FISHERIES BIOLOGY OF THE GIANT CRAB, PSEUDOCARCINUS GIGAS

FINAL REPORT TO THE FISHERIES RESEARCH AND DEVELOPMENT CORPORATION FOR PROJECTS 93/220 & 97/132

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EXECUTIVE SUMMARY

Broadscale and enduring trends in the southern Australian oceanic environment have for 35 million years supported the evolution of *P. gigas* to present day. The crabs lack internal temperature control mechanisms, but live where the steep terrain of the continental margin offers easy access to a cooler or a warmer environment. Their growth and reproduction are inherently linked with the food resources and physical character of where they live. Downslope movement into cooler water is advantageous for energy conservation through a slowing down of metabolism at times when they cannot feed. Upslope movement provides access to more abundant benthic food resources at other times.

Allozyme and then DNA techniques indicated a genetically homogeneous *P. gigas* stock structure. Another commercially exploited crab *H. acerba*, which occupies similar substrates but favours warm temperate waters is genetically the closest to *P. gigas* of all the species examined. *H. armata* an almost identical species to *H. acerba* occurs in Japanese waters and may be a clue that indicates a common Tethyan or West Indo-Pacific ancestor. Perhaps, in the Southern Hemisphere *P. gigas* evolved divergently from *H. acerba,* adapting to the cooler conditions caused by the opening of the Drake Passage and the beginning of the Antarctic Circumpolar Current.

P. gigas occur in a temperature range of 11-17°C, are well adapted for travel, and forage by following the scent of prey carried to it by water movement. Its cardiac and respiratory organs are of sufficient size to provide a large aerobic capacity and legs are protected from wear by broad hard surfaces at the tips. At any given time fishers report the crabs are at a particular depth across many miles of ground. As temperature bands do occur at similar depths over large areas, a plausible explanation for the fishers' observations is to propose that the crabs occupy a thermal niche. As the niche boundaries move, the crabs move within the niche, shallower or deeper. Excepting carrion, food boundaries are static and a function of substrate composition, but temperature is not and varies in a seasonal cycle to which the crabs growth and reproduction is synchronized. Females are captured in greatest abundance on the narrow zone of bryozoan rich substrates which begin at a depth of approximately 120 meters. This type of substrate lies beyond the scouring effects of wave action and becomes progressively muddier until at about 300 metres it grades into all mud. It extends along the entire southern margin of Australia. Circumstantial evidence suggests the females move onto the mud when they moult. Males are captured across a broader depth range than females. Most of the crabs taken as a by-catch of the lobster fishery from waters shallower than 120 metres are of this sex. In the autumn when the oceanic hydrology changes from summer upwelling to winter downwelling, the water becomes warmer and the males move outward, over the shelf into deeper, cooler water. Thus their movement is synchronised with seasonality in a biorhythm that facilitates mate selection in the Autumn and copulation in the Winter when the females have moulted and are in a soft shelled state.

Despite the crabs' largeness and hard shell acting as a deterrent to predators and so eliminating the need for a physical shelter, their occurance is limited by the abundance of food and a temperature suited to their physiology. During moulting the crabs are soft and vulnerable, but their movement to deeper cooler waters to do this, reduces their availability to predators. As their environment becomes less than optimum towards the limits of their range, there is a decrease in moult increment and the maximum size attained.

A major acheivement was the development of a cheap and effective tag that was applied in large numbers by fishers. At the end of the study nearly 18,000 crabs had been tagged and 1,700 recaptured. Their movement was along-shelf into the current except at the end of its range off West Australia where movement increasingly reversed away from the warm temperate environment where its range ends. Journeys of up to 400 km were recorded off West Australia and Victoria/South Australia. Movement into the prevailing current means the millions of larvae they produce are carried back in the opposite direction to replenish the fishing grounds. The timing of hatching, the duration of larval lifetime and the onset of summer upwelling events maximize the effectiveness of this reproductive strategy.

This project established the average female size at maturity for crab populations in each of the states and in a circumstance where the fishery was in its early stages of development, a deliberately conservative interim legal minimum size of 150mm was set, which is well above the average size at which maturity occurs for females. The crabs are highly fecund, store sperm and usually spawn in the years when they do not moult. In West Australia where the crabs mature at a smaller size, a smaller legal minimum length of 140mm was adopted in 1996.

While legal minimum length was based on egg production estimates from females, the issue of male maturity and an appropriate size at which to harvest is problematic as physiological maturity does not automatically mean the male can achieve reproductive success. Males must also become dominant over other rivals to secure a mate and function as an adult. During the transition to functional maturity one of the pincers, usually the right, becomes enlarged and we have described the point at which this occurred in the populations across Australia. We also found from an overall population sample of 80,000 crabs, that in the Autumn the increase in the average male size was due to a greater abundance of individuals that were larger than the size where this enlargement began. These size classes were also present at the same locality where newly moulted females were observed and therefore we propose they are the functionally mature section of the population. We also recognize that the onset of functional maturity is likely to be a dynamic relationship that can change.

The fact that male *P. gigas* grow to more than double the size of females may be attributed to the advantages of having a huge pincer because it allows the crushing of larger prey and so provides access to a wider range of food compared to females. As larger prey are more abundant to shore-ward this difference provides an explanation why males have a wider distribution than females and in an evolutionary sense how a maximization of growth, attainment of giantism and an optimised chance to survive is manifest in the creature we observe today.

Although the moult increment is large, growth is primarily mediated by a reduced frequency of moulting as age increases. Intermoult period estimates for *P. gigas* vary from 3-4 years for juvenile males and females (80-120 mm), with rapid lengthening in time between moulting to approximately 7 years for females and 4.5 years for males at legal minimum length of 150 mm. The female preference to aggregate on the narrow strip of bryozoan substrates means the relative abundance of egg bearers in the sections of the population above and below minimum legal size can be clearly observed and are an artefact of prior fishing history. The implication of the long intermoult, particularly for females, is that the population structure of the commercial fishery will tend to change, older and larger sizes becoming less abundant, with smaller sized recruits taking their place. In areas fished prior to a minimum size or subject to illegal removals full recovery of the population to the intended size structure will take about a decade.

Size distribution is stratified by depth and there are other highly significant differences in size which can be attributed to season and sex. Target depths can range from 75 - 250 fathoms(140 - 450 metres), but fishing operations are usually modified to ensure that the gear can be retrieved consistently. In areas subject to strong currents the depth at which the gear is set may be shallower than the optimum depth for the largest catch. As there are multiple factors that can significantly affect catches, regular communication with fishers is an important precondition for clear interpretation of trends in fishery statistics.

It has not been possible to confidently predict the crab biomass because of the broader dispersal of males out of the target fishery area and the historical inadequacy of catch and effort systems. In order to remedy this a pro-forma catch and effort form was designed to capture information at a whole fishery level and to date has been incorporated in all state fishery agency systems except Victoria.

Management of the crab fishery is a state responsibility, however the Commonwealth controls other fisheries which impact on the crab fishery. The crab fishery can be detrimentally affected by the Commonwealth managed demersal trawl and mesh-netting fisheries which are conducted in the same depth range. Demersal trawl has the deleterious effect of destroying the bryozoan substrates which are the framework for the benthic ecology.

This project could not have been possible without a large investment of research funds in training and the provision of extension materials to an Australia wide network of fishers. Combined with their material resources, existing lines of command and employment structures, consistent quality data was collected across the species range. The data was used to develop an individual based yield, egg and value per recruit model with a user friendly interface "crabsim" which allows a user to test the outcomes of their management choices. The ability to canvas multiple scenarios helps the formulation of management and improves industry confidence.

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1. Introduction

1.1. Background

The Giant Crab *Pseudocarcinus gigas* is distributed along the southern continental shelf of Australia from the Perth canyon in south-western West Australia to central New South Wales (Kailola et al 1993) (Figure 1). It is found at depths from 18 to 400 meters (Winstanley 1979) with the greatest concentration of the population occurring on the outer shelf at depths between 140 to 270 meters (Levings et. al. 1995). This is somewhat deeper than the 100-200 meters recorded by Jones and Morgan (1994) because, prior to the emergence of the targeted fishery, the small quantity of crabs that were taken were generally a by-catch from fishing directed at southern rock lobster (*Jasus edwardsii)*, and as a consequence captured from shallower water.

During 1992-1993, the period immediately preceding this study, the development of more efficient capture methods, exploration of new fishing grounds and improved post harvest methods produced a sufficient volume of product to allow market development. As the demand strengthened, higher prices were paid to fishers and a dramatic increase in fishing effort occurred.

The targeting of a previously underutilized species signified the emergence of an opportunity for diversification within the southern rock lobster fishery at a time when lobster stocks in Western Australia, Victoria and Tasmania were being subjected to high levels of fishing effort. Fisheries managers were considering how to reduce this level of effort. (Windy Harbour-Augusta working group, 1986; Victorian Rock Lobster Management Team, July 1993; Tasmanian Rock Lobster Working Group, March 1993). Fishers and managers believed that a sustainable giant crab fishery would provide an opportunity to spread fishing effort across two species of high value. However, the major impediment to a sustainable crab fishery was the lack of biological information and the absence of an assessment of the effects of exploitation on the species.

Prior to this project *P. gigas* had been little studied, with scant treatment in the literature (Hale, 1927 - 1929; Kailola et al, 1993; Jones and Morgan, 1994), other than recognition that the species showed morphology typical of xanthoids (after Warner, 1977, Jones and Morgan, 1994) with a heavy exoskeleton, relatively large body, large crushing claws, and sexual dimorphism with males having an enlarged right cheliped. Information on the basic biology of the species was non-existent. There was no information on life history, reproductive biology, population structure, feeding ecology, or growth. With the exception of Victoria, catch and effort records were non-existent or had been combined with those for other species. Experimental fishing had been conducted in Victoria (Winstanley, 1979) and Tasmania (Dix and Sumner, 1980) but generally information about the species and the level and geographic distribution of fishing effort was inadequate to manage the resource. It was apparent with the rapid development of the fishery that there was an immediate need to collect the baseline biological information which would be a pre requisite to successful resource management.

1.2. Need

In 1993 when the project commenced, arrangements to regulate the fishery were not clearly defined (see chapter 1.4.1). This and the lack of information on the biology of the species, resulted in the study being strongly supported by the industry. In 1992,

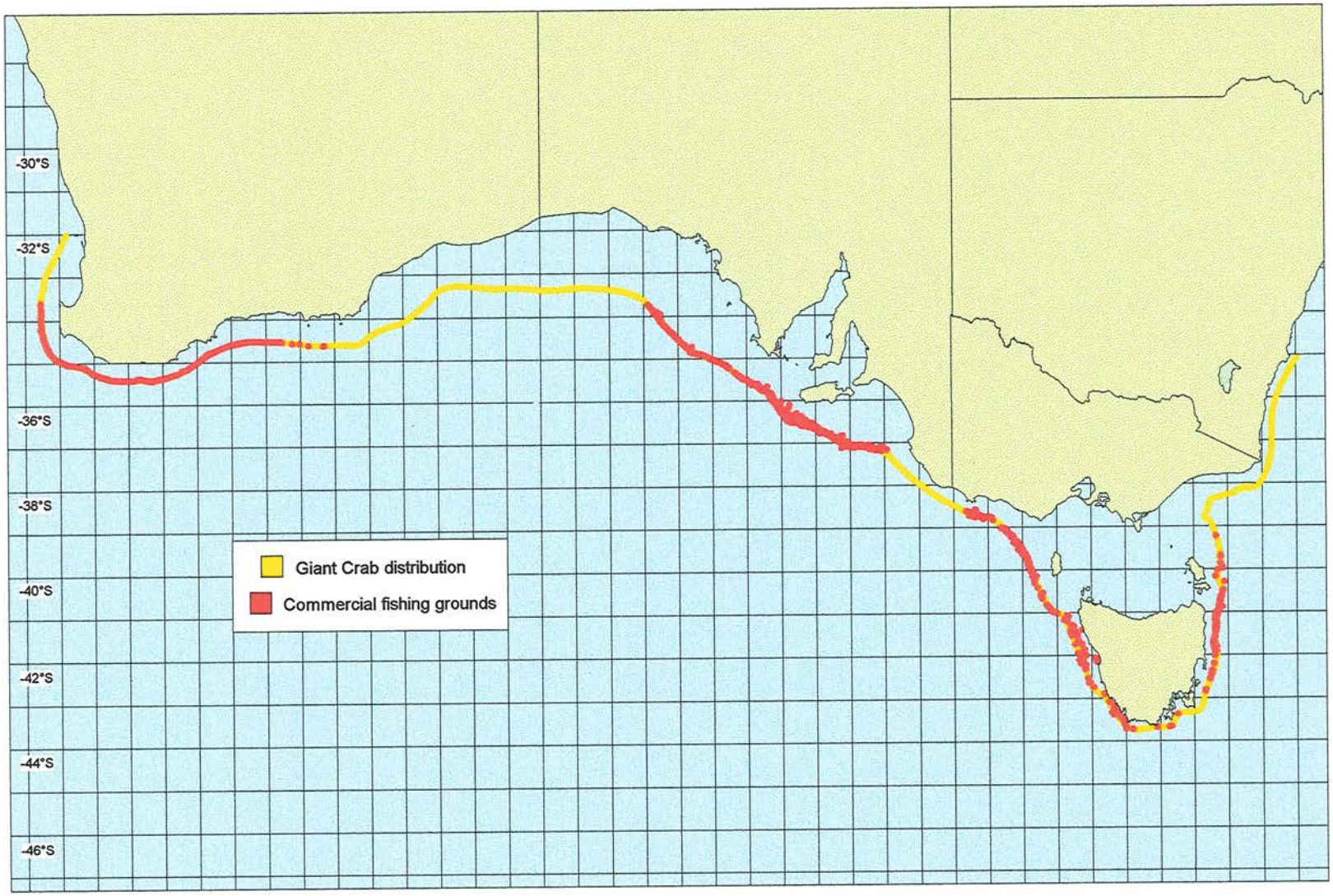


Figure 1: Commercial fishing grounds and geographic range of the Giant Crab

the Australian Southern Rock Lobster Council (an industry forum) recognised the potential for overfishing of the species and recommended the adoption of a national strategy to contain effort and provide the foundation for the establishment of a sustainable fishery. The strategy involved:
(a) An immediate ban on the taking of berried female crabs,
(b) The introduction of interim protective regulations based around existing rock lobster management policies which constrained fishing gear, fishing season and area of access,
(c) The development of a research program to determine biology and stock structure of the species,
(d) The setting of an interim minimum size limit (IMLS) to protect breeding stock.
The subsequent development of this study with the support of the FRDC, is a significant achievement for the Southern Rock Lobster Industry.

1.3. Research Objectives

The objectives of the research program funded in 1993 to run from July 1993 to June 1996, were:
1. To obtain basic biological information on the giant crab across southern Australia (Western Australia, South Australia, Victoria and Tasmania), including reproductive cycle, size at maturity, fecundity, growth, distribution and movement.
2. To determine stock structure of the giant crab across southern Australia using allozyme electrophoresis.
3. To describe the fishery for giant crab in southern Australia and its relationship to the southern rock lobster fishery.
4. To undertake preliminary stock assessment and to assist in the formulation of management recommendations.

Based upon these objectives, specific information needs were determined as summarised in Figure 2. This information was collected via several techniques, which although interrelated, broadly fell into 3 major areas:

- the tagging study,
- at sea sampling,
- interviews, surveys, and catch and effort statistics.

These areas were not entirely independent as research fishing, tagging and catch and effort information are all integral when considering issues of growth and mortality.

Some aspects of the project did not occur as originally intended. Megalopa collection was planned based on the observation that large numbers of crab megalopae were often observed found clinging to the floats and ropes of fishing gear set for rock lobster, within the range of *P. gigas,* were thought to be of *P. gigas.* However, subsequent electrophoretic analysis undertaken during this study showed that they were from another species. Planned work on this aspect ceased in 1999 after a review by state fisheries managers, biologists and the FRDC. (See Chapters 3.4 & 4.3).

Another difficulty encountered, and which is typical of many other areas of study into the Australian fauna and environment, was that the period of funding for the study was shorter than key processes in the species biology (Hamblin, 1991). This study has shown that the female intermoult period is a minimum of 4 years for young adult females and, on the basis of current information, 8 years or more for larger size

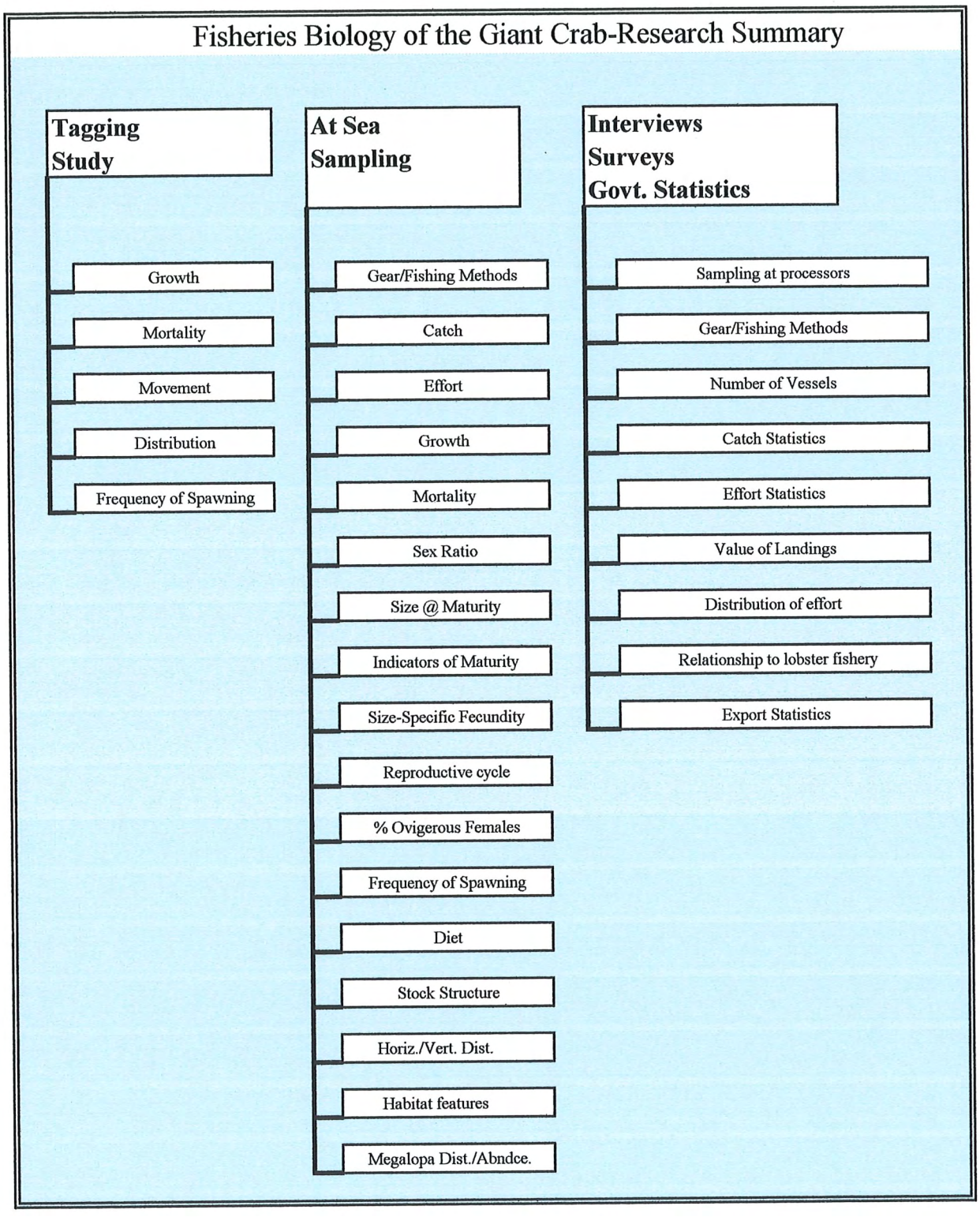


Figure 2. Summary of giant crab research plan

classes. In the absence of intermoult information early in the study, population data could not be adequately analysed and it was only after 4-5years of data was collected that intermoult period could be determined. As Hepper (1967) succinctly stated:

"In a population study a knowledge of the growth rate is essential. In crustaceans estimation of the growth rate is complicated by two factors: first, it is usually not possible to age the animals, and second, the growth rate is made up of two components, the increase in size at moulting and the frequency with which moults occur."

Additional funding was provided to extend the study from 1997 to 2000 and some supplementary objectives were added. Supplementary objectives were added in 1997;

1. To model the fishery using two methods: (a) an individual based model, (b) a spatial dynamic population model patterned after the rock lobster model used in South Australia.
2. To assess moult timing and develop a condition index which can be used for selection of premoult crabs from the wild harvest for holding in sea cages through a single moult to add value.
3. To improve genetic analysis of giant crab populations using DNA analysis in addition to protein based electrophoretic techniques to provide information of high resolution.
4. To opportunistically build and experiment with seafloor collectors to determine the feasibility of catching giant crab larvae.

1(b) and 4 were later dropped from the program with the agreement of the FRDC.

The long-term objective of research into *P. gigas* has been to develop a predictive model of yield from the fishery. However at this stage the distinction between studying the basic biology/population biology of the species and, developing predictive models of the fishery must be quite clear. As pointed out by Cobb and Caddy (1989), marine crustacean fisheries are not stable systems in equilibrium but are dynamic due to fishery and ecological interactions, changes in the physical environment and the development dynamics of the fishery. Accepting that these are the circumstances, an understanding of the relationship between exploitation and population dynamics will require a longer time frame, and it is the shorter-term individual and population biology that is the focus for this work. In the future a more robust analysis of the fishery will be possible as recapture of tagged crabs yields data on growth of larger individuals and catch and effort data collection is improved. To this end a catch and effort pro-forma was developed and is attached as Appendix 2. This has been adapted or incorporated into all state fishery catch and effort systems except Victoria.

The methods used here are primarily length-based, dependent upon the type and quality of data generated from research fishing (see chapter 3) and commercial catch sampling. The data presented were collected from trapping operations and are thus subject to the limitations of the capture technique and the fishing method. Despite these limitations the following outcomes have been achieved during the study period:

- Establishment of a uniform standard of research observations throughout the southern Australian states, by the provision of training materials for vessel captains and observers and the provision of essential data collection equipment. The collection of data across a broad geographic area was achieved through the

voluntary donation of resources of the industry (fishing vessels, gear and employment infrastructure). Ongoing observer supervision and training arrangements used existing lines of command on vessels and empowered vessel captains to train, hire and if necessary fire observers. 24 captains and 72 crew participated in this "crabcare" project. This made the greatly expanded data set possible.

- Determination of morphometric relationships between carapace length and carapace width, carapace length and whole weight, female carapace length and weight of egg mass, male carapace length and claw length.

- Analysis of size, distribution and sex ratio of crab populations at separate localities across southern Australia and derivation of cumulative egg production estimates for these different populations, the average size at maturity for females, onset of potentially sex related allometric growth in males and the quantification of the mean individual size for the different populations across the species range.

- Development of a tag that can be retained through moulting events and a method by which crabs could be tagged in large numbers at low cost. More than 18,000 crabs were tagged and the tag design and method has been adopted internationally.

- Partial description and modeling of growth. Growth modeling is limited only by the time elapsed since tagging began and the growth rate of the crabs.

- Identifying water temperature as an important factor that may affect *P. gigas* behaviour and growth.

- Production of a yield, egg and value per recruit model.

- Adaptation of crustacean moult staging methods to *P. gigas.*

- Determination of the diet of crabs from one geographic area including variation in diet according to size, sex and moult stage and the relationship between diet and the benthic ecology of the collection site.

- Determination of the stock structure by electrophoresis and DNA analysis. DNA studies of the genetic distance between various Australian crab species and *P. gigas* showed that the spiny or champagne crab, *Hypothallassia armata*, which has since been renamed *Hypothallassia acerba* (Koh and Ng, 2000) was the closest relative.

- Determination of the effects of fishing via analysis of changes in catch per unit of effort in specific geographic areas.

- Development of a 3 dimensional spatial mapping capability as an analytical tool to enable description of crab stock density by area and depth, and the production of high quality graphics for extension work.

- Classification of setae colour using the "Munsell" standardised colour system to assist low cost assessment of female reproductive status in the absence of eggs or spent egg casings at times of peak catchability.

- Determination of the economic value of the fishery and the recognition of key parameters underpinning market demand for giant crabs. This has resulted in an increased industry awareness of the physiology of the species and improved handling.

- Increased public awareness of a unique endemic Australian species via newspaper, magazine, radio and television exposure. Extension of scientific work into intergenerational contexts has occurred through talks at schools and via children's mass media such as "Totally Wild".

- Encouragement of other researchers interested in achieving an improved knowledge of the species and the establishment of formal collaborative arrangements with other *P. gigas projects.* This has ensured cost effectiveness and an exchange of information. Thus the overall benefits of research into this species have been maximised.

1.4. Industry and management consultation

1.4.1. Genesis of the Project

The targeted *P. gigas* fishery began in western Bass Strait adjacent to Portland, Victoria, in 1992 and subsequently developed off northwest Tasmania and South Australia. As these fishing operations provided a regular flow of product, markets expanded and demand increased. This research project was conceived by Andrew Levings concurrent with development of the fishery. In April 1992 the Portland Professional Fishermen's Association (PPFA), resolved to pursue the development of a sustainable fishery and took the issue to the annual meeting of the Southern Rock Lobster Council of Australia in July of that year at Apollo Bay, where management and research arrangements were discussed.

It should be noted that during the early years of the fishery's development, statutory arrangements for the management of Commonwealth fisheries were undergoing profound change with the establishment of the Australian Fisheries Management Authority (AFMA). Unendorsed Commonwealth fishing boat licenses, which conferred fishing rights to fish in all areas or fisheries not closed by fishery notices, were being replaced by a permit system, introduced under the new administration to resolve some general difficulties encountered by the Australian Fisheries Service in the development of new fisheries. This situation is outlined in detail in "New Directions For Commonwealth Fisheries Management in the 1990's" (1989).

At the time of the Southern Rock Lobster Council meeting in 1992 a policy vacuum existed in relation to *P. gigas* as the new administrative arrangements had not yet addressed the issue of a fishery for this species. The meeting recommended to AFMA that an immediate ban be placed on the taking of berried females and that future access be limited only to those persons who held a rock lobster license. It supported the development of research into the species and the establishment of an interim minimum legal size (IMLS) for the protection of breeding stock. The IMLS was intended to be reviewed at a later date in the light of improved knowledge. The PPFA

through the Victorian Fishing Industry Federation and the Australian Southern Rock Lobster Council had established a strong base of industry support. It then utilised the resources of the Portland Regional Economic Development Committee and the (then) School of Aquatic Sciences and Natural Resources Management, Deakin University, Warrnambool, to develop a research plan and a funding proposal. The Portland Regional Economic Development Committee used a National Office of Labour Market Adjustment grant to allocate $10,000 to facilitate initial planning. Deakin University, through the Fisheries Research and Development Corporation, secured funding to allow the research program to be delivered. This process took approximately one year to complete.

1.4.2. Relationship with State agencies

In developing a national project, research had to be designed to accommodate existing management arrangements and commercial activity in 5 different jurisdictions. The jurisdictions and areas are listed below, and the options for the conduct of research varied greatly. The jurisdictions were: The Commonwealth of Australia, Western Australia (WA), South Australia (SA), Tasmania (Tas.), and Victoria (Vic.), and within these a total of 10 separate management areas occurred as follows:

1. The WA rock lobster licence fishery, Zone C
2. The Augusta Windy Harbour WA rock lobster licence fishery.
3. The Albany outer zone WA rock lobster licence fishery.
4. The Esperance WA rock lobster licence fishery.
5. The Great Australian Bight outer zone WA rock lobster licence fishery.
6. The Northern Zones of the SA rock Lobster fishery.
7. The Southern Zone of the SA rock Lobster fishery.
8. The Western Zone of the Vic. rock lobster fishery.
9. The Eastern Zone of the Vic. rock lobster fishery.
10. The Tasmanian rock lobster fishery.

Recognising that research funds were limited and that the fishery was relatively small in overall value, one of the challenges faced by this project was to apply the funds that were available to maximum effect. The giant crab program, in its initial budget allocated $20,000 in 1993 and 1994 for the charter of fishing vessels for research fishing. However it was realised that this amount of money would impose severe restrictions on the number of sampling days and perhaps be insufficient to fulfil the program's objectives. Therefore self-funding research fishing operations were negotiated wherever possible. These arrangements are further discussed in Chapter 2.1.2. Initial consultation and then ongoing involvement of State agencies and other research organisations began as follows:

- Meeting with and review of research program and methodology by MAFRI in 1993.
- Discussions with Tasmanian Marine Research Laboratories (now TAFI) re methods and modeling commencing in 1994 with subsequent supply of data, equipment and information throughout the project.
- Discussions with Primary Industries South Australia (now PIRSA) in 1994.
- Discussions with West Australian Fisheries management and researchers 1994.
- Discussions with CSIRO re collaborative work in 1994.

- Discussions with the South Australian Research and Development Institute (SARDI) re a commission for them to develop a model of the fishery in 1996.
- Discussions with AGSO re the use of their bathymetry for the development of a 3 dimensional geographic information system for *P. gigas* facility by this project in 1999.

1.4.3. Relationship with other projects

In addition to the 1993 FRDC funded Deakin University project, the Tasmanian Department of Primary Industry and Fisheries also developed a project in 1994 to investigate aspects of the biology of the Giant Crab. The objectives of that project were to:

- Define general biochemical, histological and physiological patterns of yolk deposition and utilisation during ovarian development and embryogenesis.
- Determine the differences in egg quality from females of different size of moult classes.
- Obtain biological information on reproduction in male crabs, relevant to assessing the impact on the fishery of a reduction in the proportion of males in a population.
- Describe larval morphology, growth and behaviour.

Although some areas of the Deakin University and the Tasmanian project overlapped, this was considered beneficial as it provided a greater coverage of information on growth and maturity across geographic areas at a time when the preconditions for overfishing were developing. Any resources that could be applied to improve knowledge and management were seen as advantageous and where possible the methodologies used were standardised so that information collected could be pooled to yield a more robust analysis. Agreement in principal was reached on joint reporting and this liaison was formalised by a memorandum of understanding signed by the principal investigators of both projects.

1.5. Scope of this project

The project extended across the entire range of the commercial fishery from Cape Naturaliste' in Western Australia to Flinders Island in eastern Bass Strait. When it became clear that a commercially significant population of the species occurred off Western Australia, a supplementary plan for that state was developed and merged with this project.

2. Description of the Fishery

2.1. General Methods

2.1.1. Data Collected

When this fishery began commercial fishers took *P. gigas* under a fishing permit for unregulated fisheries issued under Sub-section 32(1) of the *Fisheries Management Act 1991*. The permit was not termed a crab permit *per se'*, but for this report where the permit was endorsed for giant crab, it will be described as a "giant crab permit" or "crab permit".

Most of the data relating to the *P. gigas* fishery across southern Australia were obtained from at sea sampling of the entire catch, augmented by onshore catch sampling and interviews with fishermen and processors. Fishermen in South Australia, Victoria and Tasmania have provided personal catch records and all state fisheries agencies have provided aggregated catch and effort information.

Catch and effort information was often inadequate for detailed analysis and this reflected the undeveloped support infrastructure for this developing fishery. The various systems for collating catch and effort data across the jurisdictions involved in the project are described below, together with some of the problems that were encountered:

- The Commonwealth did not record giant crab catch and effort information from permit holders. The Bureau of Resource Science's South East Fishery trawl catch statistics show that crabs have been taken but does not record the species of the crab.

- Western Australia's rock lobster catch and effort system recorded area, potlifts per day, species and landed weight. However there are 3 species of crab (spiny crab *H. acerba*, giant crab *P. gigas* and snow crab *C. bicolor*) caught along Western Australia's southern margin and fishing effort for each species is not separated. After 1999 a new logbook was introduced that provided fine spatial resolution, separation of species, pot numbers, soak-time, number of crabs caught, weight of catch and other details.

- In South Australia, crab catch until 1994, was reported by weight in the marine scale logbook. From 1994, crab catch was recorded via the rock lobster catch and effort form, which reports area, potlifts, depth, the number of crabs retained and landed weight. However the two major producers of crab in that state did not hold lobster licences and there was no catch and effort system provided for them other than by the marine scale fishery logbook.

- The Victorian catch and effort system recorded the number of pots set, the date hauled, depth, number of crabs caught, landed weight of crabs, with area recorded in narrow slices of longitude.

- In Tasmania a general fishing log introduced in late 1994 was used where date, area, type of gear, units of gear, units of effort, depth, species, weight and the form in which the product was sold, i.e. whole, gutted, etc. were recorded. In 1999, a new form was introduced that provided fine spatial resolution pot numbers, soak-time, number and sex of crabs, weight of catch and other details.

Victoria's system was superior to those employed in the other states, as catch and effort reporting areas were defined as 10 minute of a degree slices. Combined with depth, the system provides sufficient spatial resolution to study interactions between the giant crab and neighboring fisheries such as the demersal trawl fishery, and shark long lining and mesh-netting fisheries. However, the more recently introduced West Australian and Tasmanian logbooks are major improvements on the structure of all previous information gathering systems.

Based on the information sources described above, this study compiled the following information across the four states with a *P. gigas* fishery:

1. Number of vessels.
2. Geographic distribution of vessels and effort.
3. Gear used and fishing methods, including regional practices.
4. Aggregate catches.
5. Value of landings.
6. Geographic and seasonal distribution of catches.
7. Trends in catch per unit effort.
8. Processing, handling and export methods.
9. Export statistics.
10. Interrelationships with the southern rock lobster fishery, in particular:
    -seasonal effort interrelationships
    -economic interrelationships
    -fishing gear/methods requirements
    -correlation between lobster and crab catches (long-term objective)
    -correlation between catch per unit effort for lobsters and crabs (long-term objective).

Where possible the correlations between *P. gigas* and southern rock lobster were analysed on a regional basis.

A condition of the FRDC funding for this project was that it promoted the development of adequate catch and effort reporting systems by the states. AFMA was asked whether the establishment of catch and effort monitoring systems by the states would be part of the OCS settlement conditions. AFMA's response indicated this was not to be the case. Thereafter the project lobbied for improved reporting but adoption of this was hampered by the slowness of OCS negotiations and it is only recently that improvement has occurred

Independent of the data acquired from government catch and effort systems, the most valuable information for this project has been derived from the recording of the entire catch, including both undersized and sized components from commercial operations and during research fishing. The assessment of the *P. gigas* populations reported herein is largely fishery based and since much of the information has been acquired during a developmental period it should be recognised that the fishing operations resulting in the collection were conducted within the dynamic of:

- An improving their understanding of giant crab habits
- The fishing down of a virgin giant crab stock,

- An improving targeting of the most productive areas before and after the introduction of the interim legal minimum size.

Improved fishing gear, more robust vessels and the advent of global positioning systems complemented this; these factors all contributed to the development of the giant crab fishery.

The largest data set was obtained from the centre of the species range adjacent to Robe (SA) and extending westward to the south of Kangaroo Island. This data has provided a basis for comparison with other less substantial regional data sets and, combined with other knowledge, has enabled the development of propositions about the dynamics of the fishery. The substrates within this region are the most extensively described of all of the giant crab fishing grounds (Bone & James 1993), and the oceanic climate is well known (Lewis 1981, Hahn 1986, Schahinger 1987, Cai Wenju *et al.* 1991). This has greatly assisted interpretation of biological information.

2.1.2. Research Delivery Context

In 1992, prior to the start of the project, preliminary observations indicated that spring sampling would allow the detection of the newly moulted and the egg bearing components of the female population. If for example, sampling occurred in the winter, little information could be gained because the catch consisted predominantly of males, the female population not appearing to be attracted to the traps. In the early summer the onset of fouling crab shells and the cleaning away of spawn remnants, confounds the ability to split the female population into the "newly moulted" and the "ovigerous" components of which it is comprised. Crabs in this study were considered ovigerous if they were carrying eggs or spent egg casings. Thus, the period in which to sample and to obtain the most useful information about females was determined to be the spring. The spring season was usually closed to fishing for lobster and thus the use of traps. As lobster traps and crab traps were often the same piece of gear and with few exceptions a permit to fish for giant crab was generally bundled into an "unsplittable package" with the fisherman's lobster licence, special access permits to conduct research during this period were negotiated with management agencies.

One of the problems inherent in marine research is the major expense of putting vessels and personnel to sea. However solutions to this dilemma had been found in the Southeast Trawl and Scallop fisheries, where research fishing during the closed season has been permitted to be self funding from the sale of a portion of the catch. The initial budget allocated funds for the charter of a vessel for 10 days per year in Victoria only, but as the project expanded across four states, this was inadequate to obtain the amount of data needed. It was unlikely there would be enough funds available to expand pro rata this expenditure. Therefore, with the agreement of state fisheries agencies and AFMA a similar arrangement to that used in the trawl and scallop fisheries was extended to giant crab. This enlarged the closed season sampling program and with the exception of Tasmania (see this chapter below), allowed adequate samples to be obtained. All crabs captured were examined (as in chapter 3.2.2) and the unsaleable and berried portions of the catch returned to the water. In the second year of the project after tags had been developed and an interim legal minimum length introduced, all berried and undersized crabs were tagged before release.

Closed season research fishing was initiated by publicly advertising for expressions of interest, interested parties were identified and then an application made to state fisheries agencies in South Australia, Tasmania, Victoria and to the Australian Fisheries Management Authority, providing details on:

-The fishermen undertaking the research.
-The time of year for collecting samples.
-The area to be fished and sampling strategy.
-The data to be collected.
-The fishing gear to be used.
-The amount of crabs sold to fund the research.
-Any opportunities for collaborative work.
-The crab tagging program.

Fishermen were selected on the basis of experience, suitable vessel, and crab fishing gear and the possession of appropriate licenses. Ideally, fisheries agency staff were to have been involved in data collection as occurred in the first year in Victoria but generally they were unavailable and so observers were recruited from the fishing community and trained by the project officer (A. Levings). In Tasmania, the selection of interested persons was conditional on the approval by the Tasmanian Rock Lobster Fishermen's Association and the Tasmanian Marine Police.

A waterproof sampling guide (for use on deck) which described sampling protocols was provided for vessel captains and observers. This ensured that similar data was gathered across the four states with the project officer routinely monitoring its collection to ensure it was being performed to the standard required and to offer assistance as needed.

The numbers of vessels by state involved in the project were;

Tasmania: 11
Victoria: 4
South Australia: 5
Western Australia: 6

The total number of sampling days available over the study period was thus increased from 60 to 738. The breakdown of days per state is shown in table 1, chapter 3.

The budgetary saving from self-funded research fishing was redirected to:

- Underpinning the commercial integrity of putting extra vessels and staff to sea by having a budget item to offset loss in case of insufficient catch to pay for costs.
- Providing for the employment of a part time office assistant.
- The development of training materials.
- Allowing the project officer greater mobility to oversee an expanded data collection network.

The interim minimum legal size (IMLS) was recommended after discussion by fisheries managers and peak industry body representatives from South Australia, Victoria and Tasmania at a meeting convened by the Victorian Fishing Industry Federation in Melbourne in late 1993. The meeting, timed to occur immediately after the first spring sampling period, recommended that a 150 mm carapace length be set by AFMA as the IMLS. Based on the data subsequently generated by this project, the 150 mm size was found to conserve one half of the cumulative egg production from the crab population. The retention of 150mm as the ILMS was conservative given that the onset of maturity occurred in female crabs of a considerably smaller size and that the size of maturity (SOM) benchmark, defined as the point where 50% of a size class was mature, occurred at around 125 mm.

The practice of underpinning the commercial integrity became particularly important from 1994 onwards off Victoria and northwest Tasmania due to the "fished down" condition of western Bass Strait stocks and the effect of the minimum size rule. The IMLS reduced the saleable component of the research catch from 86% in 1993 to 16% in 1994 and made sampling in Tasmania tenuous. Tasmania, with a maximum of 40 pots allowed per vessel, had relatively smaller pot holdings compared with the other states where 80 or more pots were used. Correspondence with Tasmania's Department of Primary Industries and Fisheries (DPIF), initiated in an attempt to solve this problem resulted in verbal advice that most of DPIF's resources were taken up with the proposed restructure of the more valuable rock lobster fishery. It was also stated that the fishery was under Commonwealth jurisdiction and so nothing would be done until after OCS settlement (pers. comm. W. Ford, W Zacharin, Tasmanian D.P.I.F., May 1994). However DPIF did amend their general fishing logbook later that year to record giant crab catches.

In Western Australia different circumstances required a different approach. The opportunity for self funding research was absent because no closed season on the taking of crabs existed outside of the 200 metres isobath where most of the giant crab population occurred and so observers were paid to collect the data as part of the year round fishery.

In South Australia the crab fishery was developed by two fishermen who did not posses lobster licences. Both of the fishermen were known within their community to have been participating in the fishery prior to the existence of the "lobster fishers only" access policy. The project officer, having been the architect of this policy in 1992 through the Portland Professional Fishermen's Association, sought advice from the Department of Primary Industries of South Australia (PISA) about research delivery, and was referred to the Southern Zone Integrated Management Committee (SZIMC), a rock lobster management group. Separate from this approach, PISA had referred the issue of the crab fishermen's access to the same group who was able to act in a peer review capacity. After consideration of the issue, the SZIMC affirmed the two fishermen's initiative in the development the South Australian fishery and instructed them to assist the FRDC funded giant crab research project. The subsequent contribution of a continuous time series of data by one of the fishermen, K. J. Mathison, that otherwise would not have been available under the project's financial constraints, is of key importance when interpreting less robust data sets from other areas of the fishery.

However the Northern Zone Rock Lobster Fishermen's Association (NZRLFA) entered into a dispute, lobbying both AFMA and PISA to apply the "lobster fishers only" access policy (*retrospectively*) and stop the two crab fishermen from operating. This occurred at a time when the crab fishermen's efforts were demonstrating the existence of a more substantial resource than was previously realised. The NZRLFA was successful to the extent that AFMA determined that the two fishers should stop fishing. It is not clear whether this determination had taken account of the crab fishermen's investment in the fishery prior to the existence of an access policy, or the peer review process by people who had first hand knowledge of their efforts. The South Australia Primary Industries Minister of that time did take account of this and refused to support AFMA's efforts to prosecute the fishermen for alleged "illegal fishing". However following the appointment of a new minister in early 1996, and more generally the Australian National Audit Office's examination of AFMA, it was determined that the South Australian government had signed contractual arrangements with AFMA to provide fisheries enforcement services to the Commonwealth. Irrespective of circumstance, the state had an obligation to comply with these arrangements. Therefore the new South Australian minister advised the crab fishermen to stop fishing, however after the offshore constitutional settlement (OCS) on the 1st January 1997, where jurisdiction for the crab fishery was passed to South Australia, the issue was settled with the two crab fishermen being issued with miscellaneous fishing licences.

For a short period in late 1994, AFMA resisted a request from industry and government in Tasmania and Victoria to not issue more crab permits on the basis of seeking action consistently applied across the whole fishery. The delay in declaring a moratorium on further permit issue allowed continuing opportunity for persons to acquire access, and the number of permit holders increased dramatically to levels that appeared beyond the spatial capacity of the crab fishery. The fishing grounds are a very narrow strip along the continental shelf. In South Australia, despite the extended period of opportunity, only 6 of the 71 Northern Zone fishers took up a crab permit. A more profitable rock lobster fishery mitigated against diversification to crab fishing although the possession of the permit allowed the few deeper water lobster fishers to sell their by-catch of crab. The by-catch was previously discarded but with its sale became classed as a byproduct. (Anon; Environment Australia; Wildlife Protection Act (Regulation of Imports and Exports) 1982; Schedule 4 Guidelines; 2000)

Generally, as the end of the research-funding period approached it became apparent that due to cooperation from governments and very strong industry support, the project had operated substantially under budget. The industry support generated a much larger data set, more participants to train, more information to analyse and many more days travelling than was originally envisaged. Also with the transfer of control of the fishery from commonwealth to states underway, there was a continual demand for advice from stakeholders in the fishery. Future information requirements especially in relation to growth rates, indicated there was a need for continuity in the research effort. The project was extended for 6 months at the end of June 1996, running on the savings it had made previously and a proposal to capitalise on the start that had been made was developed. Backed by industry support in the form of voluntary supply of vessels and data collection valued at $1 million, it won FRDC support and a further 3 years work began from June 1997. (FRDC Project 97-132)

2.2. Number of vessels and geographic distribution of effort.
Although it became clear that only a small number of operators could fit into the thin strip of crab fishing grounds many fishermen applied for access. Whereas previously the crabs had no value and were discarded as a nuisance, or in more extreme cases, treated as vermin and killed; their increasing value led to a desire to keep them and the need to acquire a permit. Some fishermen rarely caught the species or had unsuitable vessels but it was economically rational to take advantage of an opportunity to acquire an access permit. In the future it had the potential to become a capital asset or alternatively could be activated. In the immediate term, it was a legitimate business expense that reduced taxable income.

At the time when the crab fishery was developing, the responsible management agency AFMA, was in it's early days of establishment and had begun what became a complex and protracted set of negotiations about Offshore Constitutional Settlement agreements (OCS's) with the states. It was intended that management responsibility for the giant crab fishery would be passed on to the states and during the delay it appeared that issues related to this fishery within the context of a hierarchy of issues confronting AFMA had minor ranking. As the longevity of the OCS negotiations increased so did the number of persons with access. At the time of the last OCS settlement in January 1998, 229 permits allowing the taking of giant crab had been issued. The distribution by state is illustrated in Figure 3.

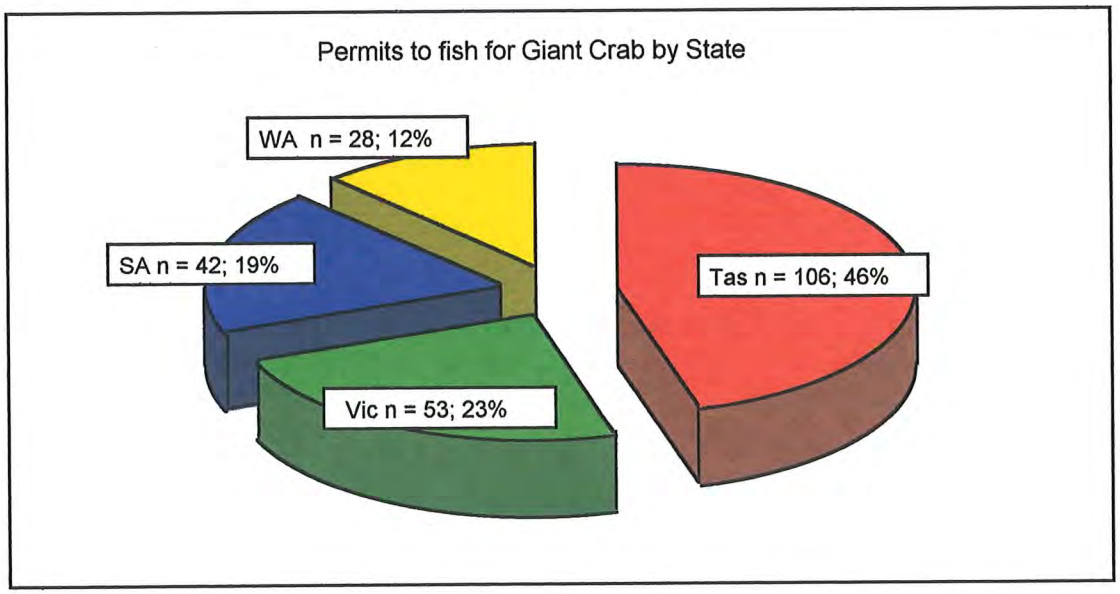


Figure 3. Permits to fish for Giant Crab by state.
Compiled from state fisheries records 2000.

The total number of pots for these vessels has not been calculated and although it may appear on first inspection that there is a large potential for latent effort this is negated by the following.

- Speculative acquisition of the fishing right has not translated into actual participation in the targeted fishery.
- Acquisition of the fishing right has occurred because of the desire to keep and sell the small crab by-catch that is taken while fishing for lobster.

- The higher economic returns from the southern rock lobster fishery in South Australia have mitigated against transferring effort to crab.

- The limited extent of the fishing grounds mean that it is physically impossible for the vessels that *are* sufficiently robust to work offshore into the available area along the shelf break.

In practice many larger Victorian vessels switch their focus from one species to the other according to the economic returns available or other circumstances such as bad weather, the need to miss days on the sea for vessel maintenance and family obligations. The attractiveness of the fishery is that traps set for crab are on softer substrates and will not chafe off in heavy weather. The gear continues to catch during the days it is not hauled or is inaccessible due to the bait remaining intact. Crabs at their adult sizes, unlike lobsters, are not subject to predation by Octopus and Leatherjackets.

In Tasmania, a limitation of 48 hours on soak time and a ceiling of 40 pots (more recently changed to 50 pots) retarded the efficiency of the commercial crab fishery. As stated above, the low pot numbers also made the collection of data tenuous. Upon implementation of lobster quota management in March 1998, the crab fishery was closed to prevent a blow out in fishing effort and to allow the development of a management plan by mid 1999.

2.3. Gear used and fishing methods

Lobster fishermen once considered *P. gigas* a nuisance because they damaged pots and deterred the entry of lobsters. Some fishermen threw them back, others killed them, but in the current decade improved prices and a more enlightened view about the resource's potential has led to a change in attitude.

Improved technology and experimentation has resulted in targeted fishing on deeper sand/mud substrates away from the hard reef areas preferred by lobster. Nearly all deep-water pots are of steel frame construction covered with resilient synthetic netting.
Typical designs are:

Tasmania:
Beehive; 1200 mm base diameter, 700 mm high, 272 mm Ø neck, 70kg.
Beehive; 1000 mm base diameter, 450 mm high, 272 mm Ø neck, 40kg.
Oblong; 1250 mm long, 1000 mm wide, 500 mm high, 272 mm Ø neck, 80kg.

Victoria and South Australia:
Beehive; 860 mm base diameter, 407 mm high, 272 mm Ø neck, 20kg.

West Australia:
Round side entry*; 1400 mm base diameter, 350 mm high, 35kg.
Round top entry; 1400 mm base diameter, 350 mm high, 272 mm Ø neck, 35kg.

** Side entry pots were disallowed in the fishery during 1995. Crab fisherman, G. Pateman, Augusta, West Australia, reported no change in catch rate since moving to top entry and less damage to pots from crabs "chewing their way out" of the (wire*

covered) pots. The side entry ramp acted as a barrier as they walked around the pot's interior, and at this point they began to bite the trap.

Unlike the lobster fishery where pots are hauled once or twice a day, crab pots are immersed for 48 to 72 hours to maximise the catch. Sometimes bad weather or strong tides result in longer soak times. A lice resistant bait such as a hock (cow's foreleg) or hide is used. Whereas much of the catch once comprised larger males and females, taken as by-catch on or next to hard substrates in the 40 to 75 fathom depth range, a smaller size range of crabs are now taken from deeper water. The shift of fishing from shallower reef bottom to deeper softer substrates from 75 fathoms out to 200 fathoms and sometimes deeper has resulted in different fishing techniques.

The soft substrate allows the crab pots to be linked into a long-line with small risk of becoming snagged. Long lining is the best adaptation to prevent gear loss from the relatively stronger tidal pressure in deeper waters. Using this system 10-20 pots are attached to a long-line up to 2 km length which is anchored at either end to prevent the tide sweeping the assembly away. This adaptation minimises the total amount of rope deployed, and an efficient operation capable of turning over at least 100 pots daily occupies long distances along the grounds. For example; 100 pots are long-lined with 10 pots a long-line at 50 fathoms separation. A gap equivalent to the length of one long-line is left between each of the 10 long-lines. This maximises efficiency as the long-lines are progressively hauled and then set as the vessel moves through the gear which occupies a 18 km strip along a target depth strata.

When the crabs are cleared from the pot care is taken to ensure their legs are not crushed or broken off and that the individuals within the pot are separated as best as possible to prevent them injuring each other. Crabs do not autotomise (shed their legs and seal the stump) as readily as southern or western rock lobster thus a crushed leg that is not shed will continue to bleed. The crab may die later, polluting the water in the catch storage area and contributing to further mortalities from poor water quality. Crabs are kept alive in circulating tanks through which large volumes of water are pumped, or in the case of smaller boats, in wells (see below). As they are removed from the pots, they are size gauged into legal and undersized components. The undersized are returned to the ocean and chelae of the saleable crabs are immobilised by binding the propodus to the merus (see Figure 4a. and 4b.). Nylon ties, widely used in the electrical industry have been adapted to this purpose. The effect of binding is to bring the tips of the chelae against the abdomen. The crabs should not be bound so tightly that the tips crack the abdominal exoskeleton as this appears to open the crab to infection and has been cited as a cause of elevated post harvest mortality (pers comm. D Gaunt & C Wong, Mullataga Pty Ltd, WA,). Processors' experience at storing the crabs indicate that it is desirable to allow a small amount of movement of the bound chelae otherwise the muscle tissue will atrophy (waste away) if the limb is completely immobilised.

A well is a tank within a boat where the hull forms the tank's bottom. The hull is perforated to allow water circulation as the rolling motion of the vessel on the ocean surface forces water in and out of the perforations. Care is taken to ensure the bottom sections of the well are not overcrowded, because relatively still conditions sometimes occur especially during the summer and autumn. With reduced boat movement, rising sea surface temperatures and water circulation cut off by overcrowding, the

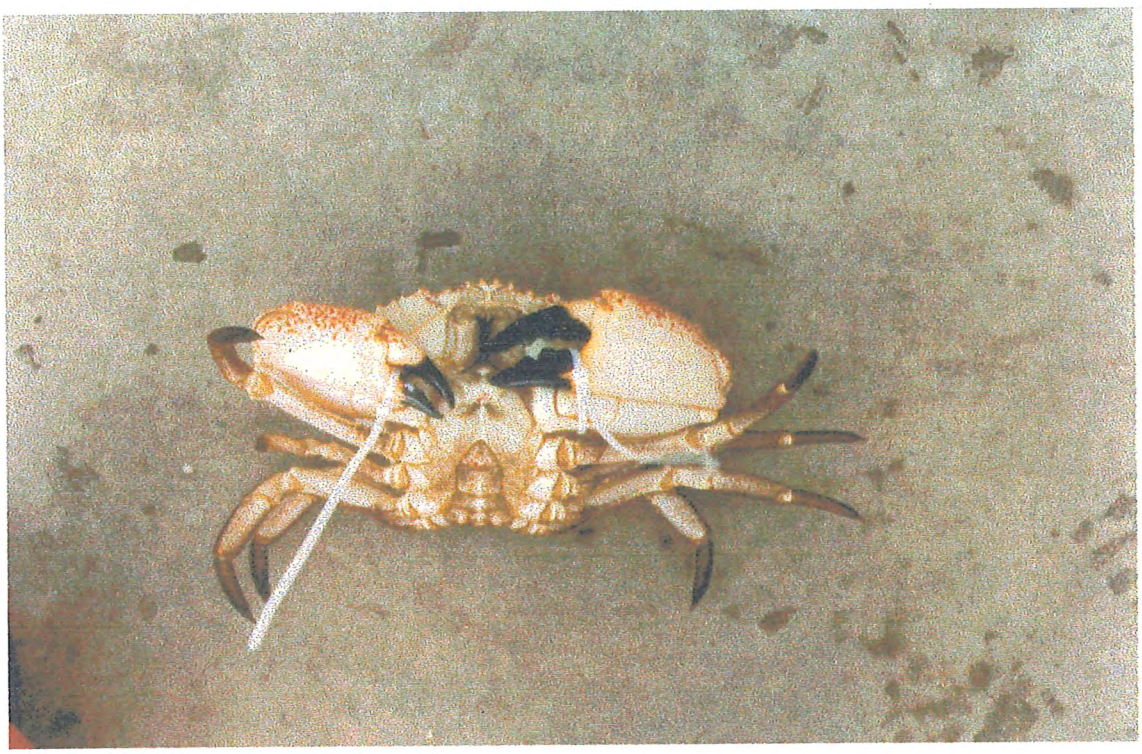


Figure 4a

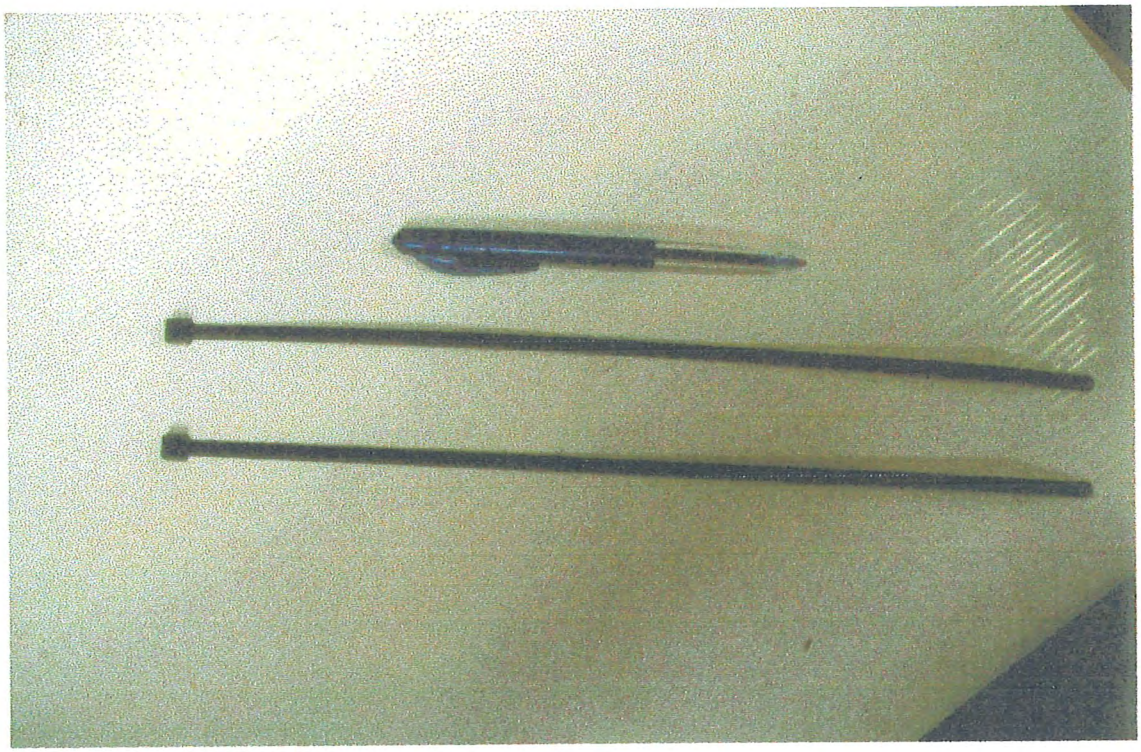


Figure 4b

Figure 4a and 4b : The chelae of the saleable crabs are immobilised using nylon ties.

Figure 5: The crabs are packed and cushioned in chilled, insulated containers for export

preconditions are set for loss of the entire catch; thus correct storage methods are of extreme concern to fishermen.

2.4. Post-harvest techniques

The crabs' value is primarily derived from ornamentation. Their bright red colour favours their use, as a centrepiece at seafood banquets especially in Asian countries where red is a cultural symbol for life, strength and prosperity. The crabs' shells fade if they are kept over extended periods in light, and therefore it is prudent that these animals should be stored in darkness. As stated above, during storage ties on the nippers should be loose or completely removed to allow a degree of movement. This ensures muscle tissue within does not loose function and shrink, thus creating a poor quality culinary experience for consumers who have paid a large amount of money for a "symbol of vitality and strength". Although consumers place advance orders, overseas merchants with limited tank space make decisions based on the best rate of profit for the least risk. The bigger individual size of this species in comparison with other crustaceans, such as western and southern rock lobster, means a greater financial loss is sustained if limbs are missing or the animal dies post harvest. Careful handling is therefore of paramount importance.

Thermal stress and dehydration during the passage from the sea floor to consumers are important post harvest issues. Long distance overland transport from the wharf to airport can cause loss unless the crabs are re-immersed in circulating tanks; their gills re hydrated and, kept in darkness, their stress levels reduced. After considerable trial and error exporters (Mullataga Pty Ltd, WA; The Fish Factory Pty Ltd, SA; Crustacea Australia Pty Ltd, Portland Vic; Hursey Seafoods Pty Ltd, Stanley, Tas) found that the crabs are best stored at 12° to 14 °C. Immediately prior to export water temperature is lowered to about 8° to 10°C and they are carefully packed and cushioned in chilled insulated containers to be exported, relaxed with a lowered metabolic rate. (See Figure 5.)

Continuity of supply is an issue since there is no trade in frozen product and no other similar species. This is unlike rock lobster where there is an alternate trade in *J. edwardsii* from New Zealand, which is also very similar in appearance to *J. lalandii,* a cool water species from similar latitudes in South Africa. Also *P. cygnus* is like *P. japonicus* except that being of Southern Hemisphere origin, it is most abundant during the southern summer when *P. japonicus* (Japan) is in short supply.

2.5. Markets

The total value of the catch across southern Australia has rose from less than $1 million in 1991 to $11 million in 1996. Total value fell due to the closure of the Tasmanian fishery in 1997, implementation of a size limit of 140mm in WA. In addition the fishery's transition from high catch rates during the fish-down of virgin stocks to lesser rates annual production, where the bulk of the catch are recruits that have grown from a previous instar below the legal minimum size, contributed to the fall. In 2000, the total value is estimated at $8 million with the re-opening of Tasmania in late 1999 and a stimulation of prices through greater product flow.

An accurate assessment of average price per kilogram has been based on financial records that document the split price structure for each sale. Wharf prices are subject to a variable weight split structure, where a premium price is paid for smaller sizes.

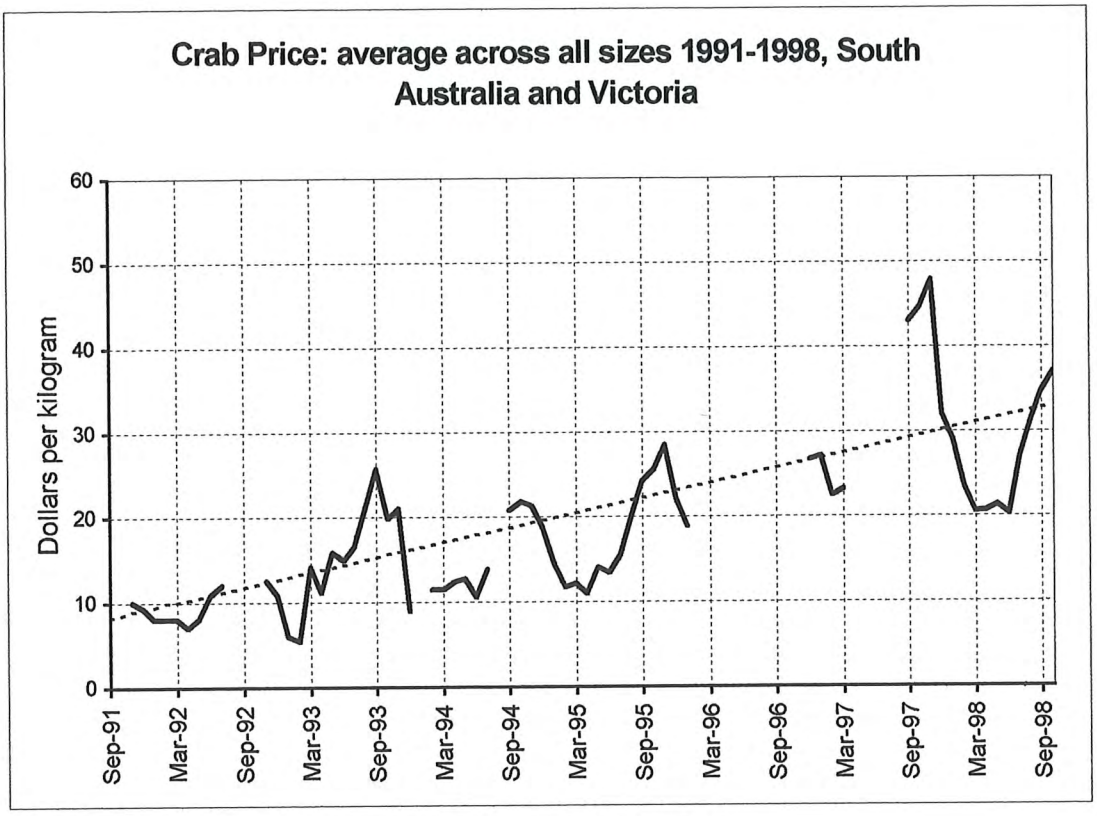


Figure 6.a: Average beach price 1992-1998, Giant Crab

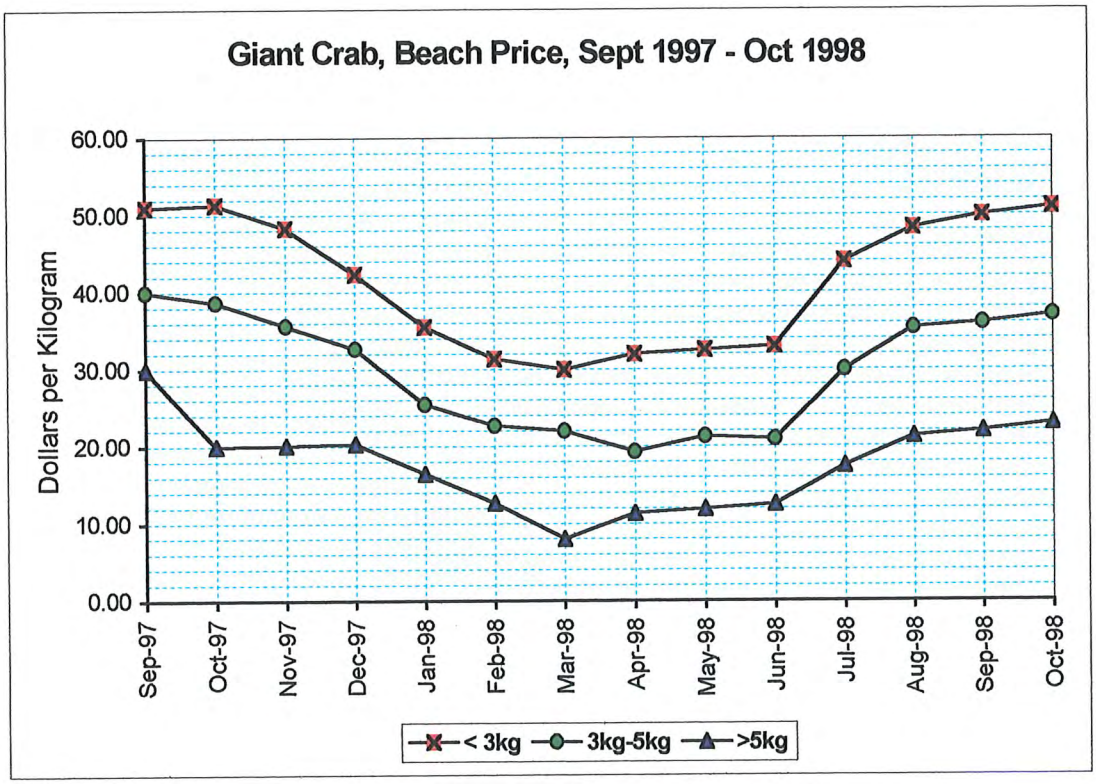


Figure 6.b: Beach price, weight split price structure, Giant Crab

The most common weight divisions are <3 kg, 3-5 kg, >5 kg in southeastern Australia and <3 kg, 3-4 kg, >4 kg in Western Australia. Other splits of < 5 kg "small" and > 5 kg "large" or similarly < 4 kg and > 4 kg are sometimes used. Males grow to more than double the weight of females which rarely exceed 6 kg, hence the larger sizes >5 kg in SA, Vic and Tas, and >4 kg in WA are predominantly males. The larger males are more difficult to handle and post harvest losses incurred by processors are generally recovered by paying fishermen reduced prices for the smaller sizes of crab.

Price is subject to annual fluctuation, rising during the winter and falling during the late summer/autumn. In December 1993 fishers in south eastern Australia were being paid $9, $7 and $5 per kg for < 3 kg, 3-5 kg, and >5kg weight classes respectively, however by December 1996 this had risen to $27, $21 and $14 per kg respectively. In the preceding August prices as high as $34 per kg for <3 kg sizes were paid. The late summer- autumn period coincides with a shift of *lobster* fishing effort to deeper water where crabs are taken as a byproduct. At this time of the year, with lobster catches at a peak, a greater volume of crabs also become available and this causes a shortage of tank holding space throughout the marketing infrastructure. The average monthly price for kilograms of crabs caught, is illustrated in Figure 6a.and shows the steady increase in the value of this species since 1992 The account of beach price in Figure 6b. is taken from the period September 1997 to October 1998 and shows the same weight - split structure of earlier years, although generally the price has increased and now surpasses that paid for southern rock lobster. In July of 2000 the price was $50, $40, and $30 for the weight classes.

Chinese communities, both domestic and in Southeast Asia provide the major markets. A weakened Japanese marketplace for Australian seafood exports has led to an increased focus on China by Australian exporters. Mark-ups from the wharf to retailers are of the order of $4 kg plus transport costs. The retailer then adds on at least another 20%, but retail price will vary greatly according to where the purchase occurs. For example the price at the Sydney Fish Market or the Victoria Market may be half that paid when purchased from a tank prior to cooking at a restaurant elsewhere in the city.

The current continuation project (FRDC 97-132) has assessed the consequences of a selective harvest of smaller sizes, which in a biological sense could be traded off with the release of larger crabs. The aim is to maximise the value of the catch while also preserving the reproductive potential of these larger economically less valuable crabs. The study commissioned by this project; "Yield, Value, and Egg per recruit of Giant crab" (McGarvey *et al* 1999), includes a user interface to allow the testing of various scenarios and their effect on yield, value and egg per recruit. It is expected to be available in September 2000, at about the same time this report is released.

2.6 Seasonal and interannual catch

There were numerous allegations from Victoria and Tasmania that overpotting was occurring and the finding of unmarked gear supported this. Fisheries managers also reported there were complaints from some processors about the existence of a market for undersized crabs. The finding at sea of mesh bags of undersized crabs, apparently stored in readiness for an opportune time to conduct illegal trade supported this. Therefore, reported catch and effort from some operators may be unreliable for the following reasons.

- Very large catches that *may* have been taken by the use of additional illegal pots *may* have been written down as having been taken by the lesser (legally licensed) amount.

- Catches of undersized that *may* have been marketed illicitly *may* have been written down as if they were of legal size.

Both practices have the potential of falsely inflating catch history in a way that would withstand normal catch validation procedures in the event of quota management.

A more general difficulty was that the Tasmanian general fishing log book required fishermen to report the weight of their catch daily, but without sophisticated equipment, weight cannot be measured reliably at sea. Though it appears the system's intent was to record landed weight, some fishermen had written down the number of crabs and not the weight. This can yield vastly different outcomes in catch and effort analysis.

In Western Australia, catches of spiny crab and giant crab have been separated but effort has not. In South Australia catches of crabs by lobster fishermen began to be recorded in lobster catch and effort data in 1994, but the catches of the 2 major giant crab producers, who were not lobster fishermen, were not documented by this system. However, these producers have voluntarily made their personal catch and effort information available to this study. Their data, along with that from other regions, is strongly influenced by the time at which fishing occurred, as there are annual fluctuations of occurrence by depth, by sex, by size and abundance.

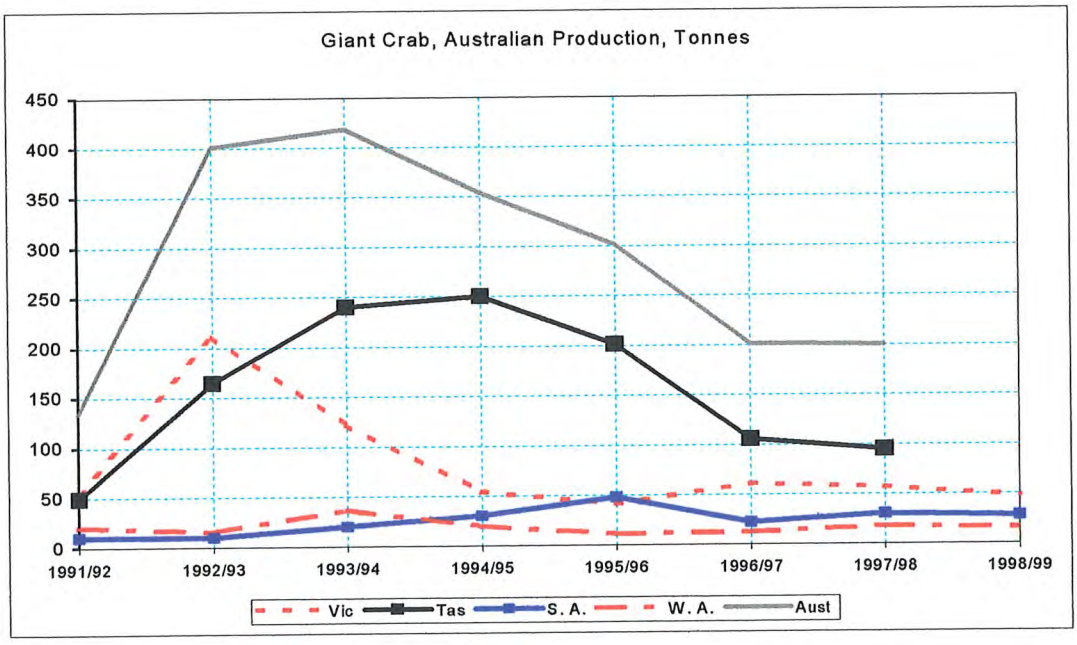


Figure 7: Catch of giant crab by state 1991-92 to 1998-99 (compiled from state fisheries records)

Therefore, figure 7 above, of total catch over time should be viewed as the nearest possible approximation based on the best available data; however, the data may be inaccurate for the reasons outlined.

Crabs are primarily targeted from early summer (December) through to late winter (August), with catches peaking in late summer-early autumn. Closed seasons vary according to state jurisdiction, with 10 week closures from September in the two most productive states, Victoria (Vic) and Tasmania (Tas).

2.7. Seasonal and interannual effort

The reporting of seasonal and interannual effort is subject to the difficulties described above, which make it impossible to report comprehensively from government catch and effort statistics. At sea sampling data has been integrated into CPUE analysis and used to study changes in catch per unit effort by season and other categories.

2.8. Seasonal and interannual CPUE

Chapter 5 uses CPUE to describe distribution by depth.
Pooled data from all regions, for both sexes, for all sizes trapped in the pot including undersized, across all seasons for all years, showed a non significant trend towards a decreased CPUE between depths of 50 m and 600 m. The inclusion of data from less than 150 m and greater than 400 m, where sample sizes were low and variability high, contributed to the fact that the trend was non significant. CPUE values ranged from .34 to 1.71 kg/pot/day between 100m - 400m, but decreased to low levels on the shallower and deeper side of this range.

The analysis then focussed at a regional level and was broken down into further sub categories. At a general level across all states, winter CPUE decreases because fishermen are handicapped if they wish to fish deeper water, balancing issues of gear recovery in stronger tidal conditions against maximisation of catch per unit effort.

2.9. Relationship to Southern Rock Lobster and other fisheries

The Southern Rock Lobster fishery is located landward of the crab fishing grounds, where the substrates gradually change from softer muddy bryozoan dominated communities to hard rocky reefs subjected to the effect of wave action which is known to extend to depths of 65 fathoms. (James. *et. al.* 1992).

Initially in 1993 with the threat of excess effort and few organisational arrangements, laws for the crab fishery were based on lobster regulation. This was useful because of the similarities in gear and annual biorhythms such as females of both species spawning their eggs in winter and hatching them in the spring. However, as the fishery has developed a more detailed knowledge has been acquired and this style of management can be substantially improved.

Target fishing for each species has a different style; a trap aimed at lobster has to land close to their home-site, but for crab, the trap is aimed at a depth strata. Lobsters are social creatures, aggregating for defence within rocky enclaves and emerging to forage nearby. Home-site availability for lobster reflects the physical effects of wave motion which, with it's erosional action, creates home-sites within rocky substrates. Beyond this effect sediment accumulation occurs and so the observed uniformity in lobster depth distribution, despite regional differences in rock type can be attributed to these physical processes. (see chapter 2.10) Crabs are independent of the need for a home-site except in the general terms of being part of the ecology at the depths they occur.

Whereas soak times of 4 to 24 hours may be suitable for catching rock lobster, this is inadequate for crab. Entrapped lobster are more vulnerable to predation by octopus, *Octopus tetricus* and *Octopus maorum* (Kailola *et. al.* 1993) and leather jacket *Nelusetta ayraudi*, but the crabs' large size and hard exoskeleton render them relatively immune to attack. The optimum soak time for crab fishing varies from 2 to 7 days and mainly occurs over soft substrate.

The fact that crabs accumulate in the trap with these extended soak times and that this occurs over softer grounds has been of major significance to deep water lobster fishermen and participants in other fisheries nearby. A new integration of fishing practices has occurred, resulting in an increased productivity from fishing operations located in this area.
Three typical examples are;

- To target lobster while at sea on a daily basis, but shift the gear onto crabs while in port during the passage of bad weather, performance of maintenance tasks, or dealing with social obligations.

- To combine drop lining for trevalla *Hyperoglype antarctica* with crab fishing in a two day cycle. Crab traps are lifted on the first day and the afternoon of the second. The hooks are set prior to daylight of the second day to capitalise on the peak trevalla catch rates during their downward diurnal migration at daybreak. A similar cycle has also been observed where long lining for school shark *Galeorhinus galeus and* gummy shark *Mustelus antarcticus* occurs instead of drop lining.

- To target pelagic species using surface longlines and to intermittently haul crab gear which is set nearby. This new pattern has emerged off the south coast of West Australia from 1999 onwards.

As the crab fishery developed a radical decline in the amount of crab by-catch taken from some of the outer lobster grounds during lobster fishing occurred. There are many anecdotal accounts about this from fishermen in South Australia, Victoria and Tasmania. In Victoria this is further supported by catch and effort statistics. The MAFRI statistics from the vessel "Jane Kerr", made available with permission from the skipper Doug McDougal, shows that his by-catch of crabs taken on the outer lobster grounds of Western Victoria diminished by 94% from the year 1992-93 to 1993-94.

When analysing by-catch data for Victoria it should be remembered that prior to the start of the targeted crab fishery in 1992, prices were low and the crabs were often not sold or recorded. Thus, analysis of changes in by-catch has focussed on the years from 1992 onwards when markets were established and there was a higher probability that all of the crab by-catch was sold and recorded.

It is proposed that the decline in crab by-catch be linked to annual movement of the crab population into deeper water in the autumn and back into shallower water in the spring. The female population that had previously overlapped onto the outer lobster grounds became exposed to capture further offshore on the deeper softer substrates of the targeted fishery and so their abundance as a by-catch of lobster fishing was

radically reduced. The male population, which ranges further inshore than females was also affected in this way, taken on the outer grounds prior to migrating inshore, or if inshore, due to their increase in value, being kept instead of being released. There was initially more of an overlap between the lobster and the crab fishery, but the dynamics of exploitation have created a greater spatial separation between the two fisheries.

However, the western and the southern extremities of the species range in Western Australia and southern Tasmania should be considered separately due to the following reasons. Western Australia is an area of convergence where warmer Leeuwin Current water travelling eastward along the south coast, overlies cooler water which moves to the west (Cresswell & Peterson, 1993). In this area, the depth of occurrence of giant crabs described in Figure 8. is substantially deeper than in South Australia, Victoria or Tasmania. The complexity of this area of convergence is reflected in a similarly complex intermingling of warm and cool temperate species. Southern rock lobster occurs with giant crab in some areas of the shelf break but its range also extends inshore in some areas, apparently having a greater tolerance to warmer water than giant crabs. The warm temperate species; the spiny crab, *H. acerba* also

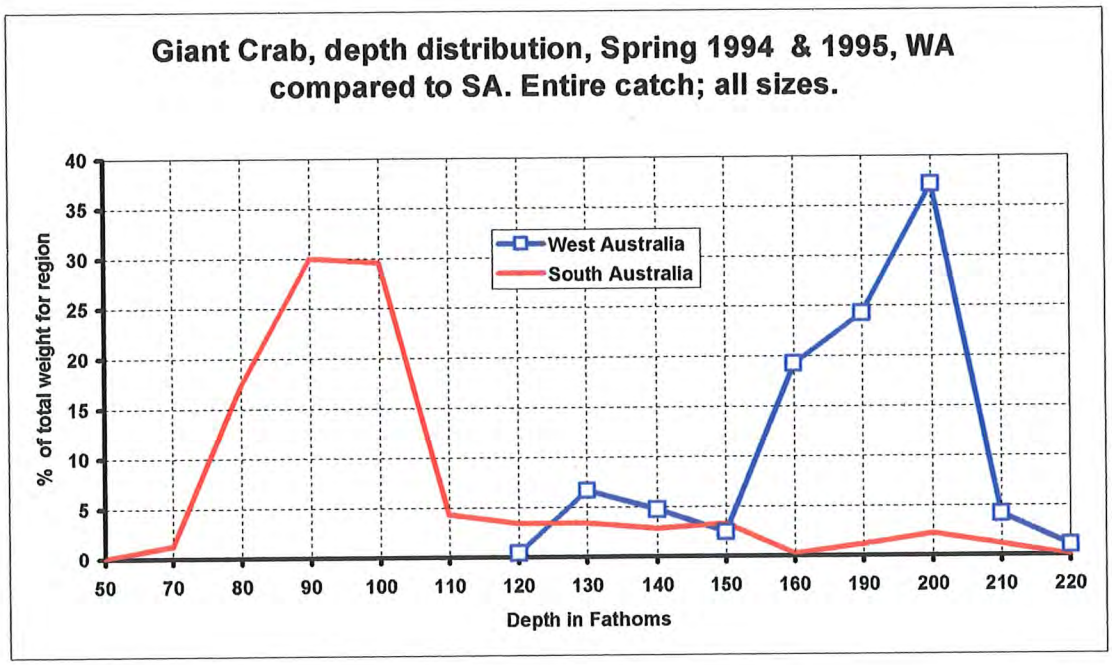


Figure 8. Giant crab catch by depth in the spring from South Australia and Western Australia is compared. In Western Australia, the spiny crab Hypothallassia acerba, a warmer water species, occupies the substrates swept by the warm Leeuwin Current, which flows across the outer continental shelf of this area. *P gigas* occupies the upper bathial slope in deeper, cooler waters.

occurs in this area but tends to be in shallower and warmer water than giant crab. At present the WA catch and effort reporting system is being redesigned, and it is hoped that in the future this will allow a much clearer analysis to be achieved than is presently possible.

Southern Tasmania, which extends into more southerly latitudes is subject to a cooler oceanic climate than the rest of the fishery, and there are many observations from fishermen that suggest the crabs are more abundant closer to shore than elsewhere.

However, this aspect cannot be resolved without access to finer resolution catch and effort data. This is currently not available due to aggregation protocols. Even if the information were available, the strength of the data is questionable. Many lobster fishermen in this area release their by-catch of crabs and as reported in chapter 2.5 above, the number of crabs taken was sometimes confused with weight of crabs in the reporting format prior to 1999. Although the anecdotal information indicates comparably more crabs inshore than elsewhere in the national fishery, it should also be remembered that crab abundance in this region is most probably limited by competition for food with the area's huge biomass of southern rock lobster.

Aggregated, *rock lobster* catch and effort data from Tasmania was analysed to investigate any changes that may have occurred in the outer lobster fishery through the 6-year period 1992 to 1997. Although this data does not record production of lobster in depths greater than 90 fathom, there are instances where fishermen have caught the species in deeper water. However, it is of insignificant scale as the entire catch from 70 fathoms and deeper represents a mere 1.2% of the total catch for the fishery over the 6-year period. During the years of development (1992-1995) of the *crab fishery* the total annual catch for lobster in this depth strata (>70 fathoms) was initially high but then declined, together with annual fishing effort and catch rate (Figure 9). Thus, the fishery dynamic for lobster over the 1992-1995 period was that fewer areas in deeper water held an accumulated stock of lobster. Targeting *lobster* was more profitable and predictable in waters shallower than 70 fathoms, and that deeper than this most of the fishing effort was aimed at *crab.*

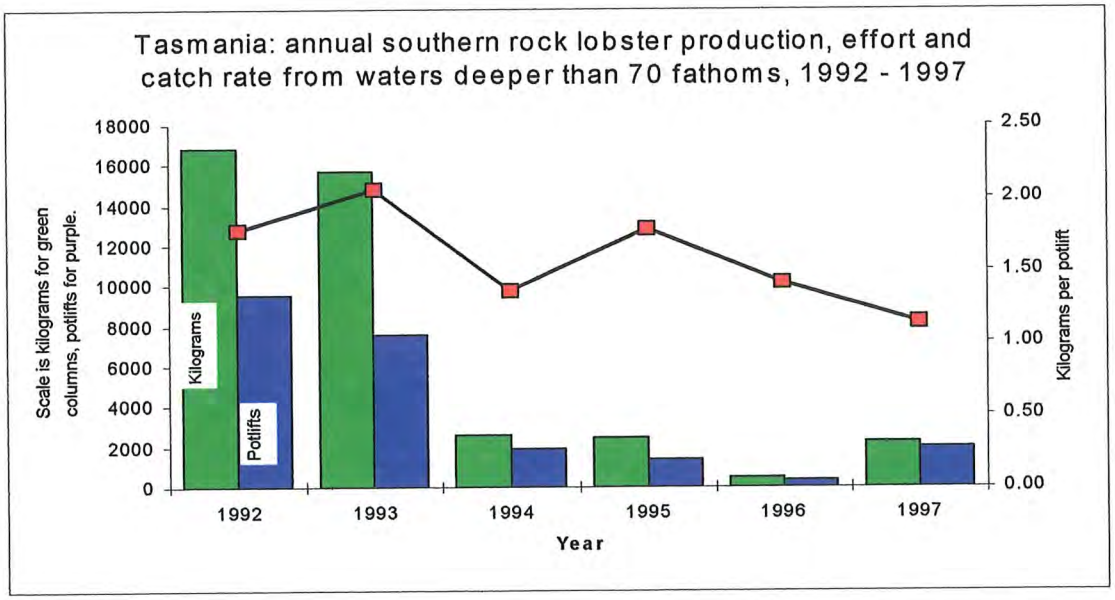


Figure 9. Rock lobster fishery during development of giant crab fishery in waters deeper than 70 fathoms (128 metres). The production, number of potlifts and catch rate for lobster decreased as the giant crab fishery developed. A few unexploited lobster colonies were found in these depths in the years 1992 and 1993, but generally, trapping of rock lobster is more reliable in shallower water and fishing in depths greater than 70 fathoms is for giant crab

Tasmanian *crab* catch and effort information was analysed from 1995 onwards. Prior to 1995, depth information was not recorded. In the 1995 data, 25% of depth information was missing, but in 1996, this value was <3%. The 1997 depth

information was fully reported. The 1996 and 1997 data was integrated into an eastern states analysis which described the depths from which production of lobster and crab was derived. The Tasmanian *crab* data showed a bi-modal distribution with peak catches at 100 and 150 fathoms (Figure 13.). This distribution may be due to the major differences in bathymetry and temperature climates of the East and West Coast Tasmanian fishing grounds. Coupled with seasonality these are most likely to be the factors affecting the statewide view, but protocols disallowing the supply of data of any finer resolution made it impossible to further investigate this aspect. Figure 10 illustrates lobster production from this outer margin in perspective with the rest of the Tasmanian lobster fishery. Figure 11 illustrates the relative size of crab and lobster fisheries in the eastern states and shows that the crab fisheries are much smaller by comparison.

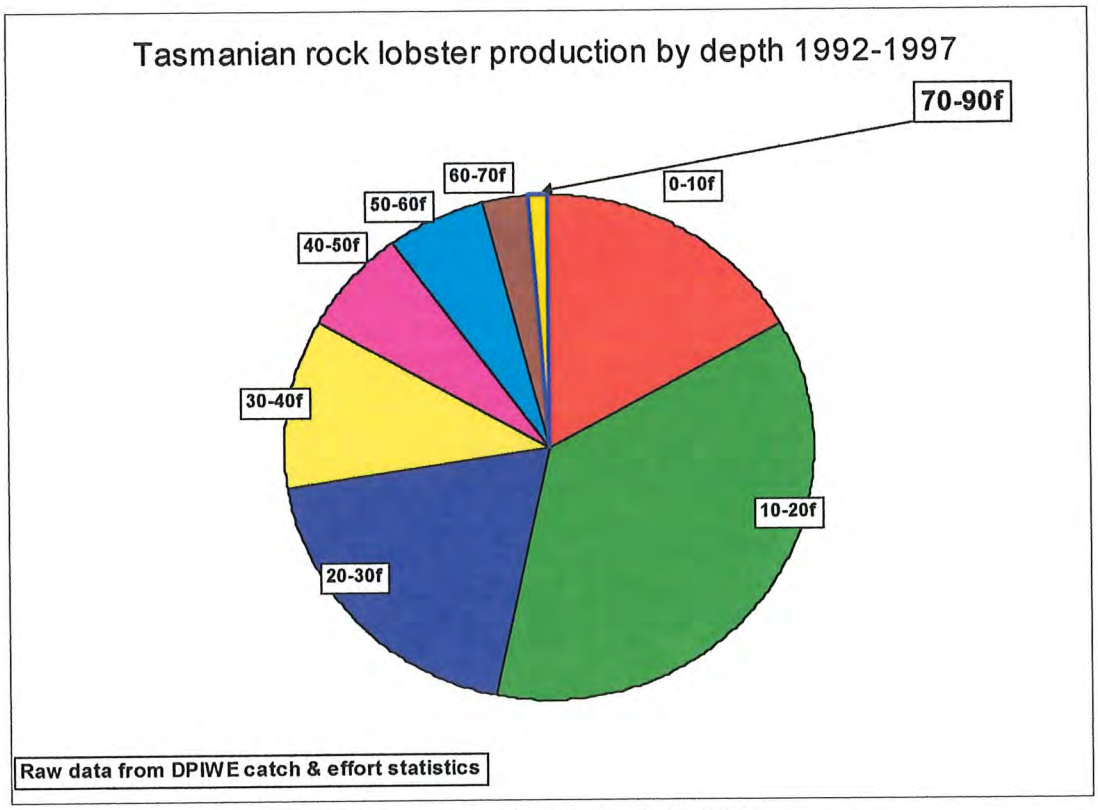


Figure 10. Tasmanian Rock Lobster production by depth 1992-97.
The relative proportion of lobster taken from the 70 to 90 fathom (128 to 165 meter) depth strata is 1.21% of the total, very small compared to elsewhere.

In South Australia the two major *crab* producers who are not lobster license holders produce about two thirds of the state's giant crab catch. Generally, the profitable lobster fishery in South Australia has mitigated against diversification to crab fishing. South Australian lobster catch and effort data records depth in metres. All of the crab fishermen's' catch is taken from depths greater than 100 metres or 55 fathoms.

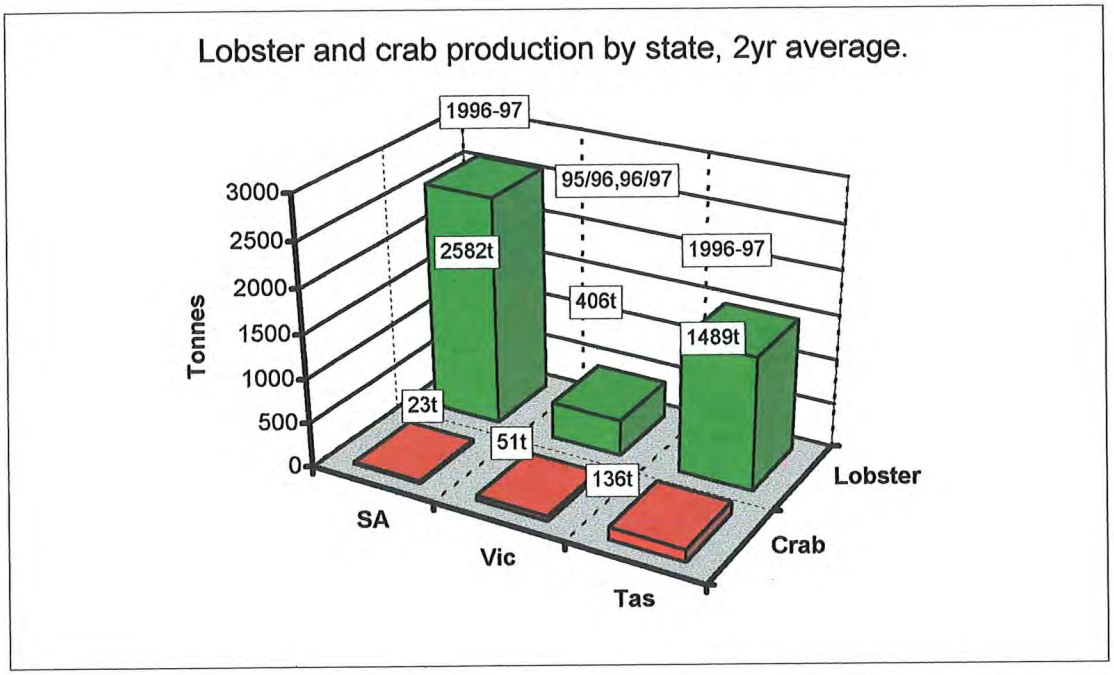


Figure 11. Annual Lobster and giant crab production by state averaged from 1996-97
South Australian crab production was lower than normal due to interrupted production in the autumn and winter of 1996 as referred to in chapter 2.1.2.

Although the lobster fishery overlaps to the extent that waters deeper than this provide 4.8% of SA's annual lobster catch, the substrates where crabs are targeted are different.

An accurate record of length and sex of all of the lobster by-catch returned to the water over two years was kept by one of the crab fishermen, and by using lobster length to weight formula's; Male wt = 0.000285*length^3.114 Female wt = 0.000271*length^3.135, An estimate of the weight of all lobster by-catch was made. When targeting crab the ratio of lobster by-catch to crab catch was 4.46% by weight across all sizes of lobster. There was only one lobster recorded below 98.5mm carapace length. For lobster fishermen an analysis of the ratio of crab by-catch to lobster catch in waters deeper than 55 fathoms yielded a value of 4.7% by weight for legal sized crab.

SARDI catch and effort information for crab taken by rock lobster producers lacks precision. Although the catch and effort report asks fishermen to specify if crabs are a target species, recording of depth is constrained to a single value which is representative of where most pots were set for the day. If for example 70% of pots are set to target lobster in 100 metres and 30% for crab in 130 metres the crab catch would be recorded as having come from 100 metres.

Figure 12. compares the South Australian *crab catch* by depth for Lobster and fulltime crab fishing sectors and Figure 13. is a comparison of the *crab and lobster* catch distributions by depth for South Australia, Victoria and Tasmania. The latter Figure 12, shows that the South Australian overlap is slightly shallower than elsewhere and this is also reflected in the data independent of the lobster catch and effort system, from the two dedicated crab fishers. The distributions of lobster and

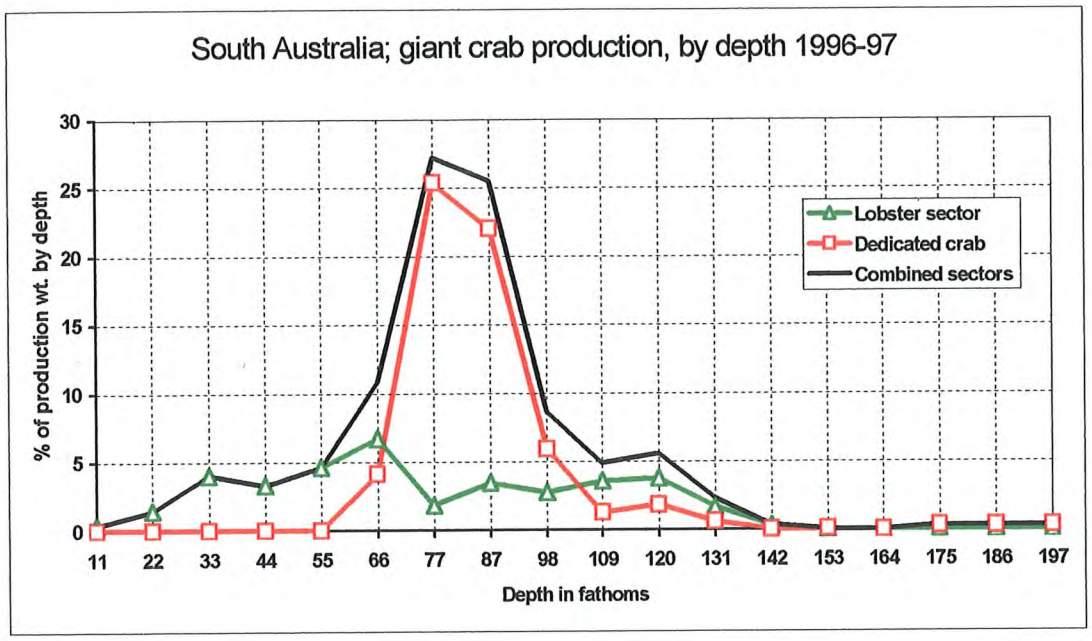


Figure 12. South Australia giant crab production by sector by depth.
Hard substrates are targeted for lobster and soft substrates for crab. Most of the lobster sector's crab catch is taken as a by-catch while targeting lobster and nearer to shoreward is increasingly comprised of male crabs

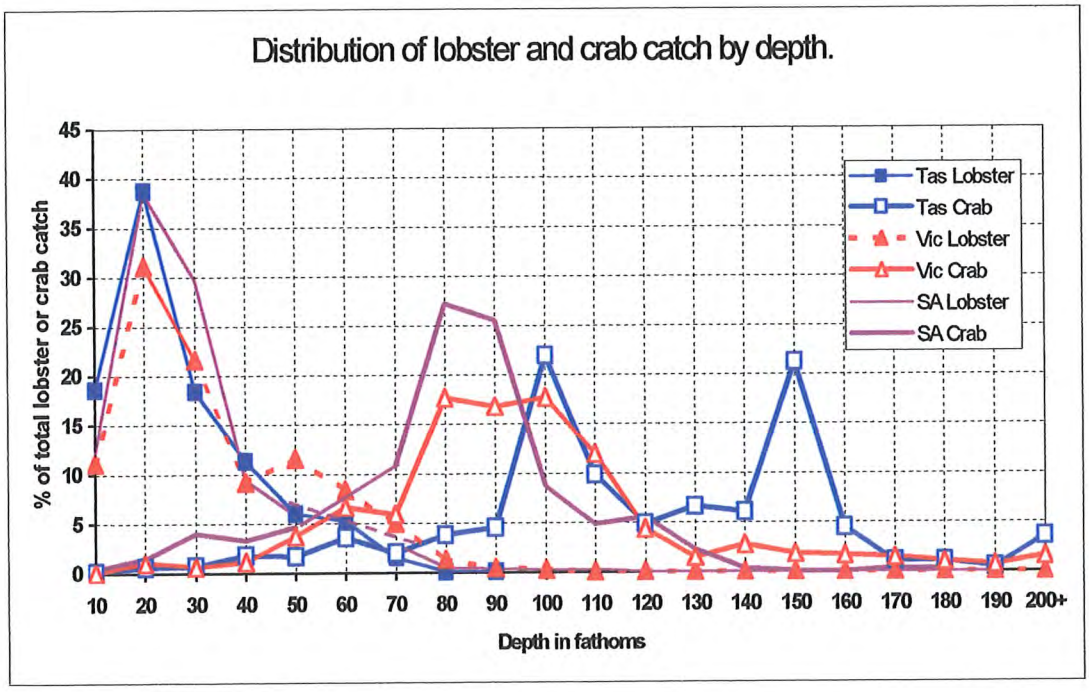


Figure 13. Distribution by depth of lobster and crab catch for South Australia, Victoria and Tasmania 1996-1997. The distributions of lobster and crab reflect the two different lifestyles of these species and the effects of seasonality. The uniformity of distribution for lobster is due to the lobsters dependence on a fixed homesite, but the nomadic lifestyle of the crab which is caught at different depths according to the time of the year, provides a variable distribution, which is also influenced by the season in which the catch was taken. Deeper in winter, shallower in summer.

crab reflect the two different lifestyles of these animals and the effects of seasonality. The uniformity of distribution for lobster is due to the lobster's dependence on a fixed home site. The variable distribution of the crab reflects it's nomadic lifestyle and occurrence at different depths according to the time of the year.

In the future it is expected that improved catch and effort reporting will provide increased accuracy, but at present Figure 13, is the best representation available.

2.10. Description of the environment.

Benthic Environment

P. gigas are endemic to Australia but there is a single instance in the fossil record of New Zealand where a fragment of a claw thought to be from *P. gigas* was found on the west coast of the south island in a sedimentary sequence deposited 5.3 Ma. (Glaessner, 1960). There is also one present day record of a single (female) crab caught off the south Island (pers com. M. Peychers, Te Anau, 1999), but no evidence of a breeding population. Most cool water decapods in Australia have evolved locally and fossil records of *P. gigas* extend from the early Oligocene period (35 Ma) to present day. The species seems typically to have inhabited the outer continental shelf and upper bathial environments of the southern margin of the Australian landmass (Jenkins 1972).

Fossil evidence indicates that *P. gigas* has gradually increased in size since the middle Oligocene. Coefficients for the width of the carapace versus its length, for the length of the fixed finger versus the length of the palm of the larger claw of males and for both claws of females have remained relatively constant. This suggests that the changes were occurring in response to a selection pressure or various pressures of virtually constant intensity. The outcome in modern times is that *P. gigas* has evolved into a very large size. It has a high carapace that accommodates larger muscles to move the limbs, a very large brachial cavity and gills and large heart to provide a satisfactory respiratory and cardio-vascular system to maintain it. The rate of increase of carapace width has been 6 to 9 mm per million years (Jenkins 1972).

P. gigas occurs along the entire southern Australian margin, inhabiting the world's largest cool water open shelf carbonate accumulation. (Connolly and von der Borch 1967, Wass et al., 1970; Marshall and Davies, 1978; Bone et al., 1991; James et al., 1992). The chemical composition of the *P. gigas* skeleton is intermediate magnesium calcite i.e. 7 -11.9 mol% $MgCO_3$ (Campbell 1996, unpublished), which is the same as most of the bryozoans that have accreted to form "cool water" limestone. The water temperature on cool water shelves thermodynamically favours a low to intermediate magnesium carbonate skeleton (Bone, 1993).

Present day observations of the outer shelf and upper slope benthos are considered a good analogue of the depositional environment of much ancient limestone. Palaeo-ecological reconstructions (Frakes & Kemp 1973) show that the associated water temperatures vary from 7 to 20 degrees. These conditions completely cover the temperature ranges of recent bryozoa and also of the crab *P. gigas*, thus it is not surprising that the fossils are found associated with these types of limestone or that in modern times the depths and location at which these bryozoans abound are also the same as where most of the *P. gigas* population lives.

The distribution of benthic faunal species on continental shelves usually occurs as three distinct zones (Day et al.1971; Maurer et al. 1982; Peres 1982; Probert & Wilson 1984; Baba et al 1986; Parry et al.1990), each characterised by a different fauna with few overlapping species. The zones are inshore, mid-shelf and offshore with the boundaries of the zones linked to the prevailing hydrology of the area. Changes in substratum type substantially affect faunal distribution with a decrease in the number and diversity of species with increasing depth (Ward & Blaber, 1994). The high-energy setting of southern Australia has resulted in the separation of muddy and grainy sediment types through the action of the wave base and this occurs at about 120 metres.

The environment below the wave base favours the growth and accretion of bryozoans, while above this the organisms are quickly abraded or swept landward. (James et al., 1992). The nutrients required to support this benthic community are most likely derived from colder water, relatively richer in nutrients compared to shelf waters, as it up wells over the shelf break (Wass et al., 1970). Bryozoans are the dominant fauna on the outer shelf break and upper slope, forming the framework of the ecosystem by providing environmental niches for other biota. Their coverage is not homogeneous, even in highly productive areas patchiness is the norm (Bone 1997, Bone & Campbell 1997). In addition to bryozoans, sponges and ascidians, other living constituents that are prey for juvenile through to adult sizes of *P. gigas* occur in this province. Table 17 in chapter 4.7 "Diet and feeding" provides a qualitative description of shellfish specimens identified from among bryozoan hash collected in a crab trap. Data derived from continental slopes elsewhere in the world (Rowe 1981) suggest that density and biomass of macrobenthic fauna decreases with increasing depth. Thus food resources are attenuated by depth and diminish in abundance and diversity as depth increases and substrates become muddier. The bryozoan rich zone is relatively narrow, the progressive gradation into all mud apparent at about 300 metres. (A. Levings, Franklin Cruise FR 03/98, unpublished data)

Female crabs often have a zone of encrusting epifauna on the lower sides of the carapace and clean surfaces on the upper lobes, suggesting that they spend periods of time semi immersed in the bottom sediments with only the upper lobes and eyes exposed. Males are generally less fouled than females but the tips of their legs show greater wear, thus it is plausible to conclude that the greater wear is caused by a more mobile lifestyle which leaves the bryozoa comparatively less opportunity to colonise their shells. Both sexes across the species range are colonised by a goose neck barnacle of the family- *Poecilasmatidae* (Annandale), species-*Poecilasma* (pers com. D. Jones, Museum of WA, 1996). Colonisation occurs very rapidly after moulting, which may be indicative of a symbiotic relationship similar to that between another gooseneck barnacle *Octolasmis* and the mud crab *Scylla serrata* (Jeffries and Voris 1992).

Oceanic Climate

Remote sensing imagery combined with information collected during the past 40 years by niskin bottles, continuous temperature depth transects (CTD's), and expendable bathythermographs (XBT's) have been integrated into the CSIRO's data set "Climatology of Australian Regional Seas, 1998". The information provided under formal agreement to this project has been used to support the hypothesis that the major parameter governing the life history of *P. gigas* is water temperature.

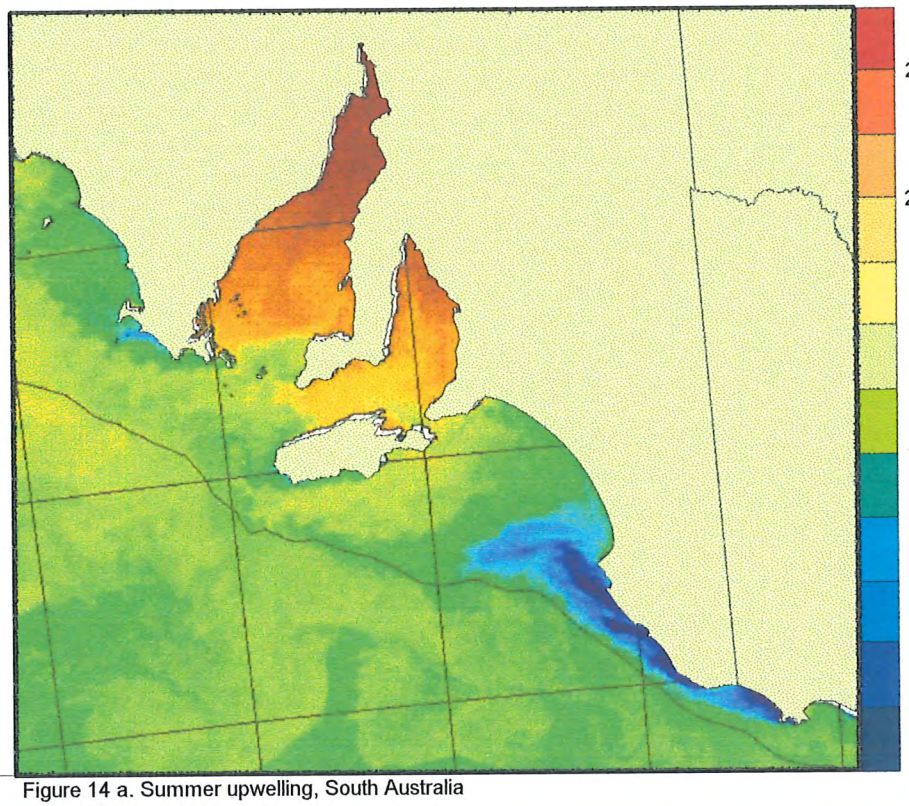


Figure 14 a. Summer upwelling, South Australia

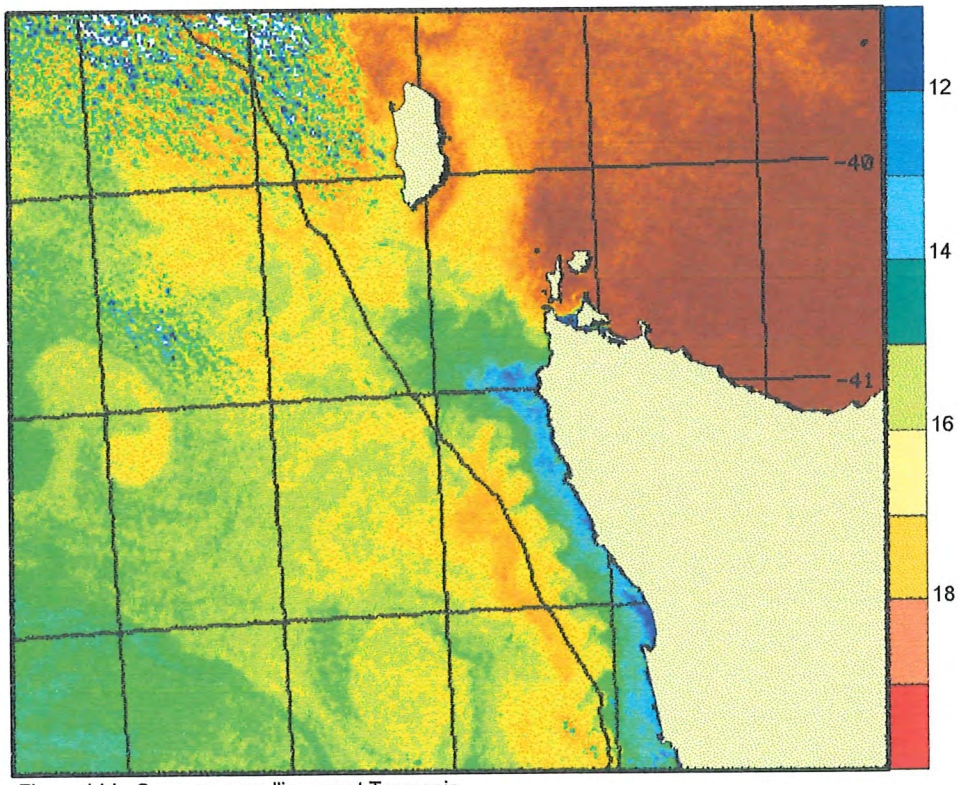


Figure 14 b. Summer upwelling, west Tasmania

Figure 14 (a) and (b): Summer southerly and southeasterly winds transport surface waters to seaward triggering an incursion of cooler and relatively richer subsurface water underneath which upwells in some areas. The upwellings appear in these SST images as green, blue and darker blue along the coastline. Degrees are in celcius.

SST Source: CSIRO Marine Remote Sensing Facility, Hobart, 1998

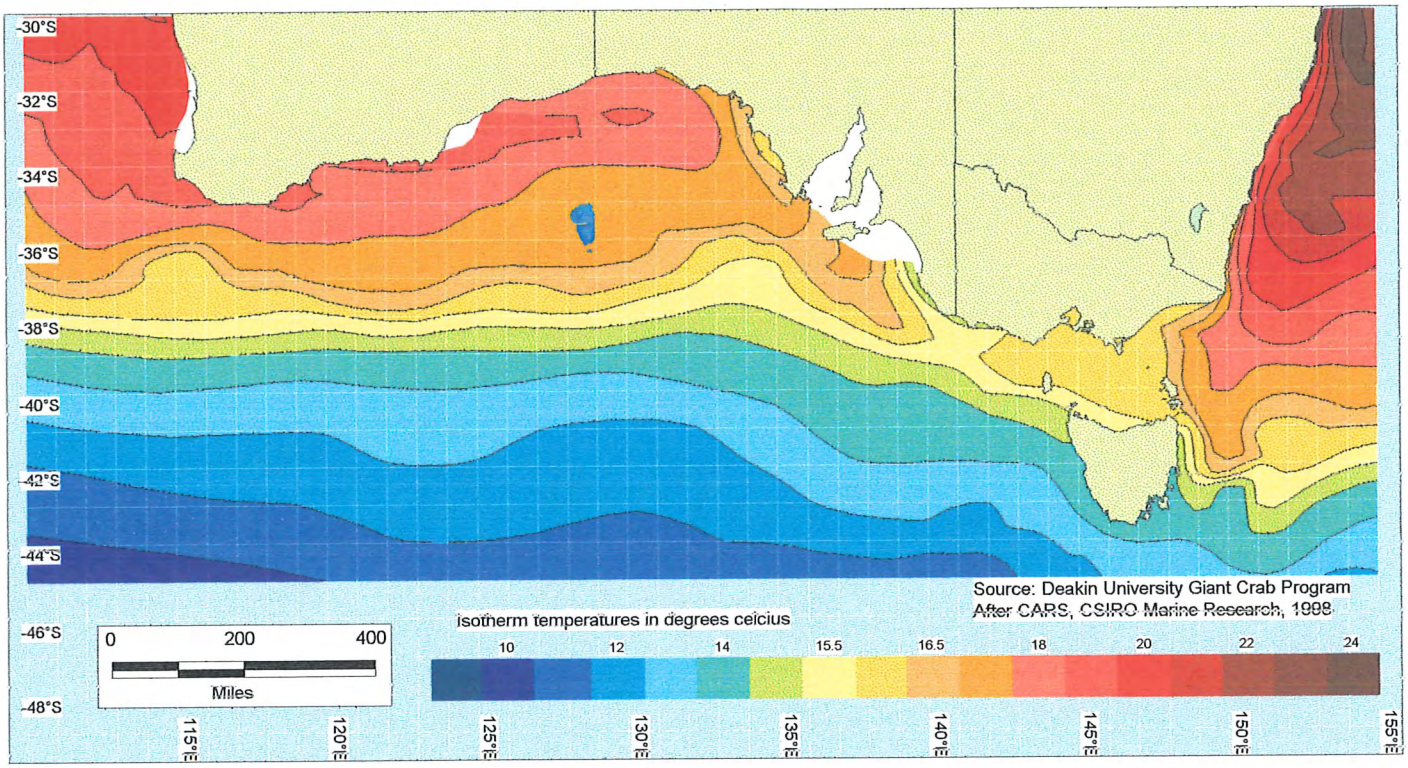


Figure 15 (a) : Summer ocean surface temperatures

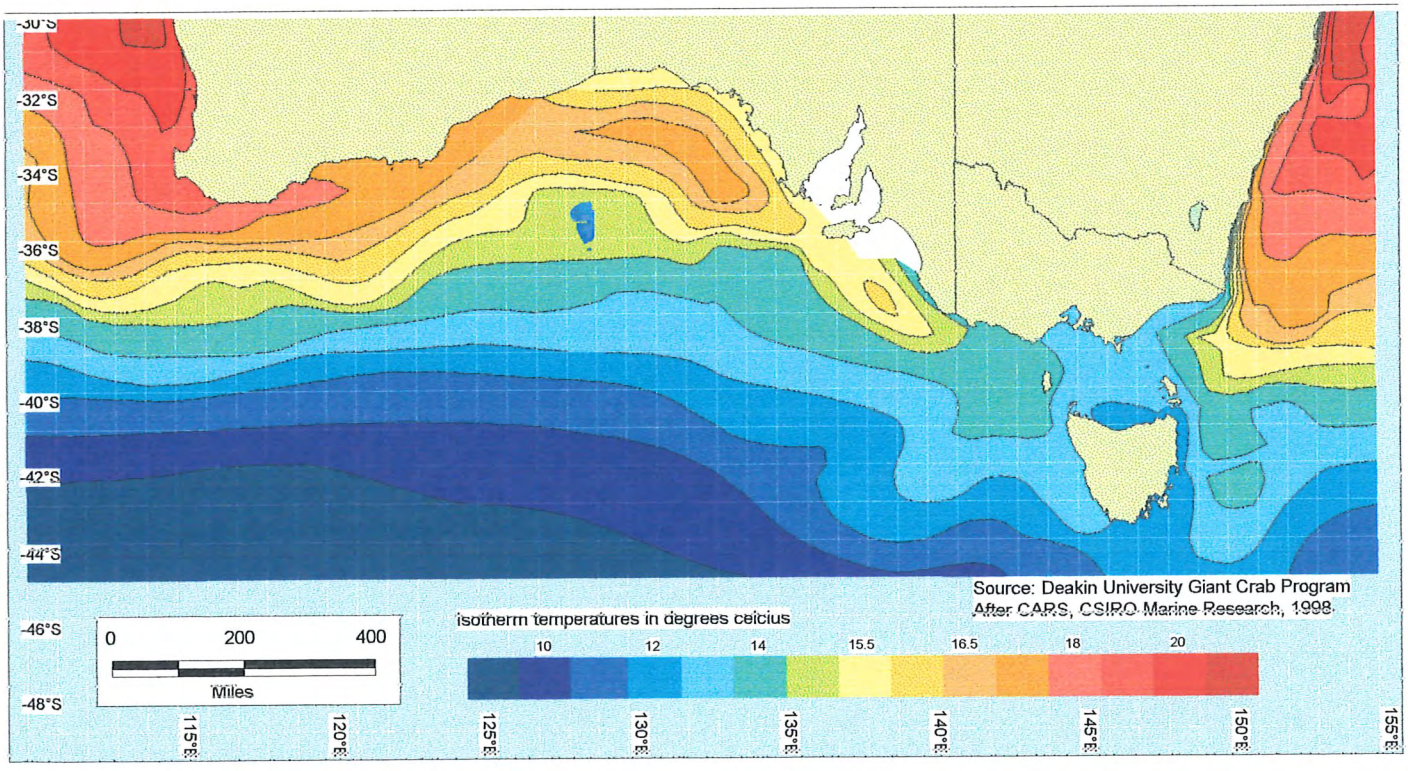


Figure 15 (b) : Winter ocean surface temperatures

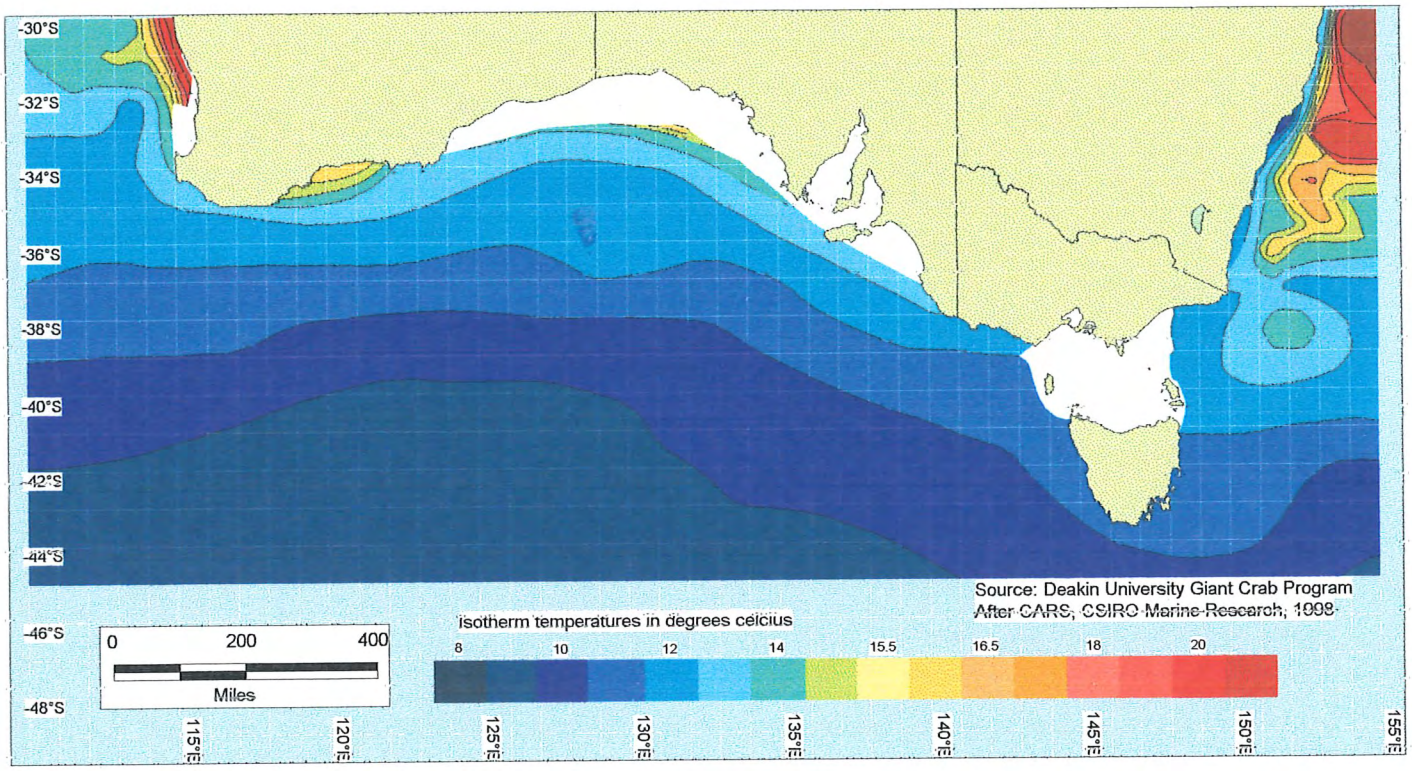


Figure 16 (a) : Summer ocean temperatures at 200 metres depth

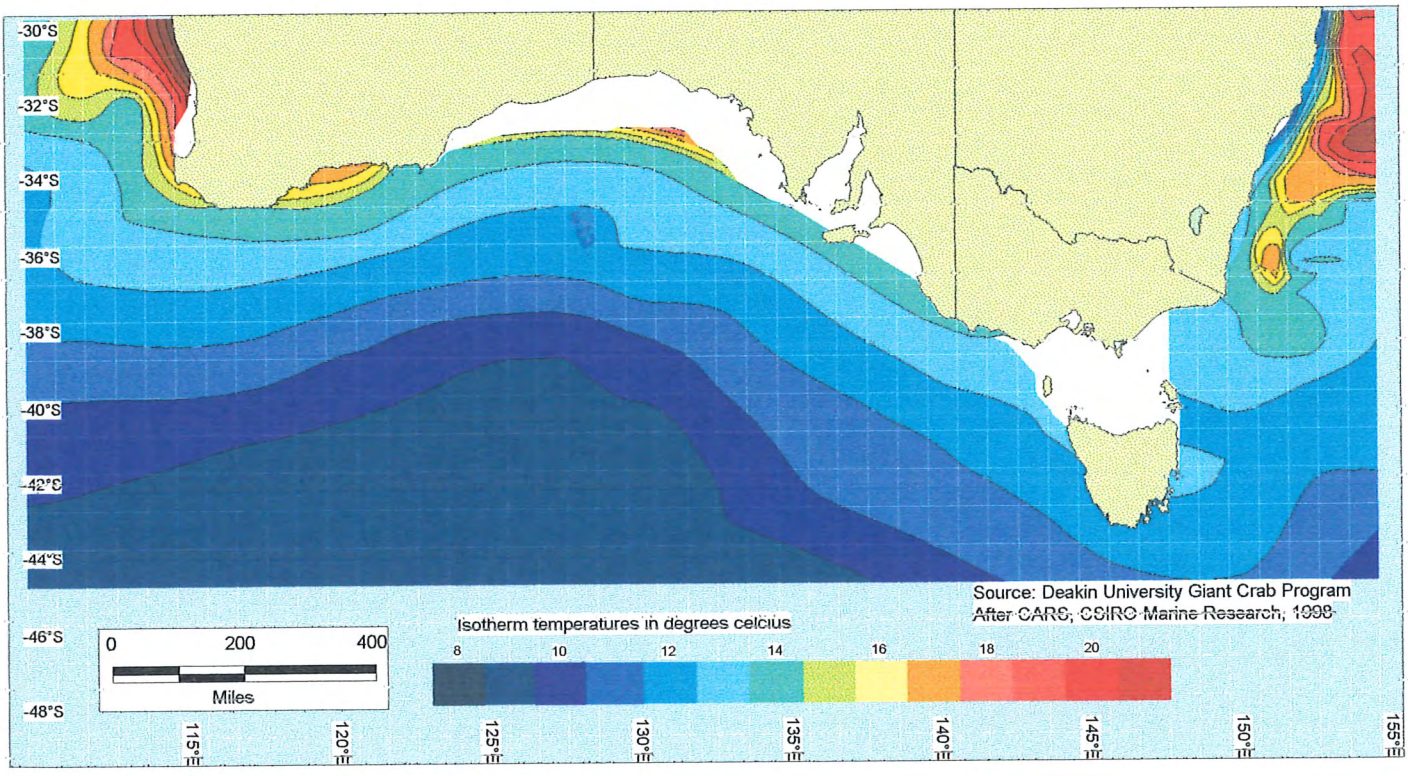


Figure 16 (b) : Winter ocean temperatures at 200 metres depth

Physical oceanographic processes are derived from the effects of wind in relation to the continental landmass of Australia. The deep mixing of surface waters is a consequence of the wind blowing onshore in the winter. In the summer, the upwelling of cooler bottom waters relatively richer in nutrients close to the continent occurs, as surface layers are blown offshore (Eckman transport) and are replaced by the underlying layer; see Figure 14a & b. The regular seasonal cycle of which summer and winter weather conditions are a part, is due to the global oscillation north or south of atmospheric pressure belts associated with the westerly and the Southeast Trade winds. Except in the areas of upwelling, ocean surface temperatures (see Figure 15a & b) are warmer in summer than in winter; but on the sea floor (see Figure 16a & b), the reverse applies. Seafloor temperatures are cooler in summer due to the upwelling circulation and warmer in winter due to deep mixing. In some areas such as central south Australia, Eckman transport does not appear to be of sufficient magnitude to change surface temperatures to the extent that it does in the south east of the state. Nonetheless, there is still sufficient movement to trigger an incursion of cooler water up and over the shelf break (Hahn, 1986; Prescott, unpublished data, 2000).

The temperature range across the area inhabited by the species varies from 17° C at 200m in WA to 12° C at 200m off Strahan, west Tasmania in July (Figure 16b). This situation has most probably prevailed at least throughout the past 20 million years during the evolution of *P. gigas*. Although fluctuations of temperature on the continental shelf can be in the order of 4° C over a short period of time a more stable temperature climate exists in deeper waters beyond the effects of surface mixing, over the edge of the shelf in the upper bathial province.

In geologic time, despite the northward movement of the Australian continent away from Antarctica, the oceanic environment has probably changed very little. There has been latitudinal oscillation during global cooling events that have occurred at 35, 15, 6, 2.4 million years ago (Kennett 1977) and again during the Holocene period, the last being only 25,000 years ago. However for over 20 million years the Southern Ocean temperature and salinity patterns, zonal water masses, surface and deep-water circulation patterns have remained essentially the same. (Frakes & Kemp 1973)

3. Biological information - methods

3.1. Sampling

As various jurisdictional arrangements prevail in each of the states across the giant crab's geographic range, three methods were used to sample the population.
The methods were as follows;

-Landed catch sampling (LCS)-samples obtained from processors.

-Commercial catch sampling (CCS)-voluntary sampling of the entire catch by commercial operators or observers at sea.

-Closed season research fishing (CRF)-sampling by observers of the entire catches during fishing in closed season with partial sale of the catch to cover costs of fishing.

The combination of the 3 methods increased the total number of sampling days available over the study period from 60 to 738. The breakdown of days per state is shown in Table 1 and the application of the various methods used in each state is summarised in Table 2.

Table 1. Sampling Days

	1993-94	1994-95	1995-96	1996-97	1997-98	1998-99	1999-00	Total
West Australia		40	20	0	50	10	11	131
South Australia	20	19	14	31	47	87	89	307
Victoria	6	35	13	4	3	4	-	65
Tasmania	9	45	30	-	26	76	49	235
Australia	35	139	77	35	126	177	149	738

3.1.1. Landed catch Sampling

It was originally envisaged that sampling of landed catch at processors could be stratified by area and time. The collection of these data was intended to supplement at-sea sampling and it was planned that the number of days to be spent sampling landed catch per interval of the commercial catch sampling period be fixed. The number of processors participating in the project as collaborators was divided by the number of sampling days to yield the number of days per processor per interval.
Each fisherman's catch was to be isolated in a separate tank and the location of capture established by interview with the fisherman. The isolation of catches was intended to ensure that repeated sampling of catches from the same fisherman could be avoided and so reduce any bias this might have introduced.

In the initial stages of the project between the lodging of the funding application and the receipt of funds for the project, more than 5,000 crabs were measured onshore at

processors. It became obvious that the intention of the initial research plan was sometimes mismatched with the reality of the fishery.

Difficulties encountered during landed catch sampling were;

- Sampling of landed catch at commercial processors occurred under a variety of circumstances that influenced the type of data that could be collected. The opportunity to sample consistently involved consideration by the researcher of how to best access the processing operation and obtain as much data as was reasonably possible without impeding it. For example, measurements taken during bagging-up immediately prior to domestic land to air transportation were restricted to length, sex, and shell state because of time constraints associated with the unfavourable dehydrating conditions for the crabs. At other times prior to overseas export when the crabs were being drained and packed into insulated boxes in a cool humid environment, weight as well as the other categories of length and sex could be obtained. During other periods within the controlled environment of the exporter's tank rooms when there were no time constraints, fuller data sets were obtained.

- Fishermen sometimes sold parts of the same catch to different processors and this created uncertainty about the status of the sample being measured and limited its usefulness.

The logistics of working with commercial processors thus resulted in deviations from a plan stratified by area and time.

3.1.2. At sea-catch sampling

At sea catch sampling conducted during commercial fishing operations required consideration of:

1) Area;

Sampling occurred in the following locations:

-South-western Victoria and
-The Lacepede Shelf of South Australia.
-The Lincoln Shelf of South Australia.
-The east coast of Tasmania
-The west coast of Tasmania
Southwestern West Australia.

These areas covered a range of catch histories including virgin stock, lightly fished and heavily fished stocks. While attempts were made to ensure an equal spread of sampling effort across these areas, the most comprehensive data set was obtained from the Lacepede Shelf, South Australia (See Figure 17).

2) Time;

Commercial catch sampling was intended to occur from November 1 until July 31. It was planned to stratify this period into 4 intervals (Nov 1 - Jan 7, Jan 8 - March 15, March 16 - May 21, May 22 - July 31). Sampling effort was intended to be distributed evenly across all 4 intervals, however the vagaries of weather and the transfer of effort from crab to lobster or lobster to crab precluded strict application of the plan.

3) Fishermen

The catches of individual fishermen were sampled at sea by the project officer or trained on-board observers. It was originally planned that the number of days to be spent sampling on-board per interval of the commercial catch sampling period were fixed. The number of fishermen participating in the project as collaborators was divided by the number of sampling days to yield the number of days per vessel per interval. However vagaries of weather and fishing patterns as follows precluded the application of this plan:

- WA fishers were allowed to use up to 4 times the amount of pots allowed in Tasmania. (160 pots compared to 40 pots). Thus it was impossible to ensure an equal spread of sampling effort across the areas listed.

- Most fishers split their fishing effort between crab and lobster and it was not possible to fully stratify sampling by time across the locations listed above. Even when the fishers were targeting crabs the vagaries of weather precluded strict application of the original research plan.

A network of fishermen based at Augusta, Albany, Esperance, Victor Harbour, Robe, Southend, Portland, Port Fairy, Warrnambool, Currie, Stanley, St Helens, Bicheno, Hobart and Kettering was formed. An illustrated, waterproof field guide was written to train them to collect data of a consistent quality.

Most of the project data was collected at sea (n = 75,456). It is stressed that at sea sampling, be it through "research fishing" during closed season, by observers, or voluntary collection during commercial fishing operations, always involved the recording of data from all of the crabs that were caught in the pots. The sample consisted of the entire catch: harvestable sizes, undersized and injured crabs, not just the commercial catch. The entire catch was sampled with sex, length, shell-state, reproductive condition and other information recorded on pro-forma data sheets.

In theory it had appeared reasonable to plan sampling over a wider range of depths than was normally fished. In practice, (except for the first year of fishing of a virgin stock), the apparent preference of the species to occupy a limited depth stratum meant that fishing elsewhere would not yield a large enough sample to meaningfully analyse statistically. Therefore the methods that have been adopted reflect a fishery-based view of stocks and bias inherent in this method can be attributed to the following;

-Fishermen only fish where the their target species is abundant.

-The sample they obtain reflects the catchability of the crab at that location, at that time of year, by the type of fishing gear they are using.

-A fishery based assessment of the stock is a reasonable approach to adopt early in the history of a fishery (Hoggarth, 1993).

In adopting this method and view of stocks it was also recognised that other factors could influence the results. For example, the range of depths targeted over a 12 month period is from 140 m- 270 m, but particular sections of it are fished according to the time of year. The pattern is one of fishing shallower depths in the summer and deeper in the winter, however the winter fishing effort is sometimes modified due to stronger

tides. During the winter fishermen make choices between fishing deeper where catch rates are higher but where there is also a greater chance of being unable to retrieve gear due to strong tides, or fishing shallower for a lesser catch but with a better chance of retrieving the gear. Therefore an individual fisherman's skill at making operational choices affects his catch and (for research purposes), the sample he obtains. Factors which may have affected fishing operations were identified during regular consultations with fishermen and if mistakes were detected in the collection of data, the remedial action was decided. Slight differences in pot design and fishing methods occurred between fishermen in different states, but the fishing technique used in South Australia where the largest data set was collected, was consistent over the study period.

Table 2. Sampling Methods

LCS - Landed catch sampling onshore
CCS - Commercial catch sampling at sea
CRF - Closed season research fishing

Year	1993-1994			1994-1995			1995-1996			1996-97			1997-98			1998-99			1999-00		
Type	LCS	CCS	CRF	LCS	CCS	CRF	LCS	CCS	CRF	LCS	CCS	CRF	LCS	CCS	CRF	LCS	CCS	CRF	LCS	CCS	CRF
Tas	X		X	X	X			X						X			X		X	X	
Vic	X	X	X	X	X		X	X						X							
SA	X	X		X	X		X			X			X	X		X	X		X	X	
WA	X	X		X			X						X			X			X		

3.1.3 Research Fishing

Normally this would be fully structured by area, depth and time of year, to generate an unbiased data set, however CPUE can be very low at times. Our research fishing took place during the closed season, solely to provide additional biological information. It was sometimes targeted to ensure that CPUE was high enough to cover costs. This approach, while not totally unbiased is considered reasonable early in the history of a fishery (Hoggarth, 1993)

The structure in more detail is:
1) Area
Research fishing was conducted on the Lacepede Shelf in South Australia, off south-western Victoria and off the east and west coasts of Tasmania. When sampling commenced southwestern Victoria and northwestern Tasmania had been subjected to constant repetitive fishing effort across the same grounds since the fishery started. South Australia had been less heavily fished with constant movement to fresh grounds with most stock removed after the introduction of the IMLS; and north-eastern Tasmania had been subject to 6 months of fishing which occurred after the introduction the IMLS.

The choice of sampling area was based upon the availability of experienced fishermen with suitably equipped vessels willing to undertake fishing during their normal seasonal break and the capacity of the project personnel to supervise fishing

operations. Areas fished during research fishing operations are shown in Figure 17. The areas sampled during research fishing included virgin, lightly fished and heavily fished areas.

2) Time
Research fishing initially took place from September 1st until November 15th, although later some sampling occurred in autumn in Tasmania during the closure of the fishery and in winter in South Australia. The original plan divided the spring period into 3 intervals of a little over 1 month, with research fishing effort spread evenly across all 3 intervals. It was intended to fix the number of research fishing days per month and, based on the number of vessels involved, the total number of "vessel days" were be spread evenly across the research fishing period. This approach called for effort to be held constant within a research fishing sampling interval. That is, total monthly effort (total pots x time of soak) would be constant. The entire catch taken during the research fishing period was recorded.

Fishable weather and tides exerted the controlling influence on fishing operations with tides often pulling floats underwater and rendering gear irretrievable. Factors such as vessel capability, the number of pots in the fleet, steaming time from port to the gear and rough weather affected the capacity to adhere to the stratification scheme proposed above. In the eastern states fishing weather often occurred in all fishing areas simultaneously with the rapid passage of frontal systems, but the lee shore effect of the north-eastern Tasmanian coast and shorter steaming times meant that this area could be fished more frequently.

3) Depth
It was originally planned that research-fishing operations in all areas would be structured to sample a wider range of depths than is normally fished in commercial operations. This would require pots to be sampled weekly, as catch rates would be less than are taken in commercial fishing operations where pots are placed at the most productive depths.

Attempts to follow structured depth sampling during research fishing in the spring of 1993 in both western Victoria and Tasmania were unsuccessful because the crabs appeared to be aggregated along a specific depth stratum. Fishing elsewhere did not provide a sufficiently large enough sample for statistical analysis or enough product to pay for the cost of the operation. As the survey progressed it became clear that catches based on a wide depth range selected via random or representative sampling techniques would be inadequate to ensure reasonable data sets and it became obvious that a narrower depth range had to be fished to meet the project's objectives. In later years this has been modified according to the abundance of regional stocks, interactions with trawlers, and sufficient pots to obtain reasonable data sets and enough catch to be financial viable.

Slight differences occurred between the research fishing techniques used in the different areas. Overall, the technique was reasonably well standardised in the different areas. A noteworthy exception was the use of larger pots in the north west of Tasmania off King Island. It is acknowledged that the data to be presented in this report is to a large degree a fishery based view of stock state. The fishery independent

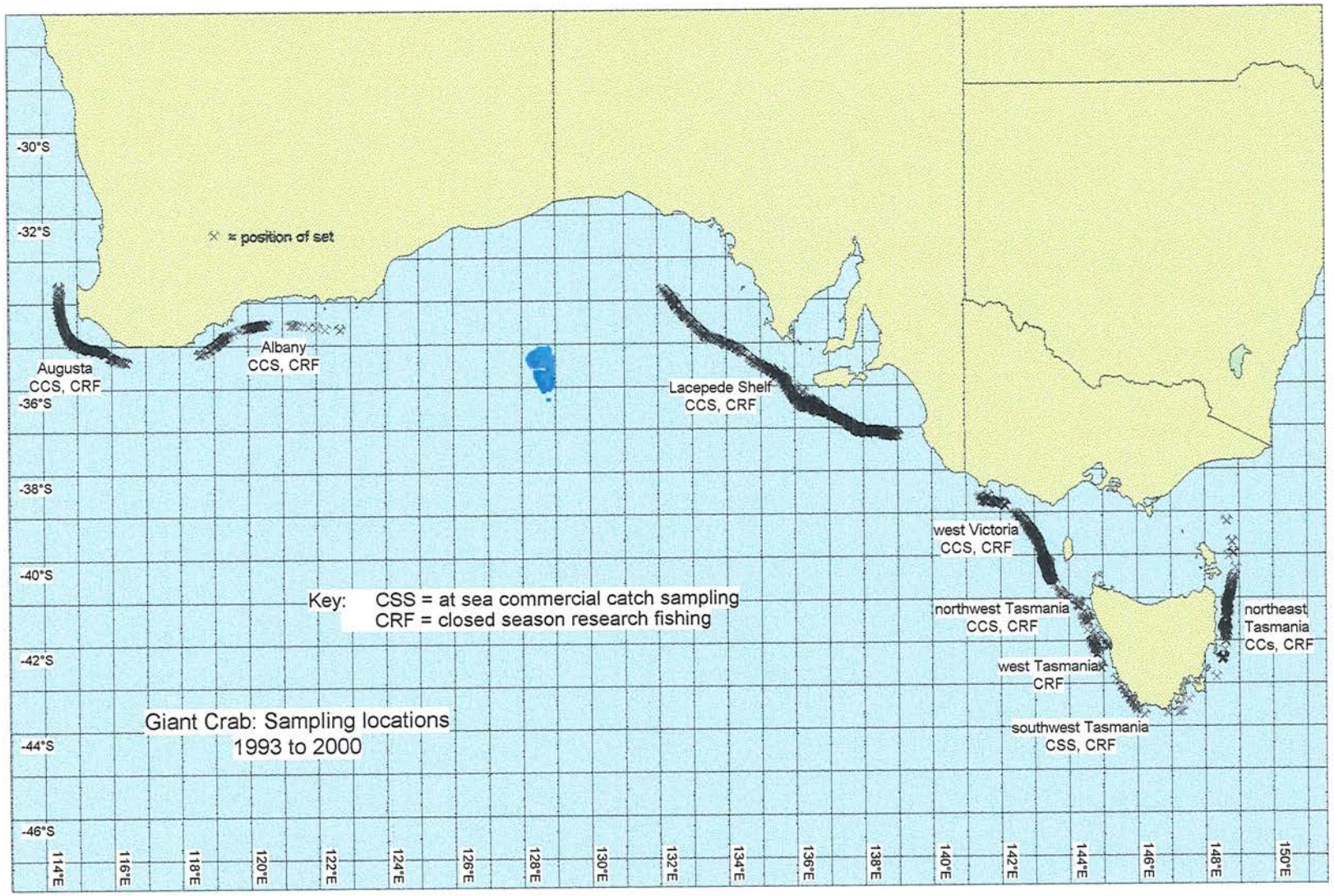


Figure 17: Sampling locations. Most of the sampling was conducted at sea where the entire catch was documented. Closed season research permits allowed sampling out of season (CRF) or in specified areas not normally accessed by crab fishers. Open season sampling is defined as CCS

Scale:
1 centimeter = 100 miles

assessment that was originally planned would have yielded very low catches, which would have meant low sample size from an unbiased study design. This report is based on high sample size but the data are not without some bias; this bias which is similar to that of commercial catch and effort statistics upon which a great deal of fisheries management is based.

3.2. Data collected

3.2.1. Landed Catch sampling

The following information was collected from sampling of landed catch at processors:

1. Sex

2. Carapace length - measured as the shortest distance from the centre of the anterior margin of the dorsal carapace between the eyes to the posterior margin of the carapace at the joint with the abdomen, (See Figure 18a), using 300 mm Mitotoyu vernier callipers (0.01 mm accuracy)

3. Carapace width - measured as the largest distance between the lateral margins of the dorsal surface of the carapace using Mitotoyu callipers as in Figure 18a.
Generally the dorsal perimeter of the shell at the left and right edge at the widest point has 2 points separated by a concave depression. However on some animals there are there are 3 points and two depressions and this would have rendered the method of measurement inconsistent because the variation would have caused confusion about where to place the gauge. Recognising the future aspect when size limitation was to be introduced and there would be a need for a consistent method of size determination, carapace length was determined to be the best way to measure the size of a giant crab. This was also consistent with the method used by fishermen to measure southern rock lobster.

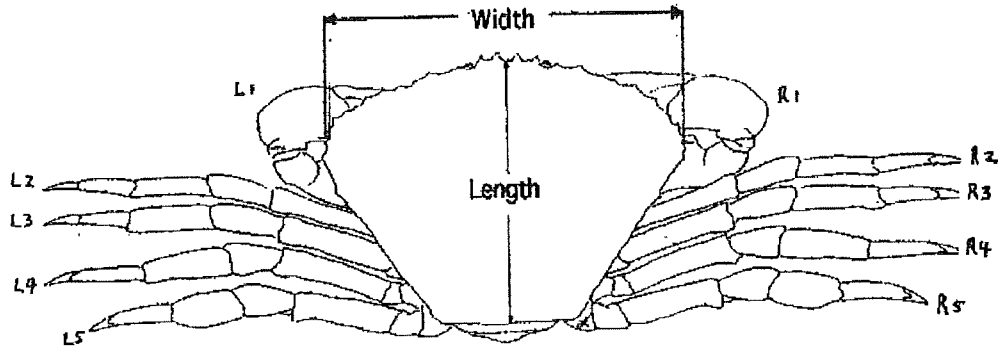


Figure 18a. Giant crab carapace length and width

4. Abdominal somite width in females - measured as the longest distance between the lateral margins of the dorsal surface of the fourth abdominal somite (Fig 18 b.) using Mitotoyu callipers as above, from a representative subsample across all size classes. This was intended to provide data to see if allometric growth of the abdomen could be used as an indicator of size at maturity.

5. Larger claw width in males; length measured as the longest distance from the ventral to dorsal margin of the propodus immediately posterior to the point of origin of the dactylus.

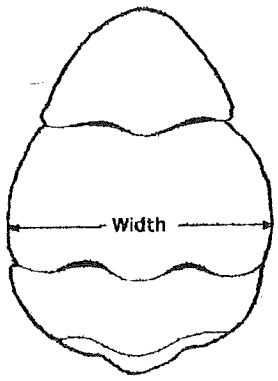


Figure 18b. Giant crab female abdominal somite

6. Larger claw length in males measured as the longest distance from the lower (underside) corner of the proximal end of the propodus to the distal tip of the propodus (Fig 18. c.) using Mitotoyu callipers as above

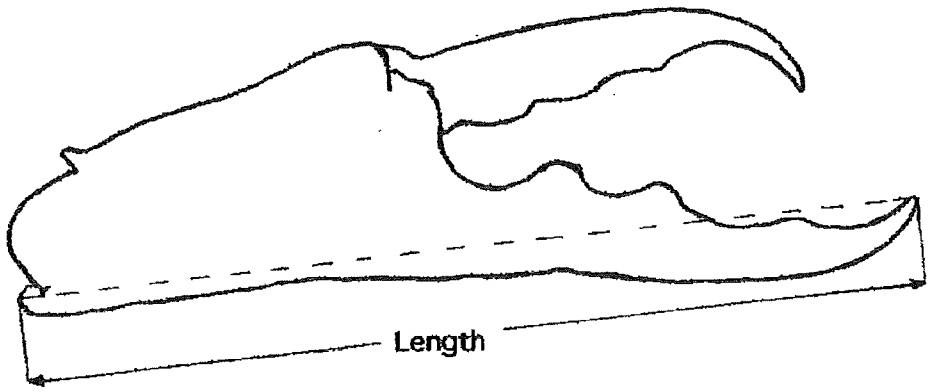


Figure 18c. Giant crab male claw length

7. Weight; using "certified accurate" processors electro balances (correct to the nearest 100 gm) with carapace length this allowed the determination of sex-specific length - weight relationships.

