Towards integrated multi-species management of Australia's SE reef fisheries: A Tasmanian example

Stewart Frusher, Colin Buxton, Neville Barrett, David Tarbath, Kevin Redd, Jayson Semmens, Hugh Pederson, Joe Valentine and Michaela Guest

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Non-technical summary

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Objectives

1. To determine the impact of rock lobster fishing on abalone population dynamics
2. To evaluate the effect of abalone fishing on the community structure of the reef
3. To understand rock lobster predator-prey relationships, particularly in relation to changes that may have occurred as a consequence of fishing

Outcomes achieved

Moving from a single species assessment approach that has been the benchmark in fisheries globally to an approach that encompasses broader ecosystem issues requires both new methods and new concepts. This project used the abalone and rock lobster fisheries in Eastern Tasmania as a laboratory for which to trial new methods that would underpin an ecosystem approach to fisheries management (EAFM) or ecosystem based fisheries management (EBFM).

Recent research into the rebuilding dynamics of abalone and rock lobster populations within a marine protected area (MPA) identified the potential for interaction between these populations. Understanding these interactions was considered important if management decisions were aimed at optimising the benefit from the combined resource. Demonstrating these interactions was seen as the first step by which to engage stakeholders so that they could recognise that managing either fishery separately could impair the productivity of the other fishery.

The key observation in the MPA was that the medium size class of abalone was missing compared to adjacent fished sites. It was considered that the increase in lobster abundance and size within the MPA was a primary driver for this observation. Using standard surveys techniques we were able to identify that abalone emerge at a larger size within the MPA and that this was probably a behavioural response to the lobster biomass, the presence of larger lobsters or both.

A series of manipulative experiments identified that newly emergent abalone were ten times more likely to be consumed by rock lobsters than either non-emergent abalone or larger abalone that had emerged earlier and therefore survived the newly emergent

phase. Using a novel approach that linked abalone shell markings to lobster attacks, we were able to provide further supporting evidence that lobsters were important predators of abalone and that the abundance and larger size of lobsters in the MPA resulted in higher mortalities.

While the above outcomes indicated that lobsters did predate on abalone, we undertook a combined stable isotope and fatty acid signature approach to evaluate the importance of abalone to lobster diet. Although this method did detect differences between diets of rock lobster found in MPAs and fished regions, the contribution of abalone to the diet was relatively minor. Stable isotopes and fatty acid signatures are normally obtained from tissue samples to provide information on dietary items ingested over periods of months, depending on tissue turnover rates. In contrast, we evaluated the use of more recent developments in dietary DNA technology to identify key dietary items that had been ingested over periods of 1-3 days. We were able to develop a quick and non-lethal technique for extracting samples for dietary DNA analysis that enabled lobsters to be returned to their place of capture (e.g. in MPAs) or to the fisher for future live export. DNA markers were developed for specific prey items such as abalone, the common urchin and the invasive long spined urchin. Aquarium trials have demonstrated that the signal can be detected between 5 and 60 hours after ingestion of the prey item. This allows for dietary information to be obtained from lobsters that have been captured in traps left on the fishing grounds for up to 3 days. The DNA dietary method holds considerable promise for evaluating the interactions between predators and their prey in marine ecosystems.

Finally, we trialled acoustic telemetry as a method to understand the behavioural responses of lobsters inside and outside MPAs. There have been very few such behavioural studies undertaken on lobster and none that address the effects of fishing on ecosystem usage. Using the latest technology in acoustic telemetry we were able to demonstrate that fishing has impacted on lobster behaviour. It was also surprising to find that lobster activity patterns within the MPA demonstrated a degree of segregation between small and large lobsters of each sex and that these different activity patterns were not reflected in catchability of lobster in traps.

The second component of this report was to evaluate the effect of abalone fishing on inshore reef ecosystems. The first section of this component used fisher's knowledge to evaluate historical changes. Outcomes from fisher's interviews indicated that the fished area of reefs is dynamic and is affected by a complex relationship between abalone abundance, the amount of catch to be taken (TAC) and the financial rewards to abalone divers. Fishers stated that abalone populations fluctuated regionally although a general trend in more resilient (measured as the observed ability to recover from fishing) populations were found further south in Tasmania. Divers also noted a wide range of ecosystem changes that had also occurred over the past 30 years. Most divers recognised that the abalone populations that they were fishing had been

severely depleted. Although not consistent across all divers, several identified that after the removal of abalone, 'preferred' abalone habitat changed to 'less preferred' habitat. This was acknowledged as a change from crustose coralline algal (CCA) dominated habitat to habitat dominated by sessile invertebrates and foliose algae (IFA),.

Fisher knowledge was also supported by an empirical study of inshore reefs. While fine scale habitat preferences could not be identified in this study, the regional differences noted by fishers were distinguishable. In particular, there was a change in understory community composition from north to south, although the Acteaons region in south eastern Tasmania was substantially difference to other sites on the East Coast.

In conclusion, this project has demonstrated a range of novel and innovative ways to address species interactions and paths the way for an improved understanding of the effects of fishing on ecosystems. Importantly, it showed that a number of factors ranging from the use of fishers knowledge to the use of recent technological advances were equally valuable in providing the science necessary to underpin the move towards an integrated multi-species approach to fisheries management.

Keywords
Integrated assessment, abalone, rock lobster, stable isotopes, fatty acids, DNA dietary markers, acoustic telemetry, home range, species interactions

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FINAL REPORT

2004/013 Towards integrated multi-species management of Australia's SE reef fisheries: A Tasmanian example

Background

Inshore reef ecosystems support Tasmania's most important fisheries, valued at approximately $150 million in 2001 (ABARE 2002). Management of these fisheries has traditionally been species based; however, there is a growing demand for more integrated management with clear consideration of the ecosystem that supports the fishery (ecosystem based management – EBM).

In a letter to FRABs in 2003, FRDC highlighted this need, stating that alternative fisheries management structures and methods that provide for EBM was a national need to ensure that fisheries natural resources are used in a sustainable way.

Understanding the effects of fishing is an important component of this as extraction of key reef species has the potential to alter ecosystem function. For example, recent studies in Tasmania and New Zealand suggest predation by lobsters may play a pivotal role in structuring their habitat. Research in the Maria Island marine protected area (MPA) suggests that the current productivity of abalone stocks on the east coast may be due to relatively low predation pressure from depressed rock lobster stocks (Buxton et al. FRDC 1999/162). Currently, management of the rock lobster fishery targets rebuilding of the biomass without consideration of the impacts on other species. To optimise the benefits of both fisheries, management needs to account for this interaction.

In response to several proposals in the 2003 round that addressed this issue, FRDC organised a workshop in Melbourne to discuss a coordinated approach to EBM, focusing on the SE region. This proposal directly addresses the outcomes of the workshop. It builds on several existing research projects and has objectives relating to specific questions associated with observed patterns. The project is ideally placed to operationalise the ESD agenda for fisheries and informs natural resource management (NRM) objectives for coastal marine systems. Significantly, collaborations between SARDI and TAFI will provide a solid foundation for this new strategic focus.

The outcomes of this work will also include a framework for a multi-species management approach for abalone and rock lobster fisheries. This includes the environmental accreditation standards of both Australian and future international schemes to improve Australia's reputation as a quality seafood exporter.

In October 2002, TAFI convened a workshop with industry and government to identify a vision and long-term strategy for addressing research to underpin ecosystem-based management.

In summary, three broad areas were identified for the next 10 years:

1. Moving towards a risk assessment approach to integrated species management.
2. Understanding the impacts of fishing on ecosystem health.
3. Gaining a greater understanding of target and by-catch species interactions.

Due to the scale of the problem, the initial focus was restricted to the reef ecosystem that supports Tasmania's key lobster, abalone and scalefish fisheries, more specifically the east coast where fishing pressure has been the most intense and fished stocks are most heavily impacted. Rock lobster and abalone fisheries were considered to be relatively benign with respect to the physical effects of fishing and by-catch species (both retained and non-retained). The research priorities were thus directed at evaluating the ecosystem consequences of removal of the target species, and the interactions between the key target and non-target species.

In March 2003 a strategic planning workshop with government and industry was held to develop the 2003–2008 Tasmanian Fisheries and Aquaculture Research Plan. This workshop confirmed the need for Tasmania to develop a strategic R&D response to ecosystem-based management.

This project will contribute to EBM by addressing several core issues including habitat utilisation of key exploited species, species interactions that have a key role in structuring the community, and trophic dynamics (food webs).

The project will progressively build layers of information to aid our understanding of the dynamics of Tasmanian reef ecosystems. Initial work will determine habitat utilisation of key commercially fished reef species (building on FRDC 1999/162). In this proposal our specific task will be to focus on abalone and rock lobster. Study sites will be comprehensively mapped to provide a baseline of the extent and quality of habitat (e.g. algal/sponge/coralline cover, dolerite boulders/sandstone shelves). Surveys using low light and infra-red (night time viewing) underwater video cameras, the latest developments in acoustic tags and visual diver observations will be used to determine habitat utilisation. By comparing unfished sites and fished sites, we will address the question of what changes have occurred in habitat utilisation due to the removal and subsequent decline in density of larger animals.

Over this habitat layer we will build a new layer focused on species interactions. Again following the requests of TAFI's stakeholders, our initial focus will be on abalone–algal community interactions and rock lobster–abalone interactions.

The next layer that is being proposed in this project is to explore trophic dynamics. Although this is a complex and immense task, our initial focus is to explore the potential of DNA markers to identify prey items of rock lobsters. By using a mixture of traditional stomach/foregut analyses and aquaria trials, we aim to determine the ability of DNA technology to provide both quantitative and qualitative measures of predation. If successful, we plan to establish a DNA library of reef organisms that can be used to screen the stomach content or faecal material of any potential predator.

The tasks identified in each of the above mentioned layers have been combined in this proposal and represent the first stage of TAFI's larger strategic focus.

Need

This project is the first of a larger strategic focus that moves away from species-based management towards integrated ecosystem management. It will give impetus to:

a) understanding the implications of management of one resource on another
b) measuring the impacts of increased utilisation of the marine ecosystem on the health of all components of the ecosystem (e.g. commercial and recreational fishing, tourism, aquaculture)
c) establishing baseline data that can be used to monitor environmental change (e.g. introduced pests, global warming)
d) meeting the increasing need of consumers for environmental accreditation (e.g. MSC, EA). This is particularly the case for diversification of future markets.

This project addresses several aspects of Australia's Marine Science and Technology Plan.
Program 1 – Understanding the Marine Ecosystem
Objective 6: To understand the biological processes in Australia's oceans
Objective 7: To understand the dynamics of Australia's marine habitats and ecosystems
Program 2 – Using and Caring for the Marine Environment
Objective 1: To ensure the maintenance of healthy and properly functioning ecosystems through the development and application of effective monitoring and assessment procedures and sustainable management practices
Objective 6: To improve the productivity and sustainability of wild harvest fisheries, and to improve understanding of the relationship between fished stocks and the ecosystems that support them.

The project addresses FRDC's strategic vision to move towards assessment and management of Australia's fisheries at the ecosystem level rather than the single species level. A concern in embracing integrated multi-species or ecosystem-based management is the breadth of ecosystem issues that can be tackled. By focusing on specific issues identified by our stakeholders, this project has the potential to demonstrate the benefits of multi-species management in two of SE Australia's most valuable fisheries, and the need for this approach to be adopted as the future management framework.

The need to develop and apply new methods is core to improving our understanding of marine ecosystems. This project encompasses this need with the use of infra-red and low light video technology, acoustic telemetry and DNA dietary studies, all of which represent frontier technologies.

At the TasFRAB Wildfish Strategic Planning Workshop held in 2003 to develop Tasmania's 2004–2009 Strategic Fisheries Plan, both industry and government recognised that a healthy and productive reef ecosystem is essential for maximising the social, economic and aesthetic returns to rural coastal populations in Tasmania.

At the Southern Fisheries Management Workshop (SFMW) held in November 2003, managers highlighted three separate approaches that needed to be addressed in pursuing ecosystem-based management. These were a systems approach that described a management unit and

incorporated all inputs into the system (e.g. Westernport Bay and associated catchments, Great Australian Bight); a risk assessment approach; and an understanding of processes that drive systems. TAFI's approach that focuses on understanding process based on observed patterns was endorsed by the SFMW. It was noted that TAFI was in the best position to undertake this research in a cost effective manner as this approach suited postgraduate studies.

Objectives

1. To determine the impact of rock lobster fishing on abalone population dynamics
2. To evaluate the effect of abalone fishing on the community structure of the reef
3. To understand rock lobster predator-prey relationships, particularly in relation to changes that may have occurred as a consequence of fishing.

1 Determining the interspecific relationship between abalone and rock lobster

1.1 Size structure of cryptic and emergent abalone and correlations with predators and competitors.

Introduction

The strong correlation between decreasing abalone abundance and increasing lobster abundance/size within the Maria Island marine reserve suggests that lobster and abalone fisheries may be closely interrelated. However, there are several potential causes of the observed decline in the abundance of abalone and all need examination. The presence of large abalone may increase intra-specific competition, resulting in delayed emergence and/or higher juvenile mortality. Increased predator numbers (lobster and fish) may lead to delayed emergence in response to behavioral changes. Finally, increased predator numbers/sizes may result in higher levels of predation. Examining the potential interactions between and within species requires a combination of correctional and experimental approaches.

Methods

The methods are described in detail by Pedersen et al (2008) (see Appendix 1).

Results

The results are described in detail by Pedersen et al (2008) (see Appendix 1).

Summary of findings

A survey of the 10 sites revealed a more than 50 millimetre difference in size of emergent abalone across the sites. The predicted size of emergent abalone (50% of the population) was considerably higher at the five sites inside the marine reserve compared to sites in adjacent fished habitats.

Significant relationships between the size of emergent abalone (probability of 50% of the population emergent at a predicted shell length) and rock lobster abundance (P=0.002, R2=0.71) and average rock lobster size (P=0.0004, R2=0.81) have been identified. Sites with high rock lobster abundance supported abalone populations with larger size at emergence. Similarly, sites with larger lobsters (mean carapace length) supported abalone populations with larger emergent abalone.

In contrast, the patterns in abalone size at emergence were not dependent upon the density of the most common crab, *Plagusia chabrus*, or a suite of predatory demersal fishes including the labrids *Notalabrus tetricus* and *Pictilabrus laticlavius* which are predators of juvenile abalone elsewhere in temperate Australia.

Discussion

The clear indirect effect of lobster fishing on abalone populations was to change the size of emergence. Outside the marine reserve, in the presence of lower numbers and smaller sized lobsters, more than half of the animals below the minimum legal size were emergent (55%). This fraction was greatly reduced inside the marine reserve (16%) where individuals greater than the minimum legally exploitable size of 136 millimetres accounted for more than half the population compared to adjacent areas where fishing has reduced the number of exploitable individuals to less than 20% of the population.

The change in size at emergence with lobster size and density has implications for the assessment and management of abalone populations. Catchability and thus catch rates will decline in areas where lobster density and average size is higher as a larger portion of the legal sized population will remain hidden. Catch rates would therefore need to be standardised against lobster density and size in regions where there are substantial differences. Furthermore, the use of undersized abalone as an indicator of potential recruitment to the fishery would be biased if rock lobster abundance and size varied between sampling regions.

Finally, there was no indication that the difference in the size composition of lobsters inside the marine reserve was due to abalone emerging at the 'fished area' size at emergence and being predated upon by the larger lobsters in the reserve.

Detailed descriptions of the size structure and abundance of lobsters and abalone in the Maria Island marine reserve and adjacent fished regions are provided in Appendix 1.

1.2 Determing size-specific predation of abalone, and the dynamics of lobster predation on abalone

Introduction

Section 1.1 demonstrated that increased densities of lobsters and larger lobsters can impact on abalone by changing their behaviour. Abalones were found to emerge at a larger size in regions where the density and average size of lobsters was substantially larger (Pederson et al, 2008). While this finding partly addresses the concern over the lack of smaller post-emergent abalone in the marine reserve, as compared to fished sites, it does not address the issue of overall predation of abalone by rock lobsters. In particular, if an increase in the biomass and size of lobsters results in increased predation on abalone then the current management objective of the lobster fishery to rebuild biomass may adversely impact on the abalone fishery.

Of current interest is the need to have more large lobsters (>135 mm CL) on reefs in an attempt to prevent the formation of 'barrens' by *Centrostephanus*. The later is becoming more abundant on Tasmanian reefs due to climate change and has the potential to denude up to 50% of reefs, similar to NSW where it originates (see Ling et al, 2008). If abalone predation was higher due to increased numbers of large lobsters then the abalone TAC would need to be reduced. However, this reduction is unlikely to be as great as the decline in abundance of abalone if extensive barrens become established as few abalone are found on barrens.

This section is aimed at understanding the predator–prey relationship between abalone and rock lobsters.

Methods

The methods are described in detail by Pedersen et al (in press) (see Appendix 2).

Results

The results are described in detail by Pedersen et al (in press) (see Appendix 2).

Summary of findings

Newly emergent abalone inside the MPA were almost 10 times more likely to experience predation compared to post-emergent adults in the same habitat. Pre-emergent abalone, that are normally hidden from predators, experienced similar levels of predation compared to post emergent abalone. In contrast, in fished sites there appeared to be no difference in the relative likelihood of mortality between the three size classes. The size at which abalone emerge from crypsis appears to be a

major factor determining their susceptibility to predation mortality and there was no overall size preference for abalone by rock lobsters.

Examination of empty shells following the tethering experiment indicated that the number of abalone mortalities directly attributed to rock lobsters (by the presence of 'chip' marks on the margin of shells) was higher inside the MPA compared to adjacent fished sites. The range of shell sizes with these characteristic 'chip' marks was also broader at sites inside the MPA, where rock lobster abundance and average size were elevated, confirming that rock lobster size plays a role in abalone mortality.

The combination of results from the manipulative experiments and surveys undertaken showed that *Jasus edwardsii* is an important predator of *Haliotis rubra* and that the likelihood of mortality is related to the abundance and size of rock lobsters.

Discussion

These results demonstrate that rock lobsters are an important predator of abalone and an increase in the average size and abundance of lobsters is likely to lead to increased abalone predation.

Inter-species management of these two species in an ecosystems context is considered important if optimal utilisation of both resources is to be achieved. Further research to optimise economic benefits from the combined use of the resource is required.

Performance indicators

(i) Report on the predators within and outside the Maria Island Marine Reserve including size specific predation by different size categories of lobsters.

The report identifies rock lobsters as the main predators of abalone inside and outside the Maria Island Marine Reserve. As the mortality of newly and post emergent abalone was not significantly different between the rock lobster inclusion treatment and partial cages where all other predators were available, other predators contribute to very little mortality.

The report identifies that larger lobsters consume a broader size range of abalone.

(ii) Visual and written documentation of abalone predation dynamics by lobsters.

The report documents the manner in which lobsters predate upon abalone through visual observation in aquarium and of tethered abalone. These observations highlighted a pattern of 'chip' marks that indicate lobster predation activities. These marks were subsequently used to identify the proportion of abalone shells that could be attributed to lobster impacts.

2 Evaluating the effect of abalone fishing on the community structure of the reef

2.1 Evaluation of the decline in extent of commercially viable abalone reef in eastern Tasmania relative to fishing pressure

Introduction

Understanding the relationships of marine herbivores with their habitat is important for improving knowledge of reef ecology and management of reef-based fisheries (Gislason et al., 2000; Tegner and Dayton, 2000; Jennings et al., 2001). In Tasmania's abalone fishery, a number of divers have consistently reported that they have noticed changes to reefs following extensive depletion of abalone populations by fishing, suggesting a level of interdependency between abalone and habitat. These changes include the reduction in coverage of crustose coralline algae and its subsequent replacement by sediment, other encrusting organisms and algae. The immediate implications to the fishing industry include a reduction of habitat type associated with abalone recruitment (Shepherd and Turner, 1985; McShane and Smith, 1988) and consequently further depletion to levels beyond which abalone may be viably fished.

Overfishing and subsequent depletion leading to the collapse of abalone populations on individual reefs and parts of the coast are common problems (Dugan and Davis, 1993; Shepherd and Baker, 1998; Karpov et al., 2000) and are difficult to detect (Keesing and Baker, 1998). While catch statistics show that overall the Tasmanian blacklip abalone fishery has been relatively robust, indications of depletion and loss of production have been evident in parts of the fishery. Following years of fishing at apparently sustainable levels, some reporting areas (blocks) of the abalone fishery in north-east Tasmania experienced rapid declines in annual catch to less than 10% of their former levels (Tarbath et al., 2007). These blocks are large (tens of kilometres), and consequently the history of abalone production from individual reefs within them is unknown. However, some divers who once worked extensively along the coastline say that many of the reefs are now too depleted to warrant economically viable fishing, and fishing activity is concentrated on the remaining productive reefs. They say that this has also occurred in other previously productive parts of the Tasmanian fishery.

The reports of depletion and changing habitat, although consistent, are not widespread, perhaps because through economic necessity, divers stop visiting reefs that are no longer productive. In addition, the Tasmanian abalone fishery covers a vast area and the location and history of production from reefs exists only as fragments of knowledge among individual divers. This project was established to identify and locate depleted reefs in eastern Tasmania by collating this knowledge and comparing where divers fished at various stages throughout the life of the

fishery. It was intended that a broad picture of the spatial coverage of the stock at various stages throughout the history of the fishery would emerge. In particular, the spatial extent of any decline could be assessed by mapping coast where divers fished in the early years of the fishery and comparing it with later years.

The information gathered from this project will be used in two ways. The first is to confirm whether any decline in commercially viable reef has occurred. If, as catch statistics suggest, there has been a decline, then more questions are raised: is the decline ongoing or did it occur earlier in the history of the fishery, thereafter leaving a stable area of productive reef? To what can the decline be attributed? If the decline is ongoing and the annual catch is being taken from a progressively smaller area of reef, then this may have implications for stock assessment. Should the area of productive reef be taken into consideration when settings limits on catch?

Second, the information will be used as a starting point to explore the nature and extent of habitat changes associated with any productive reef decline. This relates to the second part of this project: to compare biological and environmental correlates of reefs that continue to sustain commercial abalone fishing with reefs that no longer support a viable fishery. It is essential that the reefs both actively fished and depleted be identified for use in the second part. It also becomes important if small spatial scale monitoring becomes achievable in the Tasmanian fishery and there is any investigation of the characteristics of reefs with regard to variability in resilience of their abalone populations to fishing.

Methods

(a) History of fishing

Effects of abalone fishing were assumed to be most pronounced (and hence more easily detected) in areas with the greatest levels of depletion, and presumably less easily seen in areas with stable and high levels of abalone abundance. There have been no successful large-scale abundance monitoring projects undertaken in Tasmania, so there is no direct evidence that indicates that stock levels were formerly higher. However, inferences about stock levels can be made by comparing changes in levels of catch or production throughout the course of the fishery, particularly with knowledge of the critical events (e.g. management controls, market factors) made during the history of the fishery (Figure 1); in other words, productivity is a function of abalone abundance (Shepherd et al., 2001).

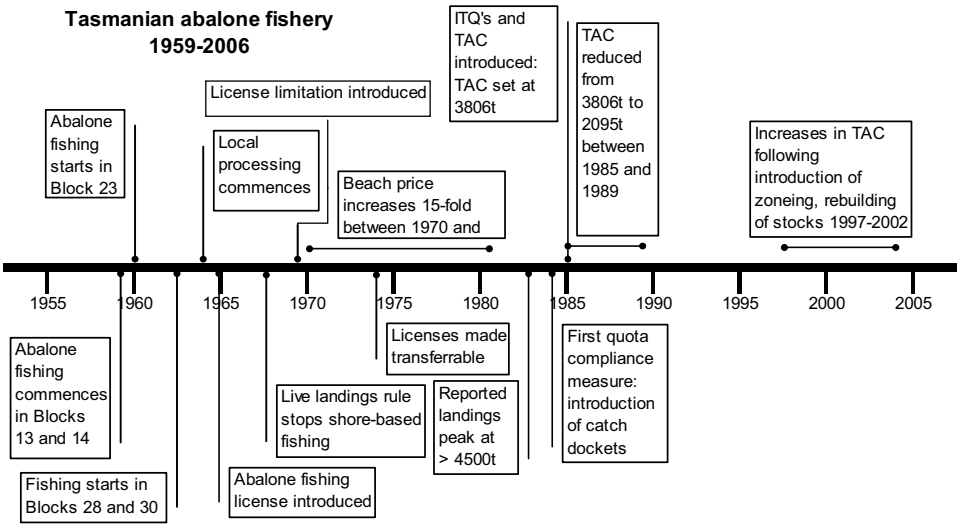

Figure 1 **Timeline of events affecting production and reporting of catch in the Tasmanian abalone fishery, 1959–2006**

The abalone fishery quickly extended around Tasmania's coastline during its formative years, and within 10 years, the annual catch increased rapidly. There are no records of annual production reported by block prior to 1975, but it is known that the eastern half of Tasmania produced most of the catch. Anecdotal information suggested that at least half the early catch was taken from just five blocks, near the fishing ports of Dover (blocks 13 and 14), Dunalley (Block 23), Bicheno (Block 28) and St Helens (Block 30) (Figure 2).

These blocks were of particular interest because (a) significant parts of the annual catch were (or still are) taken from their waters, and (b) there were large declines in annual catch between different periods of the fishery. If there were environmental consequences of abalone depletion, then they were more likely to be found in these blocks.

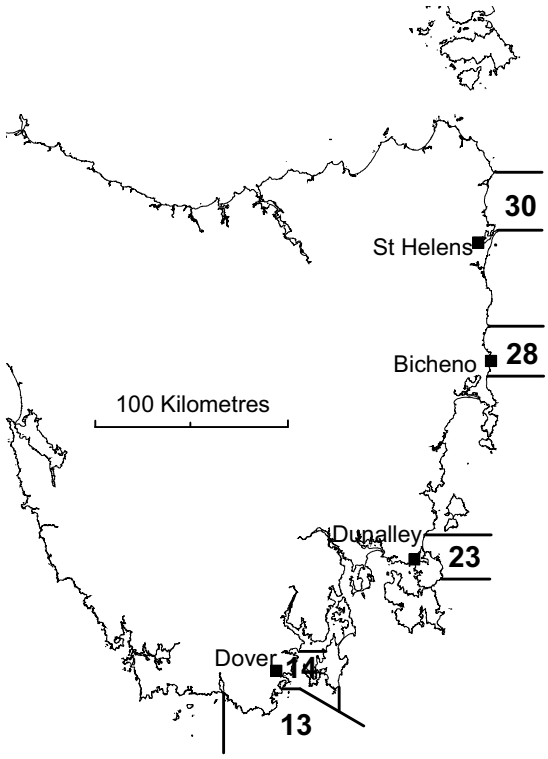

Figure 2 **Eastern Tasmania, showing the towns and coastline prominent in the early history of the abalone fishery. The numbers of the areas (blocks) from which catch was reported are shown, and their boundaries indicated by lines.**

Catch statistics from the early years of the fishery are not reliable (Figure 3). Audits of divers' and processors' income by the Australian Taxation Office during the 1980s exposed widespread under-reporting of catches. The earliest catches were reported to the Tasmanian Department of Agriculture on general fish returns prior to 1966, but estimates of annual production prepared from them are unavailable. The earliest estimates (starting 1964) of annual abalone catch were prepared from returns supplied by processors, but because much of the catch in the early part of the fishery was processed interstate, the total of the landings processed in Tasmania was less than the total catch.

In 1965, divers were required to be licensed to fish for abalone. From 1966, the Department of Agriculture collected monthly catch totals from the skipper of the vessel from which licensed divers operated, although in practice, the skipper was often one of the divers, if not the only diver. There were large discrepancies between the processor and diver annual total catches, and between 1966 and 1977, processor annual totals were always greater than diver annual totals, despite part of the catch being processed outside Tasmania.

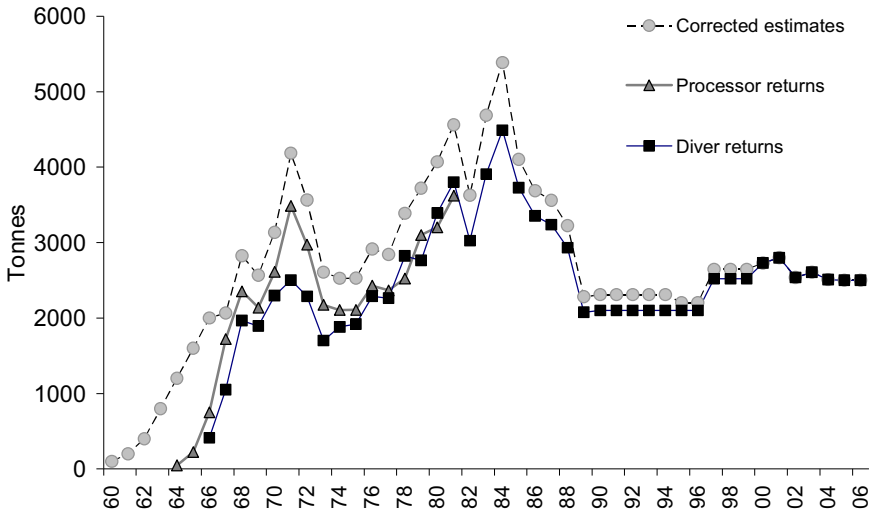

Figure 3 **Estimates of annual production (tonnes) from the Tasmanian abalone fishery, 1960–2006. Prior to the introduction of ITQs and a TAC in 1985, annual production was routinely under-reported. The earliest catches (pre 1964) were reported on general fish returns, but annual total catches are unavailable. The Tasmanian Department of Agriculture collected monthly returns of catch purchased by Tasmanian processors (processor returns), starting in July 1964. Estimates of annual processor totals did not include Tasmanian catches processed in other states. Between 1966 and 1984, the Department of Agriculture collected monthly returns of catch by block (starting in 1966) from the skippers of boats operating in the abalone fishery (diver returns). From 1985, catches were reported on a daily basis directly by divers, and catch totals became more accurate. A third series of production totals was estimated to account for under-reporting. Estimates were initially derived from anecdotes, partially supported by divers' diaries (1960–66). Between 1967 and 1984, a 20% correction factor was applied to the higher of the divers' and processors' totals. Between 1985 and 1994, the correction factor was halved, and halved again between 1995 and 1999. Catch totals were not corrected after 1999.**

Widespread concern by divers about falling stock levels in the early 1980s led to the introduction of output management controls (individual transferable quotas (ITQ) and a total allowable catch (TAC)), in 1985. It was not until the development of these controls that stricter compliance measures were introduced (catches were required to be accurately weighed and reported after landing) and estimates of annual catch became more reliable. Even so, for many years that followed, it was noticed that some processors were achieving much higher yields of product than technically possible from the abalone that were reported sold to them. It is therefore assumed that catches remained under-reported well into the 1990s, when major changes that ensured greater levels of compliance with catch-reporting requirements were introduced.

To compensate for under-reporting, a third series of annual catch estimates was prepared. Estimates of catch between 1960 and 1970 were derived using anecdotal estimates of the catches of early divers, partially supported by personal record-keeping and journals. Estimates of annual catch between 1971 and 1999 were derived by adding a correction factor to the higher of the divers' or processors' annual totals. Guided by information from former divers, processors and fisheries officers, this

correction factor was arbitrarily set at 20% for the period between 1971 and 1985. Between 1985 and 1994, the correction factor was reduced to 10%, and between 1995 and 1999, reduced to 5%. Catch totals were accepted as complete after 1999.

The annual catch totals for the five reporting blocks were prepared from state government catch data (divers' returns), and consequently, early production is under-estimated (Figure 4). It is not appropriate to apply a correction factor over such small spatial scales, because divers frequently moved their operations between blocks and there is no information about between-year variation in the spatial distribution of catch. However, to gain a better appreciation of the blocks' productivity, the size of their earlier annual catches should be considered in the context of the corrected size of the state catch.

The catch histories of blocks 14, 28 and 30 are particularly misleading. They start with relatively low but rising levels of catch followed by declines, giving the impression of rapidly developing fisheries followed by a swift boom and subsequent bust, suggesting that their stocks were of limited productivity. This is not the case. The size of the corrected estimates of statewide production in the 10 years prior to 1975, the misreporting of catches and the proximity of the blocks to fishing ports mean that these blocks had a much longer history of high levels of production than is apparent. These were among the most productive parts of the fishery. Although output controls limited the size of annual catches from 1985, their lower yields in later years are largely attributable to depletion. If environmental effects attributable to depletion of abalone by fishing exist, then they should be evident in these blocks.

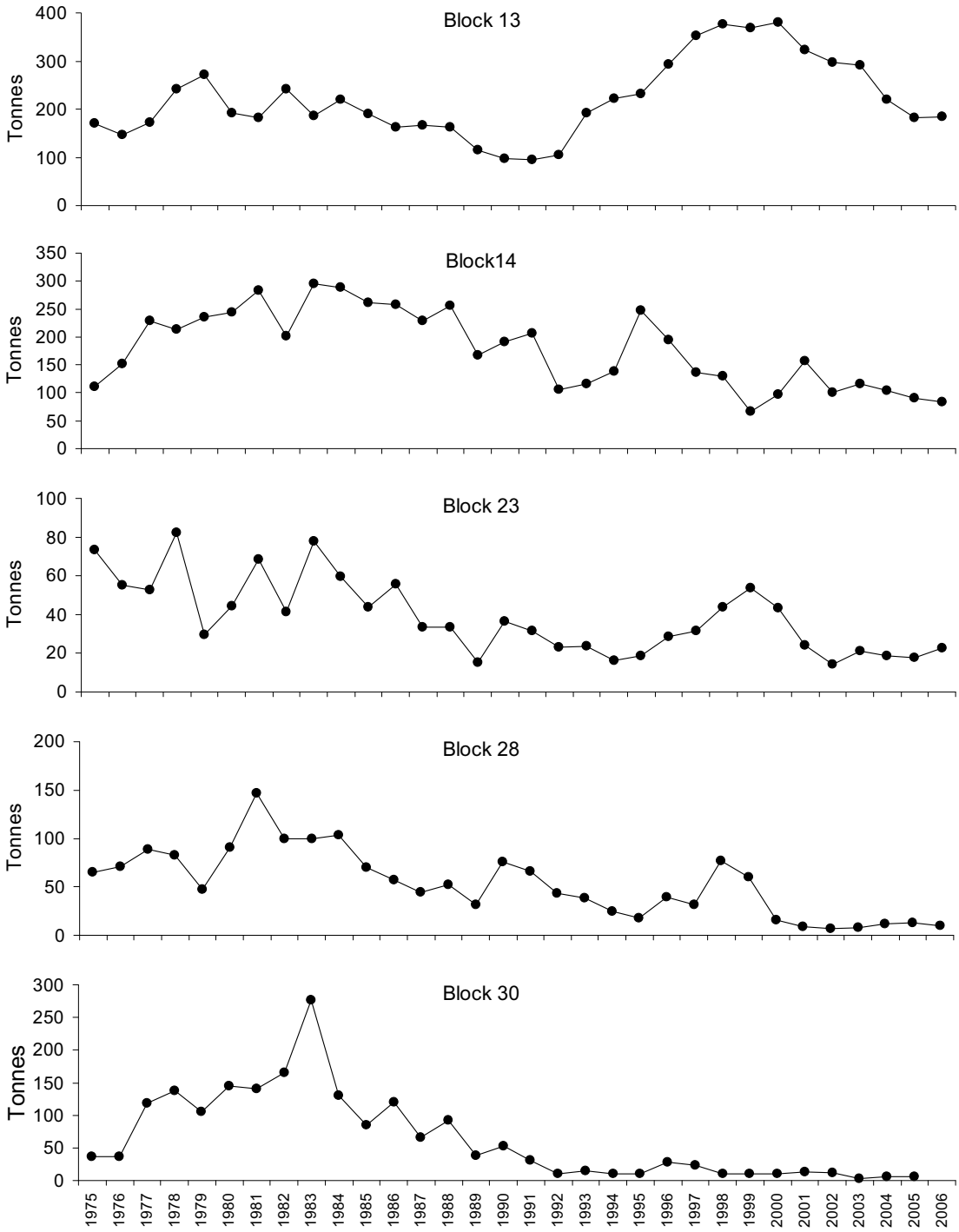

Figure 4 **Annual production (tonnes) from the five reporting blocks, 1975 to 2006. Catch reporting was introduced in 1966, but catches reported by block prior to 1975 are unavailable. Block 30 was closed to fishing in 2006. Catches were extensively under-reported during much of the early half of the fishery, and annual production prior to the introduction of catch docketing, ITQs and a TAC in the mid 1980s was probably much greater than indicated. In all blocks, except Block 13, reported annual catches trend downward, consistent with falling abalone populations. In Block 13, recent declines can be attributed to reductions in TAC.**

Blocks 13 and 23 show different patterns of annual catch. Early annual catch totals in Block 23 were relatively small (<100 tonnes), but anecdotal information indicates that

this block was one of the most heavily fished areas at the start of the fishery, that annual catches in the 10 years prior to 1975 were higher than in the following 10 years, and that by 1975, populations were in decline on many reefs. In contrast, the fishery in Block 13 has been robust. The dip in production during the late 1980s was probably due more to reductions in TAC than depletion, and the increased catch in the years that followed suggests stable or rising stock levels. The increase corresponds to the time when other blocks were declining, suggesting that divers moved there from the more depleted parts of the fishery. Post-2000 catch declines can be attributed to reductions in Eastern Zone TAC. Of the five blocks, Block 13 might be expected to show the least environmental effects attributable to abalone fishing because of its more stable stock levels.

(b) Data collection

Interviews were conducted with divers who were active in the fishery from its earliest years. The interviews were designed to collect information about where divers fished, changes in stock levels and habitat, as well as changes to their operations that might have affected the way that they fished and how they fished. The interview process involved asking a standard set of questions (Appendix 3), which included a discussion of where they had fished within the five blocks.

Divers with catch histories from three key periods were selected for interview. These periods were initially intended to be pre-1984 (early group), 1984 and later (middle group), and current, high volume divers. 1984 was considered important because east coast abalone production started to decline from that point. However, after the first few interviews it became apparent that depletion and consequent changes in the spatial distribution of effort occurred much earlier in the history of the fishery, and that the reefs fished by the middle category divers were essentially the same as those fished by current divers. Subsequently the categories were amended to pre-1972 (early group), 1972 and later (mid group), and current divers, and more early group and less middle group divers were interviewed than originally proposed. Some divers fished across more than one of the periods and were assigned to the group corresponding to the year in which they started fishing.

Divers were selected based upon the likelihood that they could supply useful information. Lists of potential interviewees were made using searches of archival material (catch returns, minutes of meetings, departmental memos) and recommendations from people who worked in the industry. Criteria for selection included their predominant fishing area, the period during which they fished and their availability for interview. The selection of later divers was made easier with the availability of computerised catch data, but also depended largely on recommendations from other divers and fish processors.

The questionnaire comprised 18 questions about the distribution of fishing activity, fishing methods used by the divers and the environment in which they fished. To minimise any bias through forced responses to interview questions, the interview

process was informal, with divers describing their lives in the fishery. Answers to most questions were obtained unprompted. This allowed them to provide extra detail about events unconnected with this project, but of great interest in its own right e.g. first sightings of *Centrostephanus*, abalone mortality events and shark attacks. The interviews were conducted with the understanding that personal information was confidential.

The maps used to locate fishing areas were mostly from the 1:25,000 Tasmap series produced by DPIW, but also included 1:100,000 Tasmaps, the TAFI Habitat Map series and RAN charts. Divers were also encouraged to draw their own 'mud maps'. Changes in the distribution of productive abalone reef during the history of the fishery were identified by comparing the maps produced by the three groups of divers.

It was originally proposed that a diver from each of the early and current groups be taken to the fishing blocks by boat, first to 'ground truth' their maps, and second to see if the visit would prompt further information. This part of the plan was abandoned after the first trip, because it became apparent that knowledge of the reefs and how they had contributed to the production of the fishery within a block was fragmented among many divers, and that to be successful, all the divers interviewed had to be present on the boat. The presence of just two individuals in the boat produced information that could not be reconciled with that from the other divers and was more confusing rather than helpful.

Results

Thirty-three divers were interviewed: 16 early group, 7 middle group and 10 current divers. Some among the early and middle groups are still current divers, but because they were interviewed about their earliest years, they were placed in the appropriate categories. A table of summarised responses may be found in Appendix 4. The places referred to in their responses are shown in maps of each block in Appendix 5.

Responses to questions

The first two questions asked for full name and contact details.

Question 3: Did you keep a diary or logbook of abalone fishing?

Seven divers (six from the early group) kept a journal of their abalone fishing activities. One diver's set of journals was destroyed. Five of the early divers' journals were seen. Three of these were purely of fishing details, listing catches, dive times, places and sales. The other two diaries combined events in the diver's personal life (marriages, births, deaths etc.) with fishing, and included prices received, details of boat maintenance, and catch details. These journals were particularly helpful in corroborating information that was received from other divers who did not keep logbooks, but relied on memory.

Question 4: What years were you actively involved in commercial abalone diving?

Start and finish years were confirmed from DPIW's catch database where records existed.

Question 5: How old were you when you started?

There was a wide variation in ages between 17 and 45. The current group of divers generally started diving for abalone at an older age than the earlier groups, presumably because the more recent high capital costs of entry to the fishery deterred younger people.

Question 6: What was your background before you started?

a. What prompted you to start diving?
b. Was your family involved in the fishing industry?
c. Where did you grow up (if raised in Tasmania)?
d. How did you first become aware of the abalone fishery?
e. Did you know any other divers at the time that you started?

During the 1960s and 70s, there was a widespread perception among the community that diving was a hazardous activity. Safe diving practices were poorly understood, and some of the early divers were injured by decompression sickness. In addition, the beach price of abalone fluctuated, and sometimes the market stopped buying fish. The health and economic factors deterred many potential entrants to the fishery who were unfamiliar with coping with the level of risk. What attracted the interviewees?

It is almost trite to say that abalone diving involves a combination of two distinctly different activities – commercial fishing and diving. However, while lack of prior involvement in either of these activities did not preclude later involvement in abalone diving, most of those interviewed were previously involved with one of the activities, principally diving.

Four of the early group had commercially fished abalone or other dive-fishery species such as mussels in Port Phillip Bay or the New South Wales south coast, and had moved to Tasmania after hearing from associates about Tasmania's large and comparatively untouched abalone stocks. Others, however, had almost no knowledge or understanding of commercial fishing. Most, but not all had prior recreational snorkelling experience. Of the early group, only three had much experience with underwater breathing equipment (but at a time when its usage was much more limited; in contrast, all current divers had previous compressed air diving experience). Mostly, the early group were spearfishermen, and they were experienced at searching for and collecting fish underwater. These early divers were attracted to abalone diving because they saw it as an extension of their recreational activities.

The early non-divers were inspired to take up abalone diving by some chance event (one – a newspaper article on the 'new' abalone fishery while he was visiting

Tasmania, another – an encounter with an abalone diver who was a passenger in his taxi). These early non-divers had more in common with the middle-group and current divers, who generally said that they were attracted by the lifestyle or the financial opportunities offered by the fishing industry, particularly abalone diving.

In part, this question was intended to show the extent to which the early abalone fishery relied upon the traditional fisheries (rock lobster, shark) during its development. Many of the large traditional Tasmanian fishing families have produced at least one abalone diver, so it seemed logical that they might be instrumental in forming some of the early fishing techniques and methods. However, only one of the early respondents came from a fishing family. While some of the methods were derived from other fisheries (mother ships, tender dinghies), most new entrants in the early group had no commercial fishing background. They were divers, not fishermen.

It is concluded that while some of the earliest abalone divers were from fishing backgrounds and were responsible for some of the development of the fishery, improvements in methods and technological developments usually came via new entrants to the fishery from the mainland. These improvements included the use of charcoal air filters, special air-breathing hose as a replacement for garden hose and mesh bags (nets) replacing hessian bags.

Question 7: What sort of equipment did you use initially?

a. Runabout or fishing boat?
b. Tow vehicle?
c. Did you use a deckhand initially?
d. Did you work from anchored boats with long hoses?
e. Wetsuit – how did you cope with cold?
f. Were you taught to dive – if so, by who?
g. Were you a diver prior to abalone fishing?

Free divers

The first of the early abalone divers were free divers (used snorkel). Some were shore-based, operating from small trucks or converted cars, while others worked from dinghies and larger open boats. The shore-based operations were mostly in the south-east and east, respondents fishing around the Forestier and Tasman peninsulas, Bruny Island and D'Entrecasteaux Channel, Bicheno and the Gardens. In 1963, two Victorian divers visited Smithton, Stanley and Couta Rocks, but did not think much of the potential for diving there, and settled at Bicheno. The early boat operations seem to have been mostly based in Dover.

Typically, the free divers swam with a net suspended at the surface from a truck tube. These nets were large enough to hold 600 pounds (~270 kilograms) of abalone. The divers drove through paddocks and along coastal tracks to an entry point on the

shore, swam until they spotted abalone below, dived and collected them, returning to the surface where they dropped the abalone in the net. Screwdrivers and modified knives were used to flip the abalone from the reef. Catch rates varied greatly between divers, some averaging a net or less per day, while others averaged two nets, and on a good day landed four nets. The depth range to which they worked also varied. Most dived less than 20 feet (~6 metres), but two of the respondents worked to 45 feet regularly and occasionally dived to more than 60 feet.

Early divers were hampered by a lack of processing infrastructure that later divers take for granted. Prior to the development of a local market, most product was air-freighted to buyers and canneries in Melbourne. In 1964, Boxall and Watt started buying abalone in the south-east, and in 1966, Safcol started canning abalone at Margate. The market wanted abalone meats, so the divers had to shuck their catch before they could sell it. Some divers dived all day, dragging their nets onto the shore where they were left overnight. The following day, the abalone were shucked and then collected for shipment to the buyer. Others alternately dived and shucked. The meats were split from their shells with a modified paint scraper into 12-gallon galvanised garbage bins. They were kept ready for shipment by either storing the bins in a freezer or salting the meats in the bins.

In 1967 a new rule was introduced to the fishery requiring divers to sell fish in a live condition to the processors. It was much more difficult for the shore-based operators to move the extra weight (of live abalone c.f. meats) along the rough bush tracks of the coast, and consequently they started working from boats. Here they found free diving disadvantageous when competing for the resource with divers breathing air underwater, and they rapidly converted to its use.

Underwater breathing apparatus

While some divers used SCUBA for a brief period, surface supply systems (hookah) quickly became universal. These comprised a small single-cylinder petrol engine (Jap, Villiers, later Honda) driving a single stage low pressure (~ 7 bar/100 psi) air compressor (typically Clisby). Air passed through filters and a distribution manifold into hoses to the divers below, who breathed through low-pressure demand-valves.

Divers were greatly concerned about the quality of air that they breathed. Typically the air was filtered through cotton waste or sanitary napkins to remove oil particles. In the late 1960s, divers who had moved to Tasmania from abalone fisheries on the mainland introduced charcoal filters, although these were crude and made ineffective by moisture.

Originally, mineral oils were used as a lubricant in the compressors, but, in the belief that mineral oil was poisonous and would damage their lungs, many switched to vegetable (cooking) oils. These were poor lubricants, however, and left deposits in the piston grooves causing the rings to stick and enable small quantities of oil to enter the compression chamber. When the compressors became hot during use (e.g. when running at high revolutions to supply divers working deep) it was thought that partial

burning of the oil took place, introducing carbon monoxide into the air. Tragically, there were several deaths among hookah divers attributed to carbon monoxide poisoning. In the 1970s specially formulated (petroleum-based) compressor oils became popular, and more recently divers have switched to synthetic oils developed for low-pressure air-breathing compressors.

The first diving hoses were PVC garden hose. When they became hot through a combination of sunlight, machinery heat and air pressure, the pressure caused localised inflation, splitting and immediate air loss, forcing the diver to quickly surface. Thin twine (couta cord') was often wrapped around to reinforce the first 10 metres of hose, but failures were still common. Purpose designed air breathing hose was introduced to the fishery via mainland divers in the mid to late 1960s, and eliminated this problem.

Compressed air divers

The early divers using hookah units usually worked from boats, either alone or with another diver. The boats were anchored at the dive site. The divers worked around the boat, each limited by the length of hose. The abalone were collected in hessian potato sacks, to which a coiled rope and small buoy were attached. A canvas lift bag was also attached to the sack, so that the buoyancy of the sack of abalone could be regulated and easily moved around the reef. When the sack was full (~60 kg), the diver let the buoy float to the surface and swam back to the boat where he collected a new sack and buoy. When he needed to shift the boat, either at the end of the day or when moving to a fresh dive site, he drove the boat around to each buoy and pulled up the sacks of abalone into the boat. The meshed bags currently in use were introduced to the fishery by divers from southern NSW or Mallacoota (Victoria) during the late 1960s, and quickly replaced the potato sacks. Initially they were large, and could hold 150 kilograms. Current divers typically use nets of one quarter this capacity.

As abalone catches became more sparsely distributed, divers found that they had to move the boat more frequently. Moving boats was time consuming and complex, particularly if more than one diver was fishing from it, and some larger boats had three divers. If a diver ran out of fish, and wanted to move, or he had jumped in on depleted reef, he would need to get the other divers back on deck, stow dive gear, weigh anchor, and motor around collecting sacks. This could take an hour, was wasteful of time and energy, and divers devised different strategies to avoid it.

The first strategy was to increase the length of hose. During the 1970s, on larger boats with multiple divers, hoses up to 1500 feet (~500 metres) in length were commonly used. The hoses were stored on hose reels usually fastened to the gunwale of the boat, and as the diver moved further away, he pulled off more hose. Frequently, the tight radius of the coils would be impressed in the hose, and as it lay loose on the surface, would intermesh with other coils causing prodigious tangles. At other times, the coils of hose would fall beneath adjacent coils preventing the hose from unrolling, or the reel would overrun and cause the hose to jam or tangle. These problems tethered the

diver at reduced range and negated the benefits of long hoses. Usually the boat's skipper or (if he was a diver) a deckhand tended the hoses to prevent tangles and keep the compressor running. The long hoses meant that divers often filled their bags at great distances from the boat. Swimming 500 metres with a full net of abalone suspended beneath a lift bag was time consuming and tiring, so the skipper or deckhand periodically drove to each diver in a dinghy to check his progress, collect full bags or ferry the diver back to the boat.

During the mid-1970s in the east and south east, diving from the deck of the larger boats mostly stopped, because stocks had become too depleted even for the long hoses, and these boats either went to work on the west coast where abalone were still abundant, or the divers worked from dinghies or small runabouts with their own compressors. These dinghies were carried on the deck of the larger boat (mother ship) when travelling or in port, but ranged far from the mother ship while working. The dinghies usually carried two divers or one diver and a deckhand.

In the earlier stages of the fishery when incomes were relatively low, most divers could not afford to pay deckhands, and either worked alone or with another diver. Beach prices increased by more than 100% between 1972 and 1974 to over 40 cents per kilogram, and deckhands became affordable. The availability of a deckhand meant that the dinghy or runabout no longer had to be anchored, but could follow the diver as he searched the shore. The diver no longer had to struggle back to the boat with a loaded bag of abalone but instead, the deckhand positioned the boat close to the diver who now only had to ascend to off-load his catch. This made fishing more efficient than with anchored boats, because there was reduced loss of time swimming between the reef and the boat, and reduced risk of the diver losing track of a patch of productive reef. By 1974, most of the divers at St Helens had adopted this method.

A further development occurred in the mid to late 1980s with the use of droplines. A dropline consisted of a rope with a weight and a spare net on one end, which was thrown to the diver working on the reef below. The diver clipped the net that he was filling to the dropline, took the empty bag and continued fishing. The deckhand hauled the filled net to the surface. During the 1990s, the method became more refined with the use of smaller, less bulky nets which were thrown to the diver at regular (e.g. 10 minute) intervals. Under some circumstance, particularly in deeper water, the method offered great improvements in efficiency because it eliminated the work done by the diver transporting the catch from the reef to the boat. It was safer because it reduced the number of ascents and consequently the likelihood of decompression sickness. It was easier for the diver, because it reduced the weight of abalone that he had to swim with as he searched, and it meant that he did not have to swim away from (and potentially lose) a patch of abalone when his bag became full.

Although these changes have been almost universally adopted, a few divers continue to work from anchored boats with large (80 kilogram) nets, particularly if they are working alone or without a deckhand, or if conditions (e.g. high stock levels) suit this style of fishing.

Abalone fishing boats

Early in the fishery there was no single style of boat such as the ubiquitous outboard-powered aluminium dinghy or 'tinny' that has become commonplace throughout the Tasmanian fishery during the last three decades. Divers used whatever they could get that would stay afloat. The larger boats were often older timber vessels that had been retired from the lobster or shark industries, or river launches and passenger ferries, or even recreational powerboats and yachts. They carried or towed smaller dinghies from which the divers worked. Fishing trips took from one to several days, and the catch was stored on deck or in tanks or wells if available.

Smaller boats were restricted to day-fishing. Until the late 1960s, these were usually timber displacement vessels with low powered inboard engines, but were also reliant on oars or sails for propulsion. Outboard powered plywood and fibreglass runabouts appeared in the fishery from the mid-1960s. Their use greatly extended the distance that divers could operate from port during a day, and the small displacement hulls were abandoned.

The planeing hulls were relatively expensive, and financially beyond reach of many divers. Some were purchased through hire-purchase agreements with high repayment levels. The irregular returns from the abalone diving left many unable to meet the monthly payments, and loan defaults were common, giving abalone divers a bad reputation among the business community. Other divers leased runabouts from recreational boat owners. These arrangements frequently became disharmonious because the boats were left in a poor state, due to lack of maintenance by the divers on boats which were not designed for work but subject to high levels of wear and tear.

Initially the planeing hulls were not trailer borne, but tied at a jetty whilst in port. In St Helens during the late 1960s, up to 15 runabouts between 4.5 and 7 metres tied at the jetty, with lesser numbers at ports further south. If a diver wanted to fish in a different region, he borrowed a trailer to move his boat to another port, or if the boat was leased, the owner moved it, or he leased another boat in the different region. Towing boats became common during the early 1970s, with greater availability of more powerful engines in utilities and the introduction of four-wheel drive light trucks, particularly the Toyota Landcruiser.

Wetsuits

Inshore water temperatures in Tasmania typically range between 11°C and 19°C, and prolonged immersion demands some type of protection from the cold. Some of the early group were well equipped from the start, with full-length neoprene wetsuits. Others started with football jumpers and a large fire on the beach where they warmed up at regular intervals. The early neoprenes were hard and inflexible and chafed the skin, sometimes causing large ulcerating sores. To reduce chafing, divers wore stockings, panty-hose or in extreme cases applied Vaseline to their skin. Early wetsuits were typically ¼-inch (~6 millimetres) thick, uncomfortable and the divers became cold relatively quickly. During the mid-1970s, more flexible neoprenes with soft inner

linings were developed and the establishment of local manufacturers meant that custom-fitted wetsuits could be produced.

Dry-suits became widely used for a period during the 1980s, but few among the current group of divers used them because they were found to be difficult to use in shallow water and unless the water was unusually cold, offered no advantage over conventional wetsuits.

Question 8: What were typical weights that you landed at the start of your diving career? Did landed weights change (get smaller, larger) in later years?

What were divers' expectations of an average day's catch, and a good catch? Did they change over time? Contrasting this crude measure of catch rates (kilogram per day) gives an approximate indication of when fishing started to impact on the virgin fishery. It also indicates the size of the catch required to operate at profitable levels.

The earliest divers working the south-east landed the largest catches. Catches of 1200 pounds were regarded as satisfactory, and occasionally catches reached 2400 pounds. Further north at Bicheno and the Gardens, catches were much lower: between 100 and 600 pounds per. This was probably not due to regional differences in virgin biomass, but more likely affected by differences in equipment levels (e.g. whether the divers wore wetsuits or football jumpers), the capacity of the market to absorb catch and motivation to earn money.

The earliest divers regarded abalone fishing as a one-off activity; in other words, they considered that once they had collected the abalone from a reef, later fishing would not be worthwhile. Two of the early group said they were surprised when bad weather forced them to revisit Coal Point on Bruny Island one year after it had been extensively fished and left in an apparently depleted state. They found that stock levels seemed to have regenerated. This changed their perception of abalone fishing from 'mining a resource' to a sustainable activity, and forced them to consider that reefs differed in productivity.

Catch records collected incidentally with market measuring samples show a rapid decline in daily landings during the late 1960s in reporting blocks 13 and 14 (south-east). The market measuring samples also show a rapid decline in modal length of abalone shells from 160 millimetres in 1967 to effectively knife edge at the 127 millimetre size-limit by 1975 (Witherspoon, 1975), consistent with a fully exploited fishery. The early group's expectations of catch size were lower in the mid-1970s than in the 1960s.

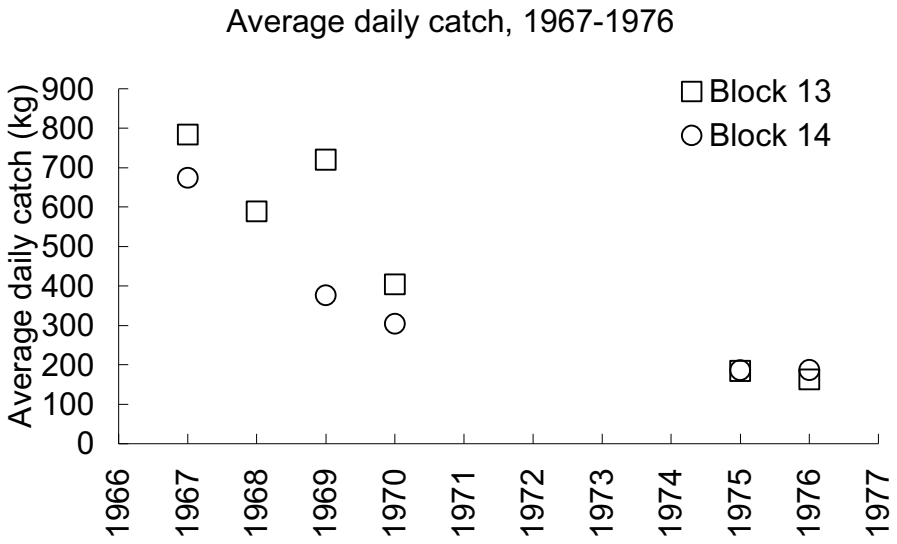

Figure 5 **Average daily landings of abalone, 1967–76, blocks 13 and 14. These statistics were taken from samples of boat landings at Dover and Southport, and are not from the entire catch. The samples were restricted to single day catches (not multi-day trips), but may represent the catches of more than one diver.**

Most divers implicitly categorised reefs by their stock levels, the catch that could be taken from them per day (catch rate) and consequently, their productivity. The early group saw the size of daily landings fall during the 1970s, and in the south-east close to ports, it was considered acceptable to fish at rates down to 100 kilograms per day (20 kilograms per hour); in other words, the reef was still considered productive at this low level.

The current group of divers experienced much better catch rates (>60 kilograms per hour) during the mid to late 1990s. During this time, most reefs were productive, and the high level of catch taken from what is now known as the Eastern Zone ensured that effort was widespread. Following the post-2000 decline in stocks, catch rates on many reefs fell below acceptable levels. Fishing patterns changed, and effort was directed mostly to reefs that produced abalone above threshold catch rates (40–50 kilograms per hour) and the less productive reefs were rarely visited.

Question 9: Who did you mostly sell to?

Question 10: What price range did you receive for your fish?

The earliest sales of abalone (1959) by divers from the early group were made to an unknown Chinese buyer in Hobart, or to a processor in Melbourne (South Pacific Cannery run by David Gilbert). Other early buyers included Safcol and Van Laine (Adelaide). During the early 1960s, the local market would accept only limited quantities of catch, and most was sold to mainland buyers. Divers usually had to pay the cost of air freighting (three pence per pound) their catch to the processor's door. In some cases the catch was reported to have arrived spoiled which meant that the diver received no payment.

Between 1960 and 1965, divers were paid six pence per pound meat-weight. (The divers had to split the meats out of the shells because the market required meats. In 1967, a rule requiring that abalone be delivered in a live condition to processors was introduced, after which landings were paid by shell weight, not meat weight.) Six pence per pound meat-weight is equivalent to 11 cents per kilogram, or assuming 40% recovery rate, 4.4 cents per kilogram shell-weight. To put this price in a contemporary context, one diver said that between 1960 and 1962 he could make more money from catching abalone on weekends (fishing on Saturday, processing on Sunday) than he could working at his trade as a panel beater during the week. Another diver said that he could make more money in one day's fishing than a carpenter could make in a week. In 1960, a building worker's wage averaged the equivalent of $35.70 per week, and a loaf of bread cost 15 cents (Vamplew, 1987). However, during the 1960s trade wages were relatively low, and it may be more valid to compare differences in the consumer price index. The 1960 CPI was 9.2% of the 2005 index (Australian Bureau of Statistics, 2005). In today's terms, a diver would need to catch approximately 300 kilograms of abalone to make $100 (net of air freight to Melbourne but before other costs, or, in other words, equivalent to today's beach price).

During the mid 1960s, a number of processors (e.g. Dover Fisheries, Albert Thompson, Bennie Boxall) started buying abalone in Hobart, facilitating the development of the fishery in the south and south-east. Prices rose from six pence per pound meat-weight to 11 cents per pound shell-weight by 1969. Greenlip abalone attracted prices up to 50% greater.

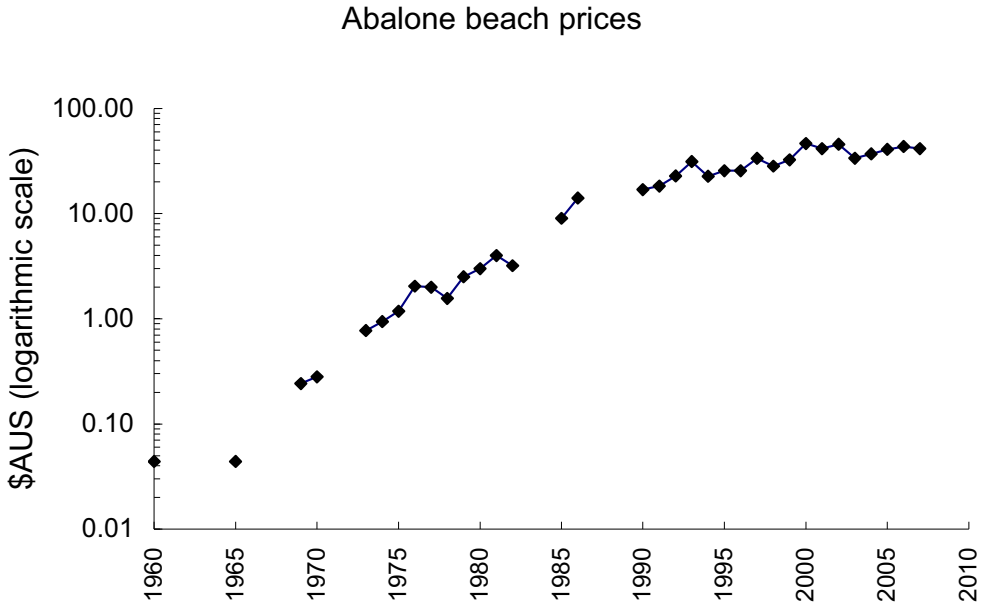

Figure 6 **Beach price received for blacklip abalone in Tasmania between 1960 and September 2007. Prior to 1966, abalone were sold by meat weight, and prices have been converted to live weight using a conversion factor of 0.4. Early beach prices are net of freight, but not of other processing costs. Price data were obtained from early divers, Harrison (1983), Department of Primary Industries and Water, and the Tasmanian Abalone Council.**

Beach prices were more unstable than they currently are. Occasionally the market stopped buying and on a number of occasions (e.g. 1967, 1972, 1977–78, 1982), prices plummeted. Almost all sales of processed abalone were to Japan. The price instability was often due to market manipulation by overseas buyers resulting in oversupply of product, which forced price collapses. In 1977, substitution of Chilean loco (*Concholepas concholepas*) for Australian abalone on the Japanese market cause a price collapse in the Australian abalone fisheries. Generally, however, there was a rapid and sustained increase in beach price between 1970 and 1981, rising from 28 cents per kilogram (March 1970, paid by Dwyers at St Helens) to over $4.00 per kilogram (Harrison, 1983), and many among the early group considered that it was during this period that the fishery became prosperous (Figure 6).

Question 11: Where did you start fishing?

a. What region?
b. What town?
c. What bays?
d. What depths?
e. Were other divers working nearby?
f. In hindsight, was it a good place to dive for abalone?

Question 12: Where did you get good catches when you first started?

a. List places where you could always get good catches.
b. List places that used to be good (commercially viable or better), but stopped being so.
    i. Did any of those places eventually recover?
    ii. How many years to recovery?

These questions were usually asked and answered with the aid of maps, particularly the 1:25,000 Tasmap series. TAFI habitat maps were used infrequently and then mostly to locate offshore patch reefs. Abalone fishing took place within only a fraction of the reef area shown on TAFI habitat maps, and most divers had difficulty reconciling their memories of reefs with the topography and reef boundaries shown on the maps.

Most divers were reluctant to write-off a piece of coast as 'failed' or 'no good', because abalone abundance is variable, and even reliable reefs could fish poorly at times. One diver produced a log book with entries showing a number of catches that were twice the daily average of the time, from a reef in Block 30 that was otherwise poorly regarded and seldom fished. In his opinion, the reef provided excellent catches, but took a long time to recover between fishing events. To further illustrate the dilemma, Block 30 has produced only a small fraction (<10%) of its former annual catch during each of the past 15 years, yet some current divers believe that the block supports

adequate stock levels. This is because under the right conditions they can land catches equal in size to those from blocks that are more widely recognised as productive. Even the most depleted reefs carry isolated populations which can occasionally be fished at high catch rates. The converse also applies (i.e. under some circumstances divers can have difficulty taking good catches from reefs that are recognised as holding abundant abalone stocks).

A second difficulty arose because during the intervening years since they had stopped diving, some early divers had lost the knowledge of spatial detail required to describe the places where they used to fish. It was originally intended to take divers back to the places where they used to fish but this was found to be not particularly helpful – they remained confused and disorientated.

A third difficulty stemmed from the use of the term 'commercial' viability. At what point does a reef stop producing commercially viable catches, particularly if the return to the diver increases as beach prices increase? For example, in 1964, the Director of Fisheries, R. H. Scott, wrote to a prospective fish buyer advising him that the abalone-bearing reefs around Bicheno had been fished out, and that the buyer would have to wait until more reefs could be found before he could be supplied with any product from Tasmania. One of the divers who worked at Bicheno at the time was interviewed. He said that they were being paid six pence per pound for meats. Freighting the meats to Melbourne cost three pence per pound, and they thought that the net return was insufficient to warrant further fishing, particularly since they had taken the easily accessible fish within the port.

In contrast, current divers receive approximately $6.00 per kilogram for catching Eastern Zone abalone. The industry is heavily capitalised, with high ongoing costs. Out of the $6.00 per kilogram fee, the divers have said that they must run and maintain boat(s) and a tow vehicle (with associated costs for fuel, repairs, depreciation of vessels, vehicles and machinery, and insurance), pay a wage to themselves and a deckhand, pay industry levees and license fees, and account for bank interest or loss of opportunity on the several hundred thousand dollar capital value of their diving entitlement and equipment. Experienced divers have learnt that they can only stay in business if their catches are above a threshold level; reefs that were productive at low catch rates when levels of industry capitalisation were lower are now effectively no longer part of the fishery.

In addition, because of the relatively small margins, it was economically disadvantageous for current divers to roam the coast looking for abalone. They were aware that when they visited unfamiliar coast, they might fail to catch sufficient abalone to ensure a profit. This was a disincentive to spending the necessary time searching for fresh reef and unexploited stocks. Their best business plan was to habitually fish areas where they knew they would catch fish. This has limited the knowledge of the distribution of productive reefs, and it was unusual to find a current diver with the same level of knowledge of the fishing reefs in a region, compared with that of the earlier divers.

In contrast, the two earlier groups of divers were more active explorers. Both groups operated when levels of capitalisation were relatively low and the diving entitlement and quota were combined. The early group had the added advantage of the strong likelihood of high catch rates when they encountered fresh reef, and the middle group received relatively larger returns than current divers. During interviews, divers from both groups said that they knew of reefs that had not been fished for many years because they had been forgotten or were unknown to current divers. Despite the time interval and fragmented knowledge, some early divers, particularly those who were still actively fishing (many still worked in the fishing industry) had accurate recall of productive coast and reefs, and were able to provide detailed spatial information.

In Block 13 (Southport Lagoon Beach to Whale Head), respondents from all three groups who had fished there considered that the area had usually provided good catches. They said that there were only isolated and inconsequential places which could be considered as formerly productive but now non-productive (e.g. small patch reef near George III Rock). However, a map of Recherche Bay and its early abalone fishing grounds developed from talks with early divers and then shown to current divers evoked surprise and doubt – firstly surprise that there were so many reefs in Recherche, and secondly doubt that they were ever worth fishing.

Also in Block 13, the southern end of the Big Actaeon Bight was described by the early divers as having dense abalone populations. Currently, after heavy fishing, populations become greatly depleted, but most current divers who fished at the Actaeons were reluctant to dismiss it as unproductive.

Block 14 was a key part of the abalone fishery from its earliest times, producing between 200 tonnes and 300 tonnes during the 1970s and 1980s. Block 14 consists of the lower D'Entrecasteaux Channel (including Port Esperance, Southport and Great Taylors Bay), the southern shores of Bruny Island east to Boreel Head (including Cloudy Bay, the Friars and the southern shore of the Labillardiere Peninsula) and the northern parts of the Actaeons reef systems (including Southport Island, Blanche and George III Rocks). During the earliest years, much of the catch was caught in the Channel, particularly Port Esperance (Dover) or nearby. Planing hulls were uncommon and divers who day-fished using small timber dinghies were effectively restricted to a range less than 10 nautical miles. It was reported that in 1964, daily catches of up to 600 kilograms were taken from Port Esperance (Hope Island, southern shore between Hawkers and Lomas Points), Blubber Head north to Roaring Beach, the coast south of Dover, including Scotts Point, Tower Bay, Lady Bay and Sisters Bay, and Partridge Island and the Pineapples. Ten years later, abalone populations in the area had become depleted (Witherspoon, 1975), but were still heavily fished. In 1975, a resident diver said that it was common to see half a dozen divers fishing the Port Esperance southern shore in south-westerly weather, with catches typically 100 kilograms per day. A fish farm was established in Port Esperance during the late 1980s, after which divers said that the kelp along the Stringers Creek shore became covered in sediment, the clarity of the water decreased, and abalone became very

depleted. In 2004, some recovery of populations had occurred, and isolated catches of up to 200 kilograms per day were landed from the southern shore and Hope Island.

The southern shores of Bruny Island and the northern parts of the Actaeons continue to provide high levels of catch and were not considered to have been depleted by any of the divers. In contrast, much of the D'Entrecasteaux Channel (which was said to have contributed approximately half the Block 14 annual catch during the 1970s and 1980s) became too depleted to warrant fishing. The average annual catch between 2000 and 2006 for the western shore between Port Esperance and Southport was 15 tonnes, while on the Bruny Island shore the catch had declined to seven tonnes for that period. The Bruny Island shore is now said to be mostly depleted, although divers occasionally take good catches from the Quarries.

On the east coast, in Block 23, the first reefs to be fished were in Little Chinamans Bay, the reef immediately outside the Narrows and along the southern shore of Marion Bay past the mouth of the Narrows. These were fished by free divers in 1960, one of whom estimated that hundreds of tonnes of abalone were taken. Today, the area still supports limited catches, but is extensively depleted, marginally productive and is fished only when divers need to supply abalone and the weather is too bad to work elsewhere. Further east at Cape Paul Lamanon, the Long Reef was fished until the early 1980s. The reef extends approximately 1.5 kilometres to the north-east of the cape, at one point rising to about five metres from the surface, and extending down to 30 metres. Currently the shallow parts of the reef remain depleted, while the status of deeper water stocks is unknown but presumed depleted. Further north in Block 23, an extensive area of reef known as Eagle Reef was intensively fished between 1965 and the early 70s, but has apparently not produced commercial catches of abalone since then.

