. guttatus* may breed several times. Small male spiny lobsters are sperm-limited but large males, capable of repeated copulations (MacDiarmid & Butler 1999), may respond more strongly to the scent of large than small females regardless of ovigerous state because large females may mate again. In contrast, ovigerous females may become less responsive to male scents until after their current eggs hatch. For example, ovigerous females of *J. edwardsii* display no preference for empty or occupied shelters (MacDiarmid & Kittaka 2000).

In experiment Medium-RA, by contrast, inter-gender responses were not significant overall, but small individuals were more responsive to conspecific odours than large individuals. Moreover, it was mostly the small females that responded to male scents, and females in general that responded mostly to scents of small males (Table 2), further supporting the notion that large individuals had already decreased their reproductive activity and that the population in general was approaching the period of minimal reproductive activity. Although female spiny lobsters prefer to mate with large males, they

may become less selective when the time of egg extrusion is near (MacDiarmid & Kittaka 2000). We can only speculate that if small females were at this point they would be sensitive to male scents, and more so to scents of small males if scents of large males change when they have exhausted their sperm supply.

In intra-gender treatments, females responded significantly to female scents in experiments High-RA and Medium-RA, but the response of males to male scents differed in both experiments. In *P. guttatus*, cohabitation of multiple females in the same den with one mature male is common (Sharp et al. 1997); thus, the presence of female scent may increase the quality of that shelter to other reproductive females (Nevitt et al. 2000). More large females were reproductive during experiment High-RA than during experiment Medium-RA, hence the differential effect of size on responses shown by females to female scents in both experiments. In the latter experiment, however, the low number of replicates in treatments involving large females may have masked their response to female scents in general.

In contrast to females, males responded significantly to male scents in experiment High-RA but not in experiment Medium-RA, but it was mostly the large males that exhibited a significant response, and trials involving large males were less numerous in experiment Medium-RA. Male spiny lobsters are aggressive towards each other, particularly during the reproductive season (MacDiarmid & Kittaka 2000), and in *P. guttatus* large males confront and are capable of evicting smaller males that approach and enter their den (Lozano-Álvarez & Briones-Fourzán 2001; Segura-García et al. 2004). Therefore, when reproductive activity is high, the presence of male scent may signal to other males the proximity of a suitable den occupied by a potential competitor. This does not mean that males would congregate in a den, only that males respond to scents of other males, because the outcome of their proximity would probably depend on further agonistic interactions (e.g., Atema & Cowan 1986; Karavanich & Atema 1998; Segura-García et al. 2004).

In summary, olfaction appears to play a key role in initiating aggregations of adult *P. guttatus*, particularly during the reproductive period. However, the ability to respond to conspecific scents would not necessarily translate into an indiscriminate aggregation of lobsters, since the outcome of the initial chemical response would depend on the physiological state of individuals and on further behavioural interactions. These results may help to explain seasonal variations in cohabitation patterns of *P. guttatus* (Lozano-Álvarez et al. unpubl. data) and provide an arena for future experiments to test more specific hypotheses.

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REFERENCES

Atema, J.; Cobb, J. S. 1980: Social behavior. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters, Vol 1. New York, Academic Press. Pp. 409–450.

Atema, J.; Cowan, D. F. 1986: Sex-identifying urine and molt signals in lobster (*Homarus americanus*). *Journal of Chemical Ecology 12*: 2065–2080.

Briones-Fourzán, P.; Contreras-Ortiz, G. 1999: Reproduction of the spiny lobster *Panulirus guttatus* (Decapoda: Palinuridae) on the Caribbean coast of Mexico. *Journal of Crustacean Biology 19*: 171–179.

Bushmann, P. J.; Atema, J. 1997: Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*. *Canadian Journal of Fisheries and Aquatic Science 54*: 647–654.

Butler, M. J. IV; MacDiarmid, A. B.; Booth, J. D. 1999: The cause and consequence of ontogenetic changes in social aggregations in New Zealand spiny lobster. *Marine Ecology Progress Series 188*: 179–191.

Childress, M. J.; Herrnkind, W. F. 1996. The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. *Animal Behaviour 51*: 675–687.

Chitty, N. 1973: Aspects of the reproductive biology of the spiny lobster, *Panulirus guttatus* Latreille. Unpublished MSc thesis, University of Miami, Florida, United States.

Dunham, P. J. 1978: Sex pheromones in Crustacea. *Biological Review 53*: 555–583.

Herrnkind, W. F.; VanDerwalker, J. A.; Barr, L. 1975: Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S.V.I.: (IV) Habitation, patterns of movement and general behavior. *Natural History Museum of Los Angeles County Science Bulletin 20*: 31–45.

Karavanich, C.; Atema, J. 1998: Olfactory recognition of urine signals in dominance fights between male lobsters, *Homarus americanus*. *Behaviour 135*: 719–730.

Lozano-Álvarez, E.; Briones-Fourzán, P. 2001: Den choice and shelter occupation patterns in two sympatric lobster species, *Panulirus argus* and *Panulirus guttatus*, under experimental conditions. *Marine and Freshwater Research 52*: 1145–1155.

Lozano-Álvarez, E.; Carrasco-Zanini, G.; Briones-Fourzán, P. 2002: Homing and orientation in the spotted spiny lobster, *Panulirus guttatus* (Latreille, 1804), towards a subtidal coral reef habitat. *Crustaceana 75*: 859–873.

MacDiarmid, A. B. 1994: Cohabitation in the spiny lobster *Jasus edwardsii* (Hutton, 1875). *Crustaceana 66*: 341–355.

MacDiarmid, A. B.; Butler, M. J. IV. 1999: Sperm economy and limitation in spiny lobsters. *Behavioral Ecology and Sociobiology 46*: 14–24.

MacDiarmid, A. B.; Kittaka, J. 2000: Breeding. *In*: Phillips, B. F.; Kittaka, J. *ed*. Spiny lobsters: fisheries and culture. 2nd ed. New York, Academic Press. Pp. 485–507.

Negrete-Soto, F.; Lozano-Álvarez, E.; Briones-Fourzán, P. 2002: Population dynamics of the spotted spiny lobster, *Panulirus guttatus*, in a coral reef on the Mexican Caribbean. *Journal of Shellfish Research 21*: 279–288.

Nevitt, G.; Pentcheff, N. D.; Lohmann, K. J.; Zimmer, R. K. 2000: Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecific odours in the field. *Marine Ecology Progress Series 203*: 225–231.

Ratchford, S. G.; Eggleston, D. B. 1998: Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. *Animal Behaviour 56*: 1027–1034.

Ratchford, S. G.; Eggleston, D. B. 2000: Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. *Animal Behaviour 59*: 793–799.

Robertson, D. N.; Butler, M. J. IV. 2003: Growth and size at maturity in the spotted spiny lobster, *Panulirus guttatus*. *Journal of Crustacean Biology 23*: 265–272.

Segura-García, I.; Lozano-Álvarez, E.; Briones-Fourzán, P. 2004: Within-shelter behaviour of the spotted spiny lobster, *Panulirus guttatus* (Latreille), in simulated communal dens: an exploratory study. *Marine and Freshwater Behaviour and Physiology 37*: 17–30.

Sharp, W. C.; Hunt, J. H.; Lyons, W. C. 1997: Life history of the spotted spiny lobster, *Panulirus guttatus*, an obligate reef-dweller. *Marine and Freshwater Research 48*: 687–698.

Zar, J. H. 1999: Biostatistical analysis. 4th ed. Upper Saddle River, New Jersey, Prentice-Hall.

Zimmer-Faust, R. K.; Spanier, E. 1987: Gregariousness and sociability in spiny lobsters: implications for den habitation. *Journal of Experimental Marine Biology and Ecology 105*: 57–71.

Zimmer-Faust, R. K.; Tyre, J. E.; Case, J. F. 1985: Chemical attraction in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin 169*: 106–118.

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Stock enhancement of rock lobsters (*Jasus edwardsii*): timing of predation on naïve juvenile lobsters immediately after release

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Abstract The success of enhancement programmes hinges on the survival of released animals. One factor greatly influencing short-term survival of reseeded lobsters is the timing and intensity of predation relative to the time of release. The activity and abundance of predators varies over daily, seasonal, and annual scales and knowing the best time to release juveniles will minimise mortality. We used chronographic tethering devices and remote video equipment at 10 sites near Wellington, New Zealand and Hobart, Tasmania, Australia, to assess the relative timing and intensity of predation for released lobsters. Our studies showed that predation was greatest within the first 2 h after release ($\chi^2 = 60.425$, d.f. = 9, $P < 0.001$) suggesting that the disturbance associated with the release itself may draw the unwanted attention of predators. Relative predation rates also peaked on each of the following two mornings, possibly because of the emergence of daytime predators. The video footage obtained at the Tasmanian sites revealed that most predation was by fish (46%), but surprisingly, cannibalism comprised 16% of predation events. The limitations of tethering as a method are discussed in numerous reviews but proved useful as a relative measure for these highly mobile and cryptic animals. Further consideration needs to be given to methods of release that minimise mortality of recently seeded lobsters.

Keywords rock lobster; *Jasus edwardsii*; tethering; relative predation; stock enhancement

INTRODUCTION

Marine stock enhancement, the release of eggs, larvae, or juveniles, is typically employed to replenish depleted wild stocks or to supplement existing stocks that may be operating below maximum carrying capacity because of, for example, low settlement (Blankenship & Leber 1995; Munro & Bell 1997). Stock enhancement has been practiced since the early 1800s but the majority of early attempts met with limited success, largely because of an inadequate understanding of the ecology of early life stages of most marine organisms (Munro & Bell 1997).

Recently, a joint Australian and New Zealand research programme has been studying the behavioural ecology of juvenile rock lobsters (*Jasus edwardsii* Hutton) to determine the feasibility of their release into the wild. The impetus for this enhancement research was to provide information for managing the harvest of pueruli for ongrowing, or rearing to a larger size, in captivity in Tasmania, Australia.

Because of a current inability to hatchery-rear rock lobsters from eggs, juveniles required for aquaculture must be harvested from the wild. In Tasmania, permits for harvesting wild pueruli have been issued on the condition that a proportion of the juveniles be released after 1 year to compensate for their removal from the wild stocks. When this proportion is greater than natural survival over the same period, a level of fishery enhancement is achieved (Gardner et al. 2000).

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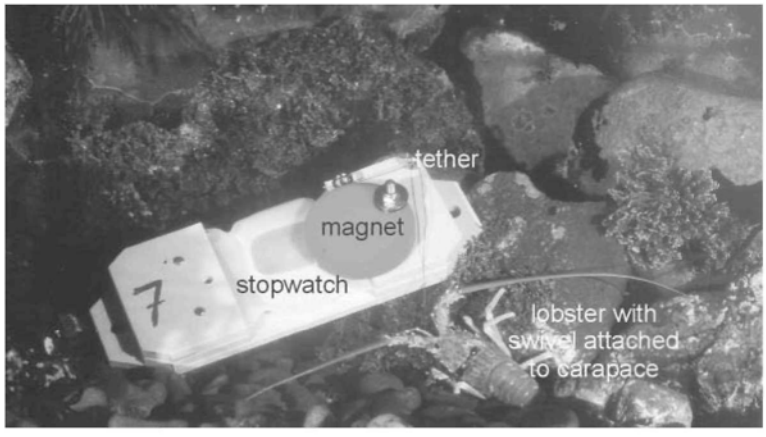

Fig. 1 Juvenile lobster (*Jasus edwardsii*) tethered to a chronographic tethering device (CTD). Lobsters were placed near suitable dens into which they could withdraw for protection.

Issues arising from this process include the possible influence of captivity on the behaviour and survival of juveniles after release (Brown & Day 2002), the suitability of habitat into which juveniles are released (Leber et al. 1996), and the methods of release (Leber et al. 1997). Research within this programme has shown that juvenile rock lobsters reared from puerulus in captivity for 1 year and released back into the wild display similar anti-predator behaviours and activity patterns as wild conspecifics (Oliver et al. unpubl. data). This indicates that apparent behavioural changes observed in captivity, such as a breakdown of strict nocturnal activity, do not affect survival after release.

Another variable that should be considered when planning enhancement programmes is the intensity and diel timing of predation (Leber et al. 1997). Fish predators, in general, vary substantially in abundance across spatial and temporal scales (Holbrook et al. 1994) and determining when predation risk is greatest may improve release protocols and juvenile survival rates. Furthermore, the act of release not only disturbs and agitates the lobsters, which may make them more vulnerable to predation, but the disturbance created by divers, boats, or simply the sudden appearance of prey animals where before there were none, may invite the unwanted attention of predatory species.

Tethering has been used successfully in several predator-prey systems to assess predation on temporal and spatial scales (Heck & Wilson 1987; Minello 1993; Peterson et al. 2001). Tethering results represent the predation potential, defined as the rate at which prey would be consumed if they were readily available to predators (Kneib & Scheele 2000) and despite its limitations (Aronson & Heck 1995; Peterson et al. 2001), is useful for measuring relative predation rates in highly mobile and cryptic animals such as lobsters.

In this paper we present the results of experiments conducted near Wellington, New Zealand and Hobart, Tasmania, Australia to determine when predation upon released lobsters was most likely to occur. Using chronographic tethering devices and video surveillance equipment at 10 sites we could assess the best time of the day to release lobsters to minimise mortality from predation.

METHODS

New Zealand experiment

Several hundred post-puerulus lobsters (10–12 mm carapace length (CL)) were collected over a period of 6 months from Gisborne, New Zealand, using crevice-type puerulus collectors (Booth & Tarring 1986), and reared in captivity in a laboratory in Wellington for 1–2 years, yielding a variety of different-sized captive-reared lobsters. The animals were kept communally in 300-litre tanks with fresh sea-water flow in excess of 1 litre/h per 100 g of body weight, and provided with aeration. Freshly opened mussels (*Perna canniculus*) were fed to the lobsters daily during daylight hours and the empty shells removed 24 h later. Predators were absent.

Twenty chronographic tethering devices (CTDs) were designed and built using cheap stopwatches with implanted reed switches. Lobsters were tethered to a magnet which, when turned during a predation event, passed over the reed switch and stopped the clock. Using this method we could calculate the time of predation. The tension of the magnet was adjusted to ensure that the strength of a lobster tail flipping would not trigger the timer. These devices were

fastened to lead anchors (c. 100 g) with steel grapple-hooks so that neither lobsters or predators could remove them.

Fifty-eight intermoult juvenile lobsters ranging in size from 37 to 41 mm CL were tethered to these chronographic tethering devices at six sites in Wellington Harbour over a period of 8 months (February–October). Lobsters were attached to the CTD (Fig. 1) using a monofilament nylon line tied around the thorax between the 3rd and 4th legs. A swivel was mounted on the dorsal surface of the carapace to reduce tangling. The tether was c. 30 cm long. Lobsters were placed in hides into which they could fully withdraw to avoid predators, and the anchor placed adjacent to the hide. Roughly equal numbers of tethered lobsters were placed out at each of the six sites for 48 h. They were monitored at 24 and 48 h intervals, after which they were removed.

We did not control for the effects of tethering by releasing un-tethered lobsters because previous movement and survival experiments on these reefs have resulted in very low resighting rates. The relative influence of emigration and predation on these low resighting rates has been difficult to tease apart and consequently we needed to eliminate the influence of emigration, by tethering, when determining predation rate in this experiment. Likewise, controls were impractical in the Tasmanian experiment outlined below because of the fixed camera angle.

The sites chosen comprised shallow Mesozoic greywacke reef areas covered with the giant kelp, *Macrocystis pyrifera*, fucoidal macroalgae, and beds of laminarian algae. All sites were c. 5 m in depth and bordered by sand on the seaward sides.

Tasmanian experiment

Lobster pueruli were collected from Bicheno on the east coast of Tasmania. Rearing conditions were similar to those in New Zealand, although lobsters were fed a mixed diet of opened fresh blue mussels (*Mytlius edulis planulatus*) and commercial prawn pellets. Lobsters were grown in tanks for 12–15 months, attaining a CL of 30–52 mm. As with New Zealand trials, animals were reared without predators and in aerated tanks with flow through water supply with exchange rates in excess of 1 litre/h per 100 g body weight, plus aeration.

Tethering trials were conducted at four sites in southern and south-eastern Tasmania of varying exposure and habitat complexity. Winter (June–August) trials were conducted at all sites and were replicated in summer (December–February) at two sites.

On each occasion, two replicate tethering trials were conducted over consecutive 48 h periods. For each replicate, 20 lobsters were tethered to 20 numbered, 100 g lead anchors with steel grapple hooks using a 25–30 cm length of nylon monofilament line. The attachment of lines to lobsters and placement of lobsters within hides was the same as per the New Zealand trials. Where necessary, macroalgal stipes were removed from the tethered range of the lobster to avoid entanglement. Positions of tethered lobsters were recorded relative to a 50 m transect line deployed across the site. For replicate trials the transect line was moved to ensure that individual hides were used only once. This was done to minimise any consistent bias from hide selection.

During each replicate, six or more lobsters were monitored using a remote infrared-capable camera system. The system consisted of six low light (0.05 lux) monochrome CCD cameras with accompanying twin infrared light sources, linked by 30 m cables to a surface pontoon. The pontoon housed an eight-channel multiplexor (to allow the signal from all cameras to be recorded on a single videotape), a time-lapse video cassette recorder (VCR), video transmitter, and batteries to power the system. Infrared lights were set by timer to come on at dusk and turn off at dawn. Tape speed on the VCR was set to record 24 h of footage on a 3 h tape, and multiplexor frame rate was set at 80 ms, providing an image from each camera every 480 ms. Camera signals could be recorded using the VCR on the pontoon, or a transmitted signal could be recorded at a remote base station.

Divers noted the presence or absence of each tethered lobster after 24 h, and again at 48 h, when all lobsters were removed. If lobsters being observed by cameras were missing after 24 h, the camera was moved to another lobster to maximise the number of predation events observed. Ninety-nine individual lobsters and their fate were recorded in roughly equal numbers across all sites.

Video footage was later reviewed in the laboratory, when time of predation and identity of predators was established.

Data analyses

We recorded when the tethered lobsters were deployed and recovered, whether the lobsters had been preyed upon and, if so, the time displayed on the watches or the video. We could then calculate the survival time and use survival analysis techniques to determine if there were any differences in survival between sites in both New Zealand and

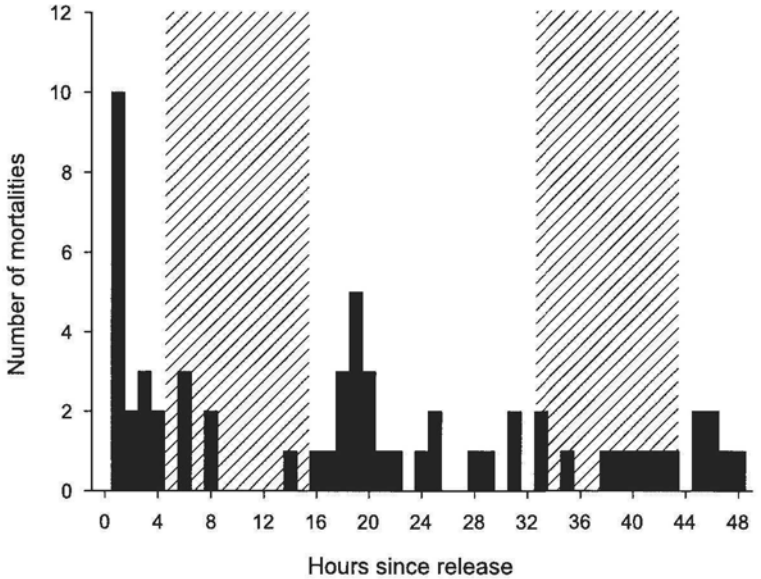

Fig. 2 Total number of mortalities at all sites since release. Shaded areas represent the hours of darkness.

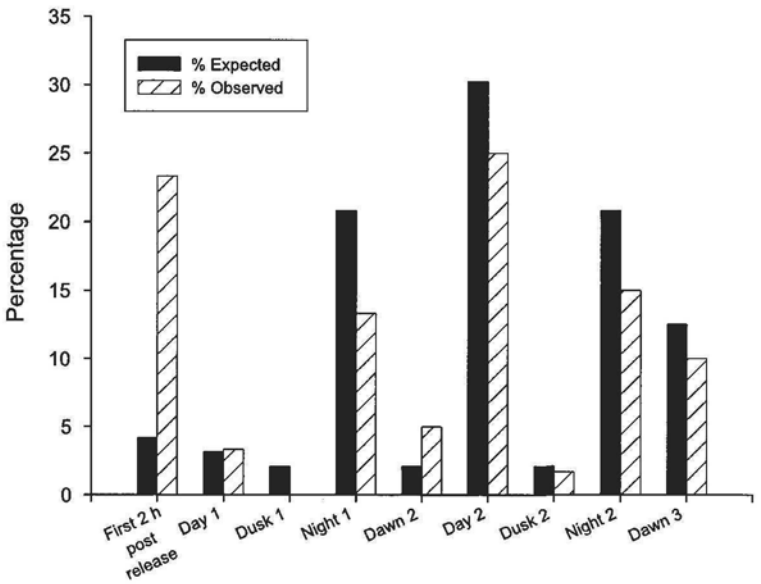

Fig. 3 Percentage of mortalities over progressive time periods since release at all sites.

Tasmania. We used the statistical package NCSS to run the analyses, including log rank tests to compare survival curves and regression analyses to investigate the influence of CL and season on mortality.

The timing of predation was analysed using chi-square tests. The 48 h experiment was divided into post-release, dawn, dusk, day, and night categories to determine the frequency of predation events within these time periods and assist analyses.

RESULTS

Survival analyses revealed that there was no significant difference in the distribution of survival rates between sites in New Zealand or Australia (Log-rank test $\chi^2 = 10.66$, d.f. = 8, $P = 0.222$). The data were then analysed without site as a factor to yield a plot of survival over time (Fig. 2). Fifty per cent of all tethered lobsters survived the 48 h experiment.

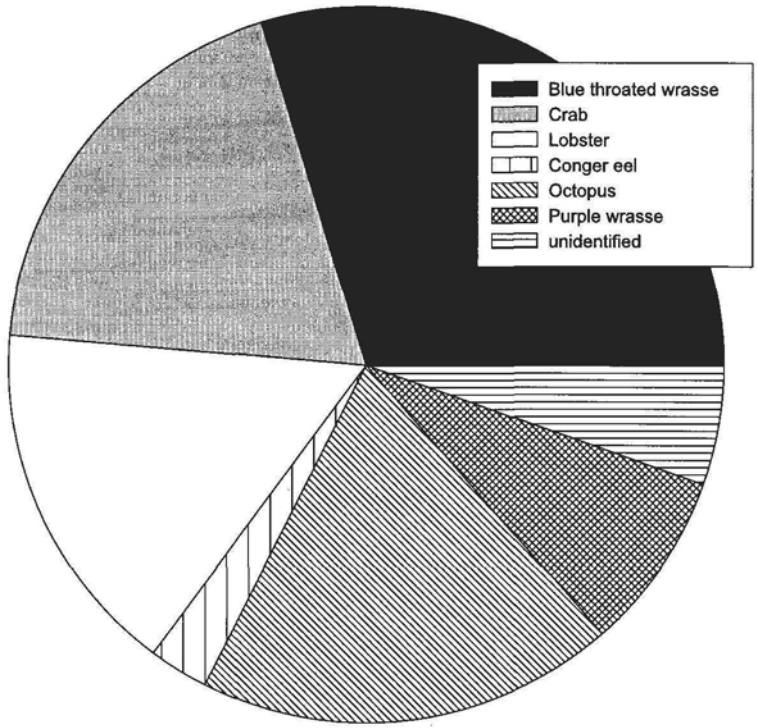

Fig. 4 Proportion of predation mortality by each predator identified using the remote video equipment in Tasmania, Australia.

Frequency distribution and chi-square analyses revealed a significantly greater chance of predation within the first 2 h after release ($\chi^2 = 60.425$, d.f. = 9, $P < 0.001$). Lobsters were 5 times more likely to be preyed upon immediately following release than expected by chance alone; this time period contributed to 87% of the chi-square statistic (Fig. 3). A smaller 4% of the chi-square statistic was explained by predation the following dawn (Fig. 3).

Regression analyses revealed there was no significant relationship between survival time and CL ($r^2 = 0.00498$, $P = 0.444$) or season ($r^2 = 0.0173$, $P = 0.152$).

Remote camera observations made in the Tasmanian experiments revealed that of 37 recorded events where the predator could be identified, lobsters were predated upon by fish 46% of the time (blue throated wrasse, *Notolabrus tetricus* 30%; purple wrasse, *N. fucicola* 8%, conger eel 3%, and unidentified species 5%) (Fig. 4). Octopus (*Pinnoctopus cordiformis*, formerly *Octopus maorum*) and crabs (*Nectocarcinus* spp.) were also key predators representing 19% of the predation events each (Fig. 4). Somewhat surprisingly, cannibalism was very high with 16% of recorded predation events being attack of the tethered lobster by a larger (estimated CL >80 mm) free-roaming lobster (Fig. 4).

Divers in Wellington also observed high predation rates by octopus and fish immediately after the tethered lobsters were placed out in the field. Small schools of a highly curious wrasse species (*Notolabrus cheliodotus*) were observed to attack and kill experimental lobsters during release, despite the ability of the lobster to withdraw on the long tether into a den.

DISCUSSION

There were no detectable differences in relative predation rates across sites in New Zealand and Tasmania probably because of the suitability of sites chosen for study. All sites provided suitable shelter in the form of dens and macroalgae cover and although predator density and composition was expected to vary on spatial (including trans-Tasman) and temporal scales, this did not induce significant differences in timing and intensity of predation across sites. Given that the lobster's ability to escape from predators was restricted by the tether, predation was relatively low, with only 51% mortality over all 10 sites after 48 h. This was to be expected given the size of tethered lobsters (31–55 mm CL) and the fact that ongrowing them for 1 year is intended to allow

lobsters to obtain a size at which they are less vulnerable to predation (Kington 1999).

The high mortality rates within the first 2 h of release suggest that predators were attracted by the activity of divers, and release protocols may need to provide for greater protection of the lobsters in the first 24 h, such as traps or cages that open to release lobsters at a set time after any disturbance abates. Further, placing lobsters outside of areas or dens not occupied by wild residents may make them more vulnerable to predation because of our anthropomorphic interpretation of den suitability and absence of group defense (Butler et al. 1999). In addition, the behaviour of fish predators varies enormously with diver disturbance. Octopus and some fish species, such as wrasse, are exceptionally curious about the activity of divers (Kulbicki 1998) and, as observed in Wellington, even small fish in large numbers are capable of immobilising and killing a lobster that has just been released without time to find shelter. These observations are consistent with studies of predation on hatchery-reared homarid lobsters released into the wild. Van der Meeren (2000) reported that juvenile *Homarus gammarus* were more vulnerable to predation immediately after release whilst searching for shelter.

Predation was also higher than expected by chance alone during the dawn following release. Crepuscular periods are times of transition between diurnal and nocturnal fish species and also periods of major activity and success of piscivores and invertebrate feeders (Helfman 1986). Previous research has demonstrated that spiny lobsters reared in captivity without predators are more conservative with emergence times when exposed to predators than wild lobsters or those with recent predator experience (Oliver et al. unpubl. data), thus we would have expected the tethered lobsters to have returned to shelter by dawn. This could be another artefact of tethering, however; if lobsters were exposed to predators because of entanglement during the course of their nocturnal activity, for example.

The high number of cannibalistic events recorded on video in Tasmania was surprising and is possibly an artefact of tethering. Lobsters are social at this size and would be expected to aggregate in dens with like-sized and larger conspecifics (Butler et al. 1999). Although cannibalism is virtually impossible to record in the wild, agonistic behaviour is associated with dominance and access to shelter and food (Thomas et al. 2003), and where these resources are scarce, as they may have been at these experimental sites, cannibalism may be common.

The relative merits of tethering techniques are discussed in numerous reviews and papers (Minello 1993; Peterson & Black 1994; Zimmer-Faust et al. 1994; Aronson & Heck 1995; Kneib & Scheele 2000). It is important to emphasise that the tethering results given here are relative measures of predation over time in representative habitats and may not reflect natural predation rates. Nonetheless, the tethering estimates are useful for indicating when tethered lobsters are most likely to be preyed upon relative to the time of release.

The chronographic tethering device used in the New Zealand study is a simple and inexpensive method of measuring survival time of highly mobile and cryptic prey such as lobsters. Despite problems with some of the mechanisms not working, we were able to record 29 predation events across six sites. The remote video equipment used in the Tasmanian study was more reliable, however, and provided valuable information about the predator.

Further consideration should be given to minimising the disturbance created by divers, boats, and the method of release. Weighted nets, pots with simple trapdoor release mechanisms, or similar devices could be used to minimise post-release mortality associated with reseeding initiatives.

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REFERENCES

Aronson, R. B.; Heck, K. L. J. 1995: Tethering experiments and hypothesis testing in ecology. *Marine Ecology Progress Series 112*: 307–309.

Blankenship, H. L.; Leber, K. M. 1995: A responsible approach to marine stock enhancement. *American Fisheries Society Symposium 15*: 167–175.

Booth, J. D.; Tarring, S. C. 1986: Settlement of the red rock lobster (*Jasus edwardsii*), near Gisborne, New Zealand. *New Zealand Journal of Marine and Freshwater Research 20(2)*: 291–297.

Brown, C.; Day, R. L. 2002: The future of stock enhancement: lessons for hatchery practice from conservation biology. *Fish and Fisheries 3*: 79–94.

Butler, M. J.; MacDiarmid, A. B.; Booth, J. D. 1999: The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Marine Ecology Progress Series 188*: 179–191.

Gardner, C.; Mills, D.; Ibbot, S.; Wilcox, S.; Crear, B. J. 2000: Preliminary investigation towards ongrowing puerulus to enhance rock lobster stocks while providing animals for commercial culture. Fisheries Research and Development Corporation Final report 1999/314.

Heck, K. L. J.; Wilson, K. A. 1987: Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology 107*: 87–100.

Helfman, G. S. 1986: Fish behaviour by day, night and twilight. *In*: Pitcher, T. J. *ed.* The behavior of teleost fishes. London, Croom Helm. 553 p.

Holbrook, S. L.; Kingsford, M. J.; Schmitt, R. J. 1994: Spatial and temporal patterns in assemblages of temperate reef fish. *American Zoology 34*: 463–475.

Kington, S. W. 1999: Factors influencing the on-growing and restocking of *Jasus edwardsii*. Unpublished MSc thesis, University of Auckland, New Zealand.

Kneib, R. T.; Scheele, C. E. H. 2000: Does tethering of mobile prey measure relative predation potential? An empirical test using mummichogs and grass shrimp. *Marine Ecology Progress Series 198*: 181–190.

Kulbicki, M. 1998: How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology 222*: 11–30.

Leber, K. M.; Arce, S. M.; Sterritt, D. A.; Brennan, N. P. 1996: Marine stock-enhancement potential in nursery habitats of striped mullet, *Mugil cephalus*, in Hawaii. *Fishery Bulletin 94*: 452–471.

Leber, K. M.; Blankenship, H. L.; Brennan, N. P. 1997: Influence of release season on size-dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary. *Fishery Bulletin 95*: 267–279.

Minello, T. J. 1993: Chronographic tethering: a technique for measuring prey survival time and testing predation pressure in aquatic habitats. *Marine Ecology Progress Series 101*: 99–104.

Munro, J. L.; Bell, J. D. 1997: Enhancement of marine fisheries resources. *Reviews in Fisheries Science 5*: 185–222.

Peterson, B. J.; Thompson, K. R.; Cowan, J. H. J.; Heck, K. L. J. 2001: Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering. *Marine Ecology Progress Series 224*: 77–85.

Peterson, C. H.; Black, R. 1994: An experimentalists challenge: when artefacts of intervention interact with treatments. *Marine Ecology Progress Series 111*: 289–297.

Thomas, C. W.; Carter, C. G.; Crear, B. J. 2003: Feed availability and its relationship to survival, growth, dominance and the agonistic behaviour of the southern rock lobster, *Jasus edwardsii*, in captivity. *Aquaculture 215*: 45–65.

Zimmer-Faust, R. K.; Fielder, D. R.; Heck Jr, K. L.; Coen, L. D.; Morgan, S. G. 1994: Effects of tethering on predatory escape by juvenile blue crabs. *Marine Ecology Progress Series 111*: 299–303.

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Review

Potential of ecological studies to improve survival of cultivated and released European lobsters, *Homarus gammarus*

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Abstract Release of hatchery-reared lobsters is often suggested for enhancing recruitment-limited populations. Because of lack of ecological considerations ahead of the releases and the unsuccessful efforts to find juvenile lobsters in the sea, little has been known about survival rates, ecological impacts of the releases, and how to improve the performance of releases. Recent studies of morphology and behaviour in hatchery-reared Homarid lobsters demonstrate that qualitative, small-scale laboratory experiments, in combination with larger-scale field studies can yield such information. This is a review of studies of rearing conditions, transportation, and handling during release that aimed to diminish the occurrence of conspicuous morphology and behaviour in the reared juveniles, causing reduced competitive ability, slow sheltering speed, and thereby high mortality rates in the sea. We need to combine small-scale studies with field studies to be able to confirm the significance of the laboratory results. Based on significant results from the laboratory, we should be able to design field studies with focus on expected ecological "bottlenecks" instead of the trial-and-error-type field studies known from the past, thereby reducing time and investment in the development of viable stock enhancement/sea ranching activities.

Keywords *Homarus gammarus*; juvenile ecology; learning, shelter use; competition; predation; laboratory versus field studies

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INTRODUCTION

Cultivation for release purpose

Cultivation of nature by rearing useful organisms has been a part of human culture for thousands of years. Three major types of population conservation or cultivation have been described: mitigation (altered or alternated habitat with recruit limitation); community change (species transplantation) (Bartley 1999); and augmentation (habitat expected to be below carrying capacity as a result of recruit limitation).

An example of mitigation to compensate for lost habitat requiring preparation of high-quality release environments (Bartley 1995) is the use of artificial reefs (Jensen et al. 2000).

Community changes occur when exotic species are introduced into a new biotope. Both intended and unintentional introductions have happened and will occur in the future. No matter if the release is intentional and based on native or exotic species or unintentional by exotic species, it is the same ecological forces that lead to either successful establishment of the introduced organisms or failure followed by disappearance of the organisms from the location.

Augmentation is suggested to reintroduce or increase the natural stock above the present level, as when the natural population for some reason has decreased to such a low level that it is reasonable to expect failure in natural recruitment. In the examples of the grey wolf (*Canis lupus*) in the United States northern Rocky Mountains, Yellowstone National Park (Fritts 2000) and white-tailed eagle (*Haliaeetus albicilla*) in Scotland (Gregory et al. 2002) re-establishment of the breeding populations were successful. An attempt to save the African rhinoceros from extinction has been made, by using captive breeding, release, and relocation (Emslie & Brooks 1999). It is not common to find successful examples from marine releases. No returns have yet been seen of reared Kemp's Ridley sea turtles (*Lepidochelys kempi*) after releases on Padre Island in Texas (Fontaine et al. 1989).

A failing of stock enhancement has been the lack of controlled research in connection to the releases, as well as missing assessments of the result of the releases (Laurec 1999). In addition, investment has been put into the construction of rearing facilities and cultivation animals in the most cost-effective way, as it is quite possible to calculate the cost and economic value of the production of these technical and fully controlled operations (Wickins & Lee 2002). Less investment has been put into biological and ecological studies of the chosen organism, the most suitable release sites, and long-term monitoring to evaluate the impact of the releases. Such studies are usually expensive and it is difficult to evaluate the economic value of the results. Even studies of the basic needs of the release organism itself (except for food, growth, and survival) are rarely accomplished. The result is that most of the release attempts worldwide have failed to give reliable conclusions on how they succeeded in enhancing the manipulated stocks. No documentation on the impact on the biotope is available.

Species thought fit for sea ranching are usually high-priced, stationary species, such as homarid lobsters, especially the European lobster (*Hommarus gammarus*), which is known to stay in a restricted area through all life stages. In contrast to sea ranching activities, cost-efficiency is not the only motivation for stock enhancement, and species mobility is no longer of importance in the same way as for sea ranching. The motivation for stock enhancement arises from a range of causes, from variable annual landings to recruitment failure, destruction or addition of suitable nursery habitat, climatic changes, food supply, and pollution (Addison & Bannister 1994; Smedstad et al. 1994; Grossman et al. 1997; Lindberg 1997; Gendron 1998; Doherty 1999; Castro et al. 2001). The aim is to reconstruct a natural stock that will be managed by fishery and natural management rules. It is natural to expect that restocking will be based on recruitment analyses showing why the stock is depleted. Ecological studies suggesting how the released animals can avoid a documented recruitment bottleneck should be a basic foundation when initiating release of hatchery-reared animals for stock enhancement purposes. However, it is quite common that knowledge of both recruitment biology and the species ecology is lacking and difficult to study (Laurec 1999; Tsukamoto et al. 1999).

Even if the motivations behind sea ranching and marine stock enhancement in many ways are different in many ways, they have the same foundation of breeding, rearing, and release of young organisms. The strategy is safe rearing of young larvae and/or juveniles through the most vulnerable life stages and release to their natural nursing grounds when they are thought to be more robust or safe from predators, to maintain a stable recruitment in the chosen area. The term "settlement" is usually a definition for the termination of a pelagic larval phase and assumption of a benthic life (Scheltema 1974), but here it is also used to define the first time an already bottom-settled organism is transferred from land-based holding facilities to natural or semi-natural habitats.

Lobster cultivation and releases

The north-Atlantic lobster (*Homarus* sp.) has been the subject for cultivation and release-programmes since around the 1880s (Dannevig 1885; Nicosia & Lavalli 1999), and particularly in Europe, as the size of the European lobster (*H. gammarus*) population is much smaller than that of the American lobster (*Homarus americanus*) (http://www.fao.org./waicent/faoinfo/fishery/statist/fisoft/fishplus/htm 2000). The European lobster has with increasing size, significant lower fecundity/length-ratio and reproduction rates than the American lobster (Aiken & Waddy 1980; Free 1998; A.L. Agnalt, Inst. of Marine Research, Norway pers. comm.). The rationale for European lobster cultivation is typical for enhancement enterprises, caused by severe stock depletion and well-functioning rearing technology, but with lack of biological and ecological data (Svåsand et al. in press). However, boosting of a local, fishery-depleted stock of lobsters (*H. gammarus*) has been successful in Norway (Agnalt et al. 1999).

Hatching and rearing of newly hatched lobster larvae turned out to be fairly straight forward, and the hatchery techniques from 1890 are still used today (Rasch 1875; Sund 1915; Dannevig 1928; Carlson 1954, 1955; Wickins et al. 1986; Latrouite & Lorec 1991; all cited in Nicosia & Lavalli 1999).

Most releases before 1960 were of settling post-larvae in moult stage IV (Nicosia & Lavalli 1999). However, no effect of the releases was found in the variation of annual lobster landings and practically all hatcheries closed down between 1950 and 1970 (Taylor 1950; Carlson 1955; Barnes 1939, as cited in Nicosia & Lavalli 1999).

A further decrease in lobster landings occurred between 1960 and 1980 in Europe (Bannister 1998) and 1969–70 in North America (Nicosia & Lavalli 1999). This gave renewed interest in lobster cultivation. Since no success had been documented after the historic post-larvae releases, it was presumed that mortality during the first months in the sea was the main reason, and the settled juveniles

were then kept individually in ongrowing facilities until 3–9 months before release (Grimsen et al. 1987; Beard & Wickins 1992). If such rearing is to be accomplished on a commercial scale, it needs to be designed to fit a commercial cost-benefit model as new hatcheries were based on efficient handling in holding trays with a high density of individually housed lobsters in a minimum of space (Grimsen et al. 1987; Borthen et al. 1999; Wickins & Lee 2002).

When tagging and recognition of released lobsters became possible through the development of the Bergman-Jefferts magnetic micro tag system (Wickins et al. 1986; Uglem & Grimsen 1995), a series of stock enhancement projects with tagged lobsters was started in Europe between 1983 and 1990 (Addison & Bannister 1994; Agnalt et al. 1999).

Different techniques have been used when releasing 5–10-month-old juvenile lobsters. Some techniques are developed to reduce the risk of predation, by releasing the lobsters on the seabed through tubes, by divers, or in closed shelters that open up after some time in the sea (Latrouite & Lorec 1991; Beard & Wickins 1992; Burton 1992; Addison & Bannister 1994; Cook 1995). In large-scale releases where tens of thousands of lobsters are released over a large area within a short period of time, surface release from small boats over 2–10 m shallow rocky bottoms was the solution (Agnalt et al. 1999). The cost efficiency of each technique can be calculated, but the survival rate in lobsters released by the different techniques is not known, as quantitative monitoring of the lobsters after release has never been achieved.

The release studies conducted in Great Britain and Norway showed that released lobsters do survive to be recaptured in the commercial fishery 5–10 years after release and they add to the natural recruitment in the same way as wild lobsters (Bannister & Addison 1994; Agnalt et al. 1999). Yet the present recapture rates, from 5% to c. 10%, is too low to make the releases economically viable (Bannister & Addison 1996). However, the large-scale release programme at Kvitsøy, Norway, between 1990 and 1997 showed that it is possible to strengthen a depleted population through releases of reared juveniles (Agnalt et al. 1999).

Life history and ecology of the Homarid lobster

Homarid lobsters differ from the Palinurid, Synaxid, and Scyllarid lobsters by having well-developed sets of claws, and by producing relatively few, large and slow-developing eggs, followed by a short planktonic larval phase (Phillips et al. 1980). However, all these large-sized decapods have to cope with much the same ecological constraints during and after settling to the bottom. Although the life history of American lobsters is well described from field studies (see Herrick 1894, referred by Factor 1995; van der Meeren & Soldal 1998; van der Meeren 2001), most studies of European lobster have been performed at hatcheries and in the fishery, and little is known from the field about ecology and life history (van der Meeren & Soldal 1998). Since basic knowledge about wild European lobsters is missing, the American lobster's life history, ecology, and behaviour have been applied for the European species. Recent comparisons between the two species imply that there might be significant differences (Mercer 2001; http://www.qub.ac.iuk/bb/prodhol/GEL/gel.html). Applying data from one species to the other should therefore be done with caution.

Early benthic phase European lobsters (4–14 mm carapace length (CL)) have never been found anywhere within the geographical range of the species (Mercer et al. 2001). They are either sparsely distributed or so well hidden that their whereabouts are a mystery. Laboratory studies show that settling lobsters prefer cobble before sand and hard substrate, much in the same way as the American lobster (Wahle & Steneck 1991, 1992; Linnane et al. 2000a). However, extensive sampling in such bottoms has failed to find any early benthic phase juveniles, even in the areas of the highest lobster landings in Europe (Mercer 2001). Lobster juveniles out of shelter are very vulnerable to predators (Mercer et al. 2001). In the same paper, it is demonstrated that juvenile lobsters were more tolerant of low salinity than adult lobsters, but the reason is not clear.

Although lobsters react quickly on visual stimuli as movements and contrasts, olfaction is probably the most important sense in *H. americanus* (Atema & Voigt 1995; Ratchford & Eggleston 1998; Derby et al. 2001). Olfactory brain cells keep proliferating throughout the lifespan in all decapod species investigated so far (Harsch & Dawirs 1996; Sandeman & Sandeman 1996, 2000; Schmidt 1997; Sandeman et al. 1998; Harsch et al. 1999; Schmidt & Harsch 1999; Steullet et al. 2000; Hansen & Schmidt 2001; Harrison et al. 2001). It has also been found that lack of stimuli induce increased cell mortality and decreased growth of such cells in an Australian crayfish species (Sandeman & Sandeman 2000). Likewise, critical periods of particular sensitivity have been found in fish larvae (Browman 1989). Neurological studies and the importance of

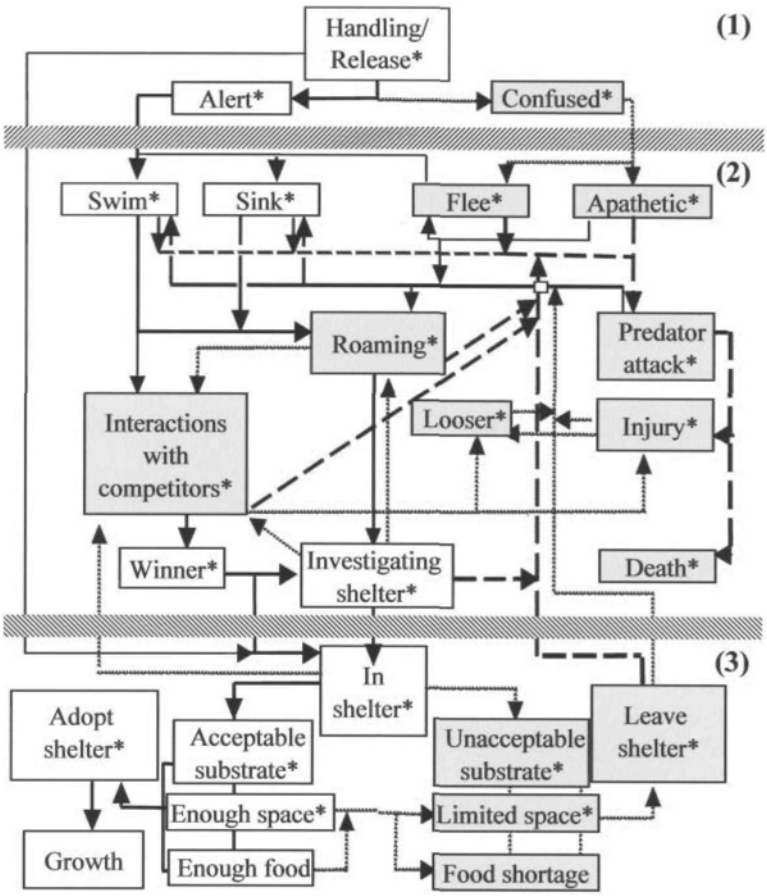

Fig. 1 Flow diagram describing the settling process of released benthic organisms. This covers the three parts: (1) "Handling and Release", which is connected to the rearing and release procedures; (2) "Roaming and Investigating"; and (3) "In shelter", which is common for all organisms, both reared-and-released and wild ones. The different actions and incidents are: Wanted actions = Risk-decrease (open boxes; full-drawn line); Other actions = Risk-increase (grey boxes; dashed line); and Unwanted incidents = Life-threatening (grey boxes; broken line). The asterisks indicate the actions presented and discussed in this paper. The thick line is expected to be the optimal development of a successful establishment. Impacts imposed on the organism by morphological or neurological abnormalities are resulting from the rearing conditions, and physical impact by temperature, currents and/or salinity is left out of this model.

olfaction has so far not been studied in Norway, and since we only had reared European lobsters available for research, it will be difficult to find out how the rearing conditions may affect brain development.