3.2.2. Research Fishing and at-sea sampling

Different circumstances required different approaches to sampling (see chapter 3.1 above), however the data collected at sea during commercial catch sampling and research fishing was similar and is listed below:

1. Geographic location.
2. Date.
3. Depth.
4. Catch - by geographic region
5. Catch - by depth
6. Effort - total soak time = number of pots x days of soak.

The catch and effort data collected were used to provide an indication of changes in CPUE during the period of the project.

7. Sex - this provided an indication of sex ratios in different localities at different times of the year.
8. Shell state -described as degree of fouling with encrusting organisms and rated (after Hoggarth 1993) as "clean" shelled (less than 5 encrusting organisms) or "undetermined" (more than 5 encrusting organisms) or "old" shelled if more than 5 encrusting organisms and with wear on the tips of the walking legs). This provided an indicator of time since moulting.
9. Carapace length - as measured in 3.2.1 for all animals at all localities - this provided information on size structure of the stock.
10. Carapace width - as measured in 3.2.1 for a representative subsample from all localities.
11. Female abdomen width -as measured in 3.2.1 for a representative subsample from all localities.
12. Larger claw length in males -as measured in 3.2.1 for a representative subsample from all localities - this allowed analysis of allometric growth of the claw as a potential indicator of size at maturity.
13. Females in berry or carrying spent egg casings, for all animals sampled from all localities- this provided percentage of ovigerous females versus size, minimum and mean size at the onset of maturity, and (once size at maturity had been determined) percentage of mature females spawning each year.
14. Indicators of mating - discoloration of gonopores, abrasions on the ventral somites of the anterior abdominal segment of females. (after Melville-Smith 1987).
15. Damage to chelae or legs.
16. Habitat features - substrate type, surface water temperature (if possible).
17. The date, position and depth of release of tagged crabs were also recorded.

Table 3. Population sampling, tagging, recaptures and moults during the survey period (July 1st 1993. to June 30th 2000.)

State	At Sea Sample	Tagged	Recaptures	Moults
Tas	16395	7154	277	31
Vic	5884	3348	431	80
SA	40276	5332	535	128
WA	12901	2160	512	111
Total	75456	17994	1755	350

Data presented in Table 3 are based on entire catch.

When onshore, sub-samples were used to determine:

1. Egg mass weight - the egg mass was stripped from the pleopods (and preserved) from a representative subsample of berried females across all size-classes. An attempt

was made to standardise the time of estimation due to egg loss during incubation. Optimal time for estimation is just prior to expected hatching (Cobb and Caddy, 1989). This occurred at the time when the colour of the eggs was a deep burgundy and catchability of gravid females rapidly increased. Egg mass was determined as wet weight (to nearest gram) after blotting dry with tissue paper using electro balances (0.100 gm accuracy).Gonads were dissected from a representative subsample of discards and weighed to nearest 0.1 gm after blotting dry. This required 5 to 10 females per size class. This could not be conducted during the commercial catch-sampling period due to the impracticality of this type of dissection during normal fishing operations. A limited data set was obtained during the research-fishing period to provide some information on gonadosomatic index (GSI).

2. Stock structure - samples of leg tissue were taken from representative locations. The tissue was frozen for electrophoretic analysis or preserved in alcohol for DNA based study.

3.3. Stock structure

The species is distributed from 35° 00' South, 150° 00' East off NSW, southerly along the edge of the Australian continental margin to 34° 00' South, 115° 30' East off WA.

Tissue samples (leg muscle) were obtained from crabs at two widely separated geographic locations off Augusta in Western Australia and Portland in Victoria. The samples were stored in liquid nitrogen. Muscle tissue was screened for genetic markers at 20 enzyme loci to determine the degree of heterozygosity using standard allozyme electrophoresis techniques (after Richardson et al, 1986).

The degree of heterozygosity exhibited by enzymes in muscle tissue of *P. gigas* was very low both within and between samples from the two areas. At the level of resolution provided by allozyme electrophoresis there was no evidence of isolation of stocks. On this basis it was assumed that *P. gigas* represented a single stock across southern Australia, however it could not be concluded that gene flow was unrestricted across the species range. Further genetic analysis of the stock with tissue obtained at Augusta, Western Australia; Portland, Victoria; and Bicheno, East Tasmania; based on DNA techniques was undertaken. (see chapter 4.2.)

3.4. Larval ecology

The original research plan called for intermittent sampling of megalopa to be conducted during the periods indicated on Figure 19. The timing of this sampling was based upon the prior accidental collection of megalopa (of an unknown species) by fishermen at these times. Given that densities and distribution of megalopa were unknown, sampling was not planned to be intensive. Megalopa were collected from ropes and floats. Artificial substrates, based upon those used to monitor puerulus settlement in *Panulirus cygnus* (Phillips and Brown, 1979), were also deployed with pots in western Victoria.

It was planned to survey;

- Megalopa distribution both horizontally (inshore and offshore) and vertically (if possible).
- Seasonal abundance.
- Electrophoretic profiles compared to adult stock.

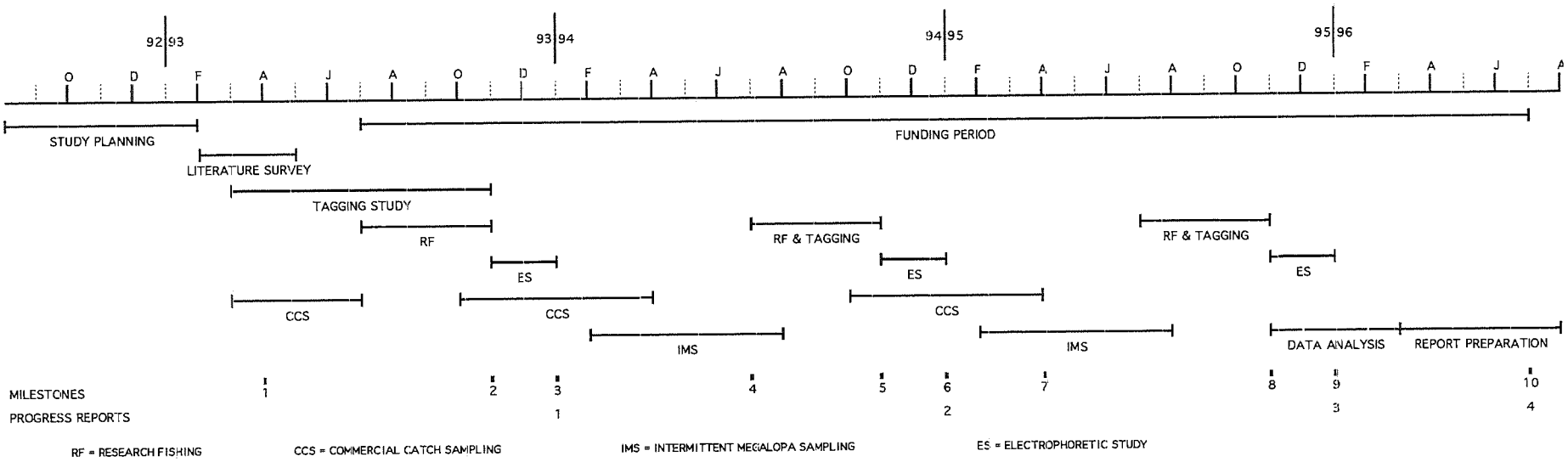


Figure 19. First phase research timetable

Megalopa from an initial collection were analysed using allozyme electrophoresis and also grown out in aquaria.

3.5. Tagging

The position of insertion for tags was based upon the use of the epimeral suture line as had been applied to other species (after Butler, 1957; Edwards, 1965; Bennett, 1974). These studies had shown that loop tags implanted at this site could be retained through a moult.

Prior to running tag trials the preliminary work listed below occurred:

1. A crab was dissected to determine its interior morphology and the effect that making a perforation through the carapace on the epimeral suture line would have on the animal. This determined that a tag inserted into this line immediately above the base of the third pair of walking legs would penetrate the brachial chamber at the rear of the gills and that it was very unlikely that bleeding or damage to vital organs would occur.

2. Field trials were conducted in August 1993 where a 3 mm hole was drilled through the suture line at the rear of the brachial cavity in 12 crabs. A test to determine if any mortality attributable to handling, perforation of the shell, or the raising then lowering of the crabs from the sea floor was performed. The crabs were placed back into the water in crab pots for a week, with 6 crabs resited at 100 fathoms (or 183 metres (and 6 crabs at 150 fathoms (or 274 metres). Of the 12 crabs treated in this way, two were absent from the pots when they were re-hauled. As no exoskeleton fragments were found in the pots it was assumed the crabs had been washed out of the pots as they were reset.

3. After the pots were re-hauled, the same crabs were placed in holding tanks at "Portland Seafoods Pty Ltd" and observed for a further 2 months to monitor healing at the perforation in the shell. During this period, but unrelated to the above trial, another crab was tagged using a single lobster T bar tag which was inserted into it's epimeral suture line. During the next week the tag was observed to disappear into the gill chamber.

The VFRI (now MAFRI) at Queenscliffe was then chosen as a suitable location to hold crabs for a tagging trial over a longer period, because it had been the site where 2 giant crabs were known to have moulted in captivity(R. Horton, pers com 1993). A tagging trial was set up in April 1994, using nylon loop tags and double T bar tags. Each animal was accommodated on a separate plastic mesh holding cage. The cages were provided with a shell grit substrate and opaque covers used to reduce light levels and to prevent fouling. Crabs were maintained in an open circulation system, at ambient temperatures of 11-21° C and fed a mixed diet of mussels and squid. Animals were sexed, measured and weighed as above prior to tagging. Observations of tag loss, mortality and moulting were made over an 11 month period.

The tagging procedures tested were:

1. Double T bar tags inserted into 27 crabs in April 1994. The earlier experience at Portland Seafoods where a single lobster T bar tag appeared to be drawn into the

brachial chamber led to the project officer designing a tag with an upper T bar added about 10 mm above the lower T, to act as a stopper. Manufacture was organised through Hallprint Pty. Ltd., South Australia and the tag consisted of a conventional T bar tag with the additional T bar filament inserted along side it and contained within the notation barrel. The tags were applied using Dennison 08958 Tagfast 11 Tag guns with a heavy- duty stainless needle. 22 crabs were housed in individual cages and the rest kept in a communal holding tank

2. Loop tags inserted through 2 holes in the epimeral suture line of 7 crabs in April 1994. The loop tag material was obtained from Hallprint Pty. Ltd. and the curved hollow insertion needles and swages to join the nylon material were manufactured by Portland Surgical Products. During the application of the loop tags it was determined this method was too intricate to be successfully applied in a large scale tagging program by fishermen working at sea. 4 crabs tagged by this method were placed in individual cages and the other 3 kept in a communal holding tank.

Discussion

No mortality was associated with application of the double T-bar tags and the shell around the tag remained in a healthy state with little erosion through wear or chitonoclastic infection. The long intermoult period of the species meant that by the end of April 1995, of the 22 animals tagged, only 5 had moulted but the tags were retained through the moult in all cases. No loss of double T tags was observed, however it should be noted that the application method can affect this, as the filament between the T's is shorter than the distance of travel of the insertion piston within the needle of the tag gun. If the needle of the gun is not withdrawn about 5 mm before the trigger is pulled, the upper T comes fast against the shell and the movement of the piston breaks off the lower T or the filament and lower T splits at their junction point. After insertion the tag should be gently pulled to test if it has come fast. Failure to do so can result in the tag falling out due to non-detection of splitting or from inadequate rotation of the lower T after it has been emplaced.

The loop tags were less successful than the double T's. Of the 7 crabs tagged, 3 had died within 2 months. In non segregated conditions other crabs seized the loops with their pincers, in 2 cases detaching it along with sections of surrounding shell around the tag site. It appeared that wherever the underlying cuticle had been touched during the tag insertion process or perhaps through other crabs pulling on the loop, infection resulted. By the end of April 1995, 1 of the crabs had moulted and retained this style of tag.

As the Queenscliffe trial proceeded it was clear that the double T-bar tagging method met the criteria of cheapness and simple application required for a full tagging program. There was however a need for caution because if the crabs were tagged in the wrong place they would be unable to moult, because the tag would snag the exuviae (cast off shell) and death would be the result. So it was most important to acquire a strong understanding of the mechanics of the moulting of this species.

During September 1994, before any crabs had moulted at Queenscliffe, the project officer visited the St. Helens Secondary College in east Tasmania, where a juvenile giant crab had been observed moulting in the science laboratory aquarium but had died before it completed the process. Inspection of the preserved specimen indicated

that the double T-bar tag would work and the certainty provided by the specimen extremely valuable, given the urgency for the commencement of a full-scale tagging program. State fisheries agencies were consulted and permission to begin a full tagging program by fishermen was obtained before the Queenscliffe trial ended in April 1994.

Tag guns, tags, release data sheets, recapture booklets, and large plastic vernier callipers were distributed. A tag return database was established and by the end of the project 17,994 crabs had been tagged, and there had been 1755 recaptures. 350 of the recaptured animals had moulted and there were only 4 reports by fishers of tag loss. Unfortunately there was anecdotal information that a fisher operating near the Victorian Tasmanian border had removed and discarded many tags. This had been anticipated and the strategy of tagging as many crabs as possible in the area was adopted. It was hoped that other fishers supportive of a sustainable fishery would capture some of these and as it eventuated this was successful.

The data from recaptures of tagged crabs was used to study:
1. Migration
2. Growth

The subsequent quantification of the differences between release and recapture lengths in figure 1.2.1.-1 of appendix 3, "Yeild, Value and Egg per recruit of Giant Crab"(McGarvey, Matthews and Levings 1999) provided a clear separation between the small differences that could be introduced by loose callipers or misreading the vernier at the edge of the slide and the much larger moult increments.

Accurate maps of release, recapture and sampling location, as well as other aspects of this study have been prepared to assist interpretation using Mapinfo and Vertical mapper software. Bathymetry is derived from the AGSO "30 Arc Second Gridded Bathymetry of the Australian Region".

The double T- bar tag is now being manufactured by Floy Tags of the USA as well as Hallprint, Australia and is used on other crab species such as dungeness crabs, *Cancer magister*, in north America and king crabs *Paralithodes camtschaticus* in Norway (pers com. Svein Loekeborg, Fisk Forsk, Tromso). The tag's cheapness and simple application has allowed fishermen to tag large numbers of crabs at sea. By 1998 the

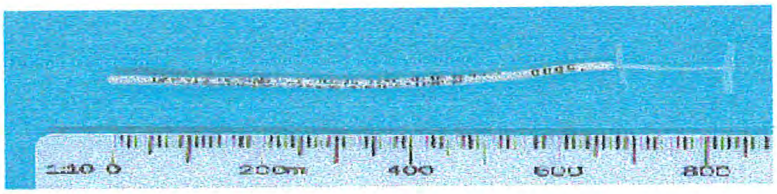


Figure 20. Levings double T bar crab tag, initially developed to study growth and movement of *P. gigas*.

tag had been shown to endure through multiple moults in *P. gigas* and in North America *C. magister* (pers com. T. Shirley, University of Alaska, 1999), with negligible tag loss or injury to the crab. The tag (Figure 20) is an effective tool to assist determination of growth rates and movement.

3.6. Reproductive Cycle and Size at Sexual Maturity

Data was obtained from at sea sampling (see 3.1.2. & 3.2.2. above) and returns from the tagging program. Combination of the data from these sources provided the following:

1. Timing of reproductive events was determined from the appearance of berried females in catches and cross referenced with the determination of gonadosomatic index. The latter was determined by onshore dissections of females across the size range 73 mm to 197 mm length, collected during the months of May 1994 to May 1996 from Western Australia, South Australia and Victoria. Due to low catchability of females during the egg incubation period, from late autumn through to early spring, samples were pooled across these sites and across years to generate enough data points to examine trends. This means that the data represents an average for all stocks and that some differences between stocks may subsequently be determined. Ovaries were weighed wet and related to wet weight of females.

2. Length of egg incubation was determined from field observations of the first incidence of eggs, their colour changes during maturation and the presence of empty egg casings after hatching.

3. Frequency of spawning was determined from the tagging study based upon successive recaptures of individual females and an examination of their reproductive state.

4. The relationship between reproduction and movement was based upon recaptures of tagged females. Reproductive condition was checked against depth and used to generate hypotheses regarding reproduction and movement cycles. The percentage of females in berry at different depths during the early part of the reproductive season (June and July) was compared to that during the late part of the season (October and November) to shed light on movement related to reproductive events.

5. Size at sexual maturity.

5.1. Female

Size at sexual maturity for females was determined via two methods based upon the relationship of size to egg bearing from field records. Females were defined as "egg bearing" if they were actually carrying eggs or if they showed signs of having carried eggs, such as empty egg cases (after Hoggarth, 1993, and King, 1995). The two methods were:

a) The minimum size at sexual maturity (Lsm) was determined from the smallest carapace length at which females were observed to carry eggs (after Hartnoll, 1969) in the different regions fished.

b) The average size of females at sexual maturity (Lm) was determined from a comparison of the percentage of females carrying eggs within different size classes. Normally this would be determined using the length at which 50% of all females in the population are egg bearing. However, in some crabs, including *P. gigas*, the relationship between percentage of egg bearing females and length does not follow the normal sigmoidal pattern. In these species the percentage of egg bearing females does not reach 100%, even in mid sized length classes with large

numbers of individuals sampled, and the proportion of females carrying eggs falls away from the asymptote in the larger size classes (Hoggarth, 1993). Cumulative normal or logistic functions cannot be fitted to the data. A reasonable estimate of size at 50% maturity can be made by fitting a curve to the lower portion of the data by eye (only) giving strongest weighting to smaller size classes based upon the assumption that the smallest females will mate and ovulate at the first opportunity available. In these species an adjustment needs to be made to take into account that less than 100% of females within any size classes are reproducing; if Lm is set at 50% using unadjusted proportions then it is artificially high (King, 1995). Based upon King (1995), the convention adopted in this study was to set Lm at the half way point between zero and the asymptotic value on the right hand portion of the curve fitted as above. Curves were initially fitted using 1mm length classes and cross referenced with a similar series, but using 5mm length classes. Whereas the use of 1mm classes was very useful for the determination of the smallest size at which 50% of crabs in that class were mature (Lm), 5mm length class series provided more clarity when analysing fecundity across the entire adult female population. The plot was less spikey and so made it easier to discern whole population trends such as that declining fecundity off east Tasmania. Correspondence between the values of Lm from these two levels of analysis was reasonable in all cases except for northwest Tasmania where the proportion of egg bearers had been grossly affected by the site's fishing history. (see table 13, chapter 4.5.4.).

Lsm and Lm were determined for the various populations fished and also compared to other biological indicators such as maximum carapace length, length of females at 50% of cumulative egg production, male and female moult increment.

5.2. Males:

When considering the issue of male maturity there is an important difference between physiological and functional maturity that should be recognised. A criterion for male maturity based solely on the existence of spermatophores within the male has limitations. It is not just the existence of sperm but rather the male's ability to deliver the spermatophore to a female and achieve reproductive success that is the key issue. Physiological maturity in males becomes of secondary importance in comparison to the need for determination of the average size at which functional maturity occurs.

This consideration applies to many crustacean fisheries (George and Morgan, 1979) and is not limited to crabs. In lobsters (*Homarus*) and (*Palinuridae*) the same situation occurs, where the presence of spermatophores in smaller sizes does not indicate the ability to function as a mature adult and participate in mating (Fielder, 1964; Heydorn, 1965). George and Morgan (1979) studying *Panulirus versicolor* examined leg length in relation to carapace length. They found that two linear relationships of leg length to carapace length fitted the data better than a single curvi-linear relationship as had been applied by Templeman (1935) in his study of *Homarus*. George and Morgan suggested the two linear growth phases of pre and post puberty were possibly the rule rather than the exception amongst many other crustaceans. The two relationships "were representative of two clear cut growth

phases during the life of rock lobsters, i.e. an early steady growth of immature animals followed by an increased, but again steady, growth of secondary sex features after gonad maturity." A similar observation had been made by Huxley (1924) who used the term "constant differential ratio" to describe the phenomenon.

As the males of *P. gigas* become adult one of the chela, usually the right grows asymmetrically and becomes much larger than the other. In this study, based on the information presented below, the large chela was considered to be a "maturity feature" and it's development was studied to shed some light on the issue of functional maturity for males.

The depth at which *P. gigas* occurs has prevented observation of courtship and mating rituals, but there are some limited observations that appear to be consistent with the behaviour of other crab species.

- Tank observations indicated the large chela of the male features in a "shield display" ritual where the crab sits back on its hind legs, rears up with claws outstretched and so appears very large.

- Damage to the chelae of *P. gigas* often consists of the imprint of the molar pegs of the large chela of another crab. The absence (in the eastern states), of other crab species that could inflict this type of damage suggests the large chela is used in combat.

- A large male *P. gigas* was introduced into a cage which contained a moulting female at Queenscliffe. The encounter began with the male stroking the female with its two fore-most legs and then using its large chela to draw the female underneath it.

In the absence of further observations on *P. gigas* it was worthwhile to consider other crab species. Sexual dimorphism of one of the chelae is observed in many species of brachyuran crabs and is a consequence of their widespread use by the male in combat, display and courtship (Hartnoll, 1974). The aggressive ritual of "shield display" is commonly observed in other brachyuran crab species and is inherent in the establishment of dominance and hierarchy (Finney and Abele, 1981). All accounts of mating for 5 species of *Cancridae* emphasised that the male treats the female gently throughout, and that the female is cooperative, sometimes in response to stroking by the male. The large chela is used to carry the female during copulation and after moulting while the female's shell hardens (Hartnoll, 1978).

Biological assays on male *P. gigas* by Gardner (1998) showed that crabs as small as 90mm had vas-differens containing well developed spermatophores. As this is much smaller size than at the onset of the adult differential growth phase, it is apparent that asymmetrical growth of the chela occurs post puberty and is a secondary sexual characteristic. This is consistent with Hartnoll's (1969) findings for other brachyuran crab species, where the development of secondary sexual characteristics did not always correspond with the ripening of the gonads. Thus it has been inferred in this study, that the asymmetrical growth of the chela in *P.*

gigas males is a secondary sexual characteristic, a typical "maturity feature" that develops in many other brachyuran crabs as well.

The method of measurement has been described in chapter 3.2.1. & 3.2.2. and claw length is illustrated in Figure 18c. The relationship between claw length and carapace length was subject to exploratory data analysis to establish the nature of the relationship or relationships between these two measurements. Subsequently a break point analysis was performed on the data for each state using minimum sums of squares analysis and the solver module in Excel V97. The breakpoint was then considered in conjunction with other biological data such as the point of separation of male and female length to weight plots and the mean moult increment. In this context the use of the breakpoint as an indicator of functional maturity was determined.

6. Relative size-specific reproductive output was determined by the relationship of wet weight of egg mass to female carapace length. Potential losses of eggs during incubation as a result of nemertian and amphipod predation (Annala and Bycroft, 1987; Kuris and Wickham, 1987; Gardner, 1997) require that females in the early stages of egg rearing be used to determine this relationship. However, the catchability of females during the early stages of egg incubation is low due to behaviour associated with ensuring that eggs are securely fixed to the pleopods (Gardner, 1998). To generate enough data points to determine the relationship between egg mass and female length; samples were pooled across sites. While this may subsequently prove to require adjustment for some sites, Gardner (1997) has shown that the relationship between carapace length and fecundity is not significantly different in Tasmania and western Victoria. On this basis data has been pooled and the relationship between wet weight of egg mass and female carapace length determined by linear regression.

7. Size-specific reproductive output allowed determination of the reproductive potential of various size classes. Cumulative egg production was based upon the number of females in the various length classes, the proportion of egg bearing females in each size class, and reproductive output (estimated from egg mass) of females within each size class. This was deemed a reasonable first approximation of reproductive output to allow the determination of an interim legal minimum size (see below). A deliberately conservative figure for protection of egg production was selected for the determination of the interim legal minimum size; this was set to protect 50% of egg production across the various stocks. Whether this level of egg production should be protected in the longer term remains to be determined. Given the state of the fishery at the time of introduction of the interim legal minimum size, it was felt that a conservative figure should be used which could subsequently be revised if additional data indicated safety in doing so.

8. Sex ratio. This is highly variable in crabs (Cobb and Caddy, 1989). Seasonal and annual deviations of the sex ratio from 1:1 were investigated for the different regional populations.

3.7. Moult Staging

Several aspects of the biology, behaviour and catchability of crabs are related to the stage of the moult cycle (Haefner Jr, 1985). Stage of the moult cycle was determined using development of the setae on the distal end of the pleopods or abdomen (Vigh and Fingerman, 1985; Mitchell and Burton, 1987). Such a procedure has been used routinely to moult stage spiny lobsters (Morgan, 1974). 54 giant crabs (21 males and 33 females) were collected from Bass Strait between Cape Bridgewater (38° 23' S, 141° 23' E) and the Victorian/South Australian border between March and July 1995. The crabs were captured by demersal trawling from a substrate of fine calcareous gravel and silt at depths between 300 and 420 metres

The crabs were immediately killed by packing on ice and remained frozen until processed. A pleopod was removed from each female and the abdomen removed from each male; these were fixed in 10% formalin for 24 - 48 hours and then preserved in 70% ethanol. On the basis of setal development on pleopods in females and on the tip of the abdomen in males, moult stage was categorised as postmoult (stages A-B), intermoult (stage C), and premoult (stage D). This information was correlated with shell-state and colour of pleopod setae in females. The results are presented in chapter 4.6.

3.8. Diet and Feeding

Description of the morphology of the digestive tract and examination of material from the oesophagus/stomach were conducted to assess diet and trophic interactions. The ability to determine diet from faecal samples is dependent upon the extent of food processing through the gastric mill. The life style of xanthoid crabs is that of a "slow walker". These animals are slow moving, protected by their heavy exoskeleton and large chelae, have small eyes and are not adapted for catching moving prey (they tend to utilise molluscs and other sedentary invertebrates) (Warner, 1977). Diet was studied to determine whether the giant crab feeds upon molluscs and some qualitative information on the distribution of prey was gathered by opportunistic collection of benthic hash that had accumulated in pots and it's subsequent microscopic examination.

Sampling

54 crabs were collected as above. Immediate freezing onboard prevented the excretion or digestion of stomach contents. Onshore storage was in a commercial freezer until laboratory work began. The crabs were sexed, weighed to the nearest 0.1 kg, and carapace length, carapace width, right cheliped length and left cheliped length measured as in Figure 18a and c. Statistical analysis of cheliped length differences within and between sexes was performed using a two-sample t-test and analysis of variance (using Minitab 9.2.1).

Digestive Tract and Feeding Morphology

The histology of the digestive tract and the morphology of the feeding structures were also investigated. Methods are detailed in Heeron and Mitchell (1997) (see Appendix 5).

Feeding Behaviour

Twenty animals were held in a recirculating seawater system at approximately 15°C and fed pieces of squid (*Nototodarus gouldii)* weighing 10 to 35 gm. During the

approximate 30 minute feeding period behaviour and the action of the feeding appendages were observed.

Stomach Content Analysis
After each animal had thawed the stomach was dissected out, relative degree of fullness was assessed and stomach contents preserved in 10% buffered formalin. Food items were sorted into representative taxa, identified and quantified using ranks based on a modification of the points method (Pollard 1973) using estimated percentage volume. Food types were ranked from highest to lowest abundance based on an estimate of relative volume. A preponderance score was then given for each food type. This score was based on the total number of food types present in any one stomach and the rank of the individual food item according to the formula:

PS = (N + 1) - r where PS = preponderance score of item i, N = total number of food items in any stomach, r = rank of the subjective volume of item i.

The individual preponderance scores for each food type were then summed over the total sample of crabs and expressed as a percentage of the sum total of the preponderance scores for all food types. This gave information on both relative abundance and association of food items. Ms Sue Boyd and Dr Gary Poore of the Department of Invertebrate Zoology, Museum of Victoria, confirmed identifications. Crabs were divided into three categories based on sex, size and moult stage. Two weight groups were selected: 0 to 2.4 kg and 2.5 to 7.5 kg. The percent relative importance of each food category was then compared both within and between different crab categories. The results are presented in chapter 4.7.

3.9. Growth

Chapter 3.5 has presented the development of the Levings double t bar tag. There have been up to 3 moults by some crabs demonstrating the tags enduring nature. Table 3 lists 350 incidents of growth from 1755 crabs recaptured. From this data, it was possible to model growth and a full description of the methods and the results are presented in chapter 4.8.

3.10. Movement

The locations of release and recapture of tagged crabs were recorded in degrees and minutes to 2 decimal figures using the fishing vessels' GPS navigation systems. Unless fitted with a differential service to eliminate the "dither effect", these systems had an accuracy of about 20 metres (± 40 metres). Booklets of recapture cards and calipers were provided to all crab permit holders. The cards provided a pro-forma for the recording of the date, tag number, water depth, location, sex, length, reproductive condition, shellstate, damage, and release location. In order to ensure this data was not purely an artefact of the target fishery location recapture kits were supplied to everyone to get a full coverage of the species range. When a recapture occurred the card was detached and forwarded to the project officer who sent back a summary of release, recapture and growth details. Inevitably, some errors were introduced through incorrect recording or data mis-entry, but spatial analysis and cross-referencing of release details with recapture cards allowed correction in many cases.

The distance and direction of movement between release and recapture positions were calculated using the geodesics described by D.Morgan (1991). As the formulae do not

account for the undulating benthic topography these calculations are an approximation and represent minimum distances. Any recaptures that occurred less than or equal to 1 km from the release point or less than or equal to 1 month at liberty were edited from the analysis. As the crab slowly sinks through the water column on release, ocean current causes it to drift away from the release point and this can confound accurate analysis of changes in depth. The size stratified nature of the population coupled with a tendency for the crabs to aggregate in a narrow depth stratum suggested it was appropriate to filter out short distance and duration recapture data. A similar procedure has been applied to *Jasus edwardsii* recaptures by Anala 1981 and Prescott et al 1997.

Changes in latitude and longitude for all recaptures were grouped by region, then summed, averaged and expressed in nautical miles. This provided a whole population movement estimate, initially along north – south (longitude) or east-west (latitude) axes. The value obtained could then be geometrically resolved to express the magnitude of movement if it was for example, south west, north west or some other direction.

3.11. Population structure

A complete series of length frequency distributions and the locations of all sites sampled across southern Australia during the period 1993 to 2000 are attached as Appendix 1. All data were collated as described in chapter 4.1. and summarised using Microsoft Excel 2000. Statistical analyses were carried out using Statview 5.0 for Macintosh and PC. Seasons were defined as summer (December to February), autumn (March to May, winter (June to August) and spring (September to November). Catch per unit effort was defined as kilograms per pot per day (kg/pot/day). Weight of each crab was predicted from the length to weight relationship. Total weight of catch was estimated by summing individual weights. Catch is defined as all crabs that were attracted to baited pots, not just the commercial component.

Australia wide population structure was analysed by;

- Maximum size
- Sex
- Mean size
- Region

Sex was analysed by;

- overall size
- region
- season
- depth

separately for male and female

Regional population structure for West Australia , South Australia, Victoria, West Tasmania and East Tasmania was analysed by;

- Years
- Season
- Depth

The results of the above analysis are presented in chapter 4.10.

3.12 Preliminary Stock Assessment

Preliminary stock assessment has been based upon the use of catch per unit effort (CPUE) as an index of relative abundance (after Miller and Mohn, 1993). The data used is a fishery based assessment of populations; fishery dependant data has the advantage of providing large sample sizes with reduced variability, but has the disadvantage that fishing may be conducted over a restricted depth range (King, 1995). While a fishery based assessment of populations has been used elsewhere to make preliminary estimates of potential yields from crab fisheries (Hoggarth 1993), the results must be considered as tentative due to the targeted nature of the fishing. Interpretation of results must take into account that actual or effective effort may change relative to measured effort as fishing techniques become more effective in the early stages of a fishery (King, 1995). While certain depths were targeted during fishing in the present study, the entire catch was sampled so biases have been minimised. The data is considered to represent the best interim indicator of population abundance available in the early stages of the *P. gigas* fishery.

As discussed by Gardner (1998), the measure of effort used in the *P. gigas* fishery is subject to error as pots may be set for irregular intervals between 1 and 5 days. The use of kg/pot/day as the measure of CPUE may introduce error due to saturation effects (reduction of catch rate with increasing catch during soak period)(Miller 1979). In the absence of fishery independent assessments of catch rate it is accepted that this measurement of effort provides the best indication of CPUE (Gardner, 1998).

Analysis of variance was performed on CPUE data according to the following scheme:

Australia wide
All data pooled between seasons
All data pooled between regions
All data pooled between sexes
All data pooled between years

By State
West Australia:
Male and Female combined;
- All data pooled between depths
- All data pooled between seasons
- All data pooled between sexes
- All data pooled between years

Male and Female separately;
- All data pooled between depths
- All data pooled between months
- All data pooled between years

South Australia
Male and Female combined;
- All data pooled between depths
- All data pooled between seasons
- All data pooled between sexes
- All data pooled between years

Male and Female separately;
- All data pooled between depths
- All data pooled between months
- All data pooled between years

Victoria
Male and Female combined;
- All data pooled between depths
- All data pooled between seasons
- All data pooled between sexes
- All data pooled between years

West Tasmania
Male and Female combined;
- All data pooled between depths
- All data pooled between seasons
- All data pooled between sexes
- All data pooled between years

East Tasmania
Male and Female combined;
- All data pooled between depths
- All data pooled between seasons
- All data pooled between sexes
- All data pooled between years

The results of the above analysis are presented in chapter 5.

4. RESULTS

4.1. Sampling

Various jurisdictional arrangements prevail in each of the states across the giant crab's geographic range and different arrangements preempted different approaches to acquiring samples. The three methods that were used to sample the population are described below and in combination increased the total number of sampling days available over the study period from 60 to 738.

Sampling methods;

-Landed catch sampling (LCS)-samples obtained from processors.

-Commercial catch sampling (CCS)-voluntary sampling of the entire catch by commercial operators or observers at sea.

-Closed season research fishing (CRF)-sampling by observers of the entire catch during fishing in closed season with partial sale of the catch to cover costs of fishing.

The breakdown of sampling days per state is shown in Table 1, and the methods used in each state in Table 2. Table 3 describes population sampling, tagging, recaptures and moults during the project period (July 1st 1993. to June 30th 2000.). Data listed in Table 3 are based on the entire catch attracted to baited pots, not just the commercial component >150mm carapace length, as would be obtained by sampling of landed catch. Tables 1, 2, & 3 are to be found in chapter 3

At the projects completion population data was processed into a data base format to facilitate ease of application of statistical analysis. The data base was set up as 2 files, where a key file listing fishing events was linked to a biological file which described the sample taken in each of the events.

The key file was structured as;
Fishing event/date set/date hauled/start latitude/start longitude/end latitude/end longitude/pots/fathoms/metres/area/fisher.

The biological file was structured as;
Fishing event/sex/carapace length/abdomen width/berried/setae colour/claw length/shellstate/damage/carapace width/claw width/area/fisher

A ready reference index was also created

The data base was then analysed to provide statistical outputs on the mean size and catch per unit effort which are presented later in this report.

4.2 Stock Structure:

The results of allozyme electrophoresis at 21 locii resolution suggested nothing other than genetic homogeneity across the entire species range. DNA techniques were then employed as they provided a higher analytical resolution to further examine if any variation could be determined and also to describe where P. gigas sat genetically in relation to other species.

4.2.1. DNA Study -1

4.2.1.1. General Introduction

DNA sequence analysis

In the last ten years DNA sequences have become the preferred tool for both population genetics and phylogenetic reconstruction (Miyamoto and Cracraft 1991). Because of wide differences in the evolutionary rate of particular gene regions it is possible to address a broad range of systematic questions ranging from kingdoms to the population level (Faber and Stepien 1997). The most common gene region studied is the mitochondrial DNA (mtDNA) due to a number of factors that make it useful for genetic studies (Simon *et al.* 1994). MtDNA provides sequences with greater variability and sensitivity to genetic drift than nuclear DNA and contains conserved genes for phylogenetic studies and highly variable regions suitable for population genetics.

Without question the polymerase chain reaction (PCR) (Saiki *et al.* 1988) is among the most significant advances in molecular biology in recent years. PCR is a rapid and simple method used to amplify a particular sequence of DNA. Until the development of PCR, sequencing of genes for phylogenetic analysis was rarely performed because it was too expensive to clone homologous genes from multiple samples (Stepien and Kocher 1997). PCR makes it possible to obtain large quantities of a particular DNA sequence by selective replication. In PCR , two small oligonucleotide primers are used to amplify a region of DNA flanked by the primers. The amplification takes place in a thermocycler and consists of three major phases: denaturation, annealing and extension. In the denaturation step, heat (usually 95(C) is used to stop all enzymatic reactions and denature the DNA from double to single strands. The annealing phase is the most critical step (Palumbi 1996) as it is where the oligonucleotides bind to the appropriate sites in the template DNA. The temperature of the annealing phase is very important, if too high then the primers won't bind, if too low then non-specific binding will occur. Each primer is different and has a different annealing temperature, therefore this needs to be established in order for optimal PCR conditions to be achieved. The final stage is extension which allows a heat stable enzyme to synthesise the target DNA segment. The enzyme most widely used is *Taq* polymerase that works well at 72(C. PCR is able to amplify target DNA via cycling (25-40 cycles) through the three phases from a very small starting concentration (e.g. <1%) to a much higher concentration (almost 100%) (Hartl and Jones 1998) which then allows direct sequencing of the target sequence.

Once the required nucleotide sequences are obtained via PCR and direct sequencing the must be aligned against each other and compared. The use of sequence data for phylogenetic analysis is straightforward compared to other methods, where the corresponding positions (A, C, G, T) are compared against each other. There are a number of methods used for analysing molecular data, each one ending in the generation of a phylogenetic tree. Each method has advantages and disadvantages,

and controversies over the relative efficiencies of each to recover phylogenetic information are abound (Swofford *et al* 1996). The major problem of phylogenetic reconstruction is that it is impossible to know the true relationships for any real set of organisms, so it is difficult to judge which tree is the correct one. The advent of advanced computer simulation and numerical resampling have made the reconstruction of phylogenies more accurate, however using multiple analytical techniques is the best way to develop accurate phylogenetic trees.

Use of population genetics in Fishery management

The role of fisheries management is to ensure the sustainable use of the resource, whilst maximising economic returns. This is best achieved by considering a wide range of issues, including information on population or stock structure. Without knowledge of the number of interbreeding populations contained within an exploited species, management policies may not effectively ensure the sustainability of resource. Population genetics attempts to identify separate populations of a species within which intermixing of individuals occur, but between which migration is rare or absent. This is evident in many freshwater species where interbreeding is difficult, or impossible due to changes in catchments (e.g. Hurwood and Hughes 1998). It is also shown in marine species, especially those with specific habitat requirements (e.g. littoral species) (e.g. Cuesta 1998), however allopatric populations are also found in pelagic species (e.g. Carvalho *et al* 1992).

Traditionally tagging and monitoring the movement of individuals was the only method for inferring population boundaries, however physical tags or markers are unlikely to be able to measure the movement of small larvae. There are a number of other methods also used but by far the greatest tool for deciding population differentiation is the development of molecular genetic methods. A genetic analysis can divulge population results much more quickly and more accurately than other studies (Hilbish 1996). The genetic consequences of migration and mutation and subsequent population mixing and interbreeding are the reasons behind the genetic approach. For example a species with no migration in or out of an area would become genetically divergent via the processes of genetic drift and natural selection, however a species capable of migration between populations will enable interbreeding without loss of genotypes via gene flow.

Molecular genetic approaches began to be used in the 1950's, initial studies were of blood group variants (Ward and Grewe 1994). Electrophoresis techniques for separating allelic variation in allozymes were developed in the 1960s and these were predominately responsible for the increased interest in molecular population genetics (Hilbish 1996). Allozyme electrophoresis is still used widely today and has provided the most genetic data to date, however the technique does have certain limitations. The resolution of allozyme electrophoresis does not always detect differences between populations and individuals (Utter and Ryman 1993) and as population geneticists have encountered more questions that cannot be resolved with allozymes, DNA methods have become more prominent. In particular mtDNA methods have been widely used for population level comparisons since the development of PCR and sequencing. There are many advantages of using mtDNA sequences for population studies, it is relatively quick and requires fewer samples than for allozyme or other methods (Hillis *et al.* 1996) and is generally thought to be more powerful. This is due

to it being haploid and maternally inherited and more sensitive to genetic change via accentuated genetic drift (Ward and Grewe 1994).

There are many other methods available at a population geneticist's disposal such as restriction analysis (RFLP's), minisatelites, RAPDs, etc and each method has advantages and disadvantages (see Hillis *et al* 1996). Ideally for a complete investigation into the population structure of a species, more than one of the available techniques is used. This is a time consuming and expensive exercise, and with constraints placed on this study it is not plausible in this case.

General Aims
The primary aim of this study was to investigate the population structure of a commercially important crustacean, the giant crab (*Pseudocarcinus gigas*) and ascertain what management proposals, if any, could be made from this data. The feasibility of sequencing various mtDNA regions for determining population subdivision was examined and those able to be obtained were used for the population study.

A secondary aim of this study was investigating the phylogenetic position of *P. gigas* in relation to other Brachyuran species, in particular other Xanthoid species. Portions of the 16S mitochondrial gene were amplified and compared in order to determine phylogenetic position.

4.2.1.2. Population Genetics of the giant crab *Pseudocarcinus gigas*.

Introduction.
The existence of *Pseudocarcinus gigas* stocks have been documented as occurring from Cape Naturaliste to Esperance in Western Australia and from the centre of the Great Australian Bight to southern New South Wales (Levings *et al* 2001 unpublished). The size of the giant crab from the western stocks is smaller than that from the eastern states. This evidence implies that there may be some population differentiation between the western and eastern stocks. However size differences do not always indicate genetic differences, as they may be caused by other factors such as diet availability and water quality. A population genetic study will, to some extent, determine the cause of these differences. Previous allozyme electrophoretic work has failed to uncover any evidence of population subdivision. It is hoped that this study will reveal any differences between the western and eastern giant crab stocks.

Previous studies have been carried out along the southern Australian coastline on the red rock lobster, *Jasus edwardsii*, (Ovenden *et al.* 1992) which occupies a similar habitat to *P. gigas*. This study examined mtDNA nucleotide sequence polymorphisms and found an absence of population subdivision in *J. edwardsii* across approximately 4600 km from Western Australia to New Zealand.

This study will concentrate generally on mtDNA sequences and there have been many previous decapod population studies using sequences from this region. The large and small subunit ribosomal RNA genes (16S and 12S respectively) and the cytochrome oxidase 1 (CO1) gene have been extensively used in these studies (see Gopurenko *et al.* 1999, Sarver *et al.* 1998, Cuesta and Schubart 1998, Tam *et al.* 1996). Initially the 12S and 16S gene regions were chosen as universal primers were available, and so

avoiding compounding problems of working with a new system and the need to develop new primer sets. In particular the 16S rRNA region has shown intraspecific variation in invertebrates (e.g. Avise *et al.* 1994, Bucklin *et al.* 1995, France and Kocher 1996). After the initial study of 12S and 16S genes, additional areas were also studied in an attempt to gain a more complete picture.

The primary aim of this study is to examine the population subdivision, if any, between *P. gigas* populations from Western Australia, Victoria and Tasmania using mitochondrial DNA sequences. To maximise the confidence in the results gained, more than one mitochondrial gene will be examined (e.g. 12S & 16S mtDNA). The results of this study are relevant to the management of the commercial giant crab fishery in southern Australia as well as to the further study of this species in relation to the reproduction

Materials and Methods:

Sample Collection.

P. gigas samples were collected from three locations in Australia, Western Australia (Albany), Victoria (Portland) and off west Tasmania through the Deakin-FRDC Giant Crab project by professional fishermen using baited pots. Samples for each site were collected from a single vessel at varying depths. Two outgroup species, *Chaceon bicolor* and *Hypothalassia acerba*, were also collected from Western Australia via the method described above. Upon capture, crabs were identified and leg muscle tissue samples were taken and placed into screwtop vials and either frozen at -20(C or stored in ethanol until analysis to ensure against DNA degradation

Total DNA isolation

Total DNA was isolated by two methods, a high salt precipitation method or a CTAB phenol-chloroform procedure. The high salt precipitation method (Crandall 1999) was developed for crayfish and uses the following protocol. All alcohol was removed from ethanol preserved tissue by blotting it dry on absorbent paper and adding 900(L of TE buffer (10mM Tris, 0.1mM EDTA, pH 8.0). This was then centrifuged and the TE buffer is drawn off and the tissue was blotted dry again. Frozen or treated ethanol preserved samples (40-50mg) were placed into 900(L of cell lysis solution (10mM Tris, 100mM EDTA, 2% SDS, pH 8.0), homogenised and 9(L of proteinase-K (20mg mL^{-1}) was added. Samples were incubated at 55(C overnight with periodic mixing until the tissue was digested, 4(L of Rnase-A (10mg mL^{-1}) were added and the sample was incubated for an hour at 37(C. After incubation 300(L of ammonium acetate (7.5M) was added and samples were vortexed and then incubated on ice for 30 minutes. Samples were then centrifuged for five minutes to pellet the precipitated proteins. The supernatant, containing the DNA, was transferred into 900(L of isopropanol and incubated on ice for 15 minutes. After the samples were centrifuged for 5 minutes to pellet the DNA, the isopropanol was carefully poured off and the DNA was washed with 750(L of 70% ethanol. It was then dried and rehydrated with 50-200(L of TE buffer depending on the size of the DNA pellet.

The CTAB phenol-chloroform protocol was developed by Doyle and Doyle (1987) for leaf tissue, but worked effectively for crab tissue. Ethanol preserved tissue was treated as per the method described above. Tissue was then added to ependorff tubes containing 700(L of CTAB, ground if necessary and 5(L of proteinase K was added and samples were incubated at 65(C for two hours.

After incubation 600(L of chloroform-isoamyl alcohol (24:1) was added to the samples, which were then mixed well and centrifuged for 30 minutes. The supernatant was then pipetted off and added to 600(L of phenol-chloroform isoamyl (25:24:1) and centrifuged for 15 minutes. The supernatant was then drawn off again and added to another 600(L of chloroform-isoamyl alcohol (24:1) and centrifuged for a further 60 seconds. The supernatant was then added to an equal volume of isopropanol and stored at -20(C for 2 hours. After which the DNA was pelleted by centrifuge and washed with ethanol, dried and rehydrated in TE buffer as above.

Amplification of DNA
The target DNA segments for each individual were amplified by the polymerase chain reaction (PCR) using combinations of various primers (Table 4). Double-stranded PCR products were obtained in a total reaction volume of 50(L, containing 5(L of 10X PCR buffer, 0.4mM of each dNTP, 0.8 (M of each primer, 4mM $MgCl_2$, 1 unit of *Taq* polymerase and 2(L of DNA extract. PCR amplification was carried out in a PC-960 Microplate Thermal Sequencer using the following temperature regime: an initial denaturation step at 95(C for 3 minutes, followed by 30 cycles of 95(C for 30 seconds(s), an annealing temperature of 50(C for 30s and an extension temperature of 72(C for 30s. This was then followed by an additional extension of 72(C for 3 minutes. PCR products were purified using a QIAGEN QIAquick PCR purification Kit, with final elution volumes of 50 (L per individual. The DNA concentrations were approximated against a Promega DNA/Hae 111 marker on a 2% agarose/TAE gel containing ethidium bromide and viewed under U.V light.

Samples were freeze-dried and sent to the Australian Genome Research Facility (AGRF), University of Queensland, for sequencing analysis. Sequencing reactions followed the protocol of Perkin Elmer, using an ABI big dye terminator reaction with custom primers. For each sample, sequencing was performed in both directions (i.e. using both primers) to allow complementary strands to be read and verify sequences. Sequence gels were analysed with ABI software 337XL collection (v.2.0) and chromatograms were viewed and edited manually using EditView and SeqPup (Gilbert 1997). Once edited sequences were aligned using ClustalX (Thompson *et al.* 1997).

Many primer pairs were trailed in order to obtain the best results possible (Table 4). These primer pairs encompassed a wide range of gene regions, including the mitochondrial regions 12S, 16S, COI and the nuclear cytochrome kinase intron. Investigating a primer pair involved optimising the PCR reaction conditions. This generally meant controlling the amount of template DNA added, varying the $MgCl_2$ volume added (e.g. a concentration series) or changing the temperature cycle. Generally altering the annealing temperature has the greatest effect on the end product.

Table 4. Primers trialed and target gene region. * Indicates successful amplification.

Name	Sequence	Gene region	Source
L1085	CAACTAGGATTAGATACCC	12S	Kitaura *et al* (1998)
H1478	GAGAGCGACGGGCGTATGTGT	12S	Kitaura *et al* (1998)
L1496	GTACATATCGCCCCTCGCTT	12S	Kitaura *et al* (1998)
H2492	CAGACATGTTTTAATAAACAGGC	16S	Kitaura *et al* (1998)
L2510	CGCCTCTTTAACAAGACAT	16S	Kitaura *et al* (1998)
H3062	CCGGTCTGAACTCAGATCA	16S	Kitaura *et al* (1998)
12s-2	AAGAACCAGCTAGGATAAAACTTT	d-loop	
11e-2	ATCAAGATAATCCTTTTTCAGGCA	D-loop	
COI RLR	TTGATTTTTTGGTCATCCAGAAGT	COI	Simon *et al* (1994)
C/N-279	TTAAGTCCTAGAAAATGTTGRGGGA	COI	Gopurenko *et al* (1999)
CK6	GATCACCTCCGCATCATCTCTATG	Nuclear intron	Palumbi (1996)
ARK7	GTGCCAAGGTTGGTGGGGCA	Nuclear intron	Palumbi (1996)

Results.

PCR amplification of the 12S rRNA (primers L1085 and H1478) and 16S rRNA (primers L2510 and H3062) yielded fragments of 390 and 535 nucleotides in length respectively, the sequences are shown in figures 21 (12S) and 22 (16S).

Figure 21. Amplified region of 12S mtDNA gene for *Pseudocarcinus gigas*

```
   1  CTTTNATATT TCTTGCNGCT GANAGTAACC CGCCAGATTA ATAGTAGATA
  51  TTTTCTTTAA ATTTAAAGAA TTTGGCGGTG ATTTAGTCTA GTCAGAGGAA
 101  CCTGTTTTTG AATCGATAAA CCACGAAAAA TCTTACTTAT CTTTGTTTTC
 151  AGTTTGTATA CCGTCATTAG CAGATAATTT TTAAAGAAAT AATTATTGTG
 201  TTTTATAAAT TTAGAAAAAT TAGATCATGG TGCAGCTTAT AGGTAAGTTA
 251  AAATGGGTTA CAATAATATT TATTTATAAC GAATAAATAA TGAAGAAAAA
 301  TTTTTAAGGT GGATTTGATT GTAATATAAG TTTAATATGC TTAGGAGGCA
 351  TGAGCTCTAA ATCATGTACA CATACGCCCG TCGCCCTTCA A
```

Figure 22. Amplified region of 16S mtDNA gene for *Pseudocarcinus gigas.*

```
   1  TGGAGGTATA AATAGTCTGG CCTGCTCACT GACACATAGA GTTTAAGAGC
  51  CGCGGTATTT TGACCGTGCA AAGGTAGCAT AATCATTAGT TTCTTAATTA
 101  GGAACTTGTA TGAATGGTCG GACAAAAGAA AAGCTGTCTC TGTTGTAAAG
 151  ATAGAAATTA ACTTTTAAGT GAAAAGGCTT AAATTTTTCA AGGGGACGAT
 201  AAGACCCTAT AAAGCTTTAT ATTTCGTTTA AATTTTATTG AATTATATAA
 251  ATAAAAATTT AATTTAATCA TTATATTGTG TTGGGGCGAC ATAGGTATAA
 301  TTTATATTAA CTGCTTGATA AGAAAACAAA TAATAAATGA TTTATAAAAA
 351  TGATCCTTTT TAAAGATTTA AGATTAAGTT ACTTTAGGGA TAACAGCGTT
 401  ATTTTTTTTG AGAGTTCATA TCGAAAAAAA AGTTTGCGAC CTCGATGTTG
 451  AATTAAAATA TCTTTATAGT GTAGCCGTTA TAAAAGAAGG TCTGTTCGAC
 501  CTTTAAATTT TTACATGATC TGAGTTCAAA CCCGG
```

The fragments obtained are both A + T rich with the 12S gene having a base composition of A-28%, T-35%, C-17% and G-20%, and the 16S gene having a composition of A-35%, T-35%, C-12% and G-18%. The extreme bias to adenine and thymine has been found for many crustaceans' mtDNA (e.g. Kitaura *et al.* 1998, France and Kocher 1996, Palumbi *et al.* 1991, Ovenden *et al.* 1997, Taylor *et al.*

1998). Sequences for the regions bordered by the other primers listed (Table 4) were unable to be obtained due to time constraints, thus sequence information could only be obtained for the 12S and 16S regions. In order to determine the nucleotide sequences for these other regions three to four weeks would have to be spent on each primer pair to effectively optimise PCR conditions, and ensure clean, easy to read sequences.

The amount of nucleotide diversity between the mtDNA of *P. gigas* from collection locations was zero. There is no evidence for historical or contemporary restriction of gene flow between populations. Large geographical distances between collection locations was not reflected by the amount of mtDNA divergence, with zero divergence between eastern collection sites and Western Australia which are separated by approximately 2000 km.

Discussion

Analysis of the mtDNA 12S and 16S regions from populations of *Pseudocarcinus gigas* from southern Australia revealed no patterns of divergence. The reason for this is probably best explained by the larval phase. The long larval phase of *P. gigas* is probably the main reason behind the lack of divergence. However the adult has been shown from tagging studies to move between 200 and 300 kilometres (A. Levings, Deakin University, personal communication) which would assist somewhat in dispersal. The giant crab has five zoel stages (Gardner and Quintana 1998) which aid in dispersal and, depending on the temperature, development is relatively long (around two months at 15(C). (Gardner unpublished data) This long development can explain the lack of divergence between populations

In the present analysis of 12S and 16S mtDNA sequences, subdivision was not detected. Similar results in the red rock lobster were shown by Ovenden *et al.* 1992, who found no population subdivision using mtDNA sequence polymorphisms. The lack of divergence found by the genes studied does not necessarily imply that *P. gigas* form a sympatric population, as complete or partial barriers between populations can exist.

High dispersal capabilities and the absence of physical barriers do not necessarily translate into panmixia. For example megalopa which contribute to adult populations may be pert of a small number of larvae not washed away by prevailing current. However the extent of larvae not lost from a population is unknown. Adaptation to local habitat is another factor that may cause population subdivision in the giant crab. Physical and chemical characters vary greatly between marine habitats and adaptation via natural selection to specific habitats could develop. Habitat specific settlement has been suggested for the genus *Jasus* (Pollock 1990) and could also be a factor for population subdivision amongst *Pseudocarcinus gigas.*

If other gene regions are studied then divergence between populations may be found. The 16S and 12S regions are fairly conservative (Palumbi 1996) and very subtle differences may not be apparent. The cytochrome oxidase 1 gene region has shown more intraspecific divergence amongst decapod crustaceans than 16S (Tam *et al.* 1996, Ovenden *et al* 1997 and Sarver *et al.* 1998). Whist this region was trialed during this study, no sequences were obtained and this area maybe a focus for further studies.

Other gene regions that may be studied include the highly variable control region, or an intron region from a nuclear gene. Little work on these regions in invertebrates has been undertaken, therefore these studies would be very time consuming and may be inappropriate for a study such as this. Microsatellite analysis is also another possible study, however is also time consuming and very expensive as individual microsatellite loci and primers have to be isolated for every taxa studied.

Since the degree of divergence cannot be determined between *P. gigas* populations cannot be measured by 12S or 16S nucleotide sequences, the populations may be exchanging more than one reproductively successful migrant per generation (Avise 1994). As the prevailing Southern Ocean current, known as the Leeuwin Current, moves from west to east, it is probable that planktonic zoel would also move in this direction. If it can be shown that *P. gigas* larvae exploit the Leeuwin Current and other Australian ocean currents then this will explain the lack of genetic divergence between supposed separate stocks. As the Leeuwin Current seems to be the main influence along southern Australia (Cresswell and Petersen, 1993), Western Australian populations may be a major source of recruits for the eastern giant crab fisheries. If future studies confirm the one-way flow of *Pseudocarcinus gigas* larvae across Australia then the Western Australian populations may deserve special attention, or conservation status.

4.2.1.3. Phylogenetic position of the giant crab, Pseudocarcinus gigas, and other Brachyuran species.

Introduction.
P. gigas is the largest member of the Oziidae family which belongs to superfamily Xanthoidea, which in turn belongs to the infraorder Brachyura or the "true" crabs. Brachyuran crabs have undergone extensive radiation and today are extremely diverse both morphologically and ecologically. Marine, freshwater and terrestrial forms exist among almost 6000 species, which are widely distributed from tropical mountain streams to deep sea hydrothermal vents (Hartnoll and Gould 1988). Brachyurans comprise more than 50% of all decapod crustaceans from Australian waters and 650 or more species have been recorded from the area. Xanthoidea is by far the largest family of brachyuran crabs in Australia. About 170 species in nearly 50 genera have been recorded from Australian waters (Jones and Morgan 1994). Xanthids are found from the tropics to southern Australia and are also widespread throughout the world's aquatic environments.

There are many discrepancies regarding the classification of Brachyura, several outstanding problems have been identified that have prevented systematists from reaching a consensus on a monophyletic classification for brachyurans (Spears 1992). Efforts to understand the evolution and phylogenetic relationships of brachyuran crabs appear to have been clouded in the past by extensive convergence in adult morphology (Spears *et al* 1992). The analyses of other areas such as larval features (Martin 1988), and the fossil record (Schram 1982) in an attempt to disregard adult morphology, have offered other classification hypotheses. There have been few molecular phylogenetic studies performed on Brachyura as a whole, with only Vaughn and Traeger (1976) and Spears *et al.* (1992) offering classification systems. Spears *et al.* used a similar method to this study, with the direct sequencing of 18S rRNA sequencing, whereas this study obtains 16S rRNA and 12S rRNA sequences.

Past studies into brachyuran classification have concentrated on the unresolved position of dromiid and raninid crabs within Brachyura (e.g. Spears *et al.* 1992). There are few studies where phylogenetic trees have been produced, providing conclusions into the evolutionary relationships of brachyuran crabs. Many classification systems have been produced, which group species into genus and family (e.g. the widely used Bowman and Abele (1982) classification), however the evolutionary relationships within and between these families are not discussed. Rice (1983) offers principal evolutionary lines among higher brachyurans based on zoel features, and Spears *et al.* as mentioned above presents a classification system based on 18S rRNA sequence data. Suggested phylogenetic positions within Xanthoidea based on megalopa characteristics were examined by Martin (1988).

The taxonomy of Xanthoidea has been the subject of numerous attempts at subdivision and a myriad of family and subfamily names have been proposed for various assemblages within the superfamily. *Pseudocarcinus* is a monospecific genus and has not been included in recent reviews of Xanthoidea (e.g. Martin 1988), however Gardner and Quintana (1998) have attempted to compare the larvae of *P. gigas* with other members of Oziidae and make phylogenetic assumptions based on this.

This study will attempt to give some insight into the phylogenetic position of the giant crab using 12S and 16S rRNA mtDNA sequences. There have been other crustacean phylogenetic studies performed using these regions (e.g. Kitaura *et al.* 1998, Ovenden *et al* 1997, Cunningham *et al.* 1992, Hanner and Fugate 1997, Crandall and Fitzpatrick 1996, Crandall *et al.* 1999), with most of these studies concentrating on relationships within families. The 12S region appears to be less conserved than the 16S (Palumbi 1996) therefore this region may be more informative for intrafamily comparisons than the 16S region. Whilst the 16S region may effectively lead to family level conclusions. Samples will be amplified using PCR and sequenced during the study and samples are also gained from GENBANK, an internet DNA database. However the number of samples that can be gained from either source is limited. The taxa gained from GENBANK are obviously limited to those that are available from previous studies of brachyuran 12S and 16S sequences. Brachyuran sequences that are obtained during this study are limited to those that can be gained within the constraints imposed.

Species studied can be seen in Table 5 and include Australian crabs which occasionally contribute to by-catch of *P. gigas* fisheries. These include the spiny crab (*Hypothalassia acerba*: Oziidae) and snow crab (*Chaceon bicolor*: Geryonidae) both found in Western Australian waters, and the velvet crab (*Nectocarcinus tuberculosis*: Portunidae) commonly found in Victorian waters. Species gained from Genbank all originate from the northern hemisphere and include species such as the stone crab (*Menippe mercenaria*: Oziidae), shore crabs (Grapsidae species) and swimmer crabs (Portunidae species).

The aim of this study, as stated, is to determine the phylogenetic position of the giant crab, *Pseudocarcinus gigas* within the superfamily Xanthoidea and infraorder Brachyura. This will be achieved by comparing the mitochondrial nucleotide sequences from the 12S and 16S rRNA gene regions.

Materials and Methods

Sample Collection
Specimens for the study were obtained through the Deakin University-FRDC Giant crab research project in collaboration with professional fishermen and the Museum of Western Australia, collected by hand from intertidal zones or sequences were obtained from Genbank. (See Table 5 for specimens studied and location of collection). Crab specimens collected were treated in the same manner as the population study.

Table 5. Species Studied

a) Australian species collected and sequenced.

Species	Classification	Collection Method
Pseudocarcinus gigas	Oziidae	Professional fishermen
Hypothalassia acerba	Oziidae	Professional fishermen
Cymo cerasma	Xanthidae	Western Australian Museum
Platypodia granulosa	Xanthidae	Western Australian Museum
Chaceon bicolor	Geryonidae	Professional fishermen
Nectocarcinus tuberculosis	Portunidae	Professional fishermen
Cyclograpsus granulosus	Grapsidae	Collected by hand

b) Northern Hemisphere crab sequences obtained from Genbank.

Species	Classification - family	Genbank accession number
Menippe mercenaria	Oziidae	U20750
Dyspanopeus sayi	Xanthidae	U75270
Uca intermedia	Ocypodidae	Z79687
Sesarma verleyi	Grapsidae	AJ225850
Pachygrapsus transversus	Grapsidae	AJ225892
Cardisoma guanhumi	Gercarcinidae	Z79653
Scylla olivacea	Portunidae	AF109321
Callinectes similis	Portunidae	U75269
Mictyris brevidactylus	Mictyridae	
Panulirus longipes	Outgroup-lobster	U96087

DNA Isolation, Amplification and Sequencing
Total DNA was isolated using the same two methods, the high salt precipitation method (Crandall 1999) and the CTAB phenol-chloroform method (Doyle and Doyle 1987), as described in the population study. Once isolated, DNA was then amplified for the 16S and 12S rRNA regions using primers L1085 and H1478 for the 12S mtDNA region (Kitaura 1998) and L2492 and H3062 (Kitaura 1998). Amplification followed the same PCR conditions and cycling regime as per the population study.

Amplified DNA was purified and sent to the Australian Genome Research Facility for direct sequencing. DNA was sequenced in both directions in order to validate base positions.

Sequence Analysis
Sequence chromatograms were viewed and edited using a combination of the computer programs EditView and SeqPup (Gilbert 1997). Sequences of crab specimens collected were then aligned with sequence data obtained form Genbank. Sequence data was not available for all species for both 12S and 16S regions. 12S data was available for *P. gigas, H. acerba, N. tuberculosis, C. bicolor, C. cerasma, P. granulosa* and *C. granulosus*. Whilst 16S data was available for *P. gigas, H. acerba, C. bicolor, N. tuberculosis, C. granulosus, S. verleyi, M. mercenaria, S. olivacea, C. similis, U. intermedia, P. transversus, C. guanhumi, D. sayi* and *P. longipes.*

Alignment is perhaps the most critical and difficult aspect of sequence analysis (Swofford *et al* 1996) and involves identification of homologous nucleotide positions amongst different sequences. Alignment places positions presumed to be homologous into the same column of an alignment matrix. The reliability of a sequence based phylogeny is dependent on this alignment. Multiple alignments were performed for both 12S and 16S data sets using the Clustal X program (Thompson *et al.* 1997) using several parameter sets. Multiple alignment parameters of gap penalties equal to 10-15 and gap extension penalties equal to 3-5 and pairwise parameters of gap penalties of 3-5 and k-tuple of 1-3 were used. Positions of uncertain alignment were then excluded to produce alignment stable data sets for both regions (Gatesy *et al* 1993).

Once aligned, sequences were then imported into PAUP* (version 4.0b2) (Swofford 1999) for phylogenetic reconstruction. Pairwise sequence divergences were calculated using the maximum likelihood model of nucleotide sequence evolution, which was implemented with the distance analysis option. Phylogenetic relationships were analyzed with three major phylogenetic procedures to compare between the different approaches in order to assess the robustness of the phylogeny. The three techniques used for the 12S data were maximum parsimony, maximum likelihood and neighbor-joining methods. The 16S data was analyzed using the same methods, however UPGMA (unweighted pair group method using arithmetic averages) trees were generated instead of neighbor-joining. All analyses were performed using PAUP*.

Maximum parsimony analyses were performed for both data sets with the heuristic search option, maximum likelihood trees were developed using the quartet puzzling option and the neighbor-joining and UPGMA methods were both implemented with the distance analysis option with sequence divergence estimated using maximum likelihood methods. Phylogenetic confidence for all analyses was estimated using bootstrapping (Felsenstein 1985) of 1000 replicated data sets. All nucleotide sites were weighted equally, although alternative weightings were also trialed.

Results
12S Data
A total of eight brachyuran sequences, including *P. gigas*, were obtained via amplification or from internet databases for the 12S mtDNA gene region. The aligned 12S brachyuran sequence matrix obtained for this study via the Clustal X alignment procedure is shown in figure 23.

Figure 23. Alignment of 12S mtDNA partial sequences of brachyuran species with regions of ambiguous alignment removed. (* - indicates consensus position amongst all species)

```
C.cerasma           TATATTCTTTAAATTTGAAGAATTTGGCGGTGGTTTAGTCTTGTTAGAGGAACCTGTTTT
P.granulosa         TACTGTCTTTAAATTTGAAGAATTTGGCGGTGATTTAATCTTGTTAGAGGAATCTGTTTT
H.acerba            TATATTCTTTAAATTTGAAGAATTTGGCGGTGGTTTAGTCTTGTCAGAGGAACCTGTTTT
N.tuberculosis      TATTATCTTTAAATTTAAAGAATTTGGCGGTGATTTAGTCTTGTCAGAGGAACCTGTTTT
C.bicolor           TATTTTCTTTAAATTTGAAGAATTTGGCGGTGATTTAATCTTATCAGAGGAACCTGTTTT
P.gigas             TATTTTCTTTAAATTTAAAGAATTTGGCGGTGATTTAGTCTAGTCAGAGGAACCTGTTTT
C.granulosus        TGTAGACTTAAATTCTTAAAAATTAGGCGGCAATTTAGTCTTTTCAGAGGAACCTGGTTT
M.brevidactylus     TAAATACTTAAAATTTAAAAGATTTGGCGGTAATTTAATCTCACCAGAGGAACCTGTTCT
                    *     *** ** * * **  *** *****   **** ***    ******* *** * *

C.cerasma           TAAATCGATACACCACGTTAAATTTCACTTGCTTTA----TT---TAGTTTATATACCGT
P.granulosa         TGAATCGATACACCACGTTAAATTTTACTCATTTTA----TT---TAGTTTATATACCGT
H.acerba            TGAATCGATACACCACGTAAAATCTTGCTCGTTTTTGTT-TT---CAGCTTATATACCGT
N.tuberculosis      TGAATCGATAAACCACGTAGTATCTTACTCATTTTTGTT-TT---CAGCTTATATACCGT
C.bicolor           TGAATCGATAAACCACGTATAATCTTACTTGGTTTTGTT-TT---TAGCTTGTATACCGT
P.gigas             TGAATCGATAAACCACGAAAAATCTTACTTATCTTTGTT-TT---CAGTTTGTATACCGT
C.granulosus        CNAATTGATAAACCACGAAAAATCTTACTTGCTCTTGTA-TGAAACAGCTTGTATACCAT
M.brevidactylus     TTAATCGATAAAACACGTTAAATCTCACTCGTCTTTGTTCT----CAGTTTGTATACCGT
                      *** **** * ****    ** *  **     *     *     ** ** ****** *

C.cerasma           CATTA TCAG ATAATCTTAAAAAAATTAGATCAAGGTGTAGCTTATAAGCAAGTTAAAATG
P.granulosa         CATTA GCAG ATAATTTTAAAAAAATTAGATCAAGGTGTAGCTTATAAATGAGTTAAAATG
H.acerba            CATTA GTAG ATAATTTTAAGAAAATTAGATCAAGGTGTAGCTTATAAATGAGTTGAAATG
N.tuberculosis      CATTA TAAG ATAATATTTATAAAATTAGATCAAGGTGTAGCTTATAAATGAGTTTAAATG
C.bicolor           CATTA TTAG ATGATTTTTATAAAATTAGATCAAGGTGCAGCTAATAACCAAGTTAAAATG
P.gigas             CATTA GCAG ATAATTTTTAAAAAATTAGATCATGGTGCAGCTTATAGGTAAGTTAAAATG
C.granulosus        CATTA CCAG ATAATTCTTAGAAAATTAGATCATGGTGCAGTTTATGGGCAAGGTAAAATG
M.brevidactylus     CATTA GCAG TTAATCATTAGAAAATTAGATCAAGGTGCAGCTTATAGGCGAGATAGGATG
                    *****   **  * **  * * ************ **** ** * **     ** *    *

C.cerasma           GGTTACAATATTTATTTACTACGAATATAAAGGAGGATTTAATTGTAAATTGAGTTTAAA
P.granulosa         GATTACAATATGTATTTATTATGAATATGAAGGAGGATTTAATTGTAATATGGGTTTAAT
H.acerba            GGTTACAATATTTATTTATAACGGATTTAAAGGAGGATTTGATTGTAATATAAGTTTAAT
N.tuberculosis      GGTTACAATATTTTTTTATAATGAATATGAAAATGGATTTGATTGTAATGTAAATTTAAT
C.bicolor           GGTTACAATATTGAACTATTACGGATTAGAAGGAGGATTTGATTGTAAAATAGGTTTAAC
P.gigas             GGTTACAATATTTATTTATAACGAATTTTAAGGTGGATTTGATTGTAATATAAGTTTAAT
C.granulosus        GGTTACAATATTGTTTTATTACGGATACAAAGGAGGATTTGATTGTGTTCTCTGTTTAAT
M.brevidactylus     GGTTACAATATTACTATTAGATGGATATCAAGGTGGATTTGGTTGTACTATAAACT-AAA
                    * *********     *   * * **   **   ******  ****    *    * **

C.cerasma           AAGCTTATGAGATATAAGCTCTAAACCATGTACACATACGCCCGTCGC
P.granulosa         AAGCCTAAAAGATATAAGCACTAAATCATGTACACATACGCCCGTCGC
H.acerba            ACGCTTAGGAGATATAAGCCCTAAATCATGTACACATACGCCCGTCGC
N.tuberculosis      AAGTTTACAAGATATAAGCTCTAGATCATGTACACATACGCCCGTCGC
C.bicolor           ATGCCTTGTAGATATAAGTTCTAAATCATGTACACATACGCCCGTCGC
P.gigas             ATGCTTAGGAGGCATGAGCTCTAAATCATGTACACATACGCCCGTCGC
C.granulosus        AAGCTAAGAAGATATAAGTTCTAAATTGTGTACACATACGCCCGTCGC
M.brevidactylus     AAGTTTAAAAGAAATGAGCACTAAATTATGTACATAT-CGCCCGTCGC
                    * *      **  ** **  *** *   ****** ** **********
```

The resulting alignment after the removal of regions of ambiguous alignment produced a region of approximately 285 base pairs (bp), of which 131 sites (46%) were variable and 78 sites (27%) were phylogenetically informative. The mean nucleotide compositions for the eight species are shown in Table 6, the overall mean base compositions are A - 34%, T – 36%, C – 13 and G – 17%.

Table 6. Nucleotide composition and length of sequences (with ambiguous alignment removed) from the 12S mtDNA region of eight brachyuran crabs including *Pseucarcinus gigas*.

Taxon	A	C	G	T	# Sites
C.cerasma	35	12	16	36	281
P.granulosa	35	11	17	37	281
H.acerba	32	13	19	36	284
N.tuberculosis	34	12	16	39	284
C.bicolor	32	13	18	37	284
P.gigas	32	13	18	37	284
C.granulosus	33	15	19	33	287
M.brevidactylus	35	15	18	32	282
Mean	34	13	18	36	285

Estimates of genetic distances between the eight species are presented in Table 7. Sequence divergence ranges from a low of 11% between the two Xanthidae crabs, *C. cerasma* and *P. granulosa*, to a high of 30% between *C. granulosus* (Grapsidae), and the out-group *M. brevidactylus*. The genetic distance between the giant crab and other species ranges from 12% with *H. acerba* and 23% with the outgroup *M. brevidactylus*.

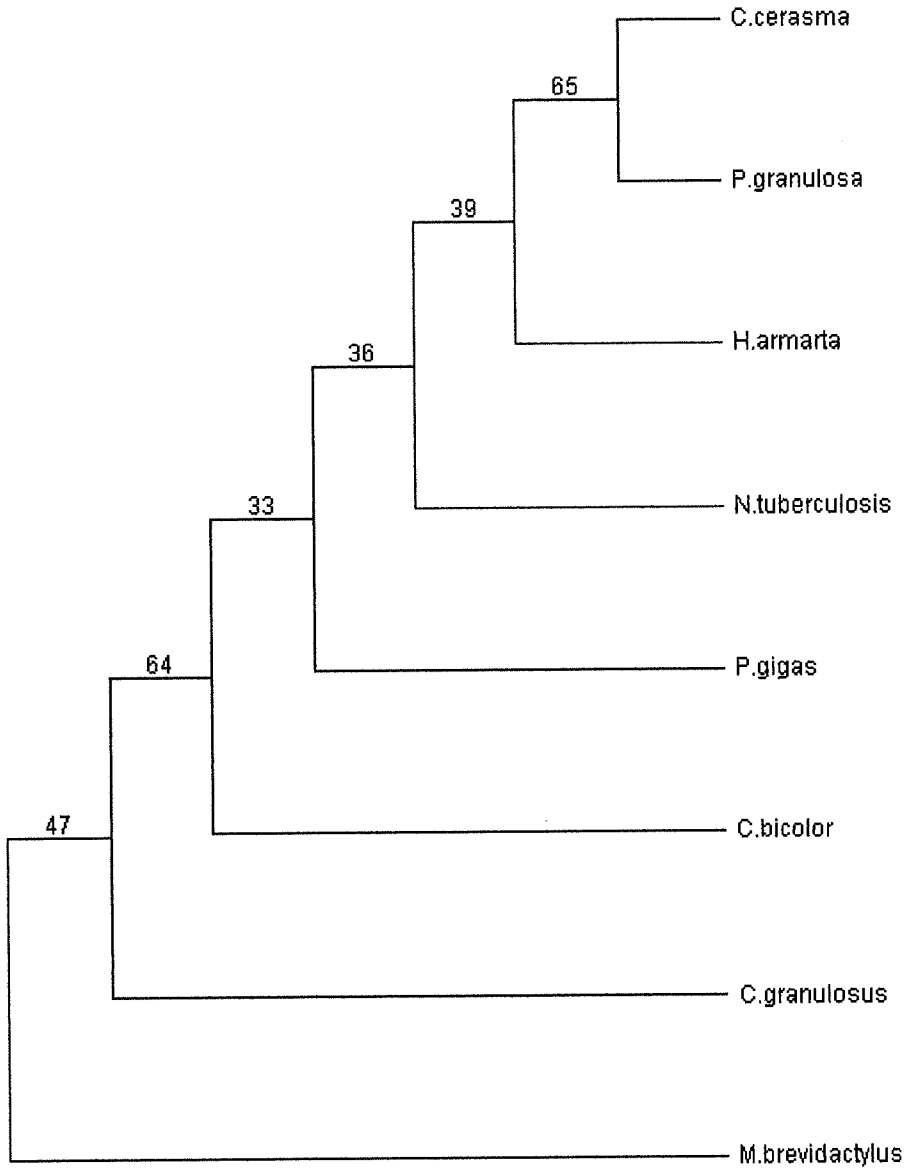
Table 7. The percent pairwise distance matrix of aligned 12S mtDNA sequences among Brachyuran species including *Pseudocarcinus gigas*.

	1	2	3	4	5	6	7
1 *C.cerasma*	-						
2 *P.granulosa*	11	-					
3 *H.acerba*	12	13	-				
4 *N.tuberculosis*	19	15	12	-			
5 *C.bicolor*	18	18	14	19	-		
6 *P.gigas*	16	16	12	14	15	-	
7 *C.granulosus*	26	30	24	27	25	22	-
8 *M.brevidactylus*	27	28	25	27	29	23	29

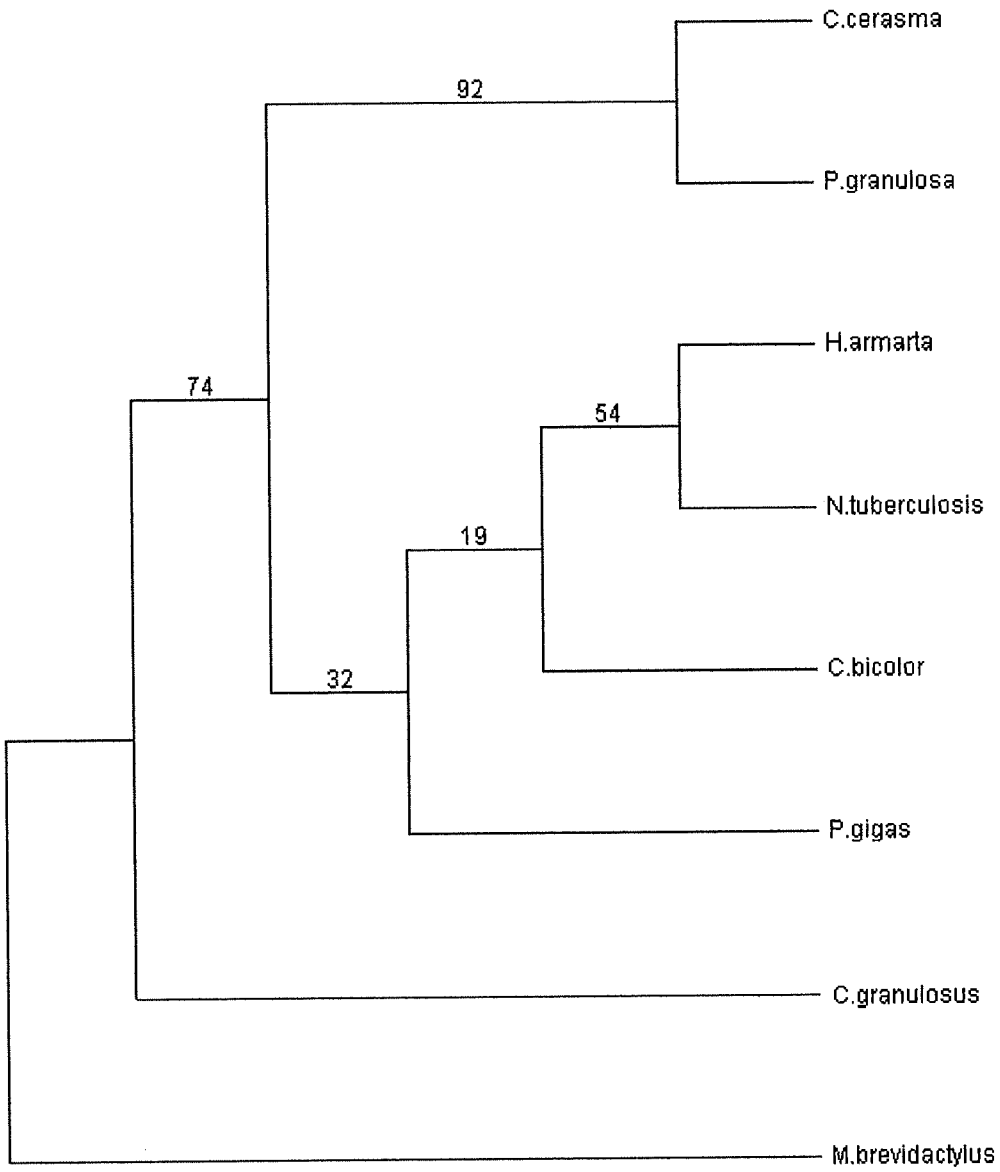
The reconstruction of evolutionary relationships through phylogenetic trees is shown in figure 23. All trees (maximum parsimony, maximum likelihood and neighbor-joining) show a similar topology, however confidence in these trees, as shown by bootstraps, is fairly low. All tree have grouped the two xanthids, *C. cerasma* and *P. granulosa*, on the same branch with high confidence (65 – 92%) and the position of *C. granulosus* and the outgroup *M. brevidactylus* on the outer of the relationships is also clear. However the relationships of the remaining crabs, including *P. gigas*, are ambiguous. The maximum likelihood method unites these four species as one clade (with low confidence – 32%) whereas the parsimony analysis gives a trichotomy with the *C. cerasma* - *P. granulosa* clade and the neighbor-joining cladogram suggests an alternative set of relationships.

Figure 24: Phylogenetic relationships amongst representatives of the family Brachyura based on the 12S mtDNA gene region. (a) Maximum parsimony tree, (b) maximum likelihood tree and (c) neighbor-joining tree. Bootstrap values were obtained from 1000 replications. *H. armata* has been renamed *H. acerba* (Koh & Ng, 2000).

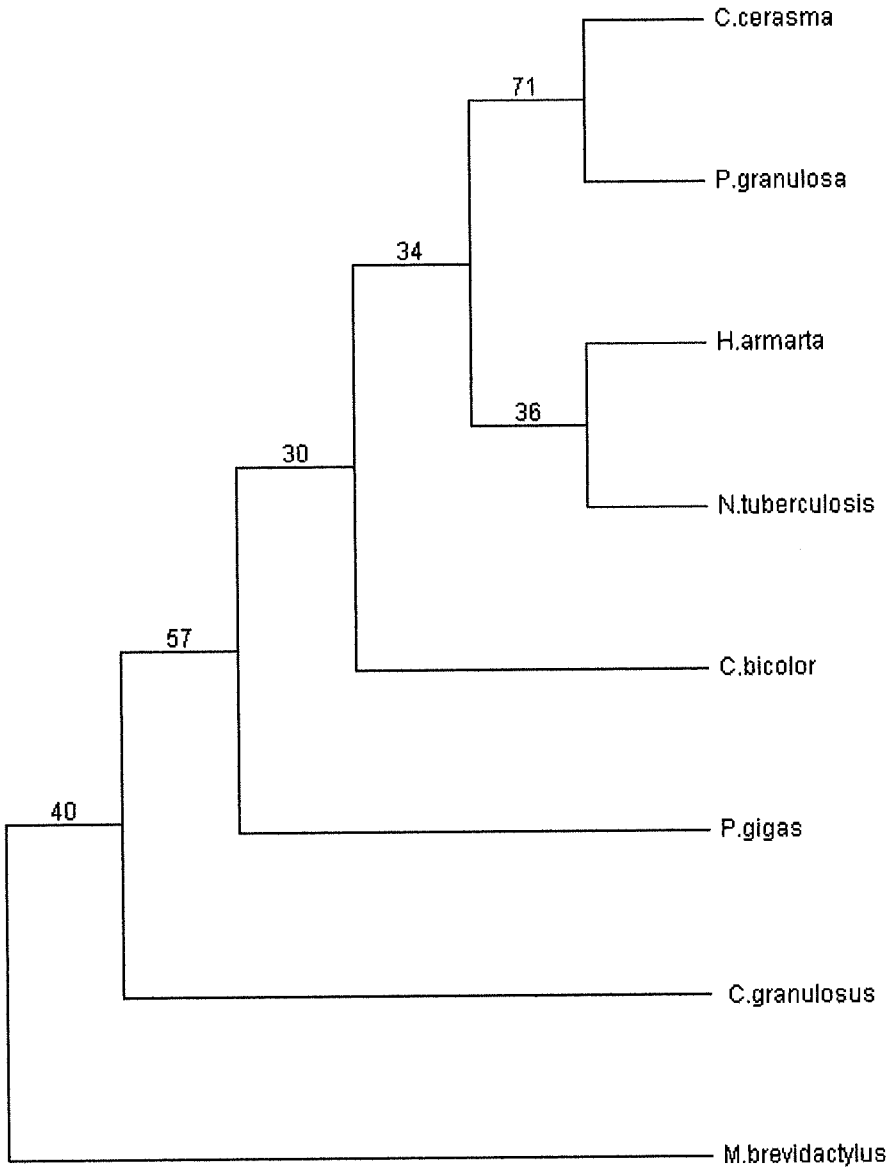
(a) Maximum parsimony tree



(b) Maximum likelihood tree



(c) neighbor-joining tree



The aligned 16S data set, consisting of 13 brachyuran species and the out-group, *Panulirus longipes*, is shown in figure 25.

Figure 25. Alignment of 16S mtDNA partial sequences of brachyuran species and the outgroup *Panulirus longipes* with regions of ambiguous alignment removed. (*indicates consensus position amongst all species)

```
P.gigas          AGCCGCGGTATTT-TGACCGTGCAAAGGTAGCATAATCATTAGTTTCTTAATTAGGAACT
H.acerba         AGCCGNGGGATAT-CGACCGTGCAAAGGTAGCATAATCATTAGTTTCTTAATTGGAAGCT
N.tuberculosis   AGCCGCAGTATTT-TGACTGTGCAAAGGTAGCATAATCATTAGTTTCTTAATTGGTAACT
M.mercenaria     AGCCGCGGTATTT-TGACTGTGCAAAGGTAGCATAATAATTAGTTTTTTAATTGAAAGCT
S.olivacea       AGCCGCGGTATTT-TGACCGTGCAAAGGTAGCATAATCATTAGTTTTTTAATTGAAAACT
C.similis        AGCCGCGGTATCT-TGACCGTGCAAAGGTAGCATAATCATTAGTTTCTTAATTGGGAACT
C.bicolor        AGCCGCGGTATCC-TGACCGTGCAAAGGTAGCATAATCATTAGTTCTTTAATTGAGAACT
U.intermedia     GGCCGCAGTAATT-TGACCGTGCAAAGGTAGCATAATAGTTAGTTTTTTAATTGGAATCT
S.verleyi        GGCCGCGGTATTTCTGACTGTGCAAAGGTAGCATAATAATTAGTTTCTTAATTAGAATCT
P.transversus    GGCCGCGGTATTC-TGACCGTGCAAAGGTAGCATAATCGTTAGTTTCTTAATTGGGATCT
C.granulosus     GGCCGCGGTATCT-TGACCGTGCAAAGGTAGCATAATCGTTAGTTTTTTAATTGGAATCT
C.guanhumi       GGCCGCGGTATTT-TGACCGTGCAAAGGTAGCATAATCGTTAGTTTTTTAATTGGAATCT
D.sayi           AGCCGCGGTATTT-TGACCGTGCAAAGGTAGCATAATCATTAGGGGTTTAATTGGAACCT
P.longipes       GGCCGCGGTANNA-TGACCGTGCTAAGGTAGCATAACA-TTTGTCCCTTAATTGGGGACT
                  ****  * *     *** **** ************   ** *    ******     **

P.gigas          TGTATGAATGGTCGGACAAAAGAAAAGCTGTCTCTAGAAATTAACTTTTAAGTGAAAAGG
H.acerba         TGTATGAATGGTCGGACAAAGGAAAAGCTGTCTCTTGAAATTAACTTTTAAGTGAAAAGG
N.tuberculosis   TGTATGAAGGGTCGGACAAAAGAAAAGCTGTCTTTTGAATTTAACTTTTAAGTGAAAAGG
M.mercenaria     TGTATGAATGGTCGGACAAAAGAAAGACTGTCTTTAGAATTTAACTTTTAAGTGAAAAGG
S.olivacea       TGTATGAATGGTTGGACAAAGAAAAAGCTGTCTCTTGAAATTAACTTCTAAGTGAAAAGG
C.similis        TGTATGANTGGTTGGACAAAGAAAAATCTGTCTCTTGANTTTAACTTCTGANTGAAAAGG
C.bicolor        TGTATGAACGGCCGGACAAGAGAAACCCTGTCTCTAGAATTTAACTTTTAAGTGAAAAGG
U.intermedia     TGTATGAATGATTGGACAAAAGAAAGCCTGTCTCCCGAATTTAACTTTTGAGTGAAAAGG
S.verleyi        TGTATGAATGGTTTGACAAGAAAAAATCTGTCTCTTGAATTTAACTTTTAAGTGAAAAGG
P.transversus    TGTATGAATGGTTGGACAAAAGAAAATCTGTCTTTTGAATTTAACTTTTGAGTGAAAAGG
C.granulosus     TGTATGAATGGTTGGACAAAAGAAAATCTGTCTTGTGAATTTAACTTTTAAGTGAAAAGG
C.guanhumi       TGTATGAATGGTTGGACAAAGGAAAATCTGTCTCGTGAATTTAACTTTTAAGTGAAAAGG
D.sayi           GGAATGAAGGGTTGGACAAAGGAAAAGCTGTCTCTTGAAATTTACCTTTAAGTGAAAAGG
P.longipes       GGTATGAACGGCTGAACAAGAAATTGACTGTCTCTTGAAATTAACGTTTAAGTGAAAAGG
                  * **** *     ****   *    ******   **  ** ** * * * ********

P.gigas          CTTAAATTTTTCAAGGGGACGATAAGACCCTATAAAGCTTTATATTTCGTAATTTTATTG
H.acerba         CTTAAATGTTTCAAGGGGACGATAAGACCCTATAAAGCTTAATATATAAAAATTTAATCA
N.tuberculosis   CTTAAATAATTTAGGGGGACGATAAGACCCTATAAAACTTTATATATTATAATTTTATTA
M.mercenaria     CTTAAATTATTCAGTGGGACGATAAGACCCTATAAAACTTTATATGTTATAATTTAATTG
S.olivacea       CTTAGATTTTCTAGAGGGACGATAAGACCCTATAAAGCTTTATAGATTGAGATTAAACCA
C.similis        CTCAGATTAGCCAGAGGGACGATAAGACCCTATAAAGCTTTATAAATTTAAATTTCTTCT
C.bicolor        CTTAAATTTTTCAAGGGGACGATAAGACCCTATAAAGCTTTATATATTAAGAATTTATTA
U.intermedia     CTCAAATAATTTAAAAAGACGATAAGACCCTATAAAGCTTGATGAATTAATATTCGATTG
S.verleyi        CTTAAATAAGTTAAAAAGACGATAAGACCCTATAAAGCTTAATATTATATTATTTAATAA
P.transversus    CTCAAATAAATTAAAGGGACGATAAGACCCTATAAAGCTTGATATTAGGATATTAACCTT
C.granulosus     CTTAAATATATTAAAGGGACGATAAGACCCTAGAAAGCTTAATATTAAAATATTTAGTTA
C.guanhumi       CTTAAATGAATTAAAGGGACGATAAGACCCTATAAAGCTTAATATGGAAAAGTTTAGTTG
D.sayi           CTTAAATAAATCAAAGGGACGATAAGACCCTATAAAGCTTTATAAGTTATAGTTTAATTG
P.longipes       CTTAAATGAGATAGGGGGACGATAAGACCCTATAAATCTTGATGGTCAAATATTAATTTT
                 ** * **     *    *************** *** *** **          *

P.gigas          AATTAATAATATTGTGTTGGGGCGACATAGGTATAATTTATATTAACTGC--TTGATA-A
H.acerba         AATTAATAATATTTTATTGGGGCGATATAGGTATAAGTTGTATTAACTGT--TTAAAT-T
N.tuberculosis   AATTTATAATATTTTGTTGGGGCGACAAAGGTATAATTTATATTAACTGT--TTAATT-T
M.mercenaria     AATTTATATTATTTTGCTGGGGCGGCATAAGTATAAATTATATTAACTGC--TTAGTA-A
S.olivacea       ATTTAATATTATTTGGTTGGGGCGACAAATGTATAATGTTAAATAACTGC--TATTAAAT
C.similis        ATTTTATATTATTTGGTTGGGGCAACCGAAGTATAATTAAAGATAACTGC--TAATAT-T
C.bicolor        AATTTATAATATTTAGTTGGGGCGACGAAAGTATAATTGATAATAACTGC--TTAAAC-T
U.intermedia     AATTAATATTATTATGTTGGGGCGACAATAGTAAAATGATTATTAACTGC--TAAAAT-T
S.verleyi        AATTTATAATATTTTATTGGGGTGATAATGATAAAATGGTTATTAACTGT--TAGTTA-T
P.transversus    AATTTATATTATTATATTGGGGCGATAGAAGTAAAATGATTGGTAACTGC--TTCTTT-T
C.granulosus     AATTTATATTATTTTATTGGGGCGATAAGAGTAAAATGATTGTTAACTGC--TTGATT-T
C.guanhumi       AATTGATAGTATTGTATTGGGGCGATAAAGGTAAAATGATTATTAACTGC--TTATTG-T
D.sayi           ATTTTATATTATTTTATTGGGGCGATATGAGTATAATTTTT-TTAACTGC--TTAAAA-T
P.longipes       TATGGTTACTATTTTGTTGGGGCGACAGGGGTATAATTA---GTAACTGC-CTTGAGTAA
                   *   ** ****    *****          ** **       ******   *
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P.gigas          GAAAACAA-ATAATAAATGATTTAAAAATGATCCTTTTT-AAAGATTTAA-GATTAAGTT
H.acerba         AAATACAATATAATAAGTGGGTTATAATTGATCCTTTTT-AGAGATTAAAAGACTAAGTT
N.tuberculosis   ATAAATACTGCGATAATTGATTTATATAAGATCCTTGTT-AGAGATTTAAAGACTAAGTT
M.mercenaria     TAATACAA--TAGTAGTTGAATTATAGATGATCCTTTTT-AAAGATTTAA-GAACAAGTT
S.olivacea       TTAAACAA--TTATATTTGATAAATAAATGATCCTTAAT-AAAGATTAAAAGATCAAGTT
C.similis        TTATACAA--TGATTTTTGTTTTATAATTGATCCTTAAA-AAGATTAAAGACACCAAGTT
C.bicolor        TAATACAA--TAATAAATGATTTTTAATTGATCCTTTTT-AAAGATTAA-AGACCAAGTT
U.intermedia     TAAAACAA--TTATATAGGTGAATTAAATGATCCTAAAT-AAAGATTAAAAGTTTAAGTT
S.verleyi        TAAAACAA--AAATAAATGAGTATTAAATGATCCTGTATTAGAGATTAAAAGTTTAAGTT
P.transversus    TTAGACAA--AAATAAGTGAGTAATAAAGGATCCTTTAT-AAAGATTTAAAGAATAAGTT
C.granulosus     TAAATACA--TTATAAATGATTGATAAATGATCCTAGTT-GAAGATTAAAAGTTTAAGTT
C.guanhumi       TTAAACAA--AAGTAAGTGATTGATAAAGGATCCTAGTT-GTGGATTAAAAGATTAAGTT
D.sayi           AAATACAA--ATTTGAGTGAATAATAAATGATCCTTTTT-AAAGATTAAAAGACTAAGTT
P.longipes       AGAATTAA--TTATTTTTA--TTGTTTGAGATCCTTCTTTGAAGAT-ATCAGATCAAGTT
                   *         *              ******         *        *****

P.gigas          ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCATATCGAAAAAAAAGTTTGCGAC
H.acerba         ACTTTAGGGATAACAGCGTTATTTCTTTTGAGAGTTCATATCGAAAAAGGAGTTTGCGAC
N.tuberculosis   ACTTTAGGGATAACAGCGTTATTTCTTTTGAGAGTTCATATCGAAAAAGAAGTTTGCGAC
M.mercenaria     ACTTTAGGGATAAGAGCGTTATTTTTTTTTAGAGTTCTTATCGAAAAAAAAGTTTGCGAC
S.olivacea       ACTTTAGGGATAACAGCGTAATTTCTTTTAAGAGTTCTTATCAAAGAAGGAGTTTGCGAC
C.similis        ACTTTAGGGATAACAGCGTAATTTATCCTGAGAGTCCTTATCAAAGGAGAAGTTTGCGAC
C.bicolor        ACTTTAGGGATAACAGCGTAATTTCTTTTGAGAGTTCATATCGAAGAAGAAGTTTGCGAC
U.intermedia     ACTTTAGGGATAACAGCGTTATTTTCCTTGAGAGTTCTTATCGAAAGGAAAGTTTGCGAC
S.verleyi        ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAAAAAAAGTTTGCGAC
P.transversus    ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAAAAAAAGTTTGCGAC
C.granulosus     ACTTTACGGATAACAGCGGTATTTTTTTTGAGAGTACTTATCAAAAAAAAAGTTTGCGAC
C.guanhumi       ACTTCAGGGATAACAGCGTTATTTTTTTTGAGAGTTCATGTCGAGAAAAAAGTTTGCGAC
D.sayi           ACTTTAGGGATAACA-CGTTATTTCTTTTGAGAGTTCATATCNAAAAACAANATTGCGAC
P.longipes       ACTTTAGGGATAACAGCGTAATCTTCTTTGAGAGTCCATATCGAAAGGAGGGGTTGCGAC
                 **** * ****** * **  ** *    * ***** * * ** *         *******

P.gigas          CTCGATGTTGAATTAAAATATCTTTATAGT-GTAGCCGT
H.acerba         CTCGATGTTGAATTAAAATATCTATATGGT-GTAGCCGT
N.tuberculosis   CTCGATGTTGAATTAAAATACCTGAATAGT-GCAGCCGC
M.mercenaria     CTCGATGTTGAATTAAATTGTCTACATGGT-GCAGTAGC
S.olivacea       CTCGATGTTGAAGTAAAATGTCTTTATAGT-GCAGCAGC
C.similis        CTCGATGTTGAATTAAAATGTCTATTCAGT-GCAGCAGC
C.bicolor        CTCGATGTTGAATTAAAATATCTTTATAGT-GCAGCAGC
U.intermedia     CTCGATGTTGAATTAAAATTCCCGTTCAATTGCAGAAGT
S.verleyi        CTCGATGTTGAATTAAAATATCTATATAATTGTAGTAGT
P.transversus    CTCGATGTTGAATTAAAAATTCTTTACAATTGCAGCAGT
C.granulosus     CTCGATGTTGAATTAAAATATCTTTATAATTGCAGTAGT
C.guanhumi       CTCGATGTTGAATTAAAATATCTGTACAATTGCAGTAGT
D.sayi           CTCNATGTTGAATTAAAATATCTATATAAT-GCAGCCGT
P.longipes       CTCGATGTTGAATTAAAGAACCTTTGTGGT-GNAGCAGC
                 *** ******** ****    *       * * **  *
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The data set, with ambiguous alignment areas removed constitutes approximately 390 bp. Average nucleotide composition is shown in Table 8 and is similar to that found in the 12S region, A – 35%, T – 34%, C – 11%, and G – 19%. The 16S gene region sequenced consists of 191 (48%) variable nucleotides and 133 (33%) of these are phylogenetically informative, this coincides with the 12S region (36% and 27% respectively).

Table 8. Nucleotide composition and length of sequences (with ambiguous alignment removed) from the 16S mtDNA region of thirteeen brachyuran crabs including *Pseudocarcinus gigas* and the outgroup *Panulirus longipes*.

	A	C	G	T	# Sites
P.gigas	36	11	18	35	391
H.acerba	35	11	20	33	393
N.tuberculosis	35	11	19	36	393
M.mercenaria	34	10	19	36	390
S.olivacea	36	12	19	33	392
C.similis	33	14	19	33	391
C.bicolor	35	14	18	33	390
U.intermedia	37	12	19	33	392
S.verlayi	38	9	17	37	394
P.transversus	35	11	20	34	392
C.granulosus	36	10	19	36	392
C.guanhumi	34	10	22	33	392
D.sayi	36	12	18	33	389
P.longipes	30	14	24	32	387
Mean	35	11	19	34	391

Pairwise sequence differences are shown in Table 9 and range from 12% divergence between *P. gigas* and *H. acerba*, to 36% between *S. verleyi* and the outgroup, *P. longipes*. Divergence between *P. gigas* and other species ranges from 12% with *H. armarta* to 30% with *P. longipes* (outgroup). The mean difference between the Australian species *P. gigas, H acerba, N. tuberculosis* and *C. bicolor,* 13%, is at the lower end of the observed differences whilst the mean difference between these species and all other species is 22%. This indicates that the Australian species are more closely related to each other than to other species.

This is reflected in varying degrees by the phylogenetic trees (figure 26) created by the maximum likelihood, UPGMA and maximum parsimony methods. The maximum likelihood tree indicates the presence of three clades, one containing the four Australian species mentioned above, along with xanthoids *M. mercenaria* and *D. sayi*. Within this clade the giant crab is most closely related to *N. tuberculosis* and *M. mercenaria*. This is supported by weak bootstrap values (49%); the entire group is also supported by weak bootstraps (42%). This tree also supports two other clades, one containing *U. intermedia, S. verleyi, P. transversus, C. granulosus and C. guanhumi* and the other containing two portunids, *S. olivacea* and *C. similis*. Both of these clades are supported by high bootstrap values 96% and 100% respectively.

The UPGMA also supports these three clades; the first clade (containing *P. gigas*) is present with a higher level of confidence (77%) in this analysis. The giant crab is placed on the same branch as *H. acerba* within this group, although again the bootstrap levels are relatively low (49%). The other relationships within this clade are also different, with all the Australian crabs more closely related to each other than to the two northern hemisphere crabs, *M. mercenaria* and *D. sayi*. Again the confidence

levels within this clade are low (39-45%). The other two clades are evident again, with slightly lower confidence levels (70% and 86%).

Table 9. The percent pairwise distance matrix of aligned 16S mtDNA sequences among Brachyuran species including *Pseudocarcinus gigas* and the outgroup *Panuliris longipes*.

	1	2	3	4	5	6	7	8
1 *P.gigas*	-							
2 *H.acerba*	12	-						
3 *N.tuberculosis*	13	14	-					
4 *M.mercenaria*	15	19	16	-				
5 *S.olivacea*	19	20	21	22	-			
6 *C.similis*	27	26	26	27	17	-		
7 *C.bicolor*	13	15	16	17	18	20	-	
8 *U.intermedia*	25	27	26	26	24	28	25	-
9 *S.verlayi*	18	20	21	23	24	32	23	19
10 *P.transversus*	19	22	22	23	22	25	23	19
11 *C.granulosus*	20	21	22	24	23	30	22	19
12 *C.guanhumi*	19	19	20	23	24	29	23	21
13 *D.sayi*	17	15	18	20	22	28	20	26
14 *P.longipes*	30	32	31	35	33	35	30	34

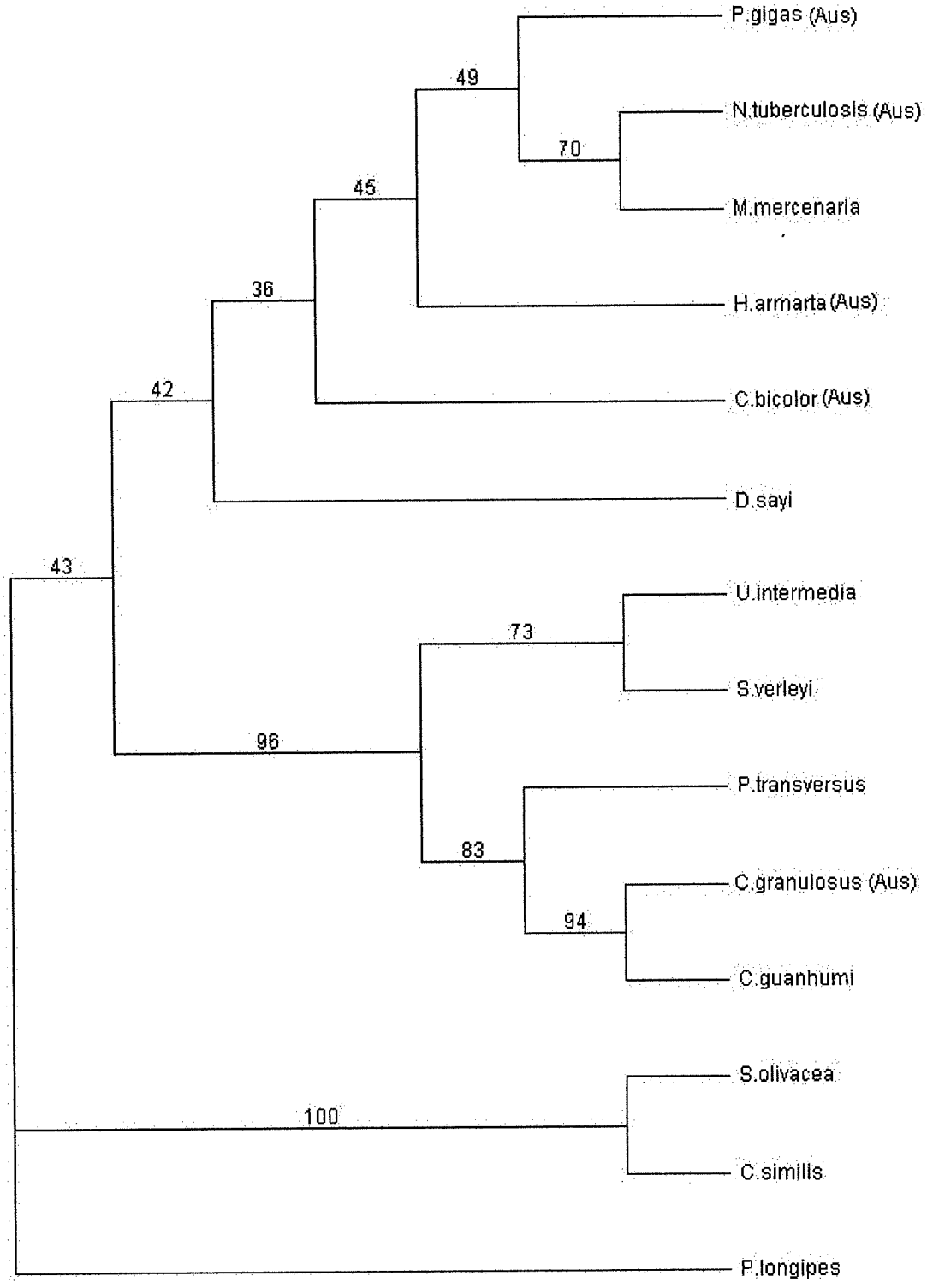
	9	10	11	12	13	14
9 *S.verlayi*	-					
10 *P.transversus*	16	-				
11 *C.granulosus*	15	14	-			
12 *C.guanhumi*	16	14	12	-		
13 *D.sayi*	21	21	20	18	-	
14 *P.longipes*	36	32	32	35	36	-

Very low confidence levels hamper the parsimony tree. However if these low numbers are ignored, two clades present in the previous analyses are apparent within this phylogenetic tree. The group containing *U. intermedia, S. verleyi, P. transversus, C. granulosus* and *C. guanhumi* is present with a high bootstrap (75%) and the other containing two portunids, *S. olivacea and C. similis* is visible at a high confidence level (90%). The other clade obvious from the preceding analyses has been split up this time with very low bootstraps (<30%) which are not shown, as they are so low as to be misleading. The maximum parsimony results are generally ignored due to very low bootstrap values which intimate low confidence levels with the relationships projected by this analysis.

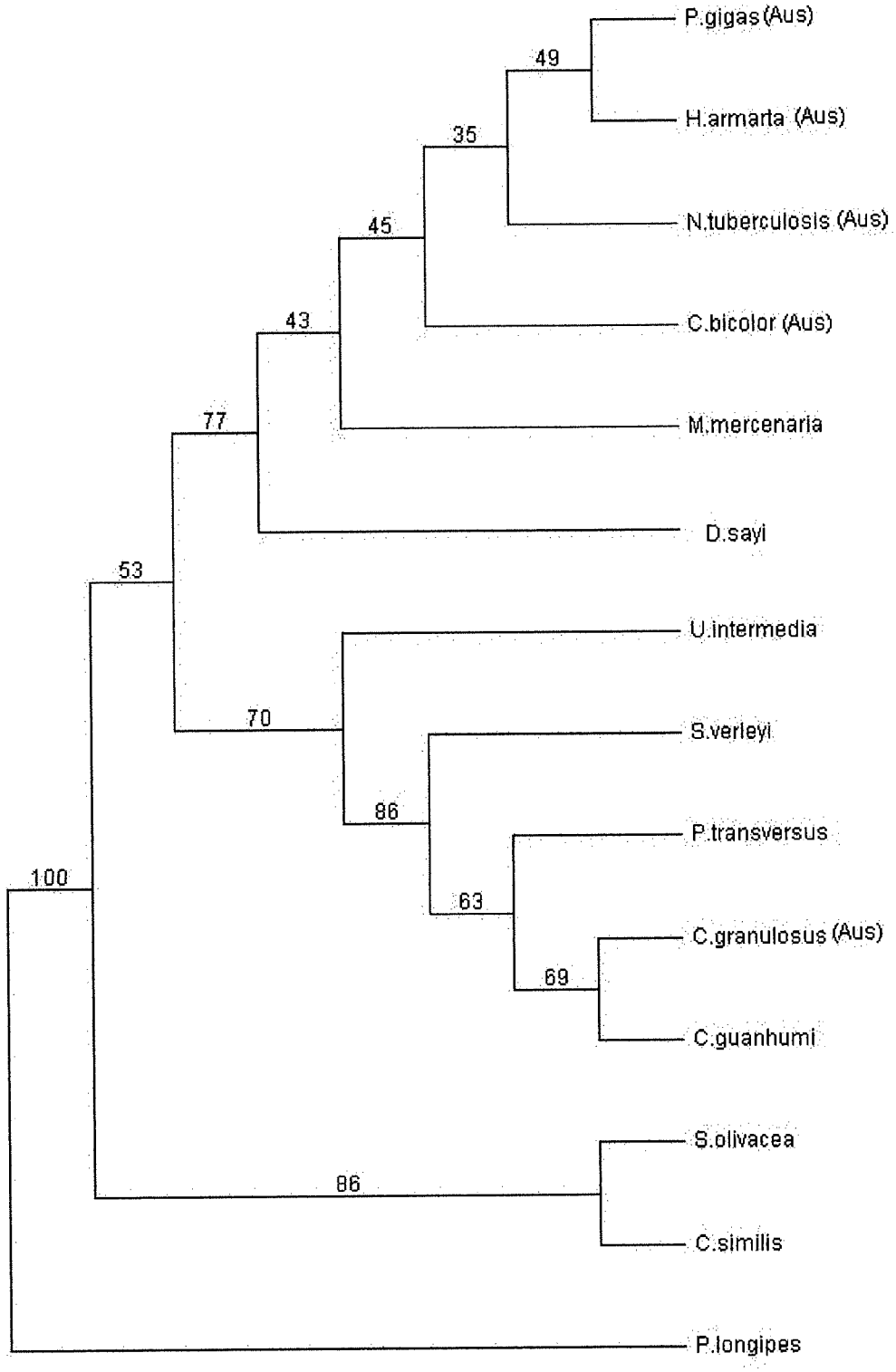
Overall, stable relationships are found with the 16S data set between the *S. olivacea* and *C. similis* and between the larger group containing *U. intermedia, S. verleyi, P. transversus, C. granulosus* and *C. guanhumi.* Whilst another group is evident from two of three analyses containing *P. gigas, H. acerba, N. tuberculosis, C. bicolor, M. mercenaria* and *D. sayi.*

Figure 26: Phylogenetic relationships amongst representatives of the family Brachyura based on the 16S mtDNA gene region. (a) Maximum likelihood tree, (b) UPGMA tree and (c) maximum parsimony tree. Bootstrap values were obtained from 1000 replications. *H. armata* has been renamed *H. acerba* (Koh & Ng, 2000)

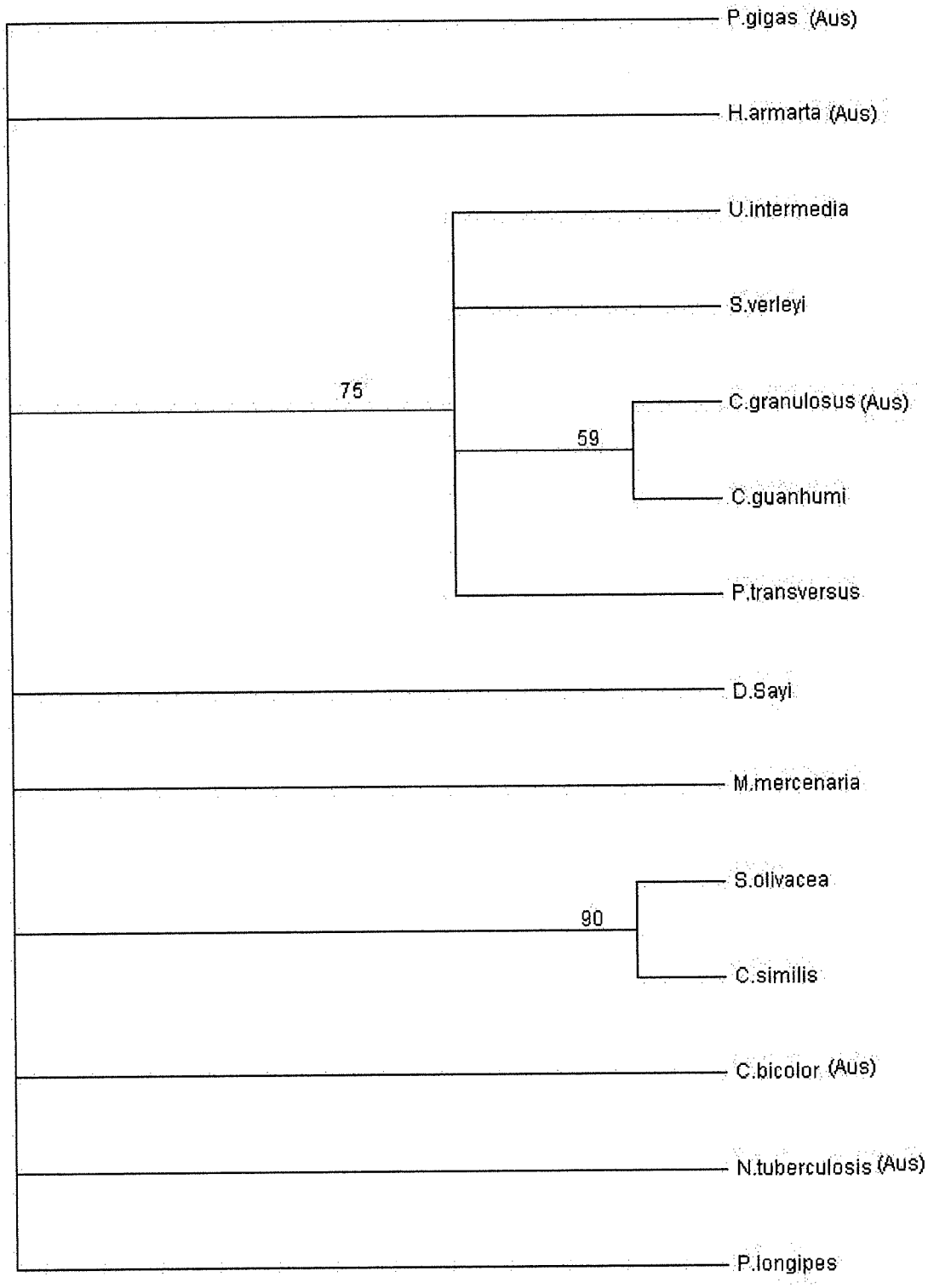
(a) Maximum likelihood tree



(b) UPGMA tree


P.gigas (Aus)
49
H.armarta (Aus)
35
N.tuberculosis (Aus)
45
C.bicolor (Aus)
43
M.mercenaria
77
D.sayi
53
U.intermedia
70
S.verleyi
86
P.transversus
100
63
C.granulosus (Aus)
69
C.guanhumi
S.olivacea
86
C.similis
P.longipes

(c) maximum parsimony tree



12S and 16S comparisons.
Sequences could only be obtained for five species over both 12S and 16S gene regions. Pairwise nucleotide divergences between these species for both regions are shown in Table 10. Mean differences for the two mtDNA regions are very similar, 12S – 18% and 16S – 17%, the two regions showing little difference when compared to each other.

Table 10. Percent nucleotide distances between species compared between 12S and 16S mtDNA regions.

Species	Compared with	12S distance	16S distance
P.gigas	*H.acerba*	12	12
	C.bicolor	15	13
	N.tuberculosis	14	13
	C.granulosis	22	20
H.armarta	*C.bicolor*	12	15
	N.tuberculosis	14	14
	C.granulosis	24	21
C.bicolor	*N.tuberculosis*	18	16
	C.granulosis	25	22
N.tuberculosis	*C.granulosis*	27	22
Mean		18	17

Discussion.
The results indicate a number of key points for *Pseudocarcinus gigas'* taxonomy and brachyuran taxonomy as a whole. There appear to be anomalies with the giant crab's position within the family Oziidae and superfamily Xanthoidea, this is especially apparent from the 12S mtDNA gene region. The 16S mtDNA region provides a more overall picture of brachyuran taxonomy, from this data set there appear to be irregularities with the classification of Australian brachyuran crabs within northern hemisphere classification systems.

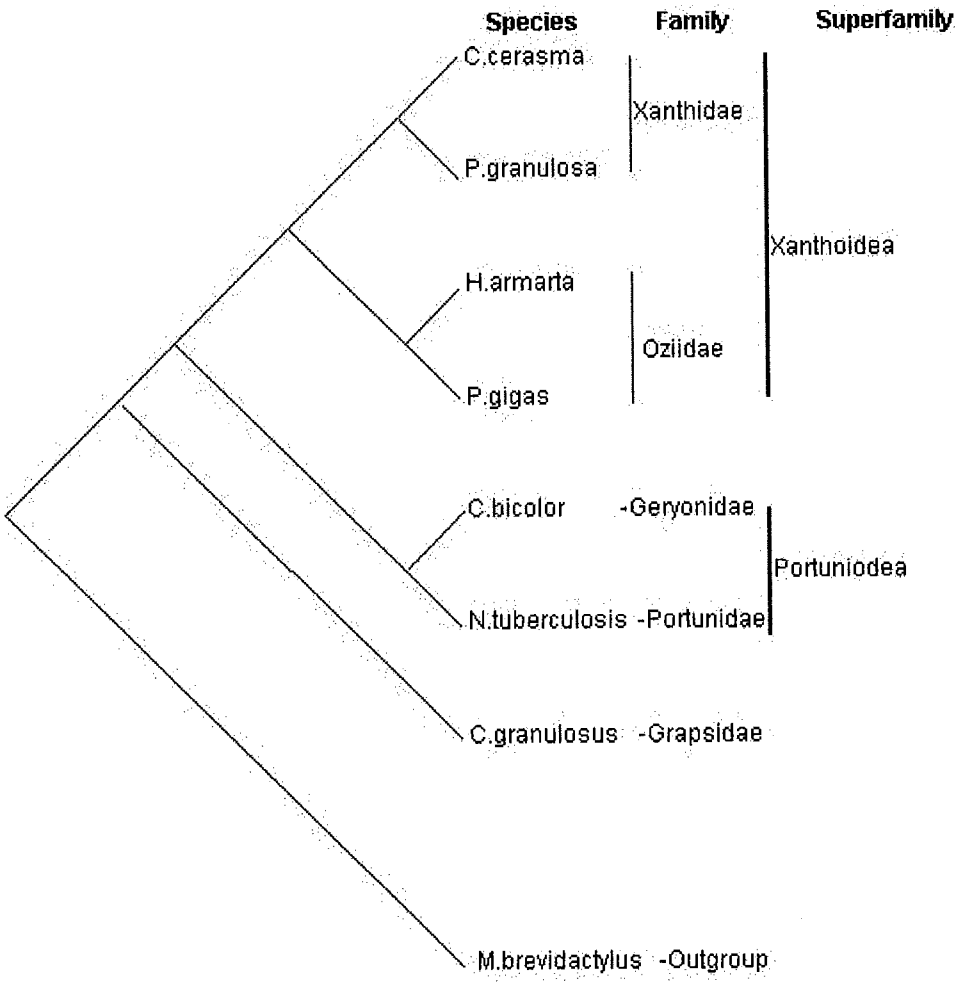
The 12S and 16S regions both exhibited characteristics expected of them. The high adenine and thymine (A and T) bias observed (A+T approximately 70%) for both gene regions is a common trait found for many crustaceans' mtDNA (e.g. Ovenden *et al* 1997, Kitaura *et al* 1998, Sarver *et al* 1998, Taylor *et al* 1998). The number of base pairs (12S – 285, 16S – 390) amplified for both regions is similar to that used in previous studies (e.g. 12S – Palumbi *et al.* 1991, Hanner and Fugate 1997. 16S – Tam *et al* 1996, Geller *et al* 1997).

Differences between 12S and 16S evolution have been found in the past for crustacean mtDNA. Taylor *et al.* (1998) found that 12S mtDNA evolved at approximately 1.5 times the rate of 16S for Daphnia species. This may suggest that 12S data is unsuitable for this study due to it evolving too quickly to ascertain the broad nature of the phylogenetic data. However similar nucleotide divergence between species for both regions (Table 10) show that the 12S and 16S regions appear to be evolving at approximately the same rate. This trend is also evident by a similar proportion of phylogenetically informative nucleotide positions for each region (12S –

27%, 16S – 33%). If the 16S region was evolving at a slower rate then it would contain relatively fewer informative sites. Therefore both gene regions should be suitable for this study.

The 12S data set indicates that the position of the giant crab within the Xanthoidea superfamily is questionable. Figure 27 shows the evolutionary relationships predicted before analyses based on current taxonomic understanding. If this figure is then compared with the relationships as determined by 12S mtDNA data (figure 23) the differences between the two are evident. According to current taxonomy, *P. gigas* is placed within the family Oziidae, which is joined with the family Xanthidae encompassed within the superfamily Xanthoidea. The 12S data does not reflect this view, as *P. gigas* is not within the same clade as the other Oziidae species, *H. acerba*, nor is it within the same clade as the other Xanthoidea species. Instead *N. tuberculosis* and *C. bicolor*, both members of superfamily Portunoidea seem to be more closely related to the superfamily Xanthoidea than the giant crab is. This is shown in two of three analyses, with the giant crab being found between these two species in the other. The data indicates that the two Oziidae species do not share a recent common ancestor, and that the giant crab does not share a common ancestor with the Xanthidae species (*C. cerasma, P. granulosa*) studied either. A common ancestor between Xanthidae and Oziidae is apparent with two analyses placing *H. acerba* on the same branch as the Xanthidae species.

Figure 27. Predicted cladogram of evolutionary relationships between species studied for the 12S mtDNA region based on current classifications. *H. armata* has been remamed *H. acerba* (Koh & Ng, 2000)



The 12S analyses suggest, as stated above, that *Pseudocarcinus gigas* does not belong within the family Oziidae, or within the superfamily Xanthoidea. Current classification, based on morphological characteristics, places the giant crab within these groups. However molecular data has been shown in previous studies to dispute phylogenies obtained via morphological attributes. Cunningham *et al* 1992 showed the close evolutionary relationship between king crabs and hermit crabs using mtDNA, despite the two groups being distinct morphologically.

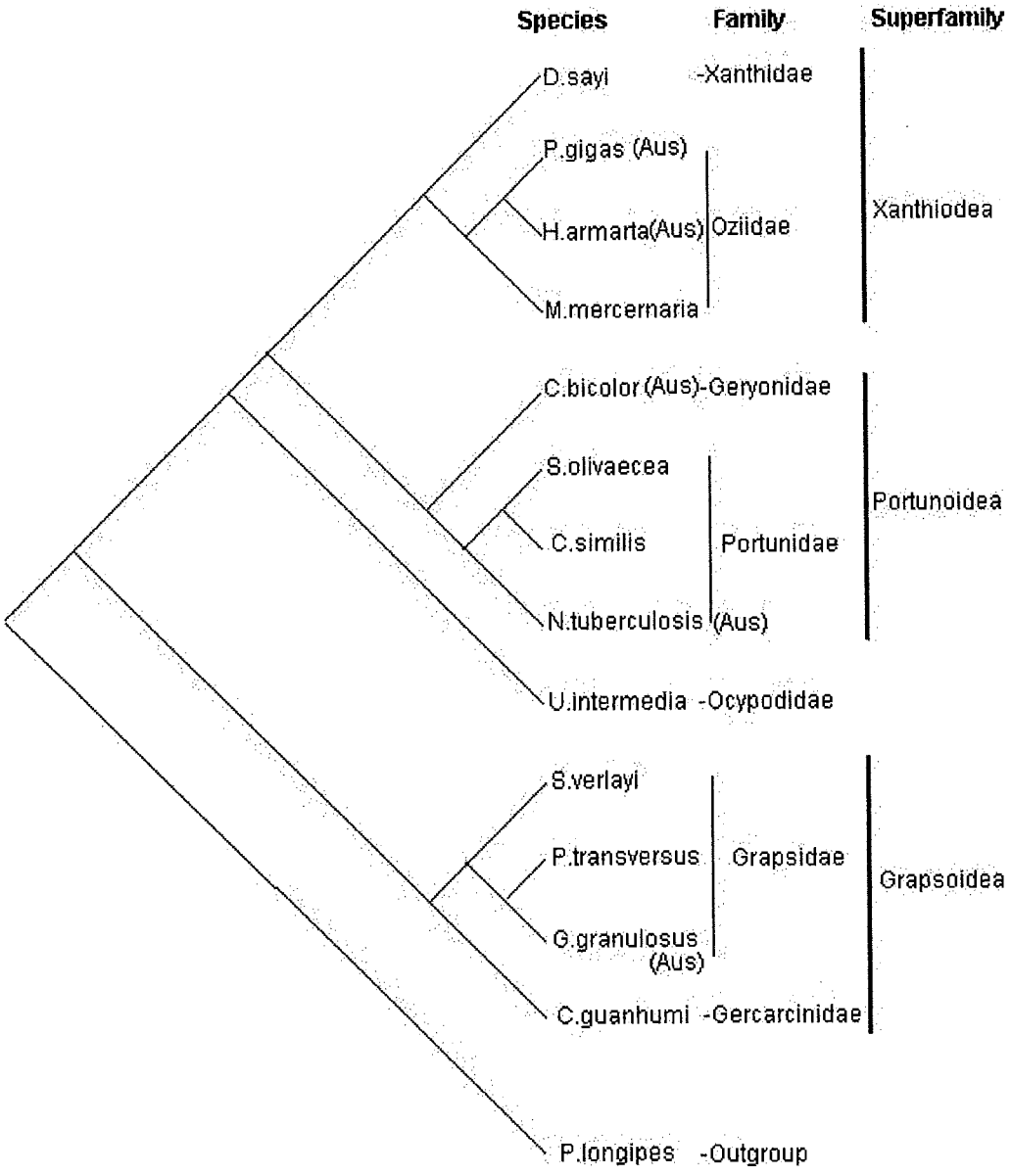
These results do need to be treated with caution, as the confidence levels of all analyses are low, shown by low bootstrap values. This indicates that the phylogenies derived from the 12S gene, whilst giving definite indications that there are problems with the classification, may not be entirely accurate. Further work will hopefully result in higher levels of confidence.

The position of the giant crab in relation to the 16S gene region is debatable. As stated the 16S maximum parsimony analysis is to be ignored due to low confidence in the results produced, therefore any inferences made are based on the maximum likelihood and UPGMA results. One tree confers with the 12S data with *P. gigas* occupying a

branch away from *H. acerba*, the other placing the two species on the same branch. This reinforces, in some way the results gained from the 12S region, but is further proof that more work needs to be undertaken in this area.

The apparent separation of Australian and Northern Hemisphere Brachyura is the main inference of the 16S mtDNA analyses. As per the 12S region, a suggested tree based on current taxonomic classifications is shown in figure 28. From this it can be seen that there are three distinct clades which were studied, Xanthoidea, Portunoidea and Grapsoidea, each clade contains both Australian crabs and Northern Hemisphere crabs. However further investigation of these species using 16S mtDNA shows that this classification scheme is questionable. The superfamily Portunoidea contains the portunid species from the Northern Hemisphere, *S. olivacea* and *C. similis*, as well as the Australian species *N. tuberculosis* (Portunidae) and *C. bicolor* (Geryonidae). It can be seen from the 16S phylogenetic trees produced that the two Northern Hemisphere species are well separated from the Australian species. The separate groups are not situated in the same clade, with the northern hemisphere species in an obvious clade of their own in all analyses. The two groups do not seem to have a recent evolutionary relationship, which would be indicated if they were more closely grouped together.

Figure 28. Predicted cladogram of evolutionary relationships between species studied for the 16S mtDNA region based on current classifications. *H. armata* has been renamed *H. acerba* (Koh & Ng, 2000)



This pattern is repeated to a lesser extent within the other two superfamilies studied Xanthoidea and Grapsoidea. Xanthoidea is represented by two Northern Hemisphere species, *M. mercenaria* (Oziidae) and *D. sayi* (Xanthidae), and two Australian species, *P. gigas* and *H. acerba* (both Oziidae). The results show that the split between Northern Hemisphere and Australian crabs is evident within this group as well. Figure 28 shows the predicted relationship between these species is not reflected by the molecular data (figure 26). The Xanthoidea species should be closely linked to each other, instead the clade containing these species is broken up by the Australian Portunoidea species, *N. tuberculosis* and *C. bicolor*. If the current classification is accurate then it would be expected that all four Xanthoidea species would share a unique evolutionary history. However the mtDNA data implies that *N. tuberculosis* and *C. bicolor* also share this evolutionary history. The UPGMA tree in particular suggests a breakup between the Australian and Northern Hemisphere Xanthoidea, however not to the same extent as the Portunoidea species.

The final group, Grapsoidea, contains the Northern Hemisphere species *S. verleyi, P. transversus* (Grapsidae) and *C. guanhumi* (Gercarcinidae), and the Australian *C. granulosus* (Grapsidae). The molecular relationships shown between the Australian and northern hemisphere crabs is also evident in this group. The current classification (figure 28) places *C. granulosus* within the Grapsidae, sharing a close relationship with Northern Hemisphere species of this family. However the 16S data (figure 26) shows that *C. granulosus* share a closer affinity with the Gercarcinidae species, *C. guanhumi*. Whilst both species belong to the same superfamily, they are members of separate families, suggesting that there are differences between Australian and northern hemisphere Grapsidae species.

There is distinct evidence that genetic separation between Australian and Northern Hemisphere crab species is present. This is most obvious when looking at Portunoidea, and to a lesser extent Xanthoidea and Grapsoidea. Genetic differentiation between apparently similar species from Australia and the northern hemisphere has been shown before in marine algae species. Woolcott and King (1998) found DNA sequence differences between Australian and Northern Hemisphere species of seaweed, *Bangia*. However no significant studies have been performed between Australian crustaceans and their northern counterparts.

4.2.1.4. Conclusions and scope for further study.

Population Genetics
The complete resolution of the stock structure of *Pseudocarcinus gigas* is an important issue. In order to ensure correct management decisions are made towards fishing regulations, knowledge of giant crab stocks is needed. The giant crab should not be treated as a single stock on the basis of these results. If this was to occur then a collapse of the fisheries may be a result. If the giant crab fishery is to be a sustainable industry then further work needs to be undertaken on the genetic structure *P. gigas* populations.

Initial work should follow on from this study, concentrating on the mitochondrial genome. Other, more variable gene regions such as COI gene and the control region may contain valuable information. Ideally the control region, or D-loop, would be studied as it has been shown to be highly variable for fish population studies (Faber

and Stapien 1997). However this region is relatively understudied in invertebrates and would require the development on new primers, a time consuming process. The COI (cytochrome oxidase) gene has been previously used in decapod population studies and has shown significant variation (e.g. Tam *et al* 1996, Ovenden *et al* 1997, Gopurenko *et al* 1999). Therefore this region would be the next gene to be examined. There are also nuclear gene regions, which may show sufficient variation, these are amplified by EPIC (Exon Primed Intron Crossing) primers and new developments are being made in this area.

Phylogenetics

The data obtained from the 12S and 16S gene regions indicate a breakdown within current classification schemes for Brachyura and subsequent families. Whilst the results are not conclusive, they point to definite anomalies within these classifications. Australian crabs, previously classified into classifications developed by Northern Hemisphere taxonomists, appear to be significantly divergent from their northern counterparts. The classification of *Pseudocarcinus gigas* is also under doubt, although more samples from within the Xanthoidea group need to be examined before any conclusions are made.

These results suggest that there is definite scope for further work in this area. A failing of the current study is the lack of species studied, as exemplified by the unresolved phylogenetic position of *P. gigas*. Further work would add to results gained from this study and more confident decisions could be made. These additional studies should include the examination of evolutionary relationships between more supposed "sister taxa" from Australia and the Northern Hemisphere. That is species currently classified within the same families or subfamilies from both Australian and Northern Hemisphere waters should be studied in order to gain a bigger picture and to determine the extent of the differences between the species already studied here.

If significant differences are found within Brachyura between Australia and the Northern Hemisphere, this will have serious implications for current classification systems. These implications may not just be confined to crab species, and may reach across a number of taxonomic groups. Northern Hemisphere studies based on morphological characteristics have developed the majority of classification systems and molecular studies may indicate flaws within contemporary schemes. As no significant works have been carried out previously, these results may lead into uncharted territory.

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4.2.2. DNA Study -2

4.2.2.1. Introduction

This study focuses on aspects of the molecular genetics and systematics of the giant crab, *Pseudocarcinus gigas*, and involves the collection of mitochondrial nucleotide data from populations of *P. gigas* in order to determine the genetic population structure of this commercially important species.

4.2.2.2. Genetic stock structure of the Giant Crab, *Pseudocarcinus gigas.*

Previous genetic studies of the giant crab including allozyme electrophoresis (Levings *et al.* 1996) and mitochondrial DNA (mtDNA) analysis (Murphy 1999) have indicated no evidence of stock isolation. Indeed no inter or intra-population variation has been detected to date, however it is possible that genetic variation has been overlooked. Allozyme electrophoresis does not always have the sufficient resolution to detect more recent population isolation, and also the mitochondrial gene regions examined by Murphy (1999) (12S and 16S rRNA) are reasonably conserved gene regions. Thus it is still possible that genetic variation and stock isolation may exist within the species but has not been detected using the genetic methods applied so far. This study will therefore investigate more rapidly evolving mitochondrial gene regions that are more sensitive to recent population isolation and evolutionary divergence. By investigating these regions, stock structure may be determined by either detecting stock isolation or providing more valid evidence of a potential single stock. Either way the elucidation of the *P. gigas* population structure is considered an essential component of the larger project by Levings and others examining the biology and sustainable exploitation of the species.

Murphy (1999) suggested that based on preliminary morphological and biological data obtained (Levings *et al.* 1996), that two distinct stocks of *P. gigas* may exist consisting of discrete western and eastern populations. The status of these stocks have, however, since been reassessed and new data presented this final FRDC report suggests there are no grounds for inferring the existence of more than a single stock. To further investigate the stock structure of this species the goal of this study was to find genetic variation within populations to allow for a direct, statistically based test for stock isolation.

Materials and methods.

Sample collection
P. gigas tissue samples were obtained from previously collected samples, used by Murphy (1999). Crab samples were collected from three locations in Australia by professional fisherman in Western Australia (Augusta), Victoria (Portland), north-western Tasmania (Stanley) and Northeast Tasmania (Bicheno). For this study an additional location was sampled, this being the East Coast of Tasmania. As well additional individuals from Portland (Victoria) were obtained. Samples were collected from a single vessel from various depths. Upon capture leg muscle tissue samples were taken and placed into screw-top vials and either frozen at –20°C or stored in 80-90% ethanol until analysis. The collection of all crab samples was arranged and

facilitated by Andrew Levings, Deakin University with the help of fishers Graham Pateman of Augusta, Shannon Churchill of Portland, Mark Hursey of Stanley and Michael White of Bicheno.

Total genomic DNA isolation

Total genomic DNA was extracted from the ethanol preserved muscle tissue following the tissue extraction protocol described by Crandall *et al.* (1999). Fifty mg of tissue was blotted dry to remove excess alcohol and was then added to a 1.5-mL microcentrifuge tube containing 900 µL TE buffer (10mM Tris, 0.1mM EDTA, pH 8.0). The samples were briefly centrifuged, the TE buffer drawn off and the tissue blotted dry again. The tissue was placed into 900 µL of cell lysis solution (10mM Tris, 100mM EDTA, 2% SDS, pH 8.0), homogenised and 9 µL of Proteinase-K (20mg mL^{-1}) added. The samples were then incubated at 55°C for several hours to overnight, with occasional mixing. After the tissue was digested, the samples were cooled to room temperature and 4 µL of Rnase-A (10mg mL^{-1}) was added. The samples were incubated at 37°C for 1 hr and were then cooled again to room temperature. Three hundred µL of 7.5 M ammonium acetate was added to the samples, which were then vortexted for 10 s and placed on ice for 15 min. Next, samples were centrifuged for 5 min at 14,000 rpm to pelletise the cell debris. The supernatant containing the DNA was transferred to a 2-mL tube containing 900 µL of isopropanol; followed by incubation on ice for 15 min. Samples were again centrifuged for 5 min to pelletise the DNA. The isopropanol was carefully poured off and the DNA was washed with 750 µL of 70% ethanol. The ethanol was poured off and the samples were left to dry. The DNA pellet was finally resuspended in 50-200 µL TE buffer depending on its size.

Amplification of mtDNA

Double stranded PCR amplifications were performed in 50 µl volumes consisting of: 1x PCR buffer, 200 nM magnesium chloride, 200 µM dNTP, 1 µM of each primer, 2 units *Taq* DNA polymerase and 2-3 µl of extracted DNA. Primers used to amplify 4 targeted gene regions are given in Table 11.

PCR amplifications were performed in a Corbett PC-960 Microplate Thermal Cycler. The following temperature regime was used for the 16S rRNA, 12S rRNA and cytochrome b gene regions: initial denaturation step of 95 °C for 5 minutes, followed by 32 cycles of denaturation at 95°C for 30 seconds, annealing at 55°C for 30 seconds, and extension at 72°C for 30 seconds. The program terminated with a 5 minutes cycle at 72°C.

The cytochrome oxidase 1 gene region used the following touch-down temperature regime: initial denaturation step of 95°C for 3 minutes, followed by 8 cycles of annealing at 55°C for 30 seconds, extension at 70°C for 2.5 minutes and denaturation at 95°C for 45 seconds. This was followed by 21 cycles of annealing at 53°C for 30 seconds, extension at 70°C for 2.5 minutes and denaturation at 95°C for 45 seconds. The program was terminated with a single cycle of annealing at 53°C for 30 seconds and extension at 70°C for 4 minutes.

Table 11. Primers and target gene regions used in this study.

Name	Sequence	Gene region	Source
L1085	CAACTAGGATTAGATACCC	12s	Kitaura et al (1998)
H1478	GAGAGCGACGGGCGTATGTGT	12s	Kitaura et al (1998)
L2510	CGCCTCTTTAACAAGACAT	16s	Kitaura et al (1998)
H3062	CCGGTCTGAACTCAGATCA	16s	Kitaura et al (1998)
CO1A	AGTATAAGCGTCTGGGTAGTC	CO1	Palumbi et al (1991)
CO1F	CCTCGAGCAGGAGGAGAYCC	CO1	Palumbi et al (1991)
CytB.F	TTACCTTGAGGACAAATATCAT	Cytochrome b	Murphy (pers.com)
CytB.R	CACCTCCTAATTTATTAGGAA	Cytochrome b	Murphy (pers.com)

Primers "CytB.F and CytB.R" were designed by Nick Murphy directly from *Penaeus* and *Drosophila* sequences obtained from Genbank.

Purification and sequencing

The PCR product was purified using a QIAquick PCR purification kit (QIAGEN Gmbh). The purified DNA was quantitatively analyzed against DNA marker (Promega DNA/Hae 111 marker) of known concentration on a 1% agarose / TAE gel containing ethidium bromide and viewed under UV light. The purified DNA was dried and resuspended in 16 µl deionised water containing 3.2 picomol of primer. Dried DNA samples were sent to the Australian Genome Research Facility (AGRF), University of Queensland, for direct sequencing using an Applied Biosystem Automated Sequencer. Sequence reactions followed the standard protocol for ABI Prism DYE-Terminator Kits (Perkin Elmer). Chromatograms were viewed using EditView software and aligned and edited using SeqPup (Gilbert 1997).

Results.

PCR amplification of the 12S rRNA (primers L1085and H1478), 16S rRNA (primers L2510and H3062), and cytochrome b (primers CytB.F and CytB.R) gene regions were successful and yielded high quality sequences for fragments of approximate lengths of 350, 455 and 430 nucleotides respectively. The proportion of nucleotide sites that could not be confidently scored (N's) being on average less than 4.5% of the total fragment length. The cytochrome oxidase 1 (CO1) gene region was also successfully amplified (primers CO1A and COLF) yielding a product of approximately 530 nucleotides in length. However only medium quality sequences were obtained with the proportion of N's ranging from 2.9 – 15.0 % per fragment sequenced. These low quality sequences are most likely due to non-specific primers. Time and cost constraints prevented further investigation of alternative CO1 primers.

Sequences from Murphy's (1999) study were reused for this study for the direct comparison with the Tasmanian East Coast samples. Murphy (1999) sequenced 5 individuals from Western Australia, Victoria and West Coast Tasmania for both the 16S and 12S gene regions. For this study a single crab sample was sequenced from the Western Australian, and Tasmanian West Coast locations for the 12S rRNA and 16S rRNA gene regions to verify the sequencing procedures used in this study. An additional 5 crabs from the Tasmania East Coast were sequenced for these 2 gene regions. All sequences for these crabs were found to be identical to each other and identical to the sequences obtained by Murphy (1999) for the 2 rRNA gene regions. Therefore, between 5 and 6 crabs have been sequenced from each of the 4 locations across southern Australia and all have yielded identical mitochondrial haplotypes for

the 12S rRNA and 16S rRNA gene regions sampled with the exception of one nucleotide position within the 16S rRNA gene region. These sequences are provided in Genetics Appendix A. attached to this section. Sequences for the 12S rRNA and 16S rRNA gene regions for Western Australian, Victorian and Tasmania West Coast sample locations were obtained from Murphy (1999).

Three individuals were successfully sequenced from each of the four-sample sites for the cytochrome b gene region. The sequences for all 12 individuals were found to be identical again with the possible exception of one nucleotide position. Due to difficulties in obtaining consistent and reliable sequences for the CO1 gene region only 2 Tasmanian East Coast, 2 Tasmanian West Coast, 2 Victorian and a single Western Australian sample were sequenced. No variation was found within or between populations. The sequences obtained for the cytochrome b and CO1 gene region for the giant crab are given also in Genetics Appendix A.

The status of 2 possible polymorphic nucleotide sites, one within the 16S rRNA gene region and the other within the cytochrome b gene region, is uncertain. Interpretation of the chromatograms was ambiguous and it is possible they represent PCR artifacts. Further investigations using alternative sequencing chemistries are required to determine if these 2 positions represent polymorphisms.

An attempt was also made to amplify the control region and a fragment spanning from the 16S rRNA to the 12S rRNA gene regions. However, in both cases after trialing a range of PCR parameters, amplification was unsuccessful and no PCR products of sufficient quality for sequencing were obtained.

Discussion.
The results of this study combined with those of Murphy (1999) mean that an average of 4.2 crabs per site, from 4 sites across southern Australia, ranging over 4000 km, have been examined for mtDNA nucleotide variation at 4 independent gene regions. The total number of nucleotide sites examined across all gene regions comes to almost 1800 bp per individual. Despite this wealth of data, no unambiguous nucleotide variation among giant crabs was detected either within or between populations. Therefore based upon this evidence it appears that the giant crab populations are genetically homogenous across southern Australia and the fishery can be managed as a single stock.

These results are consistent with previous allozyme studies reported by Levings *et al.* (1996) and recently obtained information on the population biology of the crab. No allozyme variation was found at all at 20 enzyme loci for samples of crabs obtained from Victoria and Western Australia. Low levels of allozyme variation is not unusual, however, in large, highly mobile crustaceans (Hedgecock *et al.* 1982).

Hilbish (1996) suggests that genetic homogeneity across broad geographic scales may be largely a function of high gene flow capacity generated by larval dispersal in marine species. Recent research on the larval life cycle of the giant crab suggests that larval dispersal may explain the genetic homogeneity of the *P. gigas* stock. The larval phase of *P. gigas* is approximately 60 days (Gardner and Northam 1997) and it appears that giant crab larvae exploit surface currents providing the opportunity for large-scale dispersal (A.Levings, Deakin University, pers.com). According to this

research, larvae hatch in September, a time of year characterized by gale force winds that generate strong surface currents in a west to east direction along most of the southern continental margin. Thus pelagic *P. gigas* larvae may be transported substantial distances by inhabiting surface currents during this period. In addition, recently obtained data from tagging studies by Levings (Deakin University, pers.com) indicate there is a net adult migration in a westerly direction. Individuals appear to be foraging into the current and moving to the west. Analysis of distance traveled recaptured tagged crabs yeilded an *(unweighted)* average annual migration ≈ 4.5 nautical miles or 8.3 km westerly, however the data was widely scattered with some individuals found to have migrated much further. Throughout the tagging study 8 individuals have moved ≈ 350km over a 6 year period. Therefore, adult westerly migration coupled with easterly larval advection has the capacity to lead to high gene flow, the homogenization of genetic variation and the breaking down of local adaptation and any effects of local population isolation, throughout the giant crab population across most of southern Australia.

High levels of genetic similarity over large geographical distances have been found in a variety of marine organisms. Ovenden *et al.* (1992) found no evidence of population subdivision for the Southern Rock Lobster, *Jasus edwardsii*, throughout its distribution across southern Australia and New Zealand using mtDNA 16S rRNA data. This is of special relevance in the context of the giant crab, as *Jasus edwardsii* has a similar geographical distribution to *P. gigas* across the southern Australian coast and they have similarities in a number of biological traits especially in relation to larval vagility, fecundity and adult mobility. The absence of stock structure across southern Australia has been reported in other marine species. The Australian gummy shark (*Mustelus antarcticus* Gunther), a highly mobile species, also appears to be composed of a single stock based on samples ranging from Bunbury in Western Australia to Eden in New South Wales (Gardner and Ward 1998). In contrast, other species such as snapper (*Pagrus auratus*) (Meggs and Austin 2000), and abalone (*Haliotis rubra*) (Brown 1991) are composed of several stocks over a similar geographical range to that of the giant crab. In the case of these species, the finding of stock structure is consistent with the life history of the species. Both abalone and snapper have relatively brief larval life cycles; adult abalone are highly sedentary and adult snapper do not disperse widely.

Although the DNA nucleotide data generated in this study and by Murphy (1999) indicates genetic homogeneity in the giant crab and is consistent with allozyme data (Levings *et al.* 1996) and recent biological information, the absence of stock structure is yet to be unequivocally demonstrated. High dispersal capabilities and the absence of physical barriers do not necessarily lead to panmixia (Ovenden *et al.* 1992). Physico-chemical and biological features vary widely between marine habitats; therefore local adaptation via natural selection combined with local restrictions in gene flow could still lead to stock isolation in *P. gigas*. Ovenden *et al.* (1992) suggests that for *Jasus edwardsii* locations may exist where larvae might not be swept away by prevailing currents. If this is also the case for *P. gigas*, locations may occur where megalopa are recruited from locally produced larvae, providing the possibility for localised adaptation via natural selection and therefore possible population isolation. To demonstrate the absence of stock structure in the giant crab polymorphic genetic markers are required.

Recent studies involving decapod crustaceans (Ovenden *et al.* 1997; Gopurenko *et al.* 1999), insects (Crozier *et al.* 1989) and fish (Waters and White 1997), have successfully used mtDNA cytochrome oxidase 1 and the cytochrome b gene fragments for phylogenetic analyses of closely related species. However, due to the reasonably rapid rate of evolution of these protein genes they are extremely useful for population studies, as they are highly sensitive to more recent patterns of evolutionary divergence. Finding the 16S rRNA, 12S rRNA, cytochrome oxidase 1 and cytochrome b gene regions to be monomorphic indicates that either the giant crab population consists of a single stock or stock isolation has occurred quite recently. If stock isolation has occurred recently then it is not altogether surprising that the 12S rRNA and 16S rRNA gene regions are invariant. These are the two slowest evolving mitochondrial genes (Hanner and Fugate 1997; Cuesta and Schubart 1998). Further it is also possible that the cytochrome oxidase 1 and cytochrome b regions do not evolve rapidly enough, despite evolving more rapidly than the rRNA gene regions, to allow detection of gene pool isolation in the giant crab.

Further testing for stock structure in *P. gigas* will require the analysis of quickly evolving genes such as the highly variable mtDNA control region and / or possibly nuclear intron regions. These regions are extremely sensitive to recent patterns of genetic divergence, hence appropriate for this kind of study (Atkinson and Adams 1997). The control region was trialed during this study; however, no useable PCR products were obtained. Little work has been done on these particular regions in crustaceans and therefore the development of specific primers and the optimisation of PCR conditions are required which is initially time consuming, hence it was not possible to fully investigate these regions in this study. Microsatellite loci are also a possibility for further study, however this alternative is both costly and time consuming, as primers usually have to be developed for individual species (Hillis *et al.* 1996).

In summary, based on the evidence from mtDNA data presented in this study and by Murphy (1999), it appears that the giant crab consists of a single population across southern Australia and can therefore be managed as a single stock. However, this conclusion needs to be more rigorously tested using more rapidly evolving genetic markers than were available for this study.

4.2.2.3. Literature Cited.

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4.2.2.4. Appendix.

Genetics Appendix A. Sequence data for the giant crab *Pseudocarcinus gigas*.

12S rRNA