In Block 28, the early diving (1963) was done in the immediate vicinity of the Gulch at Bicheno, and extended south to Rice Pebble beach and north into Waubs Bay (i.e. within the town boundaries). The reefs in these areas were reported depleted later in 1964, and the two divers working there left the area. In 1965, more divers arrived in Bicheno, and they worked along the coast both north and south of the town. The areas of reef closer to Bicheno became depleted, forcing the divers further afield, until eventually those reefs in turn became depleted. Some of the reefs at Bicheno have recovered and supported limited fishing before declining again. For example, there has been limited recovery at the southern end of the Gulch, around the Blowhole shore and the western shore at Rice Pebble Beach. None of the interviewed divers remembered catching abalone from the area around Governor Island now incorporated into a reserve, so it is likely that this coast was always a poor abalone habitat. Butlers Point to the south of Bicheno was mentioned by two divers who said that the abalone there were consistently larger than anywhere else near Bicheno, and that they were more plentiful. Although granite is the prevailing rock type on most of this coast, at Butlers Point the rocks are sedimentary, with folded beds of quartz wacke tilted almost vertically. The broken beds formed many more open crevices

which exposed the abalone to the diver and made them easier to find than on the adjacent granite coast.

In blocks 27, 28, and 29 there are extensive patches of reef lying off long beaches (e.g. Friendly, Dennison, Douglas, and Templestowe beaches). Large quantities of abalone were taken from these beaches between 1967 and the mid 1970s. In the 1960s, they were productive at depths down to 20 metres, but in later years were more productive at shallower depths. By the late 1980s, the reefs were no longer fished. The reefs' abalone populations still occasionally make limited recoveries which support fishing at high catch rates for a short period, but they are reported to quickly decline.

In the northern part of Block 30, three areas of reef were identified by two divers as being productive when they first started, but declined some years later and have never recovered. These reefs were at Pebbly Bight, Ansons Bay and at the Ring of Kelp (also known as Red Rocks). Interestingly, the early group divers were dismissive of these reefs, and said that they had never held worthwhile quantities of abalone. However, between 1980 and 1986, the reefs produced abalone at rates up to 300 kilograms per diver day, and it was roughly estimated that between 10 tonnes and 20 tonnes per annum were taken from each reef during this period. There are broad similarities between the reef at Butlers Point in Block 28 and the reef between Pebbly Bight and Ansons Bay: they share the same characteristic of undulating ridges and channels, they are shallow hundreds of metres offshore and they have similar broken quartz wacke strata.

Question 13: Did you notice that fishing improved any areas (i.e. started bad, but then produced fish)?

Several early group divers said that parts of Maria Island and the Tasman Peninsula were initially not good abalone fishing areas. They dived around the island in the early 1960s but abandoned it for the proven fishing opportunities at St Helens. Maria Island was made a reserve, and closed to fishing from 1966 until 1980. Since opening, it has been generally productive, and one of the early divers (who had contact with the fishery for many years) was surprised to hear that Maria Island was producing quantities of abalone.

Two of the early group divers said that the Tasman Peninsula between Tasman Island and Eaglehawk Neck never produced worthwhile catches during the 1960s. One, who was one of the first to fish the area, said that he had systematically worked from one end of this coast to the other for low returns, and eventually left disappointed. He returned some years later after others had fished there successfully and found much higher stock levels.

These responses imply either that there were fluctuating levels of abundance due to natural causes, or that the divers did not see the abalone. However, both explanations are not particularly plausible, and raise more (unanswerable) questions: why would virgin abalone stocks be too low to warrant fishing, and why would experienced divers miss the abalone?

The northern reefs in Block 30 (Pebbly, Ansons and Ring of Kelp) all apparently improved from unproductive to productive. This observation was not based upon the response of a single diver, but established after talking to several divers.

Question 14: Did fishing make some areas worse immediately – you fished it once and it was never any good after?

Several divers said that abalone populations on small isolated patch and fringe reefs usually did not recover after being heavily fished. Examples given included tennis-court sized patch reefs in Block 30, small fringe reefs in blocks 23 and 24 at the northern end of the beach at Marion Bay and fringe reefs in South Cape Bay such as Lion Rock (Block 13). They believed that fishing at the 127-mm size limit had left no viable spawning stock, and that populations on the reefs collapsed. This was confirmed by research population sampling in eastern and south-eastern Tasmania which showed that the 127 mm and 132 mm size-limits were inadequate in terms of management plan guidelines that seek to 'allow abalone to grow to a size where they have had two breeding seasons through the use of appropriate size limits' (Anonymous, 1999). It was apparent that heavily fished populations were increasingly at risk when fished at sizes smaller than 138 mm (Tarbath et al., 2001).

Question 15: Did you notice that the area of 'scungy' bottom increased?

This question was also rephrased as 'were there habitat changes on the reefs where you caught abalone?' and after some discussion, led to a further question 'did you notices habitat changes that might be associated with changes in abalone abundance?'

The term 'scungy' bottom was explained to divers, but most knew what was meant immediately – they also used this term, 'brown rock' or similar terms. It refers to benthos that is not recognised as supporting abalone populations. Scungy bottom is an all-encompassing term that includes a variety of encrusting reef coverings such as sponges and ascidians, as well as sediment (sand, silt), and algae (green, red and brown).

All divers were aware of an association between crustose corralline algae (CCA) covered rock ('pink rock' or 'purple rock') and abalone, and that there was a much greater likelihood of catching abalone on CCA-covered rock than on rock covered by other forms. Some divers also explained that even though reef might be extensively covered in CCA, there was no guarantee that it was productive abalone habitat. One diver gave an example: the coast between Orford and Swansea (Block 25) has always had and still has extensive CCA coverage but its abalone populations apparently collapsed in the late 1980s after 25 years of intensive fishing. He did not think that the depletion of abalone populations led to habitat change there.

Not all divers reported seeing habitat change. Eighteen divers reported seeing changes in the reef habitat where they fished for abalone, but many qualified their remarks by stating that that these changes were not necessarily associated with abalone fishing. Some divers said that they noticed a seasonal change in the amount of reef covered in red algae and the kelp canopy (there was more between mid-spring

and mid-autumn, and it died back over winter). Most of the divers were untrained observers, and their ability to describe changes varied widely, perhaps because it is not a skill immediately relevant to catching abalone. Some of their observations are detailed below:

- A current diver, referring to reefs at Flinders Island, said that he could not understand how the reefs that his father had found to be productive in the 1970s (but were now so depleted that they were no longer fished) could support abalone fishing, so different were they from the reefs that he currently fished. He said that in the shallows the canopy cover and other algal growth was denser, that deeper reef was more encrusted, particularly by sponge, and that on many low lying reefs, fine sand and silt had spread and now covered reef where his father used to collect abalone. He believed that there had been a habitat change at the reefs where his father had fished, and he thought that it was a consequence of the removal of abalone by fishing.
- One early-group diver thought that at the Actaeons (Block 13 – Eastern Zone) the CCA cover was less extensive in the last years that he dived. He believed that abalone played a role in stabilising the habitat, and that the change in CCA cover could be attributed to low stock levels following years of intensive fishing. He said that when he first fished at South Cape Bay (Block 13 – Western Zone) in the mid 1960s, there were large populations of abalone on reefs in the shallows, which were quickly depleted. When he returned the following year, the abalone populations had not recovered, and a dense canopy of bull kelp had overgrown the reefs. He said that all visible abalone were taken (because they were all larger than the 127-mm size limit). He believed that the growth of the bull kelp canopy could be attributed to the removal of abalone.
- Another early-group diver made a similar observation about a shallow tennis court-sized patch reef in Block 30 from which in 1970, he removed all (approximately one tonne) the abalone. Following his visit, the reef habitat changed from an open canopy reef to one dominated by dense bull kelp. The diver never found abalone on the reef during subsequent visits. When the reef was visited by TAFI divers in 2004, only a few abalone were seen, although searching was made difficult by the density of the canopy. The diver observed similar changes on shallow fringe reefs further north in Block 30.
- A middle group diver repeated an observation made to him by an early diver. He said that the early diver had told him that off the south-west shore of Lagoon Bay (Block 23), good catches of abalone were taken during the 1960s. When he started fishing in 1974, he found the reef to be very weedy with sparse CCA cover and few abalone (it remains so today). The observation puzzled him because the weedy reef was not one that he associated with abalone but instead was the type of habitat that he avoided if he wanted to catch abalone.

- A diver who fished extensively throughout the D'Entrecasteaux Channel (blocks 14 and 15) during the 1980s and 1990s said that he had noticed increasing turbidity and sediment coinciding with the establishment of salmon aquaculture farms in the channel. The sediment settled on the kelp canopy and the reef. He said abalone populations on reefs in the affected areas (Port Esperance, Great Taylors Bay, Red Cliffs and Surveyors Bay) were very depleted and no longer warranted fishing.
- A current diver who started abalone fishing in 1984 noticed changes on reefs north of the Gardens in Block 30 that coincided with reduced catches and eventually the depletion of abalone populations to sparsely scattered individuals. At Ansons Bay, the bottom changed from CCA-covered rock to green lettuce weed (*Ulva*). At the Ring of Kelp, string kelp (*Macrocystis*) disappeared and sponge and dense mats of tiny mussels started to overgrow rocks. At Pebbly Beach, the algal growth (canopy and understory) became denser as the abalone disappeared. The diver thought these reefs had all provided good catches of abalone during the period (between 1984 and 1988) that he fished there. Further south in blocks 28 and 27, he noticed that as the beach reefs (Maclean Bay and Friendly Beaches) became depleted, algal growth became more dense and sponges covered more rock.
- A current diver who started in 1998 noticed that after abalone were removed from the Templestowe Beach reefs (Block 29) in the late 1990s that the reef appeared to become more sponge encrusted. This diver fished mostly around Bicheno and has swum along much of the coast near the town; coast that used to produce abalone. He had recently swum between Redbill Point and Cod Rock, which used to produce reasonable catches in the 1980s, but had seen very few abalone. He commented that there was good coverage of CCA and that it looked like perfect abalone habitat (i.e. was unchanged), apart from there being very few abalone present.
- Divers from all three categories spoke about seasonal changes in levels of red algae and canopy. They said that algae density increased from mid-spring and was partially responsible for reduced catch rates during summer, because the algae covered the abalone. At least two divers believed that given sufficient numbers of abalone, the understory algal cover could be reduced through feeding activity.
- Finally, three current divers spoke about changes that they had seen at the Actaeons (Block 13). The first said that he had noticed that a dense bed of *Caulerpa* (green algae) was spreading and encroaching on deep water (15–20 m) abalone habitat at Fishers Point, and that no abalone lived amongst the *Caulerpa*. The second said that he had noticed that the sponge and CCA cover, and algal understory cover frequently changed coinciding with changes in abalone abundance. He viewed the habitat change as a dynamic response to changes in abalone abundance, and that changes in abundance and distribution of abalone

were not necessarily caused by fishing. The third diver said that following a violent storm in 1998, much of the shallow reef between Fishers Point and Mouldy Hole was stripped bare and boulders were overturned by the water movement. He said that it took just two years for the communities to re-establish to the point where he could no longer see any difference between affected and nearby unaffected reef. His point was that whatever effect abalone fishing had on the environment, it was likely to be inconsequential compared with the devastating effect of storms, and that the habitat would eventually revert to its former type given time.

Six divers emphatically rejected the idea that habitat changes might be associated with changes in abalone abundance, either occurring naturally or due to fishing. They maintained that abalone fishing was environmentally benign. Two others were sceptical of the idea, but also said that they had never considered the possibility and could not answer the question.

Question 16: What sort of depth range did you commonly dive to? Did early divers fish deeper habitat than later divers? Were you affected by decompression sickness?

As might be expected given the paucity of information and lack of awareness about diving-related injuries, many of the early and middle group divers regularly dived deeper, and worked at depth for longer than the current divers. They were not well informed of the consequences of decompression sickness (DCS), and regarded it as an occupational hazard rather than something that must be avoided. Most of the early group did not dive strictly to decompression tables, but devised their own time/depth schedule loosely based on the tables, or what they had heard from other divers, or whatever they felt they could get away with. Some were more risk averse and either mostly worked in 10 metres or less, or worked at greater depths for only short (<1 hour) periods before spending the remainder of the day in the shallows. Others found that the only way that they could earn sufficient money was to spend time at depth, and they frequently worked for four hours at 60 feet (~18 m) before ascending to the surface, usually without a decompression stop.

One early diver, seeking to avoid DCS, developed an ingenious in-water oxygen decompression technique that was novel at the time, to which he attributed his bend-free diving despite hours at depth. He consistently fished deeper water than the other divers, explaining that he preferred to fish in 60 or 70 feet for a couple of hours, then go home, compared with the others who caught the same weight after working in 10–40 feet all day. He had a dedicated regulator on a short hose fitted to an oxygen cylinder on his boat. When he ascended, the deckhand would lower the regulator to him, and he would breathe from it below the boat at a depth of a few metres for approximately 10 minutes. He was aware that breathing 100% oxygen would accelerate the removal of nitrogen from his body, and reduce the risk of DCS, and was also aware that breathing oxygen at high partial pressures could make him unconscious. He said that he had to be careful – the initial flow of oxygen through the regulator occasionally ignited particles of flammable material and sparks would shoot

out. In his diving career, he never had symptoms of DCS, and today remains free of its debilitating effects. Because of the risk associated with breathing oxygen under pressure, it is doubtful whether any informed diver would use this technique today. This example typifies the readiness of early divers to improvise and take risks when faced with the unknown.

Current divers were better informed about the consequences of unsafe diving practices and had access to dive computers and more conservative dive tables. While seven of the ten were prepared to work at any depth necessary to catch fish, they generally worked shallower than the earlier groups, and stayed within the limits of their dive computers, which greatly reduced the time they could spend at depth compared with the earlier divers.

Unfortunately not all divers were as successful at avoiding DCS. Four of the 16 early group divers and three of the seven middle group divers were affected by DCS. Some of these had bone damage associated with DCS. One of the early group suffered an air embolism, but it was not clear that this was due to working at greater depths. None of the current divers had suffered from DCS.

The consequence of current divers working more safely is that less effort is spent on deeper reefs. A major shift in effort to shallower water would indicate a reduction in fishing mortality on deep water stocks at the expense of shallow water stocks, and that a potentially significant part of the fishery is no longer exploited. However, it has not been possible to quantify the shift in effort, nor to locate the position and extent of deep reefs on maps, nor to estimate the contribution from the deep reefs to the annual catch, for the following reasons:

1. No early or middle group divers possessed dive computers, and few of the current divers retained depth logs from their computers. The depth recorded on fish dockets lodged with their catches was the maximum depth and gave no indication of the time spent there. Consequently, apart from anecdotes, there is no historical information about changes in the distribution of effort by depth, and sparse recent information.
2. In nearly all cases, the divers were unable to locate the reef where they fished from the TAFI habitat maps. Because maps are produced from soundings taken up to 200 m apart, they were of insufficient resolution to show key features of the reef which divers could use to navigate. A few divers were able to draw extensive 'mud maps', marking details such as bombies, gutters and sand edges. On the rare occasions when divers managed to locate productive reef on the habitat maps, their perceptions of the reef were much different from those shown on the maps, and they thought that the maps were incorrect (Figure 7).

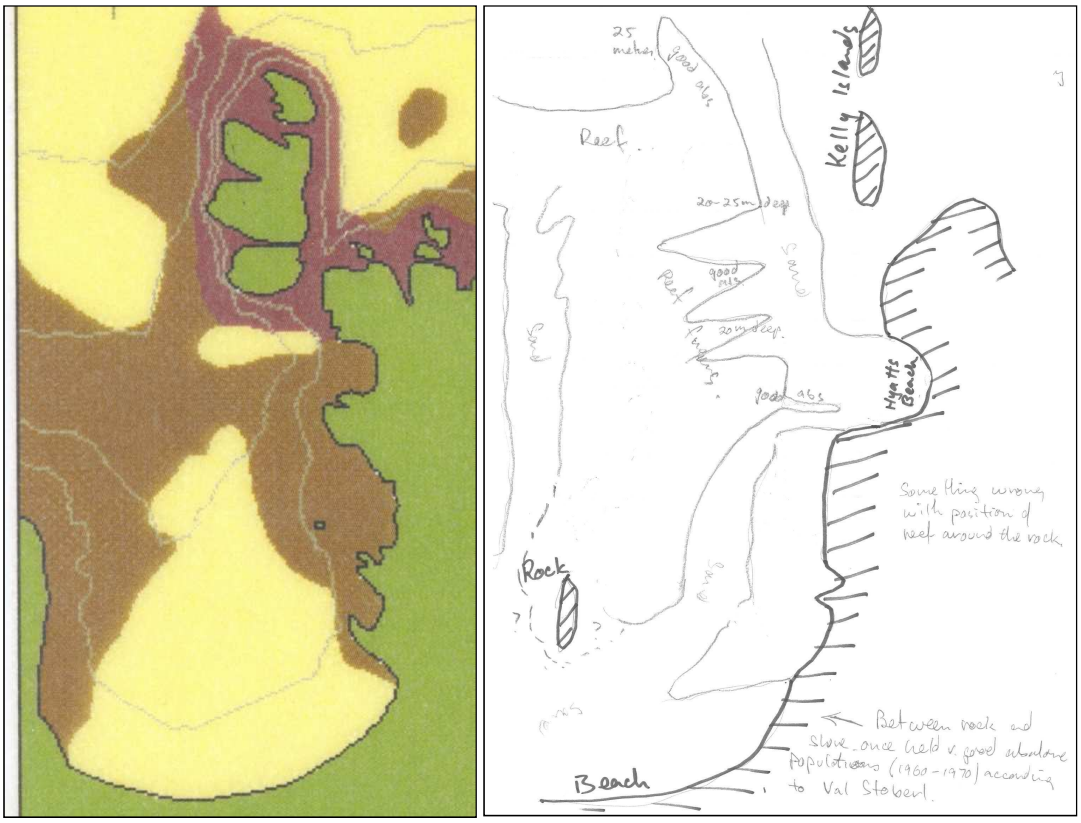

Figure 7 **Comparison between a TAFI habitat map and a map developed from memory by a diver who for many years worked on the reefs shaded in brown in the habitat map. Although the scale of features such as the islands is obviously wrong, the diver's map shows much greater detail of the reef, and illustrates some of the problems faced by divers while attempting to understand the habitat maps.**

3. The spatial reporting of catches has always been on a scale of many kilometres. In 2000, the scale was reduced when the former reporting blocks were subdivided, but it is still too large to determine if catches are taken on shallow reef or deep reef. In 2004, divers started reporting effort across three depth ranges (0–10 m, 10–20 m, >20 m), which has made it possible to detect changes of operational depth. For example, it is now possible to see a shift in effort to deeper water when divers on King Island started using Nitrox breathing apparatus in 2006 (Figure 8). The deeper reefs had not been fished since the mid-1980s, and there were many more abalone at depth than in the depleted shallows. However, while the shift in effort is indicative, it is still not possible to precisely determine how much the deeper reefs contribute. The example from King Island may be an exception, but it appears likely that the location of the Eastern Zone deep water stocks has been forgotten, and that unless divers are willing to outlay considerable expense for Nitrox equipment, these stocks may never be fished at significant levels again.

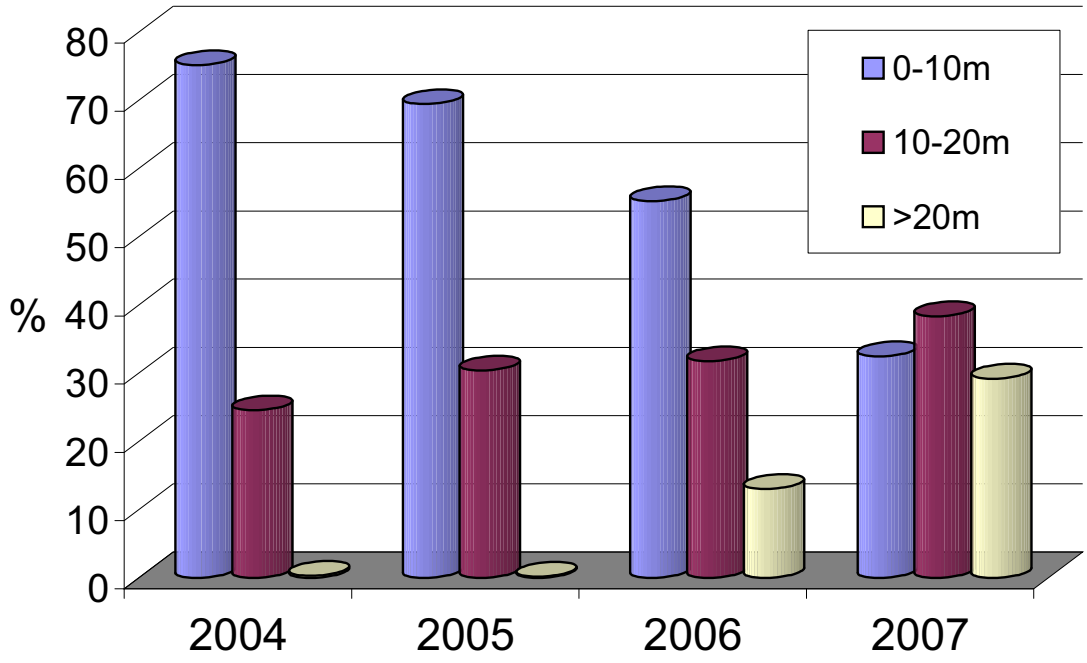

Figure 8 **Percentage effort (hours) by depth range (0–10 m, 10–20 m, >20 m) between January 2004 and May 2007, King Island blacklip fishery**

Question 17: Seasonal changes in catch rates – were East Coast catches always variable?

Question 18: Why do East Coast catches vary, but not West Coast?

Abalone are harder to catch in summer and early autumn on the east coast and most parts of south-east Tasmania, yet there appears to be no seasonal variation in catchability in the west and far south of the state. These questions were asked to determine if seasonal variations had always occurred or were a recent phenomenon, and to establish why they might occur.

All three groups of divers said that abalone were harder to catch in the warmer part of the year on the east coast. Some divers explained that the kelp canopy and algal understory grew thicker and hid the abalone, and it was not until the shorter hours of daylight and increased water movement during autumn that the weed died back, making the abalone easier to find. They said that on the west and south coasts which are more exposed to ocean swell, weed growth is restricted by the greater levels of water movement, and the abalone are more visible. The increased water movement also forces the abalone into deeper habitat where the kelp canopy is less dense, which makes the abalone more conspicuous.

The second most common response was that the abalone become cryptic (hide under rocks) when the water is warmer. Why this should be so was not clear, but they explained that the east coast water gets warmer in summer than in the south and west, which is why this behaviour is not seen there. On the northern part of the east coast and in Bass Strait (where the water is generally warmer), blacklip abalone tend to be found more often in crevices and under boulders compared with more southern

abalone, and southern divers often had difficulty finding abalone in the north until they came to terms with this change in behaviour.

Their responses indicate that seasonal variation in catches has always occurred, and that it is not related to low levels of abundance nor most importantly, to loss of habitat or long-term changes in habitat.

Changes in fished coastline

During the interviews, divers were encouraged to mark on maps, and in some cases aerial photographs, the position of reefs and coast where they had fished. This was quite imprecise, because there were no maps with which they could accurately locate where they had fished. The best representation of fished coast and reef was achieved by marking lines along the coast. No attempt was made to account for variations in width of fringing reef and differences in fishing area, because this information was mostly unavailable or unreliable. Examples of divers' maps are shown below (Figure 9).

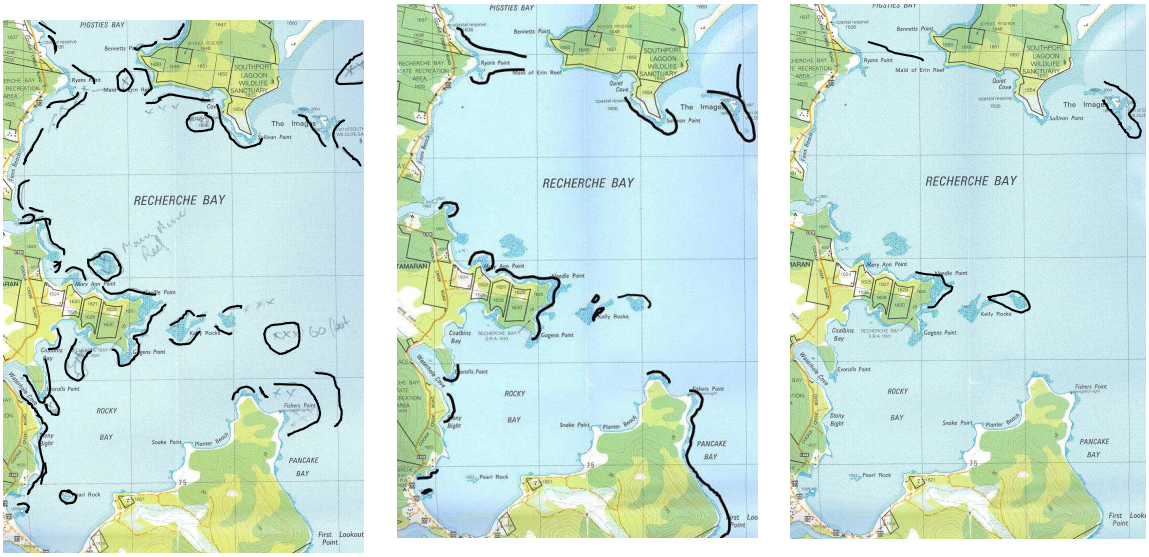

Figure 9 **Recherche Bay, Block 13, showing changes in productive abalone fishing reef (black lines) during the course of the fishery. The left-hand map was produced by early group divers, the other two maps by current divers. Base maps reproduced with the permission of Tasmap.**

The individual maps were combined, the length and position of the lines compared between groups, and the length of fished coastline measured with a curvimetre map measure (Kartenmesser, Germany). Currently fished coastline was expressed as a percentage of the maximum length of coastline identified as productive (Table 1).

The method was inaccurate where there were extensive areas of offshore reef distant from land, because there were insufficient close reference points for divers to plot the positions of fished reef on maps. For example, there were difficulties locating and describing offshore reefs at the Actaeons (Block 13). However, all divers, including

three with long (>30 years) and continuous experience in the area were unanimous in their opinions that only a few minor parts of the reef (including the reserve at George III Rock) are now unfished (i.e. the fished area of reef is essentially unchanged). In Block 30, the position of offshore fishing areas (the Gardens, Sloop Rock, Ansons Reef and the Ring of Kelp) were identified with the use of aerial photographs. This area was visited with two divers, one from the early group and one current, who were able to locate the position of past and present fished reefs.

The problem with this method of assessing changes in reef productivity is that it is reliant on the memories and observations of a small proportion of the people who worked there, and as has been previously noted, individuals generally had an incomplete knowledge of the fished reefs in a region. Additionally, much hinges on the interpretation of what individuals considered 'good' or productive bottom because, as has also been shown, this judgement varied widely between individuals.

An independent means of validating these changes in productive coastline was devised. Loss of productive coastline was assumed to be correlated with falling effort within a block; in other words, if coastline has been lost, recent mean levels of effort should be a smaller fraction of peak levels of effort. It was assumed that (a) effort could be transferred out of a block to more productive areas if necessary, and (b) that effort did not change with increasing efficiency.
Accordingly, for each block, the mean of the total annual effort for the previous five years (2002–06) was compared with the mean of the five highest years of recorded effort prior to 2002 (percentage peak mean effort, Table 1). In blocks 13, 28 and 30, there is good correspondence between levels of mean effort and fished coastline. In Block 13, two of the years of highest effort are comparatively recent (1999, 2000), indicating that the identification of fished reefs is recent and hence most probably reliable. In Block 30, the year of highest effort (1983) was excluded because the annual catch was 66% greater than the next highest catch and regarded as anomalous.

In Block 14 the percentage peak mean effort was somewhat less, and in Block 23 much less than fished coastline, implying that the length of currently productive coastline was greater than might be expected. Potentially, the peak mean effort from Block 23 could have been higher, because it was reported to be more heavily fished in the years prior to the collection of spatial catch data. The extent of fished shoreline on the Block 23 coast between Monument Bay and the Marion Bay Narrows, and parts of the Block 14 coast along the southern shores of Bruny Island varied between current divers, and could be responsible for the variation.

This comparison using the historical distribution of effort assumes that effort would flow proportionally to the most productive fishing reefs. However, there are several critical factors which invalidate this assumption and affect the reliability of this method. In particular, it assumes that factors influencing the spatial distribution of

effort (e.g. buyers' preferences for different sizes of abalone, relative costs of fishing, and relative cost of labour) remain unchanged over the period of comparison. There are no effort data prior to 1975, and given high levels of catch prior to that year, maximum mean effort may be underestimated. It also depends upon the fishery being unconstrained by management intervention. For example, constraints on level of catch may mean that if there are more abalone to be caught than allowed by a TAC, then the distribution of effort may be influenced by economic factors, rather than productivity of fishing reefs. In addition, there have been changes in catching efficiency during the course of the fishery, and it could be expected that to achieve the same amount of catch, more hours would be expended earlier in the fishery than in later years (Harrison, 1983; Tarbath et al., 2007). However, with these reservations, the use of historical distribution of effort confirms the decline in productive reef area within these blocks.

Table 1 **Currently fished coastline, as a percentage of historically productive coastline. Currently fished coastline was estimated from the length of coast plotted on maps and compared with the length of historically fished coast. For comparison, the recent (2002–06) mean effort expressed as a percentage of the mean of the five years of highest effort is shown. Effort was derived from divers' catch records collected by Tasmanian government fisheries agencies from 1975–2006.**

Block	% currently fished coastline	Identified areas of reduced effort	% peak mean effort	Years of highest recorded effort
13	90	Recherche Bay	90	1978, 1979, 1982, 1999, 2000
14	50	Lower Channel	32	1981, 1983, 1984, 1985, 1988
23	90	Eagle Reef, Long Reef, Marion Bay Narrows	22	1975, 1976, 1977, 1978, 1983
28	10	Block wide	10	1976, 1977, 1981, 1982, 1984
30	10	Block wide	6	1983 excluded, 1980, 1981, 1982, 1984, 1986

Conclusions

There are two clear conclusions from this series of interviews: first, that divers once fished a much greater area of reef than that now supporting the current Eastern Zone TAC, and second, that large-scale ecosystem changes have been observed by divers.

Reduction of reef area

The reduction of fished reef area is a consequence of three factors:

a. biological depletion of reef
b. economic depletion of reef, and
c. reduced effort in deep water.

Biological depletion occurs when rates of recruitment and growth fall below losses caused by natural mortality and fishing. Changes in blacklip abalone abundance and the extent of biological depletion can be measured relatively easily using several recognised methods (Gorfine et al., 1996; Mundy et al., 2006). Unfortunately, Tasmania has never had a fishery-independent abundance monitoring program, so changes in abundance and the extent of depletion have to be inferred from a variety of sources, and principally from changes in catch. (Long-term catch rates are of no use as an index of abundance; firstly because search time is not proportional to density, and consequently catch-rates can be hyper-stable (Sluczanowski, 1986; Prince, 1992; Shepherd and Partington, 1995); and secondly, because in Tasmania, there have been many improvements in fishing efficiency which have reduced the effort required to catch abalone, and confound interpretation of catch rates as an index of abundance (Harrison, 1983; Tarbath et al., 2007)).

In parts of south-east Tasmania, abalone stocks were reduced from virgin levels to an extensively depleted state within the first 15 years of the fishery (Witherspoon, 1975). Information from the CSIRO catch sampling program (Figure 5) and from the early group divers confirm that daily landings fell during this period to a fraction of their former levels. Reported annual catches were as high as 3500 t, almost 40% higher than Tasmania's current TAC (Figure 3). In addition, abalone were caught at a smaller size limit than those of more recent years, and it is probable that egg production from the surviving mature abalone was insufficient to provide adequate recruitment to support such high levels of fishing mortality.

No major reefs were reported where abalone were fished to localised extinction. Even on the reefs about which divers expressed the most concern (e.g. the Block 30 reefs between Eddystone Point and the Gardens, or the reefs offshore of the beaches in McLean Bay, or Eagle and Long reefs in Marion Bay), abalone were present albeit mostly as scattered individuals and these reefs still sustain limited populations.

The reported productivity of individual reefs varied greatly. Some reefs have consistently supplied good catches since the start of the fishery. Examples include the offshore reefs in Block 13, the Goat Hills in Block 23 and Long (Seymour) Point at the northern end of Block 28. Typically these reefs feature complex cryptic habitat which makes abalone difficult to find, providing protection for adults from fishing.

Others reefs supplied good catches for many years, but then declined, and now are fished only after periods of recovery, which may take many years. Examples include the fringe reefs of the D'Entrecasteaux Channel (Block 14), Eagle Reef and Marion Bay (Block 23), parts of the granite coastline at Bicheno (Block 28) and the coast between Binalong Bay and the Gardens (Block 30). Some of these reefs are isolated by long stretches of beach, or are offshore, or particularly in the granite areas, may lack sufficient suitable cryptic habitat. At the smaller size limits operating until recently, many abalone would have been taken before they became sexually mature, greatly reducing the size of the spawning stock (Nash, 1992; Tarbath et al., 2001). The isolated nature of some of these reefs and typically limited dispersal of the abalone larvae

(Prince et al., 1987; McShane et al., 1988) meant that minimal recruitment was likely following extensive reduction of stocks by fishing, and any subsequent recovery would be slow.

The two blocks with the greatest decline in productivity (blocks 28 and 30) are geologically distinct from the other three. Blocks 28 and 30 are on the granite belt which covers much of the northern half of the east coast, whereas the other three are on dolerite (Forsyth et al., 2005b; Forsyth et al., 2005a). The structure of the granite beds, particularly on the coast surrounding Bicheno and Binalong Bay, is striking, typically comprising massive slabs and boulders. The size of the boulders is typically much greater than those from the dolerite coast, and the cryptic habitat appears to be more open and less able to conceal abalone. This may be a limiting factor in the resilience of the granite reefs to withstand heavy fishing pressure.

From the perspective of fishermen, reef productivity is influenced by the price paid for the catch, and when prices are sufficiently high, reefs with low stock levels may become productive. Conversely, when prices are low, stock levels need to reach levels where they can be economically harvested before they are classed as productive i.e. they may be economically depleted.

Economic depletion is determined more by financial considerations (e.g. profitability) than by reduction in stock levels. Profitability depends upon the level of return to the diver, which itself is determined by a variety of factors such as financial cost of fishing, the physical difficulty of fishing, the price received for catching abalone and the diver's expectations of reward. Divers usually try to maximise their financial returns, and most have a threshold level of expectation of catch: if their expectations of catch on a reef are low, they will attempt to find somewhere more productive.

To illustrate the effects of economic depletion, contrast the divers who stopped fishing virgin stocks at Bicheno in 1964 because they had caught the easily accessible fish and the price was too low to warrant moving further afield, with the divers fishing depleted stocks at Dover in 1975 at very low catch rates (100 kg/day) but who received 10 times the beach price of the early Bicheno divers. These are extreme examples, and the state of the current fishery lies somewhere between them; however, the point is clear: the extent of reef fished on the coast now covered by the Eastern Zone is determined as much by economics as by biology.

It is outside the scope of this project to present a detailed review of the economic aspects of catching abalone both past and present, but the current divers who work on contracts state that the level of payments they receive for catching abalone limited them to higher-yielding sections of reef. They believed that the financial rewards to the earlier divers whose right to take an unlimited amount of fish (quota) was bound to their fishing license were greater, and enabled them to profitably fish at lower levels of abundance.

In recent years the reported annual catch from the area now covered by the Eastern Zone has been at the lowest levels since catches have been spatially recorded (1975),

and from estimates provided by the early group divers, probably since 1965. Current divers report that because of the relatively low levels of fishing mortality, stock levels have increased, and their catch rates have risen correspondingly. They have concerns that if any future increases in TAC are too large, stock levels on the current productive reefs will eventually fall, forcing them to the less productive (and currently unfished) reefs, raising the cost of fishing. While this would force them to work over a greater area of reef, they could only afford to do so if the increased costs were met by the quota owners. Similar situations have arisen following the implementation of zones in the abalone fishery, which has forced divers to work in remote areas that had not been fished for many years. While initially some of these reefs had high stock levels, intensive fishing has been met by falling catch rates and quota owners have been compelled to offer higher rates to divers to induce them to fish there.

Loss of reef caused by reduced effort in deep water may be of less consequence than indicated by the reverse situation at King Island (Figure 8). In the east and south east, divers from all groups believed that the shallows were more productive than the deep water habitat, and although the deep water reefs may have initially supported good catches, they were very slow to recover. Several early group divers estimated that only 5–10% of their eastern catch was taken from water deeper than 40 feet (~12 m), and this occurred mostly in the more exposed coast of the south.

In summary, the extent of fished reef area is dynamic, and is affected by a complex relationship between abalone abundance, the amount of catch to be taken (TAC) and the financial rewards to the divers. While the abundance of abalone on individual reefs has never been directly monitored, it appears that in the south and south-east, populations seem better able to recover following fishing than in the north-east, and consequently the extent of area of fished reef fluctuates. In the north-east, where populations appear to be less resilient to fishing, large areas of formerly productive reefs were identified which have been reduced to becoming at best marginally productive, and the loss of productive reef area is much greater and less dynamic.

The effect of inter-annual changes to productive reef area on the stock assessment process needs to be considered. If the area of non-producing reef continues to increase because of either biological or economic depletion, then unless the overall catch is reduced, stocks on remaining reefs will be jeopardised by increasing levels of fishing mortality (Keesing and Baker, 1998). However, the converse also applies, and both early and middle group divers said that because the Eastern Zone TAC is low and current divers are content to fish on established productive reefs, there is lost production from unfished reefs which have either been forgotten or where populations have recovered unobserved. Knowledge of changes in fished reef and its affect on remaining populations would therefore help to manage the fishery sustainably and productively.

Stock assessment of the Tasmanian abalone fishery is mostly dependent on fishery derived information. It has always been assumed that effort flows to the most productive reefs (i.e. fishermen attempt to maximise their returns), and that

monitoring changes in catch and (over short periods of time) effort between reporting blocks should be indicative of gross-scale changes in reef production. Unfortunately, the relationship between TAC and the size of the stock is rarely optimised to the extent that it enforces predictable flows in effort and consequently the decision about where to fish is often based on more complex reasons than abundance. This means that divers can deplete successive reefs within a reporting block without necessarily triggering changes in annual catch indicative of stock collapse. Unless a means of detecting small-scale changes in effort (e.g. the current FRDC funded GPS diver tracking project) or fishery-independent monitoring of abalone abundance is used, the current stock assessment process will continue to fail to detect stock declines and changes in the area of fished reef.

Ecosystem changes

A wide range of ecosystem changes were observed by divers, although they did not necessarily associate them with changes in abalone abundance. Prior to this project, it had been noted that divers catch most of their abalone on CCA-encrusted reef (pink/purple rock), and least abalone on reef encrusted with sponges, ascidians or other encrusting biota including dense understory and canopy algae (brown rock). Some divers had said that following particularly intensive fishing such as occurred during the Bass Strait pulse fisheries and in heavily fished areas surrounding Bicheno and the Gardens which led to extensive depletion, the habitat changed. They believed that the coverage of CCA on the reef where they used to catch abalone had become less extensive, that the pink rock had changed to brown rock and that there were much less abalone on the reef. The possible consequences of this habitat change include reduced reef area for settlement of veligers, reduced egg production from the depleted populations and consequent destabilisation of the primary abalone habitat leading to further population declines. This habitat change may be the reason why abalone populations on some of the depleted reefs in blocks 28 and 30 have failed to recover to former levels, despite low levels of catch being taken.

Not all divers noticed changes to the habitat in which they worked. Most agreed that algal growth increased during the warmer months, but by and large, they were less interested in their surroundings and more concerned with catching abalone. Of the changes that were noticed, most were transient and inconsequential, such as fluctuations in algal growth or the consequences of storm damage.

Only a few divers noticed significant habitat changes. Three divers noticed changes that they associated with gross-scale depletion of abalone. In all three cases, the changed habitat states and reduction in abalone numbers have persisted for many years. They had assumed that the removal of the abalone was responsible for the habitat change, although they conceded that other factors, such as sand scour or damage caused by storms could also have contributed to the changes.

Three different divers spoke about reefs in other areas, where abalone populations had also been grossly depleted. These places included reefs at Bicheno, in Block 25

between Swansea and Orford and on a small area of reef on the west coast south of Cape Sorell (Block 9). In contrast to the reefs where habitat changes had occurred, they said that these reefs remained 'pristine abalone habitat', with substantial areas of CCA-covered rock.

An important detail that emerged from the talks was that these six divers were aware that the extent and size of the abalone populations that they were fishing had been severely diminished, and they had a good knowledge of the abalone habitat before and after the removal of abalone. This contrasts with many of the others, who once aware that depletion had taken place, lost interest in an area once they knew it was not worth fishing, and consequently did not observe habitat change.

The only reasonable conclusion that can be developed from these observations is that abalone habitat may undergo extreme changes, and there may be multiple causes, one of which is the depletion of abalone.

2.2
Biological and environmental correlates of reefs with contrasting abalone densities

Introduction

Fishing is the most widespread human exploitative activity in the marine environment (Jennings & Kaiser, 1998) and it is now well recognised that ecologically sustainable development of marine resources requires an ecosystem-based approach to planning and management due to the extensive interactions that occur between target species and other organisms (Jennings & Kaiser 1998). Assessing the ecological role of a fished species represents a fundamental stage in an ecosystem-based management approach.

Blacklip abalone (*Haliotis rubra*) is the dominant herbivore in subtidal habitats on exposed coastlines of Tasmania and the focus of the world's largest abalone wild fishery (>2500 tonnes per annum). While not confirmed, it is widely held that abalone activity contributes to the dominance of crustose coralline algae (CCA) in understorey communities (C. Mundy, pers. comm.). Anecdotal evidence from some commercial abalone divers indicates that a shift from CCA dominance (so called 'pink rock') to a community dominated by sessile invertebrates and foliose algae ('brown rock') is associated with depletion of abalone from reefs (Chapter 2.1). On some Tasmanian reefs there is evidence that abalone numbers have been heavily depleted, with annual catches representing only 4% of the long-term average catch (Tarbath et al. 2004). If abalone play a key role in the maintenance of CCA, then substantial reductions in biomass and numbers of abalone through fishing may lead to changes in ecosystem structure and function. Additional impetus for understanding 'abalone–ecosystem' interactions is the fact that the majority of abalone (*Haliotis* spp.) fisheries around the world have collapsed or are in serious decline (Shepherd et al. 2000), raising the possibility that altered ecosystem function may have occurred due to removal of this key herbivore.

Reduced cover of CCA has implications both for natural processes and for the long-term existence of abalone populations, as other life history stages of abalone and invertebrates also rely significantly on CCA. For example, the recent recruitment failure of black abalone in California has been linked with changes in CCA abundance following mass-mortality of black abalone populations (Miner et al. 2006). Larval abalone are known to preferentially metamorphose and subsequently feed on CCA or associated bacteria and diatoms until they reach approximately 15 mm in length (Shepherd 1973b; Saito 1981; Shepherd & Turner 1985; Tarr et al. 1996; Daume et al.

1999). Shell pigmentation (pink colouration) associated with this feeding activity also aids camouflage and provides protection from predators during this critical early life history phase.

While an experimental approach is required to ultimately determine the effect of abalone removal on the reef ecosystem, a necessary prerequisite to experimental manipulations is the use of a correlative studies to identify taxa that could be potentially influenced by abalone abundance (Jenkins 2004). The primary objective of this study was to examine benthic communities on reefs with contrasting fishing histories, comparing biological and environmental correlates of reefs that continue to sustain commercial abalone fishing with reefs that no longer support a viable fishery. The original study objective required modification because of the complexities associated with assigning productivity status to individual reefs (see Chapter 2.1). Consequently, the primary objective was adjusted, focusing on biological and environmental correlates of reefs with contrasting abalone densities, reflecting the need to quantify abalone abundance on survey reefs.

Methods

Study sites

Surveys focused on four areas of the Tasmanian Eastern Zone fishery including St Helens (blocks 30, 31), Bicheno (blocks 28, 29) and Dunalley (blocks 23, 24) on the east coast and the 'Actaeons' (blocks 13, 14) region on the south-east coast. The east coast regions were chosen because it is well documented that numerous reefs in the region have experienced significant declines in abalone abundance, reflected by declining catch and effort in recent years (e.g. Figure 10). In contrast the Actaeons area has many reefs that have remained productive throughout the history of the fishery (Figure 10). The focus of the study was understorey communities in the 6–8 m depth range on exposed coastlines, since this is typically where most abalone fishing activity takes place. The influence of depth on abalone abundance and benthic community structure was investigated for the Dunalley region, where a shallower depth range (2–3 m) was also included at a restricted number of sites.

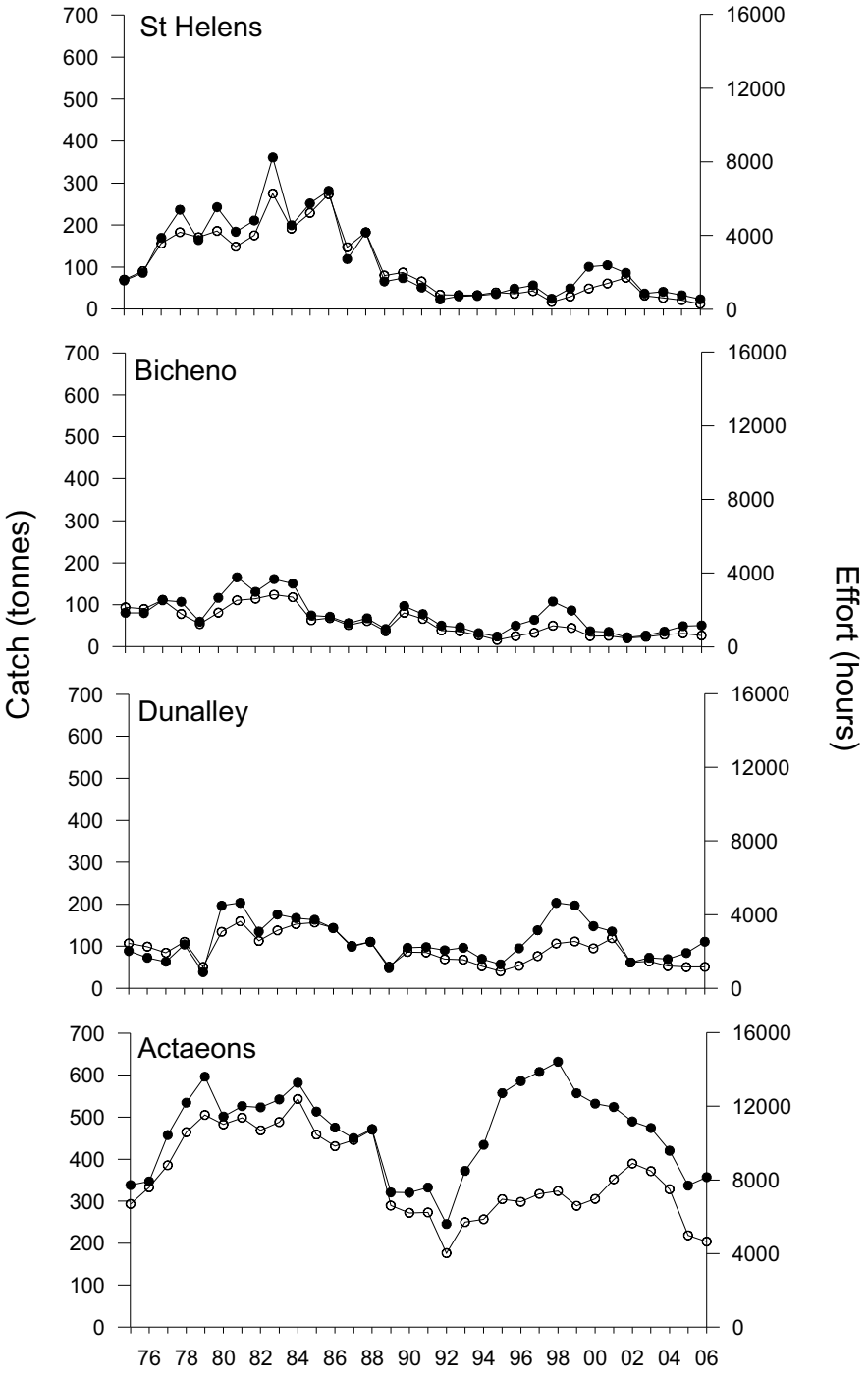

Figure 10 **Comparison of *Haliotis rubra* catch (●) and effort (○) for the St Helens (Blocks 30, 31), Bicheno (Blocks 28, 29), Dunalley (Blocks 23, 24) and Actaeons (Blocks 13, 14) regions.**

Potential survey reefs in each region were selected based on anecdotal evidence, information gained through diver interviews (Section 2.1) and knowledge of experienced abalone research scientists at the University of Tasmania. Reefs were categorised as 'failed' if they were formerly productive but now considered depleted (with respect to abalone) and 'productive' if they were considered to have been productive since the inception of the fishery and currently remain productive. Where possible, marine protected areas were also included in the survey. It was originally

anticipated that at least 10 reefs would be sampled in each region, including equal numbers of 'productive' and 'failed' reefs. The location of survey sites are shown in Figure 11.

A problem with the original survey design was that for the east coast regions (St Helens, Bicheno, Dunalley) the number of 'productive' reefs available was severely limited, because most reefs in the area are no longer considered productive. On the other hand, a small number of 'failed' reefs were available in the Actaeons region. Due to these restrictions, equal numbers of 'failed' and 'productive' sites could not be sampled and the data could not be analysed using a conventional orthogonal design. As a consequence, an alternative regression-based approach was implemented, so reefs with contrasting abalone densities could be compared. This approach was also more appropriate because there were sometimes discrepancies between divers as to the productivity status of reefs (see Section 2.1). Furthermore, reef status was not always a reliable indicator of abalone abundance.

Survey protocol

1 Biological correlates of reefs with contrasting abalone densities

At each survey site a 100 m transect was deployed from the boat along the 6–8 m depth contour. Five 20 m^2 quadrats were positioned at 20 m intervals along the transect and in each quadrat the number of abalone and other grazers (e.g. sea urchins) was recorded. Total abalone abundance was split into two separate categories of 'cryptic' and 'emergent' based upon the location of individual animals. Cryptic abalone were defined as those hidden in cracks and crevices, while emergent abalone occupied exposed reef surfaces. Abundance of canopy-forming algae in each quadrat was also estimated by classifying cover of different species according to the following categories: 1 = 0–10%; 2 = 11–30%; 3 = 31–50%; 4 = 51–75%; 5 = 76–100%.

Abundance of understorey organisms (including algae and sessile invertebrates) was assessed in terms of percentage cover. Percentage cover was estimated with a 0.25 m^2 'sub-quadrat' using a point intercept method. The sub-quadrat was divided with a grid of 49 evenly spaced intersections and was laid flat on the reef during algal assessment. Algae occurring under each intercept and one corner of the sub-quadrat were recorded, to give a total of 50 intersections per sub-quadrat. Five randomly positioned sub-quadrats were assessed in this way for each 20 m^2 quadrat. Organisms were identified *in situ* to the highest taxonomic resolution possible. For canopy algae, identification to species level was possible; however, it was necessary to allocate other species to species complexes or guilds (e.g. crustose coralline algae, foliose red algae, sessile invertebrates).

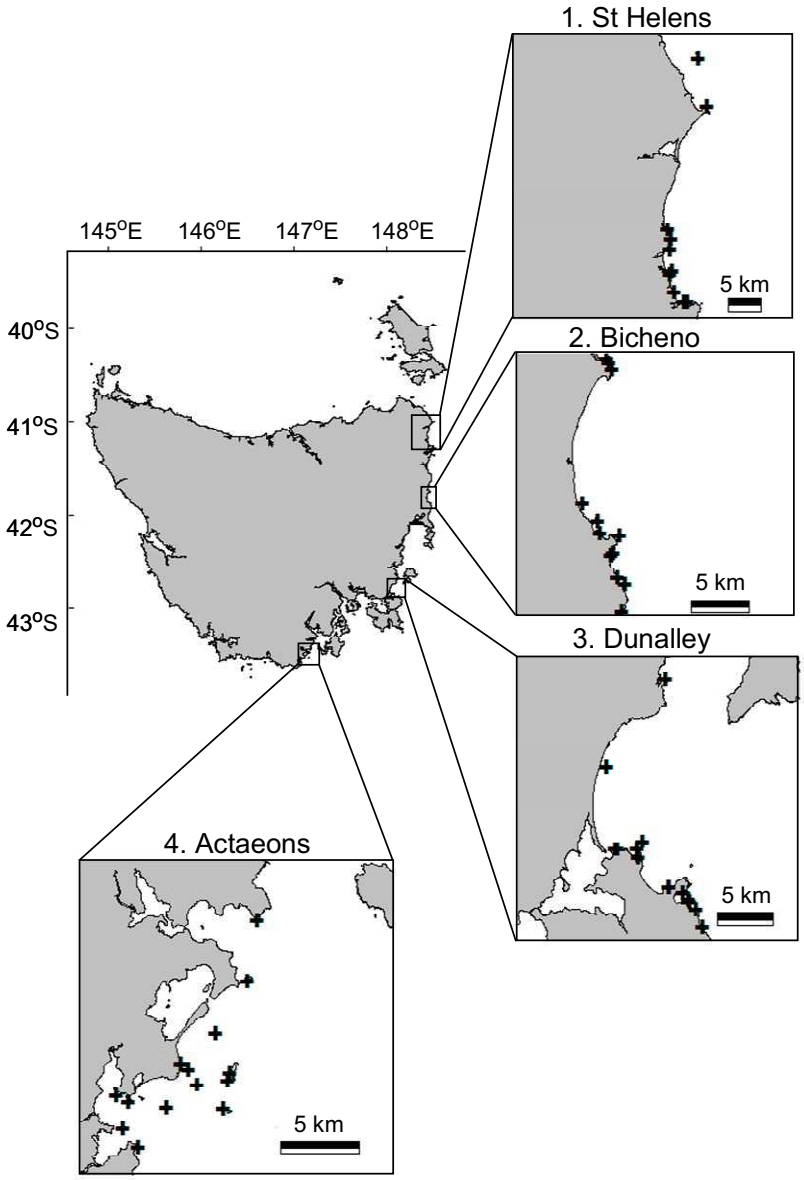

Figure 11 Map showing location of four study regions and survey sites (✚)

2 *Environmental correlates of reefs with contrasting abalone densities*

To investigate environmental correlates of reefs with contrasting abalone densities, additional site level variables were recorded, including structural complexity and relative wave exposure. Relative wave exposure was calculated according to the methods of Rice & Kenchington (1990). This wave exposure index is based upon the number of 9° sectors radiating from the site that are fully open to seaward for 7.5 km or further and does not account for prevailing winds, currents or ocean generated swell. Structural complexity was calculated using two methods: a 'rope and chain' method (Luckhurst & Luckhurst 1978) and a categorical classification. For the 'rope and chain' method a 10 m chain tape was moulded over the substratum through the centre of each quadrat and a measuring tape was then pulled straight to determine the

linear distance that the 10 m chain passed over. The categorical classification of substratum types was based on the average diameter of the dominant substratum type: 1 = flat rock/boulders >5 m diameter; 2 = boulders 2.5 – 5 m diameter; 3 = boulders 1 – 2.5 m; 4 = rocks 0.2 – 1 m; 5 = cobble 0.1 – 0.2 m; 6 = pebble 0.01 – 0.1 m; 7 = sand.

It should be emphasised that because the primary focus of the study was to understand the influence of abalone on understorey communities, the range of environmental characteristics was restricted (i.e. 6–8 m depth range; exposed coast reefs). These constraints were necessary because sampling different depths and a greater range of exposures would have reduced the power to detect the influence of abalone on benthic community structure. A survey design with a greater range of depths and wave exposures would have potentially given greater insights into factors influencing abalone abundance; however, this would have been at the expense of the adequate description of 'abalone-ecosystem' patterns.

Analysis

Relationships between abalone categories (total, emergent, cryptic) and the dominant benthic groups were explored using scatterplots and linear regression. For individual taxa, Spearman rank correlations were also used to identify taxa that were most strongly correlated with total abalone abundance at the regional level. While abundance of other grazers (sea urchins, gastropods) was very low, at four sites in the St Helens region the sea urchin *Centrostephanus rodgersii* was abundant in some quadrats. Because this grazer can have a major influence on algal community structure (Fletcher 1987), quadrats where *C. rodgersii* was abundant were excluded from regression analyses.

Analysis of variance (ANOVA) was used to compare abalone abundance and cover of dominant understorey groups in relation to depth for the Dunalley region. Abalone abundance was analysed by a two-way Model III ANOVA, while a three-factor Model III nested ANOVA was used for cover data. Both analyses included depth (fixed factor, two levels) and site (random factor, five levels). The nested ANOVA included the effect of segment nested within all combinations of Depth*Site as a random factor.

Multivariate patterns in understorey community structure among sites were examined using non-metric multidimensional scaling (MDS), an unconstrained ordination method that allows overall patterns and potential differences in relative within-group dispersions to be visualised. The nMDS routine in Primer (Clarke 1993) was used for these analyses. A constrained ordination method was also used to visualise multivariate patterns with respect to particular hypotheses. Constrained ordinations were conducted using the 'CAP' method (Canonical analysis of principal co-ordinates) in accordance with Anderson & Willis (2003). This method is a traditional canonical discriminant or canonical correlation analysis (depending on

whether the hypothesis involves group differences or continuous predictors) on a subset of coordinate axes from a metric multidimensional scaling (Anderson & Willis 2003; Willis & Anderson 2003). Separate CAP analyses were conducted to visualise the relationship between multivariate variation in understorey community structure and (i) abalone density and (ii) spatial variability at the 'regional' level. The canonical correlations in each case were tested using a permutation method, involving 4999 permutations of the raw data. All multivariate analyses were based on Bray-Curtis similarity matrices derived from average percentage cover data at each site. Data were fourth root transformed to reduce the influence of dominant species.

Standard multiple regression was used to determine the environmental parameters that had the greatest influence on abalone (emergent, cryptic, total) abundance. These parameters were relative exposure, reef complexity (chain), reef complexity (categorical), and a spatial component ('region'). The independence of these measures was examined by screening pair-wise correlations of independent variables. The two rugosity methods were highly correlated, so only one method ('rope and chain') was included in the multiple regression model to reduce problems associated with collinearity (Rao 1998). The resulting squared multiple correlation (R^2) is an expression of the proportion of the total variability in the dependent variable (abalone abundance) that is predictable from the best linear combination of the independent variables (Tabachnick & Fidell 1989). Semipartial correlation coefficients were also used to express the unique contribution of each independent variable to the total variation in abalone abundance (Tabachnick & Fiddell 1989). Multiple regression analyses were performed using the JMP© software program.

Results

Biological correlates of reefs with contrasting abalone densities

Regional level comparison of 'failed', 'productive' and 'marine reserve' reefs

Broad-scale comparisons of failed, productive and marine reserve reefs at the regional level are shown in Figure 12. Whilst differences could not be statistically tested due to the lack of balance in the dataset, it nonetheless shows some important patterns. Cover of CCA was consistently higher on productive reefs compared to failed reefs, although the magnitude of the difference was not dramatic considering the range of abalone densities observed. Abalone density was more than seven times higher on the Actaeons 'productive' reefs (0.67 abalone m^{-2}) compared to 'failed' reefs at Bicheno (0.09 abalone m^{-2}). Comparison of the corresponding CCA cover on these reefs reveals a much smaller difference, with CCA cover on the Actaeons 'productive' reefs (51.0%) higher than Bicheno's failed reefs (30.3%) by a factor of only 1.7. For the remaining benthic groups, patterns in relation to fishing history were generally weak and inconsistent. Sessile invertebrate cover was generally slightly higher on 'failed' reefs, with the exception of St Helens, where 'productive' reefs had higher sessile

invertebrate cover. For understorey algae and canopy-forming algal recruits, strong patterns in relation to fishing history were not evident.

Correlations between abalone and understorey organisms

Significant correlations between total abalone abundance and understorey organisms were observed for data collected at the 'quadrat' level, although for some understorey groups, the nature of the relationship varied between regions (Fig. 4). Although significant in a number of cases, correlations were typically very weak for all understorey groups. The strongest correlation observed was between total abalone abundance and CCA at Bicheno, with an R^2 value of just 0.30. Significant associations between total abalone abundance and particular benthic groups appear to be driven largely by the abundance of emergent abalone, since most of the patterns observed were consistent between the 'total abundance' and 'emergent' categories (Fig. 4, Fig. 5). Relationships between cryptic abalone abundance and cover of understorey organisms were weak or non-existent (Fig. 6). Of the three significant correlations observed, two (Bicheno CCA, Dunalley canopy-forming recruits) were influenced by a single strong leverage point, which when removed made the relationships non-significant.

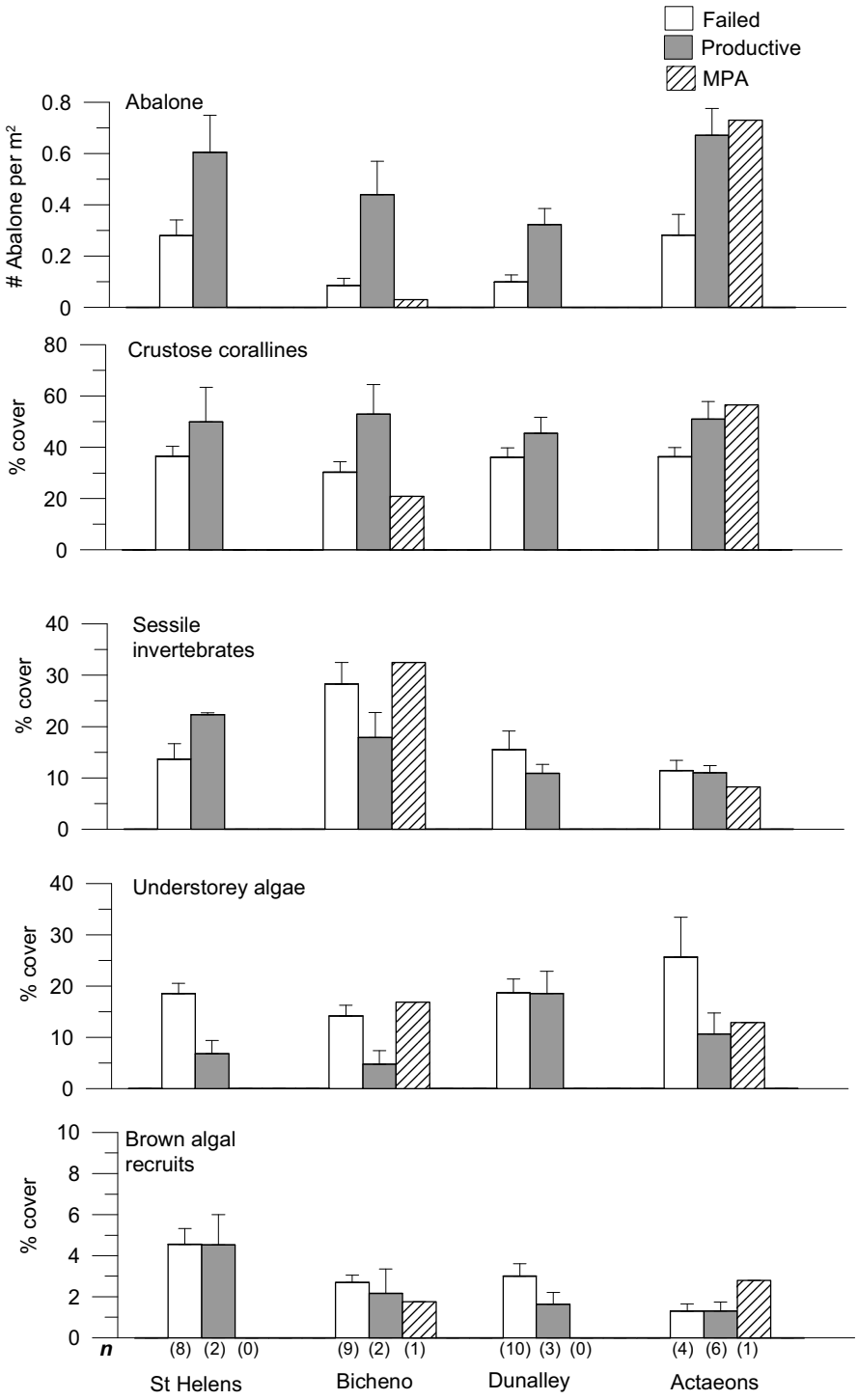

Figure 12 **Abundance of abalone and major understorey groups in relation to fishing history. Abalone abundance represents mean total abundance (cryptic and emergent) across sites, determined from five randomly positioned 20 m^2 quadrats at each site. Cover of understorey organisms was determined from five randomly positioned 0.25 m^2 sub-quadrats in each quadrat. Note that replication varied between regions; the number of replicate site variations for each 'category-region' combination is shown in parentheses.**

CCA cover was positively correlated with total abalone abundance for all survey regions. A feature of all correlations was the high level of variability and corresponding low R^2 values. While there was a general trend of higher CCA cover associated with abalone density, there were many instances where high CCA cover was observed at low abalone densities.

Sessile invertebrates were negatively correlated with total abalone abundance when data were pooled across all regions (R^2 = 0.03), but when regions were considered in isolation no significant relationships were evident (Figure 13). In contrast, significant negative correlations were evident in all regions for understorey algae. While significant, these correlations were again very weak. The 'triangular' nature of this relationship suggests that while other factors influence understorey algal abundance, abalone abundance sets an 'upper limit' to their abundance (a so called 'factor ceiling distribution' (Thompson *et al*. 1996)). Cover of understorey algae varied substantially when abalone density was low, but high values were only observed in the presence of low abalone densities. When abalone density was high, only low cover of understorey algae was observed (Figure 13).

Spearman Rank correlations confirmed the positive correlation detected in the linear regression analyses, with a significant positive correlation between abalone and CCA across all regions (Table 2). Significant correlations were rarely consistent between regions for individual taxa, with the exception of foliose red algae which was negatively correlated with abalone abundance for three of the four survey regions. Other significant correlations were evident but were only in particular regions (e.g. *Zonaria* spp. was positively correlated with abalone at Binalong Bay and Bicheno).

Correlations between abalone and canopy-forming algae

Very few significant associations were identified between abalone and the various canopy-forming algal species encountered in the study (Figure 16). The associations that were observed were extremely weak and not consistent between regions.