This paper concentrates instead on behavioural cues to discuss the range of challenges described in Fig. 1.

Studies of lobster augmentation

The main objective of much of the work reviewed in this paper was to evaluate the effect of releases on the lobster population, and put this in context with behavioural and ecological studies, at the individual level. In this way it is possible to extract data to be used in developing release strategies in ways that ensure survival of the released organism and at the same time consider how the biotope might be affected by the release. Since individuals settle, choose shelters, forage, grow, move, interact with other individuals, and eventually reproduce and/or die, it is at this level selection acts, and the properties of populations and communities emerge from the behaviour of individuals (Butler 1997).

The standardised rearing techniques might affect the morphology as well as the behaviour and thereby the ability of the lobsters to survive and respond in a functional way to complex and changing environmental challenges. Transportation and release techniques might have short-term influences on behaviour. Since wild European lobsters have been impossible to find in the sea between larval and emerging phases 2–5 years after settling, there is no reliable information available on natural demands, behaviour, and morphological development during this early life stage (Mercer et al. 2001). In addition, the benthic ecosystem of lobster biotopes has not been thoroughly studied. The biotopes and nursery grounds of the American lobster on the north-east

Atlantic coast of the United States and Canada is better described (see Lawton & Lavalli 1995), but this has not made the releases of reared juveniles more successful (Castro et al. 2001).

Most of the experimental studies have been done with European lobsters. The studies have focused on their fitness—survival, functionality, and adaptation to the variety of challenges they meet during and after release. Both experimental and field studies have been carried out, in constructed habitats in the laboratory or in natural field biotopes, surveyed by divers, and through fauna sampling. The ability of the reared lobsters to survive and adapt has been related to: (1) physical stressors before and at release; (2) temperature and light; (3) claw morphology; (4) substrate and shelter-related behaviour; (5) predators; and (6) competition, both intra- and inter-specific.

The results are discussed and used to suggest a set of ecological criteria that should be considered when rearing organisms for release purposes and when choosing how, where, and when the animals could be released to minimise their mortality, and harmful effects on the release biotope resulting from the release.

METHODS

This review presents data from a combination of field sampling and controlled experiments in the laboratory. Descriptive approaches have traditionally dominated ecological studies until the last 2–3 decades, when experimental hypothesis testing has increasingly been used (Raffaelli & Hawkins 1996). If the experiment is carefully designed, it proves to be a powerful and direct method to assess ecological mechanisms and interactions between factors.

The morphology of all lobsters that are to be used in controlled experiments was described by different variables such as origin, age, sex, CL, antennae length, claw length, claw height, claw circumference, claw depth, and live weight.

To study ecological processes and their relative contribution to the successful settling and establishment of European lobster juveniles, conducting controlled experiments in tanks was crucial, since no lobster juveniles could be found in the wild during the early benthic phase and only a few have been found in the emergent phase (Mercer et al. 2001). Fewer studies of this kind have been done with the American lobster, as the juvenile and emergent phases can be found in the sea by divers (e.g., Lavalli & Barshaw 1986; Karnofsky et al. 1989a,b; Wahle 1998).

Field studies

Field-studies can be difficult to interpret, as it is impossible to control for all the variables in a natural environment. However, field studies of the European lobster were conducted as part of the Norwegian research programme PUSH (Programme for Stimulation and Development of Sea Ranching, 1990–97) and the European Union supported research programme LEAR (Lobster Ecology and Recruitment, 1997–99). The field studies were combinations of quantitative sampling done by static fishing gear, such as trammel nets and eel pots, and active qualitative sampling done by small diver-operated suction samplers. Selected release biotopes were also visually surveyed by divers, describing the seabed substrate, algal growth, and fauna. The results were mainly of a descriptive character (van der Meeren 2000). Field data were used in their own right during releases of reared lobster juveniles (van der Meeren 1991). Fieldwork experiences were also used when sampling experimental animals for inter-specific competition experiments and designing the experiments (van der Meeren 2001, 2003; Koponen 2003).

In both programmes, divers aimed to find wild or released lobster juveniles to describe density, choice of shelter, and to estimate survival rates, but failed to do so (van der Meeren et al. 1991, 1997; Mercer et al. 2000). Instead, divers observed and recorded on video behavioural patterns in the newly released lobster juveniles, both after being released directly on the bottom, through tubes to the bottom, and when released onto the surface (van der Meeren 1993). Predators attacking the lobsters during release were also observed and video-recorded in a series of locations (van der Meeren 1991, 2000).

Searches for early benthic phase and emergent lobsters, that turned into general faunal sampling, were done by divers during the PUSH programme at Kvitsøy (van der Meeren 1991, 1996) and at the Orkneys at the same time (Burton pers. comm). This gave a qualitative description of the degree of sand, algal cover, and occurring algal and animal species in 8–13 locations, described by local fishers as "Good lobster ground", "Bad lobster ground", and "Undersized lobster ground". Although no lobster juveniles were found in these surveys, the observations should be connected to the recapture rate of released lobsters in the different areas, to evaluate the quality of these locations as nursery

grounds for released lobsters. Experiences from these surveys also provided ideas that were later put into controlled laboratory experiments (van der Meeren 2000, 2001, 2003; Koponen 2003).

The LEAR programme adopted, in addition to visual description of 0.70×0.70 m^2 quadrats, the use of an airlift suction sampler, developed for quantitative sampling of small benthos, including young-of-the year American lobsters (Holme & McIntyre 1984; Able et al. 1988; Steneck & Wahle 1991; Linnane et al. 2001; Mercer et al. 2001). The survival of crustaceans was usually 100% when sampled in this way, so this technique was used when sampling small-sized experimental animals from the sea (Koponen & van der Meeren unpubl. data).

Trammel nets and eel pots were used to sample and describe lobster predators in different habitats and seasons of release (van der Meeren 2000). This gear is commonly used to catch a wide variety of organisms, both fish and invertebrates, from 5 cm in length and up to 70 cm or more. Such gear collects qualitative samples. No attempts to sample quantitatively were made, because of the size of the release areas and the complex biotopes.

Finally, recapture data of lobsters caught up to 13 years after release is now providing a wealth of new information about growth rates, migration, maturation, and fecundity (Bannister & Addison 1998; Agnalt et al. 1999; Uglem et al. 2005).

Experimental studies

Based on field experiences from the release days, a series of behavioural experiments were run to test different hypotheses set up to explain the field observations. Important topics were post-release behaviour, aggression, claw morphology, experience in sheltering, and both intra- and inter-specific competition. The advantage of such experiments is that the variables can be controlled to such a degree that the results get clearer than they would have been in the field.

Most studies were conducted in tanks with shell sand or gravel as bottom substrate, (Wickins & Barry 1996; van der Meeren 1991, 1993, 2001, 2003; van der Meeren and Uksnøy 2000). These experiments were run as a series of replicates of each test variable, and were presented to one or two lobsters consecutively. The observed responses were then analysed to see whether the chosen variable and the responses were related. These studies revealed how and why the lobster responded to each specific test variable.

The rest of the experimental studies were of lobster groups. This was because of limitations in both time and facilities, or to study group effects (van der Meeren 1993, 2000, 2003; Linnane et al. 2000; Jørstad et al. 2001; Koponen 2003; van der Meeren et al. unpubl. data).

Such studies made it possible to characterise species-specific behavioural traits, but did not provide the data needed to analyse the underlying reasons for the observations.

Behavioural cautions

In social interactions experiments the replicates were run in single-sex groups, because both sexual differences in claw morphology is described (Phillips et al. 1980; Aiken & Waddy 1989) as well as social dominance (Scrivener 1971).

Since moult stage and aggression is connected in lobsters, setal staging was used to check the moult stage of adolescent and adult lobsters (Tamm & Cobb 1978; Atema et al. 1979; Waddy et al. 1995). Moult staging was not carried out in juveniles, since they were held under uniform conditions, which led to synchronised moult cycles (G. van der Meeren pers. obs.). Even if the holding temperature above 15°C is recommended for lobsters (Grimsen et al. 1987; Beard & Wickins 1992), most of the studies were done in colder water. Since the purpose was to study constraints on hatchery-released lobsters released at sea, the temperature should resemble natural conditions, rather than what would be optimal for the lobster.

RESULTS AND DISCUSSION

Recapture rates and survival estimates

Enhancement studies have shown that lobster juveniles that do survive after release, are capable of reproducing and can even improve local fisheries when the wild stock is depleted (Addison & Bannister 1994; Bannister et al. 1994; Agnalt et al. 1999). However, the recapture rates are usually quite low, from 4 to 9% in most instances (Addison & Bannister 1994; Agnalt et al. 2004). The fishery data is not suited to calculating mortality rate in the released stock, since trap-catch data cannot be assumed proportional to abundance (Miller 1990). Survival has been calculated to be far higher than the recapture rate indicates (Bannister et al. 1994). Monitoring the juveniles in the sea is also impossible, as they disappear within minutes of release. There is therefore a need for more information concerning the fitness of hatchery-reared lobsters, to evaluate their ability to survive in the sea and to find out whether improvements are needed and how they can be achieved.

However, preliminary results from the PUSH programme showed better recapture rates in moderately protected areas, sheltered from breaking waves, but with good water exchange, than in exposed or semi-closed areas (Fig. 2).

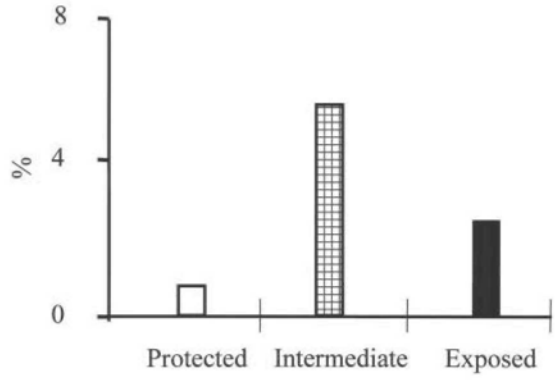

Fig. 2 Recapture frequency of legal-sized European lobsters (*Homarus gammarsu*) at Kvitsøy, Norway, hatched 1989, released 1990, and recaptured 1992–97 (n = 697), in areas that are well protected (white column), semi-protected (chequered column) and fully exposed (black column) to ocean swells.

Fitness in hatchery-reared lobsters

Lobster juveniles reared in traditional hatcheries cannot exercise and have no experience of the seasonal cycles, the use of shelters, predators and techniques for predator avoidance, foraging, social interaction, or competition. It is also a possibility that brain development in decapod crustaceans might be under-developed because of lack of stimuli (Sandeman & Sandeman 2000). As the development of the crusher claw is dependent on physical exercise between moult stages V and VIII, this development usually fails in hatcheries that rear juveniles in boxes with no supplement of coarse shell sand or shell spat (Wickins 1986). In addition, growth rate after release, nutritional status, and mobility might be different between reared and wild lobsters (Addison & Bannister 1994).

The behaviour of hatchery-reared species has been linked to increased predation rates (Olla et al. 1998; Svåsand et al. 1998) and reared lobsters may become more prone to predation (Spanier 1994). In addition, stress induced by packing, transportation, handling, and the sudden change of environment when transferred from the hatchery to the sea must have an impact on the lobster juveniles.

Stressors before and at time of release

In Norway, out-of-water (damp) transportation has been favoured for transferring lobster juveniles from the hatchery to the release site, as it is low-cost, low-tech, and allows for thousands of lobsters to be packed and transported in limited space with easy transfers between vehicles, planes, and boats (van der Meeren 1991; Linnane et al. 1997). Adult lobsters compensate for the accumulating acid metabolites resulting from hypoxia and hypercapnia by elevating their internal buffer base (Whitely & Taylor 1992). The same response is believed to function in juveniles, which are transported in boxes cooled to 3–8°C (van der Meeren 1991; Linnane et al. 1997). Immediately after release from the transportation box, c. 90% of the lobsters need several minutes to regain mobility, while c. 10% respond with tail-flapping along the bottom or upwards in the water column. Individuals climbing up and clinging to the top of high vegetation and swimming high in the water column has also been seen as a result of poor acclimatisation to the sea conditions (van der Meeren 1991; Mercer et al. 2000). Extreme behaviours such as immobility and tail-flapping lasted less than 15 min, and less harmful aggressive behaviour, such as non-physical claw display, decreased within 1 h of release (van der Meeren 1991, 2003; van der Meeren & Uksnøy 2000; Koponen 2003; van der Meeren et al. unpubl. data). Releases immediately after transportation resulted in tail-flapping lobsters that attracted fish, which preyed on the immotile lobsters on the bottom (van der Meeren 1991). Most lobsters were probably inactivated by low temperature in the transportation box, but the tail-flapping was a deleterious escape reaction induced by water deprivation and physical pressure (McLeese & Wilder 1958; van der Meeren 1991). Therefore, acclimatisation in holding tanks is necessary, since recovery to an alert state can be reached within 15 min in ambient sea water (van der Meeren 1991). Even during winter releases, no acclimatised lobsters were seen out of shelter for 30 min after release (van der Meeren 2000).

In both naïve newly released emergent lobsters, as well as adults, intra-specific fighting was quite common in the first 30 min after release, or up to 1 h if shelters were unavailable (van der Meeren 1993; van der Meeren et al. unpubl. data). This fighting behaviour was very aggressive and physical in the first minutes, and included grasping and pushing the opponent (van der Meeren 1991, 2003; Koponen 2003; van der Meeren unpubl. data). Individual aggression in adult lobsters, as well as a range of

other species has been found to peak after a period in isolation (Dunham 1972; Hoffman et al. 1975; Huntingford & Turner 1987).

Aggression and tail-flapping was also seen in lobsters released through tubes at the bottom of the sea (G. van der Meeren pers. obs.). High rates of aggression and tail-flapping are probably a fear-induced behaviour as a result of handling, but can also be an artefact from the hatchery. Temperate water and to some extent high light intensity will enforce rapid sheltering (van der Meeren 1993). The poikilothermous lobsters usually show reduced activity when the temperature is 5°C (McLeese & Wilde 1958). However, it is stress-induced activities that are most positively temperature-dependent (McLeese & Wilder 1958; Dunham 1972; Hoffman et al. 1975; Cooper & Uzmann 1977). Walking and exploring rates are less affected by low temperature (Dunham 1972; Hoffman et al. 1975; Karnofsky et al. 1989a; van der Meeren 1991, 2001).

Claw morphology

The large pairs of claws are one of the more pronounced morphological characteristics in homarid lobsters and are much used in social displays, as well as in fights (Scrivener 1971; van der Meeren & Uksnøy 2000). In American lobsters, the claws are relatively small in the early benthic phase and the anti-predator response is tail-flapping away from the threat (Lang et al. 1977). During growth, the claws increase more rapidly in relation to the CL and contribute more to the total weight. In adult American lobster, escape reflex is partially replaced by claw displays. When attacked, newly moulted lobsters, and all juveniles, throw off (autotomise) one or more claws more easily than hard-shelled adult lobsters (Atema & Voigt 1995). Thus, claws in young lobsters are probably not useful as offensive weapons. The lobster is one of the largest sized invertebrates in the temperate coastal waters of the North Atlantic Ocean (Holthuis 1950), and will eventually outgrow most of the marine invertebrate predators. The claws are used to forage on hard-shelled prey such as molluscs and snails, but male American lobsters develop claws that are disproportionately large for the prey they consume (Elner & Cambell 1981). The same is probably true in European lobsters, as potential prey found in lobster fields are quite small, compared to the size of the claws in large lobsters (van der Meeren & Uksnøy 2000; Linnane et al. 2001). Rather than tools for foraging or predator defence, large claws are probably related to intra-specific competition for shelter, food, and mates, and act as easily assessable indicators of resource holding power (Parker 1974).

Morphological anomalies such as two scissor claws instead of one scissor and one crusher claw are rarely seen in wild lobsters and have been used to recognise released lobsters when recaptured in the fishery (Wickins 1986; Tveite & Grimsen 1995). Indications are that lobsters with two scissor claws are more easily caught than lobsters with normal claws (Agnalt et al. 1999), which could be a benefit for sea-ranching enterprises but not for stock enhancement purposes. The development of double scissor claws is a rearing artifact that can be avoided by offering the juveniles shell spat, or coarse sand in the rearing box to enhance asymmetrical claw development (Wickins 1986). To what degree are two scissor claws a functional problem for the hatchery-reared lobster in the sea? The importance of large claw size on intra-specific dominance is previously demonstrated in a series of crustacean species, as is large body size (Bertness 1981; Lee & Seed 1992; Ranta & Lindstrøm 1992; Sneddon et al. 1997; Wada 1993) as well as in American lobsters (Scrivener 1971).

Hatchery-reared European lobster males with two scissor claws will, after 3–4 years in the sea, develop the same overall claw indices (CI; claw length/height/circumference) as wild lobster males of equal size, by developing one of the claws significantly more than the other (van der Meeren & Uksnøy 2000). Both claws keep the scissor shape over time and the increased volume is caused by the increase in length in one claw, whereas wild lobsters invest more in claw height and depth (Fig. 3). The smaller claw develops in the same way in hatchery-reared and wild lobsters (van der Meeren & Uksnøy 2000).

The long and slender shape of the larger claw in hatchery-reared lobsters appears to be more fragile and was broken on a couple of occasions during fights with wild lobsters (van der Meeren & Uksnøy 2000). As in other clawed crustaceans, claw loss and severe claw damage will inevitably lead to loss of dominance (Neill & Cobb 1979; Sekkelsten 1988; Abello et al. 1994; G. van der Meeren pers. obs.). Breakage of the smaller scissor claws and crusher claws was not seen during these same fights.

In American lobsters, a lobster with 50% larger CI or 18% larger CL will always win (Scrivener 1971). It has been assumed this is also true in European lobsters. Therefore, the matching of CL was applied in dominance tests, comparing recaptured hatchery-reared lobsters with two scissor claws, competing with wild conspecifics with

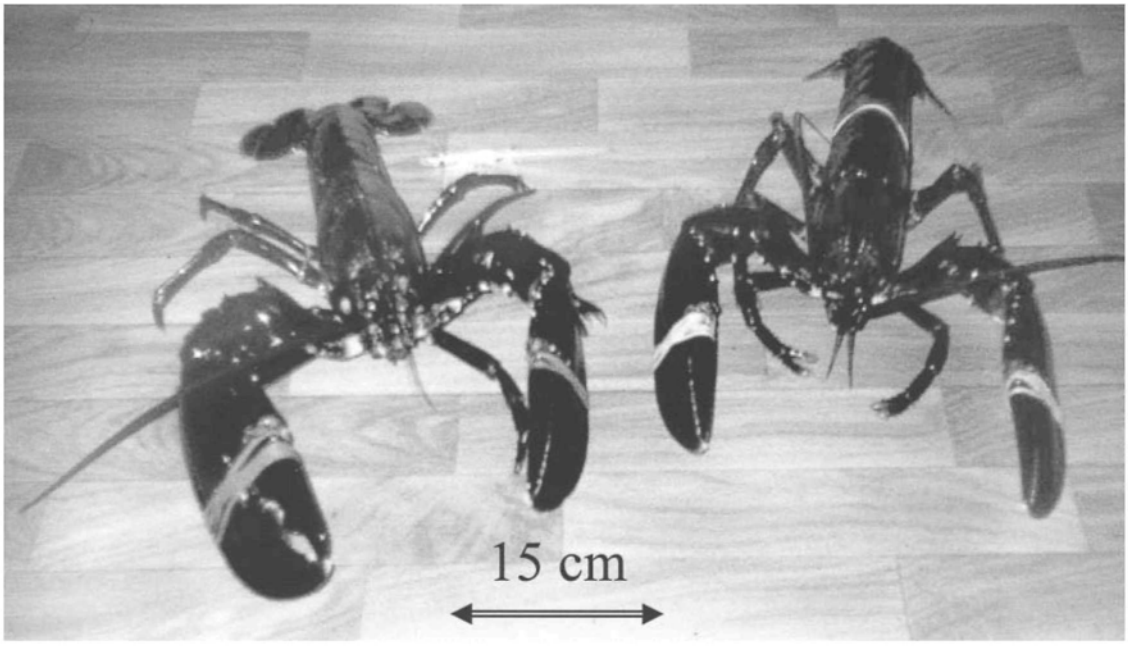

Fig. 3 Hatchery-reared and recaptured European lobster (*Homarus gammarus*) male with two scissor claws (right) and lobster male with normal set of claws (left). Note the left-hand side elongated scissor claw in the reared lobster, compared with the right-hand side crusher claw in the wild-caught lobster.

normal claws (van der Meeren & Uksnøy 2000). Both a larger CL and CI were found to be of significant importance to winning. However, very little variation was found in the correlation between CI and CL after measuring more than 100 male lobsters from 70 to 124 mm CL in Western Norway (van der Meeren & Uksnøy 2000). Thus, it has not been possible to distinguish between the two morphological factors to conclude that one was more important than the other. Since there is a significant inter-specific difference in the CL/CI relationship between the American and European lobsters, another dominance test was done to compare these species (van der Meeren et al. unpubl. data).

European lobsters invest more in prolonged CL compared to CI, whereas American lobsters have larger CI compared to the CL. However, both species show the same shelter-related behaviour (van der Meeren et al. unpubl. data) and the aggressive behaviour for both species follows the descriptions described in other studies (Scrivener 1971; Stein et al. 1975; Jacobson 1977; van der Meeren & Uksnøy 2000; van der Meeren et al. unpubl.data). The inter-specific competition tests showed that larger CI was significantly more important for the outcome of the match than larger CL (van der Meeren et al. unpubl. data). This was true for both males and females. Claw dimorphism is present in both male and female lobsters of both species, as well as a range of other decapod crustaceans (Hartnoll 1982). Because of the high risk of injury from intra-specific fights, animals possessing dangerous weapons are expected to refrain from escalated aggressive interactions if the cost is high compared to the pay-off (Caryl 1981; Maynard Smith 1982). This is so in lobsters, where the most aggressive interactions were performed as claw display only and escalated physical fights rarely resulted in physical damage to either opponent (Karnofsky et al. 1989b; van der Meeren & Uksnøy 2000; van der Meeren et al. unpubl. data).

Even if both male and female lobsters have dimorphic claws, sexual dimorphism is also present, as male lobsters, both European and American, grow substantially larger claws than females (Templeman 1935; Aiken & Waddy 1989; Free 1994; van der Meeren et al. unpubl. data). Larger, aggressive males will evolve in species where the male parental investment is little, but the inter-male competition to actually gain access to mates is pronounced (Trivers 1972). In American lobsters, male dominance can be directly correlated with mating success (Atema et al. 1979). Male-male competition in European lobsters

is found to be high and relatively insensitive to sex ratio (Debuse et al. 1999). The sexual difference in claw size seems to be at least as pronounced as in the American lobsters within the narrow size range from 85 to 100 mm CL (van der Meeren et al. unpubl. data). The data should have been tested on more animals from a wider size range, but the present result indicates that the competition between European lobster males for mates may be at least as strong or stronger than between American lobster males.

These results suggest that both size and shape of the lobster claws serve important functions. The size of the claws is one of the crucial factors that determine the outcome of intra-specific competitions, and lobsters with smaller CI have a greater disadvantage in competition for resources such as shelter, food, and mates. Resource-holding power related to the high CI of an abormally prolonged scissor claw that is prone to breakage, is more unreliable than that of a normal set of claws with a larger crusher claw and smaller scissor claw.

Sheltering behaviour

Castro et al. (2001) described that hatchery-reared young-of-the-year American lobsters spent time out of shelter immediately after release. Lab studies confirmed the results that shelter behaviour of lab-reared and wild-caught fourth and fifth stage lobsters differed. Communal rearing of European lobsters in tanks with mixed bottom substrate showed promising results in survival and growth, although the rate of claw loss was high (Kittaka 1984; Jørstad et al. 2001). Unfortunately, all knowledge on the early life stages of European lobsters is based on studies of hatchery-reared animals (Berrill 1974; Howard & Bennett 1979; Linnane et al. 2001; Mercer et al. 2001). Thus, there is no way of knowing if the available knowledge is biased resulting from artefacts from the rearing conditions, or if it really represents natural behaviour patterns in the lobster. Whether lobsters will perform in a more functional way in the sea, when reared in environments that offer natural shelter, social interaction, competition, and in the presence of predators and prey is still to be tested. Alternatively, information behaviour in hatchery-reared lobsters is vital for developing a sound rearing and release strategy in this species. Despite what background the lobster juveniles have, to survive even the first day in the sea they must be able to function when faced with predators, competitors, and eventually, foraging and reproduction.

Early benthic phase lobsters without shelter attract predators and are eaten within minutes in coastal European waters, especially in the summer season (van der Meeren 2000; Ball et al. 2001; Mercer et al. 2001). However, lobsters are usually reared without being accustomed to shelter before release (Grimsen et al. 1987; Beard & Wickins 1992). Naïve European lobster juveniles were found to seek cover in available shelters within minutes after release to the sea or to semi-natural environments, especially if they were acclimated to ambient sea temperature and kept at a low stress level by restricted handling and limited out-of-water time (van der Meeren 1993, 2000, 2001; Linnane et al. 2000a). The lobsters had an innate preference for shade and moved towards the nearest firm object from where they were released (van der Meeren 2001). The motivation to make burrows for hiding has not been found to differ owing to previous experience in early benthic phase lobsters (Wickins & Barry 1996). However, emergent phase lobsters will, with prior experience to shelter, reduce the time both to seek available cover and to hide within it (van der Meeren 2001). Juvenile lobster were occasionally seen to be passing available shelters several times before accepting them, or leaving cover after a few minutes (van der Meeren 1993, 2001). Such behaviour would have been extremely risky for juveniles in the sea; however, this behaviour was seen in wild adult lobsters released in a large tank with a limited numbers of shelters (van der Meeren et al. unpubl. data). A plausible explanation is that they found the available shelters sub-optimal and searched for better cover. It is not clear if the observed delay in sheltering is comparable to natural behaviour or if it was more a laboratory artefact, resulting from the simplified environment in the tanks where they were safe from predators. This experiment has not been carried out in the presence of predators.

Hatchery-reared lobsters given the opportunity to select, choose to settle in shelter-providing habitats, preferably pebble or pebbles on sand (Linnane et al. 2000a; Mercer et al. 2000; van der Meeren unpubl. data). However, Wickins (1999) found that more than 92% of juvenile lobsters chose artificial shelters made of short lengths of box section conduit pushed into muddy substrate when they constructed burrows, instead of digging under cobble. In Norwegian studies, all lobsters with available shelters stayed there during the day (van der Meeren 2001, 2003; Koponen 2003; van der Meeren et al. unpubl. data).

The effects of cold water and intra-specific fights increased the time the lobsters needed to reach

shelter (van der Meeren 1993, 2001). Threats such as approaching fish or moving shadows caused the lobsters to immediately stop and display their claws ("meral spread") (van der Meeren 1993, 2001). After the threat disappeared, the lobsters moved more quickly into the shelter than when not confronted (van der Meeren 2001).

Hiding in shelter-providing habitats is often seen in early benthic phase juveniles, as in other decapod species, for instance common shore crabs (*Carcinus maenas*) (Moksnes et al. 1998), blue crabs (*Callinectes sapidus*) (Heck & Orth 1980), freshwater crayfish (Astacidae) (Stein & Magnuson 1976), spiny and rock lobsters (*Panulirus argus*, *P. japonicus*, *P. cygnus*, *P. guttatus*, *P. longipes*, *P. versicolor*, *P. penicillatus*, *P. ornatus*, and *Jasus edwardsii*) (Lewis 1977; Childress & Herrnkind 1994; Yoshimura & Yamakawa 1988; Jernakoff 1990; Booth 2001; Norman et al. 1994, Yoshimura et al. 1994; Norman & Yoshimura 1995; Norman & Morikawa 1996; Dennis et al. 1997; Sharp et al. 1997), Mediterranean slipper lobster (*Scyllarides latus*) (Spanier & Almog-Shtayer 1992; Barshaw & Spanier 1994), as well as American and most recently, European lobsters (Wahle & Steneck 1991; van der Meeren 1993, 2001, 2003; Mercer et al. 2000, 2001; Ball et al. 2001; Koponen 2003; van der Meeren et al. unpubl. data).

These results confirm that nocturnal activity and shelter seeking as means of predator avoidance are inherited responses in European lobsters, but they need experience to find, accept, and settle rapidly in shelter.

Adaptation of hatchery-reared lobster juveniles to a complex biotope

When released in the sea, hatchery-reared lobsters have to cope with a new and complex environment. The release sites are usually selected from the history of the local lobster fishery and, as for type of bottom surfaces (Addison & Bannister 1994; Tveite & Grimsen 1995; Agnalt et al. 1999), cobble habitats have been preferred. It is known that wild American lobster juveniles and hatchery-reared European lobster juveniles, at least in the laboratory, settle willingly in such habitats (Incze & Wahle 1991; Wahle & Steneck 1991, 1992; Linnane et al. 2000a; Mercer et al. 2000). Laboratory studies have shown that gravel was the preferred settling habitat ahead of bricks, seaweed, or sand (Linnane et al. 2000a). However, this study might have been oversimplistic. If given a choice, significantly more juvenile lobsters dug out caves in the sand underneath hard objects placed on sand, and gravel on sand was significantly more attractive than gravel on a hard bottom (χ^2 test; $P < 0.0001$, d.f. = 1, $n = 106$, joined data from 3 replicates with no variation between them) (van der Meeren unpubl. data).

This type of bottom has been little studied by European zoologists. Therefore, little is known about the biodiversity of species richness and animal density from such habitats in Europe (Mercer et al. 2001). A suction-sampling of cobble-dwelling fauna in Europe comprised a range of different phyla and specimens, with amazingly high densities (Mercer et al. 2000, 2001; Linnane et al. 2001).

Potential lobster food organisms such as annelids, echinoderms, and small molluscs were present, with up to 100 specimens per m^2 in the Norwegian samples, as well as 17 crustacean species, sized from 5 to 50 mm carapace size. Potential competitors and predators of early benthic phase lobsters constituted 59% of the sample, and numbered up to 150 specimens per m^2 (Mercer et al. 2000; Ringvold & van der Meeren unpubl. data). No juvenile lobsters were found (Mercer et al. 2000, 2001; Linnane et al. 2001). Anomuran galathean species were the most common crustaceans found in Norway, followed by shrimps and brachyuran crabs (Ringvold & van der Meeren unpubl. data).

Hatchery-released lobsters have been able to boost a depleted lobster stock of similar type biotopes in Norway, and have been recaptured very close to the release sites (Agnalt et al. 1999, 2004). This shows that hatchery-released lobster juveniles are able to survive and grow in these biotopes, even if we have no reliable data on survival rate. However, will all hatchery-reared lobster juveniles manage to adapt to the fauna of predators, competitors and prey in the sea, or do they have individual variations in their performance? Answers to such questions are important so as to develop hatcheries that will produce juveniles with maximum fitness. It is also of interest to study how hatchery-reared lobsters may affect the wild fauna and the ecology of the release site.

Predation

Until 1988, hatchery-reared lobster juveniles in Norway were released in the summer season when water temperature was at the annual peak, in the belief that the released lobsters would gain enhanced growth rate and thermal shock would be reduced after being housed in heated water for 8–12 months (Grimsen pers. comm.). However, density-dependent prey mortality caused by aggregation of

predators was obvious, when the release of many lobsters within a limited area attracted numerous fish predators within minutes (G. van der Meeren pers. obs.). The diver's observations of the heavy predation by fish and the lack of protective responses by the lobsters at the 1988 release led to several studies (van der Meeren 1991, 1993, 2000, 2001).

Predation is the first and most risky challenge that hatchery-reared lobster juveniles face in the sea, especially within the first minutes when they are out of shelter and quite defenceless (van der Meeren 1993, 2000). Later studies of early benthic lobsters tethered out of shelters have confirmed this (Mercer et al. 2000; Ball et al. 2001). The predation pressure changes with the seasons, since there are pronounced differences in temperature and faunal composition from winter to summer season in shallow coastal waters in the North Atlantic and North Sea region (van der Meeren 2000; Ball et al. 2001). Surface water temperatures at the December–April releases were between 3 and 9°C, and 11–17°C at the May–August releases (van der Meeren 2000). The fluctuation in temperature is reflected in seasonal changes in the faunal composition, as well as the level of predation risk experienced by the lobster juveniles from each of these species (van der Meeren 2000). In December and February, 15 species were caught immediately after release. Only one of the four gadoid species, the cod, *Gadus morhua*, had eaten released lobsters. Along with the gadoids, three labrid species and four decapod crustaceans were registered but, besides the cod, remnants of released lobster juveniles were found only in an edible crab, *Cancer pagurus*. Nineteen species were registered at the March and April releases, but only edible crabs and shore crabs *Carcinus maenas*, along with the sculpin, *Myoxocephalus scorpius*, were registered as lobster predators, even if four gadoid, two labrid, and six decapod crustacean species were represented in the catch. The highest biodiversity was found in May, June, and August, when 21 species were caught and examined immediately after the releases, i.e., gadoids, labrids, and decapod crustaceans. Two of the six gadoid species, cod and *Trisopteurs minutus*, four out of five labrid species, *Ctenolabrus rupestris*, *Labrus mixtus*, *Crenilabrus melops*, *Labrus bergylta*, as well as both the crustaceans, shore crabs, and an adult lobster, were found eating lobster juveniles or had lobster remnants in the gut. In addition, the black goby, *Gobius niger*, the flounder, *Platichthys flesus*, and the eel, *Anguilla anguilla*, preyed on lobsters at these summer releases. Even if lobster juveniles have positively temperature-dependent distress activity, this is not enough to counteract the high predation pressure in the summer (van der Meeren 1993, 2000).

The release sites were typical bottom habitats that are found along the Norwegian coast. They are highly diverse, consisting of a patchwork of small areas of soft, hard, and mixed bottoms (van der Meeren unpubl. data). Within this mixture of habitat types, some of the released lobsters were expected to find good shelters in the immediate vicinity when they reached the seabed. Gravel, mussel shell substrate, and cobble offers interstitial spaces that have been preferred by early benthic lobsters, although survival over time is higher in cobble with larger interstitial spaces, where the lobsters might find more room to moult and grow without having to leave the shelter (Ball et al. 2001). Shelter scaling is probably as important in European lobsters as in the Caribbean spiny lobster, *P. argus* (Eggleston et al. 1990; Smith & Herrnkind 1992). Alternatively, since the distances between the different types of bottoms are very short, motile predators such as gadoids, labrids, and large crustaceans, usually forage in all habitats. However, predation upon released lobsters was significantly higher on open sandy bottoms than on rocky bottoms that provided shelter (van der Meeren 2000). Again, this shows how shelter-dependent early benthic phase and emergent lobsters are.

Except for the release day, no more than two released lobsters were found in fish or invertebrates during the monthly samples, which followed the same procedures as at the day of release (van der Meeren 2000). This indicates that mortality rate from large predators might be quite high at the time of release, but decreases rapidly after the first day, as the lobsters are settling into protective shelters. Most of the predators have been sampled in trammel nets and eel pots that are designed to catch large animals. Smaller, less motile predators have been observed to attack passing lobsters as they searched for and investigated shelters. Such predators could be small-sized shore- and swimming crabs (*Liocarcinus* sp.), molluscs (octopus), and cnidarians (Dahlia anemones) (Mercer et al. 2000; Ball et al. 2001; G. van der Meeren pers. obs.). Burrowed American lobsters have been seen caught by burrowing crabs (Lavalli & Barshaw 1986). Tail-flapping lobsters that are moving backwards into a crevice to escape from a threat have been seen caught by crevice-dwelling crabs, whereas more alert lobsters with lower stress-levels would always probe the crevice with antennae and claws before entering (G. van der

Meeren pers. obs.). The robustness of the shelter is also important. Common shore crabs are able to excavate sand and gravel and can get into shelters dug in the sediment (Barshaw & Lavalli 1988).

Settlement, as well as the first benthic phase days is considered to constitute a predation bottleneck in the life history of a range of marine species (see Gosselin & Qian 1997; Hunt & Scheibling 1997 for review). Lobster juveniles are dependent on functional shelters but, unlike the American lobster, they were never seen sharing shelters with conspecifics (Cooper et al. 1975; Sheehy 1976; Cooper & Uzmann 1977; O'Neill & Cobb 1979; Pottle & Elner 1982; Koponen 2003; van der Meeren 2003). Hence, a negative bias between available shelters and released lobsters might result in a number of lobsters being prone to predation, as they will be left out of shelter or occupy low-quality shelters. Studies show that lobsters would even prey on each other when reared communally, and newly moulted lobsters are especially prone to being eaten by conspecifics (Cobb & Tamm 1975; Aiken & Waddy 1995; G. van der Meeren pers. obs.). A surplus of food and shelters might counteract this, as cannibalism is not known from field studies (Karnofsky et al. 1989b; Jørstad et al. 2001).

The results confirm that lobster juveniles are extremely vulnerable to a range of predators while staying out of shelter, and are attractive as prey for both pelagic and benthic fish and benthic invertebrates. Although the loss to predators is more pronounced immediately after release, this can be reduced by cold-water releases. However, even in crevices and other interstitial spaces the lobsters can be attacked by both digging and shelter-dwelling predators. As long as no wild or hatchery-reared early benthic or emerging phase lobsters have been found in the field, their natural shelter as well as the long-term mortality in these life stages remains unknown.

Intra-specific competition

Shortages of shelters will result in increased competition over those that are available. Rearing studies in communal tanks have shown that intra-specific interactions in lobsters are pronounced. This is probably caused by the bimodal size distribution that establishes after 1–4 months, where one group outgrows the remainder of the lobsters (Van Olst et al. 1975; Sastry & Zeitlin-Hale 1977; Carlberg et al. 1979; Aiken & Waddy 1988, 1995; Jørstad et al. 2001). Cannibalism occurs under these conditions (Aiken & Waddy 1995). Since shelter is so important for the survival of lobster juveniles, intra-specific competition should be expected over limitations of this resource. In such instances, both juvenile and adult lobsters with missing claws will avoid dominant lobsters and will be displaced from shelter within a day (Scrivener 1971; van der Meeren & Uksnøy 2000; van der Meeren et al. unpubl. data). Fierce fights can also result in injuries and loss in dominance rank (van der Meeren & Uksnøy 2000; van der Meeren et al. unpubl. data). Hatchery-reared lobster juveniles were observed in escalated fights immediately after release. They also showed highly aggressive displays and threats towards conspecifics close to their shelters (van der Meeren 1993, 2003; Koponen 2003). Lobsters missing both claws were, without exception, found without shelters, even when shelters were in surplus (Fig. 4) (Mercer et al. 2000). When shelter competition was high, survival rates in the lobsters decreased until the lobster density became extremely high with more than 88 ind/m^2 (Mercer et al. 2000; Koponen 2003; van der Meeren 2003). When held at extreme densities, the lobsters were practically immobile and inactive (Mercer et al. 2000). The reason for this was not investigated, but the reduction in aggressive interactions is possibly the cause for the stabilised survival rate.

The large-scale releases in Norway since 1990 have been carried out during daytime in winter and early spring when the sea temperature is below 7°C

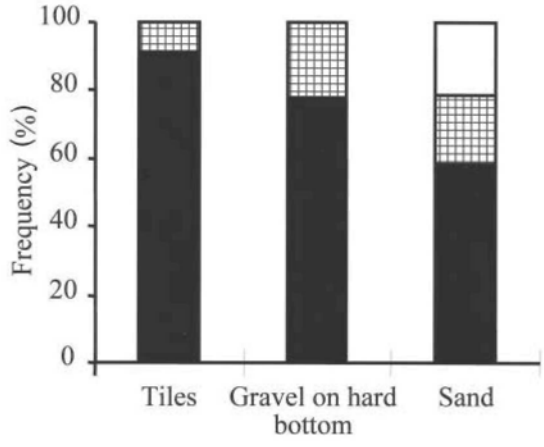

Fig. 4 Distribution of lobster juveniles with two claws (black), one claw missing (chequered), and no claws (white) after three days in a habitat with open sand, tiles, and gravel on hard bottom. There were three replicate tanks with 12 shelters and 17 lobsters in each replicate, n = 23, 9, and 19 lobsters under tiles, gravel and on open sand, respectively (Mercer et al. 2001).

(Agnalt et al. 1999; van der Meeren 2000). Although shelter-seeking speed can be reduced because of the temperature, the cold water also reduced aggression and caused them to stay in shelter. This is presumably because the cold water led to lower energy demands and thereby delayed moulting in newly released lobsters as well as reducing loss from predation (van der Meeren 1993, 2000).

If intra-specific mechanisms were important to regulate lobster populations, a negative correlation between cohorts and year classes would be present, as found in shore crabs (Moksnes 1999). This is typical for an opportunistic species with high fecundity, short life duration, and limited survival expectancy (MacArthur & Wilson 1967; Alerstam et al. 1985). The life strategy in lobsters is quite the opposite, with late maturation, low fecundity, potentially a long life span and low population density (Aiken & Waddy 1980; Sheehy et al. 1996; Wahle 1998). The settling of larvae in high densities, as in shore crabs, is probably not so for lobsters, with few and perhaps scattered larvae. Another regulating mechanism can be cannibalism by larger conspecifics, as we recovered a released juvenile from an adult lobster (van der Meeren 2000). However, it is not known if larger cannibalistic lobsters will have regulating effects on the settling cohorts and if shelter scaling might be important to avoid such effects. Although the recapture rates at Kvitsøy vary for each released cohort, no inter-cohort patterns can be documented (Agnalt et al. 2004). There is also a risk of juveniles released in the spring predating on naturally settling young-of-the-year lobsters in the summer. This is yet to be studied. Between 1990 and 1998, only two natural cohorts seemed to have settled successfully in western Norway, according to reports from fishers (G. van der Meeeren pers. obs.). The recruitment to the Kvitsøy fishery of wild lobsters during 1991–97 was different from other places in the region, so the hatchery-reared lobsters seemed to have been a significant addition and not a replacement (Agnalt et al. 1999, 2004).

If shelters are scarce, subordinate lobsters are displaced from shelters because of intra-specific competition and left unprotected from predators (Koponen 2003; van der Meeren 2003). Even with predators present, sheltered lobsters protected their shelters aggressively from approaching conspecifics trying to enter (G. van der Meeren pers. obs.). It is not known if sheltering habitats in the sea are limited thus causing a bottleneck in survival of early benthic phase lobsters in Norway. However, as the breeding population is at a historic low and fecundity is naturally low, this is hardly likely. Alternatively, large-scale releases of hatchery-reared lobster juveniles might result in unnatural high juvenile densities in the release area, resulting in displaced juveniles left out in the open as a result of insufficient shelters and thereby open for predator attacks.

Inter-specific competition

European lobsters are known to be highly aggressive, keeping their distance from conspecifics and can even cause edible crabs to avoid lobster-holding traps (Addison 1995; Addison & Bannister 1998). Hatchery-reared juvenile lobsters will successfully defend their shelters against smaller shelter-dwelling crustaceans such as galatheans and porcelaind crabs (Koponen 2003; van der Meeren 2003). Slightly larger galatheans and brachyuran crab competitors however, will have a negative effect on the sheltering rate of the lobsters (Koponen 2003; van der Meeren 2003), as small shore crabs can even catch and hold on to lobsters their own size (Institute of Marine Research unpubl. data).

It is not clear if small, bentic, shelter-dwelling but motile, nocturnal crustaceans such as crabs, galatheans and porcelain crabs, and lobsters actually compete over the same resources in the sea, or if they occupy discrete territories (Barrash 1982). Shelter shape and scaling, depth, salinity, and shelter manipulation are mechanisms that can keep potential competitors in separate niches. Both the lobster and the other species prefer to hide in hollows in the sand that are dug out underneath a solid roof (small tiles), but occupy the shelter in different ways (van der Meeren 2001). The difference in species-specific morphology and shelter-related behaviour also indicates that the studied species may benefit from character displacement (Brown & Wilson 1956). The hatchery-reared lobsters were found to be more shelter-restricted than the other species that competed for the same type of shelters, probably because of a narrower choice of shelters (Koponen 2003; van der Meeren 2003). A group of lobsters released to a semi-natural bottom habitat in an exhibition tank in Bergen Aquarium for three months, established tunnels from the brim of gravel on sand, underneath a belt of gravel, cobble, and stones. When the tank was drained, they had eventually tunnelled to the wall and underneath large boulders placed in the back of the tank (Fig. 5) (van der Meeren unpubl. data).