```
1    GCCAGATTAA  TAGTAGATAT TTTCTTTAAA TTTAAAGAAT TTGGCGGTGA
51   TTTAGTCTAG  TCAGAGGAAC CTGTTTTTGA ATCGATAAAC CACGAAAAAT
101  CTTACTTATC  TTTGTTTTCA GTTTGTATAC CGTCATTAGC AGATAATTTT
151  TAAAGAAATA  ATTATTGTGT TTTATAAATT TAGAAAAATT AGATCATGGT
201  GCAGCTTATA  GGTAAGTTAA AATGGGTTAC AATAATATTT ATTTATAACG
251  AATAAATAAT  GAAGAAAAAT TTTTAAGGTG GATTTGATTG TAATATAAGT
301  TTAATATGCT  TAGGAGGCAT GAGCTCTAAA TCATGTACAC ATACGCCCGT
351  CGC
```

16S rRNA

```
1    GTCTGGCCTG CTCACTGACA CATAGAGTTT AAGAGCCGCG GTATTTTGAC
51   CGTGCAAAGG TAGCATAATC ATTAGTTTCT TAATTAGGAA CTTGTATGAA
101  TGGTCGGACA AAAGAAAAGC TGTCTCTGTT GTAAAGATAG AAATTAACTT
151  TTAAGTGAAA AGGCTTAAAT TTTTCAAGGG GACGATAAGA CCCTATAAAG
201  CTTTATATTT CGTTTAAATT TTATTGAATT ATATAAATAA AAATTTAATT
251  TAATCATTAT ATTGTGTTGG GGCGACATAG GTATAATTTA TATTAACTGC
301  TTGATAAGAA AACAAATAAT AAATGATTTA TAAAAATGAT CCTTTTTAAA
351  GATTTAAGAT TAAGTTACTT TAGGGATAAC AGCGTTATTT TTTTTGAGAG
401  TTCATATCGA AAAAAAAGTT TGCGACCTCG ATGTTGAATT AAAATATCTT
451  TATA
```

Cytochrome Oxidase 1 (CO1)

```
1    GAGGAAAAAA GGTATGTATT AACACCAATA AATATTACTA GAAAATGAAT
51   TTTCAATCAT TTAGGGTTTA TGGATAGTCC TGTAAATAAT GAAAATCAAT
101  GAGCAATTCC GCCAAAAATA CCAAATACAG CACCCATGGA TAGAACATAG
151  TGAAAATGAG CCACAACGTA GTACGTGTCA TGAAGGATAA TATCAATAGA
201  AGAGTTAGCT AATACAACTC CTGTTAGTCC ACCTACAGTG AATAGGAAGA
251  TAAATCCGAG GGCTCAAAGC ATGGAAGGAC TATAATTGAT TTGTGTTCCA
301  TGAAGAGTTC TTAATCATCT AAAAATTTTA ATTCCAGTGG GGACTGCAAT
351  GATTATTGTT GCAGACGTAA AGTAAGCTCG TGTATCAACA TCTATTCCTA
401  CTGTAAATAT ATGGTGGGCT CAAACAACAA ATCCTAAAAT TCCAATTGCC
451  AATATAGCGT AAATTATACC TAAGGTCCCA AAGGATTCTT TTTTTCCAGA
501  CTCTTGCTTA CAATATGAGA AATTATACC
```

Cytochrome b (Cyt b)