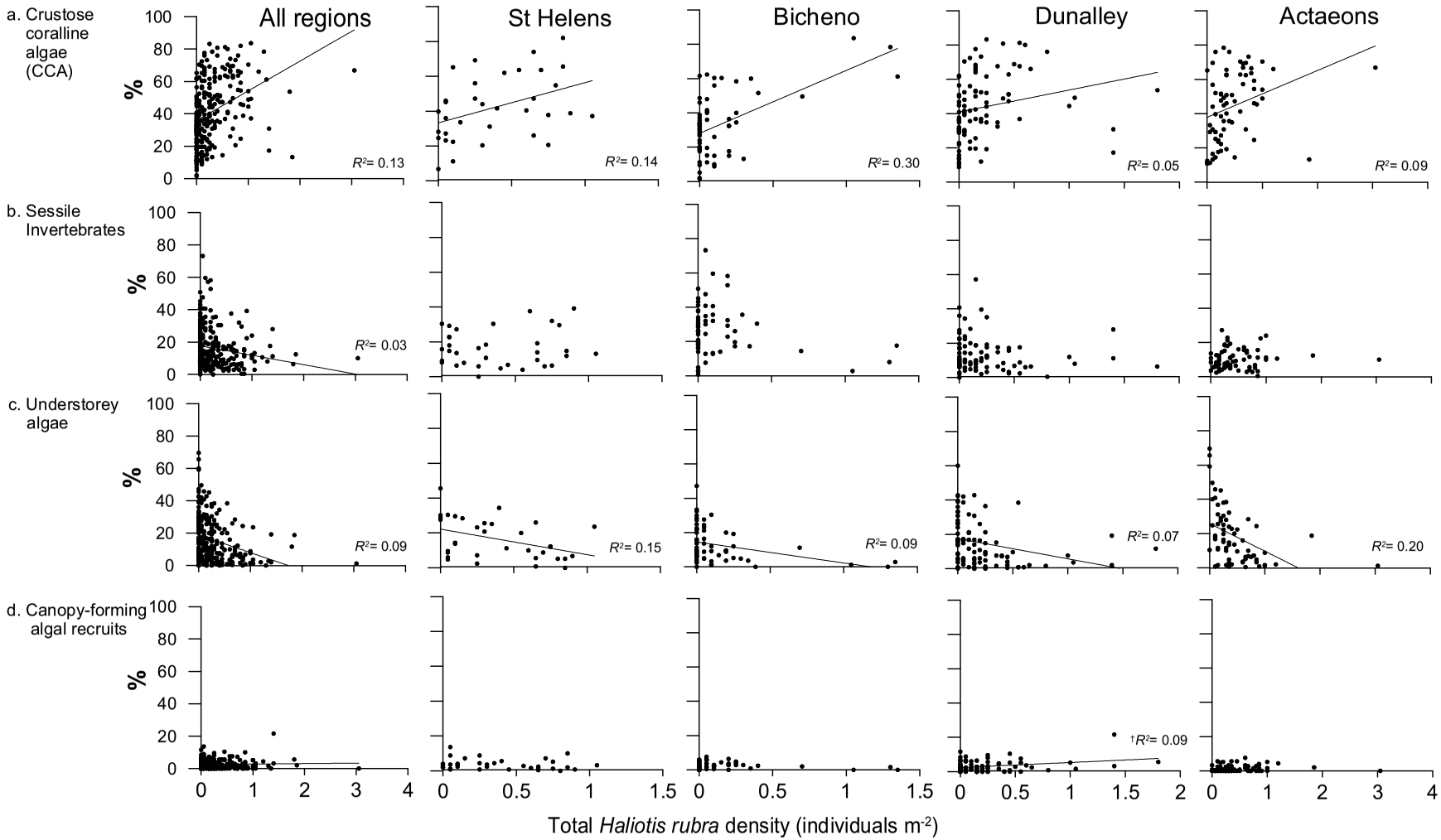

Figure 13 **Relationship between total abalone abundance and understorey organisms. Significant regression lines (α = 0.05) and corresponding R^2 values are shown. Note different scales on the x-axes. †Relationship strongly influenced by outlier with strong leverage.**

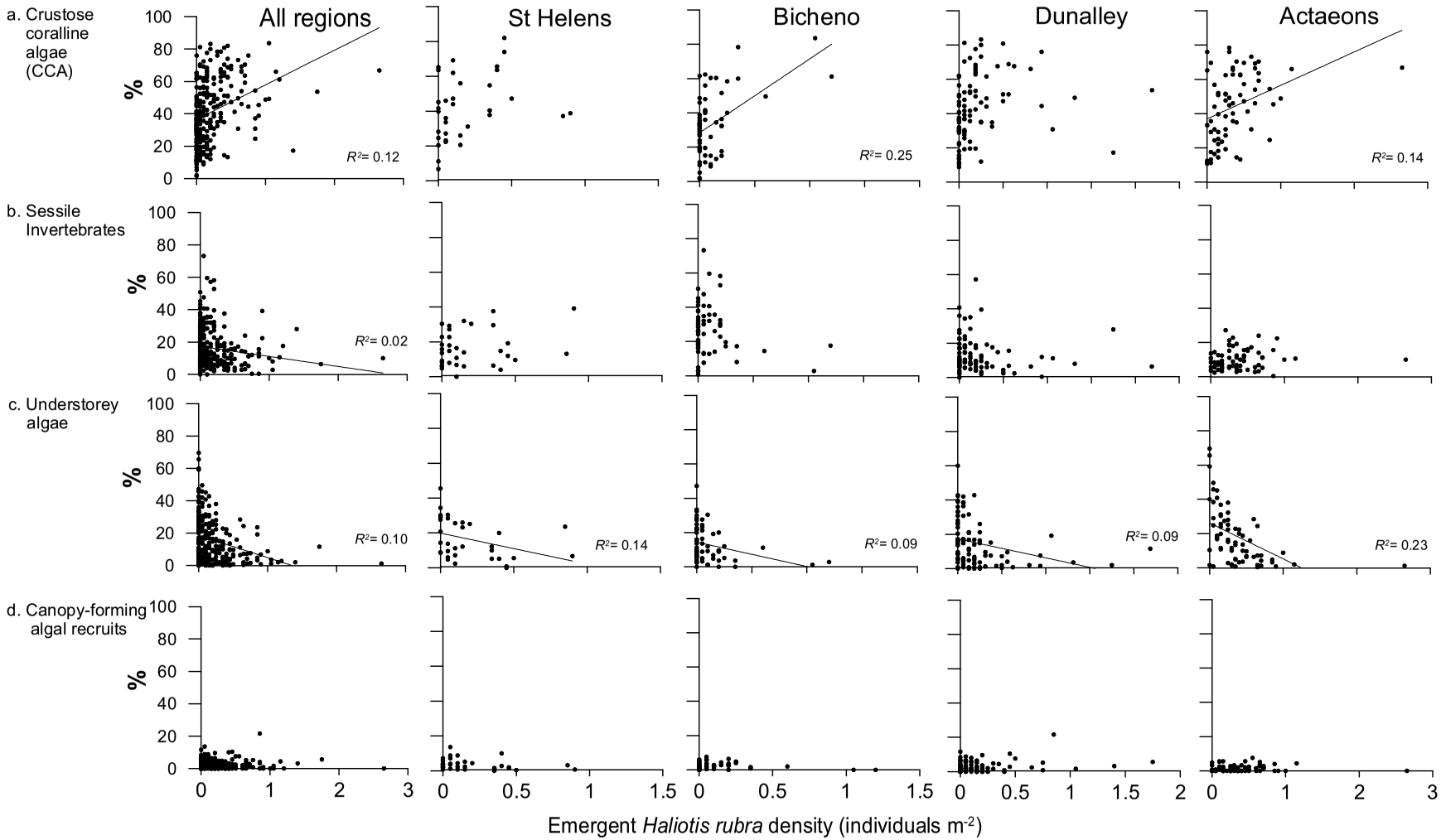

Figure 14 **Relationship between emergent abalone abundance and understorey organisms. Significant regression lines (α = 0.05) and corresponding R^2 values are shown. Note different scales on the x-axes.**

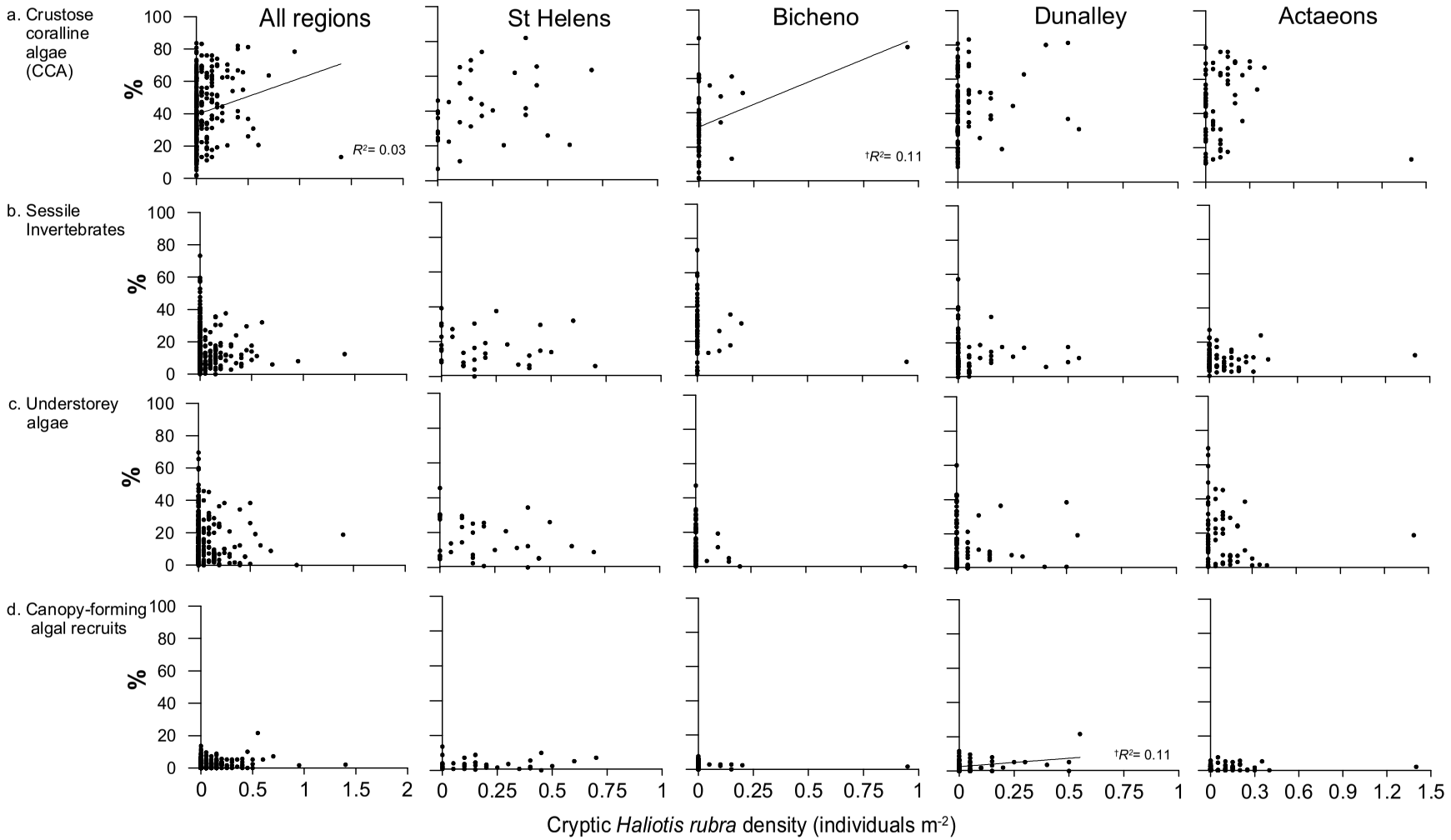

Figure 15 **Relationship between cryptic abalone abundance and understorey organisms. Significant regression lines (α = 0.05) and corresponding R^2 values are shown. Note different scales on the x-axes. †Relationship strongly influenced by outlier with strong leverage.**

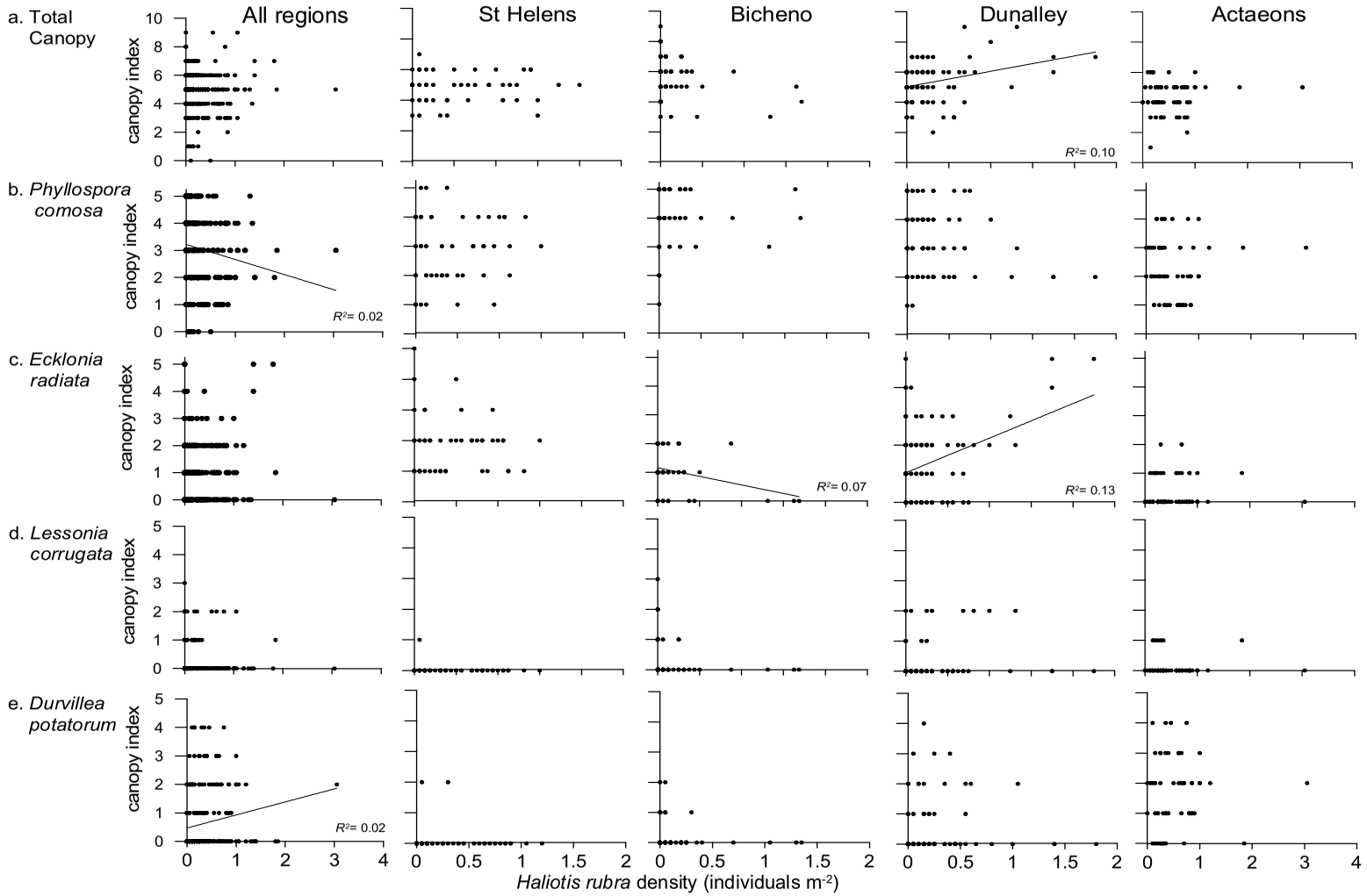

Figure 16 **Relationship between total abalone abundance and canopy-forming algae. Significant regression lines (α = 0.05) and corresponding R^2 values are shown. Note different scales on the x-axes.**

Table 2 **Spearman rank correlations of algal and invertebrate groups, derived from regional level data. Abbreviations include NCERA = non-coralline encrusting red algae (includes the algal genera *Peyssonnelia* and *Hildenbrandia*), and CCA = crustose coralline algae. Where taxa were not recorded in a particular region, the notation 'NA' applies. Significant p-values (α = 0.05) are shown in boldface.**

Variable	St Helens		Bicheno		Dunalley		Actaeons	
	S Rank	p	*S Rank*	p	*S Rank*	p	*S Rank*	p
Encrusting algae								
NCERA	-0.235	0.1004	0.0461	0.7265	0.1901	0.1293	0.1606	0.2414
CCA	0.3525	**0.0121**	0.3706	**0.0036**	0.3683	**0.0025**	0.4836	**0.0002**
Geniculate coralline algae	-0.0849	0.5577	-0.3005	**0.0197**	-0.2868	**0.0205**	0.14	0.308
Foliose understorey algae								
Carpoglossum confluens	-0.1189	0.4108	NA	NA	-0.2475	**0.0468**	-0.0198	0.8861
Carpomitra costata	-0.1475	0.3067	0.1401	0.2858	0.1206	0.3384	-0.1374	0.317
Caulerpa flexilis	-0.1512	0.2947	-0.287	**0.0262**	-0.1047	0.4066	-0.4569	**0.0005**
Caulerpa rhizome	NA	NA	-0.1241	0.345	NA	NA	-0.0545	0.6926
Colpomenia spp.	-0.269	0.0589	NA	NA	NA	NA	NA	NA
Filamentous red	-0.1494	0.3004	-0.0232	0.8604	0.2411	**0.053**	-0.0104	0.9401
Foliose red algae	-0.2254	0.1156	-0.4295	**0.0006**	-0.2929	**0.0179**	-0.6188	**<0.0001**
Filamentous green	NA	NA	-0.2166	0.0964	-0.1346	0.2849	0.276	**0.0414**
Halopteris spp.	0.2238	0.1183	0.3022	**0.019**	-0.3975	**0.001**	NA	NA
Red recruits	-0.0794	0.5836	-0.0722	0.5838	0.2105	0.0924	-0.029	0.8338
Sonderapelta spp.	0.1026	0.4782	0.0835	0.526	-0.3892	**0.0014**	-0.2632	0.0522
Xiphophora gladiata	NA	NA	-0.0634	0.6301	0.1451	0.2488	-0.2996	**0.0263**
Zonaria spp.	0.3048	**0.0314**	0.3162	**0.0138**	-0.1067	0.3978	0.2277	0.0945
Canopy-forming algal recruits								
Ecklonia radiata	-0.1666	0.2475	-0.1286	0.3275	-0.1558	0.2151	-0.1369	0.319

Cystophora moniliformis	NA	NA	NA	NA	-0.2369	0.0574	NA	NA
Cystophora retroflexa	NA	NA	NA	NA	-0.1341	0.287	0.1031	0.4539
Phyllospora comosa	-0.16	0.2671	0.2922	**0.0235**	-0.1974	0.115	0.108	0.4326
Sargassum decipiens	NA	NA	NA	NA	-0.1013	0.4219	NA	NA
Sargassum spp. recruit	-0.1847	0.1991	0.0444	0.7362	-0.0148	0.9071	0.0982	0.4755
Invertebrates								
Barnacles	-0.0932	0.5197	-0.1241	0.345	0.1312	0.2976	NA	NA
Bugularia dissimilis	-0.128	0.3759	-0.0434	0.742	-0.3404	**0.0055**	-0.257	0.0582
Variable	St Helens		Bicheno		Dunalley		Actaeons	
	S Rank	p	*S Rank*	p	*S Rank*	p	*S Rank*	p
Colonial Ascidian	NA	NA	-0.016	0.9032	NA	NA	0.1867	0.1724
Encrusting bryozoa	0.148	0.3049	-0.0586	0.6563	0.0677	0.5922	0.3606	**0.0068**
Erect sponge	-0.2785	0.0502	0.0465	0.724	-0.1346	0.2849	-0.0644	0.6403
Encrusting mussels	NA	NA	-0.0686	0.6024	NA	NA	NA	NA
Encrusting sponge	0.0917	0.5264	-0.0312	0.8127	-0.0275	0.8279	-0.0953	0.4888
Orthoscuticella phoeniceum	-0.2271	0.1127	-0.0598	0.65	-0.3012	**0.0148**	-0.0713	0.6051
Solitary Ascidian	0.3083	**0.0294**	-0.0019	0.9884	0.0005	0.9969	0.265	0.0505

Influence of depth on abundance of abalone and understorey organisms

Important insights into the influence of depth on patterns of abalone abundance and understorey community structure were provided by the Dunalley surveys (Figure 17). Depth-related patterns were site specific, with the exception of the 'canopy-forming algal recruit' category, indicated by a significant Depth*Site interaction in the ANOVA models (Table 3). For some of the understorey groups, differences attributable to depth were evident at the same sites where differences in abalone abundance were found. For example, CCA cover was significantly higher in the shallow depth zone at sites s1, s3 and s5. Abalone abundance was also higher for these same sites, although statistically significant differences were only evident for sites s1 and s5. Similar patterns were evident for understorey algae. For 'sessile invertebrates' and 'canopy-forming algal recruits' strong depth related patterns were not apparent. These patterns highlight the potential for confounding when examining correlations

between abalone and benthic community structure. In this particular example, differences in CCA abundance between depths could be related to abalone abundance; however, these differences are clearly confounded by depth and could also be explained by changes in the physical environment that also vary with depth (e.g. wave energy, light, sedimentation).

Community level patterns

MDS analysis reflected regional differences in understorey community structure, with 'Actaeons' sites generally distinct from the three east coast regions (Figure 18a). The bubble plot (Figure 18b) also tended to show sites with high abalone density forming a distinct group, but this grouping could also be attributable to regional differences in understorey community structure. CAP analyses demonstrated a significant correlation between understorey assemblage composition and both 'region' and 'abalone'; however, regional correlations were much stronger than those attributable to abalone density (Table 4). The four regions separate clearly in the canonical axis for 'region' (Figure 19a), demonstrated by the high squared canonical coefficient. The canonical axis for 'abalone density' shows some clustering of sites consistent with abalone density as a structuring influence, although there are a number of instances of overlap between sites with contrasting densities (Figure 19b).

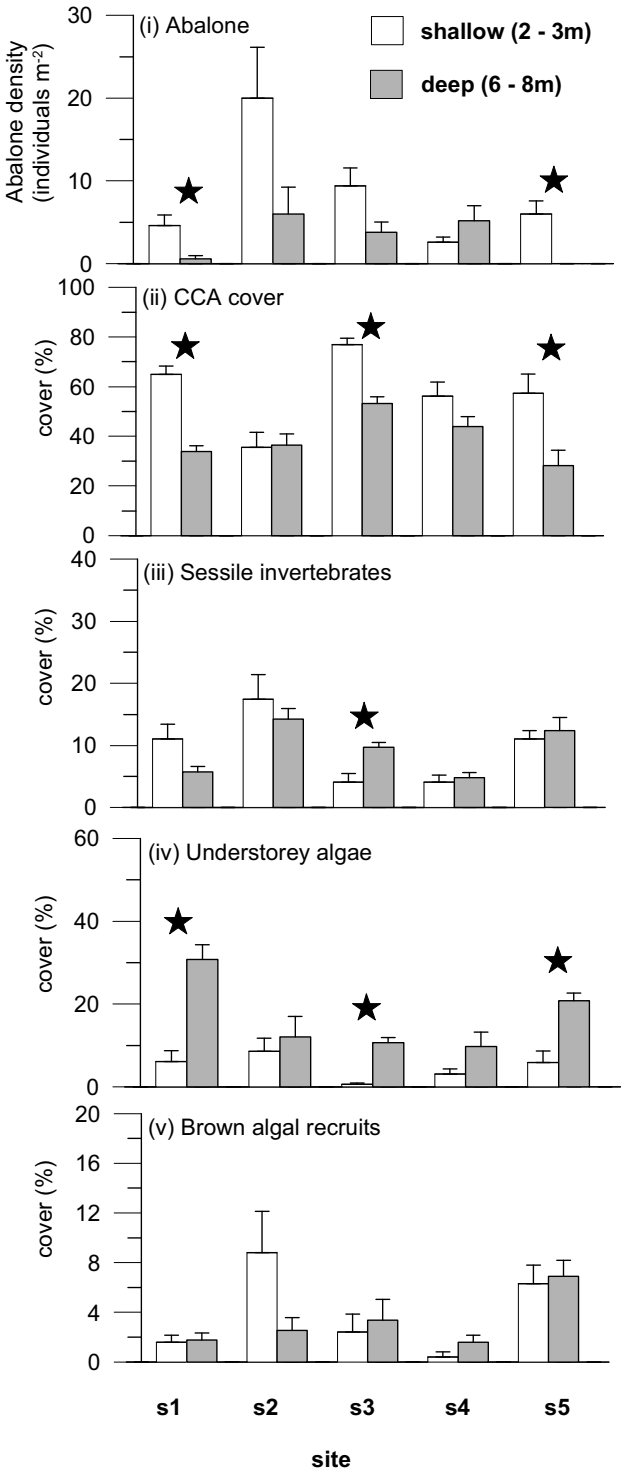

Figure 17 **Influence of depth on patterns of (i) abalone abundance and (ii-v) understorey cover for the Dunalley region. Abalone abundance represents mean (+SE) abundance across five randomly positioned 20 m^2 quadrats at each site. Cover of understorey organisms represents mean (+SE) percentage cover across quadrats (n = 5) determined from five randomly positioned 0.25 m^2 sub-quadrats within each 20 m^2 quadrat. Symbol (★) indicates site where a significant difference between depths was evident (α = 0.05).**

Table 3 **Influence of depth on (a) abundance of understorey organisms and (b) abalone. Results describe the overall ANOVA examining the effect of different depths (2–3 m vs 6–8 m) on understorey and abalone abundance. Significant p-values (α = 0.05) are shown in boldface. Transformations are expressed in terms of the untransformed variable, Y. †Transformation improved data structure considerably but did not achieve normality and homoscedasticity**

a. Benthic groups	Source of Variation							
	Depth		Site		Depth*Site		Segment (Depth *Site)	
	F (df = 1, 4)	p	F (df =4, 40)	p	F (df =4,40)	p	F (df =40, 200)	p
Crustose coralline algae (no transformation)	10.31	**0.033**	9.94	**<0.001**	3.79	**0.011**	2.10	**<0.001**
Sessile invertebrates ($\sqrt{Y}$)	0.01	0.917	12.32	**<0.001**	4.43	**0.0047**	1.18	0.2331
Understorey algae [ln(Y+0.1)]	13.93	**0.020**	4.08	**0.007**	2.64	**0.048**	2.22	**<0.001**
Canopy-forming algal recruits† [ln(Y+0.1)]	0.70	0.407	3.13	0.148	2.26	0.079	1.91	**0.002**

b. Abalone	Source of Variation					
	Depth		Site		Depth*Site	
	F (df = 1, 4)	p	F (df = 4, 40)	p	F (df = 4, 40)	p
Abalone [ln(Y+0.1)]	5.98	0.071	5.06	**0.002**	3.93	**0.009**

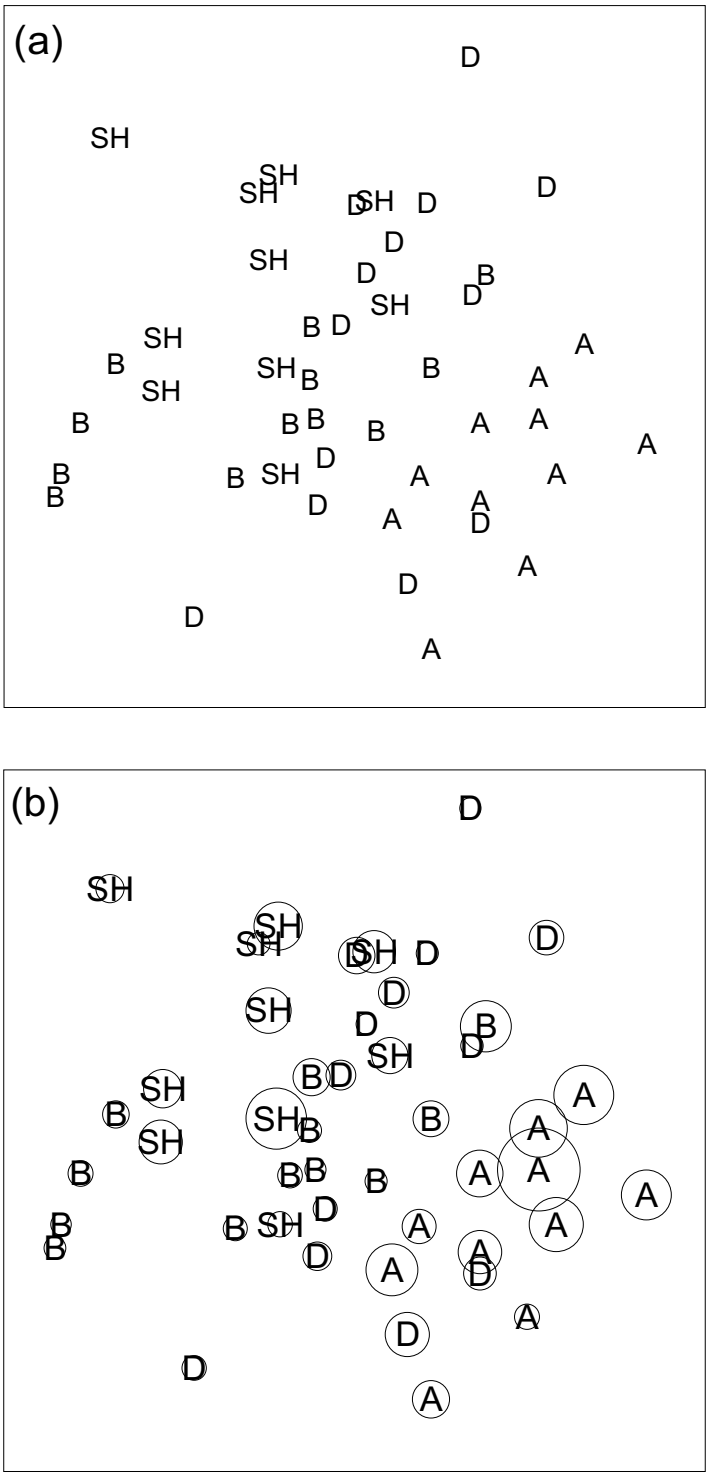

Figure 18 **MDS plots based on mean understorey community composition at each site (fourth root transformation, Bray Curtis similarity; stress = 0.2). (a) MDS indicating individual sites; SH = St Helens, B = Bicheno, D = Dunalley, A = Actaeons; (b) MDS indicating individual sites (as above) superimposed with a bubble plot representing average abalone density at each site.**

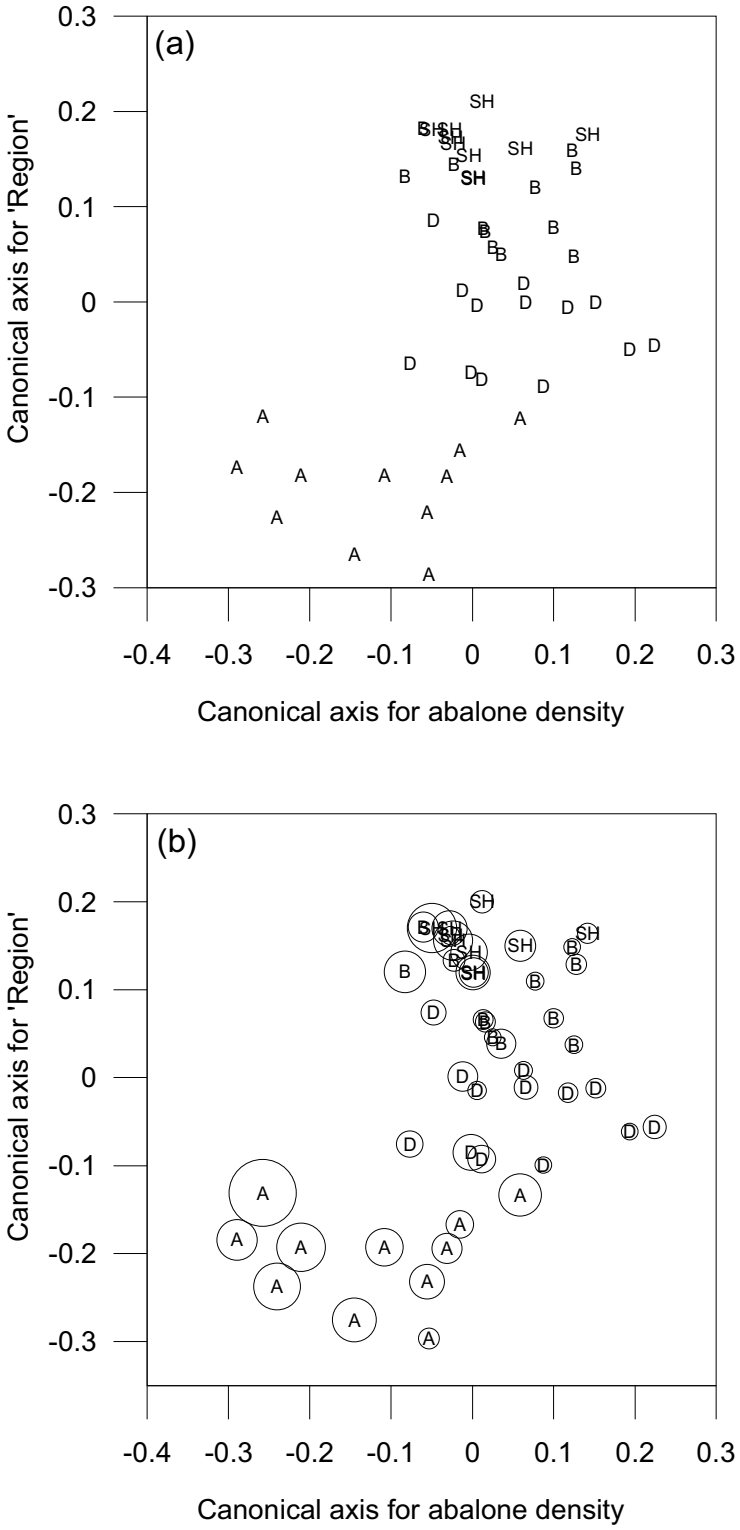

Figure 19 **(a) Two-dimensional scatterplot of the canonical axes for abalone density and 'region', based on understorey community composition at each site (fourth root transformation, Bray Curtis similarity; SH = St Helens, B = Bicheno, D = Dunalley, A = Actaeons. (b) Canonical axes plot superimposed with a bubble plot representing average abalone density at each site.**

Table 4 **Results of canonical analysis of principal coordinates examining the effects of 'region' and abalone density on understorey assemblages. %Var = percentage variation explained by the first *m* principal coordinate axes; allocation success = percentage of points correctly allocated into each group; δ^2 = squared canonical correlation.**

Factor	*m*	%Var	Allocation success (%)					δ^2	p
			Group 1	Group 2	Group 3	Group 4	Total		
Region	9	85.3	90.9 (Actaeons)	61.5 (Dunalley)	83.3 (Bicheno)	100.0 (St Helens)	82.6	0.90	0.0002
Abalone density	12	95.1						0.55	0.003

Environmental characteristics of reefs with contrasting abalone densities

For each abalone abundance category, the environmental factors that were considered in the present study explained only a very small proportion of the total variation in abundance (Table 5). Squared multiple correlation (R^2) values ranged from 0.15 for cryptic abalone to 0.25 for the emergent abalone population. The environmental factor that accounted for the majority of the variation for each abalone abundance category was 'region', with a maximum R^2 of 0.20 observed for the 'emergent' component of the population. The unique contribution of rugosity and relative wave exposure to the total variation in abalone abundance was extremely low, highlighted by the low 'squared semipartial correlation' (sr^2) values for all abundance categories (Table 5).

Table 5 **Standard multiple regression analysis examining the influence of environmental factors on the abundance of emergent, cryptic and total abalone abundance. Squared semi-partial correlation (sr^2) expresses the unique contribution of each independent variable to the total variance.**

Abalone	Regression					Squared semi-partial correlation (sr^2)		
	F	df	p	R^2		Relative exposure	Rugosity	Region
Emergent	15.33	5, 224	< 0.001	0.25		0.051	0.006	0.203
Cryptic	7.60	5, 224	< 0.001	0.15		0.002	0.003	0.128
Total	13.73	5, 224	< 0.001	0.23		0.041	0.008	0.187

Discussion

Evidence for abalone as a structuring influence on subtidal reef communities

The correlative evidence arising from the present work provides limited evidence for dramatic ecosystem change associated with abalone depletion. The most consistent pattern across regions was the existence of a weak positive correlation between total abalone abundance and CCA, and a weak negative correlation between total abalone abundance and understorey algae. The rare and inconsistent patterns observed between abalone abundance, other understorey groups (sessile invertebrates, canopy-forming algal recruits) and canopy-forming algae provide further evidence of a weak structuring role. Although multivariate analyses demonstrated a significant correlation with abalone density, stronger correlations were observed based on regional differences in understorey community structure.

There are a range of possible reasons that may account for the observed weak correlations between abalone and understorey organisms. Abalone activity may indeed have only a minor influence on understorey community structure. This would be expected if abalone feed on drift algae and display limited movement patterns around a 'homesite' or 'scar'. While this mode of behaviour explains the limited structuring influence of *H. roei* on algal communities in Western Australia (Scheibling 1994), similar evidence for blacklip abalone is lacking. Although blacklip abalone are thought to be generalist herbivores, feeding mainly on drift algae (Shepherd 1973a), detailed studies incorporating movement and feeding behaviour across broad spatial and temporal scales are vital to better understand ecological interactions between abalone and benthic communities. Recent work conducted in a sheltered bay on the east coast of Tasmania has shown limited movement by blacklip abalone (Lansdell 2006), with >80% of animals moving less than 30 cm per day. The generality of this recent work requires further investigation.

It remains possible that abalone activity influences community structure outside the immediate homesite; however, the ability to detect these potential effects will depend on the density and distribution of abalone and the scale of influence of individual animals. Because of the inherent patchy nature of subtidal reefs at small scales (e.g. Kennelly 1987; Fowler-Walker and Connell 2002), such relatively small-scale effects would have been difficult to detect in the present survey, which was designed to detect 'reef-scale' differences in community structure. Clearly the scale of any potential influence of individual abalone is a question that must be addressed in future research. If abalone activity can be demonstrated to structure understorey communities, the underlying mechanisms require further investigation.

Whilst the correlations observed in the present study are consistent with grazing effects (i.e. positive correlations between abalone and CCA, negative correlation with understorey algae), structuring mechanisms are not necessarily restricted to grazing, since mucus production (Johnson & Strathmann 1989; Searcy-Bernal et al. 1992) and

bulldozing (Dayton 1971; Hawkins 1983) by grazing molluscs also have the potential to modify benthic communities.

Environmental and habitat conditions are also a major consideration when interpreting the results of the current study. The current survey focused on the 6–8 metres depth range on exposed coastlines because of its relevance to the abalone fishery. The possibility exists that abalone may play a more important structuring role in habitats that were not considered in the present study. For example, stronger correlations might exist for deeper water abalone populations, for sheltered sites, or in other biogeographic regions.

Differences in the effects of abalone depletion in relation to environmental and habitat conditions may in fact explain why there are differing opinions among divers as to the effects of abalone removal on benthic community structure (Section 2.1), since divers' perceptions may be strongly influenced by the region and depth range they most regularly fish. Whether or not abalone activity influences understorey community structure, the present study clearly shows that factors other than abalone grazing contribute to variation in benthic community structure.

Factors affecting abundance of understorey organisms

A range of factors have been reported to influence the distribution and abundance of understorey organisms. Herbivory is most commonly identified as the source of disturbance that maintains dominance of encrusting algal communities, preventing fouling by turf-forming algae (Steneck 1986). In benthic marine systems, most studies of plant–herbivore interactions have focused on the grazing influence of sea urchins, which can have a dramatic impact on benthic community structure (e.g. Chapman 1981; Johnson & Mann 1993; Scheibling et al. 1999; Bulleri et al. 2002; Tuya et al. 2004). In the present study density of grazers other than abalone were generally very low and could not account for the high cover of CCA that was frequently observed in the absence of high abalone densities.

Canopy-forming algal canopies can also influence understorey community structure through several physical mechanisms including shading, prevention of sediment accumulation and the scour-effect associated with algal fronds abrading the substratum (Kennelly 1987; Melville & Connell 2001). Each of these mechanisms can maintain dominance of CCA by inhibiting the establishment of foliose algae and invertebrates. Both the canopy species composition (Irving et al. 2004; Irving & Connell 2006) and plant density (Kendrick et al. 1999) have also been shown to influence understorey community structure. In the absence of a macroalgal canopy and grazers, some authors have shown that CCA are capable of maintaining dominance by sloughing and shedding epithallial cells (Breitburg 1984; Johnson & Mann 1986), or through production of allelopathic substances (Kim et al. 2004).

Recent advances in understanding understorey community structure across temperate Australia have involved understorey communities occurring beneath a canopy of the common kelp *Ecklonia radiata* (Fowler-Walker & Connell 2002; Connell 2003; Irving et al. 2004). This work has shown that inside kelp forests, the presence of the canopy may be more important than grazers in facilitating maintenance of CCA dominance. For example, beneath kelp canopies cover of CCA was found to be high (>75%) on Western Australian and South Australian reefs, despite the virtual absence of grazers, while CCA cover remained low (<10%) outside kelp canopies (Fowler-Walker & Connell 2002). The present study was not designed to contrast community structure inside and outside canopies so it is difficult to make direct comparisons with the aforementioned studies. Nonetheless, canopy-forming algal cover was generally very high across all sites in the present survey (mean cover >75%), so if the same processes hold in Tasmanian waters, the apparent weak influence of abalone on understorey communities should not be an unexpected result. It would be of great benefit to test whether the shade and sweeping effects of dominant canopy-forming species in Tasmanian waters (e.g. *Phyllospora comosa*, *Durvillea potatorum*) facilitate the monopolisation of CCA-dominated habitats in the same way that *E. radiata* does on Western and South Australian coastlines (Connell 2005). If canopy-mediated physical processes are the main driving force influencing CCA abundance, habitat alteration caused by abalone removal is unlikely. Under these circumstances, improved understanding of the factors influencing the distribution and abundance of canopy-forming algae should be a focus of future research, leading to a better understanding of the environmental and biological factors that underpin resilience of reefs to fishing.

Limitations of correlative approach to infer effects of abalone depletion

There are significant limitations when using correlative studies to infer the impact of abalone removal on ecosystem structure and function. Confounding factors represent a serious issue, since differences in understorey communities attributed to differences in abalone density could also be caused by other factors (e.g. depth, exposure, regional biogeography). For example, The 'Actaeons' region had a distinct understorey community but also the highest abalone density so the influence of abalone is confounded by 'region' in this particular situation. Similarly, effects of abalone on understorey communities were clearly confounded by depth for the Dunalley region.

The correlative approach also cannot identify the factors driving associations between abalone and understorey communities. While this discussion focuses on the potential influence of abalone on understorey communities, it is also plausible that benthic communities may influence abalone abundance, as opposed to abalone activity structuring understorey communities. Understanding the mechanisms underlying abalone–understorey associations is an important question with relevance to the productivity of abalone populations. The apparent resilience of the Actaeons region could be attributable to the presence of a community that is more favourable to abalone populations, potentially providing superior conditions for on abalone growth,

reproduction and recruitment in comparison with the less resilient northeast coast reefs.

Clearly the only way to demonstrate causality is through manipulation of abalone densities. Considerations for an experimental approach to understanding effects of abalone fishing (e.g. plot size, target densities, statistical power) have been discussed previously (see Jenkins 2004); however, there remains no published work examining manipulation of abalone densities. Experimental studies involving manipulation of abalone densities are currently underway in Tasmania and Victoria and these will enable a much greater understanding of ecosystem effects on benthic community structure. The ability to generalise from these studies will be a significant issue, however, since the spatial distribution of abalone on the reef provides exceptional challenges in this regard. For example, adult abalone populations along the Victorian coast are typically associated with crevices and caves (McShane 1999), whereas adult abalone populations on the east coast of Tasmania are generally associated with exposed reef surfaces (e.g. exposed surface of boulders). Similar differences in abalone distribution can be evident over much smaller scales (J.P. Valentine, pers. obs.). The inherent variation in abalone abundance that occurs at multiple spatial scales presents major challenges when quantifying abalone abundance (e.g. Officer et al. 2001; McShane 1994); these same challenges also need to be considered when examining the effects of abalone depletion in future work.

Factors influencing resilience of reefs to abalone fishing

Consideration of potential environmental factors influencing abalone abundance is an important component of understanding why reefs differ with respect to resilience to fishing activities. Unfortunately the present study provided limited insights into the importance of environmental factors in relation to abalone abundance; the environmental factors that were considered accounted for a very small proportion of the observed variation in abundance. Interestingly, 'region' explained the highest proportion of variation in abalone abundance. While not an environmental factor in its own right, 'region' incorporates a number of factors that were not quantified directly and are likely to contribute to variation in abalone abundance. For example, regional differences in (i) the spatial structuring of reef habitat (e.g. Jordan et al. 2005b), (ii) ocean generated swell, (iii) macroalgal productivity and (iv) hydrodynamics could all contribute to differences in abalone abundance.

The limited influence of reef structure on abalone abundance was a somewhat unexpected result, since reef complexity is often thought to influence abalone abundance. The amount of 'cryptic habitat' (cracks and crevices within the reef), for example, is generally thought to be a good indicator of abalone abundance. Although the results from the present survey provide weak evidence for reef complexity as an important structuring factor, the complexity measures used in the present study may not have been sufficient to identify the fine-scale habitat structure that is likely to be of

importance to abalone populations. Future work should consider additional methods to quantify reef complexity over a range of spatial scales.

The lack of insight from the present survey into environmental factors influencing abalone abundance may be partly due to the necessity to alter the original project objectives. If reefs could have been objectively assigned to a particular 'productivity' status, environmental factors influencing resilience (rather than abalone abundance) could have been addressed. A complexity with the approach used in the present work is that abalone abundance is not necessarily a good indicator of reef productivity (and vice versa). Surveys were conducted during a period of apparent recovery of abalone stocks on the east coast (Tarbath et al. stock assessment reference), in which case formerly depleted reefs may have recorded high abalone densities. This apparent recovery could have obscured any ecosystem changes, although the fact that abalone populations recover over relatively small temporal scales provides indirect evidence that any ecosystem change does not have long-term effects on the process of abalone population recovery.

To adequately address the question of reef resilience, quantitative data on fishing behaviour at the scale of individual reefs is essential. The development of GPS technology (e.g. FRDC 2006/029) provides the tools to gather this information, providing quantitative data on abalone catch and effort at fine spatial scales. This information will allow reefs with differing resilience to fishing activities to be identified, enabling a more detailed assessment of the environmental and biological factors that may influence reef resilience. Previous work conducted over large spatial scales has identified spatial structuring as an important factor influencing the resilience of reefs to abalone fishing (Jordan et al. 2005b); however, a range of factors should be considered in future work. Factors that must be considered include the importance of ocean generated swell, local hydrodynamics, nutrient levels, algal productivity and drift algal abundance. Many of these factors cannot be examined using a 'snap shot' survey approach and will need to be quantified over a range of spatial and temporal scales.

Conclusions

The lack of a strong consistent pattern between communities with contrasting abalone densities suggests that dramatic reef-scale shifts in benthic community structure are unlikely following depletion of abalone stocks. While this may be of some relief to managers of subtidal reefs, a number of questions must be addressed to adequately address impacts of abalone depletion. Experimental studies are clearly required in habitats with varying physical characteristics and the scale of influence of individual abalone must also be critically examined. The relative influence of abalone removal is likely to depend on the physical characteristics of particular reefs, so a major question will be to identify these characteristics so reefs that are at most risk of ecosystem change following depletion of abalone stocks can be identified. The risk of ecosystem

change will also depend on the resilience of reefs to abalone fishing. This is a particularly challenging area of research that should be enhanced with improved understanding of abalone fishing behaviour, achievable with the on-going development of GPS tracking technology (FRDC 2006/029).

3 Determining the diet of rock lobsters

3.1 Evaluation of methods for determining rock lobster diet, with particular emphasis on non-destructive sampling

Introduction

Predator-prey interactions are fundamental to understanding the dynamics of ecosystems. The diet of lobsters, the dominant macro-invertebrate on southern temperate reefs is poorly understood. Part of this reason is the difficulty in identifying prey items once they pass through the grinding mandibles and into the foregut. After the foregut they become less distinguishable as the gastric mill grinds them further. While certain prey items are distinguishable from fragments of shells, spicules, bones etc., other fleshier prey items (eg. abalone, ctenophores) can not be distinguished. Additionally, to account for differences in regions, depths, size of lobsters and season variations in diet a large number of lobster would need to be sampled. We propose to explore methods that are non-destructive such as faecal examination. This would enable sampling of lobsters in reserve populations where destructive sampling would be prohibited. Similarly while sampling from fisher's vessels would reduce sampling costs, purchasing of lobsters for destructive sampling would be prohibitive.

The first aim of this section was to develop a non-destructive sampling technique for obtaining dietary information from lobsters.

Methods and results

First we developed a quick and non-deleterious method of collecting rock lobster faecal material to provide samples for DNA dietary analysis.

A 'cradle' device (Figure 20) was designed and built for the purpose of restraining lobsters while samples could be taken from the hindgut region. Lobsters are placed in the 'cradle', which holds the animal upside-down and immobilizes the posterior four pairs of walking legs. The anterior telson is held firmly by the researcher to stabilize the abdominal region/ tail while collecting faeces.

Lobster faeces are collected using a Pipetteman™ 100-1000 µL pipette with disposable tips. For each faecal sample a new sterile tip is used to prevent contamination between samples. The tip is inserted directly into the anal pore of the lobster to remove faeces from the hindgut region (Figure 21). The collected faecal material is immediately pipetted into a 1.5 mL micro centrifuge tube containing 500 µL of 70% ethanol. Ethanol has been shown to be an effective preservative for field samples and does not require freezing or any special handling. The volume of collected faeces varies from approximately 10 µL to over 1 ml depending on the size of lobster and fullness of hindgut at the time of sampling.

Figure 20: **The 'cradle' device designed and built for restraining lobsters while samples can be taken from the hindgut region.**

Figure 21: **Faecal collection technique using a Pipetteman™ 100-1000 µL pipette with disposable tip inserted directly into the anal pore of a rock lobster.**

Second we determined if faecal material could be used to identify prey using molecular methods. Results were extremely positive and are reported in Redd et al. (2008) (see Appendix 6).

Thirdly, we needed to determine over what time period a prey species DNA signal would be detected in lobster faecal material. A key driver for this was to determine if the prey DNA signal could be obtained from lobsters sourced from traps during routine fishing operations. Results from this study are reported in Redd et al. (2008) (see Appendix 6). In summary these results demonstrated that the prey DNA signal

was initially detected in all samples at 7 h after feeding and was consistently detected in all samples until 60 h after the feeding episode. There were no detections in any of the samples taken at 3 and 5 h or for the six sampling times from 66 h to 96 h after commencement of feeding.

Finally, we examined the diet of wild rock lobsters using a genetic clone library approach to screen prey diversity in the collected faecal samples. This approach is commonly used in microbial ecology to determine bacterial community composition from environmental isolates. We utilized this novel approach to prey detection by targeting the mitochondrial 16s rDNA region, known to be present in multiple copies in every prey cell and also widely used for phylogenetic analysis. We first amplified this DNA region by PCR using universal primers and then cloned the DNA fragments into bacterial plasmids. We grew the bacteria on agar plates and then isolated and sequenced the plasmids. We use the National Center for Biotechnology Information (NCBI) GenBank Nucleotide Database to query our sequences against all published DNA sequences using the BLAST suite of algorithms.

By using this sequence analysis we were able to identify several prey species of interest in wild lobster faecal samples collected around Tasman Island (43° 14' S, 148° E) in an area frequently visited by commercial rock lobster fishing vessels (Table 6).

Table 6: **The following species have been detected in four rock lobster faecal samples by using genetic clone library techniques to screen prey diversity. Included are; the relative similarity, as percent match, between our samples and the GenBank Nucleotide Database, the common name of the prey species detected, the highest taxonomic group to which the DNA could be matched accurately and a comment about the prey.**

Species	Percent match in GenBank	Common name	Match To highest level	Comment
Octopus maorum	98%	Maori Octopus	Species	Important species
Plagusia and *Dromia*	92%	Red Bait Crab and Sponge Crab	Infraorder	Group includes many crabs
Jasus edwardsii	100%	Southern Rock Lobster	Species	Cannibalism or predator DNA
Florometra serratissima	91%	Temperate Water Crinoidea	Subclass	Poorly sequenced group, not well documented in GenBank, no species from Tasmania in database

Discussion

In the original project description we planned to evaluate serology as an alternative technique to evaluate diet in lobsters. Given the success of the DNA trials the serological work was not pursued. Like the DNA method, the serological method requires the development of specific antibodies to link to specific food items. However, unlike the DNA method, the serological method requires the use of rabbits which need to be sacrificed in development of the antibodies. This requires ethics approval and is considerable more expensive. As the DNA method we have developed is non-destructive, doesn't require ethics approval and is simpler and

cheaper, future developments in dietary studies for lobsters are expected to pursue the DNA approach described and developed in this report.

The trial to use the clone library method to determine the range of predatory items consumed by lobsters was exciting but we considered it to be too time consuming and costly as a large component of the samples were potentially 'self' samples of the predator (i.e. cells sloughed off from the digestive track). The focus of future studies should focus on the development of specific DNA markers and, as these aggregate in genetic databases, a broader range of potential prey items can be screened.

There is a new method being developed that excludes predator DNA and this holds promise for maximising the return from the clone library style approach. This could hold promise for future dietary studies.

DNA primer development

The element to determine the diet of rock lobsters has focused primarily on non-lethal prey detection assays. Of particular interest is the use of the polymerase chain reaction (PCR), a powerful molecular technique to amplify DNA from environmental samples. We identified a need to detect the DNA from a wide range of reef species by PCR and have developed a suite of assays to perform this function.

Design of PCR primers for detection of species present on Tasmanian rocky reefs has been completed. The PCR primers are designed to bind selectively to regions in the 16s Ribosomal RNA sequence. This region has both highly conserved regions as well as regions which are unique to individual species. We have used species variation and a software based computer platform, Amplicon (Jarman 2004), to design PCR primers based upon aligned prey sequence data. Initially prey DNA sequences for were found in the NCBI GENBANK nucleotide database (NCBI 2006). Prey species for which no previous sequence data were available were collected as reference specimens. Several important invertebrates on southern temperate reefs have been sequenced as a part of this sequence analysis process including; *Centrostephanus rodgersii, Heliocidaris erythrogramma,* and *Nectocarcinus tuberculosus*.

The PCR primers designed range in specificity from the phylum level down to the level of individual species. General primers have already been published in detail (Jarman et al. 2006). Table 7 describes recently developed primers listing the sequence of each primer and specificity of each set.

Table 7: **PCR Primers designed for detection of southern temperate reef species. Name of each primer is listed as is the primer sequence, specificity and target organism on which each primer works.**

Primer Name	Sequence (5'-3')	Specificity	Target
Hali16sF	GGGGTGACTGGGGAACAATAGT	Genus	*Haliotis sp.*
Hali16sR	CTACACCCTCAGGACACCTTAATCC	Genus	*Haliotis sp*
Plag16sF	GACGTGCAAAGGTAGCATA	Genus	*Plagusia sp.*
Plag16sR	TAATTCAACATCGAGGTCGCA	Genus	*Plagusia sp.*
Pallidus16sF	CTCGGTGAGATATAA	Species	*Octopus pallidus*
Pallidus16sR	GTCCCTTTAA	Species	*Octopus pallidus*
Maorum16sF	GCTCGGTGAGAATAAAAT	Species	*Octopus maorum*
Maorum16sR	GTCCCTTTAAA	Species	*Octopus maorum*
Jas16sF	TCAAATATCCTGGGGGACGATAAGACCCTATA	Species	*Jasus edwardsii*
Jas16sR	CCTTGCCTTCGATAAGGACTCTC	Species	*Jasus edwardsii*
Centro16sF	TTATTCTCCCCCTGAAATTCACATC	Species	*Centrostephanus rodgersii*
Centro16sR	CCCTTAAAAGCTTCTGCACT	Species	*Centrostephanus rodgersii*
Helio16sF	AGCTTACAGCAAAAGT	Species	*Heliocidaris erythrogramma*
Helio16sR	GGTAACTTGTTCCTTTG	Species	*Heliocidaris erythrogramma*

Additional effort has been directed at developing a novel nucleic acid hybridization approach for prey detection. Hybridization relies upon exact matches of probe sequences to the DNA in environmental samples. These techniques have primarily been applied to microbial systems but have potential to be used in any form of molecular detection assay (Mei et al. 2003). We have examined the utility of hybridization techniques for food web analysis in the southern temperate reef ecosystem and are currently pursuing a suite of assays which can be applied to any dietary sample collected. Table 8 describes the oligonucleotide probes designed for DNA hybridisation assays.

Table 8: Molecular probes designed for detection of southern temperate reef species by hybridization assay. Name of each probe is listed as is the probe sequence, specificity and target organism to which each probe binds.

Probe Name	Sequence (5'-3')	Specificity	Target
Abalone	CTACACCCTCAGGACACCTTAATCC	Genus	*Haliotis sp.*
Lobster	CCTTGCCTTCGATAAGGACTCTC	Species	*Jasus edwardsii*
Mussel	CCTACCCTTAGAGGCTTCTACACCTCT	Species	*Mytilus edulis*
Shore Crab	AATTACCGCGGCCTTTAAATTTTTA	Species	*Plagusia chabrus*
Octopus1	GATGCGGCCTCGATGTTGGATTAAAAATAAC	Species	*Octopus maorum*
Octopus2	AGATTGCGACCTCGATGTTGGATTAAAAATAAC	Species	*Octopus pallidus*

3.2 Evaluation of stable isotopes and fatty acid signature methodology

Introduction

In addition to the DNA method we also explored the use of other molecular techniques, specifically stable isotopes and fatty acid signatures.
The DNA method detects what has been eaten in the last one or two meals depending on gut and intestinal evacuation rates. In contrast, the tracer techniques look at what has been incorporated into the body tissue and thus provide an indication of longer term (months) feeding preferences depending on tissue turnover rate.
Although the stable isotope and fatty acid tracers are less species specific, we envisaged that a combination of the DNA and the tracers will provide the best resolution of dietary intake by lobsters in the future.

To demonstrate the applicability of the combined stable isotope and fatty acid signature approach we examined a sub-set of the data based on a primary producer (benthic macro algae) and primary consumer (abalone) (Guest et al. 2008; see Appendix 7). We then expanded this work to look at differences in these two forms of metrics for rock lobsters between fished and non-fished locations (Guest et al. (in review); see Appendix 8).

Materials and methods

See appendices 7 and 8 for details.

Results and discussion

Contradictory to common belief, the stable isotope and fatty acid signature analyses demonstrated that abalone, from the sites sampled on the East Coast of Tasmania, preferred to consume brown rather than red algae. This was the first indication of the preference for brown algae for southern temperate reef abalone. Future studies need to determine if this preference is consistent across all temperate reef species.

Unfortunately the signatures for 'healthy' brown algae and decaying brown algae that could enter the diet through the detrital pathway could not be separated. Future studies that attempt to elucidate these pathways should be investigated.

Southern Australia has a rich and diverse macroalgal community and determining which species contribute to the abalone diet requires further work. The development of DNA specific markers for each of the potential brown macroalgae species would be an appropriate future option.

The comparison of rock lobster diet was based on a relative comparison of urchin, mollusc (abalone and turbo), ascidians, brown and red algae components of the diet. The stable isotope analysis did provide evidence of differences in the diets of rock lobsters within marine reserves compared to adjacent fished sites. Fatty acid signatures did not find significant differences between reserve and fished sites but did provide insights into the diet preference for lobsters.

A surprising result was the preference for ascidians in the fished sites and Turbo (gastropod mollusc) in the reserve site. While divers had reported observations of lobsters eating ascidians in the field, they have seldom been reported in previous studies of lobster diets. Although no quantitative assessment of ascidian abundances in the reserve and fished sites is available, ascidians, due to their sessile nature and requirement to filter feed would be located on relatively exposed habitat (cf. pre-emergent juvenile abalone or urchins). An increase in the density and abundance of lobsters in a reserve would be expected to reduce a normally abundant food source and thus require a shift to an alternative species. The switch to Turbo in the reserved sites may reflect the decline in ascidians due to increased predation pressure and the switch to an alternative food source. This is further reflected in the increase in the proportional contributions of other species including abalone and urchins.

Performance indicators

Identification of the most appropriate method for undertaking predator prey analyses. If successful, both the serological and DNA markers would be used on other species known to interact or compete with lobsters. If the DNA method were successful then these markers would commence a database of southern temperate reef species. The most expensive component of the DNA work is the development of the marker. Once developed, the marker would be available for other researchers at a substantially cheaper cost. As more markers are added to the database, animals will be able to be screened for a range of potential prey items.

The project found that DNA markers were a preferred method of obtaining dietary information from lobsters in contrast to gut analysis that requires sacrificing the animal. The limitation of the DNA work is that it is only suitable to detect the presence of prey items that already have primers (markers) developed. This project has developed a number of markers for southern temperate reefs that will be lodged on genetic databases for future researchers. New projects are already using these markers (e.g. FRDC *Centrostephanus* project) and it is anticipated that this database will increase as future projects focus on new species.
The project also developed a non-lethal method for collecting lobster faecal material that allows samples to be collected from marine reserves and commercial vessels.

4 Comparison of the foraging range and habitat usage by lobsters in fished and unfished regions

Introduction

Although the impacts of exploitation on abundance and size composition have been widely reported for exploitable fish stocks, there remains a lack of knowledge on the likely alteration of the behaviour of exploited stocks as a result of these impacts. The vast majority of studies examining animal behaviour in the marine environment have been undertaken on populations where size- and density-dependent effects cannot be examined due to the impacts of exploitation on population structure. The global implementation of marine protected areas (MPAs) provides a valuable opportunity to examine the behaviour of targeted species in situations where community dynamics and species interactions more closely resemble those pre-dating fishing. Importantly the MPA provides a baseline against which comparisons can be made to fished locations to explore the effects of fishing.

The southern rock lobster *Jasus edwardsii* is a dominant predator of benthic invertebrates in eastern Tasmania (Pederson & Johnson 2006), and supports fisheries worth in excess of AU$70 million per annum (ABARE, 2007). However, commercial and recreational exploitation has significantly reduced the abundance and average size of lobsters (*Jasus edwardsii*) in eastern Tasmania to between two and eight per cent of the virgin legal-sized biomass (Frusher, 1997). Since the declaration of marine protected areas in eastern Tasmania in 1991, the abundance and average size of *J. edwardsii* inside the protected areas has significantly increased compared to adjacent fished habitats (Edgar & Barrett, 1999; Buxton et al., 2006; Barrett et al., 2007). Most notably, lobster biomass inside the largest MPA at Maria Island (MIMPA) is now estimated to be 20 times that of adjacent fished areas and may now resemble lobster populations pre-dating the fishery (N. Barrett. pers. comm.). Coinciding with the increases in average size and abundance of rock lobsters inside the MIMPA have been anecdotal reports that the behaviour of individuals may be density and size dependent and moderated by intra-specific competitive interactions. Large lobsters (>130 mm CL females and >140 mm CL in males), which are rare in adjacent areas open to fishing, are often observed by divers foraging during both the day and the night, while the activity of small lobsters, both males and females is largely unknown.

The development of ultrasonic acoustic transmitters over the past two decades has revolutionised the way in which the movement, activity and behaviour of marine species, including lobsters, are being recorded (Atkinson et al., 2005; Golet et al., 2006).

When used in conjunction with automated telemetry systems the location of individual transmitters can be triangulated in near real-time with a positional accuracy of 1–2 metres and over extended periods (VRAP systems, VEMCO Ltd, Halifax, Canada). With the advent of this technology, the implementation of MPAs, and the expanding acceptance of geographical information systems in fisheries science, the behaviour of many marine species can be investigated in much greater detail than previously possible. We established a network of remote ultrasonic acoustic receivers to record the fine-scale movement patterns of rock lobsters in a fished and non-fished (MPA) site in eastern Tasmania to determine if exploitation and the removal of large lobsters has altered the behaviour of this species and thus its role in temperate reef ecosystems.

Methods

Site selection

The movement and behaviour of lobsters (*Jasus edwardsii*) was documented at two sites in eastern Tasmanian between May 2006 and November 2007 to determine the possible impacts of exploitation to unfished stocks. To examine size-specific effects we monitored the movement activity of lobsters inside a marine protected area and at a sited where fishing has reduced the average lobster size and abundance. Movement and behaviour of lobsters was derived from data collected using an ultrasonic acoustic telemetry system to determine the precise location of tagged individuals (see below) for periods up to eight weeks in duration.

Following 18 years of protection from fishing activity, reefs within the Maria Island Marine Protected Area (MIMPA) on the east coast of Tasmania support diverse macroalgal, demersal fish and invertebrate communities distinctly different to those in surround habitats open to fishing (Edgar & Barrett, 1999; Buxton et al., 2006; Barrett et al., 2007). Lobster populations within the MPA are made up of a broad range of size classes but are dominated by large mature individuals, and considered to resemble populations prior to the establishment of both commercial and recreational fisheries. In contrast, lobster populations at sites exposed to fishing activity in eastern Tasmania have fewer size classes and are dominated by small individuals below the minimum legally exploitable size of 105 and 110 mm (CL) for male and female lobsters respectively.

The study site inside the MPA was located approximately 500 metres from shore on an isolated patch of medium-profile rocky reef, interspersed with seagrass beds (*Zostera tasmanica*), sand flats and patch reef (clumps of boulders interspersed by sand). The average depth at the site was 12 metres and situated on the deepest and most extensive section of continuous reef inside the MPA. The site exposed to fishing activity (referred to hereafter as the fished site) was situated 50 kilometres away on the Tasman Peninsula and open to both recreational and commercial fishing activity. The habitat at the fished site was dominated by large areas of contiguous low-profile

reef and supported similar communities of macroalgae as the MIMPA. However, it was more exposed to ocean swell and had an average depth of 26 metres. While suitable sites, similar in exposure and depth range, may have been selected closer to the MIMPA and within Mercury Passage, the site on Tasman Peninsula was considered representative of areas targeted by both recreational and commercial fisheries and better suited to the deployment of the telemetry system, which requires land-based facilities to operate the radio base-station.

Habitat classification and feature identification

A detailed survey of the benthic habitats was conducted in April 2006 prior to the establishment of the acoustic telemetry system following the methods detailed by Jordan et al. (2005a). Four main habitat categories (contiguous reef, patch reef, sand, and seagrass) were easily defined through variations in the first and second echoes in the echogram collected by a single-beam scientific sounder (Simrad EK60). Habitat boundaries were identified from stored echograms and ground-truthed using video footage and attributed into the vessel track log using ArcPad v6.0 (Environmental Systems Research Institute, ESRI) with the resulting habitat map generated in ArcGIS (Figure 22).

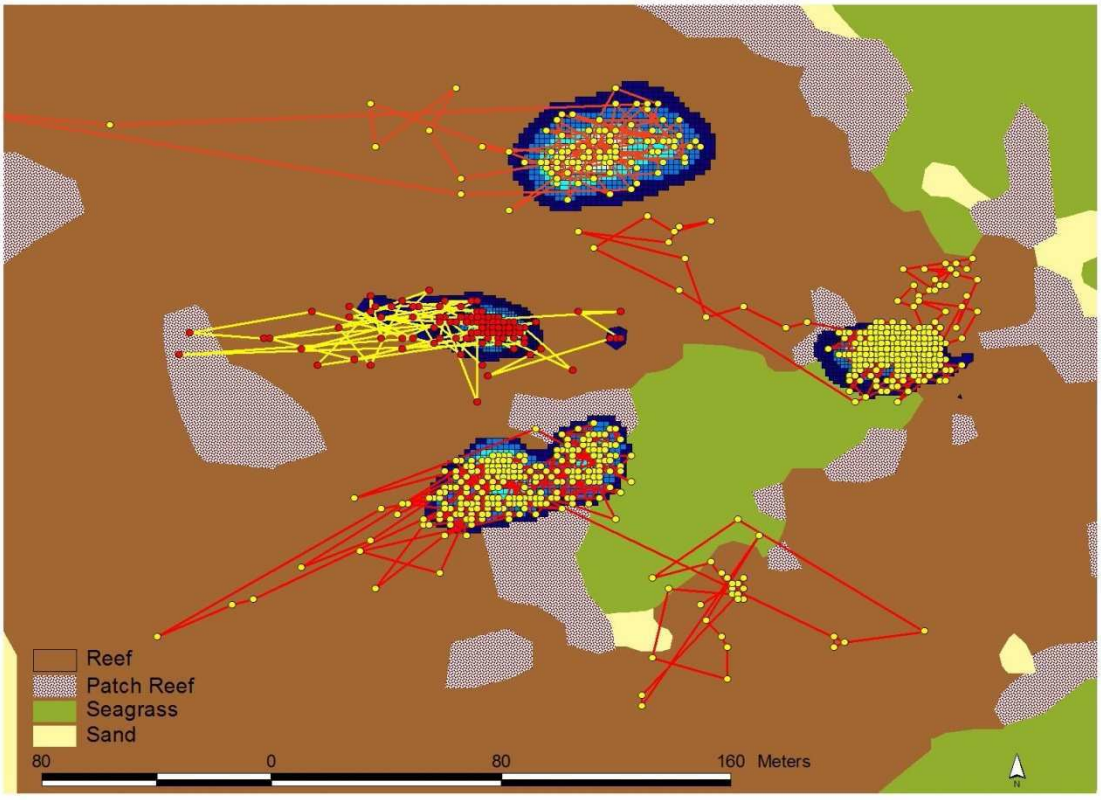

Figure 22 **Example of habitat map with lobster movements (red and yellow lines) and 95% (dark blue) and 50% (light blue) probability kernels to define home ranges.**

To determine how lobsters interact with the fine-scale topological features, a benthic complexity model, which can identify fine-scale morphometric features in reef habitat,

was generated for the site following the methods described by Lucieer & Pederson (2008, Figure 23). Briefly, bathymetric data was processed to create a uniform grid at a pre-defined resolution (5 m x 5 m grid cells in this case), and the relationship between the elevation of each cell with the eight neighbouring cells was determined. The process was iterated until the grid cell size reached 25 m x 25 m and 25 neighbourhood elevation relationships had been classified for each grid cell. The neighbourhood elevation relationships were compiled, with each cell being assigned to one of six feature classes for each of the iterations. The greater the number of classifications to the same class, the higher the probability that a cell was identified correctly at multiple spatial scales. The resulting model placed cells into six distinct morphometric features: ridges, planes, peaks, pits, passes or channels (see Lucieer & Pederson (2008) for details). This procedure was performed on bathymetric data collected at each site to produce individual habitat complexity maps to allow site-specific habitat associations to be determined.

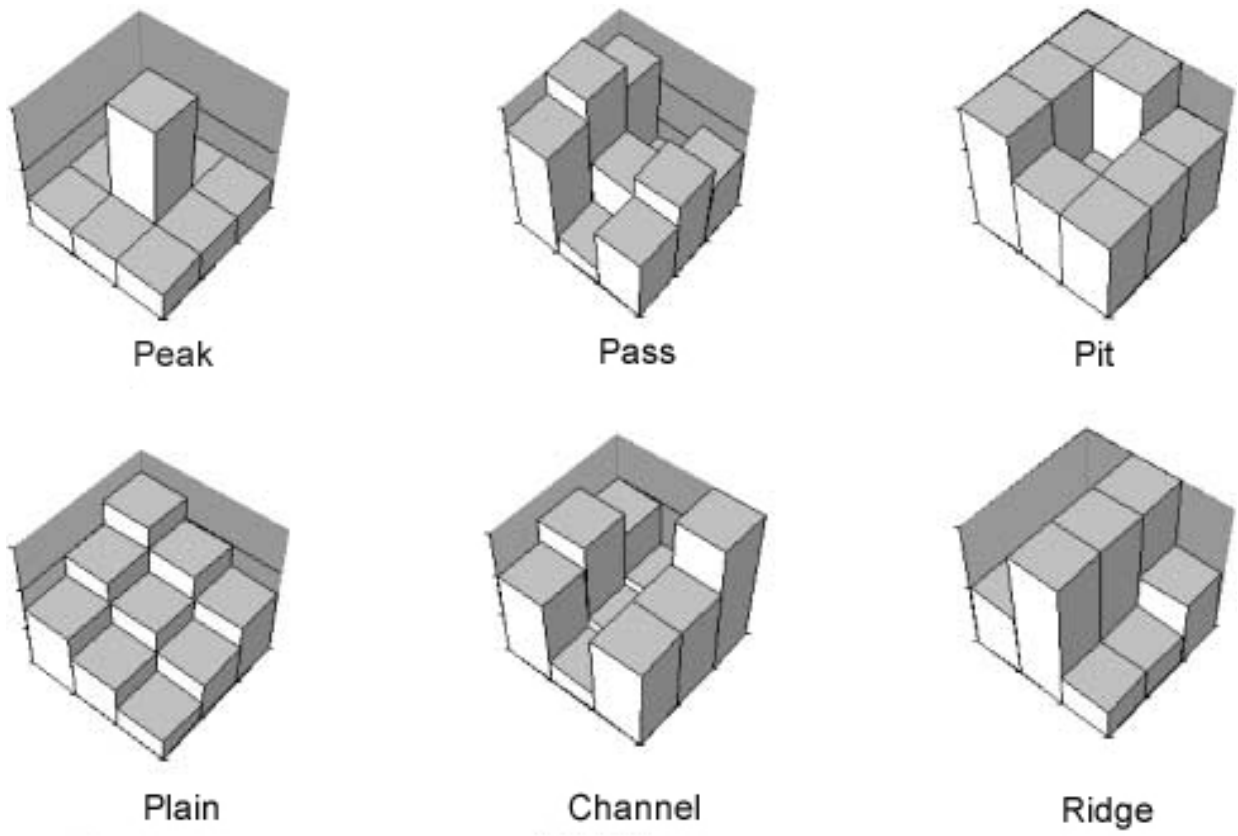

Figure 23 **From bathymetric digital elevation models, distinct reef morphometric features could be classified and quantified based upon their three-dimensional shape. Six features, including peaks, passes, pits, plains, channels and ridges, could be readily identified at Tasman Peninsula and Maria Island sites (figure modified from Wood (1996)).**

Table 9 **Schedule of acoustic tagging events.**

	2006								2007											
	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Unfished (MPA)	**35**									**36**			**21**						**16**
Fished						**8**			**18**			**18**					**12**		
Life history																			
Peak Activity								■	■	■									
Mating	■											■	■						
Moulting					■	■						■	■				■	■	
Egg release						■	■										■	■	

Lobsters were tagged during four distinct seasons over a 12-month period to capture movement activity during the peak of activity (anecdotal reports), mating, moulting and egg release (Table 9). Due to the low abundance and complete absence of large lobsters, a total of 56 small lobsters were tagged at the fished site. Within the MIMPA, 108 lobsters were tagged over the four seasons.

Lobster tagging and telemetry

Lobsters were collected from the reef habitats within each study site by experienced SCUBA divers to ensure individuals were not physically damaged but were handled carefully to reduce tagging-associated biases. Lobsters, including males and females, ranging in size from 92–200 mm (CL) from the MIMPA, and 85–115 mm (CL) from the fished site were tagged using two styles (coded and continuous) of acoustic transmitters (Amirix Systems, Vemco Division). Prior to the attachment of acoustic transmitters, lobsters were brought to the surface, the length of the carapace was measured using knife-edge callipers, and the lobsters were separated into two size classes. Lobsters <105 mm for females and <110 mm for males (representing the minimum legal catch size in the adjacent fishery) were classed as small and lobsters >130 mm for females and >140 mm for males were considered large. To ensure each tagged lobster would carry a similar weight proportional to their mass, the carapace length of each individual was used to derive a wet weight from a predetermined relationship and assigned a transmitter whose in-water weight was no more than 5% of the lobster's body weight to reduce any impediment to normal movement (Caccamise & Hedin, 1985). Transmitters were inserted into a section of silicon tube approximately 10 millimetres longer than the transmitter to facilitate easy attachment to the lobsters. The carapace of each lobster was then dried using compressed air to ensure sound attachment of the transmitter using a two-part fast setting exopy resin applied to both the silicon tubing and the dried carapace.

Tagged lobsters were tracked at each site using a radio acoustic positioning system (VRAP, Amirix systems – Vemco Division; see O'Dor et al. (1998) and Klimley et al.

(2001) for details) and proprietary software (VRAP 5.1, Vemco). Three VRAP receivers were moored to the sea floor to form an equilateral triangular array with a separation of 150 metres between receivers within the MIMPA and 300 metres at the fished site at the Tasman Peninsula. Ground-truthing of the array indicated positional precision of ca. ±2 metres inside the triangle and ca. ±4 metres up to 200 metres from the array within the MIMPA, and ±5 metres inside the triangle and ca. ±15 metres up to 500 metres from the array at the fished site. The spacing of the telemetry array was varied between the sites, to ensure maximum performance at each site, but was replicated precisely during each deployment at each site to maintain consistency between seasons. Due to the availability of only one VRAP system, studies were run consecutively to ensure that at least four continuous weeks of information was recorded within each of four separate seasons at each site.