This result supports the hypothesis that lobster juveniles avoid competition by forming shelters out of reach of the numerous commonly found

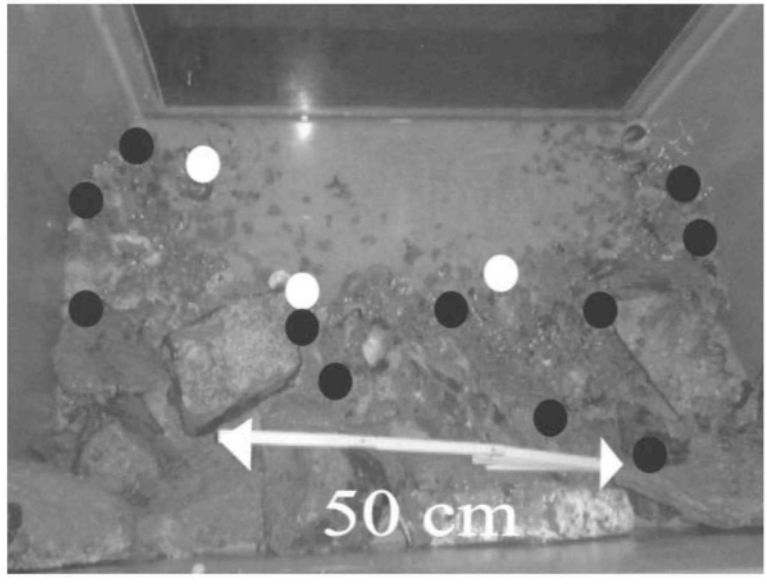

Fig. 5 Position of undisturbed lobsters visible in tunnel entrances (white spots) and hiding places after the tank was drained (black spots) in an aquarium tank three months after release (van der Meeren unpubl. data).

crustaceans living in European cobble ground (Mercer 2001; Koponen 2003; van der Meeren 2003).

Early benthic phase American lobsters are frequently found in the intertidal zone, where they hide under rocks during low tide (Cowan 1999). Small European lobsters have also been observed above the low water level (Linnane 2000b). During the studies of European lobsters and galatheans, it was also observed that the hatchery-reared lobsters stayed well inside their shelters when the tanks were drained, whereas the galatheans left their shelters and tail-flapped about on the open sand (G. van der Meeren pers. obs.). This implies that the lobsters responded to "low tide" in a functional way as for littoral life, whereas the galatheans seem to be adapted for a life below the low tide line. It may be that the response to tidal changes is a way of establishing a different niche from galatheans. The smallest European lobsters have been found in shallow waters, from depths of 15 m to the littoral zone (Linnane 2000b; Mercer 2001). Both the sublittoral and the littoral zone can be occupied by a high density of crabs. Even edible crabs are occasionally foraging above the low water line at high tide (Christiansen 1969; Karlsson & Christiansen 1996). It is not known how wild lobster juveniles avoid these competitors and potential predators, but both shelter shape and environmental conditions might be important. The apparent water permeability (AWP) in a range of decapod crustaceans has been shown to correlate to the habitat salinity of each species, where the estuarine species have a better ability to alter AWP than species living in more stabile salinity (Rudy 1967; Rainbow & Black 2001). A study of the AWP in lobsters at different life phases, as well as in potential competitive decapoda species, could be useful, as it has been found that early benthic phase lobsters are more tolerant to lower salinity than adult lobsters (Mercer et al. 2001).

How hatchery-reared lobsters manage to cope with the competition for shelter and food in the sea is unknown, as they disappear within hours of being released (van der Meeren 2000). Any type of competition seems to result in lower survival rates in lobsters. Even with competitors that are smaller than the lobsters, i.e., small galatheans and cobble-living snapper shrimps, *Athanas nitescens*, the survival rate will be significantly reduced (Mercer et al. 2000). This implies that mortality might occur in connection to the moult, when the lobster is particularly vulnerable. It is not known whether growth rate is affected in the same way (Mercer et al. 2000).

A good shelter that can be developed into a multi-entrance burrowing system that will sustain the lobster over time, and also meet its food requirements, seems to be the optimal habitat where the lobster would have the best chance to grow and survive (Wickins et al. 1996). The present results shows that hatchery-reared lobsters are able to dominate other small-sized crustaceans, even if

competition functions as a mechanism that affects survival rates over a long period. To survive in the sea, the early benthic and emergent phase lobsters probably need to find living space that is separate from other species with the similar requirements for shelter. Their morphology, behaviour, and hydrographic tolerance should enable them to establish in discrete shelters out of reach of the majority of both predator and competitor species.

Ecological criteria that affect the outcome of release activities

Usually the outcome of a release is measured and evaluated based on recapture data and population dynamic models (i.e., Borthen et al. 1999; Giske & Salvanes 1999). The use of ecological models should be applied to develop release procedures to increase the survival of the released animals, as well as protecting the biotope from damaging manipulation that, over time, can lead to negative side effects, i.e., loss of biodiversity or decreased value of other activities in the area.

In Norway, sea ranching and stock enhancement was the subject for a national research programme, to study the potential of commercial enterprises that would benefit communities along the coast, and to a lesser degree the ecology concerning the release organisms (Svåsand et al. in press). In addition to lobsters, the Atlantic salmon, *Salmo salar*, Arctic char, *Salvelinus alpinus*, and cod has been studied. Low recapture rates in the salmonid species led to some indications that improvements can be obtained, but the recapture rate from 0.5 to 3.8% is too low to make it economically viable. The Arctic char had better recapture rates, but too high mortality rates in the first-time seaward migration. Some new information about migration was achieved during the research programme, but not enough to find out if the species could be cultivated in a more cost-effective way. None of these studies has given much data on natural recruitment mechanisms in these species.

The studies on cod releases, however, have resulted in new information about natural recruitment mechanisms. In closed ecosystems and for areas where the organisms are dependent on local food production, enhancement of organisms high in the trophic level, such as cod, cannot be achieved through releases of juveniles, unless food supply is sufficiently high to sustain a natural recruitment that is above average (Salvanes et al. 1992). When juvenile cod were released at the open coast, the mortality from predation by birds and fish was too high to facilitate sufficient recapture rates to make it economically viable, even though hatchery-reared cod can be trained to more adaptive predatory defences (Johansen et al. 1999; Kristiansen 1999; Nøtvedt et al. 1999; Otterå et al. 1999a,b; Skreslett et al. 1999).

The lobster releases resulted in the best recapture rates and no stray lobsters were found outside the released area (Bannister et al. 1994; Agnalt pers. comm.). An economic simulation model showed that only small increases in recapture rates could make lobster releases economically viable, if the released females reproduced at least once before being recaptured and their offspring settled in the same area (Borthen et al. 1999). The gap between the release and the first recapture 3 years later leaves us short of the ecological information needed to find out why the recapture rate is as modest as it is. This is possibly a result of high mortality rates during or after releases or the adult lobsters avoiding the traps.

Tsukamoto et al. (1999) emphasised the importance of improving both release technique, quality of the release organism, and the environmental conditions to improve stock efficiency. The present studies show that trials and tribulations on an individual level are important for the survival rate. A range of ecological and behavioural criteria has proven to affect the immediate success of releases. Fig. 1 shows some main ecological factors that influence the survival chances of the release organism, and how they are connected, from the rearing phase to final settlement or death. The organisms must be established in a place where their ecological requirements are met in full to be able to survive and remain there (Wickins & Lee 2002).

CONCLUSION

To be able to develop models for evaluating the benefit of a release enterprise, or refining release procedures, both qualitative and quantitative data collection is needed. This pertains to physical subjects such as temperature, salinity, and depth, and to behavioural and ecological subjects, i.e., the location where wild conspecifics live and how much they interact with the rest of the benthic society they settle in. Classical ecosystem theory is in general too abstract and over-simplified to address real-world issues (Suter 1981). Individual-based ecological models have now been developed for a range of taxonomic groups, also for aquatic fish and smaller planktonic crustaceans. Most of them are based on

more realistic assumptions than state variable models, and are designed to understand how the system's properties emerge from the behaviour of individuals that make up the system (Grimm 1999). Laboratory studies of European lobsters during the last decades have provided a series of incidences that might help us to identify possible nursery habitats. These studies have already been useful in improving lobster release techniques. Unfortunately, no large field studies have been accomplished that were based on a combination of all the newly acquired data. As long as we are unable to locate wild and released lobster juveniles in the sea, data on shelter requirements, inter-specific and intra-specific competition, predation, and food availability will be suggestions based on incidence and observations of hatchery-reared animals in the laboratory. Stock enhancement and sea-farming enterprises for European lobsters will continue to be based partly on educated guesses and partly on luck, as with most of the other marine release programmes worldwide. It is possible to enhance our knowledge by performing small-scale investigations outside the field and construct testable hypotheses. It is also clear that these hypotheses need to be tested in the field before evaluating their relevance and importance in relation to larger-scale enhancement actions. Fieldwork costs a great deal in economic investments, is time-consuming, and is risky for the environment if carried out without basic understanding of the biotope. Therefore, the importance of preliminary laboratory experiments is to be able to design field studies that are as cost- and time-effective as possible, and with a minimum of risk for negative unintentional long-term effects on the biotope. Terrestrial conservation and reintroduction projects in both birds and mammals worldwide show that well-planned release programmes based on thorough ecological studies, followed by strict management rules based on basic ecological comprehension, can lead to successful population increase over time.

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REFERENCES

Abello, P.; Warman, C. G.; Reid, D. G.; Naylor, E. 1994: Chela loss in the shore crab Carcinus maenas (Crustacea: Brachyura) and its effect on mating success. *Marine Biology 121*: 247–525.

Able, K. W.; Heck, K. L. Jr.; Fahay, M. P.; Roman, C. T. 1988: Use of salt-marsh peat reefs by small juvenile lobsters on Cape Cod, Massachusetts. *Estuaries 11*: 83–96.

Abrahamsson, S. A. A. 1965: A method of marking crayfish *Astacus astacus* Linné in population studies. *Oikos 16*: 228–231.

Addison, J. T. 1995: Influence on behavioural interactions on lobster distribution and abundance inferred from pot-caught samples. *International Council for Exploration of the Sea, Marine Science Symposia 199*: 294–300.

Addison, J. T.; Bannister, R. C. A. 1994: Re-stocking and enhancement of clawed lobster stocks: a review. *Crustaceana 67*: 131–155.

Addison, J. T.; Bannister, R. C. A. 1998: Quantifying potential impacts of behavioural factors on crustacean stock monitoring and assessment: modelling and experimental approaches. *In*: Jamieson, G. S.; Campbell, A. *ed.* Proceedings of the North Pacific symposium in invertebrate stock assessment and management. *Canadian Special Publication of Fisheries and Aquatic Sciences 125*: 167–177.

Addison, J. T.; Bell, M. C. 1997: Simulation modelling of capture processes in trap fisheries for clawed lobsters. *Marine and Freshwater Research 48*: 1035–1044.

Agnalt, A.-L.; Jørstad, K. E.; Kristiansen, T.; Nøstvold, E.; Farestveit, E.; Næss, H.; Paulsen, O. I.; Svåsand, T. 2004: Enhancing the European lobster (*Homarus gammarus*) stock at Kvitsøy Islands: perspectives of rebuilding Norwegian stocks. *In*: Leber, K. M.; Kitada, S.; Blankenship, H. L.; Svåsand, T. *ed.* Stock enhancement and sea ranching—developments, pitfalls and opportunities. London, UK, Blackwell Publishing. Pp. 415–426.

Agnalt, A.-L.; van der Meeren, G. I.; Jørstad, K. E.; Næss, H.; Farestveit, E.; Nøstvold, E.; Korsøen, E.; Ydstebø, L.; Svåsand, T. 1999: Stock enhancement of European lobster (*Homarus gammarus*): a large-scale experiment off southwestern Norway (Kvitsøy). *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, Blackwell Scientific Press. Pp. 401–419.

Aiken, D. E.; Waddy, S. L. 1980: Reproductive biology. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. New York, United States, Academic Press. Pp. 215–275.

Aiken, D. E.; Waddy, S. L. 1988: Strategies for maximizing growth of communally reared juvenile American lobster. *World Aquaculture 19*: 61–63.

Aiken, D. E.; Waddy, S. L. 1989: Lobster culture. *In*: Boghen, A. D. *ed.* Coldwater aquaculture in Atlantic Canada. Moncton, New Brunswick, Canadian Institute for Research on Regional Development. Pp. 77–122.

Aiken, D. E.; Waddy, S. L. 1995: Culture of American lobster *Homarus americanus*. *In*: Boghen, A. D. *ed.* Coldwater aquaculture in Atlantic Canada. Moncton, New Brunswick, Canadian Institute for Research on Regional Development. Pp. 145–188.

Alerstam, T.; Karlsson, J.; Otto, C. *ed.* 1985: Populations ekologi. Stockholm, Sweden, Liber Förlag. 279 p. (In Swedish.)

Ali, Y.; Wickins, J. F. 1994: The use of fresh food supplements to ameliorate moulting difficulties in lobsters *Homarus gammarus* (L.) destined for release to the sea. *Aquaculture and Fisheries Management 25*: 483–496.

Appelöf, A. 1909: Undersøkelser over hummeren (*Homarus vulgaris*) med særskilte hensyn til dens optræden ved Norges kyster. Aarsberetning vedkommende Norges fiskerier, 1ste hefte. Særtrykk. Bergen, Norway, A. S. John Griegs Boktrykkeri. 160 p. (In Norwegian.)

Atema, J.; Voigt, R. 1995: Behavior and sensory biology. *In*: Factor, J. R. *ed.* Biology of the lobster *Homarus americanus*. San Diego, Academic Press. Pp. 313–348.

Atema J.; Jacobson, E.; Karnofsky, E.; Olerszku,-Szuts, S.; Stein, L. 1979: Pair formation in the lobster, *Homarus americanus*: Behavioral development, pheromones and mating. *Marine Behavior and Physiology 6*: 277–296.

Ball, B.; Linnane, A.; Munday, B.; Browne, R.; Mercer, J. P. 2001: The effect of cover on in situ predation in early benthic phase European lobster (*Homarus gammarus*). *Journal of Marine Biology Association, UK 81*: 639–642.

Bannister, R .C. A. 1998: The assessment and population dynamics of the European lobster, *Homarus gammarus* (L.). *In*: van der Meeren, G. I.; Soldal, O. *ed.* Proceedings of the seminar at Kvitsøy 1995: the European lobster *Homarus gammarus* (L.). *Fisken og Havet 13*: 58–71.

Bannister, R. C. A.; Addison, J. T. 1998: Enhancing lobster stocks: a review of recent European methods, results and future prospects. *Bulletin of Marine Science 62*: 369–387.

Bannister, R. C. A.; Addison, J. T.; Lovewell, R. J. 1994: Growth, movement, recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* Linnaeus, 1758) released into the wild on the English east coast. *Crustacean 67*: 156–172.

Barnes, E. W. 1939: Methods for protecting and propagating the lobster, with a brief outline of its natural history. *In*: Special report of the development of conservation relative to the feasibility and cost of propagation of lobsters by the Commonwealth of Massachusetts, Appendix A. Boston, Massachussets, Massachusetts House Doc. 2051, State Library. Pp. 10–32.

Barrash, D. P. 1982: Sociobiology and behavior. New York, Elsevier Science Publishing. 426 p.

Barshaw, D. E.; Lavalli, K. L. 1988: Predation upon postlarval lobster *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crab *Neopanope sayi* on three different substrates: eelgrass, mud, and rocks. *Marine Ecology Progressive Series 48*: 119–123.

Barshaw, D. E.; Spanier, E. 1994: Anti-predator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bulletin of Marine Science 55*: 375–382.

Bartley, D. M. 1995: Ocean ranching. *Ceres 151*: 42–45.

Bartley, D. M. 1996: Conservation of biological diversity in hatchery enhancement programmes. *In*: diCastri, F.; Younès, T. *ed.* Biodiversity, science and development. Towards a new partnership. Oxon, CAB International; Oxon and Paris, International Union of Biological Science. Pp. 424–438.

Bartley, D. M. 1999: Marine ranching: a global perspective. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, Blackwell Scientific Press. Pp. 401–419.

Beal, B. F.; Chapman, S. R. 2001: Methods for mass rearing stages I-IV larvae of the American lobster, *Homarus americanus* H. Milne Edwards, 1837, in static systems. *Journal of Shellfish Research 20*: 337–346.

Beard, T. W.; Wickins, J. F. 1992: Techniques for the production of juvenile lobsters. MAFF Directorate, Fisheries Research, Lowestoft. *Fisheries Research Technical Report 92*. 22 p.

Berrill, M. 1974: The burrowing behavior of newly-settled lobsters *Homarus vulgaris* (Crustacea-Decapoda). *Journal of the Marine Biology Association,UK 30*: 285–287.

Bertness, M. D. 1981: Competitive dynamics of a tropical hermit crab assemblage. *Ecology 62*: 751–761.

Booth, J. 2001: Habitat preference and behaviour of newly settled *Jasus edwardsii*. *Marine and Freshwater Research 52*: 1055–1066.

Borthen, J.; Agnalt, A.-L.; van der Meeren, G. I. 1999: Lobster stock enhancement in Norway—a bioeconomic model. Presenting of model and evaluation of some main results. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, Blackwell Scientific Press. Pp. 583–596.

Browman, H. I. 1989: The biology and behavioural ecology of ontogenetic critical periods in fish. *In*: Blaxter, J. H. S.; Gamble, J. C.; von Westernhagen, H. *ed.* The early life history of fish. The Third ICES Symposium, Bergen, 3–5 October 1988. Rapports et procès-verbaux des reunions, Conseil International pour l'Exploration de la mer 191. Pp. 469–470.

Brown, J.; Wilson, E. O. 1956: Character displacement. *Systematic Zoologist 14*: 145–162.

Burton, C. 1992: Techniques of lobster stock enhancement. Sea Fish Industry Authority, Marine Farming Unit, Ardtoe, Scotland. Seafish Reports 396. Pp. 1–35.

Butler, M. J. 1997: Benthic processes in lobster ecology: report from a workshop. *Marine and Freshwater Research 48*: 659–662.

Böck, A. 1869: Om det norske hummerfiske og dets historie. *Tidskrift for Fiskeri 3*. (In Norwegian.)

Carlberg, J. M.; Van Olst, J. C.; Ford, R. F. 1979: Potential for communal rearing of the nephropid lobsters (*Homarid* spp.). Proceedings of Annual Meeting. *World Maricuklture Society 10*: 840–853.

Carlson, F. T. 1954: The American lobster fishery and possible applications of artificial propagation. *Yale Conservation Studies 3*: 3–7.

Carlson, F. T. 1955: Evaluation of the artificial propagation of the American lobster with special reference to the Connecticut lobster Fishery. New Haven, Yale University Conservation program. 132 p.

Caryl, P. G. 1981: Escalated fighting and the war of nerves: games theory and animal combat. *In*: Bateson, P. P. G.; Klopfer, P. *ed.* Perspectives in ethology, 4th ed. New York and London, Plenum. Pp. 199–224.

Castro, K. M.; Cobb, J. S.; Wahle, R. A.; Catena, J. 2001: Habitat addition and stock enhancement for American lobster, *Homarus americanus*. *Marine and Freshwater Research 52*: 1253–1262.

Childress, M. J.; Herrnkind, W. F. 1994: The behavior of juvenile Carribean spiny lobster in Florida Bay: seasonality, ontogeny, and sociality. *Animal Behaviour 51*: 675–687.

Christiansen, M. E. 1969: Decapoda Brachyura. Marine Invertebrates of Scandinavia 2. Olso, Universitetsforlaget. 143 p.

Cobb, J. S.; Tamm, G. R. 1975: Dominance status and molt order in lobster (*Homarus americanus*). *Marine Behavior and Physiology 3*: 119–124.

Cook ,W. 1995: A lobster stock enhancement experiment in Cardigan Bay. Final report. Lancaster, North Western and North Wales Sea Fisheries Committee. 33 p.

Cooper, R. A.; Uzmann, J. R. 1977: Ecology of juvenile and adult clawed lobsters, *Homarus americanus*, *Homarus gammarus* and *Nephrops norvegicus*. *Circulations—Commonwealth Science and Industrial Organisation, Division of Fisheries and Oceanography 7*: 197–208.

Cooper, R. A.; Clifford, R. A.; Newell, C. D. 1975: Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. *Transcriptions of the American Fisheries Society 104*: 669–974.

Cowan, D. F. 1999: Method for assessing relative abundance, size-distribution, and growth of recently settled and early juvenile lobster (*Homarus americanus*) in the lower intertidal zone. *Journal of Crustacean Biology 19*: 738–751.

Dannevig, A. 1928: The rearing of lobster larvae at Flødevigen. *Report of the Norwegian Fisheries and Marine Investigations 3*: 1–15.

Dannevig, A. 1936: Hummer og Hummerkultur. *Report on Norwegian Fishery and Marine Investigations 12*. 60 p. (In Norwegian.)

Dannevig, G. M. 1885: Artificial hatching and rearing of salt-water fish and lobster in Norway. *Bulletin of the U.S. Commission of fisheries and Fishes 5*: 437–440.

Debuse, V. J.; Addison, J. T.; Reynolds, J. D. 1999: The effects of sex ratio on sexual competition in the European lobster. *Animal Behaviour 58*: 973–981.

de Maude, M. A. 1858: Rapport sur un mémoire de Monsieur Chauvin relatif à la culture la mer. Bulletine Societè de Impériale d'Acclimatation. [sited in D. Latroite and J. Lorec (1991)]

Dennis, D. M.; Jernakoff, P.; Phillips, B. F. 1997: Severe mortality in a breeding population of ornate rock lobster *Panulirus ornatus* (Fabricius) at Yule Island, Papua New Guinea. *Journal of Experimental Marine Biology and Ecology 162*: 134–158.

Derby, C. D.; Steulett, P.; Horner, A. J.; Cate, H. S. 2001: The sensory basis of feeding behaviour in the Carribean spiny lobster, *Palinurus argus*. *Marine and Freshwater Research 52*: 1339–1350.

Doherty, P. J. 1999: Recruitment limitation is the theoretical basis for stock enhancement in marine populations. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, Blackwell Scientific Press. Pp. 9–21.

Dunham, P. J. 1972: Some effects of group housing upon the aggressive behavior of the lobster *Homarus americanus*. *Journal of Fisheries Research Board of Canada 29*: 598–601.

Eggleston, D. B.; Lipcius, R. N.; Miller, D. L.; Coba-Cetina, L. 1990: Shelter scaling regulates survival of juvenile spiny lobster, *Panulirus argus*. *Marine Ecology Progress Series 62*: 79–88.

Elner, R. W.; Cambell, A. 1981: Force, function and mechanical advantage in the chelae of the American lobster *Homarus americanus* (Decapoda: Crustacea). *Journal of Zoology 193*: 269–286.

Emmel, V. E. 1908: The problems in feeding methods. *Rhode Island Commision for Inland Fisheries Annual Report 38*: 98–114.

Enslie, R.; Brooks, M. 1999: African rhino. Status Survey and Conservation Action Plan. IUCN/SSC African Rhino Specialist Group. Gland, Switzerland and Cambridge, UK, IUCN. Pp. ix + 92 p.

Factor, J. R. *ed.* 1995: Biology of the lobster *Homarus americanus*. San Diego, Academic Press. 528 p.

Ferrero, E. A.; Privileggi, N.; Scovacricchi, T.; van der Meeren, G. I. 2002: Does lunar cycle affect egg hatching and juveniles moulting frequency of reared lobsters? *Ophelia 56*: 13–22.

Fontaine, C. T.; Manzella, S. A.; Williams, T. D.; Harris, R. M.; Browning, W. J. 1989: Distribution, growth and survival of head-started, tagged and released Kemp's ridley sea turtles (*Lepidochelys kempi*) from year classes 1978–1983. *In*: Caillouet, C. W. Jr.; Landry, A. M. Jr. *ed.* Proceedings of the first international symposium on Kemp's ridely sea turtle—biology, conservation and management. Report from Texas A&M University Sea Grant Program. Pp. 124–144.

Free, E. K. 1998: Reproduction in the European lobster (*Homarus gammarus* (L.)). *In*: van der Meeren, G. I.; Soldal, O. *ed.* Proceedings of the seminar at Kvitsøy 1995: the European lobster *Homarus gammarus* (L.). *Fisken og Havet 13*: 4–27.

Fritts, S. H. 2000: Review of carnivores in ecosystems: the Yellowstone experience. *Ecology 81*: 2351–2352.

Gendron, L. *ed.* 1998: Proceedings of a Workshop on Lobster Stock Enhancement held in the Magdalen Islands (Quebec) from 29 to 31 October 1997. *Canadian Industry Report of Fisheries and Aquatic Sciences 244*. 135 p.

Giske, J.; Salvanes, A. G. V. 1999: A model of enhancement potentials in open ecosystems. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, Blackwell Scientific Press. Pp. 22–36.

Gollasch, S.; Leppäkoski, E. 1999: Initial risk assessment of alien species in Nordic coastal waters. *Nord 1999*. 244 p.

Govind, C. K.; Kent, K. S. 1982: Transformation of fast fibers to slow, prevented by lack of activity in developing lobster muscle. *Nature 298*: 75–757

Gosselin, L. A.; Quian, P. E. 1997: Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series 146*: 265–282.

Gregory, R. D.; Noble, D. G.; Robinson, J. A.; Stroud, D. A.; Campbell, L. H.; Rehfisch, M. M.; Cranswick, P. A.; Wilkinson, N. I.; Crick, H. Q. P.; Green, R. E. 2002: The state of the UK's birds 2001. Sandy, Bedfordshire, United Kingdom, The Royal Society for Preservation of Birds, British Trust for Ornithology, World Wildlife Trust, and Joint Nation Conservation Committee. 24 p.

Grimm, V. 1999: Ten yers of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling 115*: 129–148.

Grimsen, S.; Jaques, R. N.; Ernest, V.; Balchen, J. G. 1987: Aspects of automation in a lobster farming plant. Modelling. *Identification and Control 8*: 61–68.

Grossman, G. D.; Jones, G. P.; Seaman, W. J. 1997: Do artificial reefs increase regional fish production? A review of existing data. *Fisheries 22*: 17–23.

Hansen, A.; Schmidt, M. 2001: Neurogenesis in the central olfactory pathway of the adult shore crab *Carcinus maenas* is controlled by sensory afferents. *The Journal of Comparative Neurology 441*: 223–233.

Harrison, P. J. H.; Cate, H. S.; Steulett, P.; Derby, C. D. 2001: Structural plasticity in the olfactory system of adult spiny lobsters: postembryonic development permits life-long growth, turnover, and regeneration. *Marine and Freshwater Research 52*: 1357–1365.

Harsch, S.; Dawirs, R. R. 1996: Neurogenesis in the developing crab brain: postembryonic generation of neurons persist beyond metamorphosis. *The Journal of Neurobiology 29*: 384–398.

Harsch, S.; Miller, J.; Benton, J.; Beltz, B. 1999: From embryo to adult: Persistent neurogenesis and apoptotic cell death shape the lobster deutocerebrum. *The Journal of Neuroscience 19*: 3472–3485.

Hartnoll, R. G. 1982: Growth. *In*: Abele, L. G. *ed.* The biology of the crustacea, vol. 2. Embryology, morphology, and genetics. London, Academic Press. Pp. 111–196.

Heck, K. L.; Orth, R. J. 1980: Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapaek Bay—Decapoda Crustacea. *Estuaries 3*: 289–295.

Herrick, F. H. 1894: The habits and development of the American lobster and their bearing upon its artificial propagation. *Bulletin of the United States Commission for Fish and Fisheries 13*: 75–86.

Hoffman, R. B.; Dunham, P. J.; Kelly, P. V. 1975: Effects of water temperature and housing conditions upon the aggresive behavior of the lobster *Homarus americanus*. *Journal of Fisheries Research Board, Canada 32*: 713–717.

Holme, N. A.; McIntyre, A. D. 1984: Methods for the study of marine benthos. Oxford, Blackwell Scientific Publications. 139 p.

Holthuis, L. B. 1950: Decapoda (K IX) A. Natantia, Macrura Reptantia, Anomura en Stomatopoda (K X). *Fauna Ned 15*: 1–166.

Holthuis, L. B. 1991: Marine lobsters of the world. Key to species *Homarus americanus*, *Homarus capensis*, *Homarus gammarus*. *In*: Holthuis, L. B. *ed.* An annotated and illustrated catalogue of species of interest to fisheries known to date. *FAO Fisheries Synopsis 125(13)*: 57–60.

Howard, A. E. 1977: The influence of topography and current on size composition of lobster populations. International Council for the Exploitation of the Sea, Council meeting K:31. 5 p.

Howard, A. E.; Bennett, D. B. 1979: The substrate preference and burrowing behavior of juvenile lobsters (*Homarus gammarus* (L.)). *Journal of Natural History 13*: 130–133.

Hughes, J. T.; Shleser, R. A.; Tchobanoglous, G. 1974: A rearing tank for lobster larvae and other aquatic species. *Progressive Fish Culturist 36*: 129–132.

Hunt, H. L.; Scheibling, R. E. 1997: Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series 155*: 269–301.

Huntingford, F. A.; Turner, A. 1987: Animal Conflict. London, UK, Chapman & Hall Animal Behaviour Series. Pp. 1–318

Incze, L. S.; Wahle, R. A. 1991: Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus*. *Marine Ecology Progress Series 79*: 77–81.

Jacobson, S. 1977: Agonistic behavior, dominance and territoriality in the American lobster, *Homarus americanus*. Unpublished PhD thesis, Boston University, Massachusetts, United States. 136 p.

Jensen, A. C.; Collins, K.; Lockwood, A. P. M. 2000: Artificial reefs in European seas. Dordrecht, Kluwer Academic Publishers. 508 p.

Jernakoff, P. 1990: Distribution of newly settled western rock lobsters *Panulirus Cygnus*. *Marine Ecology Progress Series 66*: 63–74.

Johansen, R.; Pedersen, T.; Barrett, R. T. 1999: Cormorants (*Phalacrocorax carbo carbo*) as predators in a cod (*Gadus morhua* L.) enhancement area in North Norway. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 334–349.

Jørstad, K. E.; Agnal, A.-L.; Kristiansen, T. S.; Nøstvold, E. 2001: High survival and growth of European lobster juveniles (*Homarus gammarus*), reared communally with natural bottom substrate. *Marine and Freshwater Research 52*: 1431–1438.

Jørstad, K. E.; Farestveit, E.; Rudra, H.; Agnalt, A.-L.; Olsen, S. 2002: Studies on red king crab (*Paralithodes camtschaticus*) introduced to the Barents Sea. *In*: Crabs in cold water regions, management, and economics. Alaska Sea Grant College Program Report AK-SG-02-01. Pp. 425–438.

Karlsson, K.; Christiansen, M. E. 1996: Occurrence and population composition of the edible crab (*Cancer pagurus*) on rocky shores of an inlet on the South coast of Norway. *Sarsia 81*: 307–314.

Karnofsky, E. B.; Atema, J.; Elgin, R. H. 1989a: Natural dynamics of popuation structure and habitat use of the lobster, *Homarus americanus*, in a shallow cove. *Biological Bulletin 176*: 247–256.

Karnofsky, E. B.; Atema, J.; Elgin, R. H. 1989b: Field observations of social behavior, shelter use, and foraging in the lobster *Homarus americanus*. *Biological Bulletin 176*: 239–246.

Khalanski, M. 1997: Industrial and ecological consequences of the introduction of new species in continental aquatic ecosytems: the zebra mussel and other invasive species. Bulletin Francais de la Peche et de la Pisciculture. Pp. 187–203.

Kittaka, J. 1984: The breeding of lobster hybrids. Report on scientific research achievements of 1983. Japan, Kitsato University. Pp. 1–33.

Kristiansen, T. S. 1999: Enhancement studies of coastal cod (*Gadus morhua* L.) in Nord-Trøndelag, Norway. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 277–292.

Kuzmin, S.; Olsen, R. 1994: Barent sea king crab (*Paralithodes camtschatica*): the transplantation experiments were successful. International Council of the Exploration of the Sea, Council meeting 1994/K:12. 12 p.

Lang, F.; Govind, C. K.; Costello, W. J.; Green, S. I. 1977: Developmental changes in escape behaviour during growth of the lobster. *Science 197*: 682–685.

Latrouite, D.; Lorec, J. 1991: L'expérience française de forçage du recrutement du Homard Européen (*Homarus gammarus)*: résultats préliminaires. *ICES Marine Science Symposium 192*: 93–98.

Laurec, A. 1999: Can the conditions for a successful enhancement or sea ranching be defined? *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 1–5.

Lavalli, K. L.; Barshaw, D. E. 1986: Burrows protect postlarval lobsters *Homarus americanus* from predation by the non-burrowing cunner *Tautogolabrus adspersus*, but not from the burrowing crab *Neopanope texani*. *Marine Ecology Progressive Series 32*: 13–16.

Lee, S. Y.; Seed, R. 1992: Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Marine Ecology Progress Series 84*: 151–160.

Lewis, R. K. 1977: Rock lobster puerulus settlement in the south east. *SAFIC 13* (Magazine of the Department of Fisheries and the Australian Fishing Industry Council, South Australian Branch). Pp. 9–11.

Lindberg, W. J. 1997: Can science resolve the attraction-production issue? *Fisheries 22*: 10–13.

Linnane, A.; Uglem, I.; Grimsen, S.; Mercer, J. P. 1997: Survival and cheliped loss of juvenile lobsters *Homarus gammarus* during simulated out-of-water transport. *Progressive Fish-Culturist 59*: 47–53.

Linnane, A.; Mazzoni, D.; Mercer, J. P. 2000a: A long-term mesocosm study on the settlement and survival of juvenile European lobster *Homarus gammarus* L. in four natural substrata. *Journal of Experimental Marine Biology and Ecology 249*: 51–64.

Linnane, A.; Ball, B.; Munday, B.; Mercer, J. P. 2000b: On the occurrence of juvenile lobster *Homarus gammarus* in intertidal habitat. *Journal of the Marine Biology Association, UK 80*: 375–376.

Linnane, A.; Ball, B.; Mercer, J. P.; van der Meeren, G. I.; Bannister, R. C. A.; Mazzoni, D.; Munday, B.; Ringvold, H. 2001: Searching for the early benthic phase (EBP) of the European lobster: a trans-European study of cobble fauna. *Hydrobiologia 465*: 63–72.

MacArthur, R. H.; Wilson, E. O. 1967: The theory of island biogeography. Princetown, New Jersey, United States, Princetown University Press. 224 p.

McLeese, D. W.; Wilder, D. G. 1958: The activity and catchability of the lobster, *Homarus americanus*, in relation to temperature. *Journal of Fisheries Research Board, Canada 15*: 1345–1354.

Mather, F. 1900: Lobsters. *In*: Modern fish culture in fresh and salt water. New York, Forestry and Stream Publications Corporation. Pp. 296–300.

Maynard Smith, J. 1982: Evolution and the theory of games. Cambridge, UK, Cambridge University Press. 226 p.

Mercer, J. P.; Bannister, R. C. A.; van der Meeren, G. I.; Debuse, V.; Mazzoni, D.; Linnane, A.; Ball, B. 2000: The influence of competitive interactions on the abundance of early benthic stage European lobster (*Homarus gammarus* L.) and hence on the carrying capacity of lobster habitat. Carna, County Galway, Ireland. Final Report. Lobster ecology and recruitment (LEAR), EU Conserted Action Project, fourth framework Agriculture and Fisheries (FAIR). Shellfish Research Laboratory. Pp. 158.

Mercer, J. P.; Bannister, R. C. A.; van der Meeren, G. I.; Debuse, V.; Mazzoni, D.; Lovewell, S.; Browne, R.; Linnane, A.; Ball, B. 2001: An overview of the LEAR (Lobster Ecology and Recruitment) project: the results of field and experimental studies on the juvenile ecology of *Homarus gammarus* in cobble. *Marine and Freshwater Research 52*: 1291–1302.

Miller, R. J. 1990: Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences 47*: 1228–1251.

Moksnes, P.-O. 1999: Recruitment regulation in juvenile shore crabs *Carcinus maenas*: importance of intra-specific interactions in space limited refuge habitats. Unpublished PhD thesis, Gothenburg University, Sweden. Pp. 1–42.

Moksnes, P.-O.; Pihl, L.; van Montfrans, J. 1998: Predation an postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. *Marine Ecology Progress Series 166*: 211–225.

Neil, D. M.; Macmillan, D. L.; Robertson, R. M.; Laverack, M. L. 1976: The structure and function of thoraric exopodites in the larvae of the lobster *Homarus gammarus* (L.). London, UK, Philosophical Transcripts of the Royal Society 274B. Pp. 53–68.

Nicosia, F.; Lavalli, K. 1999: Homarid lobster hatcheries: their history and role in research, management, and aquaculture. *Marine Fisheries Review 61*: 1–57.

Norman, C. P.; Morikawa, Y. 1996: Rock face incline and height above sea bed of holes used as shelters by pueruli and juvenile Japanese spiny lobsters *Panulirus japonicus*. *Crustacean Research 25*: 121–128

Norman, C. P.; Yamakawa, H.; Yoshimura, T. 1994: Habitat selection, growth rate and density of juvenile *Panulirus japonicus* (Von Siebold, 1824) (Decapoda, Palinuridae) at Banda, Chiba Prefecture, Japan. *Crustaceana 66*: 366–383.

Nøtvedt, M.; Fernö, A.; Gjøsæter, J.; Steingrund, P. 1999: Anti-predator behaviour of hatchery-reared and wild juvenile Atlantic cod (*Gadus morhua* L.) and the effect of predator training. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 350–362..

Olla, B. L.; Davies, M. W.; Ryer, C. H. 1998: Understanding how the hatchery environment represses or promotes the development of behavioural skills. *Bulletin of Marine Science 62*: 531–550.

O'Neill, D. J.; Cobb, J. S. 1979: Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). *Marine Behavior and Physiology 6*: 33–45.

Otterå, H.; Kristiansen, T. S.; Svåsand, T.; Nordeide, J. T.; Nævdal, G.; Borge, A.; Pedersen, J. P. 1999a: Enhancement studies of Atlantic cod (*Gadus morhua* L.) in an exposed coastal area in Western Norway. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 257–276.

Otterå, H.; Kristiansen, T. S.; Svåsand, T.; Nøtvedt, M.; Borge, A. 1999b: Sea ranching of Atlantic cod (*Gadus morhua* L.): effects of release strategy on survival. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 293–305.

Parker, G. A. 1974: Assessment strategy and the evolution of fighting behavior. *Journal of Theoretical Biology 47*: 223–243.

Phillips, B. F.; Cobb, J. S.; George, R. W. 1980: General biology. *In*: Cobb, J. S.; Phillips, B. F. *ed.* The biology and management of lobsters. New York, United States, Academic Press. Pp. 1–82.

Pottle, R. A.; Elner, R. W. 1982: Substrate preference behavior of juvenile American lobsters, *Homarus americanus*, in a gravel and silt-clay sediments. *Canadian Journal of Fisheries and Aquatic Science 39*: 928–932.

Rainbow, P. S.; Black, W. H. 2001: Effects of changes in salinity on the apparent water permeability of three crab species: *Carcinnus maenas, Eriocheir sinensis* and *Necora puber*. *Journal of Experimental Marine Biology and Ecology 264*: 1–13.

Ranta, E.; Lindstrøm, K. 1992: Power to hold sheltering burrows by juveniles of the signal crayfish, *Psifastacus leniusculus*. *Ethology 92*: 217–226.

Raffaelli, D.; Hawkins, S. 1996: Intertidal ecology. London, UK, Chapman & Hall. 372 p.

Rasch, A. 1875: Om forsøg med kunstig udklækning af hummer. Nordisk Tidsskrift for Fiskerier, Ny Serie, 2en Aargang: 184–185. (On the artificial propagation of the lobster.) (In Norwegian, translated to English in Reports from the Commission of Fish and Fisheries 1873–74 and 1874–75. Pp. 781–812).

Ratchford, S. G.; Eggleston, D. B. 1998: Size- and scale-dependent attraction contribute to an ontogenetic shfft in sociality. *Animal Behaviour 56*: 1027–1034.

Rudy, P. P. 1967: Water permeability in selected Decapod Crustacea. *Comparative Biochemistry and Physiology 22*: 581–589.

Rørvik, C. J.; Tveite, S. 1982: A stock assessment of lobster (*Homarus gammarus*) on the Norwegian Skagerrak coast. International Council for the Exploration of the Sea, Council meeting 1987/K:7. 20 p. (Mimeo.)

Salvanes, A. G. V.; Aksnes, D. L.; Giske, J. 1992: Ecosystem model for evaluating potential cod production in a west Norwegian fjord. *Marine Ecology Progress Series 90*: 9–22.

Sandeman, R. E.; Sandeman, D. C. 1996: Pre- and postembryonic development, growth and turnover of olfactory receptor neurons in crayfish antennules. *The Journal of Experimental Biology 199*: 2409–2418.

Sandeman, R. E.; Sandeman, D. C. 2000: "Impoverished" and "Enriched" living conditions influence the proliferation and survival of neurons in crayfish brain. *The Journal of Neurobiology 45*: 215–226.

Sandeman, R. E.; Clarke, D.; Sandeman, D. C.; Manly, M. 1998: Growth-related and antennular amputation-induced changes in the olfactory centers of crayfish brain. *The Journal of Neuroscience 18*: 6195–6206.

Sastry, A. N.; Zeitlin-Hale, L. 1977: Survival of communally reared larval and juvenile lobsters, *Homarus americanus*. *Marine Biology 39*: 297–303.

Scheltema, R. S. 1974: Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavia 10*: 263–296.

Schmidt, M. 1997: Continuous neurogenesis in the olfactory brain of adult shore crabs, *Carcinus maenas*. *Brain Research 762*: 131–143.

Schmidt, M.; Harsch, S. 1999: Comparative analysis of neurogenesis in the central olfactory pathway of adult decapod crustaceans by *in vivo* BrdU labeling. *Biological Bulletin 196*: 127–136.

Scrivener, J. D. E. 1971: Agonistic behaviour of the American lobster, *Homarus americanus* (Milne Edwards). *Fisheries Research Board of Canada Technical Report 235*: 1–128.

Sekkelsten, G. I. 1988: Effect of handicap on mating success in male shore crabs *Carcinus maenas*. *Oikos 51*: 131–134.

Sharp, W. C.; Hunt, J. H.; Lyns, W. G. 1997. Life history of the spotted spiny lobster, *Panulirus guttatus*, an obligate reef dweller. *Marine and Freshwater Research 48*: 687–698.

Sheehy, D. J. 1976: Utilization of artificial shelters by American lobster (*Homarus americanus*). *Journal of Fisheries Research Board, Canada 33*: 1613–1622.

Sheehy, M. R. J.; Shelton, P. M. J.; Wickins, J. F.; Belchier, M.; Gaten, E. 1996: Ageing the European lobster *Homarus gammarus* by the lipofuscin in its eyestalk ganglia. *Marine Ecology Progress Series 143*: 99–111.

Skreslett, S.; Albrigtsen, I.; Andersen, A. P.; Kolbeinshavn, A.; Pedersen, T.; Unstad, K. 1999: Migration, growth and survival in stocked and wild cod (*Gadus morhua*) in the Vestfjord Region, North Norway. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 306–333.

Smedstad, O. M.; Salvanes, A. G. V.; Fosså, J. H.; Nordeide, J. T. 1994: Enhancement of cod in Masfjorden: an overview. *Aquaculture and Fisheries Management 25 (Suppl. 1)*: 117–128.

Smith, K. N.; Herrnkind, W. F. 1992: Predation on early juvenile spiny lobsters *Panulirus argus* (Lateille): influence of size and shelter. *Journal of Experimental Marine Biolology and Ecology 157*: 3–18.

Sneddon, L. U.; Huntingford, F. A.; Taylor, A. C. 1997: Weapons size versus body size as a predictor of winning fights between shore crabs, *Carcinus maenas* (L). *Behaviour and Ecological Sociobiology 41*: 237–242.

Spanier, E. 1994: An artificial reef for lobsters. *Crustaceana 67*: 173–186.

Spanier, E.; Almog Shtayer, G. 1992: Shelter preference in the Mediterranean slipper lobster: effect of physical properties. *Journal of Experimental Marine Biology and Ecology 164*: 103–116.

Stein, L.; Jacobsen, S.; Atema, J. 1975: Behavior of lobsters (*H. americanus*) in a semi natural environment at ambient temperatures and under thermal stress. Woods Hole Oceanographic Institution Technical Report. 50 p.

Stein, R. A.; Magnuson, J. J. 1976: Behavioral response of crayfish to a fish predator. *Ecology 57*: 751–761.

Steullet, P.; Cate, H. S.; Derby, C. D. 2000: A spatiotemporary wave of turnover and functional maturation of olfactory receptor neurons in the spiny lobster *Palinurus argus*. *The Journal of Neuroscience 20*: 3282–3294.

Sund, O. 1915: Beretning om anlæg av statens Hummeravlsstation og driften 1913. *Norges Fiskerier*: 525–532. (Report on the construction of the Governmental Lobster Hatchery and its running 1913.) (In Norwegian.)

Svåsand, T.; Agnalt, A.-L.; Borthen, J.; Heggberget, T.; Skilbrei, O. T. 2005: An integrated development programme for marine stocking: the Norwegian example. *FAO Fisheries Technical Paper 429*. 213 p.

Svåsand, T.; Skilbrei, O. T.; van der Meeren, G. I.; Holm, M. 1998: Review of morphological and behavioural differences between reared and wild individuals: implications for sea ranching with Atlantic salmon, *Salmo salar* L., Atlantic cod, *Gadus morhua* L., and European lobster, *Homarus gammarus* L. *Fisheries Management and Ecology 5*: 473–490.

Tamm, G. R.; Cobb, J. S. 1978: Behavior and crustacean molt cycle: changes in aggression of *Homarus americanus*. *Science 200*: 79–81.

Taylor, C. C. 1950: A review of lobster rearing in Maine. Department of Sea Shore Fish, Augusta. *Maine Research Bulletin 5*. 16 p.

Templeman, W. 1935: Lobster tagging in the Gulf of St. Lawrence. *Journal of the Biological Board, Canada 2*: 269–278.

Trivers, R. L. 1972: Parental investment and sexual selection. *In*: Campbell, B. *ed.* Sexual selection and descent of man. Chicago, United States, Aldine. Pp. 136–179.

Tsukamoto, K.; Kuwada, H.; Uchida, K.; Masuda, R.; Sakakura, Y. 1999: Fish quality and stocking effectiveness: behavioural approach. *In*: Howell, B.; Moksness, E.; Svåsand, T. *ed.* Stock enhancement and sea ranching. London, UK, Blackwell Scientific Press. Pp. 205–218.