```
1    CCAACCTCTT CTCAGCTATT CCATATATTG GTACAGATTT AGTGCAATGA
51   ATTTGAGGAG GGTTCTCAGT AGACAATGCA ACATTAACAC GATTTTTTAC
101  TTTTCACTTT GTTCTCCCAT TTATTGTAGC CGCGGCTACA ATAGTCCATA
151  TTCTATTTTT ACATCAGTCA GGGGCTAATA ACCCCTTAGG TATCTCAAGT
201  CAAGTAGATA AAGTACCCTT CCACCCATAT TTTACATTTA AAGATATTGT
251  AGGGTTTATC GTAATATTGT CAAGATTACT TTTTCTGTCA CTTCTTTATC
301  CATATCTTCT AGGAGACCCT GATAATTTTA TCCCTGCAAA TCCTTTAGTC
351  ACCCCTGCCC ATATTCAACC AGAATGATAT TTCCTATTTG CTTACGCTAT
401  CTTACGATCA ATTCCTAATA AATTAGG
```

4.3 Larval ecology

Numerous large megalopa were acquired during the initial collection however electrophoresis indicated the megalopa were genetically different to *P. gigas*. A grow out trial established that they were of the species *Plagusia chabrus* , the cleft fronted shore crab and so after initial collections sampling did not occur during the periods of research fishing as indicated by the timetable (figure 19). No megalopa of *P. gigas* were collected during the study.

The 1994 research program developed jointly by the University of Tasmania and the Tasmanian Department of Primary Industry and Fisheries to describe larval morphology, growth and behaviour, provided a description of the zoeal stages of *P. gigas* (Gardner, 1998). This information was intended to be applied during a trial of larval collectors in 1998-1999 by this project; this aspect of the project was discontinued following the outcome of a review of *P. gigas* research instigated by Tasmanian scientists and managers at Adelaide in 1999. At that stage the larval collectors that had been built for this study were in the water being conditioned.

4.4 Tagging

As described in Table 3 nearly 18,000 giant crabs were tagged across the geographic range of the species. The tags will continue to endure through multiple moults. In time it is expected that recaptures will provide the complete growth description and the means by which to validate the current predicted growth rates for the various regions across the range of the species. During the development of the Yeild, Value and Egg per recruit model a collaborative effort was made to quantify the errors of measurement sometimes observed when comparing size at release and size at recapture. The most common error, which could be corrected, was ± 5mm, which is the difference between the edge of the sliding arm of the vernier calliper and the (0) zero mark at which the vernier should be read. As the vernier becomes worn and slides more easily, other small errors in the order of < 2 mm occur as the vernier is lifted away from the carapace. The 1755 recaptures have provided important information on movement and growth described in chapters 4.8 and 4.9 of this report.

4.5. Reproductive cycle and size at sexual maturity

4.5.1 Timing of Reproductive Events

Biological assay of 112 female crabs provided the ratio of ovary weight to whole body weight (gonadosomatic index) and egg weight to whole body weight (egg index). The data was pooled across all regions (figure 29). Trends in maximum monthly GSI values indicated a mid year spawning but low catchability and reduced fishing activity limited the acquisition of specimens during late autumn and winter months. Monthly GSI values were highly variable which appeared to be due to some of the crabs preparing to moult. Gardner (1998), sampling the East Tasmanian population, also found there were some crabs that were neither going to spawn or moult and so there is a possibility that a similar situation may also have contibuted to some of the low GSI values obtained by this study.

The depth at which *P. gigas* occurs makes direct observation of mating events in the wild difficult. In some species of crab, males mate with newly moulted females but this varies widely between species (Hartnoll, 1969). The scant evidence for *P. gigas* suggests mating with recently moulted females, the single mating event at the Bicheno aquarium, east Tasmania in 1998, occurred with a female that had recently

moulted. Chapter 5 also shows that males are present in the same depths as moulting females during the winter. Many females observed during this study bore scars on the internal surface of their abdomen and it was established by placing male and female crabs in various positions, that these scars were caused by the telson of the male abdomen during mating. The observation of unhealed abrasions in clean shelled females provided another indication that mating occurs shortly after moulting. Small melanised areas were sometimes observed at the periphery of the vulvae but this was less frequent. It is of note that the *P. gigas* spermathecae allows opening by muscular action and that the structure of the vulva and the vagina offers no impediment to mating during any part of the moult cycle (after Hartnoll 1969).

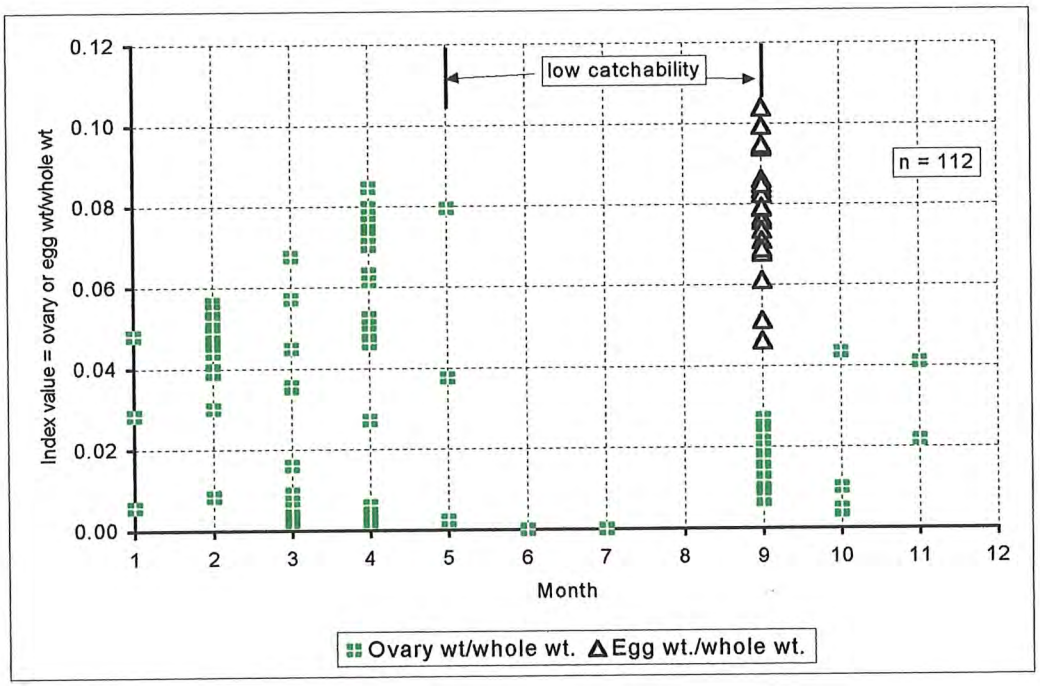


Figure 29. Gonadosomatic (GSI) and egg indexes
Values for the ratio of ovary weight to whole body weight (gonadosomatic index) and egg mass weight to whole body weight were pooled across all regions. The wide scatter of values for GSI is caused by the female population containing a mioxture of crabs that arre goin to spawn and show higher GSI values, and thoise that are going to moult with GSI values below .02 in months 1 (January) to 7 (July).

After spawning the eggs are incubated for about 4 months until they hatch in the months of September, October and November (Levings. *et. al.* 1996). As eggs ripen the colour changes from a creamy orange to a dark burgundy, as the eye of the embryo develops and the yolk mass diminishes (see figure 30).

Science students at the St Helens Secondary College in east Tasmania filmed the hatching process. The female crab vigorously opened and closed her abdominal flap to wash the pre-zoea hatchlings out of the mass of eggs, empty egg casings and funicular threads. This activity was punctuated by periods of grooming where the female used her two front legs to separate and tease out individual sections of the mass attached to each of her pleopods before the next abdominal spasm.

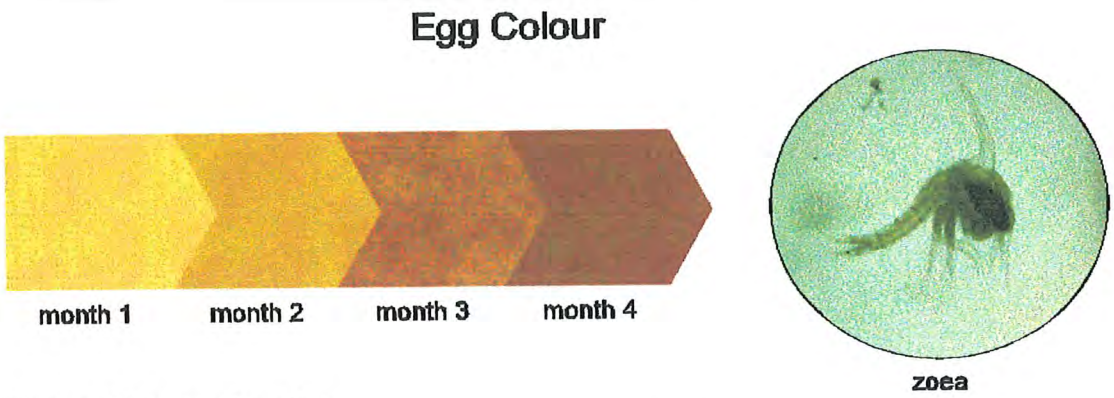


Figure 30. Egg ripening
After spawning the eggs are incubated for about 4 months, the colour progressively changing from a creamy orange to a dark burgundy as the eye of the embryo develops and the yolk mass diminishes.

Figure 31 is a snapshot of the sequence of egg hatching across regions in 1994, and suggests incubation of eggs may be linked with water temperature; hatching occurs earlier in western Australia where temperatures are higher, and later in north western Tasmania where temperatures are lower. The CSIRO's "Climate of Australian Regional Seas" data set provides long term average water temperatures at 200 metres, and these vary from 13°C off Augusta (WA) to 11°C off Strahan (Tas) in the spring. However this is far from conclusive as the depth distribution of female *P. gigas* in West Australia in the spring of 1994 was about 160 metres deeper than in South Australia.(330m *cf* 170m) At this depth the temperature may be preferable (12°C), but there is little food here compared to the bryozoan rich substrates which occur about 160 metres up the slope in shallower water (*after* Chinnock, 1996).

4.5.2. Frequency of Spawning

Multiple recaptures of tagged individual females have shown they do not produce eggs in the years they moult. They have an extended intermoult period of about 4-6 years for the 120-145 mm length classes and it is expected even longer for larger sizes. Female *P. gigas* carry stored sperm which reduces the need to mate to long periods. The stored sperm is used to fertilise successive broods and dissection indicated it can be carried through a moult; similar observations having been recorded by Gardner (1998). In the absence of mating the storage is most probably used to fertilise more broods after the moulting event. The sizes at which egg bearing is first observed and the incidence of mating scars are similar and appear to be linked to puberty. The ability of crabs to store sperm through moulting events means that the presence or absence of mating scars in the sizes above puberty is not a reliable indicator that mating has occurred. The many egg bearing crabs that lacked these marks most probably mated in a prior instar.

Off eastern Tasmania in 1994, 1995, 1998 and 1999 patterns of declining fecundity (figure 38t–w, 5mm series) in larger sizes not typical of other areas occurred. These patterns are shown below. Gardner (1998) also sampled this area and found that some crabs (n = 15) of a total sample (n = 101) did not moult or spawn; 12 of the 15 in this group were below 150mm. Reproductive inactivity has been recorded for other species of crab (Wenner *et al*, 1974, Hankin *et al*, 1989) where individuals may slow neither moulting nor spawning in some years. The fecundity pattern of this area appears to have existed prior to first targeted exploitation by pots, and may be linked

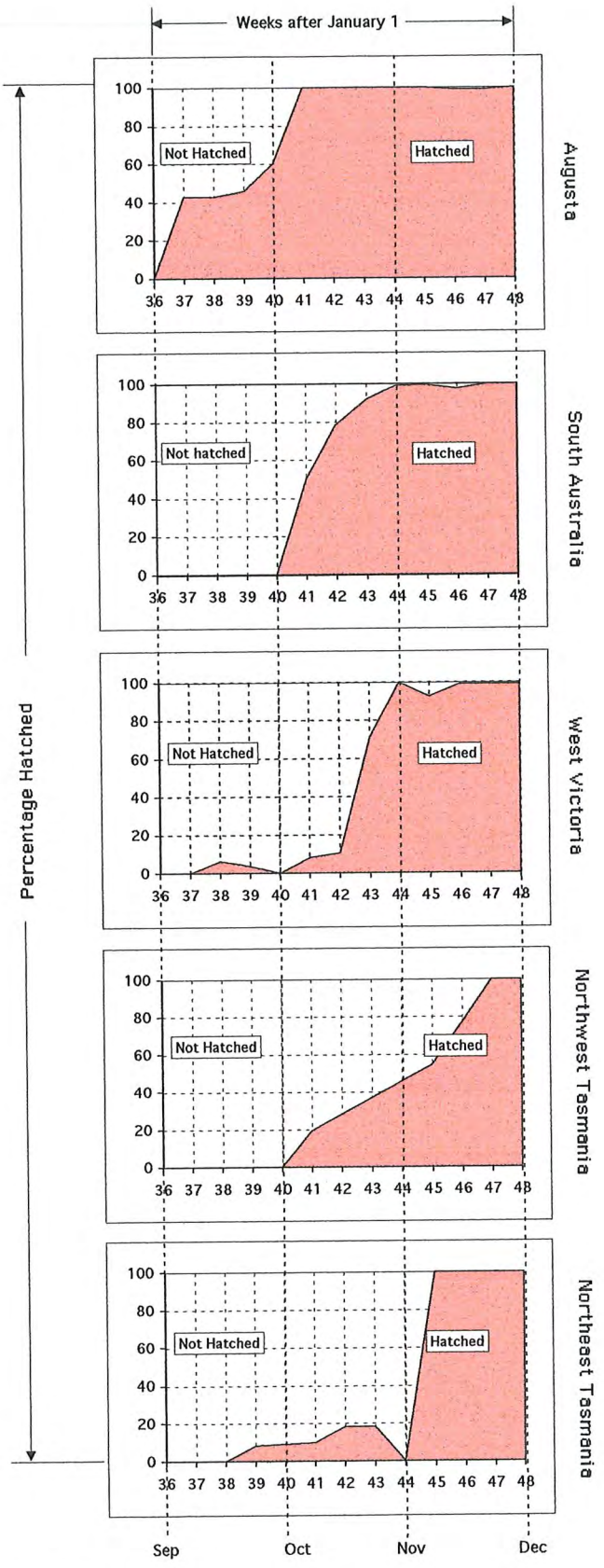


Figure 31. Giant crab egg hatching, spring 1994.
A snapshot of egg hatching across 5 southern Australian regions indicates a sequence of earlier hatching in Western Australia where bottom temperatures are higher to later hatching off South Australia, Victoria and Tasmania, where temperatures are lower.

to a lower abundance of reproductively active males.The male to female sex ratio of

this area which is described in chapter 4.10 on population structure, has not been observed to rise above 20% at any time of the year compared with winter peaks of 80% elsewhere (figure 50) and it is suggested the reason for the declining proportion of larger females bearing eggs in this population is a lack of mates.

The percentage of egg bearing females in different length classes which are presented in figure 37 & 38a – w, 1mm & 5mm series, show much variability across regions. As observations of *P. gigas* can be affected by area, fishing history, migration, seasonal behaviour and recruitment processes, care must be taken in attributing cause to the effects that are observed in the data.

In summary, female *P. gigas* show multiple spawns between moults, and with sperm storage ability, multiple spawns across moults. There is no evidence to suggest they moult and spawn in the same year; the more likely scenario is moult in year 1, spawn once in each of the subsequent 4 or 5 years, then moult, mate and begin a similar but longer sequence of annual spawnings until the next moult years later.

4.5.3. Egg Production

Whereas the average femaler size at maturity (Lm), is the smallest size class at which 50% of crabs of that class are bearing eggs, cumulative egg production (L50) progressively totals the contribution that the smallest to the largest size classes make to the total egg production output by the entire population. This analysis allows determination of the threshold at which 50%, or any other percentage, of the total egg production is reached. L50 values ranged from 137 mm to 172 mm carapace length, but most values were between 145 mm to 155 mm, varying from year to year and from site to site.(figure 36). There was no overall trend, even though there is an apparent difference in size at maturity across sites from west to east. Most populations, except Albany in 1994 and Augusta in 1997, yielded few egg bearing females smaller than 115 mm carapace length. The Albany 1994 and Augusta 1997 samples contained females smaller than this where eggs or spent eggs were observed. The nature of the relationship at the lower end of the range (ie. 90 to 115 mm carapace length) needs to be more thoroughly investigated at this site.

Egg production by individual females across a range of sizes was obtained late in the incubation period and is described as the weight of the egg mass plotted against carapace length in figure 32. The size range of females in the sample was 118 to 197 mm carapace length and production is described by a linear relationship of the form *$y = 3.824x-397.77$, where y = egg mass and x = carapace length.* The goodness of fit of this model to the data was .7811. Egg numbers were not determined in the present study but Gardner (1997) has shown that egg numbers in *P. gigas* increase with female size and vary from 706,000 in a female with a carapace length of 131 mm to 2,545,000 at a length of 203 mm. Although individual egg size increases with increasing female size, a slight but significant trend for egg number to decrease with a decline in carapace condition was noted by Gardner who concluded that egg number does not follow a simple volumetric relationship like southern rock lobster *J. edwardsii* .

Studies of seasonal behaviour of other species (e.g. *Cancer pagurus and Cancer magister*) have indicated berried females are less likely to enter pots and that catch data can be biased in favour of non berried females (Edwards, 1979; Howard, 1982;

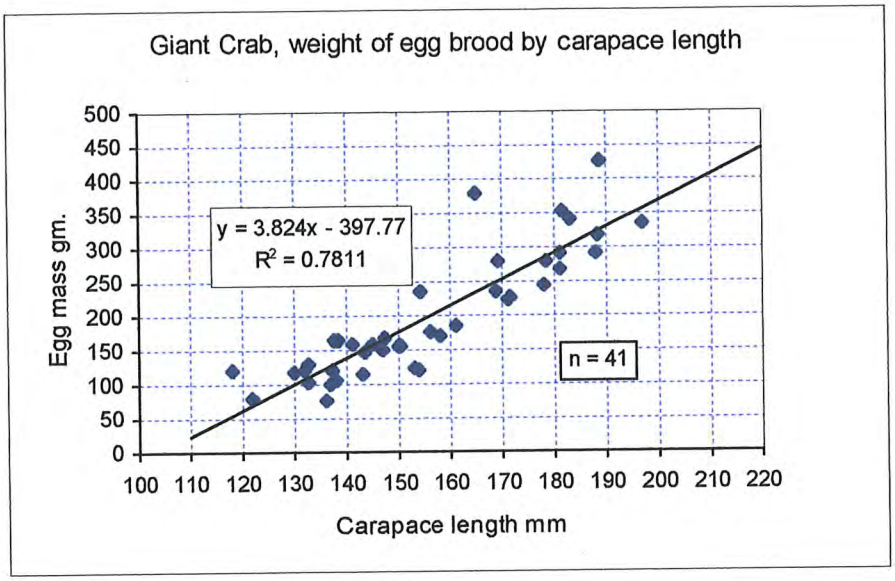


Figure 32. Weight of egg brood by carapace length

Schultz *et al*, 1996). Gardner (1998) conducted winter sampling off east Tasmania and concluded that his results as well as this study's analysis of egg production based apon sampling off northwest Tasmania were biased by an over representation of non egg bearing crabs more vulnerable to capture than those with eggs. He concluded that the *"the current size limit does little to protect egg production"* and that *"the current minimum size limit is unsuitable for Tasmania"*.

However his conclusion appears to be incorrect. Our study found that in *P. gigas* , as one group of the female population moults the other group spawns, and low catchabilty during the period from late autumn through to spring affects both groups and therefore the potential for this type of bias is less. Where a longer time series of data has been available, for example from South Australia, catch per unit effort from the female population showed the highest catchability was in the late spring/early summer after eggs had hatched when females began to actively forage. The ratio of females to males in the catch also rose to a seasonal maximum (see chapter 5). CPUE analysis of the unexploited section of the population below 150mm, illustrated in figure 33a, which shows that peak catch rates occurred in October. Figure 33b provides no support for Gardner's suggestion of sampling bias. Non berried recruits were not more catchable compared to berried crabs; in fact after hatching in October the opposite occurred and observation of the empty egg casings provided most of this study's information about which group carried eggs and was used in the initial analysis on which the minimum size limit was set. Gardner's analysis also ignored the effects of previous exploitation.

The effects of fishing on the exploited and unexploited sections of the female population off South Australia and north west Tasmania are illustrated in figure 34a. and b. Figure 34a is recapitulated in figure 35 but at the finer length class resolution of 1mm instead of 5mm. Successful size regulation illustrated in figure 35 below shows that the relative proportion of berried females above 150mm has decreased but that the nonexploited size classes below 150 mm have been conserved. The relative

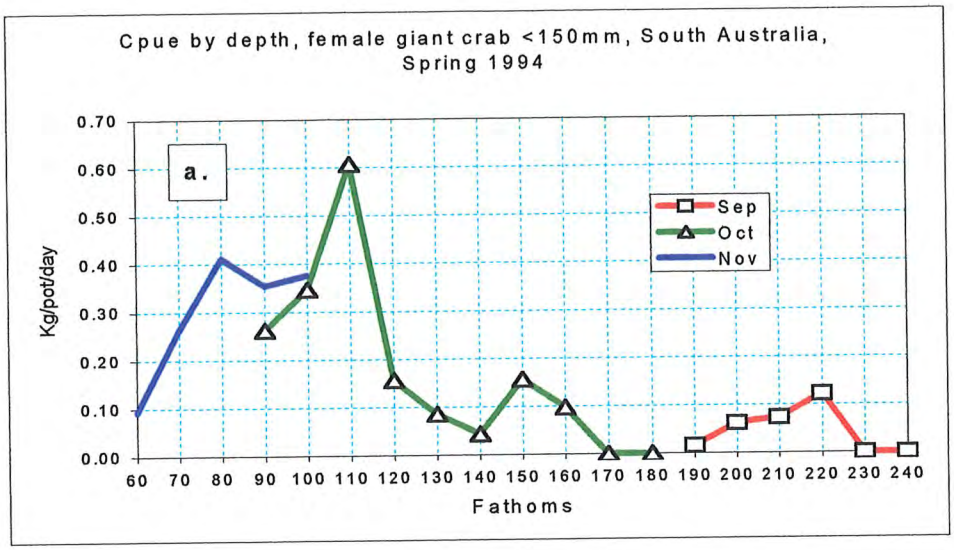


Figure 33a. Catch per unit effort by depth. Catchability of the unexploited section of the female giant crab population <150mm peaked in October 1994 in 110 fathoms or ≈ 200metres.

abundance of nonberried to berried females reflects two temporally distinct events. Fishing mortality of 12 months or more is reflected in the lower abundance of the berried part of the population. The nonberried component which has moulted in the

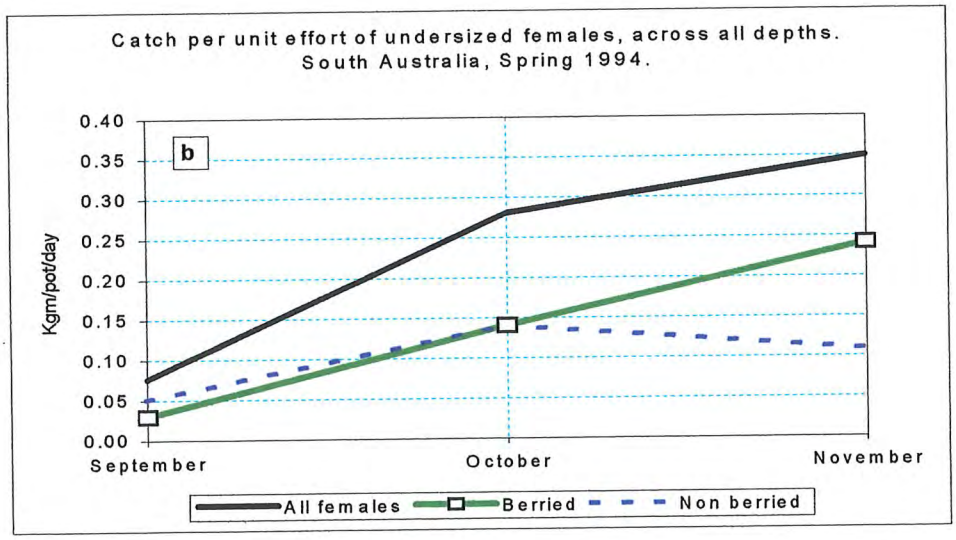


Figure 33b. Catch per unit effort of the unexploited section of the female giant crab population <150mm by reproductive state. Catch rate for berried and nonberried groups increased at a similar rate during September. Catch rate then decreased for nonberried crabs, but continued to rise for those that had carried berry (now spent casings) in November.

winter has sustained little fishing mortality in the three months up to spring sampling. Intense fishing effort was applied to the north western Tasmanian population before the introduction of the size limit. As much of the virgin population was removed, the relative abundance of egg bearing to non egg bearing females was skewed by an influx of newly moulted non egg bearing recruits into the area previously occupied by the egg bearing crabs (that had been caught). In the absence of a size limit as was the case in the Tasmanian example, this is reflected across the entire population, but for

South Australia where most exploitation occured after the size limit was introduced, the influx is reflected only in the exploited section above 150mm.

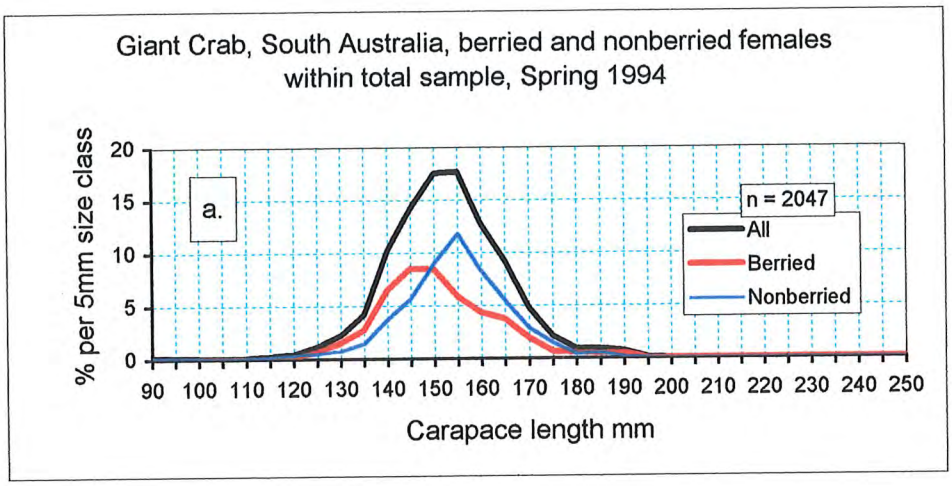


Figure 34a. Effects of fishing on a female population, South Australia.

Figure 35 shows the retention of the bell shaped size distribution through the entire size range including the sections above and below the size limit indicates that for some reason irrespective of whether the female is carrying eggs there is an apparent preference for the targeted area as evidenced by the influx.

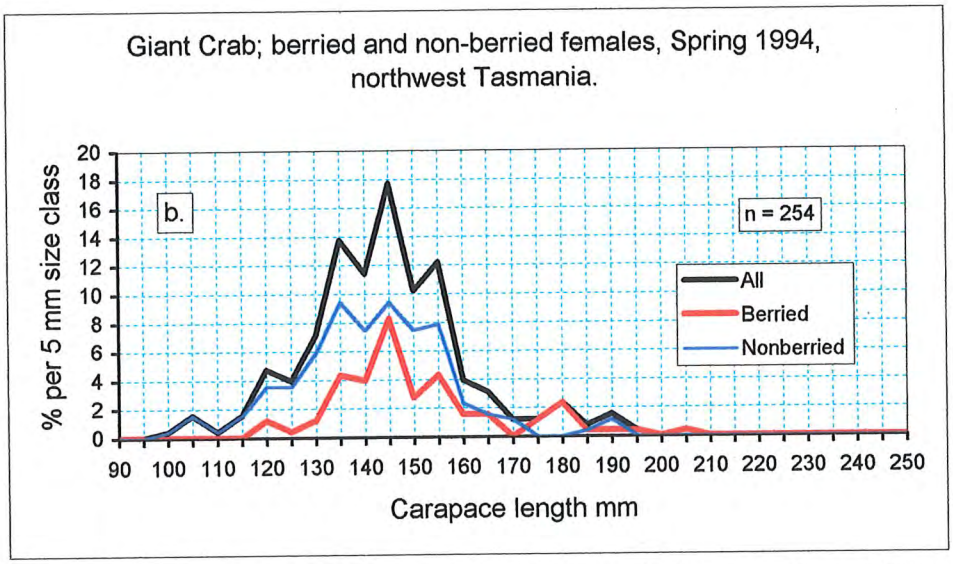


Figure 34b. Effects of fishing on a female population, northwest Tasmania.
Northwest Tasmania was subjected to heavy fishing effort prior to prior to size regulation and collection of this sample. Therefore the egg bearing section of the population had sustained fishing mortality across all size classes, but there had also been an influx of new recruits into the fishery that have moulted through from smaller sizes.

Statistical analysis presented in chapter 4.10 showed that with the exception of west Australia, *P. gigas* populations are size stratified where mean individual size decreases significantly with increasing depth. Although the level of analysis did not show significant differences with depth for west Australia, a commercial fisher (G

Pateman, Augusta. 1999) has observed a similar trend. Initially in Victoria before the fishery was regulated and as fishermen improved their skills, fishing was targeted at the depth that yielded the biggest weight of crabs. The value of L50 was an artefact of the population size distribution at this depth. After the size limit was introduced fishermen had to fish in shallower water for larger crabs, and L50 changed from 145 mm in 1993 to 160mm and 157mm in 1994 and 1995 respectively. While the smallest sized individual with eggs (Lsm) and the average size at first maturity (Lm) may vary between populations and as proposed here reflect existing natural conditions, L50 is an artefact of the way the population of a particular area is fished, given the prevailing constraint of a legal minimum length. The first assessments for the interim legal minimum size were made from data collected at the depth where the catchable biomass was at it's highest, fished in the absence of regulatory constraints. As indicated earlier, the size was set to protect 50% of egg production in a deliberately conservative management strategy until further evidence was available. It was contemplated that some adjustment could be made to the interim legal minimum size if subsequent analysis proved that this was overly conservative, or there were regional differences in Lsm, or if separate consideration for the protection of males was justified.

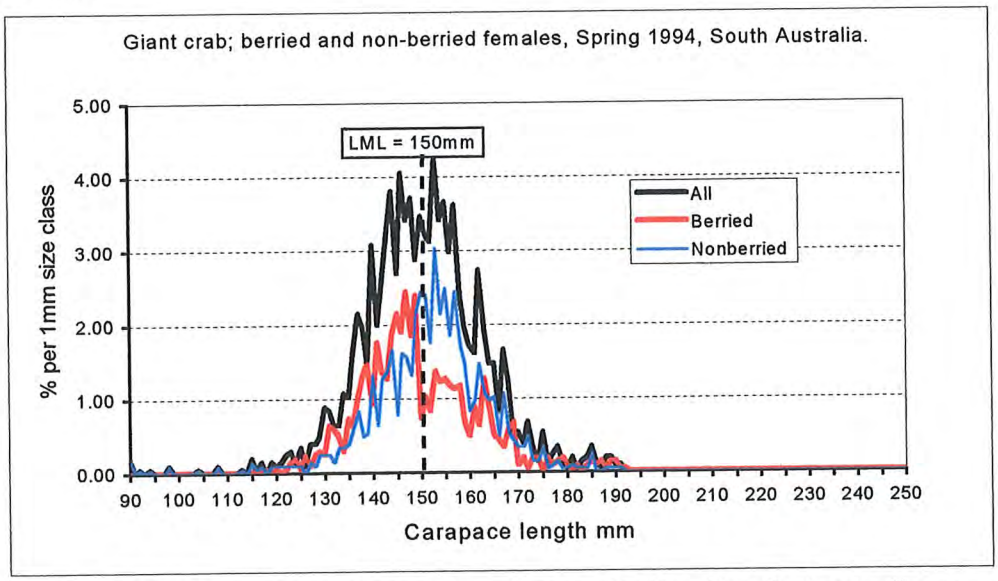


Figure 35. Effects of fishing on a female population, South Australia. At a 1mm size class resolution figure 35 is a repeat of figure 34a. Presented at a finer scale the effect of fishing to a legal minimum size is clearly illustrated in the sharp drop in abundance of berried crabs at the 150mm size limit threshold.

One of the difficulties in making fecundity assessments into the early summer is that remnants of the hatched brood such as empty egg casings and funicular threads gradually disappear. Qualitative assessment shows the rate of disappearance may be highly variable between individuals. However the colour of the setae changes from a light gold through to a dark olive with the crab's progression through the intermoult period. Therefore setal classification by standardised colour observations via the "Munsell" system may provide the means for low cost field assessments of population fecundity conducted at other times of the year despite an absence of egg remnants.

The cumulative egg production by entire female populations is illustrated in Figure 36 and summarised in Table 12.

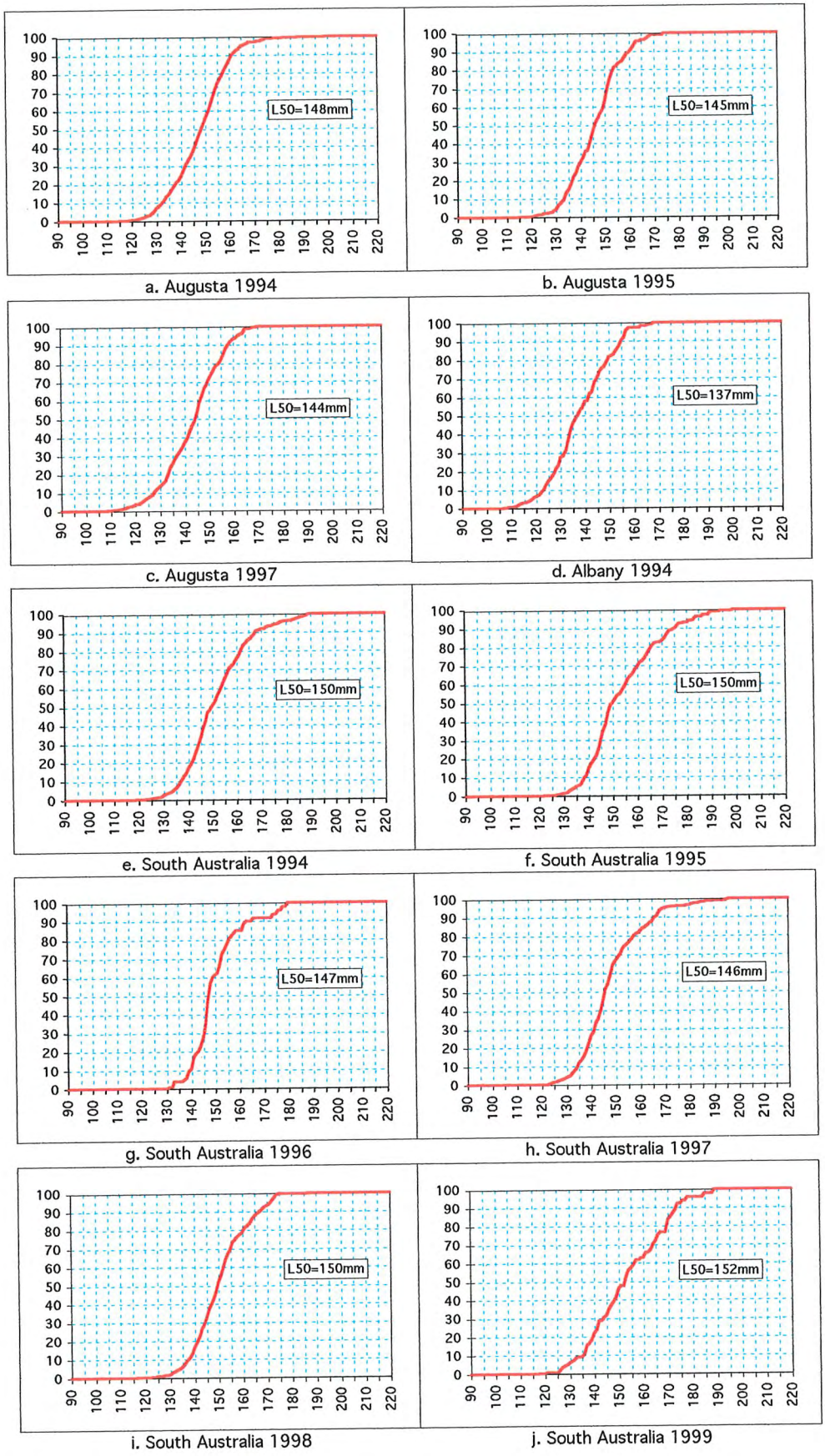


Figure 36 a.-j. Cumulative egg production by crab population

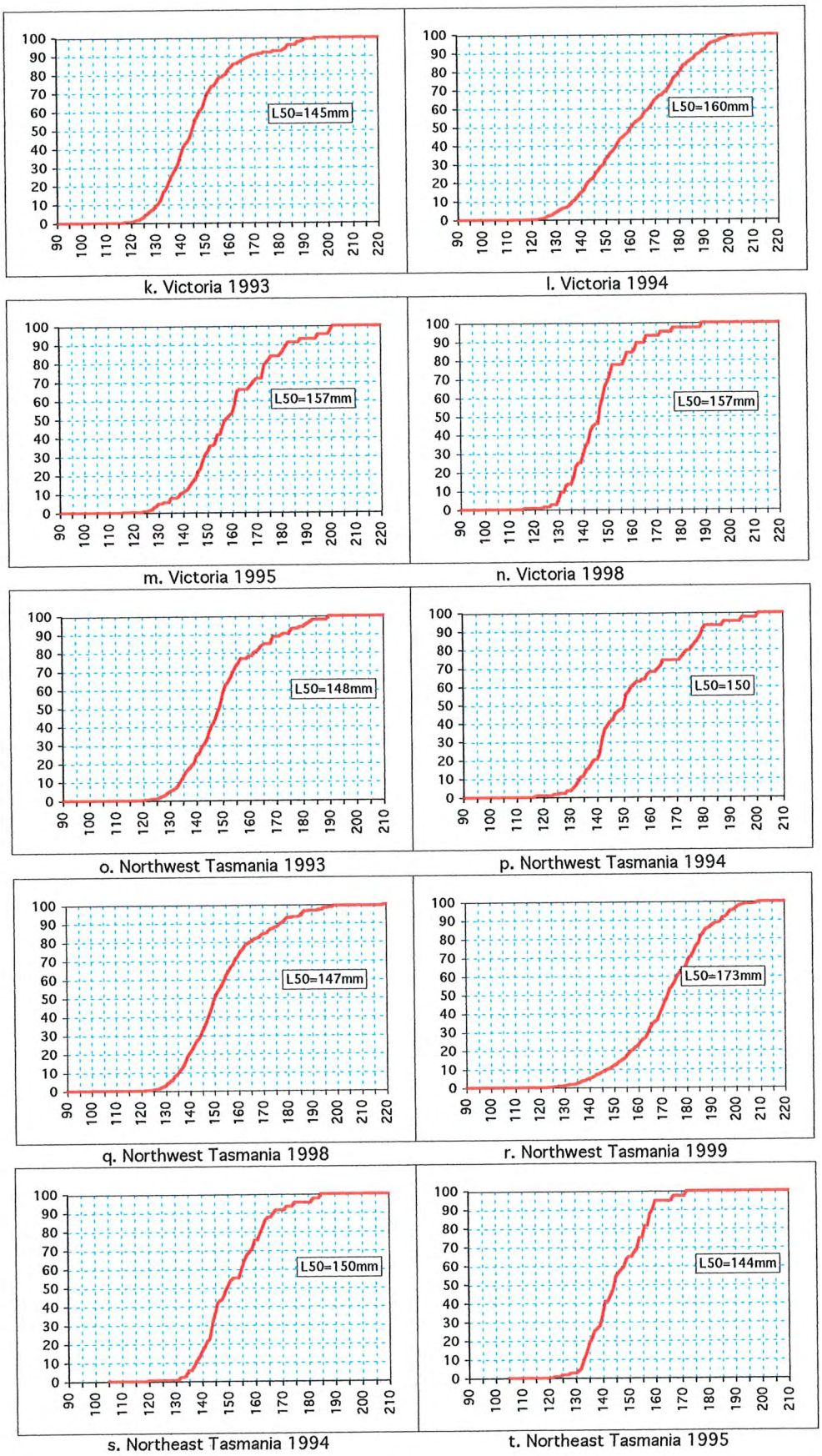
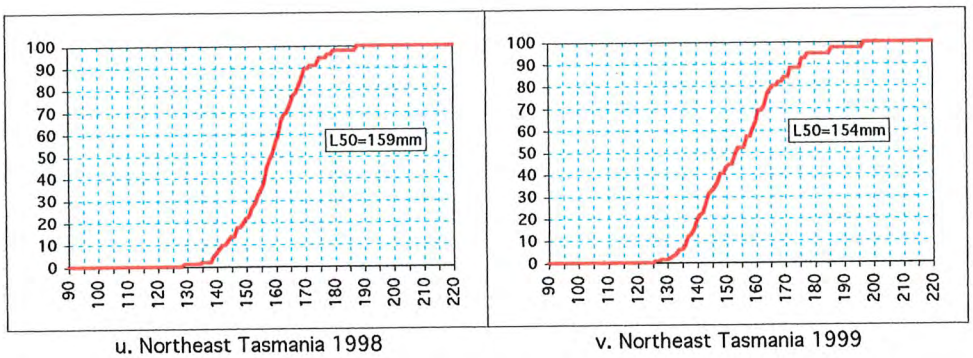


Figure 36 k.-t. Cumulative egg production by crab population



u. Northeast Tasmania 1998 v. Northeast Tasmania 1999

Figure 36 u.-v. Cumulative egg production by crab population

Table 12: Summary of size at 50% cumulative egg production

Area	Year	50%	40%	30%	20%
Augusta	1994	148	145	141	137
	1995	145	143	140	136
	1997	144	141	137	134
Albany	1994	137	134	131	127
Sth. Australia	1994	150	146	144	141
	1995	150	147	145	142
	1996	147	146	145	143
	1997	146	144	142	139
	1998	150	147	145	142
	1999	152	149	144	140
West Victoria	1993	145	140	138	135
	1994	160	154	148	143
	1995	157	153	148	145
	1998	147	143	140	137
Northwest Tas.	1993	148	145	143	139
	1994	150	144	146	138
	1998	150	148	144	140
	1999	172	169	164	158
Northeast Tas.	1994	150	145	144	141
	1995	144	140	139	135
	1998	159	156	153	149
	1999	153	148	144	140

4.5.4 Female size at sexual maturity

The proportion of egg bearing females per length classes for the different regional populations are shown in figures 37 a. to w. (1 mm length classes).

In virgin populations or in populations protected by minimum size regulation a plot of the percentage of size classes carrying eggs or egg cases, shows a rapid transition from juvenile to adult stages. The plot shows a knife edge jump from the zero values of juveniles to a 40 to 70% peak. It then plateaus out with little gradient in virgin populations, or falls away toward zero again in size classes above 150 mm in fished populations.

Catchability of females reaches a peak at the final stages of egg maturation through to post hatching of eggs, some females even being caught while egg hatching was in progress. In the weeks prior to this event fishermen target what appears to be a movement of crabs from deeper to shallower water. The catch includes smaller males (which may not be functionally mature), clean shelled females that have just moulted, and berried females. The shallower substrates are much richer in food resources and may as fishermen suggest, be occupied by "resident crabs". If this were true the influx of newly moulted crabs from deeper water occurs at the same time that the egg bearers are becoming unburdened of their brood. The two events would increase competition for food, increase in foraging activity and result in a higher level of catch in baited pots.

Tagging has shown that mature female crabs have an intermoult period of at least 4 years in smaller size classes and it is estimated, 7 years at 150 mm. In regions that were fished prior to the 150 mm minimum size, the proportion of non berried to berried females in the smaller size classes was higher and the knife edge jump referred to above not so pronounced, especially if using 5mm size classes in the analysis (Figures 38p, q, r, and s; 5mm series). Graphically the effect is that the midpoint between the asymptote and the x axis moves towards the larger length classes. This type of change is not accompanied by a change in the minimum size at which egg production is observed. In virgin or protected populations the midpoint represents the average size at sexual maturity, but in populations exploited prior to size regulation, this type of change is attributable to the dynamic of fishing mortality and then recruitment. Under these circumstances the midpoint is not a true indicator of size at maturity (Lm).

Western Australia shows different patterns which may be linked to it's different ecology. In the 5mm series, figure 38a, b and c were taken during a fishing regime which observed a voluntary 150mm size restriction, and figure 38d., a voluntary 135 mm size restriction.

Victorian sampling as illustrated in the 5mm series figure 38l. to n. below, occurred across the years 1993 to 1995. After 1994 most fishermen fished slightly shallower water to maximise the take of above 150 mm crabs in a population that was stratified by size according to depth, however the drop towards lesser abundance of berried females occurred at 130-135 mm. If the size limit had been observed by all fishermen, then by 1995 the change in relative abundance between berried and non berried crabs should have begun to show for the class immediately above and below 150 mm, but this effect is absent in figure 38n.

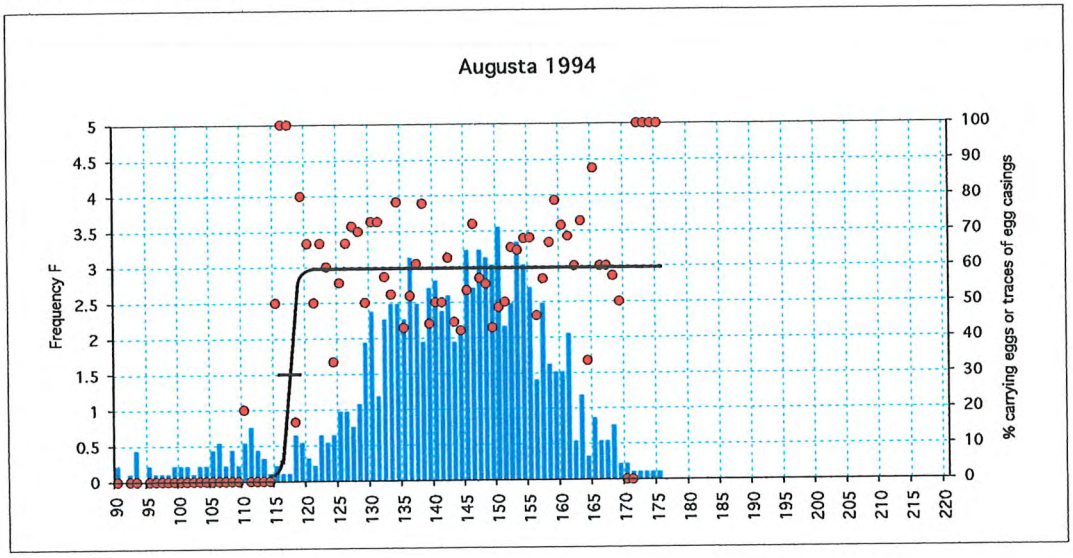


Figure 37a. Asymtote value = 60% Lm value midway between asymtote and X axis is 117 mm

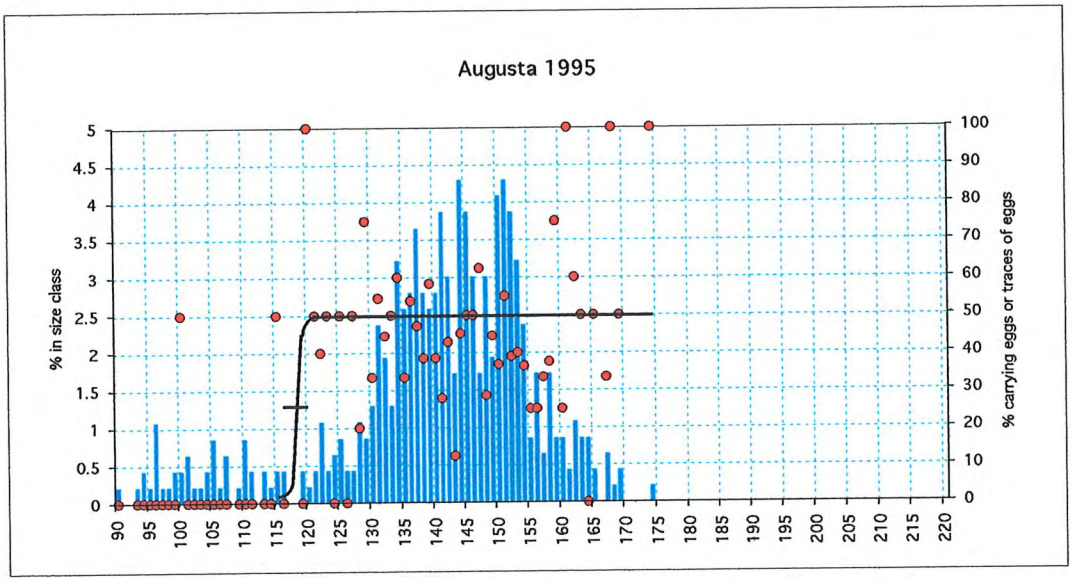


Figure 37b. Asymtote value = 50% Lm value midway between asymtote and X axis is 117 mm

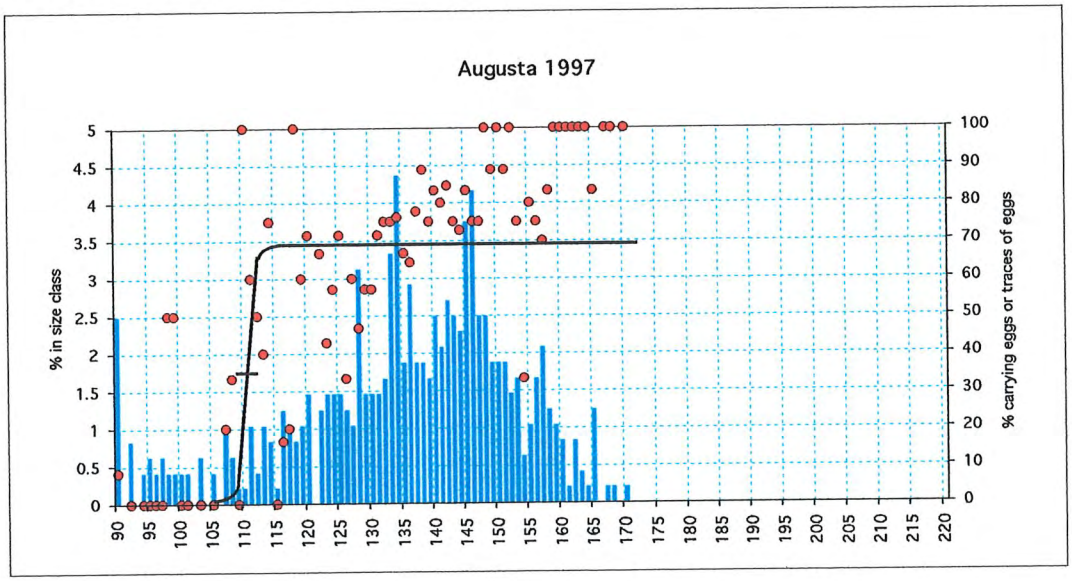


Figure 37c. Asymtote value = 75% Lm value midway between asymtote and X axis is 111 mm

Figures 37a.-c. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

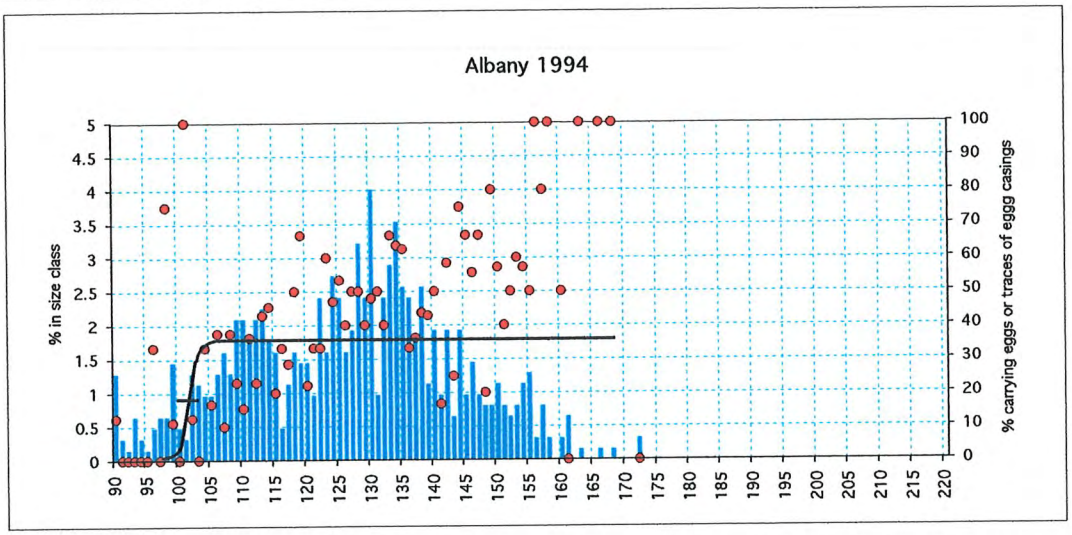


Figure 37d. Asymtote value = 35% Lm value midway between asymtote and X axis is 102 mm

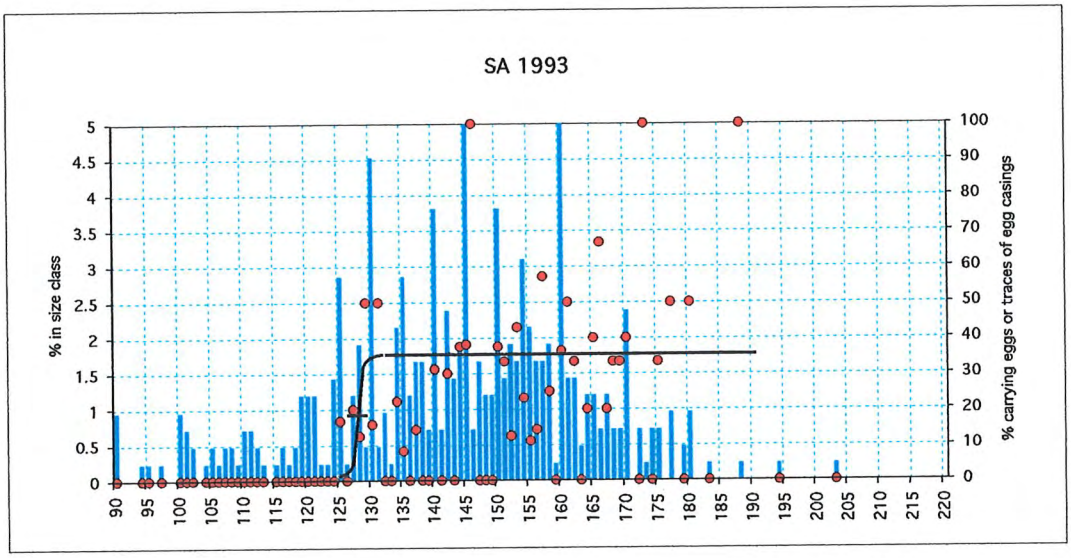


Figure 37e. Asymtote value = 35% Lm value midway between asymtote and X axis is 127 mm

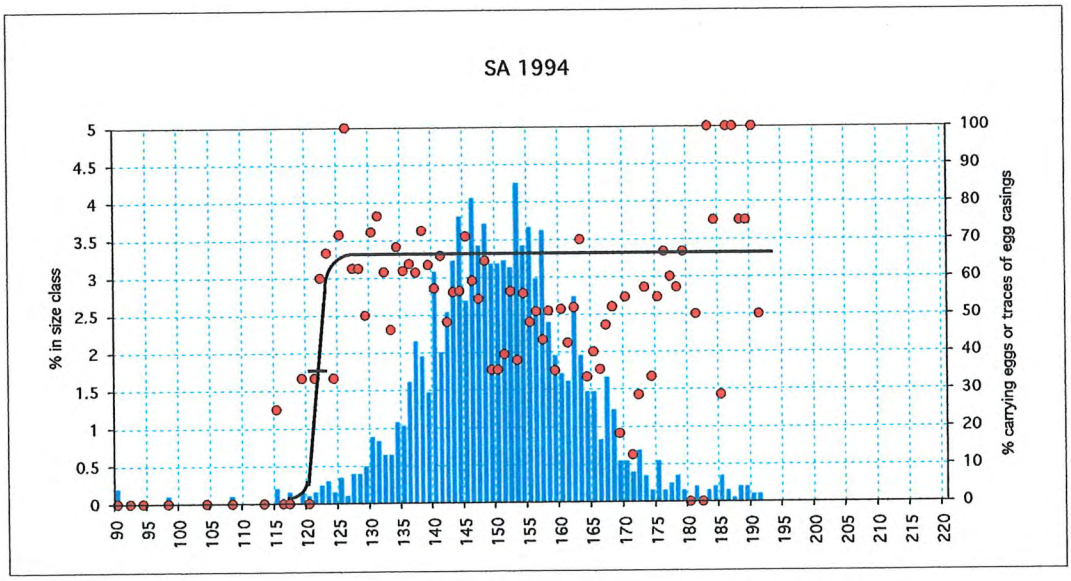


Figure 37f. Asymtote value = 68% Lm value midway between asymtote and X axis is 122 mm

Figure 37d.-f. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

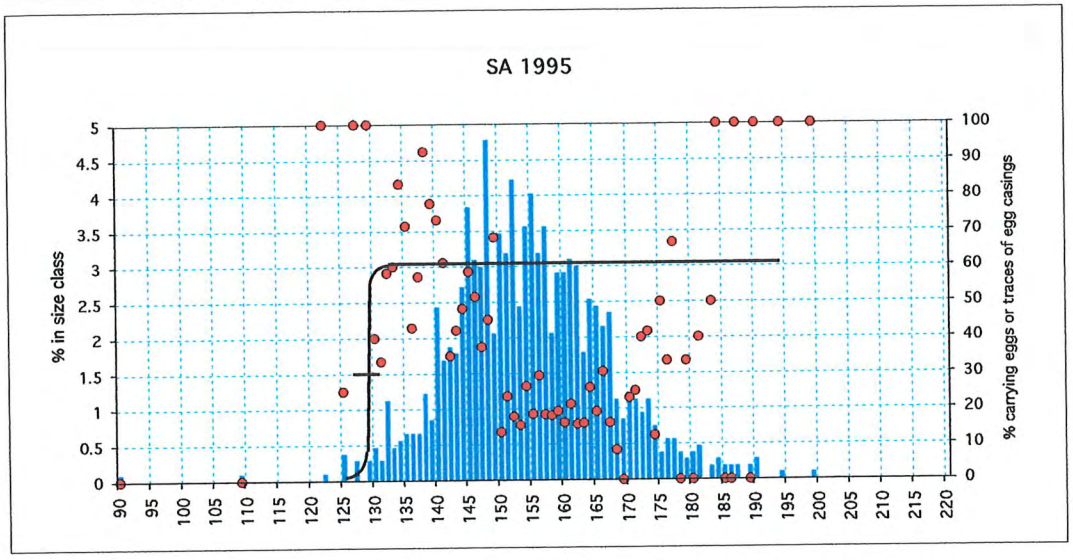


Figure 37g. Asymtote value = 62% Lm value midway between asymtote and X axis is 128 mm

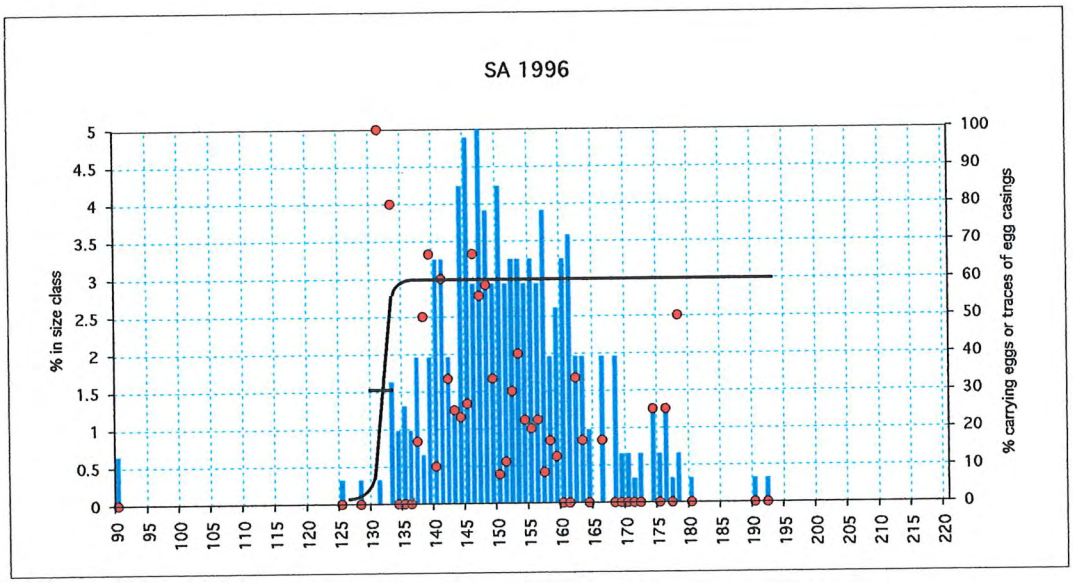


Figure 37h. Asymtote value = 60% Lm value midway between asymtote and X axis is 132 mm

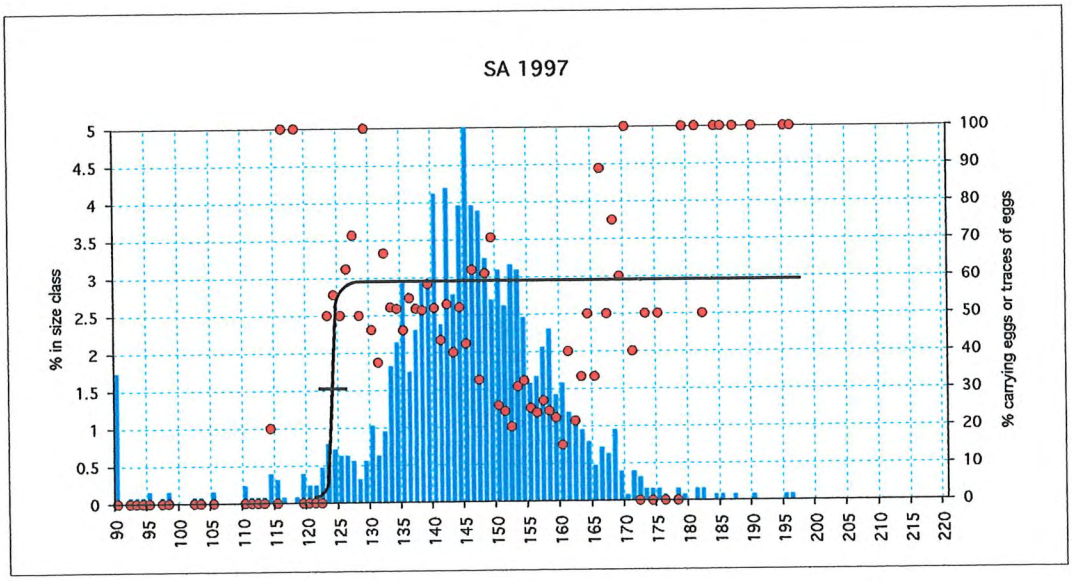


Figure 37i. Asymtote value = 30% Lm value midway between asymtote and X axis is 123 mm

Figure 37g.-i. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

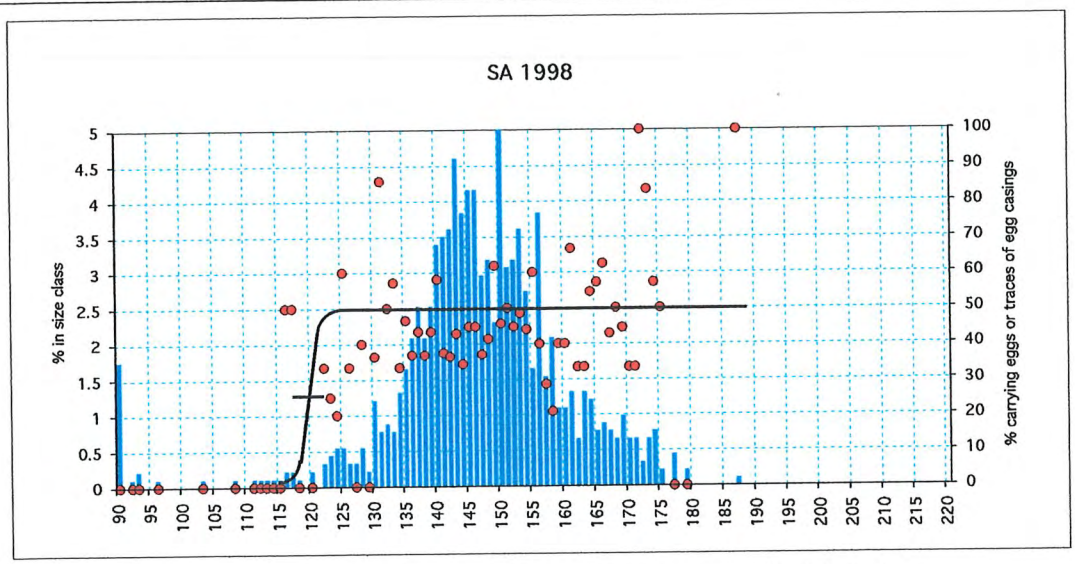


Figure 37j. Asymtote value = 50% Lm value midway between asymtote and X axis is 120 mm

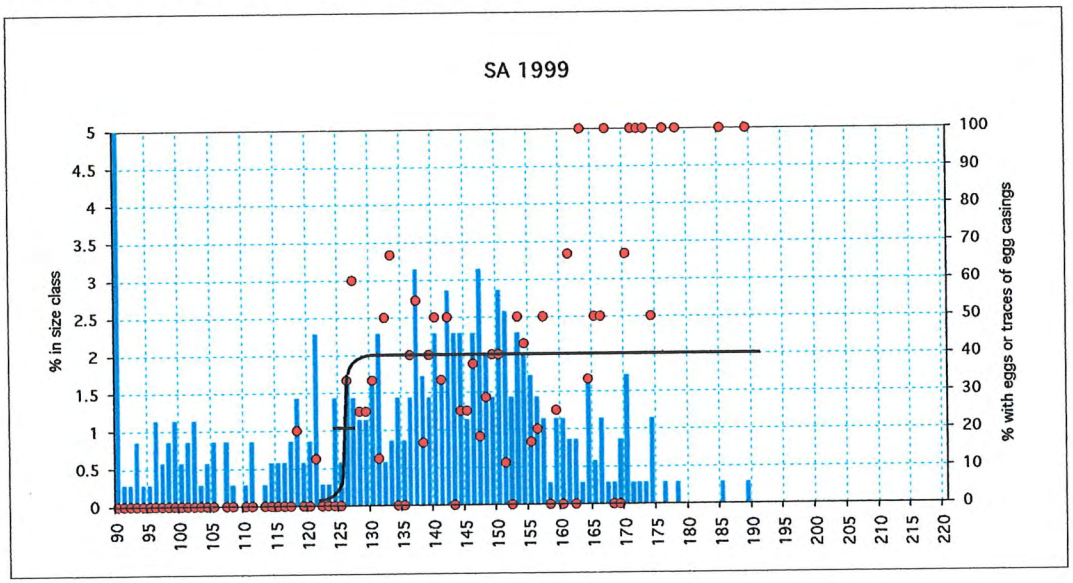


Figure 37k. Asymtote value = 40% Lm value midway between asymtote and X axis is 126 mm

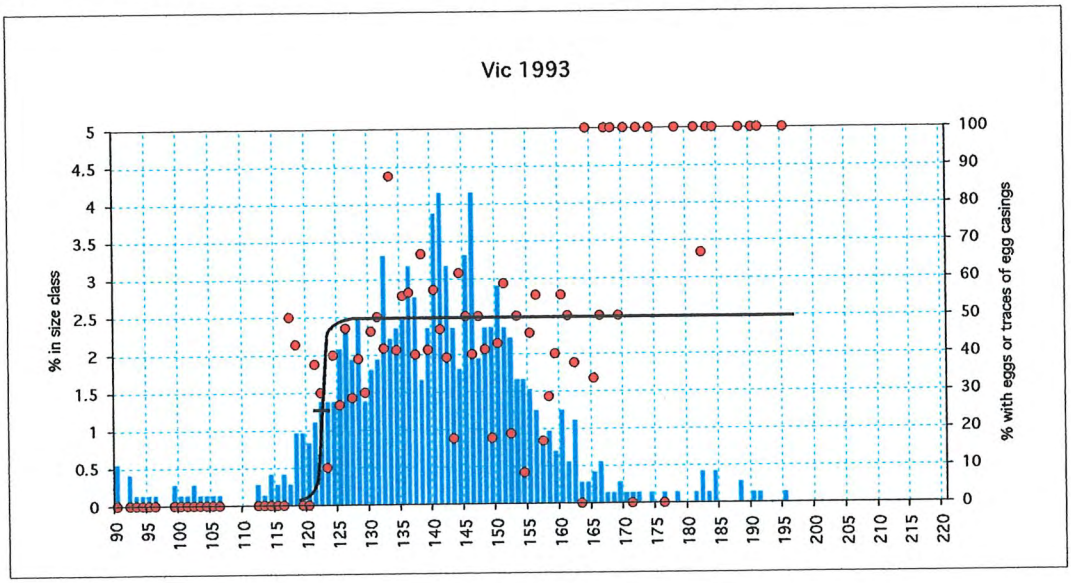


Figure 37l. Asymtote value = 50% Lm value midway between asymtote and X axis is 122 mm

Figure 37j.-l. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

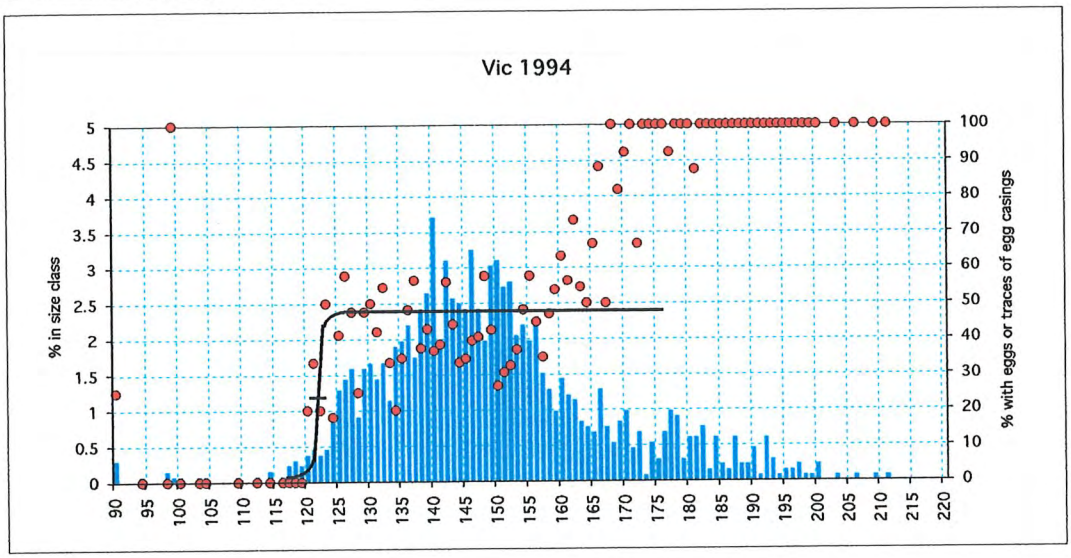


Figure 37m. Asymtote value = 48% Lm value midway between asymtote and X axis is 122 mm

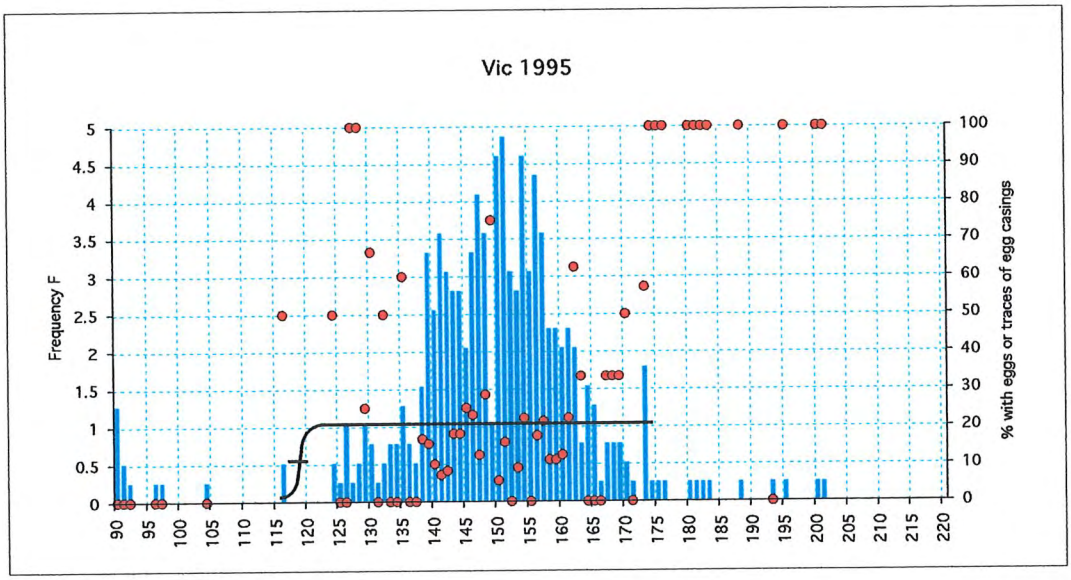


Figure 37n. Asymtote value = 20% Lm value midway between asymtote and X axis is 118 mm

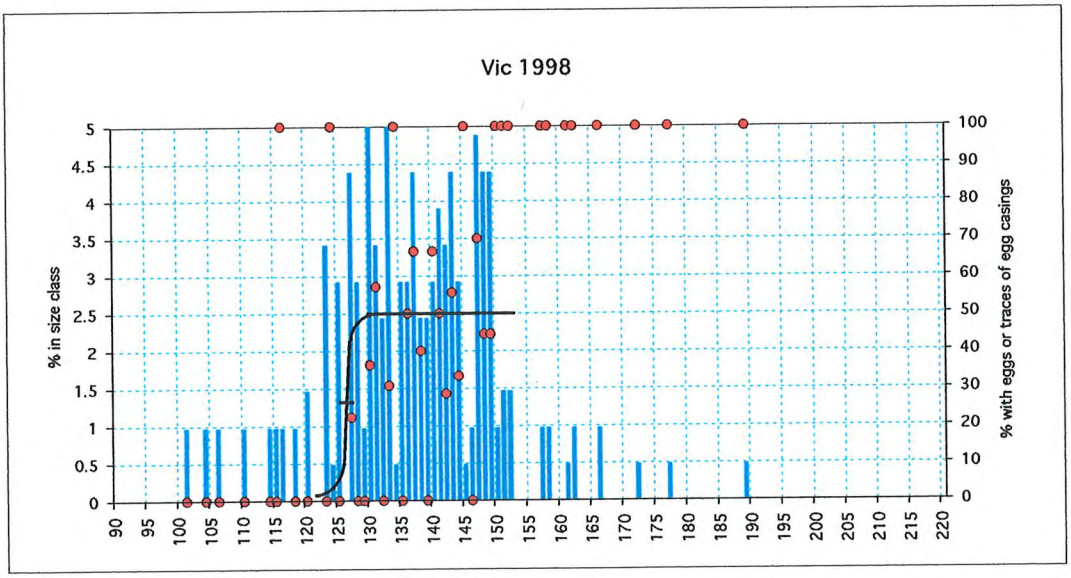


Figure 37o. Asymtote value = 50% Lm value midway between asymtote and X axis is 126 mm

Figure 37m.-o. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

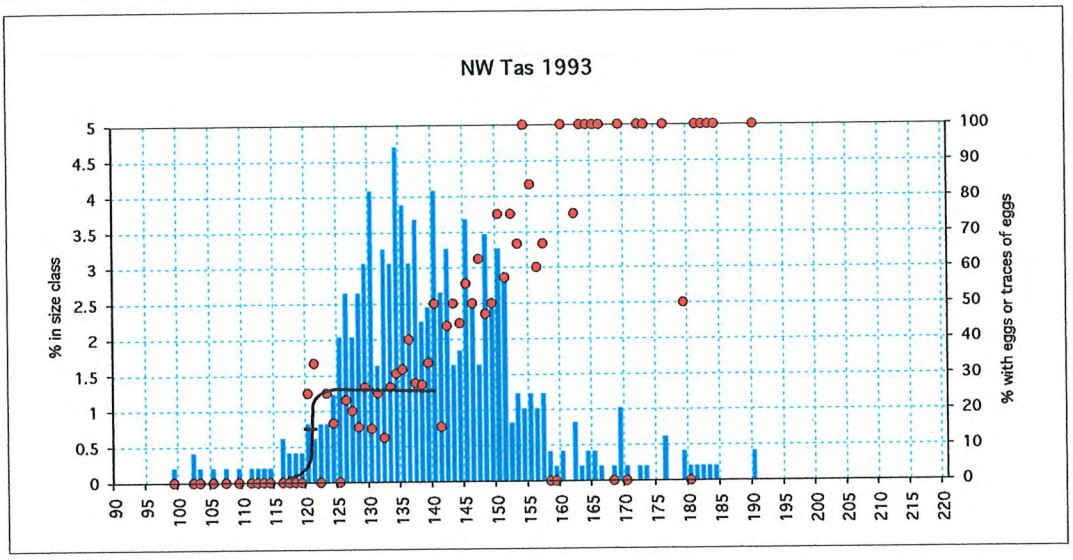


Figure 37p. Asymtote value = 45% Lm value midway between asymtote and X axis is 130 mm

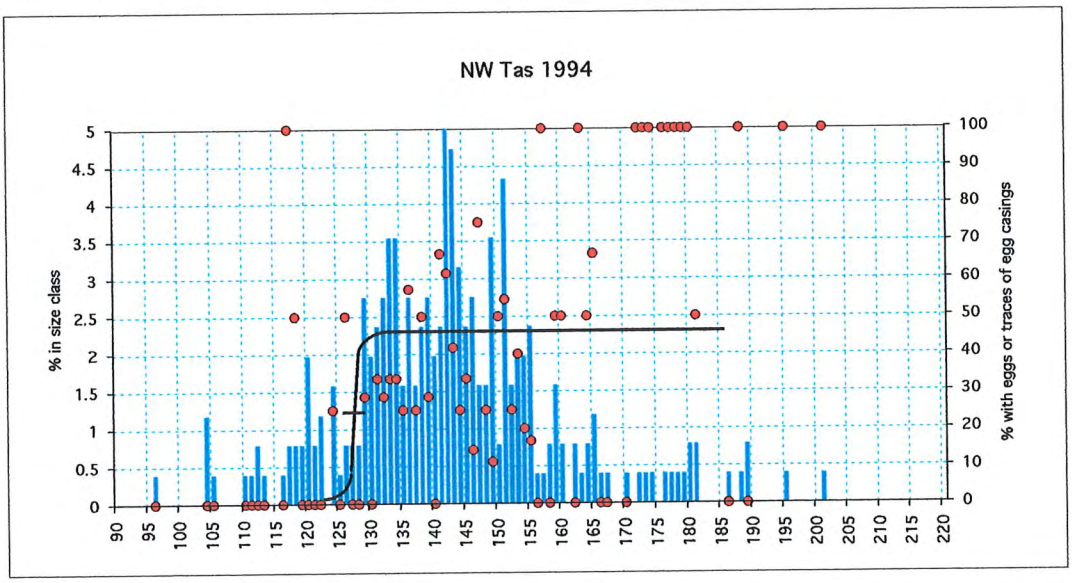


Figure 37q. Asymtote value = 47% Lm value midway between asymtote and X axis is 127 mm

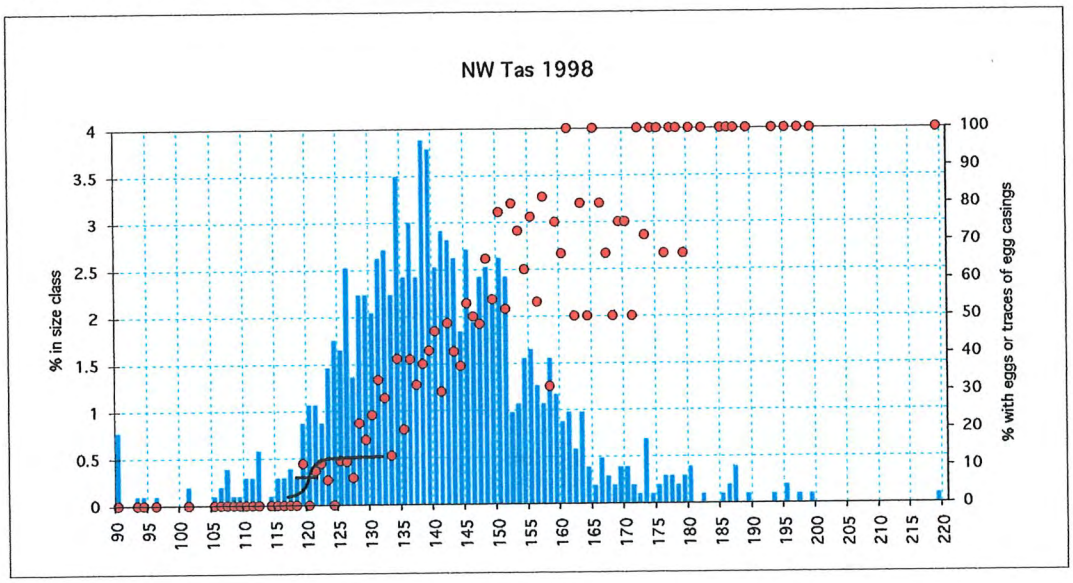


Figure 37r. Asymtote value = 10% Lm value midway between asymtote and X axis is 120 mm

Figure 37p.-r. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

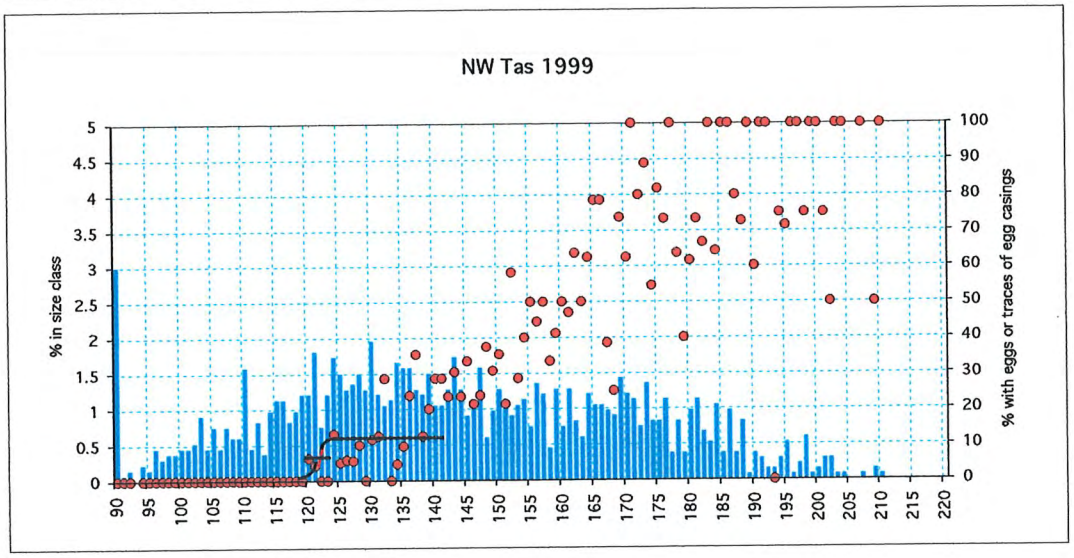


Figure 37s. Asymtote value = 12% Lm value midway between asymtote and X axis is 122 mm

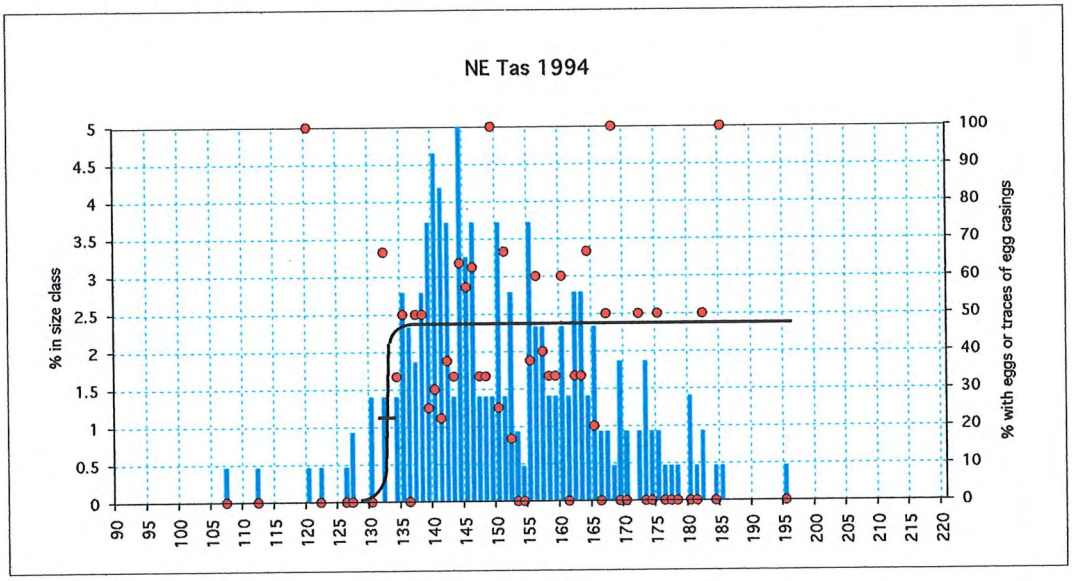


Figure 37t. Asymtote value = 48% Lm value midway between asymtote and X axis is 133 mm

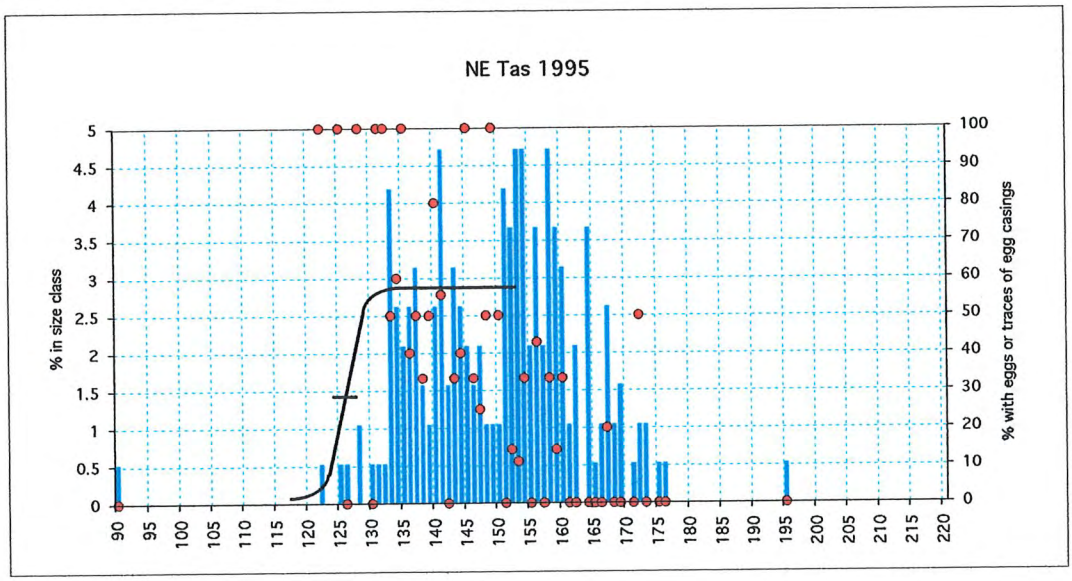


Figure 37u. Asymtote value = 58% Lm value midway between asymtote and X axis is 126 mm

Figure 37s.-u. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

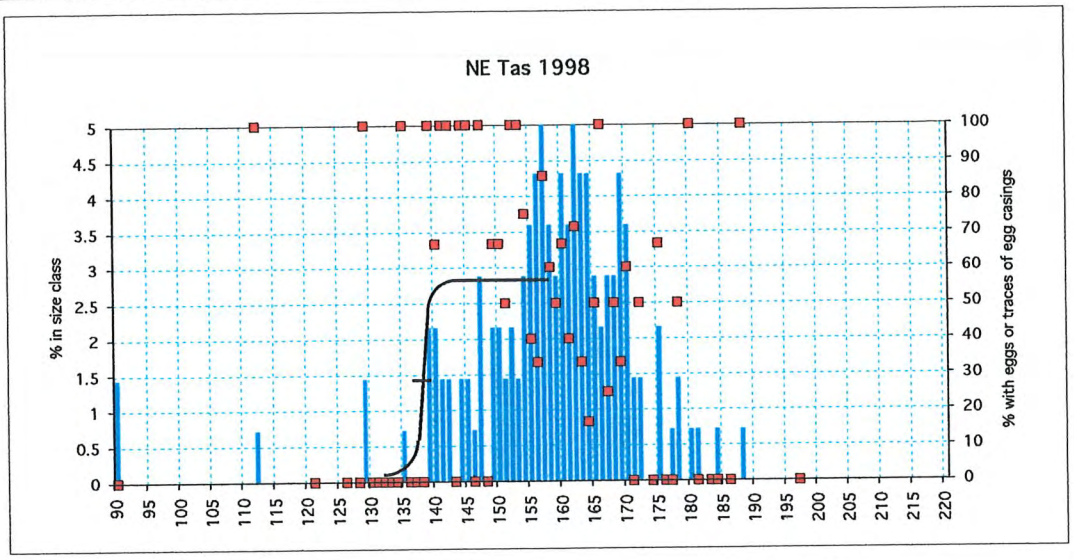


Figure 37v. Asymtote value = 58% Lm value midway between asymtote and X axis is 137 mm

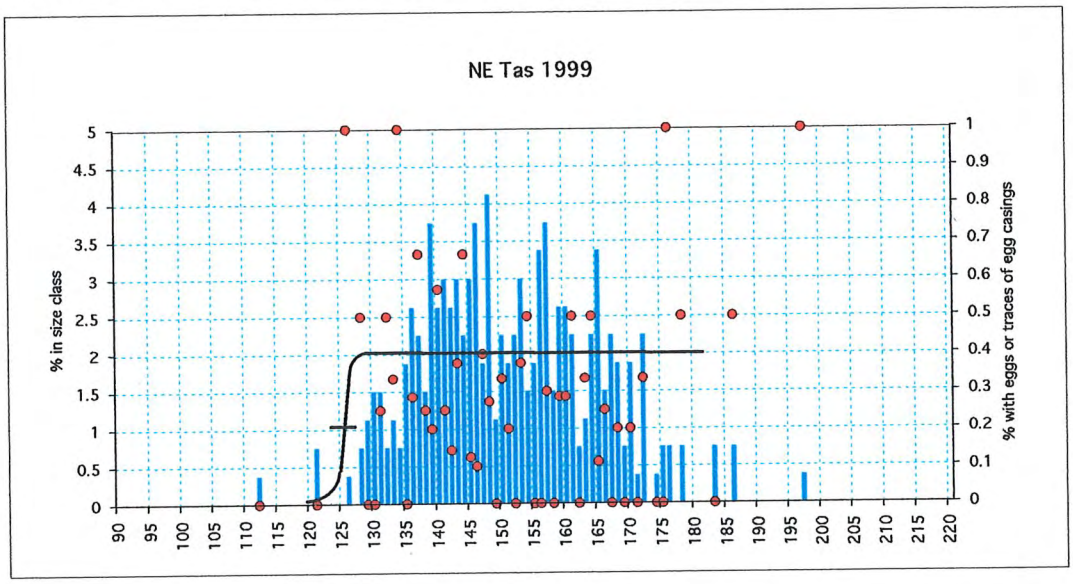


Figure 37w. Asymtote value = 40% Lm value midway between asymtote and X axis is 125 mm

Figure 37v.-w. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

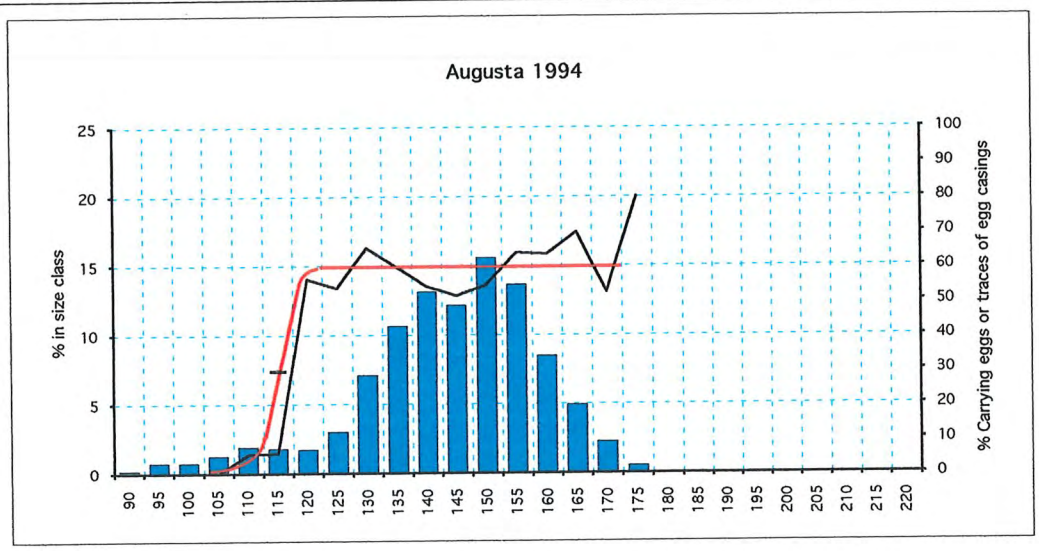


Figure 38a. Asymtote value = 60% Lm value midway between asymtote and X axis is 115 mm

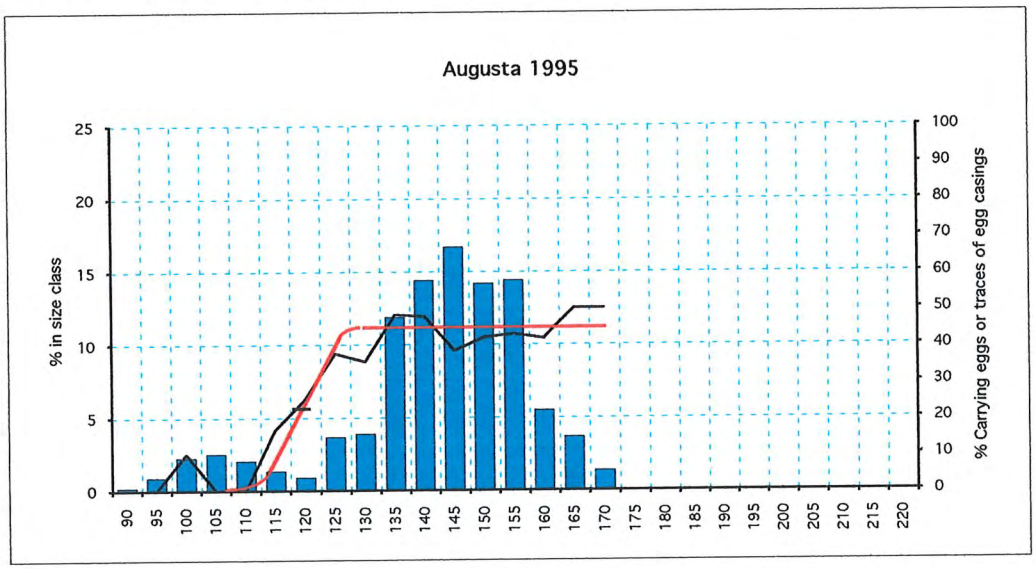


Figure 38b. Asymtote value = 45% Lm value midway between asymtote and X axis is 120 mm

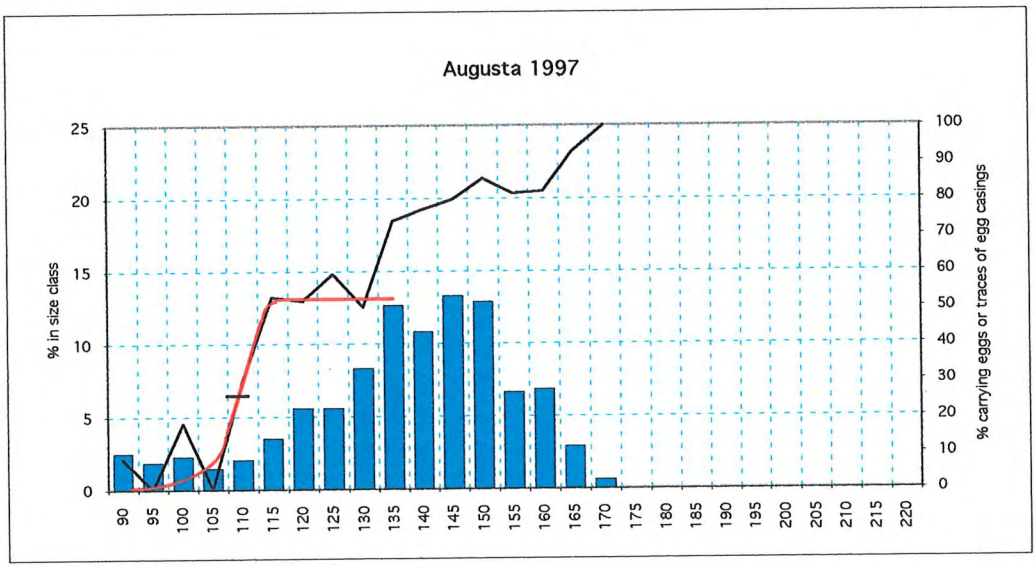


Figure 38c. Asymtote value = 53% Lm value midway between asymtote and X axis is 110 mm

Figures 38a.-c. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

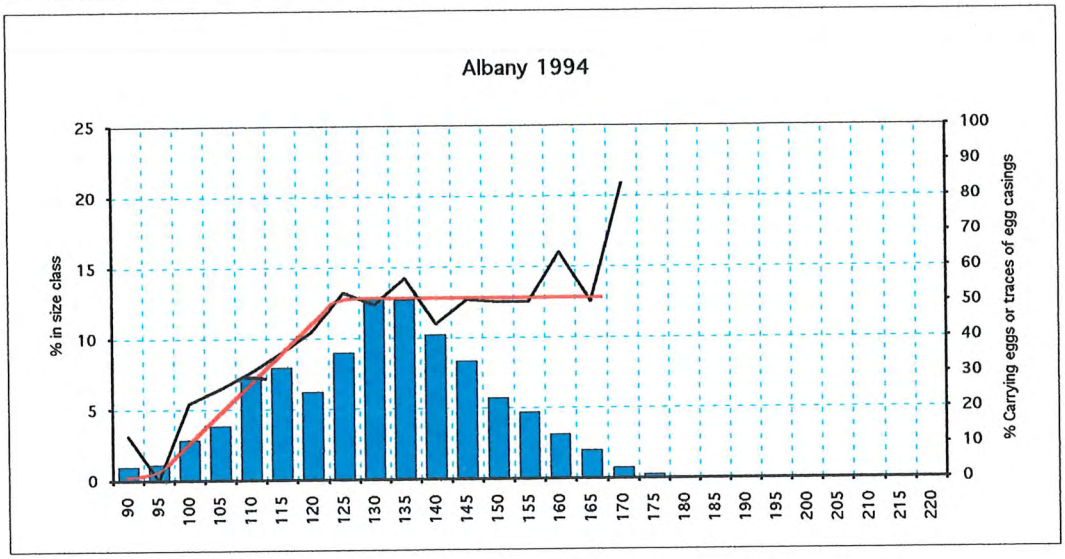


Figure 38d. Asymtote value = 51% Lm value midway between asymtote and X axis is 110 mm

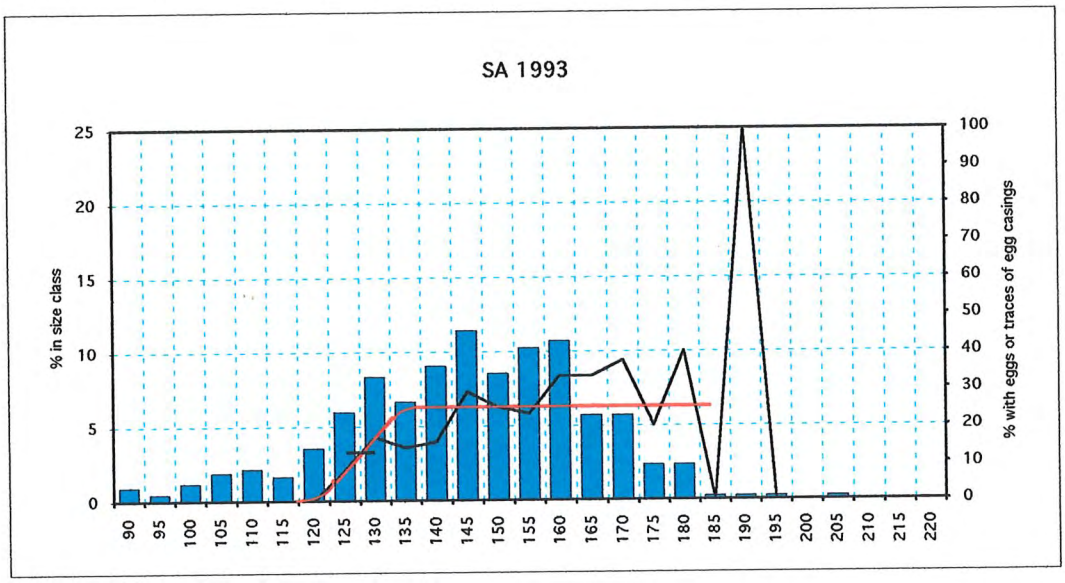


Figure 38e. Asymtote value = 25% Lm value midway between asymtote and X axis is 130 mm

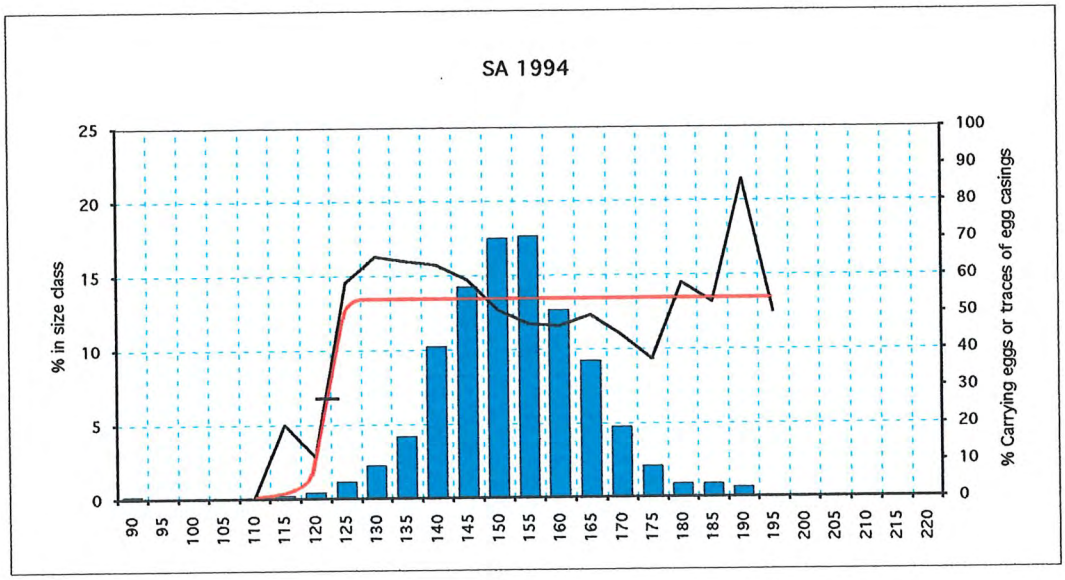


Figure 38f. Asymtote value = 55% Lm value midway between asymtote and X axis is 120 mm

Figure 38d.-f. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

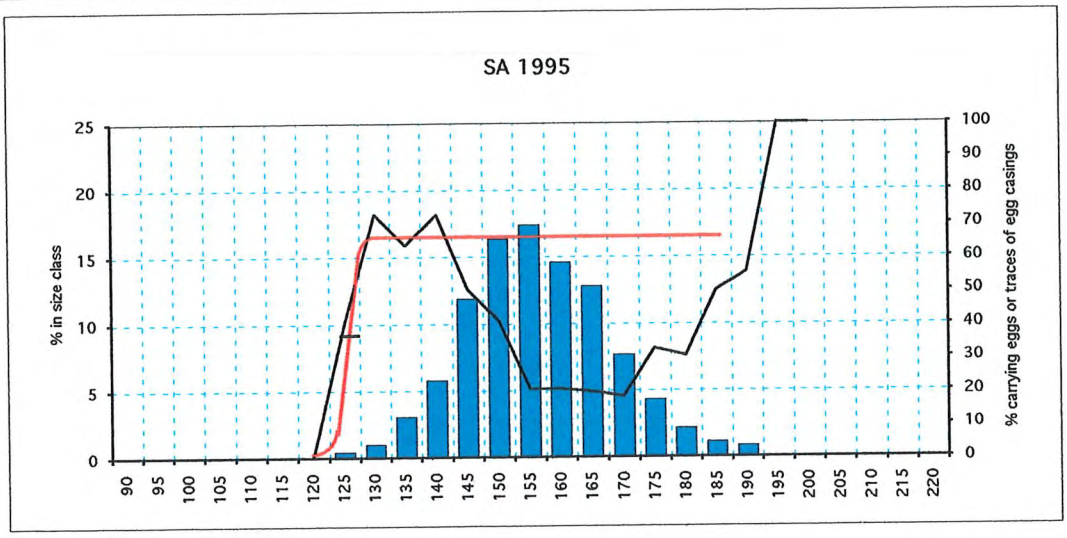


Figure 38g. Asymtote value = 68% Lm value midway between asymtote and X axis is 125 mm

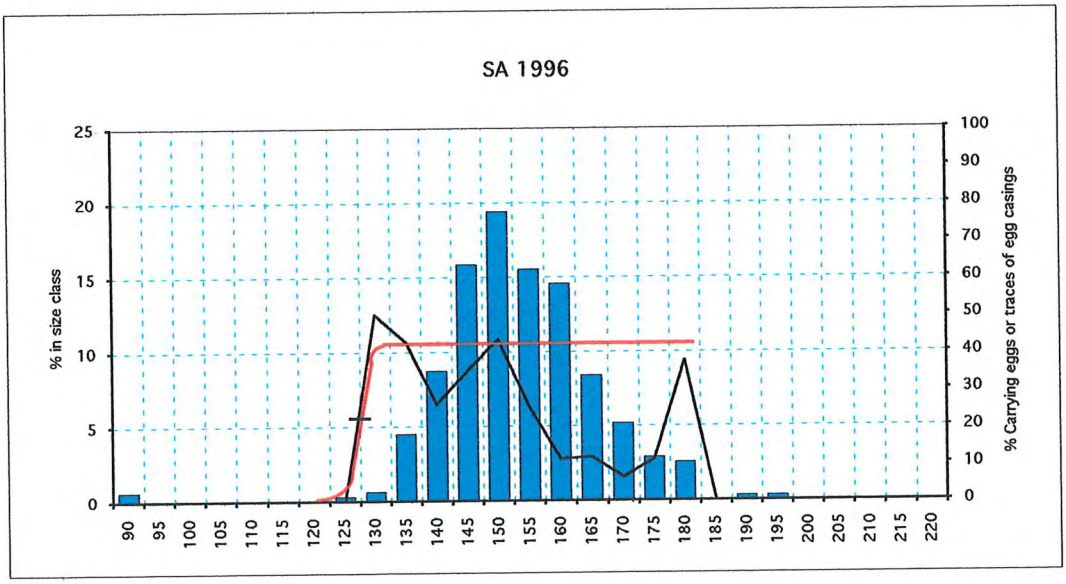


Figure 38h. Asymtote value = 44% Lm value midway between asymtote and X axis is 130 mm

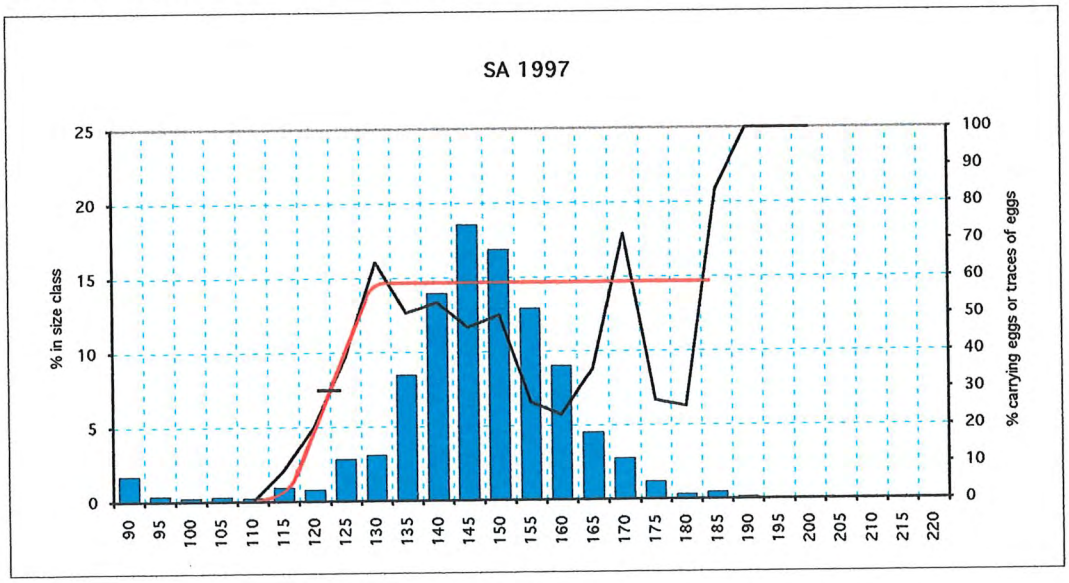


Figure 38i. Asymtote value = 59% Lm value midway between asymtote and X axis is 125 mm

Figure 38g.-i. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

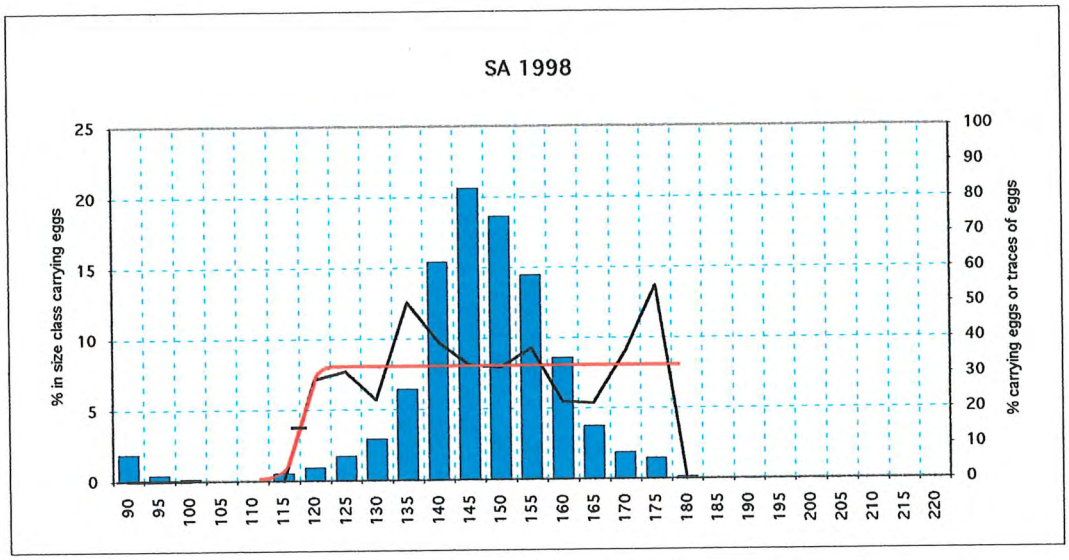


Figure 38j. Asymtote value = 32% Lm value midway between asymtote and X axis is 120 mm

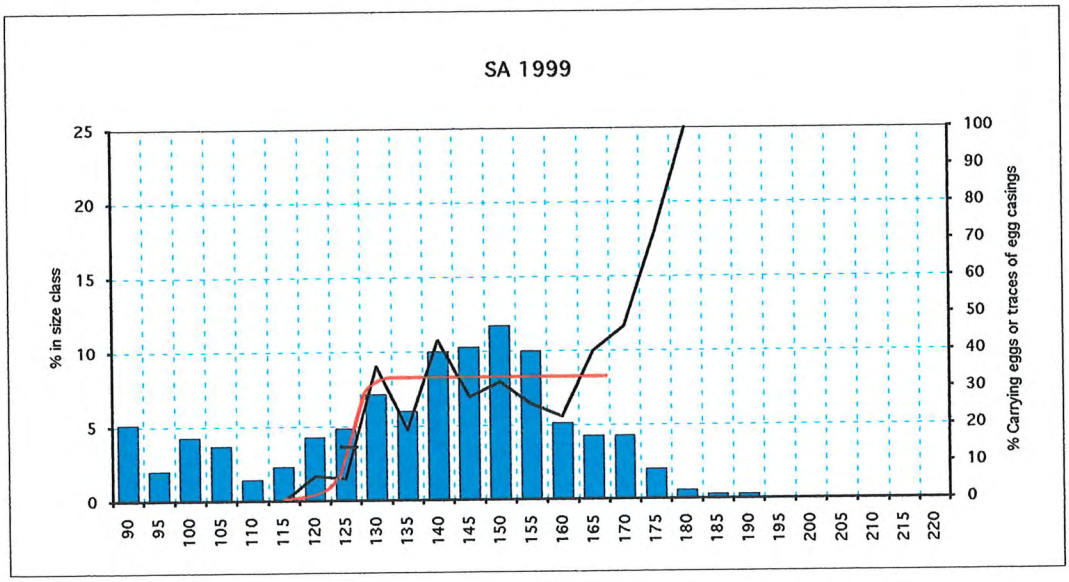


Figure 38k. Asymtote value = 33% Lm value midway between asymtote and X axis is 125 mm

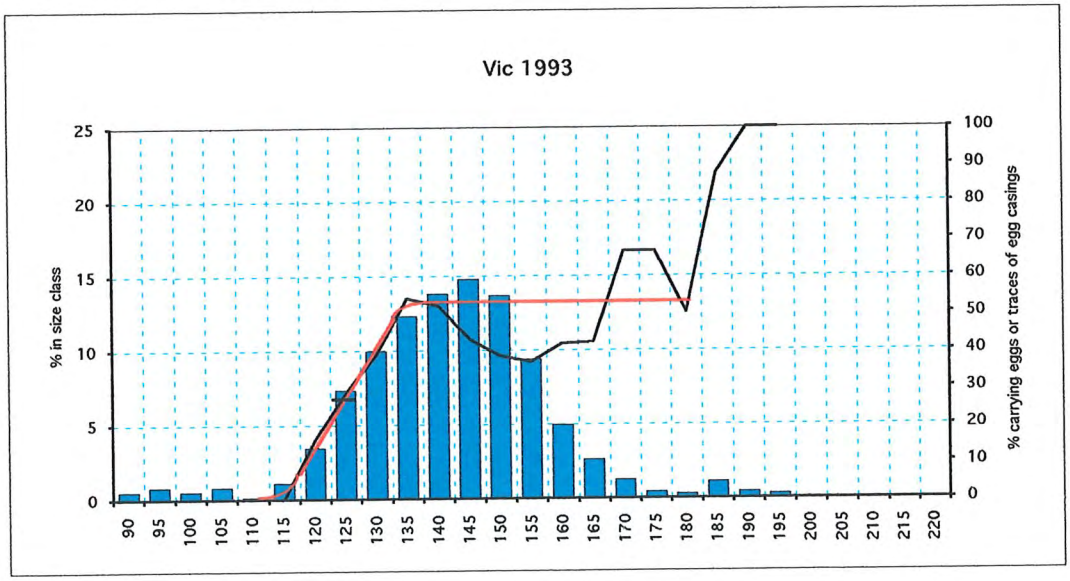


Figure 38l. Asymtote value = 53% Lm value midway between asymtote and X axis is 125 mm

Figure 38j.-l. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

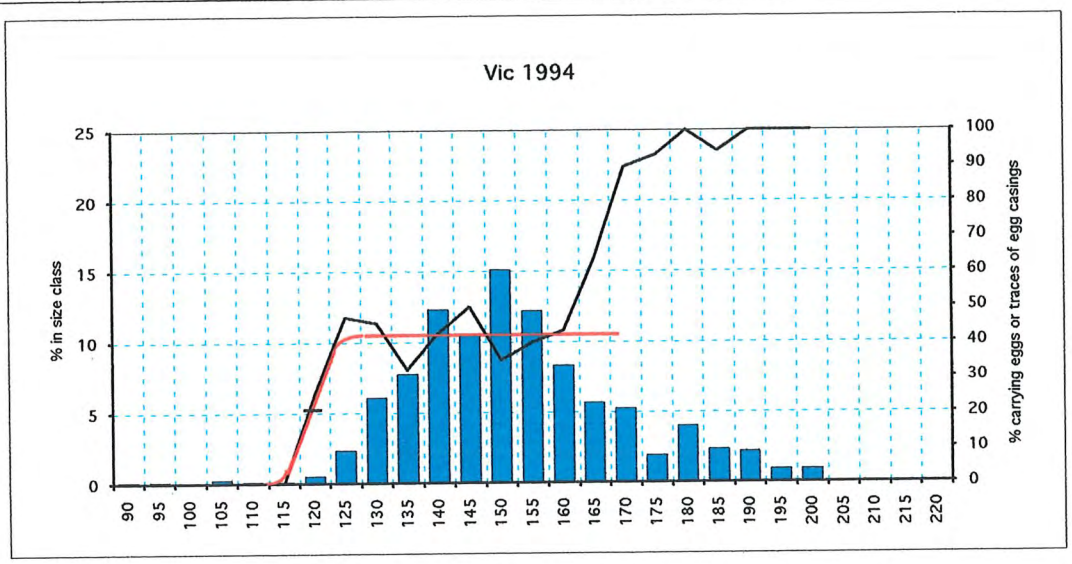


Figure 38m. Asymtote value = 43% Lm value midway between asymtote and X axis is 120 mm

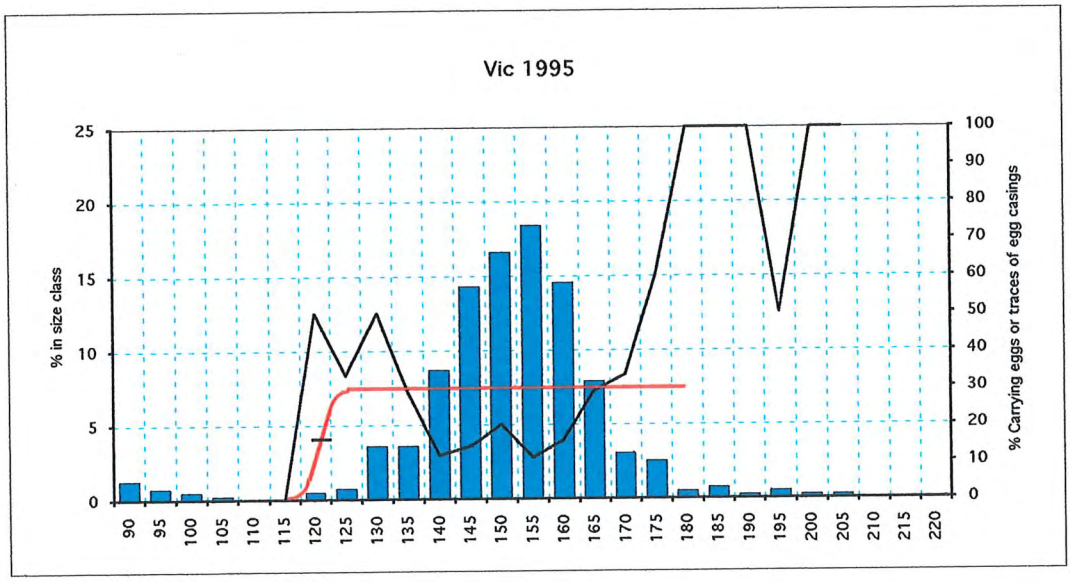


Figure 38n. Asymtote value = 30% Lm value midway between asymtote and X axis is 120 mm

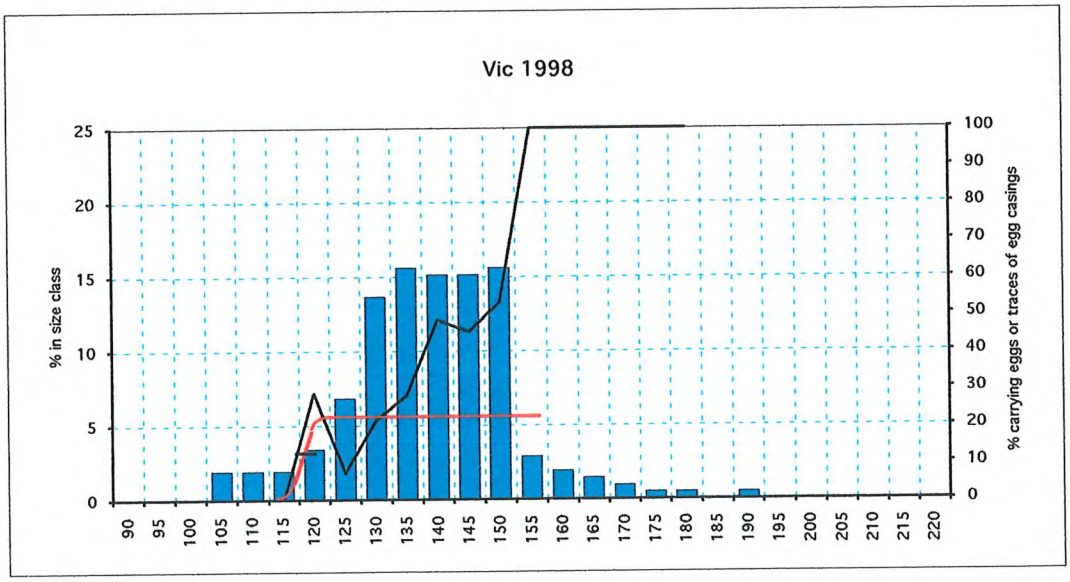


Figure 38o. Asymtote value = 22% Lm value midway between asymtote and X axis is 120 mm

Figure 38m.-o. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

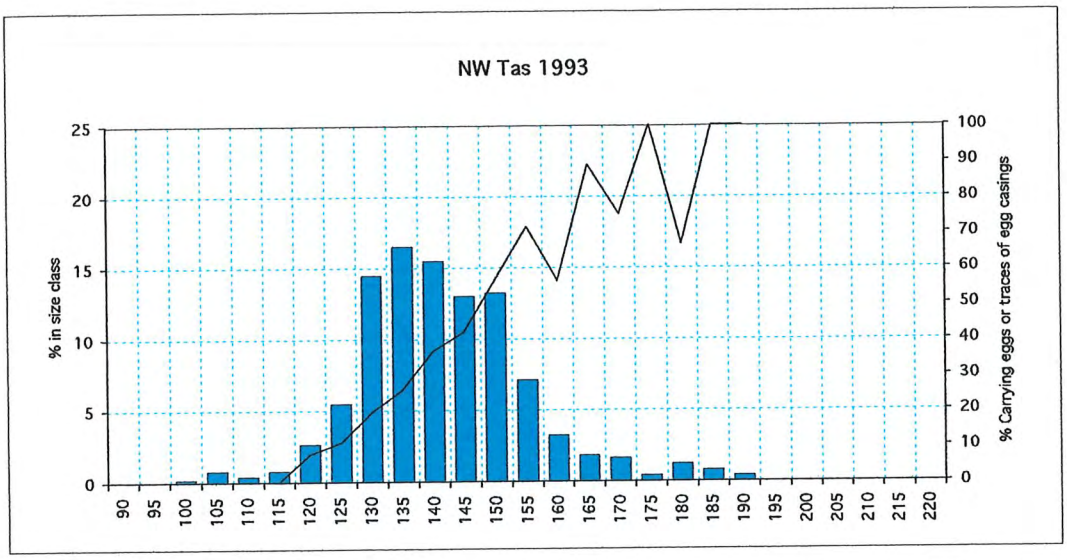


Figure 38p. Asymtote value undetermined Lm value established by using 1mm size classes and is 130 mm

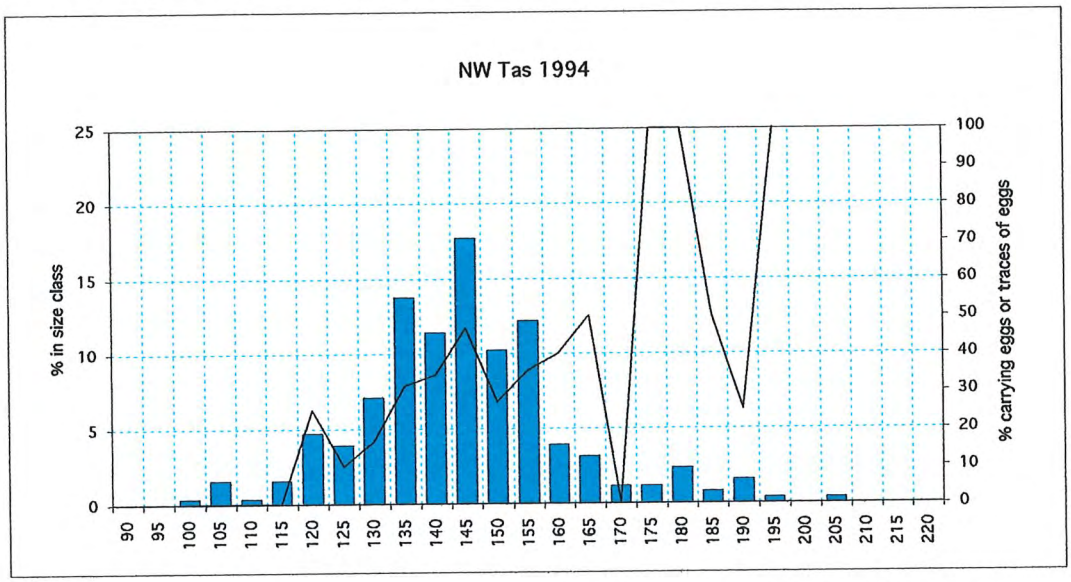


Figure 38q. Asymtote value undetermined Lm value established by using 1mm size classes is 127 mm

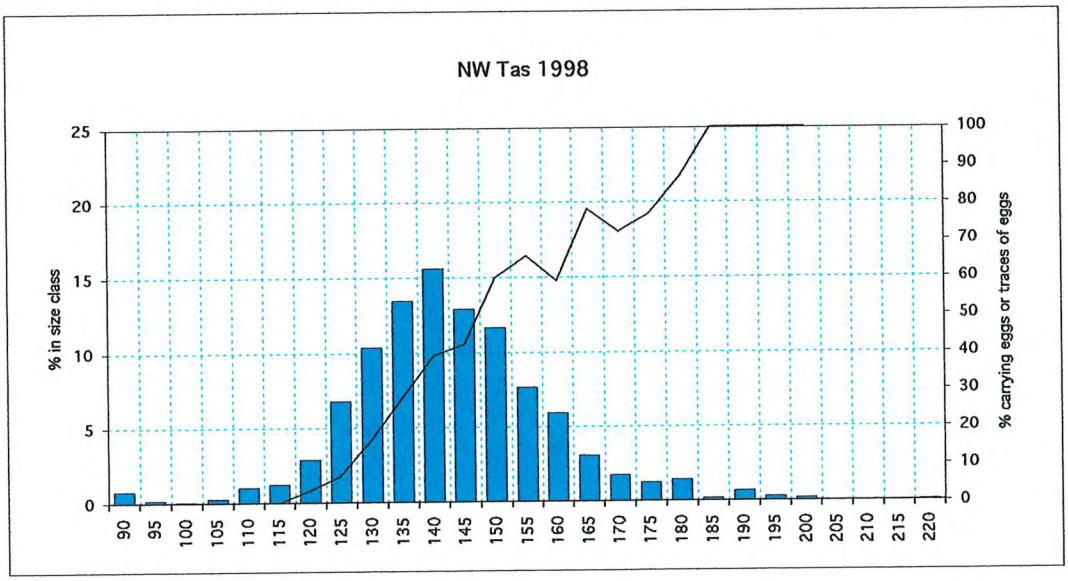


Figure 38r. Asymtote value undetermined Lm value established by using 1mm size classes is 120 mm

Figure 38p.-r. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

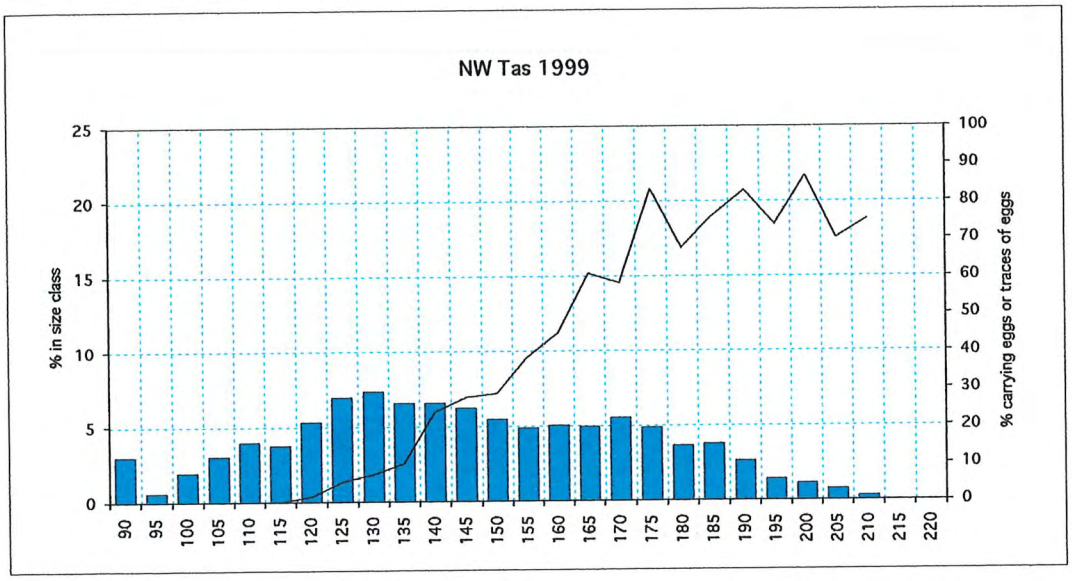


Figure 38s. Asymtote value undetermined Lm value established by using 1mm size classes is 120 mm

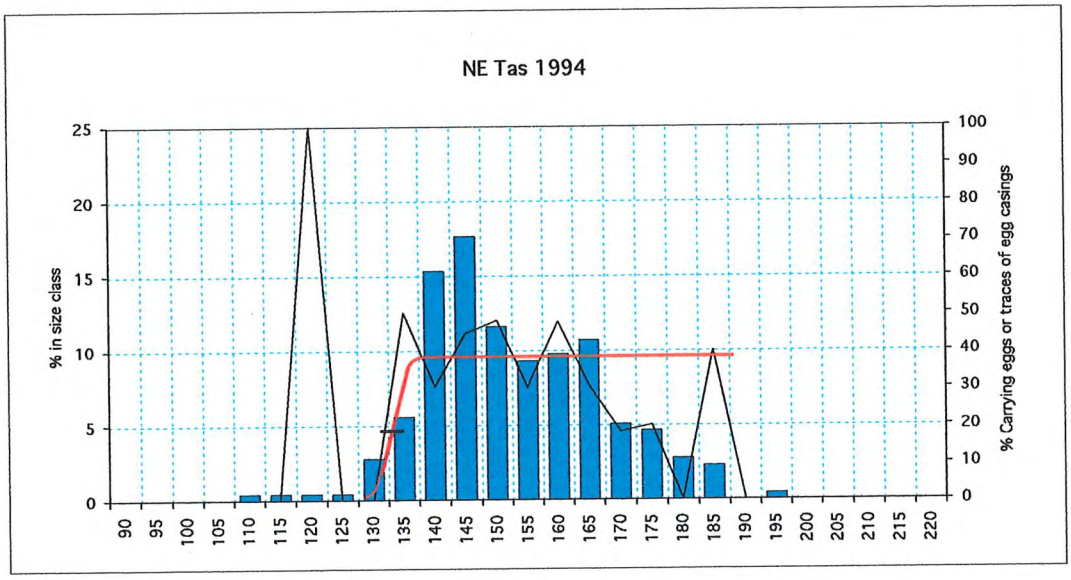


Figure 38t. Asymtote value = 38% Lm value midway between asymtote and X axis is 130 mm

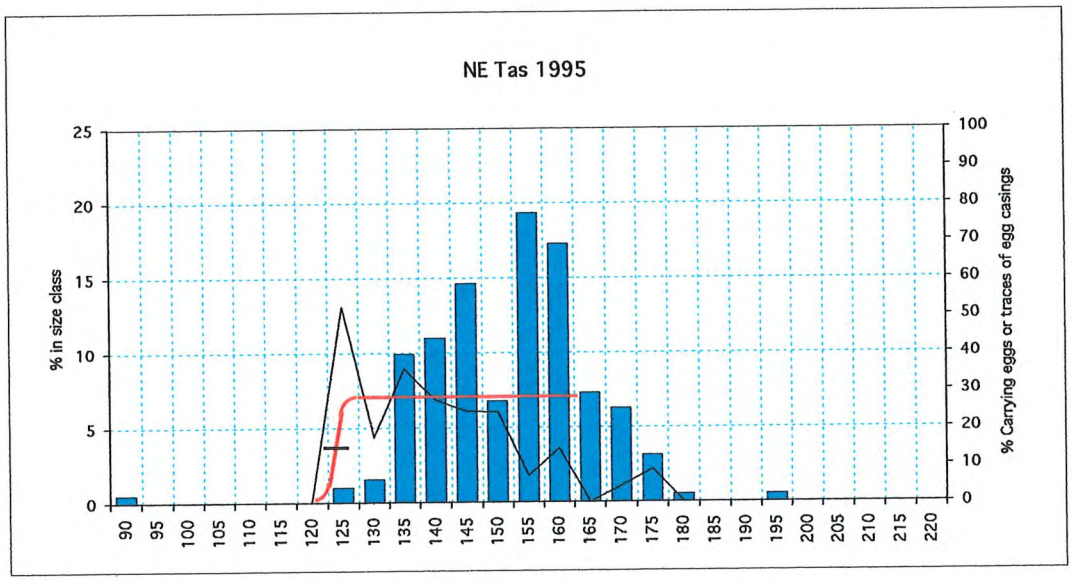


Figure 38u. Asymtote value = 28% Lm value midway between asymtote and X axis is 125 mm

Figure 38s.-u. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

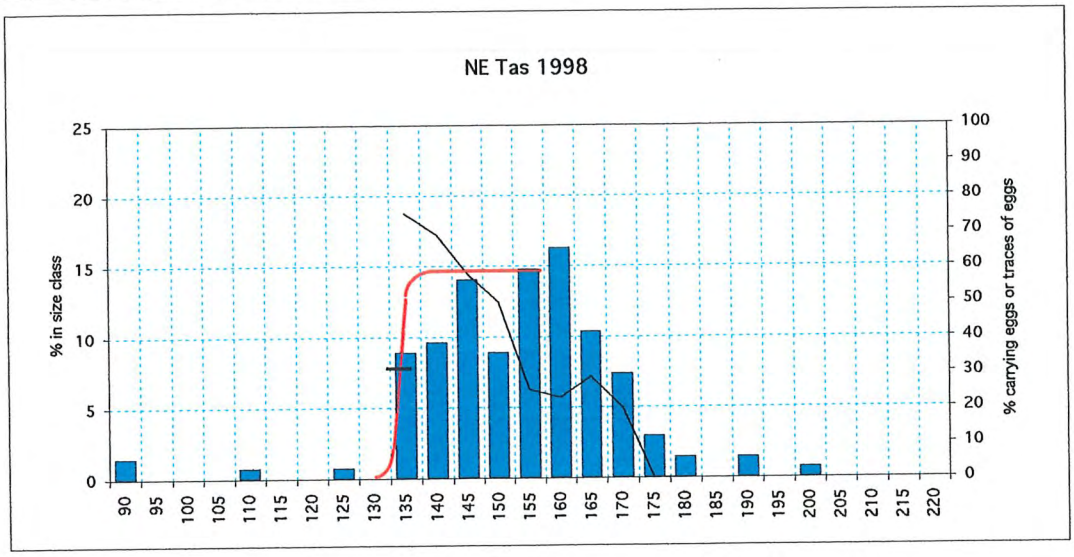


Figure 38v. Asymtote value = 60% Lm value midway between asymtote and X axis is 135 mm

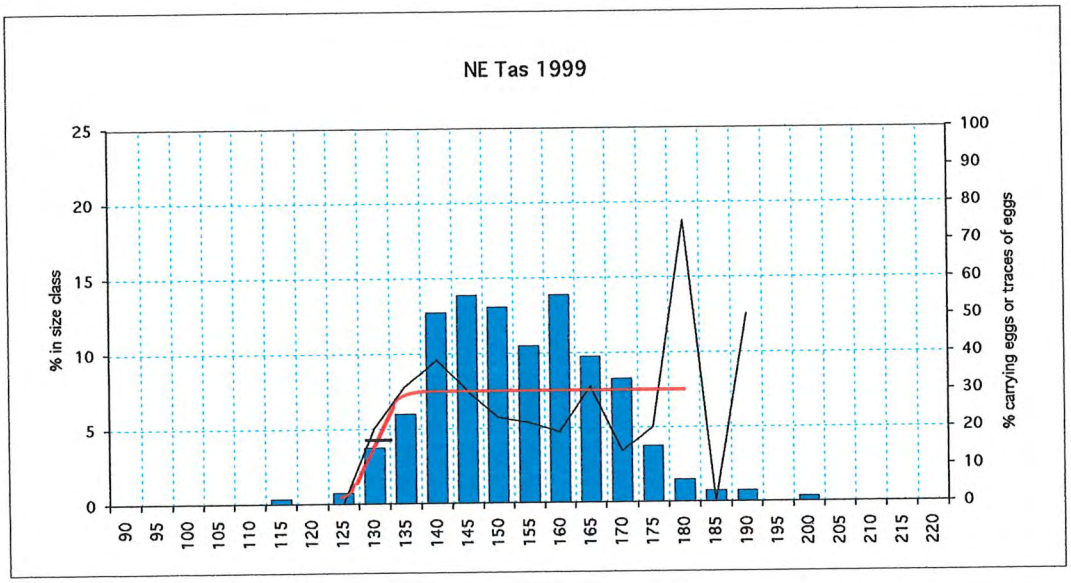


Figure 38w. Asymtote value = 30% Lm value midway between asymtote and X axis is 130 mm

Figure 38v.-w. Percentage of crabs carrying eggs or egg traces per size class (y2 axis). y1 axis is size class expressed as a % of total population. X axis is carapace length (mm)

Northwest Tasmanian sampling as illustrated in the 5mm series of figure 38p and q occurred in the years 1993 and 1994. The effect of fishing prior to the 150 mm minimum size regulation grossly affected the proportion of non berried to berried females across smaller size classes. Also the population distribution in 1994 was taken in shallower water than that of 1993 as the deeper water held few crabs above the newly introduced legal minimum length. Sampling in 1998 (figure 38r) showed little had changed, the absence of an accumulated egg bearing population below the size limit indicative that undersized were still being taken. The 1999 sample (figure 38s) showed a similar result in the same area, but the broader size distribution is derived from the inclusion of data from a more southerly site fished late in the survey. There were insufficent sized crabs available closer to the Victorian border to recover the costs of the survey, hence the shift to the more southerly location.

Off north east Tasmania (see figure 38t, u, v, w; 5mm resolution) a pattern of declining fecundity with size is evident. The ratio of males to females in this area is much lower than all other sites and so there will be less opportunity for moulting females to mate. As the crabs grow larger moult frequency (and so mating frequency) becomes less, sperm reserves become limited and are manifest in the decline in fecundity with increasing size.

All eastern Australian samples except east Tasmania showed the same trend of a higher proportion of egg bearing females in the larger but less abundant section of the population, usually in size classes larger than 170 mm. These larger size classes are rarely observed in western Australia and initial indications are that the less than favorable environment has limited growth. This manifests as smaller moult increments up to 170 mm, and with increasing age the inability to survive the moult into sizes larger than 170 mm.

Four major patterns were evident in the data.
1) In stocks from South Australia, the percentage of egg bearing females reached a peak within the range of 50 to 75% in the smaller size classes and then declined to within the range of 20 to 50% in the mid to larger size classes in 1994 and then further to between 10 to 35% in 1995 and 1996. The decrease in the middle size classes with large numbers of animals sampled is attributed to the effects of fishing down the population above the minimum size of 150mm. The percentage of egg bearing females increased in the largest size classes but the numbers of crabs in these groups were low and variability was high.
2) In Victoria, the pattern was similar to 1 above except that the initial peak in percentage of egg bearing females (40 to 55%) was lower, the dip in the mid size classes was less pronounced but the range of values at the low point of the dip (10 to 35%) was approximately the same. Victoria was heavily fished in 1992 and 1993 prior to the introduction of the 150 mm minimum size. During this period maximum catches were obtained by fishing the section of the population which although made up of smaller sized crabs yielded the most weight. The percentage of egg bearing females in larger size classes increased and sample sizes in these classes were larger than those obtained in South Australia.
3) In stocks from Augusta, Albany and north west Tasmania, the percentage of egg bearing females reached an asymptote within the range of 45 to 75%, with a slight degree of variability evident in the larger size classes. The latter was most likely due to the low numbers of animals sampled in the larger size classes.

4) In east Tasmania, the percentage of egg bearing females reached a peak of 35 to 50% in the smaller size classes and then declined to less than 20% in the mid to larger size classes. The east Tasmania pattern contrasted markedly with that of north west Tasmania and is further discussed in hypothesis 3 below. The trend towards declining percentages of egg bearing females in larger size classes and the occurrence of asymptotic values less than 100% have both been reported elsewhere (Wenner et al, 1974, and Hoggarth, 1993).

The patterns described above represent interactions between fundamental features of reproductive biology, occurrence, behavior and fishing history. Several hypotheses may be advanced to account for the patterns observed . These include:

1)The asymptote at less than 100% reflects the moult-spawn cycle of females in that females do not spawn in years when they moult (see above). Gardner, (1997) noted a tendency in *P. gigas* towards declining fecundity between successive clutches. If sperm reserve depletion was a limiting factor it would be an advantageous strategy to reduce clutch size to optimize future survival rather than risk mortality during moulting (Begon and Parker 1986). As the reduced frequency of moulting in larger size classes is accompanied by reduced mating then the probability that a female will be carrying eggs will decrease, the probability of a female not being in berry increases and consequently the rapid fall off from a sigmoidal distribution of egg bearing females would occur.

2) If females only mate with males larger than themselves, but there is a low abundance of large males (east Tasmania) then egg output in larger female size classes may be reduced. The low number of potential mates available for larger females combined with increased intermoult period may result in an exhausted sperm reservoir and may mean that during some years females neither moult nor spawn. This may explain the difference between west and east Tasmania. In east Tasmania the proportion of males in the population is noticeably lower than elsewhere.

3) Some larger females may become senescent and reproductive output may decrease. Gardner (1997) has shown a slight decline in fecundity of larger females that may reflect sperm limitation (see above) or could indicate that large females undergo reproductive senescence. Although they appear not to undergo a terminal reproductive moult, there is difficulty in establishing age classes within instars.

4) The introduction of the interim legal minimum size had implications for populations with a history of fishing and where numbers of larger females have been reduced. Larger females above the interim legal minimum size which were in intermoult and likely to spawn in the next spring were caught. Newly moulted and smaller females, unlikely to spawn until the following spring, moved into the area from which the previous residents had been caught.

Based upon the analysis of the percentage of egg bearing females in different length classes by population, average size at sexual maturity (Lm) and minimum size at sexual maturity (Lsm) were determined and are summarised in table 13 below.

Table 13: Size at sexual maturity. Values obtained using 1mm and 5mm size classes are listed

Site	Year	% Ovig at asymtote		Lm		Lm Average	
		1mm	5mm	1mm	5mm	1mm	5mm
WA (Augusta)	1994	60	60	117	115		
	1995	50	45	117	120		
	1997	75	53	111	110		
WA (Albany)	1994	35	51	102	110	**112**	**114**
SA	1993	35	25	127	130		
	1994	68	55	122	120		
	1995	62	68	128	125		
	1996	60	44	132	130		
	1997	30	59	123	125		
	1998	50	32	120	120		
	1999	40	33	126	125	**125**	**125**
Vic	1993	50	53	122	125		
	1994	48	43	122	120		
	1995	20	30	118	120		
	1998	50	22	126	120	**122**	**121**
NW Tas	1993	45	na	130	na		
	1994	47	na	127	na		
	1998	10	na	120	na		
	1999	12	na	122	na	**125**	**na**
NE Tas	1994	48	38	133	130		
	1995	58	28	126	125		
	1998	58	60	137	135		
	1999	40	30	125	130	**130**	**130**

The populations show a general trend of increasing Lm from west to east across southern Australia. Due to the manner in which Lm has been determined tests of significance cannot be performed on the data until a larger time series is available. Albany showed the smallest average size at maturity with a mean carapace length of 110 mm and north-west Tasmania showed the largest average size at maturity with a mean carapace length of 135 mm. There was also some suggestion of a similar west to east trend in Lsm across southern Australia. Lsm is not an indicator of female size at first mating because, as Gardner points out (1998), females may store sperm through moults and may not produce eggs until they have passed through one or more moults following first mating. For this reason, Lsm is unlikely to prove to be very useful for the management of *P. gigas*.

Based upon field observations the proposed reproductive cycle of female *P. gigas* is summarised in figure 39 below.

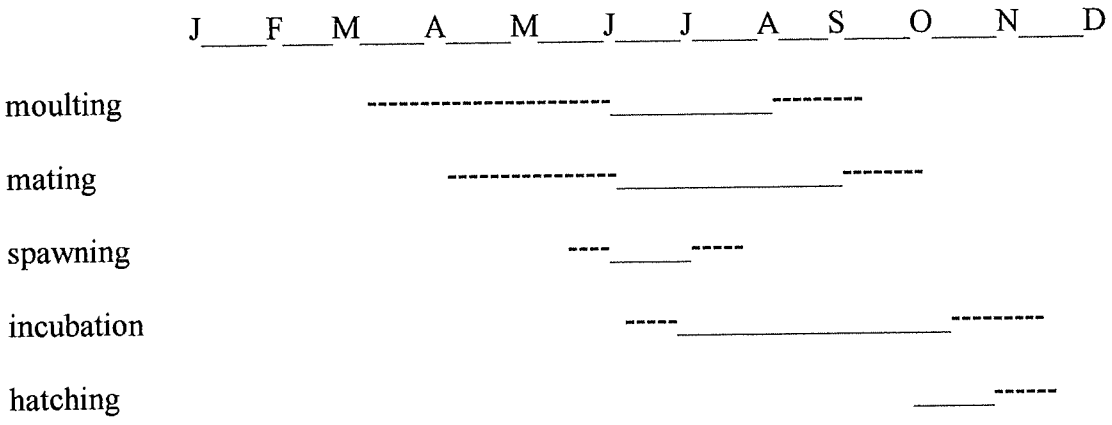


Figure 39. Proposed reproductive cycle of female *P. gigas*: Solid lines represent peak periods in the events listed, broken lines represent a low levels of these activities

4.5.5. Male size at sexual maturity

Preliminary analysis of pooled data across all states indicated a curvilinear relationship existed between chela length and carapace length. Chela length exhibited a positive allometry, with chela length increasing at almost twice the rate of carapace length as individual size increased. On closer inspection the chela length versus carapace length relationship (figure 40 below) was found to show linearity for smaller sizes below a point termed the break-point and curvilinearity above it with high R^2 values indicating a close fit between the observed data and each of the linear and curvilinear equations fitted to it. The equations were:

LINEAR: *Carapace length = m(chela length) + c,*

CURVILINEAR: *Carapace length =a(chela length)^b*

The values for *m, c, a* and *b*, together with the associated R^2 values for each of the states and an analysis of covariance are set out in the following tables 14 and 15.

Table 14. Allometric growth of largest male chela in relation to carapace length

State	*Less than or equal to break-point* *Carapace length =m(chela length)+c*			Break-point	*Greater than break-point* *Carapace length =a(chela length)^b*		
	m	*c*	*R2*	*Carapace length mm*	*a*	*b*	R^2
West Australia	1.15	-16.37	0.96	127	0.0011	2.41	0.86
South Australia	1.56	-61.22	0.88	141.6	0.0004	2.60	0.88
Victoria	1.19	-24.74	0.87	125.9	0.003	2.20	0.93
Tasmania	1.16	-18.10	0.98	142.4	0.0015	2.32	0.84

Table 15. Analysis of covariance above and below the break-point. Paired comparisons are made between states using $\log_{10}$ transformed carapace and claw lengths for male *Pseudocarcinus gigas*.

Comparison	Comparison (ANCOVA): P value*					
	≤ break point			> break point		
	slope	elevation	R^2	slope	elevation	R^2
SA x WA.	0.00	----	0.96	0.00	----	1.00
SA x Vic	0.00	----	0.92	0.00	----	1.00
SA x Tas.	0.02	----	0.94	0.57*	0.00	1.00
Tas x Vic	0.66*	0.00	0.94	0.00	----	1.00
Vic x WA.	0.00	----	0.96	0.00	----	1.00
Tas x WA	0.10*	0.00	0.99	0.00	----	1.00

1: OBL (**orbital** carapace length, mm)
CL, (**claw** length, mm)
* not significant (P>0.05)

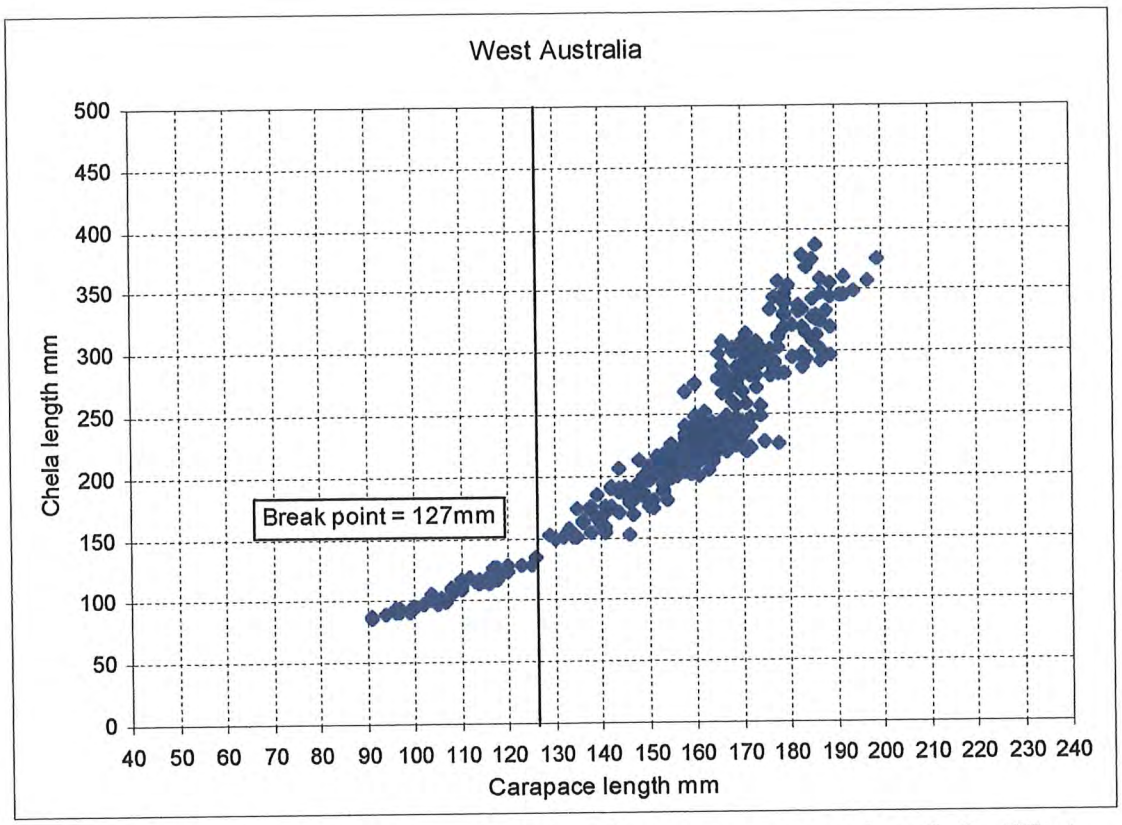


Figure 40a. Scattergram of large chela length versus carapace length for West Australia.

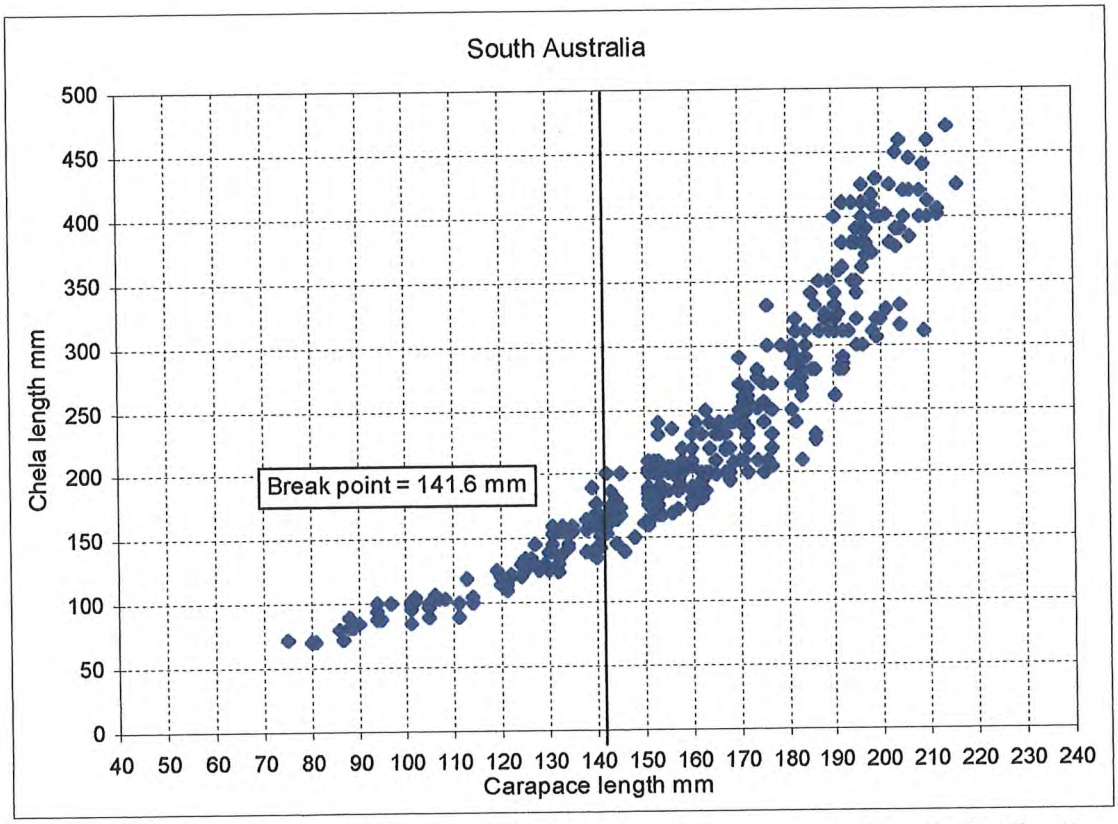


Figure 40b. Scattergram of large chela length versus carapace length for South Australia.

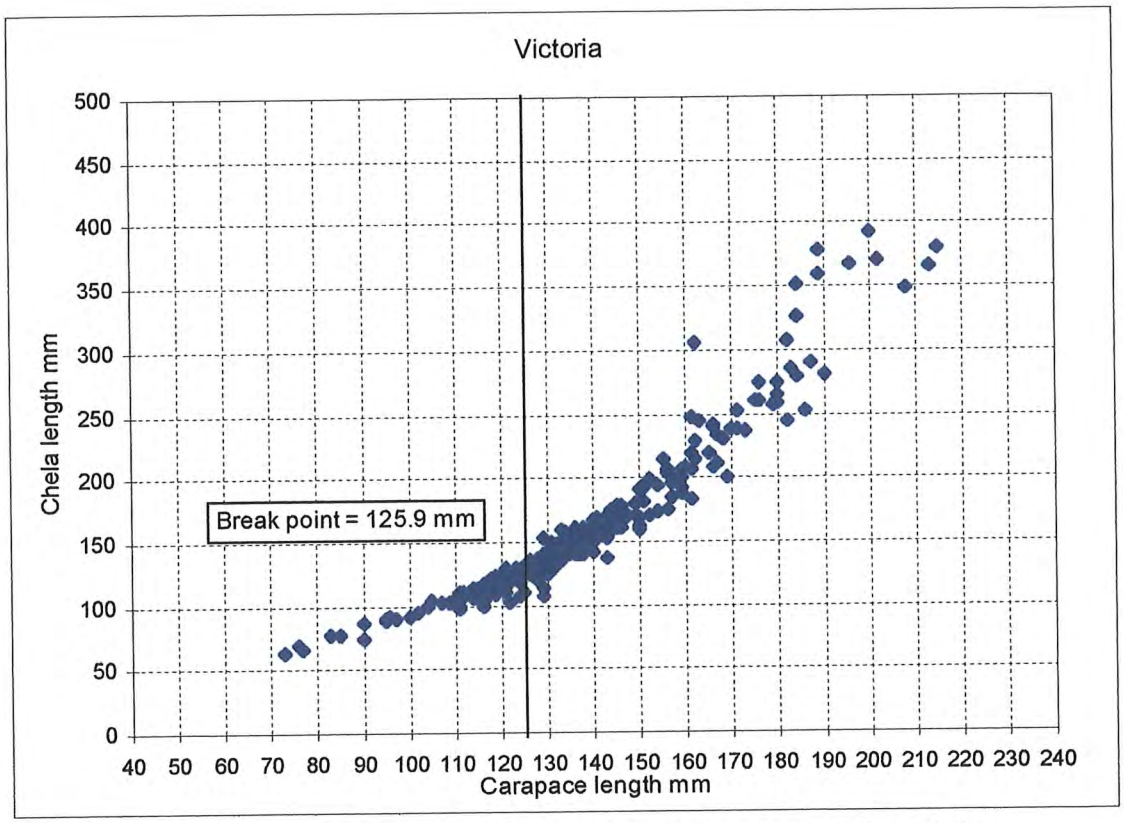


Figure 40c. Scattergram of large chela length versus carapace length for Victoria.

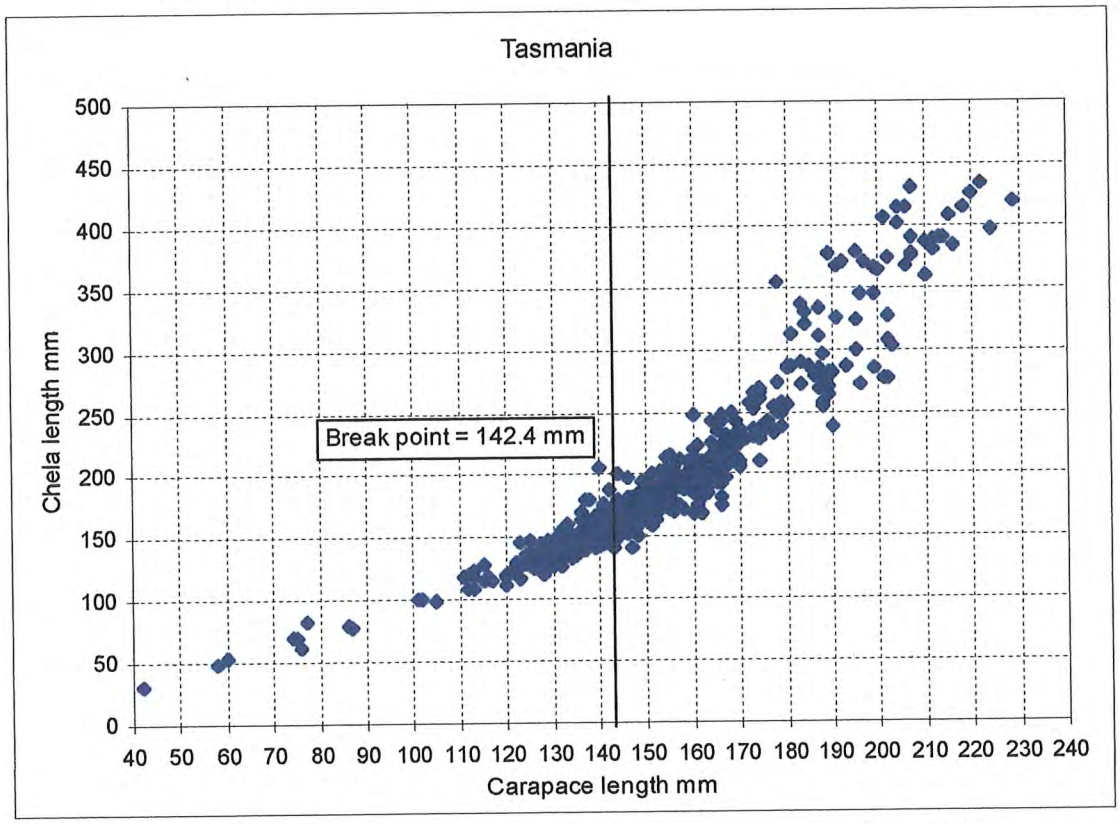


Figure 40d. Scattergram of large chela length versus carapace length for Tasmania.

Unlike the trend in the values observed for the average size at maturity of females (Lm), where Lm occurred at smaller sizes off West Australia compared to larger sizes off Tasmania, there was no corresponding pattern observed in the breakpoint analysis of chela growth for males.

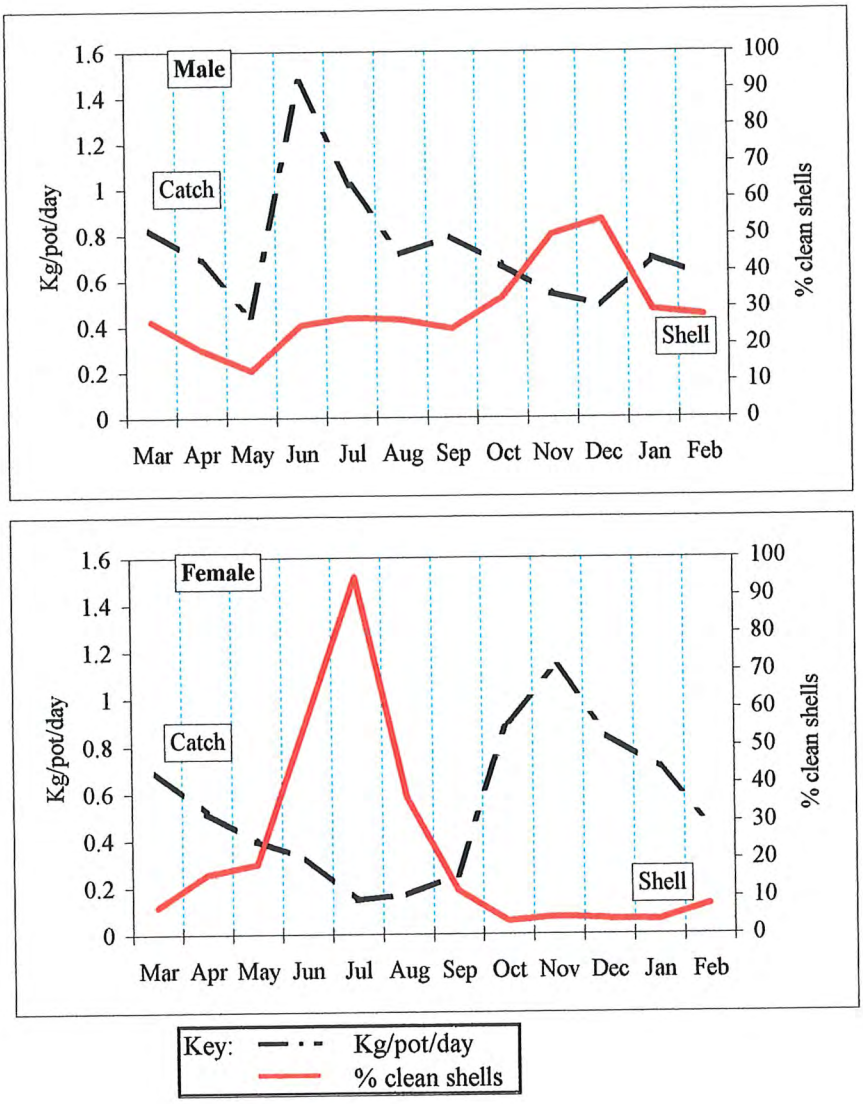
It should be noted that the breakpoint lies below the legal minimum lengths (LML's) for the states, ie:-
The West Australia break point is 127mm *cf* the LML of 140mm,
The South Australia breakpoint is 141.6mm *cf* the LML of 150mm,
The Victorian breakpoint is 125.9mm *cf* the LML of 150mm,
The Tasmanian breakpoint is 142.4mm *cf* the LML of 150mm,

Gardner (1998) also studied the morphology of the large chela and the reproductive tract in relation to carapace length from Tasmanian samples and despite a wide spread of values was able describe three groups, which after he "morphologically immature", "morphologically adolescent" and "morphologically adult" (*after* Comeau and Conan, 1992) Similar groupings were observed by this study from other regions and are probably representative of 3 consecutive moult classes. However the terminology "immature", "adolescent" and "adult" is misleading (Sainte Marie *et. al.* 1995) and has since been misinterpreted by others such as Zacharin & Ward, 2000, who said *"there is evidence that only large males mate successfully"*. Gardner (1998) found that all "immature" males greater than 90mm carapace length contained numerous well-formed spermatophores, thus "morphologically immature" are also "physiologically mature" and commented *"Without direct measures of mating it is not possible to ascribe definatively the maturation of P. gigas-----."*

Worldwide, the use of morphological indices for assessing maturity is controversial Gardner, 1998; Sainte Marie *et. al.* 1995; Paul 1992; Comeau and Conan, 1992). Although our analysis of allometry shows regional differences, the lack of observations of mate selection and behavioral interactions in the wild make it difficult to form conclusions about the significance of this analysis. Tank observations show the chela is used in shield display rituals, but in the wild *P gigas* occurs at depths where there is minimal to zero light penetration ($\approx$ 1% at 200m, Anderson, 1994.) and so the question arises as to whether the display is visible to another crab. Nonetheless there is obviously an ability to locate a mate in this dark province.

Our population studies have shown the presence of the middle-sized (*"morphologically adolescent"*) and larger (*"morphologically adult"*) groups of males at the edge of the shelf break where most of the females occur, in the Autumn.
In the winter as the catchability of females declined to an annual minimum, circumstantial evidence indicated mating occurred while the females were soft shelled in the deeper waters of the upper bathial slope. The middle and larger sized groups of males were present at the same locality where most newly moulted females were observed.

Therefore we propose these are the functionally mature section of the population, but recognize that the onset of functional maturity is likely to be a dynamic relationship that can change according to the population structure and mating hierarchy. Variability is to be expected in the middle sized group due to innate individual differences and post puberty mating dynamics reflected in each crab's development.



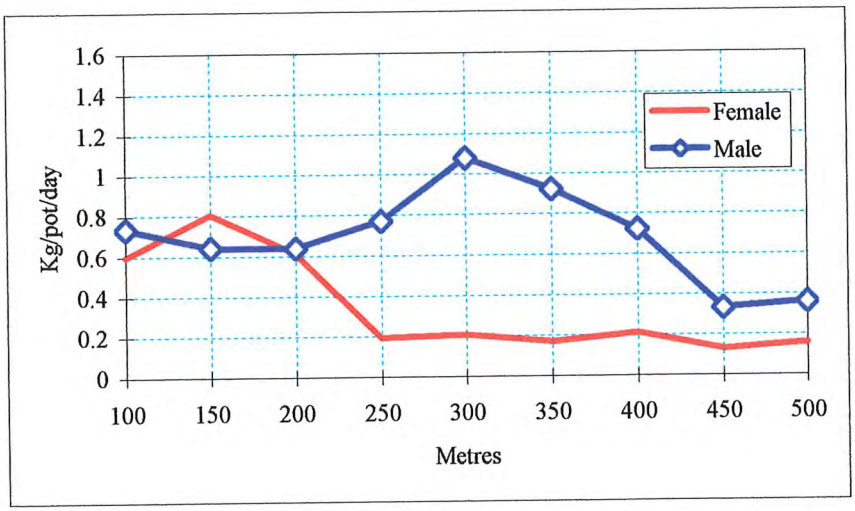


Figure 41. Circumstantial evidence indicates that mating occurs while the females are soft shelled on the mud of the upper bathial slope. Female catch rates are low in the winter but the incidence of clean shells is at its annual peak. Elevated catch rates of the middle and larger size groups of males are taken in the same depth and location at this time.

4.6. Moult Staging

Sub stages within each moult stage were not determined. The characteristics used to categorise moult stages are summarised below:

Table 16. Moult stageing, pleopod and exoskeleton characteristics

Stage	Pleopod characteristics	Exoskeleton characteristics
A-B	Thin cuticle, setae golden yellow in colour, fine granules visible within setae, setal lumen not pinched off.	No epifaunal growth present, flexible shell, fine layer of dense setae, vivid colouration.
C	Thick, translucent cuticle, setae range from yellow to tan in colour, setal lumen pinched off forming cone-like structure in setae, egg fragments may present in females.	Epifaunal growth may be present, shell no longer flexible, setal layer has reduced, colouration has dulled somewhat.
D	Thick, translucent cuticle, setal development is evident beneath cuticle, setae are dark brown in colour.	Epifaunal growth present, shell is not flexible, setal layer almost absent, worn shell and appendages, colour of shell is dull

Stage A-B (postmoult) occurs immediately after ecdysis. The cuticle of the pleopods was thin and almost transparent. The setal elements were characteristically golden yellow in colour and contained fine granules. The presence of granular protoplasm within the setae is considered a major criterion for defining stage A-B (Lyle and Macdonald, 1983). The setal lumen near the base of setae was not pinched off. The transition from stage A to stage B is defined when the granules become fibrous and the setal cones characteristic of stage C begin to form (Van Herp and Bellon-Humbert, 1978). However, this distinction is difficult to determine and all crabs possessing granular setae were classified as stage A-B. The exoskeleton was free of epifaunal growth, flexible enough to allow it to bend without cracking under pressure and was covered by a fine layer of small, brown, densely packed setae. The shell had a vibrant colour with sharp contrast between the red and white colouration.

Stage C (intermoult) is the longest stage of the moult cycle (Aiken, 1980; Lowry, 1988). The pleopod cuticle was thickened and became translucent. The setae became darker and ranged in colour from yellow to tan. Several females were observed to have the remains of eggs adhering to the pleopods. Stage C is when setal cones first become evident. The setal lumen was pinched off at the base of the setae, forming a characteristic cone-like structure. This is a distinguishing feature of stage C (Vigh and Fingerman, 1985). The exoskeleton was sometimes colonised by epifaunal growth. The shell was thickened and could not be flexed indicating that mineralisation had been completed. Many of the setae covering the shell had been worn away and shell colour had begun to fade.

Stage D (premoult) is characterised by active synthesis of the new cuticle, resorption of muscle tissue and demineralisation of the exoskeleton (Aiken, 1980; Lowry, 1988). The pleopod cuticle was still translucent and new cuticle and setal development was visible under the surface. A zone of separation between old and new cuticle was

usually visible. Setal elements were dark brown with no obvious change in setal lumen near the base of setae. The exoskeleton was colonised by many epifaunal organisms. Shell colour had lightened and the fine covering of seta was almost absent. Thoracic appendages all showed signs of wear with the distal end of each dactylus being blunted.

Crabs with the largest accumulation of epifauna were in stages C and D. Typical organisms found amongst the epifauna were tubeworms (*Galeolaria* sp.), encrusting bryozoans, stalked barnacles (*Lepas* sp.) and small sponges which usually occurred on the underside of the carapace and in the spaces between pereopods.

4.7. Diet and feeding

Feeding Structure Morphology

The general morphology of the mouthparts of *P. gigas* is the same as that of other decapods described in the literature (Barnes, 1968; Warner, 1977; Barker and Gibson, 1978; Phillips et al, 1980; McLoughlin, 1983; Skilleter and Anderson, 1986; Dorit et al, 1991). The mouthparts are the same in both sexes. The structure and function of the mouthparts are described in detail in Heeren and Mitchell (1997), attached as Appendix 3. The mouthparts show adaptations for a carnivorous diet with the third maxillipeds having small cristae dentatae which aid in gripping food. Similar structures used for gripping large food items have been described in other carnivorous crabs (Borradaile, 1922; Caine, 1974; Williams, 1978; Skilleter and Anderson, 1986). A beak-like projection is present on the aboral surface of the right mandible of *P. gigas* and a molariform structure is present on the oral surface of both mandibles. These structures have not previously been described in other brachyurans and may be used to help grip, puncture and crush food items on which the large chelipeds of *P. gigas* are unable to fully close. This may be particularly important for males in that closure of the dactylus and propodus in the hypertrophied right cheliped of males is incomplete.

Digestive Tract Morphology and Histology

The morphology and histology of the digestive tract of *P. gigas* are described in detail in Heeren and Mitchell, Appendix 3 (1997), and both are similar to that in other decapods (Johnson, 1980). The function of the foregut, midgut and hindgut is also described in Heeren and Mitchell (1997).

Feeding Behavior

The chelipeds of *P. gigas* are dimorphic with the right being significantly larger than the left in both sexes ($P < 0.001$ in females, $P = 0.02$ in males). The right and left chelipeds of males are significantly larger ($P < 0.001$) than for females of the same carapace length (see figure 1, Heeren and Mitchell, 1997). Both chelipeds have a series of longitudinal denticles that line the inner aspect of the dactylus and propodus. As crabs grow larger the chelipeds develop larger molariform pegs on the propodus. The dactylus and propodus increase in length as the animal grows and tend to curve towards the body.

The chelipeds of *P. gigas* are the largest of any known decapod (Hale, 1927). The dimorphism is similar to that of another xanthoid, *Ozius truncatus* (Skilleter and Anderson, 1986). The larger cheliped of the male appears to be used for territorial defence and during copulation when it is used to hold the female close to the male

while sperm is being transferred. The shape and size of the chelipeds determine how crabs manipulate food (Vermeij, 1977). The morphology of the chelipeds of *P. gigas* is characteristic of chelipeds used for crushing prey items (after Warner, 1977). Denticles of the form present on the propodus and dactylus of *P. gigas* have been noted in other carnivorous crabs that feed on molluscs and other hard food items (Vermeij, 1977; Williams, 1978; Zipser and Vermeij, 1978; Grahame, 1983; McLoughlin, 1983; Lowell, 1986; Schram, 1986; Skilleter and Anderson, 1986). The smaller left cheliped of males is used to present food to the mouthparts. Females, with two smaller chelipeds, appear to be able to process their food more rapidly.

When crabs were presented with food in tanks, food seeking behavior was initiated and food located using outstretched walking pereopods. The animal would then surround the food with its entire body and legs. The chelipeds were used to present food to the third maxillipeds which then gripped the food. The cheliped holding the food item was then pulled away from the mouth thus tearing pieces from the food. The smaller pieces retained by the third maxillipeds were then processed by the mouthparts. Females used both chelipeds in a similar manner while feeding. Owing to the size of the right cheliped in males their role in feeding was reduced. Food gathered by the right cheliped was immediately transferred to the smaller left cheliped which then passed it to the maxillipeds. The right cheliped was used primarily to fend off other animals if they approached too closely while feeding, however observations of its use were limited by the food provided which did not include hermit crabs or large molluscs.

Diet

The crabs for this study were gathered from the wild as previously described in chapter 3. 48% of crabs had food items in their stomachs. Most crab stomachs contained a single food item; the mean number of items per stomach was 2 and the maximum number was 4. Mean percentage composition of food items in the diet of *P. gigas* is presented in Table 17. Dominant food items were two species of gastropod molluscs, a single species of asteroid echinoderm and decapod (other *P. gigas*, spider crabs of the family *Majidae*, or hermit crabs of the order *Paguroidea*) fragments. Carrion comprised less than 5% of diet and stomachs did not contain sediment or other material inadvertently ingested during feeding. Males consumed more asteroids than females (46% of diet composition compared to 8%) while females consumed more gastropods than males (total of 44% of diet composition compared to 29%). Smaller crabs (less than 2.5 kg) of both sexes fed mainly on gastropods (44% of diet composition) while larger crabs (over 2.5 kg) consumed more asteroids (53% of diet composition) and decapods. Large males did not contain gastropod fragments but these constituted 25% of diet composition in large females. Larger males consumed a narrower range of food items than comparably sized females. Premoult animals all had empty stomachs. Postmoult animals consumed mostly asteroids, this being the only item in larger postmoult animals. Intermoult animals consumed more gastropods with larger animals including significant proportions of fish and decapods. Diet diversity was very low and was dominated by slow moving benthic forms.

Table 17. Mean percentage composition of the diet of *P.gigas* from 300-420 metres,Western Victoria Autumn, 1995

	Food Item[a]								Number of
	Aster	Brach	Carr	Anom	Gast 1	Gast 2	Osteic	UM	Crabs
Overall	22	8	5	3	24	14	4	21	22
Sex - Male	46	0	4	4	18	11	7	11	10
- Female	8	12	6	2	28	16	2	26	12
Size - < 2.5kg									
Overall	18	5	7	0	30	16	2	23	13
Male	44	0	5	0	30	17	0	4	4
Female	0	8	8	0	32	18	3	32	9
Size - > 2.5kg									
Overall	33	14	0	10	10	10	10	14	9
Male	38	0	0	13	0	0	25	25	6
Female	33	25	0	8	17	8	0	8	3
Moult Stage									
A-B - Overall	50	17	6	6	11	11	0	0	17
- < 2.5kg	36	21	7	7	14	14	0	0	3
- > 2.5kg	100	0	0	0	0	0	0	0	2
C - Overall	13	5	5	2	28	15	5	27	17
- < 2.5kg	13	6	6	0	32	17	2	25	10
- > 2.5kg	14	0	0	14	0	0	29	43	7
D - Overall	0	0	0	0	0	0	0	0	7

[a] Food Items: Aster = Asteroidea; Brach = *P. gigas,* Majidae; Carr = carrion(including equine/ bovine hairs and feathers); Anom = Paguroidea; Gast 1 = Gastropoda species 1; Gast 2 = Gastropoda species 2; Osteic = osteichthyes; UM = unidentified material

Only 22 crab stomachs (48% of the total sample) contained food. However, 20 to 30 stomachs have been shown to be sufficient to achieve asymptotic stabilisation for the curve of cumulative trophic diversity in other crabs (Williams, 1981; Cartes, 1993). Cartes (1993) found that the feeding activity of the deep-sea crab *Paromola cuvieri* was low with only 27.5% of crabs stomachs examined containing food items. The diet of *P. gigas* was comprised of mostly sedentary organisms as expected for xanthoids which have small eyes and are unable to move quickly or capture fast moving prey (Warner, 1977). The number of food items in *P. gigas* stomachs was very low compared to studies of other species from similar depths, for example, *P. cuvieri* (38 items) and *Geryon longipes* (17 items) (Cartes 1993). Crabs from shallower habitats tend to have more diverse diets (Comoglio et al 1989, Jewett et al 1989). Interestingly, the latter study showed that *Paralithodes camtschatica* trawled from 16 - 31m depths consumed similar diet items to *P. gigas* with bivalves, gastropods, brittle stars and brachyurans being most common. The apparent preference of *P. gigas* for asteroids has not been recorded elsewhere in other species; if echinoderms are ingested they are generally echinoids or holothuroids (Jewett et al 1989, Cartes 1993). The presence of fish in the diet is probably the result of scavenging fish remains resulting from commercial fishing operations in the area as reported in studies of other species by Wassenberg and Hill (1987) and Cartes (1993).

The low diversity of diet items in *P. gigas* could reflect one or more of 3 situations. *P. gigas* may feed selectively on the diet items recorded as they offer the greatest energy return for the amount of energy invested in capture. Diet would also be influenced by the body form of *P. gigas* and it may be restricted to relatively slow moving prey. The majority of prey items recorded are slow moving. Seasonal availability of prey may also be involved in these two hypotheses; stomachs were sampled during autumn and this may influence food availability.

The restricted diet diversity probably reflects reduced food availability due to demersal trawling sweeping the area bare of surface cover or to a naturally low diversity beyond 270m where the substrates are mostly mud. Inspection of a sample of bryozoan deposits from a crab pot set on untrawled grounds in western Bass straight contained many potential prey items for smaller juvenile to larger adult sizes of *P. gigas*. The items from this sample were identified by S. M. Slack-Smith (presently at Museum of W.A.) and are listed in Table 18.

Table 18. Shellfish specimens collected among bryozoan assemblage on western Bass Strait crab fishing grounds.

Phylum: Mollusca	
Class: Gastropoda	
Family Siliquariidae:	? Pyxipoma sp.
Family Turritellidae:	? Gazameda sp.
Family Muricidae:	undeveloped juveniles
Family Marginellidae:	juvenile
Class: Bivalvia	
Family Limopsidae:	Limopsis tenisoni (Tenison Woods, 1877)
Family Mytilidae:	Modiolus sp. juveniles
Family Pectinidae:	Chlamys(Talochlamys) ? famige juvenile (Iredale,1925)
Family Kelliidae:	? Marikelli sp. or? M. yorken(Cotton & Godfrey, 1938)
Family Carditidae:	Vimentum dilectum (E.A. Smith, 1885),
	Venericardia bimacul juvenile (Deshayes, 1852
	Venericardia rosulen juvenile (Tate, 1886)

Female *P. gigas* consumed more gastropods than males and larger males had fewer food items in their stomachs than females of similar size. These differences could be attributable to sexual dimorphism in cheliped morphology. *P. gigas* has large crushing chelipeds with rounded denticles typical of xanthoids (Warner, 1977). In males the right cheliped becomes larger than the left after the onset of sexual maturity. A hypothesis that *"larger males have only one actively mobile cheliped and may be unable to forage for molluscs and that females may be better able to use their chelipeds to forage for food"* was supported to some degree by the fact that the stomachs of smaller males contained equivalent proportions of molluscs to that of similar sized females.

However, information subsequently integrated into the project may lead to modification of these hypotheses. Large and heavy gastropod shells typical of shallower grounds inshore from where the trawled samples were gathered are occupied by hermit crabs. These shells are often observed to be damaged in a way consistent with the crushing action of the large cheliped of *P. gigas*, with holes

apparently caused by the molar pegs of the chela. Thus the initial hypotheses that were formulated from trawled samples, such as *"Larger males thus have only one actively mobile cheliped and may be unable to forage for molluscs"* and *"Females may be better able to use their chelipeds to forage for food"*, became increasingly arguable as information drawn from a spatially larger area or other sources was considered.

Differences in diet between males and females have been reported for several species of crab (Elner, 1980; Choy, 1986; Woods, 1993) and these were attributed to differences in cheliped size. An initial hypothesis by this investigation that *"larger male P. gigas targeted a narrower range of diet items than comparable sized females, selecting larger more sedentary items, further reinforcing the effect of dimorphism in cheliped size"* was supported to some degree by the fact that the stomachs of smaller males contained equivalent proportions of molluscs to that of similar sized females. However the highly altered state of the trawled substrates (Caton & McLoughlin, 1999) from which the samples were taken had to be considered. The narrower range of diet from this location is probably more an artefact of the altered condition of the substrates rather than the habits and abilities of the crab.

Giant crabs held in tanks at MAFRI displayed the ability to crack open shellfish. The Bicheno Aquarium also reported the crab's ability to break open shells and consume hermit crabs. On several occasions crabs in tanks have been observed to engage in intra-specific predation. The killing method was in each case similar. The predator crab attacked its prey from behind with its larger claw and plunged the dactyl tip through the carapace into the cardiac chamber before eating the prey.

Of the crabs in moult stage A-B only 36% had food in their stomachs; 53% of the crabs in stage C had food in their stomachs. The absence of food in the stomachs of premoult (stage D) animals correlates with the cessation of feeding in preparation for moulting which involves the separation of the digestive tract and the loss of antennal chemosensory processes. Differences in feeding activity during different stages of the moult cycle have been recorded for other crustaceans; food consumption of *P. argus* decreases in stage D (Aiken, 1980; Lipcius and Herrnkind, 1982). The higher proportion of stomachs containing food in stage C animals suggests that this is the most important feeding period; this correlates with stage C being the period of active tissue growth.

4.8. Growth

In the second stage of this FRDC project Deakin University commissioned the South Australian Research and development Institute to develop an individual based model for the fishery. The following section of the report is based on a manuscript entitled "Moulting growth of Australian Giant Crab (Pseudocarcinus gigas)" by Richard McGarvey, Andrew Levings and Janet Matthews, submitted for publication to Marine and Freshwater Research. At present the manuscipt has been reviewed and is awaiting final revision for acceptance.

The recapture sample of 1,755 tagged crabs yielded 190 females and 160 males that had moulted at least once. This allowed the modes of moult increment to be readily identified and the determination of instances where multiple moults had occurred. Analysis of shell condition assisted determination of the timing of moulting and the intermoult period was estimated.