Telemetry data processing and analysis

Assessing the impact of procedural artefacts on the behaviour of test subjects is often overlooked in animal movement and behavioural studies. For *Jasus edwardsii* the impact on normal behaviour as a result of carrying a transmitter is thought to be negligible (Atkinson et al., 2005; MacArthur et al., 2008). However, alteration to post-release behaviour of lobsters as a result of being brought to the surface was likely (Jernakoff, 1987; Jernakoff et al., 1987) as the majority of individuals spent several hours roaming over the habitat, and up to 48 hours to relocate to the shelter where they were captured. Therefore, positional estimates of tagged lobsters recorded in the 48 hours following release where discarded from all analyses. Positional data was exported from the VRAP software (v5.1) before being processed and visualised using Eonfusion v1.2 (Myriax software). Positional data was projected using the GDA system 1994 (GDA MGA 1994 Zone 55) for accurate distance and area unit calculation.

While the accuracy and precision of the VRAP system was determined prior to the study, random error in positional estimates still occurred. Error in positional estimates can occur for a number of reasons (Golet et al., 2006) but were easily removed using a step-wise data filtering approach, similar to that described by (Golet et al., 2006). Position estimates were calculated by the 'position average' algorithm in the VRAP software (v5.1) using the 'best' 80% of signals from each transmitter in each five-minute sampling period.

Erroneous data points were identified using a three-step process using the Eonfusion software package. First, a proportion of the erroneous data points were easily identified when the path lengths were extreme (several hundred metres), the position estimate was on land, or the second data point in a sequence of three consecutive points was considered to be a 'flyer'. Flyer positions were easily identified as the first and third positions in the series were often close together (2–5 metres), with the second position isolated some distance from the other two. Using the heading of each individual path segment, the acute angle between the two headings, termed the return

angle, can be calculated and was then used to automatically identify and remove flyer points from positional data using an acceptance threshold of 20 degrees. The final stage of error removal was to identify path segments when the average speed of movement between two consecutive data points exceeded a pre-determined maximum of three metres per minute. Segments identified as exceeding the maximum average speed were manually investigated for validity. The filtering process resulted in a reduction of position estimates and potential conservative estimates of the total distance travelled.

Tagged animals must display a level of site fidelity before the extent of their home range can be calculated (Spencer et al., 1990). The most useful method of assessing site fidelity was to compare the actual sequence of paths travelled with a random arrangement of the paths (Hooge et al., 2001). Once site fidelity for each tagged lobster was established, home range and activity centre areas were calculated using the kernel probabilistic method (Worton, 1989) which applies least-squares cross-validation (Seaman & Powell, 1996), in the 'Animal Movement' extension (Hooge et al., 2001) in ArcView 3.2 (ESRI). Home range areas were defined by the probability contours encompassing 95% of all positional estimates of each lobster and were considered to be the area utilised during foraging and residency. Activity centres were defined by the probability contour encompassing 50% of all positional estimates of each lobster and typically identify the area of residency (Hooge et al., 2001) (Figure 24).

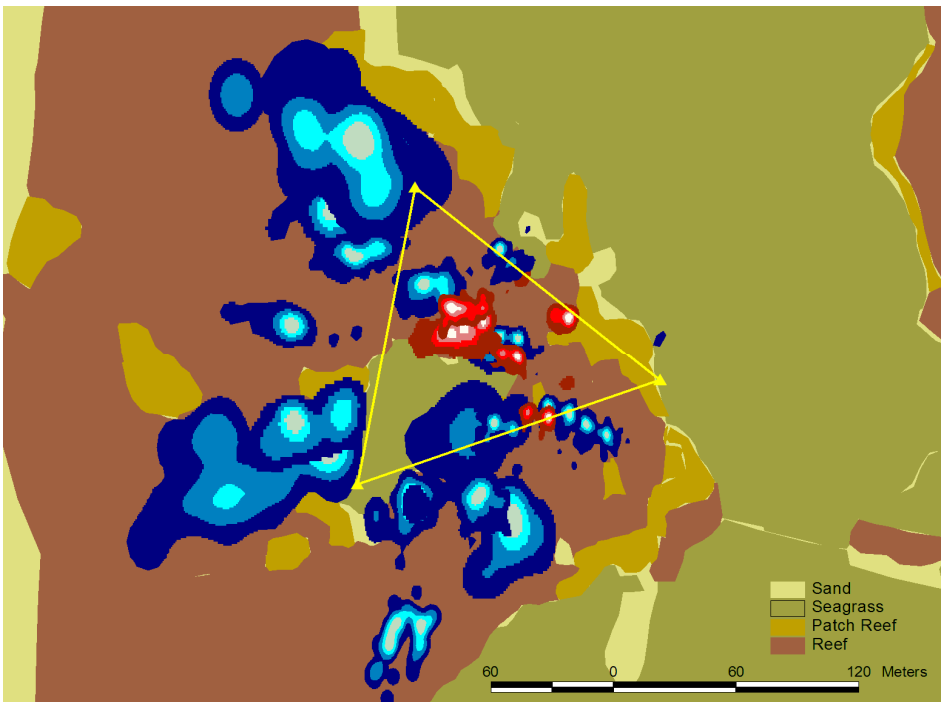

Figure 24 **Home ranges of tagged male (blue) and female (red) lobsters inside the MIMPA during May 2006. The area delineated by dark shading represents the area utilised 95% of the time by an individual lobster with the area delineated by lighter shading the activity centre of individual lobsters.**

Patterns of habitat utilisation were identified by quantifying the area of spatial overlap of activity centre and home range areas with the benthic habitat map and habitat complexity model. Data were processed using ArcView GIS (v3.2, ESRI) and differences in the patterns of habitat utilisation between individuals analysed using ANOSIM (Primer v6.0, Plymouth Marine Laboratories).

The timing of lobster activity was determined by calculating the distance between consecutive positional estimates, removing distances of <5 metres in length (average acceptable positional error of the VRAP system) and attributing the proportion of day length in which each movement event occurred. Movement events for each animal where then summed by proportion of day length and the frequencies of occurrence converted to proportions of the total movement counts to reduce biases by individuals moving more frequently than sedentary individuals.

The degree of static and dynamic interaction between rock lobsters was determined using the RANGES 7 software package (ANATRACK, Ltd). Static interactions, where pairs of rock lobsters utilise the same space, were identified when home ranges (95% kernel probability contours) or activity centre areas (50% kernel probability contours) overlapped using the OVERLAP routine. While static interactions are useful in identifying the amount of overlapping territory, they may conceal the true nature of the relationship between individuals in time. Dynamic interactions, in which Jacob's index (Jacobs, 1974) is used to examine the time series of movements, were calculated to identify cohesion and avoidance between pairs of rock lobsters using the INTERACTION routine. Significant differences between groups of rock lobsters (size and sex) were determined using a Wilcoxon signed rank test in the statistical package R.

Results

Timing of movement activity

The timing of movement and activity was influenced by both the size and the sex of lobsters. In the absence of large lobsters at the fished site, and access to a much wider range of lobster sizes within the MIMPA, the influence of size was examined initially within the MIMPA using the most extensive data set collected during the mating period of 2006. When activity data were pooled across sizes within each sex, differences between male and female lobsters were observed (Figure 25). Both male and female lobsters, regardless of size, were active throughout the morning; male activity decreased in the early afternoon whereas female lobsters remained active for several hours before becoming more sedentary following sunset.

When separated by sex, differences in the activity of male lobsters based on carapace size were also evident (Figure 26). Large male lobsters (>140 mm CL) where predominately more active during the daylight hours and sedentary at night when

small males (<140 mm CL) were most active. The increases and decreases in activity patterns of male lobsters at either end of the day coincided with both sunrise and sunset. Female lobsters, which were sampled in lower numbers than males, also showed differences between sizes in the timing of activity (Figure 27). The most prominent difference was observed in the late afternoon when the activity of large females (>130 mm CL) was greater than that of smaller females. Similar to male lobsters, changes in female lobster activity patterns coincided with both sunrise and sunset.

Due to the paucity of large lobster and males of any size at the fished site, comparison of temporal trends in the activity of lobsters between and within the fished and MPA sites was restricted to small (<130 mm CL) female lobsters. Female lobsters at the fished site on the Tasman Peninsula displayed similar patterns of activity during spawning (Oct–Nov) and peak catchability (Jan–Feb), with movement restricted to the hours between sunset and sunrise (Figure 28). The activity of female lobsters during the mating season was difficult to interpret due to the extremely low numbers of positional estimates obtained from the VRAP system. However, examination of the unresolved positional estimates indicates that the transmitters were functional and therefore female lobsters were most likely sedentary. Activity during the spawning season was consistent between the two-year sampling periods of 2006 and 2007. Due to the low numbers of male lobsters found at the fished site, it was not possible to tag sufficient numbers to determine patterns of activity.

The activity patterns of small (<130 mm CL) female lobsters inside the MIMPA were similar during mating (2006), peak catchability (2007) and spawning in 2007 (Figure 29). In contrast, the activity of female lobsters recorded in the mating season of 2007 was substantially different to that at the same time in 2006, indicating a large amount of inter-annual variability in behaviour during mating. The low levels of female activity in the mating season of 2007 reflect a similar pattern of inactivity for females at the fished site during the same season. With the exception of the mating season in 2007, the activity of female lobsters inside the MIMPA was predominantly during the day as opposed to the fished site where the majority of activity was during the evening. This was particularly evident during the seasons of peak catchability (Figure 30) and spawning (Figure 31) in 2007 when females inside the reserve were active during the day and sedentary during the night; the opposite occurred at the fished site.

Male lobster activity was relatively consistent between peak catchability, mating and moulting during the night, but showed increased and highly variable activity during the day (Figure 32).

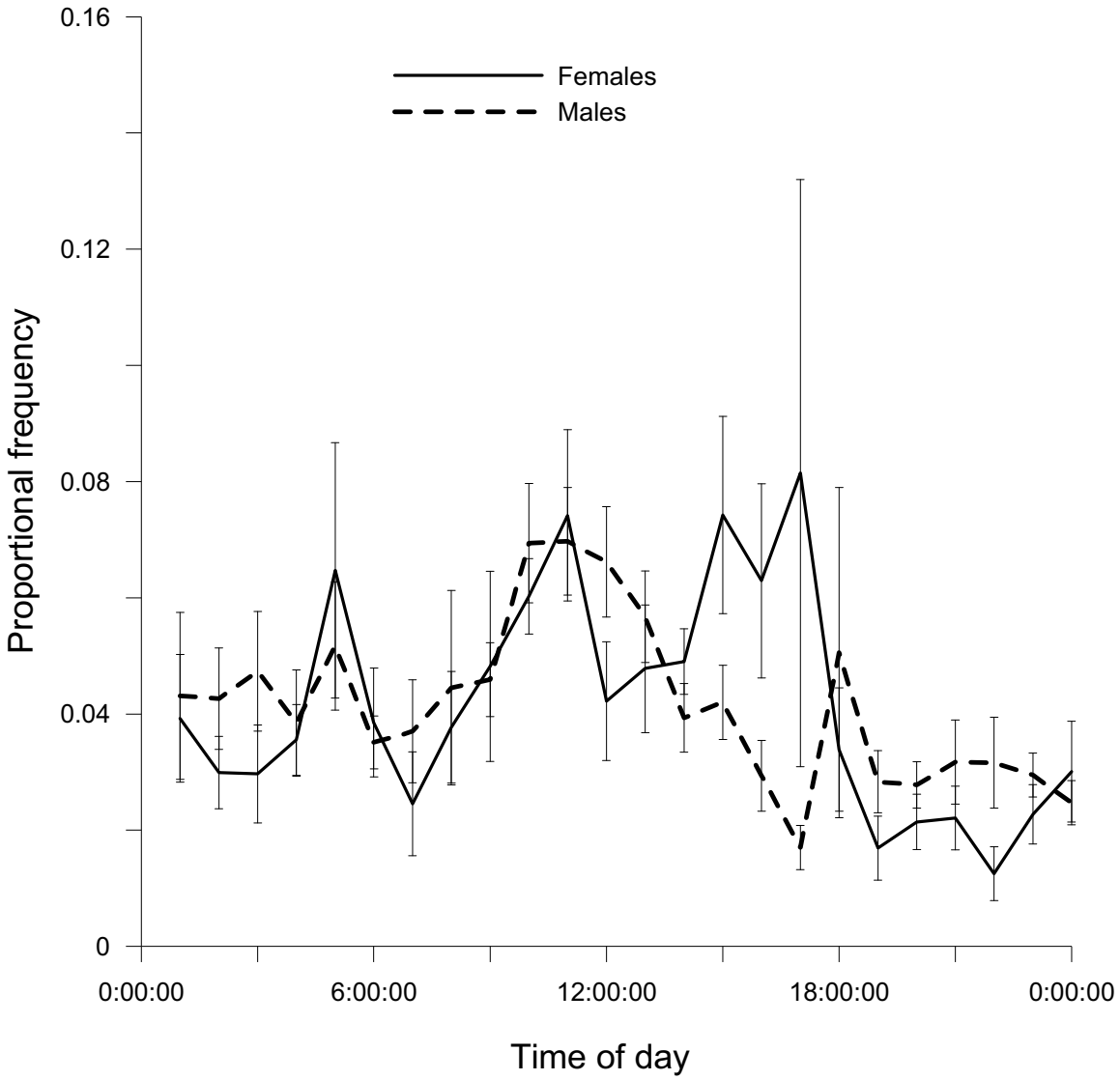

Figure 25 **Activity patterns of male and female lobsters within the MPA (mating 2006) with data pooled across carapace size within each sex. Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

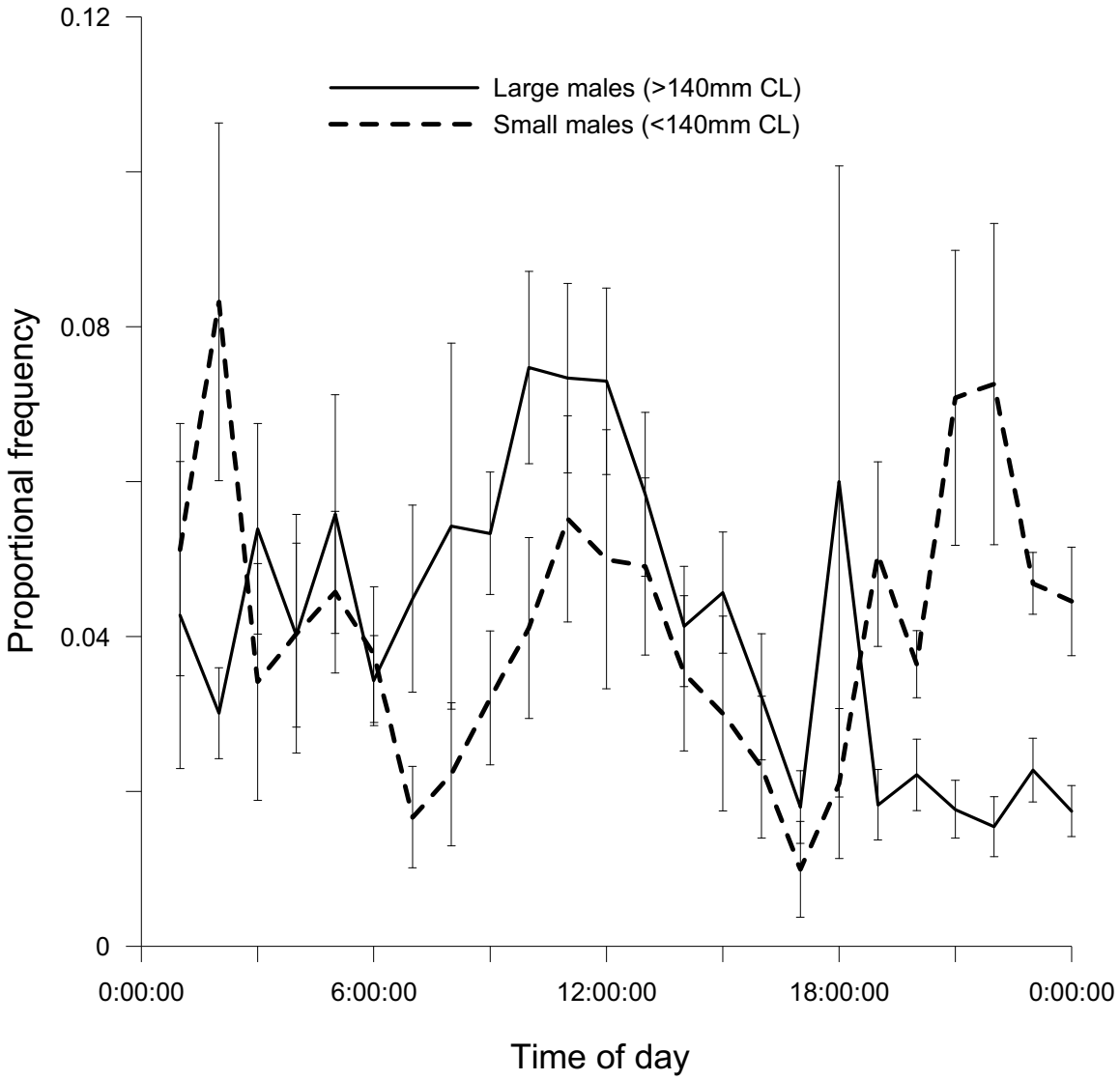

Figure 26 **Comparison of small (<140mm) and large (>140mm) male lobster activity within the MPA (mating 2006). Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

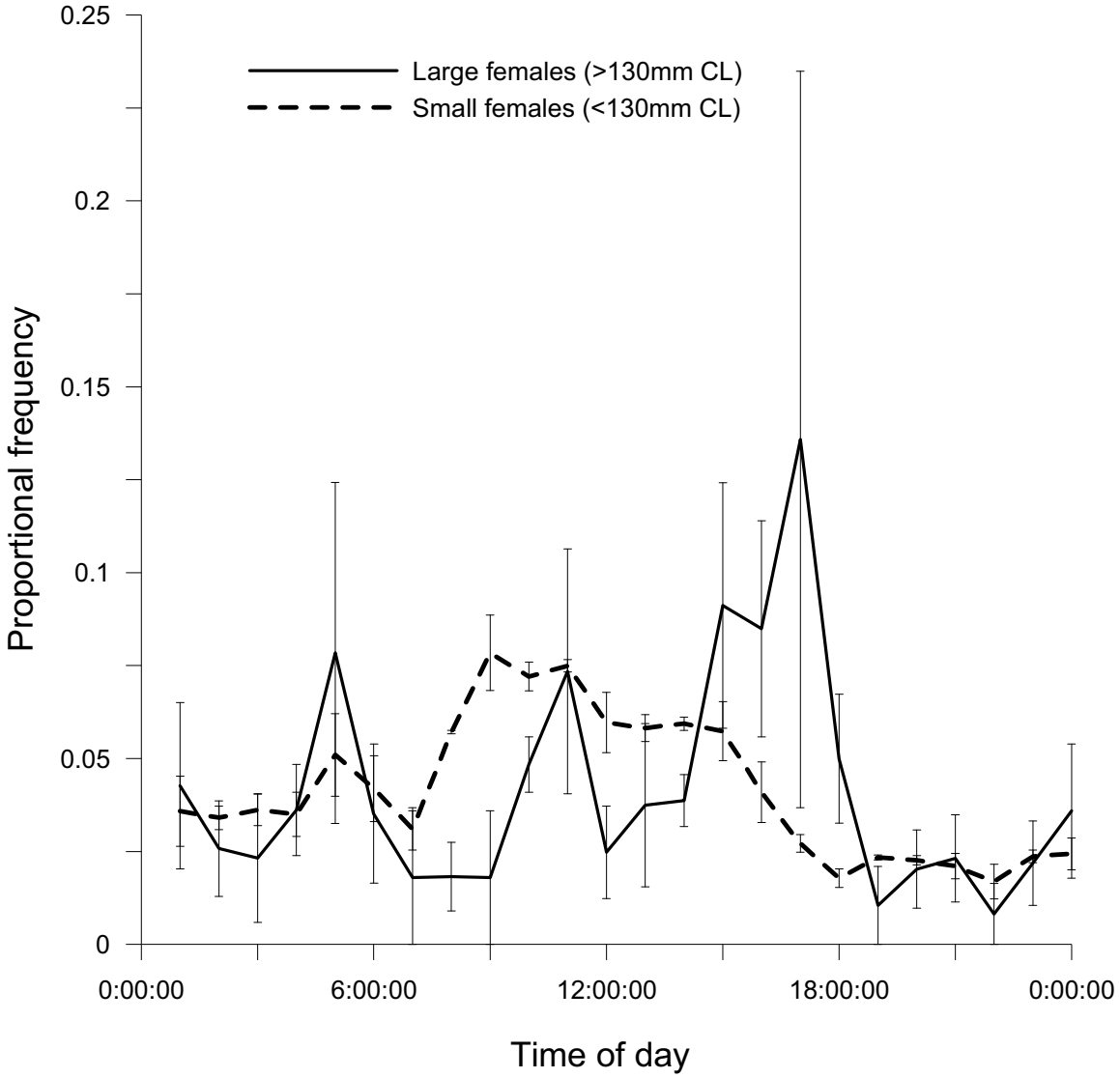

Figure 27 **Comparison of small (<130mm) and large (>130mm) female lobster activity within the MPA (2006). Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

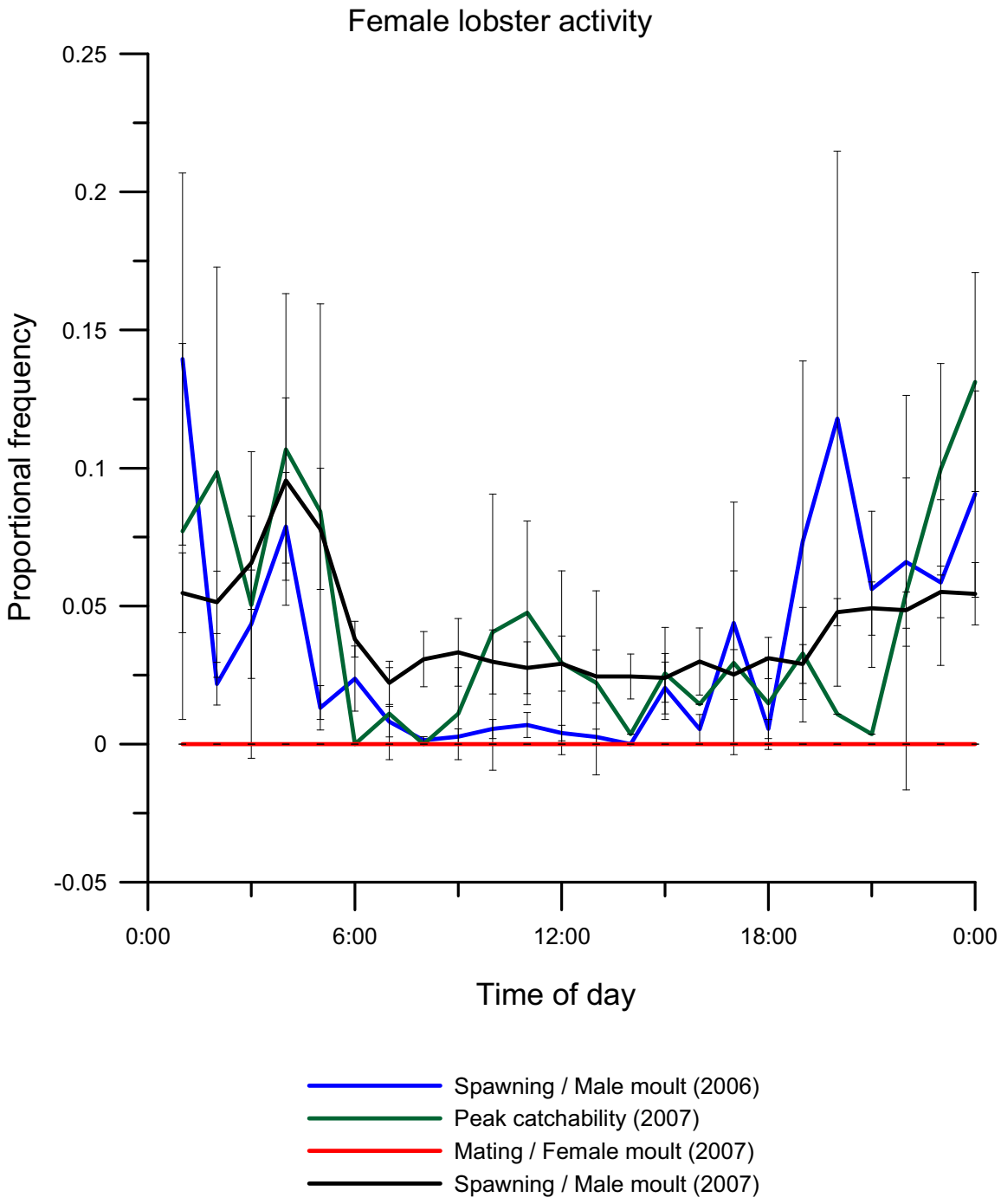

Figure 28 **Activity patterns of small female lobsters (<130mm CL) at the fished site by season. Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

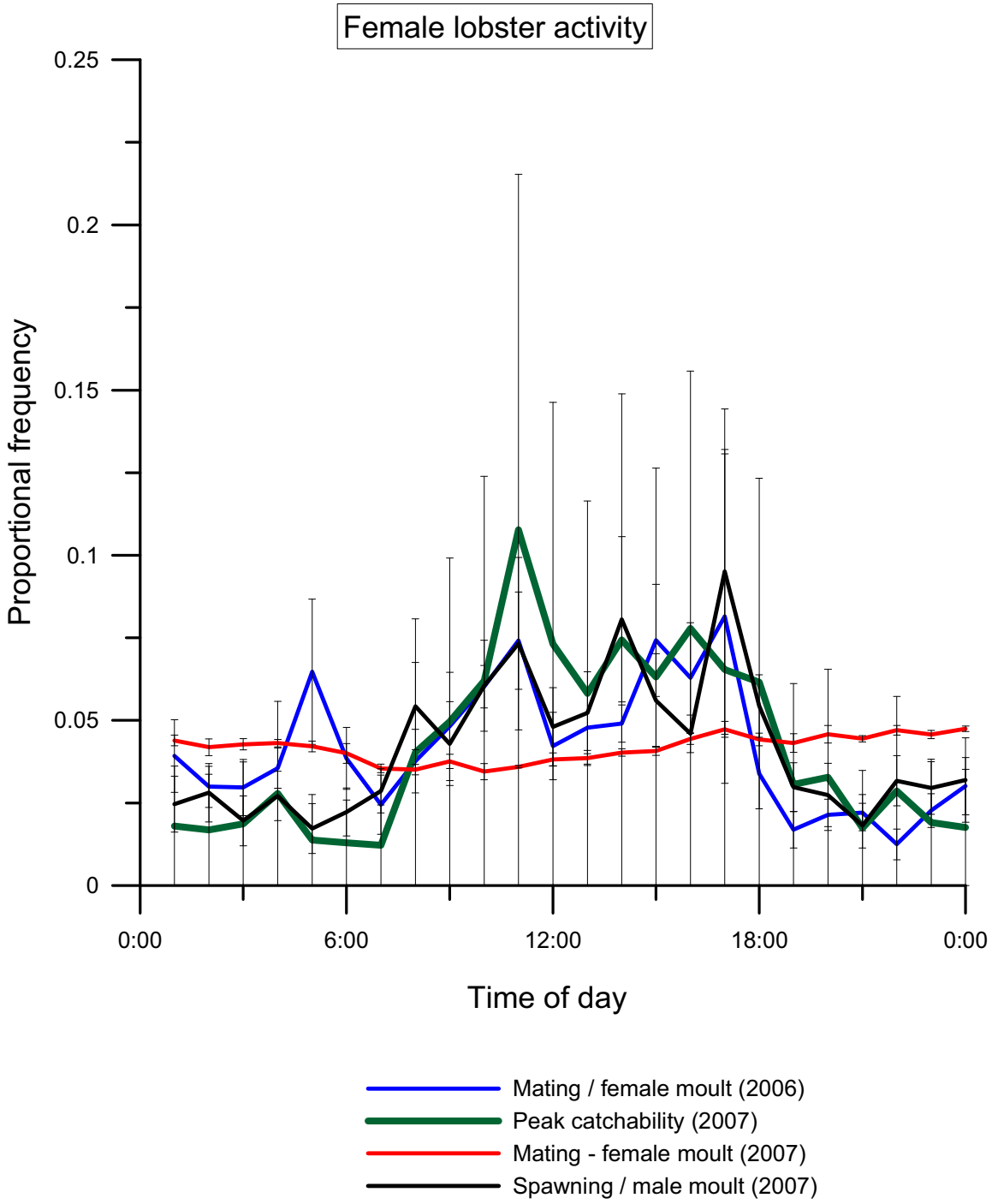

Figure 29 **Activity patterns of small female lobsters (<130mm CL) inside the MPA by season. Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

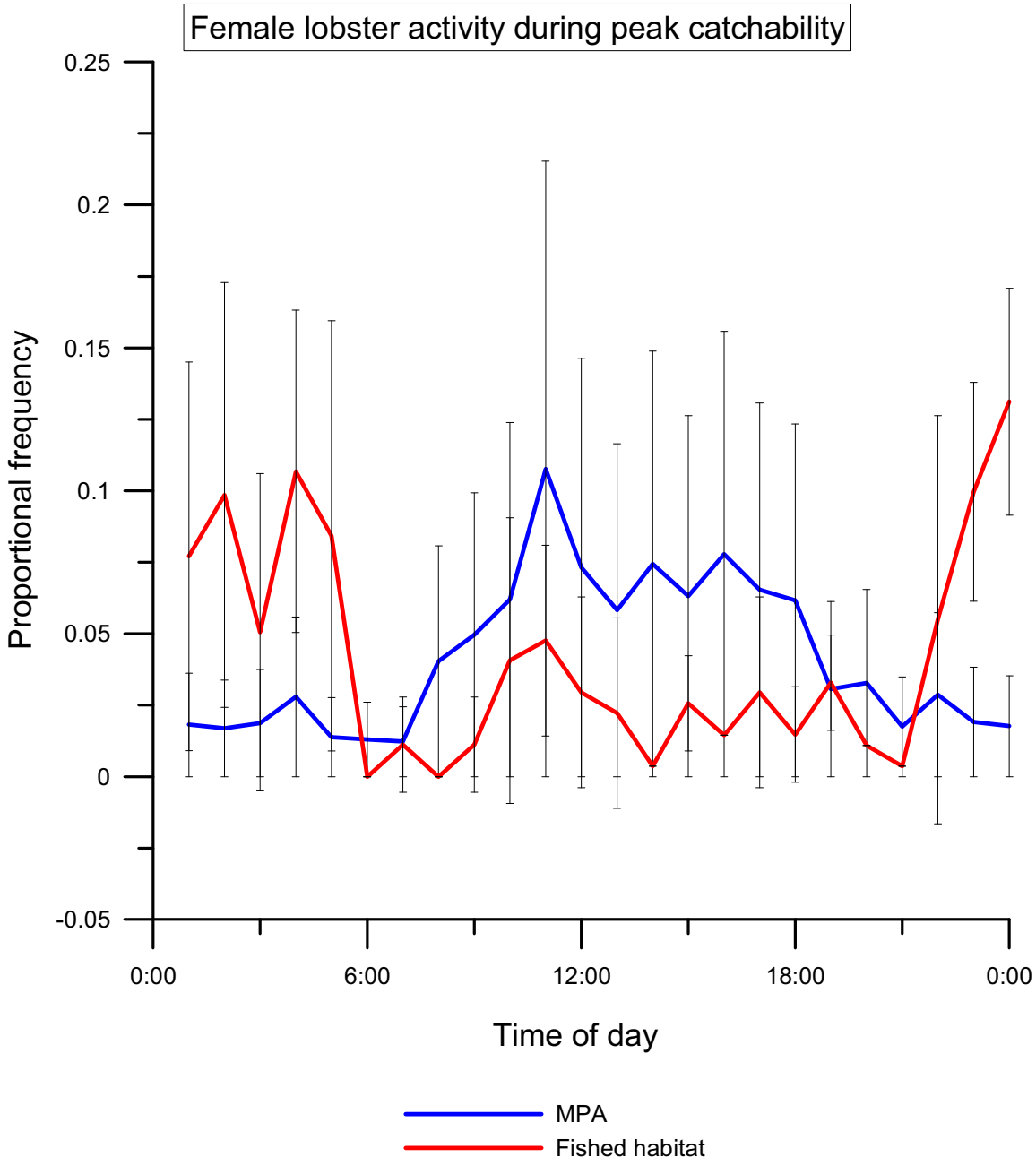

Figure 30 **Activity patterns of female lobsters in fished and unfished habitats during times of peak catchability. Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

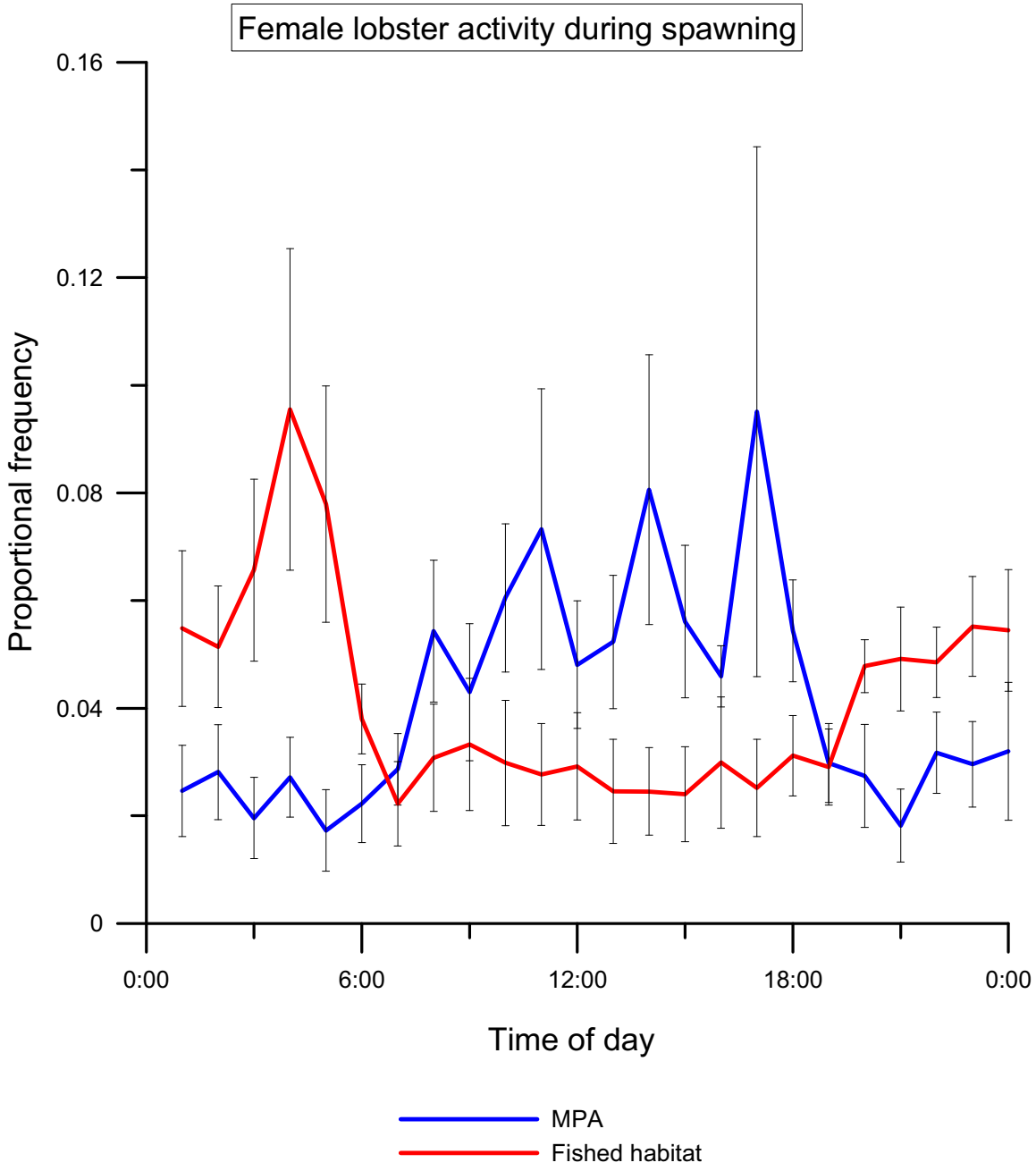

Figure 31 **Activity patterns of female lobsters in fished and unfished habitats during spawning (2007). Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

Home range area

Using the positional informational obtained from the VRAP system, estimates of lobster home ranges were calculated using a kernel density probability algorithm. During the mating season in 2006, lobsters inside the MIMPA showed no distinct relationship to carapace length for either male or female lobster (Figure 33). Intermediate-sized male lobsters within the reserve displayed the greatest variability in home range area.

The size of the female lobster home range remained relatively consistent between seasons within the MIMPA but showed substantial variation for male lobsters over a similar time period (Figure 34). The average home range area for male lobsters during mating in 2006 was less than one third of that of male lobsters during the mating season in 2007.

There was an increase in the home range of lobsters found during the 2006 and 2007 mating periods compared to either the spawning or male moulting period or the peak catchability period inside the MIMPA (Figure 35).

The home range size of female lobsters at the fished site showed significant variation between seasons, with larger average home ranges in the spawning season of 2006 compared to the other sampling periods (Figure 36).

As demonstrated by the activity patterns, home range could not be obtained for female lobsters at the fished site as females did not move beyond their dens during the survey. During spawning 2006 there was a considerable increase in the home range area that was not reflected in the 2007 spawning period, which showed similar home range sizes to the period of peak catchability (Figure 37).

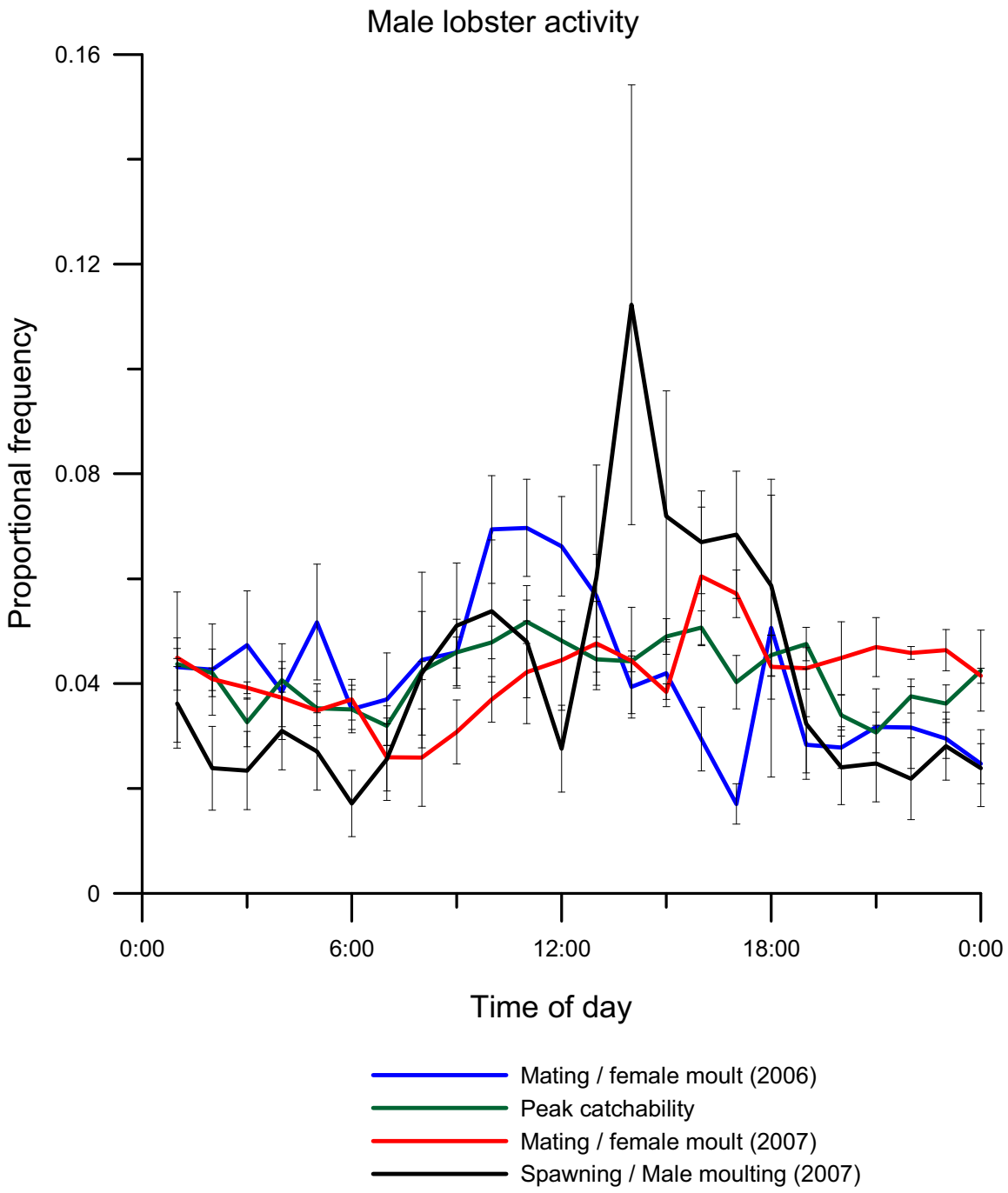

Figure 32 **Comparison of male lobster activity inside the MPA over four seasons. Lines represent the mean proportional activity recorded in each one hour block throughout the day (± s.e.).**

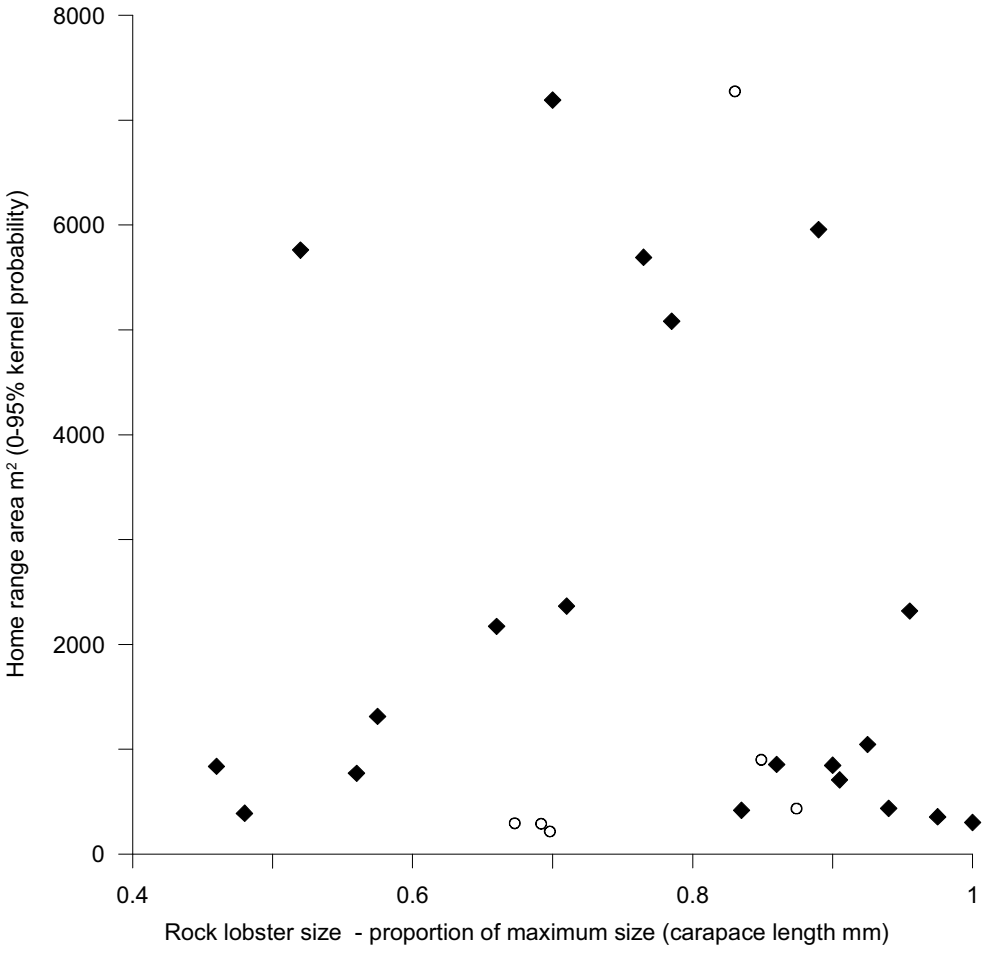

Figure 33 **Relationship between rock lobster carapace length and home range area (represented by kernel probability contours 0–95%) for male (◆) and female (○) rock lobsters during the mating season 2006 inside the MIMPA.**

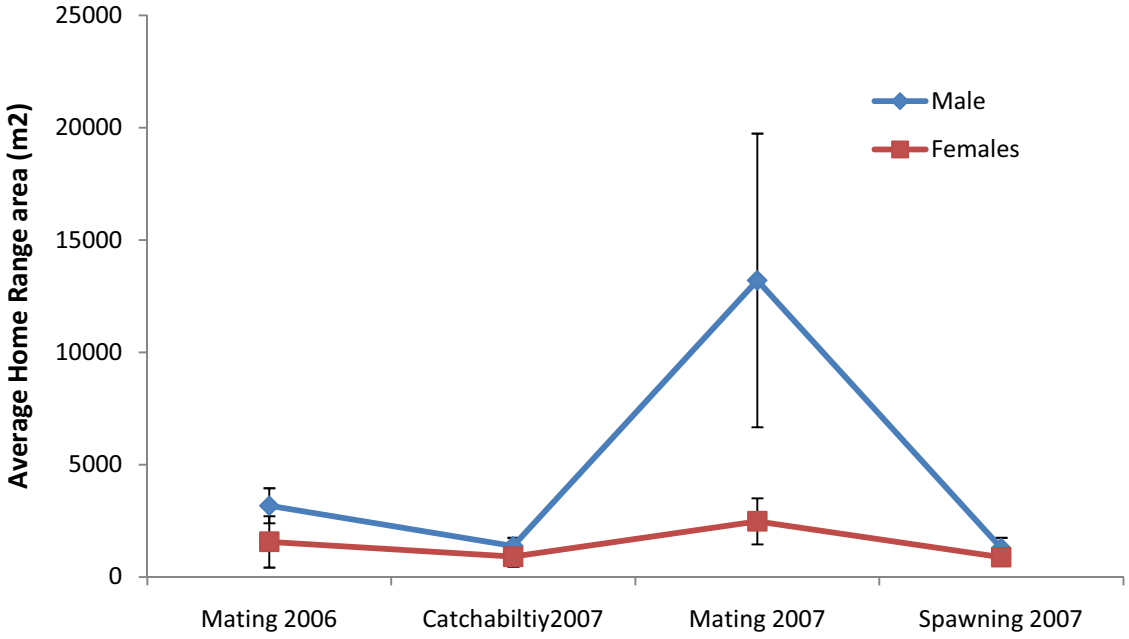

Figure 34 **Seasonal trends in home range area for male and female lobsters inside the MIMR reserve during mating, peak catchability and spawning in 2006 and 2007.**

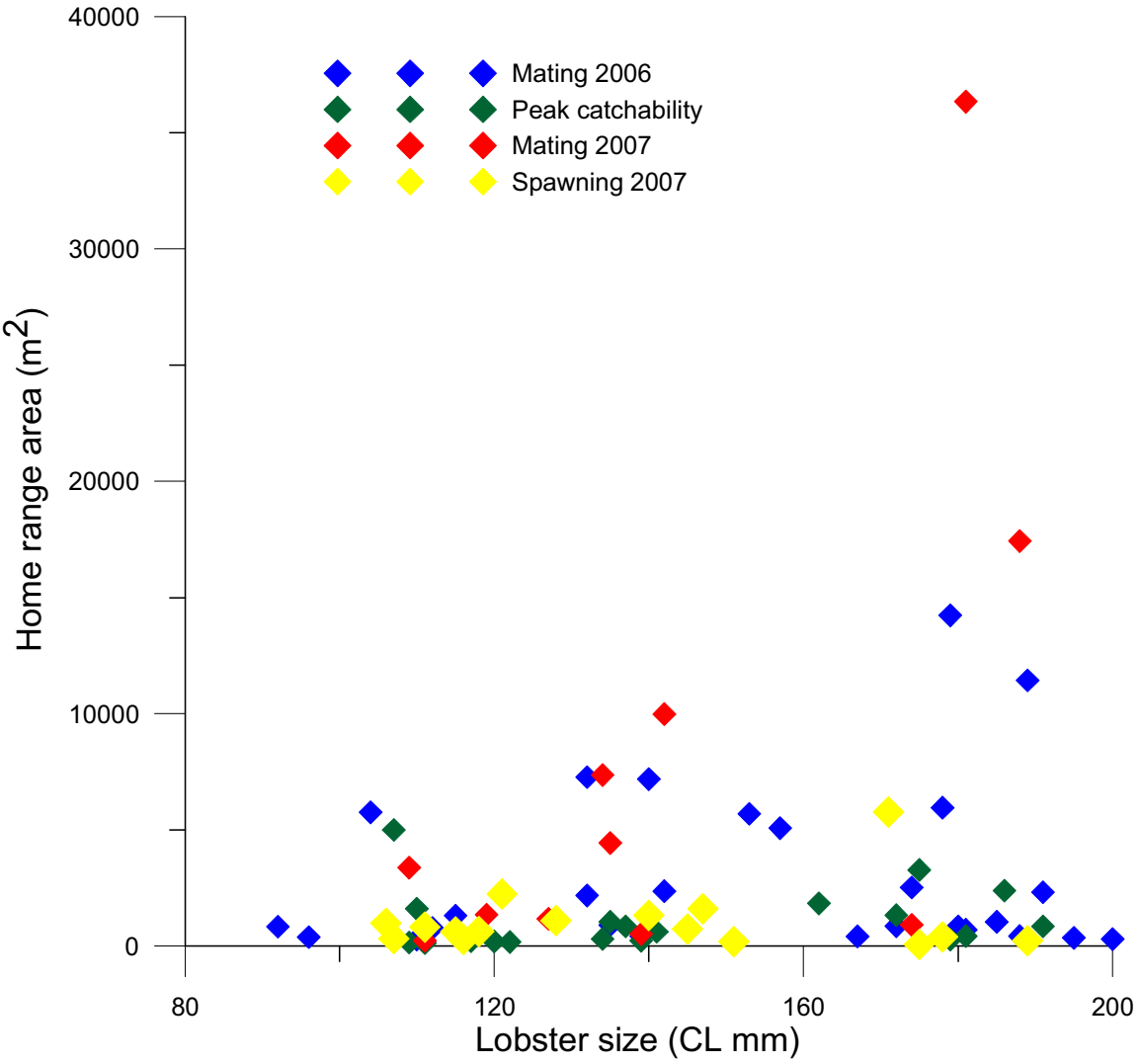

Figure 35 **Seasonal trends in home range area as a function of carapace length for all lobsters tagged inside the MPA during mating, peak catchability and spawning in 2006 and 2007.**

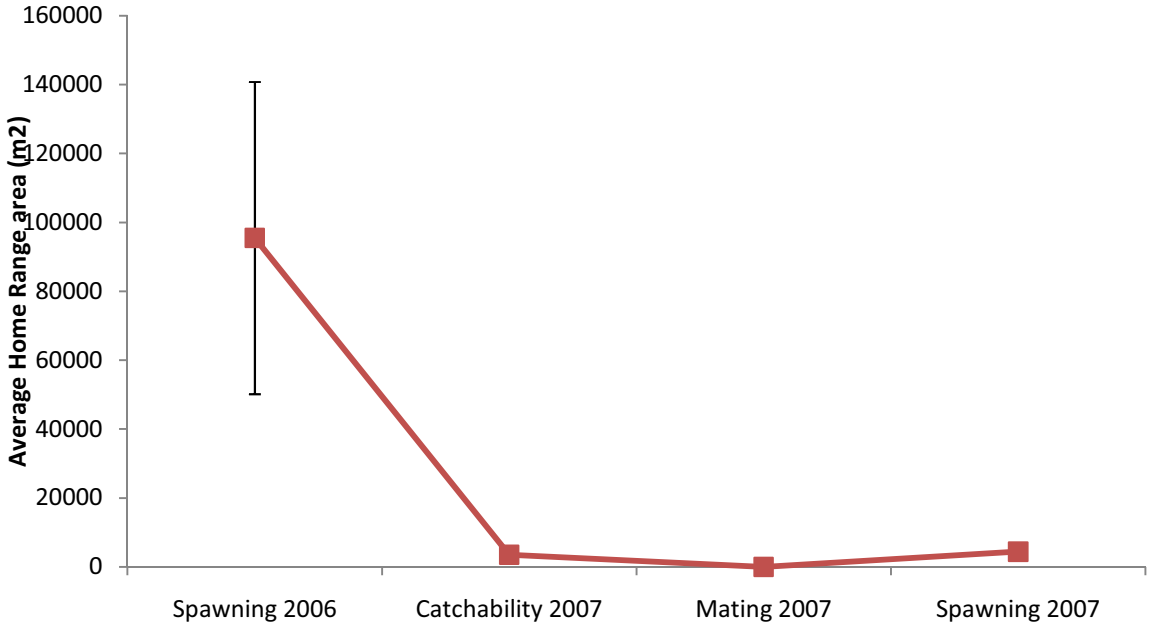

Figure 36 **Seasonal trends in average home range area (± se) for female lobsters at the fished site during spawning, peak catchability and mating in 2006 and 2007.**

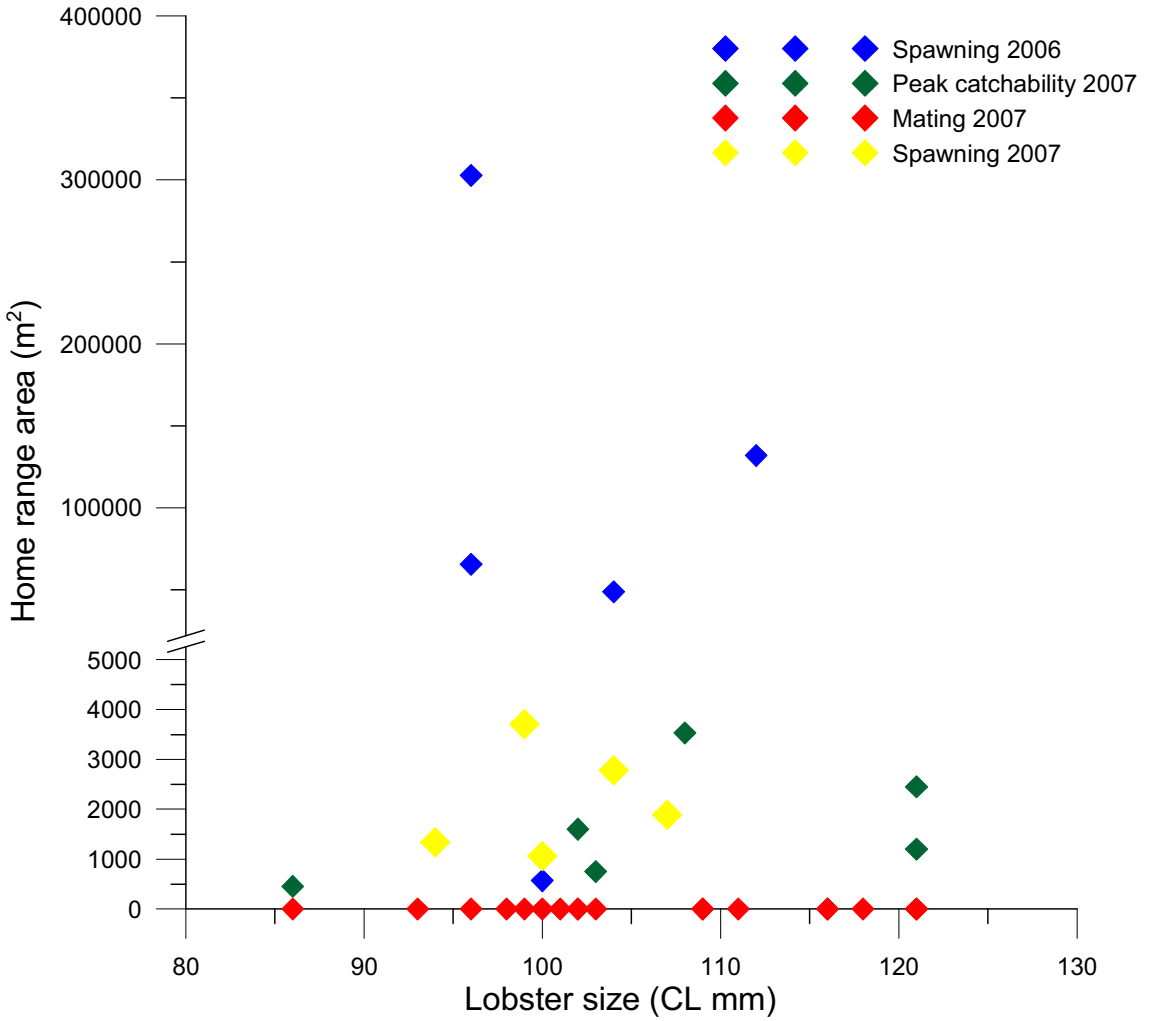

Figure 37 **Seasonal trends in home range area for female lobsters as a function of carapace length at the fished site during spawning, peak catchability and mating in 2006 and 2007.**

Distance travelled

With the exception of the mating periods when male and female lobsters travelled similar distances, male lobsters travelled, on average, greater distances than female lobsters inside the MIMPA (Figure 38).

Outside the MIMPA, the total distance travelled by female lobsters was different to that which occurred inside the MIMPA, with increased total distance travelled occurring in the spawning season (Figure 39).

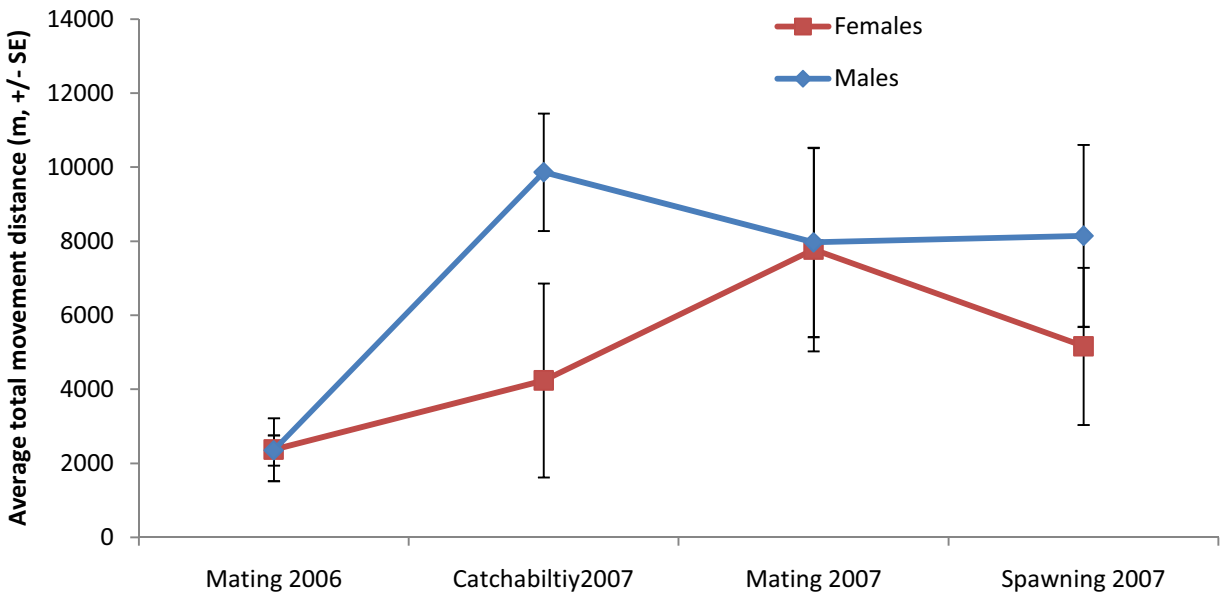

Figure 38 **Seasonal patterns in the total distance travelled by male and female lobsters inside the MPA between mating 2006 and spawning 2007.**

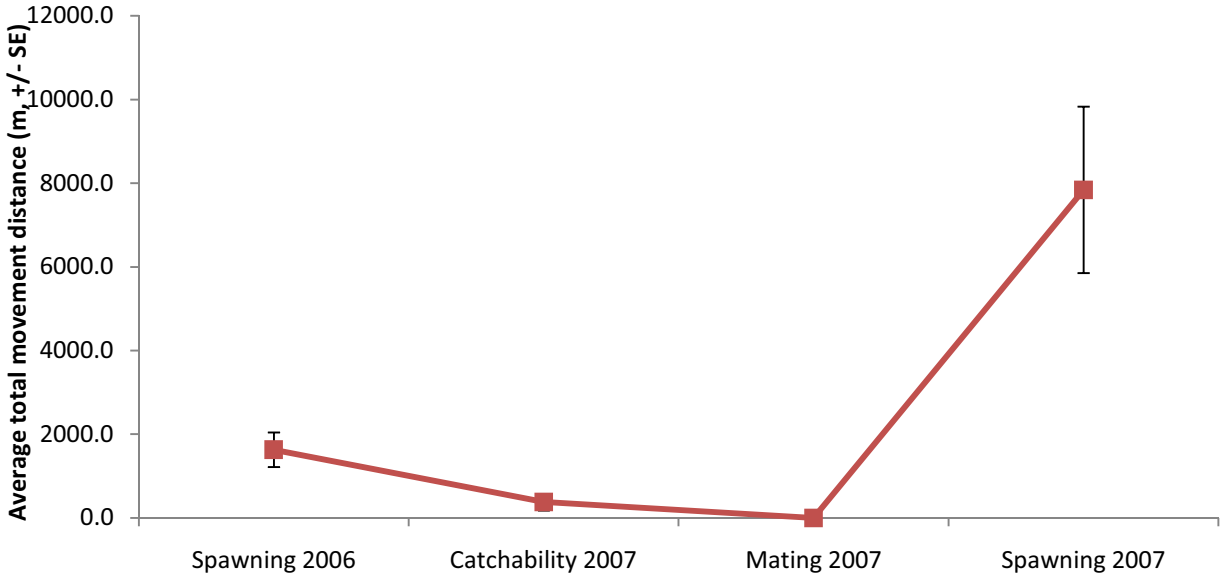

Figure 39 **Seasonal patterns in the total distance travelled by female lobsters at the fished site between spawning 2006 and 2007.**

Habitat utilisation

Kernel probability home ranges were calculated using filtered positional estimates and the resulting shapefiles were used to determine the quantity of each habitat utilised by each tagged lobster. Because the configuration and quantity of habitats was not consistent between the two sites, patterns in habitat utilisation were analysed between seasons within each site to examine temporal changes.

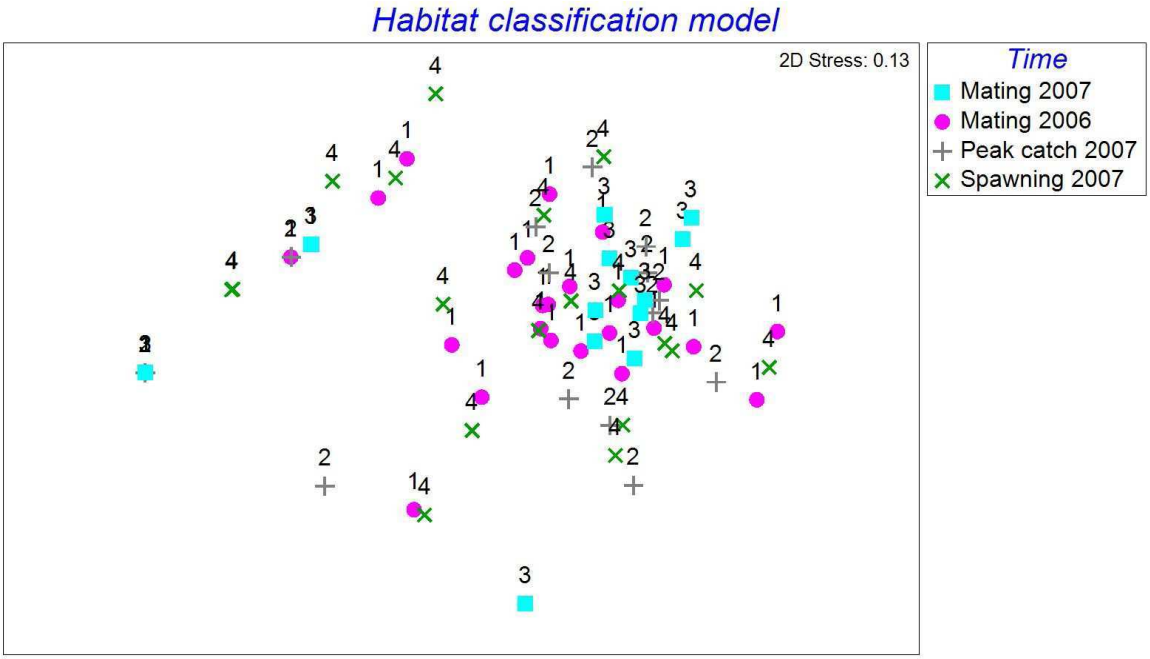

Figure 40 **Non-metric MDS plot representing seasonal trends in the utilisation within the MIMPA of habitat morphometric features identified using the classification model.**

Using analysis of similarity the pattern of habitat utilisation was not significantly different between seasons within the MIMPA (P = 0.55, Figure 40). In comparison, habitat utilisation at the fished site was significantly different between seasons, with the spawning season of 2006 significantly different from all other time periods sampled (P < 0.01, Figure 41). The SIMPER routine in the PRIMER software package identified the higher contribution of channels within the reef contributing to the differences. Examples of habitat classifications and lobster movements at the fished site are presented in
Figure 42 and Figure 43.

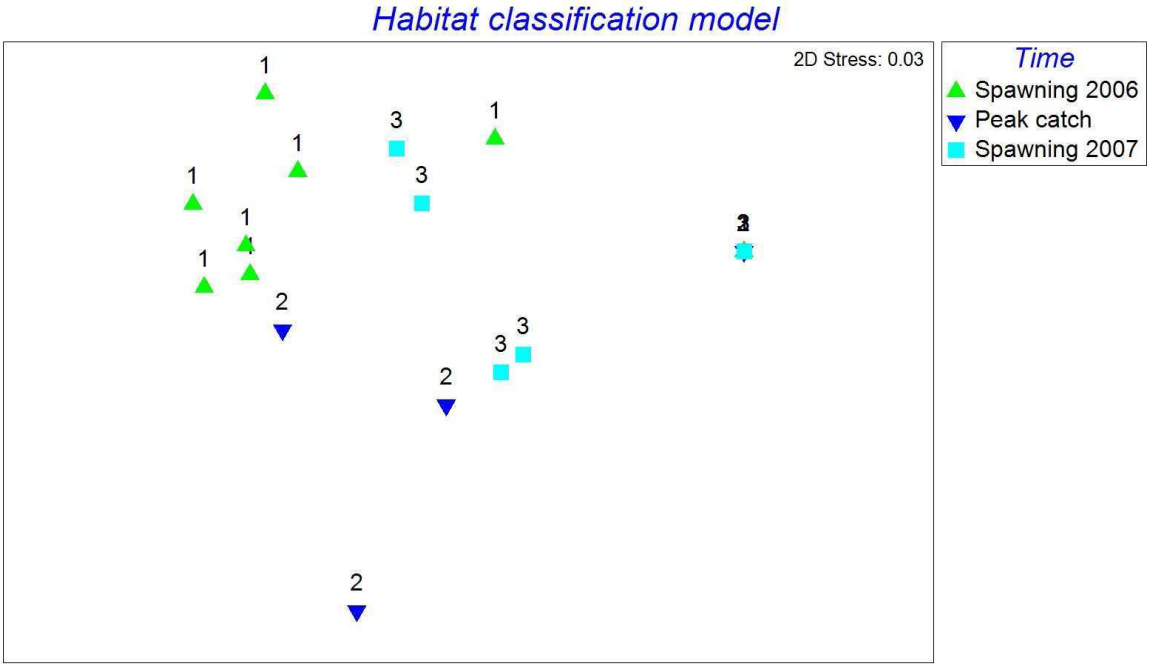

Figure 41 **Non-metric MDS plot representing seasonal trends in the utilisation at the fished site of habitat morphometric features identified using the classification model. Although habitat utilisation for the period of mating in 2007 was assessed and represented in the ANOSIM the data has been exclude from the MDS plot to display the arrangement of the other three seasons without the bias of the sample taken during the mating season. Insufficient sample size of the positional data collected during the mating season did not allow accurate home range and habitat utilisation parameters to be calculated.**

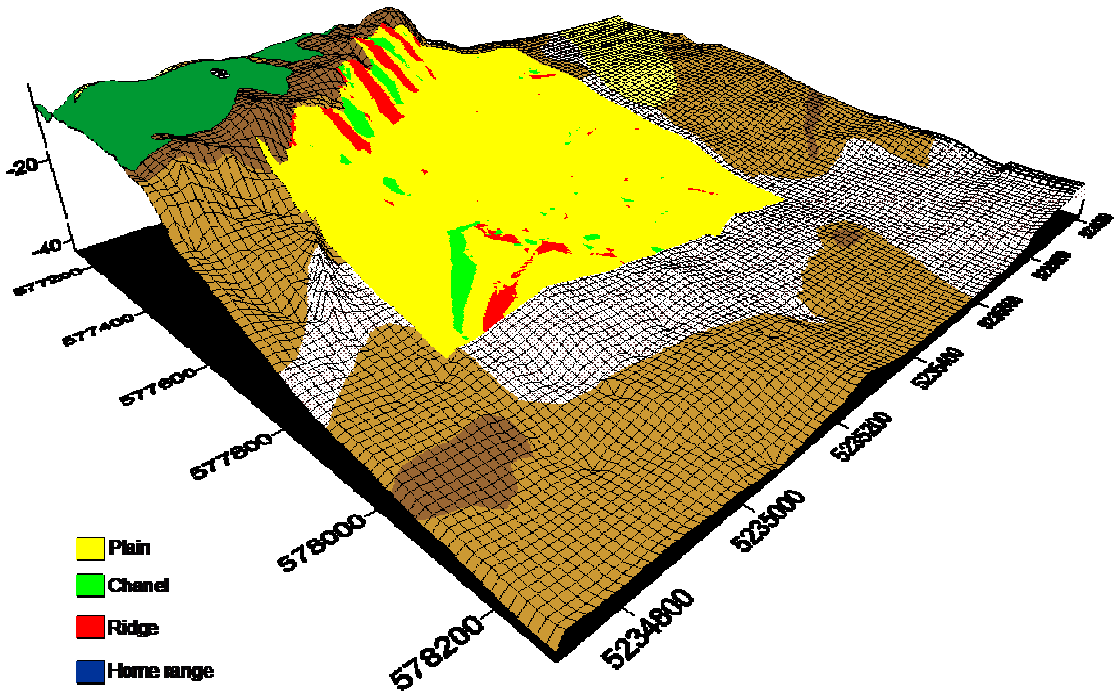

Figure 42 **Habitat maps and classification models for the experimental site located on Tasman Peninsula.**

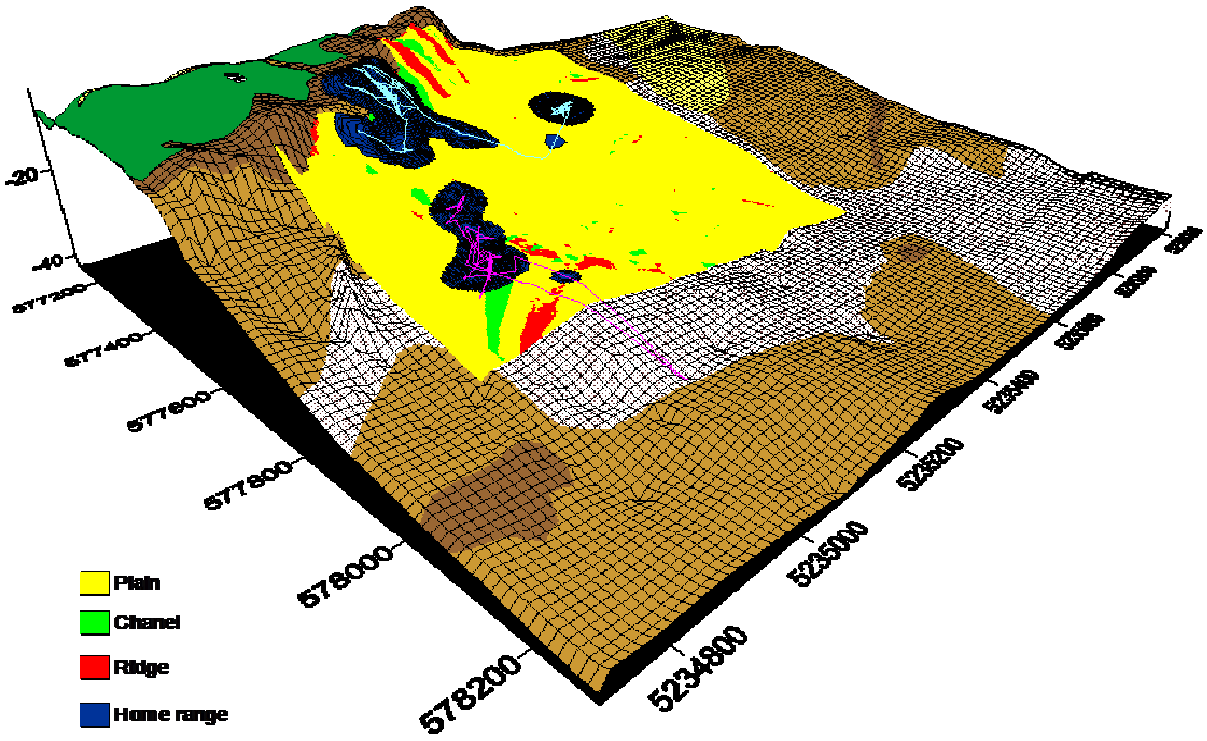

Figure 43 **Movement paths of two lobsters carrying acoustic tags (pink line = female lobster, blue line = male) on the Tasman Peninsula overlayed on habitat classification models.**

Discussion

There are substantial differences between the behaviour of lobsters in fished and unfished sites in eastern Tasmania as well as differences in seasonal activity within these sites. A major surprise was the increased activity of female lobsters during the day in the MIMPA. Sampling from traps set in the reserve during day and night (Frusher, per obs) captured virtually no female lobsters during the day. Thus, the increased activity of these lobsters is not a reflection of feeding activity. In contrast, the dominance of large males caught in lobster traps set during the day in the MIMPA is reflected in the activity patterns of large males. Similarly, smaller males were only caught in traps set during the night when small male lobster activity is highest. This pattern of male lobster activity is also reflected in fishing activity as fishers only set their traps overnight in shallow water regions. At the fished site the activity pattern of females was completely different, with activity primarily associated with night-time activity.