Tveite, S. 1991: Hummerbestanden i Norge med særlig vekt på Skagerak. Havforskningsinstituttet, Flødevigen Forskningsstasjon, *Rapportserie 4*. 12 p. (In Norwegian.)

Tveite, S.; Grimsen, S. 1995: Survival of one year old artificially raised lobsters (*Homarus gammarus*) released in southern Norway. *International Council for the Exploration of the Sea, Marine Science Symposium 199*: 73–77.

Uglem I.; Grimsen S. 1995: Tag retention and survival for lobster juveniles (*Homarus gammarus* (L.)) marked with coded wire tags. *Aquaculture Research 26*: 837–841.

Uglem, I.; Belchier, M.; Svåsand, T. 2005: Age determination of European lobsters (*Homarus gammarus* L.) by histological quantification of lipofuscin. *Journal of Crustacean Biology 25*: 95–99.

U.S. Fish and Wildlife Service, Nez Perce Tribe, National Park Service, and USDA Wildlife Service 2002: Rocky Mountain wolf recovery. 2001 Annual Report. Meier, T. *ed.* Helena, MT, United States Fish and Wildlife Service, Ecological Services. 43 p.

van der Meeren, G. I. 1991: Out-of-water transportation effects on behaviour in newly released juvenile atlantic lobsters *Homarus gammarus*. *Aquacultural Engineering 10*: 55–64.

van der Meeren, G. I. 1993: Initial response to physical and biological conditions in naive juvenile lobsters *Homarus gammarus* L. *Marine Behaviour and Physiology 24(1)*: 79–92.

van der Meeren, G. I. 2000: Predation on hatchery-reared lobsters *Homarus gammarus* released in the wild. *Canadian Journal of Fisheries and Aquatic Science 57*: 1784–1793.

van der Meeren, G. I. 2001: Effects of experience with shelter in hatchery-reared juvenile European lobsters *Homarus gammarus*. *Marine and Freshwater Research 52*: 1487–1494.

van der Meeren, G. I.; Soldal, O. *ed.* 1998: The European lobster *Homarus gammarus* (L). Proceedings from the seminar at Kvitsøy 1995. *Fisken og Havet 13*. 100 p.

van der Meeren, G. I.; Tveite, S. 1998: Fishery and management of the lobster (*Homarus gammarus*) in Norway. *In*: van der Meeren, G. I.; Soldal, O. *ed.* Proceedings of the seminar at Kvitsøy 1995: the European lobster *Homarus gammarus* (L.). *Fisken og Havet 13*: 72–76.

van der Meeren, G. I.; Uksnøy, L. E. 2000: A comparison of claw development and dominance between wild and cultured male European lobster *Homarus gammarus*. *Aquaculture International 8*: 77–94.

van der Meeren, G. I.; Farestveit, E.; Næss, H. 1991: Rapport fra feltarbeid 12/8–16/8 1991, Kvitsøy. Institute of Marine Research, Bergen, Norway. Intern Rapport L. nr. 15/91. 8 p. (In Norwegian.)

van der Meeren, G. I.; Agnalt, A.-L.; Næss, H.; Jørstad, K. E. 1997: Interne toktrapporter nr. 4 toktrapport fra hummertokt ved Kvitsøy, Juli 1996. Institute of Marine Research, Bergen, Norway, *Interne notater nr 6*. 18 p. (In Norwegian.)

van der Meeren, G. I.; Ekeli, K. O.; Jørstad, K. E.; Tveite, S. 2000: Americans on the wrong side—the lobster *Homarus americanus* in Norwegian waters. International Council of the Exploration of the Sea, council meeting 2000/U:20. 13 p.

Van Olst, J. C.; Carlberg, J. M.; Ford, R. F. 1975: Effects of substrate type and other factors on the growth, survival, and cannibalism of juvenile *Homarus americanus* in mass rearing systems. Proceedings from Annual Meeting. *World Mariculture Society 6*: 271–292.

Wada, K. 1993: Territorial behavior, and size of home range and territory, in relation to sex and body size in *Ilyoplax pusilla* (Crustacea: Brachyura: Ocypodia). *Marine Biology 115*: 47–52.

Waddy, S. L.; Aiken, D. E.; DeKlein, D. P. V. 1995: Control of growth and reproduction. *In*: Factor, J. R. *ed.* Biology of the lobster *Homarus americanus*. New York, United States, Academic Press. Pp. 217–266.

Wahle, R. A. 1998: A trans-Atlantic perspective on *Homarus* recruitment and enhancement. *In*: van der Meeren, G. I.; Soldal, O. *ed.* Proceedings of the seminar at Kvitsøy 1995: the European lobster *Homarus gammarus* (L.). *Fisken og Havet 13*: 36–43.

Wahle, R. A.; Steneck, R. S. 1991: Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck. *Marine Ecology, Progressive Series 69*: 231–243.

Wahle, R. A.; Steneck, R. S. 1992: Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. *Journal of Experimental Marine Biology and Ecology 157*: 91–114.

Whitely, N. M.; Taylor, E. W. 1992: Oxygen and acid-base disturbances in the haemolymph of the lobster *Homarus gammarus* during commercial transport and storage. *Journal of Crustacean Biology 12*: 19–30

Wickins, J. F. 1986: Stimulation of crusher claw development in cultured lobsters, *Homarus gammarus* (L.). *Aquaculture and Fisheries Management 17*: 267–273.

Wickins, J. F.; Barry, J. 1996: The effect of previous experience on the motivation to burrow in early benthic phase lobsters (*Homarus gammarus* (L.)). *Marine and Freshwater Behaviour and Physiology 28*: 211–228.

Wickins, J. F.; Lee, D. O. C. 2002: Crustacean farming, ranching and culture. Oxford, UK, Blackwell Science. 446 p.

Wickins, J. F.; Beard, T. W.; Jones, E. 1986: Micro tagging cultured lobsters for stock enhancement trials. *Aquaculture and Fishery Management 17*: 259–265.

Wickins, J. F.; Roberts, J. C.; Heasman, M. S. 1996: Within-burrow behaviour of juvenile European lobsters *Homarus gammarus* (L.). *Marine and Freshwater Behaviour and Physiology 28*: 229–253.

Wilson, D. E.; Reeder, D. M. *ed.* 1993: Mammal species of the world. Washington, United States, Smithsonian Institution Press. 1206 p

Wilson, G.; Bomford, M.; O'Brien, P.; Dexter, N. 1993: Pest animals in Australia: a survey of introduced animals. Canberra, Australia, Seven Hill Books: 64 p.

Yoshimura, T.; Yamakawa, H. 1988: Microhabitat and behavior of settled pueruli and juveniles of the Japanese spiny lobster *Panulirus japonicus* at Kominato, Japan. *Journal of Crustacean Biology 8*: 524–531.

Yoshimura, T.; Yamakawa, H.; Norman, C. P. 1994: Comparison of hole and sea weed habitats of post-settled pueruli and early benthic juvenile lobsters, *Panulirus japonicus* (Von Siebold, 1824). *Crustaceana 66*: 356–365.

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Feeding ecology of juvenile spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico

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Abstract Many aspects of the early life history of the red lobster *Panulirus interruptus* are little known, including the relationship between habitat structure, food resource availability, and nutrition of juveniles. We investigated the spatial and temporal differences in food intake, diet composition, and nutritional condition of juveniles at two sites along the Pacific coast of the Baja California Peninsula (Mexico) with contrasting oceanographic and biological conditions. One site (Arvin) is located inside a protected bay, Bahía Tortugas, where the waters are cooler and temperate seagrasses and macroalgae are the dominant benthic flora. The second site (Queen) in Bahía Sebastían Vizcaíno was located along a more open coastline where seawater temperatures were higher and the benthic flora more indicative of warmer seas. At both sites, we randomly sampled epifauna within vegetated habitats to estimate the seasonal availability of food resources for juvenile lobsters from autumn 2001 until summer 2002. Concurrently, we used traps to sample *P. interruptus* juveniles for stomach content analysis. At both sites, Amphipoda, Gastropoda, and Polychaeta dominated the epifauna assemblages, as determined by an Index of Importance. Juvenile *P. interruptus* primarily consumed crustaceans (mostly amphipods and isopods) and vegetal material (surf-grass *Phyllospadix* spp. and calcareous algae), but their food spectrum was wide. Manly's Index of Resource Selection indicated that lobsters preferred some prey (e.g., Brachyurans) over others despite their low Index of Importance. Despite marked differences in the types of food and their availability between sites, there were no significant differences in the nutritional condition (e.g., relative weight of the digestive gland) of lobsters at the two sites. However, the nutritional condition of lobsters was effected during some seasons. In particular, their condition deteriorated during the spring (April 2002) at Arvin, as did the proportion of individuals with empty stomachs. This study shows the feeding adaptation capacity of the juvenile California spiny lobster *P. interruptus* to different environmental conditions prevalent in Centre Baja California Peninsula.

Keywords feeding ecology; spiny lobsters; *Panulirus interruptus*; juveniles

INTRODUCTION

Spiny lobsters are a commercially important resource in Mexico. Profits from these fisheries are the fifth most valuable in Mexico, and are estimated to be worth US$18 million from a catch of 744 t (SAGARPA 2003). Along the Pacific coast of the Baja California Peninsula, three spiny lobster species are exploited: red lobster *Panulirus interruptus* (Randall, 1840), blue lobster *P. inflatus* (Bouvier, 1895), and green lobster *P. gracilis* (Streets, 1871). *P. interruptus* represents 95–97% of total production (Vega et al. 2000).

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The red lobster, *P. interruptus*, occurs along the west coast of the Baja California Peninsula as far south as Isla Margarita (c. 24.5°N) (Vega et al. 1996), and small populations are also found along parts of the east coast of the Peninsula (Ayala et al. 1988). However, it is most abundant off the central part of the Baja California Peninsula from Punta Abreojos (c. 26.7°N) to Isla Cedros (c. 28.3°N) (Johnson 1960a,b; Vega et al. 1996, 2000), where it lives in rocky areas from the low intertidal zone to depths of c. 150 m. Our understanding of the biology and ecology of *P. interruptus* along the Mexican Pacific coast is limited to a few studies on reproduction, puerulus settlement, growth, and genetic structure (e.g., Ayala 1976; Pineda et al. 1981; Guzmán del Próo & Pineda 1992; Guzmán del Próo et al. 1996; Perez-Enriquez et al. 2001).

Information on the natural diet and feeding habits of *P. interruptus* is scarce, although the species has been characterised as omnivorous with a diet consisting of gastropods, fish remains, decapods, and red and brown algae (Díaz-Arredondo & Guzmán del Próo 1995). This is true of palinurid lobsters in general (Kanciruk 1980), which are omnivorous and consume, among other things, crustaceans, gastropods, fish, and marine plants (Lindberg 1955; Engle 1979; Colinas-Sánchez & Briones-Fourzán 1990; Díaz-Arredondo & Guzmán del Próo 1995; Briones-Fourzán et al. 2003); although *P. inflatus* and *P. gracilis* do not appear to eat plants (Lozano-Alvárez & Aramoni-Serrano 1996). In this study, we compared spatial and seasonal differences in food intake, diet composition, and nutritional condition of juvenile *P. interruptus* at two sites on the central part of the Baja California Peninsula.

MATERIALS AND METHODS

Study sites

Our two study sites on the Pacific coast of the Baja California Peninsula (Mexico) occur within the zone where *P. interruptus* is most abundant (Vega & Luch-Cota 1992). The "Arvin" site lies inside a protected bay, Bahía Tortugas whereas the second site ("Queen") is located on the coast of Bahía Sebastian Vizcaíno, a more open coastline (Fig. 1). We selected these sites because older juvenile lobsters (40–60 mm carapace length (CL)) had previously been observed there, and because the two sites have different physiographic and marine conditions (Lluch-Belda 2000) that are indicative of those that occur along the western Baja California coast. Mean bottom seawater temperature at Arvin (17.3°C) was cooler than at Queen (19.9°C) during September 2001 and October 2002 and the dominant benthic flora also differ. At Queen, one surf-grass species *Phyllospadix torreyi* and two brown algae *Padina caulescens* and *Sargassum agardhianum* are the dominant species. At Arvin, two marine grass species *P. scouleri* and *Zoostera marina* and three brown algae *Macrocystis pyrifera*, *Sargassum muticum*, and *Cystoseira osmundacea* are the dominant species. Along Bahía Sebastían Vizcaíno, tropical species of macroalgae related to an oceanographic gyre have been described (Dawson 1951, 1952), as has the absence of the kelp *M. pyrifera* for c. 300 km of coastline within its broad distribution range (Ladah & Zertuche-González 1999).

Sampling of *P. interruptus* juveniles

To determine the feeding habits of juvenile *P. interruptus* and whether those habits varied among seasons and sites, we sampled both sites during four seasons: September 2001 (autumn), January 2002 (winter), April 2002 (spring), and June 2002 (summer). In each season, juveniles were caught with octopus traps made with galvanised wire and baited with fish (*Scomber japonicus*). Ten traps were set in the afternoon (1900 h) because lobsters feed actively during the night (Herrnkind et al. 1975; Lipcius & Herrnkind 1982). At 0800 h, we checked the traps and collected juveniles under 65 mm CL (measured from between the rostral horns to the posterior margin of the carapace). For each lobster we recorded: sex, CL (± 0.1 mm), and total weight (TW ± 0.1 g). Individuals were dissected in the field to extract their stomach, pleopods, and digestive gland. Stomachs were preserved in 10% formaldehyde in sea water and pleopods in 70% ethanol for later analysis. The digestive gland was blotted dry and weighed (WDG = weight of digestive gland ± 0.01 g), and its relative weight (RWDG = WDG/TW (×100)) was obtained as an index of the nutritional condition of individuals. Starved or poorly fed individuals have significantly lower values of RWDG than do well-fed individuals (Dall 1974).

In the laboratory, juveniles were classified as postmoult, intermoult, or premoult, based on the determination of their stage in the moulting cycle from observation of a pleopod under a microscope (Lyle & MacDonald 1983). The percentage fullness of the stomach was visually calculated and categorised according to the following scale: 0% (0–5%), 10% (6–15%), 25% (16–35%), 50% (36–65%),

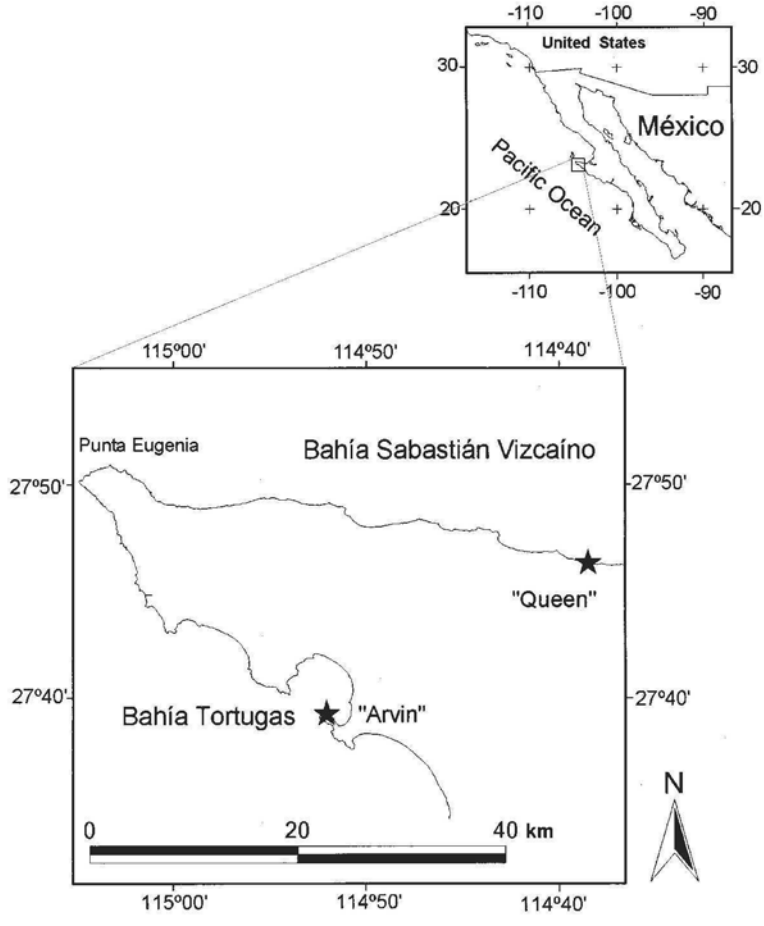

Fig. 1 Study area on the Pacific coast of northern part of Baja California Sur, México.

75% (66–90%), and 100% (91–100%) (Briones-Fourzán et al. 2003). Diet analysis was performed only on juveniles with stomachs 10% full (Joll 1984). Stomach contents were obtained and stored in 70% ethanol until sorting and identification under a stereo-microscope to the lowest taxonomic level possible (Smith & Carlton 1975; Brusca 1980; Morris et al. 1980; Kozloff 1987). Frequency of occurrence (FO = number of stomachs containing a given food category/total number of stomachs examined (×100)) was determined for each food category.

For each individual stomach, the total volume of the contents was determined using a 10-ml graduated glass cylinder (ml ± 0.1). The stomach contents were then squashed to a uniform depth on a large Petri dish on which 100 squares (each one: 40.96 mm^2) were imprinted (VWR®). Thirty of these squares were randomly selected and the number of squares covered by each type of food was measured under a stereo-microscope to estimate the percentage contribution by volume (V%) of each food type in each stomach (Krebs 1999). This technique standardises estimates of volume, irrespective of the size of the lobsters (Hyslop 1980; Joll & Phillips 1984; Briones-Fourzán et al. 2003). Finally, we calculated an Index of Relative Importance (IRI) to assess the importance of each food category in the stomachs of lobster by season and site (Yáñez-Arancibia et al. 1976). The IRI per trophic group is calculated as:

$$IRI = (FO \times V)/100$$

where FO = percentage frequency of occurrence, and V = volumetric percentage of each trophic group.

Sampling of epifauna

We also compared the resources consumed by juvenile *P. interruptus* to the availability of food in the habitats frequented by juvenile lobster during different seasons. In the same areas where juveniles were caught for stomach analysis, we established

three 200-m transects running parallel to the shore at depths of 1 m, 2–3 m, and 4–6 m. Along each transect, all biological material in five randomly positioned 0.25-m^2 quadrats was collected at both the Arvin and Queen sites during each sampling time. Samples for quantitative analysis were collected by hand, using a net bag with a 1-mm^2 mesh. In the field, biological material was placed in plastic bags, labelled, and preserved with a 10% formalin seawater solution. In the laboratory, the samples were washed with fresh water and the macrofauna retained on a 1-mm^2 mesh sieve were kept for identification based on taxonomic keys for the region (Smith & Carlton 1975; Brusca 1980; Morris et al. 1980; Kozloff 1987).

For each sample, 10% of the total macrofauna weight was analysed according to previous minimum-weight calculations performed on five samples (Margalef 1998). We used a stereo-microscope to separate the epifauna into the taxonomic groups that we observed in the stomach contents (Marx & Herrnkind 1985). For each group, the relative frequency and biomass (± 0.01 g) percentages by season and site were calculated to generate an Index of Importance Value (IIV) defined as:

$$IIV = (RF \times RB)/100$$

where RF = relative frequency (%) of the macrofauna group, and RB = relative biomass (%) of the same group.

Data analysis

Contingency table analyses were used to test the association between stomach fullness and sex, moult stage (intermoult or premoult), season (autumn, winter, spring, or summer), and sampling area (Queen or Arvin) (Oh et al. 2001). Comparisons of the logarithmic transformation of the relative weight of digestive glands over moult stage, seasons, and sites were made with a three-way factorial ANOVA (Sokal & Rohlf 1998). The logarithmic transformation was needed to yield data that were normally distributed with homogeneous variances (Zar 1999).

Manly's alpha index was used to estimate the preference of juvenile lobsters for each faunal group (Manly et al. 1993; Krebs 1999). We compared both IRI of the trophic group and IIV of the same taxon category in the environment by season and site. We obtained these estimates for each season by site combination, using "Programs for Ecological Methodology" (Charles J. Krebs 2000©).

RESULTS

We caught 377 juvenile *P. interruptus*, of which 215 were from Arvin (size and weight range: 30.0–61.9 mm CL and 36.7–237.2 g) and 162 from Queen (size and weight range: 39.4–65.5 mm CL and 55.5–272.0 g). Of the total, 67 were caught in summer, 80 in autumn, 98 in winter, and 132 in spring (Table 1). There were 122 females and 255 males. Based on moult stage, 169 were in premoult and 208 in intermoult. Postmoult individuals were absent in both study sites. There were significant differences in stomach fullness of lobsters between sites, seasons, and moult stage, but sex had no effect on stomach fullness (Fig. 2).

There was no significant difference in the RWDG in relation to site ($P = 0.8$) or moult stage ($P = 0.5$). However, the RWDG was greater in juveniles caught in autumn (390.1 g) and statistically different from juveniles caught in spring (306.5 g), but not in winter or summer (main effect: $P < 0.05$), regardless of the site. However, the specimens were affected by season in relation to the site (interaction: $P < 0.05$). The greatest RWDG was for juveniles collected from

Table 1 Summary of measurements of *Panulirus interruptus* juveniles arranged by site and season. Mean ± SD. (CL, carapace length; WDG, weight of digestive gland.)

Site	Season	*n*	CL (mm)	Total length (mm)	Total weight (g)	WDG (g)
Arvin	Autumn	40	56.7 ± 4.3	183.4 ± 15.0	174.9 ± 35.5	7.7 ± 2.3
	Winter	60	55.4 ± 5.9	182.3 ± 20.3	173.4 ± 40.2	6.9 ±2.3
	Spring	83	54.0 ± 4.4	172.3 ± 13.9	144.3 ± 30.3	4.3 ± 1.2
	Summer	32	55.9 ± 3.4	178.1 ± 11.6	165.4 ± 29.4	6.1 ± 1.7
Queen	Autumn	40	56.1 ± 4.5	179.5 ± 14.9	158.1 ± 29.3	5.8 ± 1.6
	Winter	38	53.8 ± 6.2	176.2 ± 20.8	151.3 ± 49.9	5.6 ± 2.2
	Spring	49	57.0 ± 5.1	184.9 ± 16.3	167.8 ± 42.3	6.2 ± 2.3
	Summer	35	55.8 ± 3.2	176.9 ± 9.6	161.2 ± 24.1	6.2 ± 0.9

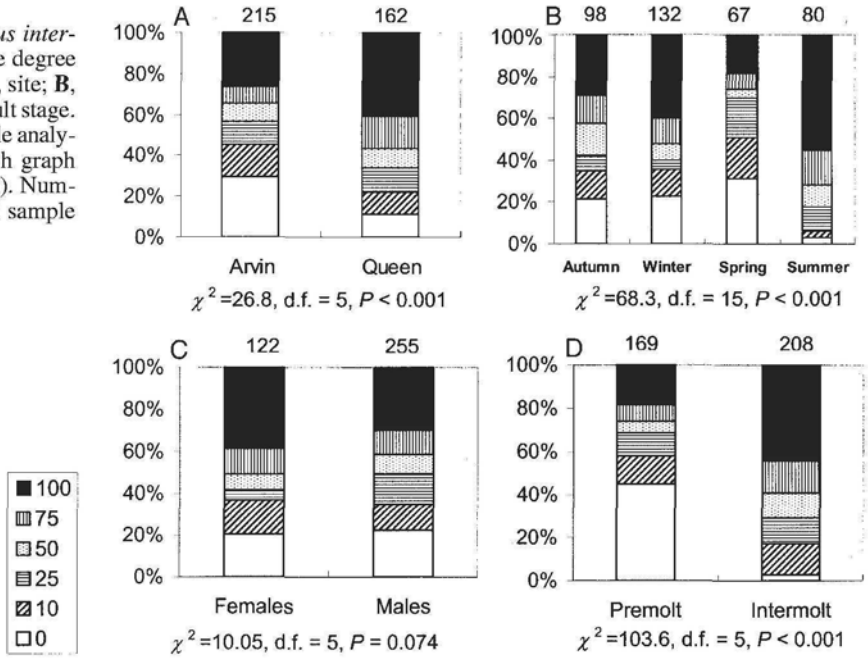

Fig. 2 Juvenile *Panulirus interruptus*. Comparison of the degree of stomach fullness by: **A**, site; **B**, season; **C**, sex; and **D**, moult stage. Results of contingency table analysis (χ^2) appear below each graph (d.f. = degrees of freedom). Numbers above bars represent sample size.

Arvin in autumn, and the lowest was from juveniles caught in Arvin in spring (Fig. 3).

At both sites, a large percentage of the juvenile stomach contents was the bait used in the traps to collect them. At Arvin, it varied from 28 to 61% (FO) and 9 to 25% (V); at Queen, it varied from 12 to 67% (FO) and 5 to 47% (V). The percentage of unidentified organic matter varied from 0 to 63% (FO) and 0 to 10% (V) at Arvin. At Queen, it varied from 6 to 26% (FO) and from 1 to 6% (V). Bait and organic material were not considered in the statistical analysis of diet.

A total of 26 taxa and unidentified crustacea were identified in the diet; 18 were from stomach contents of juveniles caught at Arvin and 24 from juveniles caught at Queen. At Arvin, according to the IRI, the most important animal trophic groups (10) were Amphipoda during autumn and spring, Isopoda in summer, and Gastropoda in spring. Of marine plants, the surf-grass *P. scouleri* was important in winter, spring, and summer. In juveniles from Queen, the most important faunal stomach contents were Isopoda during autumn and winter. Coralline algae were important in spring and the seagrass *P. torreyi* in summer (Table 2).

We identified 35 macrofauna groups at the sites where juveniles were caught; 30 at Arvin and 32 at

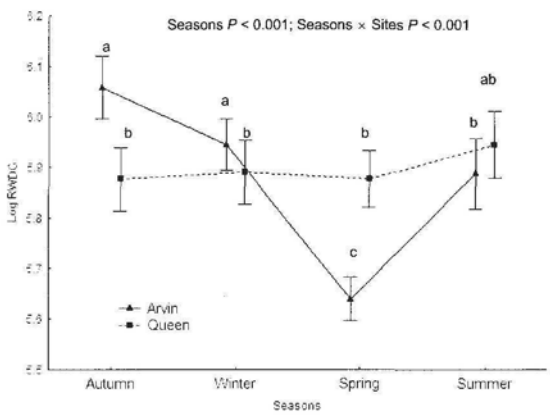

Fig. 3 Mean ± standard error in vertical bars of the relative weight of the digestive gland (RWDG) of juvenile *Panulirus interruptus* among seasons at two sites (Arvin and Queen). Results of three-way ANOVA are inserted above in the figure. Factors considered in the analysis were seasons, sites, and moult stage. The main effects are shown only when there was statistical significance. Different letters indicate significant differences (Tukey analysis).

Queen (Table 3). At Arvin, the groups with greatest importance were Amphipoda in all seasons and Polychaeta in autumn, winter, and summer. At Queen, Polychaeta and Gastropoda had the greatest importance in all seasons and Amphipoda was important from winter to summer (Table 3). Estimates of IIV of Bryozoa was not possible because relative frequency estimates are not achievable for colonial organisms. However, this group was present in many samples at both sites (73–100%); its relative biomass was lowest in spring at Arvin (0.5%) and highest in autumn at Queen (36%).

Combining the stomach content results with the availability of food resources in the environment, we compared the selectivity of lobsters for various prey types using the selection index of Manly. Although some groups were estimated as being preferred, preferences varied inconsistently among sites and seasons (Table 4).

DISCUSSION

This study of the feeding ecology of small juvenile *P. interruptus* in Baja California Sur, Mexico complements previous studies in the same region but conducted on larger specimens (57–132 mm CL) (Díaz-Arredondo & Guzmán del Próo 1995). In both studies, crustaceans, molluscs, and vegetal material were the main trophic groups exploited by juveniles; however, the relative importance of the groups was different. Crustacea were more important than Mollusca in this study, but Díaz-Arredondo & Guzmán del Próo (1995) found that the pattern was reversed. This difference may be related to the size of the juvenile specimens in the two studies. Changes in diet preferences between size classes or stages in lobsters have been observed in other species, as in *P. cygnus* (Joll & Phillips 1984), *P. argus* (Andrée 1981; Marx & Herrnkind 1985; Herrnkind & Butler

Table 2 Index of Relative Importance (IRI) of trophic groups of juvenile *Panulirus interruptus* during seasons at Arvin in Bahía Tortugas and Queen in Bahía Sebastián Vizcaíno. Bold type represents up to 10 of the IRI value.

		Arvin, Bahía Tortugas				Queen, Bahía Sebastián Vizcaíno			
		Autumn = 28	Winter $n = 22$	Spring $n = 30$	Summer $n = 29$	Autumn $n = 27$	Winter $n = 34$	Spring $n = 25$	Summer $n = 21$
Trophic group	Type	IRI	IRI	IRI	IRI	IIR	IIR	IIR	IIR
Crustacea	Brachyura	2.31	1.17	3.74	<0.01	<0.01	0.31	0.13	0.08
	Amphipoda	**14.63**	9.28	**20.61**	1.08	8.17	9.60	6.05	1.13
	Isopoda	1.69	3.79	0.70	**17.40**	**26.34**	**30.09**	1.42	4.81
	Ostracoda	4.85	–	0.11	0.1	–	0.39	–	–
	Tanaidacea	–	–	–	–	–	0.002	–	–
	Cumacea	–	–	–	–	–	–	0.01	–
	P. interruptus	–	–	–	–	0.06	–	–	–
	Unidentified	<0.01	0.04	0.58	–	–	0.02	0.12	–
Mollusca	Gastropoda	0.34	0.33	**10.93**	2.48	4.20	5.22	6.19	1.62
	Bivalvia	0.05	0.01	0.95	0.72	<0.01	0.38	3.24	–
	Polyplacophora	–	–	0.02	–	0.12	0.01	<0.01	–
	Monoplacophora	–	–	0.05	–	–	–	<0.01	–
Porifera	Demospongia	<0.01	0.13	0.03	0.02	0.11	–	0.95	0.20
Annelida	Polychaeta	–	<0.01	0.05	0.09	<0.01	<0.01		–
Ectoprocta	Bryozoa	4.00	2.10	<0.01	0.27	0.38	0.33	0.42	1.78
Nemata	Nematoda	<0.01	–	–	0.05	–	–	<0.01	0.09
Sarcodina	Foraminiferida	<0.01	–	–	–	–	0.14	0.05	0.06
Echinodermata		–	–	–	–	–	0.33	0.01	–
Cnidaria	Coelenterata	–	–	–	–	–	–	–	0.07
Algae	Coralline algae	9.54	2.64	5.01	9.98	0.57	4.54	**17.33**	0.26
	Red algae	0.41	0.05	0.17	0.18	0.01	0.2	0.33	0.80
	Brown algae	0.22	–	0.35	0.1	1.49	0.1	0.85	0.23
	Filamen algae	–	–	–	–	–	–	0.12	–
	Dictiota	–	–	–	–	–	–	0.21	–
	Macrocystis pyrifera	–	0.34	–	–	–	–	–	–
Plantae	*Phyllospadix scouleri*	4.83	**15.95**	**10.50**	**18.71**	–	–	–	–
	Phyllospadix torreyi	–	–	–	–	2.08	9.63	4.23	**37.46**

1986; Lalana & Ortiz 1991), *J. edwardsii* (Edmunds 1995), and *P. elephas* (Goñi et al. 2001). This general change in prey choice with ontogeny probably reflects an expanded foraging range and thus ability to exploit different habitats and unique prey (Andrée 1981; Edgar 1990; Briones-Fourzán et al. 2003).

In California coastal populations, Engle (1979) found a high proportion of molluscs in the juvenile *P. interruptus* diet, which could be related to the availability of molluscs in the study site or to the method used for analysis (faecal rest analysis), because digestion can lead to overestimation of the importance of groups with harder parts (Joll 1982). Like us, Engle (1979) reported differences in the diet of *P. interruptus* that depended on local habitat characteristics. This implies that local habitat

Table 3 Index of Importance Value (IIV = Relative frequency × relative biomass/100) of the epifaunal groups by season at Arvin in Bahía Tortugas and Queen in Bahía Sebastián Vizcaíno. (*, Not possible to estimate colonial organisms.) Bold type represents up to 1 of the IIV value.

		Arvin, Bahía Tortugas				Queen, Bahía Sebastián Vizcaíno			
Phyllum/ Subphyllum	Class/Order	Autumn IIV	Winter IIV	Spring IIV	Summer IIV	Autumn IIV	Winter IIV	Spring IIV	Summer IIV
Crustacea	Brachyura	0.008	0.022	0.001	0.004	0.005	0.007	0.013	0.003
	Amphipoda	**30.872**	**21.963**	**56.222**	**29.124**	0.743	**1.332**	**1.121**	**1.717**
	Amphipoda tube	–	0.001	<0.001	<0.001	0.001	0.002	<0.001	<0.001
	Isopoda	0.076	0.115	0.004	0.343	0.055	0.043	0.076	0.07
	Ostracoda	0.001	0.001	<0.001	<0.001	0.001	0.002	0.017	0.001
	Tanaidacea	0.04	0.157	0.004	0.01	0.005	0.002	0.002	<0.001
	Paguroidea	–	–	–	<0.001	–	–	<0.001	<0.001
	Caridea	<0.001	<0.001	<0.001	<0.001	–	–	<0.001	<0.001
	Cumacea	0.018	<0.001	<0.001	<0.001	–	–	–	–
Chelicerata	Picnogonida	0.003	0.001	<0.001	<0.001	0.005	0.002	0.001	<0.001
Mollusca	Gastropoda	0.062	0.035	0.028	0.013	**6.061**	**8.199**	**14.782**	**10.206**
	Bivalvia	0.012	0.001	<0.001	0.009	0.054	0.003	0.008	0.018
	Polyplacophora	–	<0.001	<0.001	<0.001	0.001	–	<0.001	0.001
	Monoplacophora	0.008	0.025	0.007	0.096	0.055	0.155	0.032	0.02
	Opistobranchia	–	<0.001	–	–	–	0.001	–	–
Porifera	Demospongia	0.001	0.003	<0.001	<0.001	0.006	0.001	<0.001	0.001
Annelida	Anelidae	0.11	0.056	0.001	0.009	0.002	0.01	0.013	0.003
	Polychaeta	**1.427**	**2.478**	0.237	**1.799**	**7.896**	**3.944**	**1.557**	**2.513**
	Clitellata (Oligochaeta)	0.013	<0.001	0.001	<0.001	0.001	0.049	0.124	0.001
Ectoprocta	Gymnolaemata (Bryozoa)	*	*	*	*	*	*	*	*
Nemata	Nematoda	–	–	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Protozoa	Sarcodina (Foraminiferida)	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	0.001	0.001
Echinodermata	Asteroidea	–	–	–	–	–	–	<0.001	–
	Ophiuroidea	<0.001	<0.001	<0.001	<0.001	0.025	0.009	0.006	0.003
	Holothuroidea	<0.001	<0.001	<0.001	<0.001	0.007	0.001	0.002	0.002
	Echinoidea	–	–	–	–	–	–	–	<0.001
Cnidaria	Anthozoa (Coelenterata)	0.073	0.624	0.081	0.109	0.022	0.031	0.035	0.01
	Anthozoa (Gorgonoacea)	–	–	–	–	0.002	<0.001	–	–
Platyhelmintes	Turbellaria	0.174	0.024	0.007	0.021	0.001	0.001	0.002	0.002
Nemertea	Nemertinos	0.012	0.029	0.004	0.006	0.001	0.002	0.007	0.001
Sipuncula	Sipunculidae	–	–	0.000	0.012	–	<0.001	–	<0.001
Entoprocta	Entoprocto	–	–	–	–	–	–	–	<0.001
Chordata	Tunicata (Ascidiecea)	0.002	<0.001	<0.001	<0.001	0.002	0.001	<0.001	<0.001
Echiura		–	–	–	<0.001	–	–	–	–

information is fundamental for understanding the feeding ecology of spiny lobsters (Edgar 1990), as is the inclusion of a range of lobster sizes even among juveniles.

We attribute differences in stomach fullness among individuals in different moult stages to be a consequence of altered foraging activity. Intermoult lobsters forage more actively than individuals in premoult condition (Lipcius & Herrnkind 1982), whereas postmoult juveniles typically remain hidden in crevices and are consequently less likely to be caught in baited traps (Herrera et al. 1991; Jernakoff et al. 1993). Briones-Fourzán et al. (2003) handcaught a similar number of intermoult and premoult juvenile *P. argus* in their study, suggesting that trap capture selects for the more active intermoult lobsters.

Using IRI analysis, we found that Amphipoda and Isopoda were important in stomach contents in some seasons and also more abundant in the environment (IIV analysis), and thus were not considered preferred food items by the Manly Index. Similarly, Díaz-Arredondo & Guzmán del Próo (1995) described seasonal variations in trophic groups related to abundance of benthic components, which suggests trophic plasticity of *P. interruptus* as in other spiny lobsters (Andrée 1981; Joll & Phillips 1984; Jernakoff et al. 1993, Briones-Fourzán et al. 2003). In contrast, the Manly Index suggests that juvenile *P. interruptus* prefer Brachyurans despite their low availability in the environment. A searcher characteristic was reported in other lobsters (Andrée 1981; Joll & Phillips 1984; Jernakoff et al. 1993; Briones-Fourzán et al. 2003).

At Arvin, the nutritional status of juveniles as determined by RWDG differed significantly among seasons, but at Queen the nutritional condition of lobster varied little seasonally. We suspect that this disparity among sites is related to differences in local environmental conditions, specifically, the warmer and less variable seawater temperatures at Queen. Like juveniles from Queen, *P. argus* juveniles caught in a tropical reef lagoon showed no seasonal differences in mean RWDG (Briones-Fourzán et al. 2003).

At Arvin, we observed the lowest value for RWDG in juveniles caught in spring, which coincided with the largest number of lobsters with empty stomachs. Baited traps promote the capture of starved animals (Dall 1975), which is related to a lack of available food (Chittleborough 1975; Colinas-Sáchez & Briones-Forzán 1990). In this

Table 4 Selective index (Manly's alpha index (α_i)) of trophic groups by season from data of Index of Importance Value (IIV) of the group in the environment versus Index of Relative Importance (IRI) in the stomach contents of juvenile *Panulirus interruptus* for the seasons at Arvin in Bahía Tortugas and Queen at Bahía Sebastián Vizcaíno. Bold type indicates preferred groups using the Manly α_i.

		Arvin, Bahía Tortugas				Queen, Bahía Sebastián Vizcaíno			
Fauna	Trophic group	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Crustacea	Brachyura	0.052	**0.334**	**0.101**	–	–	0.03	0	0.01
	Amphipoda	0	0.003	0	0	0.016	0.005	0	0
	Isopoda	0.004	**0.208**	0.006	0.017	**0.71**	**0.452**	0	0.023
	Ostracoda	**0.942**	–	**0.274**	**0.491**	–	0.116	–	–
	Tanaidacea	–	–	–	–	–	0.001	–	–
	Cumacea	–	–	–	–	–	–	–	–
	P. interruptus	–	–	–	–	–	–	–	–
	unidentified	–	–	–	–	–	–	–	–
Mollusca	Gastropoda	0.001	0.059	0.016	0.064	0.001	0	0	0
	Bivalvia	0.001	0.094	**0.1**	0.026	–	0.077	0.004	–
	Polyplacophora	–	–	**0.457**	–	**0.245**	–	–	–
	Monoplacophora	–	–	0	–	–	–	–	–
Porifera	Demospongia	–	**0.303**	0.046	0.029	0.027	–	**0.995**	0.084
Annelida	Polychaeta	–	–	0	0	–	–	–	–
Ectoprocta	Bryozoa	–	–	–	–	–	–	–	–
Nemata	Nematoda	–	–	–	**0.373**	–	–	–	**0.842**
Sarcodina	Foraminiferida	–	–	–	–	–	**0.32**	0.001	0.039
Echinodermata		–	–	–	–	–	–	–	–
Cnidaria	Coelenterata	–	–	–	–	–	–	–	0.002
	Manly α_i	0.17	0.17	0.1	0.13	0.2	0.125	0.143	0.125

study, significant differences in stomach fullness of lobsters among seasons could not be related to availability of food items because the dominant and preferred trophic groups of epifauna did not change drastically in any season at either site. Changes in seasonal nutrition may be related to differences in the quantity and quality (Dall 1975) of trophic groups eaten one season earlier. Although crustaceans and gastropod prey are protein sources essential to the structure and overall function of lobsters (Kanazawa 2000), vegetal material may also be important in the diet of lobsters. Joll & Phillips (1984) state that cellulose fibre stimulates growth and the assimilation of nitrogen in lobsters on high protein diets. When on low protein diets, the plant material acts as an extender, making a low protein diet adequate for normal growth and survival. Coralline algae may also serve as a source of calcium for the juveniles as suggested by Lindberg (1955) and Engle (1979). Joll & Phillips (1984) observed than coraline algae (*Corallina cuvieri*) can be digested by *P. cygnus,* with absorption efficiencies up to 35%.

In *P. inflatus*, Aramoni-Serrano & Lozano-Alvarez (1995) found higher densities of lobsters with diminished nutritional condition in winter. They mentioned that this impoverishment could be the result of intra-species competition for food by migration of lobsters to the coastal habitat. Vega et al. (1996) found a migration of reproductive females to shallow waters (1–25 m) into the juveniles' habitat (<4 m) to carry out egg extrusion and hatching during spring-summer. This suggests that further research on possible trophic competition among size classes from migration patterns of *P. interruptus* needs to be clarified.

Our study shows local and seasonal changes in natural diet, preferences and nutritional condition of small lobsters, a phase poorly studied in Palinuridae, which complements the knowledge of *P. interruptus* feeding ecology in the region.

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REFERENCES

Andrée, W. S. 1981: Locomotory activity patterns and food items of benthic postlarval spiny lobsters *Panulirus argus*. Unpublished MSc thesis, Florida State University, United Sates.

Ayala, Y. 1976: Aspectos biológicos de la langosta roja *Panulirus interruptus* (Randall 1846) del área comprendida entre Punta Malarrimo y La Lobera (5 km al sur de Punta Eugenia, B.C.S.). *In*: Villamar, A. *ed.* Memorias del Simposio sobre Recursos Masivos de México, Vol. Especial sobre Abulón/ Langosta, 28–30 Sept. 1976, Ensenada, México, Instituto Nacional de la Pesca. Pp. 37–72.

Ayala, Y.; González-Avilés, J. G.; Espinoza-Castro, G. 1988: Biología y pesca de langosta en el Pacífico Mexicano. *In*: Los Recursos Pesqueros del País. México, D.F., Secretaría de Pesca. Pp. 251–286.

Briones-Fourzán, P.; Castañeda-Fernández de Lara, V.; Lozano-Álvarez, E.; Estrada-Olivo, J. 2003: Feeding ecology of the three juvenile phases of the spiny lobster *Panulirus argus* in a tropical reef lagoon. *Marine Biology 142*: 855–865.

Brusca, R. C. 1980: Common intertidal invertebrates of the Gulf of California. Tucson, Arizona, The University of Arizona Press. 513 p.

Chittleborough, R. G. 1975: Environmental factors affecting growth and survival of juvenile wester rock lobster *Panulirus longipes* (Milne-Edwards). *Australian Journal of Marine and Freshwater Research 26*: 177–196.

Colinas-Sánchez, F.; Briones-Fourzán, P. 1990: Alimentación de las langostas *Panulirus argus* y *P. guttatus* (Latreille 1804) en el Caribe Mexicano. *Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 17*: 89–109.

Dall, W. 1974: Indices of nutritional state in the western rock lobster, *Panulirus longipes* (Milne Edwards). I. Blood and tissue constituents and water content. *Journal of Experimental Marine Biology and Ecology 16*: 167–180.

Dall, W. 1975: Indices of nutritional state in the western rock lobster, *Panulirus longipes* (Milne Edwards). II. Gastric fluid constituents. *Journal of Experimental Marine Biology and Ecology 18*: 1–18.

Dawson, E. Y. 1952: Circulation within Bahía Vizcaino, Baja California, and its effects on marine vegetation. *American Journal of Botany 39*: 425–432.

Díaz-Arredondo, M. A.; Guzmán-del-Próo, S. A. 1995: Feeding habits of the spiny lobster (*Panulirus interruptus* Randall, 1840) in Bahía Tortugas, Baja California Sur. *Ciencias Marinas 21*: 439–462.

Engle, J. 1979: Ecology and growth of juvenile California spiny lobsters (*Panulirus interruptus,* Randall). Unpublished PhD dissertation, University of Southern California, Los Angeles, CA, United States.

Edgar, G. J. 1990: Predator-prey interactions in seagrass beds. I. The influence of macrofaunal abundance and size-structure on the diet and growth of the Western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology 139*: 1–22.

Edmunds, M. 1995: The ecology of the juvenile southern rock lobster, *Jasus edwardsii* (Hutton 1875) (Panlinuridae). Unpublished PhD dissertation, University of Tasmania, Hobart, Australia.

Goñi, R.; Quetglas, A.; Reñones, O. 2001: Diet of the spiny lobster *Panulirus elephas* (Decapoda: Palinuridea) from the Columbretes Islands Marine Reserve (north-western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom 81*: 347–348.

Guzmán-del-Próo, S. A.; Pineda, J. 1992: Análisis poblacional de la pesquería de langosta roja (*Panulirus interruptus*) de 1971–1975 en la Bocana-Abreojos, B.C.S, México. *In*: Guzmán del Próo S. A. *ed.* Memorias del Taller México-Australia sobre Reclutamiento de Recursos Bentónicos de Baja California. México, SEPESCA-IPN. Pp. 167–177.

Guzmán-del-Próo, S. A.; Carrillo-Laguna, J.; Belmar-Perez, J.; De la Campa J. S.; Villa, B. A. 1996: The puerulus settlement of red spiny lobster (*Panulirus interruptus*) in Bahia Tortugas, Baja California, Mexico. *Crustaceana 69*: 949–957.