4.8.1 Summary and Introduction

The growth of Australian giant crabs (*Pseudocarcinus gigas*) has not been previously studied. A tagging program was undertaken in four Australian states where the species has become subject to commercial exploitation in the last decade. A recapture sample of 1372 females and 383 males were reported by fishers. 190 females and 160 males had moulted at least once. Modes of growth increment were readily identified and interpreted as 0, 1, and 2 moults during time at large. Single-moult increments were normally distributed except for lognormally fitted Western Australian females. Male moult increments were constant with length, while 3 of 4 female data sets showed a gentle decrease. From monthly proportions captured with newly moulted shells, *P. gigas* moulting in South Australia peaked strongly in winter (June and July) for females and was more widely spread through the year for males with a peak in summer (November and December). Intermoult period estimates for *P. gigas* varied from 3-4 years for juvenile males and females (80-120 mm), with rapid lengthening in time between moulting events to approximately 7 years for females and 4.5 years for males at legal minimum length of 150 mm.

Keywords: crustacean growth; Australian giant crab; moult increment; intermoult period

Introduction

The commercial exploitation of Australian giant crabs (*Pseudocarcinus gigas*) in lobster traps began in the early to mid 1990's in the states of Victoria, Tasmania, South Australia, and Western Australia. Previous work has been undertaken on *P. gigas* larval (Gardner 1996; 1997) and reproductive biology (Gardner 1997; 1998). A tagging program in cooperation with commercial harvesters was undertaken in 1994 to provide growth and movement information (Levings et al. 1996). In this paper we present results for four features of giant crab growth: moult increment, seasonal timing of moulting, intermoult period, and weight-length relationship.

An extensive literature has been devoted to modeling the dependence of mean moult increment on crustacean (pre-moult) length. A large number of studies regress post-moult versus pre-moult length, usually taken as linear (Gray and Newcombe 1938; Ennis 1972). These 'Hiatt (1948) growth diagram' regression lines have often been fitted to juveniles separately from adults, the percentage moult increment, the slope of the Hiatt diagram line, usually disjointly smaller for mature animals, particularly females (Hiatt 1948; Butler 1961; Kurata 1962; Conan and Gunderson 1979; Sainte-Marie et al. 1995). Nonlinear relationships have also been proposed including hyperbolic (Mauchline 1976), exponential via log regression (Mauchline 1977) and quadratic (Taylor and Hoenig 1990). Somerton (1980) improved the two-

line approximation method, and Easton and Misra (1988) suggested the formula of Misra (1957) for fitting to Hiatt diagrams.

The alternative approach, increasingly favoured (Botsford 1985; Wainwright and Armstrong 1993), is to model the moult increment directly versus pre-moult length (Weber and Miyahara 1962; Cooper and Uzman 1977; Kondzela and Shirley 1993; Groeneveld 1997; Zheng *et al.* 1995). Wainwright and Armstrong (1993) compared the methods of Somerton (1980) and Easton and Misra (1988), originally developed for use in Hiatt diagrams, for fitting moult increment versus length, finding roughly equal goodness of fit among *Cancer magister* data sets, as Easton and Misra (1988, Table 5) did for Hiatt diagrams. We fitted to moult increments of recaptures classified as having moulted once during time at large, determined from the growth increment mode at one moult.

More difficult is to infer the timing and frequency of moulting since methods for ageing crustaceans are not yet developed. The intermoult period (or its inverse, moult frequency) can be directly obtained by observation of moulting captive animals in laboratory tanks. Kondzela and Shirley (1993) and Hewett (1974) raised Alaskan Dungeness crabs (*Cancer magister*) and European common lobsters (*Homarus vulgaris*) respectively in tanks over long times and monitored the dependence of all moulting characteristics on temperature. For some species, moulting and reproductive life history moult instars have been identified by length-frequency modes, including juvenile *Cancer magister* (Butler 1961; Ebert *et al.* 1983; Orensanz and Gallucci 1988), and male snow crabs *Chionecetes opilio* (Sainte-Marie *et al.* 1995). For adult male Alaskan king crabs (*Paralithodes camtschaticus*), Weber and Miyahara (1962) and, in a comprehensive length-based model estimator, Zheng *et al.* (1995) used the trawl survey proportions of newly moulted shell to old shell crabs to infer moulting frequency. We applied the monthly variation in proportion of newly moulted shell giant crabs in the commercial catch as a relative measure to identify the season of moulting for males and females.

To estimate intermoult period with tag-recovery data, indirect inference is required (Caddy 1987). A range of approximate methods have been applied, including the 'anniversary' method where only recaptures in the water for approximately a year are used and percent moulted is calculated directly, generally as a function of pre-moult size (Hancock and Edwards 1967; Bennett 1974). The approach we applied here is a generalisation of the anniversary method, incorporating recaptures at large for longer than a single moulting season.

The growth of Australian giant crabs is presented in four sections: moult increment, seasonal time of moulting, intermoult period, and weight versus length.

4.8.2. Materials and Methods

Data

The double T- bar tagging technique, first developed for this giant crab study (Levings et al. 1996), used the epimeral suture line as a tag insertion site. This tag insertion point was first devised by Van Engel in 1956 for Atlantic blue crab *Calinectes sapidus* and applied using loop tags (Butler 1957; Mistakidis 1960; Edwards 1965; Bennett 1974). However loop tags are difficult to apply at sea. Testing indicated that single-T lobster tags would be drawn into the large branchial chamber of *P. gigas*, and it was therefore modified with the addition of a second T-bar about 10 mm above the lower T to act as a stopper. Tags were inserted through the suture line with a Dennison 08958 Tagfast 11 tag gun with a heavy-duty stainless

steel needle. The double T-bar tag has now been used with other crab species, remaining in place through multiple moults in *P. gigas*, *Cancer magister* in Alaska (T. Shirley, University of Alaska, Juneau, pers. comm.), and *Paralithodes camtschaticus* (Svein Loekeborg, Fisk Forsk, Tromso, Norway, pers. comm.) in Norway.

A tagging program was undertaken in cooperation with commercial harvesters in the four states. Length was measured using vernier callipers as carapace length (CL) in mm, the shortest distance from the centre of the anterior margin of the dorsal carapace between the eyes to the posterior margin of the carapace at the joint with the abdomen.

Fishers primarily target giant crabs from early summer (December) through late winter (August), with catches peaking in late summer to early autumn. Closed seasons vary according to state jurisdiction, with 10-week closures from September in the two most productive states, Victoria and Tasmania. The season is closed in South Australia for 5 months in winter. Thus tag releases and, to a greater extent, recaptures were less frequent in winter months. Most tagged and released crabs were those not legal to land and thus returned by fishers to the water in the course of day-to-day operations, i.e. those below the legal minimum length (LML) of 150 mm, and 'berried' , i.e. ovigerous, females. Thus, the distributions by months of tagging and recapture (due to closures or lower fishing levels in winter) and by lengths of tagged crabs (due to LML) are non-uniform. Substantial numbers of females greater than 150 mm were released, the majority ovigerous, in spring before egg hatching.

Clear separation of the 3 peaks in growth increments of recaptures were adequate to differentiate 0, 1 and 2 moults during time at large (figure 42). For (~ 5) recapture points whose length increments fell near the separation boundaries between moult categories, the time-at-large of each recapture was also taken into consideration. Borderline recaptures with shorter times-at-large, equal to or less than the mean intermoult period, for instance 2 years or less for males, were taken to represent a single moult, in a similar method to that of Conan and Gunderson (1979) and Taylor and Hoenig (1990). Three male recaptures at large for long times of 4.1, 5.1 and 5.3 years from Victoria, the subpopulation of fastest growth, appear to have moulted three times. This yielded a data set of 30 to 70 moulting recaptures from each state by sex (Table 19). Crabs recaptured more than once were treated as separate recaptures.

Moult increments

Moult increments were investigated using recaptures that moulted once. Sample sizes were sufficient to subdivide spatially into 7 single-moult recapture data sets, 4 of females and 3 of males, by state. With only two moulted male recaptures reported to date, Tasmanian males (Table 19) were excluded. The analysis was undertaken in two stages: (i) assuming no dependence of moult increment on length, and (ii) modeling dependence on pre-moult length by a linear relationship.

(i) Combining all moulted recaptures regardless of pre-moult length, three continuous distribution functions were assessed for approximating the spread of moult increments observed; normal, lognormal, and gamma likelihood fits were undertaken for each data set. For the case of the lognormal (Patil et al. 1984), the pdf for each moult increment observation was written

$$f(i_k \mid m,s) = \frac{1}{s\ i_k \sqrt{2\pi}} \exp\left[-\frac{(\log(i_k) - m)^2}{2\ s^2} \right] \qquad (1)$$

where i_k is the kth single-moult increment, and m and s were parameters to be estimated. The likelihood is

$$L = \prod_{k=1}^{n} f(i_k \mid m,s) \qquad (2)$$

where n = the number of moult increments in each data set. The two parameters of each moult increment data set distribution were estimated by minimising the minus log likelihood. The same procedure was followed for the normal and gamma distributions. Confidence bounds for estimated parameters were obtained using a standard bootstrap (Efron and Tibshirani 1993) as standard deviations of 1000 samples with replacement from the moult-increment data sets. To assess the statistical goodness of fit, one-sample two-sided Kolmogorov-Smirnov tests (Conover 1980) were applied to each fitted (likelihood-maximised) distribution.

(ii) The second stage of moult increment analysis examined dependence on length. Visual examination (Figure 44) showed no trend or only modest decline. We therefore modeled mean moult increment versus pre-moult length by a linear trend and assessed whether the slopes are significantly different from zero. Females, notably in Western Australia, show some visual indication (Figure 44a) of a declining mean moult increment versus length.

With modest or zero slopes and no strongly visible trend in the spread of moult increments versus length (Figure 44a), we adopted the choices of moult increment distribution about the linearly varying mean from stage 1 above, i.e. we assumed a normal likelihood for the same 6 of 7 linear regressions. For Western Australian females, the scatterplot (Figure 44a) suggested an upper tail as it did for the moult increments taken as constant with length (Table 20; figure 43); we therefore modeled this linear regression also assuming a lognormal likelihood.

For both normal and lognormal fits, variance versus length was modeled by letting the coefficient of variation (CV) be constant for both normal and lognormal likelihoods. A constant CV implies that the variation (as standard deviation, SD) about the mean varies in proportion to the expected mean moult increment itself. This growth model error structure is also used for continuously growing animals (Francis 1988) and is intuitively more reasonable than a constant SD implicit in least-squares fits. This may be seen by example. For crustaceans whose mean moult increments vary considerably over the range of pre-moult lengths from, say, 1 mm to 11 mm, the spread of observations about the small 1 mm mean moult increment will, with CV constant, be correspondingly smaller. Constant variance across all pre-moult lengths would predict significant probability of negative moults for small, and unrealistically low variance for large, mean moult increments.

The linear dependence of mean moult increment on pre-moult carapace length (l) was written

$$\bar{i}(l) = a_m + b_m \cdot l \qquad (3)$$

for both normal and lognormal fits. For the normal case, by definition of CV, $\sigma = \bar{i}(l) \cdot CV$. For both normal and lognormal likelihoods, we let the respective third parameters, CV and s, associated with variance, vary freely. For the lognormal case,

since the mean of the distribution is given by (Patil et al. 1984), linear dependence of mean moult increment on l (Eqn 3) is obtained by setting m equal to the following function of length:

$$m = \ln[a_m + b_m \cdot l] - s^2/2 \qquad (4)$$

The lognormal CV (Patil et al. 1984) is independent of m and given by $[\exp(s^2)-1]^{1/2}$. Thus, for normal and lognormal likelihoods we estimated 3 parameters, $\{a_m, b_m, CV\}$ and $\{a_m, b_m, s\}$ respectively.

Confidence bounds were obtained using a bootstrap of 1000 runs. We sought maximum-likelihood-conditional confidence intervals, i.e. for each parameter we ran a separate bootstrap, holding the other parameters fixed at their estimated maximum likelihood values.

To determine whether the slopes of the regressions of moult increment versus length have a linear trend, we tested the null hypothesis that the slope, b_m, of each data set regression is zero using the likelihood-ratio chi-square test (Rice 1988). The likelihood ratio statistic is written T = - 2 log Λ, where Λ is the ratio of the maximised likelihoods from the two models:

$$\Lambda = \frac{L(b_m = 0)}{L(b_m\ free)} . \qquad (5)$$

For the null hypothesis model, $b_m = 0$ fixed and only 2 parameters were freely estimated, $\{a_m, \sigma\}$ for the normal, or $\{a_m, s\}$ for the lognormal likelihood. The full model has one more parameter thus one more degree of freedom. The estimated slopes, b_m, from the full model are significantly different from zero at the p > 95% level if T > 3.84. More generally, the p-value for each data set was obtained by evaluating the (cumulative) chi-square distribution with one degree of freedom at T.

Seasonal timing of moulting

Shell state of crabs captured in the commercial harvest was used as indicator of recent moulting. The degree of fouling has been widely employed in crab population studies as a measure of how recently individual crabs last moulted. For Australian giant crabs, 'clean' shell state was determined (after Hoggarth 1993) by the presence of less than 5 encrusting organisms, excluding barnacles which may colonise very rapidly after moulting as occurs with mud crabs *Scyyla serrata* (Jeffries and Voris 1996).

A sample of 7298 female and 6638 male crabs were assessed for shell state from a single commercial fisher, J. Mathison, off South Australia, for whom the measure of clean was felt to be highly reliable. Data over three years of sampling (1997-99) were pooled, and the proportion 'clean' were calculated and plotted by month.

Intermoult period

Intermoult period was inferred from the proportions of crabs that moulted and the number of times they moulted over different time periods at liberty. Males and females were analysed separately. Estimation of intermoult period as a function of pre-moult length requires more data than moult increment, and sample sizes were not sufficient to further subdivide by state. We grouped the recaptures for each sex into those that were at large over times that included from 1 up to 5 moulting seasons at

large (MSAL's). Recaptures that were either tagged or recaptured during the moulting season, (June and July for females and November or December for males) were excluded.

Intuitively, if moults occur exactly, say, every four years, and the times to the moult prior to first capture are uniformly distributed among the sample of those recaptured, then approximately 1/4 will have moulted after one moulting season, 1/2 after two, 3/4 after three, and all crabs at liberty for four moulting seasons will have moulted.

More, generally, if it can be assumed that (1) moulting is asynchronous among individual animals, meaning the times back to the moult prior to first capture (when each animal is tagged and released) are randomly distributed among crabs of a similar size; (2) perfect non-varying intermoult period for animals of similar size, for instance exactly 4 four years between moults with no variation, and (3) no mortality, then the anniversary method and its extension described here apply as given.

From each recaptured crab, intermoult period was calculated from the number of moults and the number of moulting opportunities (i.e. MSAL's) while at liberty. We calculated the moulting rate (f_m), an extension of the "average moult frequency" of Hancock and Edwards (1967) and the "percentage annual moult frequency" of Bennett (1974) to the case where multiple moults are explicit and the numbers of moulting opportunities can vary. Let

$$\overline{N}_m(t,l,s) = \frac{\sum_{r=1}^{n_r(t,l,s)} n_m(r,t,l,s)}{n_r(t,l,s)} \tag{6}$$

be the mean number of moults, n_m, averaged over recaptured crabs (r, from 1 to n_r) of a given time at large (t, in moult seasons at large, MSAL), carapace length bin (l), and sex (s). Each value of $\overline{N}_m(t, l, s)$ is plotted as a single point in the plots of Figure 47. Then the observed moulting rate, for each carapace length and sex, was obtained as the slope of the linear regression of $\overline{N}_m(t, l, s)$ versus t as MSAL. A weighted regression was employed, each point weighted by its number of recaptures, $n_r(t, l, s)$.

The formula for the slope, f_m, of the weighted regression (Snedocor and Cochran 1980, p. 230) is written

$$f_m(l,s) = \frac{\sum_{t=0}^{n_t} n_r(t,l,s) \cdot t \cdot \overline{N}_m(t,l,s)}{\sum_{t=0}^{n_t} n_r(t,l,s) \cdot t^2}. \tag{7}$$

The regression intercept was fixed at zero.

The slope is the estimate of mean moulting rate, the average number of moults per MSAL. The intermoult period (IP), here calculated as the number of moulting opportunities, i.e. seasons, between moulting events, is calculated as the reciprocal of the moulting rate:

$$IP(l,s) = \frac{1}{f_m(l,s)}. \tag{8}$$

These estimates of *IP* can also be obtained graphically in Figure 47 as the intersection points of the regression lines with the horizontal line of y = 1.0.

In calculating observed moulting rate, double and triple moulters, n_m = 2 or 3, were incorporated in the average number of moults, $\overline{N}_m(t, l, s)$ and thus implicitly assigned to the length class from their time of release. In some cases the first of two or the second of three moults will move the animal to the next higher length category. We neglected this change in length, in particular, since we have no information on when, during the time at large, the second and third moults occurred. However there are few double and very few triple moulters, and the smallest length categories, in which the majority of double moulters occur, are approximately two moult increments in width.

Formal justification for this extension of the anniversary method follows from the maximum likelihood estimator for moulting frequency of Willoughby and Hurley (1987), specifically their Equation 3 which assumes zero mortality. Their Equation 3 confirms the intuitive relationship of intermoult period as the reciprocal of fraction moulted divided by days at liberty. Like the anniversary method, Willoughby and Hurley (1987), in application to aquatic insects captured in the wild and kept in captivity till moulting, assumed only one moulting opportunity is presented to the animals under study. We extend that to several moult seasons of time at large.

To combine results from different times at large, point values of $\overline{N}_m(t)$ were treated as separate experiments, the weighted slope of the line passing through all points taken as overall estimate of moulting frequency, for each recapture data set by length class and sex.

Weight versus length

The weight of crabs (kg) and their carapace length (mm) was measured directly in catch samples. Weight versus length was highly consistent among states, so a single relationship was derived for males and females combining data from all states. Mean weight versus length was modeled by an allometric relationship:

$$\hat{w}(l) = \alpha\, l^{\beta}. \tag{9}$$

The weight versus carapace length data were fitted assuming a normal variation of observations about the mean weight at each length. The standard deviation of the normal likelihood was assumed to vary linearly with carapace length, l:

$$\hat{\sigma}_w(l) = \sigma_{w1}\, l. \tag{10}$$

The intercept of this linear relationship is fixed at zero, i.e. we assume at length zero crabs have zero weight, and thus also zero variance in weight. This weight-length model has 3 freely estimated parameters, α, β, and σ_{w1}.

Confidence bounds were estimated by a bootstrap of 1000 runs. As typical with most allometric curves, there is large negative covariance of α and β. When both are freely estimated in bootstrap, they covary with each bootstrap sample; if one rises, the other declines to compensate, but the overall resulting curve is effectively unchanged. As above, to avoid unrealistically large confidence bound estimates, conditional confidence intervals for each parameter were generated in a separate bootstrap, setting the other 2 parameters fixed at their maximum likelihood values.

4.8.3. Results

Moult increments

We analysed the distributions of moult increments in two stages: (i) assuming no dependence on length, and (ii) with that dependence modeled as linear.

(i) The best likelihood fit obtained was a normal distribution for 6 of 7 (single) moult increment data sets analysed (Table 20). Western Australian females had a longer tail at the upper end due to the 3 points set above the main group of recapture moult increments (Figure 44) and were thus best fitted by a lognormal. The gamma distribution was the medium fitting choice of the three distributions tested in all 7 cases.

Parameter estimates for the 6 normal moult-increment distributions (Figure 43) were given directly as their mean and standard deviation (Table 21). For the lognormal density of Western Australian females (Figure 43), the estimated parameter values were $m = 2.769$ and $s = 0.1988$, with 95% confidence intervals of ±1.85% and ±20.4% respectively.

(ii) Visual examination of the scatterplots of moult increments versus length (Figure 44) suggests that, overall, dependence on length is weak. Female *P. gigas* showed some evidence of a declining trend (Figure 44a); males did not (Figure 44b). The likelihood regressions confirmed the visual assessment. The slopes of the linear trend of moult increment versus length (b_m in Table 22) were not significantly from zero for all male recapture data sets, implying a constant moult increment for all pre-moult lengths observed. South Australian and Western Australian females with slopes of -0.10 and -0.12 were highly and very highly significant. Victorian females also showed a negative slope of -0.14 but due to greater variation (notably one lower outlying point classified as a moult, Figure 44a) yielded a lower significance. Tasmanian females showed no declining trend.

As noted in the Introduction, for many species, the models of moult increment on pre-moult length are formulated as 'Hiatt diagram' regressions, that is, of post-moult length versus pre-moult length, or as 'growth factors', percent change in length versus pre-moult length. In order to compare Australian giant crab with other species reported in the literature, following the discussions of Kurata (1962) and Easton and Misra (1988), we can express the values expected from Hiatt model fits and growth factors in terms of b_m and a_m from Table 22. The Hiatt diagram regression is $l + \Delta l = a_H + b_H \cdot l$, where Δl is moult increment and l is pre-moult carapace length. This implies that $\Delta l = a_H + (b_H - 1)\, l$. In the regression fits above of mean moult increment versus length, we had $\Delta l = a_m + b_m \cdot l$. Thus equating Δl in the two descriptions, we see that $b_m = 0$ and $b_H = 1$ both imply moult increment constant with respect to length. Also, statistical distribution and fitting method differences apart, $a_H = a_m$. While these two forms of regression can yield (usually only modestly) different outcomes for the same data set due to differences in the nature of the distributions and implied or explicit likelihoods of the different regression forms, in general, an increasing moult increment with length is indicated by $b_m > 0$ and $b_H > 1$.

Easton and Misra (1988) note that rearrangement of terms further implies that the 'growth factor' should vary as $\Delta l / l = a_H / l + b_H - 1$. Thus, regressions of percent change in length versus length are nonlinearly related to the Hiatt and moult increment versus length models. Furthermore, often it is change in weight that is used in fishery dynamics models and stock assessment. Combining the allometric relationship of weight to length (Eqn 9) we obtained a form for the predicted change

in weight as a proportion of pre-moult weight versus pre-moult carapace length, in terms of derived a_m and b_m, namely

$$\Delta w / w = [\, b_m + 1 + a_m / l \,]^{\beta} - 1. \qquad (11)$$

We plotted the predicted curve from Eqn 11 using the b_m and a_m regression coefficients (Table 22) estimated above, and on the same graph plotted a direct least-squares allometric (power law) fit to proportional weight change of each recapture (Figure 45). This comparison provided a way to evaluate the extent that statistical properties of the linear likelihood regression and possibly other statistical complications such as the ratio of $\Delta w/w$ impact on the inferences about growth, specifically change in weight with each moult, that would be drawn in using the estimated regressions $\Delta l = a_m + b_m \cdot l$ in stock assessment, for these data sets. Only females were plotted since they showed a linear trend for moult increment versus length. The plots from the power fits and Eqn (11) agree closely (Figure 45), suggesting that the regressions of moult increment versus length and weight versus length (Eqn 9) provide a self-consistent description of growth by weight under moulting.

Seasonal timing of moulting

The proportions of crabs judged to be in a 'clean' shell state in each month (Figure 46) show a short moulting season for females, and a more extended season of moulting for males.

Females (Figure 46) showed a strong peak spanning June (57%) and July (56%). The higher than average proportion of clean shells in August (36%) may partly reflect crabs that moulted in July, particularly towards the latter half of July and were captured in early August. Note that the monthly proportion clean reaches relatively low proportions of 11% and 3% in September and October, suggesting that the time lag after moulting that a female crab is judged 'clean' does not last much longer than a month, reiterating the short season of female moulting, with 'clean' reported at low levels of 3-8% from October through March. Allowing for some lag, we conclude that June and July are the principal months of moulting for South Australian females.

For males (Figure 46), the monthly proportions clean shelled suggests a peak moulting season in November (51%) and December (55%). However, the monthly proportions clean never dropped below 13% (May), were lower than average in April (18%) and remained at or above 24% for all other months. This suggests two, not mutually exclusive hypotheses: (1) the moulting of males can occur throughout the year, and/or (2) the time lag after moulting for which a male giant crab is judged 'clean' is longer than a month, and may extend to a number of months. A longer time for the males' shells to stay unfouled is plausible given their generally more widely ranging movements at shallower depths on the shelf. Females are often captured in the mud of the shelf slope where they partly bury themselves in winter at time of moulting, offering colonising organisms more immediate contact with their shells.

Intermoult period

Moulting rates were estimated by length category and sex as weighted regression slopes of the mean number of moults versus time at large (Figure 47). The resulting estimates of intermoult period were tabulated with confidence bounds for each (Table 23). Both males and females show a steady lengthening in estimated intermoult

period with length, with a considerably more rapid slowing in moult frequency for females. The trend in intermoult period with length is substantially greater than that of moult increment, suggesting, as with many crustacean species, that the slowing of growth with size is mediated primarily by the frequency of moulting events.

The rapid lengthening in intermoult period could indicate a terminal moult for females at size above 174 mm, the largest for which we had sufficient data to analyse. Females reach a maximum size in fishery length frequency samples of around 180 mm in Western Australia and 200 mm in South Australia, that is, about one moult increment above 174 mm.

Weight versus length

Coefficients of the weight-length relationship (Table 24) show a difference in the morphology of males versus females. Isomorphic growth, that is, no change in physical shape or body density with increasing size, would be indicated by a value of 3 for the exponent parameter, β. For male *P. gigas*, β is greater than 3, and for females, less than 3. The values for β (β_{males} = 3.43 and $\beta_{females}$ = 2.83) are nearly identical to those reported by Bennett (1974: β_{males} = 3.44 and β_{males} = 2.89) for a related species, *Cancer pagurus* off southwest England. The higher values for males are, as Bennett (1974) notes, likely to result from the greater proportion of body weight allocated to the large claw, the chela, which increases in relative size as males progress through adult moults. Gardner and Williams (in press) quantified this change in *P. gigas* morphology to identify instars of the adult male, finding three.

4.8.4. Discussion

A terminal moult for giant crabs has been demonstrated for other Brachyran crabs, notably male snow crab *Chionoecetes opilio* (Sainte-Marie et al. 1995), and others reviewed by Hartnoll (1985). The mean moult increment of ~ 25 mm, and a moulting frequency of every 2-3 years would allow larger male crabs than observed in length frequency samples unless there is either a terminal moult or low survivorship at these sizes. We have not found firm evidence of terminal moult, tagged giant crabs having been in the water for only five years to date, with few males in the large (legally harvestable) size range. A terminal moult for males is compatible with the 3-instar classification of Gardner and Williams (in press), the largest instar category extending to maximum observed male carapace lengths.

Although characterising the distribution of moult increments is valuable, likelihood methods have not been widely adopted with notable exceptions McCaughran and Powell 1977; Zheng et al. 1995). The benefit of a maximum likelihood fit by comparison with raw histograms or of fitting continuous densities to histogram points or even weighted bin averages is illustrated in Figure 43, where with Tasmanian females, the likelihood fit curve fell somewhat to the right compared with the 5-mm bin histogram. This difference in the position of the likelihood and histogram modes is due to the fact that the lengths of a majority of the recaptures in the peak 15-20 mm histogram bin fell towards the upper end of the bin. Statistically the best (minimum-variance, unbiased) fit to any distribution is obtained with a maximised likelihood, provided the appropriate probability density form can be ascertained.

A more difficult problem is the estimation of intermoult period. The assumption of equally likely times to the moult prior to first capture allows the use of the intuitive estimator of Willoughby and Hurley (1987) in graphical regression, providing a readily available method in the absence of a full likelihood estimation

algorithm. We named the quantity given by the slope of the regression 'observed moulting rate' rather than moult frequency because it does not explicitly consider variation in times to prior moult. A more rigorous estimator for intermoult period from tag recoveries, which makes explicit the distribution of times to the prior moult, is currently under development. However, in the absence of the mathematical machinery needed to program and fit a full estimator, the graphical method shown above provides a simple way to estimate intermoult period from tag recoveries using a spreadsheet or statistical package, employing only weighted linear regression.

This approach offers a number of advantages over the traditional form of the anniversary method (Hancock and Edwards 1967). By (1) combining the recaptures for a number of years via the weighted regression rather than considering just a single year at large, and (2) excluding those recaptured in the season of moulting rather than only including those recaptured a full year after tagging, allows a much greater number of tag recaptures to be employed (see Hancock and Edwards 1967) which are, in general practice, returned at random times by commercial or recreational fishers, in the estimate of intermoult period. This approach requires that moulting be seasonally periodic and knowledge of when the season of moulting occurs.

An additional factor neglected in the estimates of intermoult period is natural mortality, widely assumed to be high during and immediately following moulting events. The physiological stress of such large discrete body growth, percentage weight gains on the order of 75-90% for male giant crabs and 40-60% for females, is likely to be high. Rates of predation and cannibalism are also presumed higher when the exoskeleton has been shed. Infectious pathogens and parasites are also likely to find easier entry. This higher mortality with natural moulting has not been quantified but would induce an overestimation bias in the intermoult period estimates from tag recovery data if lower percentages of moulted animals survive to be recaptured. However, while this causes underestimation of average growth of individuals that do survive, it does not bias (or cause much less bias for) the estimate of average cohort biomass growth, to which both survival and individual growth contribute.

The seasonal timing of moulting is similar to the other principal crustacean species in southern Australian coastal shelf waters, the southern rock lobster *Jasus edwardsii*, with females moulting in early winter and males in summer. Females in both species extrude eggs at the time of moulting, carry them through winter, and hatch them in spring. Their home ranges partly overlap in shelf waters along most of the southern Australian coast. Giant crabs, particularly males, are taken as by-catch in lobster pots, but the primary home range of giant crabs, in the vicinity of the shelf edge, is in deeper water than that of lobsters.

Approximately constant moult increment versus length is found in a number of crab species, notably Alaska king crab, *Paralithodes camtschatica* (Weber and Miyahara 1962). And as with Australian giant crab, faster overall growth for adult males than females as both higher moult frequency (*Cancer pagurus* in southwest England, Bennett 1974) and larger moult increments (*Cancer magister* populations reviewed by Wainwright and Armstrong 1993) are common, with some exceptions (Hancock and Edwards 1967). High spatial and temporal variability (Bennett 1974; Wainwright and Armstrong 1993) often obscures any general observations about crab growth, and significant differences in moult increment were observed among the four Australian states for *P. gigas*. It is notable that differences in mean moult increment among states were correlated by sex (Table 21), that is, where males had largest (Victoria) and smallest (Western Australia) moult increments, so did females.

A goal in generating the most appropriate distributions for giant crab moult increments and intermoult periods is to simulate growth of giant crab for fishery stock assessment and modeling. This moulting growth description was incorporated into an individual-based model for use in evaluating fishery management regulations, notably legal minimum length, seeking to optimize egg-, yield- and value-per-recruit for Australian commercially exploited populations.

4.8.5. References

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Table 19. Number of giant crabs that were tagged and released and the total number of recaptures (including multiple recaptures of the same crab) used in moult analysis.

	Females			Males		
	Released	Recaptures	moulted	Released	Recaptures	moulted
SA	2930	432	70	2402	103	58
Tasmania	4918	244	29	2236	33	2
Victoria	2038	313	31	1310	118	49
WA	2160	383	60	987	129	51

Table 20. Kolmogorov-Smirnov test statistic as a measure of goodness of fit of the three fitted continuous distributions to moult increments for crabs assumed to have undergone one moult during time-at-large. Smaller values indicate better fit. Confidence measures of 80% (*) and 90% (**) indicate significance for two-sided rejection of agreement between fitted and observed distributions.

	South Australia		Tasmania	Victoria		Western Australia	
Fitted distribution	female	male	female	female	male	female	male
normal	0.119	0.136	0.143	0.139	0.168*	0.144*	0.121
lognormal	0.153**	0.156*	0.170	0.167	0.204**	0.105	0.154
gamma	0.141*	0.150*	0.161	0.156	0.192**	0.119	0.143

Table 21. Maximum likelihood estimates of giant crab moult increments (mm), mean and standard deviation. Bootstrap 95% confidence intervals (in parentheses) expressed as a percentage of the estimate.

	South Australia		Tasmania	Victoria		Western Australia	
	female	male	female	female	male	female[1]	male
mean	16.86 (±3.61%)	24.68 (±2.87%)	18.48 (±4.74%)	22.62 (±6.27%)	27.02 (±3.99%)	16.25 (±5.30%)	22.49 (±4.33%)
standard deviation	2.711 (±16.1%)	2.719 (±20.5%)	2.358 (±23.4%)	3.854 (±32.1%)	3.404 (±31.6%)	3.264 (±22.9%)	3.254 (±24.3%)

[1]Fitted to lognormal distribution.

Table 22. Maximum likelihood linear regression coefficients of moult increment (mm) versus carapace length (mm). Bootstrap 95% confidence intervals (in parentheses) are shown. The null hypothesis p-values for b_m indicate probability that the regression slopes are zero.

	South Australia		Tasmania	Victoria		Western Australia	
	female	male	female	female	male	female[1]	male
a_m	31.4 (±1.7%)	28.3 (±2.5%)	21.8 (±3.7%)	41.3 (±3.0%)	29.5 (±2.8%)	31.3 (±2.4%)	19.3 (±4.1%)
b_m	-0.103 (±3.6%) p=0.0018**	-0.0268 (±18.4%) p=0.62	-0.0238 (±23.8%) p=0.67	-0.141 (±6.6%) p=0.104	-0.0191 (±34.4%) p=0.64	-0.123 (±5.0%) $p=6.3\times10^{-5}$***	0.0291 (±25.7%) p=0.35
CV	0.150 (±15.8%)	0.110 (±20.8%)	0.127 (±23.5%)	0.163 (±36.0%)	0.126 (±30.6%)	0.175 (±27.1%)	0.143 (±24.5%)

[1]Regression fitted assuming lognormal likelihood.

Table 23. Estimated *P. gigas* intermoult periods, by length category and sex, from weighted regression slopes of Figure 47, with bootstrap 95% confidence intervals.

	Females				Males		
	90-120 mm CL	120-138 mm CL	138-156 mm CL	156-174 mm CL	80-120 mm CL	120-143 mm CL	143-166 mm CL
Intermoult period (years)	3.84 (±3.0%)	6.09 (±1.6%)	7.15 (±1.6%)	20.5 (±15.6%)	2.87 (±1.6%)	3.92 (±2.1%)	4.57 (±5.2%)

Table 24. Maximum likelihood estimates for weight-length parameters, with 95% confidence intervals, from bootstrapping.

parameter	females	males
α	1.517×10^{-6} (± 0.52%)	8.817×10^{-8} (± 0.81%)
β	2.826 (± 0.04%)	3.427 (± 0.05%)
σ_{w1}	0.00099 (± 11%)	0.0022 (± 12%)

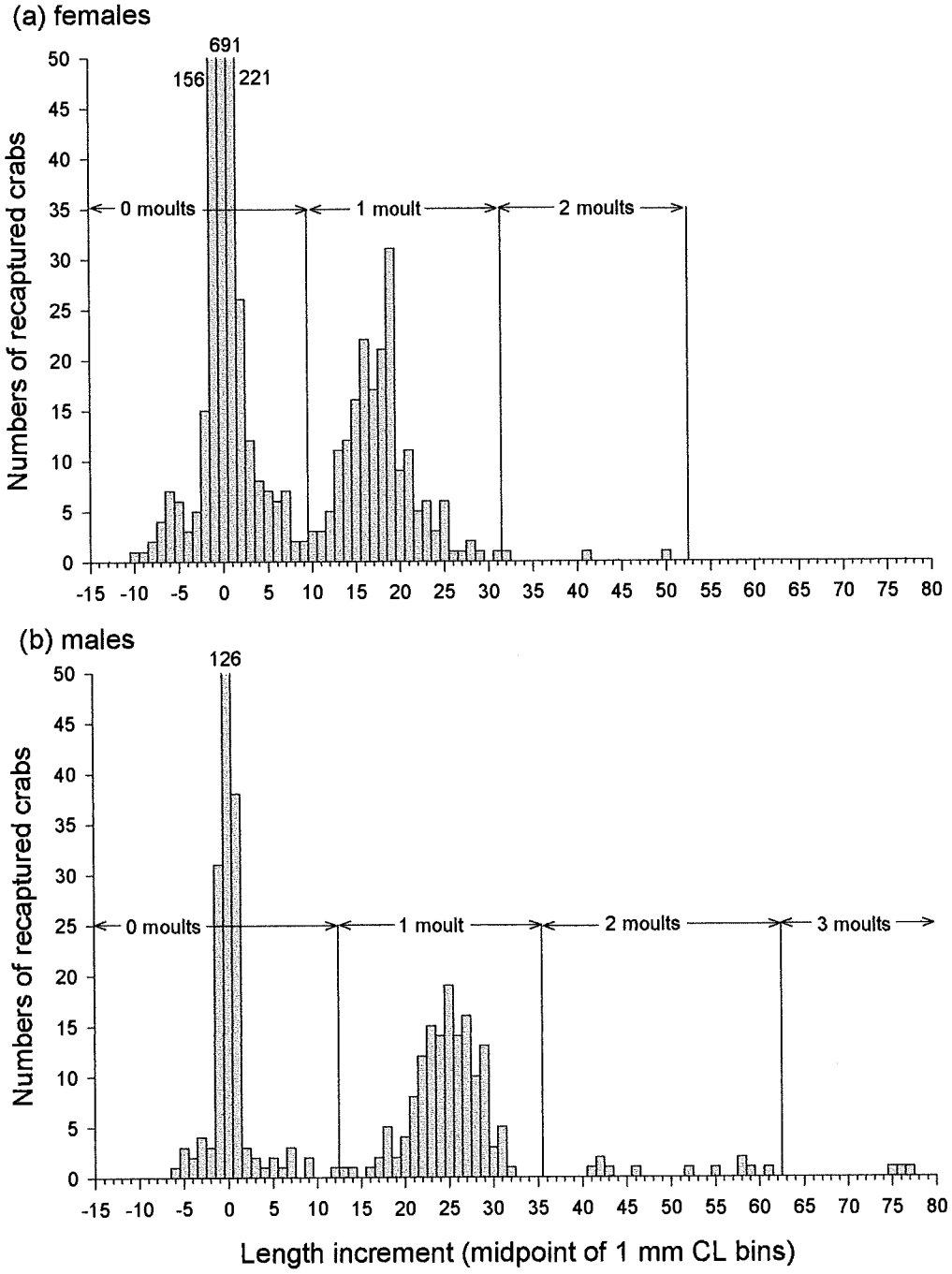


Figure 42. Length increment histograms for tag recoveries of *P. gigas*, by sex.

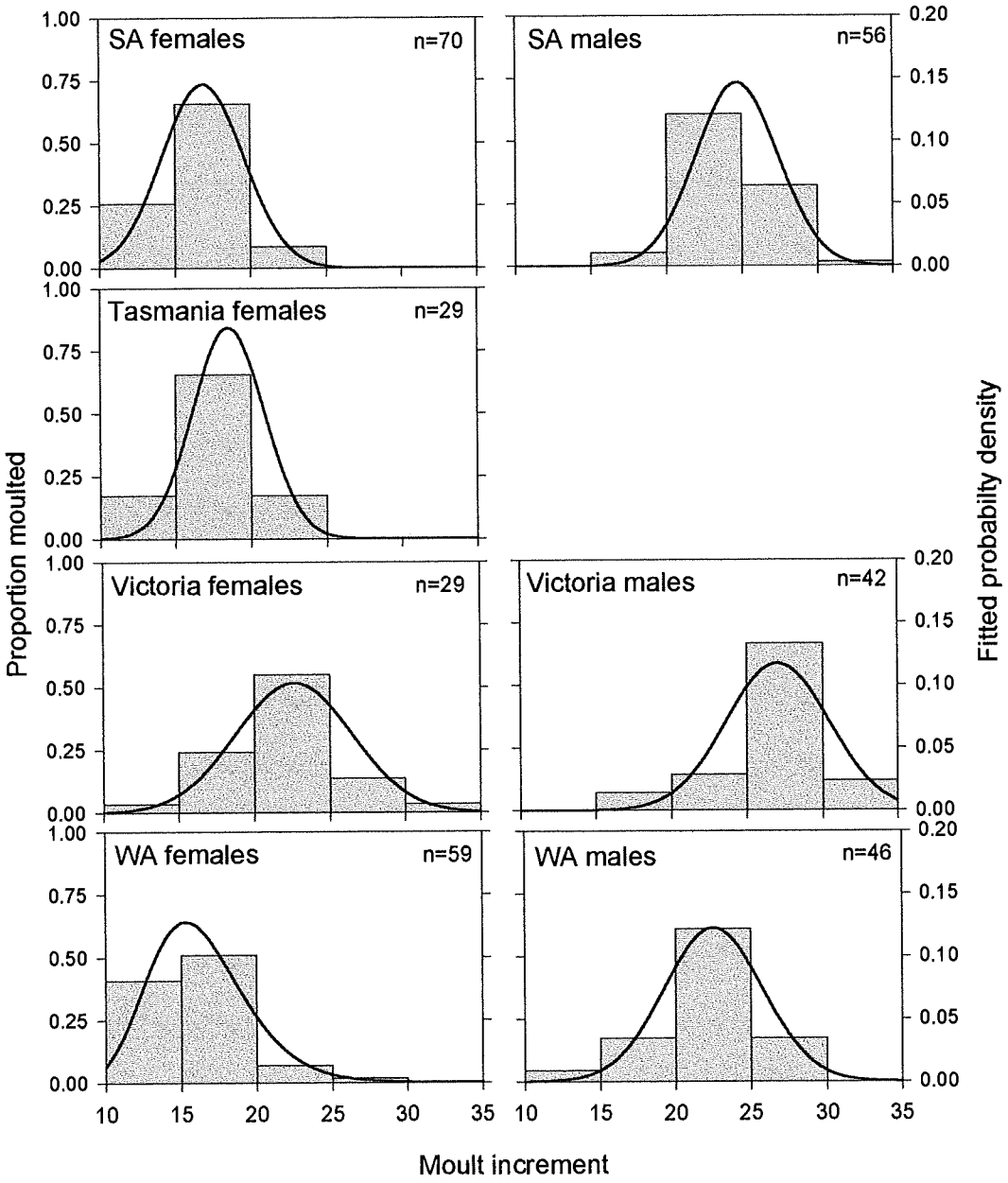


Figure 43. Moult increment probability histograms in 5 mm length bins (bars) for recaptures having moulted once. Also shown are fitted probability density curves (solid lines), normal for all cases except WA females where a lognormal yielded the best fit.

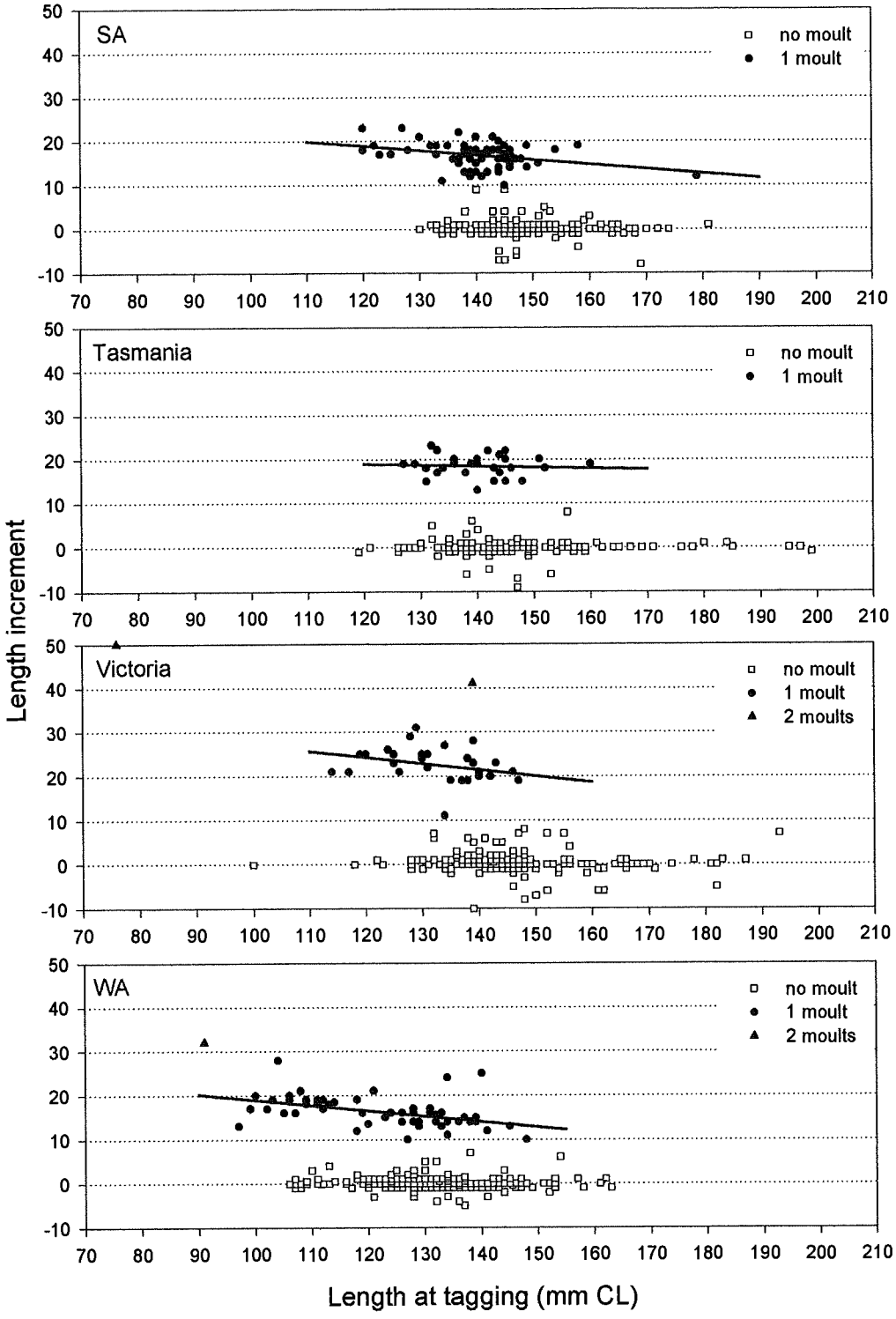


Figure 44a. Female length increments versus length, and maximum likelihood regression fits to single-moult increments, by state.

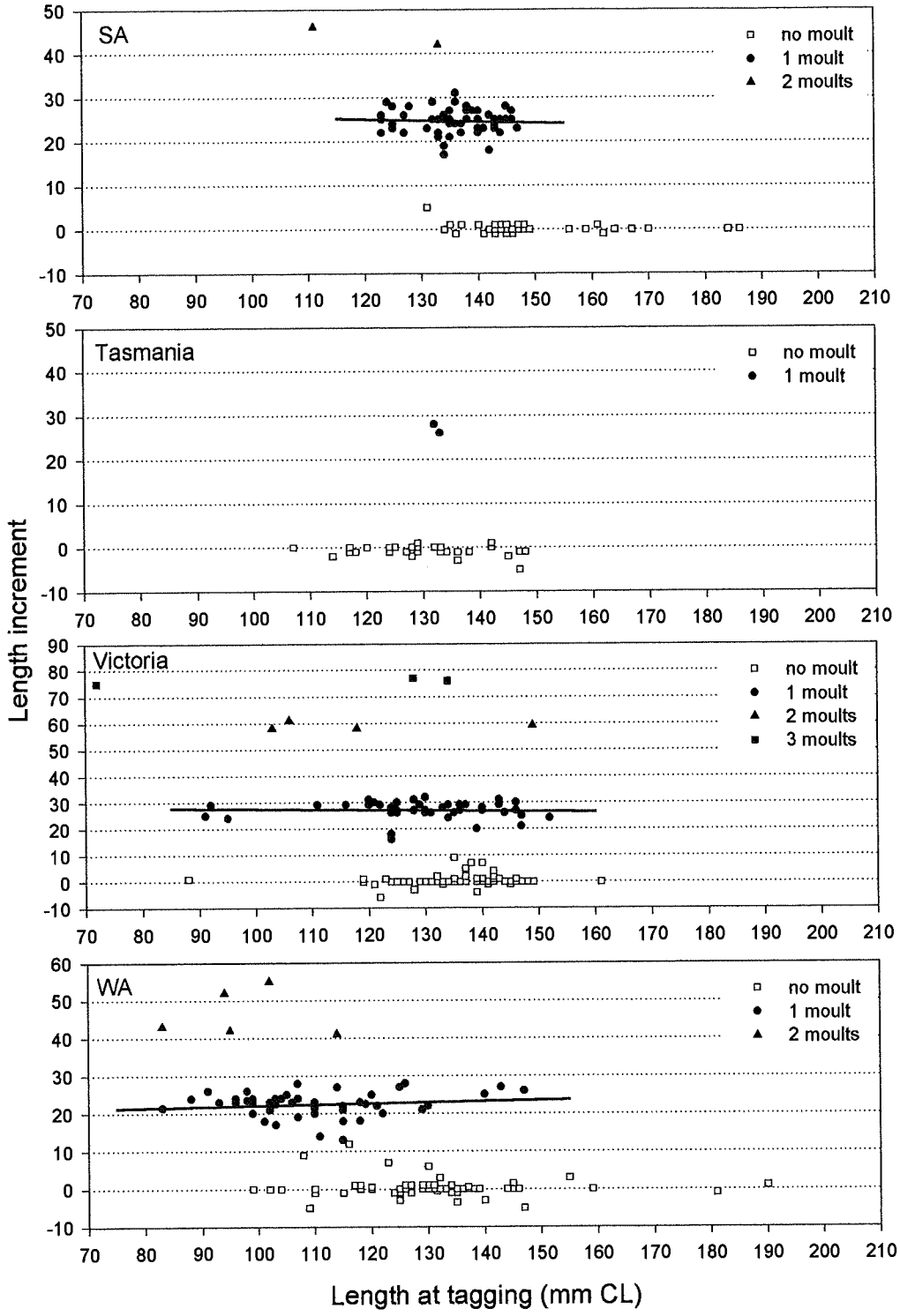


Figure 44b. Male length increments versus length and maximum likelihood regression fits to single-moult increments, by state.

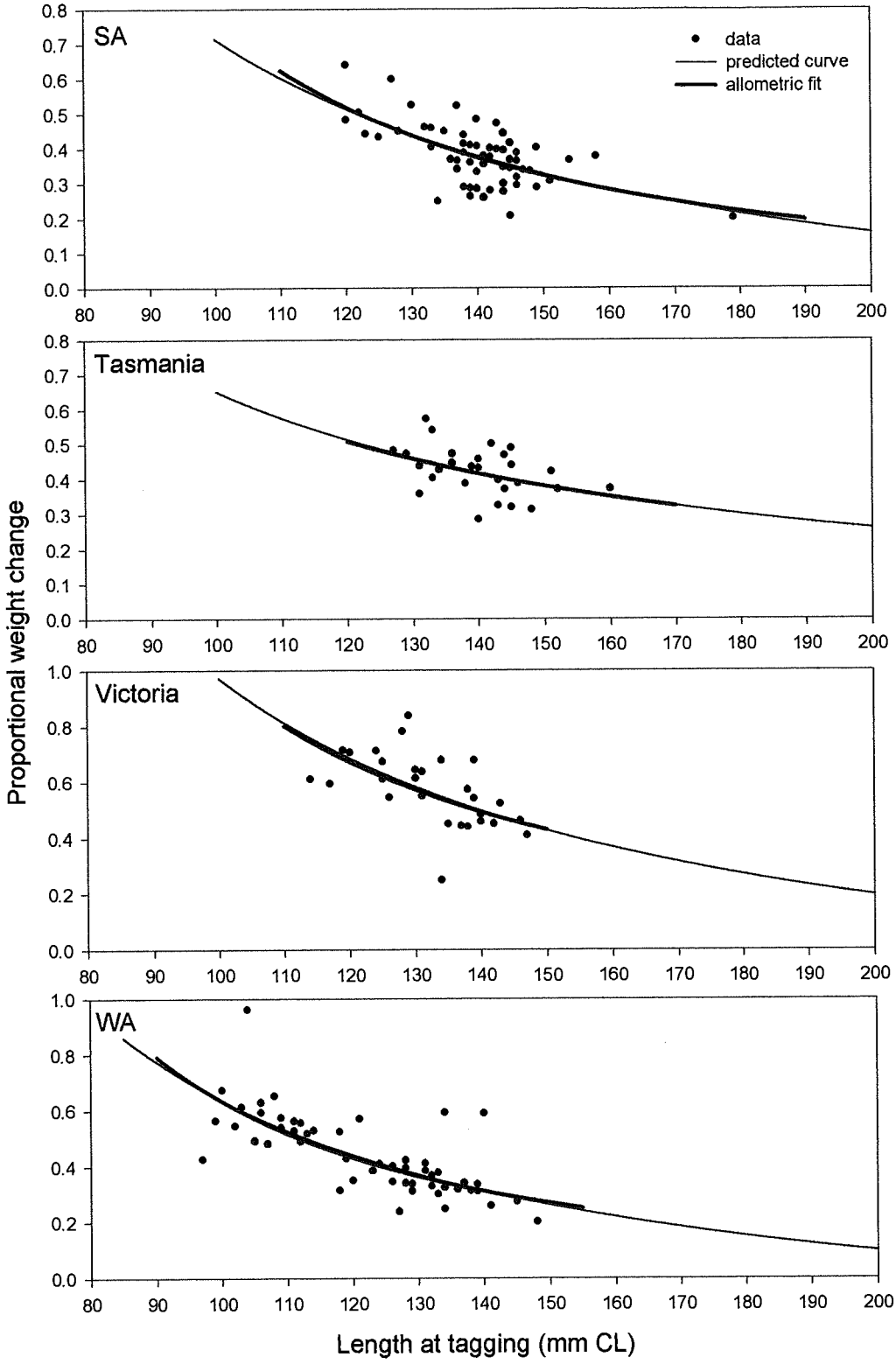


Figure 45. Female proportional change in weight under a single moult. The thin line curve is the derived relationship (Eqn 11) combining the likelihood regression coefficients of moult increment versus length (Table 21) with the fitted length-weight relationship (Eqns 9 and 10; Table 24). The heavy solid line is an allometric direct fit to the scatterplot of the individual data points shown giving proportional change in weight under moulting for recaptures that moulted once.

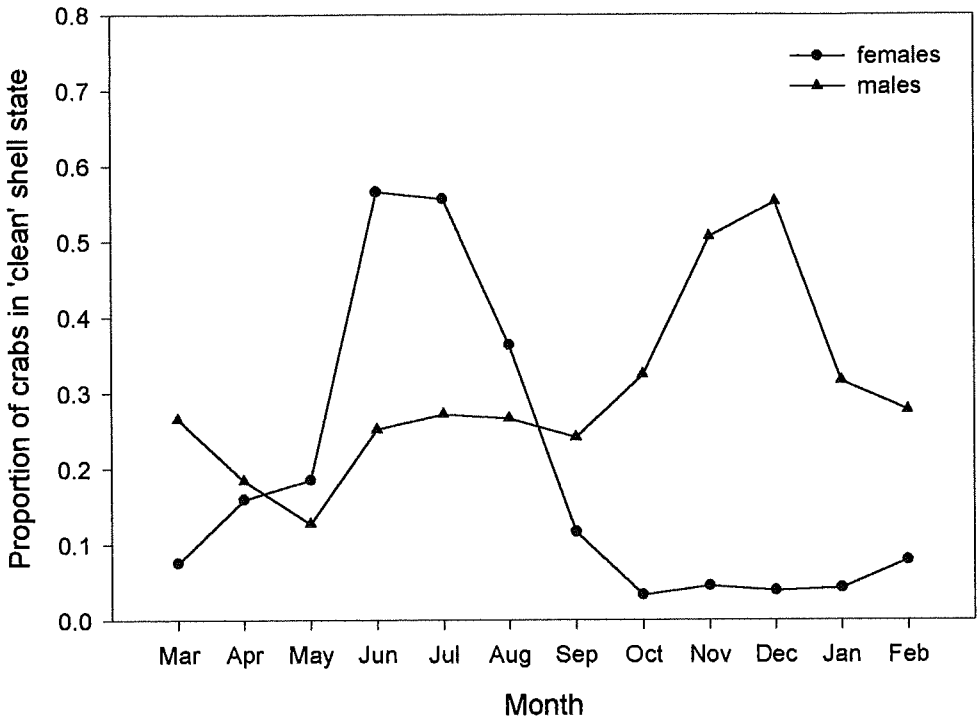


Figure 46. Monthly indicators of moulting activity, as proportions of crabs in South Australian fishery catch classified as 'clean' shell state, by sex.

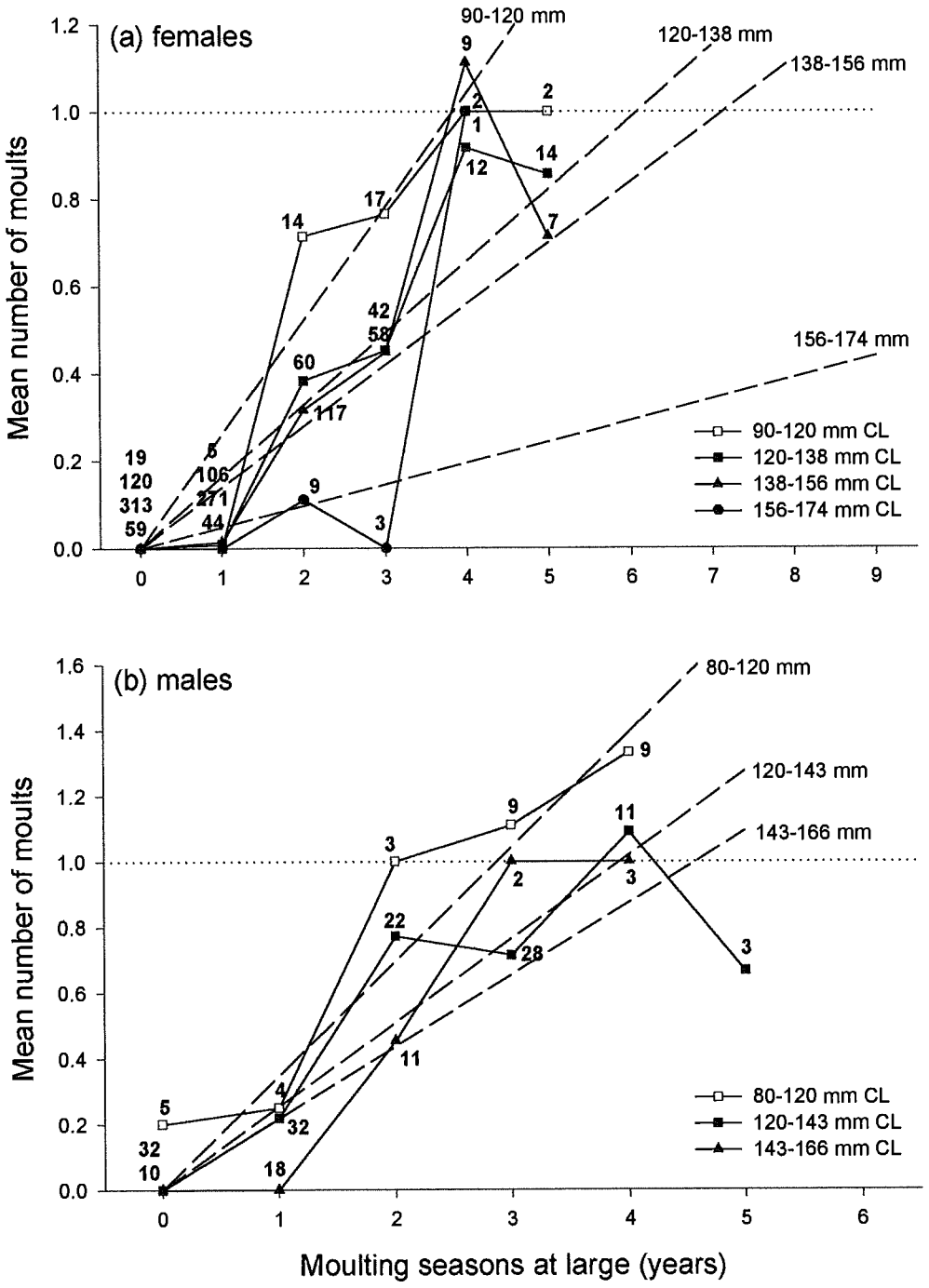


Figure 47. Proportions of recaptured crabs that have moulted, versus time at large in number of moult seasons, grouped by sex and length class. Females are assumed to moult in June/July, males in November/December. The dashed lines are weighted regressions for each length class. Sample sizes are indicated next to each symbol. Where there is more than one symbol occupying similar values, the order of the sample sizes corresponds to the order of the length classes in the legend.

4.9. Movement

Although there are a relatively small number of target fishing operations at the shelf break, many other fishers take *P. gigas* as a by product when lobster fishing in shallower water nearer to shore. In an effort to ensure that recapture data was not an artefact of the targeted fishery, kits were supplied to all permit holders licenced to retain *P gigas* either as a target or by-catch, to get a full coverage of the species range. Despite this most of the information came from the shelf break where there was a proportionally larger recapture rate for females compared to males (Table 25).

The less fouled state of male shells and greater wear on the tips of their legs (Chapter 2.10) supports the hypothesis that males live a comparatively more mobile lifestyle and disperse more widely. Although CPUE and shellstate analysis provide support for this notion in the targeted fishery further investigation is required at a whole fishery level so that the land-ward dispersal suggested by captures by lobster fishers is documented. Catch and effort information from South Australia includes the number and weight of crabs. An analysis of mean individual length by depth shows an increase in mean size from deeper to shallower water.(see chapter 4.10) Anecdotal evidence from numerous fishers indicate that most of the shallow water catch consists of males. The sexual dimorphism of males may contribute to their ability to exploit inshore food resources as their large claw can crush large gastropod shells and allow feeding on the contents (including hermit crabs, see chapter 4.7). Knowledge of the male life history can be easily improved because the crabs are large and are numerically less abundant compared to lobster. Therefore the on deck labor requirement to document males and females is not unreasonable and could be facilitated by the pro-forma catch and effort sheet which is attached as Appendix 2. This split by sex had been adopted by WA, SA, and Tasmania by 2000, although some modification to the pro forma was made to suit the specific circumstances that prevailed in each state.

The value of crab "by catch" has increased for lobster fishers and instead of being released or killed, they have become a "by-product". Although dispersal from the shelf break to shoreward has diminished in many areas because individuals of *P. gigas* are taken adjacent in deeper water, it is significant that inshore by-catch is now sold and so two components of fishing mortality, i.e. from the targeted fishery and the byproduct fishery have compounded. Figure 48 illustrates a trend towards increasing crab catch by lobster fishers off South Australia. Catch rates by this group of 254 fishers are commercially insignificant ($\approx$ .005 kg/potlift) but if aggregated across the entire fishery their annual production accounts for about one third of the reported state total, the other two thirds being taken by the 2 specialist crab fishers.

Recapture data from the shelf break was pooled according to region, i.e.

- west of 115°E longitude (off Cape Leeuwin then northerly to Cape Naturaliste' at latitude 33° 30'S, W.A.),
- Longitude 115°E to Longitude 117°E (off Cape Leeuwin east to Parryville, W.A.),
- Longitude 117°E to Longitude 121°E (off Parryville east to Investigator Island, W.A.),

- Longitude 136°E to Longitude 139°E, (Lacepede Shelf, S.A., west of Kangaroo Island to west of Robe),
- Longitude 141°E to Longitude 143° 20'E, Latitude 40°S (from S.A/Vic. to Vic/W.Tas. border),
- Latitude 40°S to Latitude 41°S (Vic/Tas border southerly to off West Point, west Tas.),
- Latitude 40°S to Latitude 42°S (off Flinders Island southerly to off Cape Lodi, east Tas.)

The data was carefully edited to remove instances where the crab had been at large for less than one month or had moved less than 1 km. These edits are summarised in Table 25. As the effect of tidal drift and steepness of shelf break bathymetry do not allow accurate recording of depth, estimates of change of depth have not been developed from recapture information at this stage.

Scatterplots of distance moved by time at large indicated that animals became increasingly dispersed after their release and that more than 50% of the recaptures had moved at least 5 km or more since tagging began. Movement of over 100km occurred in 49 instances and there were 5 records from West Australia and 1 from Western Victoria where recaptures occurred more than 350km from the release point. Hence, in contrast to *J. edwarsii* which show a high level of site fidelity (Prescott et. al. 1997), *P. gigas* is migratory.

Table 25. Regional extent of movement

Region	% of recaptures by distance travelled			Number recaptured	% edited out <1km or<1mth
	< 5 kms	≥ 5 to ≥20km	> 20km		
WA <115° Long	36	39	25	149	25.13%
WA 115° - 117° Long	43	24	13	80	20.79%
WA > 117° Long	23	33	44	181	17.73%
SA 136° - 139° Long	51	37	12	488	16.44%
wVic 141° to ≈ 143° Long	35	40	25	400	8.88%
wTas from 40° to 41° Lat	37	37	26	43	27.12%
eTas from 42° to ≈ 44° Lat	40	37	23	184	13.95%

The recaptures provided knowledge about their movements within the targeted fishery. Analysis of the frequency and direction of movement show a primary alignment with the shelf break in all regions as illustrated in Figure 52.

When the changes in latitude and longitude for all recaptures were grouped by regions, then summed, averaged and expressed in nautical miles, a predominant westerly movement was observed from most parts of the southern Australian margin. There were some exceptions; off West Australia movement off the Cape Leeuwin – Cape Naturaliste' coast was to the south, while off Tasmania movement on both sides of the island was to the north.

In the Autumn crab fishers report a run of crabs down slope into cooler deeper water coincident with the change of oceanic season when bottom temperature on the shelf increases with the onset of deep mixing downwelling winter conditions. To fishers the transition is often accompanied by a change in water colour as blue colder water from summer upwellings is displaced by warmer green shelf water advected by westerly winds.

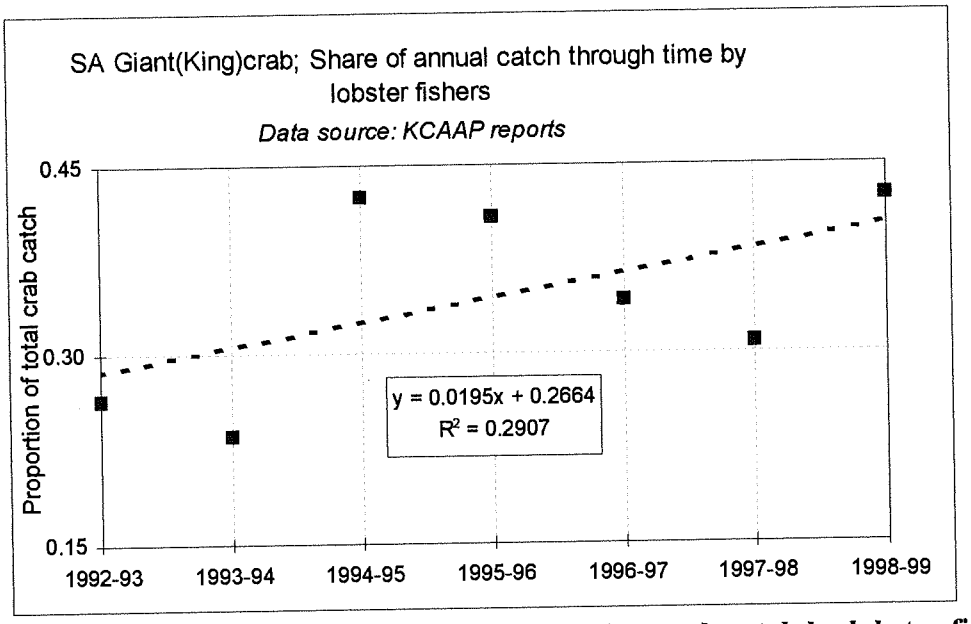
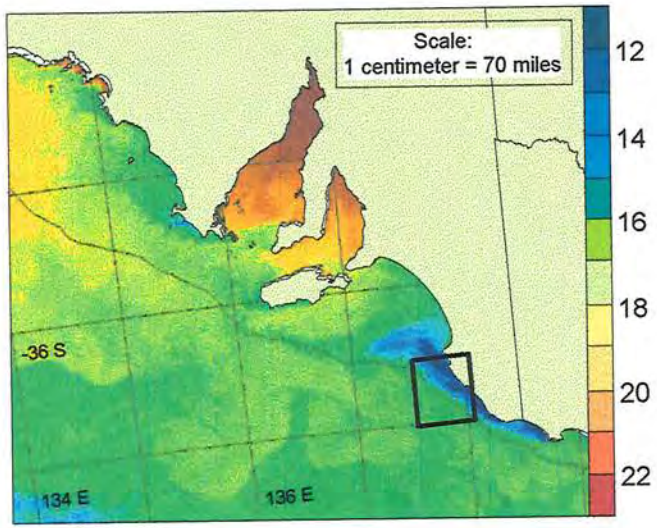
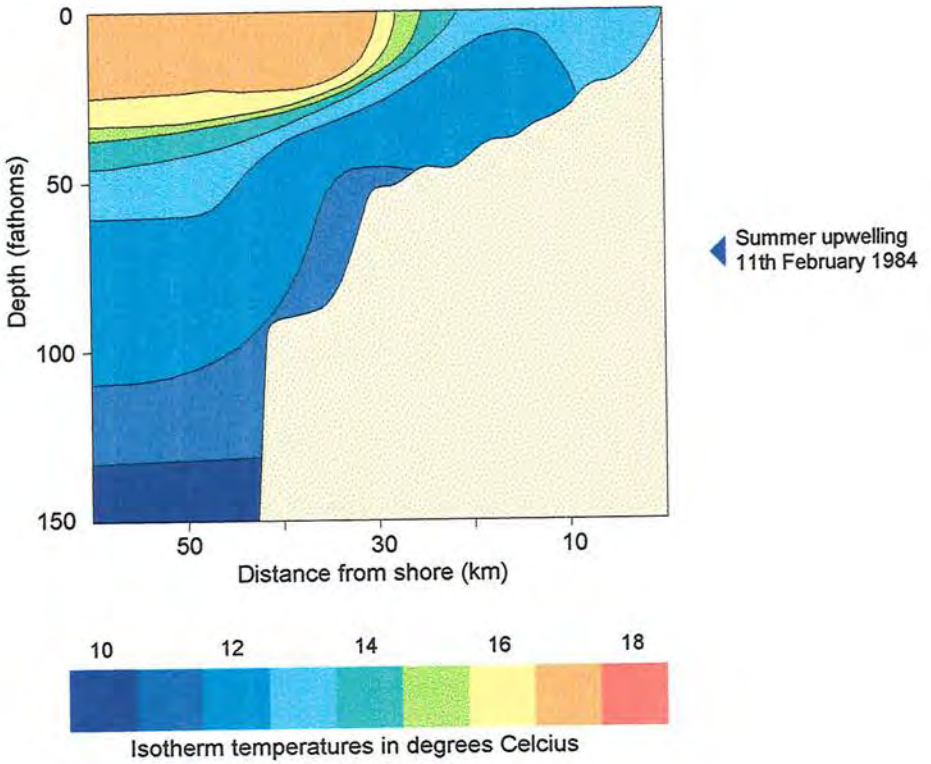


Figure 48. Proportion of total South Australian crab catch by lobster fishers.
The trendline indicates that the amount of crabs being taken is slowly increasing.

Schahinger (1987) reported a similar colour difference between water masses when studying the structure of upwelling events off South Australia. Abalone divers off Cape Nelson and Cape Bridgewater, Victoria, have also observed these effects (pers com. K. Bienssen, Portland 1995). This seasonal transition (Figure 49) is accompanied by other ecosystem changes, such as eastward migrations of Southern Bluefin Tuna *Thunnus maccoyii* from the Great Australian Bight (*after* Hynd and Robins 1967) and of Blue Whales *Balaenoptera musculus* from the "Bonney Upwelling" off the South East of South Australia (Gill, 2000).

In West Australia the edge of the warm easterly flowing Leeuwin Current and the presence of *H. armata* (now *H. acerba*, Koh & Ng, 2000), act as a natural boundary to the on-shelf and upper slope environments where *P. gigas* can survive. The location of the boundary varies with interaction of the Leeuwin current and the cooler westerly flowing "Leeuwin undercurrent" directly below it (Figure 51, *after* Cresswell & Petersen, 1993). Catch per unit effort values for *P. gigas* (Figure 50) suggest an aggregation of males at the boundary and this may explain the proportionally higher male recapture rate for West Australia compared to other locations, in Table 26 below.





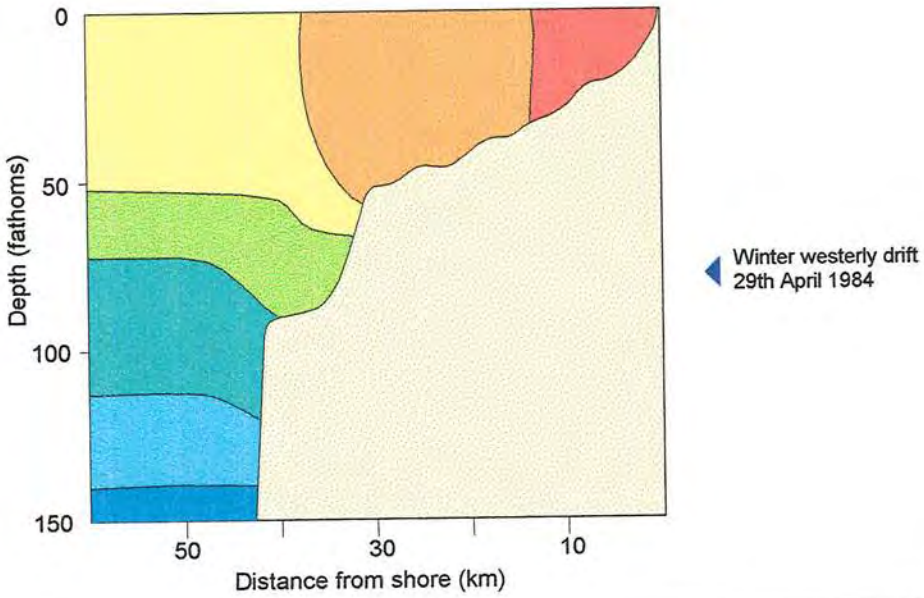


Figure 49: Oceanic Climate.

Summer upwelling, an annual feature off South Australia. See CSIRO satellite image of sea surface temperatures at top left.

Schahinger (1986) produced cross-sections from the area in the box. The top right shows Summer up-welling, the bottom right shows Winter downwelling and deep mixing of the surface waters.

Table 26. Proportion of male and female crabs tagged crabs recaptured by state.
The lower values of males for Tasmania are biased by a non typical low abundance of males off the east coast (see Figure 54).

State	Females			Males		
	Tagged	Recaptured	% Recaptured	Tagged	Recaptured	% Recaptured
SA	2930	432	14.74	2402	103	4.29
Tas	4918	244	4.96	2236	33	1.48
Vic	2038	313	15.36	1310	118	9.01
WA	2160	383	17.73	987	129	13.07

Two features are evident in the variability of catch rate by depth and month of year for West Australia (see chapter 5.2)

i. There is a large amount of variability in the catch rate at depths coincident with the interface of the Leeuwin current and Leeuwin undercurrent

ii. Maximum variability in the catch rate occurred in Autumn (figures 102 & 121) which is coincident with the passage of the leading edge of the Leeuwin current through the region during the transition from the weak and sometimes arrested summer flow to the winter maximum (Godfrey and Ridgeway 1985, Cresswell 1991, Cresswell and Peterson 1993).

A tentative hypothesis is that *P. gigas* moves into shallower areas from deeper waters to feed on the richer food resources of the bryozoan faunal assemblage, but leaves when the water becomes too warm. The warmer water is favoured by the spiny or "champagne crab", *H. acerba,* which is a potentially aggressive competitor that may have a similar diet given its distribution by depth (George 1996, Koh & Ng 2000), which locates this species over bryozoan rich substates also, bryozoa having a broader temperature tolerance (*after* James et. al. 1992) than either crab species. Thus, there are two species of crab which live on a similar substrate, that are in some ways of similar appearance. *H. acerba* favours warm temperate waters, *P. gigas* cool temperate waters. As they are the genetically closest to each other from the studies outlined in Chapter 4.2, it is reasonable to propose they may have evolved divergently from a common ancestor, probably of Tethyan or west Indo-Pacific origin.(*see* Wilson and Allen, 1987)

In all regions it appears *P. gigas* occurrence and movement are linked to the position of the interface between "oceanic" water which has constant temperature - salinity characteristics and "shelf " water which is usually warmer and exhibits a wide scatter of salinity values reflecting its mixed origins.

Off Western Australia *P. gigas* released east of 117° (Figure 52c) show a very strong westerly movement, but there is a progressive attenuation of this pattern further to the west as the limits of it's range are approached (Figures 52a & b). This is probably due to an increasingly less favourable environment and the crabs response to hunger, water temperature and competition with *H. acerba.*

When populations of crabs were initially sampled in 1994 off the Augusta and Bremer Bay areas the mean individual size for the Augusta population was larger than for

Bremer Bay to the east (*Augusta 147.67 mm cf Bremer Bay 137.44 mm - see statistical outputs for length frequencies in Appendix 1).* The westerly movement by *P. gigas* shown in Figure 52b & c and Table 27, may partially explain these differences as many of the recaptured crabs have grown during their westerly transit. Also the coolest water in the region occurs at longitudes 116° to 118° (Cresswell & Peterson, 1993). This would favour a greater access to trophic food resources on top of the shelf and a larger moult increment. Although movement and growth were unknown in 1994 and not canvassed during meetings with fishers from Albany and Esperance, some suggested that the "steep ground" off Esperance was a nursery area. The information on movement that has since emerged from the tagging program provides some explanation for this observation as larger sizes occur westerly from this area. However very small juveniles < 80mm carapace length are observed along the whole range of the WA fishery as far north as latitude 34°S adjacent Margaret River, indicating that recruitment from larval stages also occurs across this region.

Off South Australia and west Victoria the seasonal movement of crabs from shallower to deeper waters coincides with the seasonal movement of the interface between "Intermediate Antarctic" oceanic water and "Bight" water with lesser amounts of Leeuwin current and "Gulf" water, the latter three being shelf waters. Along shelf movement of *P. gigas* (Figures 52d & e) has a bimodal structure which in South Australia is consistent with the bimodal movement of current. Hahn (1986) stated,
"The southeastward flow is maintained for part of the time but is almost balanced by episodes of flow towards the northwest. The along-shelf character remains dominant."

Off East Tasmania the interface between the East Australia current and Intermediate Antarctic water lies at about 200-300 metres(Harris et al., 1987) which is also the depth from where most of the commercial catch is produced. Rochford (1960) identified an intermediate water mass which moved to the north along the east Tasmanian margin at a depth of 200-400 metres at all seasons of the year. *P. gigas* in this area show a very strong pattern of northerly movement (see Figure 52g).

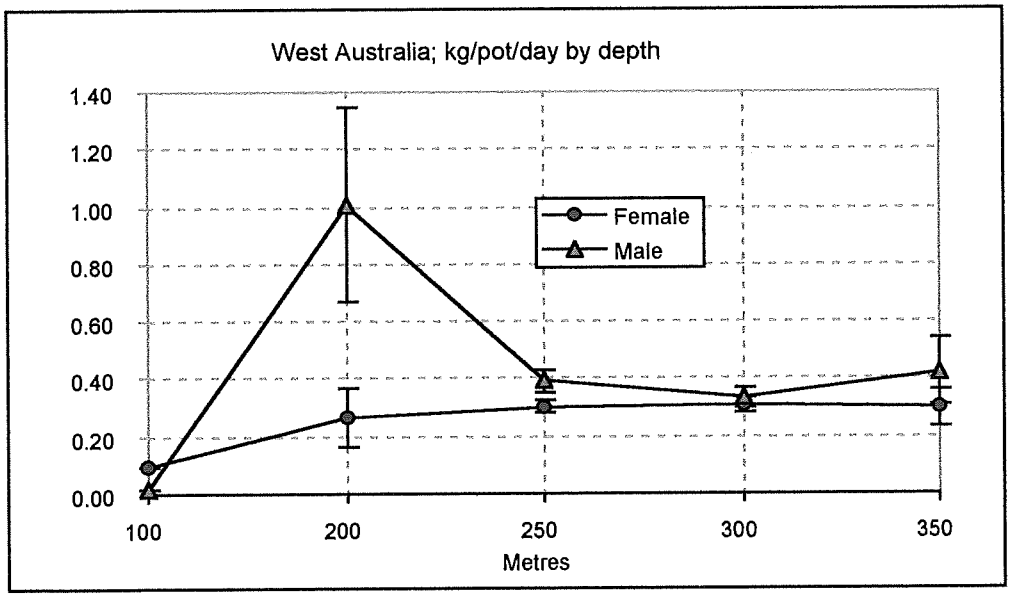


Figure 50. Catch per unit effort of P. gigas off west Australia.
There is a significantly higher catch rate of males in depths of about 200 metres. At this depth there is much variabilty in catch rates for both sexes.

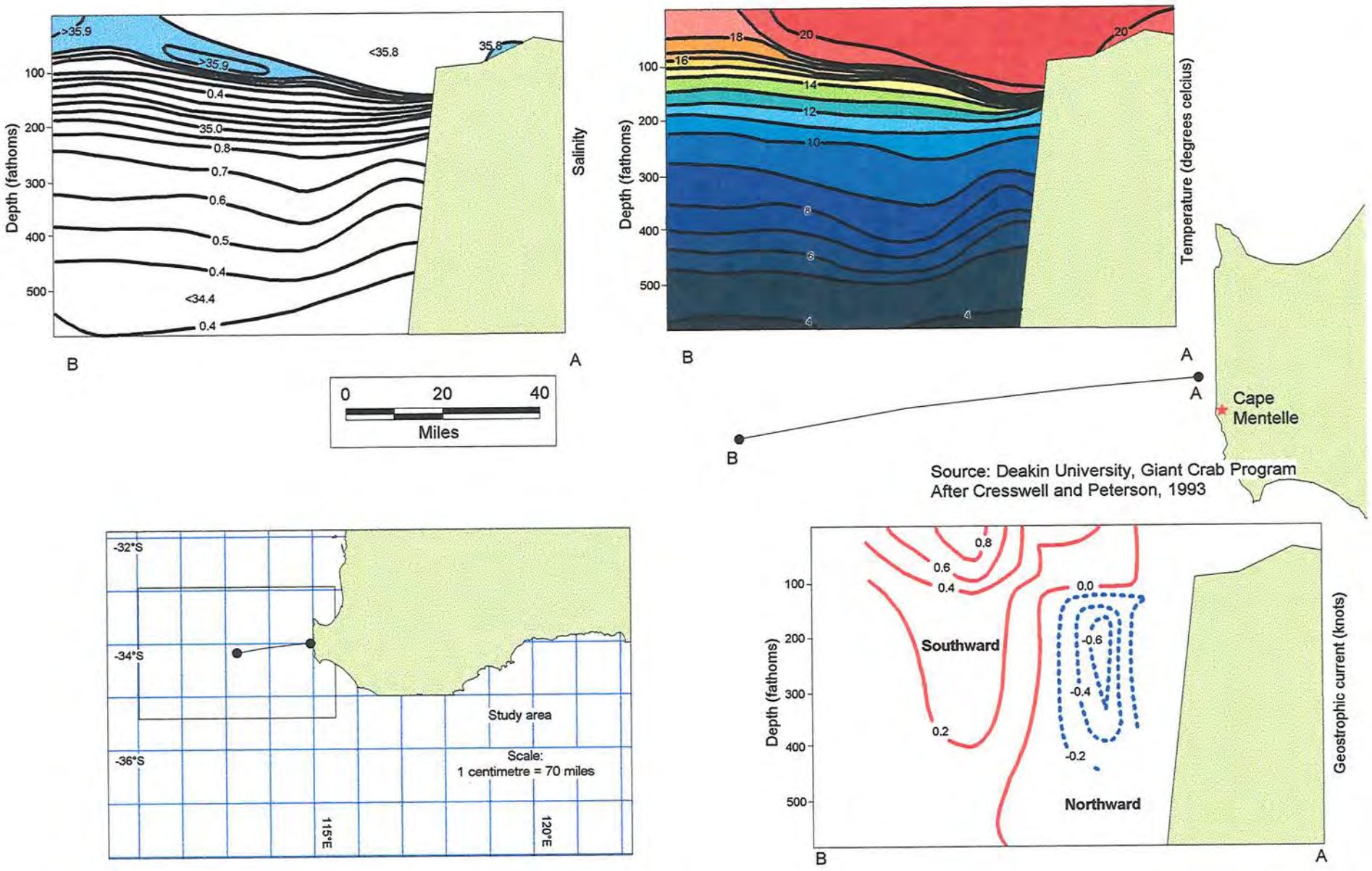


Figure 51: Temperature, salinity and geostrophic currents of the Leeuwin Current off Cape Mentelle, W.A.
In the salinity section, the shading marks the salty subtropical water beneath and seaward of the Leeuwin Current.

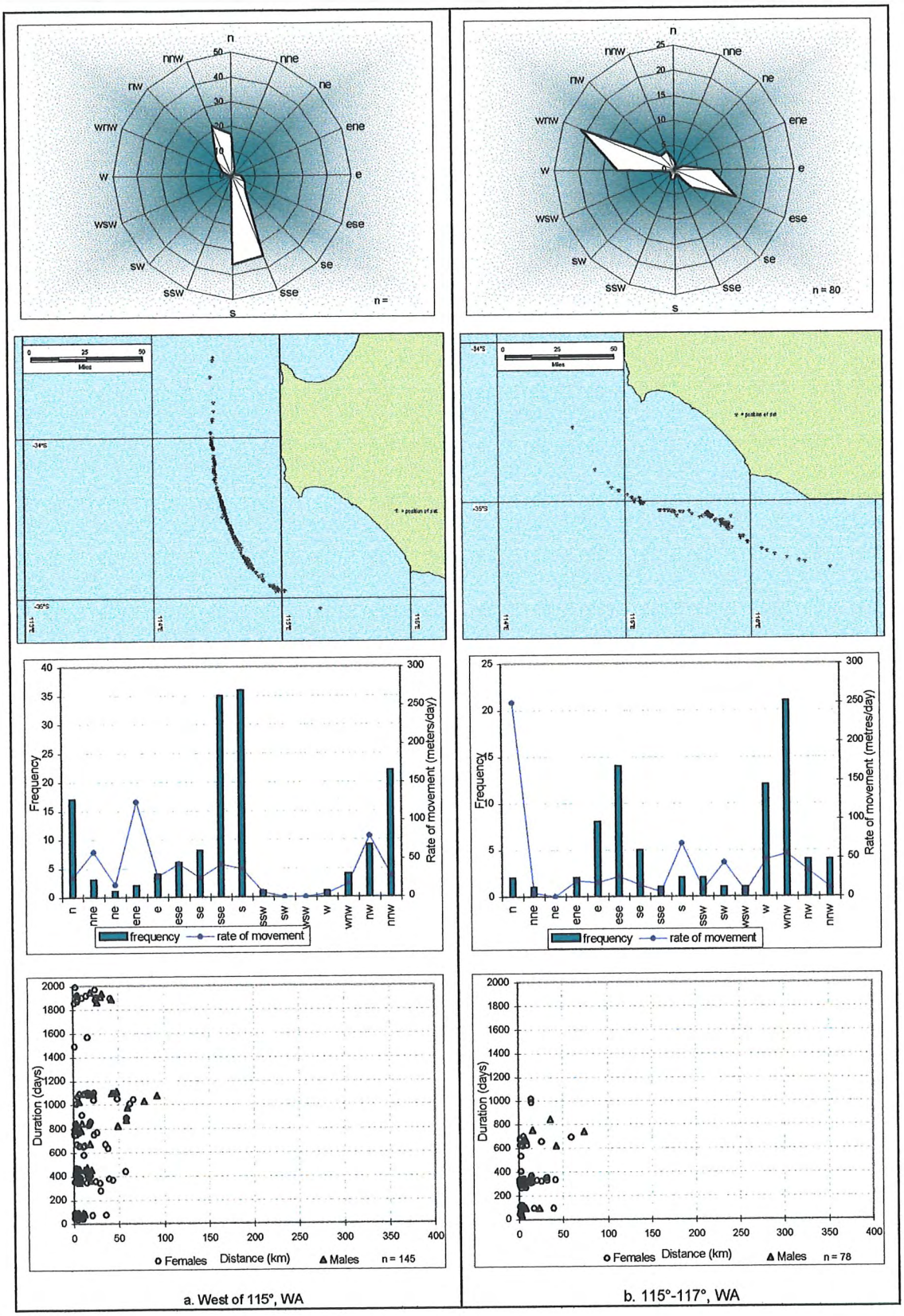


Figure 52a & b. Movement

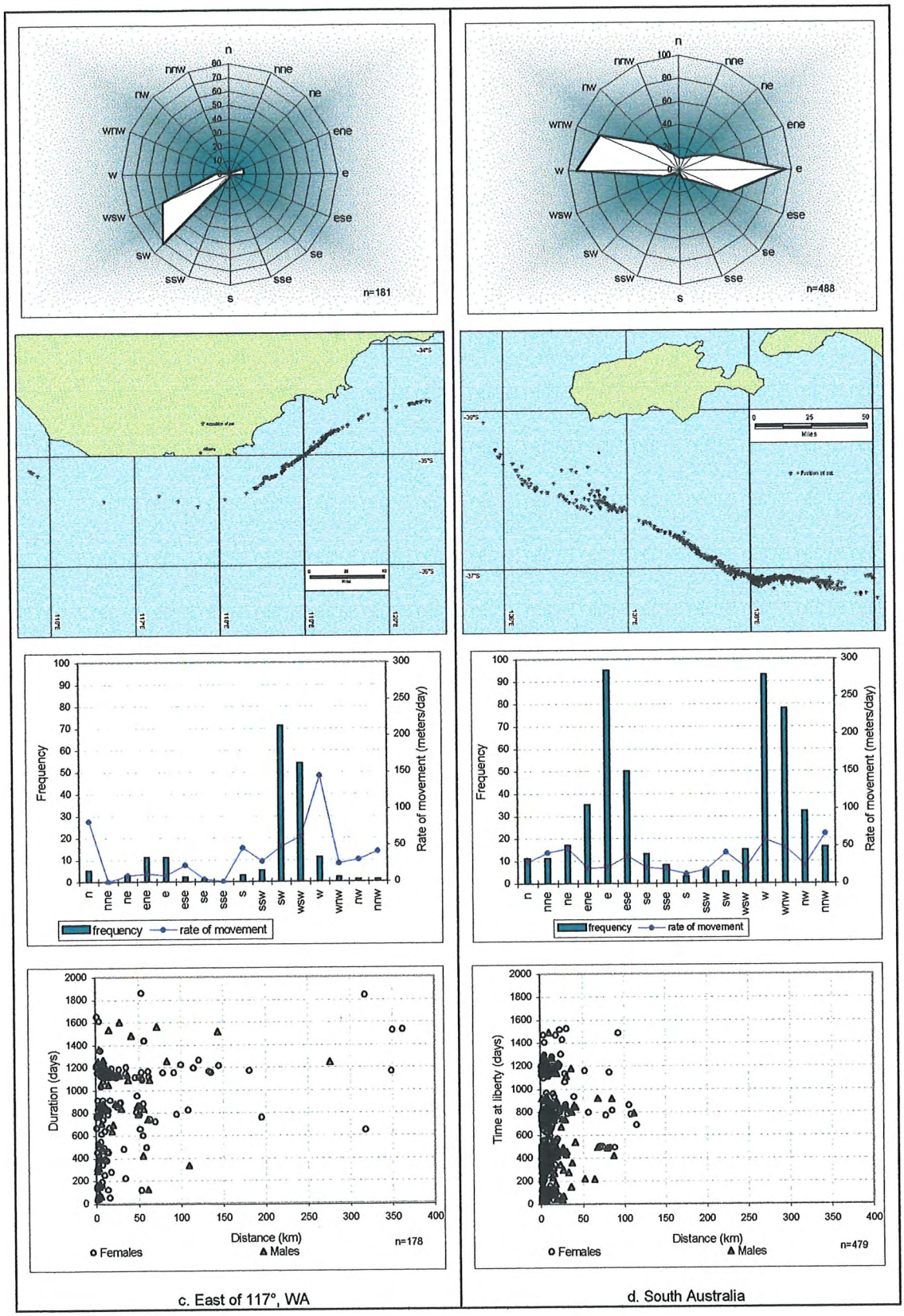


Figure 52c & d. Movement

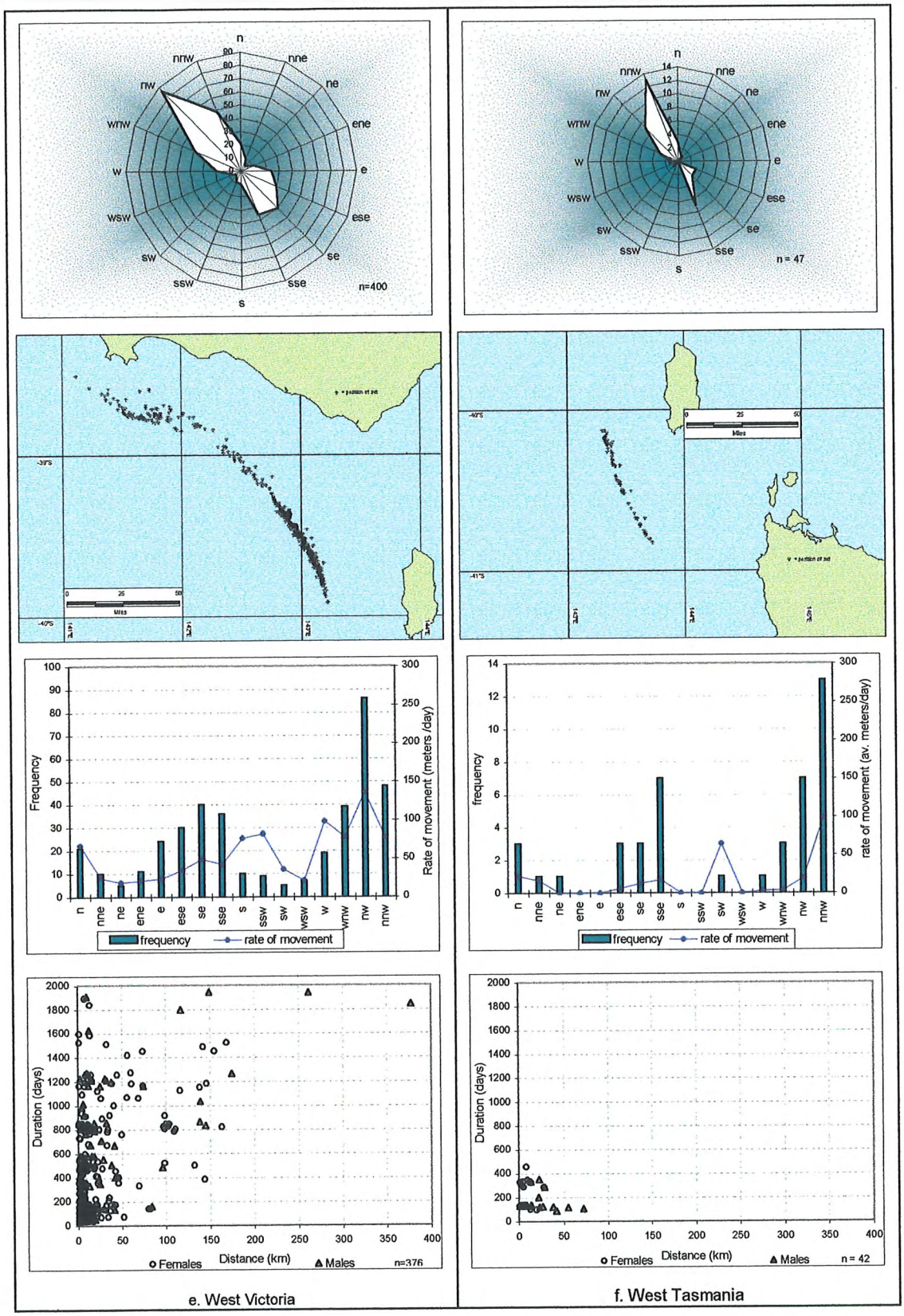


Figure 52e & f. Movement

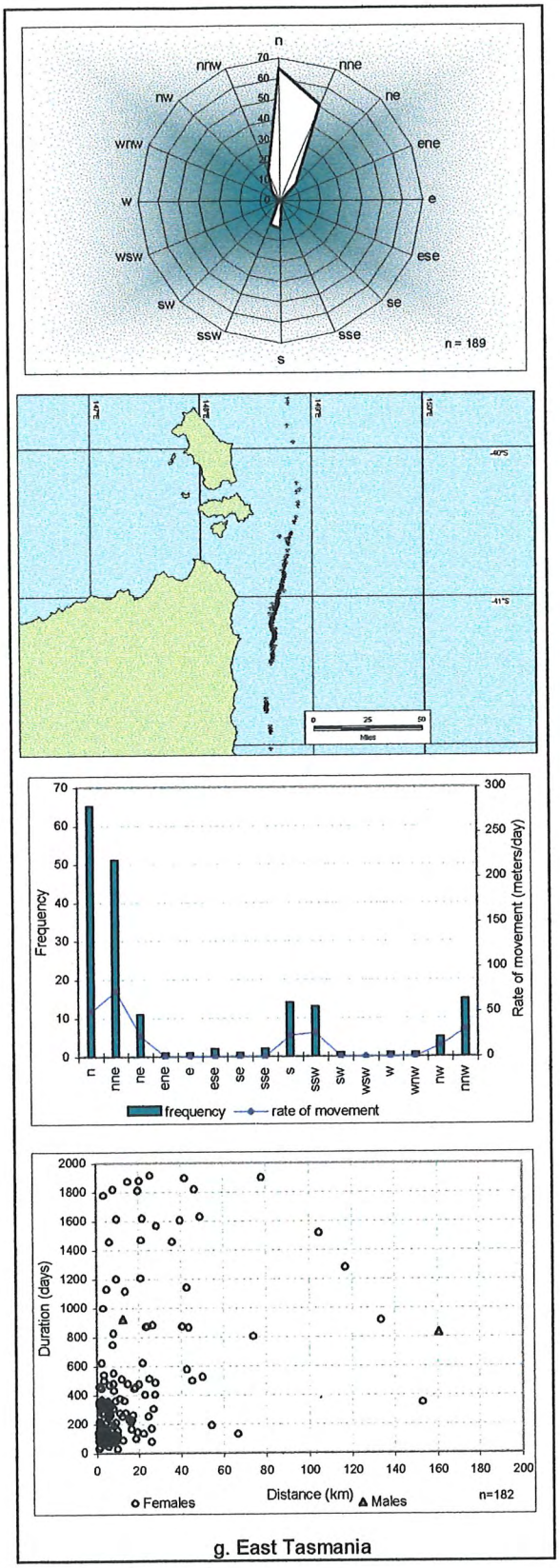


Figure 52g. Movement

Table 27; Annual movement by tagged crabs

Region	Category	Lon change	Direction	Distance*	Lat change	Direction	Distance
West Australia	*All*	0.02	east	1.03	-0.05	south	3.2 nmi
West of lon. 115°	Females	0.01	east	0.50	-0.04	south	2.43 nmi
	Males	0.04	east	2.02	-0.06	south	3.65 nmi
West Australia	*All*	-0.05	west	2.47	0.03	north	1.83 nmi
lon. 115°-117°	Females	-0.04	west	2.00	0.02	north	1.2 nmi
	Males	-0.08	west	3.96	0.06	north	3.61nmi
West Australia	*All*	-0.38	west	18.93	-0.13	south	7.82 nmi
lon.117°-121°	Females	-0.43	west	21.43	-0.13	south	7.82 nmi
	Males	-0.28	west	13.93	-0.11	south	6.63 nmi
South Australia	*All*	-0.04	west	1.97	0.02	north	1.24 nmi
lon. 136°-139°	Females	-0.04	west	1.97	0.02	north	1.24 nmi
	Males	-0.03	west	1.47	0.03	north	1.82 nmi
west Victoria	*All*	-0.11	west	5.16	0.09	north	5.4 nmi
lat. 40°-38°.40'	Females	-0.10	west	4.68	0.10	north	6.03 nmi
	Males	-0.13	west	6.07	0.07	north	4.21 nmi
west Tasmania	*All*	-0.03	west	1.35	0.08	north	4.82 nmi
north of lat. 41°	Females	-0.01	west	0.46	0.05	north	3.1 nmi
	Males	-0.04	west	1.81	0.10	north	6.01 nmi
east Tasmania	*All*	0.02	east	0.93	0.12	north	7.21 nmi
north of lat. 42°	Females	0.02	east	0.93	0.12	north	7.21 nmi
	Males	0.03	east	1.35	0.39	north	23.43 nmi

** Distance unit is nautical miles*

There is little oceanographic information for west Victoria. Information about west Tasmania (Cresswell, 2000) shows a north to south flowing current at the shelf edge. Insufficient time has elapsed since the majority of tagged crabs in this area were released to attribute much strength to the movement data. The data that has been collected shows northerly movement, which is consistant with the along-shelf movement in adjoining Victoria where there is a much longer time series.

In the future a spatial analysis which separates areas affected by Bass strait tidal flows and storm surges (Blackman et. al., 1987) and the more southerly areas of west Tasmania distant from this potential effect, should be used. A similar approach should also be used off eastern Bass strait where a winter salinity cascade (Tomczak, 1981) has the potential to affect crab movement.

Wyrtki (1971) identified a northerly component in the movement of the Intermediate Antarctic water mass between Antarctica and Australia, the undercurrents and upwelling water masses along Australia's southern margin being derived from this. Initially it seemed reasonable to speculate there may be a northerly flow under the south flowing Zeehan Current, the SST image in Figure 14a seemed to support this possibility, but the studies by Cresswell (2000) provided no evidence of this scenario.

Thus in attempting to explain the movement of *P. gigas* off west Tasmania and within the broader whole fishery context it became difficult to accept a hypothesis that the crabs travel with the current in this region or elsewhere. Therefore the alternative hypothesis, that the crabs move against the current, was explored. This hypothesis provided a plausible explanation for the crab's movement which sat well with the existing body of knowledge from many disciplines in published literature, the long time series experience of fishermen and the information collected by this investigation.

4.10. Population Structure

4.10.1. Maximum size

Hale (1927 – 29) states the maximum size recorded for a male of the species is at least 13.6 kg. Portland fisherman John Guidera has preserved a crab that was 14.5 kg. Maximum size recorded for a female of the species is 6.0 kg (Levings et. al. 1995). The species by weight, grows to be the second largest in the world after the giant Japanese spider crab, *Macrocheira kaempferi.* (Jones & Morgan, 1994)

Many thousands of individuals have been examined during this study and the mean sizes of the 10 largest crabs for each region of each sex were determined (Figure 92) The most common sizes taken by fishermen range between 2 to 8 kg. Even in areas that had been subjected to very little fishing effort the bulk of the targeted fishery catch prior to implementation of size limits was comprised of crabs that were 130 to 190 mm long and equivalent to a weight range of 1.6 to 5.4 kg. Figure 53 below, describes pack-out information provided by F. Trewartha and Sons (Warrnambool, Victoria), during the fish down of virgin stocks in 1992-93. Minimum size regulation (150mm) was not in force at this time. A 150mm female weighs approximately 2.14 kg, a 150mm male approximately 2.46 kg.

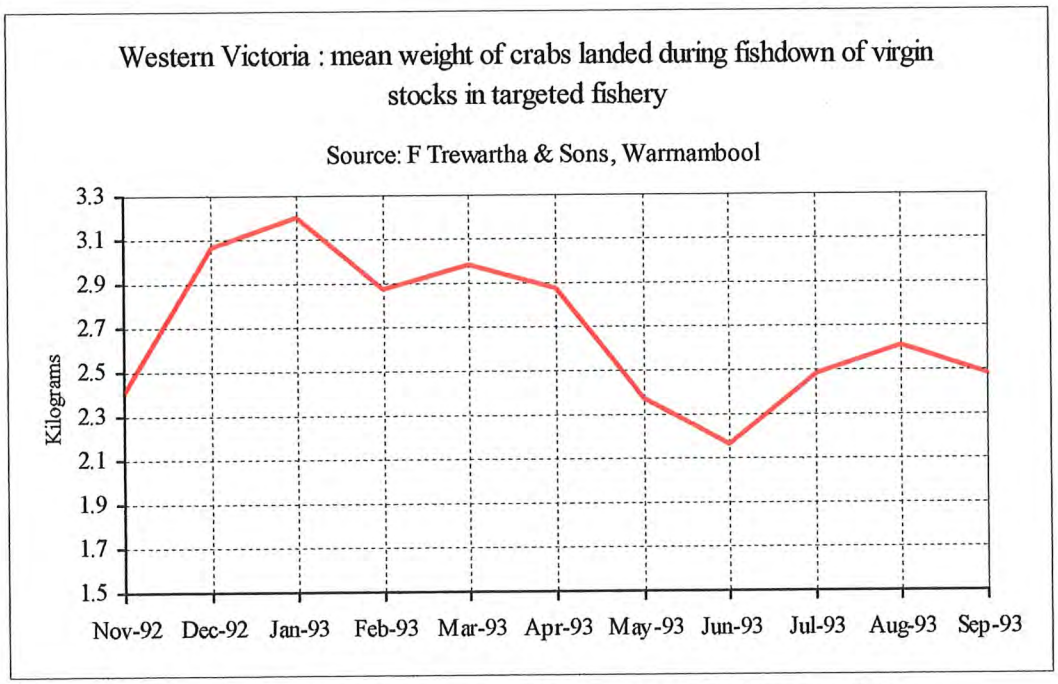


Figure 53. Processor pack out records of average individual weights.
Although *P. gigas* males reach 14.5 kg and females 6.0 kg, the targeted fishery has always been based on smaller sizes.

4.10.2 Sex Ratio

Sex ratios in the total catch for all sites from spring 1993 to autumn 2000 are described in Figure 54. South Australian data provide a nearly continuous time series along with seasonal snapshots from other sites. In South Australia the proportion of females increased from spring to summer and decreased from autumn to winter. Females were numerically more abundant in the catch from the targeted fishery for sizes below approximately 170 mm in all seasons, with the exception of winter where the proportion of males increased and exceeded that of females. Most of the population larger than 170 mm carapace length are males which grow to more than double the size of females.

Across sites, the proportion of sexes varied from 18% females in winter in South Australia to 89% females in spring in eastern Tasmania. The eastern Tasmanian sex ratios were not typical and fishermen report that there is a low abundance of males during all seasons in this area. Sex ratio is highly variable in crabs and local variation from 1:1 reflects differential mortality, migration and habitat selection (Cobb and Caddy 1989). Temperature differences between sites may modify the timing of seasonal patterns in the proportions of sexes within a year and interannual variation is also likely to occur.

The abundance of crabs in all samples reflects feeding activity and the response to baited traps. Tank holding of crabs indicate that they do not feed when they are moulting or extruding and fixing their eggs, thus sex ratio in the catch is linked to these activities.

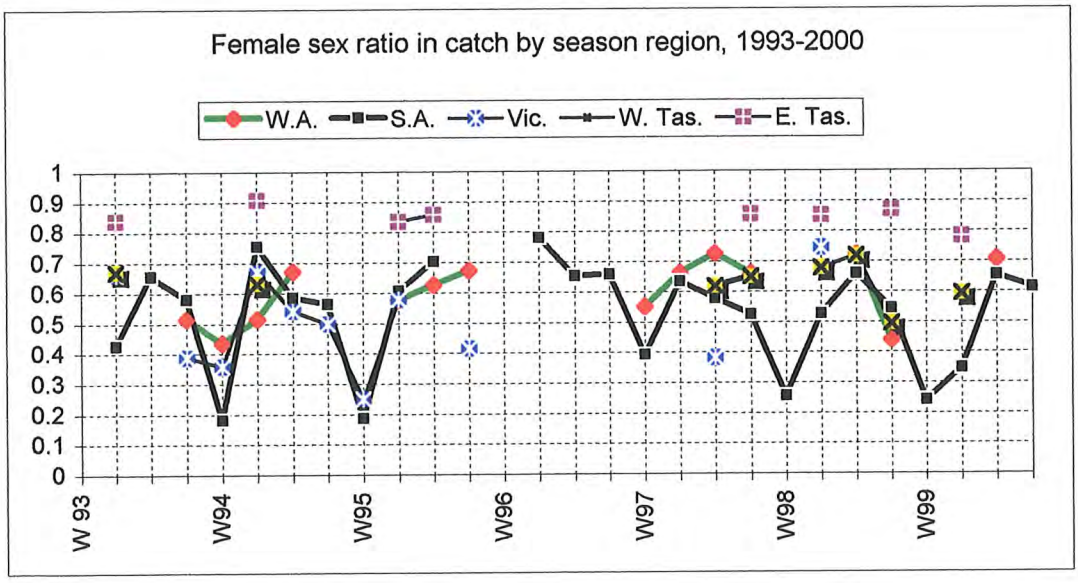


Figure 54. Female sex ratio in catches

Female abundance in the catch is low during the winter when moulting or egg extrusion and fixing occurs. East Tasmania has a low abundance of males irrespective of season.

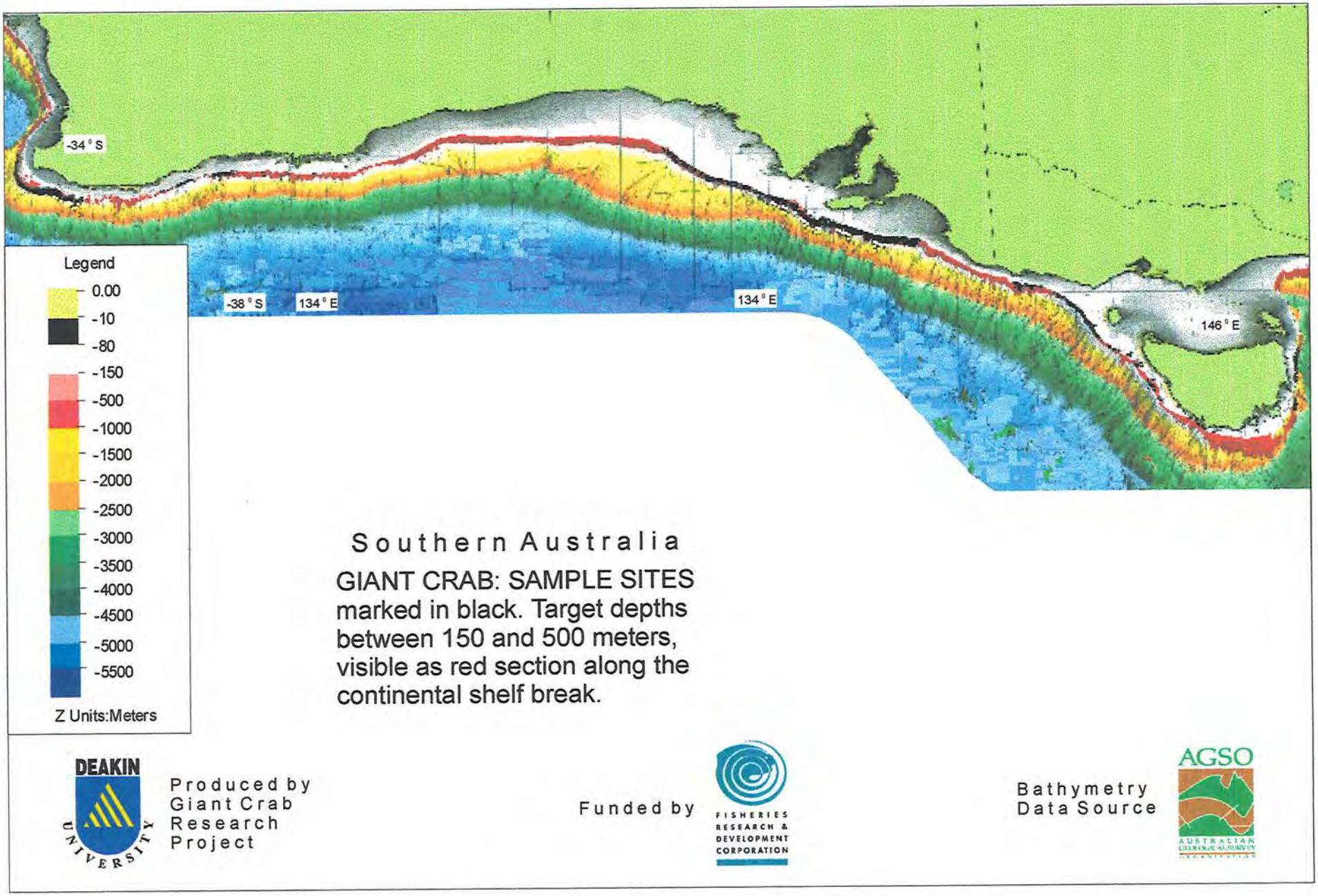

-34 ° S
-38 ° S
134 ° E
134 ° E
146 ° E
Legend
0.00
-10
-80
-150
-500
-1000
-1500
-2000
-2500
-3000
-3500
-4000
-4500
-5000
-5500
Z Units:Meters
Southern Australia
GIANT CRAB: SAMPLE SITES marked in black. Target depths between 150 and 500 meters, visible as red section along the continental shelf break.
DEAKIN UNIVERSITY
Produced by Giant Crab Research Project
Funded by
FISHERIES RESEARCH & DEVELOPMENT CORPORATION
Bathymetry Data Source
AGSO
AUSTRALIAN GEOLOGICAL SURVEY ORGANISATION

Figure 55:

4.10.3.1. Australia; population analysis, male & female combined

Australia wide; the carapace lengths of all of the sampled populations, male and female were combined and were analysed in the following series of means tables, interaction plots and Student Newman-Keuls significance tests; by the effects of year, depth, region, sex and season. Sampling locations off southern Australia are shown in Figure 55.

Both sexes combined; carapace length for the entire fishery was analysed by;

-Year
-Depth
-Region
-Sex
-Season

Male and female components were then analyzed similarly but separately.

Australia wide; Male & Female combined

Table 28

ANOVA Table for Car Lgth

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Year	7	390583.64	55797.66	137.14	<.0001	960.00	1
Depth Rang	10	989062.89	98906.29	243.10	<.0001	2430.98	1
Region	4	1453058.14	363264.53	892.86	<.0001	3571.42	1
Sex	1	1260210.04	1260210.04	3097.43	<.0001	3097.43	1
Season	3	672063.21	224021.07	550.61	<.0001	1651.84	1
Residual	77135	31382915.39	406.86				

Analysis of variance of pooled data (above) showed highly significant differences (P<.0001) within the categories of year, depth, region, sex and season. Mean size within any given sample will therefore reflect these effects and so must be interpreted in this light. These are the variables within this fishery based assessment.

YEAR

Table 29

Means Table for Car Lgth
Effect: Year

Year	Count	Mean	Std. Dev.	Std. Err.
1993	6002	141.04	19.03	0.25
1994	16744	149.31	20.44	0.16
1995	13238	153.25	22.30	0.19
1996	5177	152.78	18.34	0.26
1997	6523	148.01	21.95	0.27
1998	14456	151.66	22.87	0.19
1999	14263	151.57	23.25	0.20
2000	758	144.04	16.32	0.59

The interaction plot for mean carapace length by year is presented below;

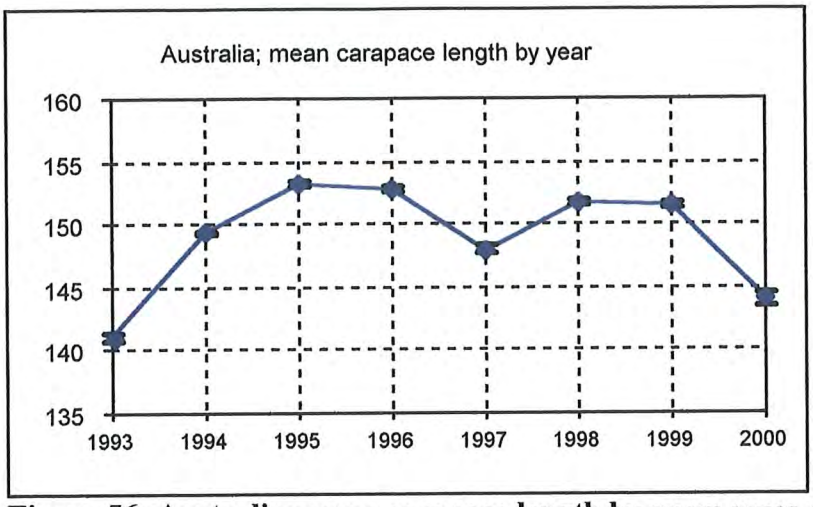


Figure 56: Australia; mean carapace length by year; sexes combined

A post hoc Student - Newman-Keuls test of significance, tabulated below, showed there were significant differences between all years except where 1995 was compared with 1997, and 1998 was compared with 1999.

Table 30

Student-Newman-Keuls for Car Lgth (both sexes)
Effect: Year
Significance Level: 5%

Year	1993	1994	1995	1996	1997	1998	1999	2000
1993		**S**	**S**	**S**	**S**	**S**	**S**	**S**
1994			**S**	**S**	**S**	**S**	**S**	**S**
1995				**S**	*NS*	**S**	**S**	**S**
1996					**S**	**S**	**S**	**S**
1997						**S**	**S**	**S**
1998							*NS*	**S**