While observations from trap catches would suggest that there are no differences in the behaviour of lobsters between day and night in both fished and unfished regions, this project has demonstrated that there are substantial differences in activity patterns. The main difference between the MIMPA and the fished site is the overall abundance

of lobsters and the increase in the number of large lobsters. Thus, these results infer that fishing has influenced the behaviour of lobsters.

Although there were differences in overall activity patterns between fished and unfished sites for females, there were consistent patterns between seasons, with female lobsters showing limited activity during the mating season. This is not surprising given that females moult before mating and are often guarded by males during the mating season (MacDiarmid, 1991. For males there was increased activity during the spawning period which coincides with the pre-moult period for males. Increased activity during this period is also reflected in the male commercial catch and is considered to be associated with lobsters increasing their metabolic reserves (feeding) prior to the energy draining process of moulting.

Although there was proportionately greater activity during the male moult period inside the MIMPA, the only change to the average home range was observed during the mating season. Again, this reflects the male behaviour of seeking out female lobsters during this period (MacDiarmid, 1991. While there were differences in the seasonal activity patterns of female lobsters, this activity appears to be primarily restricted to their home range regions in the MIMPA. In contrast to the MIMPA, there was a substantial increase in home range during spawning in 2006 at the fished site. However, this increase in home range was not reflected in the spawning period of 2007. Despite a large home range for spawning in 2006, the average distance moved by female lobsters at the fished site was less in 2006 compared to 2007, suggesting that a greater number of female lobsters moved considerable distances (i.e outside their home range) during 2007. These larger movements are believed to be associated with egg release when female lobsters move to offshore regions to release the newly hatched phyllosomas into the stronger offshore currents associated with these regions (see Figure 44 for an example of this movement).

Distance travelled by male lobsters is also not reflected in the pattern of home range variation, indicating that during catchability and pre-moult (spawning for females) there were a number of long-distance excursions by lobsters beyond the home range. In constrast, during mating the movement of lobsters was more reflected by more frequent but smaller movements within the adjacent reef region, resulting in an increased home range (see Figure 45 for an example of medium- and long-range movements of male lobsters within the MIMPA). This activity pattern supports the theory that male lobsters are visiting female lobsters within their approximate den, rather than undertaking larger feeding forays.

The larger abundance of lobsters within the MIMPA has resulted in virtually all regions of the reef being used, suggesting that carrying capacity is most likely to be associated with food availability (Figure 46). In contrast, when the abundance is reduced, such as in the fished site, seasonal differences in habitat utilisation were

revealed. Female lobsters used channels in the reef structure to move to offshore areas during spawning.

This study has been the first to reveal differences in the behaviour of lobsters in MPA and fished sites and as the major difference between these sites is the reduction in lobster abundance and average size due to fishing, this indicates that fishing has impacted on the behaviour of lobsters. These behaviour trends will have gone largely unnoticed as we have identified activity patterns that are independent of catch rates or catch composition.

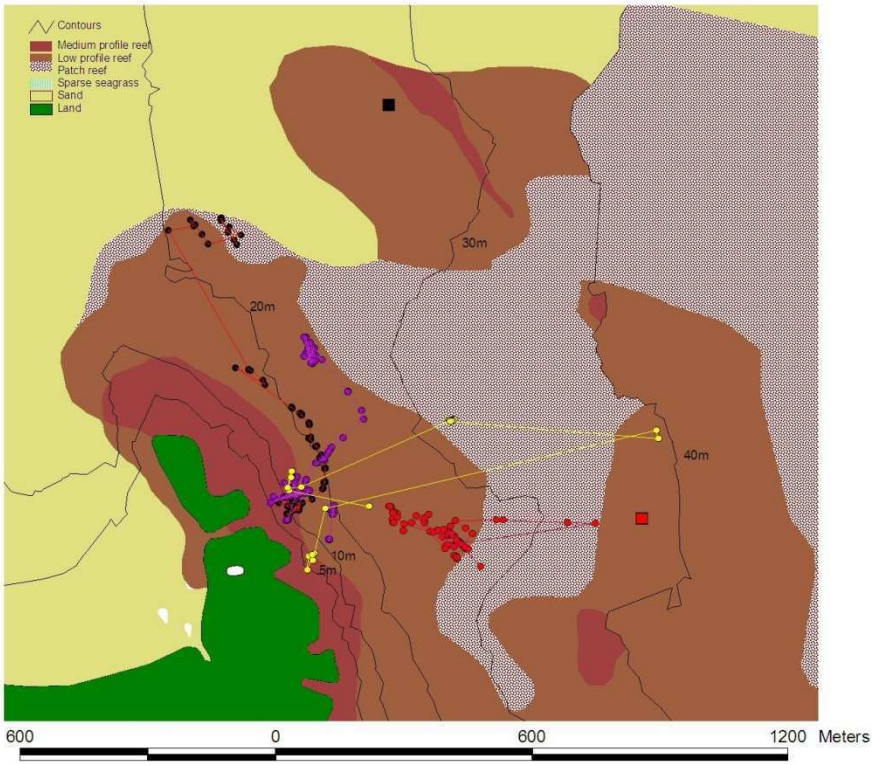

Figure 44 **Movement paths (lines) of egg-laden female lobsters over a two week period at the fished site. Coloured dots represent locations determined by VRAP system. Square represents last location observed by divers.**

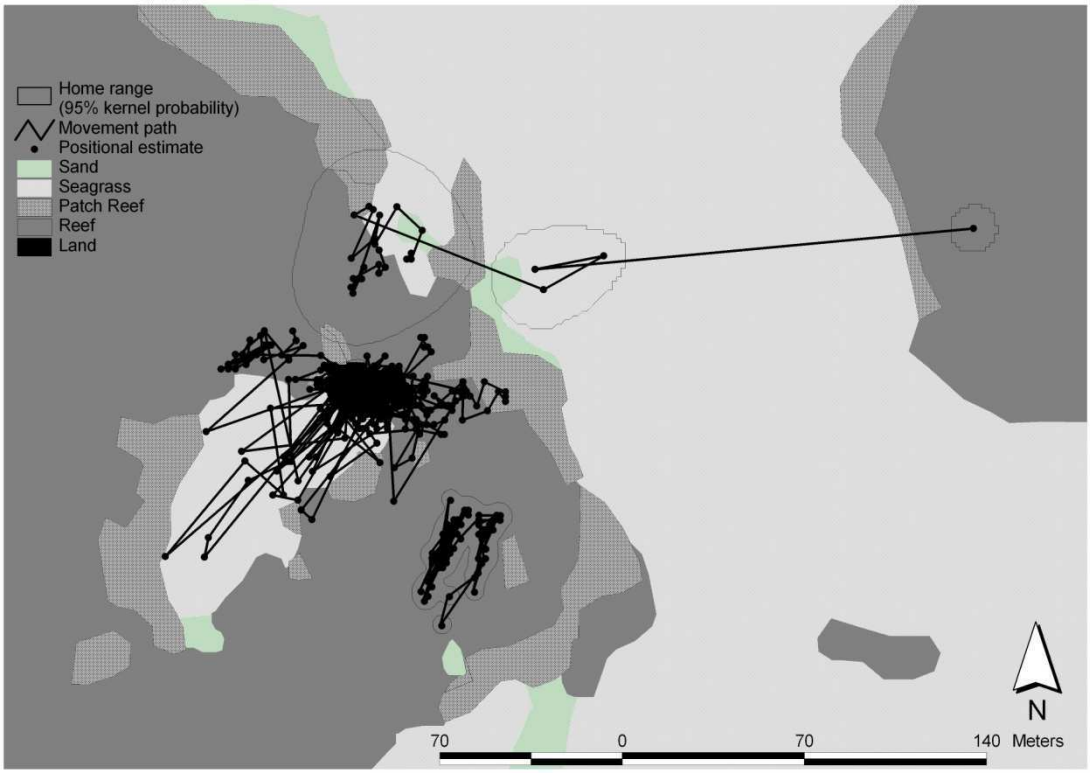

Figure 45 **Examples of small movements within the home range (bottom), medium movements outside the home range region (middle) and larger movements which result in changes in home ranges during the survey (upper) at the MIMPA.**

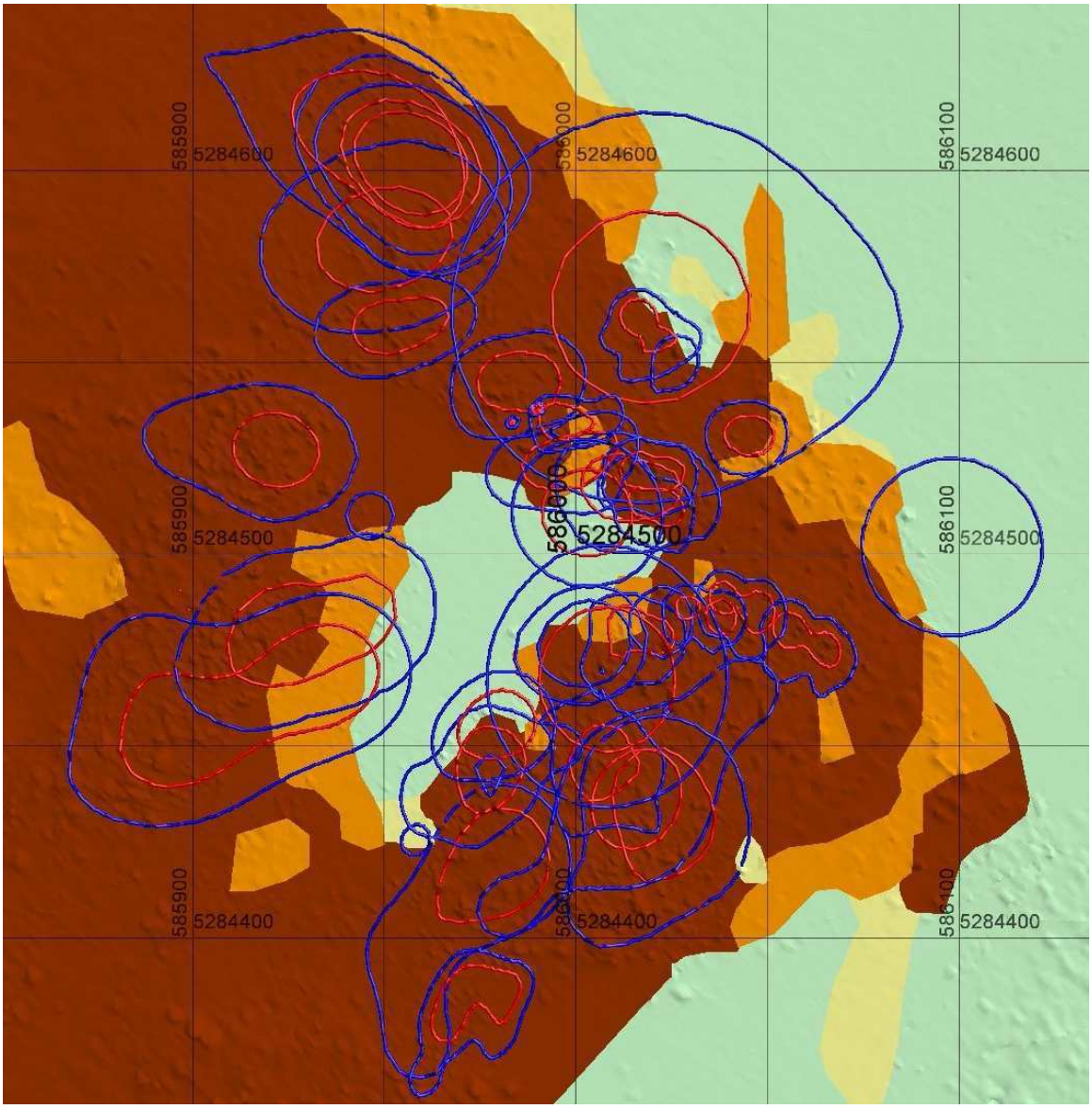

Figure 46 **Example of overlapping home ranges of male (blue) and female (red) lobsters at the MIMPA.**

Benefits

Fisheries managers, scientists, industry and the community will all benefit from this project. Fisheries managers have an example of direct and indirect impacts of fishing and will be able to contextualise the need for multi-species management. For abalone and rock lobster fisheries management, this project provides direct evidence of the relationship between these two valuable commercial species. This information can then be used (and is being used by managers in South Australia and Tasmania) to address EPBC Act concerns.

Scientists will benefit from this project as it provides a framework for tackling multi-species management issues and identifies new and innovative ways of understanding the direct and indirect effects of fishing. Several of these methods have already been adopted by other projects including the DNA dietary technique to identify *Centrostephanus* in the diet of lobster translocated into *Centrostephanus* barrens (FRDC 2007/045) and the use of fine-scale acoustic telemetry to delineate the movement patterns and home ranges of lobsters translocated into barrens (FRDC 2007/045). The fine-scale acoustic telemetry is also been used to understand the behaviour of undersized lobsters translocated to improve yield in southern rock lobster fisheries (2006/220).

This project has demonstrated to the fishing industry that the large and often amorphous statements about ecosystem management are, in reality, achievable goals. The industry now has an example of the how an issue can be addressed and that there is the appropriate technology and scientific skills to understand key issues between species.

Further development

This project has tackled a couple of key ecosystem issues on shallow temperate rock reefs. Developing several of the methods to address pelagic and deep water benthic communities will be required. Manipulative experiments and acoustic telemetry will be challengers for these ecosystems. In contrast, the trophic linkage methodologies that involved stable isotopes, fatty acid signatures and DNA dietary analysis are broadly applicable to fisheries in any ecosystem. Further development of these methods holds considerable promise for a cost-effective means of constructing appropriate food webs or validating existing theoretical food web linkages. The DNA technology is also advancing rapidly and the quantification of dietary intake is currently in development. Additionally, a new DNA technique called *pyrosequencing* holds promise for describing all prey items in a faecal sample. Both these techniques should be explored for use in understanding ecosystem interactions between the different living components of marine ecosystems.

The use of fishers' knowledge to inform scientific investigations has not been readily supported in Australian fisheries. Future developments should evaluate ways of incorporating fisher knowledge into a scientific framework.
The development of a combined ecosystem approach based on a combined model for these two important fisheries is still required and beyond the scope of a single project. We are making significant inroads to addressing this issue through PhD projects and developing components in associated projects where the outcomes are mutually beneficial. Currently the rock lobster model is being upgraded and the abalone model is still being adapted and trialled.

Planned outcomes

To incorporate this knowledge into the EA assessments of both the rock lobster and abalone fisheries, thus addressing the needs identified in the initial assessments of both fisheries for a greater understanding of ecosystem effects of fishing.
The information obtained from this report has been supplied to South Australia and Tasmania for incorporation into their EA assessments.

Uptake of these results will lead to a new integrated approach to stock assessment in both the rock lobster and abalone fisheries that will optimise the ecological, social and economic benefits of both fisheries.
The outcomes of this study indicated that the interaction between rock lobster and abalone was primarily behavioural (changes in size at emergence) with predation being relatively minor.

Outcomes of the project have demonstrated to industry and community representatives that there are interactions between species that can be assessed and quantified. By focusing on specific issues identified by our stakeholders, this project has demonstrated that there is a need for multi-species management in two of south-east Australia's most valuable fisheries, and the need for this approach to be adopted as the future management framework. While we do not expect managers and industry to move to an EBFM approach immediately, these results have progressed the debate and now await the new generation of multi-species models that can be linked to assessment models. We are currently progressing this concept through a PhD student (see below).

In a new project (FRDC 2007/045) that is evaluating ways of managing the increase in urchin barrens by *Centrostephanus rodgersii*, an option is to increase the number of larger sized lobsters (urchin predators) on inshore reefs. The Tasmanian rock lobster assessment model has been altered to provide an output of large lobster biomass. In addition, the abalone dietary DNA marker will be used to determine the consumption of these larger lobsters of abalone. This will enable the rock lobster assessment model to also estimate abalone mortality which can be incorporated into abalone

assessments. However, the development of an abalone model is currently underway. Nevertheless, outputs will raise the awareness of both managers and industry of additional sources of abalone mortality that need to be considered in assessment of the fishery. This assumes that there is a change in abalone mortality with increased size of rock lobster as identified in this project

If the negative interaction between lobsters and abalone and abalone and habitat are confirmed by this project, they will demonstrate the need for both industry and management to adopt the ESD agenda.

The methodologies demonstrated in this project have been demonstrated to industry which is becoming increasingly aware of the need to take an ecosystem approach to fisheries. Evidence of this is the support for and push for solutions to the increased prevalence of the barrens-forming urchin *Centrostephanus*. As highlighted above, the FRDC project that industry and management supported has adopted the methods developed in this project. Industry and management are aware of the four-way interaction between kelp, urchins, abalone and rock lobster and are proactive in seeking a combined solution.

The use of individual-based models to describe ecosystem processes in stock assessments.

Individual-based models were not explored in this project, although the development of methods to assess lobster behaviour, movement and diet at the individual level was demonstrated in the project. We have appointed a PhD student to develop both qualitative and quantitative models to evaluate the dynamics of the combined algae, rock lobster, abalone and urchin ecosystem dynamics. We plan to use agent-based modelling (similar to individual-based modelling with agents being individuals or collections of individuals or similar entities) to build the biological model. This model will then interface with the fisheries' assessment models to provide biological fisheries parameters (exploitatable biomass etc). The rock lobster model is currently being adjusted to incorporate economic data (FRDC 2006/220) and bio-economic data on fleet dynamics (PhD project).

Appendices

Appendix 1

The effect of predator-prey and competitive interactions on size at emergence in black-lip abalone (*Hailotis rubra*) in a Tasmanian MPA

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Abstract

Following more than a decade of protection from fishing activity the direct and indirect effects of fishing on benthic community structure are becoming apparent inside no-take marine protected areas (MPAs) on Tasmania's east coast. Gradual increases in the abundance and average size of putative abalone predators inside the no-take Maria Island Marine Reserve (MIMR) have coincided with increases in the minimum size of emergent abalone (*Haliotis rubra*). This suggests that the threat of predation may influence the structuring of abalone populations. The abundance of emergent abalone was negatively associated with predator abundance, especially rock lobsters (*Jasus edwardsii*), inside the MPA and in adjacent fished areas. Abalone leave cryptic habitat at smaller sizes in fished areas compared to abalone inside the MPA. Although the patterns in abalone size at emergence were strongly correlated with rock lobster abundance and average size, the abundance of other predators (demersal predatory fish and crabs) or competitors (sea urchins) did not influence the patterns in abalone size at emergence. However, predation mortality in isolation could not account for the differences we observed in abalone size frequency distributions between MPA and adjacent fished locations. We suggest that a combination of factors

including predation, intra and interspecific competitive interactions are responsible for patterns in abalone size at emergence.

Keywords: Abalone, size at emergence, predator-prey interactions, behaviour, MPAs, *Haliotis rubra*

Introduction

Historically, research on the effects of fishing has been focused on determining the impact of removing target species from marine ecosystems, with most studies limited to examining changes in biomass and size structure. However, after several decades of exploitation the indirect effects of fishing to non-target species and ecosystems are being observed in a range of temperate ecosystems (Babcock et al. 1999; Mayfield & Branch 2000; Tegner & Dayton 2000; Karpov et al. 2001; Rogers-Bennett & Pearse 2001; Shears & Babcock 2003; reviewed by Tegner & Dayton 2000). Among the most prominent indirect effects of fishing are changes to predator-prey relationships (Estes & Palmisano 1974; Simenstad et al. 1978; Tegner & Dayton 1981; Cowen 1983; Tegner & Levin 1983; Vadas & Steneck 1995; Tegner & Dayton 2000) and competitive interactions between species (Tarr et al. 1996; Karpov et al 2001). In many cases, assessing both the direct and indirect effects of fishing has only been possible via the advent of marine protected areas in which fishing is prohibited (no-take MPAs). The effectiveness of MPAs to increase the abundance, average size and biomass of exploited species (Edgar & Barrett 1999; McClanahan & Arthur 2001; Russ & Alcala 2003; Willis et al. 2003), reverse trophic cascades and restore ecosystems towards pre-fishing states is now well recognised (Shears & Babcock 2003).

Following a decade of protection from exploitation, changes in the abundance, average size and diversity of species have been observed in no-take MPAs along Tasmania's east coast (Edgar & Barrett 1999, Buxton et al. 2006). The most notable changes have occurred in the largest no-take reserve at Maria Island, where populations of the two commercially important species, rock lobster (*Jasus edwardsii*) and black-lip abalone (*Haliotis rubra*), have undergone significant change compared to adjacent fished locations (Edgar & Barrett 1999; Buxton et al. 2006). In the absence of fishing, the average size and relative abundance of rock lobsters increased significantly inside the MPA. In contrast, emergent abalone populations have undergone an unexpected decline in relative abundance inside the MPA, attributable to a decline in smaller size classes (Buxton et al. 2006). This observed decline was attributed to one of several different factors: an increase in predation mortality of small individuals as predator abundances increased in the absence of fishing; the emergence behaviour of juvenile abalone inside the MPA may have changed in response to non-lethal interaction with the increased number and size of predators inside the MPA; intraspecific competition for resources (food and space) as the average size of adult emergent abalone increased; or from inter-specific competition with sea urchins.

Although factors such as competitive interactions between abalone and sea urchins (Shepherd 1973a; Andrew & Underwood 1992; Karpov et al 2001) and predation of juvenile abalone (Rogers-Bennett & Pearse 2001; Shepherd 1998; Shepherd & Clarkson 2001; Mayfield & Branch 2000; Day & Branch 2002) have been examined, very little information exists on the mechanisms contributing to emergence behaviour. Using results from a survey of abalone populations at several sites inside the MPA and adjacent fished locations, we compare patterns of abalone size at emergence with the abundance of predators and competitors to determine the possible mechanisms leading to the observed changes in emergent abalone populations.

Methods

Site selection

The population structures of benthic invertebrates and demersal fish species were surveyed at 10 sites in Mercury Passage on Tasmania's east coast between May and July 2005. The sites surveyed were representative of those used in the long-term monitoring of the effectiveness of the no-take Maria Island Marine Reserve (MIMR) established in 1991 (Edgar & Barrett 1997). Study sites were located on medium profile rocky reefs at a depth of 5 m, were similar in exposure to prevailing weather conditions, and supported communities of large brown macroalgae and understorey algal species typical of moderately exposed coastlines in south-eastern Tasmania (Edgar 1984). Five of the sites were located inside the MPA, with a minimum separation of 0.8 km between sites, which is greater than the inter-annual movement of rock lobsters inside the MPA (Buxton et al 2006) to ensure estimates of rock lobster abundance were independent of each other. Five sites were located adjacent to the MPA where commercial and recreational rock lobster and abalone fisheries continue to operate (hereafter referred to as fished sites).

Survey techniques

Benthic invertebrates and demersal fishes were surveyed using underwater visual census techniques described by Edgar and Barrett (1997). At each site, four 50-m transects were deployed randomly along the 5 m depth contour and the abundance and size structure of rock lobsters (*Jasus edwardsii*) and emergent black-lip abalone (*Haliotis rubra*) were recorded by divers searching a 1 m strip parallel to each transect. Within the same search area the abundance of sea urchins (*Heliocidaris erythrogramma*) and crabs (*Plagusia chabrus*) were also recorded. Abalone size at emergence estimates were obtained by two divers searching habitat 5 m either side of the transect and restricted between the 3 m and 7 m depth contours. Emergent abalone were defined as individuals not hidden from the divers' view in deep crevices but exposed to predators, whereas cryptic individuals were hidden from the divers' view in crevices and under boulders. Estimates of cryptic abalone size structures were obtained by lifting and searching underneath small boulders (*ca*. 0.5 – 0.75 m diameter) in the area in which emergent individuals were measured. To remove observer-induced biases in

the classification of cryptic and emergent abalone, the same divers were used to survey all sites in the study. A minimum of 200 abalone (cryptic and emergent combined) were classified and measured *in situ* at each site using knife-edge calipers. To ensure that accurate estimates of size at emergence could be calculated a minimum of 75 cryptic individuals were recorded in each sample where possible.

The abundance of the dominant predatory demersal fish, including the labrids *Pictilabrus laticlavius*, *Pseudolabrus psittaculus*, *Notolabrus fucicola*, *N. tetricus*, *Dotalabrus aurntiacus*; the monocanthids *Acanthaluteres vittiger*, *Meuschenia australis*, *Meuschenia freycineti*; the latrid *Latridopsis forsteri*; and the cheilodactylids *Cheilodactylus nigripes* and *C. spectabilis*, were recorded by divers surveying a 5 m wide strip immediately above the reef along both sides of each transect. Due to the low abundances of several species, data were pooled into a group (hereafter called demersal fish) for comparison in statistical tests.

Statistical analysis

The relationship between abalone shell length and the state of emergence (cryptic or emergent) was determined using logistic regression as the technique is most suited when the dependent variable (emergence) is binomially distributed as a function of the parameters of the independent variable (Hosmer & Lemeshow 2000). Abalone size at emergence was estimated using a probit regression model that assumes that the percent response (emergence) is related to the log of the independent variable (shell length) as a cumulative normal distribution (Finney 1971). The percentage of abalone emergent can be estimated using the log of shell lengths from the cumulative normal distribution with the most reliable comparisons between sites made using the fiftieth percentile.

Relationships between abalone size at emergence and the abundance of putative abalone predators and competitors were defined using a multiple step-wise (addition) regression and fitted using ordinary least squares. The most parsimonious model was reached when the lowest Akaike Information Criterion (AIC) value and highest adjusted R^2 values were obtained and a normal Q-Q plot of residuals followed a 45° line. All analyses were undertaken using the SAS statistical software package (© v. 9.1 SAS Institute).

Abalone size frequency distributions were compared between MPA and fished populations using a randomisation procedure with the Kolmogorov-Smirnov test statistic (D). Data were pooled across sites within each treatment and the test statistic calculated (D_{obs}). Size frequency data from the two distributions were then pooled and randomly reallocated back to each original distribution and the test statistic recalculated (D_{rand}). The procedure was repeated 1000 times and the test of significant difference between the two distributions made by comparing the value of the D_{obs} to the distribution of D_{rand} values obtained by the randomisation procedure. Significant

differences were identified when less than 25 of the D_{rand} values obtained from the randomisation procedure exceeded the value of D_{obs} following the procedure described by Haddon (2001).

To ensure meaningful comparisons between the population structures could be made, without the bias of absolute abundances, the size frequency distribution from the MPA population was rescaled to match the scale of the fished population. Rescaling was achieved by calculating a common slope and intercept of the linear relationship between frequency and shell length, between 10 mm and 104 mm shell lengths (smallest individuals sampled and the mid point between the two size at emergence estimates respectively), for each population. The common slope and intercept were then used to calculate the rescaled relative frequencies of each size class (2 mm bins) of the MPA population. The rescaled MPA population was then plotted against the unchanged fished population to allow relative comparisons between the population structures to be made.

Results

Patterns in abalone size at emergence and population size structure

Estimates of abalone size at emergence (SAE) varied considerably at both MPA and fished locations (Figure 47, Table 10), but was consistently larger inside the MPA. When the data from sites within each treatment were pooled, abalone SAE in the MPA was significantly greater than at adjacent fished sites (117.8 mm and 87.6 mm respectively, $p < 0.001$).

The size frequency distributions of abalone populations from inside the MPA were significantly different from those in adjacent fished locations ($D_{obs} = 0.389$, $p < 0.0001$), with abalone larger than 140 mm accounting for the greatest difference in the size frequency distributions (Figure 48). In the MPA a smaller fraction of the population was between the size at emergence and the minimum legal size of 136 mm compared to the fished sites (16% and 55% respectively). In contrast, the proportion of the population above the minimum legally exploitable size was much greater in the MPA than at fished sites (55% and 18% respectively). Despite the observed differences between emergent individuals, the proportion of each population remaining cryptic was similar (27% fished and 29% MPA).

When the size frequency distribution of the MPA population was rescaled relative to the fished population, to remove biases in absolute abundance, there was no evidence that predation mortality had significantly reduced the proportion of abalone below the size at emergence estimate inside the MPA (Figure 49). Instead, the relative differences between the rescaled frequency distributions indicated the fished and MPA populations where similar in structure up to the minimum legally exploitable size of 136 mm ($D_{obs} = 0.039$, $p = 0.43$), after which there was a clear effect of protection on abalone size structure ($D_{obs} = 0.389$, $p < 0.0001$).

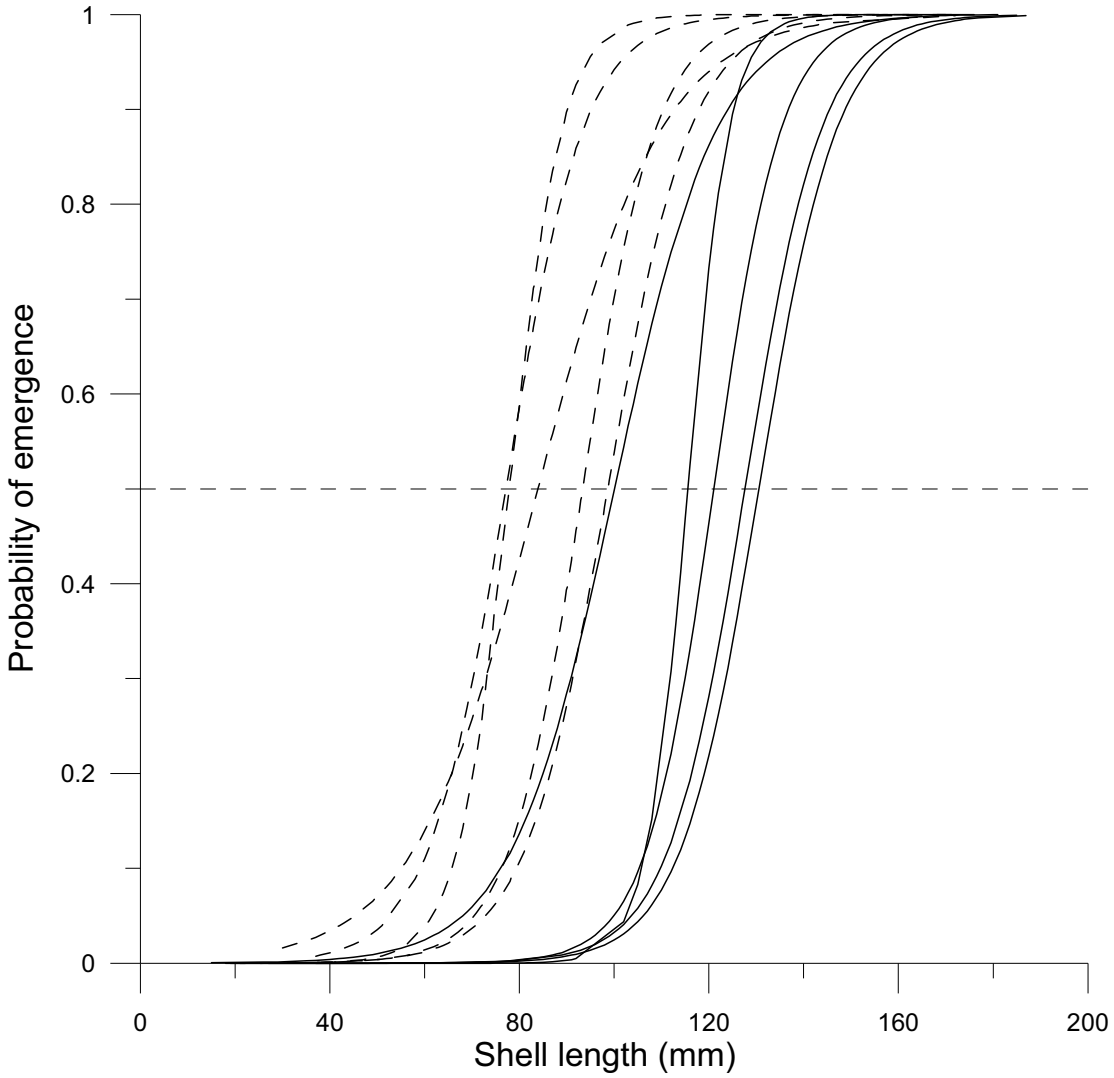

Figure 47 **Size at emergence (SAE) of abalone at ten sites within Mercury Passage. Individual plots represent the probability of abalone being emergent at any given shell length (mm) with solid lines representing size at emergence estimates for sites inside the MPA, dashed lines representing abalone populations at adjacent sites open to fishing. Horizontal dashed line indicates a 0.5 probability of abalone being emergent at the corresponding shell length.**

Table 10 **Summary of abalone size at emergence estimates (±95% CI) at five sites open to fishing and five sites inside the Maria Island a no-take MPA. Size at emergence estimates represent the shell length when there is a probability of 0.5 that an individual will be emergent. Estimates of size at emergence for MPA and fished populations were calculated on data pooled across sites within each treatment.**

Site	Size at emergence (mm)	% of sample < SAE	N
Fished			
1	77.2 (72.6-81.1)	15.7	185
2	77.9 (73.1-82.1)	21.6	194
3	93.4 (91.4-95.2)	29.3	259
4	83.9 (80.2-87.1)	25.7	222
5	98.7 (94.6-102.5)	45.9	211
Pooled	87.6 (86.8-88.4)	27.6	1071
MPA			
1	121.1 (118.5-124.3)	27.1	259
2	127.6 (124.4-130.4)	24.6	183
3	130.6 (128.5-132.4)	39.4	259
4	115.6 (110.9-119.0)	29.4	238
5	100.1 (96.8-102.9)	30.8	234
Pooled	117.8 (117.1-118.5)	30.2	1173

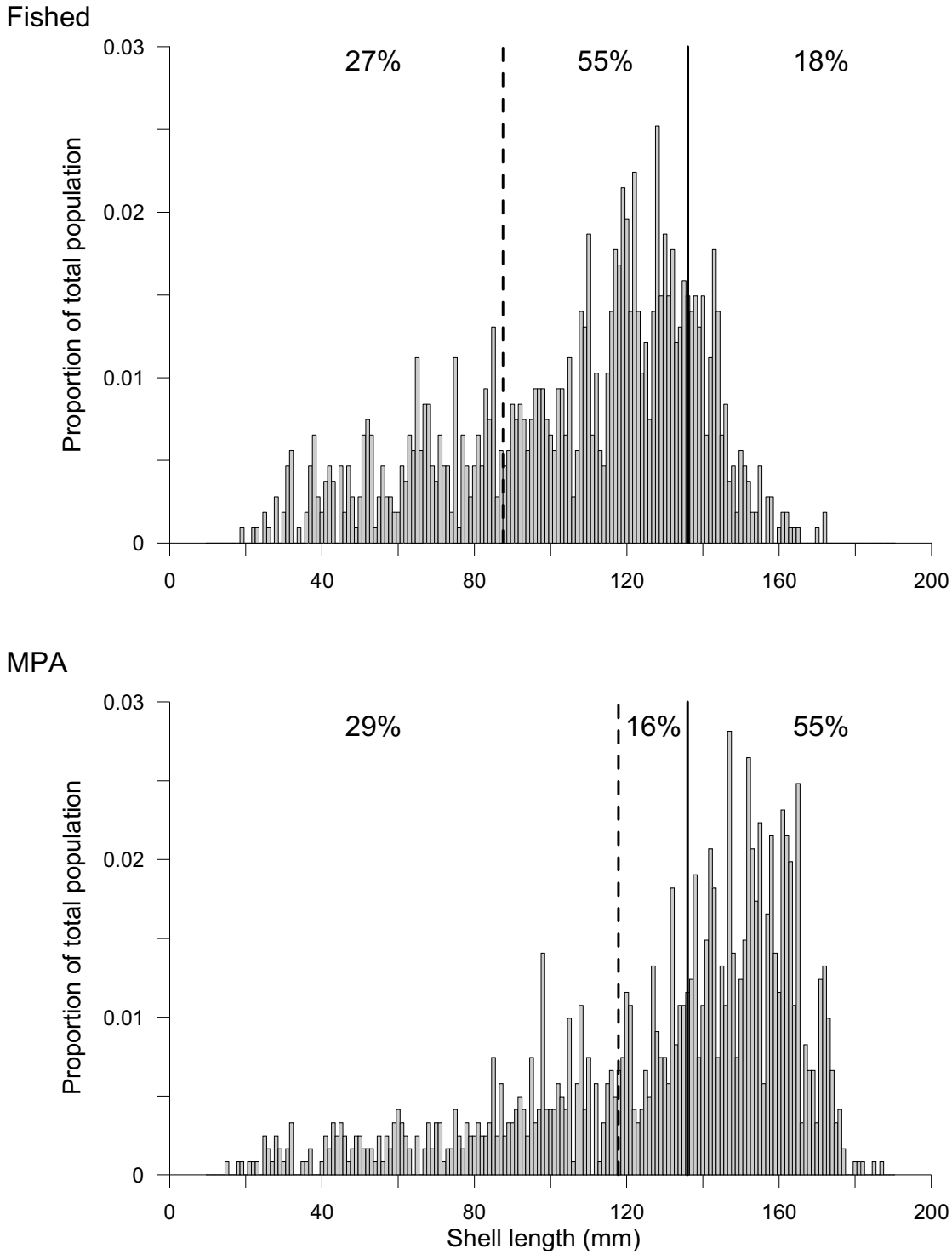

Figure 48 **Size frequency distributions of abalone in populations at fished sites within Mercury Passage and inside the MPA. Distributions were constructed by pooling size data across five sites within each treatment (N = 1071 fished, N = 1209 MPA). The distributions of abalone sizes were significantly different (D_{obs} = 0.389, p < 0.0001), with the maximum divergence between distributions at shell lengths of 140 mm. Dashed vertical lines represent size at emergence estimates for data pooled across sites within each treatment. Solid vertical lines represent the minimum legally exploitable size for abalone in the region (136 mm).**

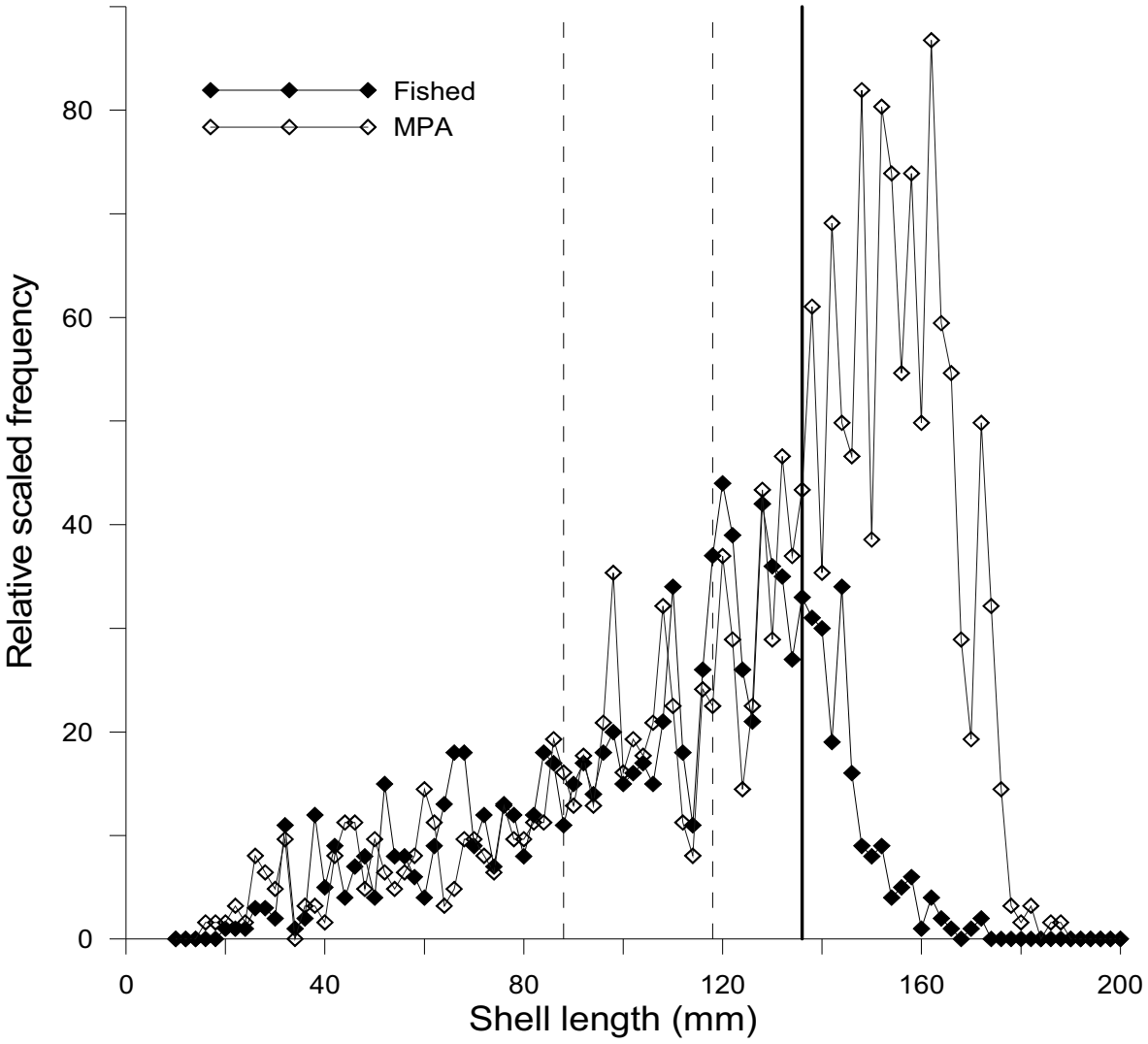

Figure 49 **Comparison of relative scaled frequency distributions for abalone populations at fished sites within Mercury Passage and the Maria Island MPA. The distribution from the MPA has been rescaled, using a slope and intercept common to both distributions from the linear regression between frequency and shell length (between 10 and 104 mm shell lengths) for each population. Dashed vertical lines represent the mean size at emergence in fished and MPA populations (88 and 118 respectively) and the solid vertical line the minimum legally exploitable size (136mm).**

Relationships with predators and competitors

The most parsimonious multiple regression model explaining the patterns in abalone size at emergence included the individual terms of rock lobster abundance (*Jasus edwardsii*), mean size of rock lobsters (carapace length), and the interaction between rock lobster and sea urchin abundance (Table 11, $_{adj}R^2 = 0.73$, $F_{3, 36} = 35.77$, $p < 0.001$, AIC =303.9). The individual terms of crab (*Plagusia chabrus*), predatory demersal fish, emergent abalone, emergent abalone >140 mm, and sea urchin abundance (*Heliocidaris*

erythrogramma) were not related to abalone size at emergence and not significant components in the most parsimonious model (Figure 50).

Table 11 Summary of the most parsimonious multiple regression model explaining patterns in abalone size at emergence (dependent variable)

Coefficients	Estimate	S.E.	p
Intercept	78.42	3.37	<0.001
Rock lobster abundance	3.97	0.75	<0.001
Mean rock lobster size (mm)	0.13	0.047	<0.01
Rock lobster * Sea urchin abundance	-0.013	0.003	<0.001
Multiple R^2 = 0.75, Adjusted R^2 = 0.73, $F_{3, 36}$ = 35.77, p <0.001, AIC =303.9			

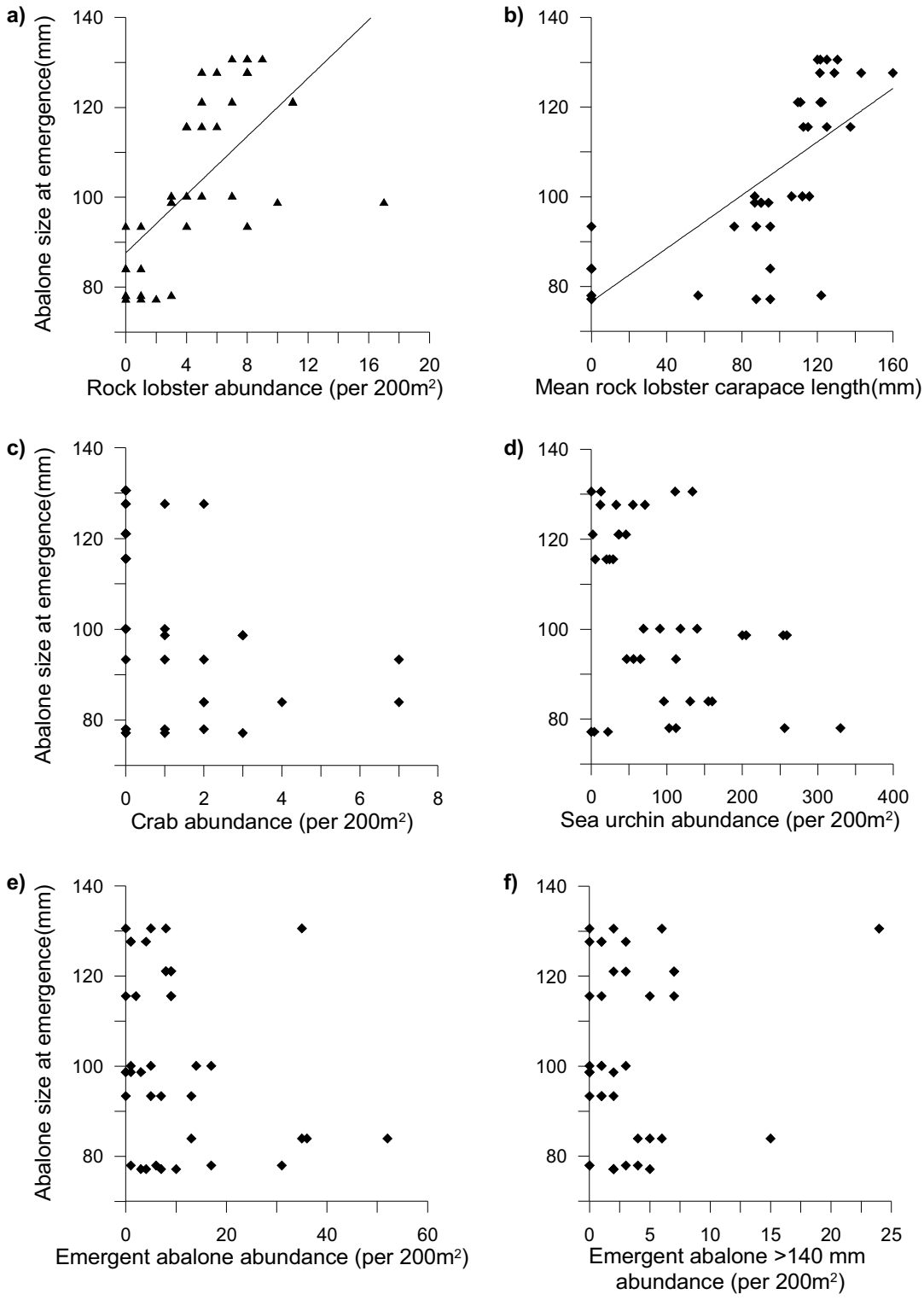

Figure 50 **Scatterplots showing the distribution of abalone size at emergence estimates in relation to, a) rock lobster abundance ($p < 0.001$, $R^2 = 0.44$), b) mean rock lobster carapace length ($p < 0.001$, $R^2 = 0.55$), c) crab abundance, d) sea urchin abundance, e) emergent abalone abundance, and f) emergent abalone >136mm abundance. Trend lines represent significant relationships between abalone size at emergence and single independent variables for fitted using ordinary least squares regression.**

Discussion

Abalone are amongst the most exploited of all temperate inshore fisheries. Although a large volume of literature on abalone biology and abalone fisheries exists, there is a paucity of information on the indirect effects of fishing on abalone populations, specifically behaviour of abalone and the stimuli responsible for emergence behaviour. Our study found significant variation across small spatial scales (10^3 m) in the size at which abalone emerge from cryptic habitat, which correlated with both the abundance of and mean size of rock lobsters (*Jasus edwardsii*). Lobsters are predators of other benthic invertebrates including sea urchins (Shears & Babcock 2002; Pederson & Johnson 2006) and juvenile abalone (Tarr et al 1996; Mayfield et al 2001) in temperate ecosystems.

In contrast the patterns in abalone size at emergence were not dependent upon the density of the most common crab, *Plagusia chabrus*, or a suite of predatory demersal fishes including the labrids *Notalabrus tetricus* and *Pictilabrus laticlavius* which are predators of juvenile abalone elsewhere in temperate Australia (Shepherd & Turner 1985; Shepherd & Clarkson 2001). This result is not surprising given the abundance of both *N. tetricus* and *P. laticlavius* have not responded to the effect of protection inside the MPA (Barrett et al 2007).

While patterns in abalone size at emergence correlate with the abundance and mean size of rock lobsters, size-specific predation of small abalone could not account for the differences in size at emergence estimates between fished sites and the MPA. For this to have occurred there would have been a distinguishable gap in the size frequency distribution immediately below the size at emergence inside the MPA. This was not the case. Our results indicate the structure and relative abundance of abalone below the minimum legally exploitable (136 mm) inside the MPA were similar to those in the adjacent fished areas. Instead, mortality appears to have acted uniformly across a wide range of size classes and reduced the absolute abundance of small abalone inside the MPA compared to the adjacent fished sites.

The clear indirect effect of lobster fishing on abalone populations was to change the size of emergence. Outside the MPA, in the presence of lower numbers and smaller sized lobsters, more than half of the animals below the minimum legal size were emergent (55%). This fraction was greatly reduced inside the MPA (16%) where individuals greater than the minimum legally exploitable size of 136 mm accounted for more than half the population compared to adjacent areas where fishing has reduced the number of exploitable individuals to less than 20% of the population.

While competitive interactions between other abalone and sea urchin species have been documented (North & Pearse 1970; Lowry & Pearse 1973; Shepherd 1973a; Tegner & Levin 1982), the effect of sea urchin (*Heliocidais erythrogramma*) abundance on abalone emergence behaviour was not evident over the scales and habitats we

surveyed. Similarly, the lack of any correlation between abalone size at emergence and the density of emergent abalone suggests that density-dependent inter and intra-specific competition does not play a major role in determining abalone emergence behaviour. However, because of the problems associated with accurately quantifying the abundance of cryptic abalone in three-dimensional substrate, we cannot rule out that emergence behaviour is linked to the abundance of cryptic abalone.

Since the abundance of rock lobsters is correlated with patterns of abalone size at emergence, and predation mortality cannot account for the differences between MPA and adjacent fished locations in isolation, how do we explain the patterns in abalone size at emergence within Mercury Passage? Although the patterns in abalone size at emergence correlated with the abundance and mean size of rock lobsters, the pattern may be the result of non-lethal interactions with rock lobsters. Cryptic abalone inside the MPA may encounter rock lobsters more frequently inside the MPA as rock lobster abundance increases and their foraging intensifies (Barrett. pers. obs). The result of the increased non-lethal interaction with rock lobsters may alter the behaviour of small abalone and delay their emergence until they reach a suitable size refuge. The non-lethal interaction may be further enhanced by intraspecific competition with the large emergent abalone during competition for space and food and delay the onset of emergence. Patterns in abalone size at emergence are likely to be the result of a complex combination of factors including predation, intra- and inter-specific competitive interactions.

While our observations apply to the Maria Island MPA, the generality of the inter-specific interaction described here has yet to be tested more broadly. While clear responses to protection by both rock lobster and abalone populations have been observed within the Maria Island MPA (Edgar and Barrett 1997; 1999, Buxton et al 2006), trends have not been as evident in three smaller MPAs in eastern Tasmania where rock lobster increases were not always associated with abalone declines. The difference in response to protection within the smaller MPAs has been attributed to the differences in area under protection (*ca*. 1000 ha within Maria Island vs. 45–60 ha in the other MPAs), lack of sufficient space to place replicate survey sites within reserves (power), prominent edge effects, higher intensity of fishing effort close to boundaries, and habitat differences (Buxton et al 2006). The variation in responses highlights the need to have a series of sufficiently large MPAs, with sufficient statistical power, to effectively assess the impact of protection on population dynamics and species interactions.

Appendix 2

Population structuring of black-lip abalone *Haliotis rubra* by the southern rock lobster *Jasus edwardsii*

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Abstract

The southern rock lobster (*Jasus edwardsii*) is a prominent invertebrate on rocky reefs in Tasmania. While *J. edwardsii* is a major predator of sea urchins, its ability to structure populations of other macro-invertebrates is not clear. Following more than a decade of protection from fishing activity, rock lobster populations inside the largest Marine Protected Area (MPA) on the east coast of Tasmania (Maria Island) have expanded to more than 20 times the biomass of adjacent areas subject to fishing. Concurrent with the increase in rock lobster biomass has been a noticeable reduction in the abundance of emergent black-lip abalone (*Haliotis rubra*) and the gradual increase in minimum emergent abalone size. These observations suggested that rock lobsters inside the MPA were having a negative effect on abalone populations. In a series of manipulative experiments, tethered abalone experienced higher mortality rates inside the MPA than those of equivalent size at fished sites, and newly emergent abalone inside the MPA were almost an order of magnitude more susceptible to predation than larger conspecifics. Approximately 50% of all mortalities inside the MPA were attributed to rock lobsters, by the presence of characteristic damage to abalone shells, compared to only 30% at fished sites. Experimental manipulations (caging) revealed the mortality of abalone was higher in the presence of rock lobsters but the effect was not size (abalone) dependent. Results from the manipulative experiments suggest that *J. edwardsii* is an important predator of *H. rubra* in eastern Tasmania and has the potential to structure abalone populations.

Key words: Reef fisheries, abalone, rock lobster, predator-prey, marine protected areas, population dynamics

Introduction

The southern rock lobster *Jasus edwardsii* is a dominant macro-invertebrate of rocky reef ecosystems in Australia and New Zealand, plays a vital role as a benthic predator (Shears & Babcock 2002, Johnson et al. 2004, Langlois et al. 2006a, Pederson & Johnson 2006) and supports lucrative recreational and commercial fisheries (ABARE 2007, Anonymous 2007). Because of their economic value, *J. edwardsii* fisheries have been exploited over many decades (Frusher 1997, Kelly et al. 2000) and therefore knowledge about the biology and ecology of the species comes from populations that are already impacted by fishing. In eastern Tasmania, exploitation has reduced the legal-sized biomass of the southern rock lobster *J. edwardsii* to 2–8% of the virgin stock (Frusher 1997), with exploited populations dominated by recent recruits (Edgar & Barrett 1999). With the advent of no-take marine protected areas (MPAs), the population density and size structure of *J. edwardsii* within MPAs was expected to revert to a population structure unaffected by fishing.

Since the declaration of four no-take MPAs in eastern Tasmania in 1991 there have been significant changes in subtidal community structure compared to those in adjacent habitats open to fishing activity (Edgar & Barrett 1999, Buxton et al. 2006). The most notable changes have been recorded in the largest MPA at Maria Island where rock lobster (*Jasus edwardsii*) biomass has increased to more than 20 times that of adjacent fished habitats with the population inside the MPA now dominated by large adults that are effectively absent in the neighbouring fishery.

While dramatic changes in rock lobster biomass and size structure have been observed, a similar effect for another heavily exploited species, black-lip abalone (*Haliotis rubra*), has not been apparent. Over the same time period abalone biomass inside the MPA declined, with significant decreases in abundance and changes in size structure compared to adjacent fished locations (Buxton et al. 2006). Several mechanisms explaining the declines in abalone biomass inside the MPA were suggested (Buxton et al. 2006) with predation by rock lobsters considered to be the most likely given that the observed declines in abalone biomass were strongly correlated with the increase in rock lobster biomass. Subsequent studies indicated that much of the observed decline in newly emergent abalone could be accounted for by spatial variation in size at emergence and not predation mortality in isolation (Pederson et al. 2008). Although the patterns of abalone size at emergence were suggested to be the result of a combination of factors, including predation mortality and competitive interactions, the contribution of any one factor could not be determined.

A series of manipulative experiments were conducted to determine the importance of predation on the structuring of abalone populations, particularly the component attributable to rock lobsters. These experiments were designed to estimate the relative

difference in abalone mortality inside the MPA and at adjacent sites where rock lobsters were fished, the size-specific nature of interactions between rock lobsters and abalone, and abalone mortality rates directly attributed to rock lobsters.

Methods

Site selection

Manipulative experiments were conducted at four sites on Tasmania's east coast (Figure 51). The sites were located in rocky reef habitats that have been used previously to assess the effectiveness of marine protected areas (Edgar & Barrett 1997, 1999) and to describe patterns of abalone size at emergence in relation to the abundance of predators and competitors (Pederson et al. 2008). Two sites were located inside the no-take Maria Island Marine Protected Area (hereafter referred to as MPA sites) and two sites in adjacent areas open to commercial and recreational fisheries for rock lobster, black-lip abalone and a range of demersal fish species (hereafter referred to as fished sites). The four sites were similar in topography, exposure to prevailing weather and supported similar biological communities except for the abundance of and size structure of abalone and putative abalone predators, mainly rock lobsters.

Rock lobster abundance surveys

Rock lobster abundance was assessed at each site prior to the manipulative experiments using the underwater visual census techniques described by Edgar and Barrett (1997). Four replicate transects were assessed at each site by a diver searching the habitat in a 1 m wide strip parallel to a 50 m weighted line and recording the abundance of rock lobsters. Transects were laid parallel to the shore, without overlap, and between the 5 m and 7 m depth contours. Rock lobsters were captured where possible and carapace length measured to the nearest millimetre using knife-edge callipers. Where rock lobsters could not be captured without significant damage, a visual estimate was made and lengths recorded to the nearest 5 mm size class. The same diver (HP) conducted all surveys during the study to remove any biases associated with using multiple observers.

Manipulative experiments

Estimates of relative predation intensity were quantified at two sites inside the MPA where rock lobsters were in high abundance, and at two adjacent sites where rock lobster abundance has been reduced by fishing activity. At each site three 20 m replicated transects were placed at random and without overlap, on rocky reef between the 5 m and 7 m depth contours. Eight abalone from each of three size classes (

Table 12), namely those below the size at emergence, above size at emergence but below the minimum legal catch size, and those above the minimum legal catch size (>136 mm), were tethered to each weighted transect line. Individual abalone were tethered using a plastic tag (Leader Tags, Victoria, Australia) inserted into one of the respiratory pores on the margin of the shell and connected to the transect line using a

600 mm long stainless steel cable (0.6 mm diameter) secured using a stainless steel crimp sleeve.

Abalone used in the tethering experiments were collected from the habitats surrounding the transect lines at each site and sorted into the above size classes using the estimates for size at emergence at each site determined by Pederson et al. (2008). Tethered abalone were attached at random distances along each transect but placed in areas to ensure that they could not seek refuge in crevices or move under boulders. Restricting abalone from seeking refuge ensured that all size classes where exposed to predators to allow relative comparisons between sites while overcoming small-scale differences between habitats which could bias results.

Experiments were conducted over a 28-day period at each site during February and March 2006. Estimates of abalone survival were recorded 7, 14 and 28 days post tethering with the proportion of shells displaying signs of lethal and non-lethal interaction with rock lobsters recorded (see below). Mortalities recorded during the assessments at 7 and 14 days post tethering were not replaced.

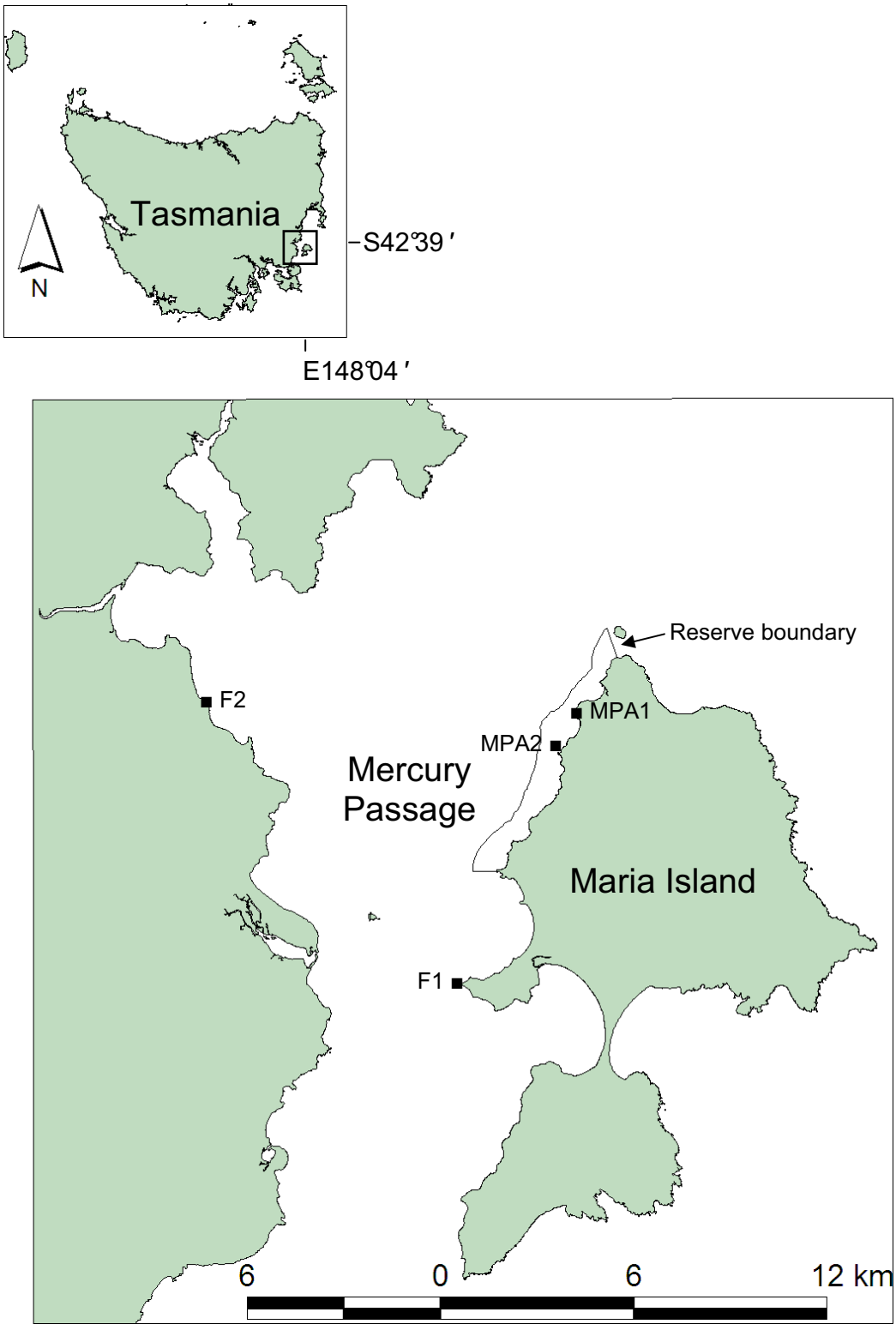


Figure 51 **Location of sites where experiments were conducted to assess size-specific predation mortality of abalone. Two sites were located inside the no-take Marine Island Marine Protected Area (MPA1, MPA2) and two sites in adjacent habitats open to fishing (F1, F2).**

Table 12 **Summary of abalone size at emergence estimates (±95% CI) at five sites open to fishing and five sites inside the Maria Island a no-take MPA. Size at emergence estimates represent the shell length when there is a probability of 0.5 that an individual will be emergent. Estimates of size at emergence for MPA and fished populations were calculated on data pooled across sites within each treatment.**

Site	Size at emergence (mm)	% of sample < SAE	N
Fished			
1	77.2 (72.6-81.1)	15.7	185
2	77.9 (73.1-82.1)	21.6	194
3	93.4 (91.4-95.2)	29.3	259
4	83.9 (80.2-87.1)	25.7	222
5	98.7 (94.6-102.5)	45.9	211
Pooled	87.6 (86.8-88.4)	27.6	1071
MPA			
1	121.1 (118.5-124.3)	27.1	259
2	127.6 (124.4-130.4)	24.6	183
3	130.6 (128.5-132.4)	39.4	259
4	115.6 (110.9-119.0)	29.4	238
5	100.1 (96.8-102.9)	30.8	234
Pooled	117.8 (117.1-118.5)	30.2	1173

Size-specific predation

To determine the size-specific predation of abalone by rock lobsters, a series of experiments was undertaken in an aquarium facility where experimental variables could be manipulated and the behaviour of rock lobsters continuously monitored using an infra-red video system (Mills et al. 2005). Rock lobsters and abalone were collected from sites in south-east Tasmania and transported back to the aquarium facility at the Tasmanian Aquaculture and Fisheries Institute. Rock lobsters and abalone were allowed 72 hours to acclimatise to storage conditions before being used in experimental trials. While abalone were fed on a diet of commercially available macroalgal pellets, rock lobsters were starved prior to use in trials to increase the likelihood of predation during each trial.

Three size classes of abalone were exposed to three separate rock lobster size classes during the series of experiments. Abalone <88 mm (pre-emergent), 89–135 mm (newly emergent) and those larger than the minimum legal catch size of 136 mm (post emergent) were used in all treatment and control tanks. Four individual fibreglass tanks measuring 2.5 m x 2.5 m x 1 m, each with a separate water supply, were used in the four replicate trials. Five abalone from each of the three size classes were placed

into each of the tanks and allowed to attach to purpose-built habitats made from sculptured aerated concrete (ca. 0.3 m x 0.3 m x 0.6 m). Three tanks were assigned three rock lobsters of a specific size class. The small size class consisted of rock lobsters < 110 mm carapace length (CL), the medium size class of rock lobsters between 111 mm and 140 mm CL and the large size class of rock lobsters >141 mm CL. Due to the lack of available tanks for replication in each trial, a single replicate of each treatment was represented in each of seven separate but consecutive trials.

Individual trials were run for a period of five days to allow four nights of rock lobster activity to be recorded by an individual infra-red camera placed in each tank covering ca. 75% of the tank area but 100% of the shelter available to abalone. Survival and mortality estimates were recorded each morning and the video footage observed to identify the method of predation. Mortalities were removed from tanks each morning and were not replaced during individual trials. Upon completion of each trial rock lobsters and abalone were returned to the wild, treatments randomly reassigned to tanks and newly acclimated abalone and rock lobsters placed in appropriate tanks.

To assess the size-specific nature of rock lobster, predation of abalone under 'natural' conditions a manipulative experiment was established inside the Maria Island MPA. Experimental cages similar in construction to Pederson and Johnson (2006) were placed on rocky reef habitat between the 7m and 9 m depth contours. Six replicate cages in each of two treatments and two experimental controls were used in the design. The two treatments involved cages where five abalone, from two separate size classes (newly emergent 115–135 mm and post emergent >136 mm), were allowed to seek refuge within the reef in either the presence or absence of rock lobsters ('+' and '-' rock lobster treatments respectively). Note that predation mortality of pre-emergent abalone could not be estimated effectively due to the variability in re-sighting individuals which were cryptic and hidden from the divers. Two rock lobsters larger than 140 mm (carapace length) were placed into each of the six '+ rock lobster' replicate cages and allowed to seek refuge in suitable dens. Rock lobsters were prevented from leaving the '+ rock lobster treatment', or entering the '– rock lobster treatment' by the addition of a roof to the top of the cage. To assess the effect of cages on abalone mortality, estimates from partial cages, which were similar in construction to the treatment cages but had openings in two of the walls and no roof, were compared with mortality estimates from '+ rock lobster' treatment cages. The openings in the walls of partial cages allowed rock lobsters and other predators to gain access to experimental abalone. The flexible netting used in the construction of the cages prevented abalone from climbing the walls and escaping via the openings (H. Pederson pers. obs). Six replicate plots, where no cage was erected but a similar sized patch of reef delineated using weighted line, served as experimental controls for the partial cage treatment. Five abalone from each of the two size classes were placed into each replicate control plot.

Before cages and control plots were stocked with experimental abalone, the habitat was thoroughly searched and resident abalone removed. Experimental abalone, collected from a neighbouring part of the same reef, were then placed into crevices previously occupied by resident individuals to ensure experimental animals would find suitable refuge. Abalone mortality was assessed once a week for eight consecutive weeks between April and May 2006. Abalone mortalities were recorded and removed from cages and control plots but not replaced.

Abalone shell survey

A survey to quantify the potential size range of abalone vulnerable to predation by rock lobsters was conducted at the four experimental sites in May 2006. Discarded abalone shells were sampled in rocky reef habitats at each site, recording the length of each shell and the presence of 'chip' marks, similar to those on predated abalone in the aquarium trial. Due to unequal sample sizes, and the scarcity of shells at some of the sites, data from the two fished sites were pooled with the resulting size frequency distribution compared to the distribution of pooled data from the MPA sites.

Statistical analysis

Relative differences in predation intensity of tethered abalone were assessed using logistic modelling in which a generalised linear model (GLM) was applied to the binomially distributed response variable (mortality) using a log-link function (Hosmer & Lemeshow 2000; Quinn & Keough 2002). In addition the logistic models were able to estimate the relative likelihood of abalone mortality in unfished and fished areas. Fully saturated logistic models were constructed using the four main effect terms (MPA, site, abalone size and transect) and all possible interactions. Model terms were removed from the fully saturated model via the step-wise process until a significant decrease in model fit (χ^2) was observed resulting in the most parsimonious model.