Herrera, A.; Ibarzábal, D.; Foyo, J.; Espinosa J. 1991: Alimentación natural de la langosta *Panulirus argus* en la región de Los Indios (plataforma SW de Cuba) y su relación con el bentos. *Revista de Investigaciones Marinas 12*: 172–182.

Herrnkind, W. F.; Butler IV, M. J. 1986: Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. *Marine Ecology Progress Series 34*: 23–30.

Herrnkind, W. F.; van der Walker, J. A.; Barr, L. 1975: Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St John, U.S. Habitation, patterns of movement and general behavior. *Natural History Museum, Los Angeles City, Science Bulletin 20*: 31–45.

Hyslop, E. J. 1980: Stomach contents analysis a review of methods and their application. *Journal of Fish Biology 17*: 411–429.

Jernakoff, P.; Phillips, B. F.; Fitzpatrick, J. J. 1993: The diet of postpuerulus Western rock lobster *Panulirus cygnus* (George) at seven Mile Beach, Western Australia. *Australian Journal of Marine Freshwater Research 44*: 649–655.

Johnson, M. W. 1960a: Production and distribution of larvae of the spiny lobster *Panulirus interruptus* (Randall) with records on *P. gracilis* (Streets). *Bulletin of Scripps Institute Oceanography, University of California 7*: 413–446.

Johnson, M. W. 1960b: The offshore drift of larvae of the California spiny lobster, *Panulirus interruptus*. *California Cooperative Oceanic Fishery Investigation Report 7*: 147–161.

Joll, L. M. 1982: Foregut evacuation of four foods by the Western rock lobster, *Panulirus cygnus,* in Aquaria. *Australian Journal of Marine and Freshwater Research 33*: 939–943.

Joll, L. M. 1984: Natural diet and growth of juvenile Western rock lobster *Panulirus cygnus* (George). Unpublished PhD thesis, University of Western Australia, Perth, Australia.

Joll, L. M.; Phillips, B. F. 1984: Natural diet and growth of juvenile Western rock lobster *Panulirus cygnus*. *Journal of Experimental Marine Biology and Ecology 75*: 145–169.

Kanazawa, A. 2000: Nutrition and food. *In*: Phillips, B. F.; Kittaka, J. *ed.* Spiny lobsters: fishery and culture. 2nd ed. Oxford, United Kingdom, Fishing News Books, Blackwell Science. 679 p.

Kanciruk, P. 1980: Ecology of juvenile and adult Palinuridae (spiny lobsters). *In*: Cobb, S. J.; Phillips, B. F. *ed.* The biology and management of lobsters. Vol. II. New York, Academic Press, Inc. 390 p.

Krebs, C. J. 1999: Ecological methodology. 2nd ed. Menlo Park, California, Addison-Wesley Educational Publications. 620 p.

Krebs, C. J. 2000: Ecological methodology, version 5.2 software program. Setauket, New York, United States, Exeter Software.

Kozloff, E. N. 1987: Marine invertebrates of the Pacific Northwest. Washington, University of Washington Press. 510 p.

Ladah, L. B.; Zertuche-González, J. A. 1999: Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its Southern limit in Baja California after mass disappearance during ENSO 1997–1998. *Journal of Phycology 35*: 1106–1112.

Lalana, R. R.; Ortiz, M. 1991: Contenido estomacal de puerulos y postpuerulos de la langosta *Panulirus argus* en el Archipiélago de los Canarreos, Cuba. *Revista de Investigaciones Marinas 12*: 107–116.

Lindberg, R. G. 1955: Growth, population dynamics, and field behaviour in the spiny lobster, *Panulirus interruptus* (Randall). *University of California, Publication Zoological 59*: 157–248.

Lipcius, R. N.; Herrnkind, W. F. 1982: Molt cycle alteration in behavior, feeding and diel rhythms of a decapod crustacean, the spiny lobster *Panulirus argus*. *Marine Biology 68*: 241 252.

Lluch-Belda, D. 2000: Centros de Actividad Biológica en la Costa Occidental de Baja California. *In*: Lluch-Belda, D.; Elourduy-Garay, J.; Lluch-Cota, S. E.; Ponce-Díaz, G. *ed.* Centros de Actividad Biológica del Pacífico Mexicano. La Paz, B.C.S., Mexico, Centro de Investigaciones Biológicas del Noroeste. 367 p.

Lozano-Álvarez, E.; Aramoni-Serrano, G. 1996: Alimentación y estado nutricional de las langostas *Panulirus inflatus* y *Panulirus gracilis* (Decapoda: Palinuridae) en Guerrero, México. *Revista de Biología Tropical 44*: 453–461.

Lyle, W. G.; MacDonald, C. D. 1983: Molt stage determination in the Hawaiian spiny lobster, *Panulirus marginatus*. *Journal of Crustacean Biology 3*: 208–216.

Manly, F. J.; McDonald, L. L.; Thomas, D. L. 1993: Resource selection by animals: statistical design and analysis for field studies. London, Chapman & Hall. 177 p.

Margalef, R. 1998: Ecología. Barcelona, Spain, Omega. 951 p.

Marx, J.; Herrnkind, W. F. 1985: Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. *Bulletin of Marine Science 36*: 423–431.

Morris, R. H.; Abbott, D. P.; Haderlie, E. C. 1980: Intertidal invertebrates of California. Stanford, California, Stanford University. 690 p.

Oh, C. W.; Hartnoll, R. G.; Nash, R. D. M. 2001: Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea. *Marine Ecology Progress Series 214*: 211–223.

Perez-Enriquez, R.; Vega, A.; Avila, S.; Sandoval, J. L. 2001: Population genetics of the red lobster (*Panulirus interruptus*) along the Baja California Peninsula, Mexico. *Marine and Freshwater Research 52*: 1541–1549.

Pineda, J.; Díaz de León, A. J.; Uribe, F. 1981: Fecundidad de langosta roja *Panulirus interruptus* (Randall 1842) en Baja California. *Ciencia Pesquera, Instituto Nacional de la Pesca, México 1*: 99–118.

SAGARPA 2003: Anuario Estadístico de Pesca 2002. México, Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación.

Smith, R. I.; Carlton, J. T. 1975: Light's manual: intertidal invertebrates of the Central California Coast. California, University of California Press. 716 p.

Sokal, R. R.; Rohlf, F. J. 1998: Biometry. The principles and practice of statistics in biological research. 3rd ed. 4th printing. New York, W. H. Freeman.

Vega, V.A.; Lluch-Cota, D. B. 1992: Análisis de las fluctuaciones en los volúmenes de langostas (Panulirus spp.), del litoral oeste de la Península de Baja California, en relación con el desarrollo histórico de la pesquería y la variabilidad del marco ambiental. *In*: Proceedings of México-Australia workshop on recruitment on benthic marine resources of the Baja California Peninsula, 25–29 November, La Paz, B.C.S., México. Escuela Nacional de Ciencias Biológicas, Centro Interdsciplinario de Ciencias Marinas, Instituto Politécnico Nacional. Pp. 191–212.

Vega, V. A.; Espinoza-Castro, G.; Gómez-Rojo, C. 1996: Pesquería de langosta *Panulirus* sp. *In*: Casas-Valdez, M.; Ponce-Díaz, G. *ed.* Estudio del potencial pesquero y acuícola de Baja California Sur, Vol. I. La Paz, México, Centro de Investigaciones Biológicas del Noroeste. 350 p.

Vega, V. A.; Espinoza-Castro, G.; Gómez-Rojo, C. 2000: Langosta. *In*: Sustentabilidad y pesca responsable en México, evaluación y manejo. Secretaria del Medio Ambiente Recursos Naturales y Pesca (SEMARNAP). D.F., México. Pp. 263–298.

Yáñez-Arancibia, A.; Curiel-Gómez, J.; De-Yáñez, V. L. 1976: Prospección biológica y ecológica del bagre marino *Galeichthys caerulescens* (Gunther) en el sistema lagunar costero de Guerrero, México. (Pises: Ariidae). *Anales del Centro de Ciencias del Mar y Limnología, Universidad nacional Autónoma de México 3*: 125–180.

Zar, J. H. 1999: Biostatistical analysis. 4th ed. New Jersey, Prentice Hall. 663 p.

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Fate of discards from deep water crustacean trawl fishery off the south coast of Portugal

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Abstract Trawling for crustaceans takes place on the south coast of Portugal at depths between 200 and 800 m. Large amounts of discards are released back to sea, reaching the bottom in the general area where trawling occurs. The objective of this work was to study the time taken for decomposition of the discards, to identify the most important scavenging species involved, and to evaluate the impact on the species targeted by the fishery. We conducted a series of 22 trials, using traps baited with samples of the discards. The time of immersion varied between 1 and 40 h. The amount of tissue removed from the discards was evaluated on a qualitative scale of 1–3, and quantitatively. The species caught in the traps were identified. Considerable consumption of the bait had occurred after 5 h of immersion. After 24 h of immersion only fish bones were left; past 40 h, consumption was complete. The conger eel (*Conger conger*) was the most common fish species present in the traps. Two species, the amphipod *Scopelocheirus hopei* and the isopod *Natatolana (Cirolana) borealis*, were identified as most important for the recycling of organic matter in the system. The stomach contents of a sample of species caught in trawls were analysed for the presence of small scavengers. Preliminary results show that *S. hopei* and *N. (C.) borealis* are part of the diet of some of the target species of this fishery, such as the Norway lobster, *Nephrops norvegicus* and the rose shrimp *Parapenaeus longirostris*.

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INTRODUCTION

Fishing is a source of disturbance which alters the flow of energy within ecosystems. In particular, bycatches and discards and incidental mortalities on the seabed generate carrion that would be unavailable to many facultative scavengers under normal circumstances. These energy subsidies can represent considerable sources of organic material. Among the most important fisheries, shrimp trawling and crab fisheries produce the highest proportion of discards, rejecting on average 84% and 71% of the catch (Hall 1999).

There is little information on the processes involved in the recycling of carrion on the seabed. Several studies looked at the consumption of discards from fisheries targeting crustaceans. Sheridan et al. (1984) studied the shrimp fishery in the Gulf of Mexico and concluded that discards may favour increases in the shrimp biomass by reducing fish predation and providing additional food for the shrimp. Wassenberg & Hill (1987) in Moreton Bay (east Australia), found that the sand crab was also the most important scavenger to feed on discards, suggesting that food available from the trawlers may have enabled higher population densities than there would be without trawling. Hill & Wassenberg (1990) in Torres Straight (east Australia), found that part of the discards from a shrimp fishery reaching the bottom were consumed within a few hours but none of the target species of the fishery was identified as a scavenger. In some studies, discards were found to modify the diets of bottom fish; discarded saury in Sandai Bay, Japan (Yamamura 1997) and discarded squid in the Patagonian shelf (Laptikhovsky & Fetisov 1999) were part of the diet of bottom species that in natural conditions would not have access to these species as prey.

Off the south coast of Portugal, crustacean trawling takes place on the lower shelf and slope at

depths between 200 and 800 m. In decreasing order of importance the four species targeted by this fishery are the rose shrimp (*Parapenaeus longirostris*) caught in the shallower area, Norway lobster (*Nephrops norvegicus*) caught at intermediate to greater depths, and two species of red shrimp (*Aristeus antennatus* and *Plesiopenaeus edwardsianus*) caught at the edges of marine canyons. The high value of these species makes all others uninteresting from a commercial point of view, and most of the catch is discarded.

Two studies have estimated the proportion of the catch discarded in this area: Borges et al. (2001) estimated 70% of the catch of crustacean trawlers was discarded whereas Monteiro et al. (2001) reported that a third of the catch was discarded. The amounts discarded vary considerably from tow to tow depending on the quantity of pelagic and semi-pelagic species caught in the net when it is being recovered (blue whiting, *Micromessistius poutassou*; boarfish, *Capros aper*; snipe fish, *Macroramphosus* spp.; and the swimming crab, *Polybius henslowii*). Fish make up 82% of the discards by weight with the most important species being the blue whiting, representing 36% of the total amounts discarded (Monteiro et al. 2001).

Another characteristic of the discards from crustacean trawlers is their great diversity. Erzini et al. (2002) have identified 140 species (68 fish species and 72 invertebrates). Most species are present only occasionally and they include a large variety of deep water species (macruridae and families of small sharks) as well as many deep water invertebrates. The depth at which this fishery occurs explains this composition—a comparison with fish trawling on the same coast, done at shallower depths on the platform, showed that discard composition was specific for each fishery (Erzini et al. 2002).

This study was one of a series of independent experiments aimed at understanding the recycling of discarded materials in the marine system. Other complementary studies include: the composition of discards, proportion of discards consumed by marine birds, identification of the discarded species that sink and float (Monteiro et al. 2001) and consumption of discards in the water column (Erzini et al. 2003). The results of these experiments showed that on average, 60% of the discards reach the bottom.

In view of the large amounts discarded over the community where fishing occurred, we were interested in understanding: (1) which species were involved in the recycling of carrion; (2) how fast this recycling process was; and (3) whether there was a direct or indirect impact on species targeted by the fishery.

MATERIALS AND METHODS

The work consisted of 22 experimental trials, carried out off Olhão, on the South coast of Portugal, using commercial vessels (Fig. 1). The traps were put in an area with the characteristics of the grounds where trawling occurs, but within the 6 n mile limit, an area where trawling is not allowed and therefore the risk of having the traps caught in a net was small.

The basic experimental design involved setting lines of traps where the bait consisted of the most commonly discarded fish species in the Algarve crustacean trawl fishery. The dimensions of the traps were c. 90 cm long, 40 cm wide, and 45 cm high. The mesh size of the trap's net was 10 mm, the size used by commercial fishers. Since this mesh could not retain small scavengers, half of the traps were wrapped in 1 mm mesh. When attaching the traps on the line, the two mesh sizes were alternated. The traps had an opening on the top. On each side of the opening were two bait pockets. Sometimes the bait was put loose inside the trap. The bait always consisted of whole fish obtained during the regular fishing operations of the vessels, used fresh or frozen.

The work was carried out in two phases. The first phase consisted of a pilot study conducted on board crustacean trawlers to obtain information on adequate immersion times. Times of permanence of the traps on the bottom were not pre-planned (depending on the convenience of the fishing activity of the vessel) and varied between 4.6 and 39.6 h. During this phase, up to seven traps were set in a single line. The bait used varied and included *M. poutassou*, *Phycis blenoides*, *Merluccius merluccius*, *Conger conger*, *Lepidopus caudatus*, *Loligo* spp., *Scomber japonicus*, and *Trachurus* spp. Owing to difficulties in obtaining accurate weights of the bait used and retrieved after immersion, the degree of consumption was evaluated using a qualitative scale of "discard consumption" consisting of the following categories: 0 = no consumption, 1 = only a slight indication of consumption (some bites on the body), 1.5 = bait partially consumed but still with muscle tissue present, 2 = only bones and skin present, 2.5 = only bones present, 3 = complete consumption. Thirteen trials were conducted during this phase (Table 1).

The second phase of the work was directed at estimating rates of consumption over time. To

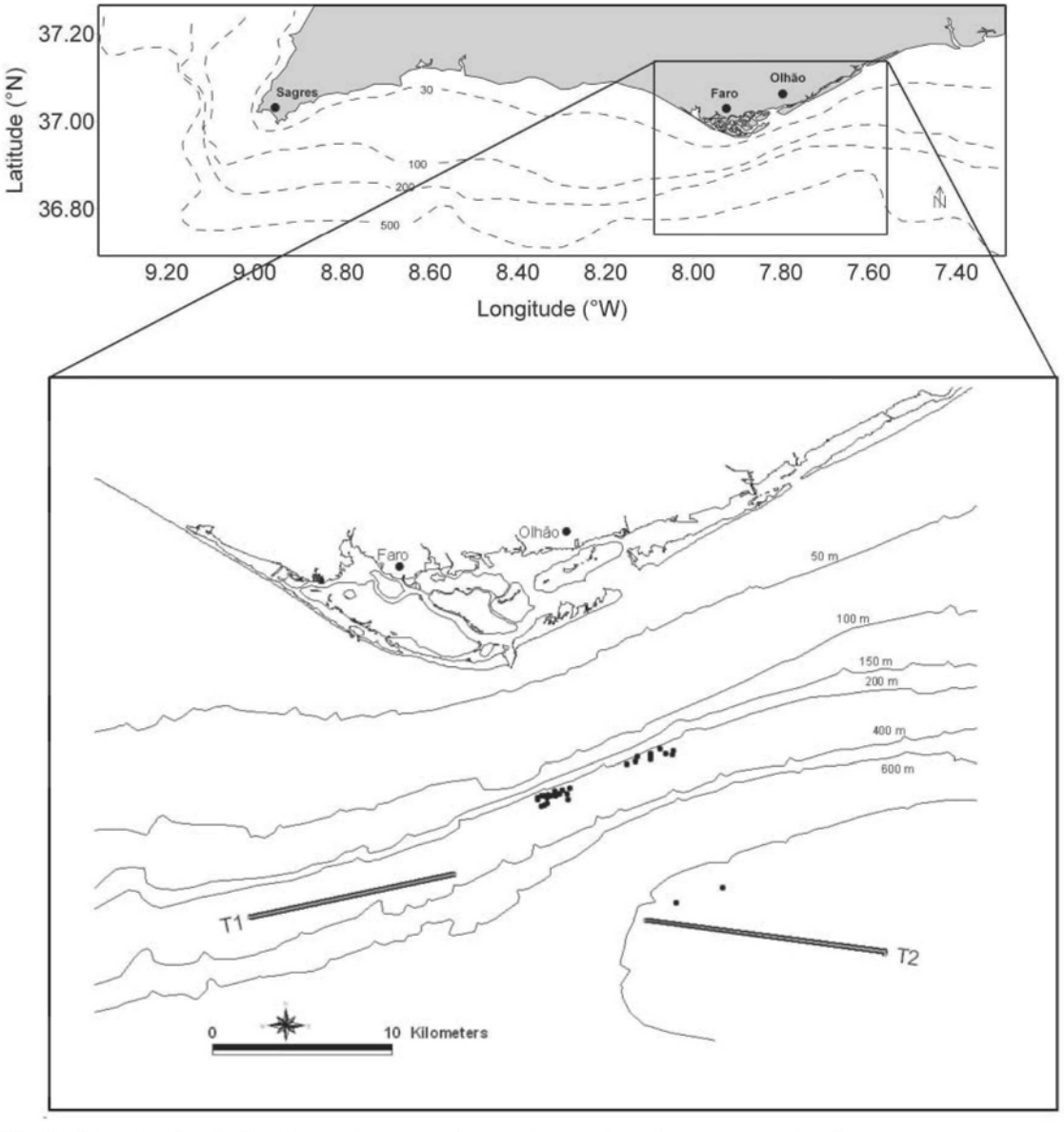

Fig. 1 Map showing the location of the tows and general area where the traps were placed.

validate for a realistic situation where the discards were not inside a trap, the bait (whole fish) was let loose inside the trap and the effect of the trap tested by attaching bait directly to the cable connecting the traps. Each trial consisted of setting five lines of traps (setting of the traps occurs within a 30 min period) and then retrieving them 1, 2, 4, 6, and 8 h after setting. The experiment was repeated nine times (trials 14–22 in Table 2). For these experiments the bait used had been deep-frozen immediately after capture by a crustacean trawler and then allowed to defrost before being weighed and put in the traps. After immersion the remaining bait was again weighed and the consumption estimated. In some instances, it was verified that the weight after immersion was higher than before. This was attributed to some dehydration resulting from the freezing process and water absorption while immersed. The weights at the beginning of the experiment (frozen bait) were therefore multiplied by a factor C = 1.093,

based on the average weight gain in fish that did not show any signs of consumption:

$$w = 1.093\ w_0$$

where w is the corrected weight and w_0 is the recorded weight of the defrosted fish.

During trials 6–13, while the traps were in the water, two tows of c. 3 h each were carried out in an adjacent area. The objective was to obtain information on the community structure. The stomachs of a sample of individuals were observed.

Descriptive statistics were used to characterise the consumption over time; for each line, initial and final weights were added and consumption recalculated. To evaluate the significance of some factors that could influence the interpretation of the results, such as effect of the trap, mesh size, and season, consumption rates for the same immersion times were compared using the Wilcoxon rank sum test (Snedecor & Cochran 1980), for the null hypothesis: median consumptions of the levels of the considered factor are equal (significance level considered was 0.05). The effect of the trap was tested by comparing consumption inside and outside for each submersion time, using data from trials 20–22 only. The effect of season was also evaluated within each submersion time category, by comparing consumptions from trials 14–16 (considered to represent cold months) versus trials 17–22 (representing warm months). To test the effect of the mesh size, data on consumption were calculated for small and large mesh traps and the values were compared within time-of-immersion categories.

Table 1 Data for the trials with baited traps for the first phase of the work. Bait consumption is registered on a semi-quantitative scale from 0 (no consumption) to 3 (complete consumption of the bait).

Trial ID	Date	Depth (m)	Immersion (h)	Type of bait	No. of traps	Consumption Min.	Max.
1	2 Mar 1997	210	12.5	*Scomber japonicus* *Trachurus* spp. *Lepidopus caudatus* *Conger conger*	6	1	1.5
2	2 Mar 1997	274	39.6	*Scomber japonicus* *Trachurus* spp. *Lepidopus caudatus* *Conger conger* *Micromessistius poutassou* *Loligo* spp.	6	3	3
3	26 Mar 1997	256	13.6	*Scomber japonicus* *Trachurus* spp. *Merluccius merluccius* *Conger conger*	7	1	1
4	13 Apr 1997	256	14.5	*Scomber japonicus* *Trachurus* spp. *Merluccius merluccius* *Conger conger*	7	1	1.5
5	13 Apr 1997	262	24.7	*Scomber japonicus* *Merluccius merluccius* *Micromessistius poutassou*	7	1	2.5
6	29 Apr 1997	567	5.2	*Micromessistius poutassou*	4	1	2.5
7	29 Apr 1997	587	5.6	*Micromessistius poutassou*	4	1	2.5
8	29 Apr 1997	458	4.6	*Micromessistius poutassou*	4	1	2.5
9	29 Apr 1997	439	4.9	*Micromessistius poutassou*	4	1.5	2.5
10	29 Apr 1997	366	5.8	*Micromessistius poutassou* *Merluccius merluccius*	4	1	1.5
11	29 Apr 1997	366	4.9	*Micromessistius poutassou* *Merluccius merluccius* *Phycis blenoides*	4	1	1.5
12	30 Apr 1997	339	5.9	*Micromessistius poutassou* *Phycis blenoides*	4	1	2.5
13	30 Apr 1997	348	4.7	*Micromessistius poutassou*	4	1	1.5

Table 2 Data for the trials with baited traps for the second phase of the work. Bait consisted of whole fish and consumption refers to the proportion of weight consumed for each individual fish placed either loose inside the trap or attached directly to the trap line.

Trial ID	Date	Depth (m)	Immersion (h)	No. of traps	No. of fish outside the traps	Proportion consumed Min.	Max.
14	23 Jan 2000	219	1	6		0.11	0.26
			2	6		0.13	0.38
			4	6		0.11	0.31
			6	6		0.19	0.47
			8	6		0.09	1.00
15	24 Jan 2000	200	1	6		0.09	0.70
			2	6		0.09	0.84
			4	6		0.10	0.41
			6	6		0.09	0.58
			8	6		0.09	0.65
16	25 Jan 2000	230	1	6		0.09	0.12
			2	6		0.11	0.23
			4	6		0.09	0.76
			6	6		0.10	0.36
			8	6		0.09	0.41
17	24 Jun 2000	210	1	6		0.25	1.00
			2	6		0.17	0.45
			4	6		0.23	0.60
			6	6		0.17	0.67
			8	6		0.23	0.86
18	1 Jul 2000	208	1	6		0.20	0.98
			2	6		0.21	0.96
			4	6		0.20	0.93
			6	6		0.15	0.30
			8	6		0.17	1.00
19	2 Aug 2001	217	1	6		0.17	1.00
			2	6		0.20	0.43
			4	6		0.20	1.00
			6	6		0.12	0.46
			8	6		0.22	0.95
20	4 Aug 2001	212	1	6	4	0.01	0.17
			2	5	5	0.05	1.00
			4	6	5	0.02	0.13
			6	6	4	0.03	1.00
			8	6	5	0.00	1.00
21	5 Aug 2001	208	1	6	5	0.06	0.24
			2	5	5	0.06	0.39
			4	6	5	0.06	0.85
			6	6	5	0.03	0.90
			8	6	5	0.03	1.00
22	6 Aug 2001	216	1	6	5	0.09	0.44
			2	5	5	0.07	0.35
			4	6	5	0.08	0.28
			6	6	5	0.07	0.77
			8	6	5	0.06	0.86

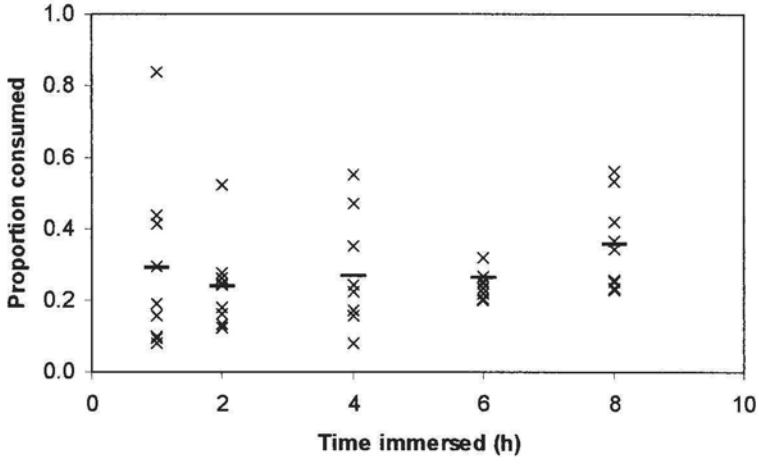

Fig. 2 Proportion of bait consumed over time. Crosses correspond to the proportion of bait consumed for each trial and time (trials 14–22), horizontal bars represent average values for each time of immersion period.

RESULTS

Testing of factors potentially affecting the interpretation of consumption data showed that none of the factors considered (trap, season, and mesh size) were significant; P values of the tests were $P > 0.28$, $P > 0.06$, and $P > 0.14$ respectively.

Consumption rates for the first set of trials are presented in Table 1. Trials 6–13, of durations between 4.6 and 5.9 h showed that considerable consumption occurred (between level 1—slight consumption, and level 2.5—only skeletons were left). Higher consumption rates were obtained with longer immersion periods, with complete consumption, in trial 2, after 39.6 h of immersion.

Data obtained in trials 14–22 (Table 2 and Fig. 2) confirmed that consumption varies widely for the same immersion times and sometimes within the same line. Average values stayed constant until 4 h after immersion (horizontal bars in Fig. 2) indicating that there is a quick initial consumption of around 20% of the bait before 1 h of immersion, followed by a slow increase in consumption after 5 h of immersion.

Table 3 shows the species caught in the traps. Two species of small scavengers, the amphipod *Scopelocheirus hopei* and the isopod *Natatolana (Cirolana) borealis* were the most abundant in number. Since many traps with a high degree of bait consumption did not have trapped animals when retrieved, it should be considered that the most important consumers of the bait escaped the traps. During trials 14–22, 267 individual traps were observed. Of these, 260 had more than 10% of the bait consumed at retrieval and only 66 had trapped individuals,

Table 3 List of species present in the traps and number of trials where each one was present out of a total of 22 trials.

Group	Species	Trials present
Fish	*Conger conger*	14
Decapoda	*Plesionika* spp.	5
	Parapenaeus longirostris	4
	Polybius henslowii	4
	Heterocarpus ensifer	2
	fam. Majidae	2
	Calappa granulata	1
	Diogenes pugilator	1
	Dardanus arrosor	1
Amphipoda	*Scopelocheirus hopei*	18
Isopoda	*Natatolana (Cirolana) borealis*	8
Equinodermata	Cl. Ophiuroidea	5
	Cl. Asteroidea	2

suggesting that small scavengers are the most important species. This is consistent with the pattern of consumption observed. Rarely was the skeleton of the fish affected when consumption was partial. Large bites were not common either. The gut was consumed first, followed by the muscle tissue, skin, and finally the skeleton.

Scopelocheirus hopei was sometimes present in very large quantities. In a single trap of trial 10, over 600 g (c. 65 000 individuals) of the amphipod *S. hopei* were caught.

Given the importance of small scavengers identified in the traps (*N. borealis* and *S. hopei*) and their possible role in transporting energy in the system, the stomachs of a sample of fauna from the

Table 4 Stomach contents analysis, absence/presence of *Natatolana (Cirolana) borealis* and *Scopelocheirus hopei*. The individuals observed represent a sample from the catch of two tows done in the vicinity of the grounds where the traps were set. Species where either *N. (C.) borealis* or *S. hopei* were present are shown in bold.

		No. of stomachs		
Group	Species	Observed	with *borealis*	with *S. hopei*
Fish	***Chimaera monstrosa***	2	1	
	Citharus linguatula	1		
	Conger conger	4		
	Etmopterus pusillus	7		
	Galeus melastomus	1		
	Helicolenus dactylopterus	5	1	
	Hoplostethus mediterraneus	3		
	Lepidorhombus boscii	1		
	Lophius piscatorius	6		
	Merluccius merluccius	4		
	Microchirus azevia	1		
	Nezumia sclerorhynchus	14	4	3
	Phycis blennoides	5	1	
	Scyliorhinus canicula	3		
	Trachyrhynchus trachyrhynchus	1		
	Trigla lyra	1		
Decapoda	*Aristeus antennatus*	11		
	Calappa granulata	6		
	Nephrops norvegicus	36	3	
	Dardanus arrosor	2		
	Parapenaeus longirostris	15	2	
	Plesionika edwardsii	8		
	Majidae	2		
	Polybius henslowii	1		1
Gastropoda	*Cassidaria tyrhena*	1		
	Ranella olearia	5		
Cephalopoda	*Ilex coindetii*	13		
	Sepiola rondeleti	1		
	Todaropsis eblane	1		
Equinoidea	*Echinus acutus*	4		

area were analysed for presence-absence of these two species. The results are presented in Table 4. For *P. longirostris* and *N. norvegicus*, the most important target species of the fishery, *N. borealis* was present. Another species of some importance is the scorpaenid (*Helicolenus dactylopterus*) a fish that is not targeted but kept for landing, where one out of five stomachs contained *N. borealis*. For the other species with no commercial value, small scavengers were part of the diet of the deep water fish species *Chimaera monstrosa*, *Nezumia sclerorhynchus*, and *P. blennoides* and the swimming crab *P. henslowii*.

DISCUSSION

The results obtained with baited traps showed that small rather than large scavengers are mostly responsible for discard consumption on the bottom. Other species may be important but not be detected with the use of traps (such as *Lophius* spp., which were present in the vicinity of the traps but were never caught). However, parallel experiments with fish attached to the cables of the traps showed that the trap effect was negligible and that slow consumption by these small scavengers dominated the

recycling process. Two species, the lysianassid amphipod *S. hopei* and the isopod *N. (C.) borealis*, were identified as the most important for the recycling of organic matter in the system, with over 65 000 individuals of *S. hopei* found in a single trap.

Most studies of consumption of marine carrion have found that small scavengers, especially amphipods and isopods play a dominant role in the recycling of organic matter. Both *S. hopei* and *N. (C.) borealis* were reported to be important scavengers in the Clyde Sea (Nickell & Moore 1991), the North Sea (Fonds & Groenewold 2000), and the Mediterranean (Bozzano & Sardá 2002). *S. hopei*, along with other amphipod and isopod species, was attracted to baited traps in the Irish Sea (Ramsay et al. 1997) and together with another lyassianidae amphipod, *Orochomene manus*, was an important scavenger in west Scotland (Bergmann et al. 2002). Large parcels of fish at 1310 m in the Santa Catalina Basin were scavenged mainly by fish and ophiuroids, but also by two species of lysianassid amphipods (Smith 1985). In general, the importance of small scavengers, in particular lysianassid amphipods, seems to increase with depth. At relatively shallow depths of 40 m in the Irish Sea, for example, the most important species consuming discards were crabs, a gastropod, and a starfish (Ramsay et al. 1997). However, studies using cameras or traps designed to catch larger scavengers may have missed the importance of these species in shallower waters.

In this study, considerable consumption of the bait had occurred after 5 h of immersion. After 24 h only fish bones were left and after 40 h consumption was complete. Soft tissues were consumed rapidly, and hard tissues took up to 2 days to be consumed. These values are comparable with results from other authors. Bergmann et al. (2002) in west Scotland and Groenewold & Fonds (2000) in the North Sea, reported major consumption between 24 and 48 h. Ramsay et al. (1997) with immersion times that were longer than this study (16.5–76 h) found consumption from 0.00 to 0.47, values lower than those found in our study where complete consumption was found in some traps. Bozzano & Sardá (2002), using a time-lapse camera set at 100–319 m and immersion periods from 9.5 to 30.6 h, found that the attached bait was almost completely consumed during the longer immersion periods.

The high consumption rates and the frequent presence, often in large quantities, of the small scavengers suggests that trawl fishery discards may have a significant impact on the population dynamics of these species. Britton & Morton (1994) reported that marine fisheries impact scavengers in two ways: by removing them from the sea and by artificially promoting their success. These authors consider the second impact more important, and it is certainly so in the region of our study, where the two small scavenger species do not suffer mortality from the fishing activity but benefit from consuming the discards. In the North Sea, it has been suggested that beam trawling may generate up to 7% of the annual food demand of the entire scavenger population Fonds & Groenewold (2000). In the deep sea, large food falls are rare but represent extremely important local sources of energy, providing c. 11% of the respiratory requirements of the benthic community at a depth of 1310 m in the Santa Catalina Basin (Smith 1985), and significantly affecting abundances and species composition of bottom communities (Stockton & DeLaca 1982). In the system we studied, with ecology similar to the deep ocean in absence of local primary production, the artificial increase in food-fall caused by fisheries discards could significantly modify the ecosystem by stimulating the abundance of highly efficient scavengers, such as those identified, in particular *S. hopei*.

Although large amounts of the catch are discarded, discards are dispersed over a large area, since they are thrown overboard during sorting while the vessel is moving. It is therefore expected that the impact is very important but at a small spatial scale. As reported by Stockton & DeLaca (1982), there is a first impact resulting from the arrival of carrion and a second one resulting from the faecal discharge from scavengers, with a border surrounding the area benefiting from the food fall. Ramsay et al. (1997) suggest that the importance of the impact of carrion is higher when local natural food supply is low, but data on standing biomass and production in systems such as the one studied here (between the edge of the shelf and mid slope), are not abundant. Most studies designed to understand and quantify the recycling of organic matter were undertaken in deep waters, abyssal plain and trenches, where addition of organic matter and scavenging have been more frequently studied in connection to food limitation.

Scavenging amphipods and isopods in food-limited environments (e.g., deep sea) have life strategies that are adapted to rare and localised food-falls. Scavenger amphipods have the ability to withstand long periods of starvation, responding rapidly to food-falls, and maximising the rate and efficiency of food consumption (Smith & Baldwin 1982). Smith (1985) referred to this as a "tank-topping" feeding strategy, meaning that this species

will take as much food as possible when it is available and will keep eating in a strategy to profit as much as possible from occasional food. Since these species have fast digestion and high assimilations rates, importance of fecal pellets for dispersing food-falls is great (Dayton & Hessler 1972). Another adaptation of deep water amphipods relevant for food-fall recycling, is the ability to store disproportionately large meals by comparison with shallow water species (Dahl 1979). Similar adaptations have also been described for scavenging isopods. Wong & Moore (1995) refer to the cirolanidae isopod *N. borealis* as processing food in the manner of a "batch reactor" by bolting food rapidly and unselectively and storing it in its extendible hindgut for later slow digestion. Its capacity to withstand long periods of starvation is also an adaptation to infrequent food supplies. Such strategies are of high value in a food-limited environment (Smith & Baldwin 1982). The ecological niche these species occupy includes adaptations to a feeding strategy based on large meals taken at more-or-less long time intervals and randomly dispersed over vast areas (Dahl 1979).

When addressing the issue of possible obligate marine scavengers, lyssianid amphipods stand out as potential candidates (Kaiser & Moore 1999; Ruxton & Houston 2004). Reviewing the literature on scavengers in the North Sea area, Kaiser & Moore (1999) suggested that *O. manus* could be an obligate scavenger of crustacean carrion. In the North Sea this species is, with *S. hopei*, associated mainly with the consumption of fish. In the system we studied, *O. manus* is not present and *S. hopei* consumes both fish and decapods. Although decapods were not used as bait in our experiments, information could be obtained from another study conducted in the same area. Live *N. norvegicus* were put into closed cages divided into individual cells for periods of over 5 days to study their survival (Castro et al. 2003). When the cages were retrieved, all soft tissues of the dead *Nephrops* were completely clean, and some *S. hopei* were occasionally found inside the carapaces of dead *Nephrops*.

The hypothesis that the small scavengers are important links between discards and fish and crustaceans, including the target species of the fishery, was confirmed by the presence of *N. borealis* and *S. hopei* in the stomachs of fish from a region adjacent to the area where the traps were placed. It is suggested that a major potential impact of discards is the favouring of higher biomasses of small scavengers. They, in turn, are part of the diet of other organisms in higher levels of the flood chain, including fish and decapods of commercial interest that are targeted by the fishery that produces the discards. Some of the species that may have important indirect benefit from discarding identified in this study are *P. longirostris*, *N. norvegicus* (the main target species of crustacean trawling in the area of the study), the scorpaenidae *Helicolenus dactylopterus*, *C. monstrosa*, *N. sclerorhynchus*, *P. blennoides*, and *P. henslowii*. Another study of the diets of 33 deep water fish species in southern Portugal (Saldanha et al. 1995), undertaken in the same general area of our study (fish caught from 498 to 740 m) showed that amphipods and isopods (species not identified) were part of the diets of nine species: *Galeus melastomus*, *Raja clavata* and *Raja montaguii*, *C. monstrosa*, *Argyroplecus aculeatus*, *Notacanthus bonapartei*, *Capros aper*, *Hoplostethus mediterraneus*, and *Benthosdesmus elongatus*. Amphipods were more common than isopods (in seven and four species respectively). Bozzano & Sardá (2002) also suggest that the same species of small scavengers found in our study may be the source of food for other species, as they observed *N. norvegicus* feeding in the area where the bait was when *N. borealis* was present.

In conclusion it is suggested that discards have an important impact in the structuring of deep water systems, in particular when trawling occurs in these areas. Large amounts of matter are removed from the system and returned in the form of dead fish and invertebrates, providing unnatural sources of food to bottom scavengers. The continuation of these practices may have favoured mainly small scavengers, not affected by the fishing gears, but with life history characteristics adapted to quick and efficient use of marine carrion. These species may therefore reach unusually high biomasses and be the prey of species at higher trophic levels. It is suggested that ecological models for systems such as the one studied here, should consider the recycling of the discards from commercial fishing.

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REFERENCES

Bergmann, M.; Wieczorek, S. K.; Moore, P. G.; Atkinson, R. J. A. 2002: Utilisation of invertebrates discarded from the *Nephrops* fishery by various selective benthic scavengers in west Scotland. *Marine Ecology Pregress Series 233*: 185–198.

Borges, T. C.; Erzini, K.; Bentes, L.; Costa, M. E.; Gonçalves, J.; Lino, P. G.; Pais. C.; Ribeiro, J. 2001: By-catch discarding practices in five Algarve (southern Portugal) métiers. *Journal of Applied Ichthyology 17*: 104–114.

Bozzano, A.; Sardà, F. 2002: Fishery discard consumption rate and scavenging activity in the northwestern Mediterranean Sea. *ICES Journal of Marine Sciences 59*: 15–28.

Britton, J. C.; Morton, B. 1994: Marine carrion and scavengers. *Oceanography and Marine Biology: An Annual Review 32*: 369–434.

Castro, M.; Araújo, A.; Monteiro, P.; Madeira, A. M.; Silvert, W. 2003: The efficacy of releasing caught *Nephrops* as a management measure. *Fisheries Research 65*: 475–484.

Dahl, E. 1979: Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. *Oikos 33*: 167–175.

Dayton, P. K.; Hesser, R. R. 1972: Role of biological disturbance in maintaining diversity in the deep sea. *Deep Sea Research 19*: 199–208.

Erzini, K.; Costa, M. E.; Bentes, L.; Borges, T. C. 2002: A comparative study of the species composition of discards from five fisheries from the Algarve (southern Portugal). *Fisheries Management and Ecology 9*: 31–40.

Erzini, K.; Monteiro, P.; Araújo, A; Castro, M. 2003: Limited mid-water scavenging of trawl discards. *Journal of the Marine Biological Association of the U. K. 83*: 731–734.

Fonds, M.; Groenewold, S. 2000: Food subsidies generated by beam-trawl fishery in the southern North Sea. *In*: Kaiser, M. J.; de Grost, S. J. *ed.* Effects of fishing on non-target species and habitats: biological conservation and socio-economic issues. Oxford, Blackwell Science Ltd. Pp. 130–150.

Groenewold, S.; Fonds, M. 2000: Effects on benthic scavengers of discards and damaged benthos produced by beam-trawl fishery in the southern North Sea. *ICES Journal of Marine Sciences 57*: 1395–1406.

Hall, S. J. 1999: The effects of fishing on marine ecosystems and communities. Oxford, Blackwell Science Ltd. 273 p.

Hill, B. J.; Wassenberg, T. J. 1990: Fate of discards from prawn trawlers in Torres Strait. *Australian Journal of Marine and Freshwater Research 41*: 53–64.

Kaiser, M. J.; Moore, P. G. 1999: Obligate marine scavengers: do they exist? *Journal of Natural History 33*: 475–481.

Laptikhovsky, V.; Fetisov, A. 1999: Scavenging by fish of discards from the Patagonian squid fishery. *Fisheries Research 41*: 93–97.

Monteiro, P. A.; Araujo, A.; Erzini, K.; Castro, M. 2001: Discards of the Algarve (southern Portugal) crustacean trawl fishery. *Hydrobiologia 449*: 267–277.

Nickell, T. D.; Moore, P. G. 1991: The behavioural ecology of epibenthic scavenging invertebrates in the Clyde Sea area: field sampling using baited traps. *Cahiers Biologie Marine 32*: 353–370.

Ramsay, K.; Kaiser, M. J.; Moore, P. G.; Hughes, R. N. 1997: Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. *Journal of Animal Ecology 66*: 884–896.

Ruxton, G.; Houston, D. C. 2004: Energetic feasibility of an obligate scavenger. *Marine Ecology Progress Series 266*: 59–63.

Saldanha, L.; Almeida, A.; Andrade, F.; Guerreiro, J. 1995: Observations on the diet of some slope dwelling fishes of Southern Portugal. *Hydrobiologia 80*: 217–234.

Sheridan, P. F.; Browder, J. A.; Powers, J. E. 1984: Ecological interactions between penaeid shrimp and bottomfish assemblages. *In*: Gulland, J. A.; Rothschild, B. J. *ed.* Penaeid Shrimps—their biology and management. Selected papers presented at the workshop on the scientific basis for the management of penaeid shrimp held at Key West, Florida, United States, November 1981. Fishing News Books Limited. Pp. 235–254.

Smith, C. R. 1985: Food for the deep sea: utilization, dispersal and flux of nekton falls at the Santa Catalina Basin floor. *Deep-sea Research 32*: 417–442.

Smith, K. L.; Baldwin, R. J. 1982: Scavenging deep-sea amphipods: effects of food odor on oxygen consumption and a proposed metabolic strategy. *Marine Biology 68*: 287–298.

Snedecor, G. W.; Cochran, W. G. 1980: Statistical methods. The Iowa State University Press. 507 p.

Stockton, W. L.; DeLaca, T. E. 1982: Food falls in the deep sea: occurence, quality and significance. *Deep-sea Research 29*: 157–169.

Wassenberg, T. J.; Hill, B. J. 1987: Feeding by the sand crab *Portunus pelagicus* on material discarded from prawn trawlers in Moreton Bay, Australia. *Marine Biology 95*: 387–393.

Wong, Y. M.; Moore, P. G. 1995: Biology of feeding in the scavenging isopod *Natalolana borealis* (Isopoda: Cirolanidae). *Ophelia 43*: 181–196.

Yamamura, O. 1997: Scavenging on discarded saury by demersal fishes off Sendai Bay, northern Japan. *Journal of Fish Biology 50*: 919–925.

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Increased predation of juvenile European spiny lobster (*Palinurus elephas*) in a marine protected area

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Abstract One of the aims of Mediterranean marine protected areas (MPAs) is to increase populations of exploited species, such as the European spiny lobster (*Palinurus elephas*), which is considered a key species for its commercial and ecological value. Monitoring of temporal patterns in abundance of early benthic stages of *P. elephas* indicated that predation may be higher inside the Medes Islands MPA relative to adjacent control sites. Tethering experiments were performed to test whether predation rates actually differed within and outside the MPA. Relative mortality of recently-settled juveniles inside the MPA was much higher than in control sites in adjacent non-protected areas. Treatments with and without shelter indicated that predation on recently-settled juvenile spiny lobsters was moderated by the availability of suitable shelter. The decline or absence of fish predators in the fished area may be the reason why juvenile lobsters outside the MPA experience lower predation than within the MPA.

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INTRODUCTION

Overfishing is a source of concern in many regions of the world because of probable impacts on future harvests of marine resources (Dayton et al. 1995). Marine protected areas (MPAs) have been proposed as a management option to counteract this problem through the simultaneous protection of a portion of the population of numerous exploited species (Dugan & Davis 1993; Lleonart & Maynou 2003). In the Mediterranean Sea, MPAs have been created with a diverse set of objectives including the protection of threatened species and for proposed benefits to fishery resources (Goñi et al. 2000). Among the fishery resources that this management measure is intended to target is that of the European spiny lobster *Palinurus elephas* (Fabricius, 1787).