1999								**S**

S = *significant at this level*

NS = Not significant at this level

DEPTH

Table 31

Means Table for Car Lgth
Effect: Depth Range (m)

Metres	Count	Mean	Std. Dev.	Std. Err.
50	5	193.60	14.47	6.47
100	566	147.08	20.90	0.88
150	21585	155.33	17.03	0.12
200	17701	149.21	119.48	0.15
250	12555	151.87	23.63	0.21
300	14974	145.56	23.38	0.19
350	7157	147.29	25.62	0.30
400	1938	148.42	30.65	0.70
450	596	132.18	31.98	1.31
500	96	124.65	28.65	2.92
550	15	137.80	20.36	5.26

The interaction plot for mean carapace length by year is presented below;

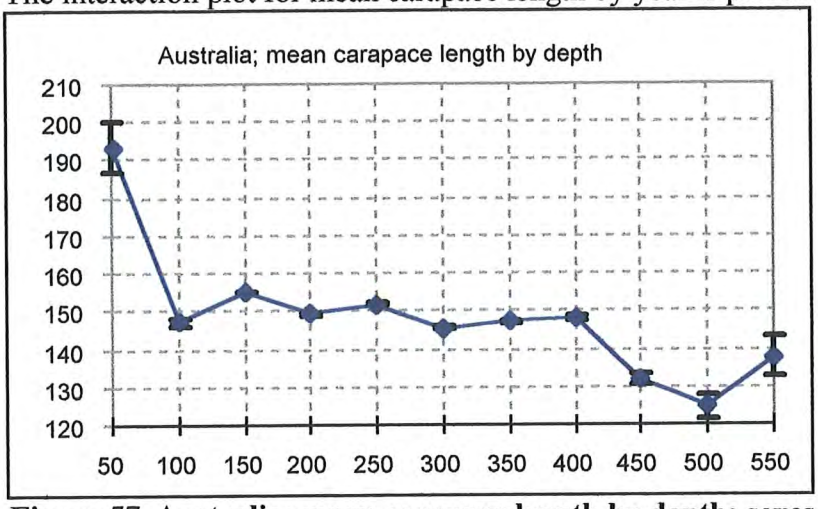


Figure 57. Australia; mean carapace length by depth; sexes combined

A post hoc Student - Newman-Keuls test of significance, tabulated below, showed there were significant differences in the mean size of crabs caught in 50 metres compared with all other depths but the small sample size (5) for 50 metres should be noted. There was a trend towards smaller sizes as depth increased from 450 metres and deeper.

Table 32

Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%

Metres	50	100	150	200	250	300	350	400	450	500	550
50		**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**
100			*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**S**	**S**	*NS*
150				*NS*	*NS*	*NS*	*NS*	*NS*	**S**	**S**	**S**
200					*NS*	*NS*	*NS*	**S**	**S**	*NS*	*NS*
250						*NS*	*NS*	*NS*	**S**	**S**	**S**
300							*NS*	*NS*	**S**	**S**	*NS*
350								*NS*	**S**	**S**	*NS*
400									**S**	**S**	*NS*
450										*NS*	*NS*
500											**S**

S = *significant at this level*

NS = Not significant at this level

REGION

Table 33

Means Table for Car Lgth
Effect: Region

	Count	Mean	Std. Dev.	Std. Err.
WA	11623	141.43	21.57	0.20
SA	44278	152.67	20.91	0.10
Vic	6705	149.34	23.25	0.28
W Tas	6038	141.53	22.79	0.29
E Tas	8517	156.81	19.93	0.22

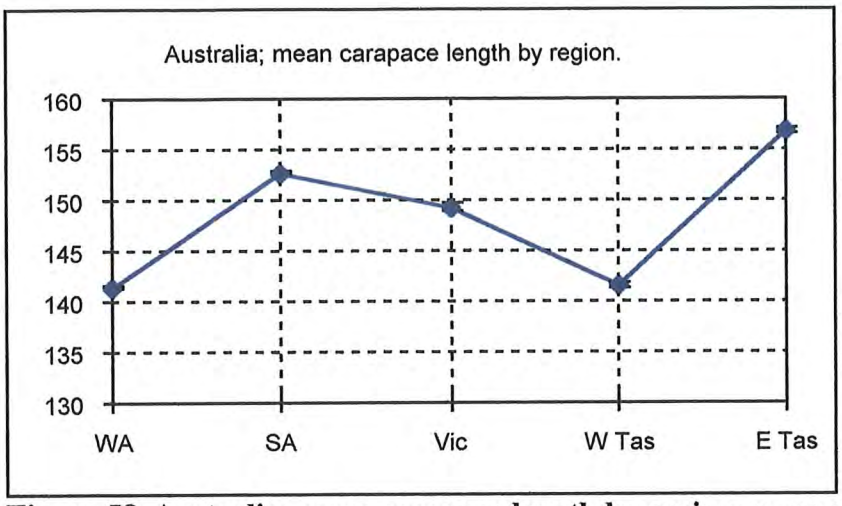


Figure 58. Australia; mean carapace length by region; sexes combined

A post hoc Student - Newman-Keuls test of significance, tabulated below, showed that there were significant differences in mean size between regions. The exception to this was West Tasmania compared to West Australia. West Tasmania and in particular in the northwest portion has been heavily exploited and fished down below the current size limit. West Australian crabs are generally smaller due to environmental effects. Although the mean size from both regions are similar the underlying reasons are quite different.

Table 34

Student-Newman-Keuls for Car Lgth
Effect: Region
Significance Level: 5%

Region	E Tas	W Tas	Vic	SA	WA
E Tas		**S**	**S**	**S**	**S**
W Tas			**S**	**S**	*NS*
SA					**S**
Vic					
WA					

S = *significant at this level*
NS = Not significant at this level

SEX

Table 35

Means Table for Car Lgth
Effect: Sex

	Count	Mean	Std. Dev.	Std. Err.
F	45008	147.35	16.79	0.08
M	32153	154.36	26.92	0.15

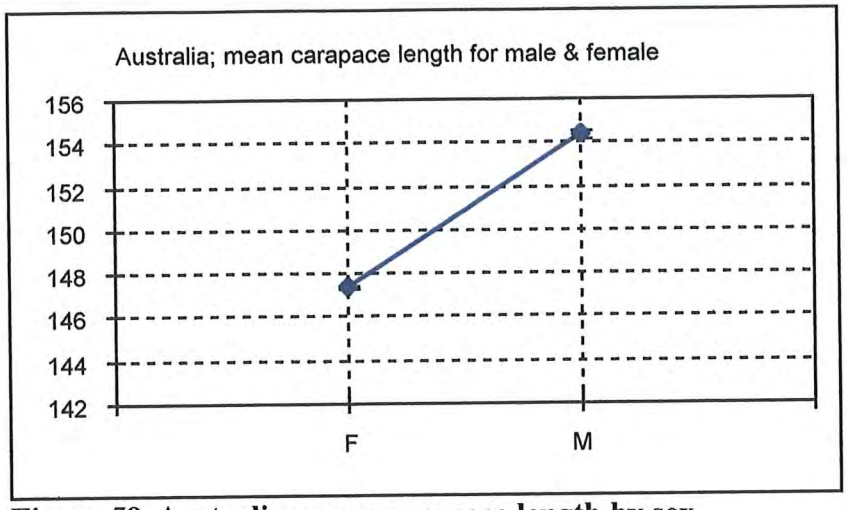


Figure 59. Australia; mean carapace length by sex

The female population has a significantly smaller mean length than the male as shown below.

Table 36

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%

	Mean Diff.	Crit. Diff.	Sig?
F, M	-7.01	0.29	**S**

S = significant at this level

SEASON

Table 37

Means Table for Car Lgth
Effect: Season

	Count	Mean	Std. Dev.	Std. Err.
Summer	17703	152.55	18.46	0.14
Autumn	16193	156.05	20.78	0.16
Winter	9295	153.06	28.06	0.29
Spring	33970	145.57	21.04	0.11

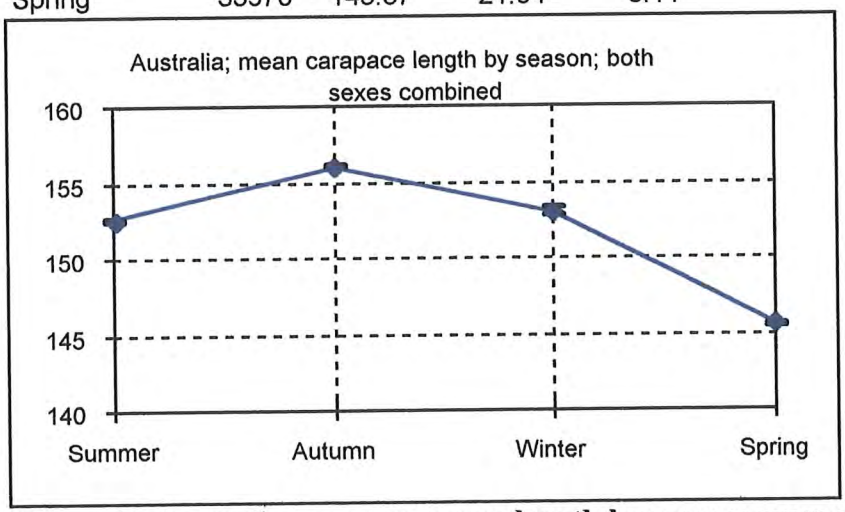


Figure 60. Australia; mean carapace length by season; sexes combined

A post hoc Student - Newman-Keuls test of significance, tabulated below, showed that there were significant differences in mean size between seasons.

Table 38

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%

Season	Summer	Autumn	Winter	Spring
Summer		S	S	S
Autumn			S	S
Winter				S
Spring				

S = *significant at this level*

4.10. 3.2 Australia; population analysis, females

Female carapace length for the entire fishery was analysed by;

- Regions
- seasons
- depths

Table 39

ANOVA Table for Car Lgth
Split by sex; female

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Region	4	992391.13	248097.78	1071.83	<.0001	4287.31	1
Season	3	208221.25	69407.08	299.85	<.0001	899.55	1
Depth Range	10	617369.06	61736.91	266.71	<.0001	2667.14	1
Residual	44990	10413924.48	231.47				

There were significant differences within the categories of region, season and depth (P = <.0001).

The following series of means tables, interaction plots and Student Newman-Keuls significance tests; analyse the effects of region, season, and depth.

REGION

Table 40

Means Table for Car Lgth
Effect: Region
Split by sex; female

	Count	Mean	Std. Dev.	Std. Err.
WA	6787	137.26	16.08	0.20
SA	23729	148.81	15.43	0.10
Vic	3645	146.68	17.46	0.29
W Tas	3632	142.22	18.05	0.30
E Tas	7215	154.95	15.49	0.18

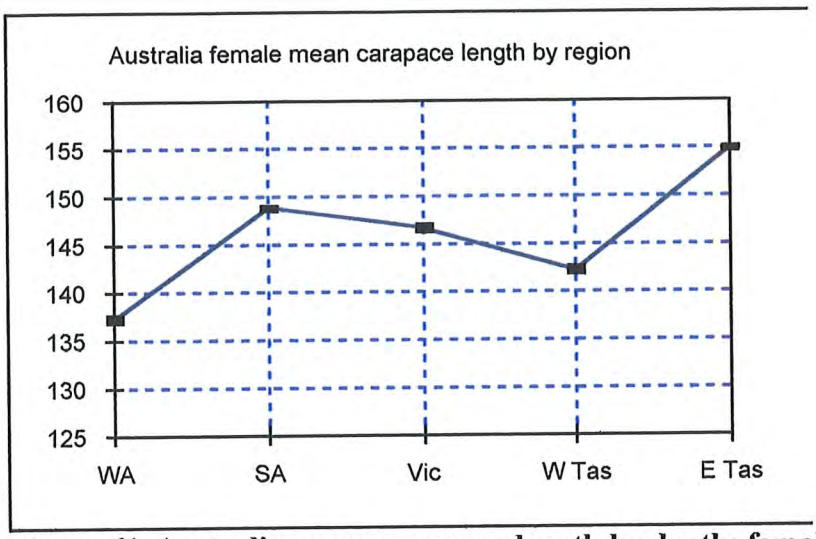


Figure 61. Australia; mean carapace length by depth; female

The Student- Newman- Kuels test (below) showed that regions were significantly different to each other excepting where West Australia was compared with West Tasmania. Although apparently similar the underlying reasons are different. West Australia's small mean size reflects a smaller moult increment and an inability by the population to successfully moult through to larger sizes, whereas West Tasmania's primarily reflects depletion of larger size classes as the result of heavy exploitation (see discussion section).

Table 41

Student-Newman-Keuls for Car Lgth
Effect: Region
Significance Level: 5%

Region	E Tas	W Tas	Vic	SA	WA
E Tas		**S**	**S**	**S**	**S**
W Tas			**S**	**S**	*NS*
SA					**S**
Vic					
WA					

S = *significant at this level*

NS = Not significant at this level

SEASON

Table 42

Means Table for Car Lgth
Effect: Season
Split by: Sex
Cell: Female

Season	Count	Mean	Std. Dev.	Std. Err.
Summer	11137	148.86	14.74	0.14
Autumn	9896	152.79	15.93	0.16
Winter	2845	143.06	22.77	0.43
Spring	21130	144.58	16.49	0.11

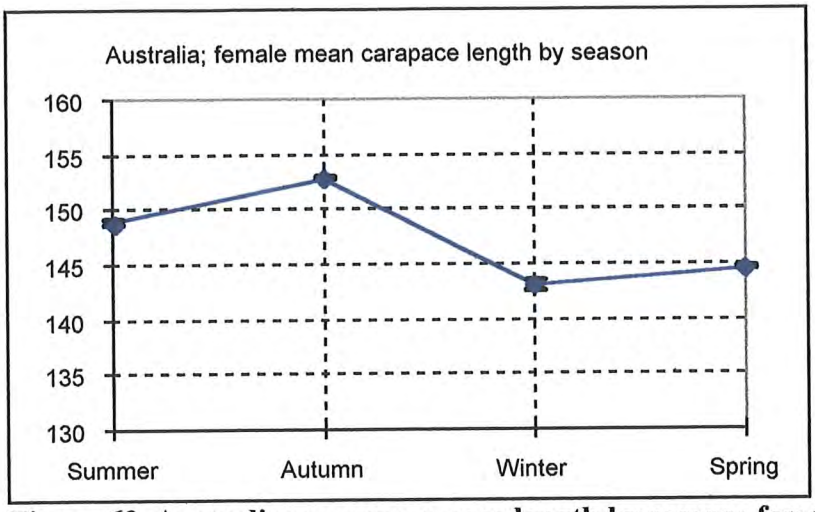


Figure 62. Australia; mean carapace length by season; female

All seasons were significantly different to each other as shown in the S-N-K test below

Table 43

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%
Split By: Sex
Cell: Female

Season	Summer	Autumn	Winter	Spring
Summer		**S**	**S**	**S**
Autumn			**S**	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant

DEPTH

Table 44

Means Table for Car Lgth
Effect: Depth Range (m)
Split By: Sex
Cell: Female

Depth	Count	Mean	Std. Dev.	Std. Err.
50	2	204.50	4.95	3.50
100	399	146.10	18.32	0.92
150	13752	151.99	13.11	0.11
200	11111	147.49	15.31	0.15
250	7303	149.22	18.65	0.22
300	8460	142.45	17.21	0.19
350	3101	139.81	18.41	0.33
400	587	134.58	23.57	0.97
450	249	126.08	28.06	1.78
500	34	121.03	24.04	4.12
550	10	135.50	19.85	6.28

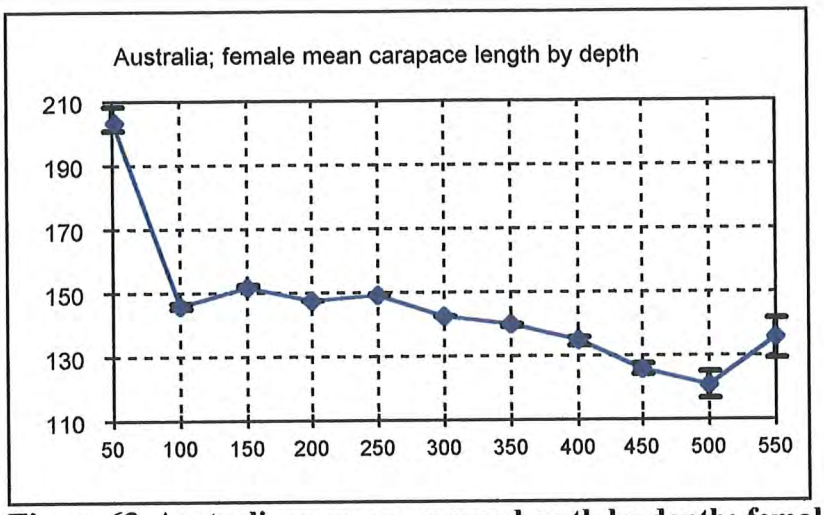


Figure 63. Australia; mean carapace length by depth; female

A post hoc S-N-K test of significance, tabulated below, showed there were significant differences in the mean size of crabs caught in 50 metres compared with all other depths but the small sample size (2) for 50 metres should be noted. There was a trend towards smaller sizes as depth increased from 400 metres and deeper but small sample sizes in the deeper samples should be noted.

Table 45

Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%
Split By: Sex
Cell: Female

Depth	50	100	150	200	250	300	350	400	450	500	550
50		**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**
100			*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**S**	**S**	*NS*
150				*NS*	*NS*	*NS*	*NS*	**S**	**S**	**S**	**S**
200					*NS*	*NS*	*NS*	*NS*	**S**	**S**	*NS*
250						*NS*	*NS*	*NS*	**S**	**S**	*NS*
300							*NS*	*NS*	**S**	**S**	*NS*
350								*NS*	**S**	**S**	*NS*
400									*NS*	**S**	*NS*
450										*NS*	*NS*
500											**S**
550											

S = significant at this level
NS = not significant

4.10.3.3 Australia; population analysis, males.

Australia wide; males

Carapace length for the entire fishery was analysed by;

- regions
- seasons
- depths

Analysis of variance in Table 46 below showed there were significant differences (P = <.0001) in the mean size of males within the categories of region, season and depth.

Table 46

ANOVA Table for Car Lgth
Split by sex; Male

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Region	4	772027.01	193006.75	297.08	<.0001	1188.34	1
Season	3	813243.98	271081.33	4117.26	<.0001	1251.78	1
Depth Range	10	444268.81	44462.88	68.44	<.0001	684.39	1
Residual	32135	20877152.14	649.67				

REGION

Table 47

Means Table for Car Lgth
Effect: region
Split by: Sex
Cell: Male

State	Count	Mean	Std. Dev.	Std. Err.
WA	4836	147.29	26.40	0.38
SA	20549	157.12	25.10	0.18
Vic	3060	152.51	28.35	0.51
W Tas	2406	140.49	28.46	0.58
E Tas	1302	167.13	33.83	0.94

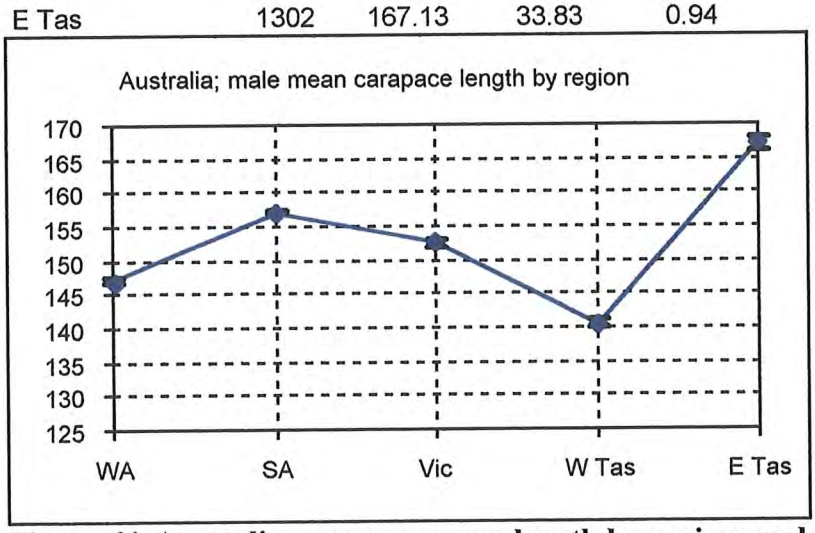


Figure 64. Australia; mean carapace length by region; male

A SNK test tabulated below showed there were significant differences between all regions.

Table 48

Student-Newman-Keuls for Car Lgth
Effect: Region
Significance Level: 5%
Split by sex; Male

Region	E Tas	W Tas	Vic	SA	WA
E Tas		**S**	**S**	**S**	**S**
W Tas			**S**	**S**	**S**
Vic				**S**	**S**
SA					**S**
WA					

S = *significant at this level*

SEASON

Table 49

Means Table for Car Lgth
Effect: Season
Split by: Sex
Cell: Male

	Count	Mean	Std. Dev.	Std. Err.
Summer	6566	158.81	22.29	0.28
Autumn	6297	161.12	25.86	0.33
Winter	6450	157.46	29.03	0.36
Spring	12840	147.19	26.83	0.24

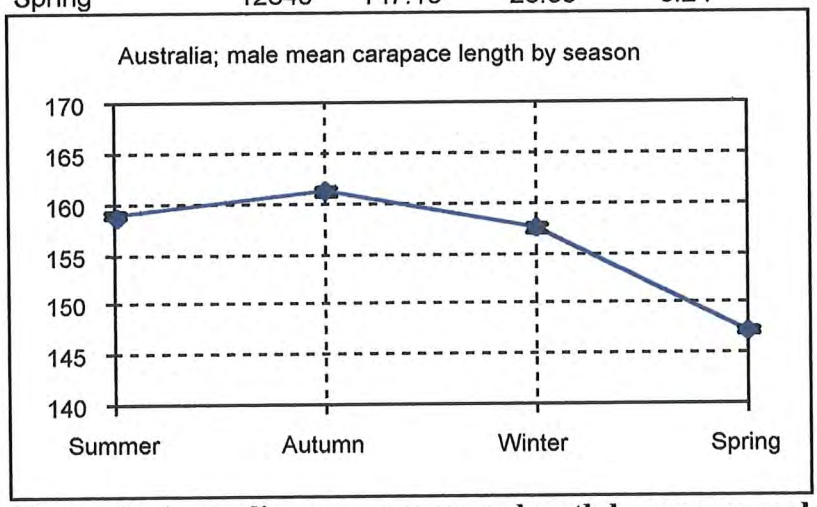


Figure 65. Australia; mean carapace length by season; male

SNK analysis (below) of male carapace length by season across all regions showed there were significant differences between seasons with autumn being the largest and spring the smallest.

Table 50

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%
Split By: Sex
Cell: Male

Season	Summer	Autumn	Winter	Spring
Summer		**S**	**S**	**S**
Autumn			**S**	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant

DEPTH

Table 51

Means Table for Car Lgth
Effect: Depth Range (m)
Split By: Sex
Cell: Male

Depth	Count	Mean	Std. Dev.	Std. Err.
50	3	186.33	14.43	8.33
100	167	149.41	25.96	2.01
150	7833	161.19	21.07	0.24
200	6590	152.10	24.71	0.30
250	5252	155.56	28.78	0.40
300	6487	149.63	29.06	0.36
350	4056	153.01	28.70	0.45
400	1351	154.43	31.43	0.86
450	347	136.56	33.89	1.82
500	62	126.63	30.89	3.92
550	5	142.40	22.90	10.24

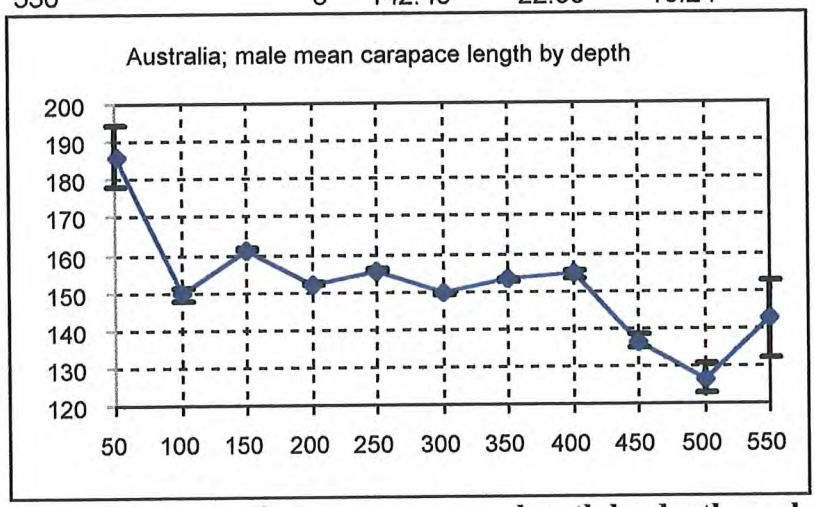


Figure 66. Australia; mean carapace length by depth; male

A post hoc S-N-K test of significance, tabulated below, showed there were significant differences in the mean size of crabs caught in 50 metres compared with all other depths but the small sample size (3) for 50 metres should be noted. There was a trend towards smaller sizes from 400 metres and deeper with crabs at 500

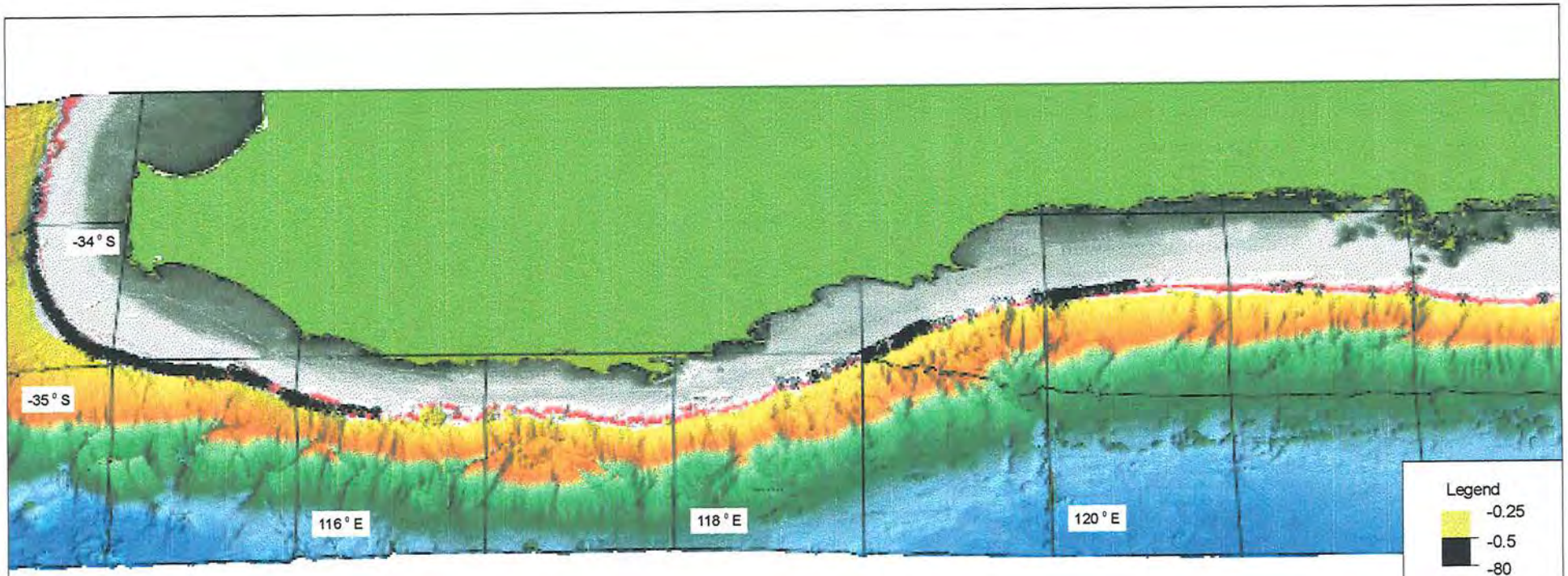
metres being significantly smaller than those in all shallower depths. The small sample size (5) at 550 metres should be noted.

Table 52

Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%
Split By: Sex
Cell: Male

Depth	50	100	150	200	250	300	350	400	450	500	550
50		**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**
100			*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**S**	*NS*
150				*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**S**	*NS*
200					*NS*	*NS*	*NS*	*NS*	*NS*	**S**	*NS*
250						*NS*	*NS*	*NS*	*NS*	**S**	*NS*
300							*NS*	*NS*	*NS*	**S**	*NS*
350								*NS*	*NS*	**S**	*NS*
400									*NS*	**S**	*NS*
450										*NS*	*NS*
500											*NS*
550											

S = significant at this level
NS = not significant



South of Western Australia

GIANT CRAB: SAMPLE SITES marked in black. Target depths between 200 and 350 meters, visible as red section along the continental shelf break.

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Bathymetry Data Source AGSO AUSTRALIAN GEOLOGICAL SURVEY ORGANISATION

Figure 67:

4.10.4. West Australia; population analysis; male and female combined

The carapace lengths of the sampled population in each of the regions were analysed with male and female combined together. The following series of anova and means tables, interaction plots and Student Newman-Keuls significance tests; show the effects of year, depth, region, sex and season on mean size. Sampling locations off West Australian are shown in Figure 67 and further broken down by season in the Appendix 1.

Table 53

ANOVA Table for Car Lgth
Split By: Region
Cell: Western Australia
Row Exclusion: Database.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	5	23162.40	4632.48	11.09	<.0001	55.44	1
Season	3	78459.60	26153.20	62.60	<.0001	187.79	1
Sex	1	261036.59	261036.59	624.77	<.0001	624.77	1
Year	6	190364.11	27194.87	65.09	<.0001	455.62	1
Residual	11606	4849108.57	417.81				

There were highly significant differences (P = <.0001) within the categories of depth, season, sex and year

DEPTH

Table 54

Means Table for Car Lgth
Effect: Depth Range (m)
Effect: region
Cell: Western Australia
Row Exclusion: Database.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
150	13	143.08	11.12	3.09
200	2	154.00	15.56	11.00
250	1755	143.32	19.77	0.47
300	6592	140.30	21.60	0.27
350	3231	142.68	22.37	0.39
400	30	143.20	16.25	2.97

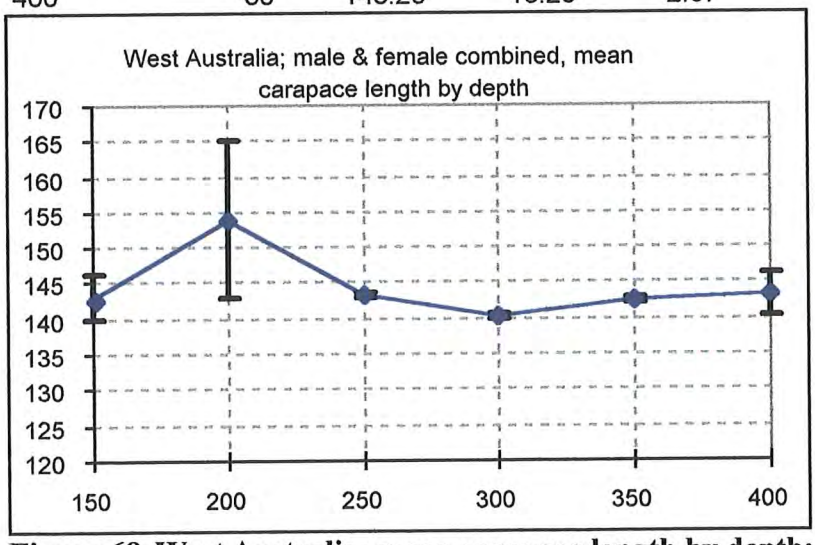

Figure 68. West Australia; mean carapace length by depth; sexes combined

A post hoc S-N-K test showed there were no significant differences between the mean size of crabs taken in depths from 150 to 400 metres.

SEASON

Table 55

Means Table for Car Lgth
Effect: Season
Effect: region
Cell: Western Australia
Row Exclusion: Database.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	3892	142.53	20.04	0.32
Autumn	863	141.90	117.82	0.61
Winter	1057	146.71	22.84	0.70
Spring	5811	139.67	22.60	0.30

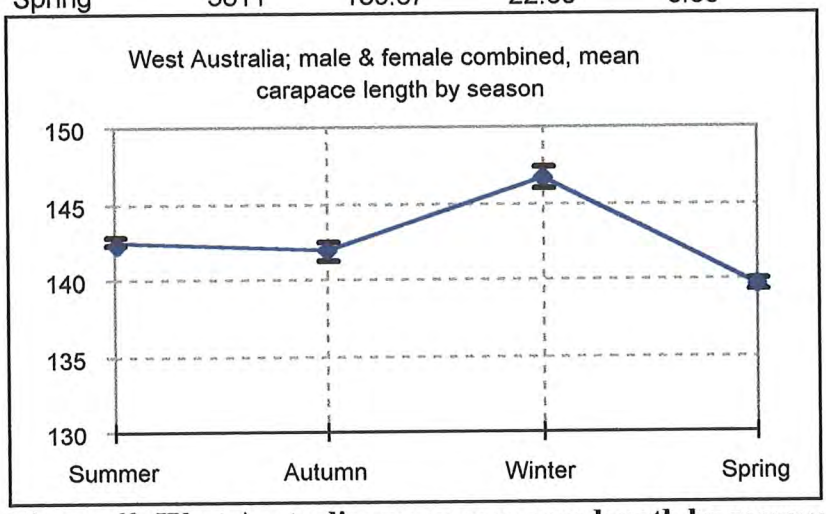

Figure 69. West Australia; mean carapace length by season; sexes combined

A post hoc S-N-K test tabulated below showed that the mean size of crabs taken in summer and in autumn were significantly smaller compared to winter and significantly larger compared with spring. There was no significant difference between summer and autumn.

Table 56

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%

Season	Summer	Autumn	Winter	Spring
Summer		*NS*	**S**	**S**
Autumn			**S**	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant at this level

SEX

Table 57

Means Table for Car Lgth
Effect: Sex
Effect: region
Cell: Western Australia
Row Exclusion: Database.ssd

	Count	Mean	Std. Dev.	Std. Err.
F	6787	137.26	16.08	0.20
M	4836	147.29	26.40	0.38

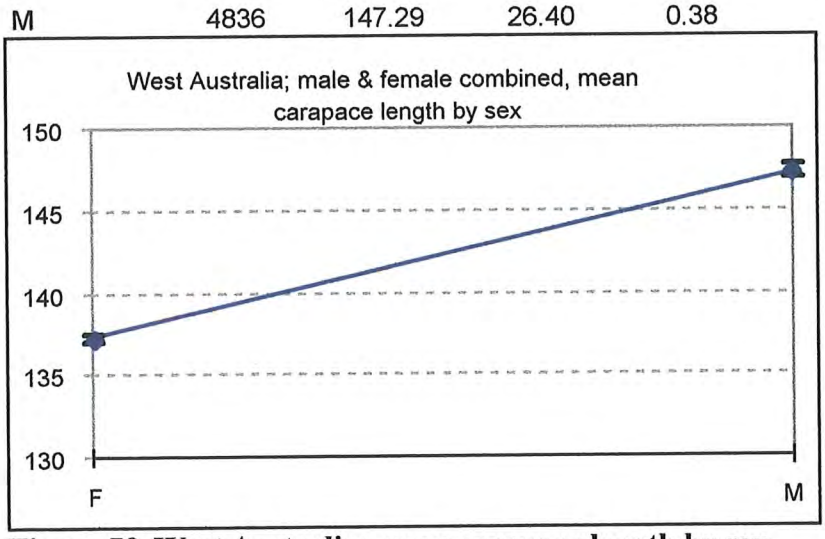

Figure 70. West Australia; mean carapace length by sex

A post hoc S-N-K test tabulated below showed there was a significant difference between the mean size of male and female crabs in the population samples.

Table 58

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%
Effect: region
Cell: Western Australia
Row Exclusion: Database.ssd

	Mean Diff.	Crit. Diff.	Sig?
F, M	-10.02	0.75	**S**

S = significant at this level

YEAR

Table 59

Means Table for Car Lgth
Effect: Year
Effect: region
Cell: Western Australia
Row Exclusion: Database.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1994	4644	142.94	22.55	0.33
1995	2383	139.82	21.29	0.44
1996	1751	148.14	21.09	0.50
1997	796	133.44	22.19	0.79
1998	316	143.26	17.30	0.97
1999	1226	136.17	15.77	0.45
2000	342	138.73	16.37	0.85

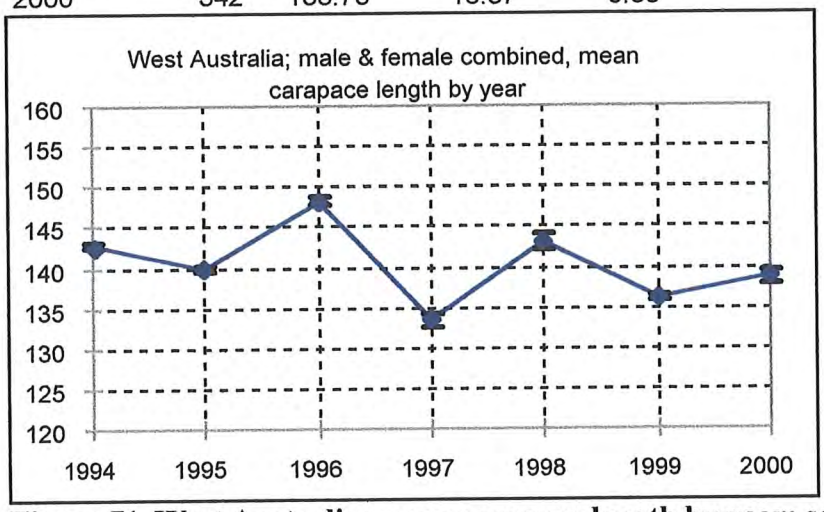

Figure 71. West Australia; mean carapace length by year; sexes combined

A post hoc S-N-K test tabulated below showed there was a significant difference between the mean size of crabs in most years except 1994 compared with 1998; and 1995 compared with 2000

Table 60

Student-Newman-Keuls for Car Lgth
Effect: Year
Significance Level: 5%
Effect: region
Cell: Western Australia
Row Exclusion: Database.ssd

Year	1994	1995	1996	1997	1998	1999	2000
1994		**S**	**S**	**S**	*NS*	**S**	**S**
1995			**S**	**S**	**S**	**S**	*NS*
1996				**S**	**S**	**S**	**S**
1997					**S**	**S**	**S**
1998						**S**	**S**
1999							**S**
2000							

S = significant at this level
NS = not significant at this level

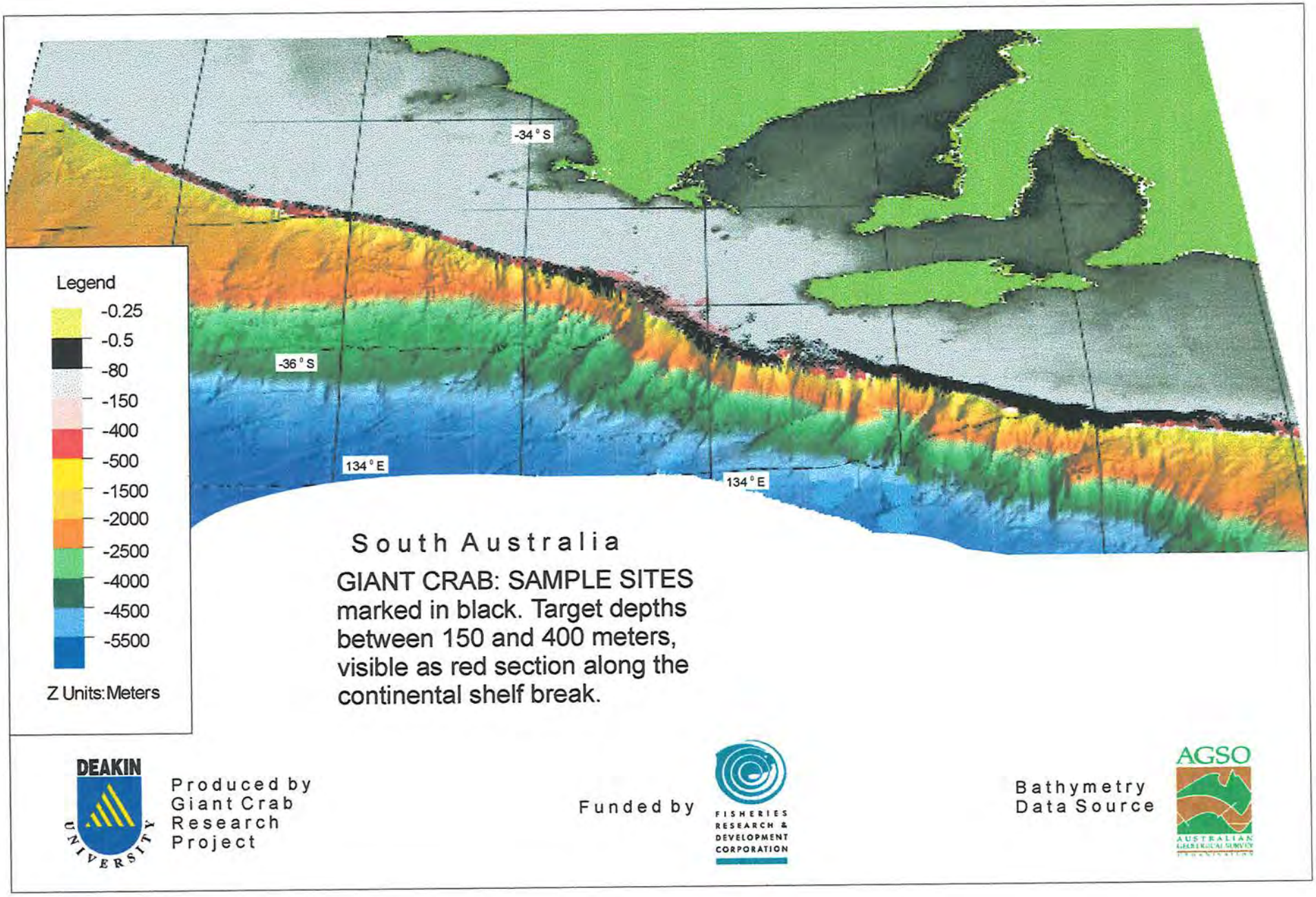
-34 ° S
-36 ° S
134 ° E
134 ° E
Legend
-0.25
-0.5
-80
-150
-400
-500
-1500
-2000
-2500
-4000
-4500
-5500
Z Units:Meters
South Australia
GIANT CRAB: SAMPLE SITES marked in black. Target depths between 150 and 400 meters, visible as red section along the continental shelf break.
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Figure 72:

4.10.5. South Australia; population analysis; male and female combined

Sampling locations off South Australia are shown in Figure 72 and further broken down by season in the Appendix 1.

Table 61

ANOVA Table for Car Lgth
Split By: Region
Cell: South Australia
Row Exclusion: Database.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Rang	9	733334.26	81481.58	211.69	<.0001	1905.23	1
Season	3	318182.71	106060.91	275.55	<.0001	826.65	1
Sex	1	962789.85	962789.85	2501.36	<.0001	2501.36	1
Year	7	183977.75	26282.54	68.28	<.0001	477.98	1
Residual	44257	17034827.10	384.91				

There were highly significant differences (P = <.0001) within the categories of depth, season, sex and year were all

DEPTH

Table 62

Means Table for Car Lgth
Effect: Depth Range (m)
Effect: region
Cell: South Australia
Row Exclusion: Database.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	15	147.33	14.19	3.66
150	19891	155.72	16.64	0.12
200	11002	150.45	17.57	0.17
250	4690	151.07	22.04	0.32
300	3169	151.44	28.84	0.51
350	3081	151.59	28.87	0.52
400	1762	149.02	30.96	0.74
450	563	130.84	32.09	1.35
500	90	125.18	29.21	3.08
550	15	137.80	20.36	5.26

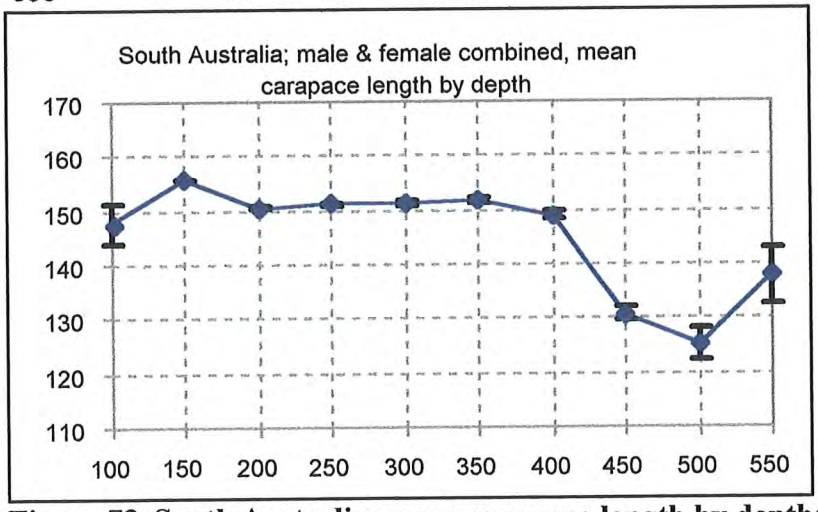

Figure 73. South Australia; mean carapace length by depth; sexes combined

A post hoc S-N-K test tabulated below showed significant differences in the mean size of crabs taken in depths from 100 to 350 metres compared with those taken in depths of 450 metres and deeper. The small sample size from 100 metres and 550 metres should be noted

Table 63

Effect: region
Cell: South Australia
Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%

Depth	100	150	200	250	300	350	400	450	500	550
100		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	**S**	**S**	**S**
150			*NS*	*NS*	*NS*	*NS*	*NS*	**S**	**S**	**S**
200				*NS*	*NS*	*NS*	*NS*	**S**	**S**	**S**
250					*NS*	*NS*	*NS*	**S**	**S**	**S**
300						*NS*	*NS*	**S**	**S**	**S**
350							*NS*	**S**	**S**	**S**
400								**S**	**S**	**S**
450									*NS*	**S**
500										**S**
550										

S = significant at this level
NS = Not significant at this level

SEASON

Table 64

Means Table for Car Lgth
Effect: Season
Effect: region
Cell: South Australia
Row Exculsion: Database.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	12701	155.08	16.79	0.15
Autumn	8344	157.08	16.64	0.20
Winter	6423	154.33	29.31	0.37
Spring	16810	148.02	20.03	0.15

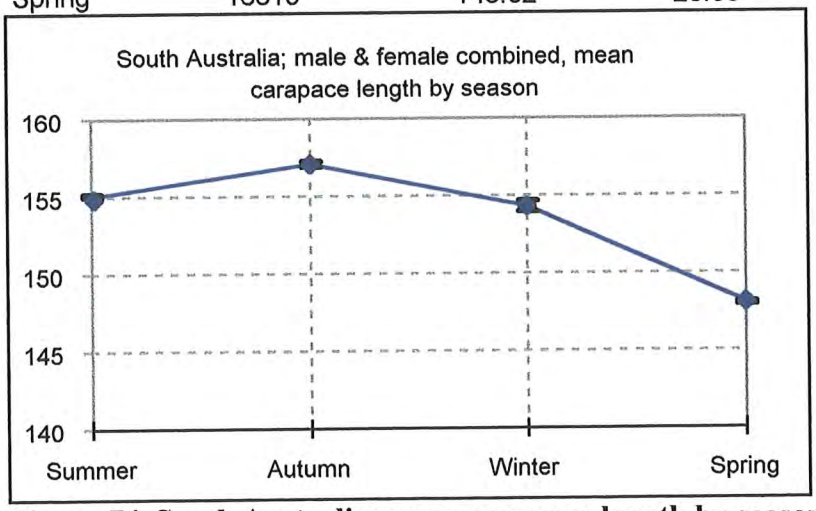

Figure 74. South Australia; mean carapace length by season; sexes combined

A post hoc S-N-K test tabulated below showed significant differences between the mean size of crabs taken during different seasons with the maximum size being in the autumn and the minimum in the spring

Table 65

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%
Effect: region
Cell: South Australia
Row Exclusion: Database.ssd

Season	Summer	Autumn	Winter	Spring
Summer		**S**	**S**	**S**
Autumn			**S**	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant at this level

SEX

Table 66

Means Table for Car Lgth
Effect: Sex
Effect: region
Cell: South Australia
Row Exclusion: Database.ssd

Sex	Count	Mean	Std. Dev.	Std. Err.
F	23729	148.81	15.43	0.10
M	20549	157.12	25.10	0.18

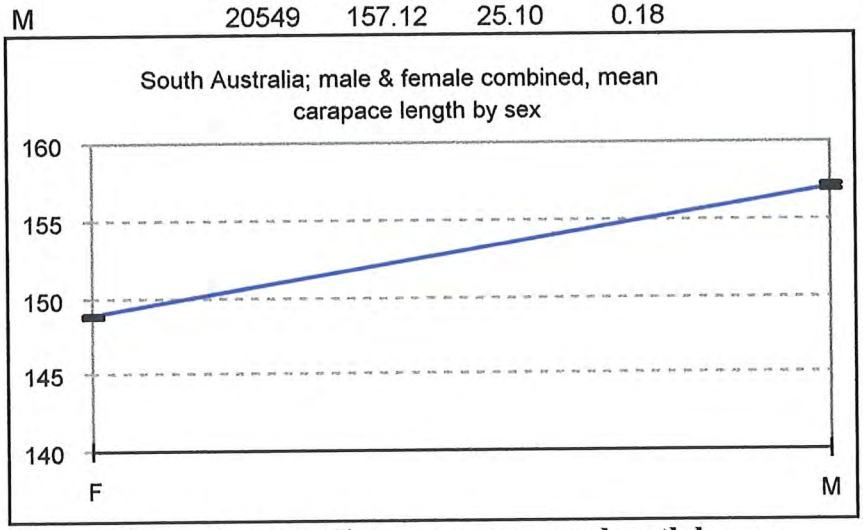

Figure 75. South Australia; mean carapace length by sex

Males were significantly larger than females as determined by the S-N-K test tabulated below.

Table 67

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%
Effect: region
Cell: South Australia
Row Exclusion: Database.ssd

	Mean Diff.	Crit. Diff.	Sig?
F, M	-8.31	0.37	**S**

S = significant at this level

YEAR

Table 68

Means Table for Car Lgth
Effect: Year
Effect: region
Cell: South Australia
Row Exclusion: Database.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	2696	143.37	18.80	0.36
1994	7140	153.32	17.39	0.21
1995	7336	156.73	20.44	0.24
1996	2897	154.28	14.90	0.28
1997	5624	150.01	21.11	0.28
1998	11027	152.14	20.09	0.20
1999	7142	153.86	25.63	0.30
2000	416	148.40	15.48	0.76

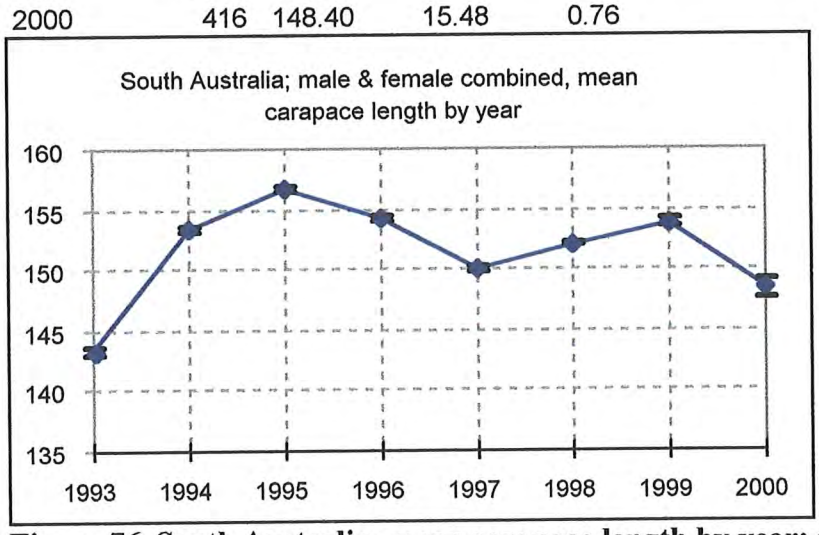

Figure 76. South Australia; mean carapace length by year; sexes combined

A post hoc S-N-K test tabulated below showed significant differences between the mean size of crabs taken in many of the years. Interpretation should be cautious as the effects of depth, season, sex and year are all highly significant. The years 1993 through to 2000 represent the beginning of the fishery, some re-fishing of the ground already exploited and from 1998 onwards, progressive exploitation of more westerly grounds. The relatively small sample size for year 2000 should also be noted. 1993 sampling primarily represents spring when sizes are smaller.

Table 69

Student-Newman-Keuls for Car Lgth
Effect: Year
Significance Level: 5%
Effect: region
Cell: South Australia
Row Exclusion: Database.ssd

Year	1993	1994	1995	1996	1997	1998	1999	2000
1993		**S**	**S**	**S**	**S**	**S**	**S**	**S**
1994			**S**	*NS*	**S**	*NS*	*NS*	**S**
1995				**S**	**S**	**S**	**S**	**S**
1996					**S**	**S**	*NS*	**S**
1997						**S**	**S**	**S**
1998							**S**	**S**
1999								**S**
2000								

S = significant at this level
NS = not significant at this level

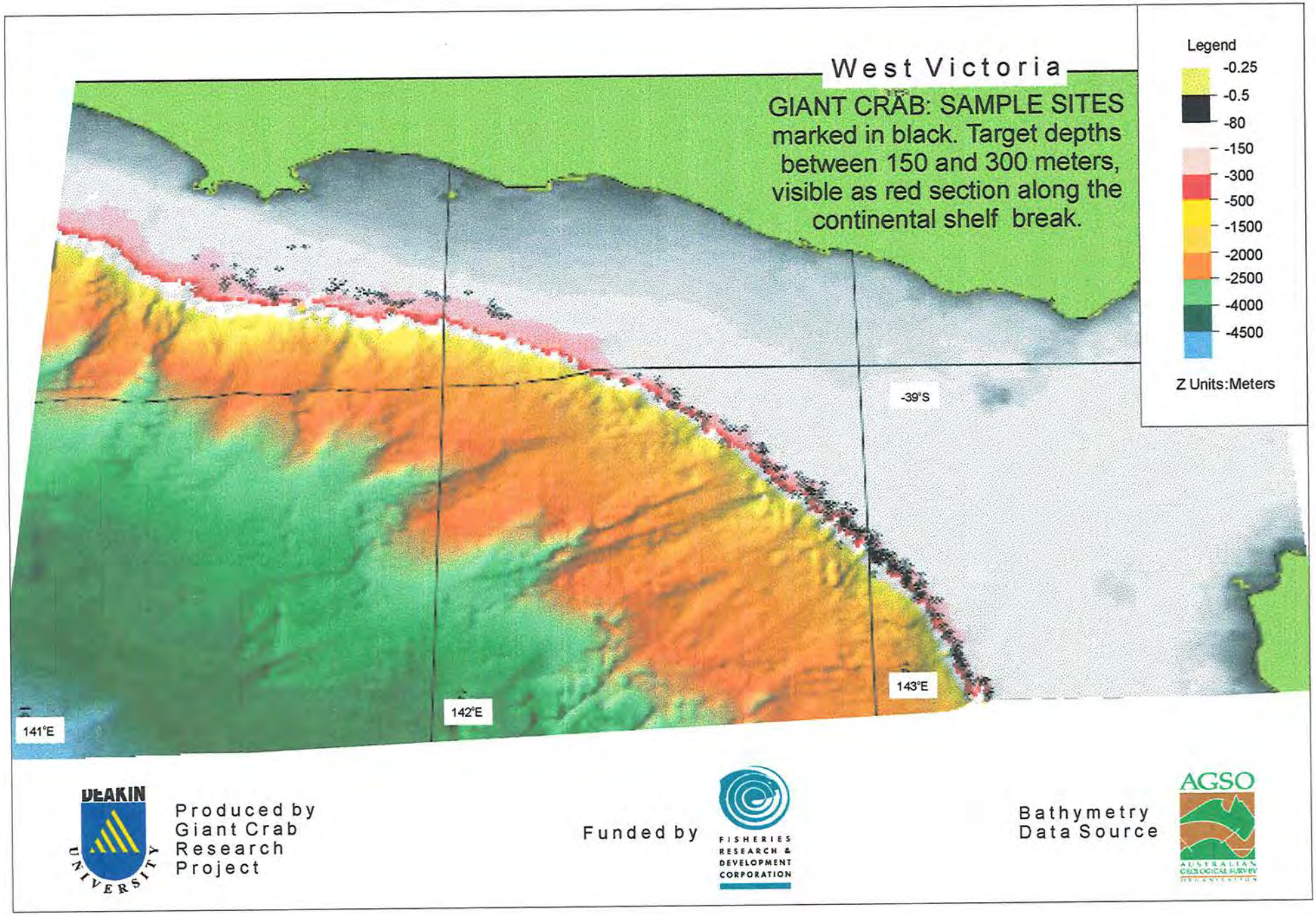
West Victoria
GIANT CRAB: SAMPLE SITES marked in black. Target depths between 150 and 300 meters, visible as red section along the continental shelf break.
Legend
-0.25
-0.5
-80
-150
-300
-500
-1500
-2000
-2500
-4000
-4500
Z Units:Meters
-39°S
141°E
142°E
143°E
DEAKIN UNIVERSITY
Produced by Giant Crab Research Project
Funded by
FISHERIES RESEARCH & DEVELOPMENT CORPORATION
Bathymetry Data Source
AGSO
AUSTRALIAN GEOLOGICAL SURVEY ORGANISATION

Figure 77

4.10.6. Victoria; population analysis; male and female combined

Sampling locations off Victoria are shown in Figure 77 and further broken down by season in the Appendix 1.

Table 70

ANOVA Table for Car Lgth
Split By: Region
Cell: Victoria
Row Exclusion: Database.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Rang	6	162331.03	27055.17	64.46	<.0001	386.76	1
Season	3	314736.06	104912.02	249.96	<.0001	749.87	1
Sex	1	32143.90	32143.90	76.58	<.0001	76.58	1
Year	5	39533.94	7906.79	18.84	<.0001	94.19	1
Residual	6689	2807497.83	419.72				

There were highly significant differences (P = <.0001) within the categories depth, season, sex and year.

DEPTH

Table 71

Means Table for Car Lgth
Effect: Depth Range (m)
Effect: region
Cell: Victoria
Row Exclusion: Database.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
150	933	153.75	20.43	0.67
200	3764	148.09	21.36	0.35
250	1170	156.61	25.24	0.74
300	656	141.71	26.32	1.03
350	135	141.66	26.84	2.31
400	41	108.46	19.54	6.05
450	...		...	...
500	6	116.67	18.05	7.37

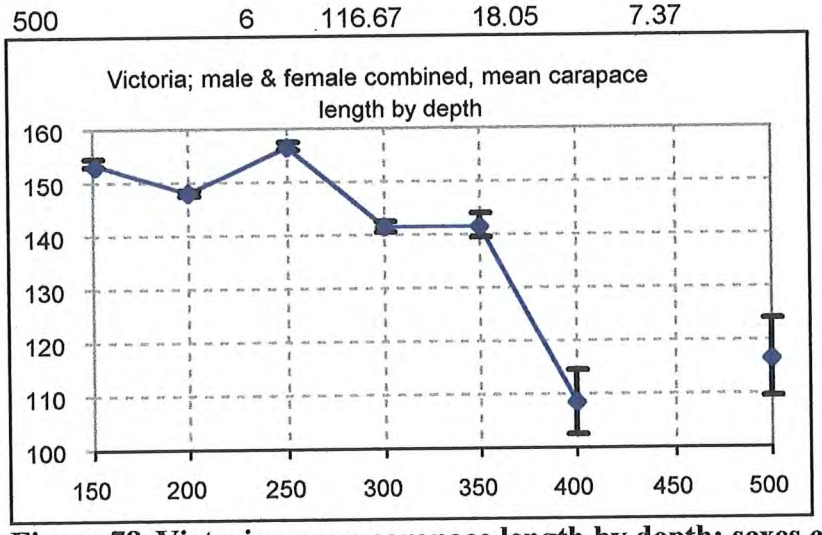

Figure 78. Victoria; mean carapace length by depth; sexes combined

A post hoc S-N-K test tabulated below showed a trend of significant differences between the mean size of crabs taken from shallower sites compared to those taken from deeper.

Table 72

Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%
Effect: region
Cell: Victoria
Row Exclusion: Database.ssd

Depth	150	200	250	300	350	400	450	500
150		*NS*	*NS*	**S**	*NS*	**S**	...	**S**
200			*NS*	*NS*	*NS*	*NS*	...	**S**
250				**S**	**S**	**S**	...	**S**
300					*NS*	**S**	...	**S**
350						**S**	...	**S**
400								*NS*
450								

S = significant at this level
NS = not significant at this level

SEASON

Table 73

Means Table for Car Lgth
Effect: Season
Effect: region
Cell: Victoria
Row Exclusion: Database.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	1073	158.35	19.14	0.58
Autumn	1256	164.41	23.18	0.65
Winter	1175	146.58	25.11	0.72
Spring	3201	141.42	19.66	0.35

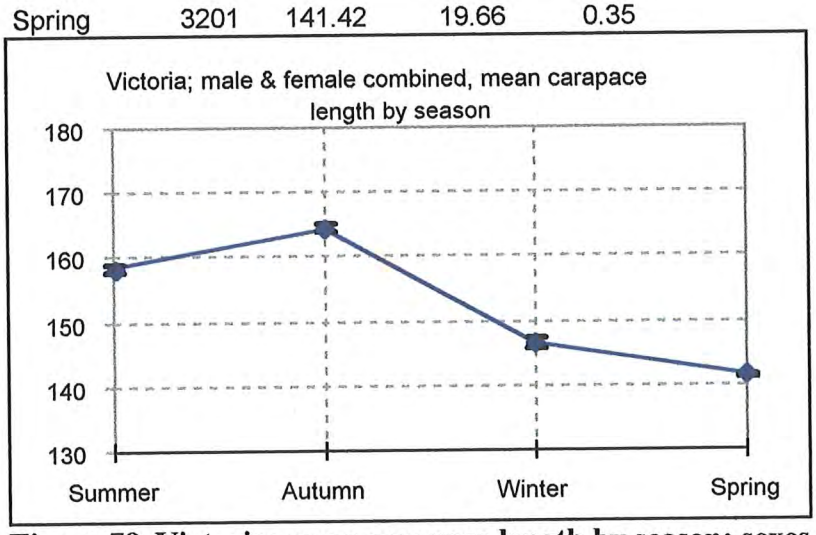

Figure 79. Victoria; mean carapace length by season; sexes combined

A post hoc S-N-K test tabulated below showed significant differences between the mean size of crabs taken during different seasons.

Table 74

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%
Effect: region
Cell: Victoria

Season	Summer	Autumn	Winter	Spring
Summer		**S**	**S**	**S**
Autumn			**S**	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant at this level

SEX

Table 75

Means Table for Car Lgth
Effect: Sex
Effect: region
Cell: Victoria
Row Exclusion: Database.ssd

Sex	Count	Mean	Std. Dev.	Std. Err.
F	3645	146.68	17.46	0.29
M	3060	152.51	28.35	0.51

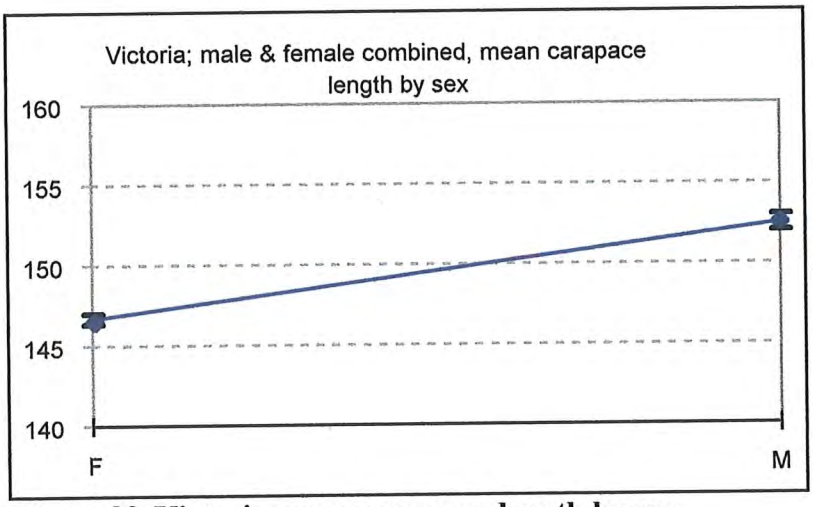

Figure 80. Victoria; mean carapace length by sex

Males were significantly larger than females as determined by the S-N-K test below.

Table 76

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%
Effect: region
Cell: Victoria
Row Exclusion: Database.ssd

	Mean Diff.	rit. Diff.	Sig?
F, M	-5.82	0.98	**S**

S = significant at this level

YEAR

Table 77

Means Table for Car Lgth
Effect: Year
Effect: region
Cell: Victoria
Row Exclusion: Database.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	1650	140.31	20.75	0.51
1994	1460	148.37	22.74	0.60
1995	2695	154.62	23.30	0.45
1996	529	159.90	21.66	0.94
1997	103	151.94	22.32	2.20
1998	268	135.38	16.91	1.03

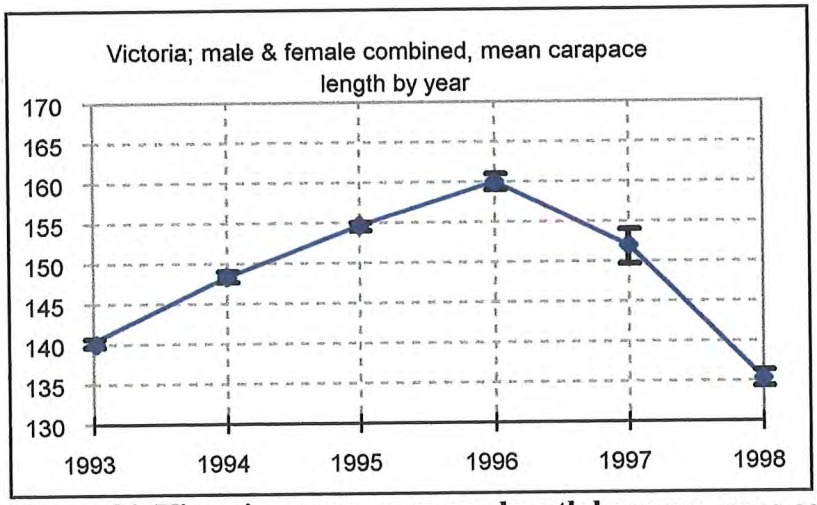

Figure 81. Victoria; mean carapace length by year; sexes combined

A post hoc S-N-K test tabulated below showed significant differences in the mean size of crabs taken in different years excepting 1995 compared with 1997. These differences reflect the transition from no minimum size to a minimum size post 1993 and a subsequent change of fishing depths. Location, season and fishing history are the contributing factors to the smallness of the mean size taken during 1998. The sample was taken in the spring when the catch is predominantly females, from the most southeasterly section of the Victorian grounds where there is evidence of illegal removal of undersized crabs.

Table 78

Student-Newman-Keuls for Car Lgth
Effect: Year
Significance Level: 5%
Effect: region
Cell: Victoria

Year	1993	1994	1995	1996	1997	1998
1993		**S**	**S**	**S**	**S**	**S**
1994			**S**	**S**	**S**	**S**
1995				**S**	*NS*	**S**
1996					**S**	**S**
1997						**S**
1998						

S = significant at this level
NS = not significant at this level

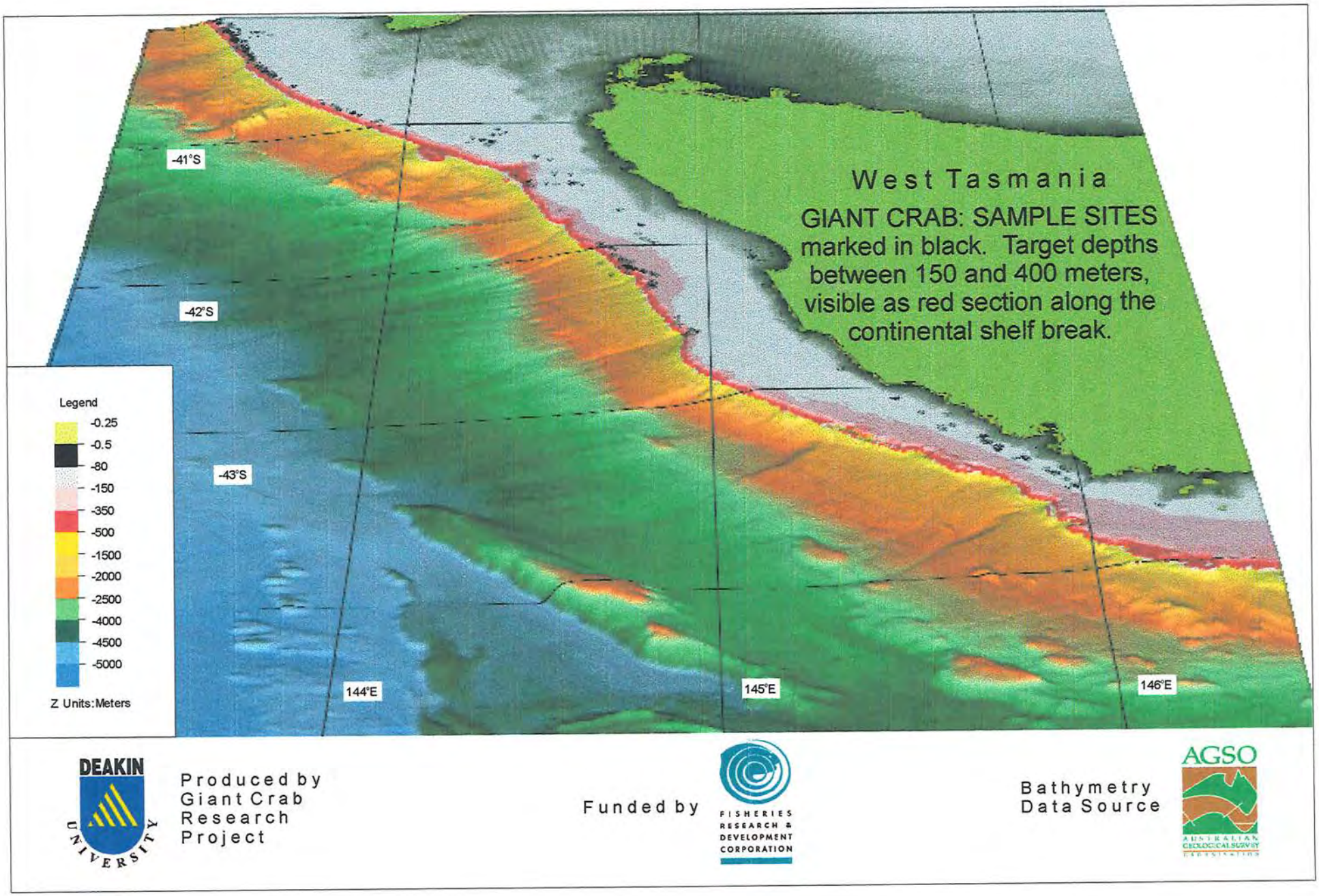
West Tasmania
GIANT CRAB: SAMPLE SITES marked in black. Target depths between 150 and 400 meters, visible as red section along the continental shelf break.
-41°S
-42°S
-43°S
144°E
145°E
146°E
Legend
-0.25
-0.5
-80
-150
-350
-500
-1500
-2000
-2500
-4000
-4500
-5000
Z Units:Meters
DEAKIN UNIVERSITY
Produced by Giant Crab Research Project
Funded by
FISHERIES RESEARCH & DEVELOPMENT CORPORATION
Bathymetry Data Source
AGSO
AUSTRALIAN GEOLOGICAL SURVEY ORGANISATION

Figure 82

4.10.7. West Tasmania; population analysis; male and female combined

Sampling locations off West Tasmania are shown in Figure 82 and further broken down by season in the Appendix 1.

Table 79

ANOVA Table for Car Lgth
Split By: Region
Cell: West Tasmania
Row Exclusion: Database.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Ra	6	108702.91	18117.15	44.76	<.0001	268.57	1
Season	2	52285.46	26142.73	64.59	<.0001	129.18	1
Sex	1	20639.80	20639.80	51.00	<.0001	51.00	1
Year	4	548397.12	137099.28	338.73	<.0001	1354.93	1
Residual	6024	2438170.68	404.74				

There were highly significant differences (P = <.0001) within the categories depth, season, sex and year.

DEPTH

Table 80

Means Table for Car Lgth
Effect: Depth Range (m)
Effect: region
Cell: West Tasmania
Row Exclusion: Database.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
50	5	193.60	14.47	6.47
100	551	147.06	21.06	0.90
150	621	144.10	20.30	0.82
200	2520	144.13	22.83	0.46
250	1545	138.52	23.18	0.59
300	727	133.21	20.98	0.78
350	69	130.73	26.69	3.21

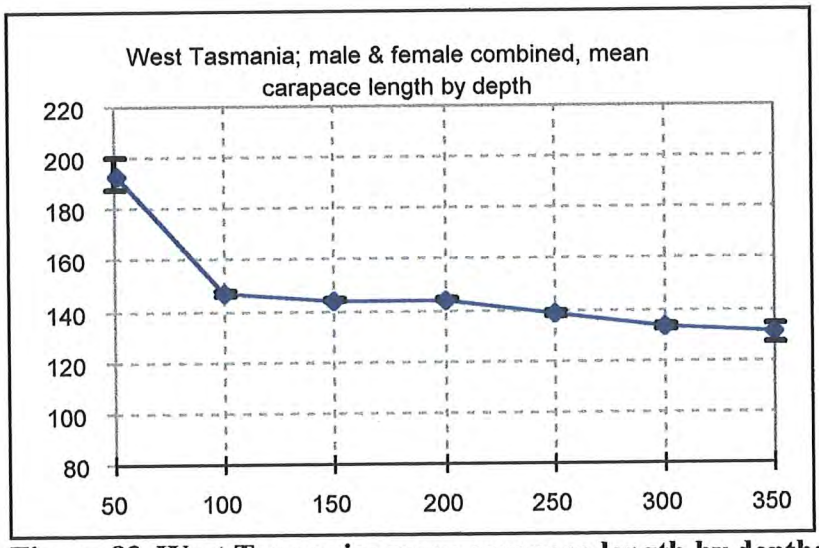

Figure 83. West Tasmania; mean carapace length by depth; sexes combined

A post hoc S-N-K test tabulated below, showed that mean size in 50 metres was significantly larger than all other depths. Also that crabs in 100 metres were

significantly larger than those taken at 300 and 350 metres. Also that those taken at 200 metres were significantly larger than those from 250 metres.

Table 81

Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%
Effect: region
Cell: West Tasmania

Depth	50	100	150	200	250	300	350
50		**S**	**S**	**S**	**S**	**S**	**S**
100			*NS*	*NS*	*NS*	**S**	**S**
150				*NS*	*NS*	*NS*	*NS*
200					**S**	*NS*	*NS*
250						*NS*	*NS*
300							*NS*
350							

S = significant at this level
NS = Not significant at this level

SEASON

Table 82

Means Table for Car Lgth
Effect: Season
Effect: region
Cell: West Tasmania
Row Exclusion: Database.ssd

Season	Count	Mean	Std. Dev.	Std. Err.
Summer	37	169.95	30.75	5.06
Autumn	1911	138.64	18.30	0.42
Winter				
Spring	4090	142.63	24.28	0.38

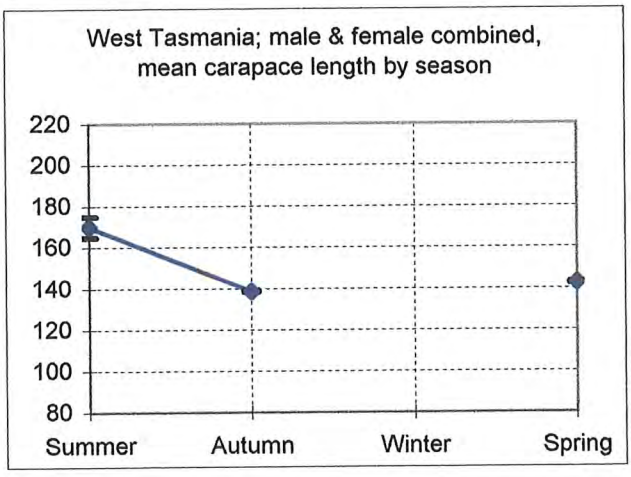

Figure 84. West Tasmania; mean carapace length by season; sexes combined

A post hoc S-N-K test tabulated below showed there were significant differences between the mean size of crabs taken in summer compared with autumn and spring, but caution should be exercised in interpretation as the depth and the

location from which these catches were taken will have a significant effect on mean size.

Table 83

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%
Effect: region
Cell: West Tasmania

Season	Summer	Autumn	Winter	Spring
Summer		**S**	.....	**S**
Autumn			.....	*NS*
Winter				.....
Spring				

S = significant at this level
NS = Not significant at this level

SEX

Table 84

Means Table for Car Lgth
Effect: Sex
Effect: region
Cell: West Tasmania
Row Exclusion: Database.ssd

Sex	Count	Mean	Std. Dev.	Std. Err.
F	3632	142.22	18.05	0.30
M	2406	140.49	28.46	0.58

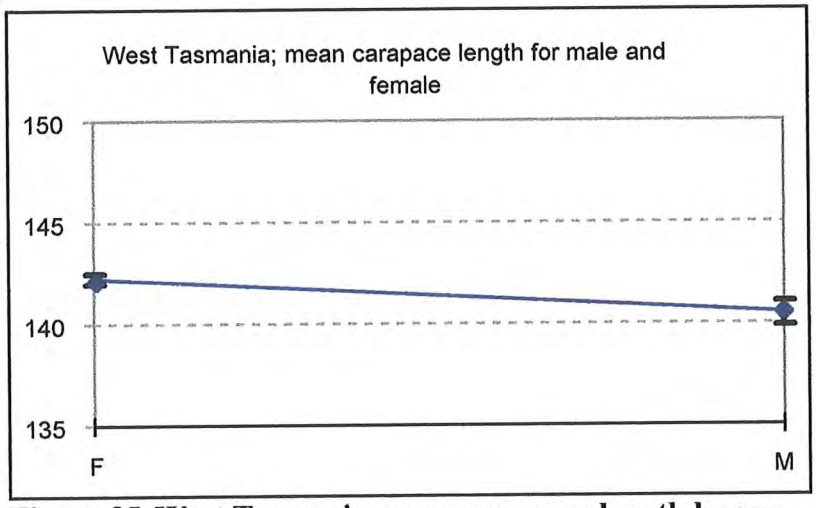

Figure 85. West Tasmania; mean carapace length by sex

A post hoc S-N-K test tabulated below showed there were significant differences between the mean size of male and female crabs, females being larger. This is due to most of the sample having been acquired in the spring in the northwest section of the grounds which have been subjected to intense exploitation.

Table 85

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%
Split By: region
Cell: West Tasmania
Row Exclusion: Database.ssd

	Mean Diff.	Crit. Diff.	Sig?
F, M	1.73	1.04	**S**

S = significant at this level

YEAR

Table 86

Means Table for Car Lgth
Effect: Year
Effect: region
Cell: West Tasmania
Row Exclusion: Database.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	1477	138.59	15.46	0.40
1994	986	152.81	27.95	0.89
1995	110	196.40	31.19	2.97
1998	1528	136.45	21.54	0.55
1999	1937	138.93	18.68	0.43

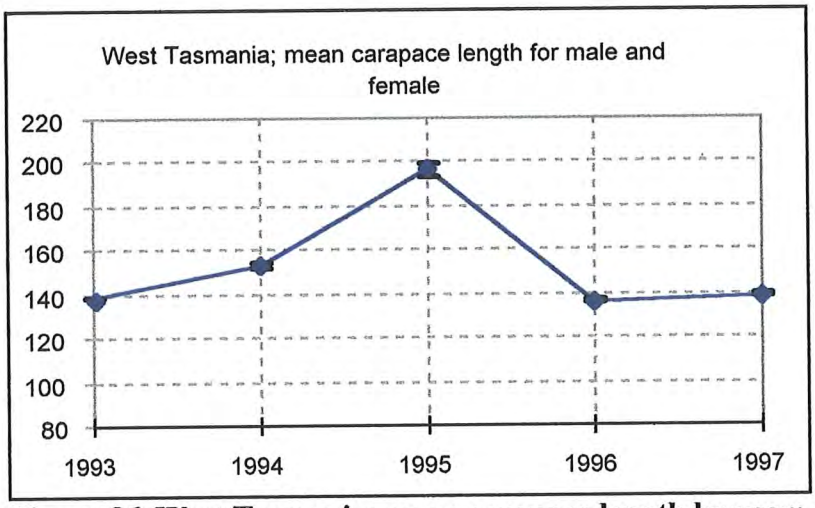

Figure 86. West Tasmania; mean carapace length by year; sexes combined

A post hoc S-N-K test tabulated below showed there were significant differences between the mean size of crabs taken in some of the years. 1993 was different to 1994 because different depths were fished, 1993 deeper, 1994 shallower. The larger mean size taken in 1995 was attributable to the samples being taken in shallower water further to the south than samples from other years.

Table 87

Student-Newman-Keuls for Car Lgth
Effect: Year
Significance Level: 5%
Effect: region
Cell: West Tasmania
Row Exclusion: Database.ssd

Year	1993	1994	1995	1996	1997	1998	1999
1993		**S**	**S**	...	...	*NS*	*NS*
1994			**S**	...	...	**S**	**S**
1995				...	...	**S**	**S**
1996					...	...	...
1997						...	...
1998							*NS*
1999							

S = significant at this level

NS = Not significant at this level

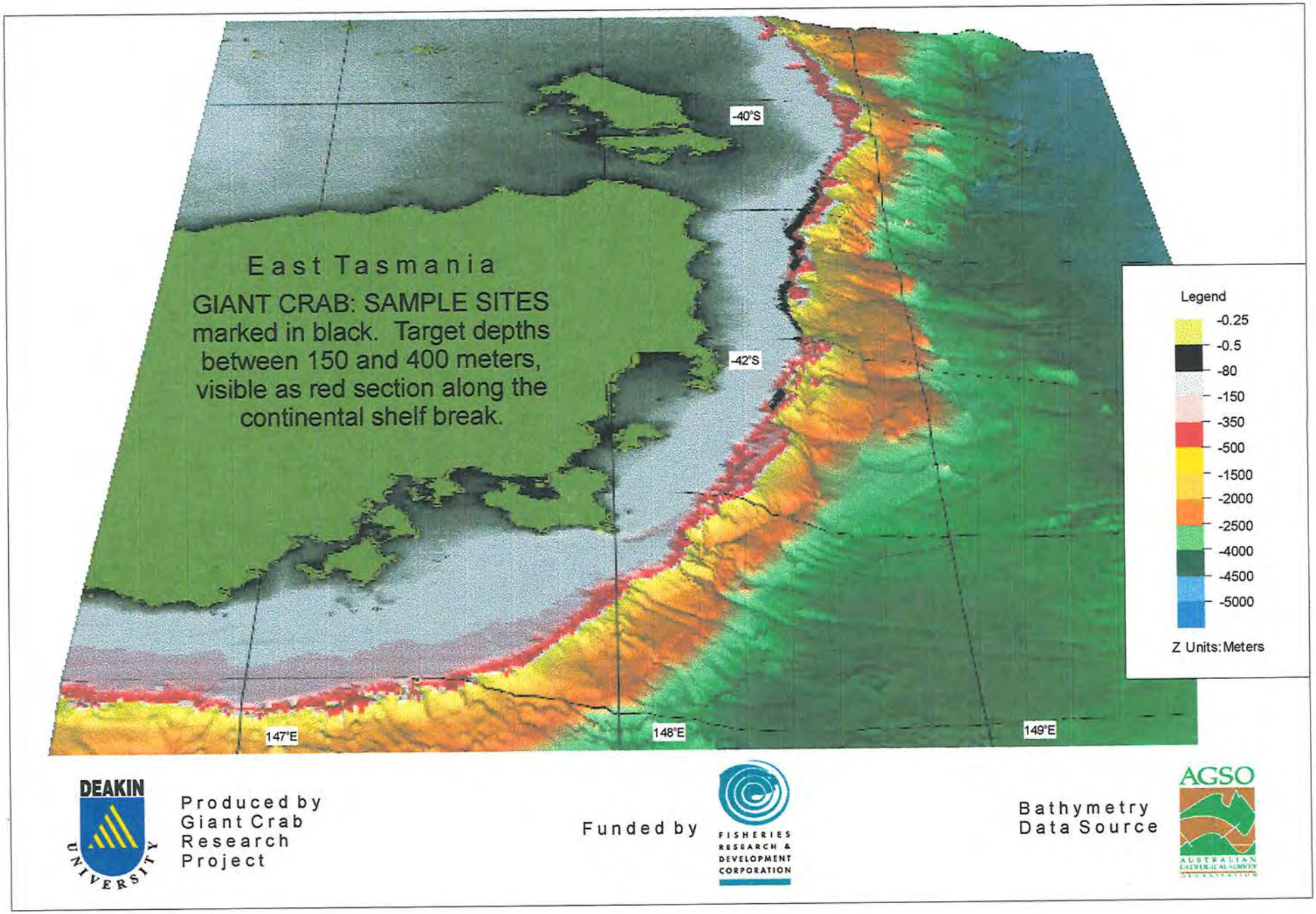
East Tasmania
GIANT CRAB: SAMPLE SITES marked in black. Target depths between 150 and 400 meters, visible as red section along the continental shelf break.
-40°S
-42°S
147°E
148°E
149°E
Legend
-0.25
-0.5
-80
-150
-350
-500
-1500
-2000
-2500
-4000
-4500
-5000
Z Units: Meters
DEAKIN UNIVERSITY
Produced by Giant Crab Research Project
Funded by
FISHERIES RESEARCH & DEVELOPMENT CORPORATION
Bathymetry Data Source
AGSO
AUSTRALIAN GEOLOGICAL SURVEY ORGANISATION

Figure 87:

4.10.8. East Tasmania; population analysis; male and female combined

Sampling locations off East Tasmania are shown in Figure 87 and further broken down by season in the Appendix 1.

Table 88

ANOVA Table for Car Lgth
Split By: Region
Cell: East Tasmania
Row Exclusion: Database.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Ra	6	68225.91	11370.98	35.41	<.0001	212.47	1
Season	2	62374.33	31187.16	97.13	<.0001	194.25	1
Sex	1	87574.03	8754.03	272.73	<.0001	272.73	1
Year	4	70780.89	17695.22	55.11	<.0001	220.43	1
Residual	8439	2727142.83	321.11				

There were highly significant differences (P = <.0001) within the categories depth, season, sex and year.

DEPTH

Table 89

Means Table for Car Lgth
Effect: Depth Range (m)
Effect: region
Cell: East Tasmania

Depth	Count	Mean	Std. Dev.	Std. err.
150	127	162.03	12.02	1.07
200	413	157.25	20.55	1.01
250	3395	161.85	22.40	0.38
300	3803	152.81	16.83	0.27
350	641	152.87	17.68	0.70
400	105	155.41	19.27	1.88
450	23	152.83	17.39	3.63

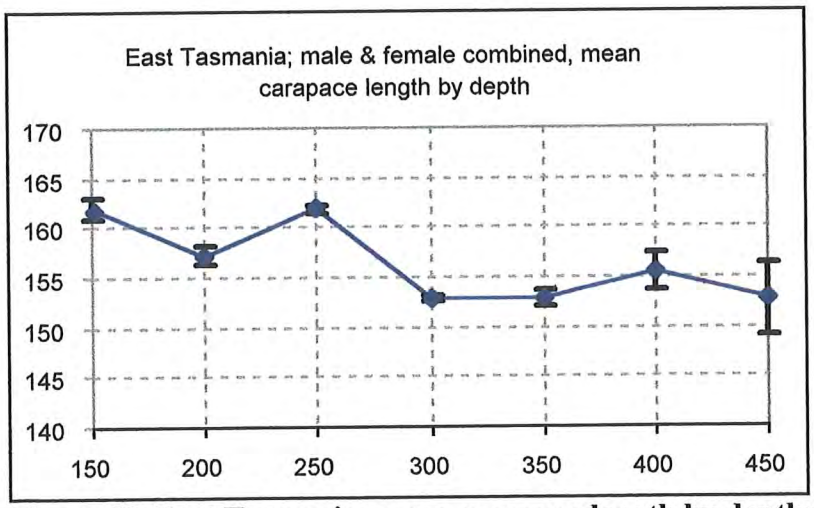

Figure 88. East Tasmania; mean carapace length by depth; sexes combined

A post hoc S-N-K test tabulated below showed significant differences with a larger mean size of crabs taken in 150 metres compared to those taken from 300 metres

and deeper. A similar pattern was observed for crabs taken in 250 metres compared to 300 metres and deeper.

Table 90

Student-Newman-Keuls for Car Lgth
Effect: Depth Range (m)
Significance Level: 5%
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

Depth	150	200	250	300	350	400	450
150		*NS*	*NS*	**S**	**S**	**S**	**S**
200			*NS*	*NS*	*NS*	*NS*	*NS*
250				**S**	**S**	**S**	**S**
300					*NS*	*NS*	*NS*
350						*NS*	*NS*
400							*NS*
450							

S = significant at this level
NS = not significant at this level

SEASON

Table 91

Means Table for Car Lgth
Effect: Season
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer				
Autumn	3819	162.98	19.65	0.32
Winter	630	162.65	23.46	0.94
Spring	4058	150.09	17.26	0.27

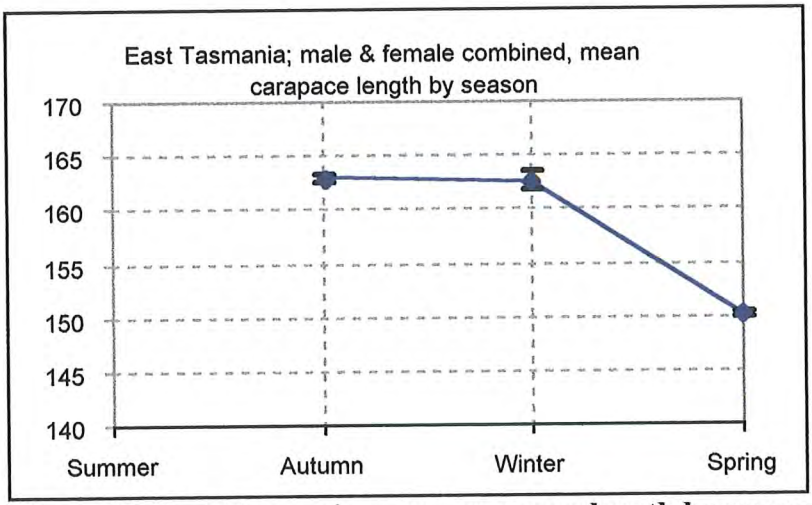

Figure 89. East Tasmania; mean carapace length by season; sexes combined

A post hoc S-N-K test tabulated below showed that there were significant differences with the mean size of crabs taken in the spring being smaller compared with autumn and winter.

Table 92

Student-Newman-Keuls for Car Lgth
Effect: Season
Significance Level: 5%
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

Season	Summer	Autumn	Winter	Spring
Summer		...	...	...
Autumn			*NS*	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant at this level

SEX

Table 93

Means Table for Car Lgth
Effect: Sex
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

Sex	Count	Mean	Std. Dev.	Std. Err.
F	7211	154.96	15.49	0.18
M	1296	167.11	33.88	0.94

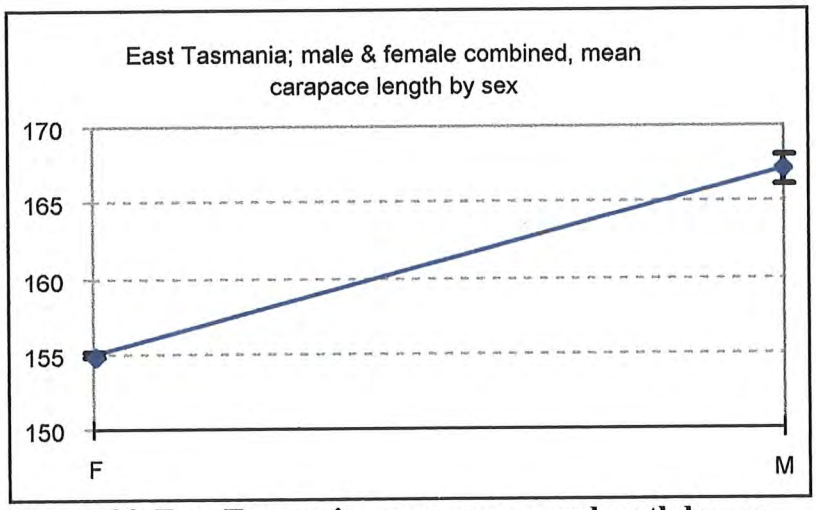

Figure 90. East Tasmania; mean carapace length by sex

Males were significantly larger than females as determined by the S-N-K test tabulated below.

Table 94

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

Sex	Mean Diff.	Crit. Diff.	Sig?
F, M	-12.15	1.06	**S**

S = significant at this level

YEAR

Table 95

Means Table for Car Lgth
Effect: Year
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	14	158.21	13.35	3.57
1994	2514	148.87	15.89	0.32
1995	714	150.61	14.02	0.53
1996				
1997				
1998	1317	170.57	26.79	0.74
1999	3948	158.39	17.53	0.28

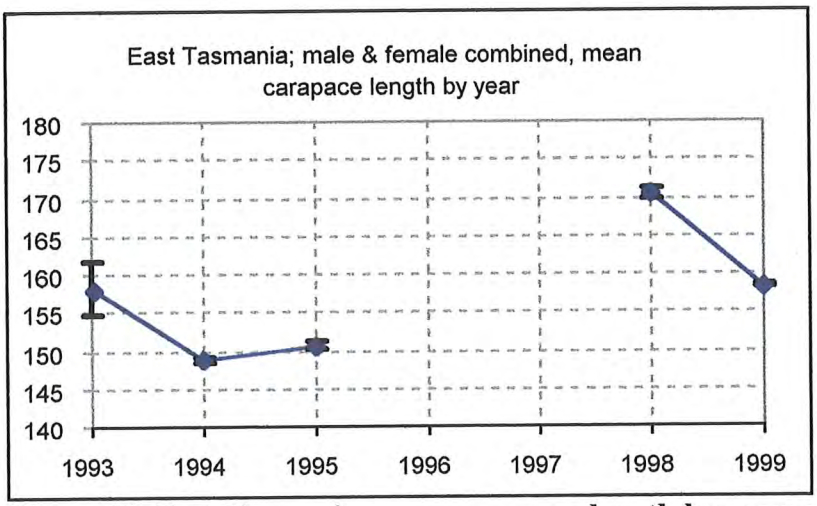

Figure 91. East Tasmania; mean carapace length by year; sexes combined

A post hoc S-N-K test tabulated below showed significant differences between the mean size of crabs taken in 1993 that were larger compared with the next two years 1994 and 1995. The significantly larger mean size in 1998 was most likely attributable to the effects of autumn sampling.

Males were significantly larger than females as determined by the S-N-K test tabulated below.

Table 96

Student-Newman-Keuls for Car Lgth
Effect: Sex
Significance Level: 5%
Effect: region
Cell: East Tasmania
Row Exclusion: Database.ssd

Sex	Mean Diff.	Crit. Diff.	Sig?
F, M	-12.15	1.06	**S**

S = significant at this level

4.10.9. POPULATION SUMMARY

Analysis of variance of Australia wide pooled data (above) showed highly significant differences (P<.0001) within the categories of year, depth, region, sex and season. A summary of these effects across regions is presented in table 97 below.

Table 97: Population analysis summary

Overall trends in mean size	W. A.	S. A.	Vic.	W. Tas	E. Tas
Males>Females	Y	Y	Y	N	Y
Decrease in size since 1993?	Y	U*	U*	Y	N
Summer/Autumn>Winter/Spring	N	Y	Y	Y	Y
Decreasing size with depth	N	Y	Y	Y	Y

U* = *undetermined at this level of analysis*
Y = *yes*
N = *no*

The general situation is that giant crab males grow faster than females and so attain a larger size. Energy is invested in somatic growth, where increased size improves their chances of successful mating, while the females invest less in growth and more in egg production. Thus the mean size of males was significantly larger than that of females at all sites except west Tasmania where very few large males were caught. The largest part of the west Tasmanian sample was acquired in the spring from the northwest section of the grounds. These grounds had been subjected to intense exploitation and based on evidence of undersized crabs in mesh bags that had been found by fishers, illegal removal of undersized animals may have been occurring. Sampling conducted in spring and autumn was stratified by depth and compared to a commercial operation, more pots than usual were set in deeper water. Consistent with the significant trend of decreasing mean size with depth off the eastern states, depth stratified sampling produced smaller size classes of both sexes in this area. A trend towards decreasing size at greater depth has been noted in other species of deep sea crabs such as *Geryon maritae* (Melville-Smith, 1987.) While there is a significant trend of decreasing mean size with depth for all sites in the eastern states, the trend is not significant in west Australia. Mean size according to season is also different to the eastern states. Both trends are most likely attributable to the effects of the hydrology, location of trophic food resources and competition with *H. acerba* (previously called *H. armata.*) (see chapter 4.9.) that are specific to that area.

The mean size of crabs from shallower waters during summer off west Tasmania was significantly larger compared with autumn and spring. Caution should be exercised in how this information is interpreted as the depth, location and fishing history of the site(s) sampled in that area has had a significant effect on mean size. Mean size peaked in the autumn off South Australia, Victoria and east Tasmania The sum of the effects of crab behavior, reproductive and moulting patterns usually

results in a higher mean size in summer-autumn compared with the winter-spring, however fishing history and depth of fishing can modify this. Notwithstanding fishing in the most extreme annual conditions in deep water in the winter, only smaller male sizes are available at this time and females with eggs or that are moulting are less likely to enter traps in winter and early spring.

Larger males become available in the summer -autumn months in shallower water. A consequence of fishermen favoring shallower depths for ease of operation is that the larger crabs of both sexes (in a depth stratified population) are removed and their position on the shallower, richer food bearing substrates is taken by smaller crabs immigrating from deeper grounds during the late spring-early summer.

Large males and clean shelled females occur together in deeper water during the winter. The increase in mean size observed in the autumn is coincident with the change of bottom water temperatures on top of the shelf from cooler summer to warmer winter values. The larger mean size observed in the autumn reflects the offshore movement into the deeper cooler waters of the upper bathial slope by males and females at this time of year.

4.11 OVERVIEW OF RESULTS

Figure 92 illustrates;

- male moult increment (M_{inc}),
- female moult increment (F_{inc}),
- the point at which growth of the large chela of males becomes allometric,
- the smallest size of females with eggs (L_{sm}),
- the average female size at first maturity (L_m),
- maximum male size (Max_m),
- and maximum female size (Max_f).

Excepting the values for the onset of allometric growth of the large chela of males, all indicators show a similar trend across the species range, where values are smaller for the population off west Australia and larger off Tasmania. Determination of the average male moult increment for east Tasmania has been impeded by the lower than normal abundance of this sex within the population.

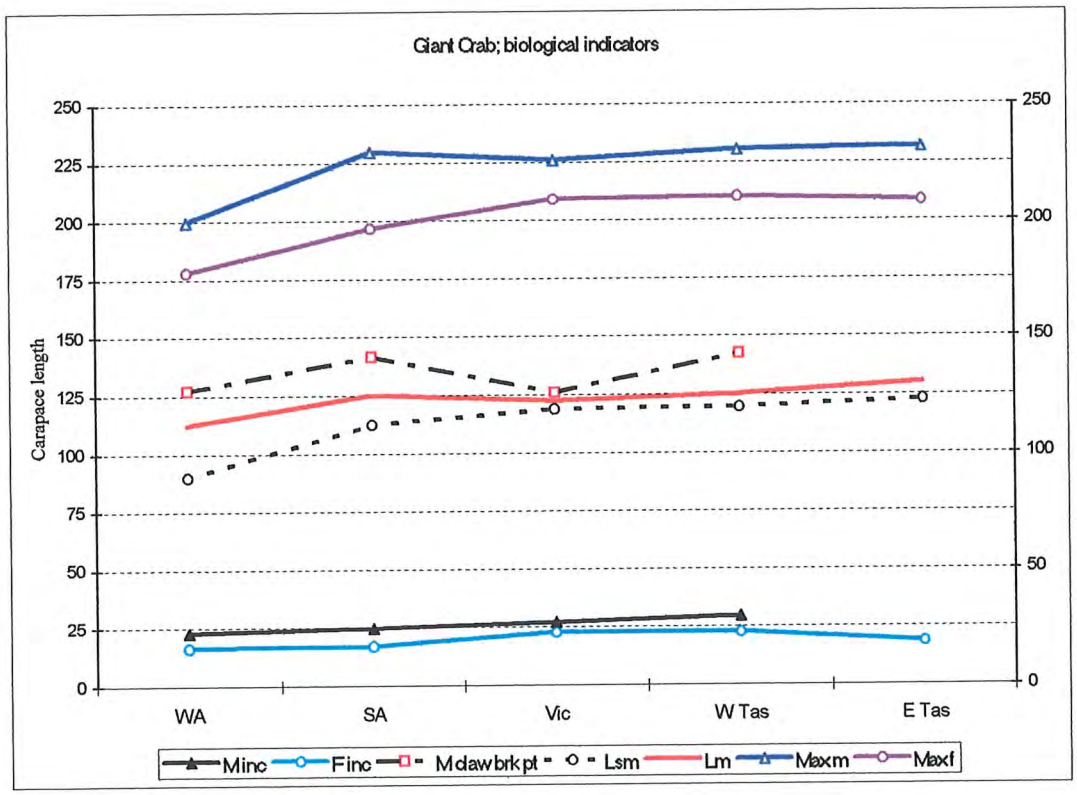

Figure 92. Biological Indicators

5. Stock assessment

5.1. Australia wide - male and female combined, all sizes attracted to baited pots are included in the following chapter, not just the commercial sizes

Table 98

ANOVA Table for kg/pot/day

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Season	3	333.76	111.25	70.16	<.0001	210.48	1
Region	4	965.95	241.49	152.29	<.0001	609.15	1
Sex	1	4.34	4.34	2.74	0.10	2.74	0.36
Year	7	176.06	25.15	15.86	<.0001	111.03	1
Residual	9385	14882.07	1.59				

There were highly significant (P = <.0001) differences within catch rates for season, state and year.

Season

Table 99

Means Table for kg/pot/day

Effect: Season

	Count	Mean	Std. Dev.	Std. Err.
Summer	2127	0.61	0.64	0.01
Autumn	2451	1.20	2.18	0.04
Winter	1226	0.61	0.95	0.03
Spring	3597	0.65	0.84	0.01

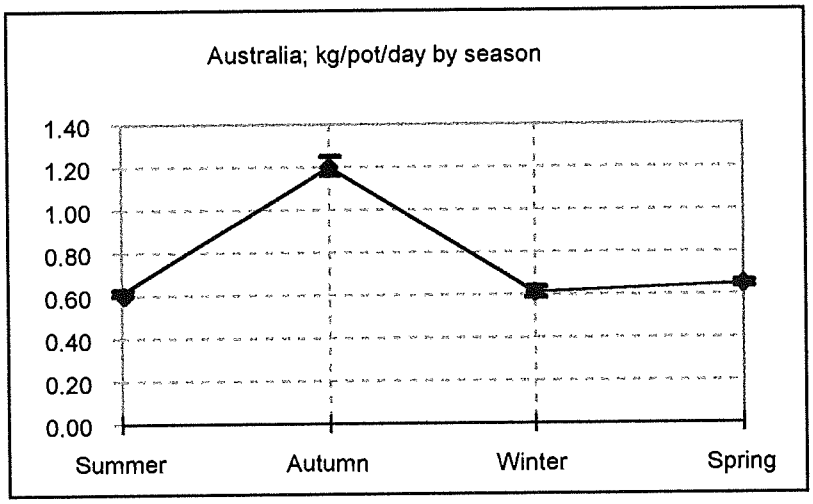

Figure 93. Australia; kg/pot/day by season; sexes combined

A post hoc S-N-K test tabulated below showed that mean catch rate was significantly higher in the autumn at 1.20 kg/pot/day compared with other seasons which were between 0.60 to 0.65 kg/pot/day.

Table 100

Student-Newman-Keuls for kg/pot/day
Effect: Season
Significance Level: 5 %

Season	Summer	Autumn	Winter	Spring
Summer		**S**	*NS*	*NS*
Autumn			**S**	**S**
Winter				*NS*
Spring				

S = Significant at this level
NS = Not significant at this level

Region

Table 101

Means Table for kg/pot/day
Effect: Region

	Count	Mean	Std. Dev.	Std. Err.
WA	861	0.34	0.50	0.02
SA	6326	0.67	0.82	0.01
Vic	602	0.62	0.81	0.03
W Tas	375	0.78	0.77	0.04
E Tas	1237	1.71	2.88	0.08

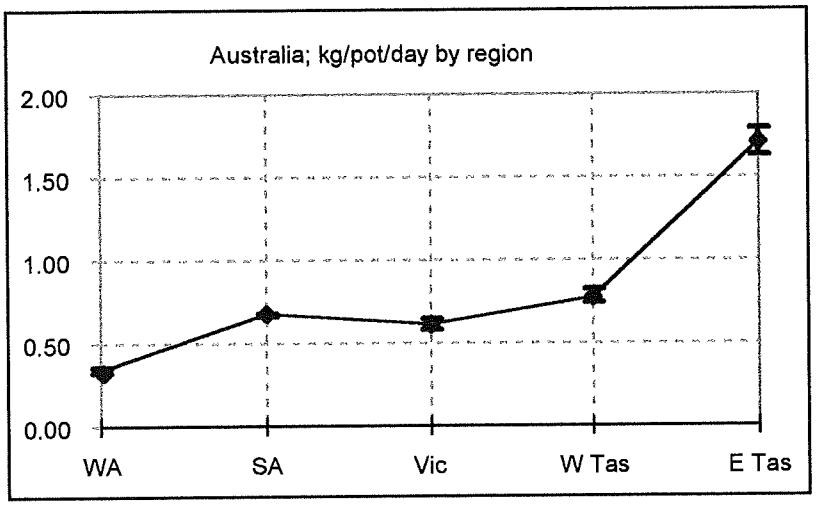

Figure 94. Australia; kg/pot/day by region; sexes combined

A post hoc S-N-K test tabulated below showed West Australian mean catch rate was significantly less than all other states, while east Tasmania catch rate was significantly higher. The west Tasmania catch rate like that from east Tasmania, included Autumn sampling obtained during the closure of this area and was significantly higher than that of Victoria.

Table 102

Student-Newman-Keuls for kg/pot/day
Effect: Region
Significance Level: 5 %

Region	WA	SA	Vic	W Tas	E Tas
WA		**S**	**S**	**S**	**S**
SA			*NS*	*NS*	**S**
Vic				**S**	**S**
W Tas					**S**
E Tas					

S = Significant at this level
NS = Not significant at this level

Sex

Table 103

Means Table for kg/pot/day
Effect: Sex

	Count	Mean	Std. Dev.	Std. Err.
F	4876	0.84	1.63	0.02
M	4525	0.71	0.90	0.01

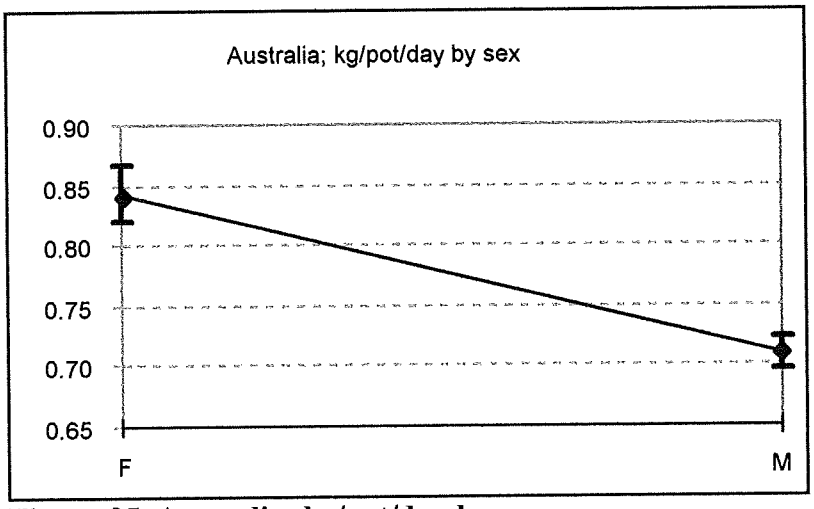

Figure 95. Australia; kg/pot/day by sex

A post hoc S-N-K test tabulated below showed the mean catch rate of females was significantly higher in this data than for males. This is to be expected as the data has a comparably larger representation of spring samples when females are in higher abundance, than for other seasons. The higher rate is also affected by regional differences. For example, East Tasmania, compared with other regions has a much higher abundance of females and due to closure produced very high autumn catch rates in 1999.

Table 104

Student-Newman-Keuls for kg/pot/day
Effect: Sex
Significance Level: 5 %

		Mean Di	Crit. Diff	Sig?
F	M	0.13	0.051	**S**

S = Significant at this level

Year

Table 105

Means Table for kg/pot/day
Effect: Year

Year	Count	Mean	Std. Dev.	Std. Err.
1993	725	0.86	1.00	0.04
1994	2016	0.76	0.83	0.02
1995	1928	0.79	0.99	0.02
1996	487	0.64	0.60	0.03
1997	834	0.40	0.36	0.01
1998	1157	0.60	0.85	0.03
1999	2174	1.05	2.27	0.05
2000	80	0.29	0.34	0.04

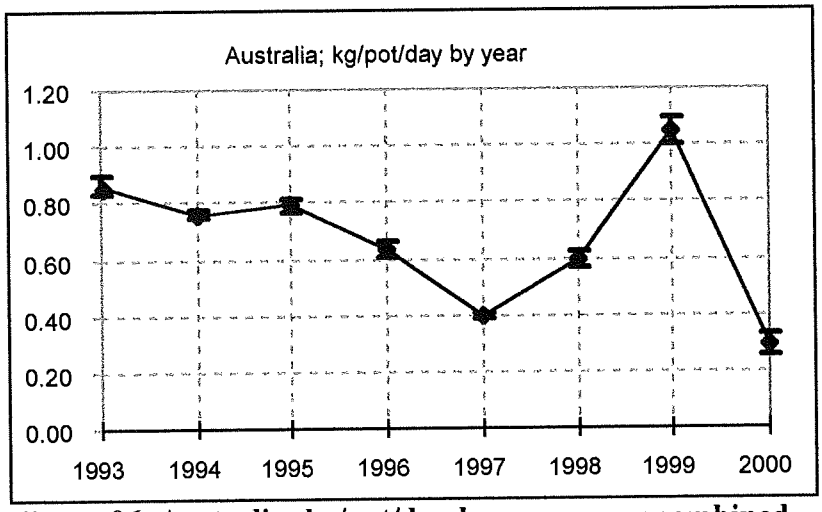

Figure 96. Australia; kg/pot/day by year; sexes combined

A post hoc S-N-K test tabulated below showed the catch rate was significantly higher in 1993 than in all years except 1999. 1999 catch rate was significantly higher than for all other years and is mostly derived from high east Tasmania values. The low values for 2000 are derived from a single sample of fishing events for a single season from a single state and should not be considered representative.

Table 106

Student-Newman-Keuls for kg/pot/day
Effect: Year
Significance Level: 5 %

Year	1993	1994	1995	1996	1997	1998	1999	2000
1993		*NS*	*NS*	**S**	**S**	**S**	**S**	**S**
1994			*NS*	*NS*	**S**	*NS*	**S**	**S**
1995				*NS*	**S**	*NS*	**S**	**S**
1996					**S**	*NS*	**S**	**S**
1997						**S**	**S**	*NS*
1998							**S**	**S**
1999								**S**
2000								

S = Significant at this level
NS = Not significant at this level

5.2. Stock Assessment - West Australia.

5.2.1. West Australia -male and female combined; all sizes attracted to baited pots are included, not just the commercial sizes.

Table 107

ANOVA Table for kg/pot/day
Split By: Region
Cell: West Australia
Row exclusion: CPUE by Event.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	4	3.705	0.926	4.01	0.0031	16.042	0.92
Season	3	0.591	0.197	0.853	0.4652	2.559	0.23
Sex	1	1.618	1.618	7.006	0.0083	7.006	0.762
Year	7	9.285	1.326	5.744	<.0001	40.207	1
Residual	845	195.132	0.231				

There were effects of were highly significant differences for the catch rates within the categories of depth, sex and year(P = .0031, .0083 and <.0001 respectively).

Depth

Table 108

Means Table for kg/pot/day
Effect: Depth Range
Split By: Region
Cell: West Australia
Row exclusion: CPUE by Event.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	2	0.05	0.06	0.04
200	41	0.65	1.21	0.19
250	358	0.35	0.42	0.02
300	414	0.32	0.44	0.02
350	46	0.28	0.38	0.06

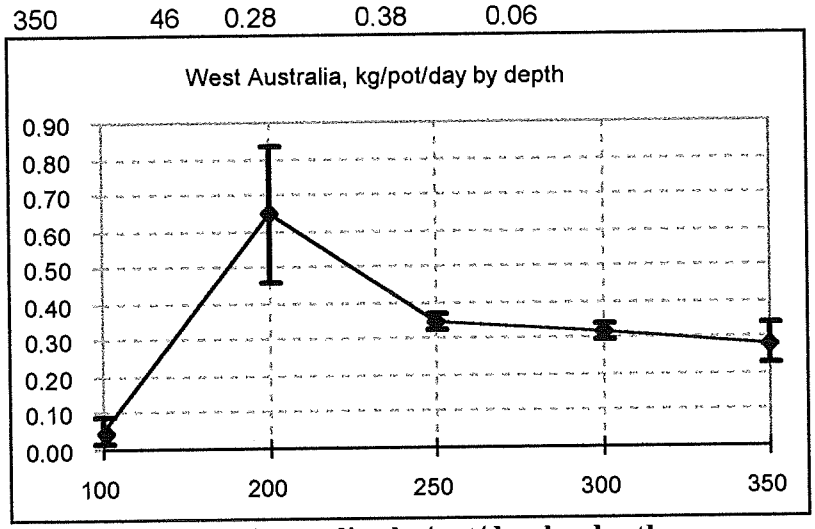

Figure 97. West Australia; kg/pot/day by depth; sexes combined

A post hoc SNK test showed there were no significant differences between depths, however the interaction plot suggests there may be a trend of declining catch as depth increases. The low sample size (2 fishing events) in 100 metres is too small to be

representative. The large amount of variability in catch rate at 200 metres may reflect variability in water temperature due to fluctuations of the border of the warm easterly flowing Leeuwin current and the cool westerly flowing undercurrent below it. (see Figure 51)

Season

Table 109

Means Table for kg/pot/day
Effect: Season
Split By: Region
Cell: West Australia
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	233	0.29	0.29	0.02
Autumn	79	0.33	0.57	0.06
Winter	84	0.27	0.24	0.03
Spring	465	0.39	0.59	0.03

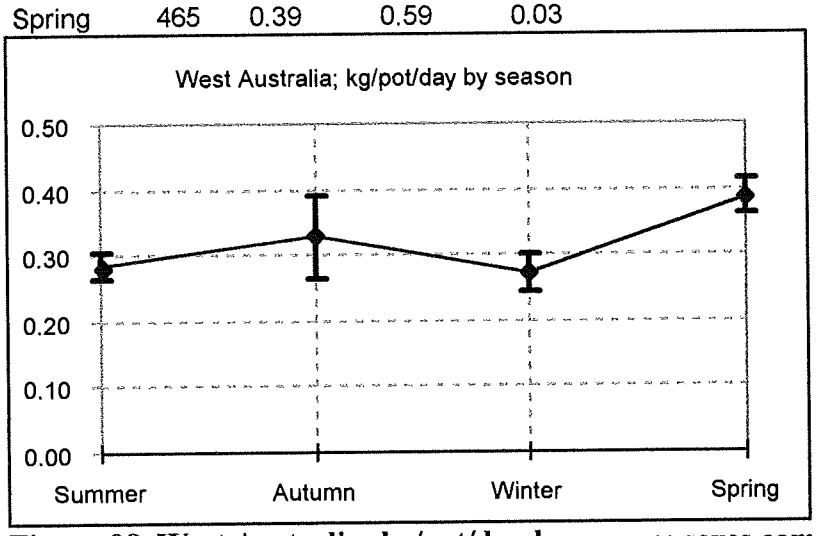

Figure 98. West Australia; kg/pot/day by season; sexes combined

A post hoc SNK test showed there were no significant differences between seasons

Sex

Table 110

Means Table for kg/pot/day
Effect: Sex
Split By: Region
Cell: West Australia
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
F	430	0.30	0.34	0.02
M	431	0.39	0.61	0.03

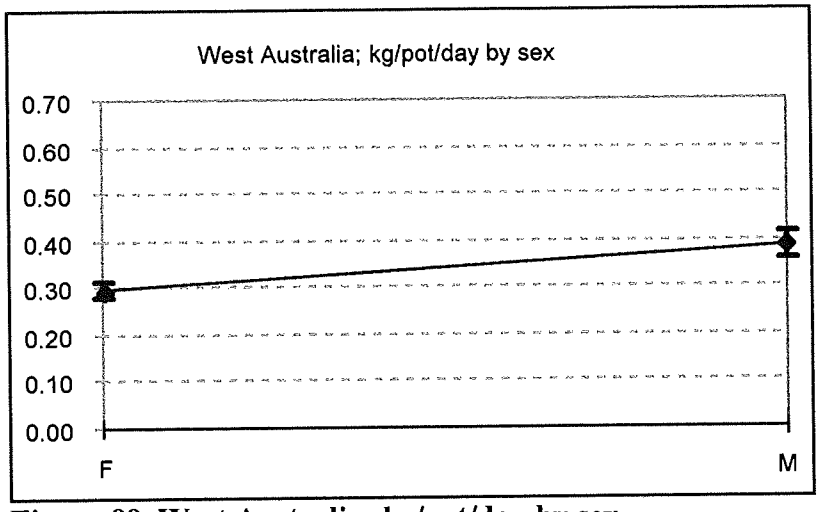

Figure 99. West Australia; kg/pot/day by sex

A post hoc SNK test showed the catch rate for males was significantly higher than for females.

Table 111

Student-Newman-Keuls for kg/pot/day
Effect: Sex
Significance Level: 5 %
Split By: Region
Cell: West Australia
Row exclusion: CPUE by Event.ssd

		Mean D	Crit. Diff	
F	M	-0.09	0.06	S

S = significantly different at this level

Year

Table 112

Means Table for kg/pot/day
Effect: Year
Split By: Region
Cell: West Australia
Row exclusion: CPUE by Event.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1994	308	0.39	0.63	0.04
1995	164	0.51	0.60	0.05
1996	81	0.33	0.22	0.03
1997	86	0.17	0.14	0.02
1998	36	0.26	0.22	0.04
1999	124	0.26	0.34	0.03
2000	38	0.17	0.11	0.02

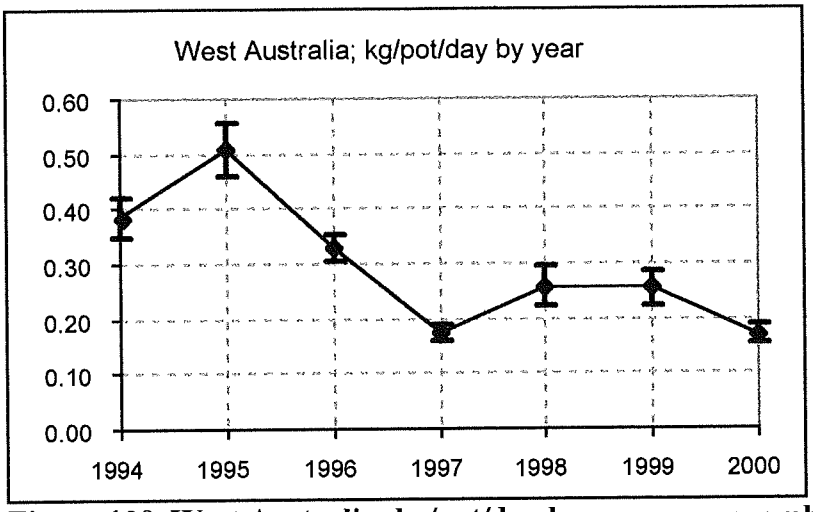

Figure 100. West Australia; kg/pot/day by year; sexes combined

A post hoc SNK test, tabulated below showed that 1995 catch rates were significantly higher than all subsequent years except 1996.

Table 113

Student-Newman-Keuls for kg/pot/day
Effect: Year
Significance Level: 5 %
Split By: Region
Cell: West Australia

Year	1994	1995	1996	1997	1998	1999	2000
1994		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
1995			*NS*	**S**	**S**	**S**	**S**
1996				*NS*	*NS*	*NS*	*NS*
1997					*NS*	*NS*	*NS*
1998						*NS*	*NS*
1999							*NS*
2000							

S = Significant
NS = Not significant

5.2.2. Stock Assessment - West Australia – female: all sizes attracted to baited pots are included, not just the commercial sizes.

Table 114

ANOVA Table for Catch (kg)/Pot/Day
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	4	0.04	0.01	0.10	0.98	0.38	0.07
Month	9	2.18	0.24	2.14	0.03	19.24	0.89
Year	6	1.10	0.18	1.61	0.14	9.67	0.61
Residual	401	45.38	0.11				

There were significant differences between months (P = .03).

Depth

Table 115

Means Table for Catch (kg)/Pot/Day
Effect: Depth Range
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	1	0.09	ï	ï
200	20	0.27	0.47	0.11
250	182	0.30	0.28	0.02
300	201	0.31	0.39	0.03
350	17	0.30	0.27	0.07

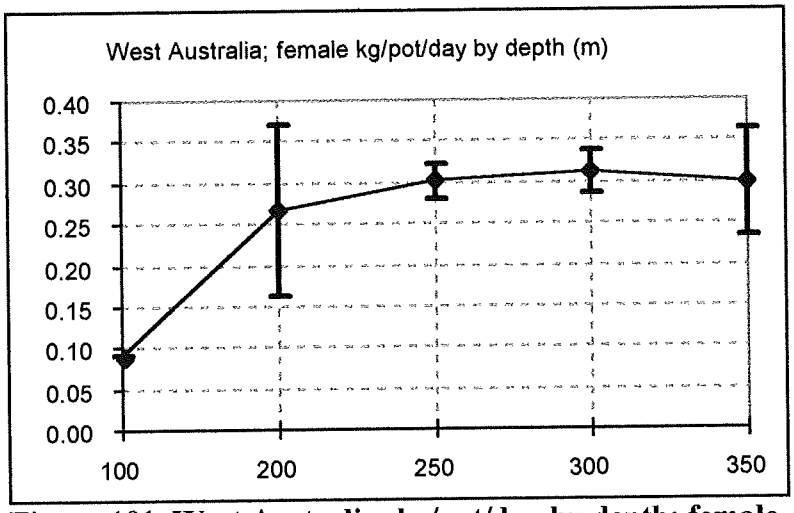

Figure 101. West Australia; kg/pot/day by depth; female

A post hoc SNK test, showed that differences between catch rates by depth were not significant.

Month

Table 116

Means Table for Catch (kg)/Pot/Day
Effect: Month
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

	Count	Mean	Std. Dev.	Std. Err.
Jan	51	0.30	0.18	0.03
Feb	17	0.23	0.16	0.04
Mar	21	0.22	0.15	0.03
Apr	10	0.48	0.72	0.23
May	9	0.15	0.08	0.03
Jun				
July				
Aug	32	0.29	0.19	0.03
Sep	96	0.20	0.15	0.02
Oct	94	0.42	0.50	0.05
Nov	41	0.26	0.18	0.03
Dec	50	0.40	0.48	0.07

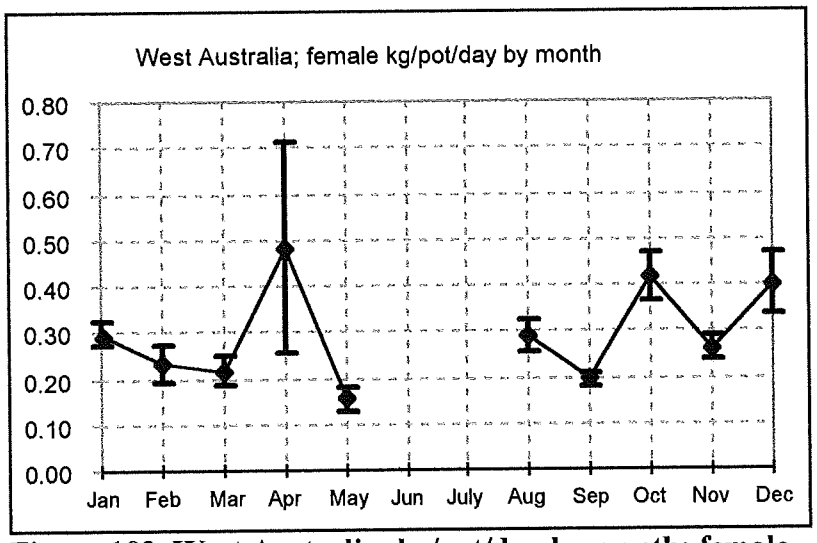

Figure 102. West Australia; kg/pot/day by month; female

A post hoc SNK test, showed that catch rate in April was significantly different to that in May. There were no other significant differences between months.

Year

Table 117

Means Table for Catch (kg)/Pot/Day
Effect: Year
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1994	163	0.26	0.31	0.02
1995	81	0.46	0.46	0.05
1996	41	0.29	0.19	0.03
1997	35	0.22	0.16	0.03
1998	20	0.26	0.23	0.05
1999	62	0.33	0.45	0.06
2000	19	0.20	0.12	0.03

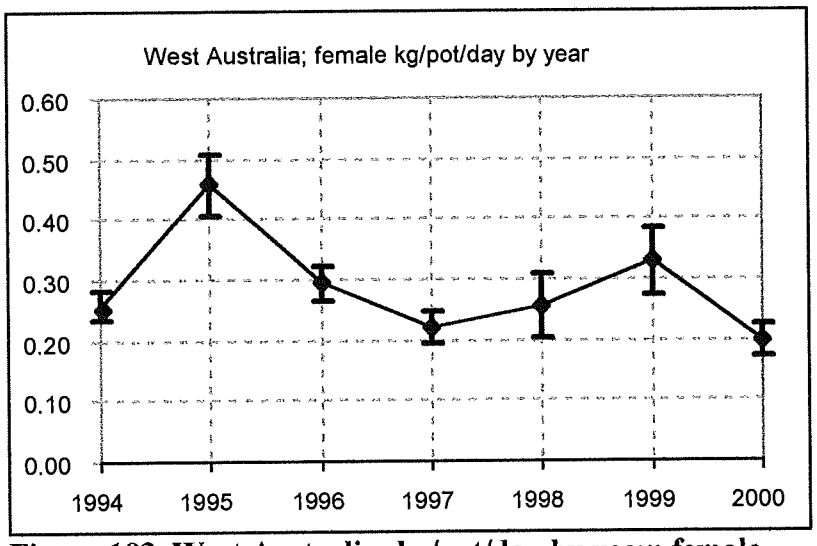

Figure 103. West Australia; kg/pot/day by year; female

A post hoc SNK test showed that 1995 catch rates were significantly different to those in 1997 and 2000. The 1995 result is attributable to improved fishing knowledge and the exploitation of new grounds.

5.2.3. Stock Assessment - West Australia –male: all sizes attracted to baited pots are included, not just the commercial sizes.

Table 118

ANOVA Table for Catch (kg)/Pot/Day
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	4	4.70	1.18	3.63	0.01	14.51	0.88
Month	9	10.50	1.17	3.60	0.00	32.39	0.99
Year	6	3.01	0.50	1.55	0.16	9.27	0.59
Residual	402	130.35	0.32				

There were significant differences between catch rates by depth (P = 0.01).

Depth

Table 119

Means Table for Catch (kg)/Pot/Day
Effect: Depth Range
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	1	0.01	ï	ï
200	21	1.01	1.56	0.34
250	176	0.39	0.53	0.04
300	205	0.34	0.48	0.03
350	19	0.42	0.51	0.12

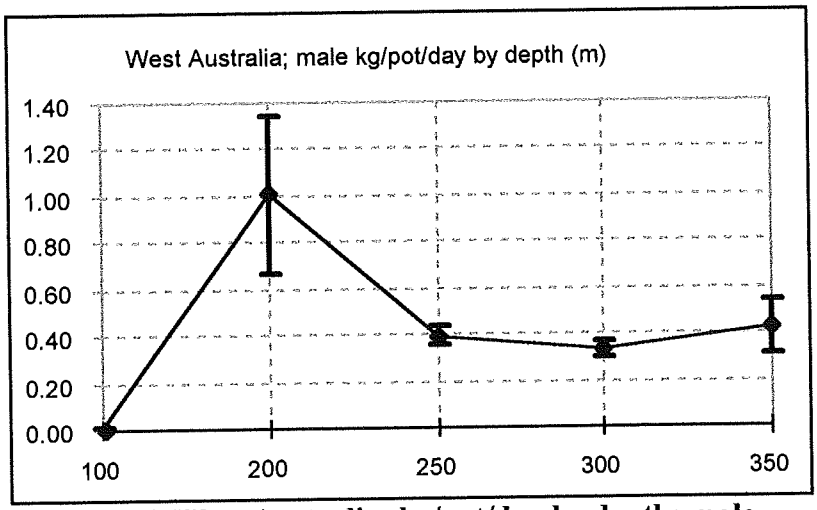

Figure 104. West Australia; kg/pot/day by depth; male

Although the interaction plot shows a higher mean catch rate at 200 metres, but it is highly variable to the extent that the SNK test (at the 5% level) was unable to establish that the catch rate was significantly different to 250, 300, or 350 metres.

Month

Table 120

Means Table for Catch (kg)/Pot/Day
Effect: Month
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

Month	Count	Mean	Std. Dev.	Std. Err.
Jan	52	0.28	0.25	0.03
Feb	16	0.27	0.19	0.05
Mar	20	0.26	0.16	0.04
Apr	10	0.74	1.37	0.43
May	9	0.27	0.12	0.04
Jun				
July				
Aug	34	0.40	0.28	0.05
Sep	96	0.34	0.32	0.03
Oct	99	0.74	1.03	0.10
Nov	39	0.14	0.09	0.01
Dec	47	0.18	0.16	0.02

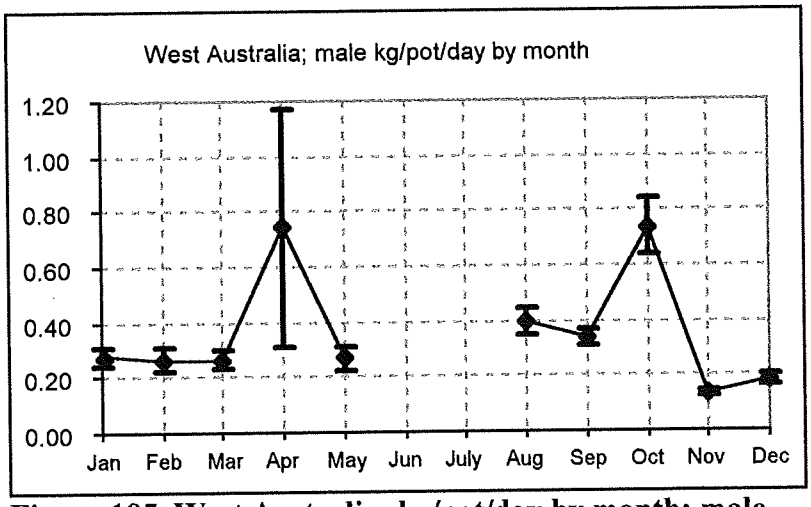

Figure 105. West Australia; kg/pot/day by month; male

A post hoc SNK test tabulated below showed there were significant differences between the catch rates of some months with a large amount of variability in April. Note that April has the second smallest number of fishing events.

Table 121

Student- Newman-Keuls for kg/pot/day
Effect: Month
Significance level: 5%

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan		*NS*	*NS*	**S**	*NS*			*NS*	*NS*	*NS*	*NS*	*NS*
Feb			*NS*	*NS*	*NS*			*NS*	*NS*	*NS*	*NS*	*NS*
Mar				*NS*	*NS*			*NS*	*NS*	*NS*	*NS*	*NS*
Apr					*NS*			*NS*	*NS*	*NS*	**S**	**S**
May								*NS*	*NS*	**S**	*NS*	*NS*
Jun												
Jul												
Aug									*NS*	**S**	*NS*	*NS*
Sep										**S**	*NS*	*NS*
Oct											**S**	**S**
Nov												*NS*
Dec												

S = Significant at this level
NS = Not significant at this level

Year

Table 122

Means Table for Catch (kg)/Pot/Day
Effect: Year
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1994	169	0.49	0.78	0.06
1995	83	0.56	0.71	0.08
1996	40	0.37	0.25	0.04
1997	33	0.14	0.12	0.02
1998	16	0.26	0.20	0.05
1999	62	0.18	0.15	0.02
2000	19	0.14	0.10	0.02

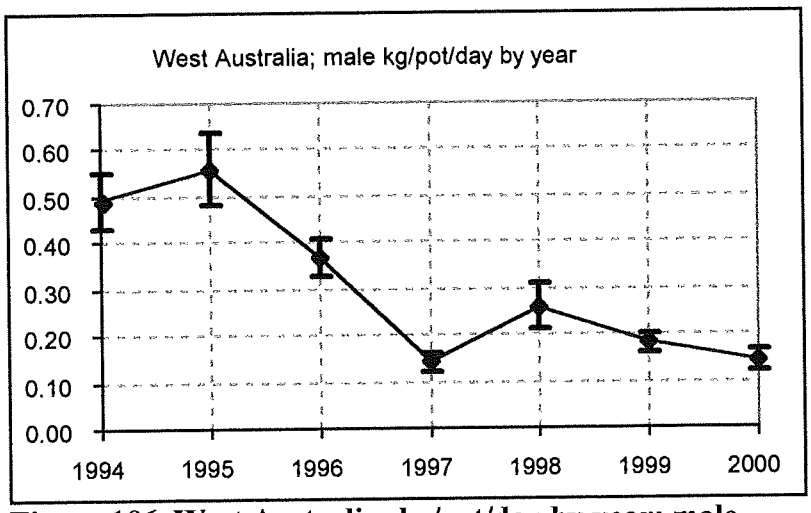

Figure 106. West Australia; kg/pot/day by year; male

There is a downward trend in catch rates with a post hoc SNK test showing significant difference between 1995 compared with 1997 and 2000.

Table 123

Student- Newman-Keuls for kg/pot/day
Effect: Year
Significance level: 5%

Year	1994	1995	1996	1997	1998	1999	2000
1994		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
1995			*NS*	**S**	*NS*	*NS*	**S**
1996				*NS*	*NS*	*NS*	*NS*
1997					*NS*	*NS*	*NS*
1998						*NS*	*NS*
1999							*NS*
2000							

S = Significant at this level
NS = Not significant at this level

5.3. Stock Assessment - South Australia.

5.3.1. South Australia - male and female combined, all sizes attracted to baited pots are included, not just the commercial sizes.

Table 124

ANOVA Table for kg/pot/day
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	8	35.16	4.40	7.11	<.0001	56.85	1
Season	3	27.32	9.11	14.72	<.0001	44.17	1
Sex	1	14.58	14.58	23.57	<.0001	23.57	1
Year	7	280.37	40.05	64.76	<.0001	453.32	1
Residual	6306	3900.14	0.62				

There were highly significant differences ($p = < .0001$) within the categories of depth, season, sex and year.

Depth

Table 125

Means Table for kg/pot/day
Effect: Depth Range
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	999	0.66	0.84	0.03
150	3082	0.73	0.76	0.01
200	860	0.63	0.93	0.03
250	441	0.52	0.80	0.04
300	421	0.70	0.94	0.05
350	331	0.60	0.93	0.05
400	156	0.48	0.66	0.05
450	27	0.23	0.29	0.06
500	9	0.27	0.43	0.14

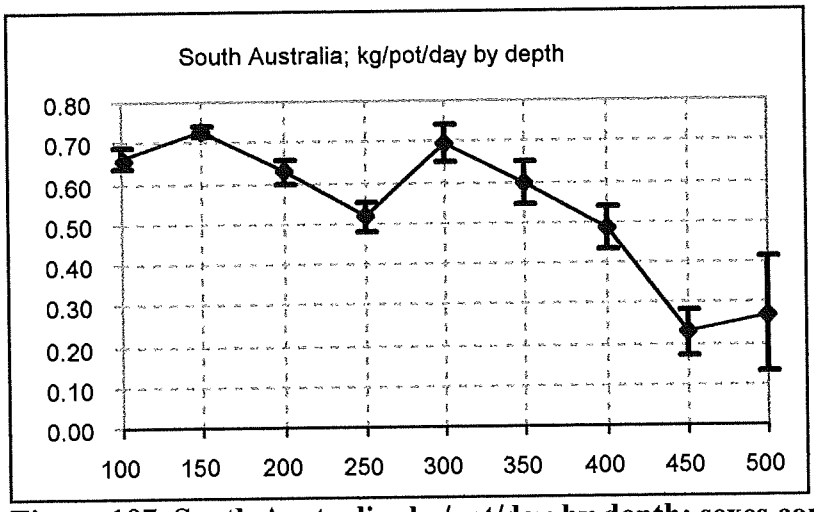

Figure 107. South Australia; kg/pot/day by depth; sexes combined

The interaction plot for both sexes combined showed a trend of decreasing catch rate with depth. The SNK test tabulated below showed mean catch rate at 300 metres was significantly lower than 150 metres and that mean catch rate at 450 metres was significantly lower than at 300 metres.

Table 126

Student- Newman-Keuls for kg/pot/day
Effect: Depth
Significance level: 5%

Depth	100	150	200	250	300	350	400	450	500
100		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
150			*NS*	*NS*	*NS*	*NS*	*NS*	**S**	*NS*
200				*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
250					*NS*	*NS*	*NS*	*NS*	*NS*
300						*NS*	*NS*	**S**	*NS*
350							*NS*	*NS*	*NS*
400								*NS*	*NS*
450									*NS*
500									

S = Significant at this level
NS = Not significant at this level

Season

Table 127

Means Table for kg/pot/day
Effect: Season
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	1773	0.65	0.66	0.02
Autumn	1562	0.65	0.81	0.02
Winter	945	0.62	0.94	0.03
Spring	2046	0.73	0.89	0.02

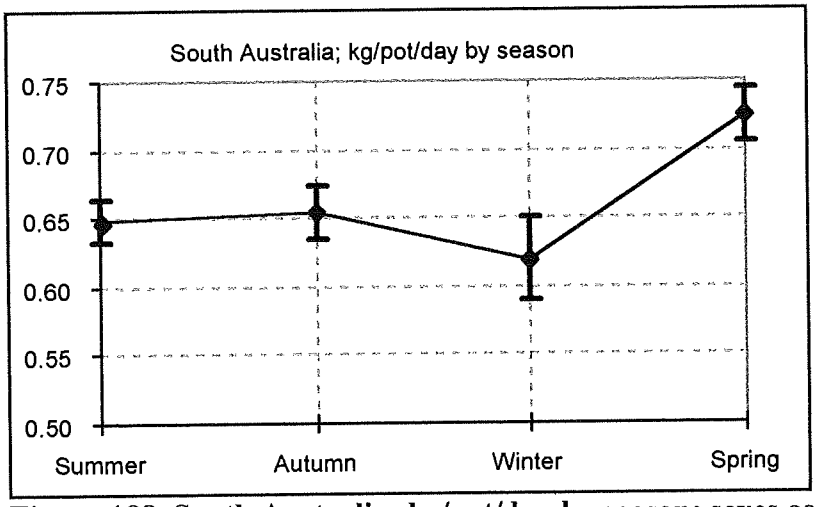

Figure 108. South Australia; kg/pot/day by season; sexes combined

A post hoc S-N-K test (tabulated below) indicated that catch rate in spring was significantly higher compared with summer, autumn and winter.

Table 128

Student-Newman-Keuls for kg/pot/day
Effect: Season
Significance Level: 5 %
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

Season	Summer	Autumn	Winter	Spring
Summer		*NS*	*NS*	**S**
Autumn			*NS*	**S**
Winter				**S**
Spring				

S = Significant at this level
NS = not significant at this level

Sex

Table 129

Means Table for kg/pot/day
Effect: Sex
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
F	3113	0.63	0.77	0.01
M	3213	0.71	0.87	0.02

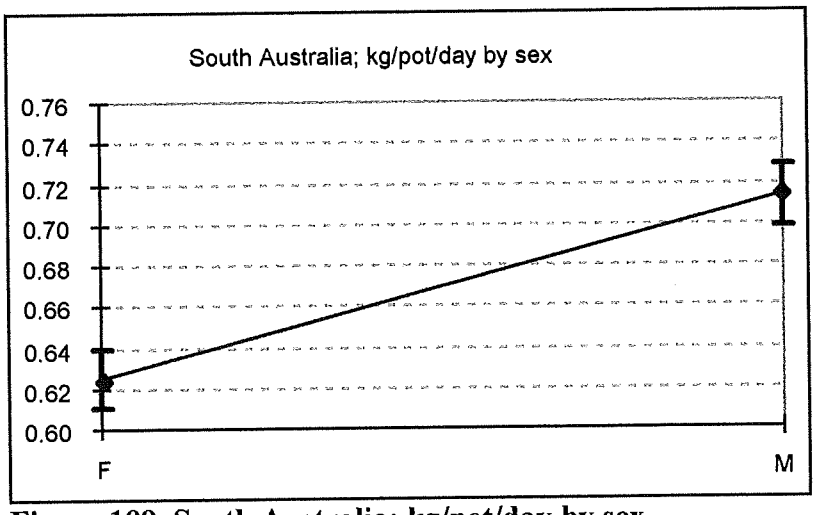

Figure 109. South Australia; kg/pot/day by sex

A post hoc S-N-K test (tabulated below) showed that the catch rate for males was significantly higher.

Table 130

Student-Newman-Keuls for kg/pot/day
Effect: Sex
Significance Level: 5 %
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

		Mean Diff.	Crit. Diff	Sig?
F	M	-0.09	0.04	**S**

S = Significant at this level

Year

Table 131

Means Table for kg/pot/day
Effect: Year
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	570	0.97	1.07	0.05
1994	1289	0.77	0.77	0.02
1995	1333	0.90	1.08	0.03
1996	342	0.71	0.64	0.04
1997	730	0.42	0.37	0.01
1998	894	0.60	0.81	0.03
1999	1126	0.35	0.38	0.01
2000	42	0.40	0.44	0.07

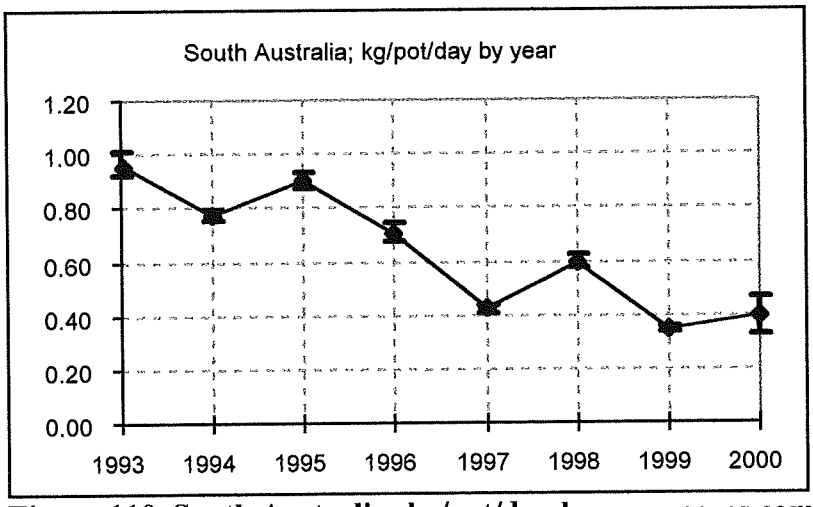

Figure 110. South Australia; kg/pot/day by year; sexes combined

Catch rate has declined since 1993 over years as targeted effort and the retention of by-catch by lobster fishers fished down the previously unexploited stocks. The SNK test tabulated below identifies significant differences within this trend.

Table 132

Student-Newman-Keuls for kg/pot/day
Effect: Year
Significance Level: 5 %
Split By: Region
Cell: South Australia
Row exclusion: CPUE by Event.ssd

Year	1993	1994	1995	1996	1997	1998	1999	2000
1993		**S**	*NS*	**S**	**S**	**S**	**S**	**S**
1994			*NS*	*NS*	**S**	**S**	**S**	**S**
1995				**S**	**S**	**S**	**S**	**S**
1996					**S**	*NS*	**S**	**S**
1997						**S**	*NS*	*NS*
1998							**S**	**S**
1999								*NS*
2000								

S = Significant at this level
NS = not significant at this level

5.3.2. Stock Assessment - South Australia – female: all sizes attracted to baited pots are included, not just the commercial sizes.

Table 133

ANOVA Table for Catch (kg)/Pot/Day
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	8	24.713	3.089	6.422	<.0001	51.38	1
Month	11	93.989	8.544	17.764	<.0001	195.41	1
Year	7	66.787	9.541	19.836	<.0001	138.85	1
Residual	3086	1484.346	0.481				

There were highly significant differences (P = <.0001) within the categories of depth, month and year.

Depth

Table 134

Means Table for Catch (kg)/Pot/Day
Effect: Depth Range
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	514	0.598	0.628	0.028
150	1580	0.806	0.819	0.021
200	403	0.612	0.974	0.049
250	196	0.193	0.232	0.017
300	185	0.207	0.258	0.019
350	144	0.169	0.207	0.017
400	73	0.21	0.297	0.035
450	14	0.129	0.09	0.024
500	4	0.158	0.15	0.075

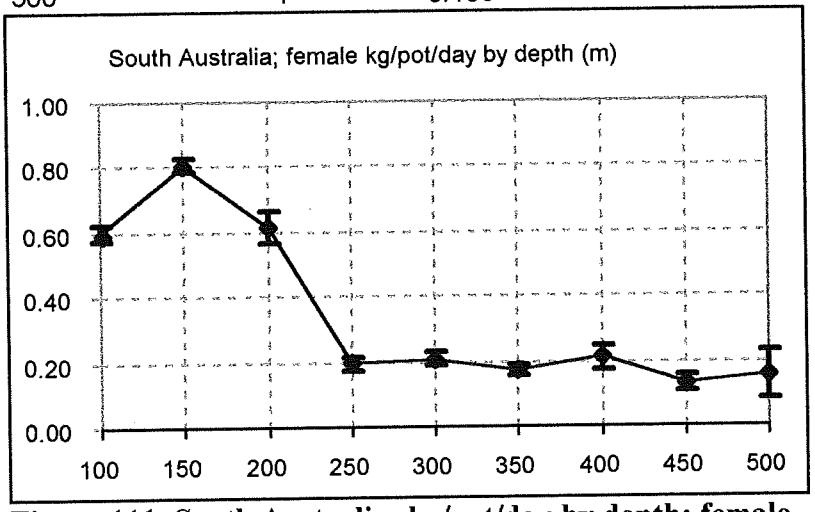

Figure 111. South Australia; kg/pot/day by depth; female

A post hoc SNK test is tabulated below, shows catch rates at 150m were significantly higher compared to those taken at 250 metres and deeper.

Table 135

Student-Newman-Keuls for Catch (kg)/Pot/Day
Effect: Depth Range
Significance Level: 5 %
Split By: Sex
Cell: F

Depth	100	150	200	250	300	350	400	450	500
100		*NS*	*NS*	*NS*	*NS*	*NS*	**S**	*NS*	*NS*
150			NS	**S**	**S**	**S**	**S**	**S**	**S**
200				*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
250					*NS*	*NS*	*NS*	*NS*	*NS*
300						*NS*	*NS*	*NS*	*NS*
350							*NS*	*NS*	*NS*
400								*NS*	*NS*
450									*NS*
500									

S = Significant at this level
NS = Not significant at this level

Month

Table 136

Means Table for Catch (kg)/Pot/Day
Effect: Month
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

	Count	Mean	Std. Dev.	Std. Err.
Jan	355	0.705	0.677	0.036
Feb	225	0.466	0.47	0.031
Mar	400	0.691	0.759	0.038
Apr	268	0.52	0.506	0.031
May	115	0.398	0.404	0.038
Jun	98	0.325	0.33	0.033
Jul	86	0.145	0.19	0.021
Aug	232	0.168	0.232	0.015
Sep	330	0.25	0.324	0.018
Oct	348	0.9	1.069	0.057
Nov	340	1.133	1.05	0.057
Dec	316	0.839	0.831	0.047

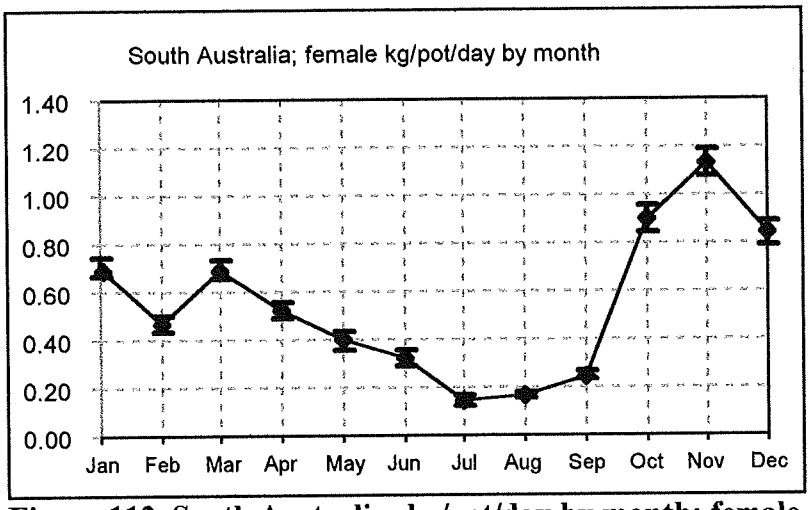

Figure 112. South Australia; kg/pot/day by month; female

A post hoc SNK test tabulated below showed there were many significant differences between monthly mean catch rates which peak in the late spring early summer, and then decline to be at a minimum in winter and early spring, when spawning and incubating of eggs are in progress. Another section of the female population is also moulting at this time.

Table 137

Student-Newman-Keuls for Catch (kg)/Pot/Day
Effect: Month
Significance Level: 5 %
Split By: Sex
Cell: F

Depth	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan		**S**	*NS*	**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	*NS*
Feb			**S**	*NS*	*NS*	*NS*	**S**	**S**	**S**	**S**	**S**	**S**
Mar				**S**	**S**	**S**	**S**	**S**	**S**	**S**	**S**	*NS*
Apr					*NS*	**S**	**S**	**S**	**S**	**S**	**S**	**S**
May						*NS*	**S**	**S**	*NS*	**S**	**S**	**S**
Jun							**S**	*NS*	*NS*	**S**	**S**	**S**
Jul								*NS*	*NS*	**S**	**S**	**S**
Aug									*NS*	**S**	**S**	**S**
Sep										**S**	**S**	**S**
Oct											**S**	*NS*
Nov												**S**
Dec												

S = Significant at this level
NS = Not significant at this level

Year

Table 138

Means Table for Catch (kg)/Pot/Day
Effect: Year
Split By: Sex
Cell: F
Row exclusion: CPUE by month by event sv.ssd

	Count	Mean	Std. Dev.	Std. Err.
1993	263	0.851	0.993	0.061
1994	666	0.867	0.829	0.032
1995	651	0.689	0.769	0.03
1996	175	0.861	0.775	0.059
1997	360	0.436	0.4	0.021
1998	440	0.537	0.911	0.043
1999	536	0.265	0.345	0.015
2000	22	0.447	0.511	0.109

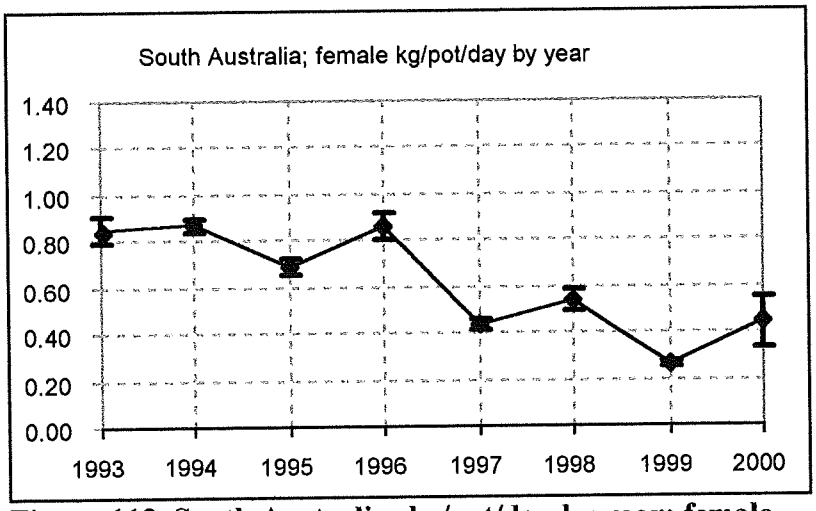

Figure 113. South Australia; kg/pot/day by year; female

Post hoc SNK testing tabulated below showed that catch rates in the more recent years 1997 to 2000 are significantly less than those of 1993 to 1996. In 1997 to 2000 most of the samples were taken from west of 137° longitude, whereas in the earlier years most samples were taken from east of this point.

Table 139

Student-Newman-Keuls for Catch (kg)/Pot/Day
Effect: I Year
Significance Level: 5 %
Split By: Sex
Cell: F

Depth	1993	1994	1995	1996	1997	1998	1999	2000
1993		*NS*	*NS*	*NS*	**S**	**S**	**S**	**S**
1994			*NS*	*NS*	**S**	**S**	**S**	**S**
1995				*NS*	**S**	*NS*	**S**	**S**
1996					**S**	**S**	**S**	**S**
1997						*NS*	*NS*	*NS*
1998							**S**	*NS*
1999								*NS*
2000								

S = Significant at this level
NS = Not significant at this level

5.3.3. Stock Assessment - South Australia –male: all sizes attracted to baited pots are included, not just the commercial sizes.

Male:

Table 140

ANOVA Table for Catch (kg)/Pot/Day
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	8	12.6	1.575	2.463	0.0117	19.705	0.916
Month	11	73.529	6.684	10.453	<.0001	114.988	1
Year	7	228.883	32.698	51.134	<.0001	357.938	1
Residual	3187	2037.921	0.639				

There were significant differences within depth (P = .0117) and highly significant differences within month and year (P = <.0001).

Depth

Table 141

Means Table for Catch (kg)/Pot/Day
Effect: Depth Range
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
100	485	0.733	1.012	0.046
150	1503	0.641	0.676	0.017
200	457	0.64	0.893	0.042
250	245	0.772	0.976	0.062
300	236	1.079	1.097	0.071
350	187	0.923	1.125	0.082
400	83	0.724	0.794	0.087
450	13	0.332	0.386	0.107
500	5	0.362	0.567	0.254

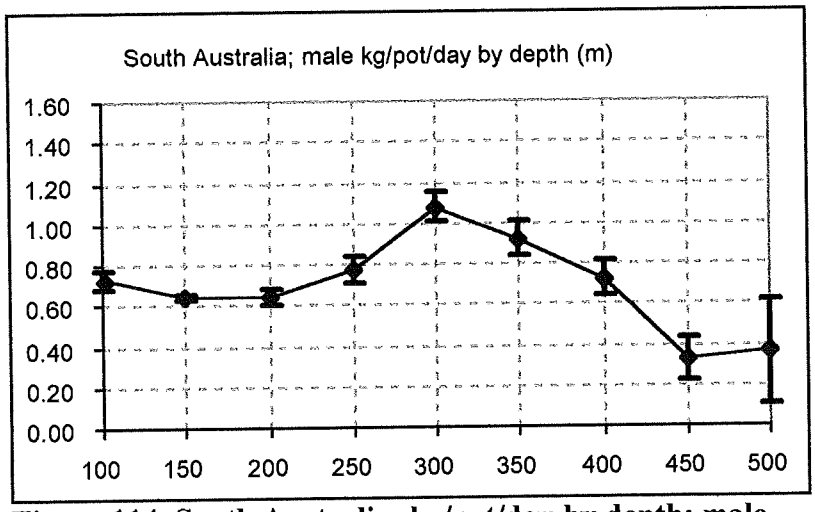

Figure 114. South Australia; kg/pot/day by depth; male

A post hoc SNK test below showed there were significant differences between 300metres compared with 450 and 500metres, however the number of fishing events in these depths was comparably small.

Table 142

Student-Newman-Keuls for Catch (kg)/Pot/Day
Effect: Depth Range
Significance Level: 5 %
Split By: Sex
Cell: F

Depth	100	150	200	250	300	350	400	450	500
100		*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
150			*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
200				*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
250					*NS*	*NS*	*NS*	*NS*	*NS*
300						*NS*	*NS*	**S**	**S**
350							*NS*	*NS*	*NS*
400								*NS*	*NS*
450									*NS*
500									

S = Significant at this level
NS = Not significant at this level

Month

Table 143

Means Table for Catch (kg)/Pot/Day
Effect: Month
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

	Count	Mean	Std. Dev.	Std. Err.
Jan	347	0.698	0.779	0.042
Feb	227	0.613	0.523	0.035
Mar	398	0.824	1.13	0.057
Apr	259	0.688	0.735	0.046
May	123	0.445	0.383	0.035
Jun	120	1.472	1.624	0.148
Jul	114	1.016	1.2	0.112
Aug	295	0.713	0.711	0.041
Sep	411	0.788	0.989	0.049
Oct	356	0.667	0.692	0.037
Nov	261	0.538	0.633	0.039
Dec	303	0.488	0.388	0.022

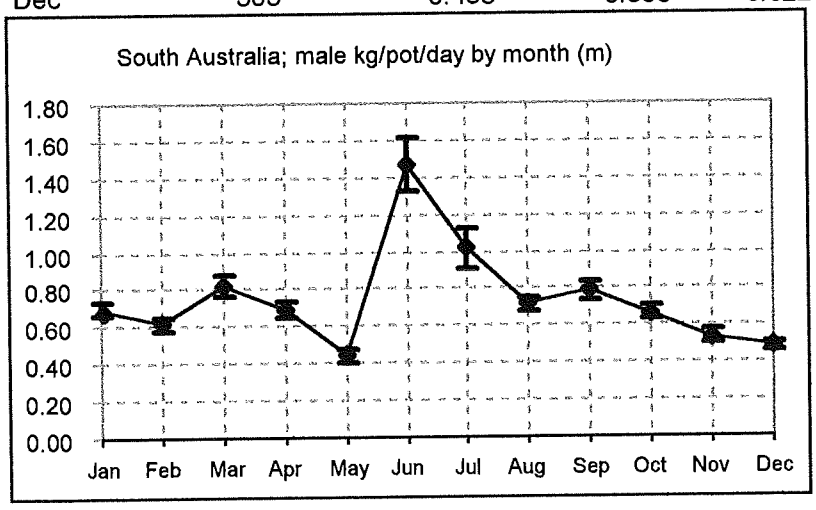

Figure 115. South Australia; kg/pot/day by month; male

A post hoc SNK test showed that June catch rate was significantly higher than all other months and that July was significantly higher than all other months except June. Other significant differences are tabulated below.

Table 144

Student-Newman-Keuls for Catch (kg)/Pot/Day
Effect: Month
Significance Level: 5 %
Split By: Sex
Cell: F

Depth	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan		*NS*	*NS*	*NS*	**S**	**S**	**S**	*NS*	*NS*	*NS*	*NS*	*NS*