Differences in average rock lobster abundance at experimental sites was examined using one-way ANOVA with separate models constructed for small (<100 mm CL), medium (111–140 mm CL) and large rock lobsters (>141 mm CL). For all ANOVAs, including those used to assess predation mortality in caging experiments (see below), the relationship between standard deviation and means of treatment groups was used to determine the appropriate transformation to stabilise variances, and transformed data were checked for both normality (using normal probability plots) and homoscedasticity. Results are expressed in terms of the untransformed variable, Y (Draper & Smith 1981). We compared means of treatment groups after ANOVA using the Ryan-Gabriel-Elliot-Welsh procedure ('Ryan's test') for multiple range tests which controls for type I error (Day & Quinn 1989).

Size frequency distributions of empty abalone shells were compared between the MPA and fished sites using a randomisation procedure with the Kolmogorov-Smirnov test statistic (D). Data were pooled across sites within each treatment and the

test statistic calculated (D_{obs}). Size frequency data from the two distributions were then pooled and randomly reallocated back to each original distribution and the test statistic recalculated (D_{rand}). The procedure was repeated 1000 times and the test of significant difference between the two distributions made by comparing the D_{obs} values to the distribution of D_{rand} values obtained by the randomisation procedure. Significant differences were identified when <25 of the D_{rand} values exceeded the D_{obs} value (see Haddon 2001).

Estimates of predation mortality attributed to rock lobsters in the caging experiment were assessed using both a two-way ANOVA and a logistic model. The ANOVA included fixed main effects of rock lobsters (with two levels: presence and absence), and abalone (two levels: emergent and post emergent), and compared abalone mortality among treatments. The logistic model compared the likelihood of abalone mortality in the different treatments, and data were pooled across replicates of the same treatment to gain adequate samples sizes for the procedure. Data collected from the caging experiment used to construct the logistic model followed a binomial distribution with the response variable, mortality, recorded as a proportion of the total test sample. The statistical package SAS© was used for all analyses.

Results

Predation mortality indices

Tethered abalone exposed to predators experienced varying levels of predation mortality between the MPA and fished sites (Figure 52). The minimum adequate logistic model explaining the pattern in abalone mortality contained the main effect terms, all of the two way interactions and the three-way interaction of protection*site*transect (χ^2 = 8.95, *df* = 2, p = 0.0114). Accurate interpretation of the results from the minimum adequate model was not possible and therefore the data were separated by the 'protection' factor and analysed independently to estimate the relative differences in size-specific effects.

Abalone size was the only term contributing to a significant model fit from data collected inside the MPA (χ^2 = 7.25, *df* = 2, p = 0.0267). Newly emergent abalone (131–135 mm at MPA1 and 116–135 mm at MPA2 respectively) inside the MPA were almost 10 times more likely to experience predation compared to post-emergent adults in the same habitat (>136 mm; χ^2 = 4.30, *df* = 1, p = 0.0381). Pre-emergent abalone, that are normally hidden from predators, experienced similar levels of predation compared to post emergent abalone (>136 mm).

The pattern at fished sites was different from that observed inside the MPA with the two-way interaction of site*transect significant in model fit (χ^2 = 10.75, *df* = 2, p = 0.005). The significant interaction term precluded further analysis of the data. However, from the average mortality estimates it appears that there was no difference in the relative likelihood of mortality between the three size classes. The likelihood of mortality for

newly emergent abalone varied between the two fished sites. In contrast, there was no difference in the likelihood of mortality between sites for pre or post emergent abalone.

Examination of empty shells following the tethering experiment indicated that the number of abalone mortalities directly attributed to rock lobsters, by the presence of 'chip' marks on the margin of shells (see below), was higher inside the MPA compared to adjacent fished sites (Figure 53). The minimum logistic model describing the patterns in rock lobster associated mortality consisted of the two-way interaction of protection*site ($\chi^2 = 4.58$, $df = 1$, $p = 0.032$) and the individual main effect terms. The significant interaction term indicated that the predation of abalone by rock lobsters was spatially variable at a scale of the distance between sites. The number of mortalities that could be attributed to rock lobsters was higher at sites inside the MPA compared to fished site 1 but not significantly greater than the number of mortalities at fished site 2 (Figure 53).

Results from the three separate ANOVA models found no significant difference between sites in the average abundance of small rock lobsters (<110 mm CL; $F_{3,15} = 1.47$, $p = 0.2720$), significant differences between sites for medium sized rock lobsters (111–140 mm CL; $F_{3,15} = 22.00$, $p < 0.0001$), and significant differences between sites for large rock lobsters (>141 mm CL; $F_{3,15} = 7.32$, $p < 0.005$). Multiple range comparison tests indicated medium sized rock lobsters were in significantly higher abundance at both MPA sites compared to both fished sites and were significantly more abundant at MPA1 compared to MPA2. Large rock lobsters were significantly more abundant at MPA1 compared to either fished site but in similar abundance to MPA2 (Figure 54). The abundance of large rock lobsters was not significantly different between the fished sites and MPA2.

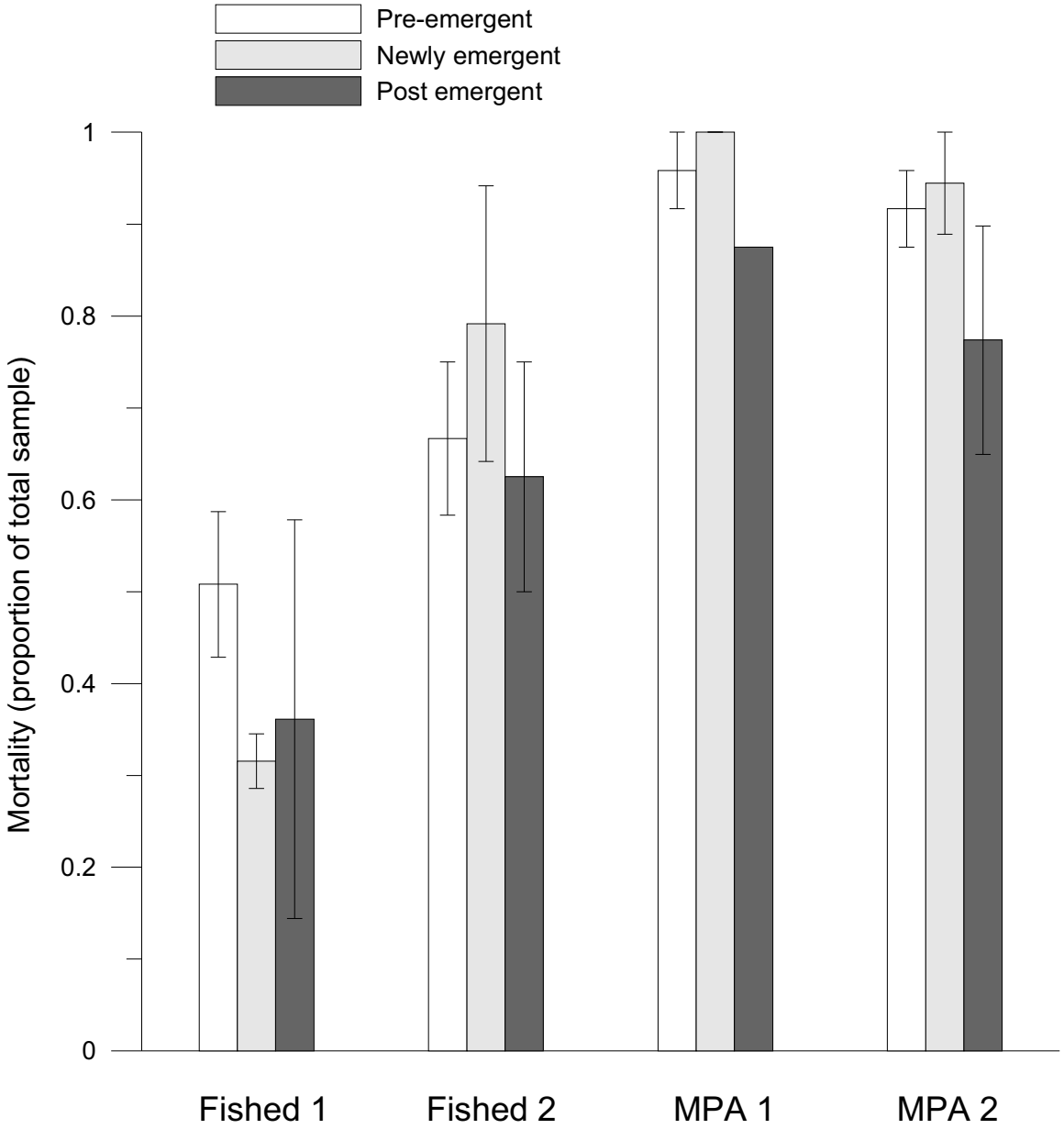


Figure 52 ***Haliotis rubra*. Estimates of relative predation mortality, represented as the proportion of mortalities in the total sample of tethered abalone at four sites over 28 days. Data series are mean estimates (± SE) from three replicate transects at each site with *n* = 8 individuals in each size class on each transect. Note that data series where the estimates of mortality were equal between replicates an error estimate (SE) is not displayed.**

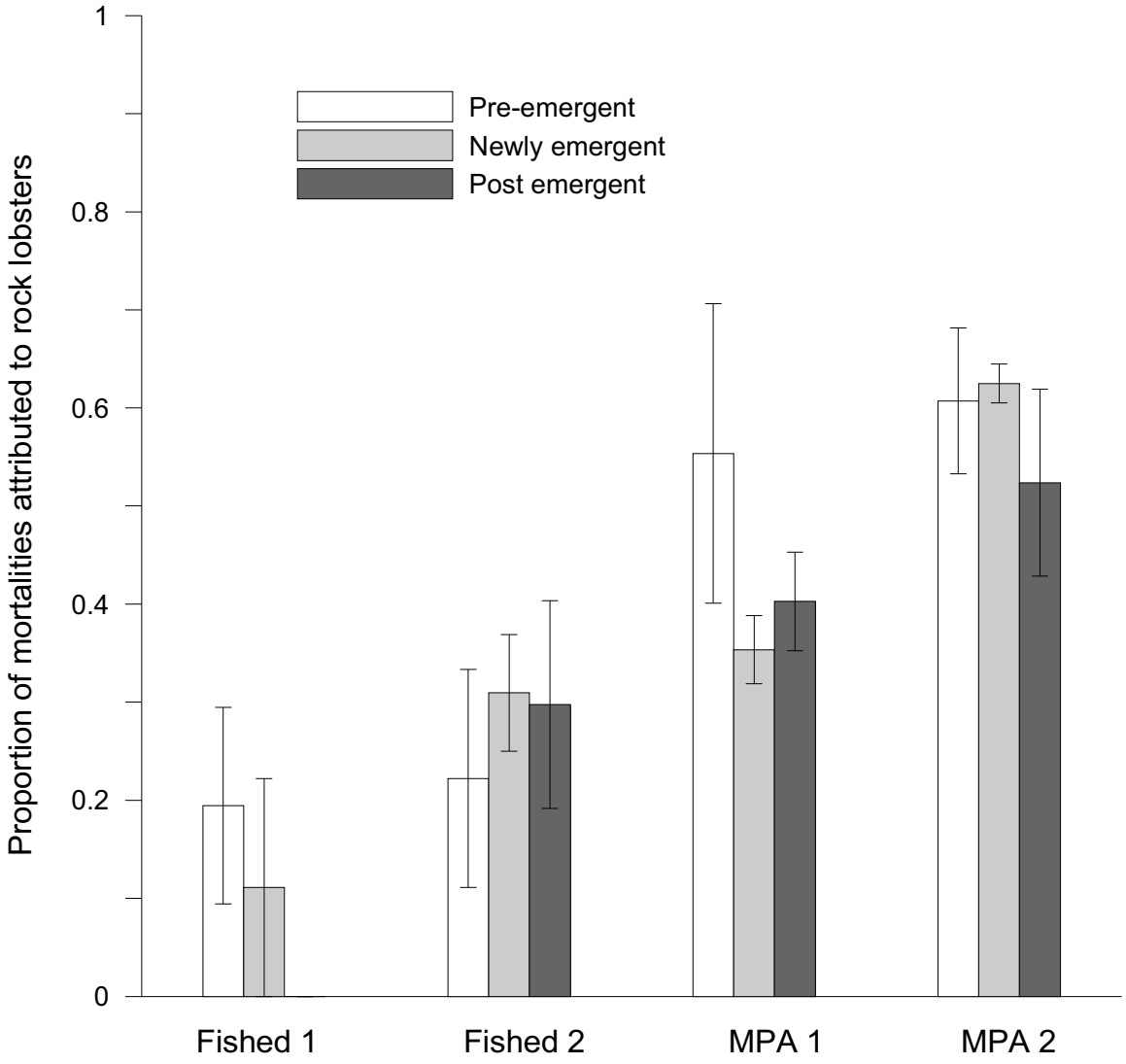
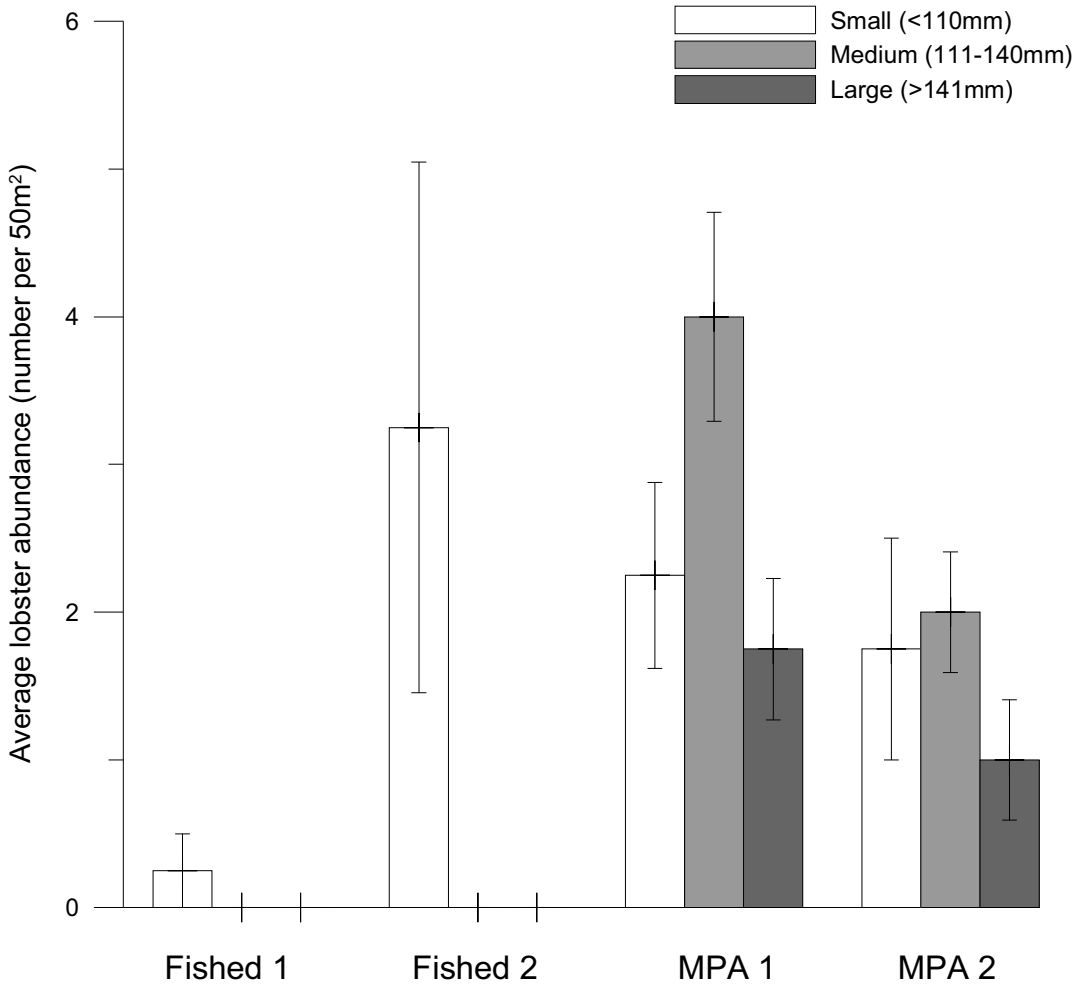


Figure 53 ***Haliotis rubra*. Proportion of tethered abalone mortalities showing distinctive rock lobster predation marks (bars). Data series are mean estimates (± SE) from three replicate transects at each site with *n* = 8 individuals in each size class on each transect.**

Surveys of the four experimental sites, where tethering experiments were undertaken, found a wide size range of empty abalone shells displaying signs of interactions (both lethal and non-lethal) with rock lobsters (Figure 55). The size frequency distribution of shells at fished sites were significantly different from those within the MPA (D_{obs} = 0.519, p <0.0001) with the maximum separation between the distributions at 123 mm.



Small	**A**	**A**	**A**	**A**
Medium	**C**	**C**	**A**	**B**
Large	**B**	**B**	**A**	**A-B**

Figure 54 ***Jasus edwardsii*. Average rock lobster abundances in each of the three size classes (small <110 mm, medium 111-140 mm and large >141 mm) at each of the four sites prior to experimental manipulations being performed. Average abundance and standard error were calculated from four replicate (50 x 1m) transects at each site with differences in average abundance assessed using 1-way ANOVA constructed for each rock lobster size class and Ryan-Gabriel-Elliot-Welsh (REGW) multiple comparison test. Sites assigned different REGW grouping were significantly different with alpha adjusted to control for Type I error ($\alpha_{adj} = 0.009$).**

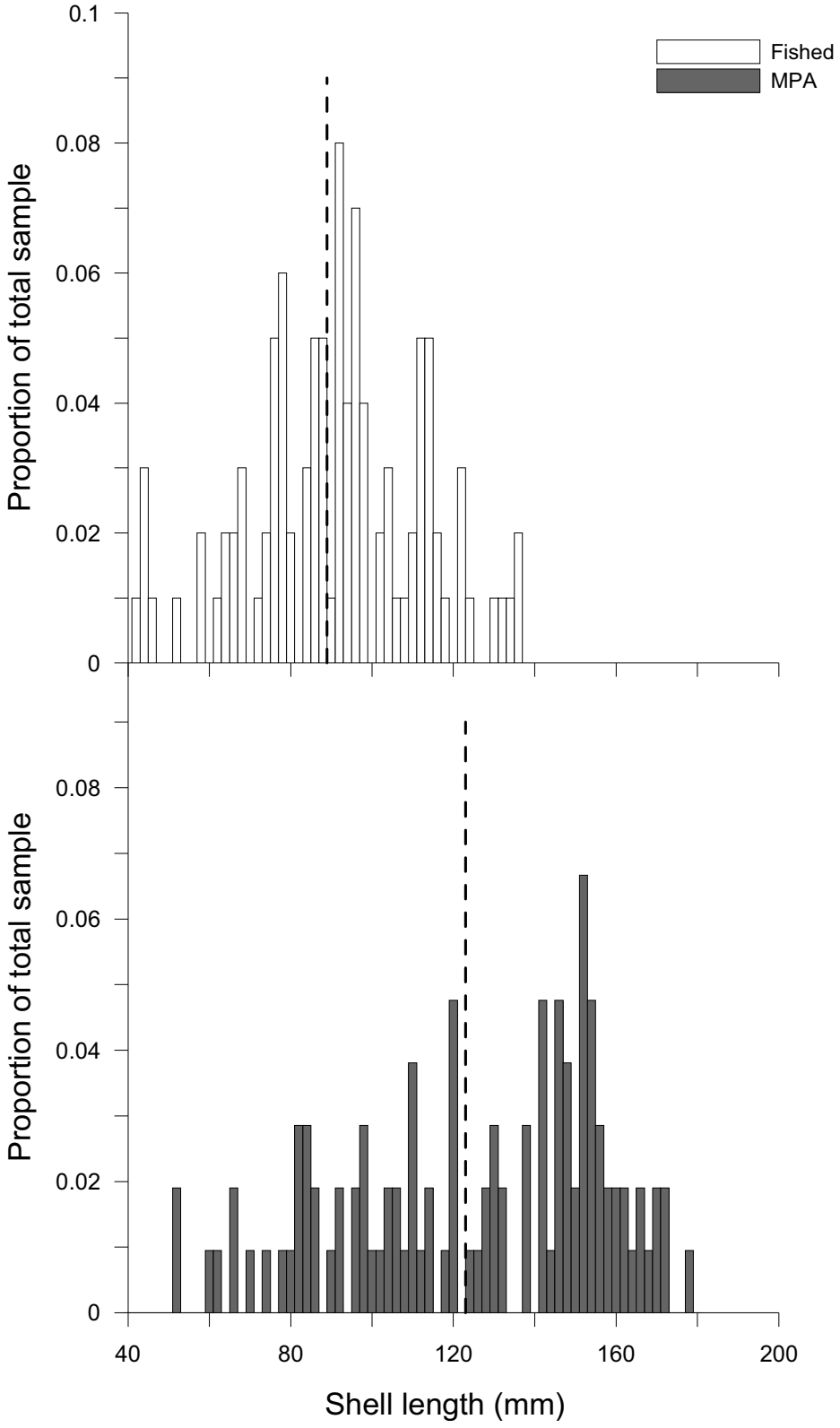


Figure 55 ***Haliotis rubra*. Size frequency distributions of empty abalone shells with characteristic markings indicating interaction with rock lobsters. Data were pooled across replicate sites (n = 2) within each treatment. Size frequency distributions were significantly different at 123 mm shell length (D_{obs} = 0.519, p <0.0001). Dashed vertical lines represent size at emergence estimates from Pederson et al. (2008) averaged across sites within each treatment.**

Size-specific predation

Direct observations of rock lobster behaviour during the aquarium experiment suggested the preferred method of attacking abalone involved rock lobsters breaking small pieces of shell from the margin of abalone shells before applying leverage using the first thoracic appendage. Predation events involving this technique were observed by several large rock lobsters but not by the medium sized (111–140 mm) or small (<110 mm) rock lobsters. Lethal interactions were only observed to occur between large rock lobsters (>141 mm) and pre-emergent abalone (<88 mm). Interactions between rock lobsters and post-emergent abalone were observed in infra-red footage but only resulted in non-lethal impacts. The result of many non-lethal interactions were characterised by the rock lobster chipping the margin of abalone shells but not successfully consuming abalone. Due to the extremely low number of mortality events observed during the aquarium experiment, a statistical analysis of the results could not be performed (Table 13). However, results from the aquarium experiments indicate that markings left on the abalone shells can be used as an indicator of either lethal or non-lethal interactions with rock lobsters (Figure 56).

Table 13 **Average number of abalone mortalities, with standard errors (parentheses), in three size classes, exposed to three different size classes of rock lobsters. Averages were calculated from seven separate but consecutive trials.**

Abalone size class	Control	Small lobster (<110 mm)	Medium lobster (111–140 mm)	Large lobster (>141 mm)
Pre-emergent (<88 mm)	0	0	0.143 (0.143)	0.429 (0.202)
Newly emergent (89–135 mm)	0	0	0	0.143 (0.143)
Post emergent (>136 mm)	0	0	0	0

Figure 56 ***Haliotis rubra*. Abalone shell (72 mm shell length) displaying damage (A) characteristic of lethal interaction with large rock lobsters (>141 mm) during aquarium trials**

Predation mortality attributable to rock lobsters

Comparison of the cage controls with the un-manipulated controls (plots) found no significant difference in abalone mortality using either ANOVA ($F_{3,20} = 0.99$, p = 0.4162) or the logistic model (treatment*size $\chi^2 = 0.1$, $df = 1$, p = 0.98; size $\chi^2 = 3.46$, $df = 1$, p = 0.07; treatment $\chi^2 = 0.62$, $df = 1$, p = 0.43). This result indicates there was no detectable effect of the cage on abalone mortality and therefore the un-manipulated control plots were excluded from further analyses.

Comparison of abalone mortality rates using the ANOVA model found a significant treatment effect ($F_{2,30} = 6.49$, p = 0.005), with abalone mortality rates significantly higher in the presence of rock lobsters (Figure 57). Newly emergent abalone experienced similar levels of predation mortality to post emergent abalone in all treatments (size $F_{1,30} = 0.43$, p = 0.52). Abalone mortality rates were not significantly different in the presence of rock lobsters at experimental densities inside cages (0.11 individuals m^{-2}) or at background densities recorded at the site (0.16 individuals m^{-2}) in partial cages where rock lobsters were allowed free access through holes in the side

of cages. This result indicates that there was no detectable effect of restricting rock lobsters inside the cages on subsequent abalone mortality.

Results from the logistic model were similar to those of the ANOVA, with a significant difference between the three treatments (two experimental treatments and the partial cage $\chi^2 = 28.23$, $df = 2$, $p < 0.001$) and no significant difference in the likelihood of mortality based on abalone size ($\chi^2 = 0.77$, $df = 1$, $p = 0.3818$). However, when multiple comparisons between treatments were made, the likelihood of abalone mortality (both sizes) was 5.1×10^{12} times higher in the presence of rock lobsters (+lobster cages) compared to when rock lobsters were absent ($\chi^2 = 28.15$, $df = 1$, $p < 0.001$), 1.3×10^{11} times more likely when rock lobsters were allowed free access to partial cages (i.e. at background density) compared to when rock lobsters were excluded ($\chi^2 = 14.77$, $df = 1$, $p < 0.001$), but no difference in the likelihood of mortality when rock lobsters where either contained inside cages (+ lobster treatment) or allowed free access to cages (partial cages: $\chi^2 = 3.44$, $df = 1$, $p = 0.0635$).

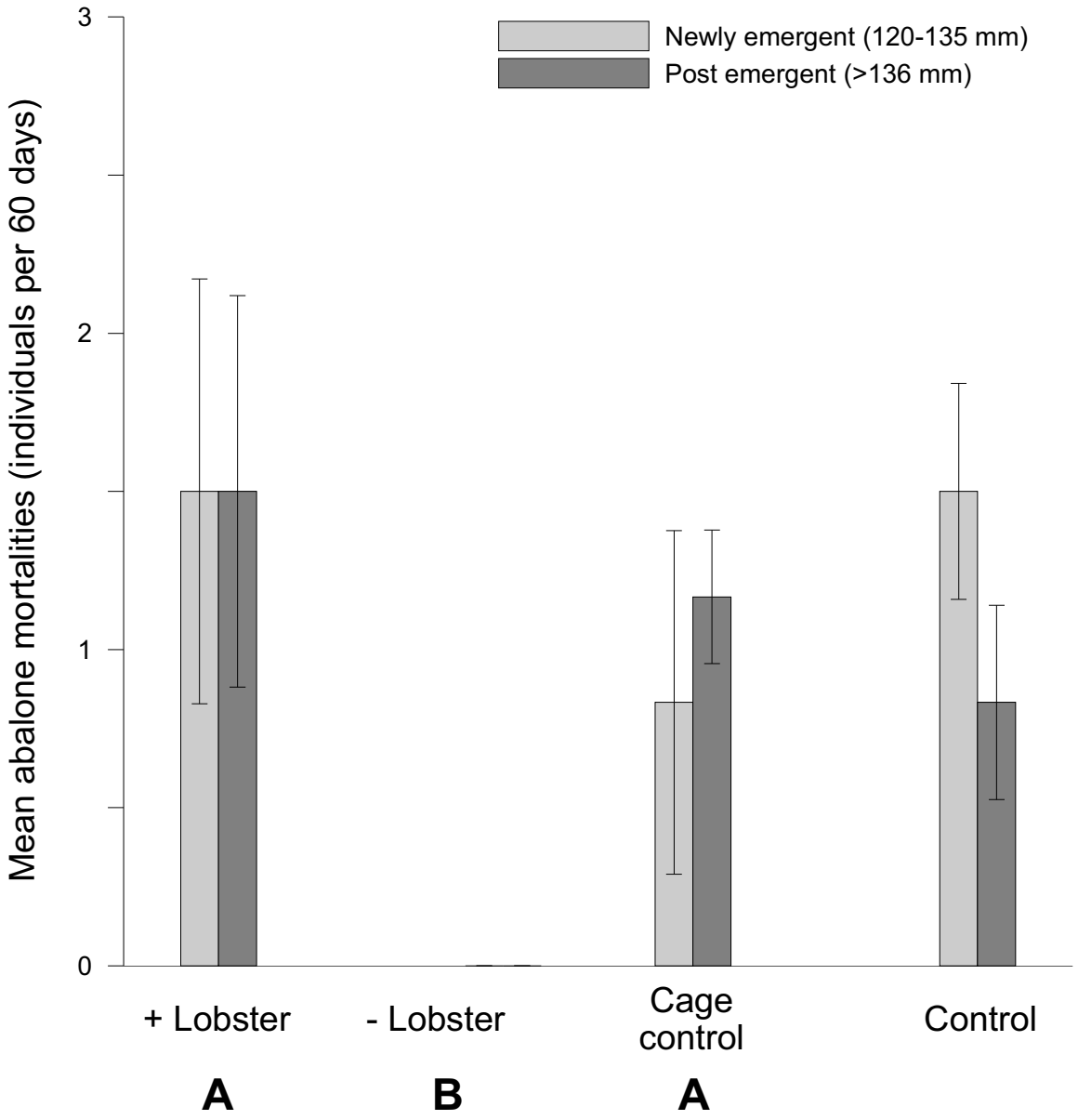


Figure 57 ***Haliotis rubra*. Mean estimates of abalone mortality over a 60 day period in the presence and absence or rock lobsters (+ Lobster, - Lobster respectively), cage controls (partial cages allowing rock lobsters and other predators access) and un-manipulated control plots allowing access by all predators. Mean estimates (± SE) were gained from six replicate treatment plots (full cages, partial cages or un-manipulated plots) with five replicate abalone in each size class in each replicate plot. Labels below series represent results from univariate ANOVA and Ryan-Einot-Gabriel-Welsch (REGW) multiple range comparison tests comparing mean abalone mortality in each treatment. Treatments assigned different REGW grouping were significantly different from each other with alpha adjusted to control for Type I error in multiple comparisons ($\alpha_{adj} = 0.017$).**

Discussion

Importance of rock lobsters

Rock lobsters are known to prey on a variety of benthic invertebrates and in some instances attack prey, leaving characteristic markings or remains (Tegner & Levin 1983; James & Tong 1998; Shears & Babcock 2002; Pederson & Johnson 2006). Rock lobsters in our aquarium trial attacked abalone in a specific way leaving identifiable marks on the marginal edge of the shell (Figure 56). These characteristic marks allowed the proportion of abalone mortalities directly attributable to rock lobsters during the tethering experiment to be calculated. Results from the tethering experiment indicated that abalone mortality was directly proportional to rock lobster abundance. Although the estimates of predation directly attributable to rock lobsters were conservative, the estimates indicated that rock lobsters contributed to a large proportion of mortalities. The remaining mortalities were attributed to a range of other predators whose identity remains unknown.

Unlike previous experiments examining the relative importance of both rock lobsters and predatory demersal fish as benthic predators (Pederson & Johnson 2006), treatments to test the effect of predatory demersal fish on abalone mortality were not conducted in this study. This decision was based on previous work where no clear relationships between supra-benthic fish abundance and either abalone abundance or size at emergence were observed at the same study sites (Pederson et al. 2008). However, the experimental design allows for the effect of predators other than rock lobsters to be estimated by comparing abalone mortality in rock lobster inclusion cages (+ rock lobster treatment) with those of the partial cages. Mortality of newly and post emergent abalone was not significantly different between the rock lobster inclusion treatment and partial cages, indicating that rock lobsters contribute to the majority of mortalities, with other predators contributing to very few mortalities. The combination of results from the manipulative experiments and surveys show that *Jasus edwardsii* is an important predator of *Haliotis rubra* and that the likelihood of mortality is related to the abundance and size of rock lobsters.

Predation intensity and rate

While tethering experiments are considered to be ineffective at estimating predation mortality rates due to potential artefacts associated with the tethering process (Peterson & Black 1994), they give a clear indication of the relative differences in predation intensity between sites and as such have been widely applied (McClanahan & Muthiga 1989; Sala & Zabala 1996; Shears & Babcock 2002; Pederson & Johnson 2006). Results from this study indicated that size-specific predation intensity was spatially variable at the scale of the distance between sites (10^3 m) and linked to the abundance of large rock lobsters. The results demonstrate that when abalone, regardless of size, are unable to seek refuge in preferred habitat, they experience high levels of mortality over short time periods when exposed to rock lobsters.

Results from the caging experiment were more reliable in estimating predation morality rates as abalone were able to establish their own position on the substrate, including locations hidden from predators which helps to reduce the likelihood of predation. Tethered abalone of similar size may not be able to select suitable attachment surfaces and suffer from higher levels of predation. Results from the caging experiment estimated annual predation mortality rates of abalone to be *ca.* 2.03 individuals m^{-2} $year^{-1}$. The rate of natural mortality, excluding predation, was lower still, with no mortalities recorded in cages where all predators including rock lobsters were excluded. These results suggest that abalone experience lower rates of natural mortality when rock lobsters are in low abundance but experience significantly higher mortality rates when rock lobster abundance is elevated. Results from a similar experiment conducted at the same site by Pederson and Johnson (2006) found the common sea urchin (*Heliocidaris erythrogramma*) to experience low levels of natural mortality and similar level of predation mortality directly attributable to rock lobsters (1.99 and 3.08 individuals m^{-2} $year^{-1}$). This result suggests that sea urchins and abalone are consumed in equal proportions under field conditions.

Size-specific predation

Unlike other prey items where size plays a role in determining the susceptibility to predation by lobsters (Pollock 1979; Tegner & Levin 1983; Robles et al. 1990; James & Tong 1998; Mayfield et al. 2001; Langlois et al. 2006a; Pederson & Johnson 2006), the physical size of abalone did not have an impact on the likelihood of predation in the current study. The results of the tethering experiment showed that behaviour was an important factor determining the susceptibility of abalone to predation. When pre-emergent abalone, which would normally be cryptic, were tethered and unable to seek refuge from predators, they experienced similar rates of mortality as their larger conspecifics. Therefore, the size at which abalone emerge from crypsis appears to be a major factor determining their susceptibility to predation mortality and may explain the patterns of abalone size at emergence previously described by Pederson et al (2008).

Although very few mortalities were recorded during the aquarium experiment, abalone were only consumed by the largest size class of rock lobsters (>141 mm CL), of which, only pre-emergent abalone (<88 mm) suffered lethal interactions. However, shell damage was observed on newly emergent (89–135 mm) and post emergent abalone (>136 mm) as a result of non-lethal interaction with large rock lobsters. The survey of empty shells at the four experimental sites found marks on abalone shells indicative of interactions with rock lobsters across a much broader range of size classes. Although the source of the mortality could not be unequivocally identified, the presence of the characteristic marks indicated that rock lobsters interact, both lethally and non-lethally, with a broad range of abalone sizes. The range of shell sizes was also broader at sites inside the MPA, where rock lobster abundance and average size were elevated, confirming that rock lobster size plays a role in abalone mortality.

Results from this study showed that rock lobsters are important predators of abalone of Tasmanian reefs, and consistent with other studies which illustrate the importance of molluscs in rock lobster diets (Jernakoff et al. 1993; Kelly 1999; Mayfield et al 2000a; Mayfield et al 2001). The experimental data reinforces the patterns observed, but not tested, in related observational studies of ecosystem changes associated with MPAs (Edgar & Barrett 1999; Buxton et al 2006). Removal of rock lobsters by fishing has a series of consequences for broader ecosystem function that need to be taken into account by fisheries and conservation management. The current stock rebuilding management strategy which has clear economic and ecological benefits including the suppression of sea urchin populations (Johnson et al 2004; Johnson et al 2005), is likely to have a synergistic effect on the Tasmanian abalone fishery currently worth in excess of AU$150 million per annum.

Appendix 3
Diver questionnaire

1. Name
2. Contact address/phone number
3. Did you keep a diary or logbook of abalone fishing?
4. What years were you actively involved in commercial abalone diving?
   Start year / Stop year
5. How old were you when you started?
6. What was your background before you started?
   a. What prompted you to start diving?
   b. Were your family involved in the fishing industry?
   c. Where did you grow up (if raised in Tasmania)?
   d. How did you first become aware of the abalone fishery?
   e. Did you know any other divers at the time that you started?
7. What sort of equipment did you use initially
   a. Runabout or fishing boat?
   b. Tow vehicle?
   c. Did you use a deckhand initially?
   d. Did you work from anchored boats with long hoses?
   e. Wetsuit – how did you cope with cold?
   f. Were you taught to dive – if so, by who?
   g. Were you a diver prior to abalone fishing?
8. What were typical weights that you landed in the 1960's
   a. Did weights change (get smaller, larger) in later years?
9. Who did you mostly sell to?
10. What price range did you receive for your fish?
11. Where did you start fishing?
   a. What region?
   b. What town?
   c. What bays?
   d. What depths?
   e. Were other divers working nearby?
   f. In hindsight, was it a good place to dive for abalone?
12. Where did you get good catches when you first started?
   a. List places where you could always get good catches
   b. List places that used to be good, but stopped being so
      i. Did any of those places eventually recover?
      ii. How many years to recovery?
13. Did you notice that fishing improved any areas (i.e. started bad, but then produced fish)?

14. Did fishing make some areas worse immediately – you fished it once and it was never any good after?
15. Did you notice that some areas of "scungy" bottom increased?
16. What sort of depth range did you commonly dive to? (trying to establish if early divers fished deeper habitat than later divers)
    a. Obviously depends upon where you fished.
    b. Were you affected by decompression sickness?
17. Seasonal changes in catch rates – were East Coast catches always variable?
18. Why do East Coast catches vary, but not West Coast?

Appendix 4

Table of summarised responses to questions

question	3	4	4	5	6a	6b	6c	6d	6e	7a	7b	7c	7d	7e	7f	7g
Diver	Diary	Start year	Stop year	Age at start	why dive abalone	Family fishing?	Tasmanian?	How became aware of abalone	Knew other divers?	Runabout or Fishing boat	tow vehicle?	use deckhand?	anchored boats/long hoses?	use wetsuit?	taught to dive?	prior diver?
early 1	no	1964	1984	24	amateur diver	no	no	amateur diving	no	dinghy	not towed	no	snorkel	yes	no	yes
early 2	no	1965	1991	24	amateur diver	no	yes	amateur diving	yes	dinghy	car	no	yes	yes	yes	Spear-fishing
early 3	yes	1966	1979	21	amateur diver	no	yes	friends	yes	dinghy	various	no	yes	yes	no	yes
early 4	no	1969	1987	26	amateur diver	no										
early 5	no	1969	1991	23	Victorian ab diver	no	no	amateur diving	yes	runabout	jeep	yes	yes	yes	no	yes
early 6	yes	1965	1986	19	amateur diver	no	yes	amateur diving	yes	shore-based		no		no	no	yes
early 7	no	1970	1976	26	friends	no	yes	friends	yes	fishing boat		no	yes	yes	no	yes
early 8	no	1965	1982	35	chance	no	no	friends	yes	fishing boat		yes	yes	yes	yes	no
early 9	no	1963	1964	21	amateur diver	no	no	amateur diving	no	shore-based		no	no	no	no	yes
early 10	no	1963	1983	19	amateur diver	no	no	amateur diving	yes	shore-based		no	no	no	no	yes

question	3	4	4	5	6a	6b	6c	6d	6e	7a	7b	7c	7d	7e	7f	7g
Diver	Diary	Start year	Stop year	Age at start	why dive abalone	Family fishing?	Tasmanian?	How became aware of abalone	Knew other divers?	Runabout or Fishing boat	tow vehicle?	Use deckhand?	Anchored boats/long hoses?	Use wetsuit?	Taught to dive?	Prior diver?
early 11	yes	1959	1980	28	amateur diver	no	no	Through amateur diving	no	shore-based		no		yes	no	yes
early 12	yes	1965		17	work	no	yes	friends	no	fishing boat		no	yes	yes	no	no
early 13	no	1958	1987	18	fishing	yes	yes	fishing industry	no	shore-based		no		no	no	Spear-fishing
early 14	yes	1969	1984		amateur diver	no	no	Through amateur diving	no	runabout	not towed	no	yes	yes	no	Spear-fishing
early 15	no	1964	1978	24	chance	no	no	News-paper	no	fishing boat		no	yes	yes	no	no
early 16	yes	1966	1988	17	amateur diver	no	no	friends	yes	fishing boat		no	snorkel	yes	no	Spear-fishing
middle 1	no	1975	2002	17	fishing	yes	yes	fishing industry	yes	runabout	not towed	yes	yes	yes	no	snorkel
middle 2	no	1978	1997	25	fishing	yes	yes	fishing industry	yes	runabout	Toyota	yes	no	yes	no	yes
middle 3	no	1975	1989	22	fishing	no	no	friends	yes	runabout	Toyota	yes	no	yes	no	yes
middle 4	no	1973	1995	26	friends	no	no	friends	yes	fishing boat	yes	yes		no	no	
middle 5	no	1976	1994	20	fishing	no	yes	chance	no	runabout	Landrover	no	yes	yes	no	no

question	3	4	4	5	6a	6b	6c	6d	6e	7a	7b	7c	7d	7e	7f	7g
Diver	Diary	Start year	Stop year	Age at start	dive why abalone	Family fishing?	Tasmanian?	How became of aware abalone fishing?	Knew other divers?	Runabout or Fishing boat	ow vehicle?	Use deckhand?	Anchored boats/long hoses?	Use wetsuit?	Taught to dive?	Prior diver?
middle 6	no	1978	1994	20	fishing	no	yes	chance	no	runabout	Landrover	no	yes	yes	no	yes
middle 7	no	1980	1996	38	fishing	no	no	chance	yes	runabout	Toyota	yes	no	yes	yes	yes
current 1	no	1993		27	fishing	no		fishing industry	yes	runabout	Toyota	yes	no	yes	no	yes
current 2	no	2000		25	fishing	no	no	chance	yes	dinghy		yes	no	yes	no	
current 3	no	1994		30	fishing	yes	yes	fishing industry	yes	runabout		yes	no		no	
current 4	yes	1986		28	chance	no	no	friends	yes	runabout	Toyota	yes	no	dry-suit	no	yes
current 5	no	1994		35	fishing	yes	no	fishing industry	yes	runabout	Toyota	yes	no	yes	no	yes
current 6	no	1988		34	fishing	no	yes	fishing industry	yes	runabout	Toyota	yes	no	yes	no	yes
current 7	no	2003		33	fishing	no	yes	fishing industry	yes	dinghy		yes	no	yes	no	yes
current 8	no	1998		24	fishing	yes	yes	fishing industry	yes							
current 9	no	1992		32	fishing	no	yes	fishing industry	yes	runabout	Toyota	yes	no	yes	no	yes
current 10	no	1998		43	fishing	no	yes	fishing industry	yes	runabout	Toyota	yes	no	yes	no	yes

question	8	8a	9	10	11	12a	12b	12b(i)	12b(ii)	13	14	15	16a	16b	17	18
Diver	typical weights	weights change?	processor?	price?	where did you start fishing?	places always good?	places good but got worse	places that recovered	years to recovery	places that improved	immediate effect	increase of scungy bottom?	depth range fished?	affected by DCS?	East Coast catches	why no variability in
early 1	600	smaller	Dover Fisheri	6d/lb	Dover	Actaeons				Block 22	yes	yes	<40 feet	no	yes	
early 2	300-400		Safcol, Planet	6d/lb	South	Dover	Kelly's Rocks, Partridge Is			no	yes	yes	<40 feet	air emb-olism	yes - too much weed	swell keeps weed cover down
early 3	200	no	many	10d-/lb	Bruny	Marion Bay		Monu-ment Bay, Hellfire Bluff	10 years	Munros		yes	shallow	no	yes	swell keeps weed cover down
early 4					East Coast	Bicheno	Bicheno			no	no	no	shallow	no	yes - too much weed	swell keeps weed cover down
early 5	300-400		Safcol		East Coast	Dough-boys, Merricks, George Rocks	W & N sides Maraud Is, Ansons, Gardens			no	no	no	all depths	no	yes	

early 6	200	bigger	SPC	6d/lb	south east	Gulch, Seymour, Temples towe etc	McLean Bay reefs			no	yes	yes	shallow	yes	yes - abs go under rocks	less cryptic habitat
question	8	8a	9	10	11	12a	12b	12b(i)	12b(ii)	13	14	15	16a	16b	17	18
Diver	typical weights	weights change?	processor ?	price?	where did you start fishing?	places always good?	places good but got worse	places that recovered	years to recovery	places that improved	immediate effect	increase of scungy bottom?	depth range fished?	affected by DCS?	East Coast catches	why no variabilit y in
early 7	250	no	Blue waters	40c-/lb	East Coast	Seymour, Hughes	McLean Bay reefs, Friendly Beaches	never to former extent		no	yes	no	45-50 feet	no	yes	
early 8	300-400		SPC	1s/lb	Storm Bay	Wedge Bay	Frederick Henry Bay		long time		yes		<60 feet	no	yes	
early 9	200-300		SPC	6d/lb	East Coast	Gulch, Rice Pebble, Cod Rock							20-30 feet	yes		
early 10	200-350	smaller	various	7d/lb	Storm Bay	Wedge Bay, Goat Hills, Actaeons	around Dover, Gardens		2-10 years	no	no	yes	<120 feet	no	yes-weed	swell keeps weed cover down

early 11	600	smaller	various	6d/lb	Storm Bay	Pt Arthur, Wedge, Pirates, Marion Bays	Port Arthur			no	no	yes	<100 feet	yes	yes - too much weed	swell keeps weed cover down
early 12	<500	fluctuated	various	10d-/lb	North East	North East, Storm Bay	if good always good			no	flat reefs	seasonal	<10m	no	yes - too much weed	swell keeps weed cover down
question	8	8a	9	10	11	12a	12b	12b(i)	12b(ii)	13	14	15	16a	16b	17	18
Diver	typical weights	weights change?	processor ?	price?	where did you start fishing?	places always good?	places good but got worse	places that recovered	years to recovery	places that improved	immediate effect	increase of scungy bottom?	depth range fished?	affected by DCS?	East Coast catches	why no variability in
early 13	depended on market		SPC	3d/lb	Dover	Actaeons	bays in South			no	no	no	all depths	yes		
early 14	300-400	fluctuated	Dwyers	11c-/lb	North East	George Rocks, Barway, Dough-boys	Fancy Reef, Gardens			no	yes		shallow	no	yes - abs go under rocks, weed	swell keeps weed cover down
early 15	150-180	bigger	Dover Fisheries		South		narrow bottom			no	yes	yes	30-35 feet	no	yes	waves, exposure
early 16	200	bigger												no		

middle 1	200	bigger	Victoria Canning Coy	95c-/kg	lower East Coast	Goat Hills, Vischer Island, Lagoon Bay	all places have off periods	Goat Hills	3-4 years	Southerly Bottom	yes reefs	no	<25 metres	yes	yes - abs go under rocks, weed	
middle 2	90-400	fluctuated	Boxalls	$2.10/kg	South	Actaeons				no	yes	no	shallow	yes	yes - abs go to sides of rocks, weed	
question	8	8a	9	10	11	12a	12b	12b(i)	12b(ii)	13	14	15	16a	16b	17	18
Diver	typical weights	weights change?	processor?	price?	where did you start fishing?	places always good?	places good but got worse	places that recovered	years to recovery	places that improved	immediate effect	increase of scungy bottom?	depth range fished?	affected by DCS?	East Coast catches	why no variability in
middle 3	150-200	no	Safcol		North East	Binalong Bay to George Rocks	Gardens, Binalong Bay	Gardens, Binalong		no	no	no	deeper	yes		
middle 4	200-300				West Coast	every-where	most get worse (when fished too hard)	most		no	no		<25 metres	no	yes	
middle 5	220-250	no		$1.20/kg	North East	Gardens, George Rocks				Maria Island	no		<30 feet	no	yes - weed cover	swell keeps weed down

middle 6	220-250	no		$1.20 /kg	North East	Gardens, George Rocks						yes	<30 feet	no	yes - weed cover	swell keeps weed down
middle 7	200-300	smaller			South	D'Entrecasteaux Channel, southern bays	narrow bottom			no	no	yes				

question	8	8a	9	10	11	12a	12b	12b(i)	12b(ii)	13	14	15	16a	16b	17	18
Diver	typical weights	weights change?	processor ?	price?	where did you start fishing?	places always good?	places good but got worse	places that recovered	years to recovery	places that improved	immediate effect	increase of scungy bottom?	depth range fished?	affected by DCS?	East Coast catches	why no variabilit in
current 1	300	fluctuated			North East	Gardens, George Rocks, Eddystone	Ansons, Gardens, Red Rocks, Pebbly	Gardens		no	no	yes	all depths	no	yes - weed cover	swell keeps weed down
current 2	200		various		South	Actaeons	Actaeons	yes	3-4 years	Breaks	no	yes	all depths	no		
current 3	200		various		South	Actaeons	Actaeons	yes	3-4 years	no	no	no	<20 metres	no		

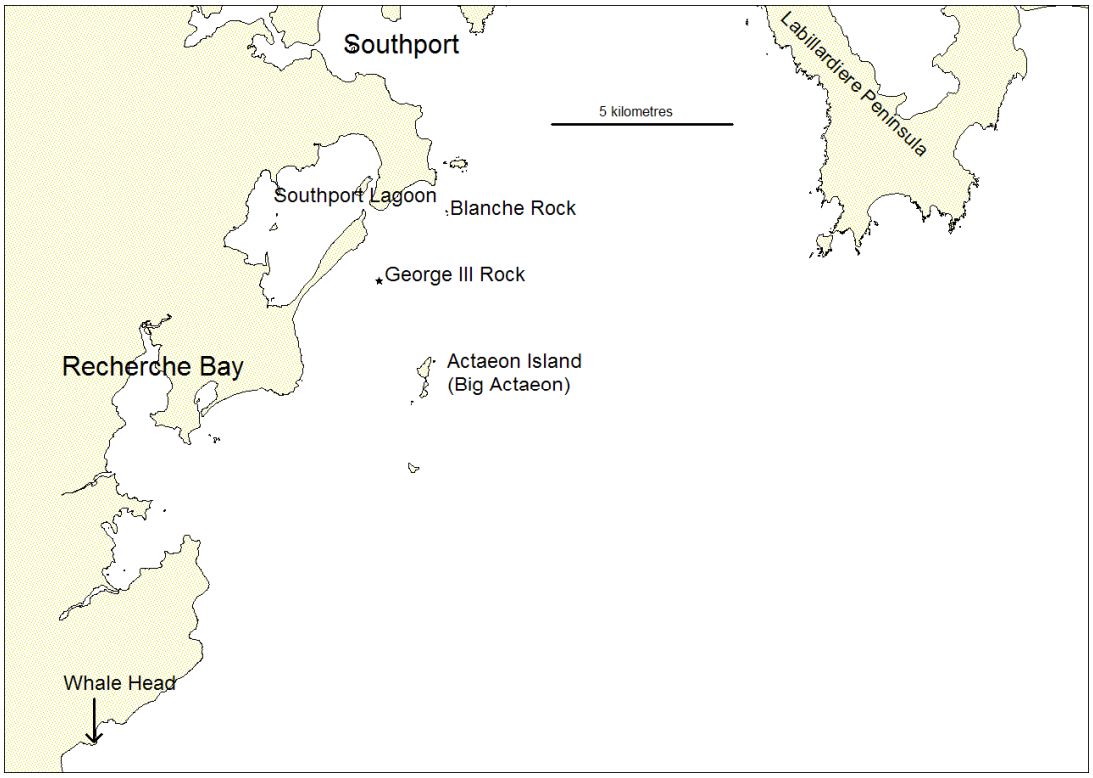
current 4			Safcol	$9-$14-/kg	North East	Gardens, George Rocks, Eddystone	Ansons, Gardens, Sloop			East Coast (1990's)	yes	not noticed	<20 metres	no	yes - abs go under rocks, weed	
current 5	250-350	no			North East	Seymour	Gardens, north part of Freycinet	Freycinet	Friend-ly Point, Iron-house	no	no	no	shallow mostly	no	yes - abs go under rocks, weed	
current 6			Dover Fisheries		Actaeons		Fishers Point after a storm	same	2 years	no	no	yes - seasonal	<10 metres	no	yes - too much weed	swell keeps weed cover down
question	8	8a	9	10	11	12a	12b	12b(i)	12b(ii)	13	14	15	16a	16b	17	18
Diver	typical weights	weights change?	processor?	price?	where did you start fishing?	places always good?	places good but got worse	places that recovered	years to recovery	places that improved	immediate effect	increase of scungy bottom?	depth range fished?	affected by DCS?	East Coast catches	why no variabilit in v
current 7			Ralphs		Actaeons					no	no	yes	all depths	no		
current 8					North East		Franklin Sound	many places in Franklin Sound	not recover-ed			yes	all depths	no		
current 9	250-300				Actaeons	Actaeons, Bruny	Actaeons	Actaeons	3-4 years		no	yes	all depths	no	yes	waves keep kelp down

current 10	200-300	smaller after 2000			Bicheno	Seymour	Bicheno	some parts of Bicheno	1-10 years	no	no	yes	5-10 metres	no	yes - too much weed	swell cuts weed back

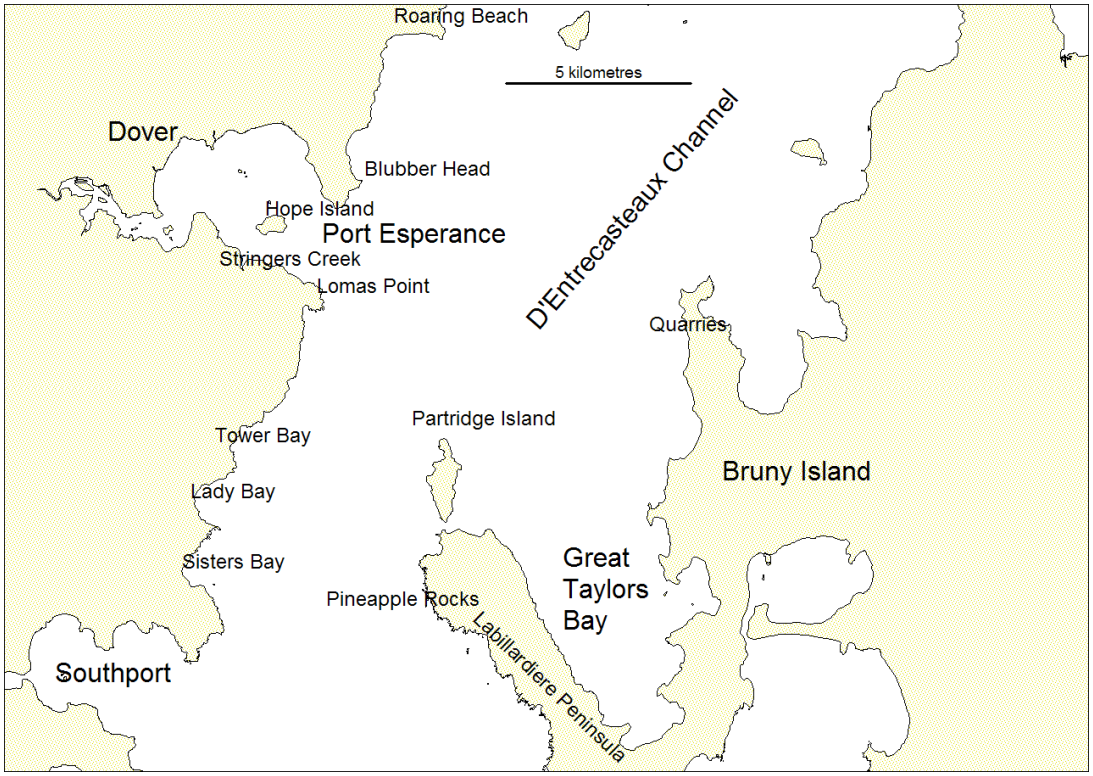
Appendix 5

Maps of the five blocks showing place-names referred to in text

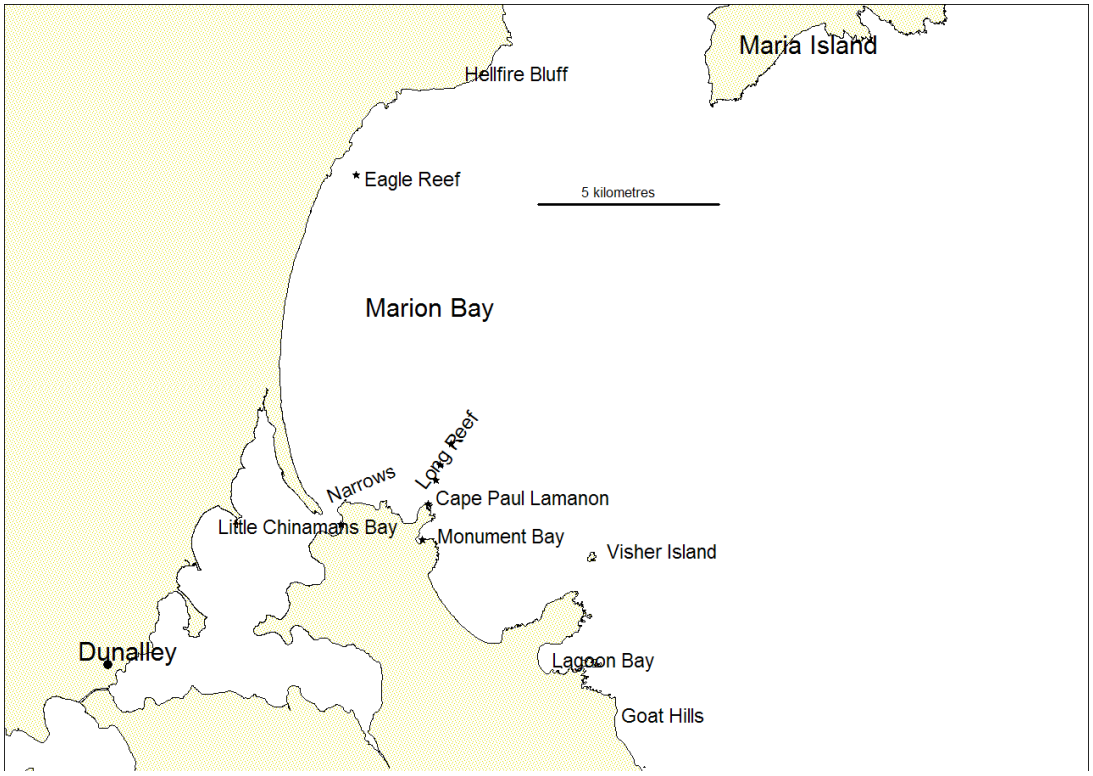
Block 13



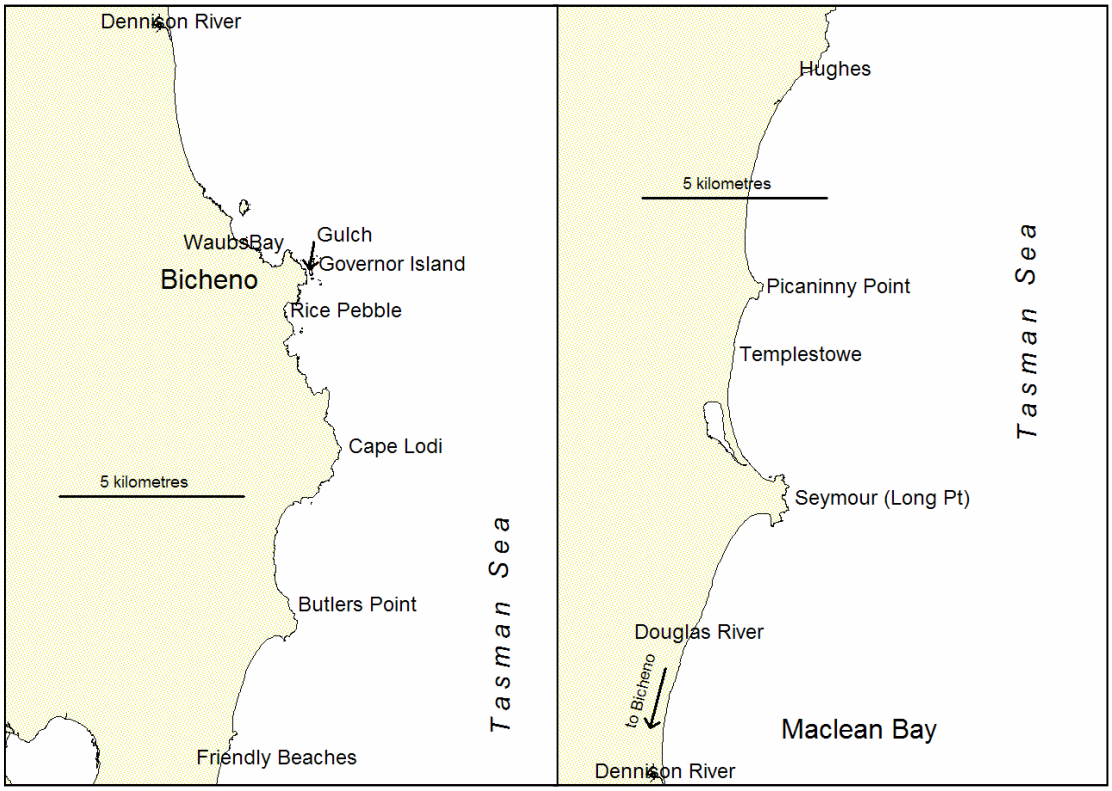
Block 14



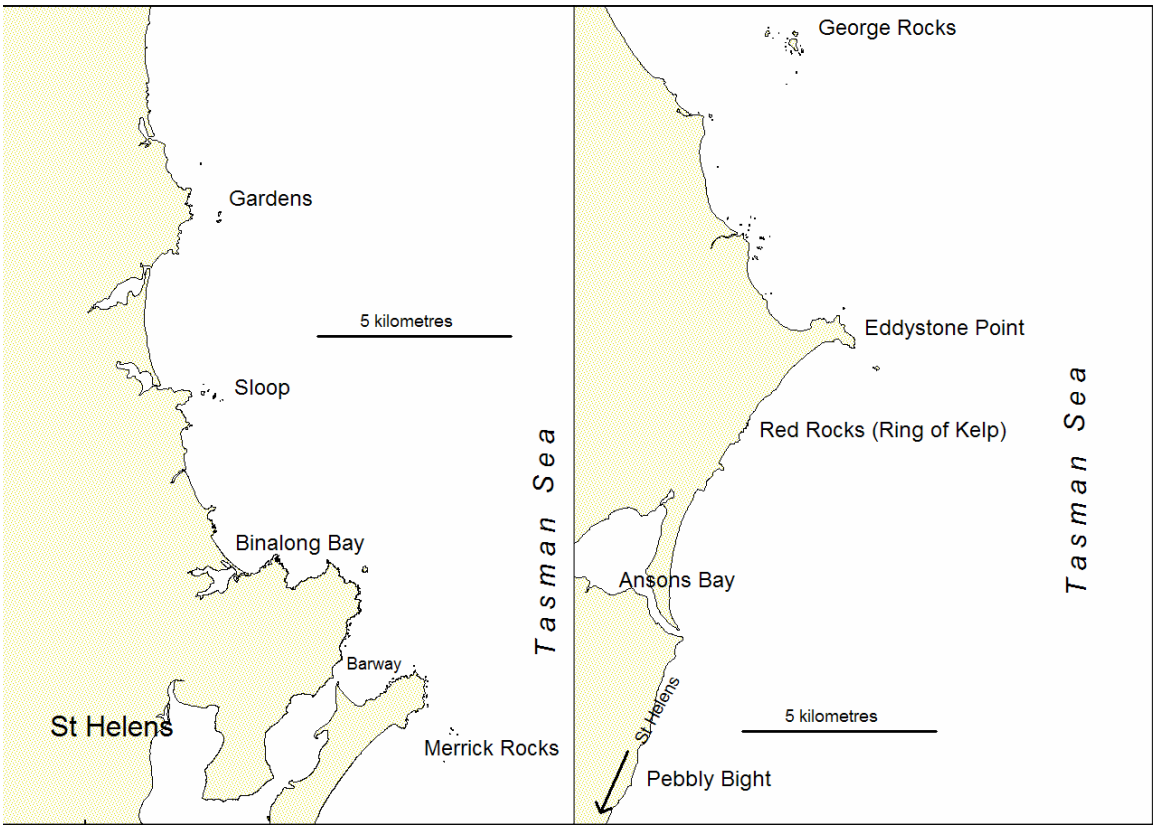
Block 23



Block 28



Block 30



Appendix 6
A molecular approach to identify prey of the southern rock lobster

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Abstract
We demonstrate the use of molecular techniques to detect specific prey consumed by the southern rock lobster (*Jasus edwardsii*). A quick and non-lethal method was used to collect rock lobster faecal material and a molecular protocol was employed to isolate prey DNA from faecal samples. The isolated DNA was amplified using the polymerase chain reaction (PCR) with PCR primers designed to target specific prey items. Feeding experiments determined that DNA from black-lipped abalone (*Haliotis rubra*) and sea urchins (*Centrostephanus rodgersii* and *Heliocidaris erythrogramma*) can be detected in rock lobster faecal samples within seven hours and remains present for up to 60 h after ingestion.
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Keywords: *Jasus edwardsii, Haliotis rubra,* polymerase chain reaction (PCR), prey detection, rock lobster diet

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Introduction
In many near-shore temperate reef ecosystems, rock lobsters are a dominant predator effecting a top-down control of benthic community structure (Tarr *et al*., 1996; Mayfield & Branch, 2000; Shears & Babcock, 2003). However, detailed knowledge of

rock lobster diets and spatial and temporal variability in diet is unknown. This information is crucial to informed management at an ecosystem level of rocky reefs and the important fisheries they support. The establishment of no-take marine protected areas (MPAs), where commercial and recreational fishing is prohibited, has provided a useful resource for monitoring of key temperate reef organisms (Edgar *et al*., 1997). This has recently led to speculation that southern rock lobster (*Jasus edwardsii*) predation may underpin an apparent decrease in densities of young abalone within the Tasmanian MPAs (Edgar & Barrett, 1999; Barrett *et al*., 2003). Currently, there is no method to test this idea or to evaluate the predation patterns of southern rock lobsters in the wild. Furthermore, these are both high value fishery species and, thus, an interesting trophic interaction to monitor.

Previous research on predator–prey relationships of crustaceans has largely involved gut dissection and relied on visual analysis to identify prey remains (Hickman, 1945; Fielder, 1965; Ennis, 1973; Jernakoff *et al*., 1993; Mayfield *et al*., 2000c). This approach has shown that the diet of lobsters varies widely with season and that lobsters are selective feeders (Joll & Phillips, 1984; Barkai *et al*., 1996; Mayfield *et al*., 2000a,b). The physical process of digestion, however, makes visual assessment of gut contents difficult, and gut content analysis has many biases due to varying rates of gut retention, digestion and erosion of prey material. The collection of foregut contents for inspection also necessitates the mortality of the studied lobster (Hickman, 1945; Williams, 1981; Joll & Phillips, 1984; Jernakoff *et al*., 1993; Mayfield *et al*., 2000a,c) so that large-scale surveys are problematic. Killing animals to identify prey is also unlikely to be acceptable if the study population resides in an MPA (Ward *et al*., 2001). Visual inspection of gut contents is known to miss soft-bodied prey organisms, such as abalone and other gastropod molluscs, and may result in up to 90% of the gut contents being unidentifiable (Mayfield *et al*., 2000c). Non-lethal techniques to determine dietary intake are essential because of the high value of live rock lobsters in the commercial fishery and to enable ongoing work inside MPAs.

For most marine predators, unbiased identification of prey is problematic, but new protocols are emerging that allow the unambiguous detection of prey species in predator diets. Recent advances in molecular biology have been used to elucidate diets of animals in a wide range of taxonomic groups, such as fish (Rosel & Kocher, 2002), giant squid (Deagle *et al*., 2005a), wasps (Kasper *et al*., 2004), spiders (Agusti *et al*., 2003) and even introduced insects capable of foraging in native forests (Sheppard *et al*., 2004). Molecular techniques take advantage of unique DNA sequences in species or in groups of organisms and can provide detailed and precise information about predator–prey relationships (Agusti *et al*., 2003; Nejstgaard *et al*., 2003; Jarman & Wilson, 2004; Deagle *et al*., 2005a; Juen & Traugott, 2005).

In the marine environment, protocols have been developed successfully to isolate prey DNA from the faeces of predators (Nejstgaard *et al*., 2003; Jarman *et al*., 2004; Deagle *et*

al., 2005b; Vestheim *et al*., 2005). The DNA is amplified using polymerase chain reaction (PCR) with specific primers that target gene regions of prey species (Jarman *et al*., 2004; Sheppard & Harwood, 2005). The techniques developed have shown that the identity of prey species can be unambiguously detected in this manner (Symondson, 2002). A major incentive for development of non-invasive techniques as an alternative to direct stomach content analysis has been to allow the non-lethal study of endangered or protected animal species (Deagle *et al*., 2005b; Farrell *et al*., 2000; Jarman *et al*., 2002; Jarman *et al*., 2004; Jarman & Wilson, 2004; Symondson, 2002).

In Tasmania, lobsters are the basis for a lucrative commercial fishery where fishers land and sell their lobsters live to discerning domestic and international markets. For fishers to support our research, it was necessary to obtain dietary information while still leaving the lobsters in perfect condition for subsequent sale. The capacity to use animals caught in traps was also important to enable researchers to obtain samples aboard commercial rock lobster fishing vessels, to access remote areas of lobster habitat and to obtain animals from deep-water reefs outside standard scuba diving depths.

The aims of this paper were threefold. First, we demonstrated a non-lethal approach to obtaining dietary samples; second, we determined if faecal material could be used to identify prey using molecular methods; and, third, we determined if the longevity of the DNA signal was sufficient to include prey items from lobsters that would be retained in traps for up to 24 hours.

Materials and methods

Feeding trials

Rock lobsters for feeding trials were captured by scuba diving in the Crayfish Point Marine Reserve at Taroona, Tasmania (42.95°S, 147.34°E) in April 2004 and May 2005. Lobsters were collected opportunistically, ensuring an even distribution of sexes and a wide range of sizes. All captured lobsters were measured and carapace length (CL) was recorded to the nearest millimetre.

Captured lobsters were immediately taken to the laboratory and kept in aerated, flow-through seawater tanks. For the duration of the feeding trials, lobsters were maintained under ambient light conditions and water temperatures in outdoor aquaria at the Marine Research Laboratories, Taroona, Tasmania.

For each trial, the lobsters were placed in one section of a 450-litre tank separated into three sections with plastic mesh and dividers. Each lobster was provided with a 400 mm × 200 mm concrete block as a shelter. All lobsters were starved for 72 hours prior to each feeding trial to facilitate gut evacuation and to remove any remaining prey DNA from the digestive tract. For each trial, approximately 15 grams of fresh food

material was given to each lobster. This material was prepared by shucking live abalone (*Haliotis rubra*) and cutting the foot tissue into approximately 15-gram portions. Common sea urchins (*Heliocidaris erythrogramma*) and long-spined sea urchins (*Centrostephanus rodgersii)* were shucked alive and approximately 15-gram portions of roe and viscera were used as food. Food was introduced to each lobster at 1700 hours and individual lobsters were monitored for feeding activity. Only lobsters that actively fed and consumed the entire food sample within the first hour were used in the feeding trials. No additional food was provided to lobsters for the duration of the trial and each lobster was sampled once per feeding trial. Lobsters were selected for faecal collection over the next five days at the times (hours after commencement of feeding) given in Table 14. Lobsters were selected randomly to eliminate any tank effect. For each sampling time, faecal material was collected from a minimum of three separate lobsters. For each of the individual faecal samples, PCR assays were performed twice to guarantee the consistency of the result. These feeding experiments were repeated over a period of 65 days with 116 faecal samples collected in total. A total of 61 lobsters were used in these trials, comprising 24 females and 37 males. Lobsters ranged in size from 53 to 161 millimetres carapace length.