The effectiveness of MPAs for increasing the abundance of exploited species within their boundaries has been demonstrated in numerous studies. Thus, several studies of coastal rocky areas have shown that piscine predators of fish and invertebrates become more abundant inside MPAs following cessation of fishing (Bell 1983; Francour 1994; Harmelin et al. 1995). Predation is a crucial structural factor in marine communities (Brooks & Dodson 1965), so it may be expected that this change in abundance of exploited predators will induce further change in the community structure inside MPAs. Planes et al. (2000) have previously noted that the increase in predators within European MPAs could act to reduce survival of some species inside MPAs, as similarly reported by Shears & Babcock (2002) and McClanahan & Shafir (1990). In the Medes Island MPA, the population of *P. elephas* has not followed a pattern of population increase. On the contrary, a substantial decline in lobster abundance has been detected over the last 10 years (Marí et al. 2002). We investigated the possible role of predation in this decline.

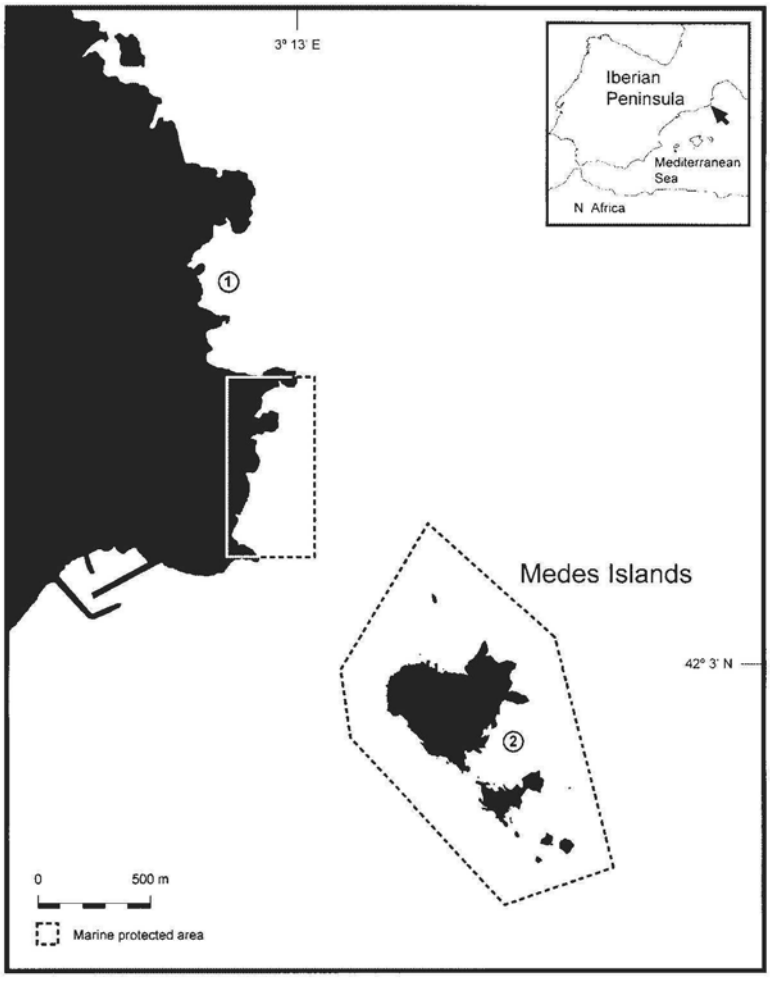

Fig. 1 Map of the Mediterranean region (inset) with Montgrí Coast and MPA (Medes Islands Marine Protected Area) shown expanded. Sites used for tethering experiments are marked with numbers: 1, Negre del Falaguer (non-MPA site); and 2, Cova de la Reina (MPA site).

Predation risk is generally considered to be applied unevenly throughout the development of individuals with periods of heightened or reduced risk. The early benthic phases must overcome critical periods of high predation, which often constitute a bottleneck in the recruitment (Gaines & Roughgarden 1987; Smith & Herrnkind 1992). During periods of high predation, the availability of shelter becomes especially crucial and can have a great influence on survival (Herrnkind & Butler 1986; Wahle & Steneck 1991).

Juvenile *P. elephas* have precise habitat preferences during the period following settlement and preferably occupy the empty holes bored by date mussels (*Lithophaga lithophaga*) in limestone rocky areas (Díaz et al. 2001). When the size of juveniles increases to c. 25 mm carapace length (CL) this type of shelter becomes unsuitable and the behaviour becomes more gregarious, gathering mainly in crevices (Díaz et al. 2001). In other spiny lobster species, such as *Panulirus argus*, this shift in behaviour and habitat with increasing size has been linked to a change in the mortality of the juvenile phases (Eggleston et al. 1990). Habitat availability thus has the potential to alter natural mortality rates between sites, although this effect would be expected to alter as lobsters grow through different sizes.

Research presented here examined the effect of potentially elevated predation risk in a MPA on recently-settled juveniles of *P. elephas* using tethering experiments inside and outside the MPA. Although this technique elevates mortality so that absolute values of mortality are biased, the technique does allow comparison of relative predation between treatments such as inside and outside MPAs (Zimmer-Faust et al. 1994). The key hypothesis

examined was: does the predation rate of juvenile lobsters differ between sites inside and outside MPAs? Where a difference was detected, we then attempted to examine the effect of shelter availability on the survival of the individuals.

MATERIAL AND METHODS

Study area

The study was carried out in the Medes Islands Marine Reserve (north-east Spain, north-west Mediterranean Sea) close to the village of L'Estartit (42°03′N 3°12′E). The MPA encompasses a small group of islands c. 1.5 km off the coast plus a small part of the mainland with total area of 93.2 ha (Fig. 1). Fishing has been forbidden since 1991 in the central core of this MPA although non-extractive recreational activities are allowed and are extensive, with over 100 000 divers per year. The high frequency of recreational diving in the Medes Islands MPA was a potential source of bias to this study because of the acclamation of large fish predators and damage to the sessile community (Garrabou et al. 1998). To minimise this bias we selected sites within the MPA well separated from the moorings used by recreational divers.

Two sites were selected to perform the tethering experiments: Negre del Falaguer (control site outside the MPA) and Cova de la Reina (within the MPA). All experiments were made in September 2002, after the well-defined window of settlement that takes place from June to August, peaking in July (Díaz et al. 2001). Juvenile densities are highest between 10 and 15 m depth. These sites were close to each other (2.5 km) and allowed divers to move between the sites rapidly so that all separate experiments were conducted within a day of each other. Both sites presented a similar geomorphological and ecological habitat with flat rubble reef and large boulders (>2 m height) with a mean depth of 11.6 ± 0.5 m. Upper surfaces of boulders were covered by a photophilic community dominated by brown algae (*Dictyota dichotoma*, *Padina pavonica*, and *Halopteris scoparia*) and red algae (*Corallina elongata*, *Jania corniculata*, and *Haliptilon virgatum*). On the sides of boulders, with inclination up to 45°, the dominant community was sciaphilous with little algal cover (Ros et al. 1989). The tethered animals were placed along the sides of the boulders where the densities of *L. lithophaga* were 124 ± 54 holes/m^2. The two sites were selected for similarity in the algal community and the physical environments of wave exposure and depth (10–15 m). Crucially, previous research had indicated that natural settlement levels were generally equivalent at the two sites (Díaz et al. 2001). Present surveys and experiments have been performed in the same study area as in Díaz et al. (2001).

Experimental design

Following preliminary testing, juveniles were tethered by slipknot between the carapace and the abdomen using nylon monofilament of 0.25 mm diam. and 2.6 kg breaking strength. Each tether was then attached to a base line. The effect of this system on natural movement and foraging of juveniles was checked by holding 12 tethered individuals of different sizes (13–23 mm CL) in a tank with several diameters of pipes as shelters to mimic the natural shelters of *L. lithophaga* holes. Behaviour was recorded for 24 h in natural photoperiod by a video camera with infrared illumination. Individuals sheltered and foraged with no apparent effect from the tether and no individual was able to escape from the tether.

All the individuals used in experiments were captured from the wild by divers one day before the experiment and maintained in holding facilities at the temperature and salinity found in the capture area. Juveniles were checked during this time for vitality and also measured (CL) and tethered with an individual number.

To compare the relative predation inside and outside the MPA we tethered 120 recently-settled juveniles (60 in each site). In each experimental site, six permanent transect lines were installed, each 15 m long, to which were attached 10 individuals. In all instances, the distance between individuals was greater than 1 m.

To test the effect of availability of shelter, each transect line had five individuals tethered by a short line (20 cm) in a region where no natural shelter (empty *L. lithophaga* holes) was available, whereas the remaining five individuals were tethered by a long line (1 m) so that they had easy access to natural shelters. The tether line did not prevent the individuals from using the shelters. We also made sure that all individuals having access to shelter were indeed using it. Each survey comprised six replicates.

Experiments started at 1900 h and ran for 24 h. All animals were checked at 0700 h the following day, with records taken of all the individuals eaten. These were replaced with new individuals at the same time. The last survey was at 1900 h of the same

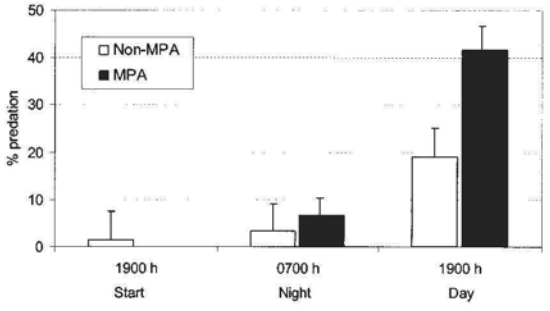

Fig. 2 Predation of early juvenile phases of *Palinurus elephas* at release and subsequent surveys at 12 and 24 h inside the marine protected area (MPA) (black columns) and outside MPA (white columns). Error bars are standard error of mean percentage mortality.

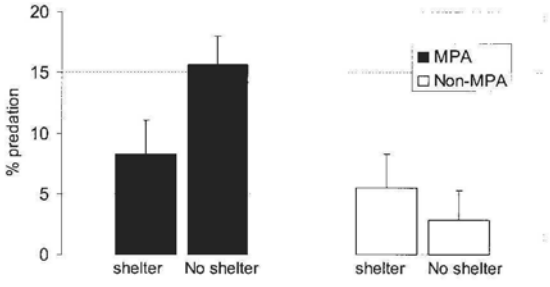

Fig. 3 Percentage mortality of early juvenile phases of *Palinurus elephas* as a function of access to shelter. Longer tether lines were used to simulate the capacity to find an optimal shelter whereas shorter tethers were used to restrict juveniles to regions of boulders where the surface was without holes. Bars show standard error of mean percentage mortality.

day. These experiments were repeated at the two sites within a day of each other.

The main predators of *P. elephas* in this region are the following finfish: *Scorpaena scrofa*, *Scorpaena porcus*, *Epinephelus marginatus*, *Serranus cabrilla*, and *Diplodus sargus*, and the cephalopod *Octopus vulgaris* (Marin 1987; Quetglas et al. 2001; pers. obs.). Potential finfish predators were quantified by García-Rubies & Zabala (1990) and García-Rubies (1999) and were significantly more abundant inside the MPA than outside.

We note that tethering experiments as applied here have been the subject of analytical discussions by Aronson et al. (2001) who made several recommendations on the application of the method. Both sites were exposed to the same suite of possible predators, with the only difference being the density of predators which is higher within the MPA than outside, both in abundance and in sizes (García-Rubies & Zabala 1990; García-Rubies 1999). This has been estimated annually for over a decade during a monitoring survey carried out inside and outside the MPA (García-Rubies et al. 2002). Linehan et al. (2001) also recommended that the timing of experiments and the depth be standardised to minimise introduction of biases from these factors.

Densities of juvenile *P. elephas* were estimated by underwater visual censuses using the methodology described by Díaz et al. (2001), which consisted of three replicate transect lines 1 m wide overall encompassing 129 m^2 at 10–15 m depth on a calcareous limestone rocky area.

Analysis

Analysis followed the methods described by Acosta & Butler (1999) for the analysis of tethering data from *Panulirus argus*. Data collected through this study on the survival of individuals were square root-arcsin transformed to produce normality and homogeneity of variance (Sokal & Rohlf 1987). The effect of the MPA on survival was tested using a *t* test for dependent-sample analysis. To check the effect of sites and shelter we used contingency table analysis and chi-squared testing with the Yates correction. All the statistical analyses have been carried out by the statistical package Statistica (Statsoft 1998).

RESULTS

Effect of MPA

Natural levels of settlement were equivalent at the two sites, but the decline in density was greatest in the MPA. This was taken as evidence of higher predation in the protected area, and we sought to test this with the tethering experiment.

Predation on recently-settled *P. elephas* was very low during the night, both inside and outside the MPA, with maximum values of 6% and 3% respectively. Greatest mortality at both sites occurred during the day, indicating that most predators were visual, with a maximum of 41% of the individuals inside the MPA predated, relative to 19% outside (Fig. 2).

Mortality was significantly higher inside the MPA for the entire 24-h period with 41% mortality inside the MPA and 17% outside ($t = -3.51$, d.f. = 5, $P < 0.05$). During this survey, predation was only directly observed by one fish species—*Serranus cabrilla*.

Effect of shelter availability

The effect of shelter availability was tested using 120 individuals with two treatments for shelter (individuals with shelter available and individuals without shelter) at two sites (inside and outside MPA). Juveniles with shelter had a mortality rate of 23%, whereas those without shelter had a mortality rate of 35%.

Differences were not detected among the two treatments of shelter availability in either the non-MPA site (χ^2 Yates corrected = 0.37, d.f. = 1, $P = 0.54$) or the MPA site (χ^2 Yates corrected = 2.64, d.f. = 1, $P = 0.10$). For lobsters without shelter, there was significantly higher mortality inside the MPA than outside (χ^2 Yates corrected = 6.11, d.f. 1, $P = 0.01$), although no difference between sites was detected for animals with access to shelter (χ^2 Yates corrected = 0.09, d.f. = 1, $P = 0.766$; Fig. 3).

DISCUSSION

The effect of MPAs on the density and biomass of exploited species has been well documented with most exploited species increasing in abundance (García-Rubies & Zabala 1990; Dayton 2003; Gell & Roberts 2003). This can have subsequent ecological impacts such as increased predation on other components of the community (McClanahan & Shafir 1990; Sala & Zabala 1996; Shears & Babcock 2002). Direct field observations of changes in lobster populations following the creation of MPAs have generally detected an increase in lobster abundance and mean size (Cole et al. 1990; MacDiarmid & Breen 1992; Goñi et al. 2001). Occasionally the reverse is reported, with populations declining after MPAs are established, such as with the populations of *Jasus verreauxi* that declined in the King Poor Islands MPA 4 years after the establishment of the MPA (MacDiarmid 1991). In the Medes Islands MPA, a substantial decline (>50%) of lobsters in transect counts has been recorded over the last 10 years (Marí et al. 2002).

Present results show that no general assumption of equivalent survival of sublegal animals inside MPAs should be taken without specific studies, since reduced juvenile survival within a MPA may well take place relative to outside the MPA because of differential predation. The reduced survival detected within the MPA in the present study appeared to be attributable to higher rates of predation from visual finfish which show higher abundance inside the MPA following protection from fishing (García-Rubies & Zabala 1990; García-Rubies 1999). The decline or absence of fish predators in the fished area outside the MPA may well be the reason why recently-settled spiny lobsters experience lower predation outside the MPA.

This effect of differential predation may constitute one of the mechanisms for the observed decline of lobsters in the Medes Islands MPA over the last 10 years (Marí et al. 2002). However, other factors are also likely to have contributed to this effect. Although *P. elephas* typically has low mobility (Goñi et al. 2003), individuals can forage beyond the boundaries of the MPA and thus become vulnerable to capture by fishers. Fishers have gained improved understanding of seasonal patterns in movement across boundaries in other MPAs, which has resulted in a reversal of previous stock rebuilding (McDiarmid & Breen 1992) and similarly may be occurring at the Medes Islands MPA. Commercial fishing along the boundaries of Spanish MPAs for *P. elephas* is often intense and would be expected to reduce abundance at least along the edges of the MPAs (Goñi et al. 2001). Other possible factors contributing to the observed decline may include poaching and disturbance by increased levels of recreational scuba diving.

Within the Medes Islands MPA, where finfish are larger and present higher densities and biomass than outside the MPA (García-Rubies & Zabala 1990; García-Rubies 1999; Macpherson et al. 2002), we observed higher mortality of juvenile *P. elephas* that did not have access to shelters relative to those that had. Lack of appropriate or optimal shelter appeared to be less crucial in the non-MPA site where fish density was lower.

Juvenile *P. elephas* use *L. lithophaga* holes and previous research has shown that the abundance of this habitat is essential for the success of settlement (Díaz et al. 2001). Results presented here suggest that the mechanism for the observed relation between availability of *L. lithophaga* holes and densities of juvenile *P. elephas* (Díaz et al. 2001) may well be predation by visual finfish, which is relatively reduced outside the MPA because of human exploitation and disturbance. The nature of the geological substratum influences the ability of *L. lithophaga* to

bore holes and thus the availability of their burrows to *P. elephas*. Accordingly, the abundance of recently-settled *P. elephas* has been found to be up to 10 times lower in metamorphic substrate areas than in adjacent "optimal" limestone areas (Díaz et al. 2001). Where shelter plays a crucial role in the recruitment of lobsters, geological type has the potential to create a bottleneck to recruitment (Howard 1988; Wahle & Steneck 1991). This implies that the geological nature of the substratum should be considered when planning spatial management methods such as the creation of MPAs if fisheries benefits to *P. elephas* are desired.

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REFERENCES

Acosta, C. A.; Butler, M. J. IV 1999: Adaptive strategies that reduce predation on Caribbean spiny lobster post-larvae during onshore transport. *Limnology and Oceanography 44(3)*: 494–504.

Aronson, R.; Heck, K. L.; Valentine, J. F. 2001: Measuring predation with tethering experiments. *Marine Ecology Progress Series 214*: 311–312.

Bell, J. D. 1983: Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage on the north-western Mediterranean Sea. *Journal of Applied Ecology 20*: 357–369.

Brooks, J. L.; Dodson, S. I. 1965: Predation, body size and composition of zooplankton. *Science 150*: 28–35.

Cole, R. G.; Ayling, T. M.; Creese, R. G. 1990: Effects of marine reserve protection at Goat Island, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research 24*: 197–210.

Dayton, P. K. 2003: The importance of the natural sciences to conservation. *The American Naturalist 162(1)*: 1–13.

Dayton, P. K.; Thursh, S. F.; Agardy, M. T. 1995: Environmental effects of marine fishing. *Aquatic Conservation Marine Freshwater Ecosystems 5*: 205–232.

Díaz, D.; Marí, M.; Abelló, P.; Demestre, M. 2001: Settlement and juvenile habitat of the European spiny lobster *Palinurus elephas* (Crustaceana: Decapoda: Palinuridae) in the western Mediterranean Sea. *Scientia Marina 65(4)*: 347–356.

Dugan, J. E.; Davis, G. E. 1993: Applications of marine harvest refugia to coastal fisheries management. *Canadian Journal of Fish and Aquatic Science 50*: 2029–2042

Eggleston, D. B.; Lipcius, R. N.; Miller, D. C.; Coba-Cetina, L. 1990: Shelter scaling regulates survival of juvenile spiny lobster *Panulirus argus*. *Marine Ecology Progress Series 62*: 79–88.

Francour, P. 1994: Pluriannual analysis of the reserve effect on icthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). *Oceanologica Acta 17*: 309–317.

Gaines, S. D.; Roughgarden, J. 1987: Fish in offshore kelp forest affect recruitment of intertidal barnacle populations. *Science 235*: 479–481.

García-Rubies, A. 1999: Effects of fishing on community structure and on selected populations of Mediterranean coastal reef fish. *Naturalista Siciliano 23 (Suppl.)*: 59–81.

García-Rubies, A.; Zabala, M. 1990: Effects of total fishing prohibition on the rocky assemblages of Medes Islands marine reserve (NW Mediterranean). *Scientia Marina 54(4)*: 317–328.

García-Rubies, A.; Hereu, B.; Zabala, M. 2002: Estudi de la població de neros de les Illes Medes i altres especies de peixos vulnerables. *In*: Zabala, M. *ed.* Evolució del patrimoni natural de les Illes Medes. Direcció General de Pesca Marítima, Generalitat de Catalunya Technical Report. Pp. 70–103.

Garrabou, J.; Sala, E.; Arcas, A.; Zabala, M. 1998: The impact of diving use on marine rocky sublittoral communities: a case study of a Mediterranean bryozoan population. *Conservation Biology 12*: 1–12.

Gell, F. R.; Roberts, C. M. 2003: Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution 18(9)*: 448–455.

Goñi, R.; Polunin, N. V. C.; Planes, S. 2000: The Mediterranean: marine protected areas and the recovery of a large marine ecosystem. *Environmental Conservation 27(2)*: 95–97.

Goñi, R.; Reñones, O.; Quetglas, A. 2001: Dynamics of a protected Western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap survey. *Marine and Freshwater Research 52*: 1577–1587.

Goñi, R.; Reñones, O.; Quetglas, A. 2003: Size maturity, fecundity and reproductive potential of a protected population of the spiny lobster *Palinurus elephas* (Fabricius, 1787) from the western Mediterranean. *Marine Biology 143*: 583–592.

Harmelin, J. G.; Bachet, F.; Garcia, F. 1995: Mediterranean marine reserves: fish indices as test of protection efficiency. *Marine Ecology Pubblicazioni Della Stazione Zoologica Di Napoli 16*: 233–250.

Herrnkind, W. F.; Butler, M. J. IV 1986: Factors regulating post-larval settlement and juvenile microhabitat use by spiny lobster *Panulirus argus*. *Marine Ecology Progress Series 34*: 23–30.

Howard, R. K. 1988: Fish predators of the western rock lobster (*Panulirus cygnus* George) in a nearshore nursery habitat. *Australian Journal of Marine Freshwater Research 39*: 307–316.

Linehan, J. E.; Gregory, R. S.; Schneider, D. 2001: Predation risk of age–0 cod (Gadus) relative to depth and substrate in coastal waters. *Journal of Experimental Marine Biology and Ecology 263*: 25–44.

Lleonart, J.; Maynou, F. 2003: Fish stock assessments in the Mediterranean: state of the art. *Scientia Marina* 67 *(Suppl. 1)*: 37–49.

MacDiarmid, A. B. 1991: Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus edwardsii* on a coastal reef in northern New Zealand. *Marine Ecology Progress Series 70*: 129–141.

MacDiarmid, A. B.; Breen, P. A. 1992: Spiny lobster populations change in a marine reserve. Proceedings of the second International Temperate Reef Symposium. *In*: Battershill, C. N.; Shield, D. R.; Jones, G. P.; Creese, R. G.; MacDiarmid, A. B. *ed*. Wellington, New Zealand, NIWA Marine. Pp. 44–56.

Macpherson, E.; Gordoa, A.; García-Rubies, A. 2002: Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. *Estuarine Coastal and Shelf Science 55*: 777–788.

Marí, M.; Díaz, D.; Abelló, P.; Zabala M. 2002: Avaluació temporal de les poblacions de llagosta (*P. elephas*) en les Illes Medes. *In*: Zabala M. *ed*. Evolució del patrimoni natural de les Illes Medes. Technical Report: Direcció General de Pesca Marítima, Generalitat de Catalunya. Pp. 62–69.

Marin, J, 1987. Exploitation, biologie et dynamique du stock de langouste rouge de Corse *Palinurus elephas* Fabricius. Unpublished PhD thesis, Université d'Aix Marseille II, Faculté des sciences de Luminy, France.

McClanahan, T. R.; Shafir, S. H. 1990: Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia 83*: 362–370.

Planes, S.; Galzin, R.; García Rubies, A.; Goñi, R.; Harmelin, J.-G; Le Diréach, L.; Lenfant, P.; Quetglas, A. 2000: Effects of marine protected areas in recruitment processes with special references to Mediterranean littoral ecosystems. *Enviromental Conservation 27(2)*: 126–143.

Quetglas, A.; Reñones, R.; Goñi, R. 2001: Trophic interactions among grouper (*Epinephelus marginatus*), octopus (*Octopus vulgaris*) and the red lobster (*Palinurus elephas*) in the western Mediterranean. *Rapports Comisión Internationale pour l' Exploration Scientifique de la Mer Mediterranée 36*. 310 p.

Ros, J.; Romero, J.; Ballesteros, E.; Gili, J. M. 1989: Buceando en aguas azules. El bentos. Chapter. 8. *In*: Margalef, R. *ed*. El Mediterráneo Occidental. Omega. Pp. 1–357.

Sala, E.; Zabala, M. 1996: Fish predation and the strucure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series 140*: 71–81.

Shears, N. I.; Babcock, R. I. 2002: Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia 132*: 131–142.

Smith, K. N.; Herrnkind, W. F. 1992: Predation on early juvenile spiny lobsters *Panulirus argus* (Latraille): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology 157*: 3–18.

Sokal, R. R.; Rohlf. F. J. 1987: Biometry. New York, W.H. Freeman & Co.

StatSoft, Inc. 1998: Statistica for Windows. Tulsa, OK, United States, StatSoft Inc.

Wahle, R. A.; Steneck, R. S. 1991: Recruitment habitats and nursery grounds of the American lobster *Homarus americanus* a demography bottleneck? *Marine Ecology Progress Series 69*: 231–243.

Zimmer-Faust, R. K.; Fielder, D. R.; Heck, K. L. Jr; Coen, L. D.; Morgan, S. G. 1994: Effects of tethering on predatory escape by juvenile blue crabs. *Marine Ecology Progress Series 111(3)*: 299–303.

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Use of fishery-dependent data for the evaluation of depensation: case study involving the predation of rock lobster (*Jasus edwardsii*) by octopus (*Octopus maorum*)

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Abstract The relationship between the level of octopus (*Octopus maorum*) predation and the daily-average number of lobsters (*Jasus edwardsii*) per pot was investigated using commercial catch statistics. Octopus predation was found to be inversely correlated with lobster catches, such that, lobsters experienced reduced survival when their daily-average density in a pot was lower. The reduction in survival at lower densities provides evidence for a depensatory mechanism underlying the predator-prey interaction between pot-caught octopus and lobster. The effect of lobster density on the feeding response of octopus is unknown so this study could not determine whether depensation was brought about by either predator saturation or predator avoidance tactics used by lobsters. The use of commercial catch statistics to investigate this depensatory effect has disadvantages because the lobster mortality estimates can be biased by the non-reporting of undersized lobsters caught inside pots, under-reporting of lobsters killed by octopus, the inability to identify unsuccessful predation attempts made by octopus, and the ability of some lobsters to escape from pots. All the sources of bias would tend to make it difficult to conclusively determine both the absolute proportion of lobsters killed by octopus and the true scale of the depensatory mortality, as the scale of the mortality may be greater than the commercial data suggest. However, the bias will not necessarily reduce our ability to detect the depensatory effect if, as seems likely, the sources of bias are relatively constant across the range of daily-average catches. Depensation in crustacean stocks affected by pot-related octopus predation has been rarely studied, and, because depleted stocks lead to fewer lobsters being caught per pot, such depensatory mortality has implications for the population dynamics and management of crustacean stocks.

Keywords depensation; *Jasus edwardsii*; predator-prey interaction; octopus predation; depensatory mortality

INTRODUCTION

Identifying the processes affecting a population and the mechanisms driving such processes is crucial to understanding population dynamics (Leonardson 1994; Cappuccino & Price 1995). Processes that reduce population growth at lower abundances (e.g., decreased survival, growth, and reproduction) are referred to as inverse density-dependent or depensation (Liermann & Hilborn 2001). Depensatory processes tend to destabilise populations, as species subjected to a strong depensation effect may be more susceptible to catastrophic population collapses. The increasing importance of managing and conserving populations has raised awareness of the role depensatory processes play in the conservation and recovery of populations (Courchamp et al. 1999).

Depensatory mortality is observed in populations with decreased survival at low population abundances. The mechanisms driving depensatory mortality restrict the level of mortality at higher prey densities through either predator saturation or predator avoidance tactics arising from group living of prey. Predator saturation arises from feeding constraints (e.g., handling time, gut capacity, and

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digestion) placed on predators which restrict the number of prey killed during a given time. This type of feeding relationship is commonly referred to as a type II functional response (Holling 1959). A number of studies support predator saturation as a depensatory mechanism by demonstrating that the rate of mortality increased at low prey densities, then decreased due to feeding constraints (Ruggerone & Rogers 1984; Fresh & Schroder 1987; Dittel et al. 1995).

It is well documented that group living and aggregative behaviour can play an important role in preventing predation of individuals (Pulliam 1973; Treisman 1975; Pulliam & Caraco 1984; Pitcher & Parrish 1993). In a group, an individual's risk of predation may be reduced through the: "dilution and selfish-herd effect" (Hamilton 1971; Vine 1971; Bertram 1978), "encounter effect" (Taylor 1977; Turner & Pitcher 1986; Wrona & Dixon 1991), "confusion effect" (Welty 1934; Landeau & Terborgh 1986; Schradin 2000), and "group-defence effect" (Milinski 1977; Bowyer 1987; Herrnkind et al. 2001). It was demonstrated that the number of prey killed increased with prey density up to a threshold level and then declined at higher prey densities as a result of the confusion effect (Welty 1934; Williamson 1984) and the group-defence effect (Mori & Chant 1966; Tostowarky 1972). These effects give rise to a dome-shape functional response, which is referred to as a type IV response.

The confusion effect occurs when predators have difficulty in capturing prey surrounded by other individuals, whereas the group-defence effect arises when the members of an aggregation collectively defend themselves against predators. It is possible that the protective advantage of group-defence may depend on both the number and size of individuals in the group. Body size can often influence predator-prey interactions strongly (Paine 1976; Osenberg & Mittelbach 1989) because size can influence whether the individual is selected by the predator. Detailed information on the influence prey size has on existence and scale of the depensatory mortality is scarce. Size-dependent mortality may potentially mask the existence of depensatory mortality depending on the influence body size has on an individual's risk of being captured.

Little detailed information exists on the affect lobster size has on reducing the risk of octopus (*Octopus maorum* Hutton 1880) predation, however is considered to be an opportunistic predator that preys on crustaceans, bivalve molluscs, and any fish that can be captured (Anderson 1999). It is unknown if the feeding response of octopus becomes saturated. There is empirical evidence that the group-defence effect may influence the feeding response of octopus as spiny lobsters (*Jasus edwardsii* Hutton 1875) have the ability to fend off predators—as aggregating lobsters collectively use their antenna to defend against predators (Cobb 1981; Zimmer-Faust & Spanier 1987). Bulter et al. (1999) found that aggregations increased the survival of larger lobsters as opposed to smaller lobsters. Octopus may also suffer from the confusion effect, as Neill & Cullen (1974) found that cephalopod find it difficult to capture a single prey from a group if it is surrounded by other moving conspecifics. This possibility is supported by the tendency of lobsters to create confusion for predators by maintaining a cohesive group while under attack (Milinski 1977).

Identifying the mechanisms that may lead to depensatory processes is important. However, identifying the depensatory mechanisms does not necessarily imply the dynamics of a population are depensatory. Often there is little evidence that any depensation is strong enough to be important in a population's dynamics (Liermann & Hilborn 2001). Detecting populations with depensatory dynamics is difficult because other non-depensatory factors (e.g., temperature, depth, and predator numbers) may act on the population processes and possibly prevent the depensatory mechanism coming into play. Contributing to the difficultly is the constraint that the species has to be at a low abundance level. Understanding the recovery dynamics of the species may be one way of establishing the importance of depensation to the population.

The implications of depensation are potentially very important to fisheries management, in particular, to the management of crustacean fisheries affected by pot-related octopus predation. Many crustacean fisheries around the world are significantly affected by octopus predation occurring inside commercial fishing pots (Garstang 1900; Rees & Lumby 1954; High 1976; Brock 2000). However, the affect that this pot-related octopus predation has on crustacean stock dynamics has rarely been studied. In this study, we test for depensatory mortality in the Tasmanian rock lobster population by investigating the possibility of octopus killing a higher proportion of lobster in pots when lobster catches per pot are lower. We investigate the reporting of lobsters killed by octopus within the fishery and its affect on the demonstration of depensation.

The following questions are specifically addressed to test for the presence of depensatory

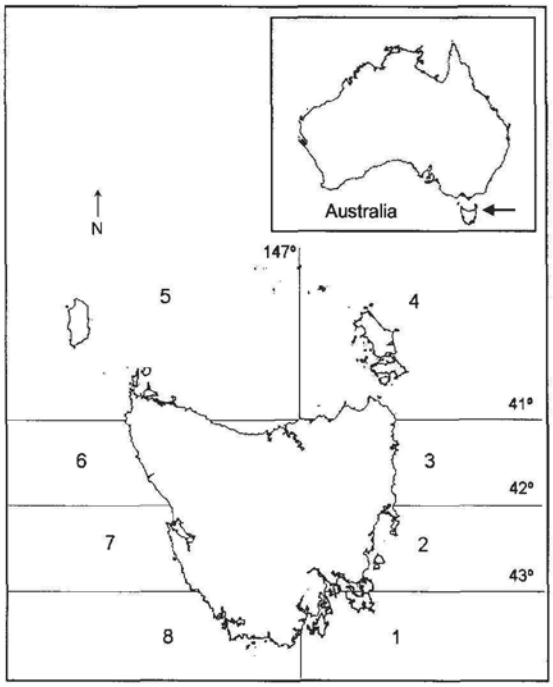

Fig. 1 Map of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia, showing the eight assessment regions.

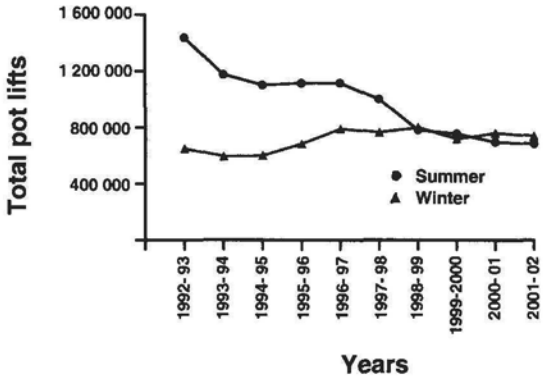

Fig. 2 Total pot lifts used in the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia, from 1992 to 2002 during summer and winter. Total winter effort now exceeds total summer effort.

mortality and to examine the affect that the temporal and spatial aspect of the predator-prey dynamics has on octopus predation. To what degree does octopus predation: (1) correlate with lobster catches (daily-average number of lobsters per pot); (2) vary in relation to lobster catches; and (3) vary temporally and spatially across the fishery in relation to lobster catches. Following these analyses, we discuss the bias affecting the relationship between octopus predation and lobster catches, the possible mechanisms influencing the interspecific interaction, and the importance of depensation in the management of crustacean stocks affected by pot-related octopus predation.

METHODS

Study area

The Tasmanian rock lobster fishery is divided into eight assessment regions (Fig. 1), which have widely different environmental characteristics. Fishing in the western regions tends to be in greater relative depths than in the eastern regions, and water temperature is warmer in the northern regions than the southern regions. Growth and sexual maturity of lobsters vary greatly around the fishery. An individual transferable quota system was introduced into the fishery in March 1998, which meant it changed to an output-controlled fishery based on a 1500 t total allowable catch. Limits on the total number of commercial pots used in the fishery and seasonal closures also remain in place.

Since the introduction of the quota system there has been a shift from summer dominated fishing to winter fishing, where the total winter effort now exceeds the total summer effort (Fig. 2). Total effort has declined with most of the reduction occurring from the summer period. In this study, the summer period is taken to extend from October to March and the winter period from April to September. The seasonal shift in effort is primarily owing to the higher selling prices of lobster during the winter months. The quota system has led to attempts at maximising the value of the catch instead of maximising the catch.

Study species

Jasus edwardsii and *O. maorum* are distributed across southern Australia and New Zealand. The commercial southern rock lobster fisheries in southern Australia are affected by octopus predation inside commercial pots (Brock 2004). It is not currently understood if the octopus predation rate of lobster is exacerbated by trapping the lobsters inside pots. Little information exists on the rate of predation outside of pots and lobsters are not always irrevocably trapped, as some lobsters have been observed

leaving pots through the main entrance (Green 2002).

Fishery dependent information

The commercial catch and effort data used in this study were obtained from daily lobster catch returns. The compulsory logbook returns enabled information to be accumulated on the catch and effort details of vessels (number of legal-sized lobsters caught, estimated weight, number of pot lifts, fishing block, depth strata, and the number of lobsters killed by octopus). The number of undersized lobsters caught inside the commercial pots was not recorded in the logbook, which acts to bias low the estimates of the number of lobsters per pot, that is, the daily-average catch. All commercial pots are equipped with escape gaps in an effort to reduce the capture of undersized lobsters.

The legal-sized and undersized lobsters killed by octopus inside the pots have been collectively recorded in the logbook since 1992, although whether all mortalities are actually reported is not known. The logbook information collected in 2003 was not included in this study owing to potential bias arising from the impact of the global outbreak of Severe Acute Respiratory Syndrome (SARS) on lobster catches in the fishery. Therefore, the study period extended from 1992 to 2002.

Reporting of octopus kills

The completeness of reporting of octopus kills in the fishery was investigated by determining whether the proportion of the logbook returns that recorded no octopus kills in each region of the fishery over the quota years from 1992 to 2002 remained relatively constant. The quota year extends from March until February of the following year. The simple equations used to calculate the values of interest in this study are provided in detail to remove the possibility of confusion. The proportion of the daily logbook returns that reported no lobsters killed by octopus was estimated using the equation:

$$w_{r,t} = \frac{c_{r,t}}{b_{r,t}} \quad (1)$$

where r indexes the region, t indexes period (a quota year or season depending on the analysis), $w_{r,t}$ is the proportion of daily logbook returns which reported no lobsters killed by octopus in region r during time-step t, $c_{r,t}$ is the number of daily logbook returns which reported no lobsters killed by octopus in region r during time-step t, and $b_{r,t}$ is the number of daily logbook returns in region r during time-step t.

Analysing the relationship between octopus predation and lobster catch per pot

Predation was characterised using the proportion of lobster killed in each pot by octopus. The proportion of lobsters killed measures the rate of octopus predation on lobster, that is, the kill rate per lobster/pot. Using the total number of lobsters killed to characterise predation would not be useful because the relationship between octopus predation and lobster catches would be confounded with the affects that changes in the number of pot lifts and lobster catches have on total lobster kills. Another way of characterising octopus predation could be through a kill rate per pot. However, this approach was not used because it fails to account for the influence that lobster numbers per pot have on octopus predation, which is essential in demonstrating the affect that lobster numbers have on depensatory mortality.

Individual pot information was not recorded in the fishery logbook, so the daily-average number of lobsters per pot had to be estimated for each vessel's daily logbook return before the relationship between octopus predation and lobster catches could be analysed. The daily-average lobster catch per pot was estimated using the equation:

$$d_i = \frac{v_i}{e_i} \quad (2)$$

where i indexes a single daily logbook record, d_i is the daily-average number of lobsters per pot for each daily record i, v_i is the total number of lobsters (live and killed by octopus) reported in daily record i, and e_i is the number of pot lifts reported in daily record i.

Analysing the seasonal and spatial variation in the predator-prey dynamics required the time-step of the analysis to be divided into a summer and winter component that used combined logbook information collected throughout the whole study period in each region during the respective season. The seasonal and spatial aspects of the predator-prey dynamics were analysed by comparing the proportion of lobsters killed by octopus in summer and winter in each region of the fishery in relation to the daily-average lobster catches. When the seasonal variation in the catch statistics was analysed across the regions for 12-month time-step, it required the summer information to be grouped across years (October–March of the following year), which meant the recorded quota year could not be used as it inaccurately represented the temporal partitioning of the information. However, the quota year was used when the seasonal variation in the statistics was not investigated.

Only the daily catch returns that recorded at least one lobster killed by octopus were used to estimate the mortality level. However, catch returns with zero kills do not mean that lobsters were not faced with the possibility of predation. Sometimes lobsters may not be killed because octopus are either more interested in the bait, or the grouping behaviour of lobsters may decrease killing success. Not accounting for these unsuccessful (zero) kills means the level of mortality will be biased upwards, especially at higher catches owing to the possibility of increased protection against predation. These unaccountable zero kills will tend to make the detection of depensation more difficult. The proportion of the returns with no reported octopus kills owing to unsuccessful killing attempts is unknown and difficult to estimate using non-visual underwater observations. Therefore, the catch returns with non-zero kills was used to estimate the proportion of lobsters killed by octopus using the equation:

$$p_{i,r,t} = \frac{k_{i,r,t}}{n_{i,r,t}} \quad (3)$$

where $p_{i,r,t}$ is the proportion of lobsters killed in daily record i in region r during time-step t, $k_{i,r,t}$ is the daily record i of the number of lobsters killed (greater than one) in region r during time-step t, and $n_{i,r,t}$ is the daily record i of the number of lobsters caught (live lobsters and lobsters killed by octopus) in region r during time-step t.

The daily records were categorised into groups of records with specific daily-average catches to estimate the average proportion killed in each density category. The daily-average catches, d_i, were grouped into a density category ranging from 0.05 to 5.95 lobsters per pot (with 0.1 increments), so if the daily-average catch was >0 and ≤0.1, then the record was grouped into a density category of 0.05. Similarly, if the daily-average catch was >0.1 and ≤0.2, then the record was grouped into a density category of 0.15. Within each category, the estimated proportions of lobsters killed were log-normal distributed, so the geometric average proportion killed for each density category was estimated using the equation:

$$a_{c,r,t} = \exp\left(\frac{\sum_{i=1}^{N_{c,r,t}} \mathrm{Ln}\left(p_{i,c,r,t}\right)}{N_{c,r,t}}\right) \quad (4)$$

where c indexes the density category, $a_{c,r,t}$ is the geometric average proportion of lobsters killed in density category c in region r during time-step t, $p_{i,c,r,t}$ is the ith observation of the proportion of lobsters killed in density category c in region r during time-step t, and $N_{c,r,t}$ is the total number of daily records relating to each density category, region, and time-step.

Testing for depensation

To test for depensation, a declining power function was fitted (using least squares) to the estimated proportion of lobsters killed, to determine if octopus predation declined significantly in relation to the increasing daily-average lobster catches. Multiplicative log-normal residual errors were assumed when fitting the power function. The correlation between both the daily-average catches and the proportion of lobsters killed and also the categorised densities and average proportion killed was estimated using linear regression.

The decline was modelled using the equation:

$$Y = ax^{-b}\, e^{\varepsilon} \quad (5)$$

where Y represents the proportion of lobsters killed by octopus during time-step t, b is the rate of change in octopus predation of lobster catches (related to the gradient of the curve), a is the expected level of octopus predation at a daily-average catch of one lobster, x either represents the daily-average catches or the categorised daily-average catches during time-step t, and ε is the normal residual error.

RESULTS

Reporting of octopus kills in the fishery logbook

Regions 1, 2, and 5 were the only regions where more logbook returns contained reports of octopus kills than no octopus kills (Fig. 3). Region 5 was the first region to have more than 50% of the logbook returns contained octopus kills, followed by regions 2 and 1. In the 2001/02 quota year, regions 3, 4, and 7 were approaching the point where more logbook returns contained reports of octopus kills than no octopus kills. The 1998/99 quota year corresponds to the period when the quota system was first introduced in the fishery. The proportion of the logbook returns which reported no octopus kills has continually decreased since around the 1998/99 quota year in all regions except regions 3, 4, and 5 which experienced a temporary increase in the proportion in the 2000/01 quota year.

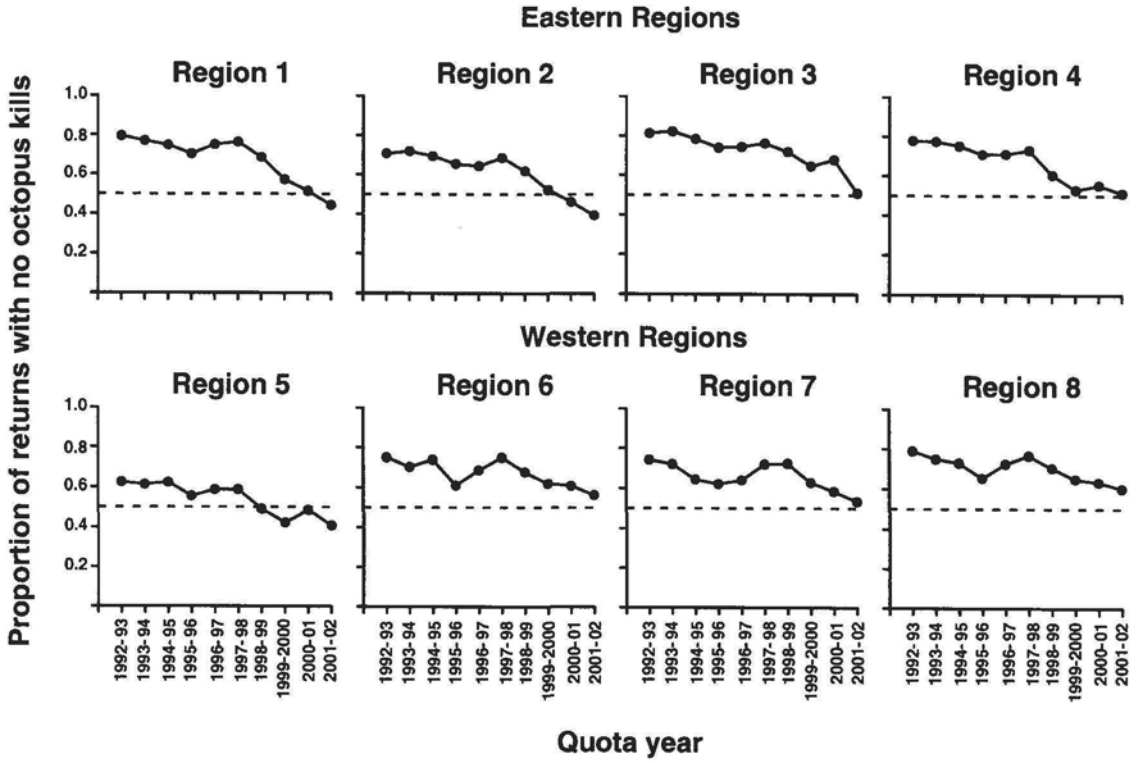

Fig. 3 Proportion of the daily logbook returns which reported no octopus (*Octopus maorum*) kills over the quota years from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia. Straight dotted line represents the situation where half the daily logbook returns reported no octopus kills and half the returns reported octopus kills in the quota year.