Feb			*NS*	*NS*	*NS*	**S**	**S**	*NS*	*NS*	*NS*	*NS*	*NS*
Mar				*NS*	**S**	**S**	**S**	*NS*	*NS*	*NS*	**S**	**S**
Apr					**S**	**S**	**S**	*NS*	*NS*	*NS*	*NS*	*NS*
May						**S**	**S**	**S**	**S**	**S**	*NS*	*NS*
Jun							**S**	**S**	**S**	**S**	**S**	**S**
Jul								**S**	**S**	**S**	**S**	**S**
Aug									*NS*	*NS*	*NS*	**S**
Sep										*NS*	**S**	**S**
Oct											*NS*	*NS*
Nov												*NS*
Dec												

S = Significant at this level
NS = Not significant at this level

Year

Table 145

Means Table for Catch (kg)/Pot/Day
Effect: Year
Split By: Sex
Cell: M
Row exclusion: CPUE by month by event sv.ssd

	Count	Mean	Std. Dev.	Std. Err.
1993	307	1.065	1.117	0.064
1994	623	0.668	0.682	0.027
1995	682	1.104	1.279	0.049
1996	167	0.548	0.405	0.031
1997	370	0.41	0.335	0.017
1998	454	0.658	0.694	0.033
1999	591	0.422	0.401	0.016
2000	20	0.343	0.345	0.077

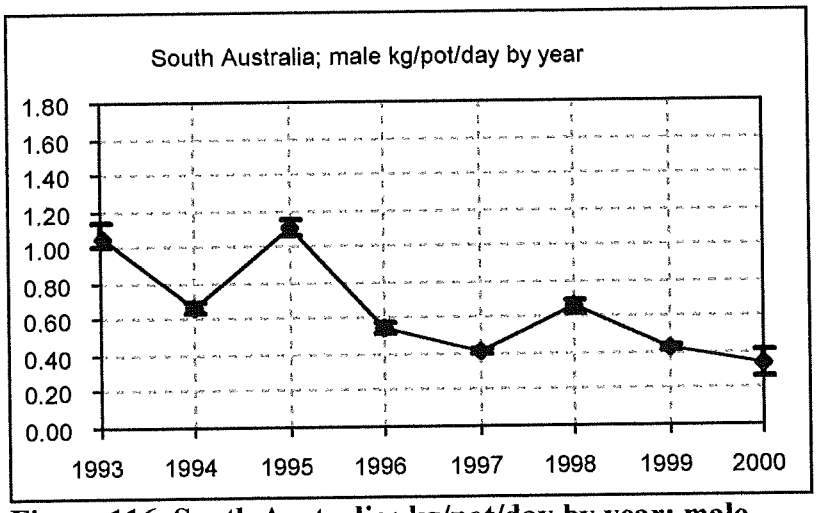

Figure 116. South Australia; kg/pot/day by year; male

A post hoc SNK test showed that male mean catch rate has decreased significantly since 1993. The increase in 1998 is linked to fishing new grounds west of 137° longitude, whereas the 1999 sample came from winter and spring sampling of even further to the west. The 2000 sample is small, of limited temporal extent and not representative.

Table 146

Student-Newman-Keuls for Catch (kg)/Pot/Day
Effect: Year
Significance Level: 5 %
Split By: Sex
Cell: F

Depth	1993	1994	1995	1996	1997	1998	1999	2000
1993		**S**	*NS*	**S**	**S**	**S**	**S**	**S**
1994			**S**	*NS*	*NS*	*NS*	*NS*	**S**
1995				**S**	**S**	**S**	**S**	**S**
1996					*NS*	*NS*	*NS*	*NS*
1997						*NS*	*NS*	*NS*
1998							*NS*	**S**
1999								*NS*
2000								

S = Significant at this level
NS = Not significant at this level

5.4. Stock Assessment – Victoria -male and female combined; all sizes attracted to baited pots are included, not just the commercial sizes.

Table 147

ANOVA Table for kg/pot/day
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	5	1.59	0.32	0.61	0.69	3.04	0.22
Season	3	32.93	10.98	20.94	<.0001	62.83	1
Sex	1	4.84	4.84	9.23	0.00	9.23	0.88
Year	5	36.54	7.31	13.95	<.0001	69.72	1
Residual	587	307.66	0.52				

There were significant differences within season and year (P= <.0001)

Depth

Table 148

Means Table for kg/pot/day
Effect: Depth Range
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
150	342	0.53	0.70	0.04
200	151	0.82	1.02	0.08
250	69	0.64	0.74	0.09
300	34	0.63	0.76	0.13
350	4	0.07	0.04	0.02
500	2	0.04	0.03	0.02

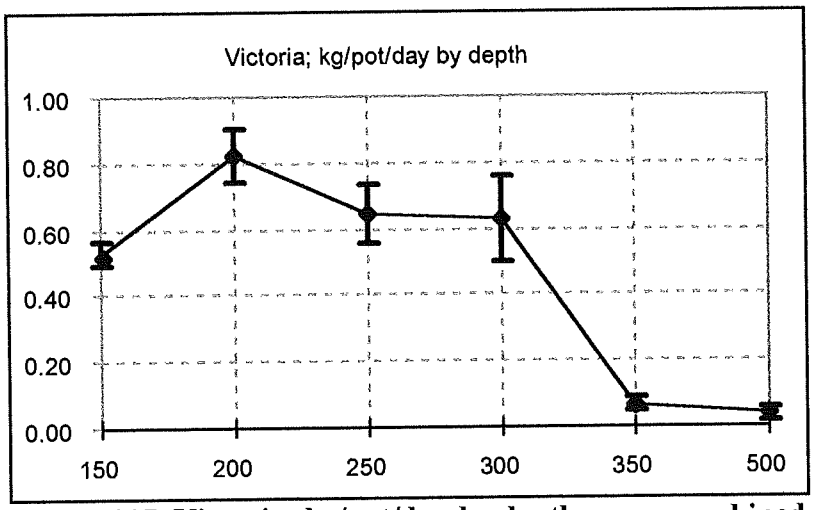

Figure 117. Victoria; kg/pot/day by depth; sexes combined

The interaction plot shows a trend of falling mean catch rate with depth from 200 m and deeper. Beyond 300 metres the rate was significantly lower.

Season

Table 149

Means Table for kg/pot/day
Effect: Season
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	100	0.75	0.71	0.07
Autumn	132	0.95	0.91	0.08
Winter	90	0.75	1.04	0.11
Spring	280	0.37	0.60	0.04

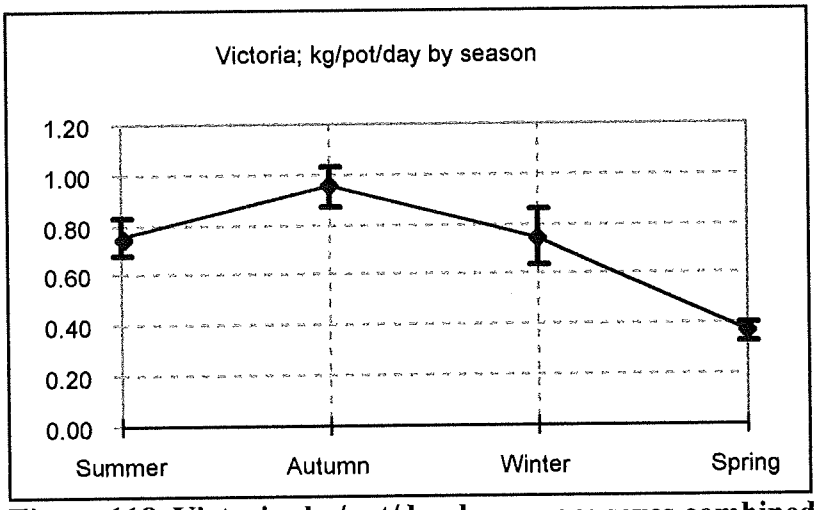

Figure 118. Victoria; kg/pot/day by season; sexes combined

A post hoc SNK test (tabulated below) showed that mean catch rates were significantly higher in autumn than in summer and spring. Spring catch rates were significantly lower than for the other seasons.

Table 150

Student-Newman-Keuls for kg/pot/day
Effect: Season
Significance Level: 5 %
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

Season	Summer	Autumn	Winter	Spring
Summer		**S**	*NS*	**S**
Autumn			*NS*	**S**
Winter				**S**
Spring				

S = significant at this level
NS = not significant at this level

Sex

Table 151

Means Table for kg/pot/day
Effect: Sex
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
F	303	0.52	0.65	0.04
M	299	0.71	0.93	0.05

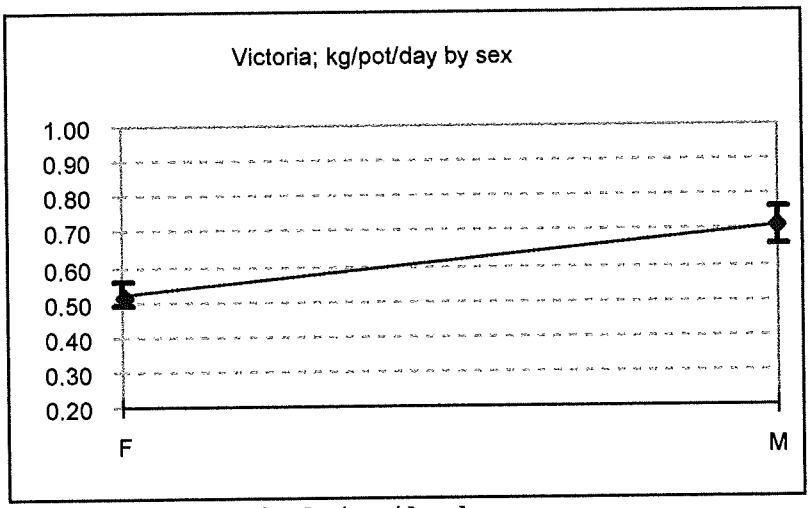

Figure 119. Victoria; kg/pot/day by sex

A post hoc SNK test tabulated below showed that male mean catch rate was higher than for females.

Table 152

Student-Newman-Keuls for kg/pot/day
Effect: Sex
Significance Level: 5 %
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

		Mean Diff.	Crit. Diff.	Sig?
F	M	-0.19	0.12	**S**

S = significant at this level

Year

Table 153

Means Table for kg/pot/day
Effect: Year
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	78	0.36	0.31	0.04
1994	103	1.11	1.16	0.11
1995	317	0.57	0.76	0.04
1996	64	0.64	0.61	0.08
1997	18	0.35	0.20	0.05
1998	22	0.05	0.03	0.01

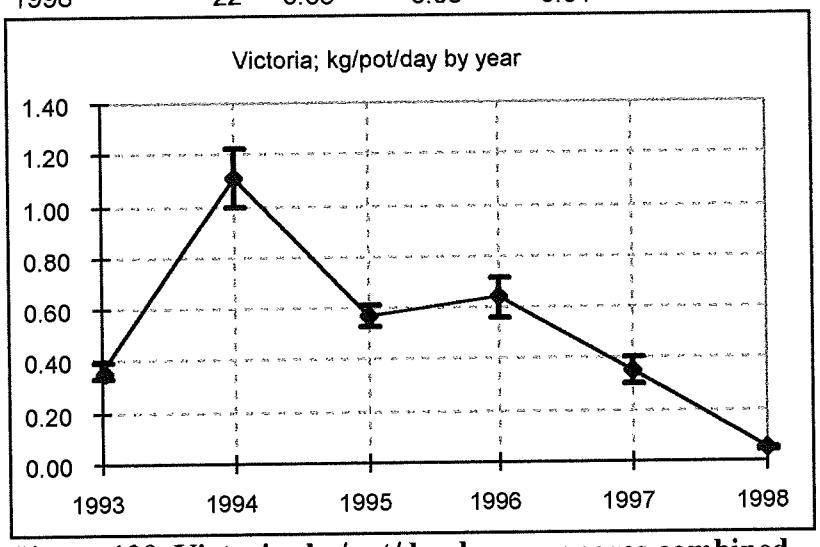

Figure 120. Victoria; kg/pot/day by year; sexes combined

A post hoc SNK test found significant differences between mean catch rates. The low value for 1993 are attributable to sampling occurring only in the Spring. 1994 values were obtained across all seasons from the shelf break east of 142° 40' however values for the years 1996, 1997 and 1998 reflect effects of sampling locations, season and sample sizes.

Table 154

Student-Newman-Keuls for kg/pot/day
Effect: Year
Significance Level: 5 %
Split By: Region
Cell: Victoria
Row exclusion: CPUE by Event.ssd

Year	1993	1994	1995	1996	1997	1998
1993		**S**	*NS*	*NS*	*NS*	*NS*
1994			**S**	**S**	**S**	**S**
1995				*NS*	*NS*	**S**
1996					*NS*	**S**
1997						*NS*
1998						

S = significant at this level
NS = not significant at this level

5.5. Stock Assessment – West Tasmania -male and female combined; all sizes attracted to baited pots are included, not just the commercial sizes.

Table 155

ANOVA Table for kg/pot/day
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	6	7.86	1.31	2.87	0	17.22	0.90
Season	2	10.33	5.17	11.31	<.0001	22.62	1.00
Sex	1	0.74	0.74	1.62	0	1.62	0.23
Year	4	7.75	1.94	4.24	0	16.96	0.93
Residual	361	164.90	0.46				

There were significant effects within season (P= <.0001)

Depth

Table 156

Means Table for kg/pot/day
Effect: Depth Range
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
50	22	0.24	0.22	0.05
100	40	0.44	0.66	0.10
150	83	1.03	0.88	0.10
200	169	0.88	0.78	0.06
250	39	0.59	0.57	0.09
300	15	0.69	0.73	0.19
350	7	0.50	0.41	0.16

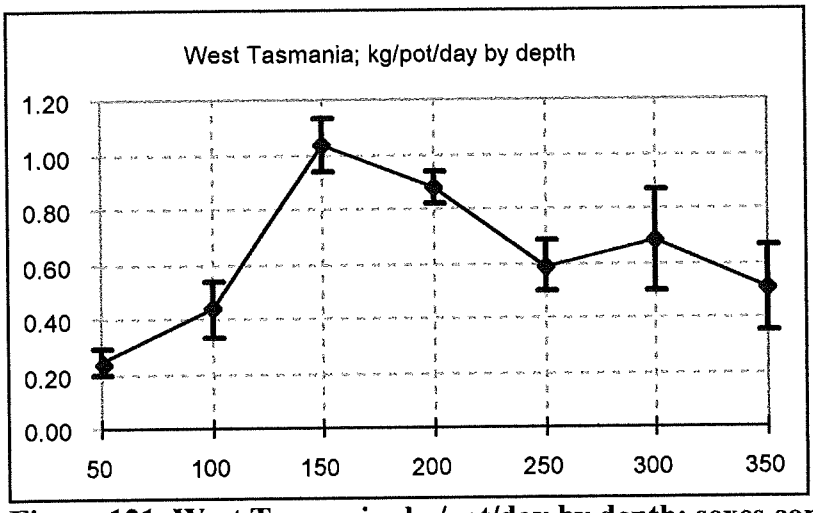

Figure 121. West Tasmania; kg/pot/day by depth; sexes combined

The interaction plot shows that mean catch rate peaks on the outer edge of the shelf break in waters of 150 –200 metres. A post hoc SNK test tabulated below showed that the catch rates at the shelf break were significantly higher than to shoreward. While there was also a trend of decreasing mean catch rate down-slope, there was also a large amount of variability.

Table 157

Student-Newman-Keuls for kg/pot/day
Effect: Depth Range
Significance Level: 5 %
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

Depth	50	100	150	200	250	300	350
50		*NS*	**S**	**S**	*NS*	*NS*	*NS*
100			**S**	*NS*	*NS*	*NS*	*NS*
150				*NS*	*NS*	*NS*	*NS*
200					*NS*	*NS*	*NS*
250						*NS*	*NS*
300							*NS*
350							

S = significant at this level
NS = not significant at this level

Season

Table 158

Means Table for kg/pot/day
Effect: Season
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer	21	0.13	0.08	0.02
Autumn	69	1.40	0.89	0.11
Winter				
Spring	285	0.68	0.68	0.04

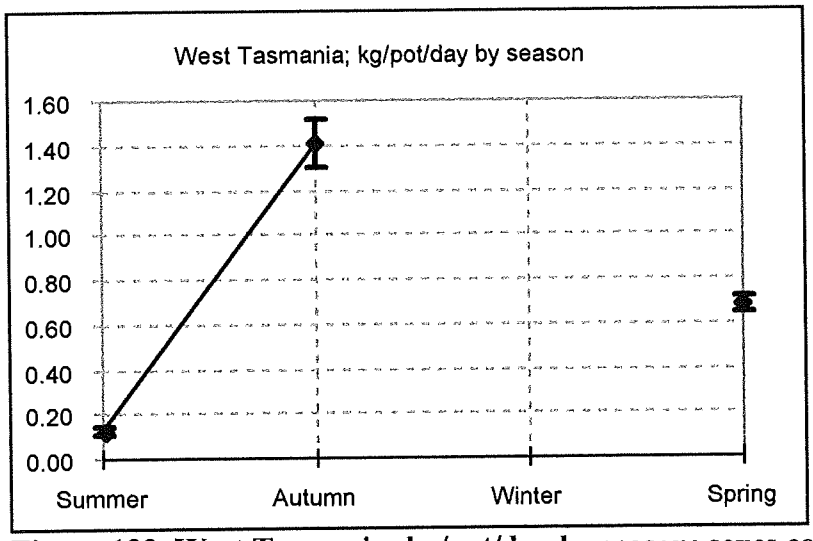

Figure 122. West Tasmania; kg/pot/day by season; sexes combined

There were no winter samples. A post hoc SNK test showed that autumn mean catch rates were significantly higher than for summer or spring. Summer catch rates reflect by catch while targeting lobster.

Table 159

Student-Newman-Keuls for kg/pot/day
Effect: Season
Significance Level: 5 %
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

Season	Summer	Autumn	Winter	Spring
Summer		**S**	...	**S**
Autumn				**S**
Winter				
Spring				

S = significant at this level

Sex

Table 160

Means Table for kg/pot/day
Effect: Sex
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
F	182	0.81	0.74	0.06
M	193	0.76	0.80	0.06

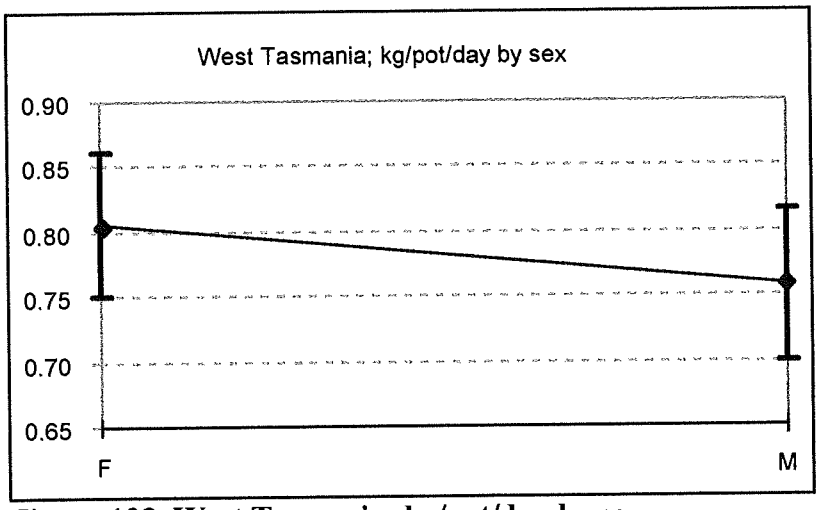

Figure 123. West Tasmania; kg/pot/day by sex

There was an insignificant trend of a higher mean catch rate for females.

Year

Table 161

Means Table for kg/pot/day
Effect: Year
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	48	0.89	0.71	0.10
1994	126	0.70	0.73	0.07
1995	10	1.32	1.38	0.44
1998	107	0.47	0.35	0.03
1999	84	1.17	0.95	0.10

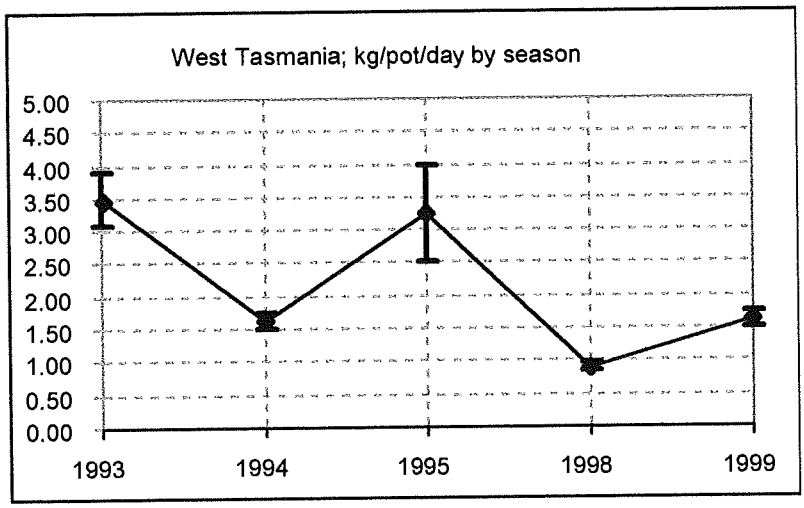

Figure 124. West Tasmania; kg/pot/day by season; sexes combined
A post hoc SNK test tabulated below showed significant differences between mean catch rates for some years. The low values for 1998 are in part attributable to spring sampling only, the much higher 1999 values reflect the effects of autumn as well as spring sampling which also included a population of larger individuals at a more southerly site. 1993, 1994 and 1995 samples were all taken in the spring, however 1994 came from shallower water than 1993. 1998 targeted depths where smaller crabs were most abundant to maximise the number of crabs that were tagged, and so while the three years reflect spring sampling, they are each influenced by depth effects.

Table 162
Student-Newman-Keuls for kg/pot/day
Effect: Year
Significance Level: 5 %
Split By: Region
Cell: West Tasmania
Row exclusion: CPUE by Event.ssd

Year	1993	1994	1995	1998	1999
1993		*NS*	**S**	**S**	*NS*
1994			**S**	*NS*	**S**
1995				**S**	*NS*
1998					**S**
1999					

S = significant at this level
NS = not significant at this level

5.6. Stock Assessment – East Tasmania -male and female combined; all sizes attracted to baited pots are included, not just the commercial sizes.

Table 163

ANOVA Table for kg/pot/day
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Depth Range	6	154.55	25.76	3.78	0.001	22.69	0.97
Season	2	949.54	474.77	69.69	<.0001	139.37	1.00
Sex	1	398.73	398.73	58.53	<.0001	58.53	1.00
Year	4	65.00	16.25	2.39	0.05	9.54	0.69
Residual	1223	8332.20	6.81				

There are significant differences between years (P= 0.05) and highly significant differences within the categories of depth, season and sex (P ≤.0001).

Depth

Table 164

Means Table for kg/pot/day
Effect: Depth Range
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

Depth	Count	Mean	Std. Dev.	Std. Err.
150	81	1.64	1.90	0.21
200	250	1.95	3.47	0.22
250	643	1.93	3.16	0.13
300	196	1.06	1.34	0.10
350	48	0.89	0.98	0.14
400	14	0.49	0.29	0.08
450	5	0.67	0.42	0.19

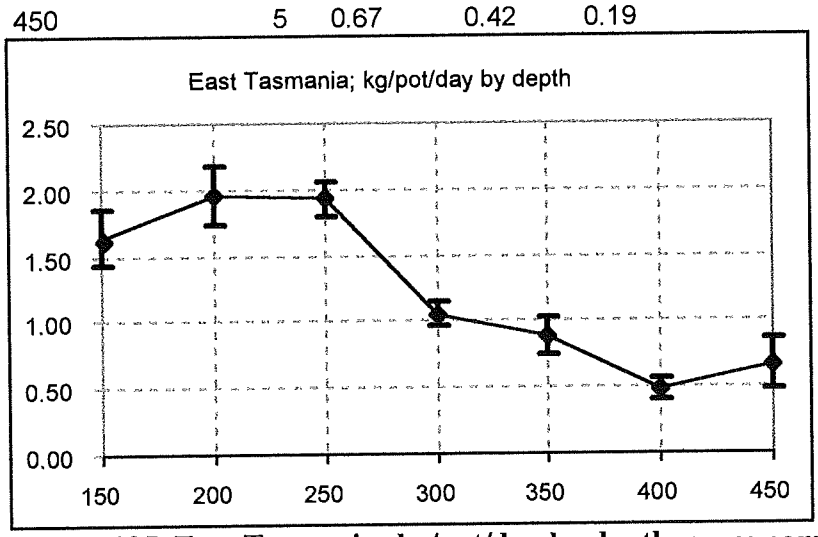

Figure 125. East Tasmania; kg/pot/day by depth; sexes combined

Analysis of variance showed differences by depth. A post hoc SNK test could not determine where these differences were although inspection of the interaction plot shows a trend of falling cpue with depth from 250 m and deeper.

Season

Table 165

Means Table for kg/pot/day
Effect: Season
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
Summer				
Autumn	609	2.75	3.72	0.15
Winter	107	0.71	1.23	0.12
Spring	521	0.71	0.90	0.04

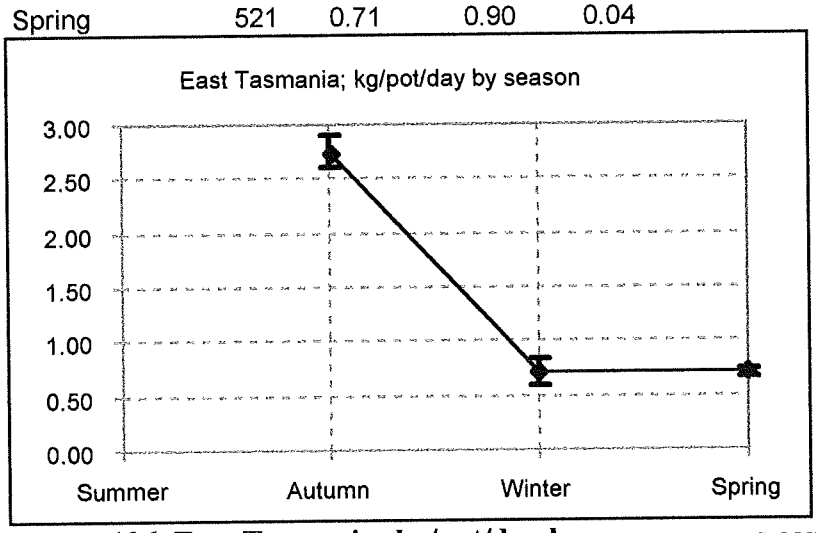

Figure 126. East Tasmania; kg/pot/day by season; sexes combined

Autumn catch rates were significantly higher than for winter and spring. There was no summer data.

Table 166

Student-Newman-Keuls for kg/pot/day
Effect: Season
Significance Level: 5 %
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

Season	Summer	Autumn	Winter	Spring
Summer		...	...	...
Autumn			**S**	**S**
Winter				*NS*
Spring				

S = significant at this level
NS = not significant at this level

Sex

Table 167

Means Table for kg/pot/day
Effect: Sex
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

	Count	Mean	Std. Dev.	Std. Err.
F	848	2.04	3.32	0.11
M	389	1.00	1.30	0.07

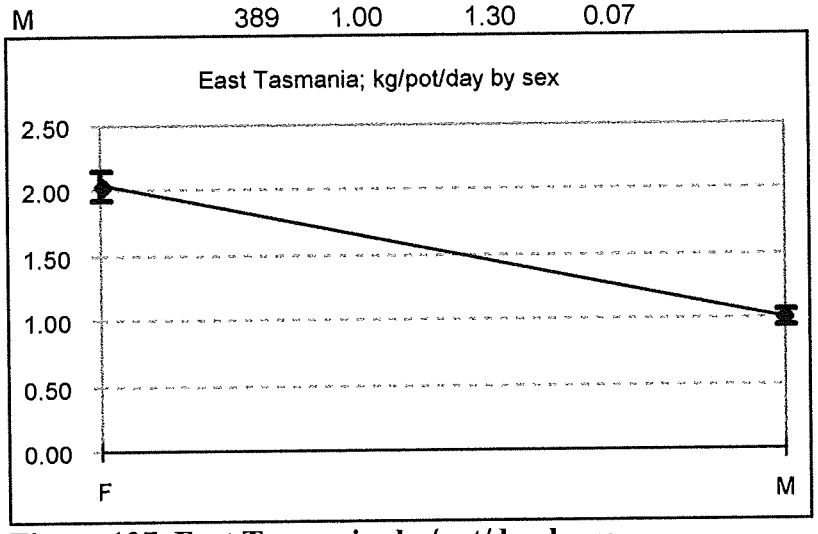

Figure 127. East Tasmania; kg/pot/day by sex

Female mean catch rate was significantly higher than male.

Table 168

Student-Newman-Keuls for kg/pot/day
Effect: Sex
Significance Level: 5 %
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

		Mean Diff.	Crit. Diff	Sig?
F	M	1.04	0.31	**S**

S = significant at this level

Year

Table 169

Means Table for kg/pot/day
Effect: Year
Split By: Region
Cell: East Tasmania
Row exclusion: CPUE by Event.ssd

Year	Count	Mean	Std. Dev.	Std. Err.
1993	5	0.11	0.05	0.02
1994	190	1.14	1.05	0.08
1995	104	0.42	0.29	0.03
1998	98	0.95	1.46	0.15
1999	840	2.10	3.35	0.12

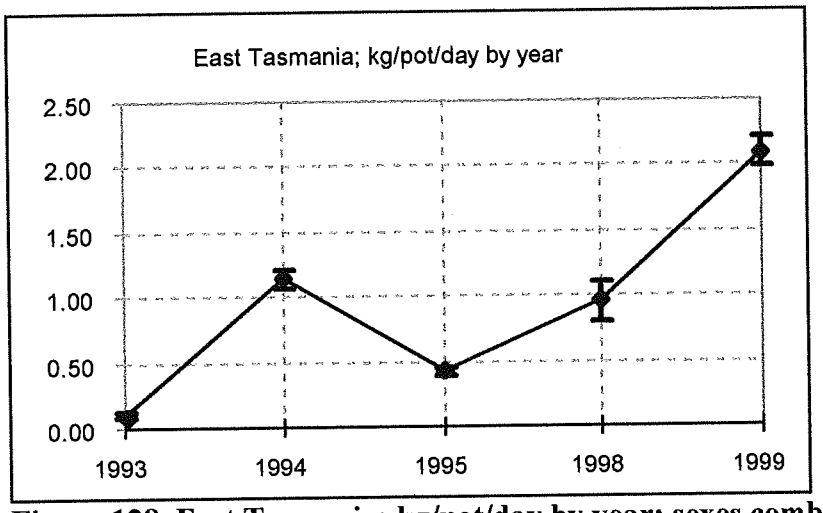

Figure 128. East Tasmania; kg/pot/day by year; sexes combined

1999 catch rates were significantly higher than for other years. The low values for 1993 reflect a very small and non-representative sample.

5.7. CPUE Summary

Table 169: Summary of catch per unit effort analysis.

The analysis refers to all crabs that entered the traps, not just the commercial component. The unit is kilograms per pot per day (kg/pot/day).

	Overall trend	WA	SA	Vic	W Tas	E Tas
Sexes	F > M	M > F	M > F	M > F	Not sig	F > M
Region	WA lowest, E Tas highest	< others	> WA, < W Tas & E Tas	> WA, < W Tas & E Tas	> Vic	> others
Years	1993 > all yrs expt 1999	1995 > all yrs expt 1996	1993 > all yrs expt 1995	1994 > 1998	Not sig	1999 > all yrs
Seasons	Au. > W, Sp, Su	Not sig.	Sp > W, Su, Au	Au .>Sp, Su	Au. > Sp, Su	Au. > Sp, W
Depths	Not analysed	Not sig.	Trend: decr. w depth	Trend: decr. w depth	Trend: decr. w depth	Trend: decr. w depth

Notes; " > " means significantly greater than, " < " means significantly less than at the .05 level.

CPUE by sexes
Australia wide: Higher female than male CPUE due to a higher abundance of females in spring sampling, a larger spring sample size and an abnormally high abundance of females off east Tasmania.

CPUE by regions
There is a general trend of increasing cpue along the southern Australian margin from west to east.

CPUE by years
1993 cpue's are higher due to the absence of a size limit. Notwithstanding the fishing of new grounds, or the recovery of stocks after closure, there is the expected decline in cpue as virgin stocks were fished down and the fishery became more dependent on recruitment from below legal minimum size.

CPUE by seasons
Autumn is usually higher due to an influx of larger males. A large sample size in SA has meant that a difference in catch rate of only .08kg/pot/day is statistically significant.

CPUE by depths
Excepting West Australia, there is a trend of decreasing cpue as depth increases on the upper bathial slope. Off WA a similar trend has been reported by fishermen(G Pateman, G Blackman)

6. Yield, value, and egg-per-recruit of Giant Crab

Introduction:

In the second stage of this FRDC project Deakin University commissioned the South Australian Research and development Institute to develop an individual based model for the fishery. The following chapter was previously released as a report to FRDC:

McGarvey, R., J.M. Matthews, and A.H. Levings. 1999. *Yield-, value-, and egg-per-recruit of giant crab, Pseudocarcinus gigas. South Australian Research and Development Corporation Report. 73 pp.*

A number of aspects of giant crab growth, notably intermoult period, moult increment, and seasonality of moulting, were subsequently reanalysed with improved statistical methods and the addition of tag recoveries received subsequent to this 1999 report. These finalised growth analyses were presented in Chapter 4.8.

The Beverton and Holt (1957) yield equation often serves as the basis of egg- and yield-per-recruit analysis in fishery assessment of changes to legal minimum length (LML). The Beverton-Holt formulation assumes (1) steady-state population structure, (2) continuous von Bertalanffy growth, (3) no dependence of reproductive life history on growth or mortality.

Several features of giant crab life history and growth fail to satisfy the assumptions of Beverton and Holt. Mean intermoult periods at LML of 2-3 (males) or 7-8 years (females) and egg production hypothesised to occur in years of non-moulting require a more detailed growth description than the continuous von Bertalanffy curve. Ideally growth is modelled by infrequent events of moulting observed for this species. High individual variability in growth, in moult increment and intermoult period, can have important implications for management, notably with regard to the question of optimal LML. Because each giant crab will bear eggs or not, or moult or not, with independent schedules, an individual-based model is preferred.

The individual-based simulation developed under this contract is dynamic, providing a prediction of both short-term and long-term effects of changes in LML. Knowledge of anticipated short-term effects in years following change in size limit, not provided by a Beverton Holt yield equation, is of value to management decision makers wher short term yield-per-recruit losses (increased LML) or gains (decreased LML) are considered in potential trade off to intended longer-term gains or losses.

A commercial fishery for giant crab operates in four states, (Western Australia, South Australia, Victoria, and Tasmania). Size of giant crabs is measured by carapace length (CL). Currently the LML is set at 150 mm CL in all states except Western Australia, where a LML of 140 mm CL was recently adopted.

This report will follow in three parts: 1. giant crab population biology relevant to questions of changes in LML; 2. a description of the individual-based model; 3. results of egg-, yield-, and value-per-recruit analysis.

6.1. Population Biology

6.1.1. Length-weight relationship

Relationships of giant crab mean weight versus carapace length (CL in mm) for males and females were fitted to weight and length data supplied by Mitchell and Levings

(1999). These data were pooled across states to obtain Australia-wide length-weight relationships (Figure 129). An allometric relationship was fitted assuming multiplicative lognormal errors. This error structure was chosen to reflect the observed increasing dispersion of weights with length.

The length-weight formulas obtained were as follows:

Males: $\text{Weight} = 0.0000001099 * \text{Length}^{3.3839}$.

Females: $\text{Weight} = 0.000001166 * \text{Length}^{2.8779}$.

6.1.2. Growth

The data set of tag recoveries obtained under previous and current FRDC programs (Mitchell and Levings 1999) provide information on giant crab growth, specifically moult increment and intermoult period. Commercially captured giant crabs were tagged and released in the four states of the fishery, with the exception of Tasmania where only two male recoveries were reported. Maximum reported times at large (times at liberty, from tagging and release to recapture) were 4 years.

6.1.2.1. Moult increment

Frequency distributions of male and female length increments (Figure 130) reveal two modal peaks, interpreted as crabs that have undergone either 0 or 1 moult during their time at large. Four additional recapture length increments greater than 40 mm CL were interpreted to represent two moults.

Visual stratification in scatterplots of growth increment versus length (Figure 131) indicate moult increments largely independent of pre-moult length over the range of observations, for both males and females.

Mean moult increments were larger for males and females in Victoria, and smaller for males in Western Australia (Table 170).

Table 170. Mean length increment (mm CL) with standard error and standard deviation for crabs that moulted once during their time at large. Only 1 moulted male recapture was reported from Tasmania.

	Males		Females	
	Mean ± SE	SD	Mean ± SE	SD
SA	24.93 ± 0.41	2.80	17.06 ± 0.38	2.36
Tasmania	26	-	18.42 ± 0.70	2.43
Victoria	26.78 ± 0.55	3.45	22.38 ± 1.03	4.61
WA	22.39 ± 0.55	3.25	17.31 ± 0.69	4.05

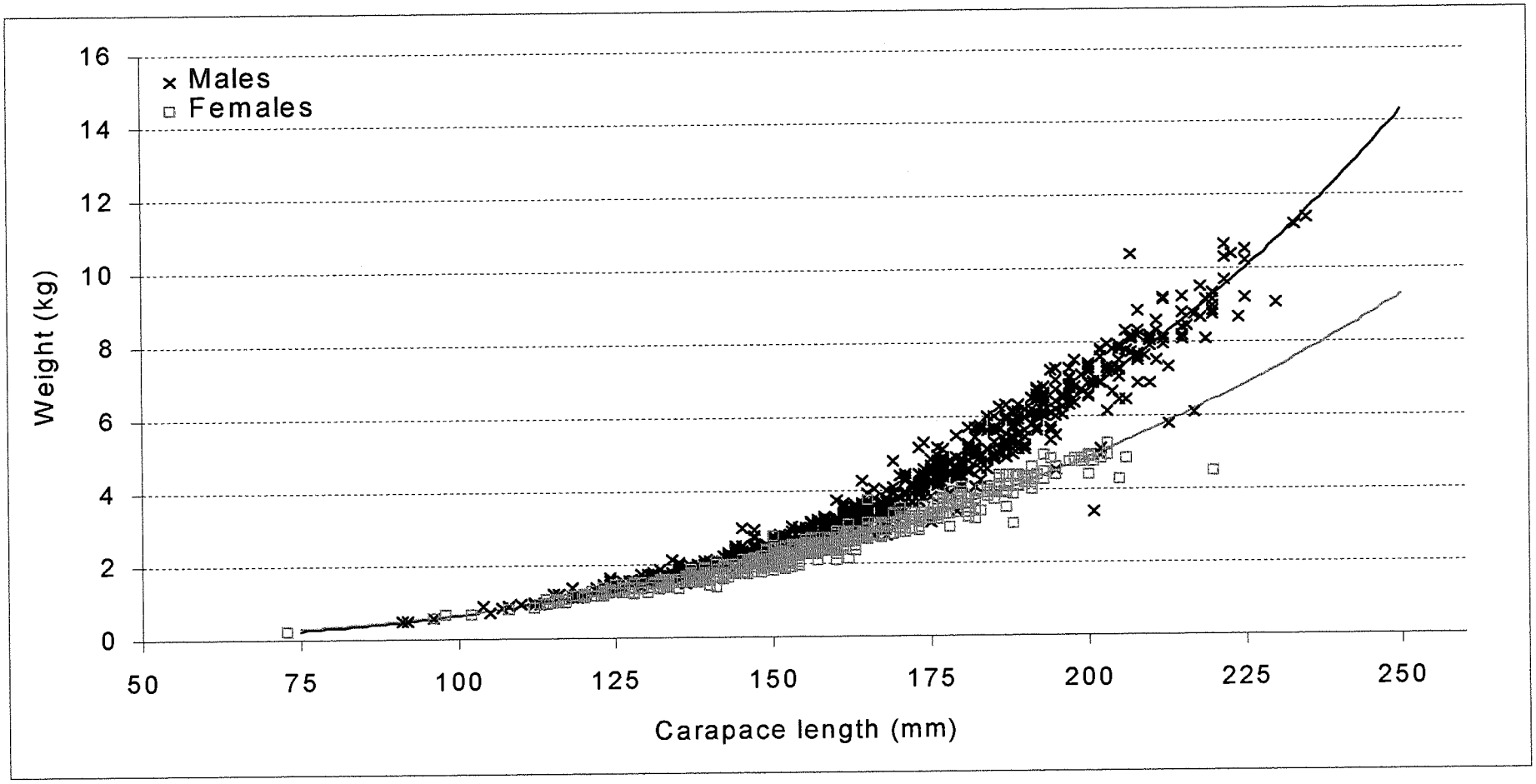

Figure 129. Length-weight curves fitted to pooled Australian data.

over all single-moult recaptures. Percentage weight gains of 77-91% for males and 40-59% for females (Table 171) reflect a life history growth strategy of very large weight increases with each moult.

Table 171. Mean % weight increment with standard error and standard deviation of giant crabs moulting once during time at large.

	Males		Females	
	Mean ± SE	SD	Mean ± SE	SD
SA	77.46 ± 1.71	11.58	39.61 ± 1.19	7.33
Tasmania	82.98	-	42.64 ± 2.15	7.43
Victoria	91.19 ± 3.30	20.63	58.50 ± 3.19	14.25
WA	90.67 ± 3.35	19.82	50.33 ± 3.52	20.53

Differences in the mean moulting length increments were tested among the four states using ANOVA. Females overall showed a significant result ($p < 0.0001$), and pairwise comparisons using protected least significant difference (LSD) showed that the mean for Victoria was significantly different from the other three states at the 1% level. South Australia, Western Australia and Tasmania were not significantly different from each other (at the 5% level). Although there was some inequality in the variances and non-normality of the residuals, these results were confirmed by alternative tests: a Kruskal -Wallis test (which does not assume normality) showed a significant difference between the median moult increments in some of the four states, and two-sample t-tests without assuming equal variance confirmed that Victoria was different to the other three states, and South Australia, Tasmania and Western Australia were not significantly different from each other

For males (excluding Tasmania), ANOVA yielded a significant result ($p< 0.0001$) and protected LSD's showed all three means (South Australia, Victoria and Western Australia) were significantly different from each other at the 1% level, with Victoria > South Australia > Western Australia. Again, there was some evidence of non-normality and variances were found to be unequal, however an ANOVA on transformed data corroborated these test outcomes.
(K. Haskard, Biometrics SA, SARDI, GP0 Box 397, Adelaide SA 5001, pers. comm.)

Moult increment distributions were obtained from crab recaptures that fell into the 1-moult length-increment range (Figure 130). The histograms were plotted at 5 mm intervals by state for males and females (Figure 132).

The relatively flat relationship of carapace length versus moult increment may be considered an accident of that definition for body growth. Often in crustacean growth analysis the proportional length increment (length increment divided by starting length) is plotted rather than absolute length increment (Mauchline 1977). This measure of growth yielded a modest decreasing trend versus length (Figure 133).

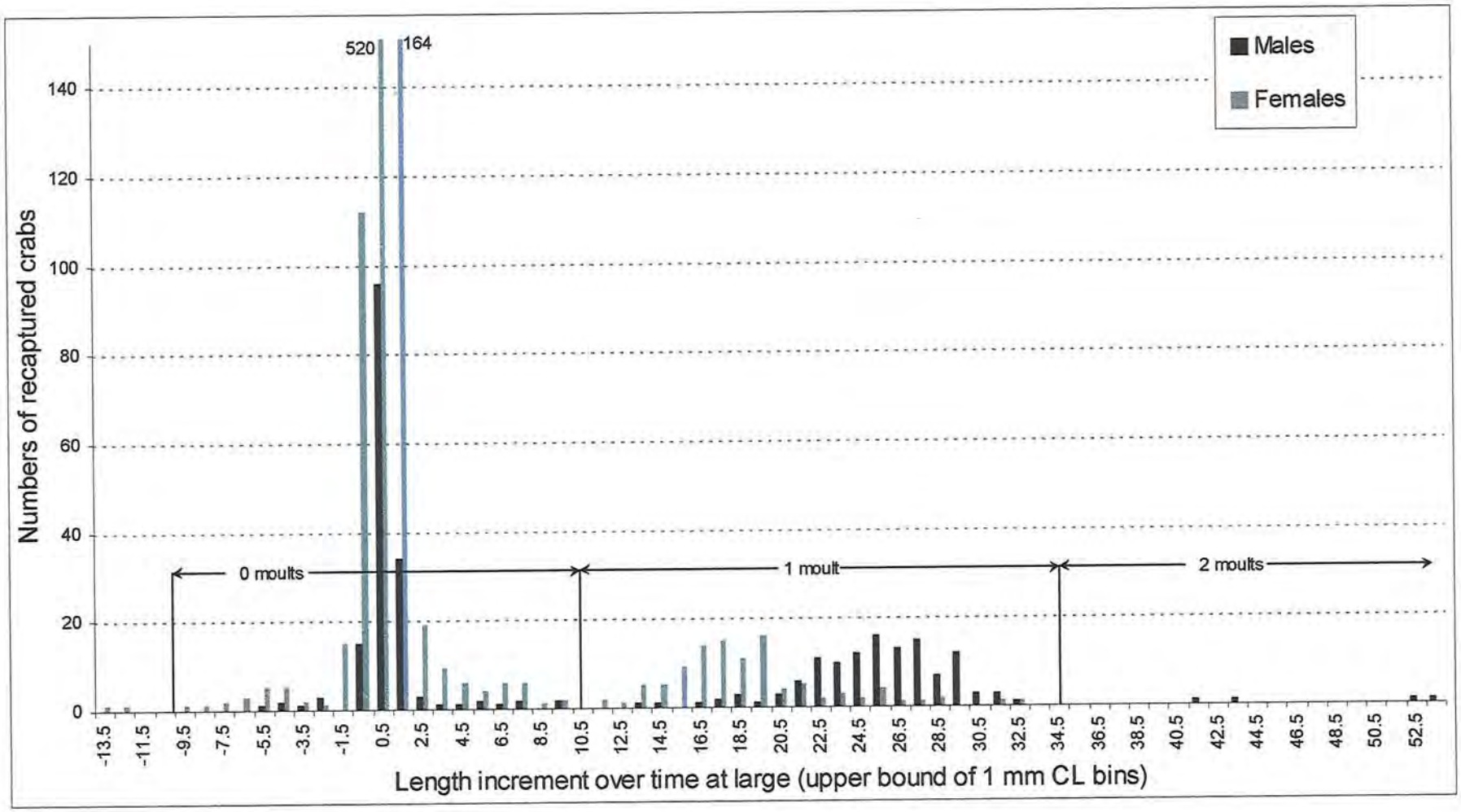

Figure 130. Length increment histograms for four states combined.

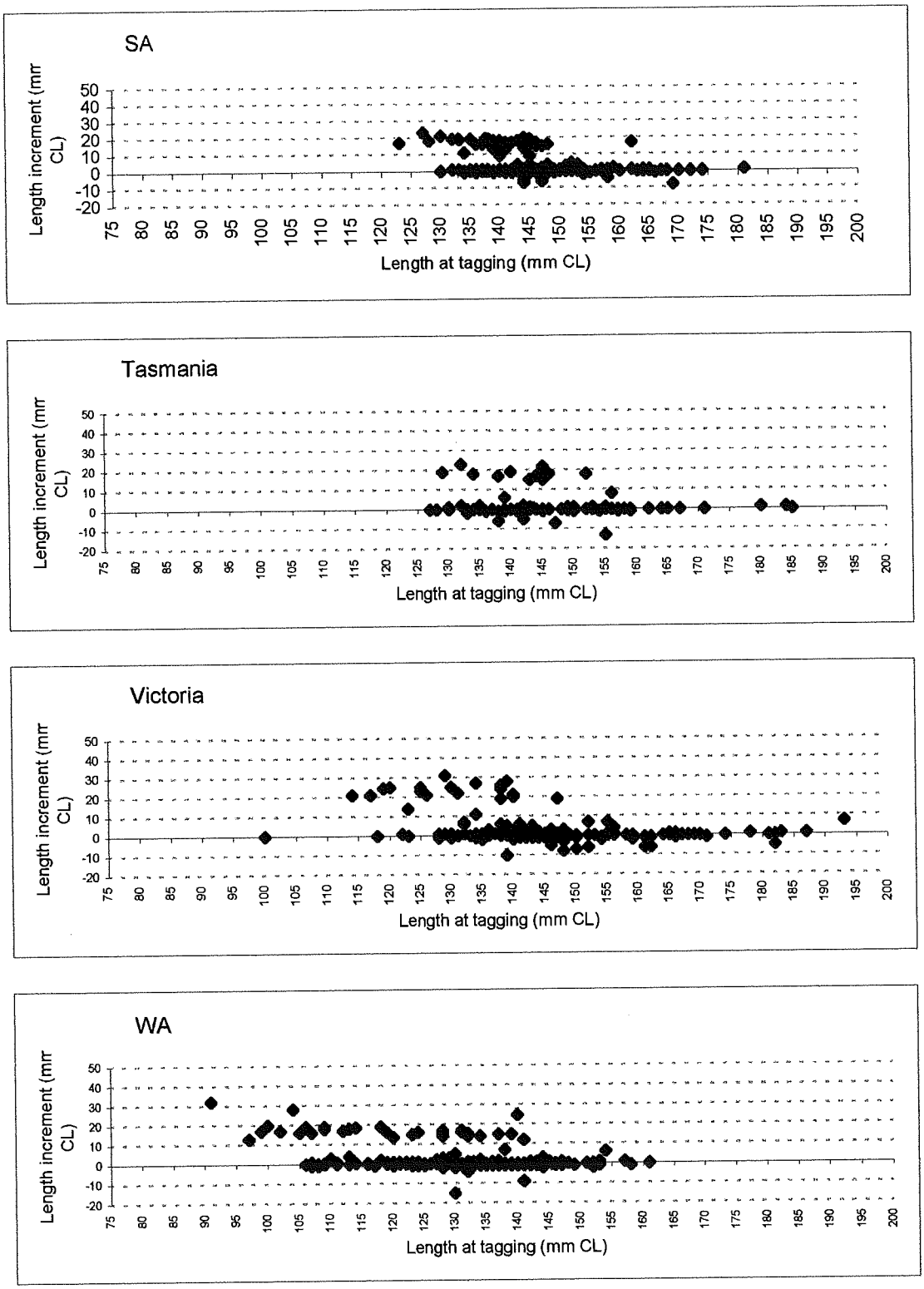

Figure 131. Female length increment scatterplots by state.

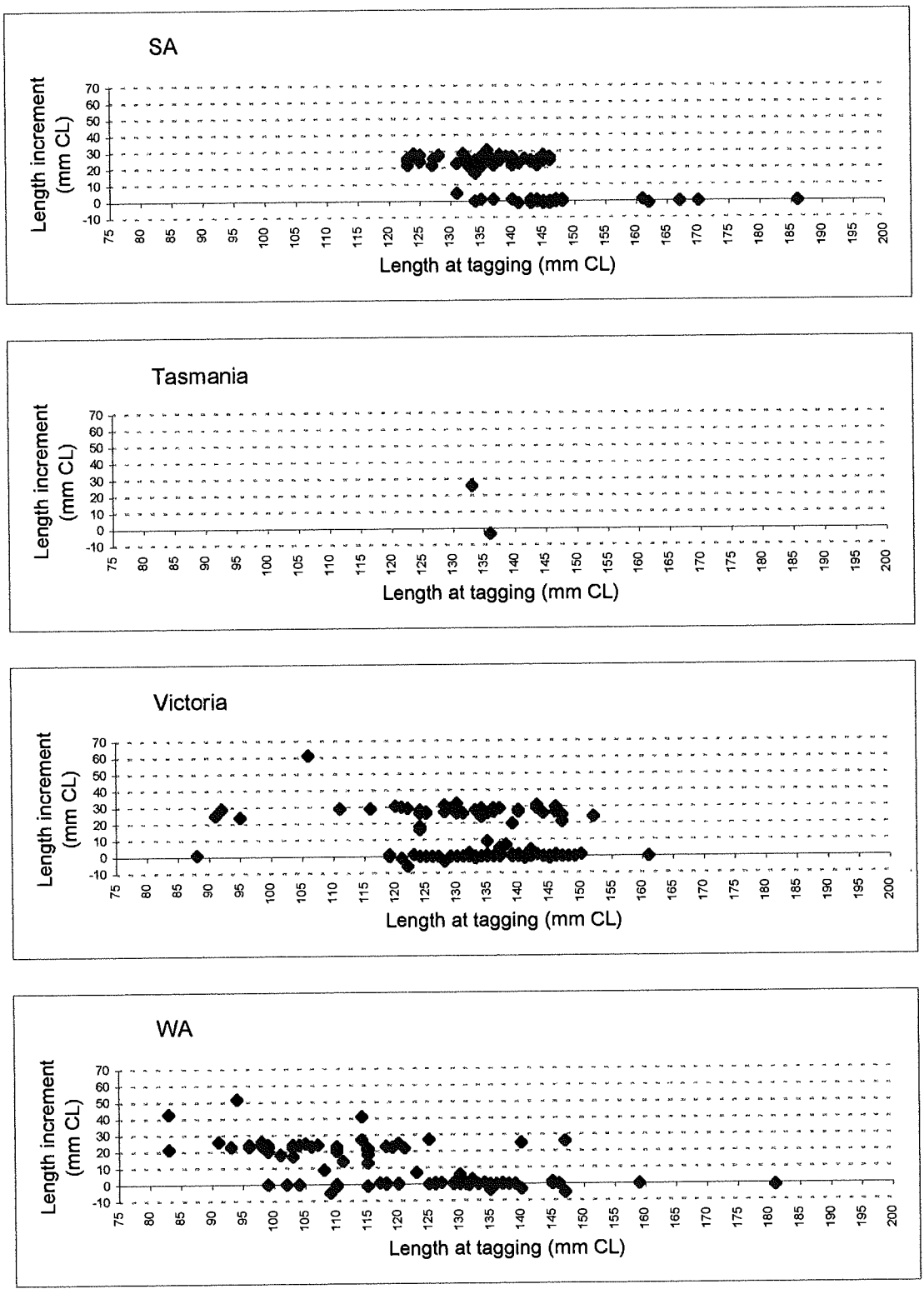

Figure 131. Male length increment scatterplots by state.

6.1.2.2. Seasonal timing of moulting

Conan (1985) in review noted that seasonal patterns for moulting are documented for a number of Brachyuran species. The giant crab tag recoveries contain information about this timing, but the (1) wide spread in times of releases and recaptures, and (2) times at liberty spanning many months and often years, make that inference indirect.

The time of year in which moulting is most frequent (if any) was analysed by considering each month in turn, and calculating the proportion of recaptures that moulted of those whose time at liberty traversed that month. The proportion of crabs that were observed to have moulted of those tagged in the 11 months prior to each month and recaptured the 11 months following, would yield a peak or substantial rise for month(s) when moulting was most frequent.

Plots of these proportions (Figure 134) over the two years available (including 11 months before the first month plotted and 11 months after the last) show little discernible trend for females. For males, there is a relatively clear rise in proportion moulted in months following December 1995 and December 1996, suggesting a moulting period of early to mid summer.

Fishers report observing greater numbers of clean shelled females in the months of following June, suggesting moulting in this time of early winter. However data samples are relatively sparse in these months--commercial fishing is closed during June and July, apart from research sampling, and weather reduces the levels of effort on the shelf edge where crabs are found. Predominantly male catch and lower levels of fishing may obscure the outcome for females by this approach, and is compatible with the sharp rise in proportions moulted in Figure 134a in November of each year when full-time fishing effort resumes.

6.1.2.3. Intermoult period

To estimate the time between moults (intermoult period, or its inverse, moult frequency), June and December were assumed to be the months of moulting for females and males respectively.

Time-at-large was quantified in units of moult periods at large (MPAL's), defined as the number of June or December moulting seasons crossed while the tagged crab was at liberty, i.e. the number of yearly opportunities to moult. Graphs of proportion moulted versus time-at-large yield a descriptive indication of intermoult period. If, for instance, all crabs (or all in a given size category) moulted every other year, then approximately half would have moulted after the first moulting time, and 100% would have moulted after two moulting seasons at large. Willoughby and Hurley (1987, Equation 3) obtained a similar result for a single moult under the assumption of uniform probability of time before tagging to previous moult. Approximately half moulting after one MPAL is roughly what was observed for males (Figure 135b), where most had moulted after two MPAL's, suggesting a mean intermoult period slightly larger than 2 years. The four male plots, one for each size class (Figure 135b), indicate a modest decrease in the slopes of the curves of percent moulted versus time at large, evidence of increasing intermoult period with size. For females (Figure 135a), a strong trend of increasing intermoult period with size is evident in decreasing regression slopes for increasing size categories, i.e. fewer larger females moulting after given times-at-large.

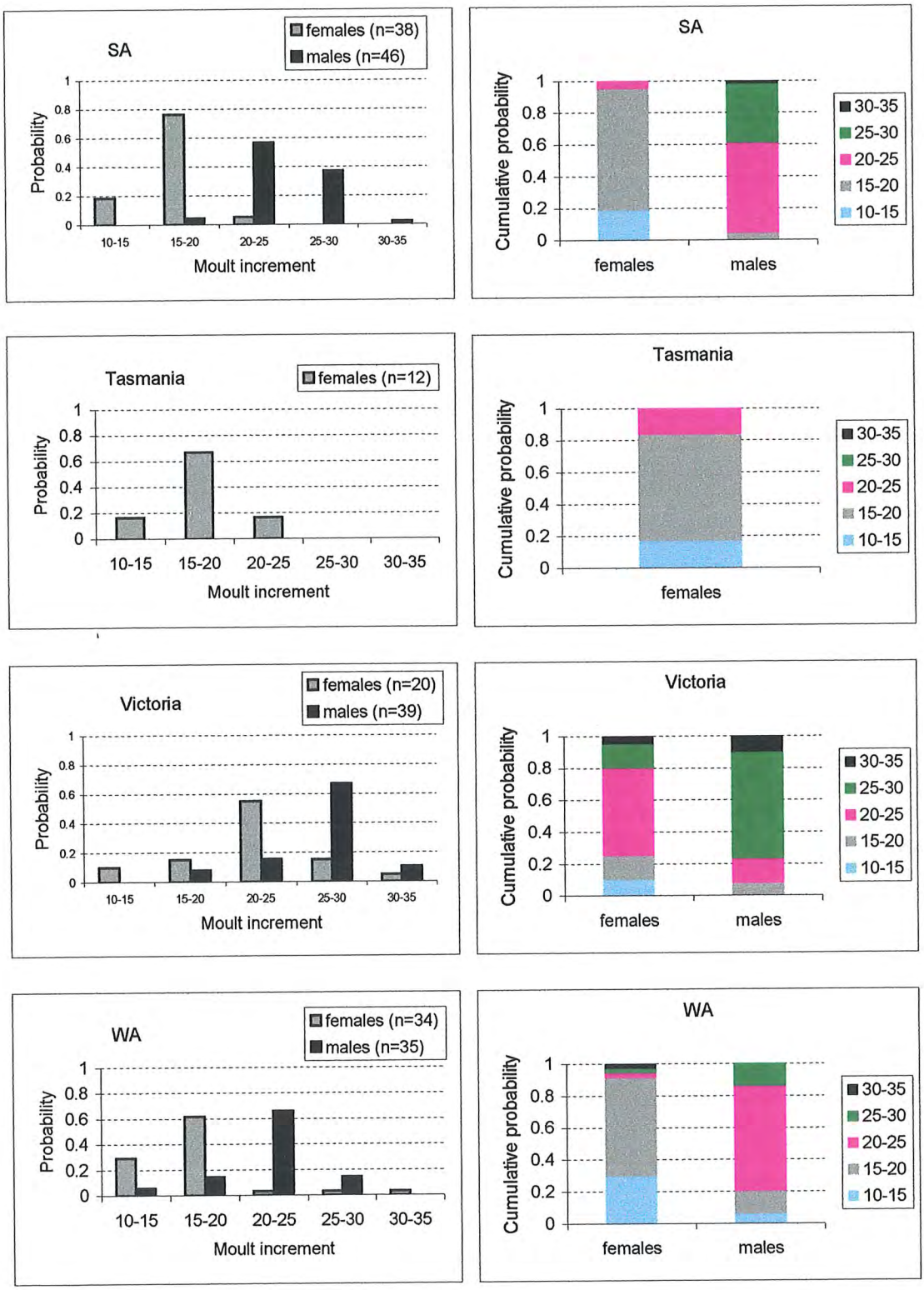

Figure 132. Moult increment probability histograms:- also displayed as cumulative probabilities, used in the individual-based model. Model length increment taken as the midpoint of the selected 5 mm bin.

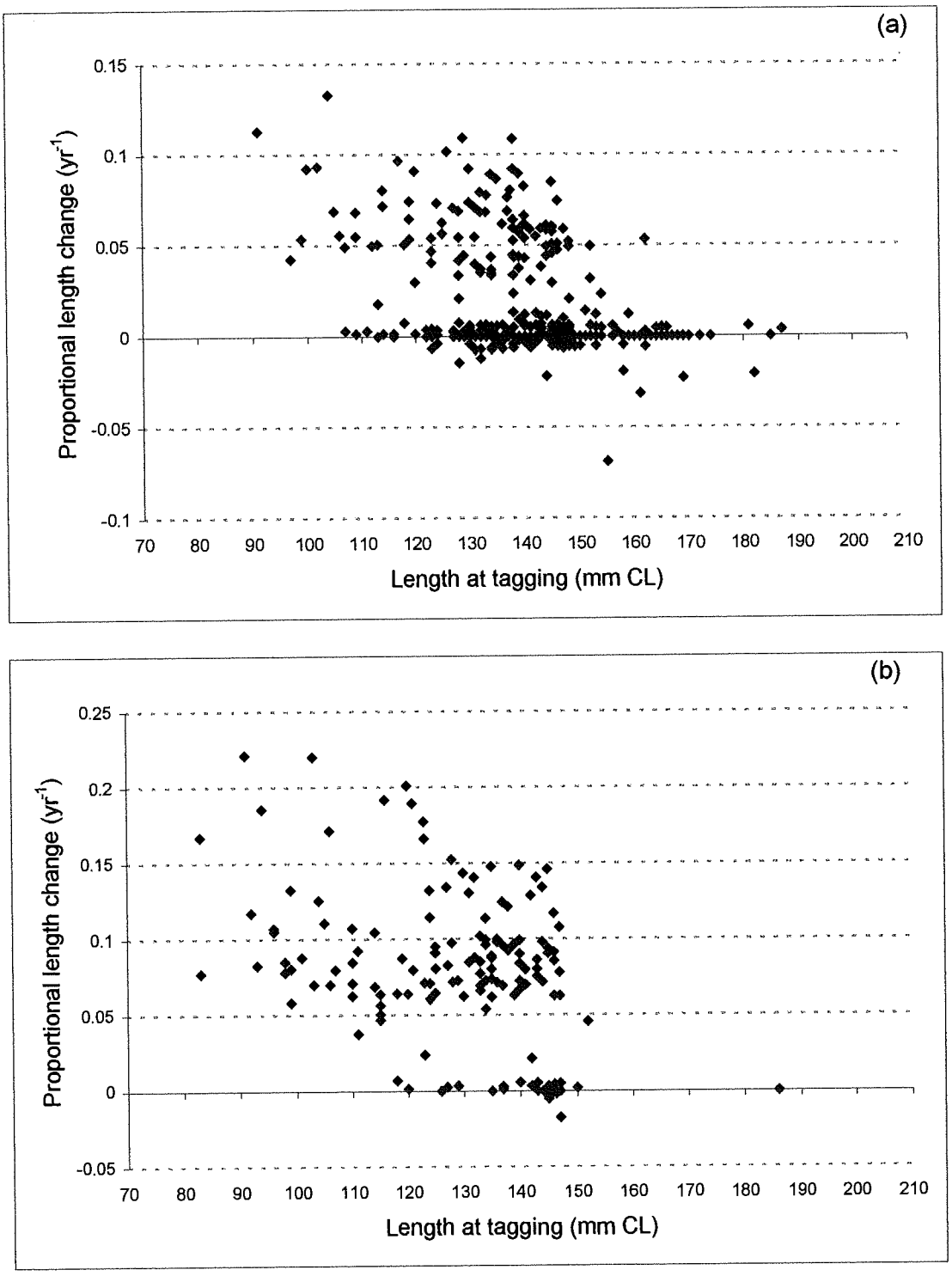

Figure 133. Change in length as a proportion of tag release length per year at large, excluding crabs at large less than one year: (a) females, (b) males.

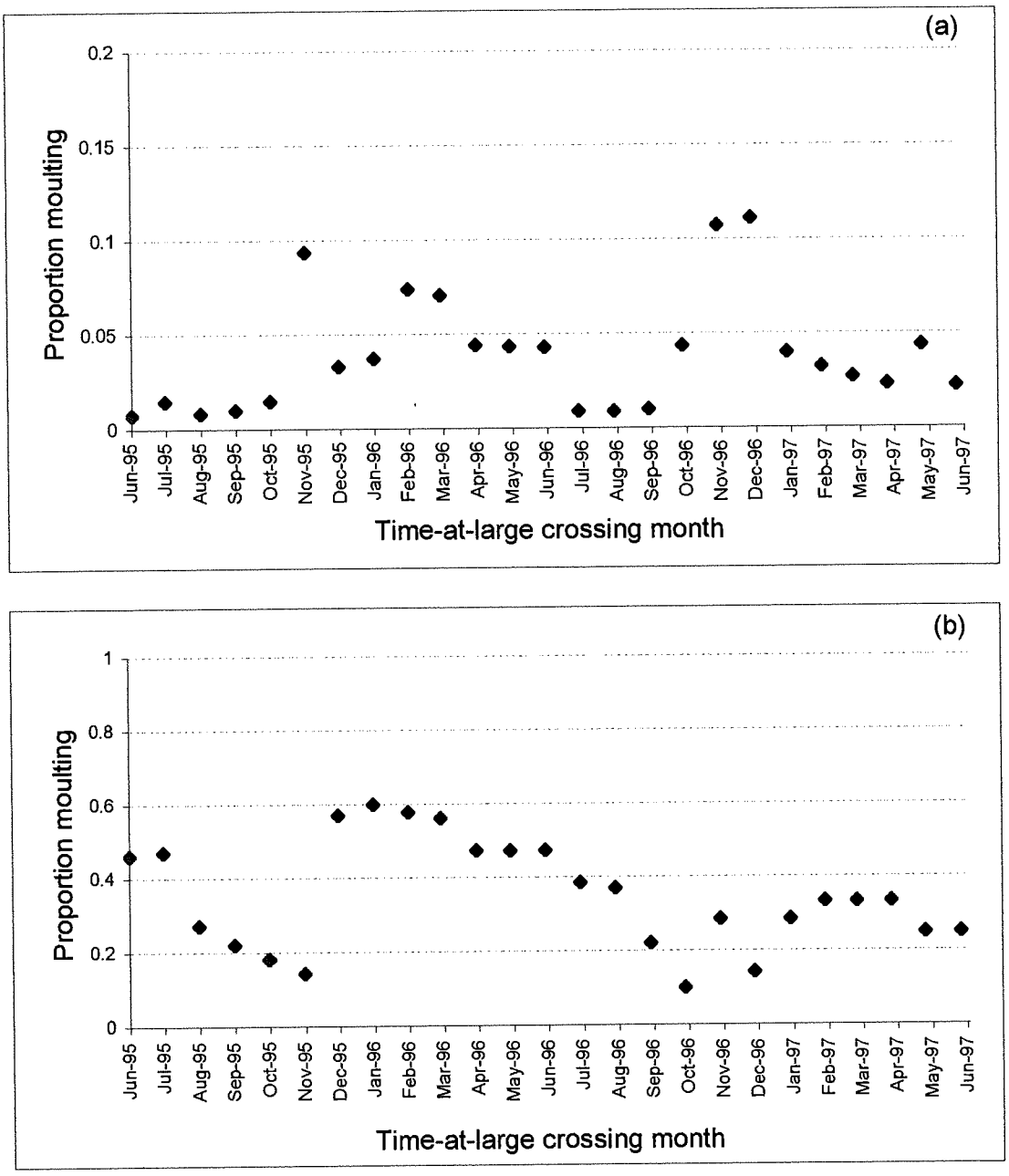

Figure 134. Proportion moulted by month. Proportion of recaptured crabs that have moulted of those tagged in the 11 month period before each possible month of moulting (time-at-large crossing month, along the x-axis) and recaptured in the 11 month period after the given moult month: (a) females, (b) males.

6.1.2.3.1. Intermoult period estimation

To derive mean intermoult period as a function of carapace length, a likelihood estimation method was developed and applied to the tag-recovery data set. Mathematical details of this estimation model are presented elsewhere. Basic assumptions are twofold:

1. Mean intermoult period varies as a quadratic polynomial with respect to pre-moult carapace length.
2. A discrete finite (and therefore renormalised) normal distribution describes the probability that a crab of given length will moult in 1, 2, 3, etc. moult periods subsequent to its prior moult.

This estimator sought to improve on previous ones (Willoughby and Hurley 1987; Hoenig and Restrepo 1989) by not assuming uniform probability of time before tagging to previous moult.

Male and female data sets were analysed separately. Because intermoult period estimation requires larger samples than quantifying moult increment, tag-recapture numbers to date were not sufficient to analyse intermoult period by state.

The resulting relationships between mean intermoult period and carapace length (Figure 136) indicated large difference by sex, as suggested by the descriptive analysis of Figure 135. Males exhibited little change in intermoult period over the size range of observations, covering the first two of three morphological phases (Gardner and Williams, in press). With moult increment effectively constant, male giant crab growth, in terms of carapace length, varies slowly with size. Mean intermoult periods of 2.4 years at pre-moult length of 120 mm, 3.5 years at 180 mm, and of 5.1 years at 150 mm CL were obtained.

Females in the size range of observations (Figure 136) moult with considerably lower frequency and exhibit a marked decline in moulting frequency with size. Mean intermoult periods of 4.5 years at pre-moult length of 120 mm, 15 years at 180 mm, and 7.4 years at 150 mm CL were estimated. If a terminal moult for females is reached at sizes above about approximately 166 mm CL, the steepness of this curve (here modelled as a quadratic polynomial) would, in reality, be effectively infinite at this size.

The inferred probability distributions of male and female intermoult period are illustrated for the cases of male and female crabs at LML (Figure 137).

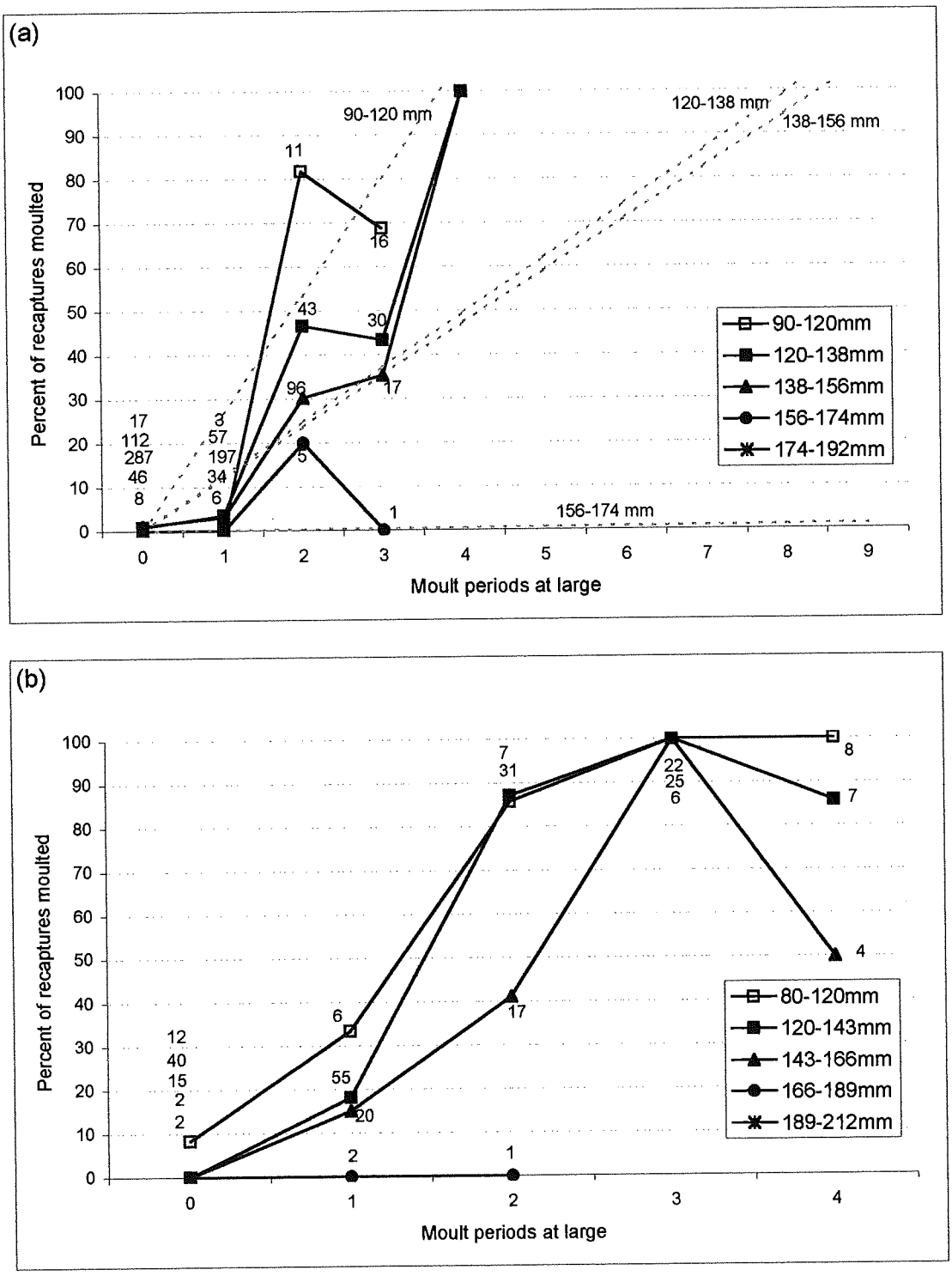

Figure 135. Percent of recaptured crabs that have moulted, versus time-at-large in number of moult periods, grouped by length class: (a) females, (b) males. Females are assumed to moult in June, males in December. The dashed lines on the female graph are weighted regressions for each length class. Sample sizes are indicated next to each symbol. Where there is more than one symbol occupying similar values, the order of the sample sizes corresponds to the order of the length classes in the legend.

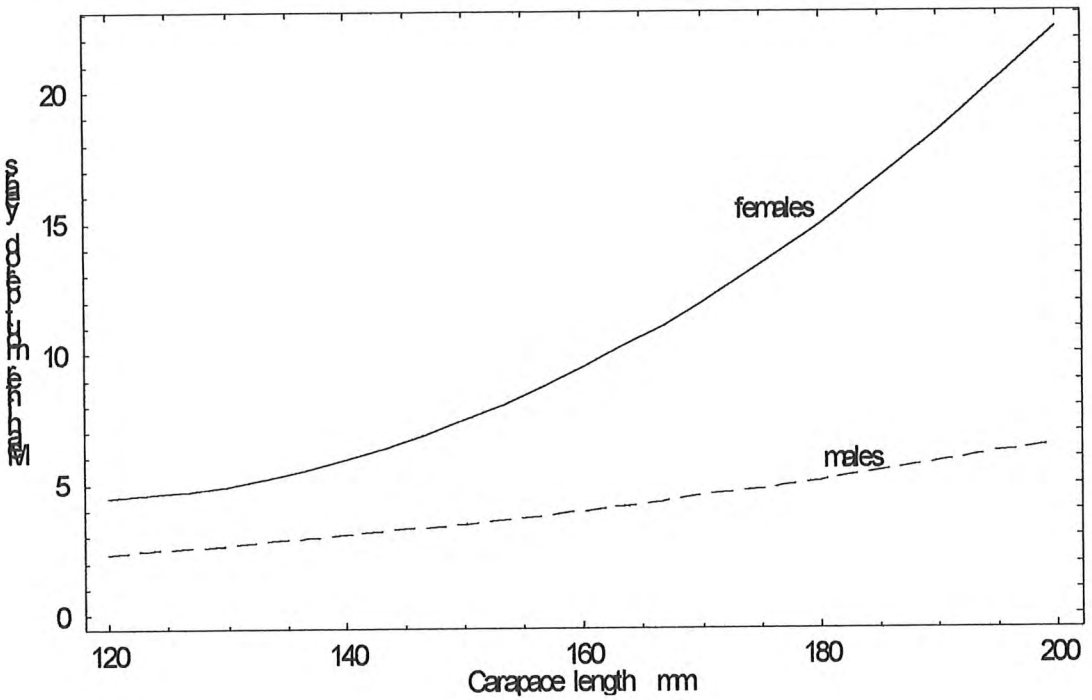

Figure 136. Estimated mean intermoult period versus (pre-moult) carapace length. Based on quadratic polynomial fit.

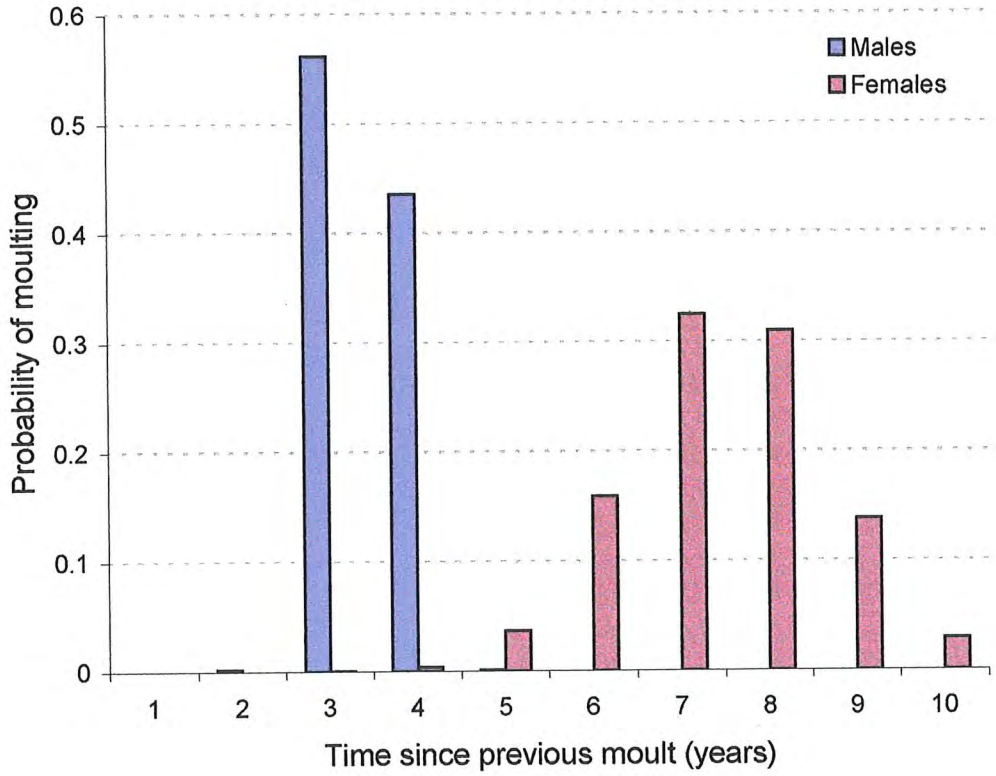

Figure 137. Estimated probabilities of intermoult period for male and female giant crabs, at size of LML (150 mm CL).

6.1.2.4. Terminal moult

Hartnoll (1985) reported that a single instar above full maturity is common among Brachyura. However, he noted that this pattern is highly flexible among Brachyura species. Morphological classification of males (based on ratio of large male claw to body length) by Gardner and Williams (in press) suggests males from eastern and western Tasmania fall into a single instar above about 180 mm.

Two additional data sources of information exist to assess the prevalence of a terminal moult for *Pseudocarcinus gigas*: length frequencies and tag recoveries. From both sources, the evidence is indirect. Tagged giant crabs have been at large only 4 years, and relatively few have been tagged in the larger size range where a terminal moult is hypothesised.

Length frequencies for captured males in the eastern states exhibit maximum sizes of about 220 mm CL, with some at 230 mm CL and a couple of occurrences at 270 mm CL. In Western Australia, very few males were captured above 200 mm CL. Female length frequencies show maximum sizes of around 195-200 mm CL in the eastern states, and two occurrences of 220 mm CL females. Western Australian females were again smaller, with maximum sizes of around 170-180 mm CL.

The spread of observed moult increments (taking the mean of the lowest state minus its SD to the mean of the highest state plus its SD) of approximately 22-30 mm CL for males and 16.5-23.5 mm CL for females, implies terminal moult above roughly 190 mm CL, and 165 for females.

6.1.3. Egg production

Egg production of individual females will be taken as a function of size. Two aspects apply: (1) measured fecundity, and (2) effective size of maturity, at which fertile eggs first begin to be hatched by females in the wild.

6.1.3.1. Fecundity

Eggs per female versus carapace length were measured in two previous studies: Levings et. al. (1996) measured weight of the egg mass and Gardner (1997) converted egg mass weight to egg numbers. The two curves were plotted together for comparison, and both appeared linear though the egg number curve was based on a power relationship (Figure 138). It is hypothesised that mature female giant crabs do not extrude and hatch eggs in years when they moult (Levings et al. 1996).

Gardner (1997) reported evidence of a decline in the number and size of eggs over years of spawning (between moults). This feature could be incorporated into the per-recruit model. The fecundity curves (Figure 139) for three defined categories of shell state (Gardner 1997) indicate a relatively small effect.

6.1.3.2. Size of maturity

Presence or not of eggs on captured females was recorded in giant crab catch monitoring. Eggs are hatched (released into the water column, after being carried over winter) in October and November (Levings et al. 1996). The length-dependent

proportions of females bearing eggs in spring (3 months averaged, September-November) were summarised in histograms of 5 mm length bins. Proportions egg-bearing versus carapace length bin were plotted for catch monitoring samples from South Australia 1994-97 and Western Australia 1994, 1995 and 1997 (Figures 140 a-g). Note that x-axis labels are bin upper bounds.

Proportion egg bearing rises quickly from a low proportion to near the mean level of older females at 120-125 mm CL in South Australia 1994 and 1997, and reaches a local maximum at 125-130 in all three years. In 1996 South Australian samples, only one female was examined in each of the size classes 120-125 and 125-130. Excluding 1996 from consideration, this suggests South Australian females reaching effective full maturity by 125-130 mm, with greater than 50% mature in the size category of 120-125.

Western Australian giant crabs matured at a smaller mean size, reaching or near the mean level of older females at 115-120 mm CL in 1994, 120-125 mm in 1995, and 110-115 in 1997.

Length frequencies for male crabs (Figure 141) in South Australia and Western Australia both show some evidence of depletion of the larger sizes in years following the first samples (Figures 141(a) & (f)) measured in the year following the opening of this population to human exploitation in these two states, but note that figure 141(c) is biased towards lower sizes by an absence of Autumn or Winter sampling.

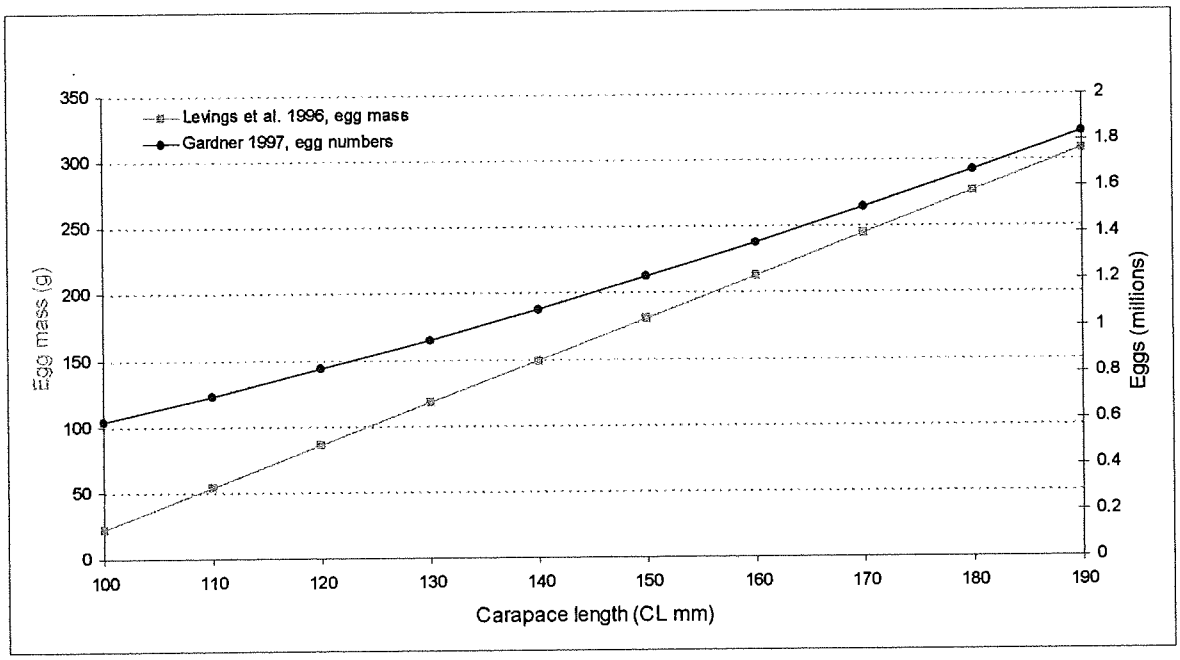

Figure 138. Fecundity versus length from Levings et al. (1996) and Gardner (1997).

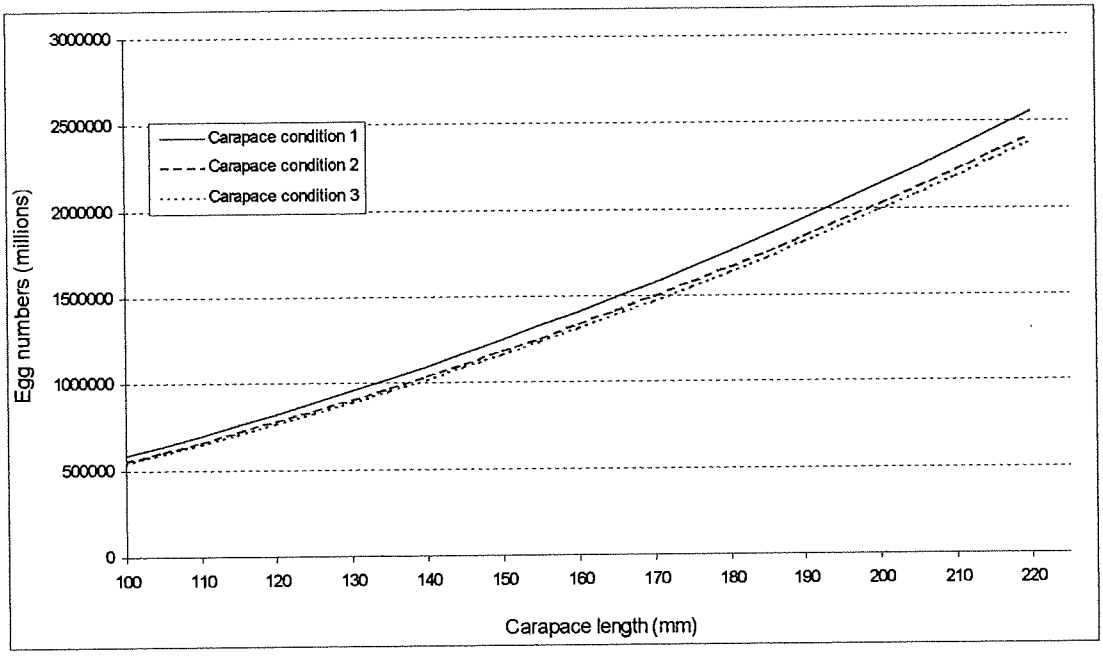

Figure 139. Fecundity curves of Gardner (1997) for three categories of carapace condition as proxy for years since prior moult.

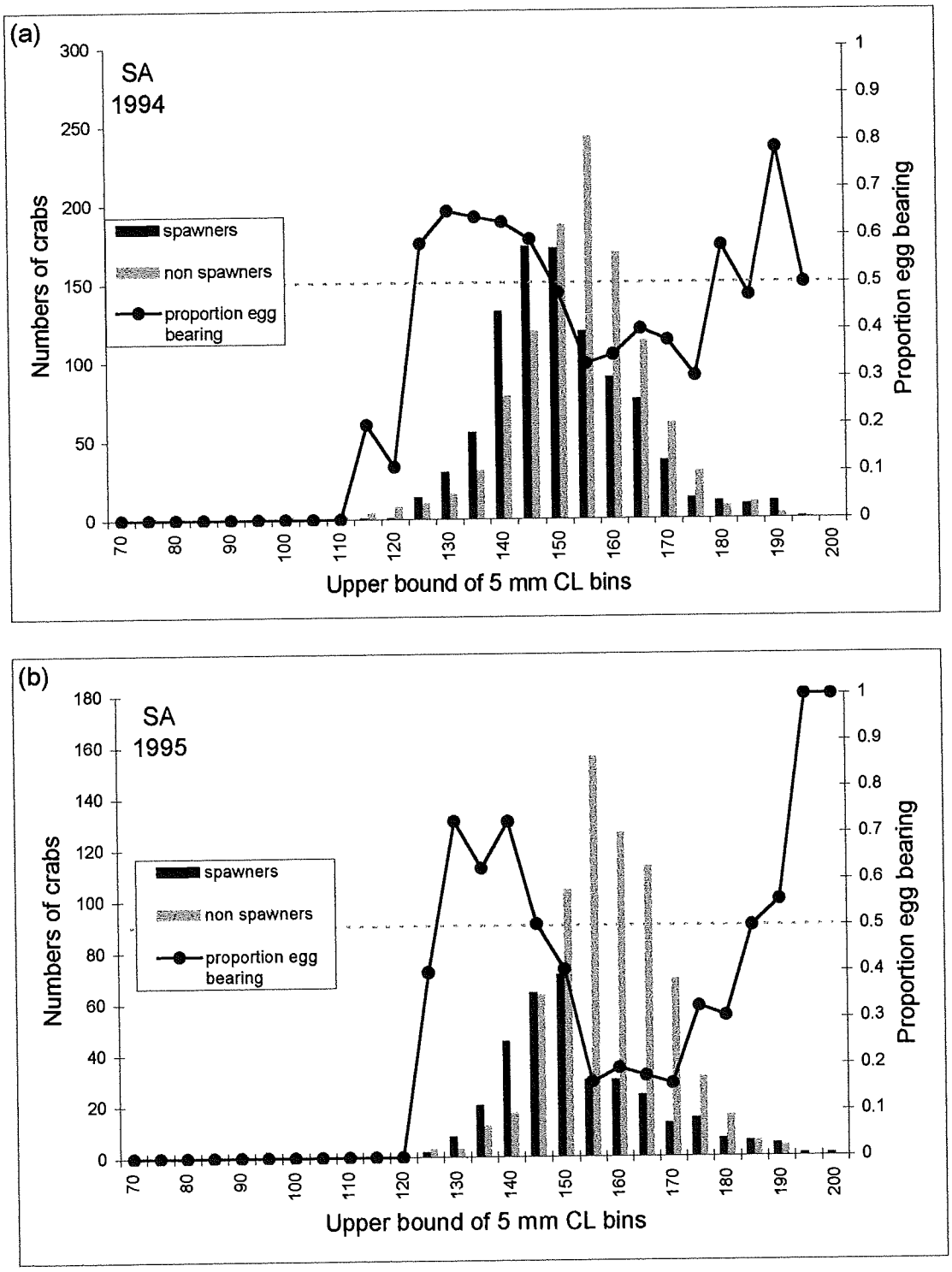

Figure 140. Female catch samples from (a-d) South Australia and (e-g) Western Australia, collected in spring: numbers and proportion ovigerous versus length.
Bars show numbers of spawners and non spawners. The line indicates the observed proportion of females that spawned, judging by the occurrence of eggs or spent egg casings.

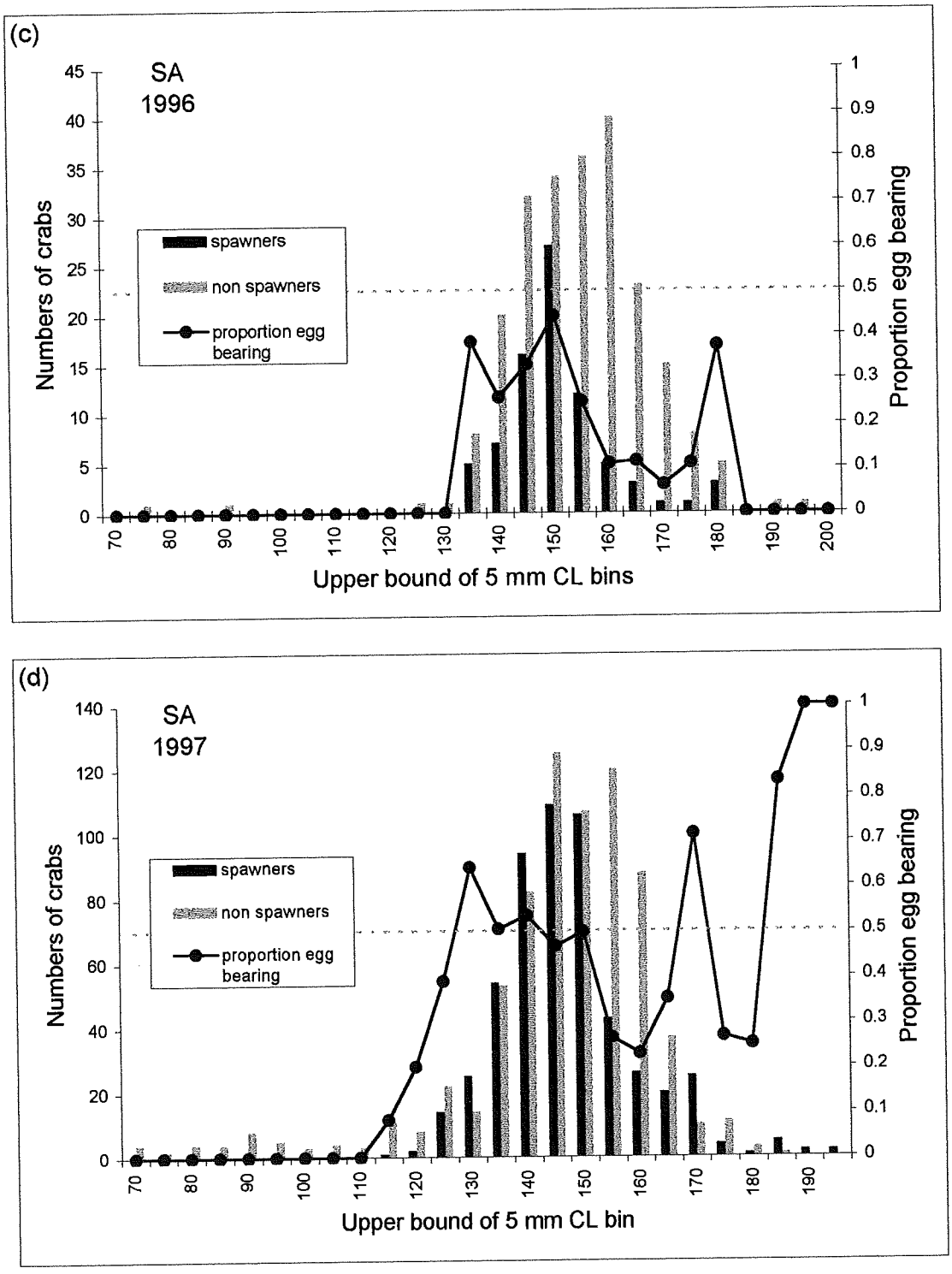

Figure 140. (c) & (d).

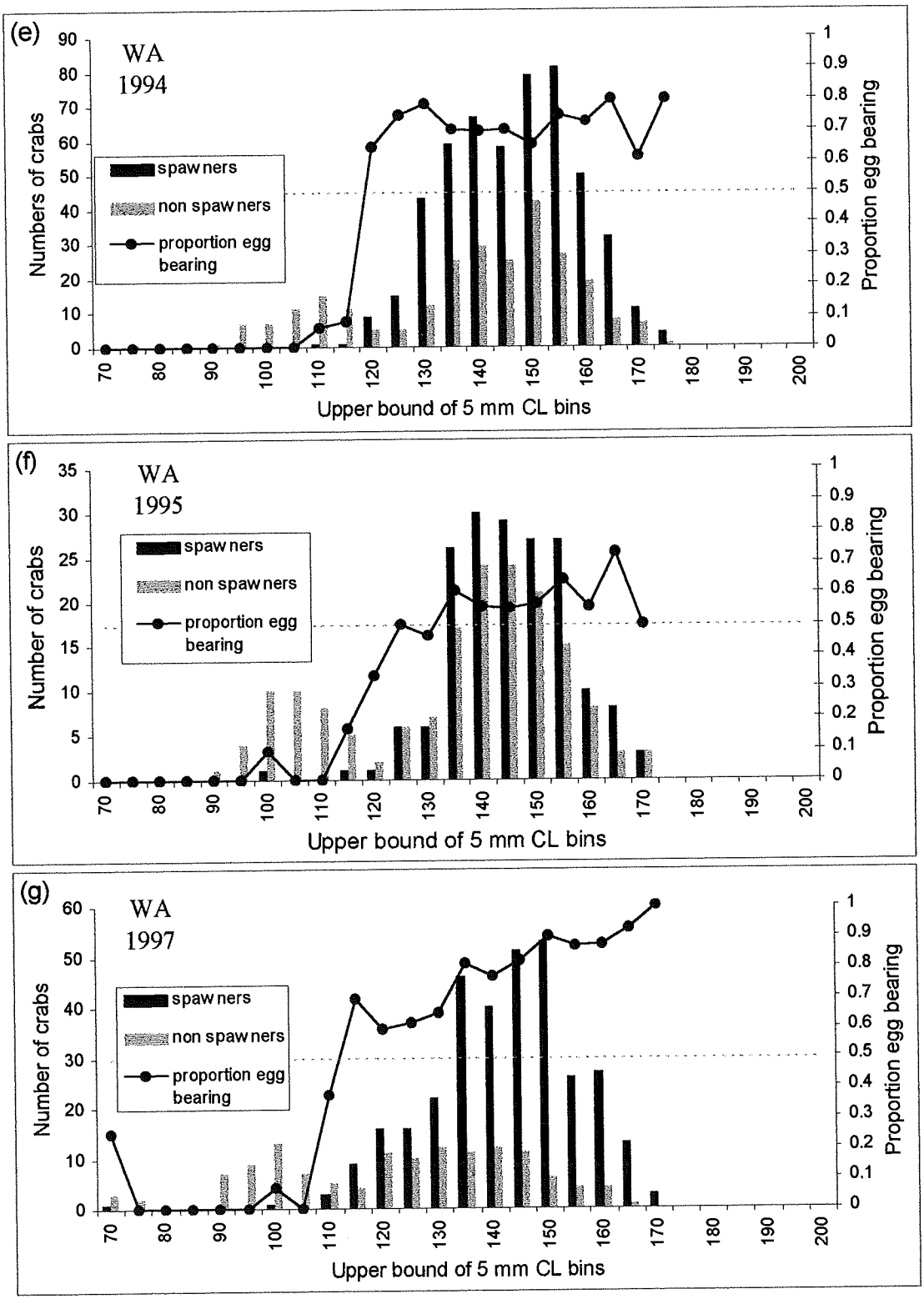

Figure 140. (e)-(g).

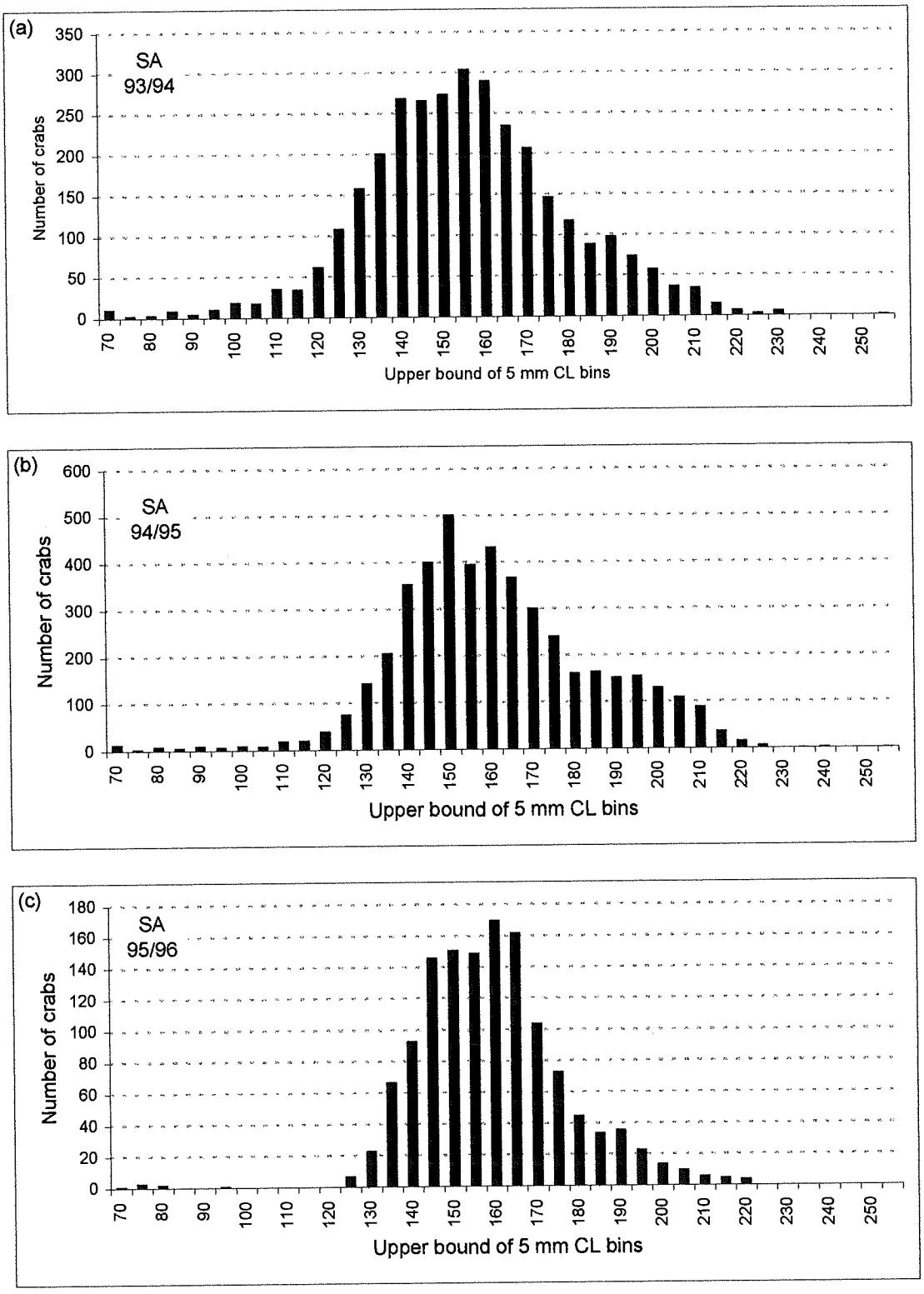

Figure 141. Male giant crab length frequencies, sampled on-board from the catch: (a-e) South Australia and (f-h) Western Australia.

South Australian samples have been aggregated into years (September-August) and Western Australian data are spring catches only.

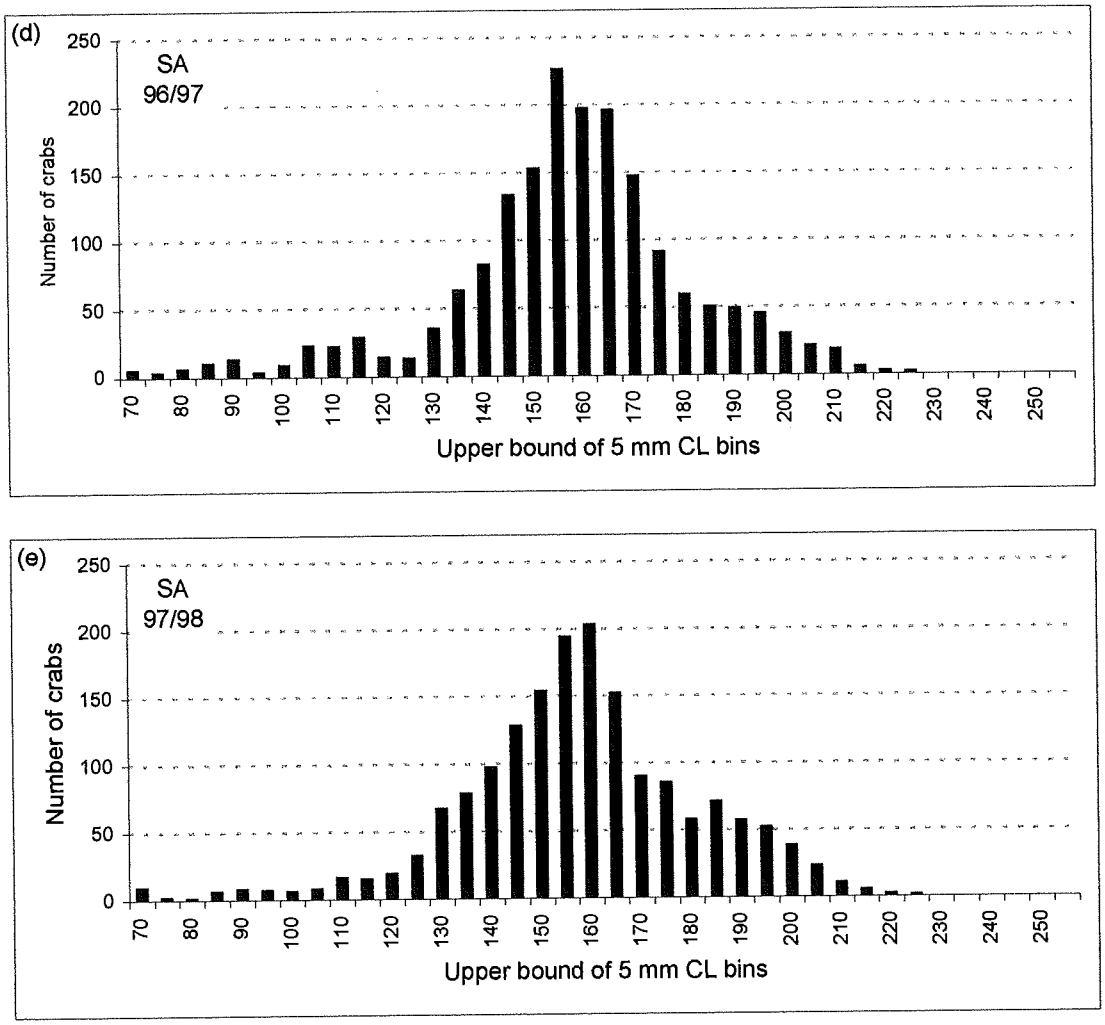

Figure 141. (d) & (e).

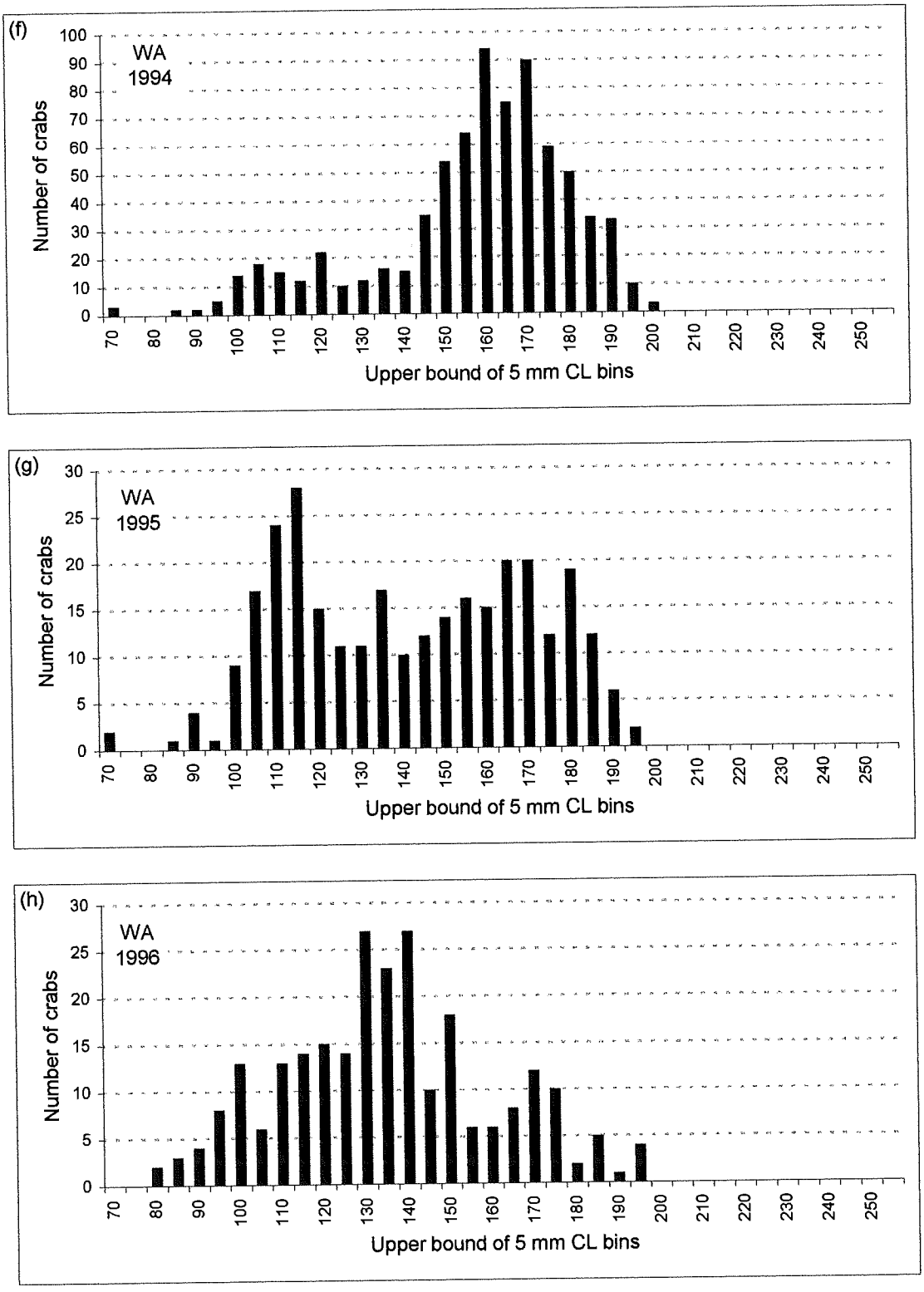

Figure 141. (f)-(h).

6.1.4. Natural mortality and fishing mortality

6.1.4.1. Natural mortality

Natural mortality of crustaceans is believed to be higher during and immediately following moulting. Percentage weight gains on the order of 75-90% for male giant crabs and 40-60% for females were quantified above (Table 171). The physiological stress of such large discrete body growth is likely to be high. Rates of predation and cannibalism are also presumed higher when the exoskeleton has been shed. Infectious pathogens and parasites are also likely to find easier entry.

6.1.4.2. Capture selectivity

Numbers of crabs captured versus length follows a general rising trend from low numbers taken below about 120 mm CL rising to a peak in the neighbourhood of LML. Assuming the crab population on the bottom follows a generally declining length structure corresponding to exponentially declining numbers with age, this peak at LML must reflect a rising trend in capture selectivity up to approximately the peak in numbers captured for sublegal giant crabs (Figure 142).

Relative selectivity of egg-bearing versus non-egg-bearing females is considered in Appendix 1.

Larger crabs bring a substantially lower price (Figure 143) and fishers therefore target these sizes with correspondingly lower fishing effort. The capture selectivity coefficient is reduced for crabs in this low price category greater than 5 kg (4 kg in Western Australia where mean size of captured giant crabs is smaller).

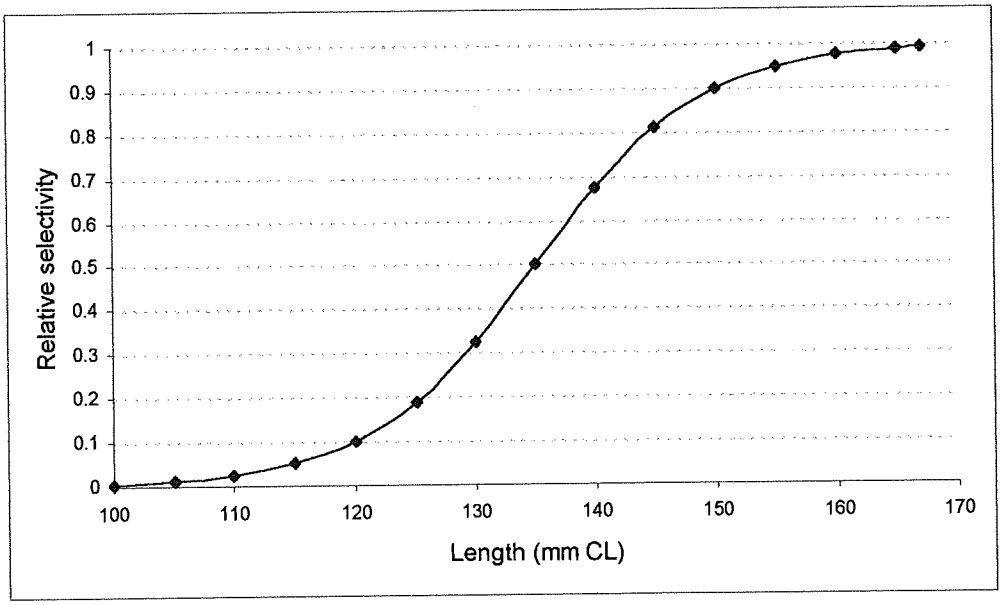

Figure 142. Fishing selectivities for undersize crabs used in the individual-based model. The selectivities follow a logistic curve up to CL = 167 mm, above which selectivity = 1.

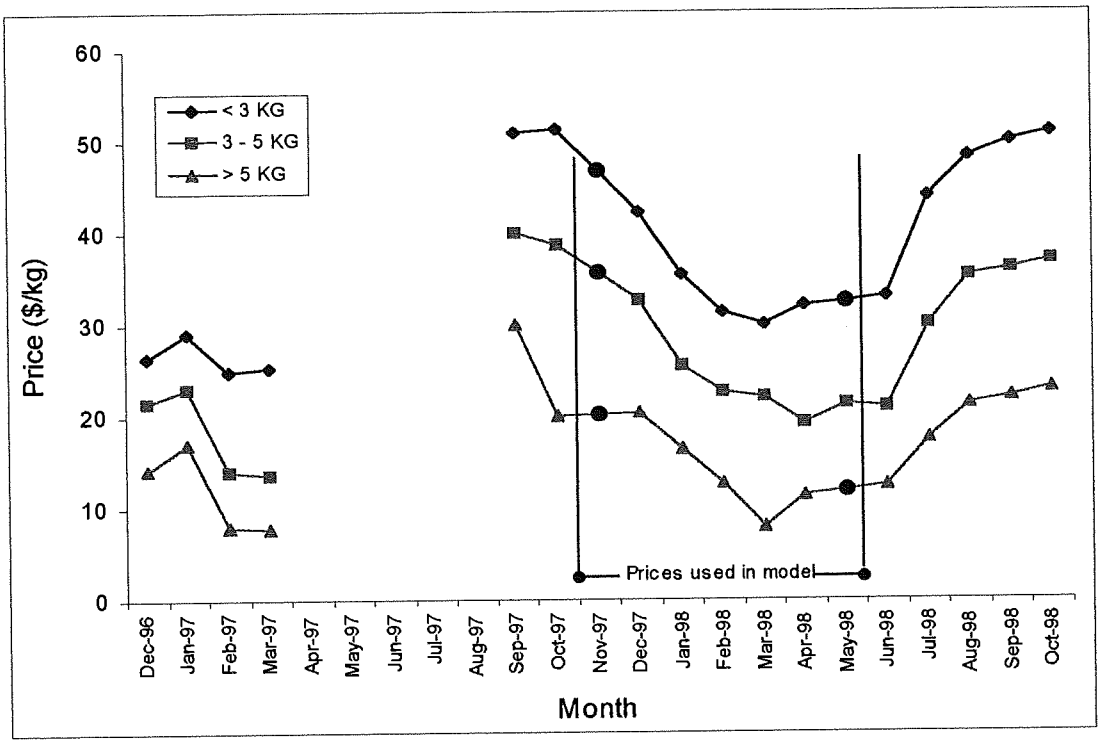

Figure 143. Landed giant crab prices for South Australia, by month and weight class. Black dots indicate the months for which price data was not available. These were interpolated as the moving average of the two prices adjacent for use in the individual-based model.

6.2. Individual-Based Model

In order to incorporate much of the detail relevant to growth and reproduction, yield-, value- and egg per recruit analyses were undertaken using an individual-based model. Each crab in the simulation has a set of biological characteristics randomly assigned when it enters the population. These traits vary through time as the crab grows and matures, generally as a function of carapace length. The simulation is run on a monthly time scale with events such as moulting, spawning, fishing and natural mortality occurring in specific months. Growth is simulated by random sampling from the data-based distributions for moult increment and intermoult period discussed in 6.1. One advantage of the individual-based modelling approach is that as more information becomes available describing the dynamics of the giant crab population, it can be easily incorporated into the simulation. The following table describes the model parameters and their baseline values.

Table 172. Parameters with definitions and baseline values used in the individual-based per-recruit model.

Parameter	Definition	Baseline value
equil	Number of years model is run to achieve equilibrium before changing to a new test value of legal minimum length (LML).	70
years	Number of years model is run at new LML.	30
oldLML	Current, i.e. default, LML (CL mm) the model uses for the first *equil* years.	150 (SA, Vic, Tas) 140 (WA)
newLML	New LML (mm) implemented at beginning of year *equil*+1.	[130, 135, 140, 145, 150, 155, 160]
F	Yearly fishing mortality rate.	[0.0, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6]
Fmon	Monthly discrete fishing mortality rate = F / # fishing months = F / 7.	[0.0, 0.057, 0.086, 0.114, 0.143, 0.171, 0.2, 0.229]
Mn	Natural mortality rate, implemented every year to all crabs, at beginning of moulting month (June).	0.05
Ms	Senescence mortality rate, in addition to natural mortality, on crabs that have had their terminal moult.	0.05
Mm	Moulting mortality rate, imposed on crabs in years of moulting.	0.2
Lmat	Length at which a female crab becomes mature and therefore able to produce eggs.	SA: 125 mm VIC: 130 mm WA: 120 mm
Sspawn (month)	Monthly fishing selectivity coefficient for spawning females (7-month fishing season).	[1/7, 3/7, 5/7, 1, 1, 1, 1]
Wold	Weight beyond which crabs incur a reduced selectivity due to drop in Asian demand and thus price of larger crabs.	5 kg (SA, Vic, Tas) 4 kg (WA)
Sold	Fishing selectivity on crabs heavier than *Wold.*	0.25
Lnomoult	Terminal moult size.	males: 189 mm females: 166 mm
Nrecruit	Number of crabs continually maintained in recruit stage (75-100 mm CL).	10,000
mpr	Years till next moult for recruits, randomly sampled from {1, *mpr*}.	males: 2 females: 2

The algorithms and relationships used in the per-recruit simulation are described below by population process. Table 173 summarises assumptions used in the individual-based model.

Table 173. Assumptions and inputs of the individual-based per-recruit model.

Description of assumption

Data
Analyses used the data set of Mitchell and Levings (1999).
Moult increments by Australian state analysed using tag-recapture data.

Recruits
Initial 10,000 recruits randomly selected. Subsequent recruits thereafter have:
sex randomly assigned, assuming 50:50 sex ratio;
length uniformly sampled from [75, 100];
initial intermoult period uniformly sampled from {1, *mpr*}.
When a recruit moults into the sublegal population a new recruit replaces it.

Intermoult period (IMP)
Recruits: IMP = 2 years for males and females. Initial IMP is randomly sampled from {1, *mpr*}.
Sublegals and legals: IMP is sampled from a discrete finite normal probability distribution, dependent on the sex and length of the crab.

Moult Increment
Moult increment is sampled from the moult increment probability distribution. The length increment is the midpoint of the 5 mm bin that is selected.
Once a crab moults above the terminal moult length for males and females (*Lnomoult*), it retains that length thereafter.

Natural mortality
Three forms of non-fishing mortality:
Natural mortality occurs once yearly at time of moulting for all crabs.
Senescence mortality occurs in addition to natural mortality for those crabs that have had their terminal moult.
Moulting mortality, at a higher rate than natural mortality, is incurred in years of moulting.

Maturity
Knife edge relationship – 100% mature for all females above *Lmat*.

Fecundity
Two fecundity relationships obtained:
Egg mass (g) (Levings et al. 1996) $eggs = 3.179 \times length - 296$.
Egg number (millions) (Gardner 1997) $eggs = e^{5.2022} \times length^{1.755} \times 1.012$.
All mature females spawn once per year in June.
No eggs produced in years of moulting, but eggs produced in all non-moulting years.

Fishing
7-month fishing season, November – May.
Fishing selectivities, ie reduced probabilities of capture, apply:
spawning selectivity (*Sspawn*) – on crabs that have produced eggs this year;
size selectivity (*Sold*) – on crabs that weigh more than *Wold*;
undersize selectivity (*Su-size*) – on sublegal crabs.
No regulated throwing back of egg bearing females.
Length-weight relationship calculated from pooled Australian data
Males: $weight = 1.099 \times 10^{-7} \times length^{3.384}$
Females: $weight = 1.166 \times 10^{-6} \times length^{2.878}$

Values indicated are 'baseline' meaning they were used in the basic estimates of egg-, yield-, and value-per-recruit. In addition, sensitivity analysis values are also specified for some parameters.

6.2.1. Moulting

6.2.1.1. Moult increment

The distribution of moult increment, the increase in carapace length with moulting, was obtained from tag-recaptures of those that did moult while at liberty. Frequencies (Figure 132) were converted to probabilities for each 5 mm length class. A separate set of probabilities were derived for each state and by sex. When a simulated crab was sampled for moulting, the size of the length increase was obtained by random selection in proportion to these discrete probabilities.

This random selection of length bin from the set of discrete probabilities, $\{P_1, P_2, \ldots, P_N\}$ follows the usual procedure: A random number, R, uniformly distributed over [0, 1], is generated. If $R < P_1$, where P_1 is the lowest moult increment bin probability, bin 1 is selected; if R falls in the cumulative probability range covered by the second moult increment bin, P_1 to $P_1 + P_2$, then the second moult increment is chosen, and so on for higher bin moult increments. The crab length is then increased by the midpoint length of the selected bin.

6.2.1.2. Intermoult period

Each time a crab has moulted, intermoult period, ie the waiting time in years till its next moult, is also chosen stochastically. Intermoult period is randomly selected from a discrete finite normal distribution (specifically, probability mass function, pmf). The latter was derived as the maximum likelihood pmf in estimation of intermoult period from tag-recapture data, described in Section 1.

Model mean intermoult period, $\overline{m}$, was written as a quadratic polynomial:

$$\overline{m}(CL) = m_0 + m_1 \cdot CL + m_2 \cdot CL^2 . \qquad (2.1.2\text{-}1)$$

Parameters $\{m_0, m_1, m_2\}$ were estimated to obtain the mean intermoult period as a function of starting carapace length. The discrete finite normal pmf, incorporating a fourth parameter, σ, the (likelihood) standard deviation of predicted intermoult period, was written

$$P(m_i) = \exp\left[-\frac{(m_i - \overline{m}(CL))^2}{2\cdot\sigma^2}\right] \Big/ \sum_{m_i=1}^{n_m} \exp\left[-\frac{(m_i - \overline{m}(CL))^2}{2\cdot\sigma^2}\right] \qquad (2.1.2\text{-}2)$$

where

$m_i \equiv$ independent variable of intermoult period, given in numbers of yearly moulting seasons. The model assumes moults happen once yearly, in the neighbourhoods of June or December, thus m_i is discrete, equal to 1, 2 , 3, ...

$P(m_i) \equiv$ following crab's prior moult to length CL, probability of subsequent moult in m_i yearly seasons;

$n_m \equiv$ maximum intermoult period, assuming finite range for possible values of m_i.

Intermoult period parameter estimates were as follows:
For females: $\{m_0 = 37.8879, m_1 = -0.581193, m_2 = 0.00252129, \sigma = 0.87254\}$;
for males: $\{m_0 = 3.6989, m_1 = -0.0492559, m_2 = 0.000317703, \sigma = 2.48382\}$.

Random selection for intermoult period followed the same algorithm as for moult increment given above, using the discrete set of $P(m_i)$ probabilities.

6.2.1.3. Terminal moult

Whether strictly genetic or resulting from a combination of environment and genetics, the growth dynamics of a population expressing significantly slower growth at large sizes can be safely approximated for purposes of fishery modelling by an effective terminal moult, a fixed upper size above which further moults are assumed negligibly probable.

In this simulation, moulting ceases once a female crab reaches 166 mm, 189 mm for males.

6.2.2. Egg production

Eggs hatched by each individual are summed yearly at time of spawning to obtain population egg production.

6.2.2.1. Spawning frequency

We assumed that females do not produce eggs in years (Novembers) following moulting (in June), but spawn in all non-moulting years.

6.2.2.2. Fecundity

Fecundity as egg mass (Levings et. al. 1996) was used in the individual-based simulation. The fecundity relationship in terms of egg numbers (Gardner 1997) was used in sensitivity analysis.

The feature of declining fecundity in years of spawning between moults (Gardner 1997; Figure 139 above) was not considered of sufficient magnitude to warrant explicit simulation (C. Gardner, Taroona Marine Research Laboratories, PO Box 192B, Hobart, Tas. 7001, pers comm.).

The sizes at (full) maturity employed in the model are South Australia: 125 mm, VIC: 130 mm, Western Australia: 120 mm.

6.2.2.3. Fraction mature and spawning selectivity

The relationship describing the relationship of percent mature, with selectivity of ovigerous females derived in Appendix 1 is:

$$s_E = R_E^C \left[\frac{T}{p_{mat} \cdot (T-1)} - 1 \right].$$

where

p_{mat} ≡ fraction of female crabs that are reproductively mature;
T ≡ female intermoult period;
R_E^C ≡ observed ratio of spawners to non-spawners in the catch;
s_E ≡ relative selectivity of spawners to non-spawners.

As detailed in Appendix 1, approximately equal numbers of berried and unberried females were observed in the spring catch length frequencies (Figures 140 a-g) and therefore we set $R_E^C = 1$. Mean intermoult period, T = 8, its estimated value at the LML of 150 mm CL, and percent mature, $p_{mat} = 1$ were assumed. This yielded an estimated selectivity of spawners 1/7 that of non-egg bearing females.

6.2.3. Natural mortality and fishing mortality rates

We modelled non-fishing mortality as a combination of three processes: 'natural mortality' set to occur yearly, 'senescence mortality' which occurs in addition to natural mortality after a crab undergoes its terminal moult, and 'moulting mortality' at a higher rate imposed only in years when crabs moult. Three sets of value for each non-fishing mortality fraction were chosen: baseline values, and sets of high and low values used for sensitivity testing (Table 174).

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For females: $\{m_0 = 37.8879, m_1 = -0.581193, m_2 = 0.00252129, \sigma = 0.87254\}$;
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Random selection for intermoult period followed the same algorithm as for moult increment given above, using the discrete set of $P(m_i)$ probabilities.

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$$s_E = R_E^C \left[\frac{T}{p_{mat} \cdot (T-1)} - 1 \right].$$

where

p_{mat} ≡ fraction of female crabs that are reproductively mature;
T ≡ female intermoult period;
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Table 174. Values used in sensitivity testing for natural mortality, senescence mortality and moulting mortality.

Non-fishing mortality level	M_n natural mortality fraction	M_s senescence mortality fraction	M_m moulting mortality fraction
low	0.025	0	0.1
baseline	0.05	0.05	0.2
high	0.075	0.1	0.3

At yearly time of moulting (June 1), prior to simulation of moulting growth processes, each crab must draw a straw: For crabs below terminal moult size, if R, a random number from [0, 1] is less than M_n, it dies from natural mortality. Crabs that have undergone their terminal moult have their natural mortality probability increased by the addition of a 'senescence mortality'. If R is less than $(M_n + M_s)$ then it dies from natural mortality. Once growth processes are simulated, for crabs that are selected to moult, a second R is drawn; if $R < M_m$, it dies from moulting mortality.

Fish are subject to fishing mortality in the open months of the South Australian season. Annual fishing rate, F, applied in monthly time steps, was set to vary over a range of values from 0.4 to 1.6. The fishing season covers seven months of the year so a fish is captured each month of the season with probability F / 7.

When crabs grow beyond marketable weight or when a female is bearing eggs, the crab becomes less vulnerable to fishing and the capture probability is reduced. A flow chart describes how capture probabilities are varied (Figure 144).

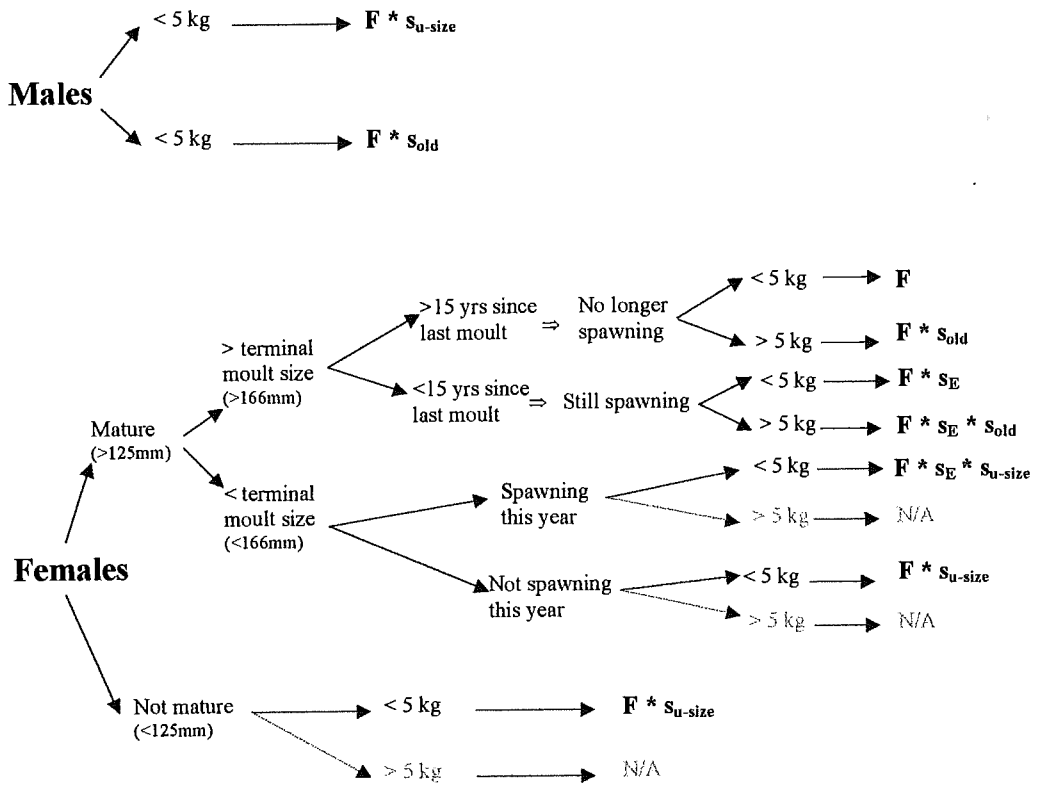


Figure 144. Model capture probability flow diagram.
The 5 kg cut off point where F is reduced by the factor s_{old} represents the size above which the market and processors offer the lowest price. In Western Australia this occurs at 4 kg. s_{old} is currently set at ¼ . s_E is the selectivity of spawners relative to non-spawners (see Appendix 1) and is currently set at ⅓ for November, ⅗ for December, ⅘ for January and 1 for February to May. $s_{u\text{-}size}$ is the capture selectivity of sublegal giant crabs.

6.2.4. Algorithm for population dynamics of the individual-based model

The population is divided into recruits, sublegals and legals as follows:

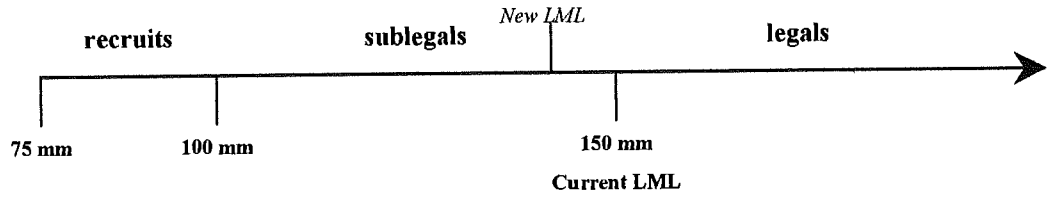


Figure 145. Life history categories of simulated giant crabs, determined by crab length.

An initial population of 10,000 'recruits' are randomly sampled, each crab assigned:

1. sex;
2. initial length between 75 and 100 mm, uniformly sampled;
3. number of yearly moult periods until next moult. (Choice of 1 or 2 moulting periods. This is equal for males and females assuming the divergence of

intermoult period by sex occurs after sexual maturity, observed to occur at sizes of 115-120 mm CL and greater.

Recruits moult every two years and suffer no natural mortality. They exist as a pool for continual supply of new crabs into the population. As each crab moults past 100 mm in length it becomes a sublegal and a new recruit is selected to replace it.

Sublegals incur natural mortality as described above, and are subject to capture probability in commercial pots with a logistic curve of undersize selectivity. All captured sublegals are thrown back, incurring no additional release mortality. Mature females (> 125 mm) spawn in all non-moulting years.

When a sublegal moults over the LML it becomes a legal and in addition to moulting, spawning, and natural mortality, becomes subject to risk of harvest.

The LML is set at the current regulation of 150 mm CL for the eastern states and 140 mm for Western Australia. This inheres for the first 70 years of the simulation. In simulations of the effect of alternative choices of LML, these are imposed at the beginning of the 71st year. This results in a reallocation of crabs between sublegals and legals depending on whether the new LML is higher or lower than the current level. The model is then run a further 30 years with the new LML in effect.

A model year runs from June 1st to May 31st. The sequence of events in any year are as follows:

1 **JUNE**

a) Natural mortality (FEMALES)
   i) Loop through all sublegal and legal females (not recruits).
   ii) For crabs below terminal moult size:
      (1) If random number R < Mn, then that crab dies of natural mortality.
   iii) For crabs which have undergone terminal moult:
      (1) If random number R < Mn + Ms, where Ms is an additional 'senescence mortality', then that crab dies of non-fishing causes.

b) Moulting and moulting mortality (FEMALES)
   i) Loop through all recruit, sublegal, and legal females.
   ii) If moultyrs(icrab) = 1 then that crab is scheduled to moult this year.
   iii) If random number R < Mm, then that crab dies of moulting mortality (sublegals and legals only).
   iv) If the crab survives moulting mortality,
      (1) sample for the
      (2) increase crab length by selected moult increment,
      (3) sample from intermoult period probabilities for next scheduled moult.
   v) If the crab crosses into the next category, make the adjustments to the relevant arrays. If it is a recruit that has become a sublegal, replace it with another.

c) Spawning
   i) Loop through all sublegals and legals.
   ii) If icrab is female, mature and hasn't just moulted then it is spawning this year.
   iii) Calculate the eggs it produces using the fecundity function and add it to the total egg production for that year.

2 **JULY** - Nothing
3 **AUGUST** - Nothing
4 **SEPTEMBER** - Nothing
5 **OCTOBER** - Nothing
6 **NOVEMBER**
   a) Fishing
      i) Loop through all legals.
      ii) Get a random number, R.
      iii) If R< fishing probability (Figure 144), the crab is harvested.
7 **DECEMBER**
   a) Fishing
   b) Natural mortality (MALES)
   c) Moulting and moulting mortality (MALES)
8 **JANUARY** - Fishing
9 **FEBRUARY** - Fishing
10 **MARCH** - Fishing
11 **APRIL** - Fishing
12 **MAY** - Fishing

6.2.5 Results: Model Validation

6.2.5.1 Length Frequencies

Fishing mortality has not been estimated for Australian giant crab stocks. A wide range of F values were tested in the per-recruit analyses. One data source for model validation are length frequencies of the catch. We limit consideration to qualitative comparison of South Australian data and model run with a baseline default F = 0.6. Quantitative agreement would require estimates of F upon which model length frequencies are dependent. For females, model length frequencies were plotted for November only, while for males we summed model length frequencies over the whole season. These time periods were chosen to match the particular commercial catch data analysed, where for females, the spring catch at time of hatching was of principal interest. Because female lengths are taken from only one month, total model numbers reported (Figure 146) are relatively low.

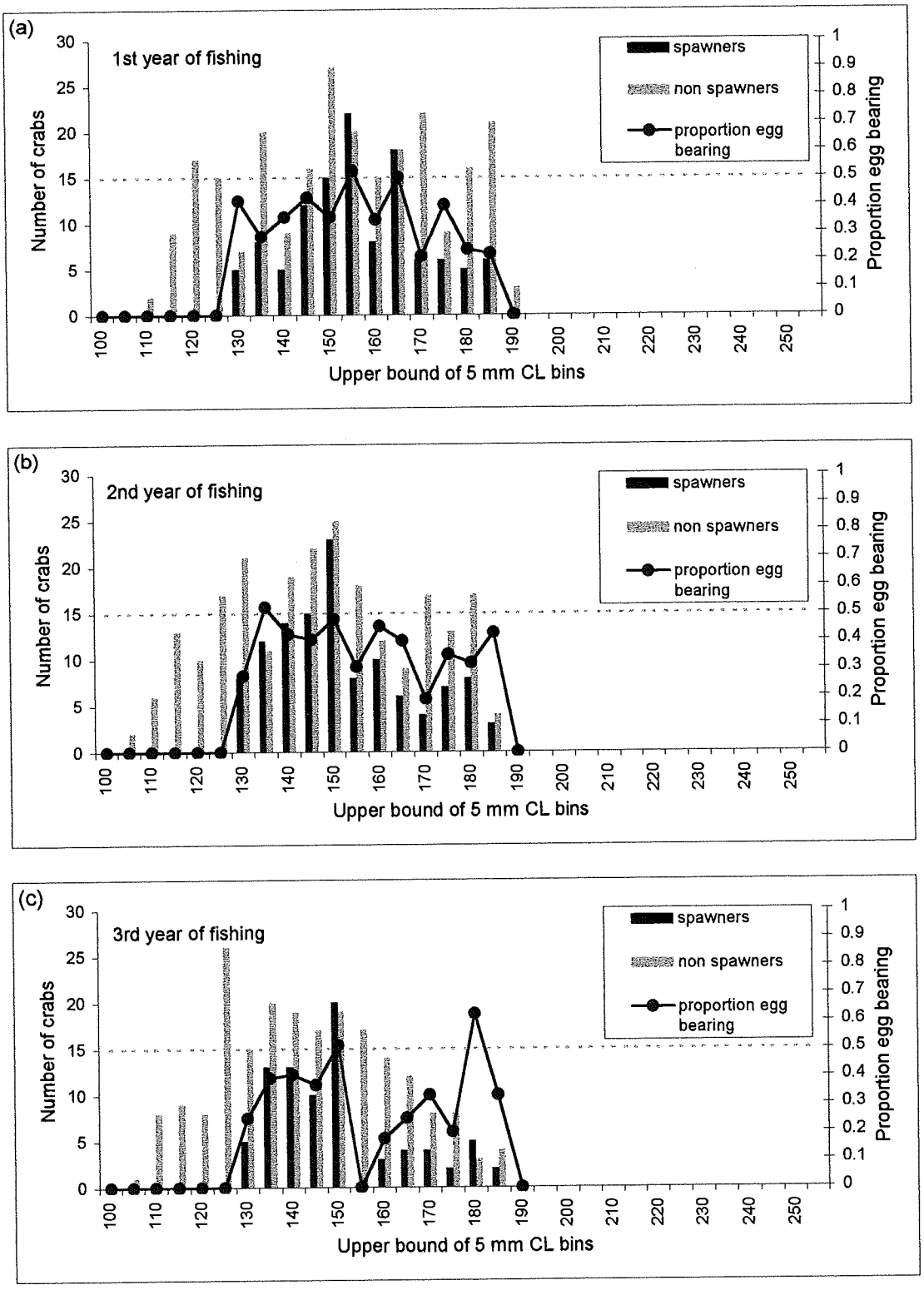
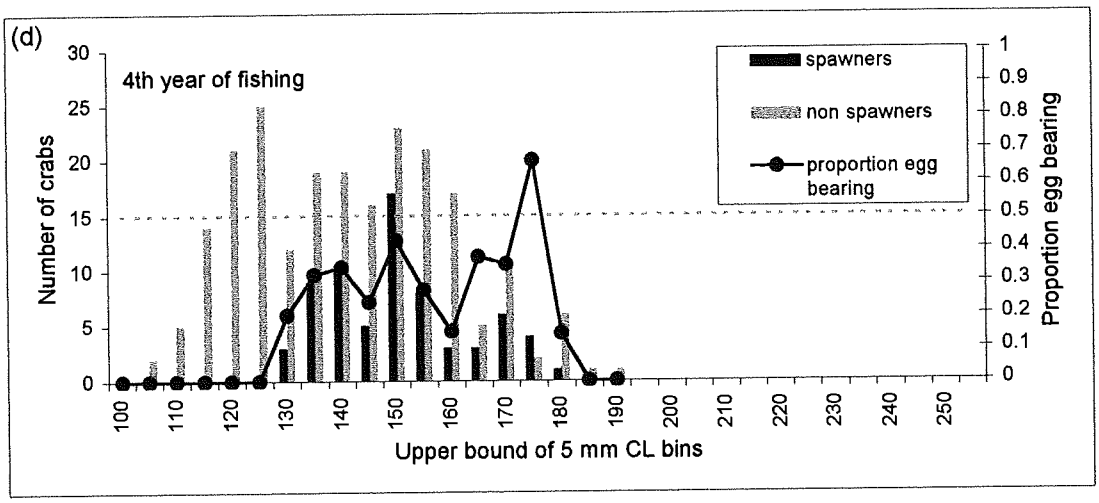
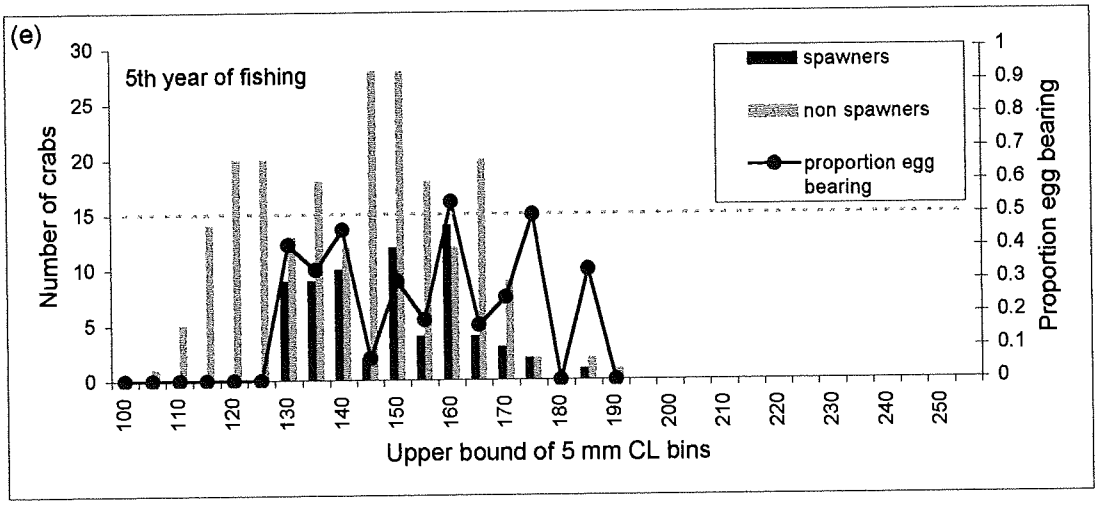


Figure 146. Simulated female catch length frequencies for nine years (a)-(i) following the introduction of exploitation. The individual-based model was run for 70 years before fishing began, after which length frequencies were recorded for November.





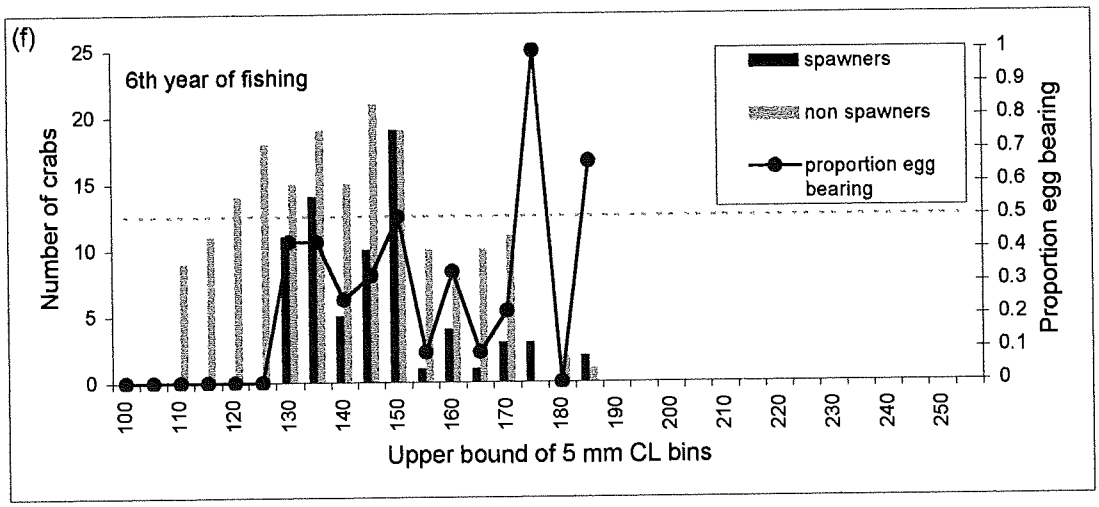


Figure 146. (d)-(f).

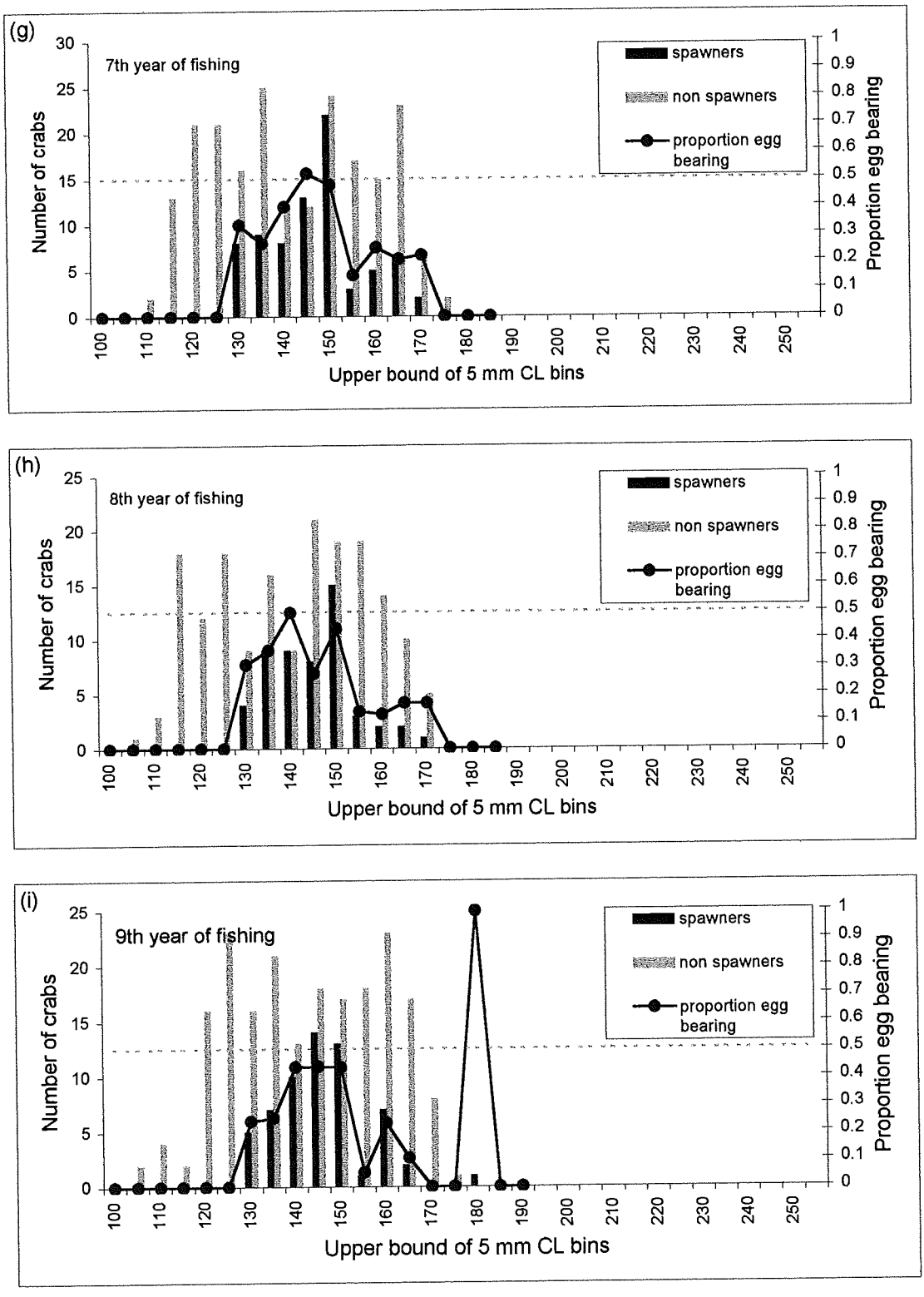


Figure 146. (g)-(i).

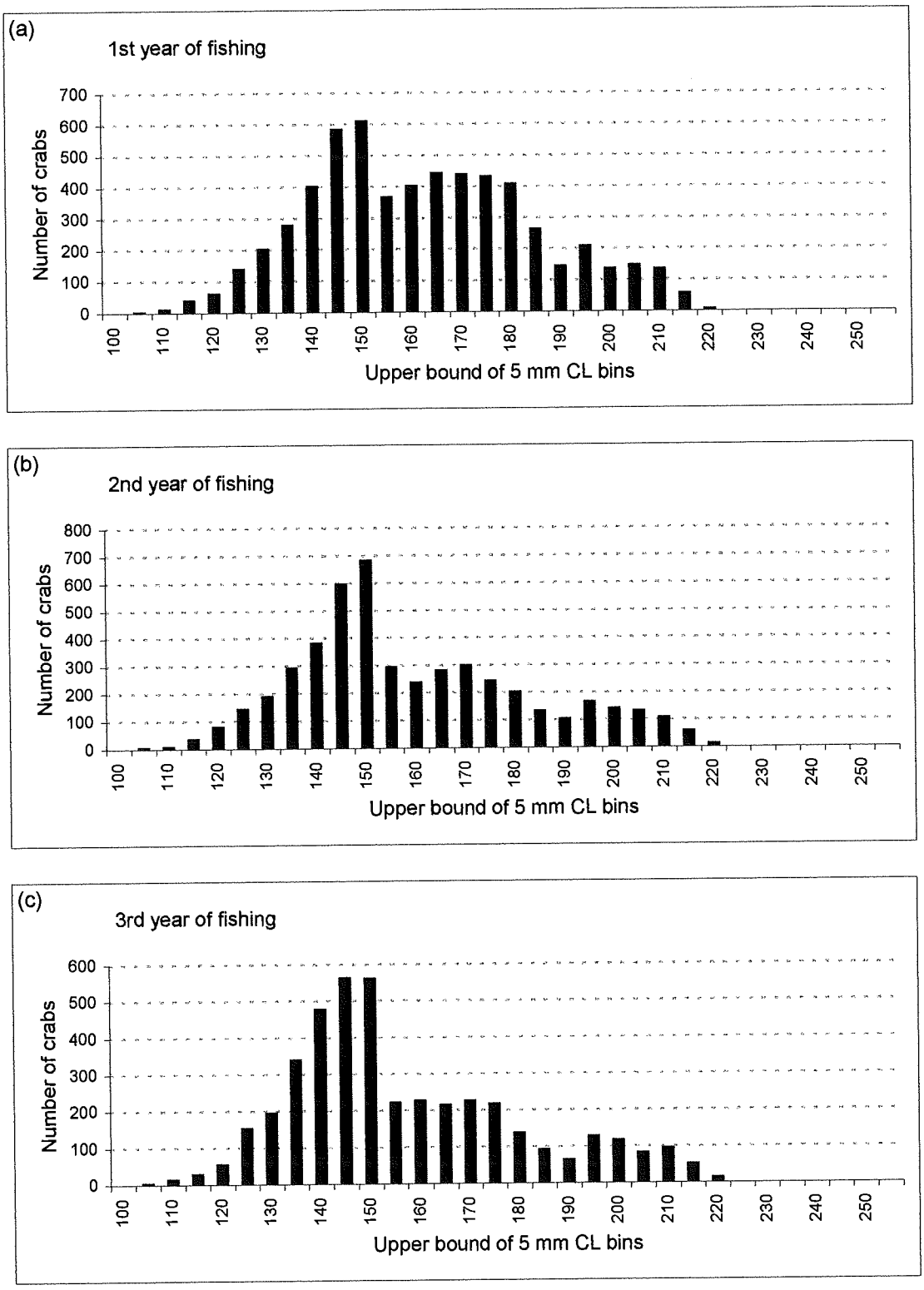
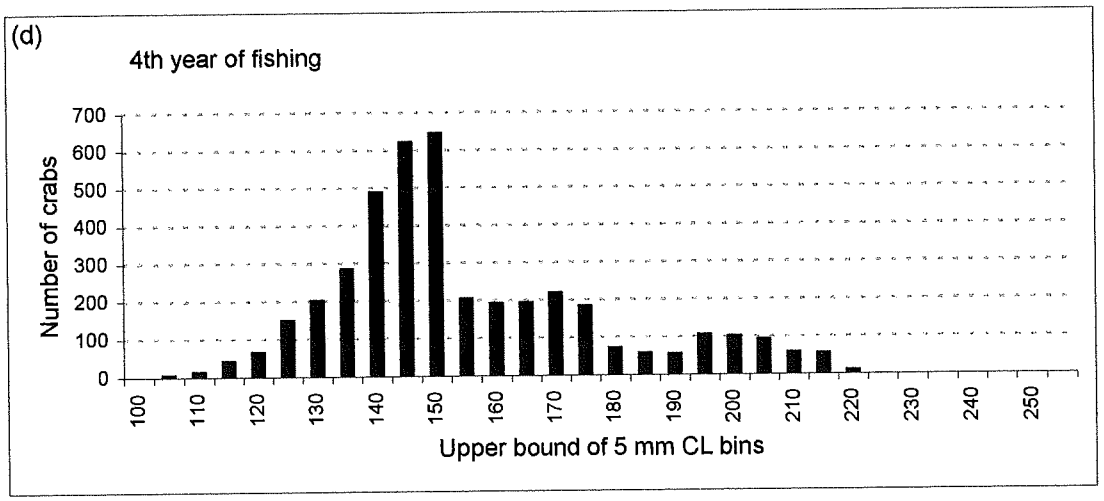
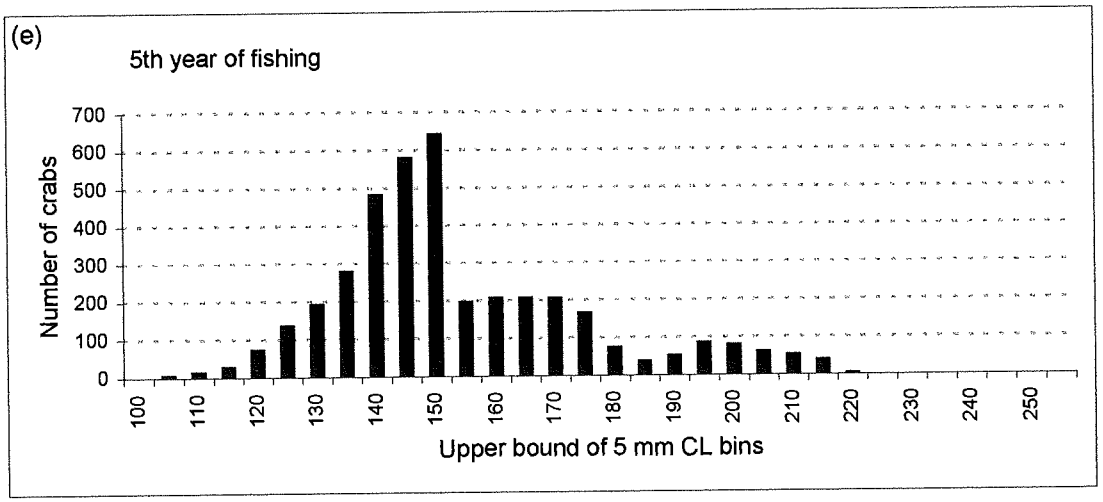


Figure 147. Simulated male catch length frequencies for nine years (a)-(i) following the introduction of exploitation. The individual-based model was run for 70 years before fishing began, after which length frequencies were summed over each season (November-May).





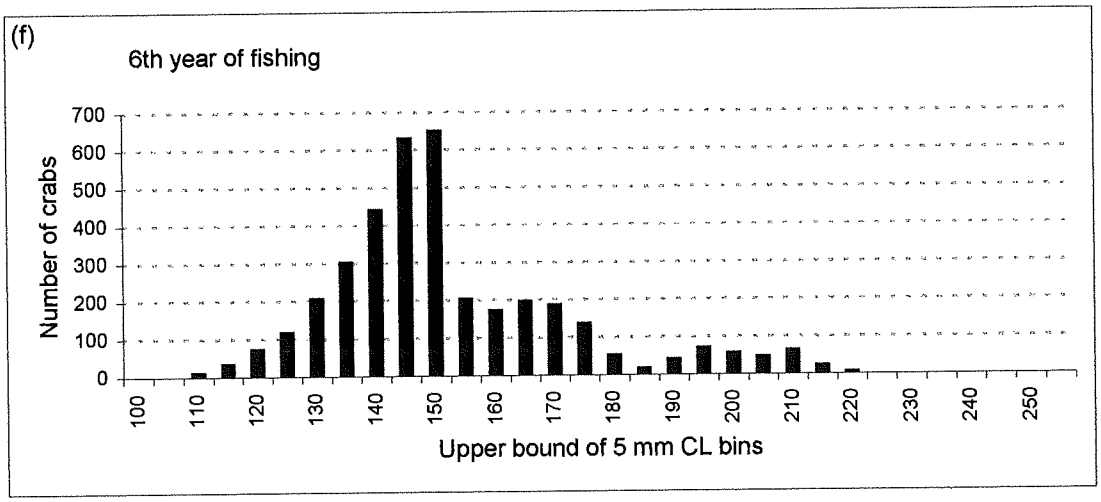
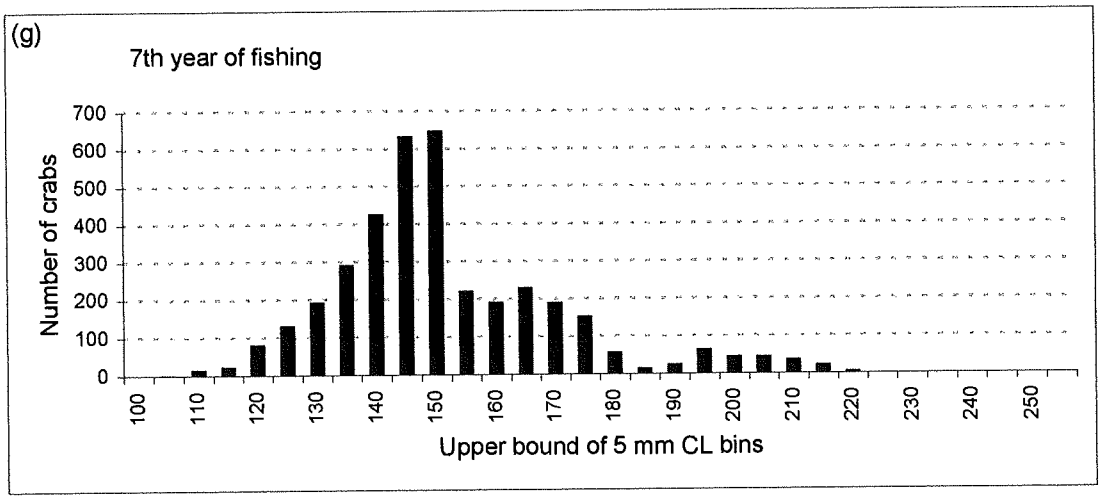
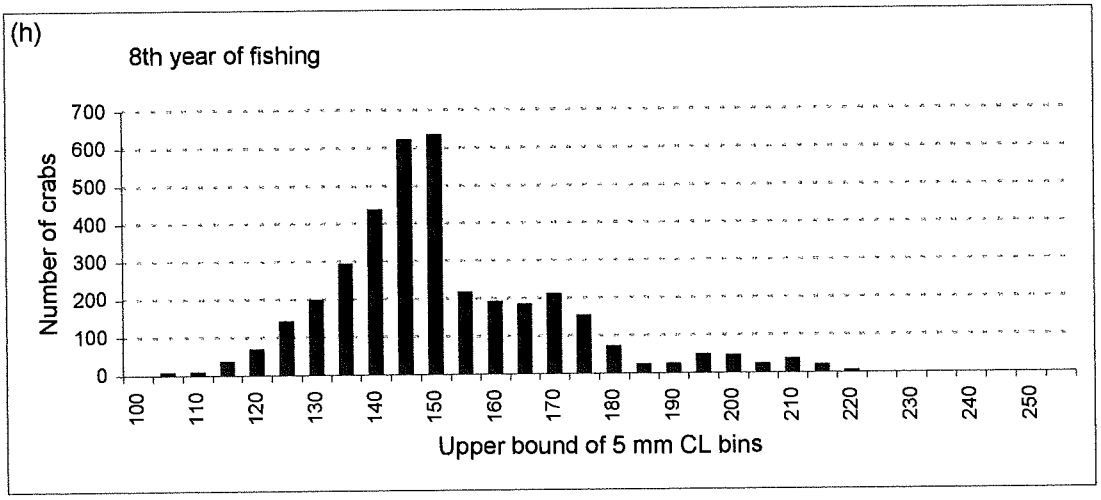


Figure 147. (d)-(f).





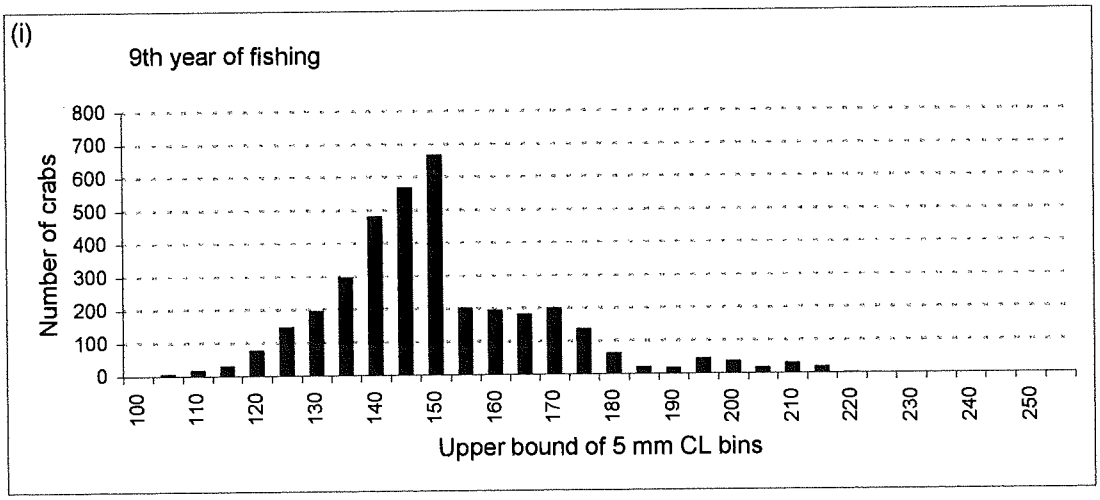


Figure 147. (g)-(i).

General qualitative agreement was satisfactory:

1. Qualitative form of length distributions for female sampled (Figure 140) compared with model (Figure 146) and male data (Figure 141) versus model (Figure 147) catches is similar in the extent of the upper tails, and the general form of the distributions.
2. After a number of years, the proportion of ovigerous females is lower for legal size than sublegal females in the catch, as observed in the catch samples.

Several more secondary differences between observation and the model-predicted lengths are noted:

1. The difference in proportion egg-bearing above and below LML took more years in simulation, roughly 6-7 rather than 2-3 years as in South Australian catch data (Figure 140), to exhibit the significantly lower proportion above LML.
2. Overall levels of proportion egg bearing for sublegals is generally below 50% in the model and above 50% in the data. This would, at least in part, be explained by the model assumption of low selectivity (s_E) for egg-bearing females for all of November, however, some females in the data were observed to release eggs prior to the end of November, and in some years, nearly all are spent by the end of October.

Both of these differences regarding proportions of ovigerous females in the catch indicate that the modelling of relative egg-bearing selectivity and possibly also catchability require further analysis.

6.2.5.2 Growth

Growth and natural mortality are the two most important input quantities for per-recruit fishery indicators. For comparison with natural mortality rate, the growth measure is relative growth rate, the mean growth in weight, as a proportion of starting weight, per year. This quantity was plotted for each tag recapture of crabs in the water longer than one year (Figure 148). For validating the growth description of the individual-based model, we chose this measure as well for comparing the moulting growth model description directly with tag data.

A model measure of proportional weight growth rate is obtained by averaging the weight increase of each crab in the simulated population, once each year. These model means were also calculated by 5 mm length bin (Figure 149).

From the data, annual growth by weight can also be obtained, if less precisely. Binning the tag recaptures (Figure 148), the mean proportional weight increases for recaptures in each 5 mm length bin from this plot were also plotted (Figure 149) for comparison.

A number of aspects of the way these data means for proportional weight growth are gathered and calculated can introduce variance or bias. These include the variations in the timing of tagging versus moulting, and leaving inexplicit the fact that crabs might have moulted one or many years prior to the time of tag and first release, which is not explicit in this data plot (but is explicit, through the intermoult period estimator) in the model moulting growth description. To try and obtain a model quantity as close as feasible to the data measure (in Figure 149), we simulated tagging in the individual-based model. A random sample of captured crabs were tagged and

released. Numbers per month were patterned after those of the South Australian giant crab tagging study. Simulated tag recaptures were then recorded and the mean proportional weight increases per year by 5 mm bin were calculated as with the actual tag recapture data (Figure 149).

Some of the difference between the model and data plots were corrected in the simulated tagging output (Figure 149). In general, the agreement between model and data is good (Figure 149). One evident area of divergence is the lower levels for simulated tagging in the size range 135-145 mm CL for both males and females. The model growth description in based on three submodels: moult increment histograms (Figure 132), intermoult period probabilities (Figure 137), and the fitted weight-length relationship (Figure 129). This general level of agreement of model growth and data suggest is satisfactory. Further investigation in the sublegal size range would be expedient.

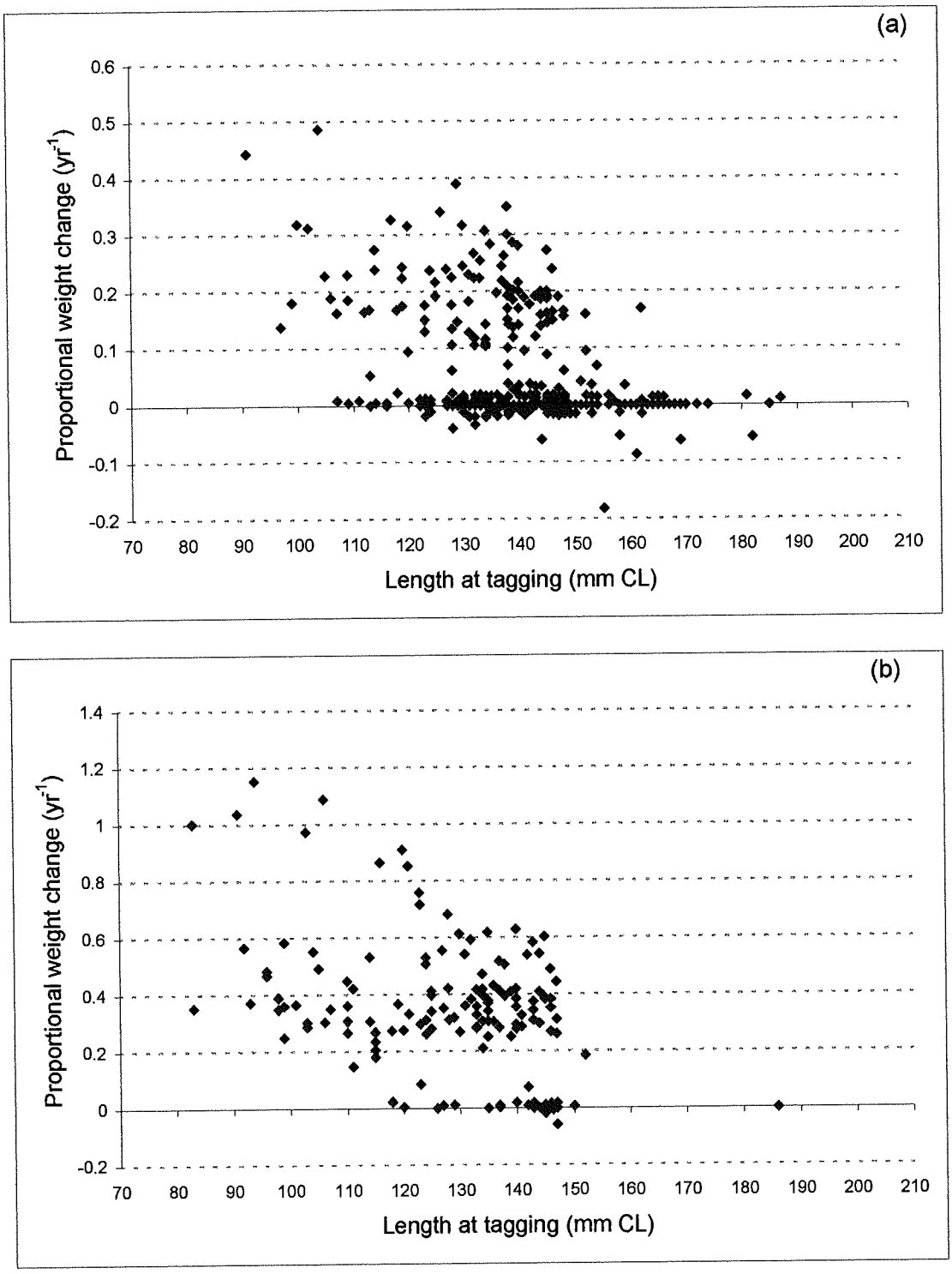


Figure 149. Change in weight as a proportion of tag release weight per year at large excluding crabs whose years at large were less than one: (a) females, (b) males.

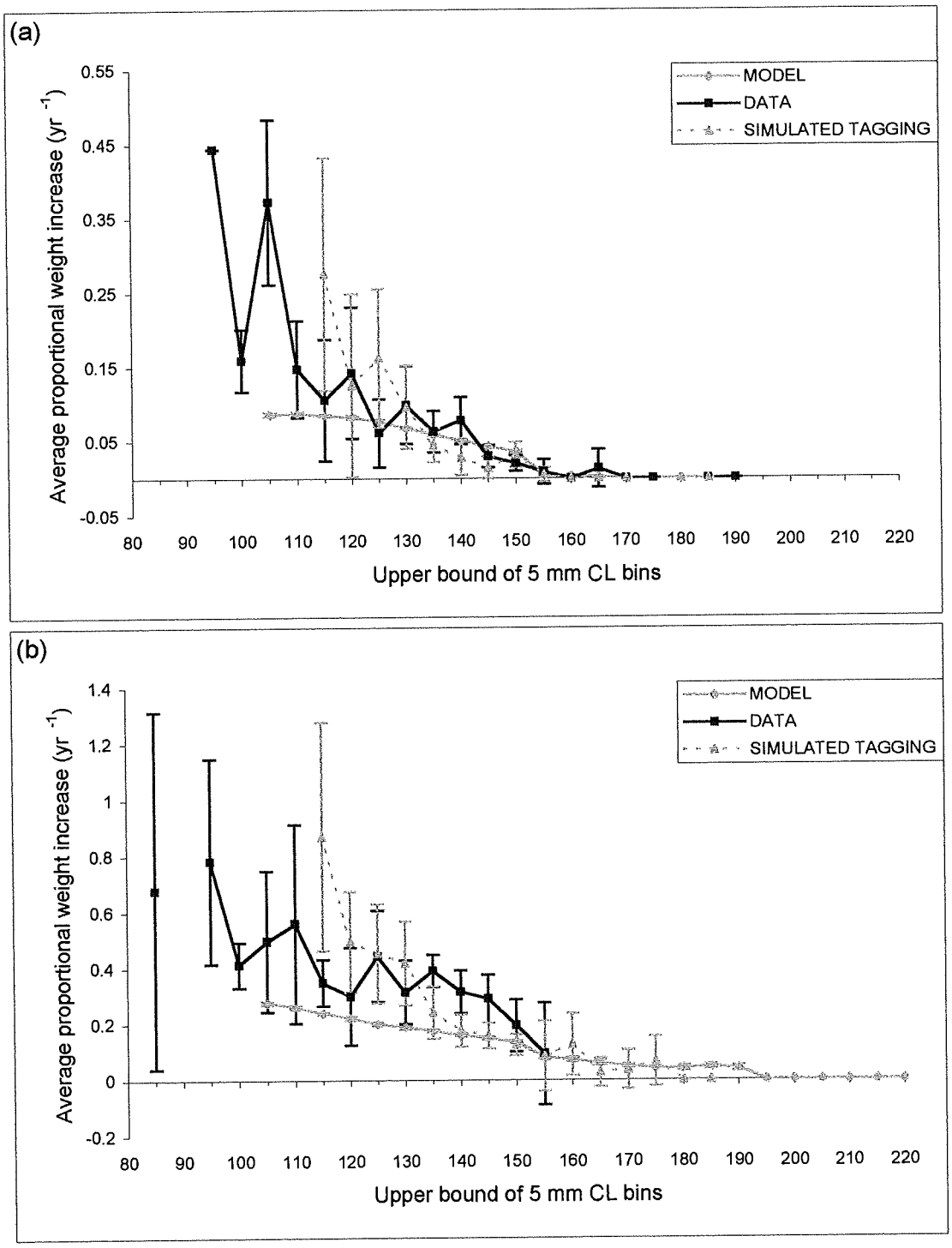


Figure 150. Observed tag-recapture, model predicted and simulated tag-recapture average proportional weight increase per year, by length. Error bars represent 95% confidence bounds on the standard error.(a) females, (b) males.

6.3. Yield-Per-Recruit (YPR), Value-Per-Recruit (VPR), and Egg-Per-Recruit (EPR) Analysis

6.3.1. Methods

The analysis was done for South Australia, Victoria and Western Australia. Tasmania was not included due to a lack of recaptures of tagged animals and therefore of growth information. The runs between states were distinguished by

1. moult increment probabilities,
2. LML (currently 150 mm in eastern states and 140 mm in Western Australia), and
3. size of reduced fishing selectivity on large crabs; (> 4 kg for Western Australia, > 5 kg for eastern states).

The simulation was identical among states in all other respects.

Seven legal minimum lengths (LML's) were tested in each state. These ranged between 130 mm and 160 mm and included the current LML of 150 mm (140 mm for Western Australia). A single run of the simulation covered 70 years to reach equilibrium at the current LML and a further 30 years after change of LML to simulate the effect of regulatory change in minimum size. For each value of LML, the stochastic individual-based model was run 5 times, resulting in five replicates of 100-year time series. Recorded outputs were annual recruitment, annual catch, annual harvest revenue (i.e. value), and annual egg production.

For the three model-derived per-recruit indicators, both the dynamic impact in years subsequent to change in LML, and the long-term ('equilibrium') impacts analogous to classic Beverton-Holt outputs are presented.

Since recruitment varied randomly between years, an overall measure of annual recruitment was obtained by averaging across all runs for years 61-100. Each of the three per-recruit indicators were calculated by dividing the relevant fishery output (catch by weight, revenue, or egg production) through by this level of mean recruitment.

The dynamic outputs all assumed a value of F = 0.6. The variation with time was plotted as averages across years and runs for:

- 5 years previous to change in LML as a measure of the steady state levels of YPR, VPR and EPR
- year of change of LML as a measure of the immediate response to change in LML
- 1 year after change in LML as a measure of the short term response
- 2 year after change in LML
- 3 year after change in LML
- 4 year after change in LML
- 5-9 years after change in LML
- 10-14 years after change in LML
- 15-19 years after change in LML
- 20-24 years after change in LML
- 25-29 years after change in LML.

Averages over the longest recorded time subsequent to change in LML (25-29 years after change in LML) were taken as the long-term equilibrium impacts. For these equilibrium indicators, 8 levels of fishing mortality (F) were simulated. Each F was tested using the seven LML's.

The range of long-term averages for the three derived per-recruit indicators, yield-, value-, and egg-per-recruit, are presented as scatterplots for each state.

6.3.1.1. Yield per recruit (YPR)

Annual catch weight was divided through by average recruitment to give annual yield per recruit (YPR).

6.3.1.2. Value per recruit (VPR)

Total harvest revenue is calculated by summing the price (per kg) times weight of each crab when captured Prices (Figure 143) varied by crab length and by month of harvest.. VPR equals total harvest revenue to fishers divided by average recruitment, i.e. the landed value per yearly recruited giant crab to the legal stock.

6.3.1.3. Eggs per recruit (EPR)

Egg per recruit is reported as a percentage of virgin egg production. Ten model runs with F = 0 averaged over years 61 to 100 provided a single measure of virgin egg production. The simulation was then run with fishing restored at the assumed range of F values. Yearly egg production sums were divided through by virgin egg production. Averages were taken across years and runs as described above to obtain dynamic and equilibrium model outputs.

6.3.2. Results

6.3.2.1. Yield per recruit

Model short-term effects on YPR of changes in LML, 0, 1 or 2 years subsequent to the regulatory change in LML (Figure 150), were the same for all states. Lowering LML results in an immediate increased catch because smaller crabs, below LML, are now taken, while recruitment is unaffected.

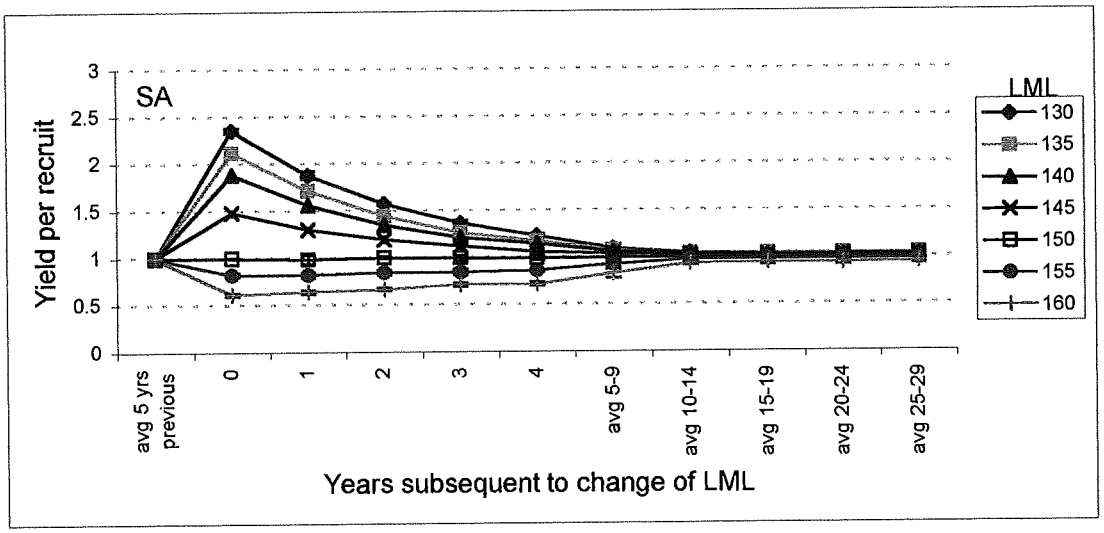
Long-term equilibrium levels of YPR were reached after about 9 years subsequent to change in LML (Figure 150), the approximate intermoult period of females.

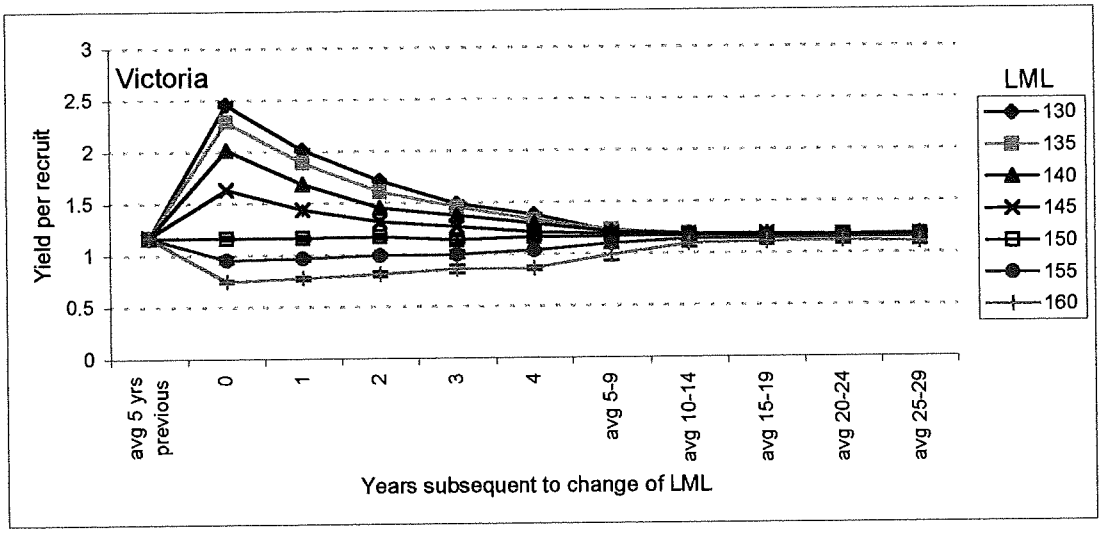
The principal result for giant crab YPR was that in Victoria and South Australia, long-term levels were only mildly affected by choice of LML. In Western Australia, lowering LML yielded no change, while raising LML from the current 140 mm yielded measurable declines in YPR (Figure 150). Western Australian moult increments were smaller and thus (model) growth is slower than the other two states, yielding a generally lower YPR.