Table 14 **Feeding trial schedule over five days, covering 96 hours after initiation of feeding episodes. Each time indicates when samples were collected and the hours after the commencement of feeding.**

Day	Sampling time (hours after commencement of feeding)
Day 1	2000 (3 h), 2200 (5 h)
Day 2	0000 (7 h), 0200 (9 h), 0400 (11 h), 0600 (13 h), 0800 (15 h), 1000 (17 h), 1200 (19 h), 1400 (21 h), 1700 (24 h), 2300 (30 h)
Day 3	0500 (36 h), 1100 (42 h), 1700 (48 h), 2300 (54 h)
Day 4	0500 (60 h), 1100 (66 h), 1700 (72 h), 2300 (78 h)
Day 5	0500 (84 h), 1100 (90 h), 1700 (96 h)

Faecal material collection

A 'cradle' device was designed and built for the purpose of restraining lobsters while samples could be taken from the hindgut region. Lobsters were placed in the cradle, which holds the animal upside-down and immobilizes the posterior four pairs of walking legs. The anterior telson was held firmly by the researcher to stabilize the abdominal region and tail while collecting faeces.

Lobster faeces were collected using a 100–1000 µl pipette with disposable tips. For each faecal sample, a new sterile tip was used to prevent contamination between samples. The tip was inserted directly into the anal pore of the lobster to remove faeces from the hindgut region. The collected material was immediately pipetted into a 1.5 ml micro centrifuge tube containing 500 µl of 70% ethanol. Ethanol has been shown to be an effective preservative for field samples and does not require freezing or any special handling (Jarman *et al*., 2004). The volume collected varied from approximately 10 µl to 1 ml depending on the size of lobster and fullness of hindgut at the time of sampling. Ethanol was removed from samples before DNA extraction by centrifuging at 10,000 g for 30 s. Excess ethanol was poured off and the sample tubes centrifuged again. Any remaining ethanol was then removed by pipette.

DNA extraction

There were no previously published studies using rock lobster faecal material as a source of prey DNA. Tissue samples from predator and prey species were collected to test PCR primer specificity and to use as both positive and negative DNA controls in later experiments. Tissue samples were taken from fresh animals and a small (~0.25 ml) portion was used for total cellular DNA extraction. Another portion (~2 ml) of the tissue was stored in 70% ethanol as a voucher specimen. The DNeasy® Tissue Kit (QIAGEN) was used to extract genomic DNA from predator and prey tissues, and the manufacturer's animal tissue protocol was followed.

The Ultra Clean™ Fecal DNA Kit (Mo Bio Laboratories, Inc.) was used for DNA extractions on rock lobster faecal samples following the manufacturer's protocols with the supplied proprietary buffers and reagents. All DNA extracted from faecal samples using this kit was ready for PCR, and the manufacturer's protocol appeared to remove any potential PCR inhibitors.

PCR amplification

Precautions were taken during preparation of PCR reactions to minimize the possibility of contamination by extraneous DNA. Aerosol-resistant barrier pipette tips were used for preparing all PCR reactions, and pipette tips were either sterile and pre-packaged or autoclaved prior to use. All PCR reactions were prepared in a dedicated hood where PCR tubes, pipettes and pipette tips were subjected to UV light for a minimum of 10 min prior to setting up each PCR reaction.

The components of the 20 µl PCRs were 50 mM KCL, 15 mM Tris.HCl pH 3.0, 5.0 mM $MgCl_2$, 100 µg ml^{-1} bovine serum albumin, 0.5 mM of each dNTP, 2 mM each primer (Geneworks), 1 unit AmpliTaq Gold® DNA polymerase (Sigma), and ~20 ng template DNA. Both positive and negative controls were run with each batch of PCRs. For negative controls, 2 µl MilliQ H_2O was used as template; and, for positive controls, ~20 ng template DNA from *Haliotis rubra*, *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* was used to confirm reaction success. PCR replication was performed by running reactions a minimum of two times to ensure a consistent result.

The PCR primer sets used in this experiment (Table 15) were developed previously to distinguish *Haliotis rubra* tissue from that of other *Haliotis* species for forensic purposes (Elliott *et al*., 2002) and for identification of echinoderms as prey items in marine ecosystems (Jarman *et al*., 2006). Primers were obtained from GeneWorks Pty Ltd Custom Oligonucleotide service and diluted to 10 µM for use in setting up PCR reactions.

PCR thermal cycling conditions for HalCO2GENA and HalCO2GENB primers were: denaturation and DNA polymerase activation at 95°C for 10 min followed by 10 initial amplification cycles: 94°C for 30 s, annealing at 60–55°C for 30 s, 72°C for 1 min with a decrease in the annealing temperature by 0.5°C for each of the 10 cycles. Twenty-five further amplification cycles were carried out: 94°C for 30 s, 55°C for 30 s and 72°C for 1 min. The final extension step was 72°C for 5 min and the reaction was held at 10°C until removed from the MJ Research PTC-2001 Thermal Cycler.

PCR thermal cycling conditions for EchinNSS18sf/EchinNSS18sr primers were: denaturation and DNA polymerase activation at 95°C for 10 min followed by 35 amplification cycles: 95°C for 5 s, annealing temperature at 51°C for 30 s, 72°C for 30 s. The final extension step was 72°C for 5 min and the reaction was held at 10°C until removed from the MJ Research PTC-2001 Thermal Cycler.

PCR products were visualised by electrophoresis on 1.5% agarose gels stained with ethidium bromide (5 µl ethidium bromide per 100 ml agarose). Each gel was loaded with 7 µl of PCR product, and a 100 bp ladder was used on every gel to determine fragment size and to confirm the results of each PCR. All agarose gels ran for 20 min at 80 V.

Table 15 **PCR primers used, including sequence of each primer, target organism or group, and DNA region amplified. DNA regions are mitochondrial cytochrome oxidase subunit I (mt COI) and the nuclear large subunit ribosomal RNA gene (18s rDNA).**

Primer	Sequence (5'–3')	Target species/group	DNA region
HalCO2GENA	CAA TYT GAA CYA TTC TMC CAG C	*Haliotis rubra*	mt COI
HalCO2GENB	CCT TAA ART CTG AGT ATT CGT AGC C	*Haliotis rubra*	mt COI
EchinNSSf1	GCG TGC TTT TAT TAG GA	Echinodermata	18s rDNA
EchinNSSr1	CGA CCA TGR TAR GCG CAT AAC G	Echinodermata	18s rDNA

Results

Feeding trials

Using HalCO2GENA and HalCO2GENB primers, fragments of 193 bp were successfully amplified from both black-lipped abalone tissue DNA and faecal samples from lobsters fed a diet of black-lipped abalone (fig. 1). Using EchinNSSf1 and EchinNSSr1 primers, fragments of 160 bp were successfully amplified from *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* tissue DNA, and from faecal samples from lobsters fed a diet of both urchin species (Figure 58). Prey was initially detected in all samples at 7 h after feeding and was consistently detected in all samples until 60 h after the feeding episode. There were no detections in any of the samples taken at 3 and 5 h or for the six sampling times from 66 h to 96 h after commencement of feeding.

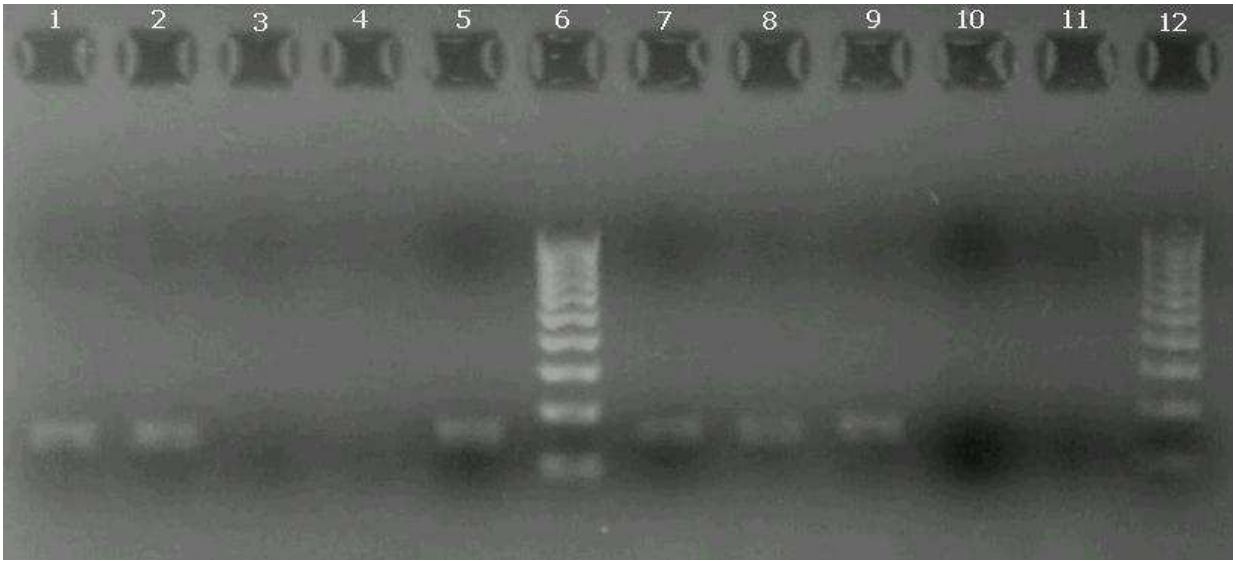

Figure 58 **Secificity of HalCO2GENA/HalCO2GENB and EchinNSSf1/EchinNSSr1 PCR primers. Agarose gel showing PCR products amplified from rock lobster feeding experiments using group and species-specific PCR primers. Lanes 1–5 show DNA amplification using PCR primers specific to *Haliotis rubra* and lanes 7–11 show DNA amplification using PCR primers specific to Echinodermata. Lanes 6 and 12 are 100 bp DNA reference ladders indicating relative size of DNA fragments in sample lanes. Lanes 1, 2 and 3 indicate PCR amplified rock lobster faecal samples from 8, 24 and 96 h after feeding on black-lipped abalone. Lane 5 shows DNA amplification using *Haliotis rubra* tissue. Lanes 7, 8, 9 and 10 show PCR amplified rock lobster faecal samples from 12, 36, 48 and 72 h after feeding on *Centrostephanus rodgersii*. Lanes 4 and 11 are negative controls with water instead of DNA sample template.**

Discussion

The faecal collection technique developed met the important requirement of being non-lethal. During the feeding trials, several individual lobsters were sampled ten times over four months using the non-destructive faecal collection technique with no obvious deleterious impacts. The ability to repeatedly sample the same individual lobster confirms the low impact nature of this method and allows for a greater range of experimentation on lobster diet and feeding behaviour. Faecal material was easily and successfully extracted from both sexes of lobsters and a wide range of size classes (53 mm CL-161 mm CL). This indicates that faecal material is useful to study ontogenetic dietary shifts and dietary changes associated with maturity and reproduction.

Molecular prey detection depends upon the ability of DNA to resist digestion in the predator gut and on the power of PCR to amplify a prey specific region of DNA from semi-digested material (Jarman *et al*., 2002; Nejstgaard *et al*., 2003; Deagle *et al*., 2005b; Parsons *et al*., 2005). The extent of DNA breakdown after digestion by rock lobsters was previously unknown, although Mayfield *et al*. (2000c) found that digestion rendered the use of serological methods unsuitable. This study shows, for the first time, that prey DNA survives digestion, can be isolated from lobster faecal material and can be successfully amplified using PCR.

The longevity of the molecular signal indicates that samples obtained from traps during routine fishing operations would retain prey DNA consumed prior to entering the trap. In *Jasus edwardsii* fisheries, traps are set for a maximum of 24 h. These results suggest that dietary information should still be available from faecal material for at least the 24 h prior to entering the trap as the dietary signal was recorded in all samples up to 60 h after the commencement of feeding.

For animals such as rock lobsters where previous dietary studies have been inconclusive, DNA holds considerable promise for assessing specific prey variability across spatial and temporal scales. Although rock lobsters and abalone are common on temperate reefs around the world (e.g. South Africa, New Zealand, Australia), there are no records of the presence of abalone in rock lobster dietary studies (Hickman, 1945; Tarr *et al*., 1996; Mayfield & Branch, 2000; Mayfield *et al*., 2000c). Commercial abalone divers often report empty abalone shells in front of lobster dens. The failure of previous studies to identify abalone in lobster guts is possibly due to the 'foot' tissue being the only part consumed by rock lobsters and without any shell fragments, this tissue would be unidentifiable. Understanding the interaction between these two valuable recreational and commercial species is one example of the potential of DNA dietary studies for improving our understanding of marine ecosystems. Importantly, the ability to obtain dietary information non-destructively enables comparisons between fished and non-fished (e.g. MPAs) regions, to better understand the trophic impacts of harvesting marine resources.

Acknowledgements

This research was a component of grant 2004/013 'Towards integrated multi-species management of Australia's SE reef fisheries: A Tasmanian example', which is supported by funding from the Fisheries Research and Development Corporation on behalf of the Australian Government. Funding was also provided by the ANZ Charitable Trust Australia's Holsworth Wildlife Research Endowment. We would additionally like to thank all the individuals at the Marine Research Laboratories who assisted with rock lobster husbandry and the collection of lobsters and prey species. All experiments were carried out in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes 7th Edition 2004.

Appendix 7

Trophic effects of fishing southern rock lobster (*Jasus edwardsii*) shown by combined fatty acid and stable isotope analyses

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Trophic effects of fishing southern rock lobster *Jasus edwardsii* shown by combined fatty acid and stable isotope analyses

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ABSTRACT: The southern rock lobster *Jasus edwardsii* is a commercial species that has benefited from the complete protection offered by no-take reserves, with higher abundances and larger animals recorded in reserves than in adjacent fished areas. What remains unclear is whether there is any change in the diet of lobsters in reserves, for example, as a result of increased intraspecific competition for food. We used combined chemical tracers to examine the diet of lobsters in fished and reserve areas in 2 bioregions in eastern Tasmania. $\delta^{15}N$ values of lobsters were richer in fished than in reserve areas, indicating that lobsters eat a greater proportion of food items from higher trophic levels in fished areas. Mixing models suggest that ascidians, sea urchins and the turbinid gastropod were all important food sources for lobsters, but the importance of these food items differed between bioregions. This spatial variability may suggest that the small size of the reserve in one bioregion is inadequate at ensuring the diet of lobsters is protected from fishing pressure. Fatty acid profiles of lobsters supported the importance of these food sources to lobsters. Differences between bioregions, or inside and outside of reserves, were not apparent using fatty acids. The present study highlights that lobster fishing has the capacity to alter the trophic status of prey for generalist predators and suggests that fatty acid analyses may be limited in detecting changes in the dietary composition of such generalist feeders.

KEY WORDS: Effects of fishing · Food webs · Marine protected areas · Stable isotopes · Fatty acids

INTRODUCTION

No-take marine protected areas, or reserves, are an increasingly common tool used to mitigate the effects of fishing and preserve biodiversity (Jennings 2000). In the absence of manipulative experiments and data that is collected prior to fishing activities, no-take marine reserves also provide a unique opportunity to test specific hypotheses about the effects of fishing on community structure and dynamics (Pinnegar et al. 2000). Typically, these hypotheses have focused on evaluating the direct effects of fishing, such as changes to the density of targeted species (e.g. Roberts & Polunin 1991, Dahlgren & Sobel 2000, Schroeter et al. 2001, Shears et al. 2006). Not surprisingly, the abundance and often mean size of fished species is generally found to increase in reserves compared with adjacent fished areas (Edgar & Barrett 1997, Follesa et al. 2007, Sonnenholzner et al. 2009). More recently, however, the indirect effects of fishing on the trophic structure of reserve and fished communities have been considered with evidence of trophic cascades in several communities following the increase of predator densities in reserve areas (Scheffer et al. 2005, Kramer & Heck 2007).

The southern rock lobster *Jasus edwardii* (Hutton) is one species demonstrated to benefit from the estab-

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lishment of marine reserves in which complete cessation of fishing is enforced (Edgar & Barrett 1997, 1999, Shears et al. 2006). Increases in the abundance of *J. edwardsii* have been linked with trophic cascades in reserves that shifted from sea urchin- to algal-dominated reef habitats (Shears & Babcock 2003). What remains unclear, however, is the potential dietary shift of lobsters due, in part, to greater lobster density after reserve establishment (e.g. via intraspecific competition) that may have unknown effects on other components of the reef community.

Chemical tracers such as stable isotope and fatty acid analyses are means by which the diet of lobsters in fished and reserve areas may be determined. As lobsters macerate their food upon ingestion, the chemical tracer approach has advantages over conventional methods of dietary analysis, such as gut content analysis where identification is often labour intensive, requires taxonomic expertise and soft bodied organisms may be overlooked (Sheppard & Harwood 2005). Moreover, chemical tracers identify food that is assimilated over a period of time and is of nutritional importance, rather than that which is ingested at one point in time (Thomas & Cahoon 1993). The basis of the chemical tracer approach is that consumers incorporate the marker, or signature, of their food source into their somatic and other tissues with minimal or predictable changes, thus providing an integrated record of the main food items in their diet (Peterson 1999, Dalsgaard & St John 2004).

Stable isotope signatures refer to the variation in the ratio of rare heavy isotopes (e.g. ^{13}C, ^{15}N) to the more common lighter isotopes (e.g. ^{12}C, ^{14}N) in the target organism relative to an international standard (Peterson & Fry 1987). As carbon changes very little between successive trophic levels (0 to 1‰, McCutchan et al. 2003), the carbon isotope can often indicate the ultimate source of primary production at the base of a consumer diet. The nitrogen isotope experiences greater fractionation per trophic level (3 to 4‰) and is thus used to infer the trophic status of a consumer (McCutchan et al. 2003). Signature fatty acids include individual fatty acids that are rare and unique ratios of commonly occurring fatty acids, both of which can be reflected in the fatty acid profile of a consumer (Dalsgaard et al. 2003). The combined use of stable isotope and fatty acid analyses therefore results in a greater capacity than that of a single technique to discriminate between potential food sources contributing to the diet of lobsters in fished and reserve areas.

The combined use of stable isotope and fatty acid analyses has been successfully applied to understanding the feeding ecology of marine invertebrates (Kharlamenko et al. 2001, Guest et al. 2008, Jaschinski et al. 2008, Soreide et al. 2008, Stevens et al. 2008), birds (Karnovsky et al. 2008, Tierney et al. 2008) and mammals (Krahn et al. 2008, Tucker et al. 2008). No previous studies have examined the diet of lobsters, including wild *Jasus edwardsii*, using combined stable isotope and fatty acid analyses. More importantly, combined tracers have not previously been applied to understanding potential differences in the feeding ecology of a consumer between spatial management zones. The present study, on the east coast of Tasmania, uses a combined chemical tracer approach to determine if lobster diet differs between fished areas with low lobster density and reserve areas with higher lobster density. In doing so, it provides insight into both the feeding ecology of lobsters and its response to spatial management, and the efficacy of chemical tracers in resolving spatial differences in a consumer's diet.

MATERIALS AND METHODS

Study sites and species. The diet of *Jasus edwardsii* was studied in fished and reserve areas in 2 bioregions in eastern Tasmania, Australia (Fig. 1). The Maria Island reserve protects ~7 km of coastline and was established principally to preserve marine habitats representative of the Tasmanian east coast, whilst the Governor Island reserve at Bicheno protects ~1 km of coastline and was established to restore recreational fisheries species such as lobster back to unfished levels (Edgar & Barrett 1999). Both regions are characterised by shallow algal reefs which support *J. edwardsii* and the blacklip abalone *Haliotis rubra*, the 2 most important fisheries species in Tasmania.

Each bioregion is represented by a single reserve with adjacent fished locations. Two locations (1 & 2) were selected within each reserve, as well as 3 locations (3 to 5; see Fig. 1) in fished areas adjacent to each reserve, to maximise habitat similarity in terms of wave exposure and macroalgal communities between treatments. There were multiple sites within each location to ensure samples were representative of each location. Reserve and fished locations in each bioregion were similar to those used by Edgar & Barrett (1997, 1999). Locations within each fished and reserve area were separated by at least 1 km, and within each location, multiple sites were separated by approximately 100 m.

At Maria Island, both total density and the density of large *Jasus edwardsii* were higher in reserves than adjacent fished areas (Edgar & Barrett 1997, 1999, Barrett et al. 2009). There were no apparent differences in the density of *J. edwardsii* at Governor Island between reserve and fished areas (Edgar & Barrett 1999, Barrett et al. 2009), but observations suggested that lobsters moved to deeper water and beyond surveying depth

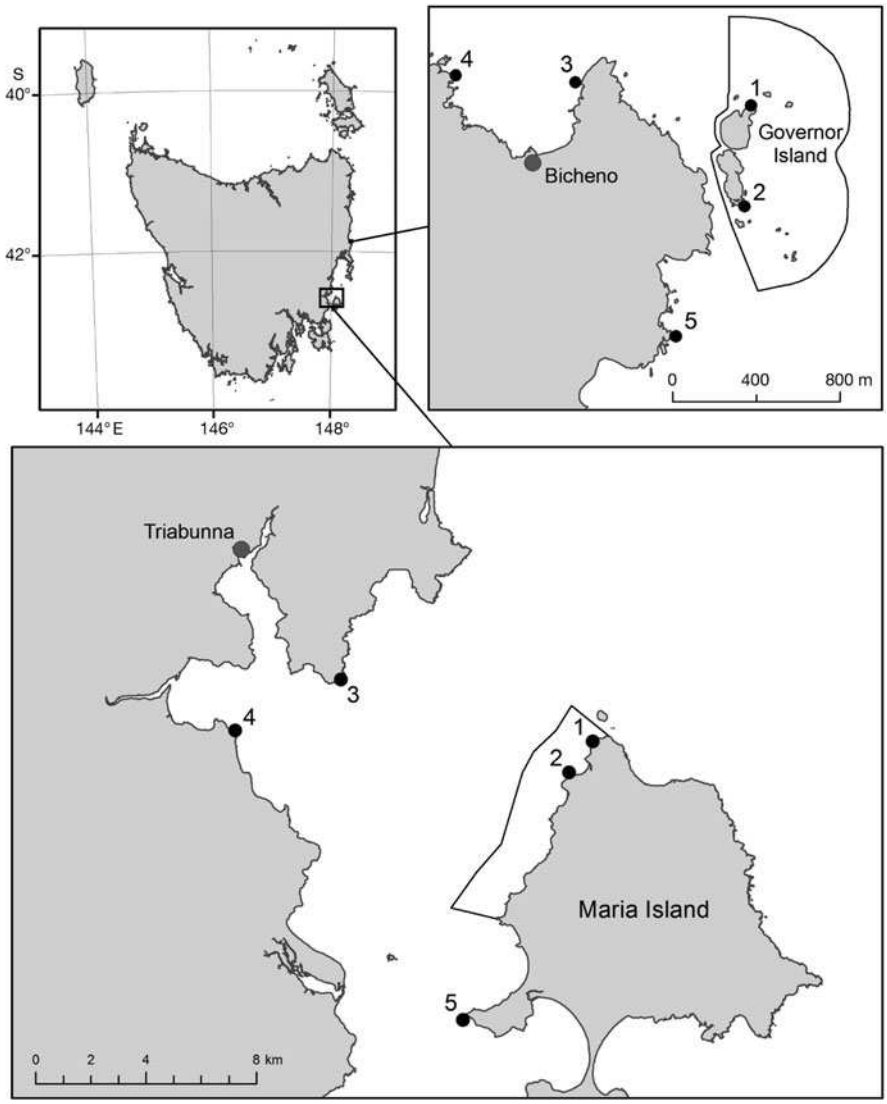

Fig. 1. Sampling locations (1 to 5) at Governor and Maria Islands, Tasmania. In each bioregion, Locations 1 and 2 are reserves (outlined) and 3 to 5 are fished

(5 m) in poor weather at this more exposed location (N. Barrett pers. comm.), making potentially higher densities of lobsters in reserves at Governor Island difficult to detect.

Potential lobster prey items included the blacklip abalone *Haliotis rubra*, the turbinid gastropod *Turbo undulatus*; the purple sea urchin *Heliocidaris erythrogramma*, the long-spined sea urchin *Centrostephanus rodgersii*, and the solitary ascidians *Herdmania momus*, *Cnemidocarpa radicosa* and *Pyura gibbosa*. The density of small abalone (*H. rubra*) was lower than large abalone in reserves than in fished areas (Edgar & Barrett 1999). The densities of *H. erythrogramma* and *C. rodgersii* were greater in fished areas compared with reserve areas for both bioregions (Barrett et al. 2009). Densities of the turbinid gastropod *T. undulatus* were similar between fished and reserve areas at Governor Island, and strong recruitment at one location at Maria Island apparently caused the significantly higher abundance of *T. undulatus* recorded there (Buxton et al. 2006). No data are available on the density of ascidians. Red algal cover at 5 m depth was 11 to 24 % at Maria Island and 10 to 20 % at Governor Island. Dominant brown algal canopy species were *Durvillea potatorum*, *Ecklonia radiata* and *Phyllospora comosa* and their total cover was 40 to 80 % at Maria Island and nearly 100 % at Governor Island (Edgar & Barrett 1999).

Sample collection and processing. A minimum of 3 samples of *Jasus edwardsii* and potential prey items were collected from each site within each location in reserve and fished areas for both stable isotope and fatty acid analyses. All samples were collected on

SCUBA by hand. Due to the limited dive time, uneven numbers of samples among species and locations and between bioregions often resulted. Sampling of *J. edwardsii* occurred inside and outside of reserve areas and was non-destructive, involving the removal of the second or third walking leg *in situ* before release. Nelson et al. (2005) showed the fatty acid profiles of leg tissue to be similar to that of muscle tissue in both wild and cultured lobsters. Where possible, *J. edwardsii* from different size classes (small: <80 mm carapace length [CL]; medium: 80–120 mm CL; large: >120 mm CL) were collected to examine potential ontogenetic shifts in diet. Common red algae *Plocamium angustum* and brown algae (*Ecklonia radiata*, *Phyllospora comosa*) were collected at the same locations as the lobsters, and all samples were taken at 5 to 10 m depth.

All samples were frozen after collection (–20°C), then thawed and rinsed in distilled water prior to processing. A leg muscle of lobster samples was removed from the exoskeleton, and a 2 cm^3 section of muscle was removed from the abalone foot for later analysis. Muscular tissue of *Turbo undulatus* was also separated from the shell and other organs. Similarly, a portion of ascidian tissue, including the tunic, washed free of epiphytes, was also removed. Samples of sea urchin, comprising the lantern only, were rinsed, and small amounts of flesh removed for analysis. From each algal sample, tissue was selected haphazardly from the tip, midline and lower portion of each frond. All samples were then freeze-dried for 24 to 48 h and ground with a mortar and pestle. Samples were then partitioned for fatty acid and stable isotope analyses.

Stable isotope analysis. The ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ for all samples were calculated as the relative per mille (‰) difference between the sample and the recognized international standard (Pee Dee belemnite carbonate for carbon; air for nitrogen) and analysed on a Micromass Isochrom continuous flow-isotope ratio mass spectrometer. Precision of the mass spectrometer calculated from duplicate samples was 0.2‰.

Fatty acid analysis. Dried animal and algal samples (15 mg of each) were trans-methylated to produce fatty acid methyl esters (FAME) using methanol–chloroform–conc. hydrochloric acid (10:1:1, 80°C, 2 h). Direct trans-methylation of samples has previously been validated against conventional methods (Christie 1982) for a microheterotroph (Lewis et al. 2000) and for striped trumpeter larvae and rotifers (M. P. Bransden & G. A. Dunstan unpubl. data). FAME were extracted into hexane–chloroform (4:1, 3 × 1.5 ml). Analysis of gas chromatograms was performed with an Agilent Technologies 6890N GC equipped with an HP-5 capillary column (50 m × 0.32 mm internal diameter), a flame ionization detector (FID), a split/splitless injector and an Agilent Technologies 7683 auto sampler using gas chromatograph operating conditions previously described (Phillips et al. 2003a). Individual components were identified using mass spectral data (Finnigan Thermoquest GCQ GC-MS) and by comparing retention times with those of authentic laboratory standards.

Statistical analyses. ***Stable isotopes:*** A nested ANOVA tested for differences in carbon and nitrogen isotope values of lobster and potential food sources among fished and reserve locations (reserve effect: fixed, 2 levels). Location was a random factor and, where possible, nested within reserve effect, but was unbalanced as 2 locations were in reserve areas and 3 were in fished areas. Tests for differences between fished and reserve areas were done separately for each bioregion using the general linear models (GLM) procedure in SAS version 9.1.3 (SAS Institute), except for ascidians where there were too few data within either bioregion among reserve and fished areas to be analysed. The GLM procedure uses the method of least squares to fit GLMs, and is particularly suited to unbalanced data (Quinn & Keough 2002). Data were checked for normality and homogeneity of variance by examination of residuals, and square root-transformed where necessary. Spearman rank correlation was used to determine if there was a relationship between lobster size and carbon and nitrogen isotope values.

Mixing model of Jasus edwardsii diet: Mixing models cannot provide a unique solution where there are more sources than elements, as in the present study. Instead, the IsoSource model (Phillips & Gregg 2003) uses the average carbon and nitrogen isotope values of lobster and its potential prey items to calculate the upper and lower limits of the contribution that each food source makes to the diet of lobster. All possible combinations of each food source contribution (0 to 100%) are examined in 1% increments. Combinations that sum to 0.5% of the lobster signature are considered feasible contributions. Results are reported as the distribution of feasible solutions for each food source as recommended by Phillips & Gregg (2003). The 1st and 99th percentiles are also given rather than the full range, which is sensitive to small numbers of observations on the tails of the distribution (Melville & Connolly 2003).

The average carbon and nitrogen isotope values of *Jasus edwardsii* and the potential prey items — abalone *Haliotis rubra*, the turbinid *Turbo undulatus*, the sea urchins *Heliocidaris erythrogramma* (Maria Island only) and *Centrostephanus rodgersii* (Governor Island only), ascidians, brown algae and the red alga *Plocamium angustum* — for reserve and fished areas within each bioregion were corrected for fractionation. Trophic fractionation for carbon is on average 0.5‰ per trophic level (McCutchan et al. 2003). For nitrogen,

fractionation is larger and on average 3.5‰ per trophic level (McCutchan et al. 2003, Waddington & MacArthur 2008). Fractionation rates can vary between species with such issues as diet type (Vanderklift & Ponsard 2003) and dietary studies are required to confirm the fractionation rates of individual species (Pitt et al. 2009). As this was beyond the scope of the present study, the sensitivity of the IsoSource mixing model was run for each species using a range of fractionation rates for carbon and nitrogen. Changes in fractionation rates between 0.5 to 1.5‰ did not change the overall order of contributions made by most prey items to lobster diet (data not shown), thus the above standard levels of fractionation were used here. Lobsters were assumed to be 2.5 trophic levels above the base autotrophic source, ascidians 1.5 levels above base autotrophic source (Bingham & Walters 1989) and the grazers, including abalone (Guest et al. 2008), turbinids and sea urchins, 1 trophic level above base autotrophic source. Isotope values for ascidians, sea urchins and brown algae were pooled within each respective phylum as, for the purposes of the model, there were insufficient differences between isotope values to discriminate individual species' contributions to lobster diet. For modelling of the reserve effect at Governor Island, stable isotope values of only one reserve and one fished location were available, and not all data were available for each species/phylum.

Fatty acid profiles: The diet of lobsters was compared between fished and reserve areas using principal component analysis (PCA) based on the fatty acid profiles of *Jasus edwardsii* and potential food sources. PCA reduces the number of dimensions produced by the large number of variables and uses linear correlations (components) to identify those fatty acids that contribute most to the separation between observed groups (Best et al. 2003). PCA was run on each species/phylum separately for fished and reserve areas in each bioregion to ensure that potential variability in fatty acid profiles of individual species/phylum due to environmental factors did not preclude subsequent trophic interpretation of data. For each species/phylum, a nested ANOVA on the scores of the first principal component (PC1, which described the majority of the variance between phyla) was then used to test for differences among bioregion (random, 2 levels), whether there was an effect of reserve (fixed, 2 levels) and for differences among location within reserve treatments (random, 5 levels) using the GLM procedure in SAS. PCA was then run on all species/phyla combined to examine the trophic relationships at fished and reserve areas in each bioregion. All analyses were performed on percent composition data, and fatty acids that contributed a mean of >1.0% of total fatty acids to the fatty acid profile for each species/phylum were used in PCA. A 1% cutoff was chosen to minimise chromatographic overlap. Results were consistent with analysis of mg g^{-1} fatty acid data (data not shown, but see Phillips et al. 2003b). The relationship between lobster size and principal component score, derived from fatty acids present in the profile of *J. edwardsii*, was examined using Spearman's rank correlation. All statistical analyses were performed using SAS version 9.1.3 (SAS Institute).

RESULTS

Stable isotopes

Carbon and nitrogen isotope values could be distinguished between broad phylogenetic groups (Fig. 2). For sea urchins, ascidian and brown algal species, the carbon and nitrogen values of similar species (e.g. *Heliocidaris erythrogramma* and *Centrostephanus rodgersii*) could not be distinguished and the isotopic values of these species were averaged for subsequent modelling of lobster diet (Fig. 3). As not all species were present in each bioregion, differences among bioregion in stable isotope values were not tested. Spearman's rank correlation showed no relationship between carbon (r_S = 0.06, p = 0.70, n = 46) or nitrogen isotope values (r_S = 0.16, p = 0.29) and size of *Jasus edwardsii*, so lobsters from all size classes were pooled for further analyses.

Nitrogen values of *Jasus edwardsii* were significantly more enriched at fished compared with reserve areas for both Maria (fished: 14.0 ± 0.3‰; reserve: 13.0 ± 0.1‰) and Governor Islands (fished: 13.9 ± 0.2‰; reserve: 13.4 ± 0.1‰; Table 1). Nitrogen values of *Plocamium angustum* were also significantly more enriched at fished (8.9 ± 0.2‰) compared with reserve areas (6.0 ± 0.1‰). Nitrogen values of *Haliotis rubra* differed significantly among locations, but not between fished and reserve areas. Carbon values of *J. edwardsii*, *H. rubra*, *Heliocidaris erythrogramma*, brown algae and *P. angustum* were significantly different among locations (Table 1). There were no significant differences in carbon or nitrogen isotope values between fished and reserve areas for any other species/phyla.

Mixing model of *Jasus edwardsii* diet

IsoSource modelling of $\delta^{13}C$ and $\delta^{15}N$ values at Maria Island suggested a singular dominant potential contributor to the diet of lobsters at fished (ascidians, 80 to 93%) and reserve areas (*Turbo undulatus*, 57 to 91%), with all other food sources making much smaller con-

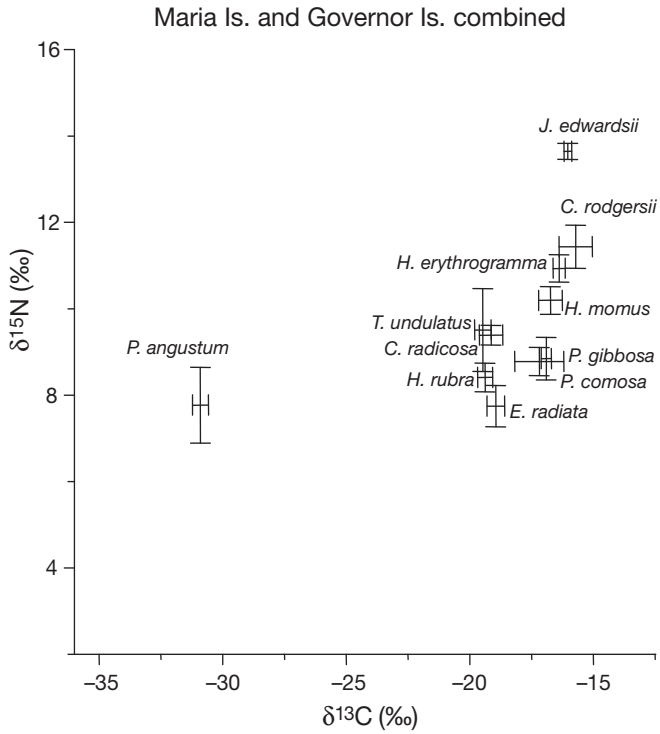

Fig. 2. Mean (±SE) stable isotope values of $\delta^{15}N$ and $\delta^{13}C$ for *Jasus edwardsii* and potential prey items by species (*Haliotis rubra*, *Turbo undulatus*, *Heliocidaris erythrogramma*, *Centrostephanus rodgersii*, *Herdmania momus*, *Cnemidocarpa radicosa*, *Pyura gibbosa*) pooled across bioregion and locations. Values for autotrophic sources (*Plocamium angustum*, *Ecklonia radiata*, *Phyllospora comosa*) are also included for comparison

tributions (Fig. 4). The pattern of likely food source contributions between fished and reserve areas was different for Governor Island. Sea urchins made substantial contributions to the diet of *Jasus edwardsii* in both fished and reserve areas but were the most dominant contributor in fished areas at Governor Island (58 to 71%). Ascidians also made a strong likely contribution to lobster diet (24 to 53%) in both fished and reserve areas but were most pronounced in reserve areas at Governor Island.

Sea urchins were the second most important potential contribution to lobster diet in fished areas at Maria Island, but, as previously mentioned, this contribution was much larger at Governor (58 to 71%) than at Maria Island (0 to 13%). Sea urchins were also an important potential contributor in the Maria Island reserve (4 to 22%) but to a much lesser extent than at Governor Island. *Haliotis rubra* was the next most important potential food source for lobster in both fished (0 to 25%) and reserve (0 to 32%) areas at Governor Island, but made a relatively minor contribution to lobster diet in fished areas at Maria Island (0 to 8%); the potential contribution of *H. rubra* in reserve areas at Maria Island (0 to 19%) was similar to that at Governor Island. *Turbo undulatus* also made a minor contribution to lobster diet in fished areas at Maria Island (0 to 7%) and in fished (0 to 16%) and reserve areas (0 to 11%) at Governor Island, and was the dominant contributor in reserve areas at Maria Island (57 to 91%). Brown and red algae were consistently estimated to be unimportant contributors to the diet of lobsters in fished and reserve areas in both bioregions (Fig. 4).

Fatty acid profiles

Fatty acids 16:0 (7.3 to 55.9% of total fatty acids), 20:4n-6 (4.4 to 19.0%) and 20:5n-3 (3.4 to 13.3%) commonly occurred in all species/phyla (Table S1 in online supplementary material, see www.int-res.com/articles/suppl/m388p169_app.pdf). For *Jasus edwardsii*, 18:1n-9 (15.7 to 16.1%) was the most abundant fatty acid, with relatively high levels of 22:6n-3 (8.2 to 8.7%), 18:0 (6.4 to 6.6%) and 16:1n-7 (3.9 to 4.1%). *Haliotis rubra* and *Turbo undulatus* were characterised by relatively high levels of 22:5n-3 (8.9 to 9.4%) which was low or absent in all other phyla. In addition to 20:4n-6 and 20:5n-3, *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* also had high levels of 20:1n-7,9,11 (13.6 to 19.7%) and 20:3n-6 (11.7 to 15.1%). Ascidians had relatively high levels of 18:0 (4.0 to 8.8%) and 22:6n-3 (1.4 to 8.3%). Fatty acids 14:0 (5.2 to 7.5%), 16:1n-7 (4.5 to 6.3%), 18:1n-9 (17.6 to 22.4%) and 18:4n-3 (3.9 to 7.3%) were common in both brown algal species. Fatty acids 14:0 (9.5 to 9.9%), 22:0 + hydroxy (OH)20:0 (3.4 to 3.9%), 16:1n-7 (2.6 to 3.1%) and 20:3n-6 (3.4 to 3.6%) were the most abundant in the red alga *Plocamium angustum*. Percentages of fatty acids for all species/phyla were similar between fished and reserve areas (Table S1) and this pattern was consistent for absolute concentrations of fatty acids (mg g^{-1}, not shown).

Spearman's rank correlation showed no relationship between lobster size and PC1 scores derived from the fatty acid profile of *Jasus edwardsii* (r_S = 0.16, p = 0.13, n = 91); therefore, lobsters from all size classes were pooled for all analyses although size classes are delineated in Fig. 5. All species/phyla could be distinguished using PCA based on fatty acids contributing more than 1% of the lobster profile (Fig. 5), with the greatest overlap between *Haliotis rubra* and *Turbo undulatus* and some red and brown algae samples. PCAs that used a subset of fatty acids based on metabolic relationships or ratios of n-3/n-6 polyunsaturated fatty acids (PUFA) can sometimes yield additional information (e.g. Alonzo et al. 2005), but displayed no additional

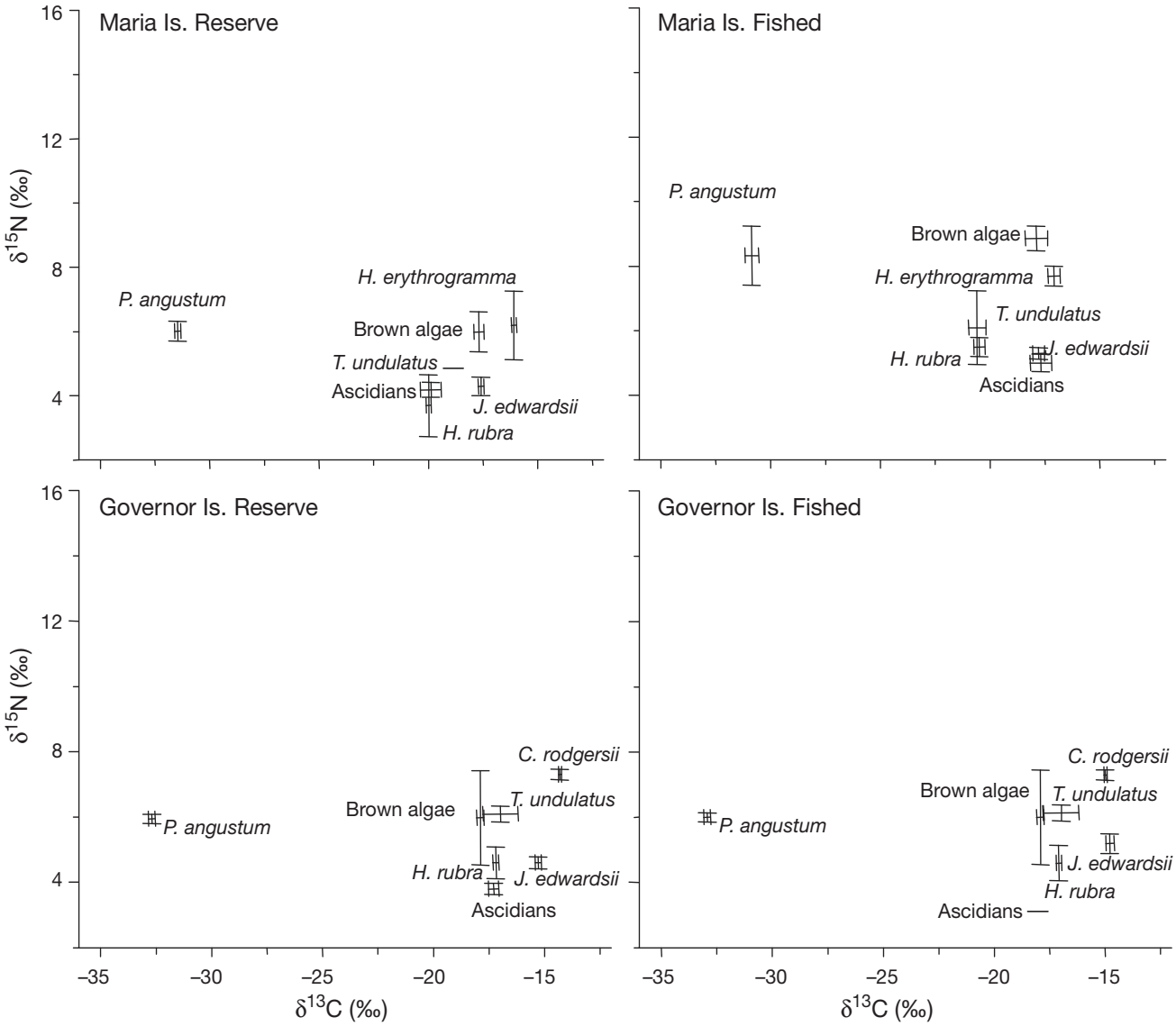

Fig. 3. Mean (±SE) stable isotope values of $\delta^{15}N$ and $\delta^{13}C$ for *Jasus edwardsii* and potential prey items corrected for fractionation (3.5‰ for ^{15}N, and 0.5‰ for ^{13}C per trophic level). Species names are given in full in Fig. 2. *J. edwardsii* is assumed to be 2.5 levels above its autotrophic source; *Haliotis rubra*, *Turbo undulatus*, *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* are assumed to be 1 level above; and the remaining ascidians are assumed to be 1.5 levels above their autotrophic source. These values were used in the IsoSource mixing model. Values are shown for reserve and fished treatments for each bioregion. Isotope values for Governor Island were unavailable for some species/phyla. For reserve areas, the red alga *Plocamium angustum* and the sea urchin *C. rodgersii* are from Governor Island fished locations; for one fished area, the turbinid *T. undulatus* and brown algae are from Governor Island reserve (n = 1). For *T. undulatus* at Maria Island reserve areas and ascidians at Governor Island fished areas, SE are too small to be seen and are shown as a single horizontal line

dietary patterns in the present study (see Nelson et al. 2002). For all species/phyla combined, at both bioregions and at fished and reserve areas, 78.8 to 82.1% of the total variance was explained by PC1 (Fig. 5). Along PC1 at fished and reserve areas, *J. edwardsii* was always closest to *H. rubra* and *T. undulatus*. Sea urchins and red algae were always furthest from lobsters, and brown algae intermediate between these groups. The major contributing fatty acids to PC1 were similar for each bioregion and reserve treatment (Fig. 5). Of those fatty acids that can indicate dietary contribution, 20:4n-6 and 22:5n-3 were important in distinguishing among species/phyla along PC1, and 20:3n-6, 20:2n-6, 22:6n-3 and 22:5n-3 were important in distinguishing among species/phyla on PC2.

PC2 explained 6.4 to 8.6% of the total variance among species/phyla observed for each bioregion,

Table 1. Results of ANOVAs using $\delta^{13}C$ and $\delta^{15}N$ values for each species/phylum. As there were insufficient replicates of all species/phyla at each bioregion and/or location, species/phyla and bioregion are analysed separately. Data are pooled across location for some species/phyla where there were insufficient data among locations for each treatment to permit analyses. Superscripts (M: Maria Island; G: Governor Island) denote the bioregion(s) analysed. Degrees of freedom are the same for $\delta^{13}C$ and $\delta^{15}N$ and thus only reported once. $\delta^{15}N$ values for *Jasus edwardsii*, *Haliotis rubra* and *Ecklonia radiata* were square root-transformed

Factor	df	$\delta^{13}C$			$\delta^{15}N$		
		MS	*F*	p	MS	*F*	p
Jasus edwardsii							
Reserve effect^{M}	1	0.517	0.13	0.740	0.178	49.49	**0.006**
Location(Reserve effect)	3	3.921	4.74	**<0.001**	0.004	0.12	0.947
Error	41	0.827			0.296		
Reserve effect^{G}	1	0.561	2.11	0.182	0.641	5.29	**0.050**
Error	8	0.265			0.121		
Haliotis rubra							
Reserve effect^{M}	1	0.483	0.01	0.920	1.321	7.44	0.072
Location(Reserve effect)	3	40.70	9.07	**<0.0001**	0.178	5.02	**0.004**
Error	50	4.487			0.035		
Reserve effect^{G}	1	0.055	0.04	0.848	0.014	0.18	0.684
Error	7	1.411			0.078		
Ascidians							
Species$^{M, G}$	1	0.133	0.05	0.824	7.847	1.41	0.244
Error	31	2.663			5.575		
Reserve effect$^{M, G}$	1	8.857	3.72	0.062	3.637	0.64	0.431
Error	31	2.382			5.711		
Heliocidaris erythrogramma							
Reserve effect^{M}	1	4.293	0.31	0.618	11.570	5.76	0.096
Location(Reserve effect)	3	13.953	6.67	**0.001**	2.009	1.19	0.331
Error	40	2.093			1.689		
Brown algae							
Species^{M}	1	35.757	6.74	**0.012**	23.962	2.05	0.587
Error	39	5.599			11.698		
Ecklonia radiata							
Reserve effect^{M}	1	0.082	0.01	0.920	1.231	9.33	0.055
Location(Reserve effect)	3	6.919	0.89	0.458	0.132	0.83	4.984
Error	28	7.759			0.159		
Phyllospora comosa							
Reserve effect^{M}	1.217	0.51	0.550	16.941	2.14	0.281	
Location(Reserve effect)	2	2.397	1.16	0.342	7.915	0.29	0.751
Error	14	2.069			27.122		
Plocamium angustum							
Reserve effect^{M}	1	18.328	0.32	0.631	36.791	34.31	**0.028**
Location(Reserve effect)	2	57.929	3.68	**0.048**	1.072	3.32	0.062
Error	16	15.750			0.323		

fished and reserve areas. Sea urchins and red algae were most remote from lobsters along PC2 and lobsters equidistant between ascidians and *Haliotis rubra*.

PCA of individual species showed that most of the total variance was explained by PC1 for all species (94 to 99%, Table 2). For some species there was insufficient data to allow a comparison of fatty acid profiles between fished and reserve areas at each bioregion. For *Herdmania momus* and *Pyura gibbosa*, ANOVA showed significant differences PC1 scores of fatty acid profiles between species (p = 0.001, Table 2) and subsequent data for each species was pooled across bioregions to test for differences in fatty acid profiles between fished and reserve areas. Differences in the PC1 scores of fatty acid profiles between *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* (p < 0.001, Table 2) and insufficient numbers of each species at a single bioregion meant only a single region for these species was used to test for differences in fatty acid profiles between fished and reserve areas. For each species/phylum analysed separately, the ANOVA on PC1 scores of fatty acid profiles showed no signifi-

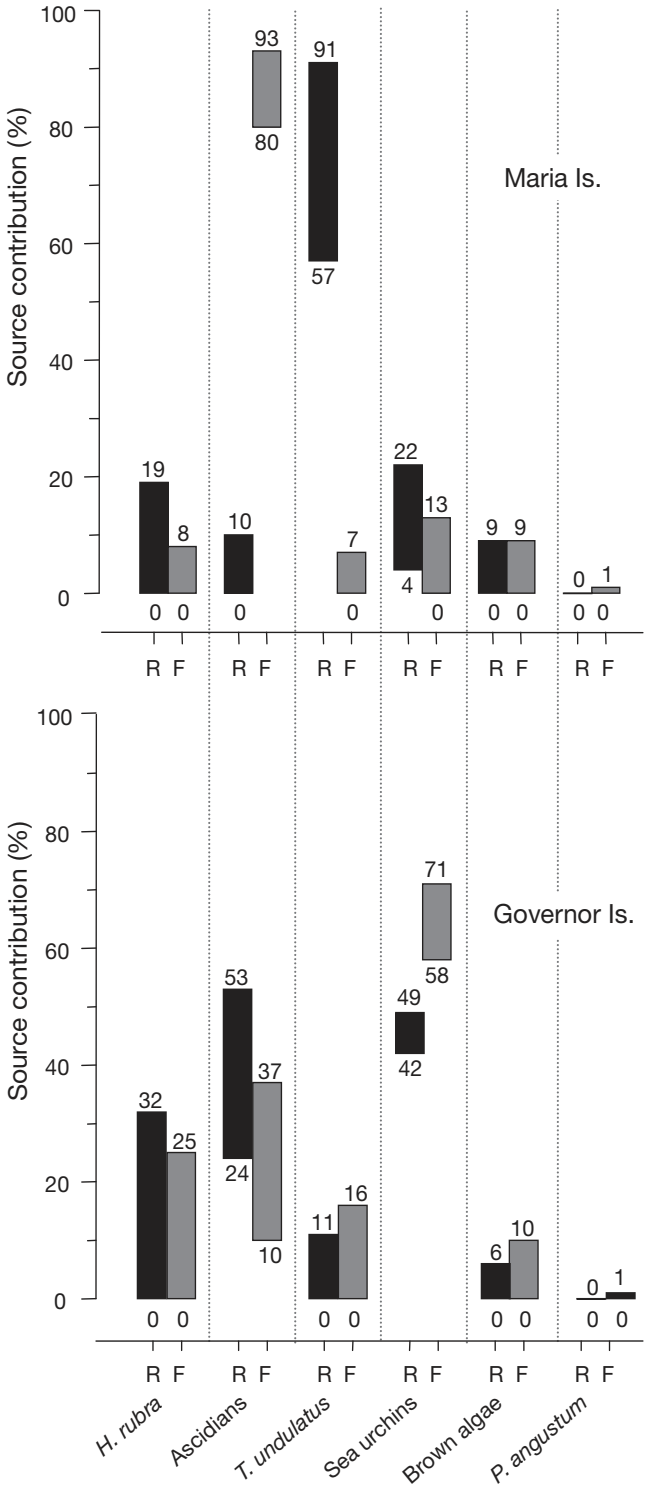

Fig. 4. Range of feasible contributions of the 6 potential food sources to the diet of the southern rock lobster *Jasus edwardsii* after correcting for both ^{15}N and ^{13}C fractionation. Bars are the 1st and 99th percentiles for the distribution of feasible contributions. Species within phyla (i.e. ascidians, sea urchins and brown algae) are pooled where isotopic signatures between species were not sufficiently distinct to be used in the model. See Fig. 2 for full species names. R: reserve area; F: fished area

cant differences between fished and reserve areas (Table 2). PC1 scores based on major fatty acids of *Haliotis rubra* ($p = 0.006$), and *H. erythrogramma* ($p = 0.039$) showed significant differences among locations (Reserve effect × Bioregion), and brown algae showed significant differences among bioregion ($p = 0.010$).

DISCUSSION

More enriched $\delta^{15}N$ values for lobsters in fished areas than in reserve areas at Maria Island and, to a lesser extent, Governor Island, provide direct evidence that the diet of *Jasus edwardsii* differs between areas of low (fished areas) and high (reserve areas) lobster density. The results of the IsoSource mixing model for Maria Island supports this apparent shift in potential food sources with the model indicating lobsters eat a larger proportion of ascidians in fished areas than they do in adjacent reserves. Differences in $\delta^{15}N$ values of lobster could not be attributed to differences in the size of lobsters between fished and reserve areas. *Turbo undulatus* was identified as the dominant food source in reserve areas at Maria Island, and although the results of the mixing model for Governor Island support the importance of ascidians in the diet of lobsters, there was only a slightly greater contribution of ascidians to the diet of lobsters in reserves compared with fished areas. Sea urchins made a similar contribution to ascidians in reserves at Governor Island and were the dominant food source for lobsters in fished areas in this bioregion. Fatty acid profiles of lobsters and potential prey items also highlighted the potential contribution of ascidians but did not suggest any difference in the diet of lobsters in fished and reserve areas. As such, all subsequent comparisons of the diet of lobsters between reserve and fished areas refer to the IsoSource mixing model results. Fatty acid profiles indicating *Haliotis rubra* and *T. undulatus* are important prey of lobsters were consistent with the mixing model results.

Lobster diet: reserve vs. fished areas

More enriched values of $\delta^{15}N$ at fished areas compared with reserve areas suggest that lobsters in fished areas obtain a greater proportion of their diet from higher trophic levels, although such differences are not large. The ascidians *Herdmania momus* and *Pyura haustor* have previously been reported to consume invertebrate larvae (Bingham & Walters 1989) and this is consistent with the higher trophic level assigned to ascidians (*H. momus* and *Pyura gibbosa*) compared with urchins, abalone and the turbinid in the present study. Note that zooplankton was observed to be a common

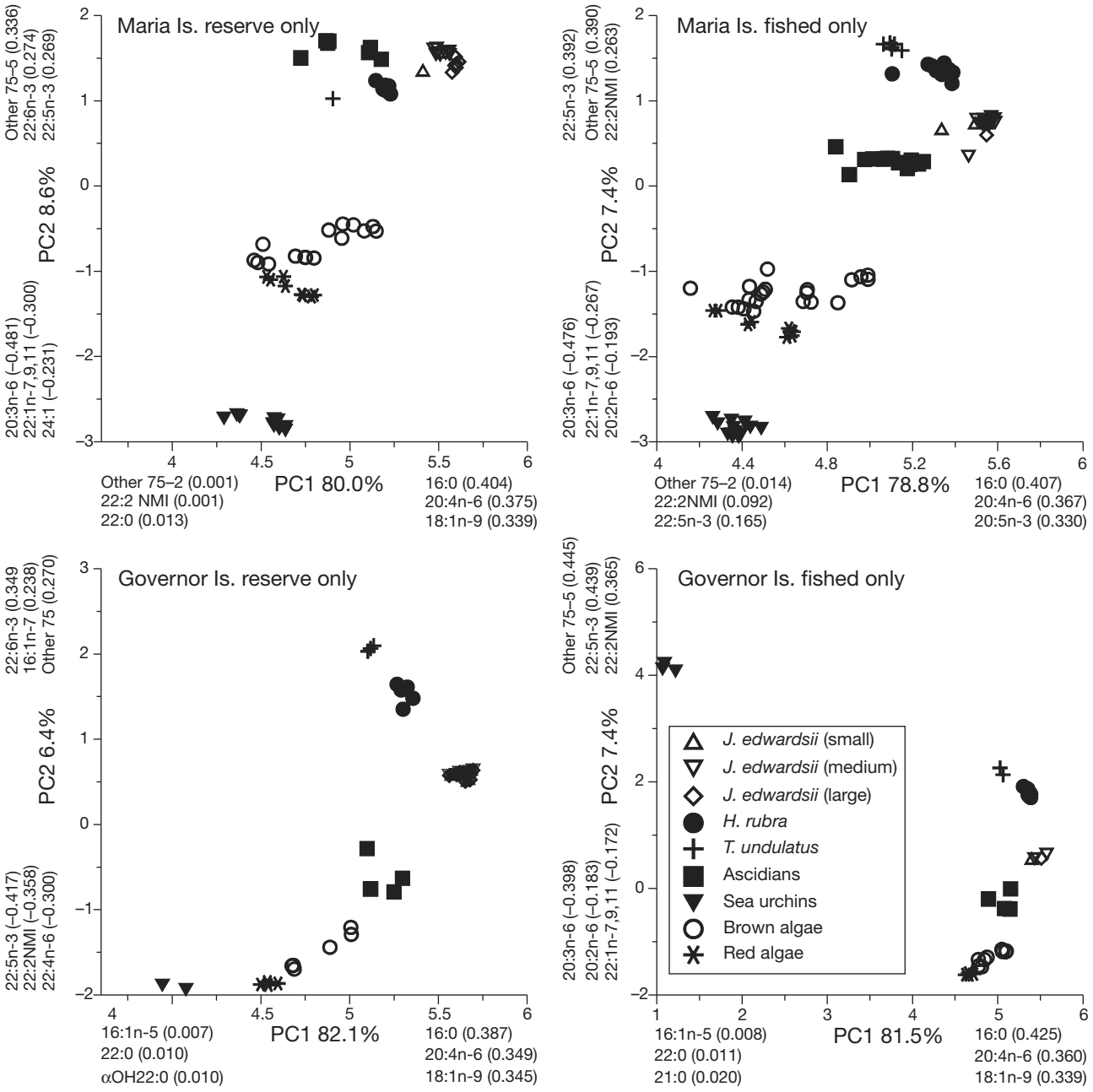

Fig. 5. Ordination of the first and second principal component (PC) scores, and corresponding loading weights (in parentheses) derived from the major fatty acids contributing >1% to the profile of *Jasus edwardsii* and potential food sources (see Fig. 2 for full species names) for Maria and Governor Islands at fished and reserve locations. Percentage variance explained by each component is marked on each axis. Fatty acids listed along each axis are those that contribute most to the distribution of phyla within each region and treatment

component of the planktonic community at the time of *Jasus edwardsii* sampling, suggesting that, at least intermittently, ascidians have access to an invertebrate food source which contributes to their higher trophic status.

Ascidians have been reported as only a minor component in the diet of *Panulirus interruptus* (Castañeda-Fernández-de-Lara et al. 2005) but a wide variety of consumers have been reported to eat ascidians (e.g. gastropods, chitons, sea stars: Kott 1997, Stotz et al. 2003; crabs: Bernárdez et al. 2000). The apparent predominance of ascidians in the diet of *Jasus edwardsii* in fished compared with reserve areas at Maria Island may be due to the reduced competition among lobsters

Table 2. Results of ANOVAs of scores of the first principal component of the main fatty acids for each species/phylum. Data are pooled across bioregion for some species/phyla where there were insufficient data for a reserve effect to be analysed. Superscripts (M: Maria Island; G: Governor Island) denote the bioregion(s) analysed. Degrees of freedom are the same for $\delta^{13}C$ and $\delta^{15}N$ and thus only reported once. Significant differences among species meant that each species was then analysed separately to test for differences among reserve and fished treatments and location nested within each. PC1 scores of *Heliocidariserythrogramma* were square root-transformed

Factor	df	MS	*F*	p	PC1 score
Jasus edwardsii					0.994
Reserve effect	1	0.001	0.08	0.829	
Bioregion	1	0.007	2.73	0.160	
Bioregion × Reserve effect	1	0.001	0.51	0.508	
Location(Bioregion × Reserve effect)	5	0.002	1.42	0.226	
Error	82	0.002			
Haliotis rubra					0.992
Reserve effect	1	0.004	0.26	0.699	
Bioregion	1	0.019	1.24	0.308	
Bioregion × Reserve effect	1	0.017	1.13	0.330	
Location(Bioregion × Reserve effect)	6	0.015	4.34	**0.006**	
Error	99	0.003			
Turbo undulatus					0.995
Reserve effect	1	0.023	1.36	0.452	
Bioregion	1	0.017	3.84	0.121	
Bioregion × Reserve effect	1	0.017	3.70	0.127	
Location(Bioregion × Reserve effect)	4	0.004	1.81	0.168	
Error	19	0.002			
Ascidians					0.961
Species	2	0.688	16.62	**<0.001**	
Error	54	2.170			
Herdmania momus[M,G]					0.987
Reserve effect	1	0.010	0.05	0.822	
Error	28	0.200			
Pyura gibbosa[M,G]					0.965
Reserve effect	1	0.065	2.01	0.187	
Error	10	0.032			
Sea urchins[M,G]					0.992
Species	1	0.200	11.33	**<0.001**	
Error	64	0.018			
Heliocidaris erythrogramma[M]					0.993
Reserve effect	1	0.001	0.86	0.412	
Location (Reserve effect)	3	0.001	3.06	**0.039**	
Error	40	0.0005			
Centrostephanus rodgersii[G]					0.995
Reserve effect	1	0.006	7.62	0.110	
Location (Reserve effect)	2	0.001	0.48	0.625	
Error	16	0.001			
Brown algae					0.992
Reserve effect	1	0.021	1.21	0.470	
Bioregion	1	0.093	13.50	**0.010**	
Bioregion ×Reserve effect	1	0.017	2.52	0.164	
Location (Reserve effect ×Bioregion)	6	0.007	1.13	0.353	
Species	1	0.500	91.69	0.066	
Species ×Reserve effect	1	0.001	3.70	0.305	
Species ×Bioregion	1	0.005	0.67	0.447	
Species ×Reserve effect ×Bioregion	1	0.0003	0.03	0.864	
Species ×Location (Reserve effect ×Bioregion)	6	0.008	1.34	0.249	
Error	81	0.006			
Plocamium angustum					0.994
Bioregion	1	0.013	0.611	0.439	
Error	38	0.021			
Reserve effect	1	0.040	1.59	0.297	
Location (Reserve effect)	3	0.025	1.20	0.322	
Error	35	0.721			

for this food source, and thus the potentially greater availability of ascidians in fished areas. Additionally, the ease with which lobster can capture ascidians may make them an attractive food source given their relatively high levels of omega-3 long-chain ($\geq C_{20}$) PUFA, particularly 22:6 (n-3), which are important for the functioning of the nervous system, adaptive processes and immunity to infections and parasitic diseases (Kolakowska et al. 2003). The absence of seasonality in the abundance of ascidians examined here may also make them an attractive food source to lobsters given their more continuous supply. Whilst there are no data on the potential difference in the density of ascidians between fished and reserve areas, *Herdmania momus* and *Pyura gibbosa* are common species on the east coast of Tasmania. It remains for future studies to examine the potential relationship between ascidian density, nutritional quality and lobster diet.

The slightly higher contribution of ascidians to lobster diet in reserve compared with fished areas at Governor Island, as suggested by the mixing model, contrasts with that recorded at Maria Island, and could be related to differences in the availability of ascidian prey between bioregions. Additionally, the small size of the reserve at Governor Island (~1 km of coastline) may not be sufficient to ensure that the trophic structure in the reserve reflects that of unfished habitat in this bioregion. The role of reserve size in preserv-

ing habitat structure and trophic function in marine systems is poorly understood and beyond the scope of the present study, but is increasingly a topic of examination (e.g. Guest & Connolly 2006, Martins et al. 2007). The greater similarity between the potential contributions of ascidians (and sea urchins) in fished and reserve areas at Governor Island indicates differences in the diet of lobsters may be attributed to differences among bioregion rather than a specific reserve effect.

Sea urchins were also identified as an important food source for lobsters at Governor Island, with a slightly greater contribution to lobster diet in reserves than adjacent fished areas. This is consistent with previous studies that also report sea urchins to be an important food source for lobsters (*Homarus americanus*: Carter & Steele 1982; *Jasus lalandii*: Mayfield et al. 2001; *J. edwardsii*: Andrew & MacDiarmid 1991, Pederson & Johnson 2006). The predominance of lower order sea urchins in the diet of lobsters at Governor Island may account for depleted $\delta^{15}N$ values of lobsters in this bioregion.

At Maria Island, sea urchins contributed less to the diet of lobsters than at Governor Island, irrespective of treatment. The density of *Heliocidaris erythrogramma* is lower at Governor Island (~10 ind. 200 m^{-2}) than at Maria Island (>200 ind. 200 m^{-2}, Barrett et al. 2009), most likely because the more exposed reef at Governor Island is less favourable to *H. erythrogramma* (Underwood et al. 1991, Edgar 2000). It is also possible that lower densities of sea urchins at Governor Island are due to the greater predation on sea urchins by lobsters in this bioregion. However, lower lobster density at Governor Island compared with Maria Island suggests that despite lower sea urchin density (Barrett et al. 2009), there may be sufficient sea urchins available to support lobsters in this bioregion.

Turbo undulatus was a major contributor to the diet of lobsters in reserves at Maria Island, but made minor contributions to the diet of lobsters in fished areas or at Governor Island, regardless of treatment. The density of *T. undulatus* did not differ inside and outside the reserve at Maria Island and thus cannot explain the larger contribution of *T. undulatus* to lobster diet in the Maria Island reserve. The shift by lobsters towards a more molluscan diet, however, indicates the potential influence of protection on lobster diet, and is likely a result of the increase in lobster density on the behaviour and/or density of alternate food sources such as ascidians, abalone and sea urchins. For example, Barrett et al. (2009) hypothesized that the apparent decline in abundance of small abalone in Maria Island reserves could be due to changes in juvenile abalone behaviour which delays the size at which abalone emerge in the presence of more and larger lobsters. Changes in behaviour of potential prey such as abalone, and low or decreased abundance of preferred prey type such as ascidians and sea urchins, may explain the predominance of *T. undulatus* in the diet of lobster at Maria Island reserves. Further work is required to determine if *T. undulatus* also alter their size at emergence in the presence of more and larger lobsters to confirm the validity of this hypothesis. Differences in the contribution of *T. undulatus* between bioregions could be due to the regional availability of this species.

Haliotis rubra was not a major contributor to lobster diet but ostensibly made greater contributions at Governor Island than that at Maria Island. While anecdotal evidence suggests that abalone are a common prey item for *Jasus edwardsii*, there are no studies that demonstrate the relative contribution of abalone to lobster diet. Mayfield et al. (2001), however, indicated that consumption of abalone by *J. lalandii* declined where more preferred food such as mussels were available. In the present study, greater consumption of more preferred and/or easily available food such as ascidians may explain the relatively low contribution of abalone to lobster diet.

Lobster diet: previous studies

Previous characterisation of lobster diet using stable isotope or fatty acid analysis has generally been as a means to describe the nutritional requirements of post-pueruli and juvenile *Jasus edwardsii* in aquaculture to maximize lobster growth rate and condition for commercial exploitation (James & Tong 1997, Crear et al. 2002, Johnston et al. 2003, Ward et al. 2003, Nelson et al. 2004). To date, no other studies have used stable isotopes of either carbon or nitrogen to examine the diet of adult, wild *J. edwardsii*. The fatty acid profile of *J. edwardsii* from the present study is similar to those of wild lobsters used in a previous study to examine nutritional and taste differences between wild and cultured lobster (Nelson et al. 2005).

For some species of lobsters, ontogenetic shifts in diet have been recorded between early and late juvenile stages owing to the different social organisation of these life-history stages (Johnston 2003). We found no evidence of any difference in diet between the lobsters of different size classes (<80, 80–120 and >120 mm CL) examined here. This is most likely due to the similarity in the size of the lobsters and the limitations of chemical tracer techniques in detecting minor shifts in the relative contributions of same-type food sources. For example, wholesale shifts in dietary choices associated with lobsters are usually between pueruli or post-pueruli and juvenile stages, where diets shift from

algal- to invertebrate-dominated (Jernakoff et al. 1993). All of the lobsters examined here were late-juvenile to adult stages, where changes in diet most likely comprise a change in the proportion of existing invertebrate food sources rather than a complete replacement of food types.

Spatial variability in chemical tracers

For some species, $\delta^{13}C$ and/or $\delta^{15}N$ values were significantly different among locations within reserve/fished areas or bioregion, however, the spatial variability of lobsters and other consumers did not track those of their potential food items among locations. Variability in $\delta^{13}C$ values of the red alga *Plocamium angustum* may indicate a difference in carbon source or the rate of productivity of red algae at Location 5, which was more depleted in ^{13}C than other locations sampled. Small-scale spatial variability in $\delta^{13}C$ values of the consumers *Haliotis rubra* and *Heliocidaris erythrogramma* could indicate minor shifts in dietary composition among locations, although for *H. erythrogramma* this is unlikely as shifts in $\delta^{13}C$ values of consumers were not consistent with those of primary producers at the same locations. *P. angustum* and *H. rubra* also showed significant differences in $\delta^{15}N$ values among locations. For *P. angustum*, variation in $\delta^{15}N$ values may be due to differences in nitrogen source (NO_2 or NH_4^+, Peterson & Fry 1987) among locations. For *H. rubra*, differences in $\delta^{13}C$ and $\delta^{15}N$ values among locations were minor and negligible in terms of food web studies, but may suggest minor variation in the proportion of bacterial and macroalgal food sources to the diet of abalone among locations.

Fatty acid profiles exhibited less spatial variability than that of stable isotopes showing no differences among treatments, and only minor differences for a few species among bioregion (brown alga) or location (*Haliotis rubra* and *Heliocidaris erythrogramma*). This suggests that fatty acids are less sensitive to proportional changes in the diet of consumers than those of bulk signal stable isotopes and are best applied to resolve large differences in dietary contribution and separating the role of potential food sources that cannot be discriminated using stable isotopes (e.g. bacteria, Guest et al. 2008).

Resolution of chemical tracers and lobster diet

The present study demonstrates the capacity of stable isotope and fatty analyses as powerful tools in distinguishing between broad phylogenetic groups (e.g. lobster, abalone, sea urchins, brown and red algae, Figs. 2 & 5), and thus determining the relative contribution of those groups to a consumer's diet. The combined chemical tracer approach, however, is limited in distinguishing the contribution of individual species within phyla to the diet of lobsters. Despite being statistically different, the stable isotope and fatty acid values of various ascidian, sea urchin and brown algae species could not be distinguished within their respective phyla for the purposes of trophic analyses (also see Johns et al. 1979, Nelson et al. 2002), and so the dietary contribution of individual species within these phyla remains unclear.