The decrease in returns reporting no octopus kill and subsequent increase in the reporting of octopus kills either indicates that octopus kills were under-reported before the introduction of the quota system, or that since the introduction of quota the number of lobsters killed by octopus has increased. When the proportion of returns reporting no octopus kill declines, there is no way of knowing if the reporting rate increased or whether increased predation decreased the days with no observed kills. Other analyses were carried out to help to distinguish between the two possibilities and conclusively interpret the reporting of octopus kills in the fishery.

There were correlations between the increases in the reporting rate of octopus kills (Fig. 3) and the reported total number of lobster killed by octopus (Fig. 4). However, in regions 3, 6, and 8 there are inconsistencies between the two sets of trends. Despite these findings, there have been no verbal reports from the rock lobster industry concerning a major rise in the levels of octopus mortality to match that reported in the commercial catch returns. The number of vessels that never reported a kill in the fishery has consistently been about eight vessels since 1998 (Fig. 5), however this number was significantly higher in 1992.

Since 1992/93, consistently 80–90% of the returns, across all regions, had low proportions of lobsters killed by octopus, between 0 and 0.1 (Table 1). The actual percentage of returns recording no octopus kills has generally decreased, especially over the recent quota years, from 83% in 1992/93 to 60% in 2001/02. These findings seem to indicate that the increase in the reporting of octopus kills since the introduction of quota is probably not because of an increase in the absolute number of lobsters killed by octopus, but because of increased reporting of octopus kills after the introduction of quota. Some of the increase in reporting may be a result of the shift to winter fishing. A general pattern emerged across the regions, with the exception of region 2, where the proportion of lobsters killed in winter

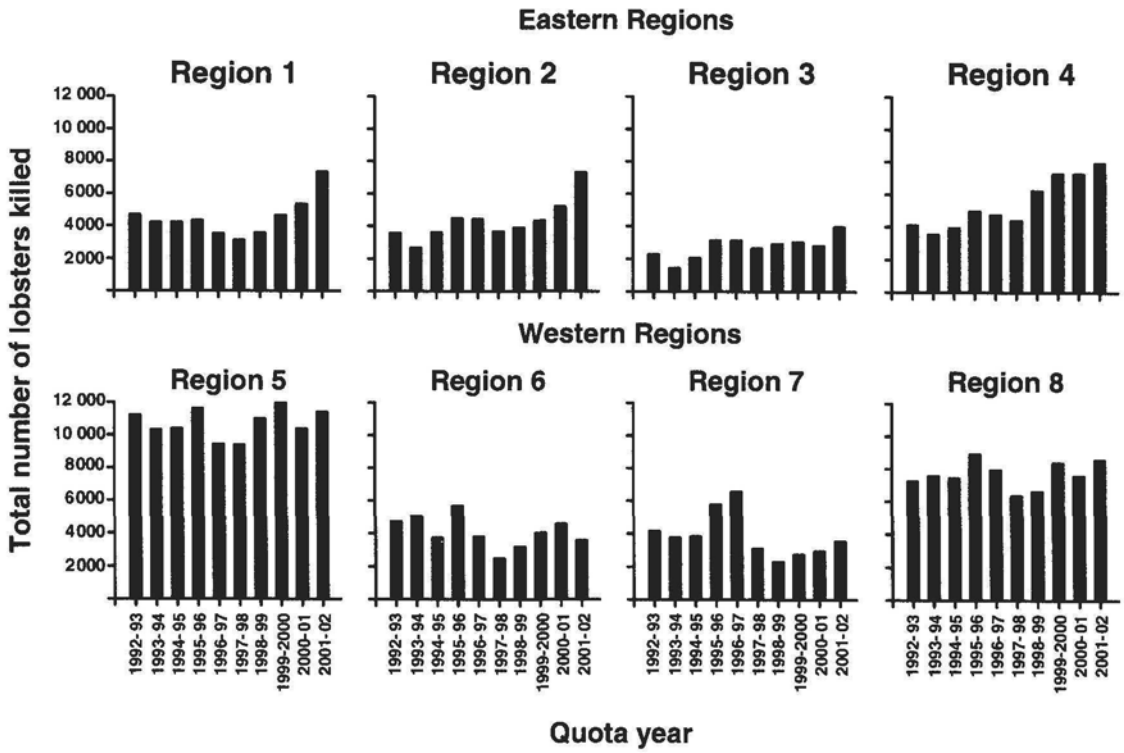

Fig. 4 Total number of lobsters killed by octopus (*Octopus maorum*) over the quota years from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia.

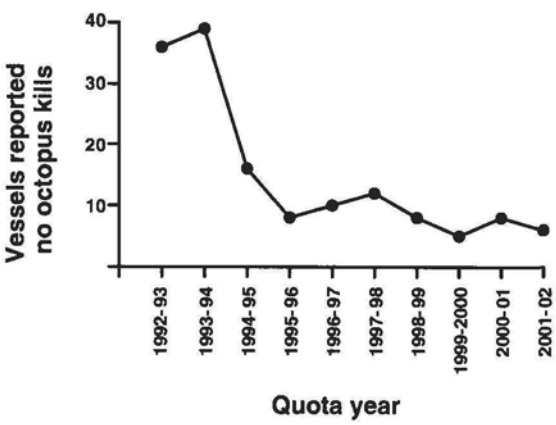

Fig. 5 Number of vessels that recorded no octopus kills over the quota years from 1992 to 2002 in the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia.

increased along with the total proportion of lobsters killed since the introduction of quota (Fig. 6).

Spatial variation in octopus predation within the fishery

The proportion of lobsters caught varied across the eight regions in relation to the catergorised daily-average number of lobsters per pot (Fig. 7). The largest proportion range was in region 3, where the percentages ranged from 0.03% at a density category of 0.05 lobsters per pot to 8.2% at a density of 0.55 lobsters per pot. Across the regions, the proportion was highest when the daily-average catch was less than two lobsters per pot, except in region 7, where the region had a higher percentage of lobsters caught at a daily-average catch around two lobsters per pot. The higher percentage of lobsters caught in region 7 at the density category around two indicates that the lobster population is less depleted in this region, particularly compared with regions 3 and 4 which both had a higher proportion of lobsters occurring at density categories less than one lobster per pot.

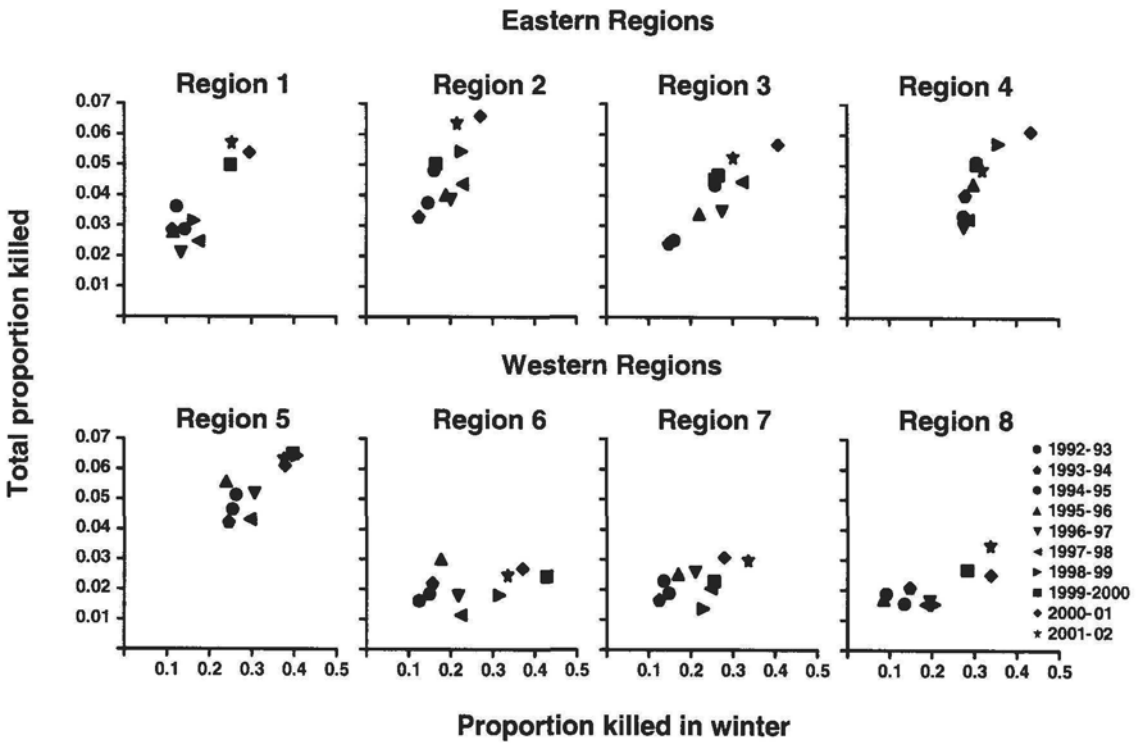

Fig. 6 Proportion of lobsters killed in winter compared with total proportion of lobsters killed during the year across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia.

Table 1 Percentage of the logbook returns from the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia, that recorded no octopus (*Octopus maorum*) kills and octopus predation levels within the proportion of lobsters killed category over the quota years from 1992 to 2002.

Quota	% returns with	Proportion killed category									
year	no octopus kills	0.05	0.15	0.25	0.35	0.45	0.55	0.65	0.75	0.85	0.95
1992–93	83	90.4	5.55	1.75	0.99	0.58	0.17	0.18	0.12	0.04	0.17
1993–94	82	89.4	5.94	1.92	1.07	0.77	0.19	0.21	0.15	0.06	0.32
1994–95	80	88.7	6.35	1.99	1.23	0.77	0.18	0.26	0.15	0.05	0.29
1995–96	75	86.9	7.49	2.32	1.43	0.90	0.17	0.27	0.12	0.05	0.33
1996–97	77	89.6	6.23	1.97	1.04	0.56	0.15	0.14	0.10	0.02	0.20
1997–98	80	90.0	5.63	1.91	1.01	0.68	0.17	0.20	0.13	0.03	0.25
1998–99	74	86.5	7.25	2.58	1.61	0.87	0.28	0.28	0.19	0.07	0.37
1999–2000	66	85.9	8.59	2.61	1.34	0.72	0.19	0.21	0.16	0.05	0.23
2000–01	66	85.8	8.76	2.64	1.20	0.81	0.22	0.19	0.16	0.05	0.20
2001–02	60	83.2	9.93	3.28	1.68	0.83	0.36	0.31	0.17	0.08	0.17

The proportion of lobsters caught at a low daily-average catch declined in all regions over the quota years from 1992 to 2002, except region 3, where there was a constant proportion of lobsters caught in the density category (Fig. 8). There was significant variation in the proportions in different years across all regions except in regions 5, 6, and 7. Owing to this variation, the correlation between the proportions and time was low across the regions (r^2 was less than 0.64 across all regions). However, the declining trend in the proportion of lobsters occurring at a low density indicates that the lobster

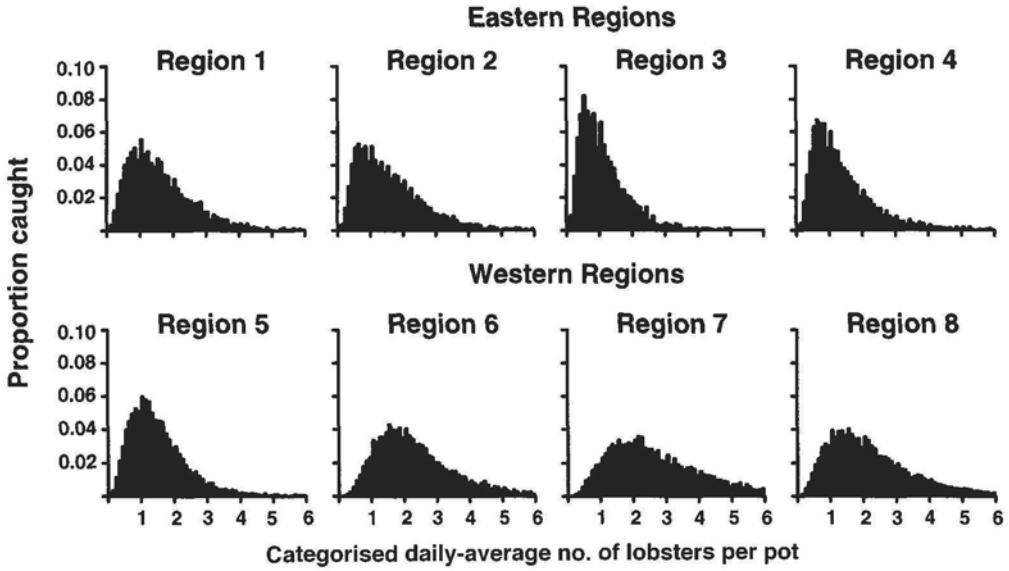

Fig. 7 Proportion of the total number of lobsters caught from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia, in relation to the categorised daily-average number of lobsters per pot. Categories into which the daily-average catches are summarised are in units of 0.1 lobsters per pot.

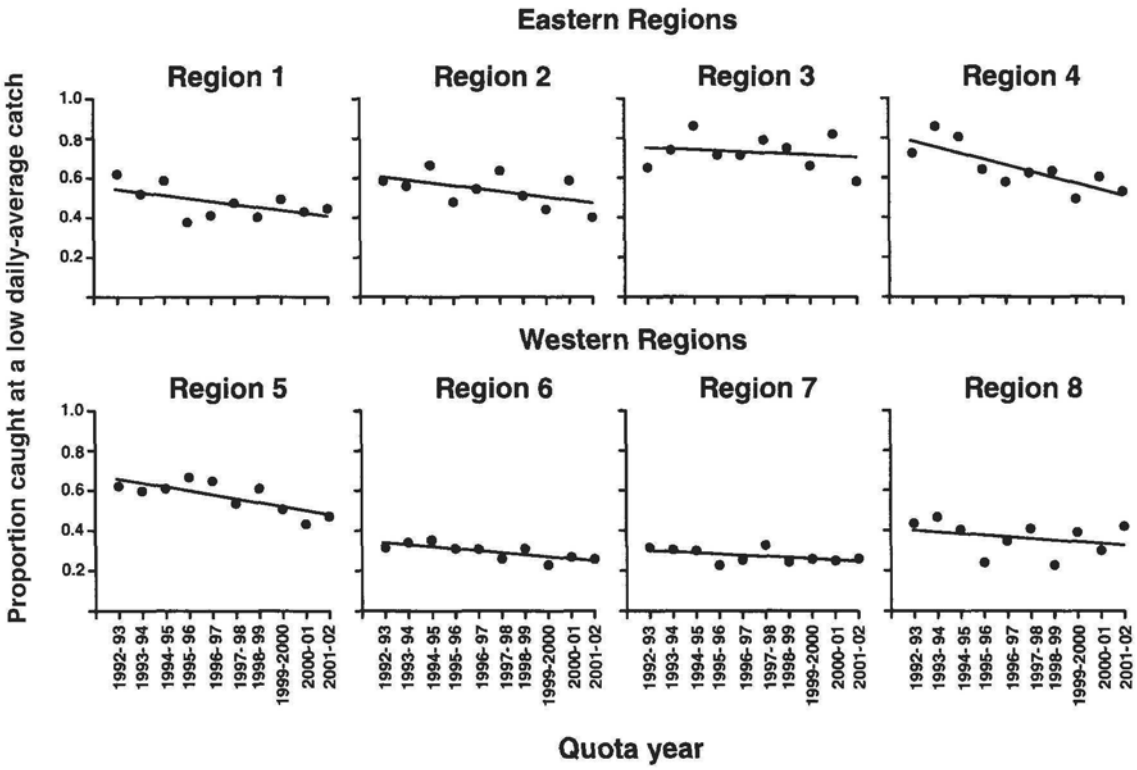

Fig. 8 Proportion of the total lobsters caught at a low daily-average catch over the quota years from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia. The low density category into which the daily-average catches are summarised is between 0.5 and 1.5 lobsters per pot.

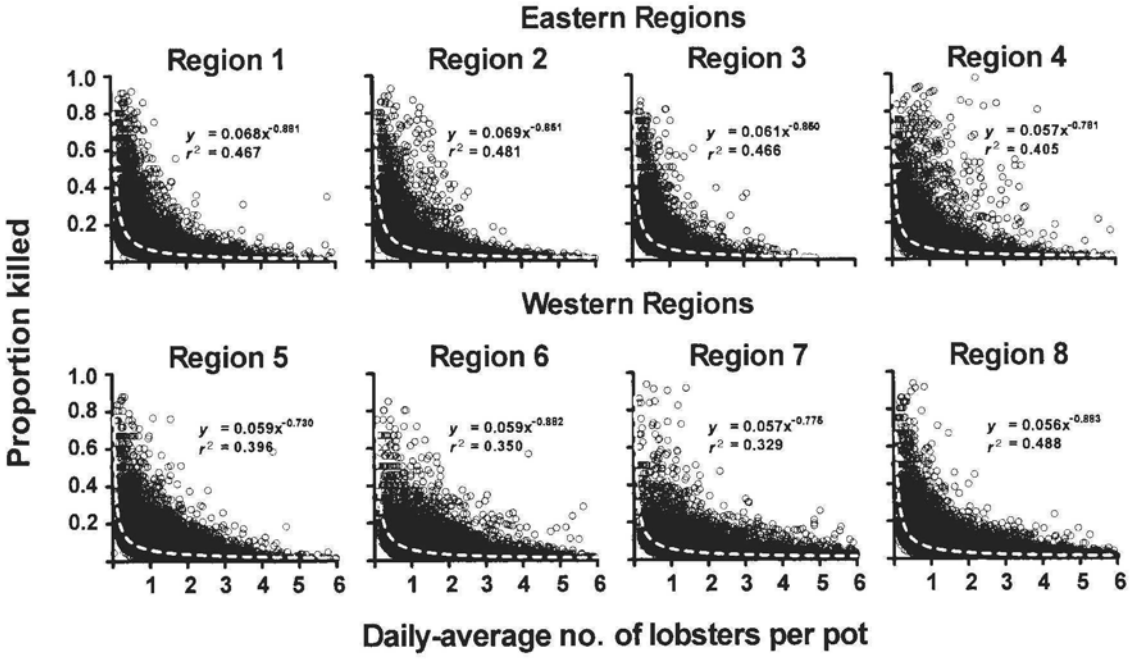

Fig. 9 Proportion of lobsters killed by octopus (*Octopus maorum*) from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia, in relation to the daily-average number of lobsters per pot.

populations in the various regions are recovering from earlier levels of depletion (except, possibly, in region 3).

The proportion of lobsters killed relative to the increasing daily-average number of lobsters per pot declined across the eight regions (Fig. 9). The decline indicates that octopus killed a higher proportion of lobsters when the daily-average catch was lower and therefore octopus predation is inversely correlated with lobster catches. The rate of change in the proportion killed, measured by the slope of the curve, varied slightly across the regions. The steepest curve in region 2 implies a greater change in the rate of octopus predation across the range of density categorises. The correlation between the proportion killed and the average-daily number of lobsters per pot was less than 0.5 across all the regions owing to the variability in the daily-average catches.

When the daily-average catches in region 1 were grouped into density categories (Fig. 10A), the estimated model parameters were similar to the parameters estimated using the uncategorised daily catches in this region (Table 2). However, the error associated with the average proportion killed for each category and the daily-average catches becomes discarded. The regression based on the daily estimates of the average catches and proportion killed provides more defensible correlation estimates, however both the uncategorised and categorised daily-average catches provided realistic parameter estimates. Therefore, the rest of the analyses were based on categorised daily-average catches because it provided realistic parameter estimates while enabling the results of the temporal comparison of octopus predation to be presented more clearly.

Temporal and spatial variation in octopus predation within the fishery

The proportion of lobsters killed relative to the increasing density categorises declined in region 1 in summer and winter (Fig. 10B). The rate of change in octopus predation relative to the density categorises varied between the two seasons across the eight regions, with the biggest seasonal difference in regions 3 and 4, which indicates some seasonal variation in the proportion killed in these regions (Table 3). Across the eastern regions there was a higher proportion of lobsters killed in winter when the categorised daily-average catch was about one, however the rate of change in the proportion killed

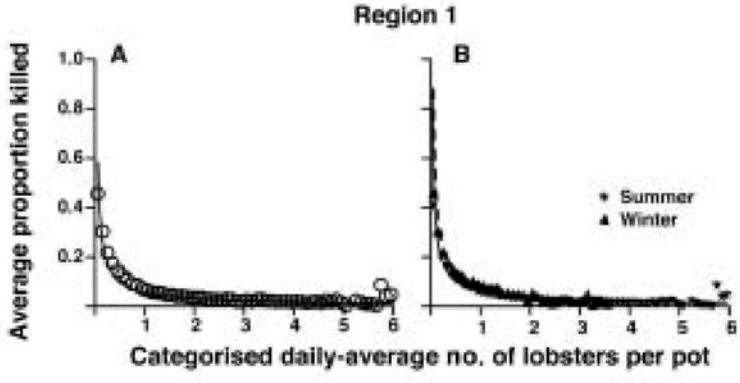

Fig. 10 Average proportion of lobsters killed by octopus (*Octopus maaruni*) from 1992 to 2002 in region 1 of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia, in relation to the categorised daily-average number of lobsters per pot: **A**, non-seasonal analysis; and **B**, seasonal analysis. Categories into which the daily-average catches are summarised are in units of 0.1 lobsters per pot.

Table 2 Model parameters describing the relationship between the average proportion of lobsters killed by octopus (*Octopus maaruni*) and the categorised daily-average number of lobsters per pot from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia.

	Model parameters		
Region	a	b	r^2
1	0.064	–0.792	0.782
2	0.064	–0.838	0.956
3	0.058	–0.828	0.838
4	0.056	–0.812	0.878
5	0.054	–0.844	0.889
6	0.054	–0.895	0.954
7	0.056	–0.747	0.969
8	0.054	–0.862	0.976

Table 3 The model parameters describing the relationship between the average proportion of lobsters killed by octopus (*Octopus maaruni*) and the categorised daily-average number of lobsters per pot during summer and winter from 1992 to 2002 across the eight regions of the Tasmanian rock lobster (*Jasus edwardsii*) fishery, Australia.

	Model parameters			
	Summer		Winter	
Region	a	b	a	b
1	0.061	–0.761	0.065	–0.913
2	0.062	–0.827	0.087	–0.660
3	0.058	–0.849	0.076	–0.633
4	0.053	–0.816	0.083	–0.403
5	0.056	–0.855	0.050	–0.869
6	0.057	–0.924	0.049	–0.852
7	0.056	–0.749	0.056	–0.771
8	0.054	–0.859	0.051	–0.925

was higher in summer across the regions except in region 1. There was little seasonal difference in the proportion killed in the western regions. The rate of change was slightly higher in winter across regions 5, 7, and 8, and the proportion of lobsters killed was a little higher in summer across regions 5, 6, and 8 when the categorised daily-average catch was about one.

DISCUSSION

This study represents an initial effort to use fishery logbook information to test for depensation by analysing the relationship between octopus predation and the daily-average number of lobsters per pot. The non-reporting of undersized lobsters may not necessarily affect the demonstration of depensation providing all undersized lobsters leave through the escape gap or are killed by octopus and are therefore accounted for through the reporting of octopus kills. However, it is likely that some undersized lobsters remain inside the pots, which means the relationship is biased given that daily mortality estimates and average catches would be respectively larger and smaller than the true level. The bias reduces the opportunity to conclusively determine the absolute proportion of lobsters killed by octopus and therefore the true scale of the depensatory mortality. Nevertheless, demonstrating depensation is still possible if the undersized lobsters remain at a constant proportion to the daily-average catches or vary randomly from the catches, as the bias would not significantly affect the slope of the relationship.

It is likely that the numbers of lobsters killed by octopus were not consistently reported in logbooks,

particularly before the introduction of the quota system. The under-reporting of octopus kills means the level of octopus predation would have been higher than the observed level. However, the bias arising from the non-reporting of undersized kills, inaccurate recording of octopus kills, the inability to include unaccountable zero kills, and the ability that some lobsters have to escape from pots are unlikely to mask the occurrence of depensation if the bias is constant or random across the daily-average catches. There was little reason to consider the bias varied substantially from the catches. By assuming this constant level of bias, the inconsistencies in the fishery information masks our understanding of the full scale of depensation, not the demonstration of depensation.

The results demonstrate that the pot-related predator-prey interaction between lobster and octopus contributed to depensatory mortality in the Tasmanian rock lobster population, given the higher proportion of lobsters killed by octopus when the daily-average catches were lower. However, the appearance of depensation may arise if the reporting of octopus kills is inversely related to lobster catches. If this occurs, such that higher numbers of lobsters caught result in lower reporting of octopus kills, it would give the appearance of a reduction in predation at higher densities. There is little reason to consider that the reporting of octopus kills varied substantially with respect to the catches. There are signs that the Tasmanian lobster stock is recovering from depletion implying higher catch rates of lobsters, and yet the rate of reporting of octopus kills is increasing steadily. This indicates that the inter-specific interaction, not the inconsistent reporting of octopus kills, contributed to depensation.

The variation in the catch frequency is unlikely to affect the demonstration of depensation, providing octopus have an equal chance of finding each pot and lobsters fall victim to octopus predation across some of the catch frequency range. This situation is likely, given the higher proportion of lobsters caught at elevated densities in region 7 did not affect the detection of depensation in this region. However, the ability to detect depensation may be influenced by lobster size. If predation is reduced when lobster catches are low owing to the presence of larger sized lobsters, then detecting depensatory mortality may be difficult because predation would be dependent on both lobster size and numbers. Since the observed predation level increased when catches were low, it seems to suggest that either there were no low catches of larger lobsters or, more likely, the presence of the larger lobsters at lower catches offered no significant protection against predation. It has been observed that larger lobsters were more commonly selected by octopus than smaller ones (Brock 2004).

Identifying the mechanisms driving the depensatory mortality is crucial to understanding the detailed dynamics of the Tasmanian rock lobster population. Little information exists on the feeding response of octopus to lobster numbers, to determine if the response is inversely related to lobster density and is influenced by prey size, predator saturation, and predator avoidance tactics (e.g., encounter, dilution, confused, and group-defence effects). This lack of information made it difficult to establish if predator saturation or a combination of anti-predator tactics is driving the depensatory mortality. It is possible that the confinement of a pot restricts both the movements of lobsters and octopus and also the time an octopus spends inside the pot, which may mean the potential of some anti-predator tactics operating in the pots is reduced. Lavalli & Spanier (2001) found that the confusion and dilution effects do not operate in the time span used in their experiments or where lobsters are restricted in their movement by a tethering device.

Understanding the mechanisms through which the level of octopus predation varies temporally and spatially within the fishery is important. The results highlighted a slightly higher level of octopus predation in some of the eastern regions during winter. The cooler temperatures may slow down lobster vigilance and increase vulnerability to predation. Ziegler et al. (2002) observed that the catchability of lobsters was highest in early summer and lowest in winter. However, the lack of seasonal difference in the proportion of lobsters killed by octopus in the western regions suggests there may be some seasonal effect other than the seasonal change in lobster vulnerability that is driving the level of octopus predation, such as the distribution of the octopus in the fishery. Lobster mortality rates were found to be positively correlated with the catch rates of octopus in the south Australian rock lobster fishery (Brock 2004).

Determining the numerical response of octopus (relationship between octopus and lobster population numbers) will help to understand the influence that the response has on the dynamics of octopus predation and depensation. Water depth may also influence the level of octopus predation in pots as the number of lobsters killed was observed to decrease as depth increased (Brock 2004). The small

difference in the proportion killed in the eastern and western regions during summer seems to indicate that the deeper water depth of fishing in the western regions played little part in reducing lobster vulnerability to octopus predation. Identifying the possible factors affecting octopus predation is important in understanding the depensatory dynamics.

Knowing that depensation threatens a population allows management to consider reducing the effect (Courchamp et al. 1999). Depensation is an important issue in the Tasmanian rock lobster population and has implications for the management of crustacean stocks. Applying the combined pressure of fishing and depensatory mortality to a severely depleted stock could potentially collapse a fishery, depending on the scale of both forms of mortality. Even with catch restrictions it is possible that the scale of the depensatory mortality could seriously threaten a depleted stock. Alternatively, the restrictions may allow the stock to recover. The resilience of all lobster fisheries to collapse may not be justified by using past observations of lobster fisheries recovering from low abundances. The scale of the depensation needs to be determined for each lobster fishery to make an accurate assessment of the impact of depensatory mortality on the recovery of dynamics of the population, since octopus predation is influenced by environmental and biological factors.

The absolute scale of depensation within the Tasmanian rock lobster fishery could not be conclusively established owing to the bias in the fishery information. Nevertheless, the demonstration of the occurrence of depensation reinforces the need to avoid severe stock depletion in the fishery and in other fisheries significantly affected by the pot-related octopus predation. There may also be financial implications for a fishery from the depensatory effect, depending on the scale of the effect. Greater restrictions on catches may be required to increase the stock than would be required in the absence of depensation. The possibility of increased threat of the depensatory effects in particular regions of the fishery should also be considered if some regions are prone to a higher predation, as indicated by the spatial variation in the proportion of lobsters killed by octopus. Linking the seasonal affects of the predator-prey interaction to increased predation means the possible effects from seasonal shifts in effort should also be considered.

To better understand the affect that the predator-prey interaction has on depensatory mortality, there needs to be pot sampling conducted in the fishery over summer and winter to collect detailed information on the number of lobsters and octopus kills per pot. Unfortunately, the fishery sampling data may be inherently biased because of the difficultly involved in establishing the exact number of lobsters present while the octopus enters the pot, given that lobsters may enter and leave the pot. The exact number of lobsters per pot needs to be observed to accurately determine how group size affects predation risk. Information on the temporal and spatial dynamics of the octopus population and the functional and numerical response of octopus is important towards understanding the dynamics underlying the interaction and depensation. Distinguishing if predator saturation or predator avoidance tactics are driving the depensation requires experiments to be undertaken. Additional experiments which examine the affect of group size and position of lobsters within the group may help to understand if lobsters use one or more predator avoidance tactics.

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REFERENCES

Anderson, T. J. 1999: Morphology and biology of *Octopus maorum* Hutton 1880 in Northern New Zealand. *Bulletin of Marine Science 65(3)*: 657–676.

Bertram, B. C. R. 1978: Living in groups: predators and prey. *In*: Krebs, J. R; Davies, N. B. *ed.* Behaviour ecology: an evolutionary approach. Oxford, Blackwell Science. Pp. 122–147.

Bowyer, R. T. 1987: Coyote group size relative to predation on mule deer. *Mammalia 51*: 515–526.

Brock, D. 2000: Trying to save thousand of lobster from the octopus squeeze. *Southern Fisheries 7(2)*: 25.

Brock, D.; Ward, T. W. 2004: Maori octopus (*Octopus maorum*) bycatch and southern rock lobster (*Jasus edwardsii*) mortality in the South Australian rock lobster fishery. *Fishery Bulletin 102*: 430–440.

Butler, M. J.; MacDiarmid, A. B.; Booth, J. D. 1999: The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Marine Ecology Progress Series 188*: 179–191.

Cappuccino, N.; Price, P. W. 1995: Population dynamics: new approaches and synthesis. San Diego, California, United States, Academic Press.

Cobb, J. S. 1981: Behaviour of the Western Australian spiny lobster, *Panulirus cygnus* George, in the field and laboratory. *Australian Journal of Marine and Freshwater Research 32*: 399–409.

Courchamp, F.; Clutton-Brock, T.; Grenfell, B. 1999: Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution 14*: 405–410.

Dittel, A. I.; Hines, A. H.; Ruiz, G. M.; Ruffin, K. K. 1995: Effects of shallow water refuge on behaviour and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bulletin of Marine Science 57(3)*: 902–916.

Fresh, K. L.; Schroder, S. L. 1987: Influence of the abundance, size and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences 44*: 236–243.

Garstang, W. 1900: The plague of octopus on south coast, and its effect on the crab and lobster fisheries. *Journal of Marine Biological Association U.K. 6*: 260–273.

Green, N. 2002: Evaluating lobster catchability using remote video and the implications for density estimates obtained from trapping surveys for a southern rock lobster *Jasus edwardsii* population. Unpublished honours thesis, University of Tasmania, Australia.

Hamilton, W. D. 1971: Geometry for the selfish herd. *Journal of Theoretical Biology 31*: 294–311.

Herrnkind, W. F.; Childress, M. J.; Lavalli, K. L. 2001: Cooperative defence and other benefits among exposed spiny lobster: inferences from group size and behaviour. *Marine and Freshwater Research 52*: 1113–1124.

High, W. L. 1976: Escape of Dungeness crabs from pots. *Marine Fisheries Review 1184*: 19–23.

Holling, C. S. 1959: The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist 91*: 385–398.

Hutton, F. W. 1875: Descriptions of new species of New Zealand fish. *Annals and Magazine of Natural History (Series 4) 16(95)*: 313–317.

Hutton, F. W. 1880: Manual of the New Zealand Mollusca. Wellington, New Zealand. 224 p.

Landeau, L.; Terborgh, J. 1986: Oddity and the 'confusion effect' in predation. *Animal Behaviour 56*: 150–160.

Lavalli, K. L.; Spanier, E. 2001: Does gregariousness function as an antipredator mechanism in the Mediterranean slipper lobster, *Scyllarides latus*? *Marine and Freshwater Research 52*: 1133–1143.

Leonardson, K. 1994: Multiple density dependence in two sub-populations of the amphipod *Monoporeia affinis*: a potential for alternative equilibria. *Oecologia 97*: 26–34.

Liermann, M.; Hilborn, R. 2001: Depensation: evidence, models and implications. *Fish and Fisheries 2*: 33–58.

Milinski, M. 1977: Do all members of a swarm suffer from the same predation? *Zeitschrift für Tierpsychologie 45*: 373–388.

Mori, H.; Chant, D. A. 1966: The influence of prey density, relative humidity, and starvation on the predacious behaviour of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). *Canadian Journal of Zoology 44*: 483–491.

Neill, S. R. St. J.; Cullen, J. M. 1974: Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *Journal of Zoology, London 172*: 549–569.

Osenberg, C. W.; Mittelbach, G. G. 1989: Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monographs 59*: 405–432.

Paine, R. T. 1976: Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology 57*: 858–873.

Pitcher, T. J.; Parrish, J. K. 1993: Functions of shoaling behaviour in teleost fishes. London, Chapman & Hall.

Pulliam, H. R. 1973: On the advantages of flocking. *Journal of Theoretical Biology 38*: 419–422.

Pulliam, H. R.; Caraco, T. 1984: Living in groups: is there an optimal group size? *In*: Krebs, J. R; Davies, N. B. *ed.* Behaviour ecology: an evolutionary approach. Oxford, Blackwell Science. Pp. 122–147.

Rees, W. J.; Lumby, J. R. 1954: The abundance of octopus in the English Channel. *Journal of Marine Biological Association U.K. 33*: 515–536.

Ruggerone, G. T.; Rogers, D. E. 1984: Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. *Fishery Bulletin 82*: 401–410.

Schradin, C. 2000: Confusion effect in a reptilian and a primate predator. *Ethology 106*: 691–700.

Taylor, R. J. 1977: The value of clumping to prey: experiments with a mammalian predator. *Oecologia 30*: 285–294.

Tostowaryk, W. 1972: The effect of prey defense on the functional response of *Podisus modestus* (Hemiptera: Pentatomidae) to densities of the sawflies *Neodiprion swainei* and *N. pratti banksianae* (Hymenoptera: Neodiprionidae). *Canadian Entomologist 104*: 61–69.

Treisman, M. 1975: Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour 23*: 779–800.

Turner, G. F.; Pitcher, T. J. 1986: Attack abatement: a model for group protection by combined avoidance and dilution. *American Naturalist 128*: 288–240.

Vine, I. 1971: Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology 30*: 405–422.

Welty, J. C. 1934: Experiments in group behaviour of fishes. *Physiological Zoology 7*: 85–128.

Williamson, C. E. 1984: Laboratory and field experiments on the feeding ecology of the cyclopoid copepod, *Mesocyclops edax*. *Freshwater Biology 14*: 575–585.

Wrona, F. J.; Dixon, R. W. 1991: Group size and predation risk: a field analysis of encounter and dilution effects. *American Naturalist 137*: 186–201.

Ziegler, P. E.; Frusher, S. D.; Johnson, C. R.; Gardner, C. 2002: Catchability of the southern rock lobster *Jasus edwardsii*. I. Effects of sex, season, and catch history. *Marine and Freshwater Research 53*: 1143–1148.

Zimmer-Faust, R. K.; Spanier, E. 1987: Gregariousness and sociality in spiny lobsters: implications for den habitation. *Journal of Experimental Marine Biology and Ecology 105*: 57–71.

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Organic matter production of American lobsters (*Homarus americanus*) during impoundment in Maine, United States

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Abstract Lobster impoundments are dammed coastal embayments utilised to hold American lobsters (*Homarus americanus*) before shipping to market. The impacts of lobster impoundments on the environment have not been previously studied. Here, the digestive functioning of American lobsters was examined to assess the quantity and quality (TVS, total volatile solids) of lobster faeces produced under the temperatures and feeding regimens these animals were subjected to during the impoundment period. Overall it was determined that quantity and quality of faeces did not differ among the experimental temperatures (5, 10, and 15°C), and that animals fed every 1–2 days produced greater quantity and quality of faeces than those fed every 3–18 days, or those animals fed less than every 18 days. As a first estimate of organic matter production in active lobster impoundments, it was calculated that a typical lobster impoundment produced 0.79 ± 0.35 (average ± 1 SD) g TVS m^{-2} day^{-1} during the impoundment period, equivalent to 3.11 ± 0.60% of the total weight of lobsters stocked into the impoundment. This level of organic matter production is below the level produced by other aquaculture operations, and that at which benthic impacts might be expected.

Keywords benthic impact; faecal production; *Homarus americanus*; lobster impoundment; Maine; organic matter; total volatile solids

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INTRODUCTION

Impoundments are an important component of the American lobster (*Homarus americanus*, H. Milne Edwards 1837) fishery. They are cordoned-off coastal areas, ranging from the simple damming of a tidal embayment, to a three-sided corral, with the fourth side being the shoreline. In all instances, there is a gate within the dam that can be opened or closed. When the gate is closed, water is prevented from draining completely from the impoundment. The water generally is dammed to a depth of 1.5 m, thus only around the period of high tide will there be water exchange over the top of the dam. When lobsters are not stocked in the impoundment, the gate is opened, and the impoundment can be drained completely, thereby exposing virtually the entire impoundment bottom.

The highest landings in the American lobster fishery occur in September–November. During this time, excess animals are stored in the impoundments. These animals then are released slowly into the market during a time (February–March; winter in the Northern Hemisphere) when fishing is unsafe and landings are generally lower. Impounding lobsters, and the subsequent slow release of impounded animals to the market, avoids a market glut in the autumn, thereby helping to stabilise market prices.

In Maine, United States, there are a total of 56 active impoundments that can hold up to 2257 t of lobster (H. Hodkins, Maine Lobster Pound Association pers. comm.). In addition to Maine's present impoundments, there is much interest in developing new impoundments. Within the last half-decade, there have been over a dozen new applications for impoundment licenses (J. Sowles, Maine Department of Environmental Protection pers. comm.). These new impoundments will be developed in prime coastal habitat, and thus it is critical to ensure that these impoundments do not significantly degrade the habitat. One method to accomplish this is to determine the holding or environmental assimilative capacity of impoundments. Thus for new impoundments, biologically feasible loadings

can be determined *a priori* as part of the effort to ensure that the industry proceeds in an environmentally sustainable manner (Rosenthal 1994; Olsen 1996; Pillay 1996), and to prevent lobster health problems that come with crowding.

To date, lobster impoundments have not had the advantage of biological monitoring to the same degree as other sectors of the aquaculture industry. Although several studies have considered environmental effects on lobster growth and health (Jansen & Groman 1993; Speare et al. 1996; Bayer et al. 1998), no studies have looked at the reverse issue of lobster impacts on the environment, especially of impoundments. This lack of information for lobster impoundments is exemplified by the fact that regulatory agencies within the Gulf of Maine do not currently have a formal environmental component associated with impoundment licensing and applications. In the past decade, the scientific and practical knowledge of how other aquaculture sectors impact the environment has increased substantially (Pillay 1992; Ervik et al. 1997). One main tenet from this environmental work is that if the industry develops in a suitable area and at a reasonable level of effort, the impacts to the environment are negligible or even non-existent (O'Connor et al. 1991; Olsen 1996; Tlusty et al. 1999).

The issue of environmental impacts in lobster impoundments is timely for three reasons. First, there is heightened public awareness of aquaculture impacts on the environment (Positive Aquaculture Awareness, 2004, "Issues in Aquaculture Farmed Salmon, PCBs, Activists, and the Media" www.farmfreshsalmon.org/images/PDFS/rptupdate.pdf, accessed 20 January 2004). Some of the initial public concern was justified, but lately the public has done a poor job of discerning perception from fact. In addition, concern about environmental impacts is often used as a proxy argument for other issues such as visual impacts and the "not-in-my-backyard" attitude. Regardless, the heightened awareness of potential impacts to the environment makes it necessary that all new aquaculture ventures promptly and effectively address this issue. Second, effluent production standards have been considered for lobster impoundments (USEPA 2002). Although the standards were not implemented, they likely will be reconsidered, and possibly acted upon in the future. If regulations are developed for impoundments without appropriate scientific backing, any policies put forth would be based on untested principles. Finally, there is current concern that lobster health in impoundments is compromised, as shell disease is often noticed within impoundments (Bayer et al 1978; Prince et al. 1995). Improper diets can lead to increased incidence of disease which can be further exacerbated if impoundments are overstocked, leading to environmental degradation. Understanding the relationship between stocking and organic matter production will assist in the analysis of disease states within these areas.

Although in use for over a century, little work has been done on the ecology of these areas—particularly regarding how the impoundment process may alter ecosystem function. One particularly interesting area concerns how the lobster's biology, specifically digestive functioning at winter temperatures, interacts with ecosystem function. Impoundments are point sources for the concentration of organic matter (USEPA 2002). The lobsters are fed during the impoundment period, and likewise excrete metabolic wastes, thus increasing the input of organic matter to the ecosystem at these points. It is unknown how completely the lobsters process the food inputs, and thus what contribution lobster impoundments have on the net organic matter loading to the ecosystem. A majority of the previous research on dietary processing of lobsters was concerned with food digestibility and time for food to pass through the lobster's gastrointestinal tract (Conklin 1995). However, in examining environmental impacts, metabolic wastes need to be considered in a slightly different light. The important features determining how metabolic wastes may impact the environment include the long-term quantity and quality of the produced wastes. Thus, the quantity and quality of faeces produced, and how these values change at different environmental temperatures and different feeding regimens, was addressed. This information was then used to estimate how much organic matter was deposited in a lobster impoundment during the period lobsters were held within. This estimate was intended to be an upper limit value, which will create a starting point to better address environmental impacts of lobster impoundments.

METHODS

To assess the faecal organic matter production by American lobsters, animals were held at the New England Aquarium, Boston, MA, United States, and fed a diet with a known content of total volatile solids (TVS). Their faeces were collected daily, and these samples were analysed for faecal output (g $faeces_{dry\ weight\ (DW)}$/g $lobster_{wet\ weight\ (WW)}$) and its TVS content. Lobsters were held individually in a recirculating

sea-water system (10% daily exchange) in 8-litre plastic containers within a larger 200-litre fibreglass tank. Each individual container had six mesh panels in the top 5 cm. Water was recirculated through each plastic tub at a rate of 4 litres/h. Each lobster was scheduled to be tested under three feeding regimes (a single food presentation, once every 4 days, and every day) at three temperatures (5, 10, and 15°C, Table 1). However, because of the length of time needed to conduct these experiments, two groups of lobsters were used. The first group was acclimated to a set temperature of 10°C for 10 days, during which time the animals were not fed. On the 11th day, the tank was thoroughly cleaned, and animals were then fed a single meal. Each animal was fed shrimp (*Panaeus monodon*) at 3% of their body weight ($food_{WW}/lobster_{WW}$). Faeces were collected daily by siphoning the particulate waste off the bottom. Midway through this trial, one lobster died. It was not replaced, and the initial data from this animal were not used in any of the analyses. After 17 days, the feeding regimen was then increased to once every 4 days (intermittent feed) for four feeding cycles. On days that the animals were fed, faeces were collected before the feeding event. At this point, the temperature of the incoming water was lowered to 5°C. These animals were then re-acclimated to the lower temperature for 8 days. During this period, they remained on the intermittent feeding schedule. Faecal samples were then collected for four intermittent feeding cycles. A second group of five lobsters was acquired, and acclimated at 15°C for 15 days, during which time they were not fed (Table 1). On the 16th day, their containers were thoroughly cleaned and the animals fed a single meal. Faecal collection started, and continued daily for the remainder of the experiment. After 8 days, the animals were then fed intermittently for four feeding cycles. Finally, this group of animals was fed daily for 8 days.

The faecal samples were processed immediately for storage. A majority of the water was removed, and the samples were then placed into 2.5 ml microcentrifuge tubes and stored at –80°C until they were analysed. Each sample was analysed for %DM and %TVS (Tlusty et al. 2000b). Samples were rinsed to remove salt, weighed, then dried for 24 h from which dry matter was calculated. Next, the samples were ashed in a muffle furnace at 500°C for 8 h, cooled, and re-weighed. TVS was determined as the % loss of mass on ignition (LOI_{500C}).

Data analyses

All data were checked for normality and equal variance. Those failing these tests were analysed utilising ranked data (Sigma-Stat 2.03). Because not all lobsters were tested at each temperature × feed-interval combination (Table 1), analysing the complete data set was difficult because the repeated-measures ANOVA was unbalanced. Relevant subsets of the data were analysed by grouping similar feeding regimen trials across temperatures, or different feeding regimens within temperature. The resultant analyses were two-way repeated-measure ANOVAs. One factor was always the number of days, which was the sequential count in the single and daily feeding regimens. In the intermittent trial, "days" was the 4 days after feeding, with values being averaged over the four replicated feeding events. The repeated measure occurred on one or

Table 1 Summary of experimental designs, and the temporal sequence in which they occurred. Two groups of American lobsters (*Homarus americanus*) were used. The first experienced 10 and 5°C, the second only 15°C. Animals were held for a acclimation (Acc.) period in which they were not fed, or fed once every for days (Acc.*). The feeding trials consisted of animals being fed a single time (Sing.), once every 4 days (Int.), or every day (Daily). Days refers to the sequential count of days for each experimental group of animals. For the five comparisons listed, the groups being statistically compared are identified by similar letters.

Animals	1–4	→→	→→	→→	→→	6–10	→→	→→	→→
Temp. (°C)	10	→→	→→	5	→→	15	→→	→→	→→
Feed trial	Acc.	Sing.	Int.	Acc.*	Int.	Acc.	Sing.	Int.	Daily
Days	1–10	11–29	30–46	47–54	55–70	1–15	16–24	24–40	41–48
Comparison									
1							a	a	a
2		b	b						
3			c		c				
4			d					d	
5		e					e		

both factors depending on whether the analysis compared the same animals at different temperatures (5 versus 10°C) or different animals at different temperatures (10 versus 15°C). Treatment comparisons were made with Tukey's test. Power was calculated with $\alpha = 0.05$.

Modelling cumulative organic matter production

The model of the cumulative production of organic matter within impoundments was accomplished by assessing production of TVS throughout the impoundment period. This required knowing the daily amount biomass of lobsters in the impoundments, the feeding schedule, and the quantity and quality (TVS content) of faeces produced specific to the feeding regimen. Data on the rate of stock addition, feeding, and stock removal for each lobster impoundment was gathered by relying on the impoundment owners to share their information. Information was supplied by three owners for four impoundments. Two of the impoundment owners supplied data for 3 years, and one for only a single year. Similarly, two owners supplied all three pieces of information (addition, feeding, and removal) whereas one owner only supplied stock addition and feeding data.

The stock addition and removal data were used to create a time series of cumulative weight of animals in the impoundment. The feeding schedule was analysed to determine the feeding regimen (days between feedings). This cumulative weight of lobsters was then multiplied by both the average weight of faeces produced and TVS content of the faeces produced (determined in the previously-described laboratory experiments) specific for the feeding regimen, to arrive at the estimation of the organic matter produced per day per impoundment. Since complete stocking data were lacking for all impoundments, the cumulative production of TVS was first calculated through the feeding period for all impoundments. The feeding period was defined as 17 days post-terminal feeding, as this was the longest observation period investigated in the laboratory study, and the point at which the model utilised a lower value for TVS production. The cumulative production of TVS throughout the entire impoundment period was then determined for the four impoundments in which there were complete data. The percentage difference between the cumulative TVS production through the feeding period and the entire impoundment period was calculated. This value was used to interpret cumulative TVS production throughout the entire impoundment period for the impoundments in which the removal data were lacking.

The total net weight of TVS produced was of little use by itself, as it varied with the total number of lobsters in the impoundment, as well as with the total area of the impoundment. Thus, this value was altered to become a valuable metric for assessing impacts of lobster impoundments on the environment, and for managers to estimate organic matter loading from lobster impoundments. To assess impact of impoundment on the environment involves shifting this number to a rate of production of TVS per area per unit time. Thus the weight of TVS produced was converted into g TVS m^{-2} day^{-1}. For managers, it is best to be able to predict TVS loading from lobster impoundments by being able to estimate TVS production with different stocking levels. Thus the total weight of TVS produced was also converted to the %TVS production, $\%TVS(kg_{DW})/lobster(kg_{WW})$, for the entire impoundment period.

RESULTS

Feeding regimen

Data from animals tested under different feeding regimens were analysed to examine how food delivery affected excretory processing. At 15°C, animals were tested under all three feeding regimens (comparison 1, Table 1). Here, a statistically significant feeding regimen × day (4 days) interaction was observed for the faecal output (two-way repeated measures ANOVA on ranked data, $F_{6,24} = 4.936$, $P < 0.002$, power = 0.920). In general, animals fed daily produced a greater amount of faeces. An analysis of simple effects demonstrated that the amount of faeces (g_{DW}) per lobster (g_{WW}) per day did not change over 4 days for animals fed a single time or daily (for all pair-wise comparisons, Tukey's test, $q < 3.17$, $P > 0.13$). However, for animals fed intermittently, more faeces were produced on day 1 than any other day (for all comparisons to day 1, Tukey's test, $q > 4.13$, $P < 0.03$, Fig. 1).

Unlike the faecal output, there was no significant day × feed regimen interaction for TVS content of the faeces (two-way repeated measures ANOVA on ranked data, $F_{6,24} = 1.694$, $P > 0.15$, power = 0.220). Animals fed daily produced faeces with a greater TVS than the other two regimens (two-way repeated measures ANOVA on ranked data, $F_{2,8} = 8.424$, $P < 0.01$, power = 0.819, for all comparisons, Tukey's test, $q > 4.69$, $P < 0.03$). There was no statistically significant difference between the faecal output of

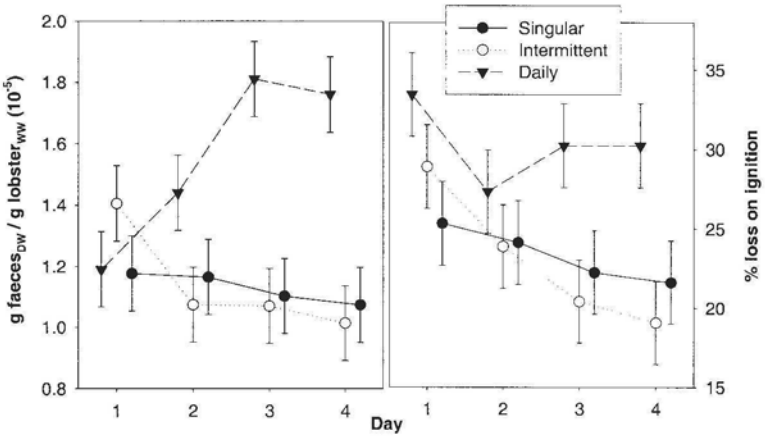

Fig. 1 Faecal output (10^{-5} g faeces$_{\text{dry weight (DW)}}$/g lobster$_{\text{wet weight (WW)}}$) and total volatile solid content of the faeces (% loss on ignition at 500°C) for five lobsters (*Homarus americanus*) fed a single time, intermittently every 4 days, or daily at 15°–C. Daily values are for the first 4 days in the single and daily trial, and averaged over the first four feeding cycles for animals fed intermittently. Data were non-normal and analysed as ranked data. Unranked values are presented here (± 1 SE) since the ranking did not significantly alter the interpretation of the analyses.

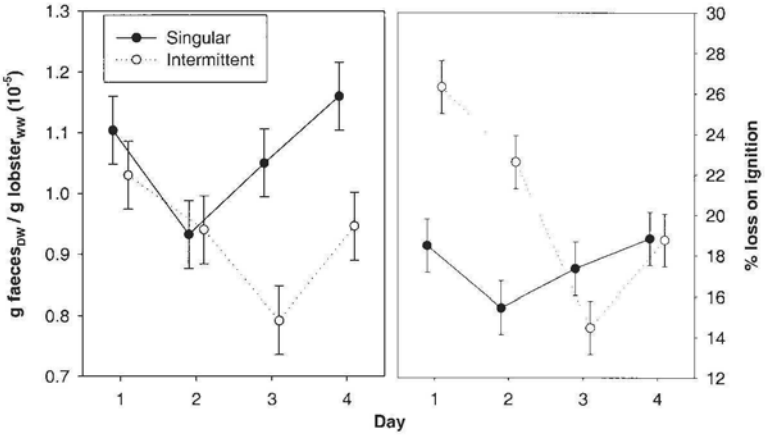

Fig. 2 Faecal output (10^{-5} g faeces$_{DW}$/g lobster$_{WW}$) and total volatile solid content of the faeces (% loss on ignition at 500°C) for four lobsters (*Homarus americanus*) fed a single time, intermittently every 4 days, or daily at 10°C. Daily values are for the first 4 days in the single trial, and averaged over the first four feeding cycles for animals fed intermittently. Data were non-normal and analysed as ranked data. Unranked values are presented here (± 1 SE) since the ranking did not significantly alter the interpretation of the analyses.

animals fed a single time compared with those fed intermittently (Tukey's test, $q = 0.625$, $P > 0.89$, Fig. 1). The number of days post-feeding did not influence TVS content of the faeces (two-way repeated measures ANOVA on ranked data, $F_{3,12} = 1.449$, $P > 0.27$, power = 0.113).

For animals tested under multiple feeding regimes at 10°C (comparison 2, Table 1), the results generally were similar to those presented above, with a few minor differences. An analysis of the rate of faecal production exhibited no significant treatment interaction term (two-way repeated measures ANOVA on ranked data, $F_{3,9} = 3.285$, $P > 0.07$, power = 0.396), and thus main effects were examined. The feeding regimen treatment was the only statistically significant factor (two-way repeated-measures ANOVA on ranked data, feed regimen $F_{1,3} = 31.708$, $P < 0.01$, power = 0.946, day $F_{3,9} = 2.014$, $P > 0.15$, power = 0.191). However, in this instance, animals produced more faeces per day when fed a single time compared with when they were fed intermittently (Fig. 2). The TVS content of the faeces did exhibit a significant day × feed regimen interaction term (two-way repeated measures ANOVA on ranked data, $F_{3,9} = 6.271$, $P < 0.02$, power = 0.772). An analysis of simple effects shows that there was no significant difference in the TVS content of faeces between days for animals fed a single time (for all comparisons, Tukey's test, $q < 2.38$, $P > 0.25$). The same animals fed intermittently exhibited a general decrease in the TVS content in their faeces over the 4 days (Fig. 2). Day 1 was not significantly different from day 2 (Tukey's test, $q = 1.59$, $P > 0.65$), day 2 was not significantly different from day 4 (Tukey's

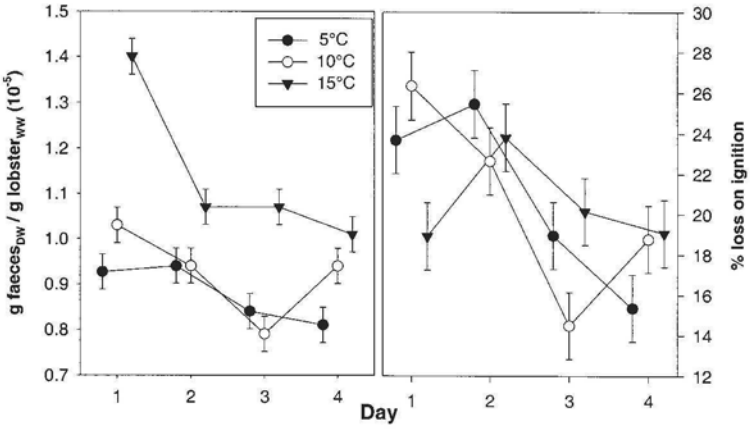

Fig. 3 Faecal output (left graph) and total volatile solid content (right graph) for each of 4 days after lobsters (*Homarus americanus*) were fed intermittently (every 4 days). Values were averaged (± 1 SE) over four feeding cycles—same four lobsters were tested at 5 and 10°C while five different lobsters were tested at 15°C. (DW, dry weight; WW, wet weight.)

Table 2 Analyses of the effect of temperature on faecal output (g faeces$_{\text{dry weight (DW)}}$/g lobster$_{\text{wet weight (WW)}}$) and total volatile solids (TVS) measured as the % loss on ignition at 500°C. Analyses are two-way repeated measures ANOVA with one or both factors repeated. Non-normal data were ranked, and indicated as such. Values for each day after feeding were averaged from four feeding cycles, and the first 4 days, except for when the lobsters were fed singly in which it was calculated over 6 days. Power was calculated with $\alpha = 0.05$.

		g faeces$_{DW}$/g lobster$_{WW}$				TVS			
Source of variation	d.f.	MSE	*F*	*P*	Power	MSE	*F*	*P*	Power
Four lobsters held at two temperatures (5 and 10°C), fed intermittently (faecal output and TVS ranked)									
Lobster	3	306.25				338.531			
Temp.	1	112.5	0.965	0.398	0.05	0.781	0.0259	0.882	0.05
Temp. × lobster	3	116.583				30.198			
Day	3	177.917	3.13	0.08	0.37	941.865	19.712	<0.001	1.00
Day × lobster	9	56.833				47.781			
Temp. × day	3	27.417	1.124	0.39	0.06	103.865	2.88	0.095	0.33
Residual	9	24.389				36.059			
Total	31	88.000				161.249			
Four lobsters held at 10°C and five lobsters held at 15ºC, fed intermittently (TVS ranked)									
Temp.	1	4.05E-09	4.269	0.078	0.34	70.313	0.366	0.564	0.05
Lobster (temp.)	7	9.48E-10				192.027			
Day	3	1.43E-09	7.465	0.001	0.94	528.205	14.083	<0.001	1.00
Temp. × day	3	4.24E-10	2.209	0.117	0.27	53.872	1.436	0.26	0.12
Residual	21	1.92E-10				37.508			
Total	35	5.91E-10				111.000			
Four lobsters held at 10°C and five lobsters held at 15ºC, fed a single time (faecal output ranked)									
Temp.	1	182.522	0.307	0.597	0.05	222.749	5.308	0.055	0.43
Lobster (temp.)	7	590.899				41.924			
Day	5	226.108	1.429	0.24	0.14	10.703	0.479	0.789	0.05
Temp. × day	5	265.72	1.68	0.167	0.21	24.599	1.102	0.378	0.07
Residual	34	158.202				22.331			
Total	52	229.647				28.116			

test, $q = 2.74$, $P > 0.25$), and day 4 was not significantly different from day 3 (Tukey's test, $q = 3.36$, $P > 0.610$). TVS exhibited a slightly different trend in that intermittent feeding exhibited significantly greater TVS values for the first 2 days than the third and fourth days, whereas animals fed singularly exhibited little day-to-day variation (Fig. 2).

Temperature

Temperatures between 5 and 15°C had virtually no impact on the quantity or quality of faeces produced by lobsters fed a single time or intermittently. In this experiment, three valid comparisons regarding temperature could be made: (1) the same animals fed intermittently at 5 and 10°C for 4 days; (2) different animals fed intermittently at 10 and 15°C for 4 days; and (3) different animals fed once at 10 and 15°C for 6 days (comparisons 3–5, Table 1). In each of these comparisons, the temperature factor and the temperature × day factor were not statistically significantly different (Table 2, Fig. 3). Of the three comparisons, the most valid pertaining to temperature was the first, as it compared faecal production in the same animals at two temperatures (Table 2). The lack of a significant temperature effect in this comparison, coupled with a lack of significant temperature effect of the other two comparisons lends further credence for failure to reject the null hypothesis of no relationship between temperature and the quality or quantity of faeces produced by lobsters (Fig. 3).

The significant day-after-feeding-treatment effect for lobsters fed intermittently (Table 2) further supports the results discussed previously that lobsters produce more faeces with a greater TVS content the first 2 days after feeding than if more time has elapsed since feeding (Fig. 3).

Duration of faeces production

The animals that experienced a single feeding regimen at 10°C had their faeces evaluated for 17 days post-feeding, whereas those animals tested at 15°C had their faeces collected for 8 days. In both trials, lobsters continually produced faeces for the first 6 days post-feeding. For the animals at 10°C, one animal did not produce faeces on the seventh and 17th days, and two did not produce faeces on the eighth day. At 15°C, one animal missed faecal production on the seventh day, and one on the eighth day. Excluding these days of no faecal production, there was no observed change in amount of faeces produced over the 17 days (one-way repeated measures ANOVA, $F_{11,33} = 1.37$, $P > 0.24$), or the TVS content of the faeces (%LOI_{500C}, one-way repeated measures ANOVA, $F_{11,33} = 1.36$, $P > 0.25$). The longest interval for which any of the feeding trials were carried out was 17 days. Although the data were collected as 24-h periods post-feed, the missed days of faecal production represented a period of between 24 and 48 h, as opposed to a stringent 48-h period.

It is likely that faecal production becomes more sporadic the longer after the animal was fed. The few days that lobsters did not produce faeces during the 17 days of monitoring was just the beginning of this pattern of reduced faecal output. Further evidence for long-term faecal production comes from lobster wholesalers. William Atwood Lobster Co, Spruce Head Island, ME, United States, held 680 t of newly caught lobsters for 3 months in an indoor flow-through system in 2003. In this production scenario, the lobsters produced c. 0.49 t of wet faecal waste. Assuming that lobster faeces were 7.3% DM (data from the previously-discussed laboratory experiments), this equates to 5.84×10^{-7} g $faeces_{DW}$/g $lobster_{WW}$ day^{-1}. This faecal production value was significantly lower than the c. 1.0×10^{-5} g $faeces_{DW}$/g $lobster_{WW}$ day^{-1} faecal production by lobsters during the feeding experiments (Fig. 2 and 3). It was likely that there was a degree of soluble loss of constituent faecal components, as well as loss of finer particles (Tlusty et al. 2000b). However, even with this loss of fine particles, these data suggested that there was a significantly lower faecal production by unfed lobsters over a 3-month period than that observed within the first 2 weeks. Thus any long-term estimate of faecal production by unfed lobsters will need to account for this decreased output.

Modelling cumulative organic matter production within lobster impoundments

The results presented above regarding the amount and organic matter content of lobster faeces, measured as TVS, can be used to estimate total organic matter production per impoundment over the course of the impoundment season. To simplify this modelling exercise, the experimental results for faecal production and TVS content of American lobster faeces needed to be pared to parsimonious trends. From the data presented above, it was first assumed that faecal production did not vary with temperature when winter-time temperatures (<10°C) were considered. Second, the quantity and quality of faeces produced did not vary with size of the meal fed as a % of the lobster's weight. In the experiments on faecal production described above, a meal of 3% g food/g body was utilised. Although this was the amount that was often fed to lobsters at the beginning of the impoundment season, by the end of the season, when temperatures were colder, food was being delivered at a rate of <1% g food/g body day^{-1} (Fig. 4). This ration was completely consumed, as American lobster will consume up to 50% (wet weight basis) of their body mass daily (Donahue et

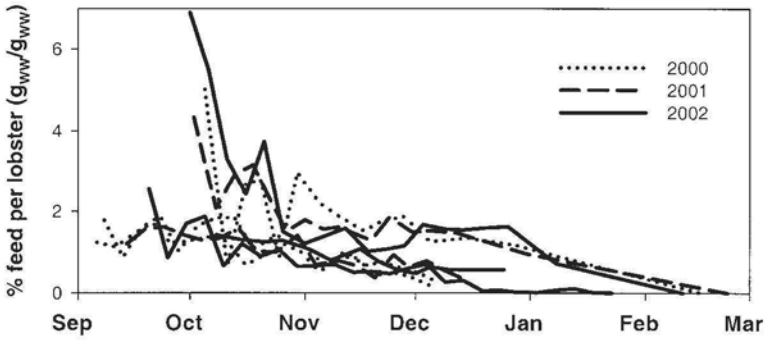

Fig. 4 Amount of food fed (% on a wet weight (WW) basis) to lobsters (*Homarus americanus*) in 10 impoundments during three seasons. Decrease in the amount of food delivered to the lobsters corresponded to a decrease in water temperature.

Table 3 Physiological conditions of faecal output used to model the cumulative production of organic matter by American lobsters (*Homarus americanus*) held in impoundments. Values were ascertained from the previous feeding trial studies. (DW, dry weight; WW, wet weight.)

Days between feedings	g $faeces_{DW}$/g $lobster_{WW}$	% volatile solids (LOI_{500C})
<3	1.10E-05	25
3–17	8.70E-06	20
>18	5.87E-07	15

al. 1997). Ration size would influence digestion via a change in the gut retention time, where larger and more frequent meals would decrease the amount of time the food was processed in the gut (Stephens & Krebs 1986; Hilton et al. 2000). In other animals, the time food is retained in the gut is negatively related to digestive efficiency (Johnston & Mathias 1996; Hilton et al. 2000). However, given the relatively low ratio of food fed in these experiments, it is questionable as to whether faecal quality would change significantly with a decrease in feeding ration. The third and final control rule was that animals fed every day or every other day produced more faeces with higher TVS than those animals fed intermittently, and animals fed every 3–18 days produced more than those animals fed once every 18 days or more (Fig. 3).

The control rules as they were used in this modelling exercise are listed in Table 3. Using these values to calculate TVS production, it was observed that TVS production varied between impoundments and years (Fig. 5). In general, the stocking of animals into the impoundment began between the first week of September and the first week of October. The impoundments were fully stocked over the next 40–75 days, and were completely stocked with an average of 3.79 ± 1.29 (± 1 SD) kg $lobster_{WW}$ m^{-2}. Animals were fed daily or every other day during the stocking period, and as the temperatures became colder and the animals "bed" down, feeding became intermittent. A majority of owners fed for 80 to 120 days following the first day of stocking, although one owner fed for 155 days (Fig. 5). Animals were removed beginning in January or February, and the impoundments were generally clear of animals by April, c. 190–210 days after the animals were first added to the impoundment (Fig. 5).

The variability in animal density, feeding protocol, rates of stocking and removal influenced the total amount of TVS produced. Through the feeding period, an average of 661.70 ± 289.89 (± 1 SD, n = 10) kg TVS were produced per impoundment. This represented 77.9 ± 15.3% (± 1 SD, n = 4) of the TVS produced during the entire impoundment period. Adjusting the impoundments lacking the lobster removal data to account for TVS production through the entire impoundment cycle, the average cumulative TVS produced per impoundment was 849.4 ± 367.0 kg_{DW}. This corresponded to a production rate of 0.79 ± 0.35 (average ± 1 SD) g TVS m^{-2} day^{-1} for the 10 impoundments examined here, equivalent to 3.11 ± 0.60% TVS_{DW}/$lobster_{WW}$ of the total weight of lobsters stocked into the impoundment.

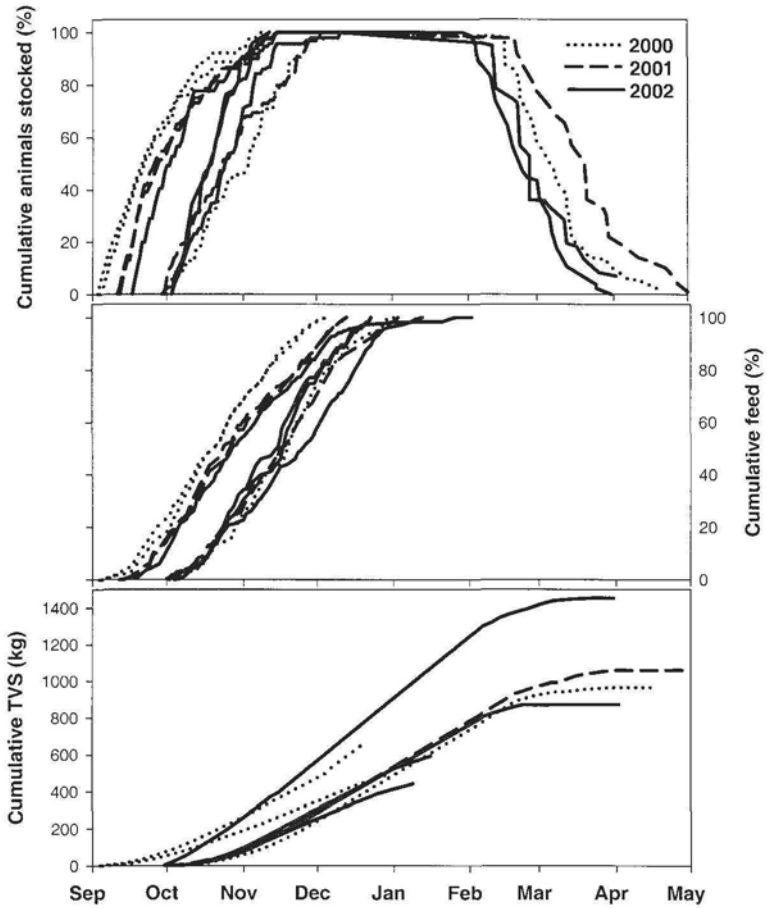

Fig. 5 Stocking (top), feeding (middle), and the modelled cumulative organic matter production (total volatile solids (TVS) measured as loss on ignition at 500°C, bottom) for 10 lobster (*Homarus americanus*) impoundments over three seasons.

DISCUSSION

The impoundment of American lobsters is best thought of as an aquaculture operation. Animals are held, fed, and occasionally medicated, for periods up to 6 months. Thus, the estimates of organic matter production within these impoundments (based on both production per unit area and per unit lobster produced) need to be compared to other types of aquaculture operations. Salmon aquaculture operations will be used as the main comparator, as it is also carried out in coastal waters of North America. The general observation has been that carbon flux rates to the benthos in excess of 1 g carbon m^{-2} day^{-1} exceed mineralisation capabilities thus causing anoxic sediments (Oviatt et al. 1987; Hargrave 1994). Above this rate, the oxidation-reduction potential of the sediment eventually becomes negative causing anoxia, subsequently leading to decreased infaunal diversity and hydrogen sulfide production (Brown et al. 1987; Findlay et al. 1995; Black et al. 1996; Brooks 2001). Total organic carbon is c. 63% of the TVS (Brooks 2001), thus the corresponding TVS loading that will not lead to increased deposition of sedimentary organic matter was 1.58 g TVS m^{-2} day^{-1}. Data from reference areas and those areas removed from anthropogenic input supported this value as they tended to have TVS deposition rates below 2.0 g TVS m^{-2} day^{-1} (Morrisey et al. 2000; Brooks 2001). Salmon farms had organic matter levels up to 18–24 g TVS m^{-2} day^{-1} observed immediately beneath the farm (Brooks 2001). The upper limit for the 95% confidence interval for TVS production in lobster impoundments examined in this study was 0.99 g TVS m^{-2} day^{-1}, which was below the value of 1.58 g TVS m^{-2} day^{-1} that was assumed to be within the ability of the environment to assimilate, thereby giving minimal impact. This analysis considers only

lobster-derived effluents, and not natural deposition. Lobster impoundments are active in the winter, a time when the natural productivity of ecosystems is low. It was unlikely that natural organic matter deposition in the impoundment areas during the winter would be equivalent to the amount being produced by the lobsters. A pulse of organic matter deposition was observed between April and September, the period when lobster impoundments are not being used, thereby corresponding to natural productivity associated with the North American summer (Tlusty 2003). Therefore, lobster impoundments were unlikely to reach the mark of 1.58 g TVS m^{-2} day^{-1}, and thus indicating that the solid waste production of lobster impoundments was low enough not to lead to an increase in deposition of organic matter to the benthos.

The estimate of organic matter production within lobster impoundments in Maine created through this procedure were an upper limit estimation. Because of the food that was utilised, and the temperatures at which the animals were held, organic matter production is likely to be greater than it would be under an actual impoundment scenario. The shrimp being fed to the experimental animals was likely to be more digestible than that in an actual working impoundment (most commonly herring or salted cod). Second, the laboratory animals were restricted in movement compared with animals in an impoundment. Finally, the lowest water temperature examined here was still greater than the 0°C commonly observed in the impoundments during winter. Furthermore, this estimated amount is the starting point before any subsequent environmental processing (soluble, transport, and consumption losses, Tlusty et al. 2000b). That being said, it was important to note the relatively low level of organic matter production observed by the lobsters under the simulated impoundment conditions. To understand how lobster impoundments compare to other aquaculture operations, this estimated upper limit value can be compared to real values for salmon and shellfish operations.

Because of the point source loading of aquaculture effluents, sediment organic matter tends to be greater adjacent to an aquaculture site than it is at a distance (Brooks 2001 and references within). The distribution of sedimentary organic matter is patchy, and although TVS content below salmon farms can range upwards of 65% (Samuelsen et al. 1988; Cornel & Whoriskey 1992; Tlusty et al. 2000b), it typically averages <20% (Hargrave et al. 1997). The Scottish Environmental Protection Agency uses 27% as the limit below which no remediative action is required (Heinig 2001). In shellfish aquaculture operations, rates of sediment deposition are comparable to that of salmon farms, although differences between faeces and pseudo-faeces can impact the quality of organic matter being deposited. Impacts ranged from negligible (Grant et al. 1999) to TVS values of between 20% and 25% (Dahlbäck & Gunnarsson 1981; Mattsson & Lindén 1983). In light of these values for TVS production, the lobster impoundment produced significantly less TVS than any other aquaculture operation, and the rate of TVS accumulation equalled that of the background areas referenced above. The TVS in surficial sediment samples from Maine lobster impoundments, measured as the $\%LOI_{500}$, averaged <5% (Tlusty 2003), and was often lower, especially within the lobster impoundments. These data further support the conclusions from modelling of solid effluent production that lobster impoundments produce relatively low levels of organic matter, which is being biologically processed instead of accumulating on the benthos.

The low levels of TVS being created and deposited in lobster impoundments compared to the greater levels around salmonid farms can assist in elucidating the factors important for minimising environmental impacts of marine aquaculture operations. The difference between these two types of aquaculture operations include differences in the digestion and feeding regimens of crustaceans compared to finfish, the length of fallowing periods utilised, stocking densities, and physical disruption of the benthos. The first factor leading to the relatively lower rate of TVS deposition was the lower rate of lobsters' faecal production compared with that of other aquacultured organisms. In addition to the different food types (although artificial diets fed to both are created similarly), the digestive system of lobsters is more complex than that of finfish. Lobsters have both a mid-gut and hind-gut caecum, which increases digestive and absorptive capabilities (Factor 1995). Salmonids have a more linear digestive system without additional ceacal capacity. These physiological differences resulted in lobster faecal TVS ranging from 15% to 25% depending on time since last feeding. In salmon, TVS content of faeces varied between 50% and 80%, although values as great as 90% in the winter were observed (Tlusty et al. 1998, 2000b). In addition to physiological differences, much of the cause behind the lower lobster faecal production in lobsters was the fact that they were fed

for c. 50% of their time in holding. Lobsters were not fed for months at a time, particularly after the temperatures reached their winter minima. Salmon were fed throughout the winter, although at a much reduced rate (Tlusty et al. 1998). These differences in digestion and feeding regimens ultimately resulted in different levels of organic matter production throughout the production cycle. During the impoundment period, TVS production was 3% of the total stocked lobster biomass. In comparison, estimates for total faecal production of salmonids through the production cycle averaged 16% (Bergheim & Åsgård 1996).

Second, lobster impoundments were not utilised continually throughout the year. They were empty, or fallowed, for up to 6 months per year. Fallowing was beneficial in that natural ecosystem functions were allowed to bioprocess any accumulated organic matter. Organic matter was assimilated through consumption, translocation, and diffusion (Tlusty et al. 2000b). Displaced organisms recolonised the disrupted areas during the fallow period, and their activity assisted to reoxygenate the benthos. This activity functioned to return the aquaculture area to a pre-disruption state. Although a low level of organic matter was deposited, the relatively lengthy fallow period further assisted in minimising the environmental impact of lobster impoundments. The benefits of fallowing within aquaculture operations are just now becoming more fully appreciated, and lobster impoundments serve as a positive example of their benefits.

Third, stocking density of lobsters was lower than that for salmonids, a function of the finish operations occurring in a volume of water as opposed to the planar stocking of lobsters. Salmon are stocked at a density of c. 18 kg m^{-3}. A salmon cage 50 m in circumference and 5 m deep, is stocked with 17 904 kg of fish. In terms of an areal impact, this would translate to a stocking density of 90 kg m^{-2}. Also, the bottom of a salmon cage is further removed from the benthos, and although this may lead to greater dispersal of organic solid waste over the area of the substrate (Findlay et al. 1995), often wastes are functionally dispersed immediately below the cages (Tlusty et al. 2000a). The dispersal of wastes on their path to the benthos would have to be significant to reduce the effluent production of salmon aquaculture sites to a level equal that of lobster impoundments.

Finally, lobsters are active on the benthos. Until winter temperatures reach their minima, the lobsters are moving around feeding. Their relatively thin walking legs will penetrate the soft surficial sediments. This serves to aerate and mix the upper few centimetres of the sediment, redistributing the pore water and ultimately maintaining a positive oxidation-reduction potential in the surficial sediment. This is similar to the idea of harrowing, which is often used to decrease the benthic impacts of aquaculture operations (Boyd 2003).

The research reported here was the first attempt to predict TVS production by impounded American lobsters. For this modelling effort, three control variables were incorporated into the model. The quantity and quality of faecal production did not vary with: (1) temperature <10°C; or (2) the feeding rate as a % of the body weight of lobsters; but (3) did vary with the feeding regimen. Specifically that more faeces of higher quality were produced when animals were fed daily or every other day compared to intermittently or not at all. The evidence for the first assumption was presented as the analysis of the feeding experiments conducted as part of this research programme. Physiologically, American lobsters respond differently to temperatures above in contrast to below 10°C. Maturity and egg development will remain in stasis or at a greatly reduced rate below 8°C, whereas above this temperature, animal growth and development proceeds rapidly (Cooper & Uzmann 1971; Aiken & Waddy 1989). It is likely that manifestation of temperature-mediated developmental differences have their basis in enzymatic and digestive functioning.

The second assumption that quantity and quality of faecal production did not vary with feeding rate as a % of the body weight of lobsters is less assured. Although the rate of 3% food/body weight was within the range of feeding rates used within the impoundments examined here, for a majority of the time, animals were fed <2% of their body weight daily (Fig. 4). In general, when animals were fed at a lower rate, gut retention time tended to increase, increasing nutrient absorption and thus leading to a decrease in TVS production (Stephens & Krebs 1986; Hilton 2000). Any decrease in faecal quantity or quality with the decreased rate of feeding likely will lead to subsequent decreases in the TVS production of the impounded animals. More work will be needed to assess the concomitant decrease in TVS production with a decrease in feeding rate. If TVS production is positively associated to feeding rate, then the estimations for TVS production can be considered an overestimation, as lower feeding rates would lead to lower levels of TVS production. Finally the third assumption, that more faeces of

higher quality were produced when animals were fed daily or every other day compared to intermittently or not at all, was also supported by the analysis of the feeding experiments conducted as part of this research programme. This observation coalesces with foraging theory (Stephens & Krebs 1986).

In addition to these control rules, there was also the implicit assumption that all food was consumed by the lobsters. The model developed here to estimate lobster impoundment TVS production assumed that all TVS is derived from faeces. If all food was not consumed by the lobsters, then the TVS content of the unconsumed feed would have to be accounted for in the estimation of TVS production. Functionally, uneaten feed would increase the amount of TVS reaching the benthos, and would increase the subsequent measure of sedimentary TVS. Food is placed in lobster impoundments directly on the bottom, and hence uneaten food would also increase the spatial variation of TVS throughout the impoundment.

The main tenet of sustainable aquaculture progress is that careful development of a suitable area at a reasonable effort can lead to an industry that has low to no impact on the environment (O'Connor et al. 1991; Olsen 1996; Tlusty et al. 1998). The best way to foresee potential impacts is to model the system to determine appropriate loading levels (Hargrave et al. 1994). It is critical to complete this work as early in the development of the industry as possible. When this work is put off the industry can outpace itself, which can result in a wide variety of environmental problems and subsequent public outcry. Proactive environmental work has the ability to quell any concerns citizen groups may have about negative environmental impacts (Tlusty unpubl. data). This work demonstrating low levels of organic matter loading in lobster impoundments and subsequent minimal impact on the naturally-occurring fauna was a necessary but long overdue component to assure the continued sustainable development of both aquaculture operations and the lobster fishing industry.

Recently, the United States Environmental Protection Agency listed lobster impoundments as aquaculture facilities that do not need active monitoring (USEPA 2002). The modelling presented here along with environmental assessments of impacts (Tlusty 2003) support the EPA ruling. However, lobster impoundment owners along with all aquaculture operators need to be cognizant of the effects and subsequent impacts that aquaculture can have on the environment. Lobster impoundments produce less organic loading to marine benthos than do respective salmon or shellfish aquaculture operations. This lower organic matter production and minimal resultant observable environmental impacts are because of the sparse feeding of impounded lobsters, a more efficient digestive process, the low organic matter production in the faeces, and the long fallow times each year. These results stress the importance of proper feed management, stocking, and fallowing in all aquaculture operations to continue to progress toward environmentally benign operations. Given the importance of lobster impoundment to the lobster fishing industry, coupled with the minor environmental impacts, it behoves regulatory agencies not to overburden the impoundment owners with unnecessary monitoring activities.

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REFERENCES

Aiken, D. E.; Waddy, S. L. 1989: Interaction of temperature and photoperiod in the regulation of spawning by American lobsters (*Homarus americanus*). *Canadian Journal of Fisheries and Aquatic Sciences 46*: 145–148.

Bayer, R. C.; Glalacher, M. L.; Leavitt, D. F. 1978: Nutrient requirement of the lobster and nutrition pathology. *Marine Fisheries Review 40(10)*: 44.

Bayer, R. C.; Riley, J.; Donahue, D. 1998: The effect of dissolved oxygen level on the weight gain and shell hardness of new-shell American lobster *Homarus americanus*. *Journal of the World Aquaculture Society 29(4)*: 491–493.

Bergheim, A.; Åsgård T. 1996: Water production from aquaculture. *In*: Baird, D. J.; Beveridge, M. C. M.; Kelly, L. A.; Muir, J. F. *ed.* Aquaculture and water resource management. London, UK, Blackwell Science. Pp. 50–80.

Black, K. D.; Kiemer, M. C. B.; Ezzi, I. A. 1996: The relationships between hydrodynamics, the concentration of hydrogen sulphide produced by polluted sediments and fish health at several marine cage farms in Scotland and Ireland. *Journal of Applied Ichthyology 12*: 15–20.

Boyd, C. E. 2003: Bottom soil and water quality management in shrimp ponds. *Journal of Applied Aquaculture 13*: 11–33.

Brooks, K. M. 2001: An evaluation of the relationship between salmon farm biomass, organic inputs to sediments, physiochemical changes associated with those inputs and the infaunal response—with emphasis on total sediment sulphides, total volatile solids, and oxidation-reduction potential as surrogate endpoints for biological monitoring. Port Townsend, Aquatic Environmental Sciences. 172 p.

Brown, J. R.; Gowen, R. J.; McLusky, D. S. 1987: The effect of salmon farming on the benthos of a Scottish sea loch. *Journal of Experimental Marine Biology and Ecology 99*: 425–433.

Conklin, D. E. 1995: Digestive physiology and nutrition. *In*: Factor, R. J. F. *ed.* Lobster biology. San Diego, Academic Press. Pp. 441–464.

Cooper, R.; Uzmann, J. 1971: Migrations and growth of deep-sea lobsters, *Homarus americanus*. *Science 171*: 288–290.

Cornel, G. E.; Whoriskey, F. G. 1992: The effects of rainbow trout (*Onchorhynchus nykiss*) cage culture on the water quality, zooplankton, benthos and sediments of Lac du Passage, Quebec. *Aquaculture 109*: 101–117.

Dahlbäck, B.; Gunnarsson, L. A. H. 1981: Sedimentation and sulphate reduction under a mussel culture. *Marine Biology 63*: 269–275.

Donahue, D. W.; Bayer, R. C.; Work, T. M.; Riley, J. G. 1997: The effect of diet on weight gain, shell hardness, and flavor of new-shell American lobster, *Homarus americanus*. *Journal of Applied Aquaculture 7(4)*: 69–76.

Ervik, A.; Hansen, P. K.; Aure, J.; Stigebrandt, A.; Johannessen, P.; Jahnsen, T. 1997: Regulating the local environmental impact of intensive marine fish farming. I. The concept of the MOM system (Modelling-Ongrowing fish farms-Monitoring). *Aquaculture 158*: 85–94.

Factor, R. J. F. 1995: The digestive system. *In*: Factor, R. J. F. *ed.* Lobster biology. San Diego, Academic Press. Pp. 395–440.

Findlay, R. H.; Watling, L.; Mayer, L. M. 1995: Environmental impact of salmon net-pen culture on marine benthic communities in Maine: a case study. *Estuaries 18*: 145–179.

Grant, J.; Hatcher, A.; Scott, D. B.; Pocklington, P.; Shafer, C. T.; Winters, G. V. 1999: A multidisciplinary approach to evaluation impacts of shellfish aquaculture on benthic communities. *Estuaries 18*: 124–144.

Hargrave, B. T. *ed.* 1994: Modelling benthic impacts of organic enrichment from marine aquaculture. Canadian Technical Report of Fisheries and Aquatic Sciences. Vol. 1949. 125 p.

Hargrave, B. T.; Phillips, G. A.; Doucette, L. I.; White, M. J.; Milligan, T. G.; Wildish, D. J.; Cranston, R. E. 1997: Assessing benthic impacts of organic enrichment from marine aquaculture. *Water, Air and Soil Pollution 99*: 641–650.

Heinig, C. S. 2001: The impacts of salmon aquaculture: the difficulties of establishing acceptability limits and standards. *In*: Tlusty, M. F.; Bengtson, D.; Halvorson, H.; Pearce, J.; Rheault, R. B. *ed.* Marine aquaculture and the environment: the perceptions of stakeholders in the Northeastern US. Falmouth, MA, Cape Cod Press. Pp. 41–68.

Hilton, G. M.; Ruxton, G. D.; Furnerss, R. W.; Houston, D. C. 2000: Optimal digestion strategies in seabirds: a modeling approach. *Evolutionary Ecology Research 2(2)*: 207–230.

Jansen, M.; Groman, M. 1993: The effect of high concentrations of iron on impounded American lobsters: a case study. *Journal of Aquatic Animal Health 5(2)*: 155–156.

Johnston, T. A.; Mathias, J. A. 1996: Gut evacuation and absorption efficiency of walleye larvae. *Journal of Fish Biology 49(3)*: 375–389.

Mattsson, J.; Lindén, O. 1983: Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. *Sarsia 68*: 97–102.

Morrisey, D. J.; Gibbs, M.; Pickmere, S. E.; Cole, R. G. 2000: Predicting impacts and recovery of marine-farm sites in Stewart Island, New Zealand, from the Findlay-Watling model. *Aquaculture 185*: 257–271.

O'Connor, B.; Hartnett, M.; Costelloe, J. 1991: Site selection and environmental monitoring in the mariculture industry: an integrated protocol. *In*: De Paw, N.; Joyce, J. *ed.* Aquaculture and the environment 1991. *European Aquaculture Society Special Publication 16*: 191–202.

Olsen, J. H. T. 1996: Developing sustainable aquaculture. *World Aquaculture 27*: 16–17.

Oviatt, C. A.; Quinn, J. G.; Maughan, J. T.; Ellis, J. T.; Sullivan, B. K.; Gearing, J. N.; Gearing, P. J.; Hunt, C. D.; Sampu, P. A.; Latimer, J. S. 1987: Fate and effects of sewage sludge in the coastal marine environment: a mesocosm experiment. *Marine Ecology Progress Series 41*: 187–203.

Pillay, T. V. R. 1992: Aquaculture and the environment. Oxford, Fishing News Books. 189 p.

Pillay, T. V. R. 1996: The challenges of sustainable aquaculture. *World Aquaculture 27*: 7–9.

Prince, D. L.; Bayer, R. C.; Gallagher, M. L.; Subramanyam, M. 1995: Reduction of shell disease with an experimental diet in a Nova Scotian lobster pound. *Journal of Shellfish Research 14(1)*: 205–207.

Rosenthal, H. 1994: Aquaculture and the environment. *World Aquaculture 25*: 4–11.

Samuelsen, O.; Torsvik, V.; Hansen, P. K.; Pittman, K.; Ervik, A. 1988: Organic waste and antibiotics from aquaculture. *In*: International Council for Exploration of the Sea Committee Meeting. 1988/F: 14, Mariculture Committee Session W.

Speare, D. J.; Cawthorn, R. J.; Horney, B. S.; MacMillan, R.; MacKenzie, A. L. 1996: Effects of formalin, chloramine-T, and low salinity dip on the behavior and hemolymph biochemistry of the American lobster. *Canadian Veterinary Journal 37(12)*: 729–734.

Stephens, D. W.; Krebs, J. R. 1986: Foraging theory. Princeton, Princeton University Press. 325 p.

Tlusty, M. F. 2003: Integrating American lobster biology into an assessment of organic matter loading to examine the environmental impacts of American lobster impoundments in mid-coast Maine. MIT Sea Grant College Program Final Report. 39 p.

Tlusty, M. F.; Anderson, M. R.; Pepper, V. A. 1998: Assuring sustainable salmonid aquaculture in Bay d'Espoir, Newfoundland. *Bulletin of the Aquaculture Association of Canada 98*: 35–37.

Tlusty, M. F.; Pepper, V. A.; Anderson, M. R. 1999: Environmental monitoring of finfish aquaculture sites in Bay d'Espoir, Newfoundland during the winter of 1997. *Canadian Technological Report of Fisheries and Aquatic Sciences 2273*. vi + 32 p.

Tlusty, M. F.; Hughes Clark, J. E.; Shaw, J.; Pepper, V. A.; Anderson, M. R. 2000a: Groundtruthing multibeam bathymetric surveys of finfish aquaculture sites in the Bay d'Espoir estuarine fjord, Newfoundland. *Marine Technology Society Journal 34*: 59–67.

Tlusty, M. F.; Snook, K.; Pepper, V. A. 2000b: The potential for soluble and transport loss of particulate aquaculture wastes. *Aquaculture Research 31*: 745–755.

United States Environmental Protection Agency 2002: Draft Guidance for Aquatic Animal Production Facilities to Assist in Reducing the Discharge of Pollutants. EPA–821–B–02–002. 100 p.

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