As stable isotopes reveal a bulk signal of all biomolecules present in a sample, the lack of separation in isotopic signatures between species shown in this and other studies is partly explained by the taxonomic and functional similarity of food items (e.g. algae, grazers). $\delta^{13}C$ is most strongly influenced by carbon source and the physiology of the target species (Farquhar et al. 1989, Raven et al. 2002), which may be similar in closely related taxonomic groups. $\delta^{15}N$ values are influenced by the trophic status of a consumer, and become difficult to detect for species of the same or overlapping trophic positions. For example, the isotopic separation of algal species, or the detection of a proportional change to lobster diet (in response to changes in lobster density) is difficult in situations where lobsters are consuming a wide range of food items from differing trophic levels. $\delta^{15}N$ values can also be influenced by diet quality (Vander Zanden & Rasmussen 2001) and can vary between the tissue types of the target species (Pitt et al. 2009). Manipulative feeding trials were beyond the scope of the present study but may help to calibrate the feeding relationships indicated by stable isotopes in the present context.

By contrast, fatty acid analyses reveal the lipid fraction of a consumer diet, which can be labile and vary according to the physiology and nutritional condition of the target species (Ju & Harvey 2004). In addition, the lipid content of the target species may influence the fatty acid profile of the tissues/species being examined (Ju & Harvey 2004), with different fatty acids mobilised at varying rates both within and between species. This variation in lipid content and the mobilisation of individual fatty acids that occurs over different time periods to that of stable isotopes may explain potential differences in the signatures between the 2 techniques. Again, manipulative feeding trials are therefore required to calibrate the feeding relationships observed here.

Previous studies show that the lipid content of most species used in the present study are low in lipids (algae, Johns et al. 1979; abalone, Nelson et al. 2002; lobster, Nelson et al. 2005). For lobsters, lipids in muscular tissues such as walking legs are primarily stored

as phospholipids, which are resilient to short-term changes in environmental and physiological factors (Cockcroft 1997), and are therefore considered useful for understanding longer term dietary changes (Corazze 1999).

Variation in the lipid content and the corresponding fatty acid profile among different tissue types within a single consumer can also indicate the diet of a consumer over different time periods. Here, the use of sea urchin lanterns for fatty acid analysis, compared to lipid-rich gonads thought to be consumed by lobsters, may explain the lower contribution of sea urchins to lobster diet indicated by fatty acid profiles compared with stable isotopes. It would be useful for future work to examine differences in fatty acid profiles of lanterns and gonads to verify the contribution of sea urchins to lobster diet using fatty acid analyses.

CONCLUSIONS

This is the first study to apply the use of combined chemical tracer techniques to examine the trophic effects of removing a significant predator from temperate reefs. The present study compared the chemical tracer profiles of lobsters in fished areas of low lobster density and reserve areas of high lobster density. Differences in $\delta^{15}N$ values of lobsters between fished and reserve areas indicated that lobsters eat a greater proportion of food items from higher trophic levels in fished areas than adjacent reserves. Differences in the stable isotope values between treatments, however, were not large and demonstrate the dietary plasticity of lobsters and the difficulty in evaluating potential trophic cascades in response to fishing pressure. Future application of chemical tracer techniques to detect changes in trophic structure and diet in response to fishing pressure may indicate more pronounced effects for dietary specialists. For generalist predators such as *Jasus edwardsii*, conclusions about fishing effects should be cautious, as it may be difficult to demonstrate potential trophic cascades until there are notable changes in the biota and functioning of reef systems. The present study also provides insight into the diet of wild *J. edwardsii* and is the first to recognise the role of ascidians and turbinid gastropods to lobster diet. Further work is required to identify the species of ascidians important to *J. edwardsii*.

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The following supplement accompanies the article

Trophic effects of fishing southern rock lobster *Jasus edwardsii* shown by combined fatty acid and stable isotope analyses

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Table S1. Mean percentage fatty acid composition (±SE) of *Jasus edwardsii* and potential prey items for fished and reserve treatments. As general linear models showed no significant differences between Maria and Governor Island bioregions (except for brown algae), fatty acid values have been pooled across bioregions for each species. SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids. All double bonds are cis geometry unless otherwise indicated. Asterisks indicate those fatty acids whose identity could not be separated due to chromatographic overlap

Fatty acids	*Jasus edwardsii*	*Haliotis rubra*	*Turbo undulatus*	*Heliocidaris erythrogramma*	*Centrostephanus rodgersii*	*Herdmania momus*
Fished	n=44	n=74	n=20	n=27	n=9	n=26
14:0	1.0 ± 0.1	1.9 ± 0.1	1.0 ± 0.0	3.3 ± 0.2	3.9 ± 0.2	2.5 ± 0.3
i15:0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.0	1.2 ± 0.1
15:0	0.6 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	0.1 ± 0.0	0.5 ± 0.1	1.0 ± 0.1
16:0	12.9 ± 0.2	19.9 ± 0.1	23.5 ± 0.4	9.1 ± 0.2	7.8 ± 0.3	13.1 ± 0.9
17:0	1.2 ± 0.0	1.9 ± 0.0	1.8 ± 0.1	0.1 ± 0.0	0.3 ± 0.0	1.1 ± 0.0
18:0	6.4 ± 0.1	6.2 ± 0.1	6.5 ± 0.2	5.0 ± 0.1	2.6 ± 0.1	4.3 ± 0.1
20:0	0.7 ± 0.0	0.4 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.6 ± 0.1	3.3 ± 0.2
21:0	0.2 ±0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.1
22:0 + OH20:0*	0.7 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	2.0 ± 0.2
Sum SFA	**24.0 ± 0.4**	**31.4 ± 0.3**	**34.6 ± 0.8**	**18.1 ± 0.6**	**16.1 ± 0.8**	**29.8 ± 1.9**
16:1n-7	3.9 ± 0.1	1.5 ± 0.0	1.0 ± 0.1	0.2 ± 0.0	0.6 ± 0.1	3.4 ± 0.3
16:1n-5	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	1.5 ± 0.1	0.2 ± 0.0	0.5 ± 0.0
18:1n-9	16.1 ± 0.4	6.8 ± 0.1	6.3 ± 0.2	1.6 ± 0.0	1.6 ± 0.1	5.1 ± 0.2
18:1n-7	3.5 ± 0.1	7.6 ± 0.1	1.8 ± 0.1	3.5 ± 0.1	2.3 ± 0.1	5.9 ± 0.3
20:1n-7,9,11 + 20:3n-3*	2.4 ± 0.1	2.7 ± 0.1	1.9 ± 0.1	13.6 ± 0.6	19.5 ± 0.4	1.8 ± 0.1
22:1n-7,9,11,13*	0.3 ± 0.0	0.8 ± 0.0	0.0 ± 0.0	4.9 ± 0.3	3.1 ± 0.2	0.9 ± 0.1
Sum MUFA	**26.4 ± 0.8**	**19.7 ± 0.4**	**11.2 ± 0.4**	**25.3 ± 1.2**	**27.3 ± 0.9**	**17.6 ± 0.9**
18:2n-6	1.2 ± 0.0	1.1 ± 0.0	3.4 ± 0.2	0.0 ± 0.0	0.2 ± 0.0	1.9 ± 0.1
18:4n-3	0.5 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	1.4 ± 0.1
20:2n-6	1.2 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 0.1	1.2 ± 0.3	0.4 ± 0.0
20:3n-6 + 20:2 NMI*	0.6 ± 0.1	0.5 ± 0.0	0.3 ± 0.0	11.9 ± 0.3	15.1 ± 0.4	0.4 ± 0.0
20:4n-6	11.1 ± 0.2	11.5 ± 0.1	12.3 ± 0.3	18.5 ± 0.4	14.6 ± 0.6	6.8 ± 0.5
20:5n-3	13.2 ± 0.3	6.1 ± 0.2	3.4 ± 0.2	10.1 ± 0.3	6.2 ± 0.3	9.5 ± 0.5
22:2NMI + C22PUFA*	0.3 ± 0.0	4.6 ± 0.1	1.2 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.2 ± 0.0
22:2NMI2 + 22:4n-3*	0.2 ± 0.0	0.1 ± 0.0	2.9 ± 0.2	0.7 ± 0.1	0.3 ± 0.1	0.1 ± 0.0
22:4n-6	1.4 ± 0.1	2.4 ± 0.0	5.4 ± 0.2	0.0 ± 0.0	0.9 ± 0.1	0.4 ± 0.0
22:5n-3*	2.0 ± 0.1	9.4 ± 0.1	9.7 ± 0.4	0.0 ± 0.0	0.5 ± 0.1	0.6 ± 0.1
22:6n-3	8.7 ± 0.4	0.2 ± 0.0	0.8 ± 0.1	0.0 ± 0.0	1.9 ± 0.3	6.7 ± 0.5
Sum PUFA	**40.5 ± 1.3**	**36.3 ± 0.6**	**39.7 ± 1.5**	**43.2 ± 1.2**	**41.4 ± 2.2**	**28.5 ± 2.0**
Sum Other >1%[a]	**4.4 ± 0.2**	**7.9 ± 0.2**	**9.6 ± 0.3**	**6.7 ± 0.2**	**8.7 ± 0.4**	**9.6 ± 0.9**
Sum Other <1%[b]	**4.8 ± 0.3**	**4.7 ± 0.2**	**4.8 ± 0.4**	**6.7 ± 0.7**	**6.5 ± 1.0**	**12.6 ± 1.2**
Reserve	n=47	n=35	n=7	n=19	n=9	n=5
14:0	1.3 ± 0.1	1.8 ± 0.1	1.1 ± 0.0	3.7 ± 0.3	3.1 ± 0.3	2.2 ± 0.5
i15:0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.0	1.0 ± 0.2
15:0	0.6 ± 0.0	0.7 ± 0.0	1.0 ± 0.1	0.1 ± 0.0	0.6 ± 0.0	0.8 ± 0.1
16:0	12.0 ± 0.2	19.8 ± 0.2	23.2 ± 0.4	8.9 ± 0.2	7.3 ± 0.2	12.7 ± 1.5

Table S1 (continued)

Fatty acids	*Jasus edwardsii*	*Haliotis rubra*	*Turbo undulatus*	*Heliocidaris erythrogramma*	*Centrostephanus rodgersii*	*Herdmania momus*
17:0	1.2 ± 0.0	1.6 ± 0.0	1.5 ± 0.0	0.1 ± 0.0	0.4 ± 0.0	1.0 ± 0.0
18:0	6.6 ± 0.1	6.6 ± 0.1	6.6 ± 0.2	5.3 ± 0.1	2.7 ± 0.1	4.7 ± 0.2
20:0	0.7 ± 0.0	0.8 ± 0.3	0.5 ± 0.0	0.5 ± 0.0	0.7 ± 0.0	3.6 ± 0.4
21:0	0.2 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	1.2 ± 0.3
22:0 + OH20:0*	0.6 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.0 ± 0.0	0.2 ± 0.0	2.0 ± 0.5
Sum SFA	**23.3 ± 0.5**	**31.5 ± 0.7**	**34.3 ± 0.8**	**18.7 ± 0.6**	**15.2 ± 0.7**	**29.2 ± 3.6**
16:1n-7	4.1 ± 0.1	1.4 ± 0.1	0.9 ± 0.1	0.2 ± 0.0	0.6 ± 0.1	2.9 ± 0.5
16:1n-5	0.3 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	1.7 ± 0.1	0.2 ± 0.0	0.4 ± 0.0
18:1n-9	15.7 ± 0.4	7.7 ± 0.2	6.2 ± 0.1	1.7 ± 0.1	1.5 ± 0.1	6.1 ± 0.3
18:1n-7	3.6 ± 0.1	7.8 ± 0.1	1.9 ± 0.1	3.6 ± 0.1	2.3 ± 0.1	4.2 ± 0.3
20:1n-7,9,11 + 20:3n-3*	2.9 ± 0.2	2.8 ± 0.1	2.0 ± 0.1	13.7 ± 0.3	19.7 ± 0.4	1.3 ± 0.1
22:1n-7,9,11,13*	0.4 ± 0.0	0.8 ± 0.0	0.0 ± 0.0	4.1 ± 0.2	3.4 ± 0.2	0.7 ± 0.1
Sum MUFA	**26.9 ± 0.9**	**20.8 ± 0.5**	**11.2 ± 0.5**	**25.0 ± 0.8**	**27.6 ± 0.8**	**15.7 ± 1.3**
18:2n-6	1.1 ± 0.0	1.1 ± 0.0	2.8 ± 0.3	0.1 ± 0.0	0.2 ± 0.0	1.9 ± 0.1
18:4n-3	0.5 ± 0.0	0.4 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	1.2 ± 0.2
20:2n-6	1.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 0.2	1.3 ± 0.3	0.2 ± 0.1
20:3n-6 + 20:2 NMI*	1.0 ± 0.1	0.4 ± 0.0	0.4 ± 0.1	11.7 ± 0.3	14.2 ± 0.4	0.4 ± 0.0
20:4n-6	11.4 ± 0.3	11.9 ± 0.2	11.7 ± 0.7	19.0 ± 0.4	15.4 ± 0.6	8.4 ± 1.1
20:5n-3	13.3 ± 0.3	5.0 ± 0.2	4.9 ± 0.5	9.2 ± 0.3	5.9 ± 0.3	9.6 ± 0.9
22:2NMI + C22PUFA*	0.3 ± 0.0	4.8 ± 0.1	1.1 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.1 ± 0.0
22:2NMI2 + 22:4n-3*	0.2 ± 0.0	0.1 ± 0.0	2.1 ± 0.5	0.7 ± 0.1	0.3 ± 0.1	0.2 ± 0.0
22:4n-6	1.5 ± 0.1	2.8 ± 0.1	5.1 ± 0.5	0.0 ± 0.0	1.0 ± 0.0	0.5 ± 0.1
22:5n-3*	2.0 ± 0.1	8.9 ± 0.2	11.4 ± 0.4	0.0 ± 0.0	0.6 ± 0.0	0.6 ± 0.2
22:6n-3	8.2 ± 0.4	0.2 ± 0.0	0.6 ± 0.1	0.0 ± 0.0	2.3 ± 0.2	8.3 ± 0.9
Sum PUFA	**40.6 ± 1.5**	**35.6 ± 0.8**	**40.5 ± 3.1**	**42.6 ± 1.3**	**41.7 ± 2.0**	**31.4 ± 3.6**
Sum Other >1%[a]	**4.5 ± 0.3**	**8.0 ± 0.3**	**9.7 ± 1.6**	**6.3 ± 0.3**	**8.3 ± 0.5**	**10.3 ± 1.9**
Sum Other <1%[b]	**4.8 ± 0.3**	**4.0 ± 0.3**	**4.3 ± 1.0**	**7.3 ± 0.7**	**7.1 ± 0.8**	**11.9 ± 1.6**

Fatty acids	*Pyura gibbosa*	*Cnemidocarpa radicosa*	*Ecklonia radiata*	*Phylospora commosa*	*Plocamium angustum*
Fished	n=6	n=5	n=36	n=24	n=25
14:0	3.9 ± 0.8	2.7 ± 0.5	6.9 ± 0.3	5.2 ± 0.2	9.5 ± 0.5
i15:0	0.8 ± 0.2	0.6 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
15:0	1.8 ± 0.2	0.8 ± 0.1	0.8 ± 0.0	0.5 ± 0.0	1.1 ± 0.1
16:0	21.4 ± 1.6	16.4 ± 1.0	20.6 ± 0.7	22.3 ± 0.5	55.9 ± 1.1
17:0	1.0 ± 0.2	1.4 ± 0.1	0.3 ± 0.0	0.5 ± 0.2	0.3 ± 0.0
18:0	4.5 ± 0.4	8.0 ± 0.6	1.4 ± 0.2	0.9 ± 0.1	1.2 ± 0.0
20:0	3.9 ± 0.2	1.0 ± 0.1	1.3 ± 0.1	0.6 ± 0.0	0.3 ± 0.0
21:0	1.1 ± 0.4	0.2 ± 0.1	0.0 ± 0.0	0.4 ± 0.1	0.0 ± 0.0
22:0 + OH20:0*	1.1 ± 0.5	0.7 ± 0.1	0.0 ± 0.0	0.3 ± 0.0	3.9 ± 0.3
Sum SFA	**39.4 ± 4.3**	**31.8 ± 2.7**	**31.4 ± 1.4**	**30.8 ± 1.1**	**72.3 ± 2.0**
16:1n-7	5.4 ± 0.4	8.0 ± 0.9	6.0 ± 0.4	5.0 ± 0.2	3.1 ± 0.1
16:1n-5	0.6 ± 0.2	0.9 ± 0.2	0.5 ± 0.0	0.6 ± 0.1	0.0 ± 0.0
18:1n-9	8.1 ± 0.8	7.4 ± 0.5	22.4 ± 0.7	17.6 ± 0.3	1.8 ± 0.1
18:1n-7	3.4 ± 0.4	5.9 ± 0.7	0.3 ± 0.1	0.2 ± 0.0	2.1 ± 0.1
20:1n-7,9,11 + 20:3n-3*	1.5 ± 0.3	0.7 ± 0.1	1.0 ± 0.1	0.8 ± 0.1	1.3 ± 0.1
22:1n-7,9,11,13*	0.7 ± 0.3	0.6 ± 0.1	0.0 ± 0.0	0.2 ± 0.0	0.0 ± 0.0
Sum MUFA	**19.7 ± 2.4**	**23.4 ± 2.4**	**30.1 ± 1.2**	**24.3 ± 0.7**	**8.3 ± 0.3**
18:2n-6	2.1 ± 0.2	2.5 ± 0.1	3.7 ± 0.1	6.2 ± 0.2	0.7 ± 0.0
18:4n-3	2.1 ±0.5	1.8 ± 0.2	7.3 ± 0.6	4.0 ± 0.3	0.0 ± 0.0
20:2n-6	0.1 ± 0.1	0.5 ± 0.0	0.0 ± 0.0	0.7 ± 0.1	0.7 ± 0.0
20:3n-6 + 20:2 NMI*	0.2 ± 0.1	0.5 ± 0.1	0.8 ± 0.0	1.5 ± 0.0	3.6 ± 0.2
20:4n-6	7.4 ± 0.7	4.4 ± 1.0	15.9 ± 0.4	17.7 ± 0.6	6.8 ± 0.6
20:5n-3	8.2 ± 1.3	12.6 ± 1.5	5.3 ± 0.2	5.0 ± 0.3	6.3 ± 0.6
22:2NMI + C22PUFA*	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
22:2NMI2 + 22:4n-3*	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
22:4n-6	1.3 ± 1.0	0.3 ± 0.1	0.0 ± 0.0	0.4 ± 0.0	0.0 ± 0.0
22:5n-3	0.2 ± 0.1	0.4 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
22:6n-3	1.4 ± 0.6	6.9 ± 1.0	0.0 ± 0.0	0.2 ± 0.0	0.0 ± 0.0
Sum PUFA	**23.1 ± 4.5**	**29.8 ± 4.3**	**33.0 ± 1.4**	**36.0 ± 1.6**	**18.1 ± 1.4**
Sum Other >1%[a]	**9.1 ± 1.6**	**5.3 ± 1.5**	**0.2 ± 0.1**	**3.6 ± 0.3**	**0.2 ± 0.0**
Sum Other <1%[b]	**8.7 ± 3.2**	**9.1 ± 2.0**	**5.2 ± 0.6**	**5.3 ± 0.7**	**1.1 ± 0.2**
Reserve	n=6	n=5	n=24	n=18	n=15
14:0	4.5 ± 0.6	1.0 ± 0.4	7.5 ± 0.4	5.2 ± 0.2	9.9 ± 0.5
i15:0	0.9 ± 0.1	0.6 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Table S1 (continued)

Fatty acids	*Jasus edwardsii*	*Haliotis rubra*	*Turbo undulatus*	*Heliocidaris erythrogramma*	*Centrostephanus rodgersii*	*Herdmania momus*
15:0	2.0 ± 0.1	0.5 ± 0.1	0.8 ± 0.1	0.5 ± 0.1	1.1 ± 0.1	
16:0	18.4 ± 0.5	10.3 ± 1.4	22.3 ± 0.3	23.1 ± 0.4	55.4 ± 2.6	
17:0	1.2 ± 0.2	1.4 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	
18:0	4.0 ± 0.5	8.8 ± 0.6	1.1 ± 0.1	0.8 ± 0.1	1.3 ± 0.1	
20:0	4.1 ± 0.3	1.8 ± 0.4	1.3 ± 0.1	0.6 ± 0.1	0.3 ± 0.0	
21:0	1.8 ± 0.2	0.3 ± 0.1	0.1 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	
22:0 + OH20:0*	2.3 ± 0.3	1.1 ± 0.3	0.0 ± 0.0	0.4 ± 0.0	3.4 ± 0.4	
Sum SFA	**39.4 ± 2.6**	**25.9 ± 3.5**	**33.4 ± 1.0**	**31.3 ± 0.9**	**71.7 ± 3.7**	
16:1n-7	4.8 ± 0.4	3.7 ± 1.3	6.3 ± 0.3	4.5 ± 0.3	2.6 ± 0.2	
16:1n-5	0.6 ± 0.0	1.1 ± 0.7	0.5 ± 0.0	0.8 ± 0.1	0.0 ± 0.0	
18:1n-9	7.8 ± 0.5	8.6 ± 0.5	22.1 ± 0.4	18.0 ± 0.4	2.1 ± 0.1	
18:1n-7	2.5 ± 0.2	6.1 ± 1.2	0.4 ± 0.1	0.3 ± 0.0	1.6 ± 0.1	
20:1n-7,9,11 + 20:3n-3*	1.9 ± 0.1	1.3 ± 0.6	1.2 ± 0.1	0.7 ± 0.1	1.1 ± 0.1	
22:1n-7,9,11,13*	1.3 ± 0.1	0.7 ± 0.4	0.1 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	
Sum MUFA	**19.0 ± 1.4**	**21.6 ± 4.7**	**30.6 ± 0.8**	**24.5 ± 0.9**	**7.5 ± 0.5**	
18:2n-6	2.1 ± 0.1	1.6 ± 0.2	3.5 ± 0.1	6.1 ± 0.3	0.6 ± 0.0	
18:4n-3	1.5 ± 0.2	1.3 ± 0.1	6.3 ± 0.5	3.9 ± 0.3	0.0 ± 0.0	
20:2n-6	0.2 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	
20:3n-6 + 20:2 NMI*	0.2 ± 0.1	0.7 ± 0.3	0.8 ± 0.0	1.5 ± 0.0	3.4 ± 0.3	
20:4n-6	7.1 ± 0.5	8.4 ± 1.2	14.8 ± 0.3	18.5 ± 0.7	6.2 ± 0.8	
20:5n-3	5.8 ± 0.7	7.6 ± 1.3	4.5 ± 0.2	4.8 ± 0.3	8.5 ± 1.3	
22:2NMI + C22PUFA*	0.2 ± 0.1	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	
22:2NMI2 + 22:4n-3*	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	
22:4n-6	0.5 ± 0.1	0.4 ± 0.1	0.0 ± 0.0	0.5 ± 0.0	0.0 ± 0.0	
22:5n-3	0.3 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	
22:6n-3	2.8 ± 0.4	3.7 ± 0.9	0.0 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	
Sum PUFA	**20.7 ± 2.3**	**24.2 ± 4.3**	**29.9 ± 1.1**	**36.5 ± 1.6**	**19.1 ± 2.5**	
Sum Other >1%[a]	**8.3 ± 1.3**	**13.0 ± 2.4**	**0.4 ± 0.1**	**2.7 ± 0.2**	**0.5 ± 0.1**	
Sum Other <1%[b]	**12.6 ± 2.9**	**14.5 ± 3.9**	**5.6 ± 0.8**	**5.0 ± 0.8**	**1.2 ± 0.3**	

[a]Other >1%: ·OH16:0 (OH denotes hydroxyl), ·OH21:0, ·OHbranched22:0, 3 fatty aldehydes (derived from plasmalogens; identified by a base peak at m/z 75)

[b]Other <1%: i14:0, 14:1n-7, 14:1n-5, 4,812TMTD (trimethyl tetradecanoic acid), a15:0, 15:1n-6, C16PUFA, i16:0, 16:1n-9, 16:1, 16:2, 16:1n-13t, 7Methyl17:1, i17:0, ,OHbranched15:0, ·OHbranched15:0, a17:0, 17:1n-8, 17:1n-6, 5 fatty aldehydes, 18:3n-6, C18PUFA, i18:0, 18:1n-9, 18:3n-3, 18:1n-7t, ·OH16:1, 18:1n-5, ,OH16:0, i19:0, ·OHbranched17:0, ·OHi17:0, ·OHa17:0, 19:1, ·OH17:0, C20PUFA, 20:2Non Methylene Interrupted (NMI), 20:4n-3, ·OH18:0, 20:1, C21PUFA, 21:5n-3, 21:1, 22:5n-6, 22:3 n-6, 23:0, C24PUFA, ·OH22:1, 22:1, 24:1, ·OH22:0, 24:0

Appendix 8

Evidence of abalone (*Haliotis rubra*) diet from combined fatty acid and stable isotope analyses

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Abstract

Abalone are common herbivores throughout temperate and tropical waters, and yet the contribution of red and brown macroalgae to the diet of wild abalone remains unclear. In the northern hemisphere, adult abalone are considered to consume predominantly brown algae, but in the southern hemisphere abalone are thought to prefer red algae. Conventional methods such as gut content analysis and feeding trials provide some insight into diet choice, but the associated biases of these techniques create uncertainty surrounding the aforementioned variability in abalone diet. We use combined stable isotope and fatty acid analysis to determine the relative contribution of red algae, brown algae and detritus/microalgae to the diet of wild abalone in Tasmanian waters. Stable isotopes of carbon suggest that brown algae and detritus are a more important source of carbon than red algae. Fatty acid analysis confirmed the larger contribution of brown algae to the diet of abalone, and also identified the bacterial and diatom component of detritus to be an important contributor to abalone diet. These results show combined use of chemical tracers to be a promising technique for resolving abalone diet, and challenge current perceptions regarding spatial variability in abalone diet choice.

Keywords: abalone diet, macroalgae, stable isotopes, fatty acids

Introduction

Abalone are widely distributed in temperate and tropical waters throughout the world (Lindberg 1992). They are a valued commercial species whose dietary preferences have been variously described, but considerable uncertainty remains as to the contribution of major algal groups to abalone nutrition. In the northern hemisphere, feeding preference trials in aquaria suggested brown algal species (e.g. *Laminaria sinclairii*, *Macrocystis pyrifera*, *Nereocystis luetkeana*, *Egregia menziesii, Ecklonia maxima*) were considered important to abalone diet (*Haliotis rufescens*, *H. fulgens*, *H. midae* Leighton and Boolootian 1963; Barkai & Griffiths 1986; Winter & Estes 1992; Nelson et al. 2002). In the southern hemisphere, feeding preference trials in aquaria indicated red algae (e.g. *Plocamium* sp. *Pterocladia capillacea*, *Asparagopsis armata*) were the preferred food of abalone (*Haliotis rubra*, *H. laevigata*, *H. roei*: see Foale & Day 1992; Shepherd & Steinberg 1992;, Fleming 1995), but brown algae (e.g. *Phyllospora comosa*, *Sargassum* sp.) have been found in the gut of wild abalone (Shepherd 1973b; Wells & Keesing 1989).

Several chemical and physical factors are thought to influence diet preference of haliotids. For example, substantial differences between polyphenolic content of northern and southern hemisphere brown algae (Steinberg 1989) have been linked to diet preference of abalone in these regions (Winter & Estes 1992). In addition, dietary preference of abalone may be influenced by algal toughness (McShane et al. 1994), nutritional value (Fleming 1995), and the abundance and therefore availability of algae to abalone (Shepherd 1973b).

The inherent biases associated with common methods of evaluating abalone diet contribute to the difficulty in clarifying the relative contribution of different algal sources to abalone diet (in combination with, or separate from, an examination of the mechanisms that dictate diet choice). For example, aquaria and *in situ* feeding trials (e.g. Shepherd & Steinberg 1992; Fleming 1995) may introduce artifacts into consumer diet choice (Peterson & Black 1994). Miller and Gaylord (2007) found cages and associated cage-controls to reduce water flow by up to 47% in high-energy subtidal and intertidal environments, thus having the potential to alter feeding behaviour that is dependent on current flow such as that described for *Haliotis laevigata* (Shepherd 1975). A common artifact associated with gut content analysis (e.g. Shepherd 1973b; Wells & Keesing 1989) is that it can overestimate those food items less rapidly digested and underestimate more labile food items (Gee 1989; Dalsgaard et al. 2003; Sheppard & Harwood 2005). For example, brown algae have been found to be digested more slowly in the gut of *H. midae* (Day & Cook 1995) and *H. rubra* (Foale & Day 1992) than red algae, thus limiting the use of gut content analysis as a means to accurately determine the relative contribution of red and brown algae to abalone diet.

Chemical tracers such as stable isotope and fatty acid analyses are means by which the identity of food that is assimilated by a consumer and therefore of nutritional

importance may be determined. The chemical tracer approach has advantages over conventional methods of dietary analysis such as feeding trials and gut content analysis, as it overcomes the need for contrived laboratory conditions and does not require food items to be present in the gut of a consumer for identification. The basis of the chemical tracer approach is that consumers incorporate the marker, or 'signature' of their food source into their somatic and other tissues with minimal or predictable changes providing an integrated record of the main food items in their diet (Peterson 1999; Dalsgaard & St John 2004).

Stable isotope signatures refer to the variation in the ratio of rare heavy isotopes (e.g. ^{13}C, ^{15}N) to the more common lighter isotopes (e.g. ^{12}C, ^{14}N) in the target organism relative to an international standard (Peterson & Fry 1987). As carbon changes very little between successive trophic levels (0–1‰, McCutchan et al. 2003), the carbon isotope can often indicate the ultimate source of primary production at the base of a consumer diet. The nitrogen isotope experiences greater fractionation per trophic level (3-4‰) and is thus used to infer the trophic status of a consumer, but may also reflect nitrogen source (McCutchan et al. 2003). Signature fatty acids include individual fatty acids that are rare, and unique ratios of commonly occurring fatty acids, both of which can be reflected in the fatty acid profile of a consumer. The combined use of stable isotopes and fatty acid analysis therefore gives a greater capacity than that of a single technique to discriminate between potential food sources contributing to the diet of a consumer.

Previous characterisation of abalone diet using stable isotope or fatty acid analysis has generally been as a means to describe the nutritional requirements of juvenile abalone in aquaculture to maximise abalone growth rate and survival for commercial exploitation (Grubert et al. 2004; Su et al. 2006). There have been no studies that have used combined stable isotope and fatty acid analysis to determine the diet of wild abalone. This study uses stable isotopes of carbon and nitrogen and fatty acid analysis to discriminate between the potential role of red and brown algae to the diet of wild abalone on the east coast of Tasmania.

Methods

The diet of wild abalone *Haliotis rubra* was studied at five locations at Maria Island, eastern Tasmania, Australia (Figure 59). Locations were separated by at least one kilometre, and within each location, multiple sites were sampled that were separated by approximately 100 metres to ensure samples were representative of each location (n = 3 for locations 1, 2 and 3 for both stable isotope and fatty acid analyses; n = 3 for locations 4, 5, for fatty acid analyses; and n = 1 for stable isotope analyses). Abalone (mean size 108 mm, ± 3.65 se, range 50–180 mm), were collected from depths of approximately 5–7 metres. Common red algae (*Plocamium angustum*, *P. dilatatum* and *Phacelocarpus peperocarpus*), brown algae (*Ecklonia radiata*, *Phyllospora comosa* and *Durvillaea potatorum*) and detritus were collected at the same locations as abalone and

always at the seven-metre depth interval with the exception of *D. potatorum* which grows more commonly in shallower waters. This species was collected as close to the five-metre depth interval as possible. Edgar and Barrett (1997, 1999) describe the red and brown algal cover at the five-metre depth interval at these locations. On average, red algal species comprised 11–24% of algal cover, and brown algae comprised about 40–80% of algal canopy cover over the six-year period. As abalone may consume live, drift or detrital algal components (via browsing the reef surface, Shepherd 1973b), detrital fragments within the reef matrix were also examined. Detritus in the current context refers to small particulate organic matter that settles into the interstitial spaces within the reef matrix. Chemical tracer profiles of large drift algae were not examined specifically as previous studies have shown that the decomposition of algae over 60–125 days causes only trivial (~1‰) changes in the carbon ratio of the source algal material (Stephenson et al. 1986; Fenton & Ritz 1988). Detritus was collected manually whilst on SCUBA by scraping surface material (sediment, organic matter and microalgae) from sandy patches nested within the reef to a depth of approximately one centimetre using a one-litre collection jar. All samples were frozen after collection.

Samples were thawed and abalone and algal samples rinsed in distilled water prior to processing. Small amounts of encrusting calcareous epiphytic algae were also removed from macroalgae, using a dull razor blade but were not examined as they were considered an unlikely component of abalone diet (Prince 1989). Where present, three samples of each algal species, and at least three abalone were analysed from each site. From each algal sample, tissue was haphazardly selected from the tip, midline and lower portion of each frond. A two cubic centimetre section of muscle was removed from the abalone foot, and both abalone and algal samples were freeze dried for 24–48 hours. Dried abalone and algal samples were then ground using a mortar and pestle and partitioned for fatty acid and stable isotope analyses.

Detrital samples for stable isotope analysis were washed through a 125 μm sieve to remove shell grit and large debris, and material passing through the mesh was then washed through a 53 μm mesh. Material retained on this mesh was added to a test tube containing colloidal silica (LUDOX™, density = 1.21), which was shaken to facilitate the separation of remaining infauna. Infauna floated to the surface and could be manually removed from the mixture. The remaining detrital fragments were again rinsed through a 53 μm mesh to remove the colloidal silica. Inspection of the remaining detrital sample showed it to be mainly small fragments of macroalgae and some diatoms. Detritus was then placed into tin capsules for subsequent stable isotope analysis. Sulfurous acid was added to each tin capsule to remove any remaining carbonates and bicarbonates. The ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ for all samples were calculated as the relative per mil (‰) difference between the sample and the recognised international standard (Pee Dee belemnite carbonate for carbon; air for nitrogen) and analysed on an Isoprime mass spectrometer. Precision of the mass spectrometer calculated from duplicate samples was 0.2‰.

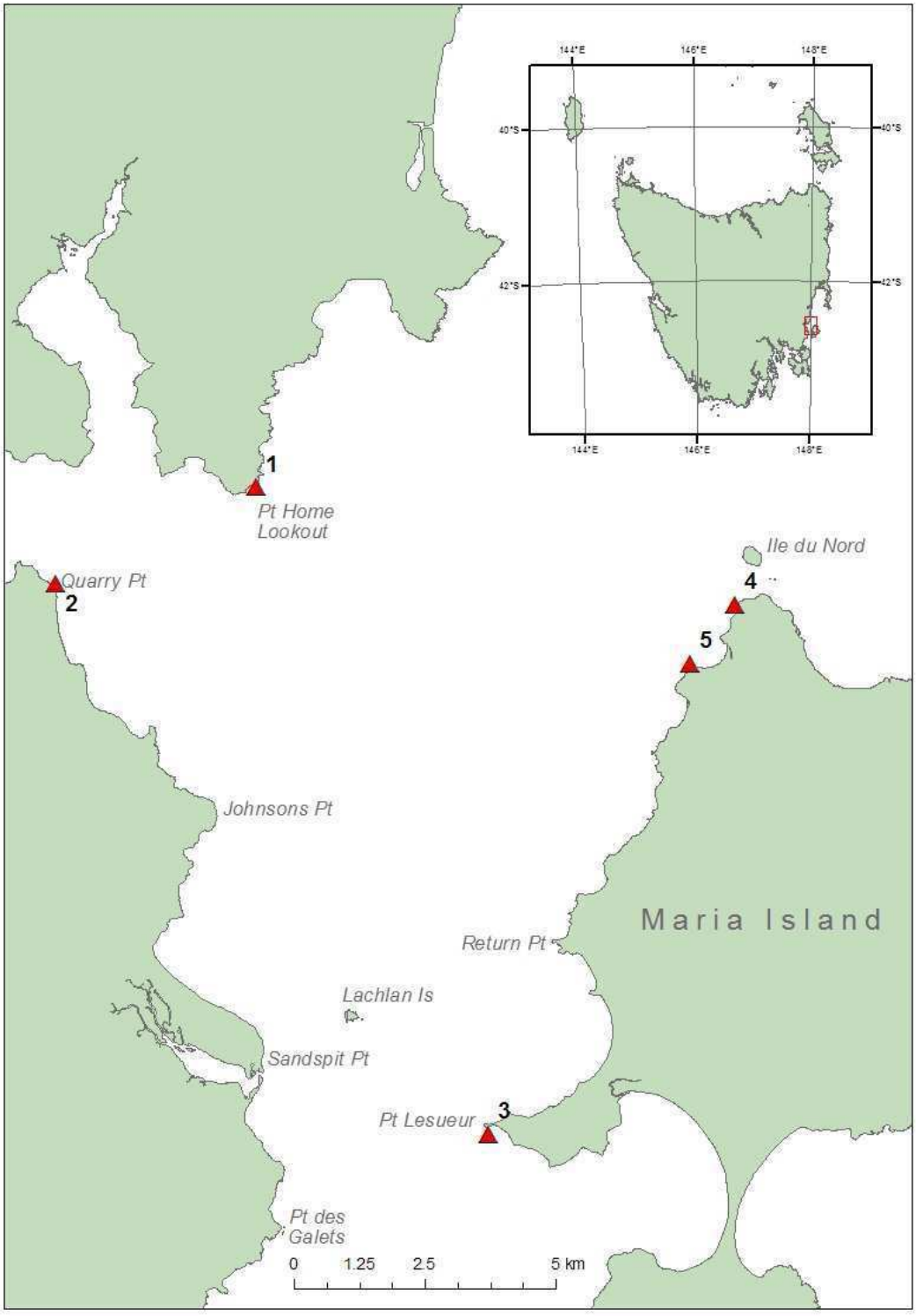

Figure 59 Sampling locations (numbered 1–5) in Mercury Passage, Maria Island Tasmania

Wet detrital samples, and 15 milligrams of each dried abalone and algal samples, were trans-methylated to produce fatty acid methyl esters (FAME) using methanol–chloroform–conc. hydrochloric acid (10:1:1, 80°C, 2 hr). Direct trans-methylation of

samples has previously been validated against conventional methods (Christie 1982) for a microheterotroph (Lewis et al. 2000) and for striped trumpeter larvae and rotifers (Bransden & Dunstan unpublished data). FAME were extracted into hexane–chloroform (4:1, 3 × 1.5 mL). Gas chromatographic (GC) analyses were performed with a Agilent Technologies 6890N GC (Avondale, Pennsylvania, USA) equipped with an HP-5 capillary column (50 m × 0.32 mm i.d.), an FID, a split/splitless injector and an Agilent Technologies 7683 auto sampler using GC operating conditions previously described (Phillips et al. 2003a). Individual components were identified using mass spectral data (Finnigan Thermoquest GCQ GC-mass spectrometer) and by comparing retention time data with those obtained for authentic and laboratory standards.

Statistical analyses

Stable isotopes

As not all species were present at all locations, species were grouped by phyla. A two-way ANOVA was used to test for differences in isotopic values between phyla (fixed, 3 levels: red algae, brown algae, abalone) and locations (sites pooled, random, 5 levels: locations 1 to 5) (SYSTAT 9 software, SYSTAT Inc Evanstil IL, USA). Differences among locations were not of specific interest, but were included to determine if differences between phyla were consistent across locations. Data were checked for homogeneity of variance using Cochran's test and no transformations were necessary. There were an insufficient number of detritus samples to permit analysis.

Mixing model of abalone diet

Data were first analysed using the carbon isotope values of abalone, red algae, brown algae and detritus averaged across all locations. Carbon isotope values for each algal species were grouped according to phyla, as algal species within each phyla could not be distinguished. As the nitrogen isotope could not distinguish between algal species or phyla, values for nitrogen were not used in the mixing model. Mixing models cannot provide a unique solution where there are more sources than elements. Instead the Isosource model uses the carbon isotope values of abalone, algae, and detritus to calculate the upper and lower limits of the contribution that each food source makes to the diet of abalone (Phillips & Gregg 2003). All possible combinations of each algal/detrital contribution (0–100%) are examined in 1% increments. Combinations that sum to 0.1% of the abalone signature are considered feasible contributions. Results are reported as the distribution of feasible solutions for each food source as recommended by Phillips and Greg (2003). The first percentile and 99th percentile are also given rather than the full range which is sensitive to small numbers of observations on the tails of the distribution (Melville & Connolly 2003). To account for the minor fractionation in carbon experienced by consumers within each trophic level, we adjusted the isotope values of carbon for abalone by 0.5‰ (McCutchan et al. 2003).

Fatty acid profiles

Fatty acid profiles were compared among phyla (abalone, red algae, brown algae and detritus) using principal component analysis (PCA), and location using non-metric multi-dimensional scaling (nMDS) ordinations generated from a Euclidean distance matrix. Analysis of similarities (ANOSIM) was used to identify similarities among locations across phyla. PCA reduces the number of dimensions produced by the large number of variables and uses linear correlations (components) to identify those fatty acids that contribute most to the separation between observed groups (Best et al. 2003). ANOSIM compares ranked similarities between and within groups selected *a priori* using a randomisation test of significance. Pairwise ANOSIM comparisons were made between all locations using 5000 simulations in each case. Fatty acids that contributed a mean of less than 1.0% (of total fatty acids) to the abalone fatty acid profile were omitted from statistical analyses. All analyses were done on percentage composition data and results were confirmed by analysis of mg/g fatty acid data (not shown, but also see Phillips et al. 2003b). Multivariate statistical analyses were done using PRIMER 6 software (PRIMER-E, Plymouth, UK).

Results

$\delta^{13}C$ and $\delta^{15}N$ values were similar between species within algal phyla (Figure 60), but as all algal species were not present at all locations, algal species were grouped into phyla (red and brown algae) for analysis and subsequent modelling of carbon isotope values. There were insufficient samples of detritus (n = 2 for stable isotope analysis, n = 3 for fatty acid analysis) to permit statistical analysis. The $\delta^{13}C$ values of all phyla were significantly different (red algae, -30.0, ± 0.9‰; brown algae, -17.9, ± 0.3‰; and abalone, -19.8, ± 0.3‰, $F = 89.9$, $P < 0.001$), with some phyla differing among locations (Phyla*Location, $F = 2.07$, $P = 0.04$). For example, brown algae were slightly more enriched at two of the five locations, but this difference only accounted for a 0.4 – 0.5‰ enrichment in carbon values. The $\delta^{13}C$ values of detritus (-15.0, ± 1.3‰) were slightly more enriched than the mean value of brown algae (-17.9, ± 0.3‰). The $\delta^{15}N$ values were unable to distinguish between phyla (red algae, brown algae and abalone, $F = 1.55$, $P > 0.10$), but there was a significant difference ($P < 0.001$) among locations.

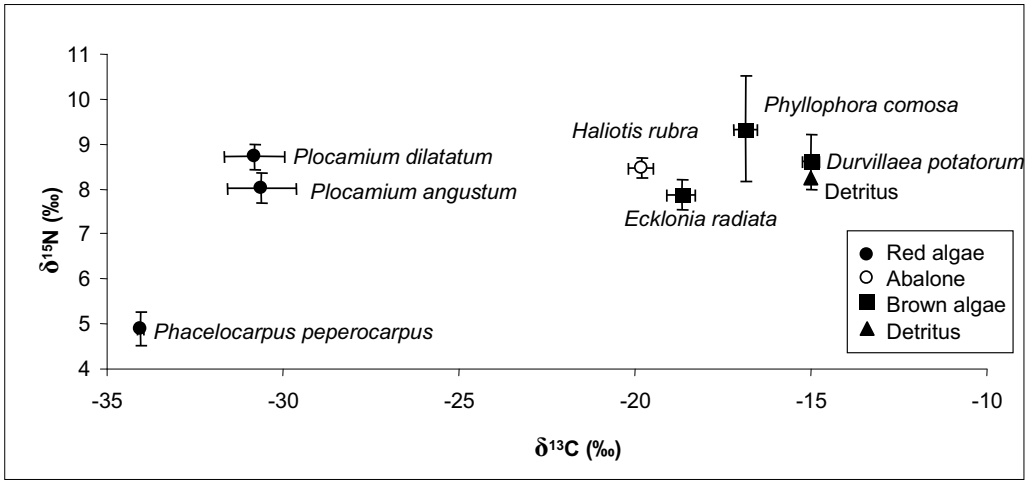

Figure 60 **Mean (± 1 SE) carbon and nitrogen isotope values of abalone, *Haliotis rubra*; red algae, *Phacelocarpus peperocarpus*, *Plocamium dilatatum*, *Plocamium augustum*; and brown algae, *Durvillaea potatorum*, *Phyllospora comosa*, *Ecklonia radiata*.**

Isosource modelling of $\delta^{13}C$ values averaged across all locations showed the range of feasible contributions to be large and uninformative for both brown algae (0–88%) and detritus (0–71%), but more restricted for red algae (12–39%). The lack of separation between the $\delta^{13}C$ values of detritus and brown algae contributed to the large range of feasible contributions calculated using the Isosource mixing model. As such, the mean of brown algae and detritus was calculated and the contributions of red and brown algae/detritus were remodelled using a single isotope, two source mixing model, Isoerror, (Phillips & Gregg 2001) which calculates source proportional contributions and standard errors. Brown algae/detritus (mean -17.8, ± 0.04‰) contributed a mean of 87.5 ± 0.04% of carbon to the diet of abalone, and red algae contributed a mean of 12.5 ± 0.04%.

Fatty acids (FA), 16:0 (19.2 – 55.7% of total FA), 20:5(*n*-3) (5.3 – 10.4%) and 14:0 (5.0 – 9.5%) were the most abundant in all algal and abalone samples with highest percentages found in red algal species (Table 16). Abalone also contained relatively high levels of FA 22:5(*n*-3) (9.5%). 22:5(*n*-3) was generally absent across all other samples with the exception of the brown alga (*Phyllospora comosa* (0.1%) and detritus (0.6%). FAs16:1(n-7)c (0.9 – 13.4%), 18:1(*n*-9)c (1.8 – 30.3%) and 20:4(n-6) (3.1 – 19.3%) were common across all species, with higher percentages present in brown algae. Detritus samples had high percentages of FA 18:1(n-7)c (22.2%), 16:0 (17.6%), 16:1(n-7) (13.4%) and 20:5(n-3) (3.2%).

Table 16 **Mean percentage fatty acid composition (± se) of Algae (by species and by group), abalone and detritus. *n is* sample size, SFA is saturated fatty acids, MUFA is monounsaturated fatty acids, PUFA is polyunsaturated fatty acids.**

Fatty acid	*Plocamium augustum*	*P. dilatatum*	*Phacelocarpus peperocarpus*	All red algae	*Phyllospora comosa*	*Ecklonia radiata*	*Durvillaea potatorum*	All brown algae	Detritus	*Haliotis rubra*
	n = 32	*n* = 6	*n* = 3	*n* = 41	*n* = 27	*n* = 45	*n* = 3	*n* = 81	*n* = 3	*n* = 80
14:0	9.4 ± 0.4	9.5 ± 1.3	4.1 ± 0.2	9.0 ± 0.4	5.0 ± 0.2	6.9 ± 0.3	5.9 ± 0.3	6.2 ± 0.2	0.6 ± 0.1	1.9 ± 0.1
15:0	1.1 ± 0.1	0.0 ± 0.0	0.8 ± 0.1	0.9 ± 0.1	0.5 ± 0.0	0.8 ± 0.0	0.5 ± 0.0	0.6 ± 0.0	1.0 ± 0.2	1.0 ± 0.0
i15:0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.2	0.1 ± 0.0
a15:0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.3	0.0 ± 0.0
16:0	55.7 ± 1.5	55.3 ± 1.1	41.6 ± 1.8	54.6 ± 1.3	21.9 ± 0.3	21.0 ± 0.6	19.2 ± 0.4	21.3 ± 0.4	17.6 ± 0.9	19.9 ± 0.1
17:0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.2 ± 0.2	1.9 ± 0.0
i17:0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.1	0.4 ± 0.0
a17:0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.0	0.1 ± 0.0
18:0	1.3 ± 0.0	1.6 ± 0.1	2.1 ± 0.1	1.4 ± 0.1	0.8 ± 0.1	1.3 ± 0.2	1.9 ± 0.1	1.1 ± 0.1	3.0 ± 0.2	6.2 ± 0.1
20:0	0.3 ± 0.0	0.3 ± 0.1	0.0 ± 0.0	0.3 ± 0.0	0.6 ± 0.0	1.2 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	0.9 ± 0.2	0.5 ± 0.1
22:0	3.8 ± 0.2	0.3 ± 0.1	0.5 ± 0.0	3.0 ± 0.3	0.3 ± 0.0	0.0 ± 0.0	0.5 ± 0.0	0.1 ± 0.0	0.7 ± 0.1	0.2 ± 0.0
Sum SFA	71.7 ± 2.2	67.0 ± 2.7	49.5 ± 2.2	69.4 ± 2.2	29.2 ± 0.7	31.5 ± 1.2	29.5 ± 0.8	30.8 ± 0.8	30.2 ± 2.5	32.1 ± 0.4
16:1(*n*-7)c	2.8 ± 0.1	4.6 ± 0.2	1.9 ± 0.2	3.0 ± 0.1	4.5 ± 0.2	5.5 ± 0.2	0.9 ± 0.1	5.0 ± 0.2	13.4 ± 1.5	1.5 ± 0.0
16:1/16:2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 0.2	0.0 ± 0.0
16:1(*n*-5)c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.1	0.4 ± 0.0	0.1 ± 0.0	0.5 ± 0.0	1.1 ± 0.1	0.3 ± 0.0
17:1(*n*-8)c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	1.1 ± 0.2	0.5 ± 0.0
17:1(*n*-6)c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 0.1	0.1 ± 0.0
18:1(*n*-9)c	1.9 ± 0.1	1.8 ± 0.2	13.1 ± 0.5	2.7 ± 0.5	17.3 ± 0.3	22.5 ± 0.5	30.3 ± 1.1	20.9 ± 0.5	5.4 ± 0.2	6.9 ± 0.1
18:1(*n*-7)c	1.9 ± 0.0	2.5 ± 0.0	2.2 ± 0.0	2.0 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	0.2 ± 0.0	22.2 ± 0.0	7.6 ± 0.1
18:1(*n*-7)t	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.8 ± 0.2	0.1 ± 0.0
20:1(*n*-7,9,11)c	1.1 ± 0.1	1.9 ± 0.5	0.0 ± 0.0	1.1 ± 0.1	0.6 ± 0.1	1.0 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	2.4 ± 0.7	2.6 ± 0.0
24:1	0.0 ± 0.0	0.0 ± 0.0	4.5 ± 0.1	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Sum MUFA	7.8 ± 0.3	10.7 ± 1.2	21.7 ± 1.2	9.2 ± 1.0	23.4 ± 0.7	29.8 ± 1.0	31.9 ± 1.3	27.6 ± 0.8	50.3 ± 4.6	19.7 ± 0.4
18:4(*n*-3)	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	4.6 ± 0.2	7.7 ± 0.5	2.1 ± 0.5	6.3 ± 0.3	0.5 ± 0.1	0.4 ± 0.0
18:2(*n*-3)	0.6 ± 0.0	0.0 ± 0.0	0.8 ± 0.0	0.5 ± 0.0	6.7 ± 0.1	3.7 ± 0.5	9.1 ± 0.1	5.0 ± 0.2	1.2 ± 0.1	1.0 ± 0.0

20:4(*n*-6)	6.5 ± 0.4	8.7 ± 0.4	3.4 ± 0.4	6.6 ± 0.4	19.3 ± 0.5	15.6 ± 0.3	17.2 ± 0.4	17.0 ± 0.4	3.1 ± 0.4	11.4 ± 0.4
20:5(*n*-3)	7.6 ± 0.7	6.5 ± 0.6	10.4 ± 1.8	7.7 ± 0.6	5.5 ± 0.2	5.3 ± 0.2	6.3 ± 0.2	5.4 ± 0.1	3.2 ± 0.9	6.1 ± 0.2
20:3(*n*-6) + 20:2 NMI	3.7 ± 0.2	4.1 ± 0.3	0.0 ± 0.0	3.5 ± 0.2	1.5 ± 0.0	0.8 ± 0.0	0.8 ± 0.0	1.1 ± 0.0	0.6 ± 0.1	0.4 ± 0.0
20:4(*n*-3)	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.0	1.0 ± 0.0	1.0 ± 0.1	0.9 ± 0.0	0.3 ± 0.1	0.1 ± 0.0
20:2(*n*-6)	0.6 ± 0.0	1.2 ± 0.0	0.0 ± 0.0	0.6 ± 0.0	0.7 ± 0.1	0.0 ± 0.0	0.9 ± 0.0	0.3 ± 0.0	0.5 ± 0.0	0.0 ± 0.0
22:4(*n*-6)	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.0	0.6 ± 0.3	2.5 ± 0.0
22:5(*n*-3) DPA	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.2	9.4 ± 0.1
22:2NMI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	4.7 ± 0.1
Sum PUFA	19.0 ± 1.6	20.5 ± 1.8	14.6 ± 2.0	18.9 ± 1.5	39.7 ± 1.2	34.0 ± 1.2	37.4 ± 2.0	36.2 ± 1.2	10.8 ± 2.9	36.1 ± 0.6
*Other > 1%	0.3 ± 0.1	0.0 ± 0.0	13.1 ± 0.8	1.2 ± 0.5	4.1 ± 0.4	0.7 ± 0.1	0.1 ± 0.1	1.9 ± 0.3	1.4 ± 0.2	7.6 ± 0.2
AA/EPA	0.9 ± 0.0	1.4 ± 0.1	0.3 ± 0.0	0.9 ± 0.1	3.6 ± 0.1	3.0 ± 0.1	2.7 ± 0.0	3.2 ± 0.1	1.0 ± 0.8	2.0 ± 0.1
**Other < 1%	1.1 ± 0.2	0.1 ± 0.0	1.2 ± 0.1	1.0 ± 0.2	3.6 ± 0.6	3.9 ± 0.5	1.1 ± 0.1	3.7 ± 0.6	7.3 ± 2.1	4.5 ± 0.2

SFA, saturated fatty acids, MUFA, monounsaturated fatty acids, PUFA, polyunsaturated fatty acids.

*Other >1%: α-OH 16:0, Other 75-5, αOH br22:0, and one unidentified fatty acid

**Other < 1%: i14:0, 14:1(*n*-7)c, 14:1(*n*-5)c, 4,812TMTD, 15:1(*n*-6)c, C16PUFA, i16:0, 16:1(*n*-13)t, 16:1(*n*-9)c, Other, 7Me17:1, αOHbr15:0, C18PUFA, i18:0, 18:3(*n*-6), αOH 16:1, 18:1(*n*-5)c, β-OH 16:0, i19:0, αOHbr17:0, αOHi17:0, αOHa17:0, 19:1, αOH17:0, C20PUFA, 20:2NMI, αOH18:0, 20:1, αOH 18:0, C21PUFA, 21:5(*n*-3), 21:1, 21:0, 22:6(*n*-3) DHA, 22:5(*n*-6) DPA(6), 22:3(*n*-6), 22:2NMI+22:4(*n*-3), 22:1(*n*-7-13)c, 22:0 + OH20:0, αOH21:0, 23:0, C24PUFA, αOH22:1, α22:1 + 24:1, 24:1, αOH22:0, 24:0 and several unidentified fatty acids.

All phyla could be distinguished using principal component analysis (PCA) (Figure 61), and this pattern was consistent with that shown in the nMDS ordination (Figure 62). 95.7% of the variability among phyla was explained by the first three principal components (PC3 not shown). Major contributing fatty acids to PC1 were FAs 16:0, 20:4(*n*-6), 20:5(*n*-3), and 14:0, which explained 72.9% of the total variance. The fatty acid profiles of abalone, brown algae and detritus were overlapping on PC1, whereas red algae could be clearly distinguished. By contrast, red algae were intermediate between abalone, detritus and brown algae on PC2 which explained 19.5% of the variance. Major contributing fatty acids to PC2 were FAs 22:5(*n*-3), 18:1(*n*-7), and 20:4(*n*-6). Abalone and detritus were separated on PC3 which explained only 3.3% of the total variance. Major fatty acids contributing to the separation of abalone and detritus on PC3 were FAs 16:1(*n*-7), 18:1(*n*-7) and 20:4(*n*-6). nMDS showed no separation of fatty acid profiles among sampling sites (not shown), and only minor separation among locations within phyla (Figure 62). The ANOSIM tests showed differences among phyla and location to be significant (Phyla, Global R = 0.98, P < 0.001, Global R for pairwise comparison of phyla ranged between 0.99 and 1.00, P < 0.001, Location. Global R = 0.24, P < 0.001; Global R for pairwise comparison of location ranged between 0.03 and 0.52, P < 0.001).

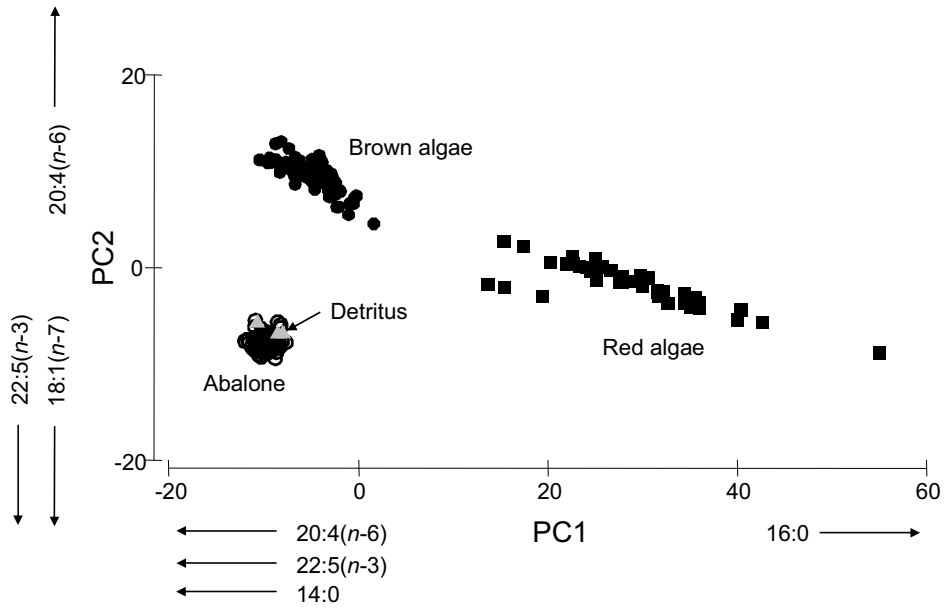

Figure 61 **Biplot of the first and second PC derived from the fatty acid composition of abalone, detritus red algae and brown algae. PC1 explained 72% of the variability between groups. PC2 explained 19.5% of the variability. Arrows indicate fatty acids contributing most to the distribution of phyla along each component.**

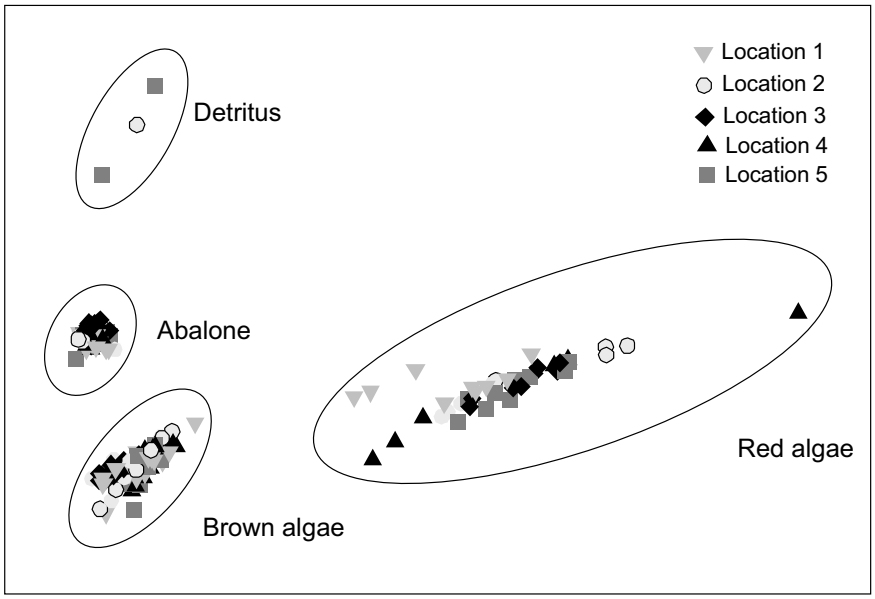

Figure 62 **Two dimensional ordination of nMDS based on Euclidean distance similarities of fatty acid profiles from red algae, brown algae, detritus and abalone (stress = 0.04). Axis scales are arbitrary in MDS and are therefore omitted.**

Discussion

This is the first study to use combined stable isotope and fatty acid analyses to assess the diet of wild adult abalone. Evidence from both stable isotopes and fatty acids indicate that brown algae and detritus (particulate macroalgae, diatoms and bacteria) make a greater contribution to the diet of abalone than red algae. The combined use of stable isotopes and fatty acids provided greater discriminatory power among food sources than that which could be achieved using a single tracer. A summary of the phylogenetic separation achieved using chemical tracer techniques is first presented to provide the context for the subsequent discussion of abalone diet.

Separation of phyla using chemical tracers

There are few studies that report both the carbon and nitrogen isotope values of red algal species, although carbon isotope values of *Plocamium* sp. in the current context are consistent with that reported previously for the same genera (e.g. *Plocamium angustum*,
-30.9‰, Fenton & Ritz 1989, *Plocamium* sp -31.0 to -34.7‰, Raven et al. 2002). Whilst other genera have more enriched carbon isotope values (*Laurencia* spp, -18.0‰, Connolly et al. 2005, *Palmaria palmata*, -16.5 to -21.6, Raven et al. 2002), they commonly have a different morphology to the red algal species examined here. A comparison of $\delta^{13}C$ values among red, brown and green algae showed that most marine macroalgae with $\delta^{13}C$ values of ≤ -30‰, are red algae species (Raven et al. 2002).

Isotope values of carbon for brown algae are typically lighter in $\delta^{13}C$ than red algae (e.g. *Laminaria longicruris* -12 to -20‰, Stephenson et al. 1984, *Macrocystis pyrifera*, -11.1 to -20.7‰, *Ecklonia radiata*, -19.3‰, Raven et al. 2002). Such differences in $\delta^{13}C$ values of red and brown algae are due to different photosynthetic pathways of CO_2 and/or active uptake of HCO_3^- (Farquhar et al. 1989, Raven et al. 2002).

In the current study, it was not possible to separate the carbon isotope value of brown algae from detritus, suggesting that detritus comprised predominantly fragmented brown algal material. Decomposition of *Ecklonia radiata* and *Laminaria longicruris* over a 60–125 day period in previous studies resulted in only minor changes (~1‰) in the $\delta^{13}C$ value of these species (Fenton & Ritz 1988; Stephenson et al. 1986) indicating that detached brown algae may retain its $\delta^{13}C$ values over the short to medium term, and this could explain the lack of separation between detritus and brown algae $\delta^{13}C$ values in the current study. The large biomass of brown algal-derived detritus fragments may also mask any $\delta^{13}C$ contribution from bacteria or microalgae. For example, it is possible that the large biomass of a single macroalgal species, *Durvillaea potaturum* (-15.00 ± 0.25‰) swamped the $\delta^{13}C$ contribution of microalgae and bacteria in the detrital sample (-15.00 ± 1.34‰) due their comparatively small biomass (see Figure 60).

There was little spatial variability in the $\delta^{13}C$ values among locations for all phyla, but the minor variability in $\delta^{13}C$ values observed for brown algae (0.5‰) may indicate a difference in carbon source or the rate of productivity of brown algae located at this site (Guest et al. 2004). Such variability is negligible in terms of food web studies and does not preclude the use of stable isotopes of carbon in the current context.

Whilst there are no data on $\delta^{15}N$ values for the macroalgal species examined here, in a similar reef system, $\delta^{15}N$ values of species within red, brown and green algal phyla were indistinguishable (Vanderklift 2002). Variation in $\delta^{15}N$ values in primary producers are due to differences in nitrogen source (N_2O or NH_4^+, Peterson and Fry 1987), and the similarity in nitrogen values of primary producers among locations suggests that nitrogen source among locations is similar for all macroalgae. There have been no previous studies that report the $\delta^{15}N$ value of wild abalone.

Separation of fatty acid profiles of red and brown algae is consistent with that recorded previously, and confirms the lack of separation among species within each phyla (Johns et al. 1979; Nelson et al. 2002). The separation among all phyla achieved by fatty acid analysis is similar to that of carbon isotope analysis, except that fatty acid profiles could more readily distinguish between detritus and brown algae, primarily due to the presence of distinct bacterial [18:1(*n*-7), Phleger et al. 2005a; Phleger et al. 2005b] and diatom [16:0, 16:1(*n*-7), C16 PUFA, and 20:5(*n*-3), Dunstan et al. 1994, Volkman et al. 1980, Virtue et al. 1993] biomarkers. As PUFA degrade quickly, the relatively low values for 20:5(*n*-3) in detritus indicate that the diatom component of

the detritus was degraded. Additional bacterial biomarkers (C_{15} and C_{17} iso- and anteiso-branched FA) further supported the presence of bacteria in detritus samples, collectively constituting 6% of the total fatty acids present in detritus. Future studies may benefit from the use of sterol biomarkers to further discriminate the identity of macroalgae (e.g. Volkman 1986) in the detritus samples.

The most common fatty acids of wild abalone in the current study are consistent with those of previous studies (Nelson et al. 2002; Su et al. 2006) including the presence of the signature non-methylene interrupted (NMI) fatty acids that occur in abalone and other marine molluscs (Ackman & Hooper 1973). Spatial variability in fatty acid profiles among locations is likely to be attributable to differences in species' composition of algal phyla among locations. Regardless of differences in fatty acid profiles among location, the trophic interpretation of abalone remains unchanged.

Abalone diet

Carbon isotope values provide primary evidence that brown algae and/or detritus contribute more carbon to the diet of abalone than red algae. The lack of discrimination between the carbon isotope values of brown algae and detritus, however, means the Isosource mixing model was unable to quantify the likely contribution of each potential food source. The certainty of results was improved using the combined average of carbon isotope values for brown algae and detritus in the single element, two-source mixing model (Isoerror), which showed brown algae and detritus to be more important in the diet of abalone compared to that of red algae. It is possible that exclusion of other sources such as microalgae or bacteria from the mixing model may overestimate the relative contribution of food sources included in the model, although the comparative dominance of brown algal-derived carbon over red algae to the diet of abalone remains unchanged.

Fatty acid profiles are consistent with those of carbon isotopes and indicate that detritus and brown algae contribute more to the diet of abalone than red algae. Graphical representation of the first two principal components show fatty acid profiles to give greater resolution regarding the contribution of brown algae and detritus, and indicated that diatoms and bacteria are a major component of detritus and are an important source of food for abalone. Shepherd (1973b) also recorded abalone (*H. rubra*, *H. cyclobates* and *H. scalaris*) to consume detritus by browsing on the rock surface and this could be the feeding mode by which detritus is consumed in the current study.

The trophic contribution of brown algae to abalone diet is illustrated by the fatty acid profiles on PC1 which explain 72% of the variability among samples. Brown algae had higher percentages of essential fatty acids (EFA) 20:4(n-6) and 20:5(n-3) than red algae, and this is consistent with the higher percentages of these fatty acids in the profile of abalone. As essential fatty acids must be derived from the diet of a consumer, the

higher proportion of EFA, and therefore higher nutritional value of brown algae compared to red algae, may explain the predominance of brown algae in the diet of abalone (Nelson et al. 2002).

It is possible that other algal species not examined in the current study are the main source of macroalgae for *H. rubra*. For red algae, although carbon isotope values may vary with differing morphology (Raven et al. 2002), fatty acid profiles of red algae are consistent across this phyla (e.g. Dunstan et al. 1996). It is therefore unlikely that sampling a wider range of red algal species would change the relative contribution of red algae to the diet of abalone examined here. Similarly, the lack of discrimination among species for brown algae, using both carbon isotopes (Raven et al. 2002) and fatty acid profiles (Johns et al. 1979), suggests that the combined chemical tracer technique is a robust means by which abalone diet may be examined.

These results obtained from chemical tracer techniques are in contrast to that observed by Shepherd and Steinberg (1992). In a feeding preference trial, three species of abalone consistently ate two red algal species and one corticated brown alga at higher rates than other algal species. Shepherd and Steinberg (1992) proposed that the toughness of laminarian algal species (e.g. *Ecklonia radiata*) and high concentration of unpalatable polyphenolics may explain the low consumption rates of *E. radiata* observed within the feeding trial. For *Haliotis roei*, they concluded that brown algae such as *E. radiata* may be consumed when the more preferred red algae were absent.

In the current context where red algae were a common feature of the reef (Edgar & Barrett 1997, 1999), it is not clear what mechanisms are determining the selection of brown algae over apparently more preferable red algal species noted by Shepherd and Steinberg (1992), Shepherd (1973b, 1975) and others. Clearly, factors that drive abalone diet choice are more complex than algal abundance alone. Nonetheless, it would make an interesting comparison to determine whether abalone residing at depths depauperate in brown algae (i.e. >15–20 m) consume a higher proportion of red algae than that observed here. Given that the polyphenolic content of algae such as *E. radiata* is thought to deter grazing by abalone (Shepherd & Steinberg 1992), it is possible that brown algae such as *Phyllospora comosa* and *Durvillaea potatorum* that are low in polyphenolics compared to *Ecklonia radiata* (Steinberg 1989) are the major algal contributors to the diet of abalone in the current study. Future application of DNA markers (e.g. Deagle et al. 2005a; Deagle & Tollitt 2006) may prove useful in separating the identity of brown algae consumed by abalone at Maria Island, that were unable to be separated using stable isotopes or fatty acids in the current study.

Nutritional value and digestibility are further characteristics of macroalgae considered to play a role in the diet choice of abalone (Shepherd & Steinberg 1992). Nelson et al. (2002) fed specific macroalgal diets to the Californian abalone *Haliotis fulgens* (mean shell length 42–69 mm) to test the importance of fatty acids EPA and AA to the diet of

abalone. Abalone growth rate was linked to temperature, and the highest growth rates occurred in abalone fed the brown alga *Egregia menziesii* compared to those abalone fed red or green algae. *E. menziesii* had highest levels of C20 PUFA and the highest ratio of 20:4(n-6) to 20:5(n-3). Brown algae in the current study also had higher proportions, on average, of C20 PUFA and 20:4(n-6) to 20:5(n-3) than red algae, and it may be this higher nutritional value of brown algae in this study that is an important determinant in its selection.

Bacteria resident in the gut of abalone in this region may also facilitate the digestion of brown algae. For example, bacteria resident in the gut of *H. midae* have been shown to play a role in the digestion of complex polysaccharides commonly found in *E. maxima* and other brown algal species (Erasmus et al. 1997). Kelp-fed animals also appeared to be able to adjust their enzymatic activity to utilize this food source (Erasmus et al. 1997). The role of gut bacteria in facilitating the digestion of brown algae for abalone (*H. rubra*) located at Maria Island requires further study.

This study provides results contrary to some common perceptions about the diet of Australian abalone and potentially provides the first evidence that Australian wild abalone are able to derive a major portion of their nutritional requirements from brown algae. We also confirm the role of diatoms and detrital matter in the diet of abalone. Further work is required to determine the mechanisms driving abalone diet choice. The value of combined chemical tracer approach is demonstrated and offers a promising tool for future dietary studies.

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Appendix 9: Intellectual Property

No commercially valuable intellectual property resulted from this research. Results are provided with no protection or confidentiality.

Appendix 10: Staff

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