Trends in long-term YPR were similar for the range of F-levels assumed (Figure 151). Thus, the result for YPR versus LML is robust with respect to the level of F applied.

These are plotted on a reduced y-axis scaling (Figure 151 versus Figure 150). Only at lowest tested F = 0.4 did the optimal level and overall trend of YPR versus LML differ (Figure 151). For YPR (not egg production considered below), optimal LML for South Australia was 140 mm CL. For Victoria, 140 to 150 mm. In Western Australia, the highest YPR is predicted for the lowest possible LML. But as noted above from the dynamic plots of YPR (Figure 150) the variation is slight, with effectively constant levels of YPR over the range 130 to 150 mm CL for higher levels of F in South Australia, 130 to 160 in Victoria, and 130 to 145 in Western Australia.

With respect to assumed levels of fishing mortality, model YPR increased with assumed F.





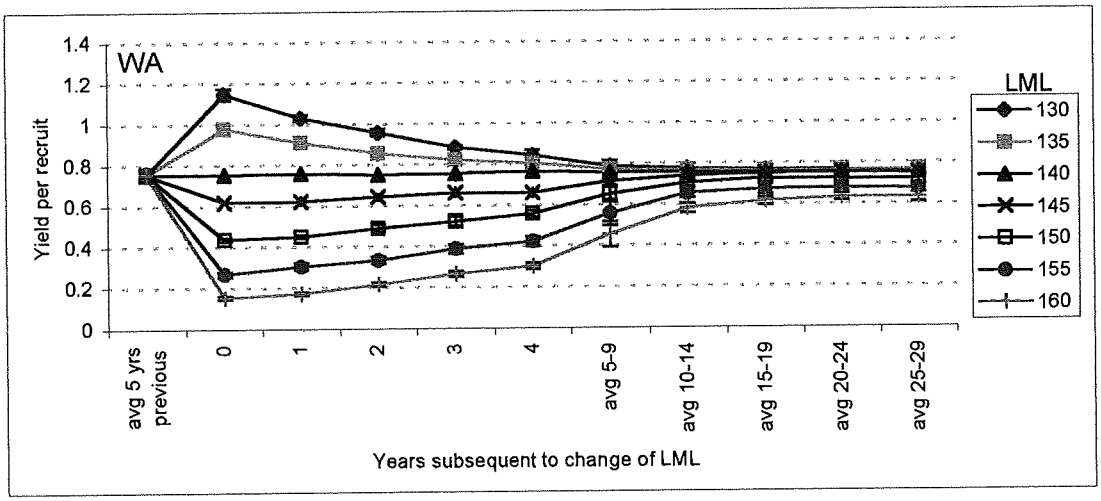


Figure 151. Time dependent (short and long term) effect on yield per recruit following a change of LML. Error bars indicate the standard deviation over five runs of the stochastic individual-based model using F=0.6.

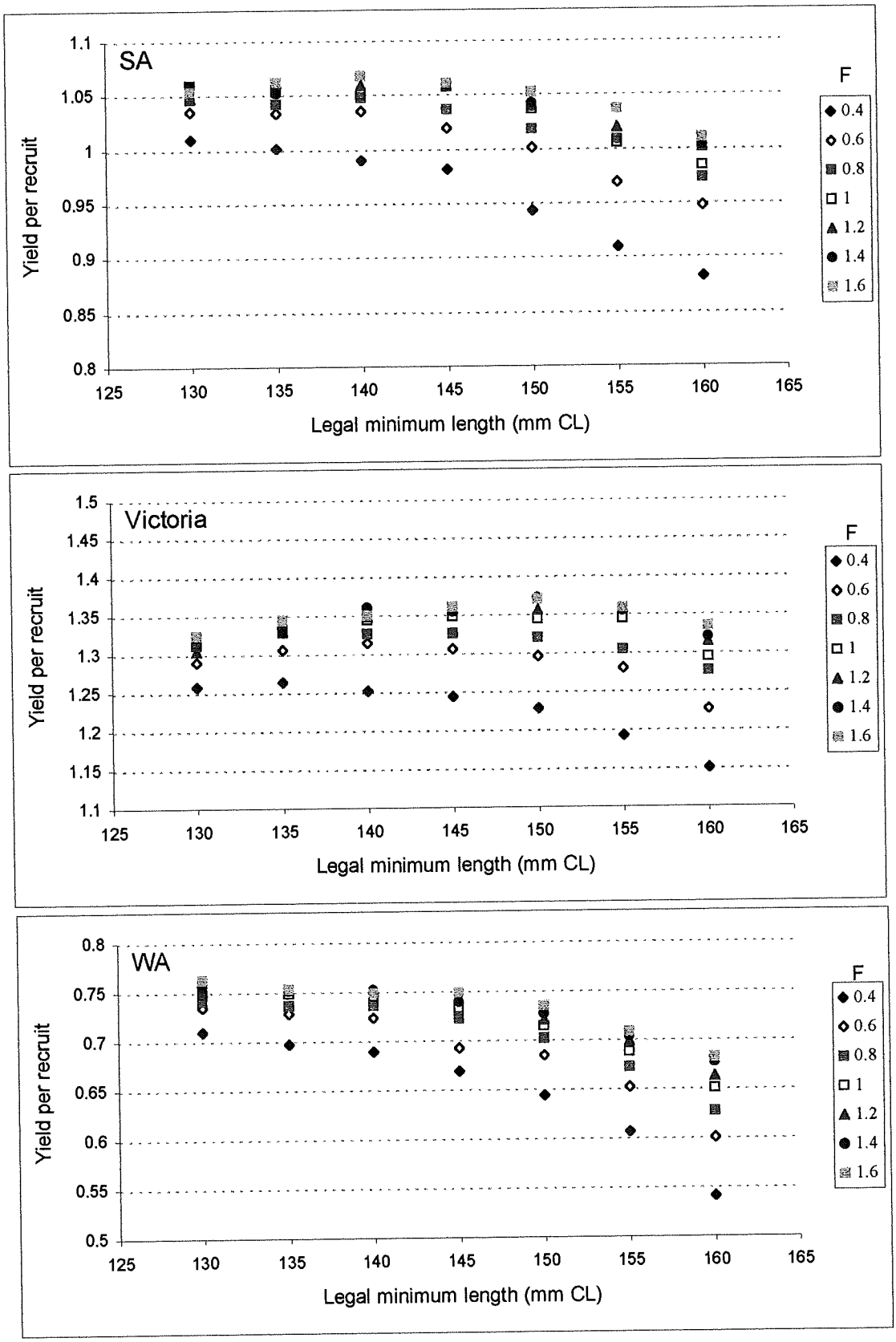


Figure 152. Time dependent (short and long term) effect on yield per recruit following a change of LML, under a range of fishing mortalities.

6.3.2.1.1. Interpretation of YPR Result: M versus weight growth

To interpret this YPR result of weak dependence on LML, we examined in more detail the results of the South Australian model population.

Male giant crabs grow faster than females. The first question is whether both sexes express this outcome. The answer is they do not. Males (Figure 152 resembled the YPR outcome overall of relatively weak dependence on LML, but lower LML yielded lower YPR. Females (Figure 152) showed stronger dependence on LML, with the opposite relationship, lower LML giving higher YPR. Analysing model output, males comprise, on average, 72% of the landed catch by weight, females 28%. Thus males dominate the YPR outcome.

YPR, in general, is a trade-off between declining rate of growth and natural deaths. The YPR outcomes for the two sexes are understood by examination of natural mortality rate and proportion weight growth versus length (Figure 153). Natural mortality dips in middle lengths due to lower moult frequency and returns to the higher value when senescence mortality come into effect at lengths above the terminal moult.

Because mature females (> 125 mm CL) grow more slowly than the rate of natural death for all sizes, it is optimal by a YPR indicator to harvest females earlier. Their growth in harvest weight will never compensate natural losses in numbers in succeeding years.

For males (Figure 153), however, the proportional weight increase per year is higher than natural mortality rate at smaller sizes, and crosses over, growth slower than deaths above the size of 150-155 mm CL. Thus potential net gain in harvest biomass is lower for recruits harvested at sizes below this cross-over length where growth is still faster than natural death. Raising LML also results in reduced yield per recruit at lengths above the cross-over, because growth has slowed to the point where more crabs are being lost to natural mortality. In simulated male South Australian giant crabs, this cross-over point occurred at the current LML. Thus the optimum size of male harvest for YPR is the current LML. The slightly higher overall YPR at 140 mm CL for South Australia (Figure 151) reflects the added influence of females, for which a lower LML yields higher YPR.

This %weight growth versus natural death rate cross-over for males, who form the majority of harvest weight and thus dominate the yield-per-recruit outcome, also explains the higher YPR with higher F. The optimum size of harvest is at the cross-over. Lower F's leave more survivors to larger lengths where losses from the harvest of numbers are not compensated for by greater weight of each crab taken.

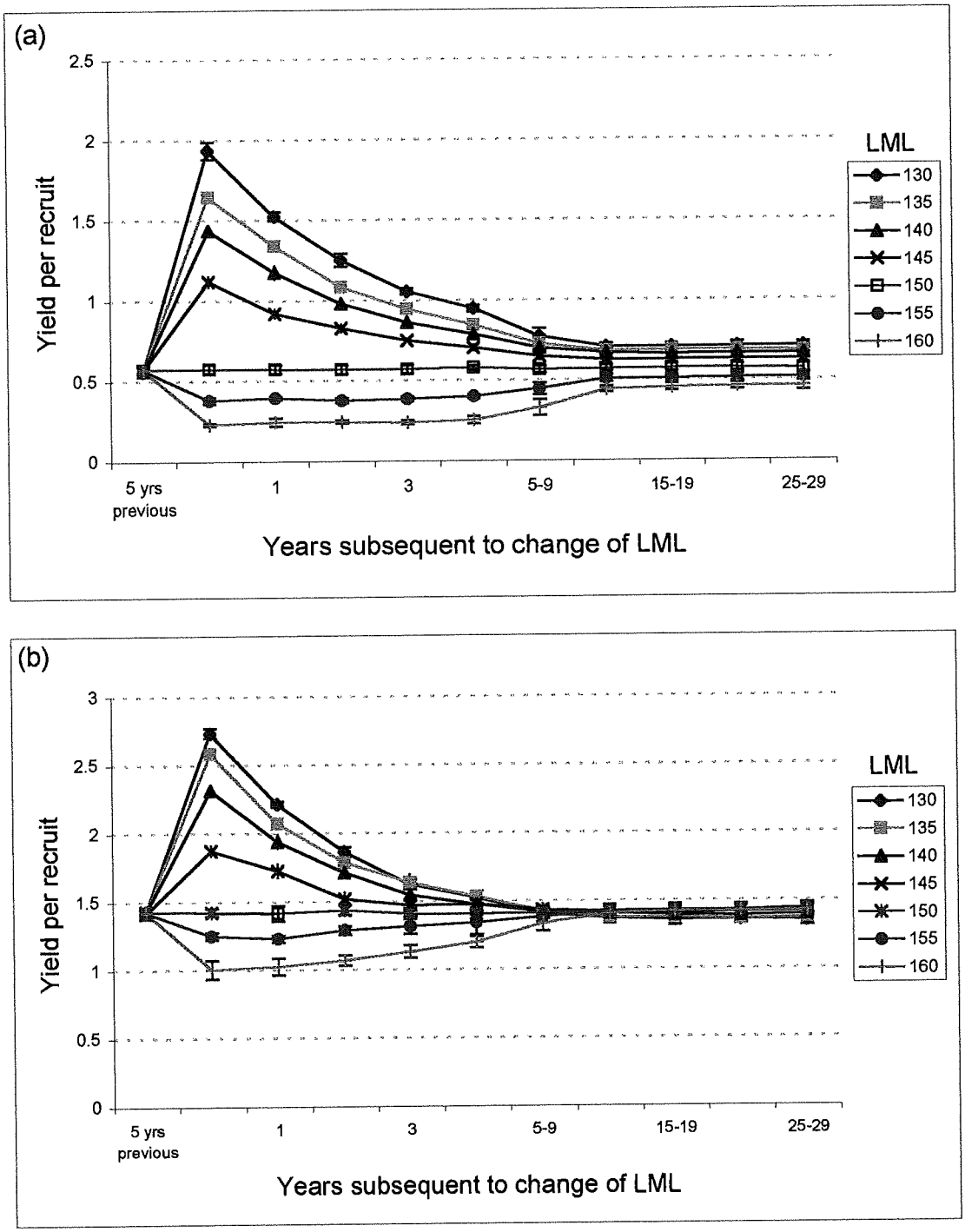


Figure 153. Yield per recruit for South Australian (a) females and (b) male giant crabs, following a change of LML. Error bars indicate the standard deviation over five runs of the stochastic individual-based model using F = 0.6. A range of years displayed indicates an average across those years.

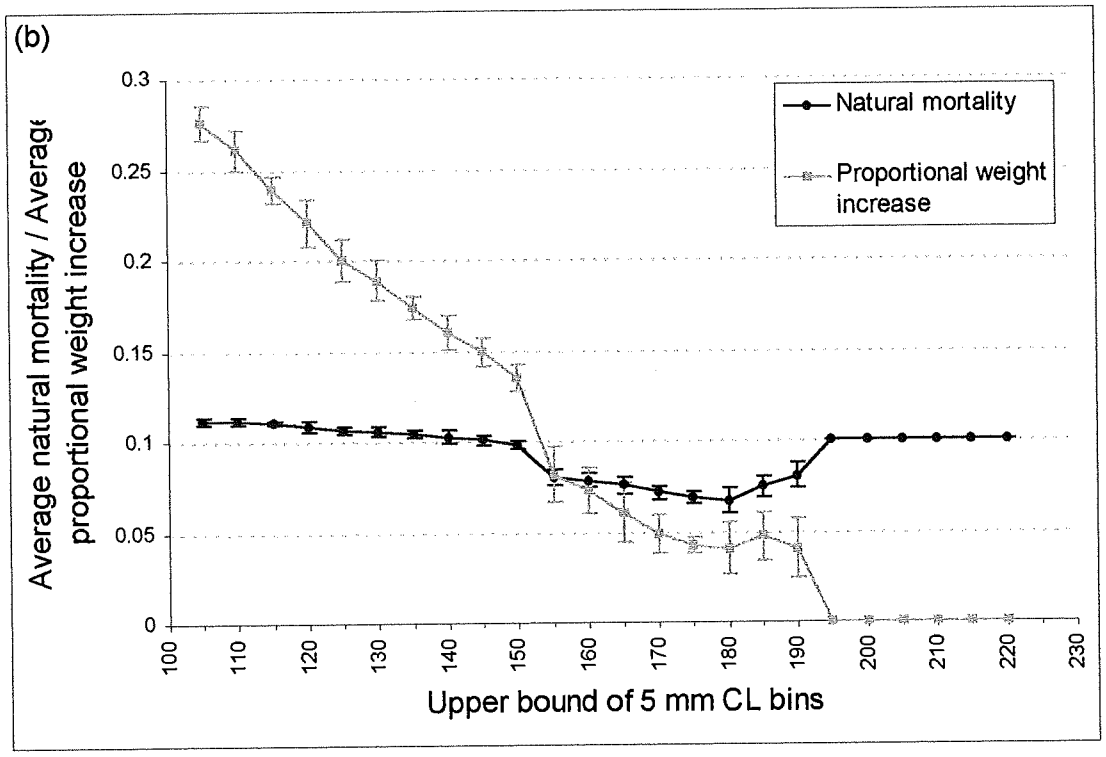


Figure 154. Average simulated natural mortality rates and proportional weight increase divided into 5 mm length bins, (a) females and (b) males. Natural mortality, Mn = 0.05, moulting mortality, Mm = 0.2, & senescence mortality, Ms = 0.05.

6.3.2.2. Value per recruit

Because gross revenue is landed weight times price paid to fishers, VPR is YPR modified by size-dependent price. Prices (Figure 143) are higher for smaller crabs, at a ratio of roughly 2:3:4 by weight category in high price months and 2:3.3:5.4 in summer and spring when catch rates and catches are high. The strong market preference for smaller crabs shifts the VPR outcome in favour of lower LML. For all three states (Figure 154) VPR was highest at lowest tested LML. Examination of the long-term model outcome (Figure 155) indicated a reduction in LML from current 150 to 140 mm CL is predicted to yield a rise from $30 to $34 per recruited (75-100 mm) crab in South Australia and $39 to $43 in Victoria. Marginal increases in Western Australia of approximately $1 are predicted for LML drop from current 140 to 130 mm CL. These specific landed values per recruit quoted were for F = 0.6. More generally, a $4 increase in South Australia and Victoria was consistent across the range of F values tested.

The model VPR breakdown by sex (Figure 156) shows that (unlike YPR), both males and females express the same dependence on LML.

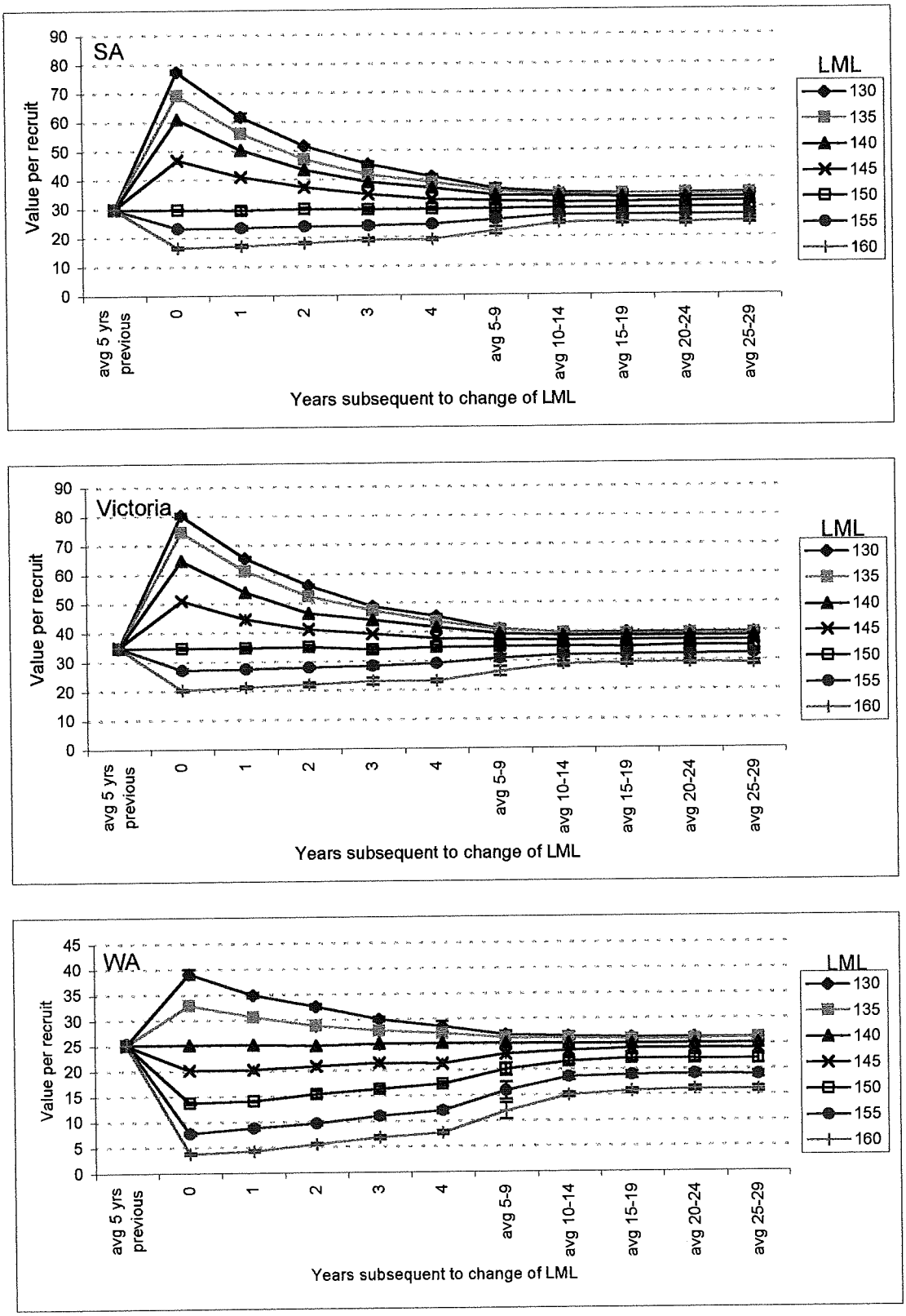


Figure 155. Time dependent effect on value per recruit following a change of LML.
Error bars indicate the standard deviation over five runs of the stochastic individual-based model using F=0.6.

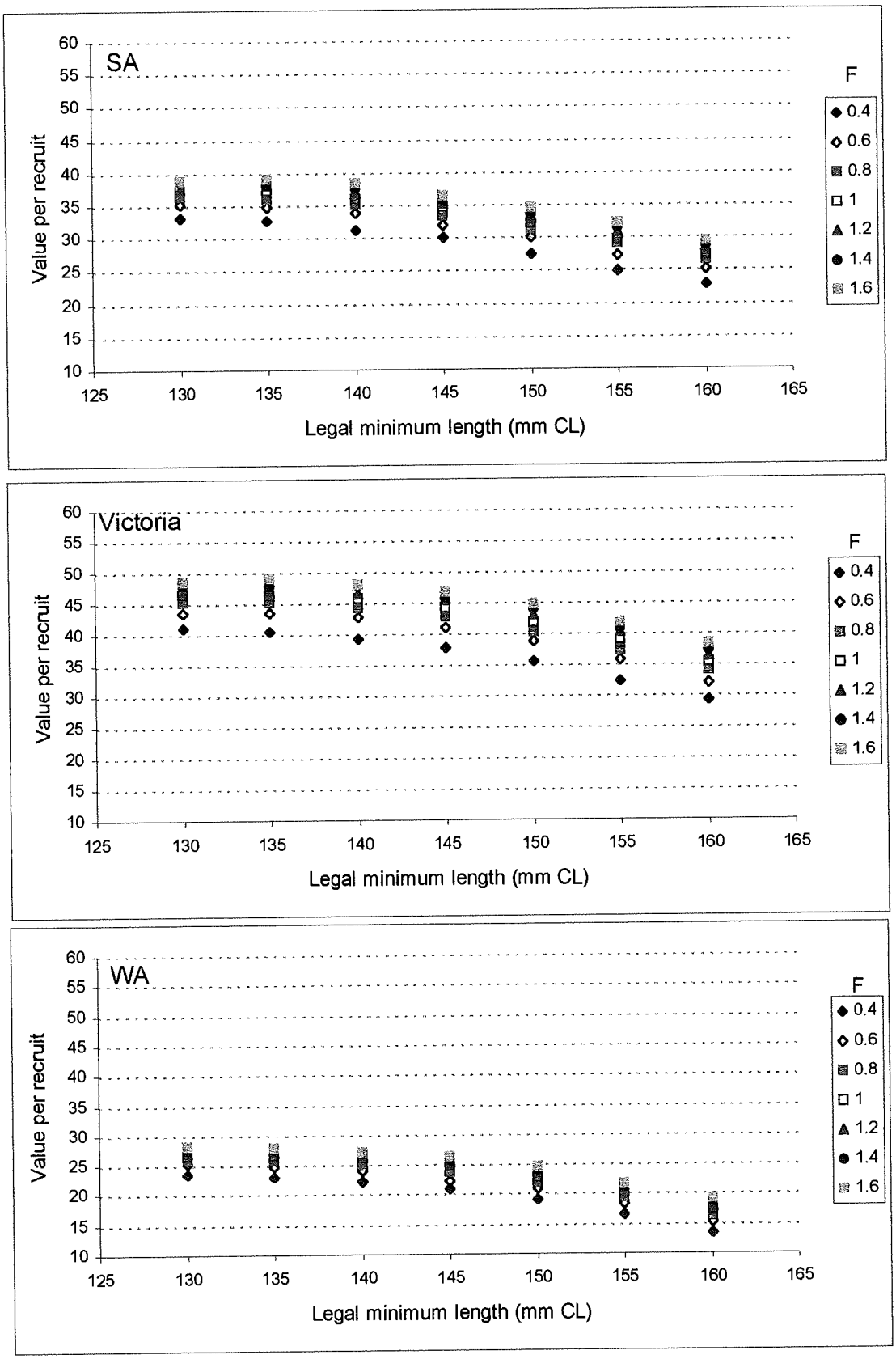


Figure 156. Long-term effect on value per recruit following a change of LML, under a range of fishing mortalities.

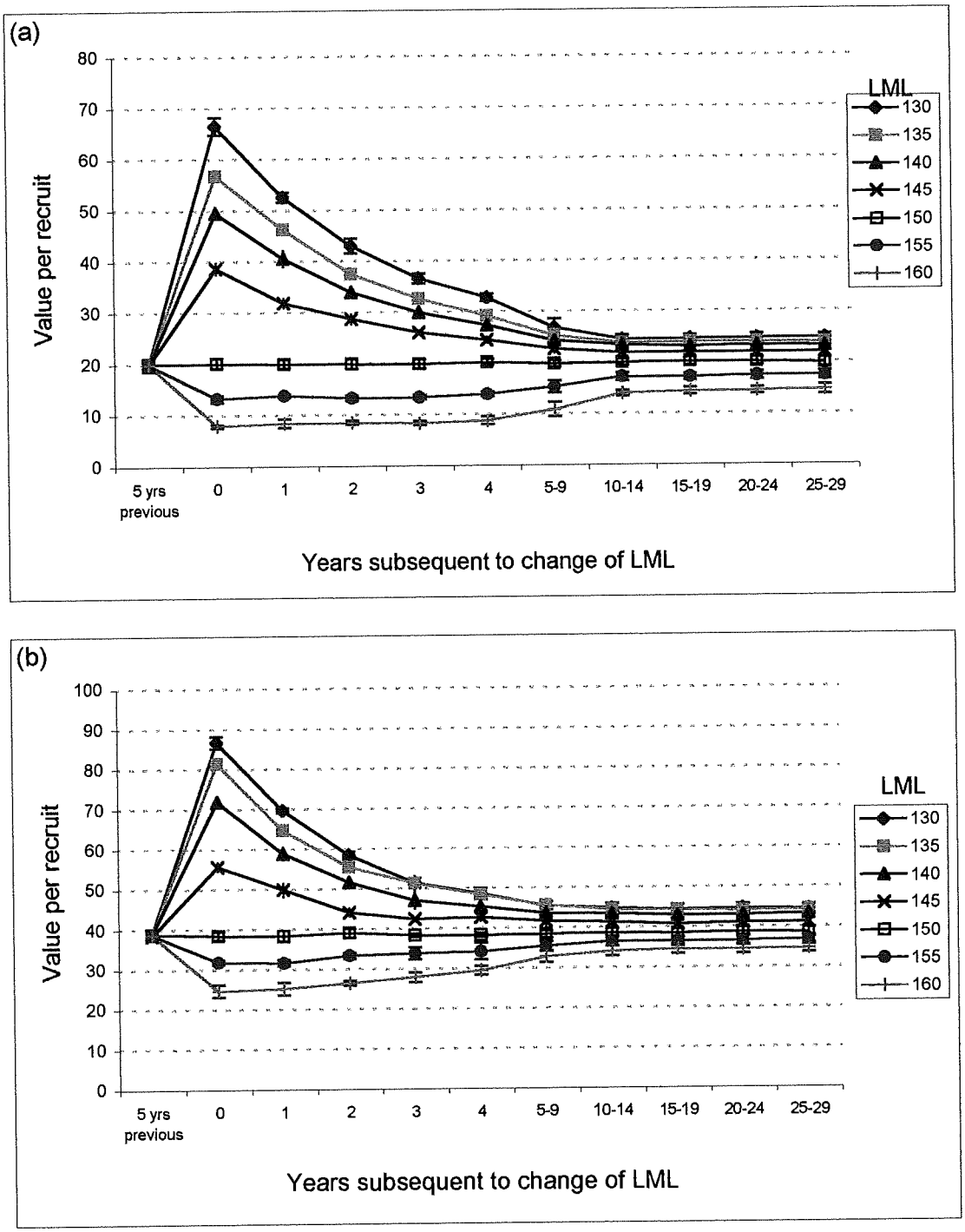


Figure 157. Sex-specific value per recruit for South Australia, following a change of LML: (a) females and (b) males. Error bars indicate the standard deviation over five runs of the stochastic individual-based model using F=0.6. A range of years displayed indicates an average across those years.

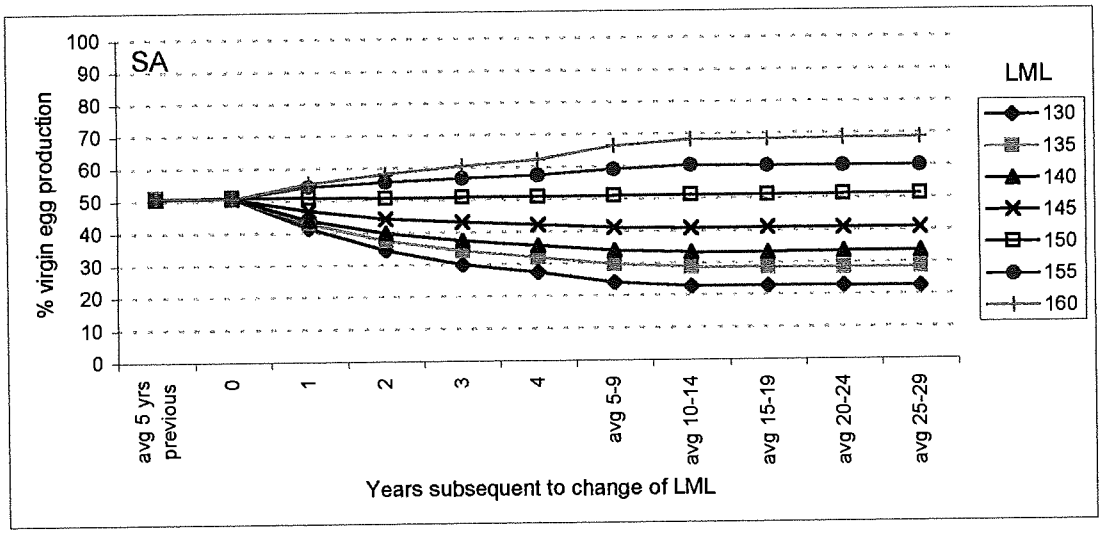
6.3.2.3. Eggs per recruit

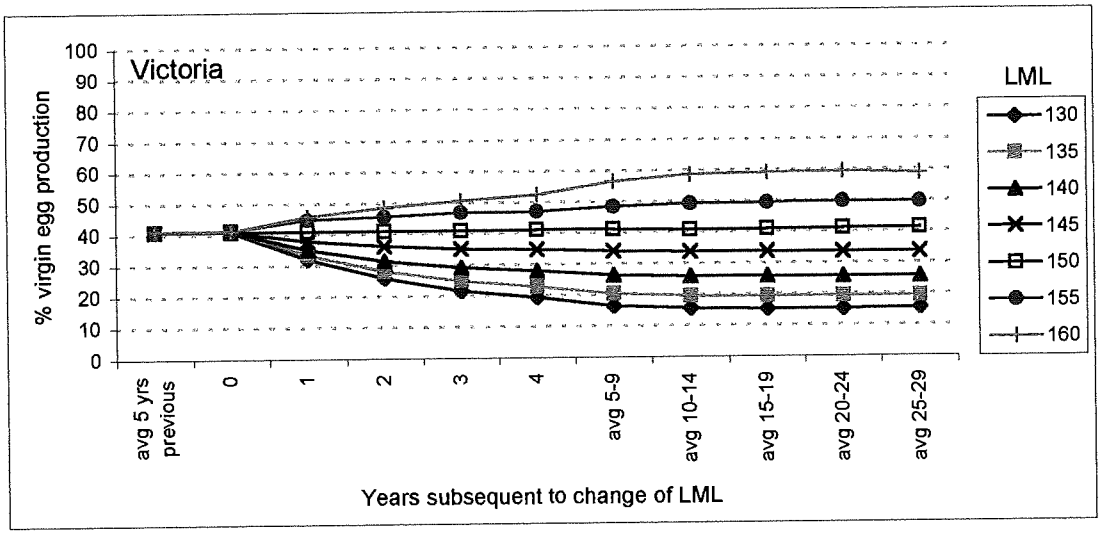
With % virgin egg production per recruit there is no trade-off between growth and natural mortality. Higher LML will always yield higher EPR, both in the short-term (Figure 157) and long-term (Figure 158). The dependence on LML in all three states was strong (Figure 157).

At current LML, assuming F is greater than 0.4, long-term percent virgin egg production in South Australia is 44-51%, 32-41% in Victoria, and 30-39% in Western Australia. Approximate 9% increases are predicted for each 5 mm CL increase in LML in Victoria and South Australia. A decrease in LML to 140 mm CL in South Australia is predicted to yield a decrease to 25-33%, and in Victoria, to 17-27%, an approximate 7-8% decrease in EPR for each 5 mm CL LML reduction.

The dependence on LML of EPR is stronger than for YPR and VPR. In strict percentage terms, losses in EPR by lowering LML are greater than gains in VPR. (As noted YPR was relatively weakly affected by LML.)
actively mating males, and the fertilisation of female eggs may be limited.

In the future, it may be possible to monitor sperm limitation in Tasmanian giant crab populations as spermathecae samples were taken in the early years of the fishery by the Tasmanian DPI & F. These samples can be compared against future samples to assess if there have been changes in the incidence of mating or ejaculate weight. Such a program would be of relatively low cost. Similar programs of spermethecae monitoring could be undertaken in all four states where giant crabs are subject to high rates of exploitation.





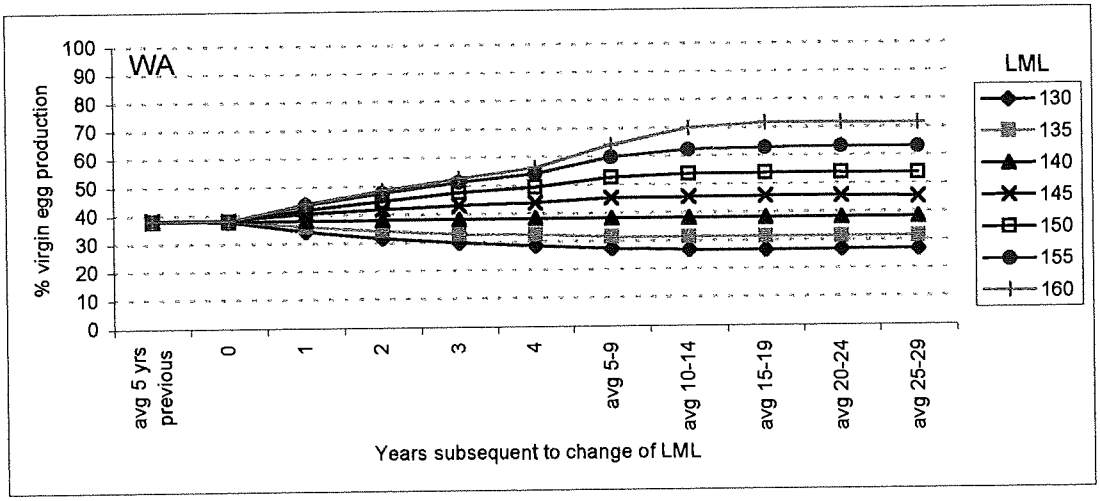


Figure 158. Time dependent (short and long term) effect on % virgin egg production following a change of LML. Error bars indicate the standard deviation over five runs of the stochastic individual-based model using F=0.6.

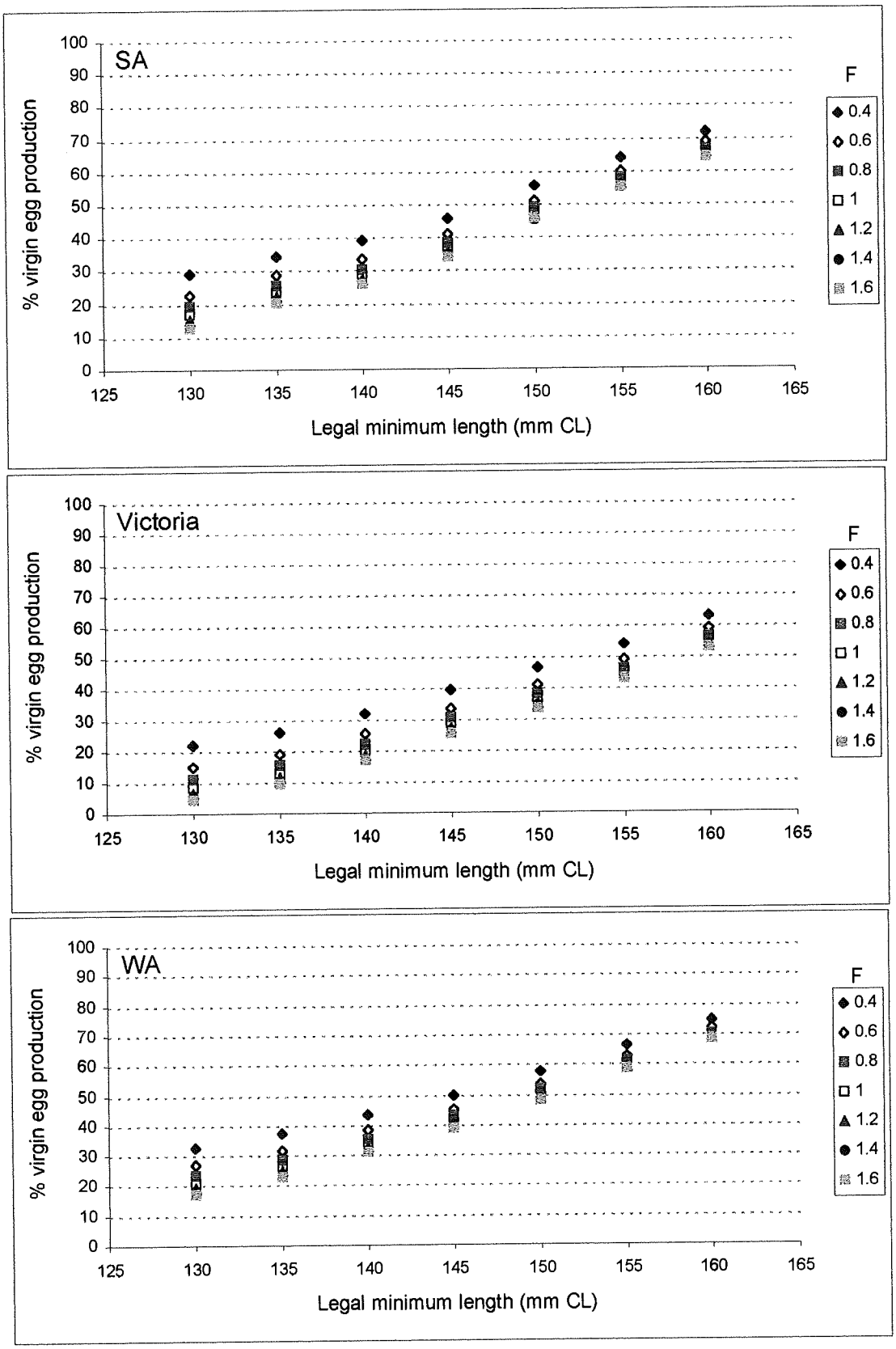


Figure 159. Long-term effect on % virgin egg production following a change of LML, under a range of fishing mortalities.

6.3.2.3.1. Interpretation of YPR Result: Egg Production by Length Class

To visualise the impact of LML on population egg production, the model-estimated female length structure and total egg production by length class were calculated and plotted (Figure 159) for a virgin stock and three choices of LML. Fishing mortality was set at the baseline value of F = 0.6 in these examples. Population egg production by length class was calculated as a product of female population numbers and average eggs per female in each length class (Figure 159). The sum under each of the egg production curves equals the total population egg production for that choice of LML.

Also illustrated are the average eggs per female which decline almost imperceptibly below the raw fecundity curve due to presumed reduction in egg output by older females, by half 10 years following, and to zero 15 years following their terminal moult. This indicates that this postulated decline in fecundity after long times is not a significant factor in final population egg production (Table 175).

These egg production totals at length were plotted together for comparison (Figure 160). It is evident that above LML, egg production declines precipitously. A LML of 160 mm leaves more than half of that in a virgin stock, while LML set at 150 mm allows about half (51%). The decline from 51% to 33% at the LML of 140 mm CL (Figures 159 (c) to (d)) is evident. Overall, with measures of fecundity and F = 0.6 employed here, giant crabs exhibit a relatively modest variation in total egg production by length class.

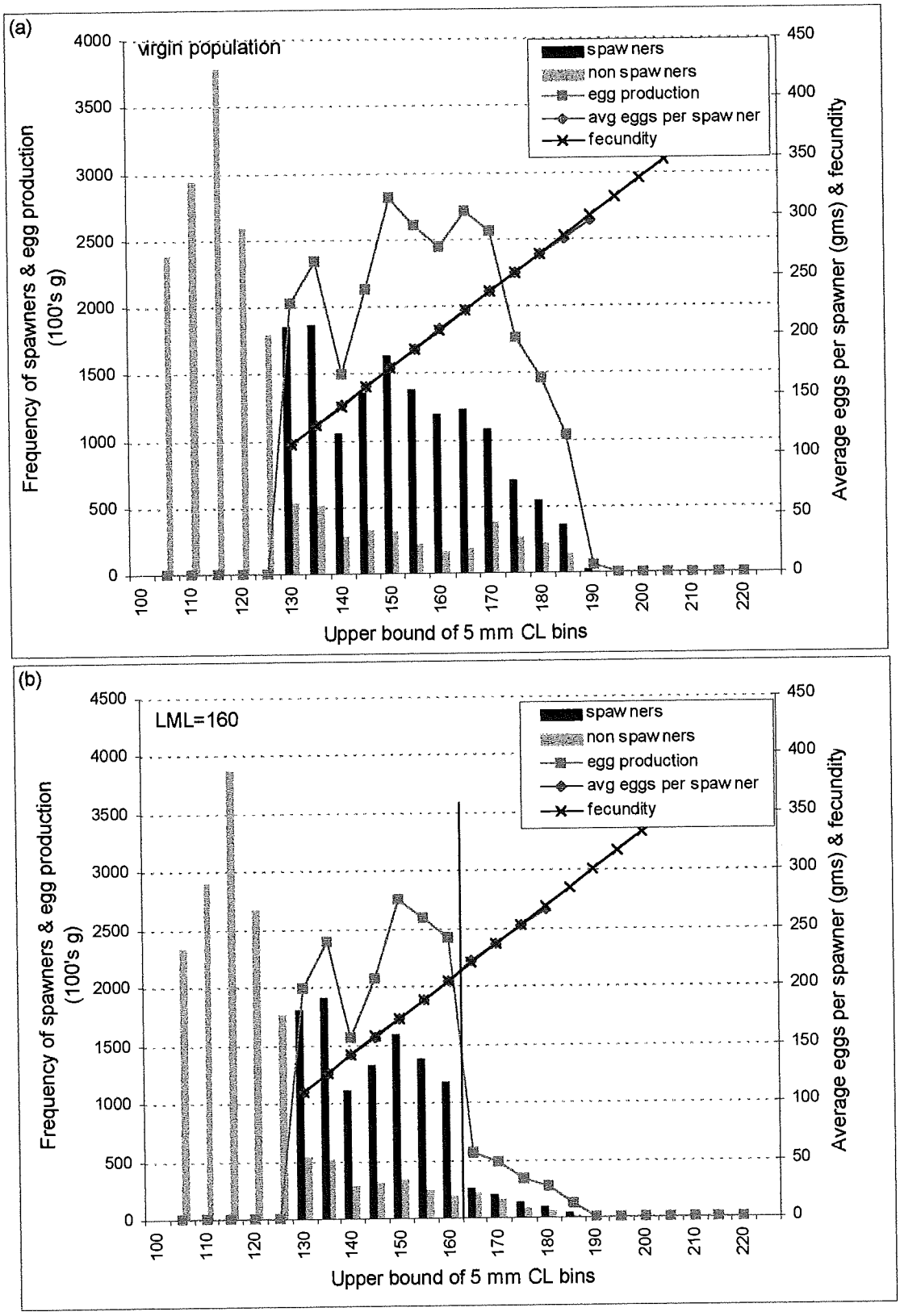


Figure 160. Population egg production, as product of spawners times fecundity, and percent egg-bearing, by length class: (a) no fishing, (b) LML = 160 mm, (c) LML = 150 mm, (d) LML = 140 mm. Yearly capture probability for all runs was F = 0.6.

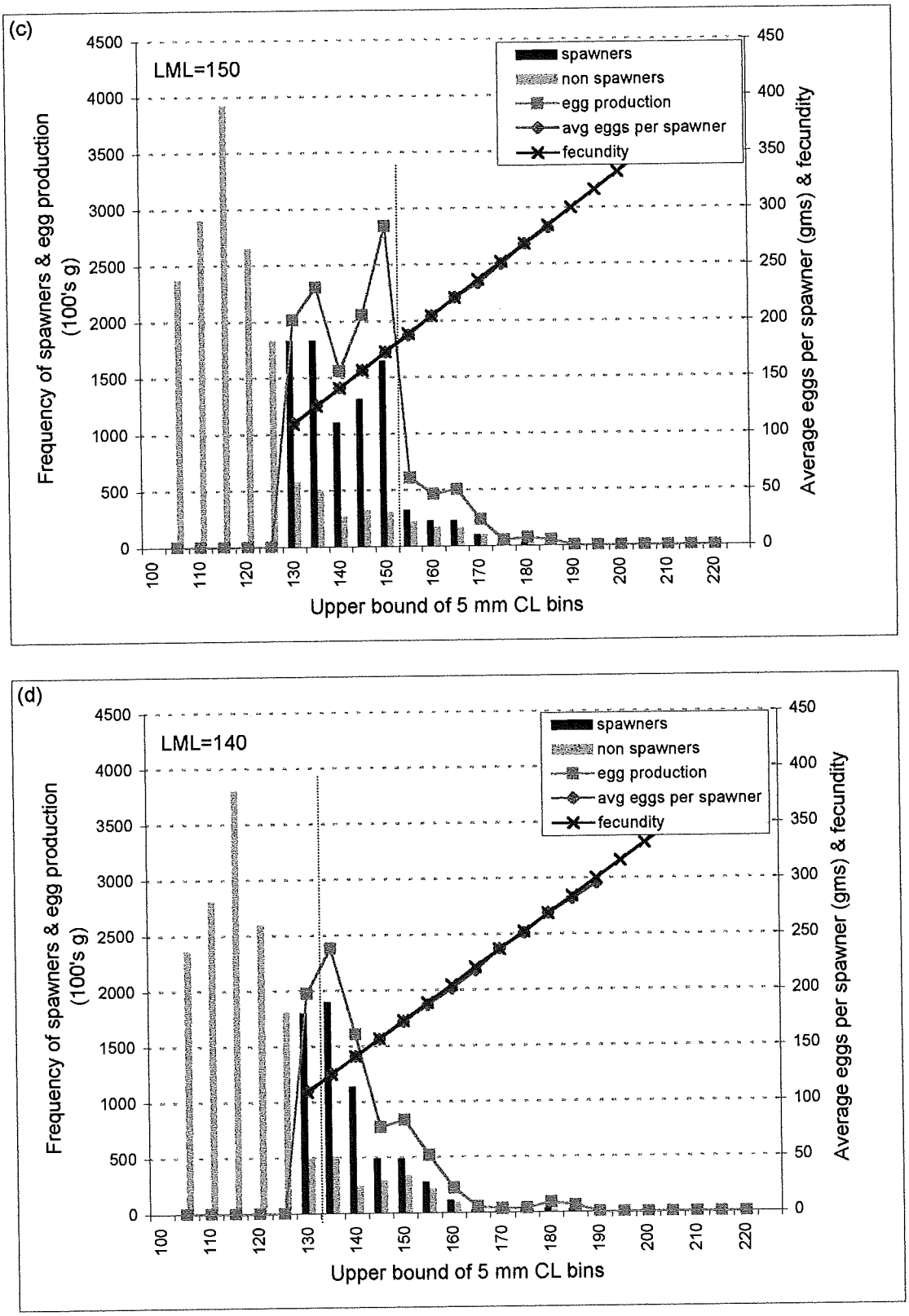


Figure 160. (c) & (d).

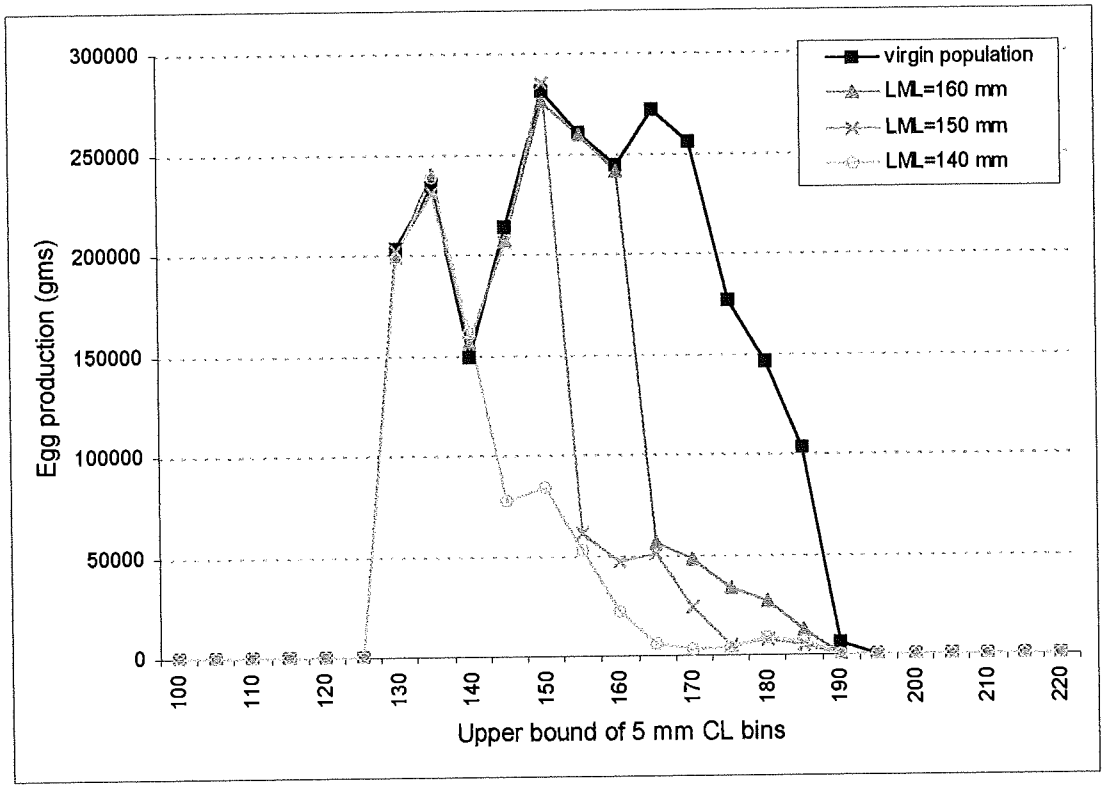


Figure 161. Population egg production by length class, for 4 choices of LML (from Figure 159).

6.3.3. Sensitivity Analysis

In order to assess how robust these results are to variation in the underlying assumptions of the individual-based model, a range of values were tested and the model rerun with each (Table 175).

Table 175. Sensitivity analysis of parameters used in giant crab individual-based model. The baseline run used South Australian data, with F = 0.6 and LML = 150 mm. Egg-, yield- and value-per-recruit were calculated as an average taken over 5 model runs and over years 25-29 in each run. Values in brackets show percentage change relative to the baseline run.

Parameter description	Baseline value	Changed Value	YPR (kg)	VPR ($)	EPR (% virgin)
Baseline run:		--	1.00	29.97	0.51
Length of full maturity	125 mm	130 mm	--	--	0.47 (-8.09 %)
Natural, senescence, and moulting mortality rate (Mn, Ms, Mm)	(0.05, 0.05, 0.2)	(0.075, 0.1, 0.3)	0.57 (-43.36 %)	16.96 (-43.43 %)	0.66 (29.74 %)
		(0.025, 0.0, 0.1)	1.76 (76.31 %)	52.79 (76.11 %)	0.34 (-32.95 %)
Terminal moult length (male, female)	(189, 166) mm	(208, 183) mm (+10 %)	1.01 (0.74 %)	30.08 (0.35 %)	0.43 (-16.00 %)
		(170, 149) mm (-10 %)	0.95 (-4.70 %)	28.67 (-4.34 %)	0.64 (25.99 %)
Fecundity versus length	(Levings et al. 1996)	(Gardner 1997)	--	--	0.55 (8.11 %)
Egg production after crossing terminal moult	Fecundity above terminal moult halved (10 yrs) and stopped (15 yrs)	No slowing of egg production after crossing terminal moult	--	--	0.46 (-9.00 %)

The estimates for percent of virgin egg production vary from 34 to 66%. Yield per recruit shows similar levels of variation. Natural morality is the parameter to which per-recruit indicators are most sensitive.

6.4. Discussion

Percent virgin egg production levels of 34-66% estimated for Australian giant crabs under the LML of 150 mm suggests a female spawning stock well protected by this size limit, in particular with comparison to other crustacean species in Australian temperate waters. The simulations indicate that in the longer term relatively few females are likely to survive to moult again after reaching legal size, with intermoult periods of order 8+ years. The bulk of population egg production is therefore expected to come from those not yet moulted above LML. Long intermoult period of females at size below LML, estimated to be 7-8 years, in combination with a LML set roughly two female moult increments above maturity results in female egg production well protected by the current LML.

One question not addressed by studies to date is that of release mortality. If removing from depth and subsequent return to the bottom results in significant rates of mortality, then commercial fishing operations could reduce spawning stock for sublegal females. This potential effect is not explicit in the individual-based model.

A second aspect of giant crab reproductive biology not considered in this individual-based per-recruit model analysis is the contribution of males to successful fertilisation. Sperm limitation due to overfishing of males is increasingly identified as a potential or demonstrated constraint on crab population reproduction. Gardner and Williams (in press) investigated reproductive fertilisation physiology of Tasmanian giant crabs, classifying males into three instars based on morphology, specifically comparing ratios of the length of the large male chela propodis (right claw) to overall body length. They showed that while some sperm are produced by males with "juvenile" claw morphology ('juveniles'), the weight of the vas deferens (male gonad) as a proportion of body weight is lower for smaller juveniles, though this effect is not observed for larger juveniles. They also found that spermathecae increase with female size, implying that larger females normally mate several times during their life and may thus require larger males for full brood fertilisation.

Thus while no direct measure of male functional maturity versus carapace length is available, there is indirect evidence that it may be a potential problem in Australian giant crabs. If, as suggested by Gardner and Williams, morphological juveniles are not functionally mature, then the current LML of 150 mm CL will protect very few actively mating males, and the fertilisation of female eggs may be limited.

In the future, it may be possible to monitor sperm limitation in Tasmanian giant crab populations as spermathecae samples were taken in the early years of the fishery by the Tasmanian DPI & F. These samples can be compared against future samples to assess if there have been changes in the incidence of mating or ejaculate weight. Such a program would be of relatively low cost. Similar programs of spermethecae monitoring could be undertaken in all four states where giant crabs are subject to high rates of exploitation.

6.5. References

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Appendix 6.1: Inferring selectivity of egg bearing females from proportion observed in catch below LML

The goal in this appendix is to derive an approximate relationship between the percent mature and the selectivity of egg bearing females at time of egg bearing and hatching in spring.

The following assumptions repeat life history observations or estimates reported above:

1. Moulting of females occurs at the time of moulting in early winter (June).
2. Hatching occurs in spring (October-November).
3. In years when females moult, they do not spawn.
4. In all non-moulting years, 'mature' females spawn (extrude and hatch fertilised eggs).
5. The intermoult period of females below LML (150 mm CL) will be approximated as a constant, T = 8 years.
6. Percent mature, p_{mat}, is assumed constant above the size of maturity. This proportion is taken to represent the fraction of females that do bear eggs in non-moulting winters. If other factors such as unsuccessful mating or fertilisation, insufficient food, or other factors prevent normal egg production, this additional reduced percentage successfully spawning and hatching eggs is subsumed in the parameter p_{mat}.
7. Relative capture selectivity of egg-bearing versus non-egg-bearing females in the spring catch, s_E, is also assumed constant. For example, if egg-bearing females are half as likely as non-egg-bearing females to be captured in a commercial trap at that time, $s_E = 0.5$.

The basic data input to be employed in inference about p_{mat} and s_E will be the fraction of egg-bearing females in the spring catch, specifically females below LML. This is recorded in on-board catch monitoring undertaken in the commercial fishery (Figures 140 a-g, from data of Mitchell and Levings 1999).

In estimating s_E versus p_{mat}, we limit consideration to sublegal females. The observed ratio of egg- over non-egg bearing is abruptly lower above LML in some catch monitoring samples, notably South Australia (Figures 140.a-d, 155 length bin). This may be due to a combination of high fishing mortality and absence of legal protection from harvest in the first spring season after moulting past LML when, being non-ovigerous, they are not being legally returned to the sea. Crabs must survive a full year after moulting above this length in order to spawn. In areas of high fishing intensity, many of these females will be captured in the first year, giving rise to the observed situation of relatively fewer reaching the second year when they recommence spawning. As time goes by, a greater and greater share of the population is comprised of newly legal-sized individuals. The observed ratio of egg- to non-egg-bearing in the catch is thus confounded by factors other than s_E, namely percent ovigerous in the legal-sized population, making its use in estimating s_E problematic.

For sublegal females, with considerable variance but little trend of variation between the two states, South Australia and Western Australia, over years and among sublegal sizes down to 125-130, percent ovigerous varied between 40% and 75% in the spring

catch samples (Figures 140 a-g). Defining "egg-bearing ratio" in the catch, $\hat{R}_E^C$, (egg-bearing:non-egg-bearing), we summarise the observed ratio as 50:50, $\hat{R}_E^C = 1$.

Define N^P_E and N^P_{NE}, and N^C_E and N^C_{NE}, as numbers of egg-bearing and non-egg-bearing females in the fishable population and in the catch. Assuming a given exploitation rate, U, the standard Schaefer (1954) catch relationship yields $N^C_E = N^P_E \, U \, s_E$ and $N^C_{NE} = N^P_{NE} \, U$. Thus

$$R_E^C = \frac{N_E^C}{N_{NE}^C} = s_E \frac{N_E^P}{N_{NE}^P} . \qquad \text{(A1.1)}$$

Proportion egg bearing in the population is determined both by the proportion mature and the proportion bearing eggs in any given spawning season. If females bear eggs in all years of non-moulting, and the moult period, T, is 8 years as assumed, if all females are mature, then, on average, 7/8 of the population will bear eggs in any given spring. More generally, the number of females spawning will be the proportion mature, times the frequency of spawning of those mature, i.e.

$$N_E^P = p_{mat} \cdot \frac{T-1}{T} \cdot (N_E^P + N_{NE}^P). \qquad \text{(A1.2)}$$

Combining (1)-(2) we obtain a formula summarising the assumptions above:

$$s_E = R_E^C \left[\frac{T}{p_{mat} \cdot (T-1)} - 1 \right]. \qquad \text{(A1.3)}$$

Two special cases are of interest:

(1) If all females are mature, i.e. $p_{mat} = 1$, and if we assume a 50:50 egg bearing ratio in the catch, then taking our assumed values of T = 8, we have $s_E = 1/7$. This is the intuitive outcome we anticipate if all are mature: With females bearing eggs 7 of every 8 years, there should be 7 times as many egg-bearing females in the population. With equal numbers of egg-bearing and non-egg-bearing females captured in crab pots, the selectivity of the pots must be 1/7.

(2) If, on the other hand, egg-bearing females are not less likely to be captured in crab fishing traps ($s_E = 1$), and we continue to set $R_E^C = 1.0$, then (A1.3) implies $p_{mat} = 8/14$.

We will assume in this population analysis that $p_{mat} = 1$, based on two observations.
1. If maturity were rising through these sizes of interest above 125-130 CL, so presumably would the proportion bearing eggs. Examining the catch samples (Figures 140 a-g), percent ovigerous exhibits no increasing trend. Thus percent mature does not vary with size.
2. The p_{mat} value will be less than 1 if for any reason a portion of females in non-moulting years do not bear eggs. One important source of evidence to test this possibility comes from the CAT scan examinations of female reproductive activity

carried out in autumn by Gardner (unpublished data, Taroona Marine Research Laboratories, PO Box 192B, Hobart, Tas. 7001) on commercial catch samples of Tasmanian giant crabs. Averaging over females above 130 mm CL, the proportion reproductively active was 88.5%. Gardner's observations also confirmed small variation in percent reproductively active with respect to crab size in a total sample of 340 females. This proportion reproductively active (88.5%) closely approximates the expected ratio of 7/8 = 0.875 predicted with the assumed $p_{mat} = 1$ and an intermoult period of T = 8.

A value of $s_E = 1/7$ was therefore set in the individual-based model.

6.6. "Crab sim", the user friendly interface of the individual based model

The giant crab individual-based model (CrabSim), developed by SARDI was designed to estimate percent virgin egg production, yield-per-recruit, and value-per-recruit with respect to current legal minimum length (LML) regulations and different levels of fishing mortality. It builds on the model described in Chapter 6.1-5. with improvements made to many of the features represented in the earlier version. Most obvious is that the model is now presented in a graphical user interface developed using the Delphi programming language, making it easy to change parameter values and view the results. The other principal change is that the history of the fishery and the regulations imposed can be varied yearly. This chapter gives a description of the model, in particular the additions made from the previous version, and how it can be used to compare various LML- and F-controlled outcomes.

Due to the detailed and variable nature of giant crab life history, a stochastic, individual-based model was developed to estimate yield and value-per-recruit and percent virgin egg production. Tag-recapture data generated by the Deakin University /FRDC program *"Fisheries Biology of the Giant Crab"* (Levings *et al* 2001) was used to estimate all of the growth parameters (Chapter 4.8) used in the model which have been included as default values in the parameter screens for SA, Victoria and WA.

The data for any management strategy, both the regulations chosen, and all associated parameters, together with all outputs are collectively described as a 'project'. Any user modifications of these parameters, as well as any set of outputs for a given tested strategy can be saved for later use by saving under a new project name. Three projects included with the model files contain default parameter estimates for South Australia, Victoria and Western Australia. These were the states for which sufficient tag recapture data were collected to enable parameters to be estimated. The parameter screens and the screens used to impose regulatory regimes to be tested are accessed through the menus at the top. The user can change any of the parameter values displayed on the screens described below.

Parameters menu

Natural mortality

In addition to natural mortality, occurring every year to all crabs in the month of moulting with probability Mn, moulting mortality and senescence mortality are also implemented for some crabs. For older crabs that have had their terminal moult, the probability of death by natural causes is increased by Ms, i.e. Mn+Ms. There is a relatively large additional probability (Mm) for crabs that are moulting in any particular year of dying due to predation or infection. This is also added to natural mortality and implemented at the time of moulting.

Length weight

A length-weight relationship was derived from catch samples pooled across states. This analysis is described in Chapter 6.1, and the results from this analysis have been used as the default values in the model. The length-weight relationship in CrabSim has been extended such that it can be varied monthly throughout the year if desired. Model years run from June to May. A plot showing male and female length-weight relationships, by month is displayed on the parameter input screen.

Growth

Giant crab growth, in particular moult increment, has been improved in this version of the model. Previously moult increments were sampled as the midpoints of 5 mm-bin histograms of tag-recapture moult increment data. In the current version, continuous

distributions of moult increment were fitted to observed moult increments by maximum likelihood.

Likelihood fits using three distributions: normal, lognormal and gamma showed moult increment data was best represented by the normal distribution in all cases except WA females where a lognormal distribution was more appropriate (Chapter 4.8).

In the growth parameter input screen, users have the choice of a normal or lognormal distribution for males and females from which the moult increment at times of moulting is sampled. Parameters describing the length-dependent (linearly declining or flat) mean of the chosen distribution, and the coefficient of variation of moult increments are displayed.

The intermoult period estimator developed for the previous version of the model remains in this version, with parameters describing it displayed in the input screen. A detailed description of this estimator is provided in Chapter 4.8.

Seasonal time of moulting has been hardwired into the model: June for females and December for males. This was based on analyses of proportion clean shelled crabs in the catch for males and females (Chapter 4.8).

Terminal moult length, beyond which crabs cease moulting, is also the length where female egg production begins to decline according to a schedule described by parameters on the "Maturity and egg production" input screen.

Maturity and egg production

In the previous version of the model, maturity was controlled by a single length, beyond which all crabs were deemed mature. Maturity is now represented by a logistic, length-dependent probability. Two parameters are required as inputs for this logistic curve, expressed as the lengths at which the probability of a crab being mature is 0.5 and 0.95. Fecundity is now expressed as a generalised allometric function: number of eggs produced = a*length^b + c, where the parameters a, b and c can be changed.

The assumption that females always produce eggs in non-moulting years has now been replaced with a probability of egg production in non-moulting years. In any given year, each non-moulting female spawns and hatches eggs with this probability.

Parameters determining the month of hatching for females are a new addition to the model. Although hatching is displayed on the egg production input screen, its only purpose in the model is to determine the months in which these females remain as egg-bearing, and therefore which class they are categorised into for the purposes of fishing selectivity.

The decline in egg production after a crab moults past the terminal moult length is modelled as a yearly reduction, with three parameters: the number of years after the final moult when the decline begins, the initial proportional reduction in egg production in the first year, and the yearly linear rate of decline in subsequent years which continues until egg production ceases.

Fishing selectivities
Fishing selectivity has been considerably extended from the previous version. Selectivities now come in two forms: those calculated as a function of length and those as a function of fishing month. The three categories of crabs: males, egg-bearing females and non egg-bearing females each have independent selectivity relationships.

Length selectivities:
The length-dependent selectivity function is comprised of a logistic curve left-hand limb for small (primarily undersize) crabs, and a linearly declining right-hand limb for larger crabs. The left-hand logistic curve has inputs as described for the maturity curve, while the right-hand decline of larger crabs (due, in the fishery, to lower price) has the same three inputs as described for declining egg production.

Month selectivities
In this input screen the fishing months are specified and corresponding relative selectivity rates entered as individual coefficients by month for the three classes of crabs.

Economic
The economic parameter screen contains the prices per kg used in the value-per-recruit calculations. Two user-input cut-off weights determine the three classes of crabs (<wt 1, wt1-wt2, >wt2). Within each class of crab, prices also vary by month, reflecting the seasonal variation.

Strategy menu
This model is designed to test the effects of changes in legal minimum length (LML). In the previous version, a single constant LML value was used in all years leading up to the year where it was then increased or decreased, and the new LML remained for all subsequent years. A chosen yearly fishing mortality (F) remained constant throughout the run.

However, the exploitation of Australian giant crab only commenced in the early 1990's at different times and with different rates of development in the different states. The LML of 150 was imposed in 1994. To represent this history of length regulation and changing levels of exploitation in this version, F and LML values can be set to vary yearly. Moreover, yearly LML- and F-"scenarios" provide the opportunity to test more dynamic management regimes than a simple increase or decrease.

The scenarios are structured such that a single F and LML value is specified for the first 70 equilibrium years. Then for the 10 years leading up to and the 10 years following the point of "management change", separate yearly LML and F values can be chosen. The last 20 years again use a single value.

Closing chosen specific years to fishing can be done by setting F values to 0. Length regulation can be removed by setting LML to 0.
Simulate
The model is stochastic. The variances in these quantities have been estimated from data and incorporated in the dynamic simulations as noted above. Each run provides a different outcome depending on variation in growth and natural and fishing mortality.

To generate a picture of the range of likely outcomes to chosen management strategies, the Simulate menu gives the user a choice of how many runs to repeat the stochastic simulation, up to a maximum of ten. The model is automatically run without fishing before the scenario-testing runs so that virgin egg production can be calculated based on the saved parameter values.

Results display

The results screen displays the short- and long-term effect of the F- and LML-scenarios on yield-per-recriut, value-per-recruit and percent virgin egg production. Plots are displayed separately for each F-scenario, controlled at the top of the screen.

The time dependent effects are displayed yearly for the ten years leading up to the management change and fifteen years following the change, then averaged in 5 year blocks for the remaining 15 yrs. The F-scenario currently displayed is shown at the top of the screen together with the average F value (taken over the ten years following the management change).

The long term (i.e. equilibrium) results of different choices of LML and F are shown in a scatterplot of the average LML value (taken over the ten years following the management change) versus the final five-year-averaged per-recruit value from the time-dependent plot. Scatterplots for all LML- and F-scenarios are displayed on the equilibrium output graph.

7. SUMMARY

7.1. Biology

Broadscale and enduring trends in the southern Australian oceanic environment have for 35 million years supported the evolution of *P. gigas* to present day. The crabs are "poikilotherms" which lack internal temperature control mechanisms, but live where the hydrology and steep terrain of the continental margin offers easy access to a cooler or a warmer environment. Their growth and reproduction are inherently linked with the food resources and physical character of where they live. Downslope movement into cooler water is advantageous for energy conservation through a slowing down of metabolism during moulting or extrusion and brooding of eggs, when they cannot feed. Upslope movement provides access to more abundant benthic food resources at other times.

Allozyme and then DNA techniques indicated a genetically homogeneous *P. gigas* stock structure. Another commercially exploited crab *H. acerba*, which occupies similar substrates but favours warm temperate waters is genetically the closest to *P. gigas* of all the species examined. *H. armata* an almost identical species to *H. acerba* occurs in Japanese waters and may be a clue that indicates a common Tethyan or West Indo-Pacific ancestor. Perhaps, in the Southern Hemisphere *P. gigas* evolved divergently from *H. acerba*, adapting to the cooler conditions caused by the opening of the Drake passage and the beginning of the Antarctic circumpolar current.

P. gigas occur in a temperature range of 11-17°C, are well adapted for travel compared to many other crab species, and forage by following the scent of prey carried to it by water movement. Its cardiac and respiratory organs are of sufficient size to provide a large aerobic capacity and legs are protected from wear by broad hard surfaces at the tips.

At any given time fishers report the crabs are at a particular depth across many miles of ground. As temperature bands do occur at similar depths over large areas and as the crabs are poikilotherms, a plausible explanation for the fishers'observations is to propose that the crabs occupy a thermal niche. As the niche boundaries move, the crabs move within the niche, shallower or deeper. Excepting carrion, food boundaries are static and a function of substrate composition, but temperature is not and varies in a seasonal cycle to which the crabs growth and reproduction is synchronized.

Females are captured in greatest abundance on the narrow zone of bryozoan rich substrates which begin at a depth of approximately 120 meters. This type of substrate lies beyond the scouring effects of wave action and becomes progressively muddier until at about 300 metres it grades into all mud. It extends along the entire southern margin of Australia. Circumstantial evidence suggests the females move onto the mud when they moult.

Males are captured across a broader depth range than females. Most of the crabs taken as a by-catch of the lobster fishery, from the wave scoured rocky reefs in waters shallower than 120 metres, are of this sex. In the autumn when the oceanic hydrology changes from summer upwelling to winter downwelling, the water becomes warmer and the males move outward, over the shelf into deeper, cooler water. Thus their movement is synchronised with seasonality in a biorhythm that facilitates mate

selection in the Autumn and copulation in the Winter when the females have moulted and are in a soft shelled state.

Despite the crabs' largeness and hard shell acting as a deterrent to predators and so eliminating the need for a physical shelter, the boundaries to their occurance are defined by the abundance of food and a temperature suited to their physiology. During moulting the crabs are soft and vulnerable, but their movement to deeper cooler waters to do this, reduces their availability to predators. As their environment becomes less than optimum towards the limits of their range, there is a decrease in moult increment and the maximum size attained.

A major output was the development of a cheap and effective tag that was applied in large numbers by fishers. At the end of the study nearly 18,000 crabs had been tagged and 1,700 recaptured. Their movement was along-shelf into the current; to the north off both sides of Tasmania, tending northwesterly off western Victoria and then westerly off South Australia. Off Bremer bay in West Australia the movement was along shelf to the southwest. Off Augusta where the shelf break begins its northerly orientation adjacent Cape Leeuwin movement increasingly reversed to be southerly, away from the warm temperate environment further northward where its range ends. Journeys of up to 400 km were recorded off West Australia and Victoria/South Australia.

Movement into the prevailing current means the millions of larvae they produce are carried back in the opposite direction to replenish the fishing grounds. The timing of hatching, the duration of larval lifetime and the onset of summer upwelling events, maximize the effectiveness of this reproductive strategy. For example: the Bonney upwelling illustrated in chapter 4 creates a peak in phyto-plankton production and within the 14°C to 16°C temperature range, concentrations of zoo-plankton including krill. While assisting larval nutrition the upwelling also reverses the direction of the current and broadcasts them further westerly during these episodic events. Settlement subsequently occurs and is demonstrated by the presence of juvenile crabs observed in lobster traps between 45 to 75 fathoms (or ~ 80 to 140 meters) below the location of the well defined thermocline at the outer edge of the upwelling.

This project established the female size at maturity for crab populations off each of the states. In the early stages of the fishery's development, an interim size limit of 150 mm was set in the eastern states in 1994. This was deliberately conservative and aimed for a target of 50% for the conservation of virgin egg production, double the 25% international benchmark. Hence females are well protected by the current size limit, as it is set well above the average size at which maturity occurs. The crabs are highly fecund, store sperm and usually spawn in the years when they do not moult. There is a trend in declining fecundity with increasing size and age in the East Tasmanian population where there is a low abundance of males. In West Australia where the crabs mature at a smaller size and over a lifetime do not grow as large as those of the eastern states, a smaller legal minimum length of 140mm was adopted in 1996. Western Australian fishers voluntarily observed size limits of 135mm off Albany and 150 mm off Augusta prior to this.

While legal minimum length was based on egg production estimates from the female section of the population, the issue of male maturity and an appropriate size at which

to harvest is problematic. Physiological maturity does not automatically mean the male can achieve reproductive success because males must also become dominant over other rivals to secure a mate and function as an adult. During the transition to functional maturity the morphology of the large chela in relation to carapace length starts to exhibit allometric growth. We have described the point at which this occurred and found from an overall population sample of 80,000 crabs, that in the Autumn the increase in male mean size was due to a greater abundance of individuals that were larger than the size where allometric growth began. These larger sizes were also present at the same locality where most newly moulted females were observed, therefore we propose they are the functionally mature section of the population. We also recognize that the onset of functional maturity is likely to be a dynamic relationship that can change. Variability is to be expected due to innate individual differences and varying population dynamics reflected in each crab's development.

The fact that male *P. gigas* grow to more than double the size of females may be attributed to the advantages provided by having a huge chela, because it allows the crushing of larger prey and so provides access to a wider range of prey compared to females. As these larger prey are more abundant to shore-ward this difference provides an explanation why males have a wider distribution than females and in an evolutionary sense how a maximization of growth, attainment of giantism and an optimised chance to survive is manifest in the creature we observe today.

7.2. Preliminary Stock Assessment

Although the moult increment is large, growth is primarily mediated by a reduced frequency of moulting as age increases. Intermoult period estimates for *P. gigas* vary from 3-4 years for juvenile males and females (80-120 mm), with rapid lengthening in time between moulting to approximately 7 years for females and 4.5 years for males at legal minimum length of 150 mm. The female preference to aggregate on the narrow strip of bryozoan substrates means that the relative abundance of egg bearers in the sections of the population above and below minimum legal size can be clearly observed in the data and are an artefact of prior fishing history. The implication of the long intermoult, particularly for females, is that the population structure of the commercial fishery will tend to change, older and larger sizes becoming less abundant, with smaller sized recruits that have moulted from below the legal minimum length taking their place. In areas fished prior to a minimum size being introduced, or subject to illegal removals, full recovery of the population to the size structure that was intended will take about a decade.

Size distribution is stratified by depth ($P =<.0001$) and there are also other highly significant differences in size which can be attributed to season and sex ($P =<.0001$). Target depths can range from 75 - 250 fathoms(140 - 450 metres), but fishing operations are usually modified to ensure that the gear can be retrieved consistently. In areas subject to strong currents the depth at which the gear is set may be shallower than the optimum depth for the largest catch. As there are multiple factors that can significantly affect catches, regular communication with fishers is an important precondition for clear interpretation of trends in fishery statistics.

It has not been possible to confidently predict the crab biomass because of the broader dispersal of males out of the target fishery area and the historical inadequacy of catch and effort systems. In order to remedy this a pro-forma catch and effort form was

designed to capture information at a whole fishery level and to date has been incorporated in all state fishery agency systems except Victoria.

Management of the crab fishery is a state responsibility, however the Commonwealth controls other fisheries which impact on it. The fishery can be detrimentally affected by the Commonwealth demersal trawl and mesh-netting fisheries which are conducted in the same depth range. Demersal trawl destroys the bryozoan substrate which is the framework for the benthic ecology and mobilises bottom sediments previously held in place by these organisms, making recolonisation difficult.

P. gigas is taken as a by-catch by trawl and meshnet methods. Southeast Fishery trawl operators are restricted to a by-catch of 5 crabs per trip, but no limitations have yet been placed on meshnet operators in regard to crab by-catch. This is significant because there is strong anecdotal evidence about damage to crab stocks off eastern Tasmania and southern Western Australia by deep water mesh netting operations. The accounts primarily concern circumstances where strong tides cause the net to come into contact with the bottom and delay retrieval. The eastern Tasmanian account deals with events over a decade ago when blue eye Trevalla were targeted. The vessel and the fishing method in that area were subsequently banned. The western Australian account is current, with crab fishers in Esperance and Albany attributing the cause of damage to crabs to be from deepwater meshnetting for dogshark and scalefish and the loss of nets which have subsequently ghostfished.

These sort of problems have occurred elsewhere in the world. Comments about the Northern Pacific king crab *Paralithodes camtschaticus,* where the early fishery was mostly based on trawl and tangle nets, are illuminating.

> "American king crab fishermen are forbidden to use tangle or trawl nets in the crab fishery, because the nets, the tangle net especially, make it difficult to return females and sub-legal males to the sea without injury". (Browning et. al., 1974).

This project could not have been possible without a large investment of research funds in training and the provision of extension materials to an Australia wide network of fishers. Combined with their material resources, existing lines of command and employment structures, consistent quality data was collected across the species range. The data which consists of many discrete snapshots of fishing events within the targeted fishery was used to develop an individual based yield, egg and value per recruit model. The model has a user friendly interface "crabsim" which allows a user to key in their management choices. The choices are integrated with biological and economic information to provide outcomes. The ability to canvas multiple scenarios helps the formulation of management and improves industry confidence. The model has wider application and is also being applied in Western Australia to the *H. acerba* fishery.

Giant crab is a small "boutique" fishery, but the large demand for the species is evident in the year 2000 price maximum of $57 per kg for smaller commercial sizes. The need for sound management practices is paramount. As the fishery generates only a small volume of a valuable commodity, continuity of supply is essential to keep up demand. It is vital that exporters are involved in formulation of future management plans to ensure the best use is made of the product.

7.2.1. Management recommendations

- That the legal minimum size of 150mm in the eastern states and 140mm in West Australia provides adequate conservation of sexually mature females to maintain high levels of egg production for resource sustainability.

- That the size at sexual maturity for males should be further researched with a view to re-asssessment of the present legal minimum length for this sex. This reassessment should be considered a priority in Western Australia where the ecology combined with the male preference for shallower substates has rendered it comparatively more vulnerable to fishing mortality than females.

- That annual surveys take into consideration that the giant crab population is not fixed to a specific location and should therefore incorporate movement information gained from tagging, into choice of sampling location.

- That a bycatch, even if only 1 or 2 crabs a trip be allowed for rock lobster fishers to assist the return of tag recapture information and provide information about migration from the shelf break to shallower waters to shoreward.

- The consequence of illegal removal of undersized crabs from the Victorian - Tasmanian border region is a decade of damage. The migratory nature of crabs indicates the damage is not limited to this area. Strong measures by the state of Victoria are required to rectify this situation.

- The issues which arise from the impacts of other fisheries may be controversial and may generate conflict between resource access holders and designated management authorities. Nonetheless they should be carefully addressed.
  The issues are;
  a/ Degradation of habitat by demersal trawling.
  b/ The effects of deepwater meshnetting.

- That the tool of 3 dimensional mapping be used to assist in a fuller description of marine ecosystem dynamics and the resolution of multiple use issues.

- Optimisation of the benefits of exploitation of giant crab requires careful integration of;
  a/ The need for continuity of supply to overseas buyers.
  b/ The need to supply premium quality product
  c/ The timing of biological events that affect quality.
  It is therefore essential to include exporters as well as fishers, biologists and managers, in discussions of this nature and work towards an integration of these issues for the best result.

8. EXTENSION OF RESULTS

This project would not have been possible without the strong partnership between industry, researchers and managers. Extension of methods and results occurred by direct contact at sea on crab fishing vessels, extensive media exposure, in correspondence, in the return of tag recapture information or in more formal settings such as the meetings of the Southern Rock Lobster Council of Australia, the Tasmanian Rock Lobster Fishermens Association, West Australian Fisheries Southern Ports tour and the Victorian Lobster and Crab Fisheries Assessment workshop. There now remains the final task of completing the extension by way of presentation of this final report as a series of seminars to crab fishers and managers in each of the states.

9. BENEFITS

The principal beneficiaries are the crab fishing industry, state governments directly responsible for the management of the resource under OCS agreement and the Federal Government who has sustainable development obligations as prescribed in Schedule 4 of the Wildlife Protection Act (Regulation of Imports and Exports), 1982.

The tag developed by this study is of international benefit and is now used on other species off North America and Europe. Little was known when the study began but the strategy of involving fishermen has paid huge dividends by providing data collection at very low cost. We provided the information required for the critical first step of setting a legal minimum size to act as a safety net for the fishery. The better the information on stock, the more confidence fisheries managers can have that their decisions will balance the criteria for conservation and economic efficiency.The population and growth information we gathered and the development of the crab - sim model provides a superior way to canvass outcomes of future management scenarios and so improves business certainty.

Our description of the crabs life history has taken a whole ecosystem approach and much of the information collated on oceanography and the 3 dimensional presentation of the marine environment have a broader application. We have sought to place the species in context with the evolution of its environment and for persons involved in the fishery and the other diverse groups who have a more general interest in the sea have provided a clarity of vision about the little known province where it occurs

10. INTELLECTUAL PROPERTY

Deakin University and the FRDC in their project agreement have agreed to jointly share the title to and the ownership of all intellectual property resulting from or arising in the course of carrying out the project. For more recent project components undertaken by the South Australian Research and Development Institute (SARDI), notably growth data analysis, individual-based modelling, egg-, value- and yield-per-recruit analysis, and the Windows per-recruit model software development, intellectual property is split evenly among FRDC, Deakin University, and SARDI. Excepting data gathered during research fishing under special permit, any fisher's personal catch history that has been voluntarily provided to this project, requires the fisher's written permission for release to other persons or institutions who may wish to use it.

11. FURTHER DEVELOPMENT

There are many analyses that are yet to be done on the huge volume of data that has been acquired. Nearly 18,000 crabs have been tagged and the recapture information that is continuing to be received is leading to an understanding of the growth rates of larger size classes. This needs to be incorporated into the yeild, value and egg per recruit model developed by this project. The ability of the species to walk long distances has meant that spatial analysis techniques have been integral to understanding the fishery's dynamics. This led to integration with information about temperature, bathymetry, substrate composition and the relationship of the crab fishery to other outer shelf and upper slope fisheries. A three dimensional representation of these relationships should be undertaken as it is a valuable analytical and educational tool with great potential to acheive the sustainability, ecosystem protection and industry development objectives of the FRDC.

12. PLANNED OUTCOMES

The growth rate of the crab, the geographic extent of its range and the huge volume of information gathered by the crabcare network created logistical problems. The time frame in which to achieve planned outcomes did not conform to original expectations and the project was subject to a considerable amount of review and prioritisation which led to the dropping of some objectives. The development of a guide to allow selection of premoult crabs from the wild harvest for holding in sea cages through a single moult was not fully progressed. Despite these difficulties all other objectives were completed and the project has successfully laid the foundations upon which more detailed biological and stock assessment work can be built.

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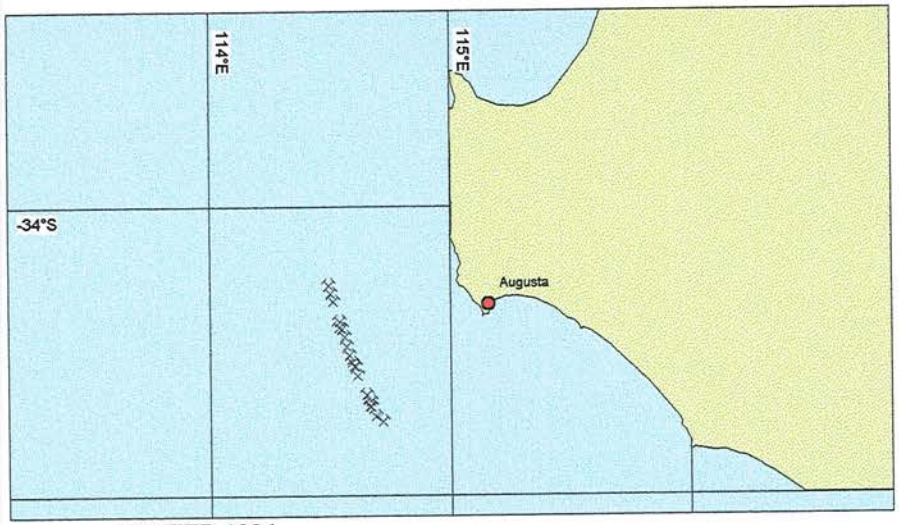
Appendix 1

Population Structure

by

Site, Season and Sex



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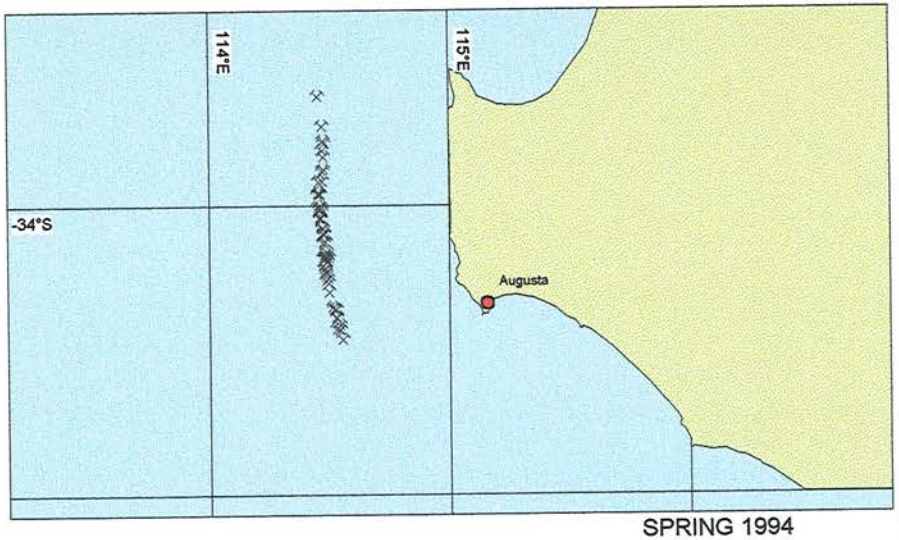
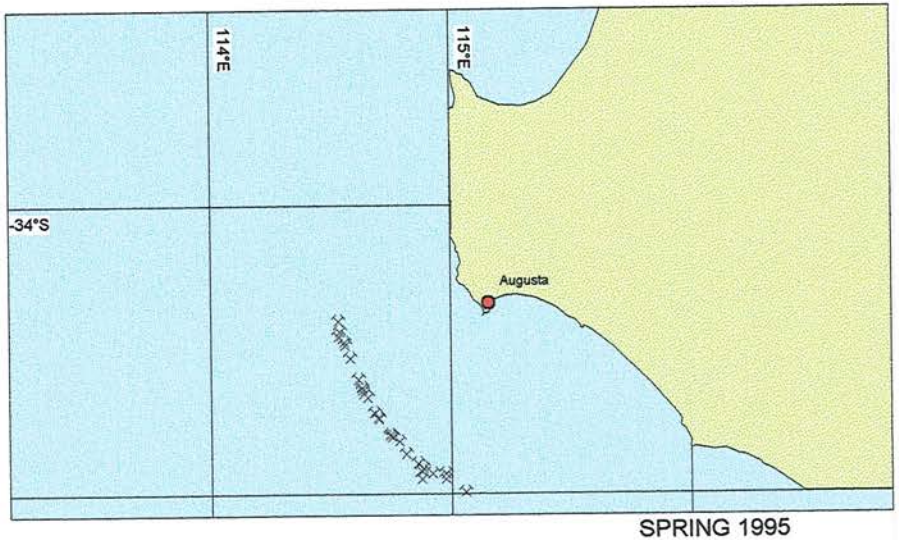


SPRING 1994

SUMMER 1994 - 1995



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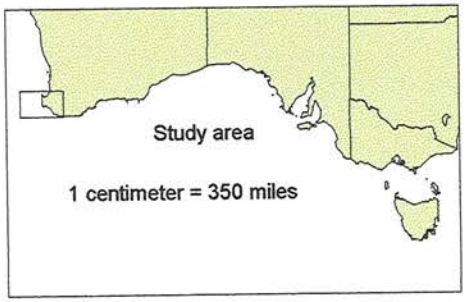
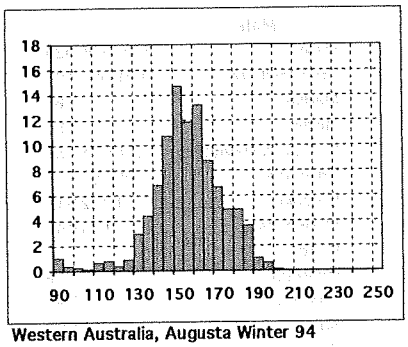


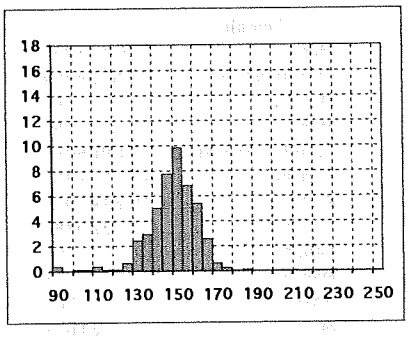
Sampling locations for the Augusta area, Western Australia

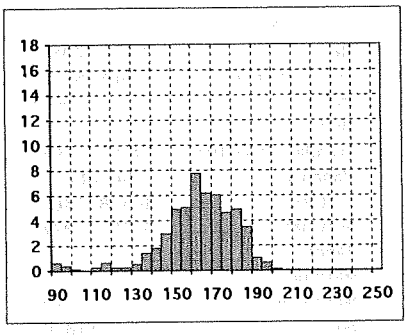
Scale:
1 centimeter = 18 miles

Western Australia, Augusta



Western Australia, Augusta Winter 94





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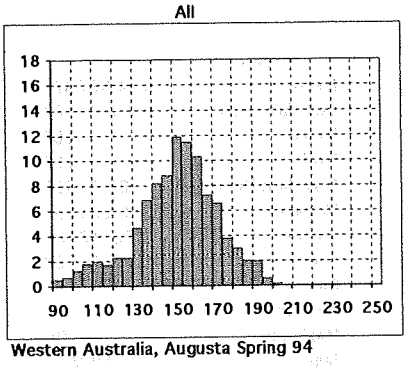

Western Australia, Augusta Spring 94

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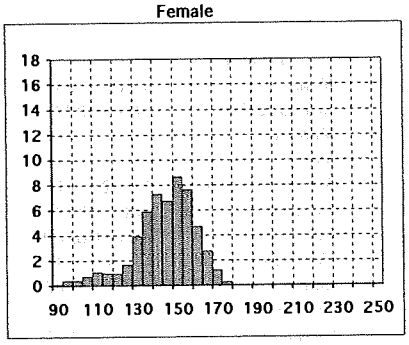

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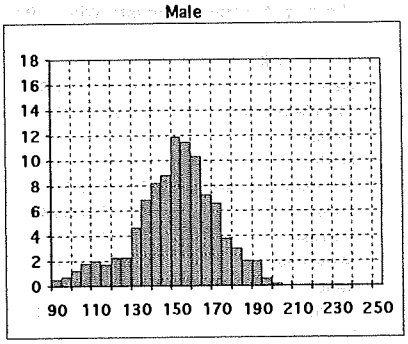

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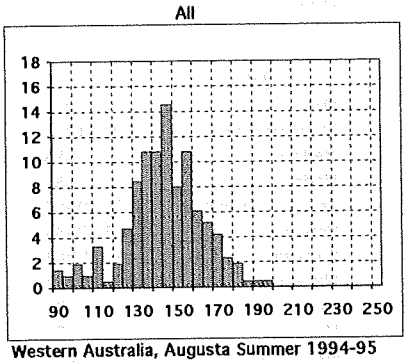
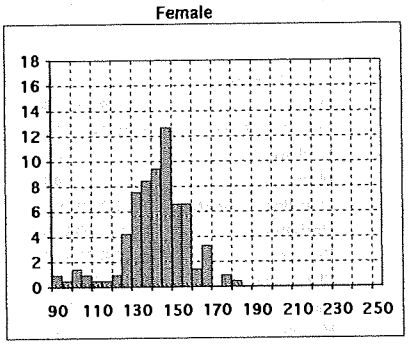


Western Australia, Augusta Summer 1994-95

Female



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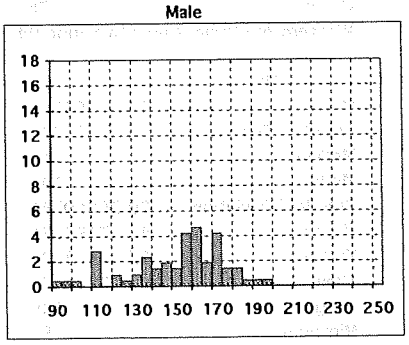

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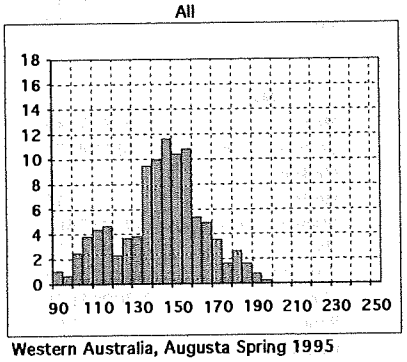
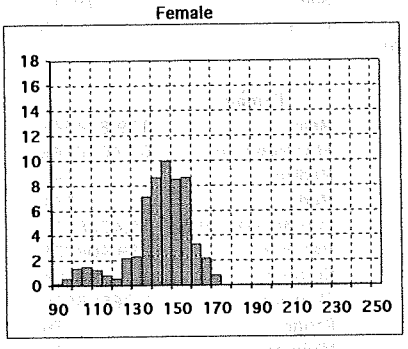


Western Australia, Augusta Spring 1995

Female



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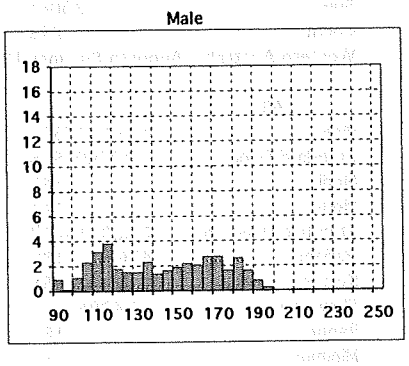
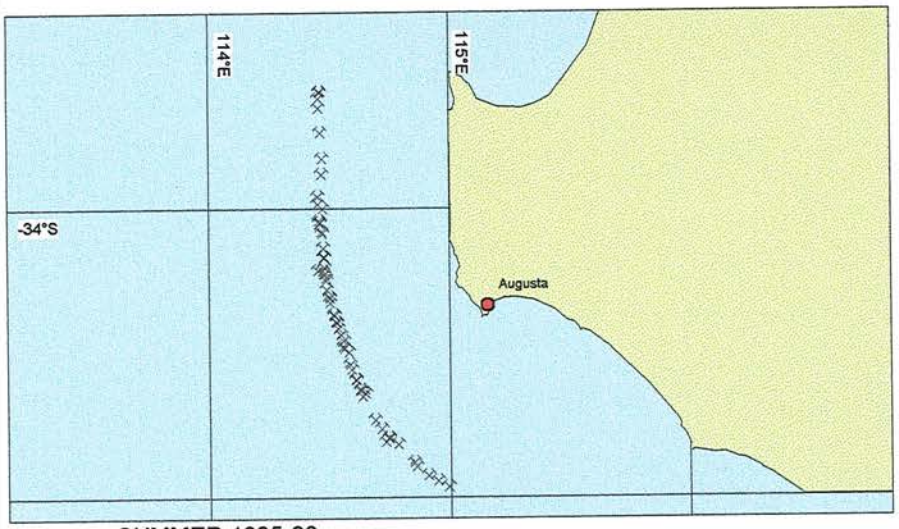
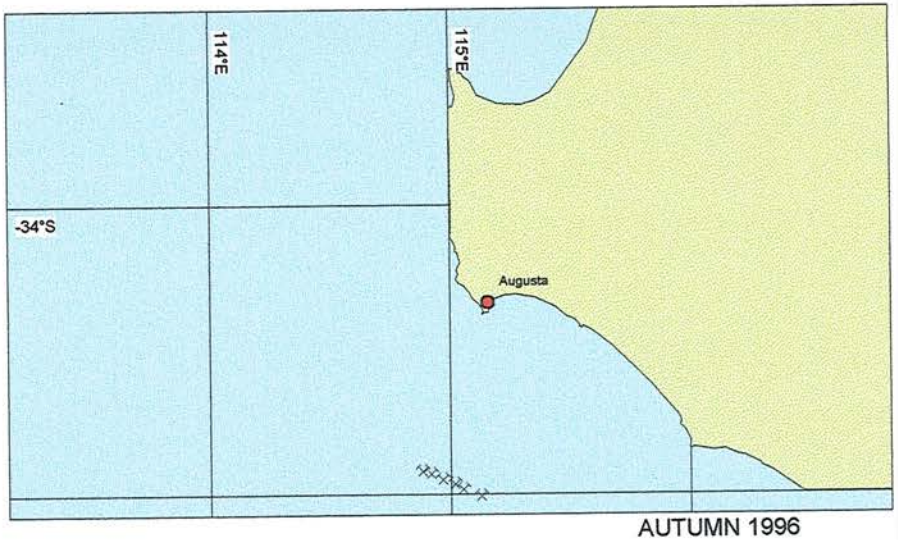


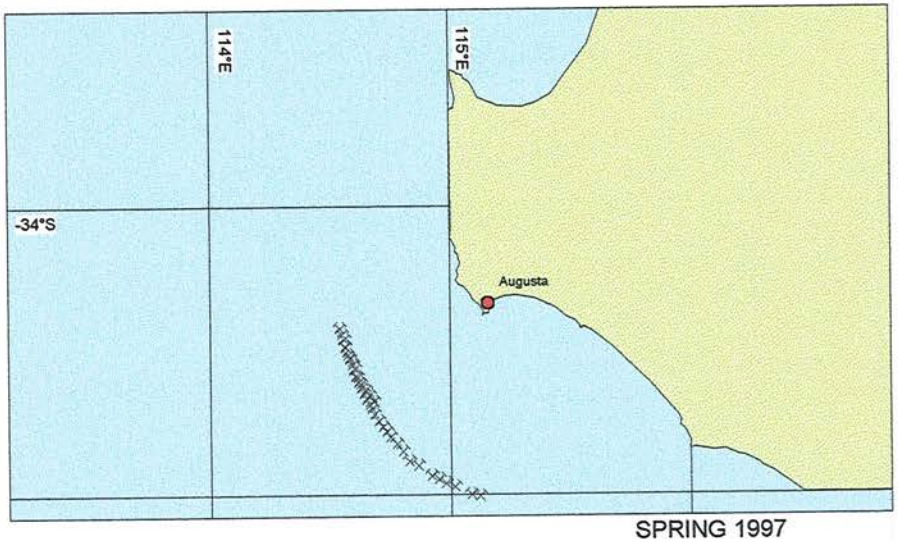


SUMMER 1995-96



AUTUMN 1996

WINTER 1997



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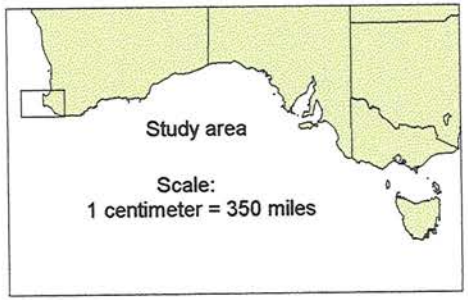
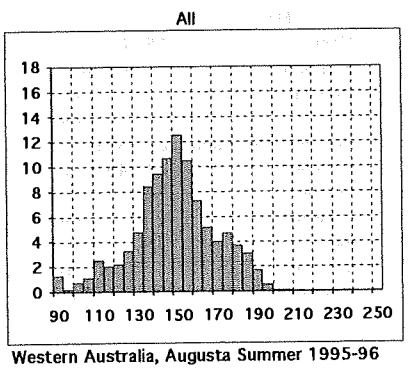


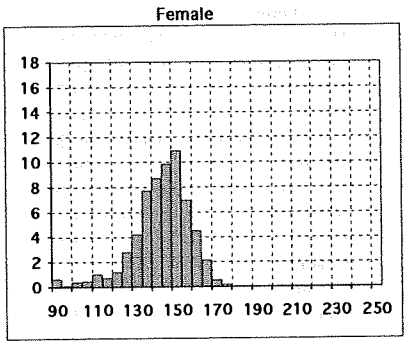
Scale:

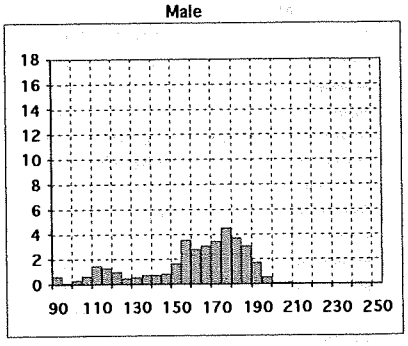
1 centimeter = 18 miles

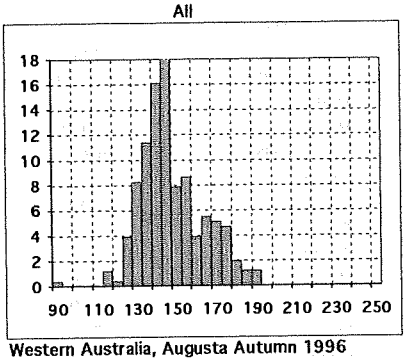
Sampling locations for southern Western Australia



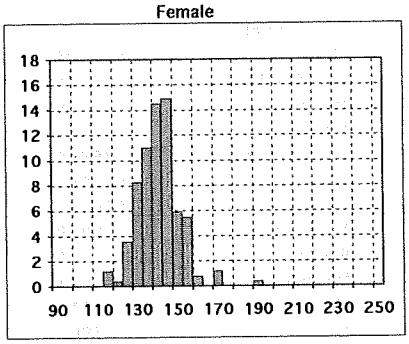
Western Australia, Augusta Summer 1995-96

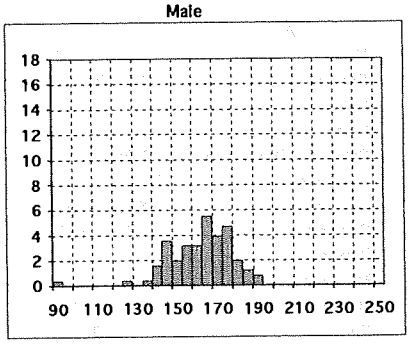


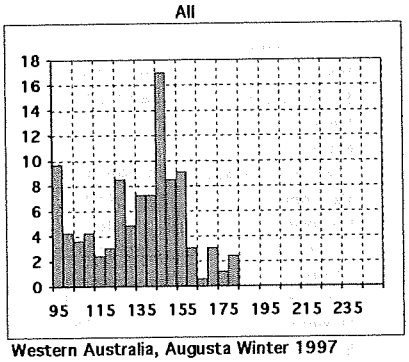




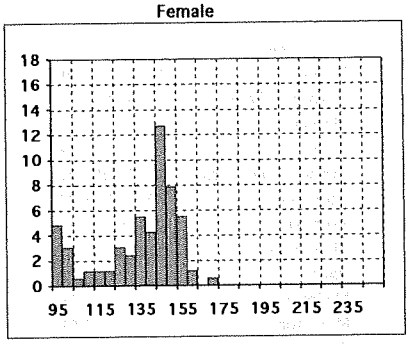
Western Australia, Augusta Autumn 1996

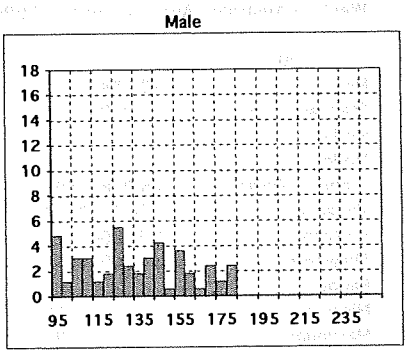


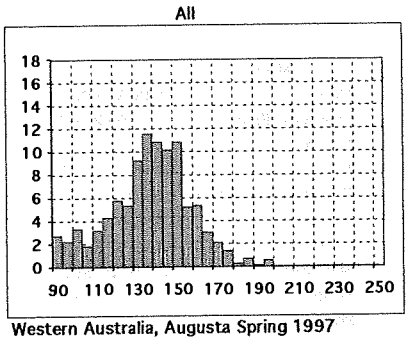




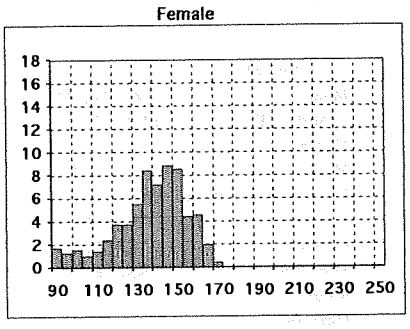
Western Australia, Augusta Winter 1997

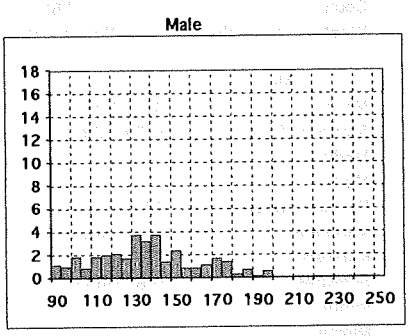


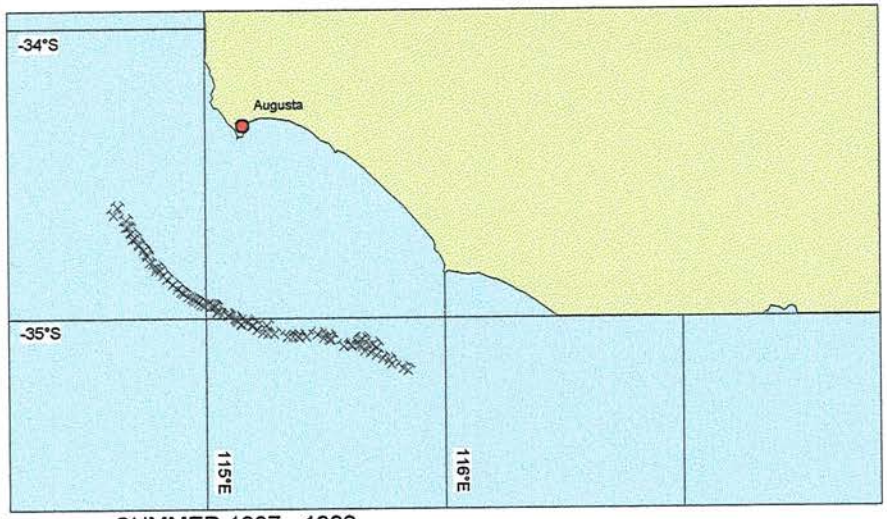




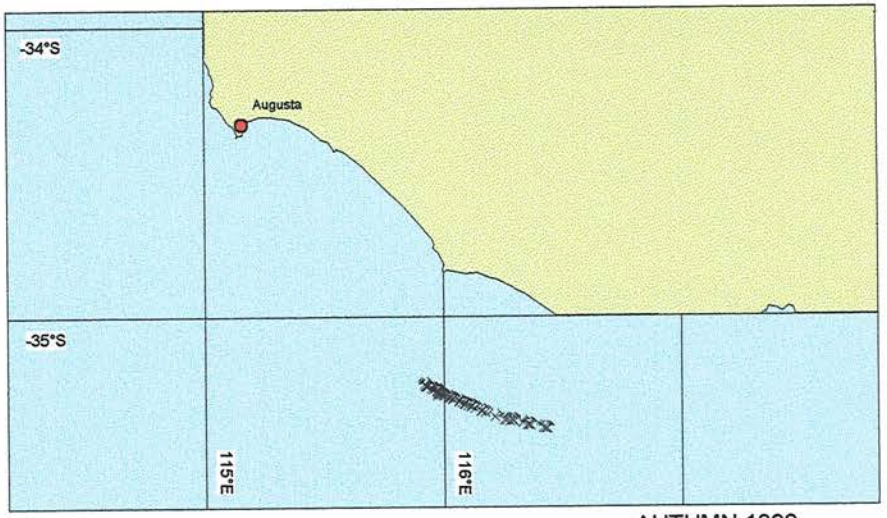
Western Australia, Augusta Spring 1997



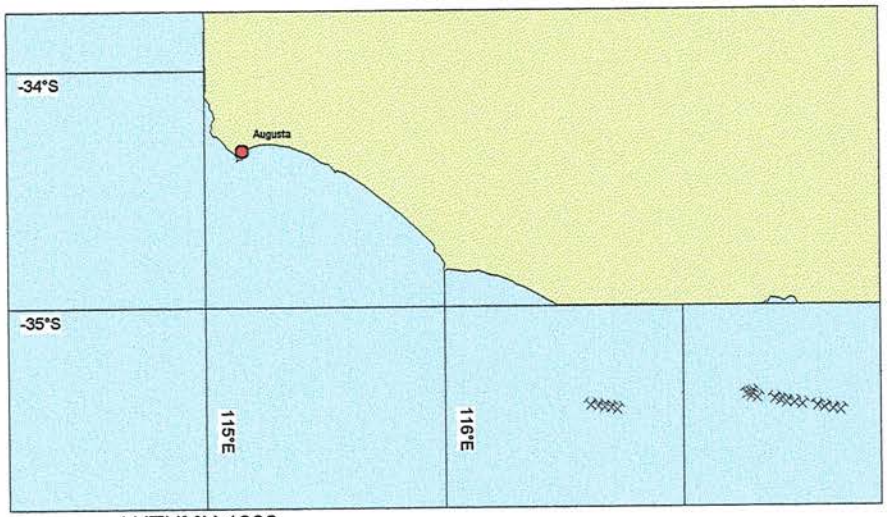




SUMMER 1997 - 1998

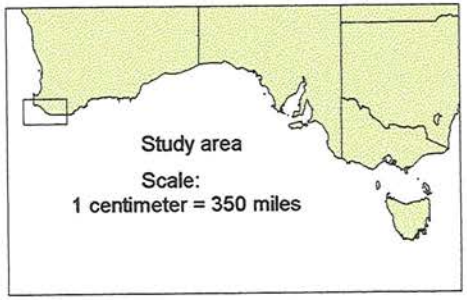


AUTUMN 1998



AUTUMN 1999

SUMMER 1999 - 2000

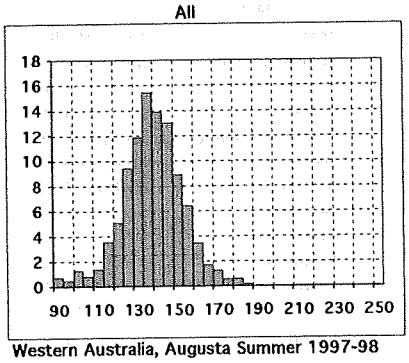


Sampling locations for the Augusta area, Western Australia

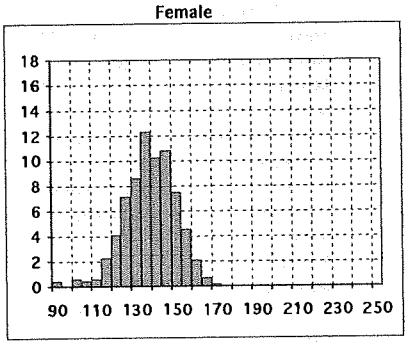
Scale:

1 centimeter = 18 miles

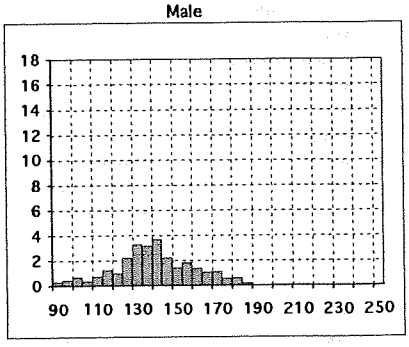
All



Female

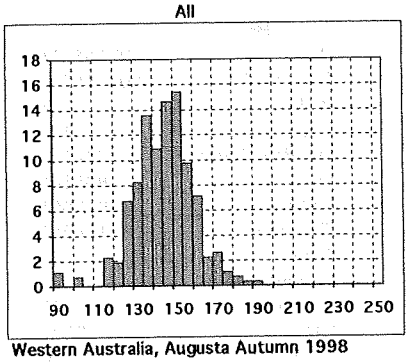


Male



Western Australia, Augusta Summer 1997-98

All



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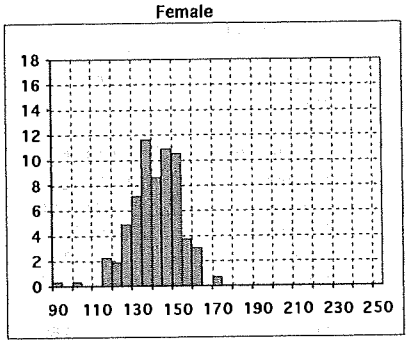
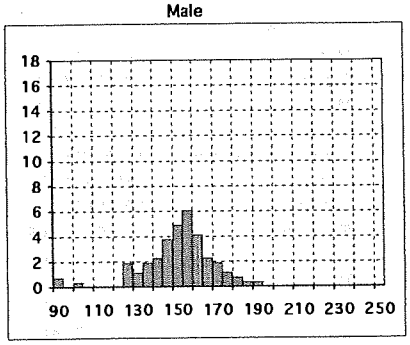
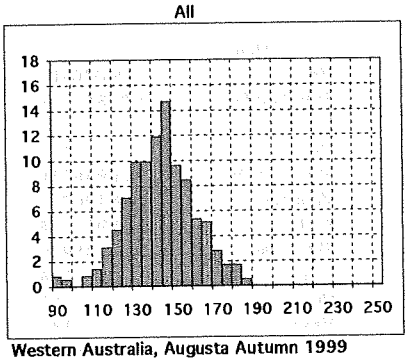


Male



Western Australia, Augusta Autumn 1998

All



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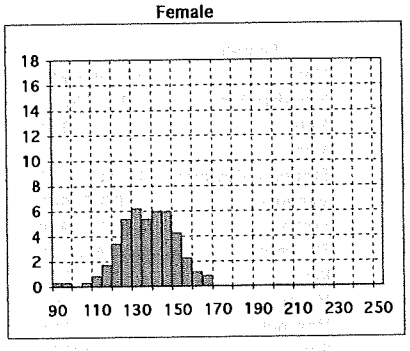
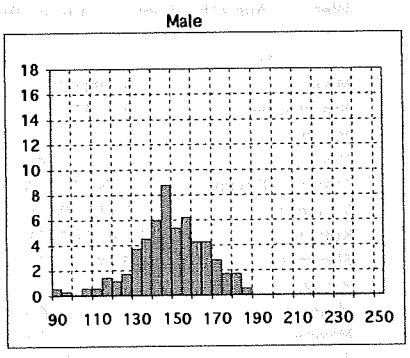
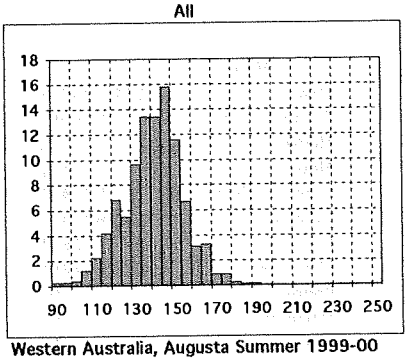


Male

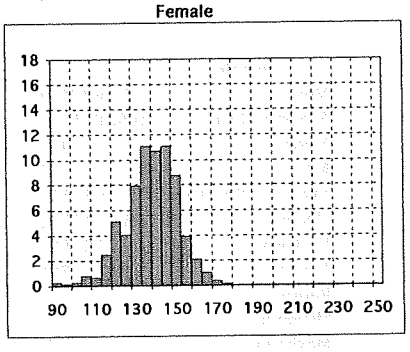


Western Australia, Augusta Autumn 1999

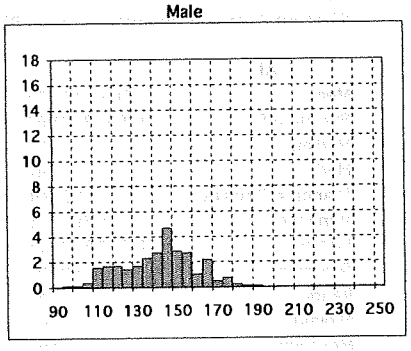
All



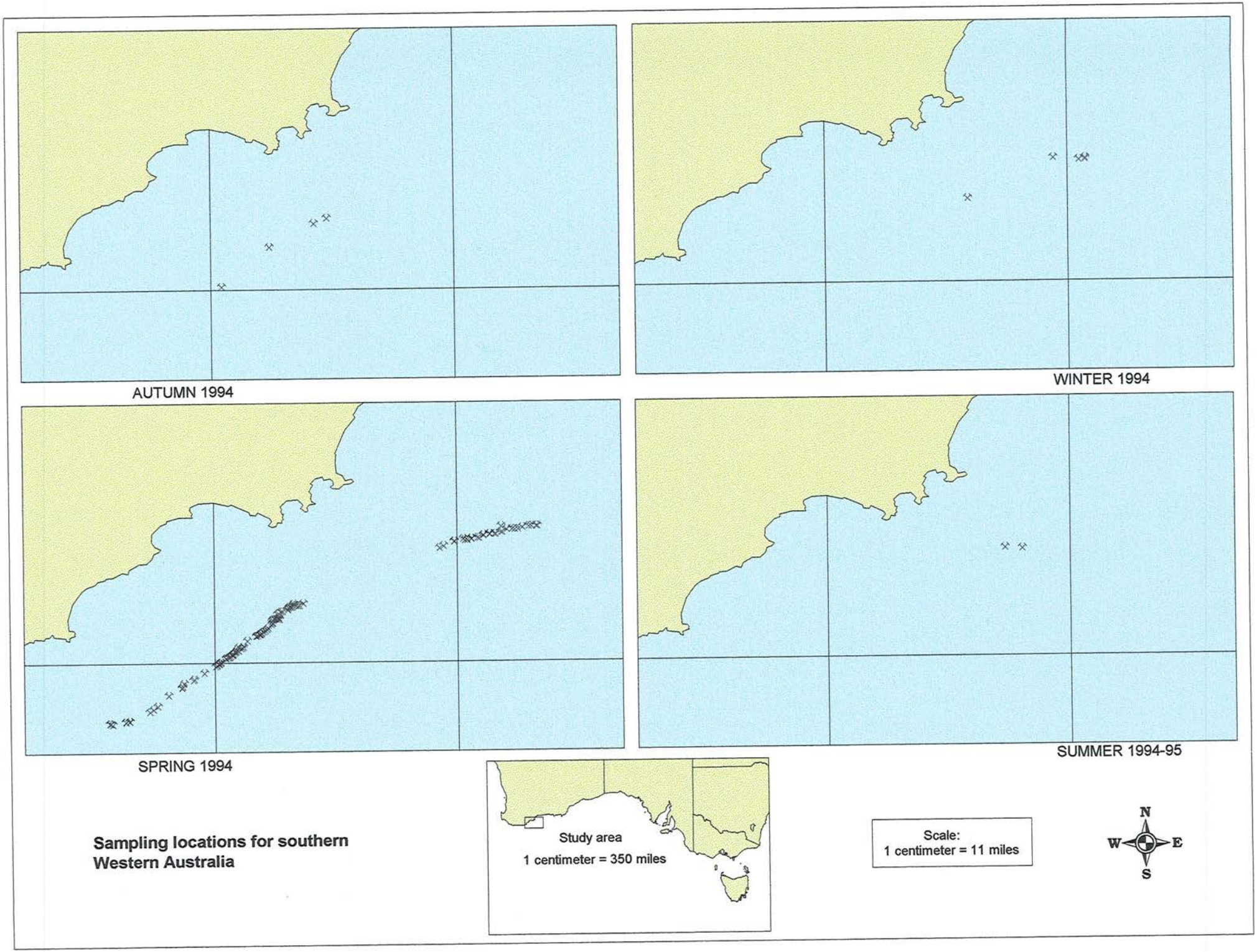
Female



Male



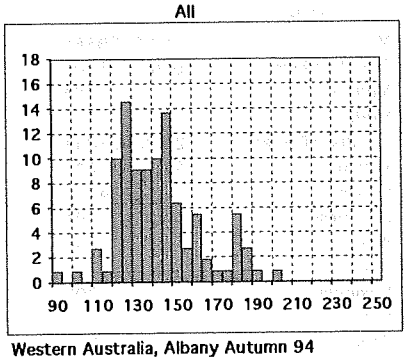
Western Australia, Augusta Summer 1999-00



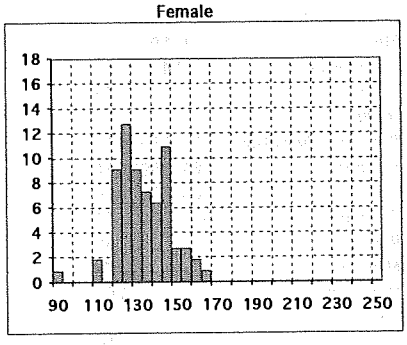
Sampling locations for southern Western Australia

Western Australia, Albany

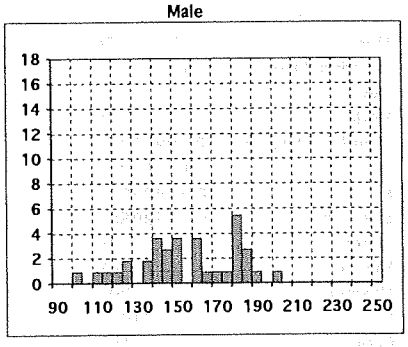
All



Female

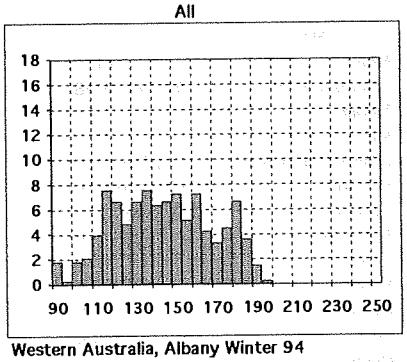


Male

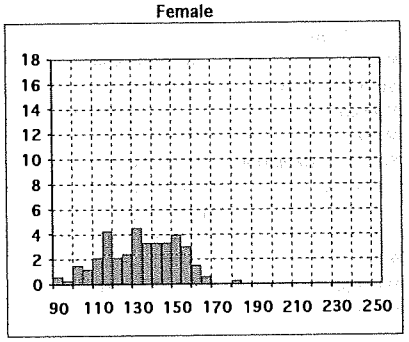


Western Australia, Albany Autumn 94

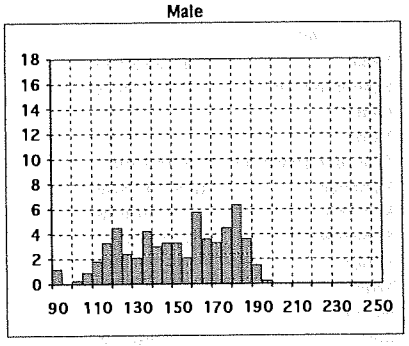
All



Female

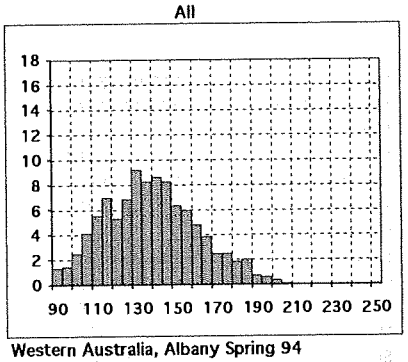


Male

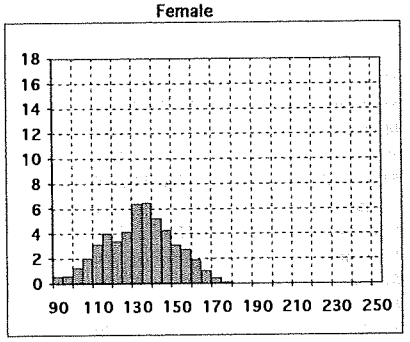


Western Australia, Albany Winter 94

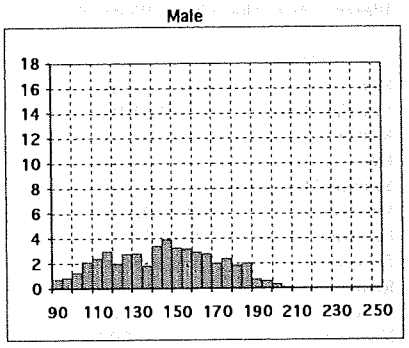
All



Female

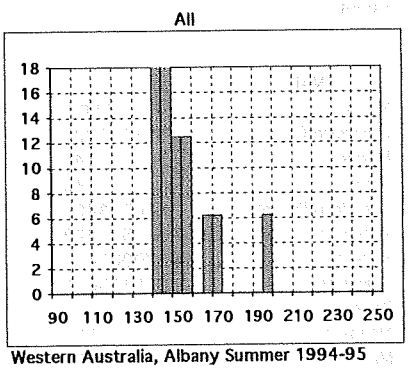


Male

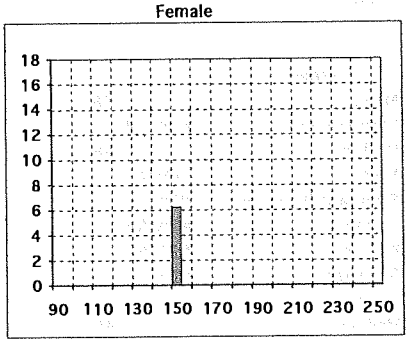


Western Australia, Albany Spring 94

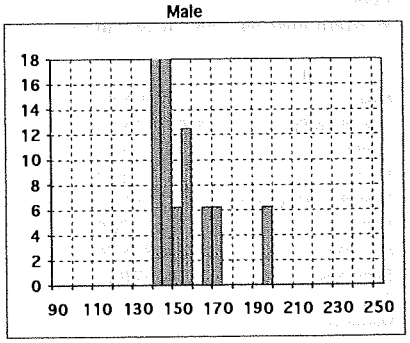
All



Female



Male

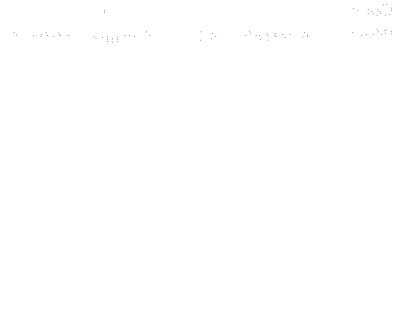


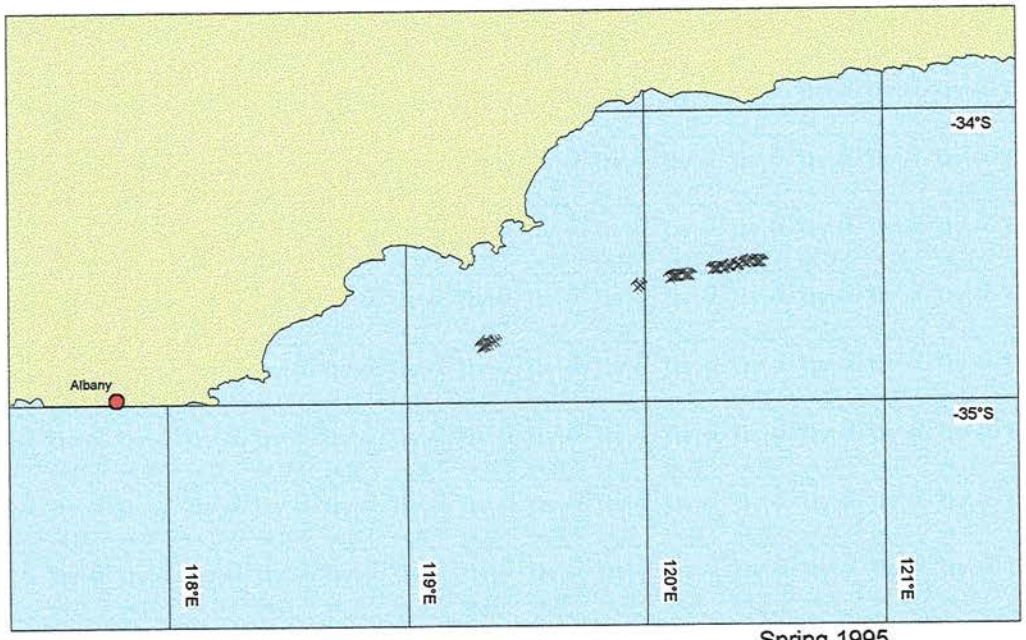
Western Australia, Albany Summer 1994-95

All

Female

Male



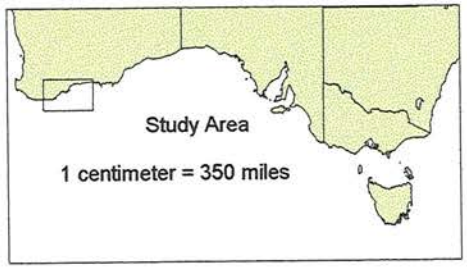


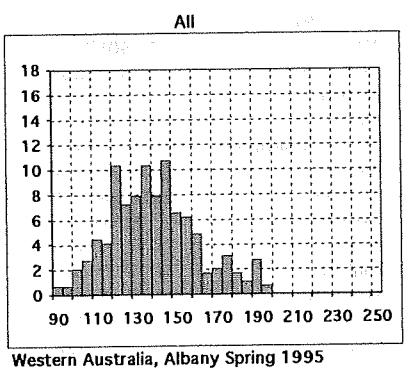
Spring 1995

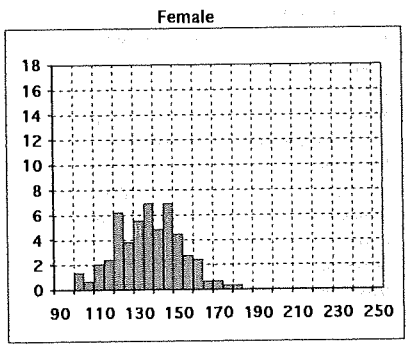
Sampling locations for southern Western Australia

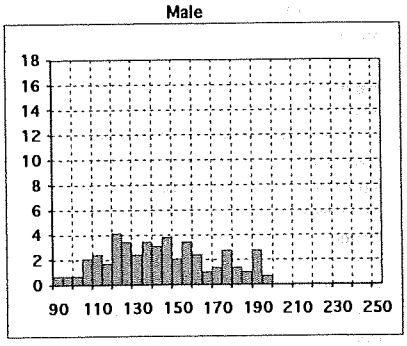
Scale :
1 centimeter = 18 miles

N
W E
S

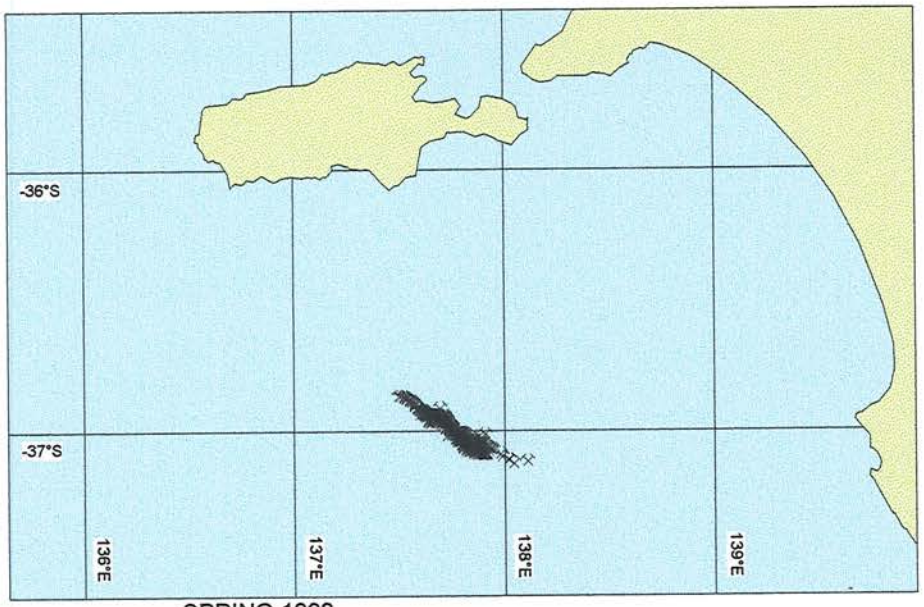




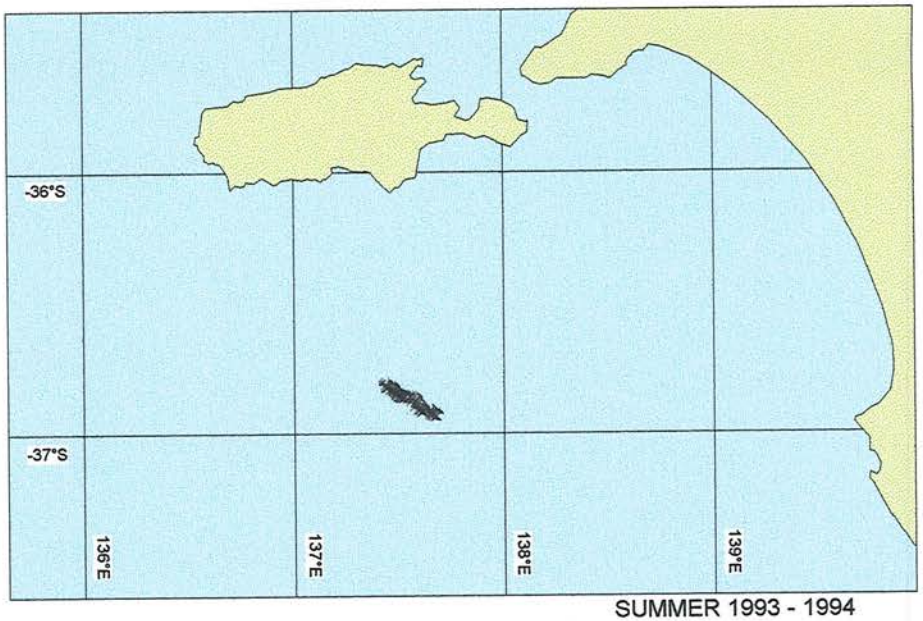




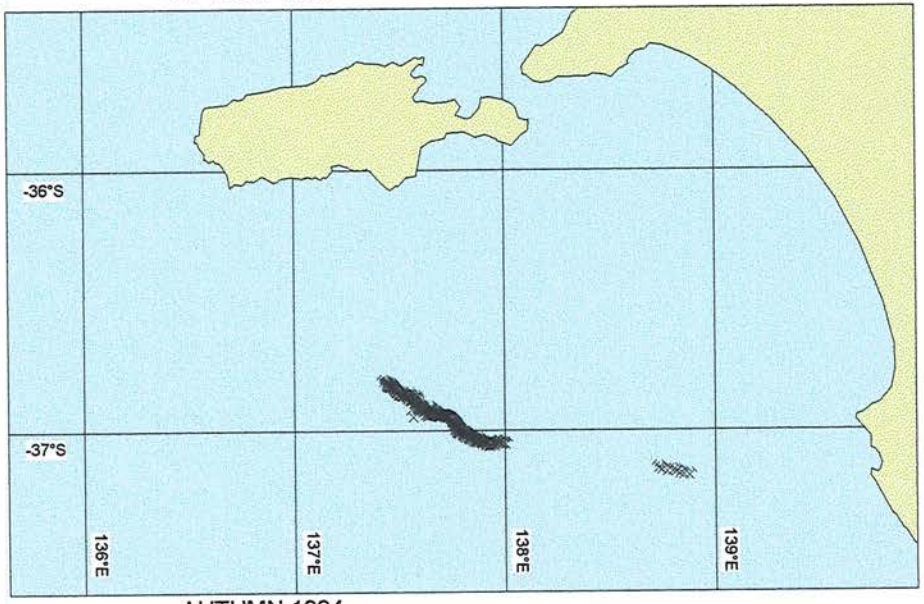
Western Australia, Albany Spring 1995



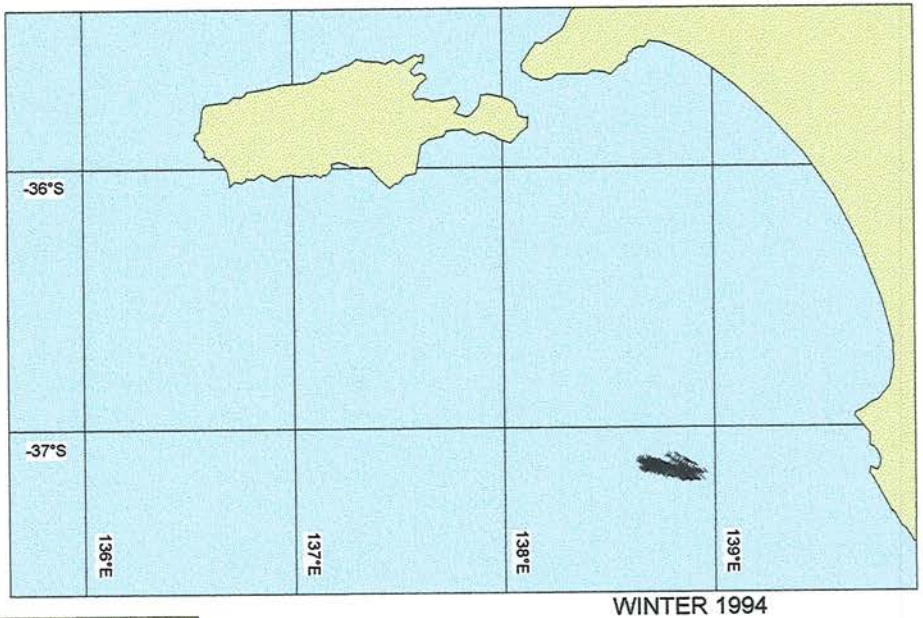
SPRING 1993



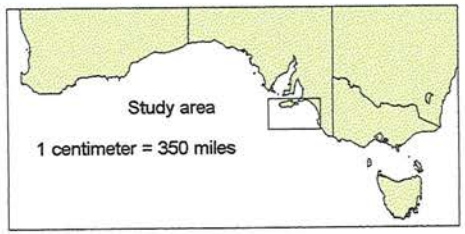
SUMMER 1993 - 1994



AUTUMN 1994



WINTER 1994

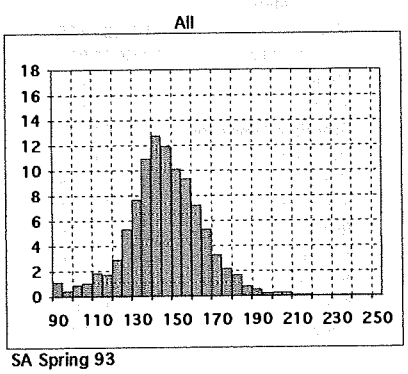


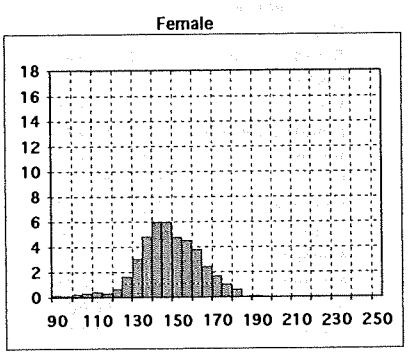
Scale:
1 centimeter = 20 miles

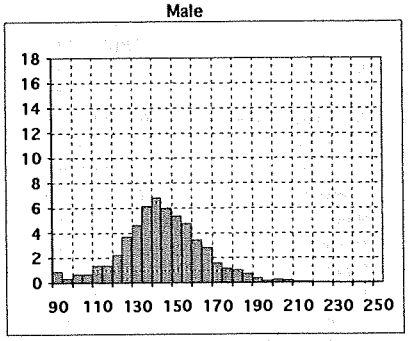
N
W E
S

Sampling locations for South Australia

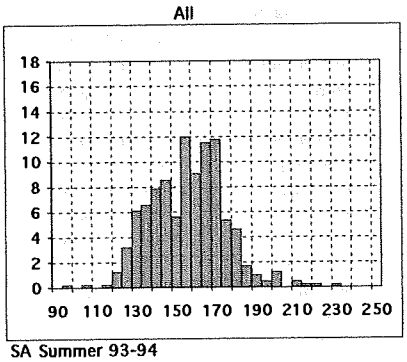
South Australia

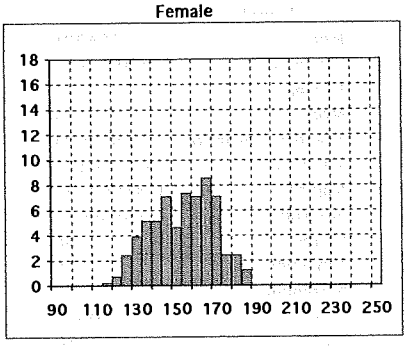


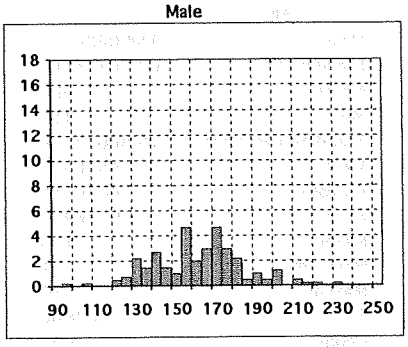




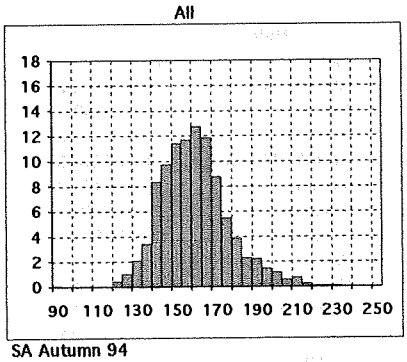
SA Spring 93

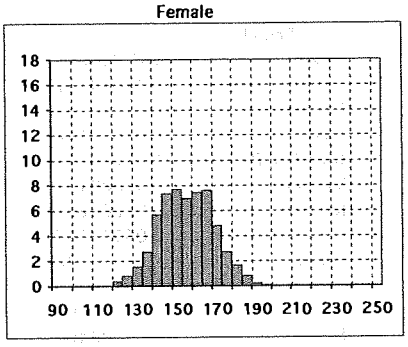


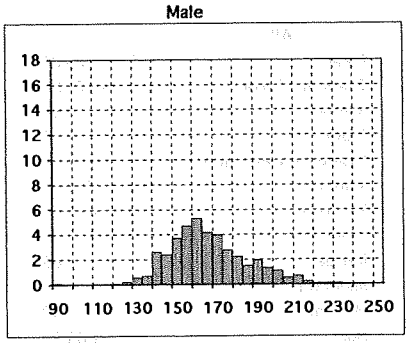




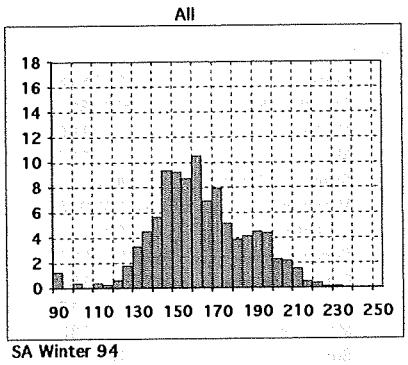
SA Summer 93-94

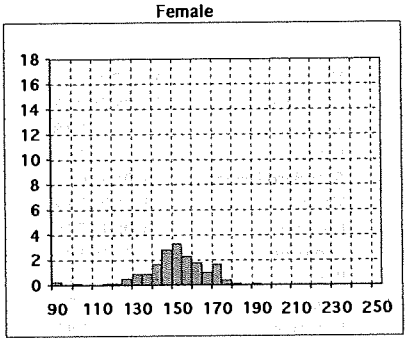


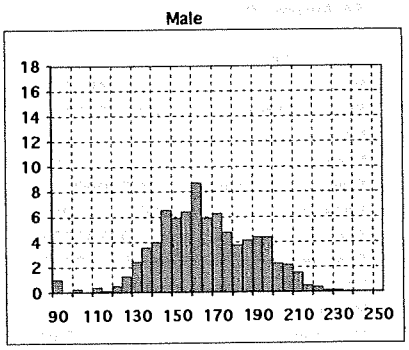




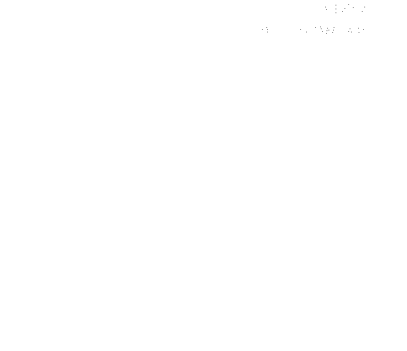
SA Autumn 94

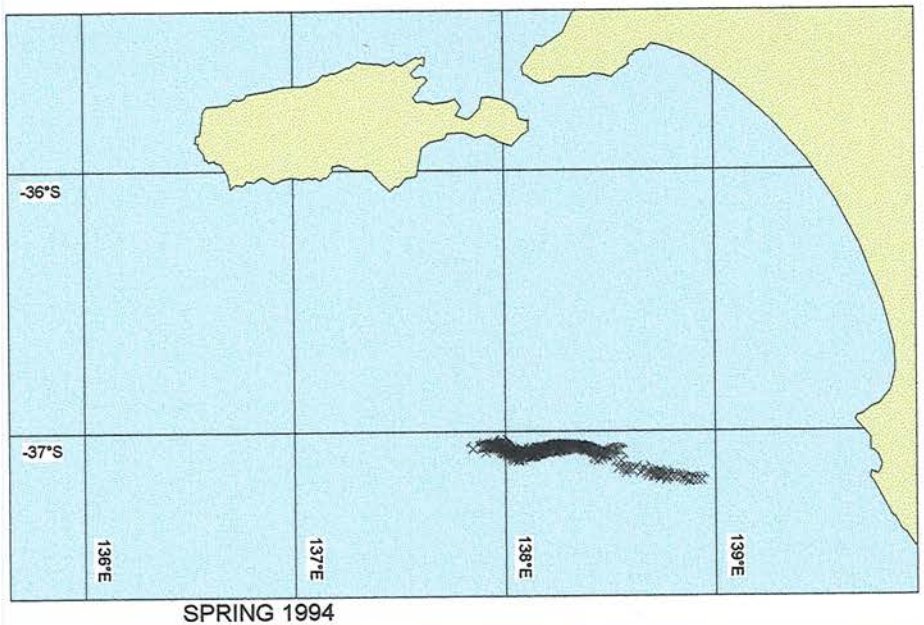




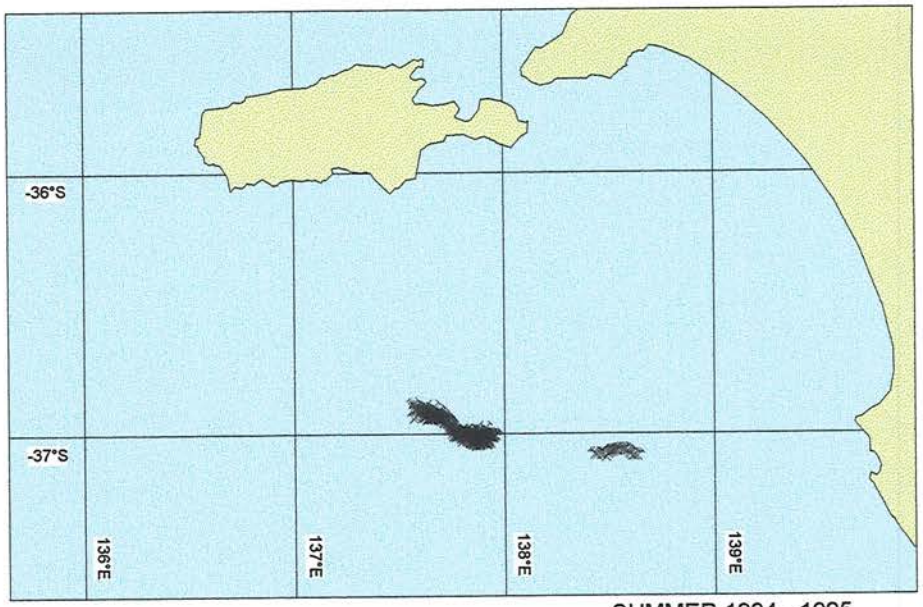


SA Winter 94

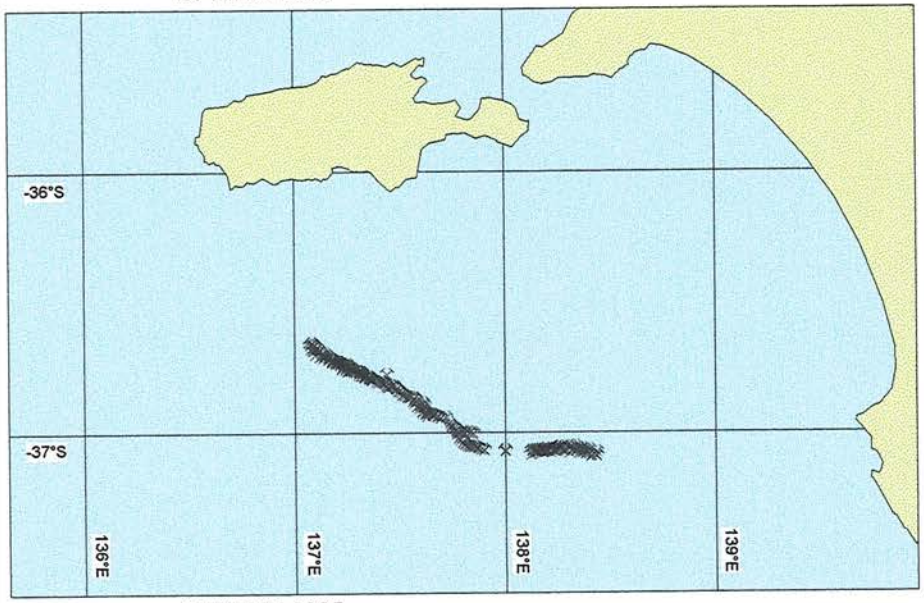




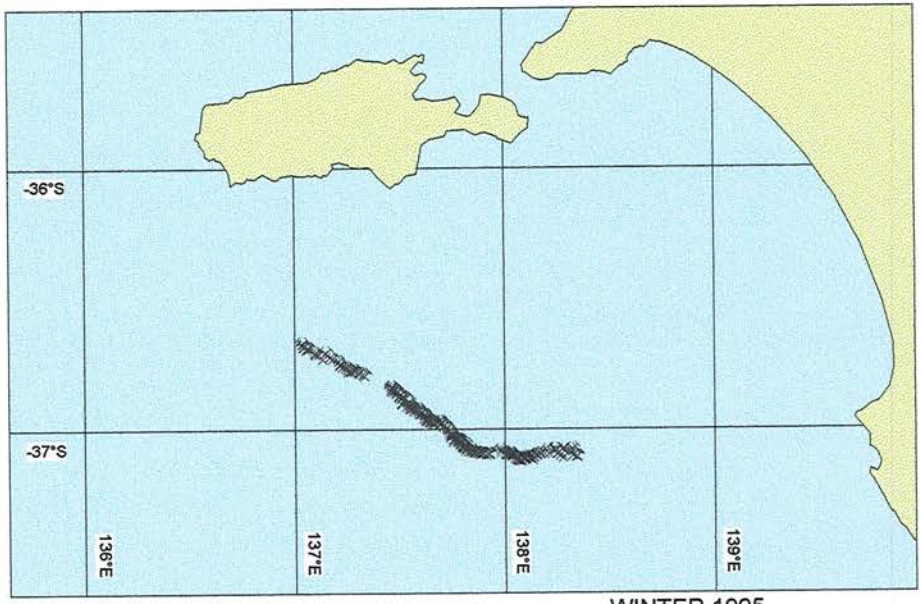
SPRING 1994



SUMMER 1994 - 1995

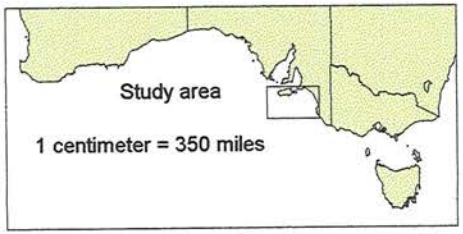


AUTUMN 1995



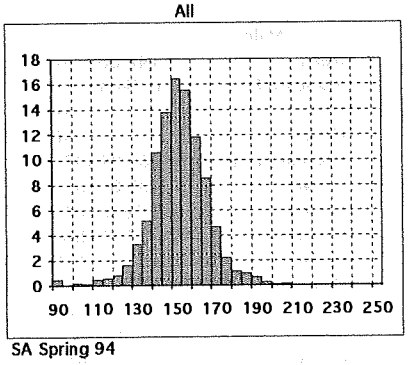
WINTER 1995

Sampling locations for South Australia

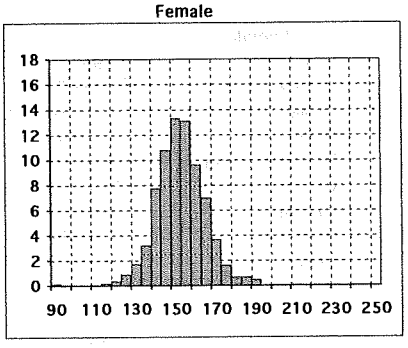


Scale:
1 centimeter = 20 miles

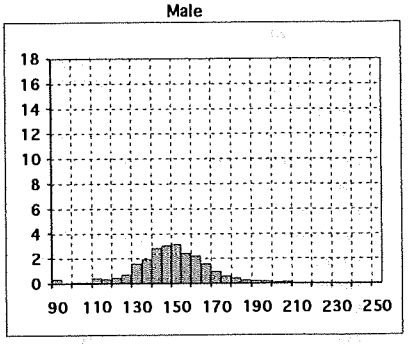
All



Female

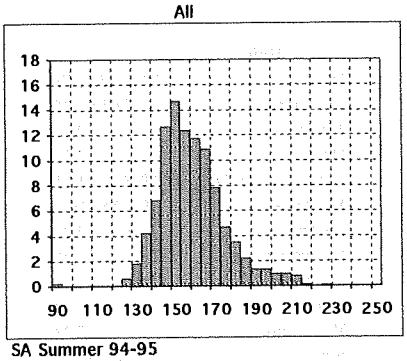


Male

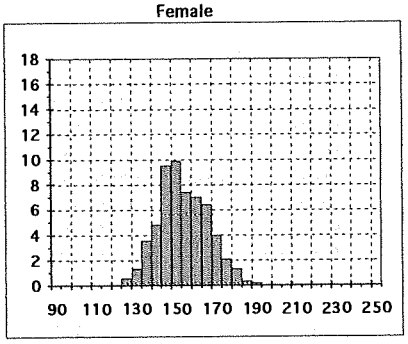


SA Spring 94

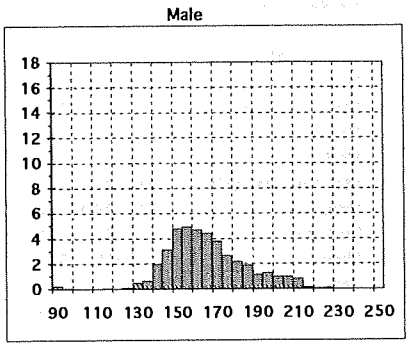
All



Female

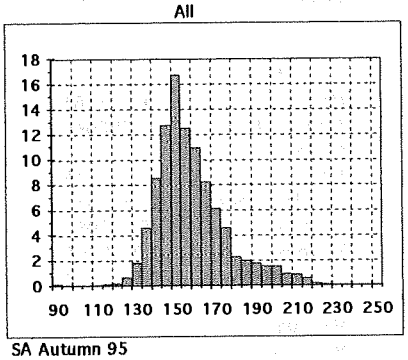


Male

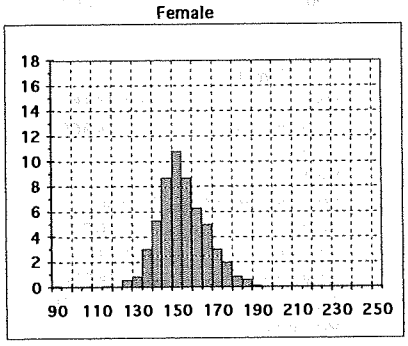


SA Summer 94-95

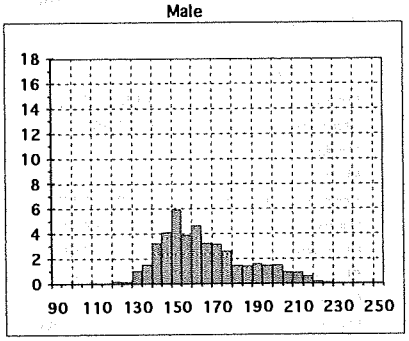
All



Female

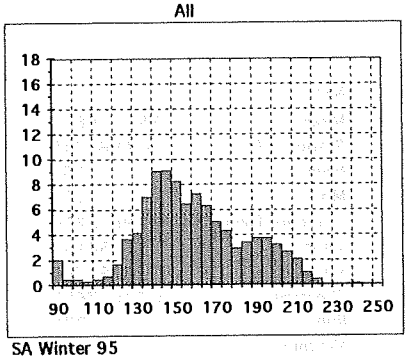


Male

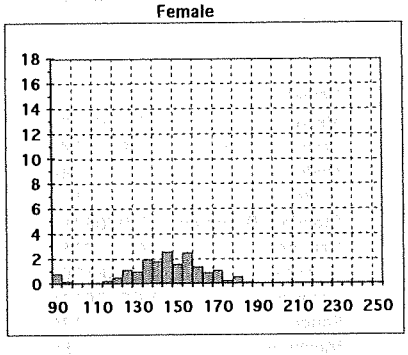


SA Autumn 95

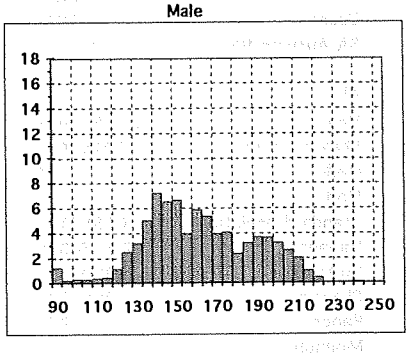
All



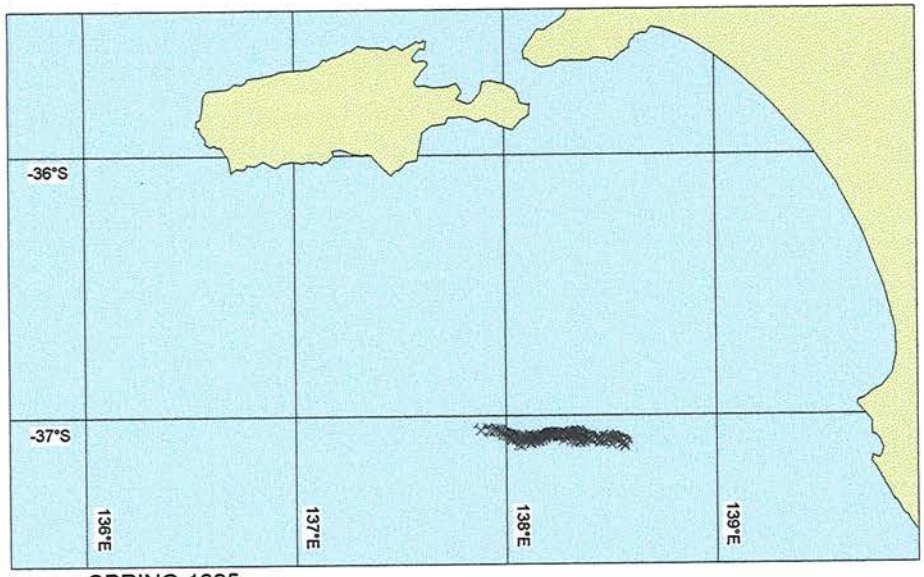
Female



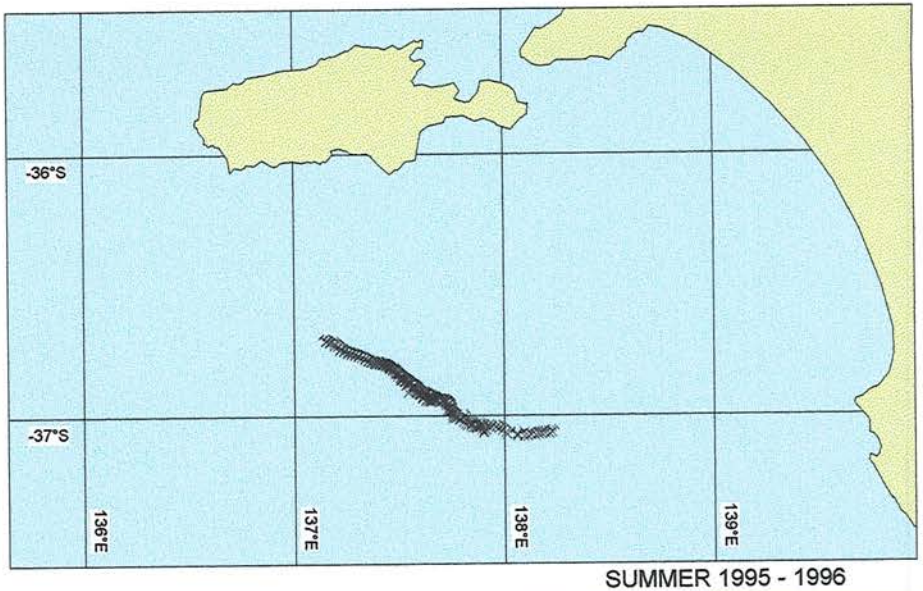
Male



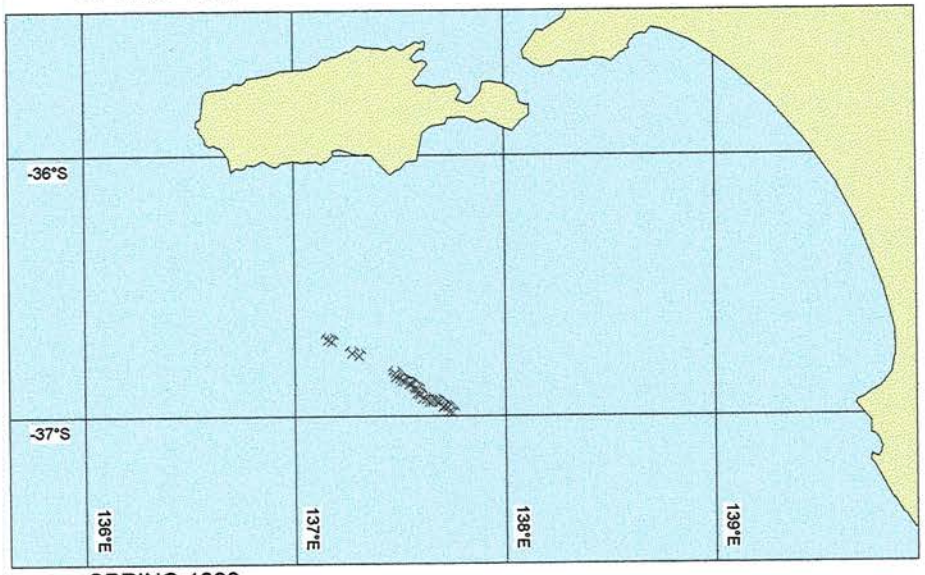
SA Winter 95



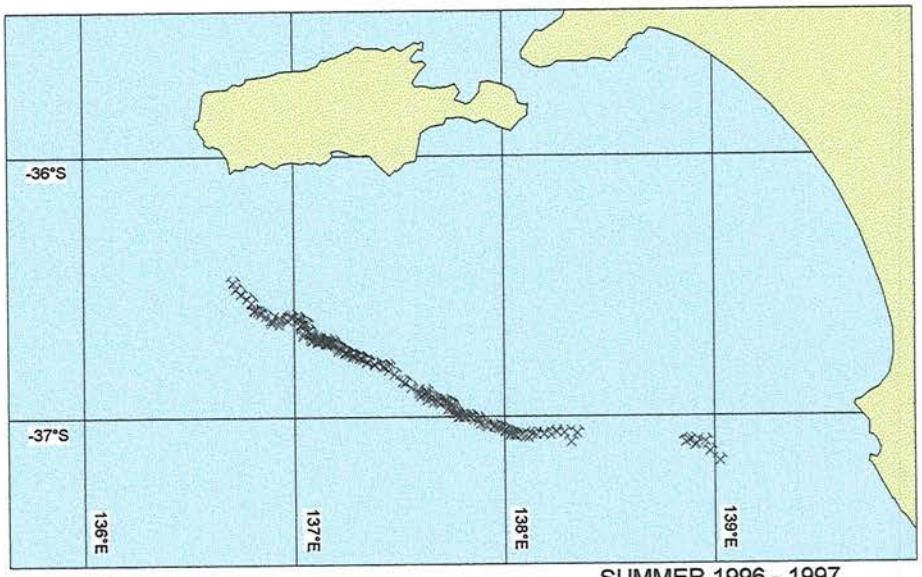
SPRING 1995



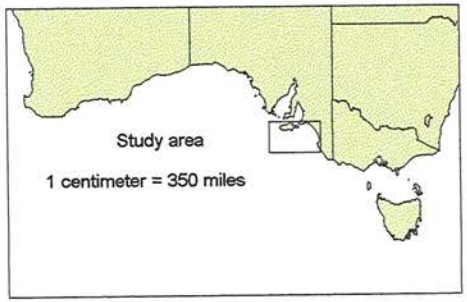
SUMMER 1995 - 1996



SPRING 1996



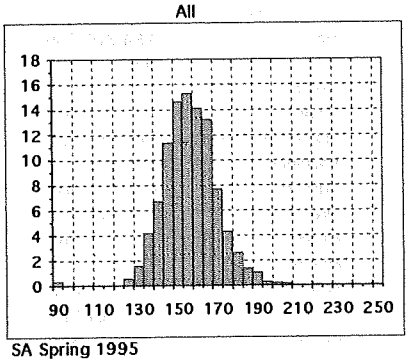
SUMMER 1996 - 1997



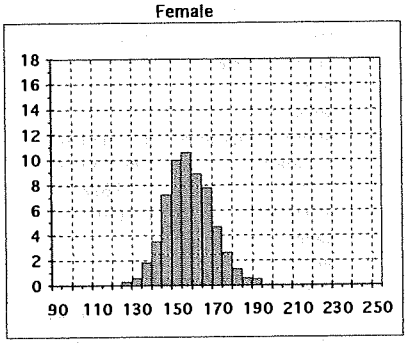
Sampling locations for South Australia

Scale:
1 centimeter = 20 miles

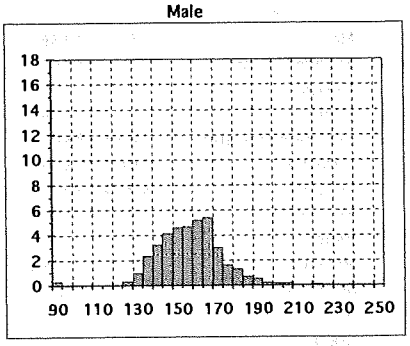
All



Female

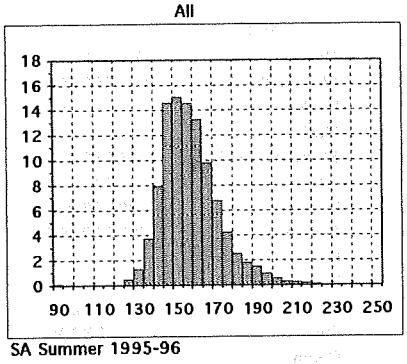


Male

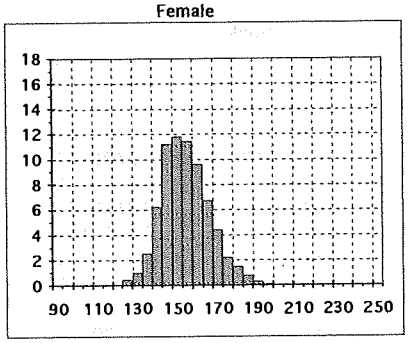


SA Spring 1995

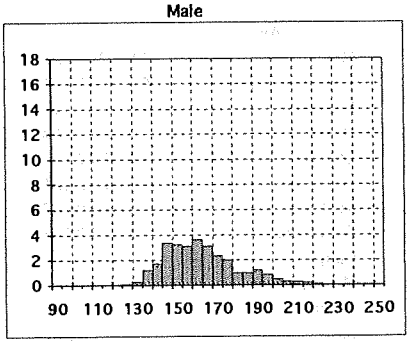
All



Female

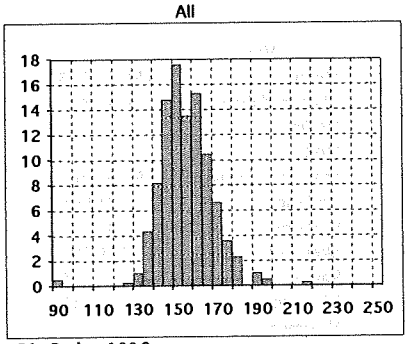


Male

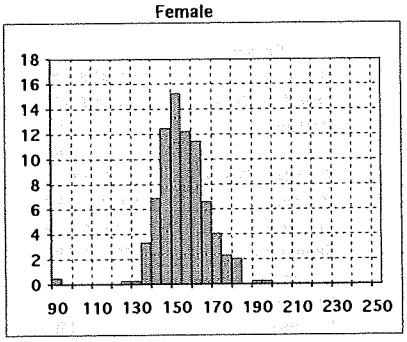


SA Summer 1995-96

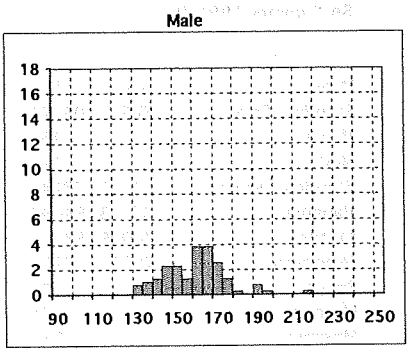
All



Female

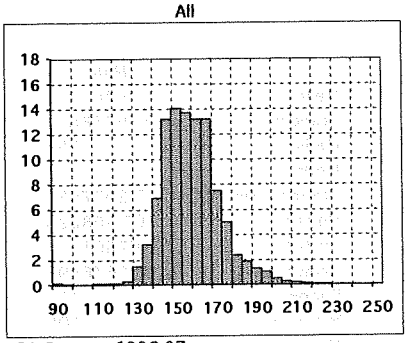


Male

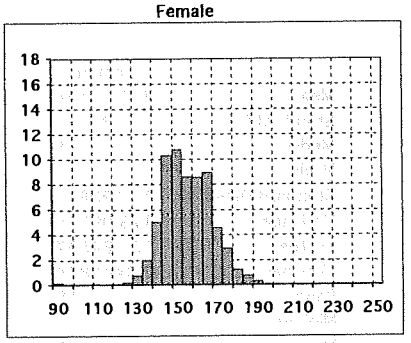


SA Spring 1996

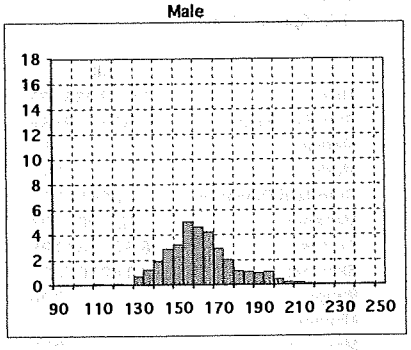
All



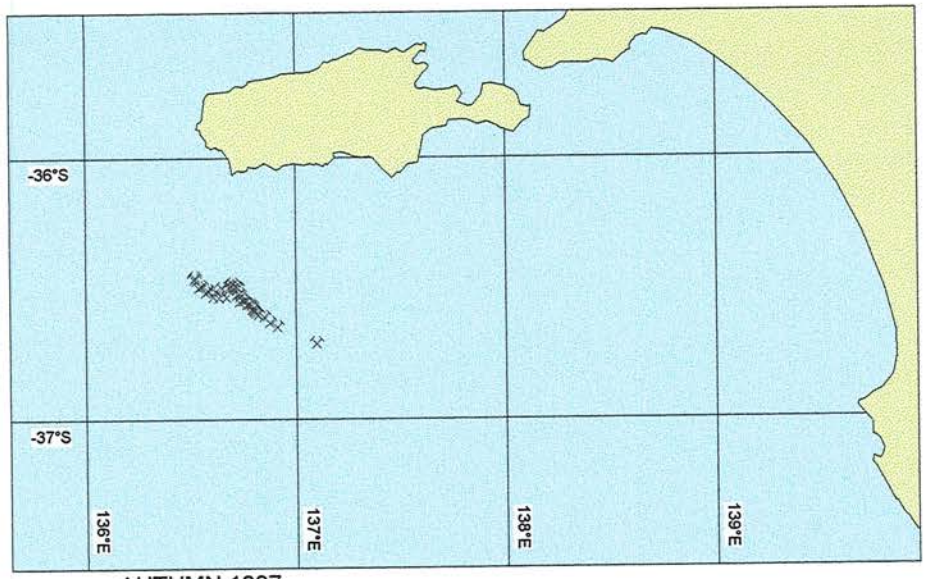
Female



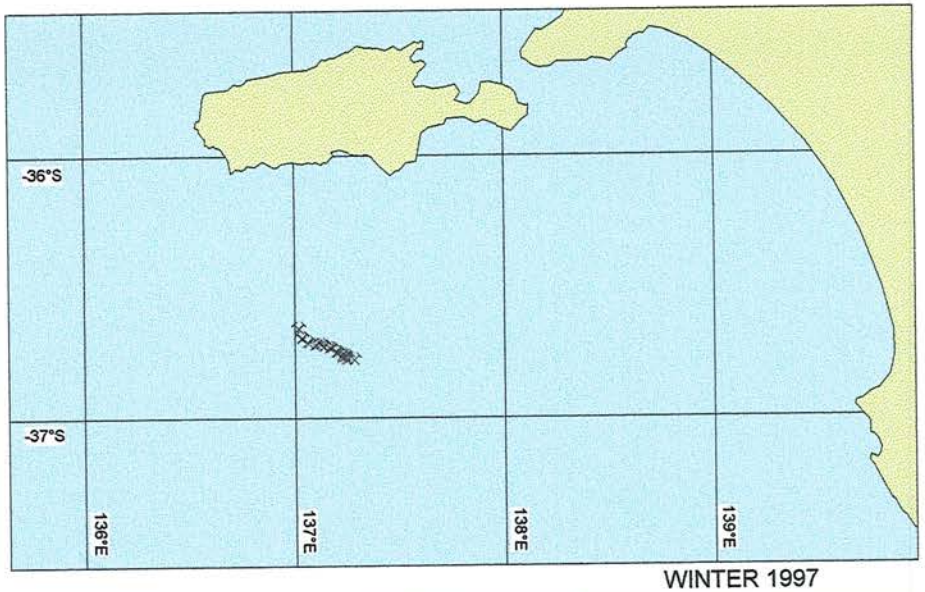
Male



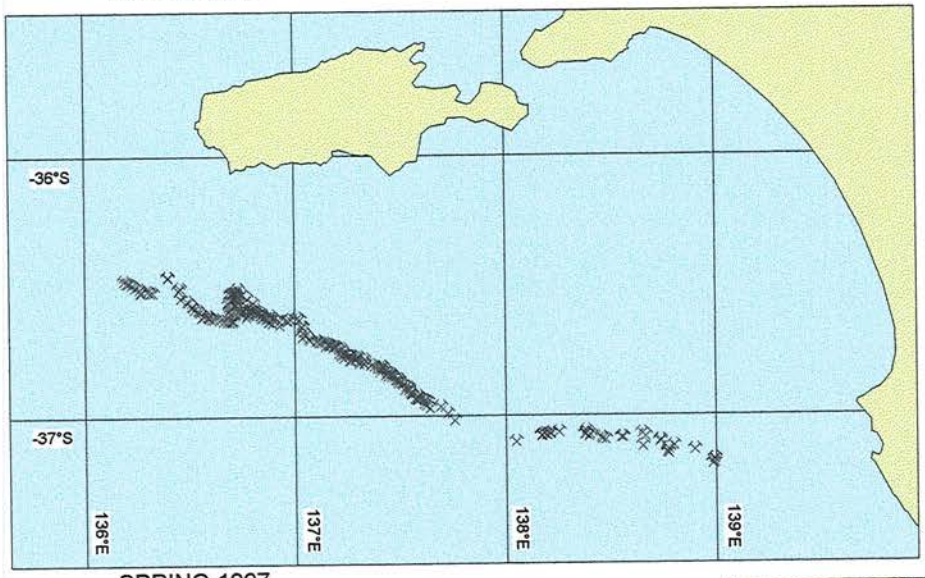
SA Summer 1996-97



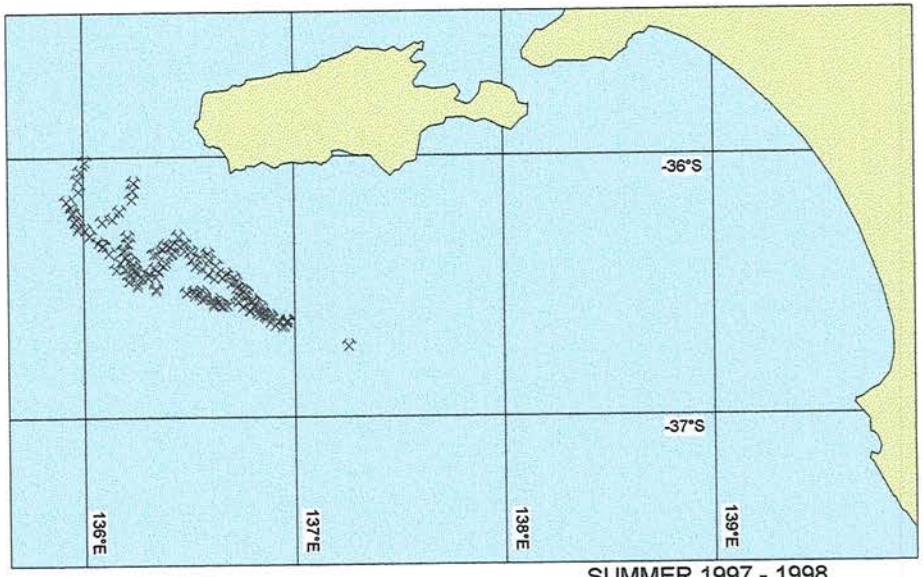
AUTUMN 1997



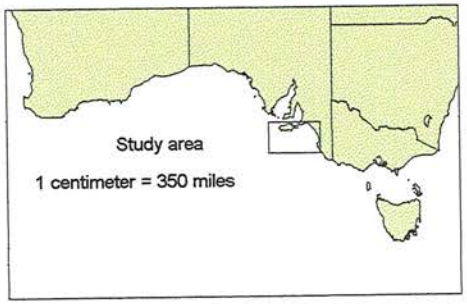
WINTER 1997



SPRING 1997



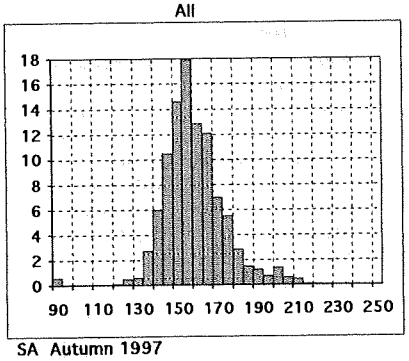
SUMMER 1997 - 1998



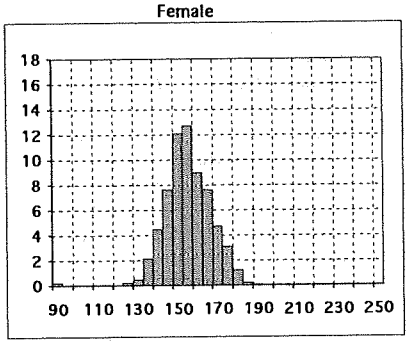
Sampling locations for South Australia

Scale:
1 centimeter = 20 miles

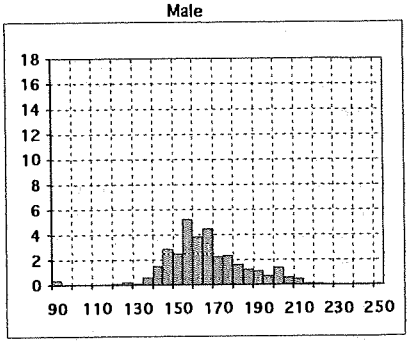
All



Female

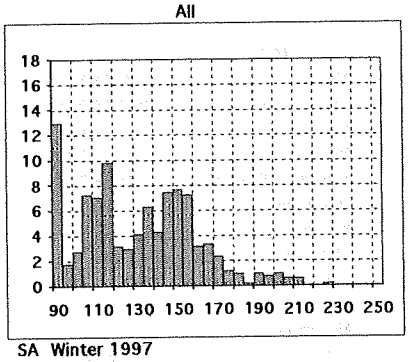


Male

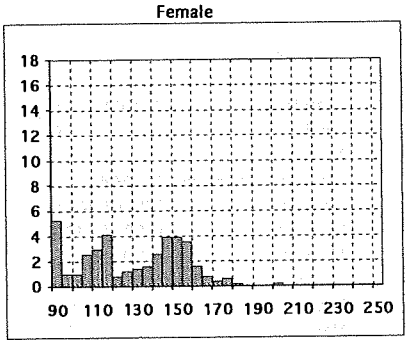


SA Autumn 1997

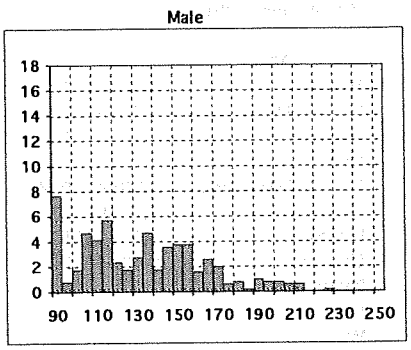
All



Female

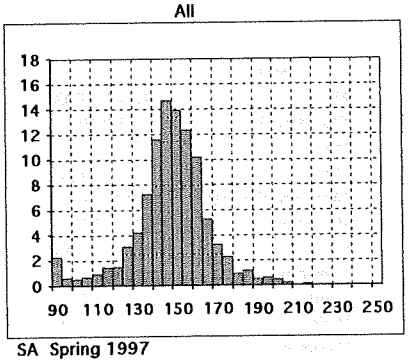


Male

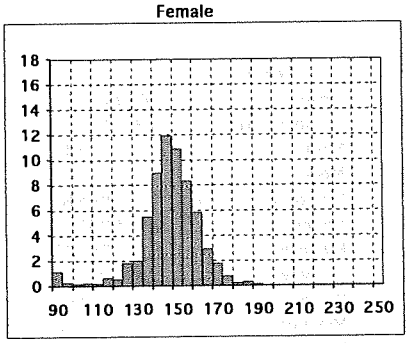


SA Winter 1997

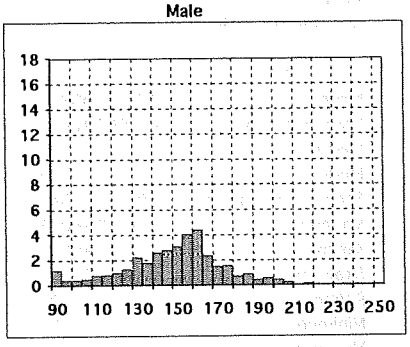
All



Female

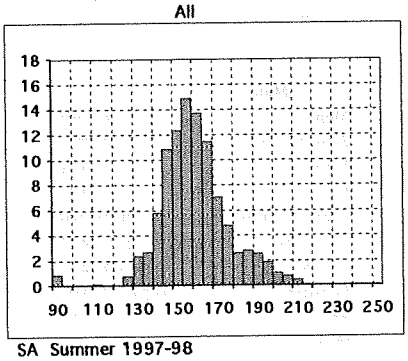


Male

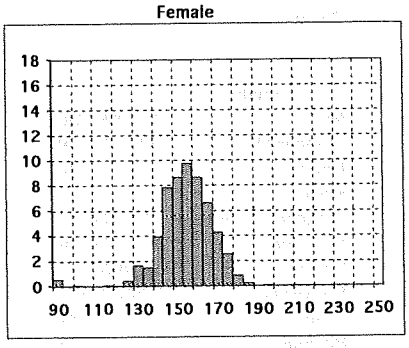


SA Spring 1997

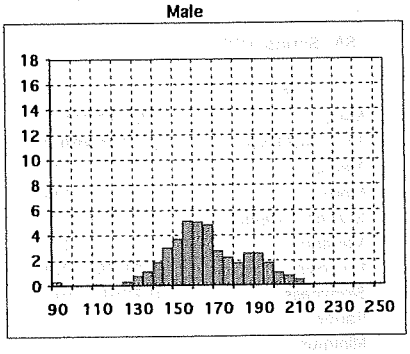
All



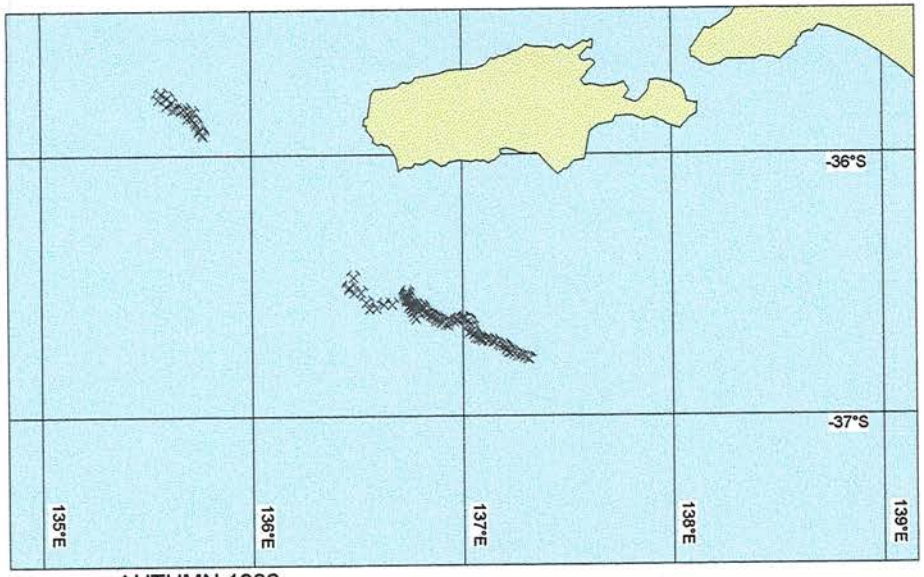
Female



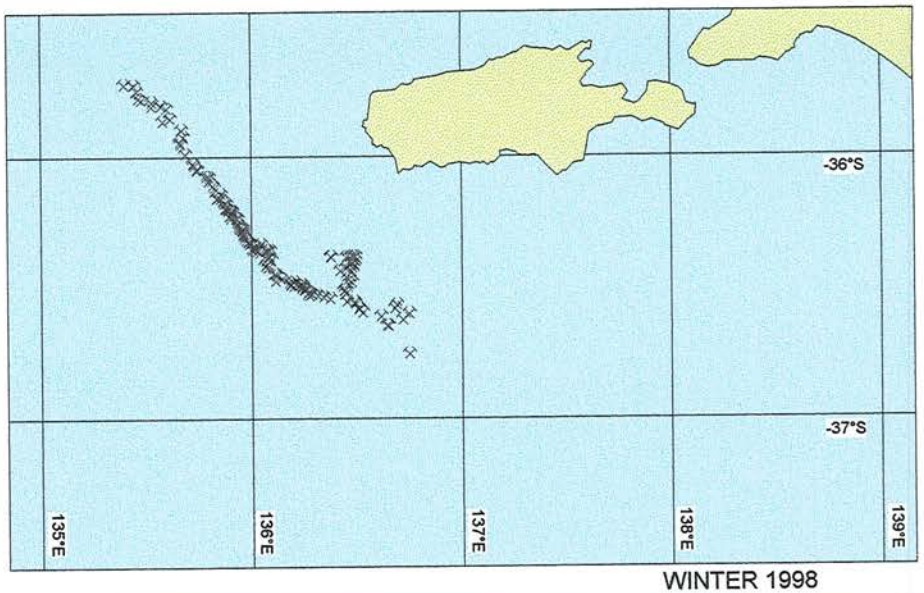
Male



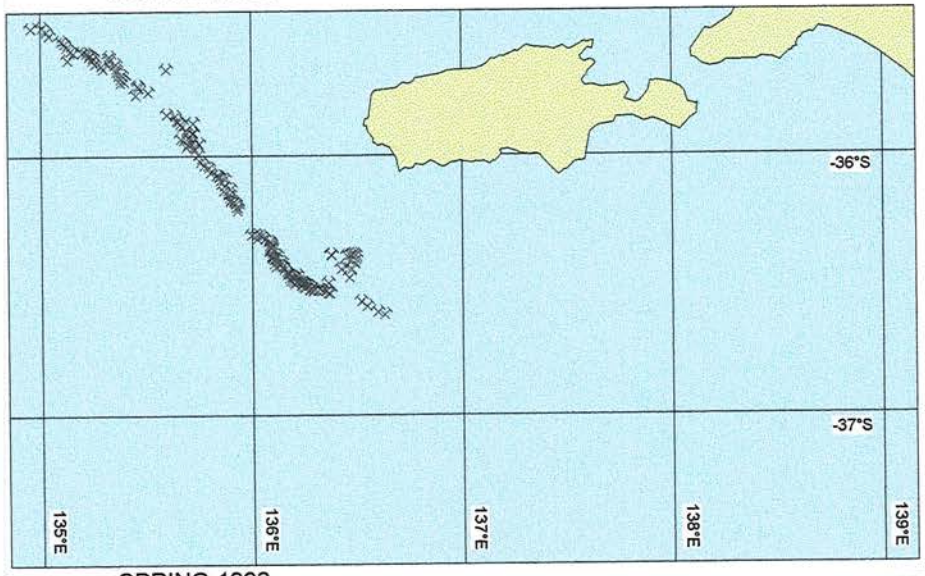
SA Summer 1997-98



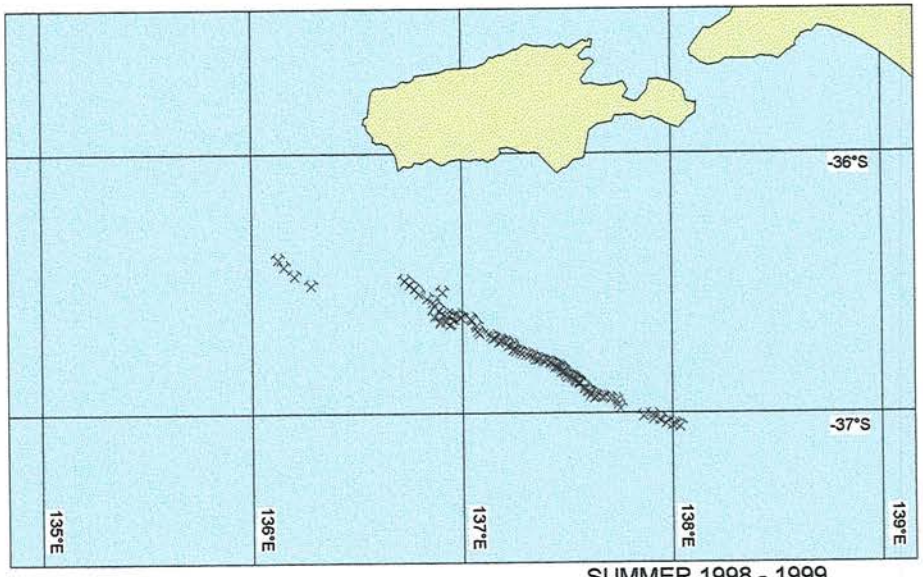
AUTUMN 1998



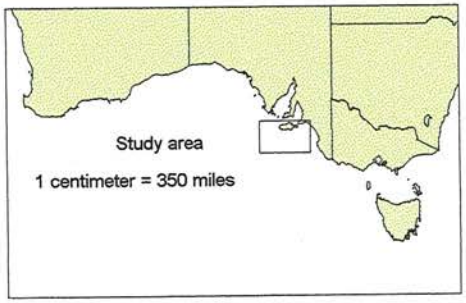
WINTER 1998



SPRING 1998



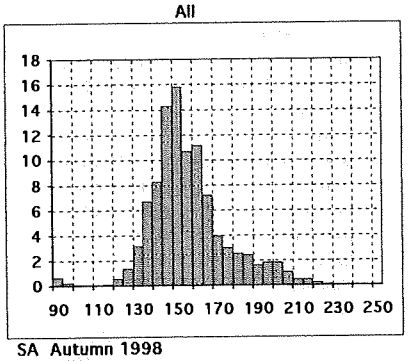
SUMMER 1998 - 1999



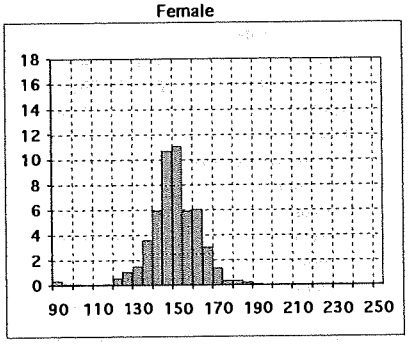
Sampling locations for South Australia

Scale:
1 centimeter = 20 miles

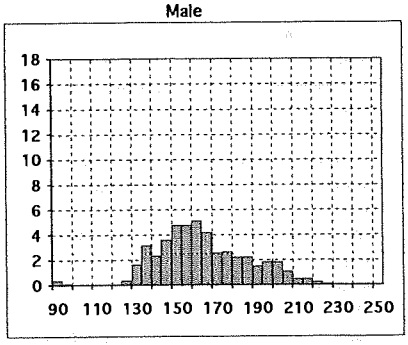
All



Female

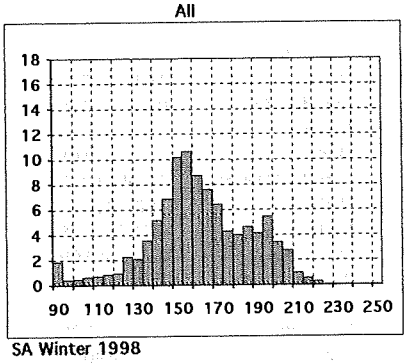


Male

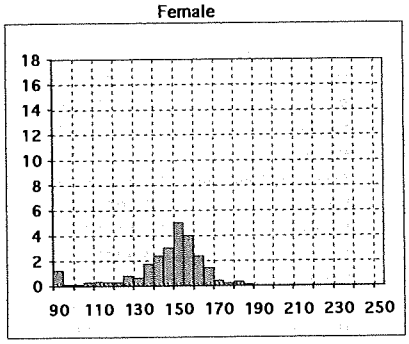


SA Autumn 1998

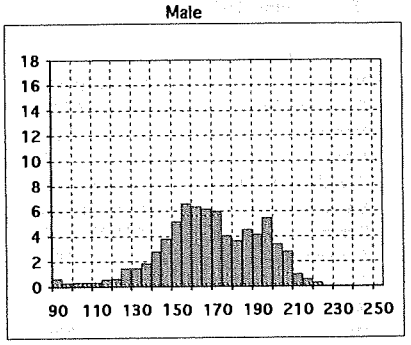
All



Female

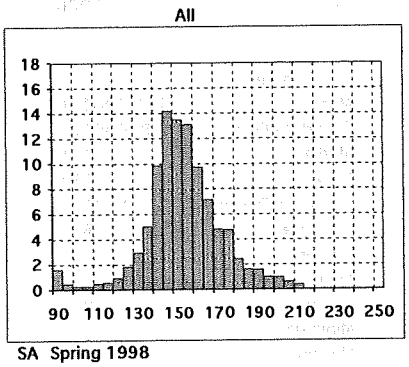


Male

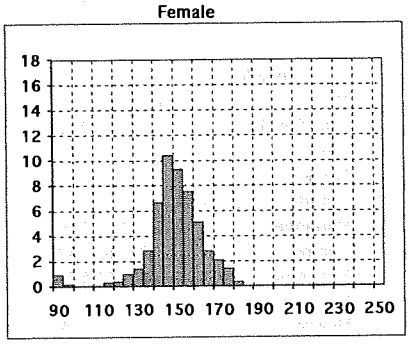


SA Winter 1998

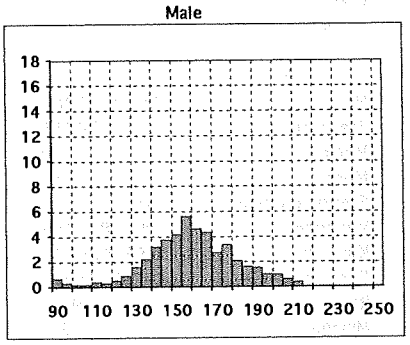
All



Female

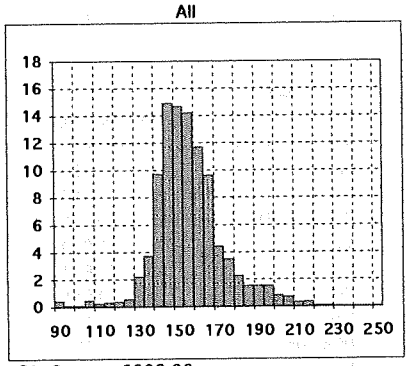


Male

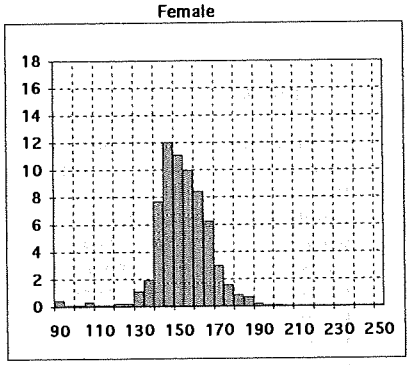


SA Spring 1998

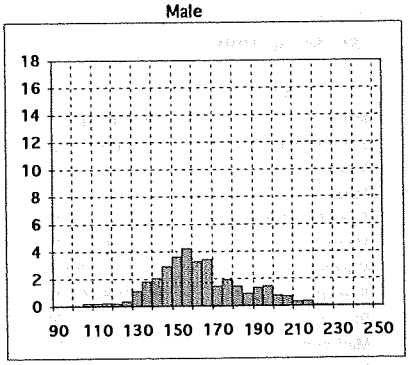
All



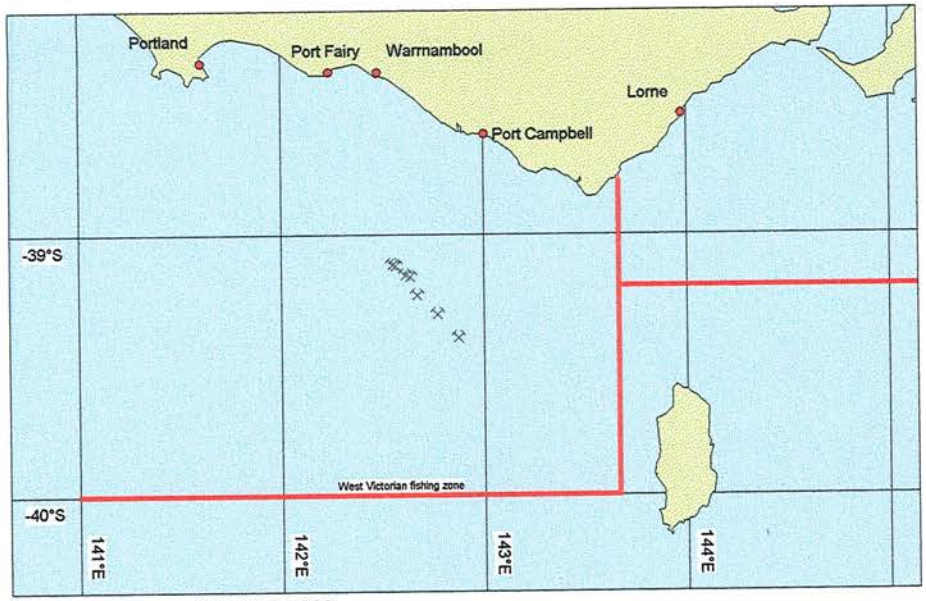
Female



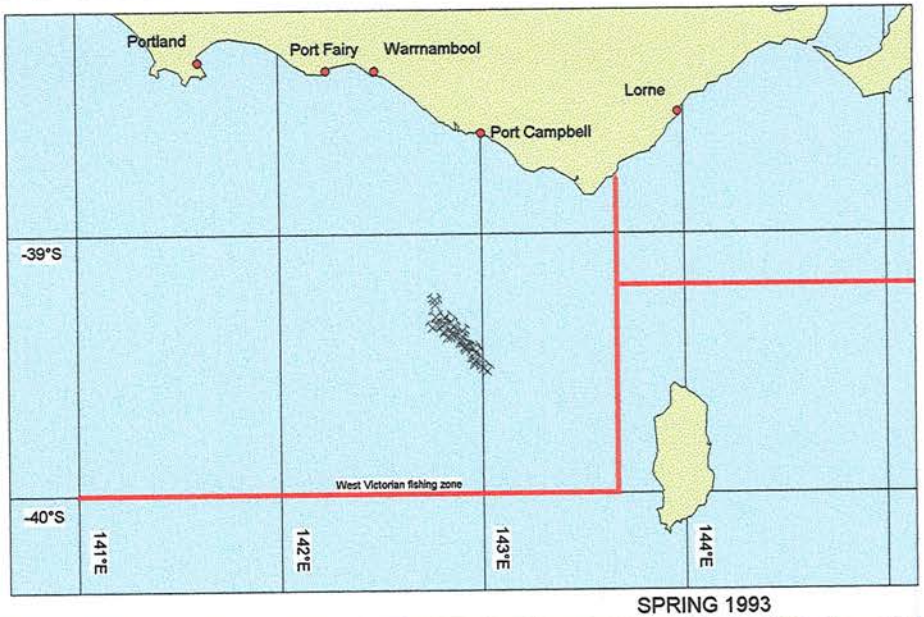
Male



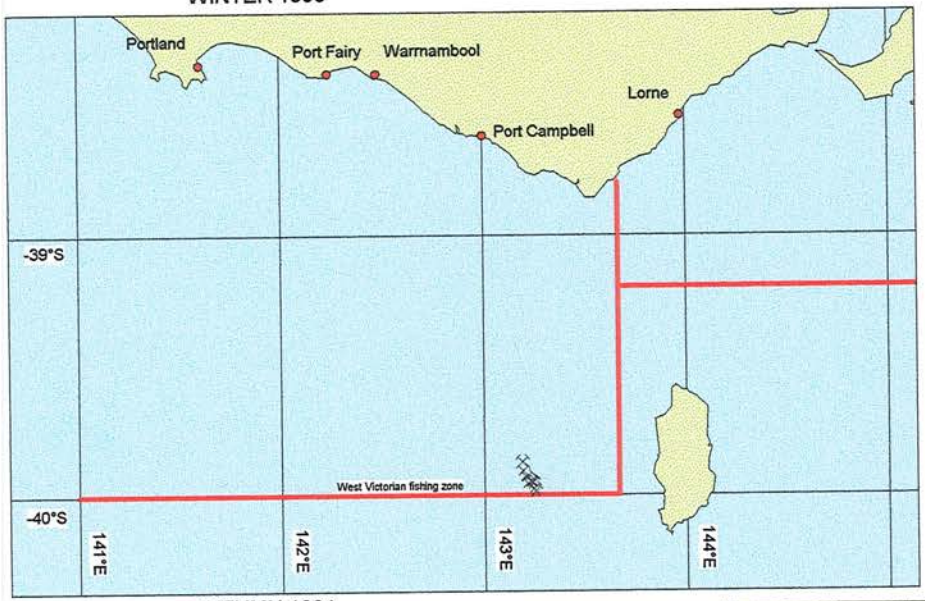
SA Summer 1998-99



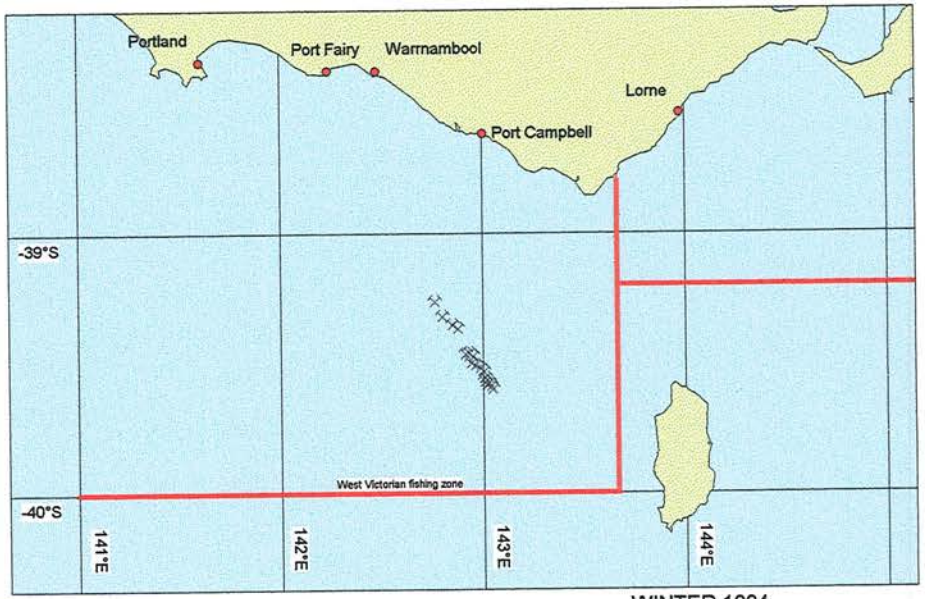
WINTER 1993



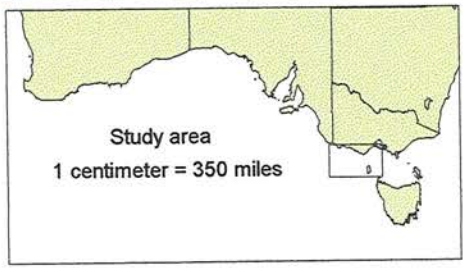
SPRING 1993



AUTUMN 1994



WINTER 1994

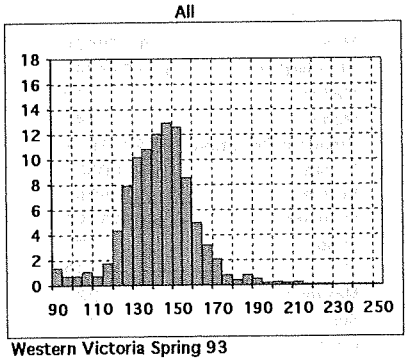


Scale:
1 centimeter = 20 miles

Sampling locations for western Victoria

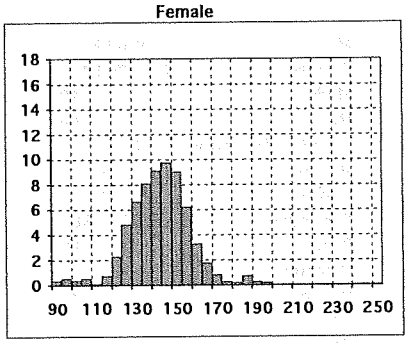
Western Victoria

All

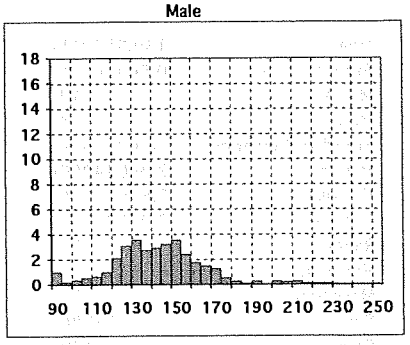


Western Victoria Spring 93

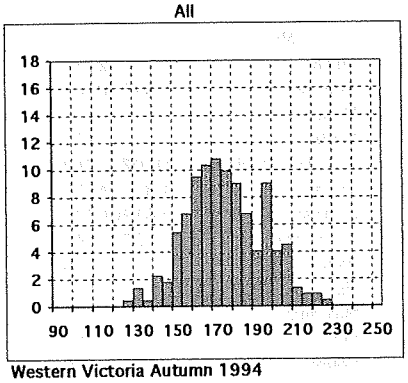
Female



Male

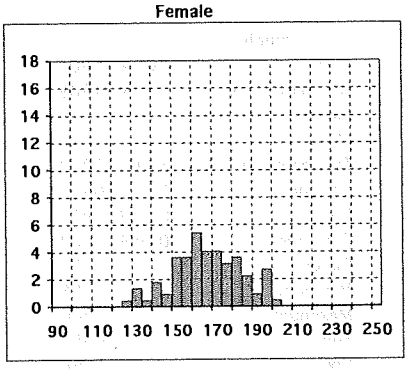


All

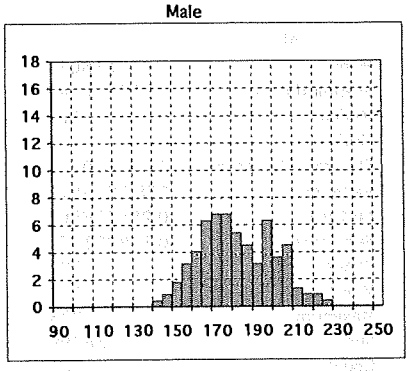


Western Victoria Autumn 1994

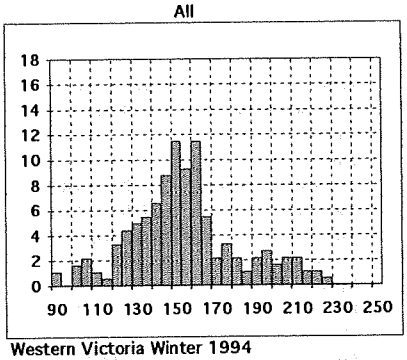
Female



Male

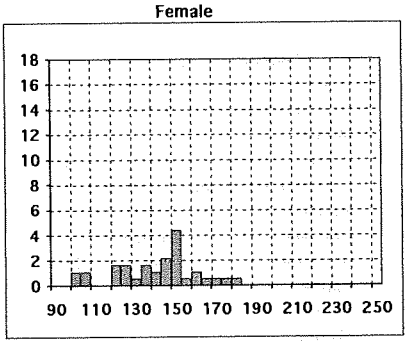


All

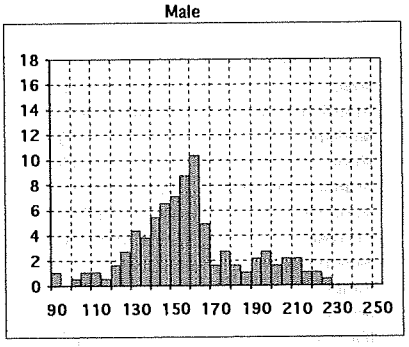


Western Victoria Winter 1994

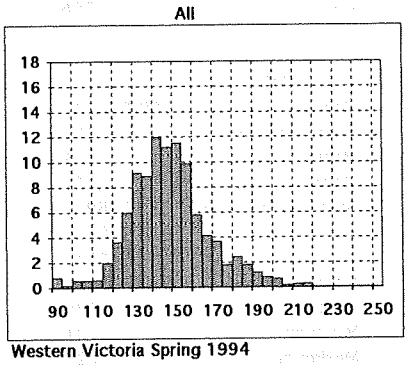
Female



Male

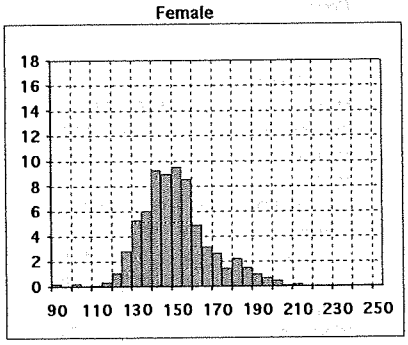


All

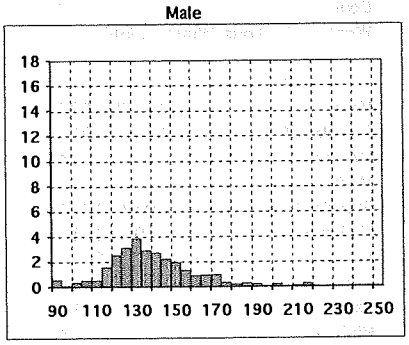


Western Victoria Spring 1994

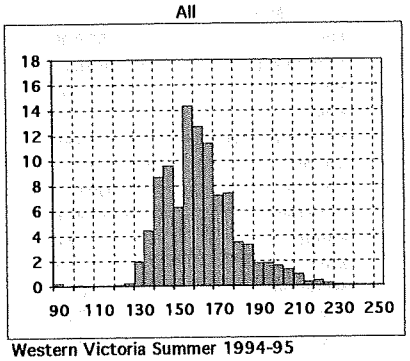
Female



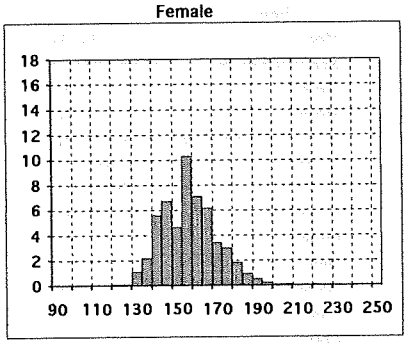
Male



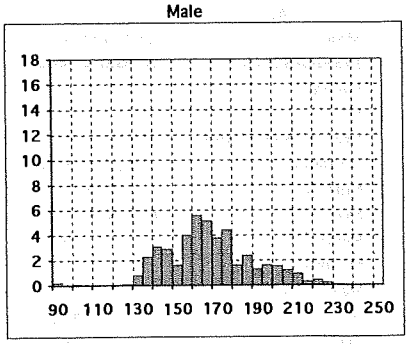
All



Female

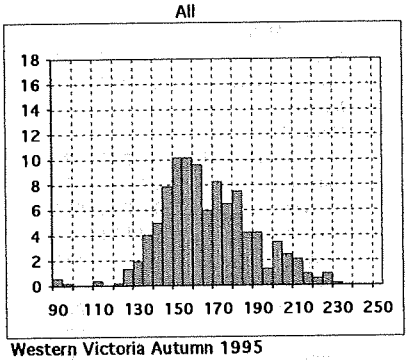


Male

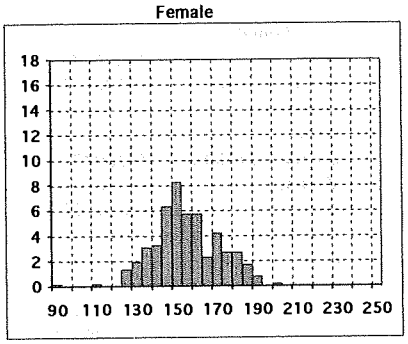


Western Victoria Summer 1994-95

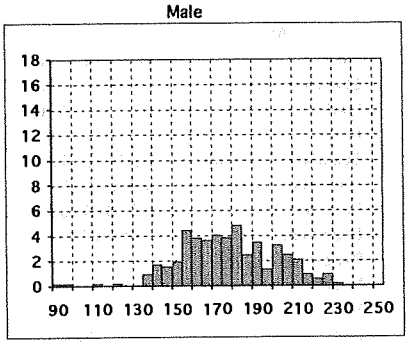
All



Female

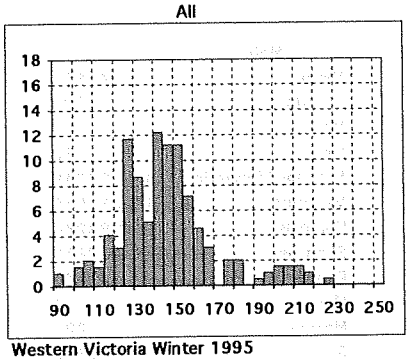


Male

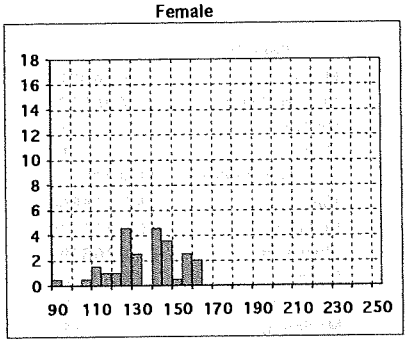


Western Victoria Autumn 1995

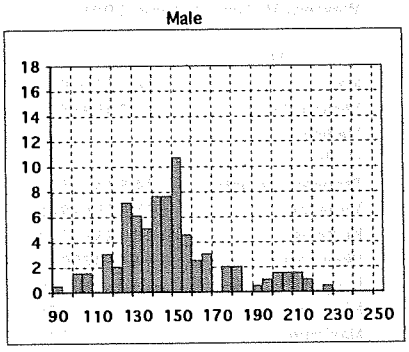
All



Female

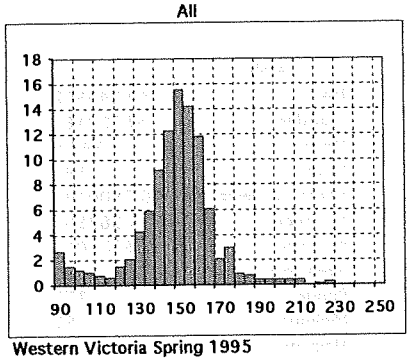


Male

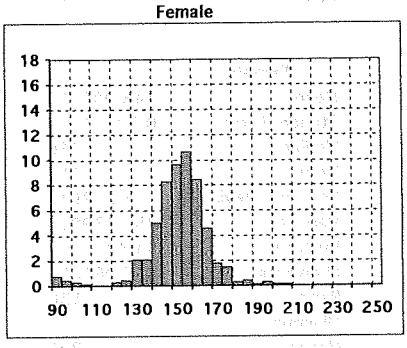


Western Victoria Winter 1995

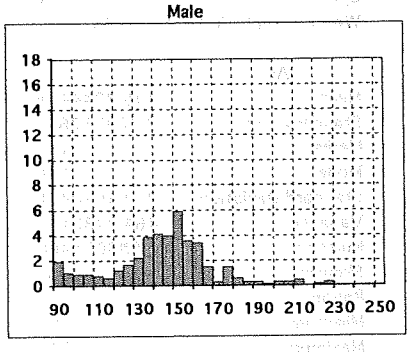
All



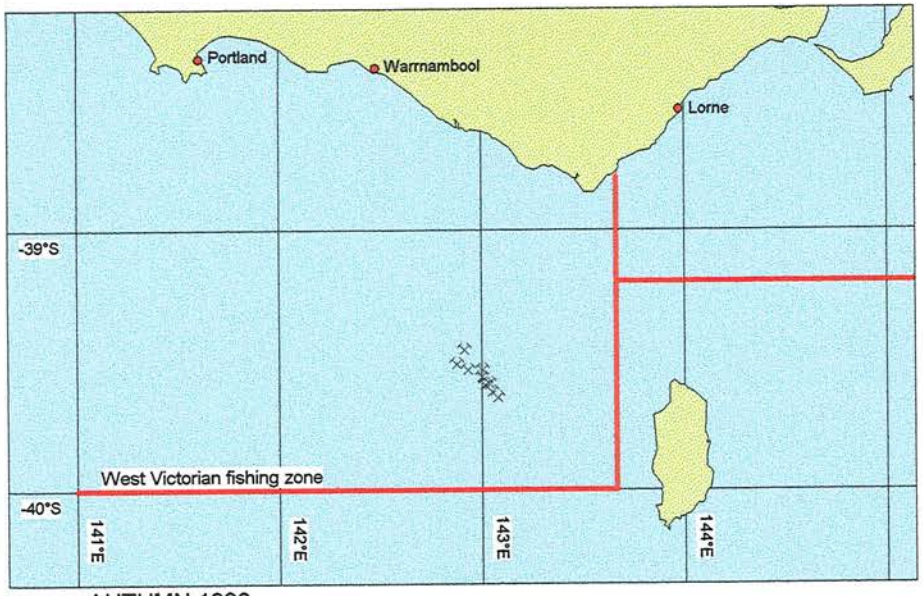
Female



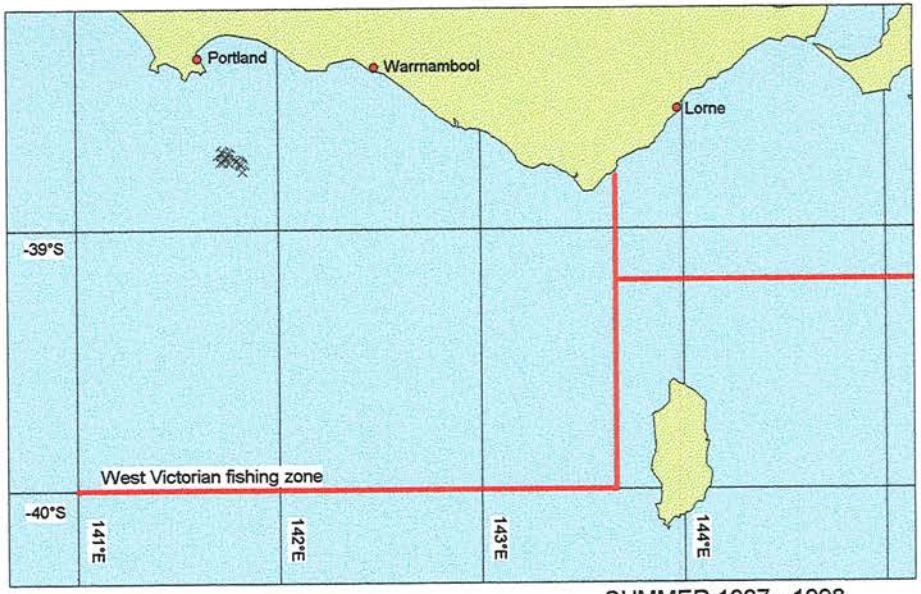
Male



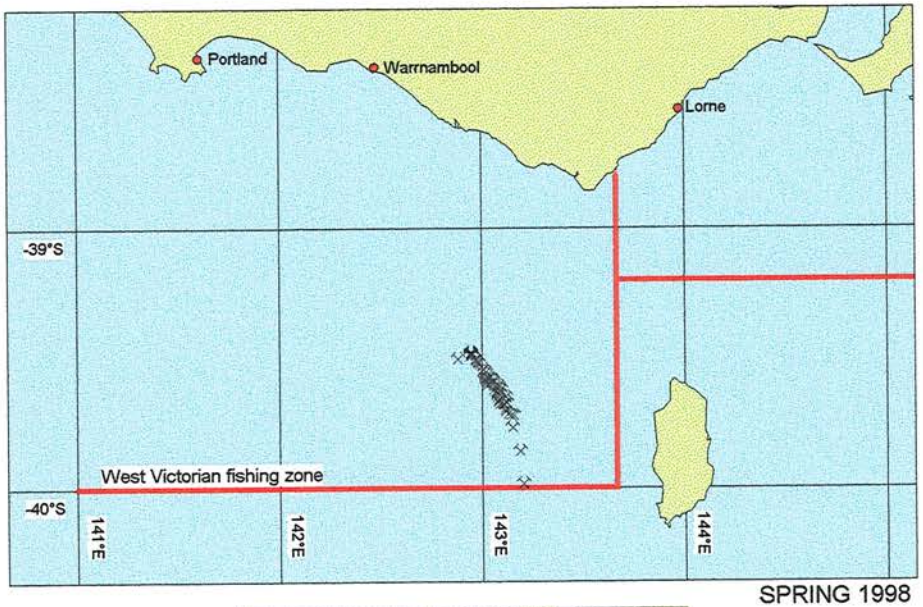
Western Victoria Spring 1995



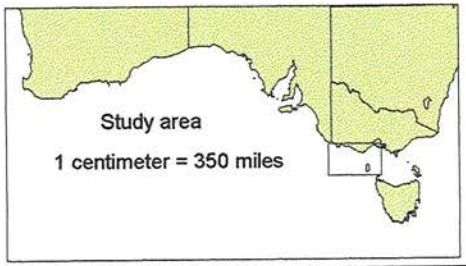
AUTUMN 1996



SUMMER 1997 - 1998

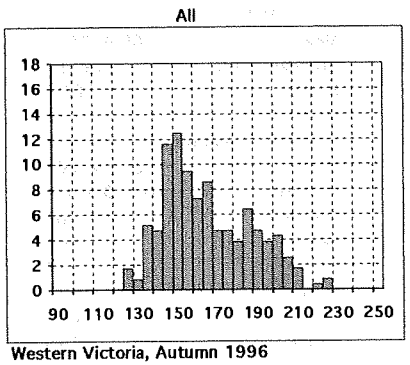


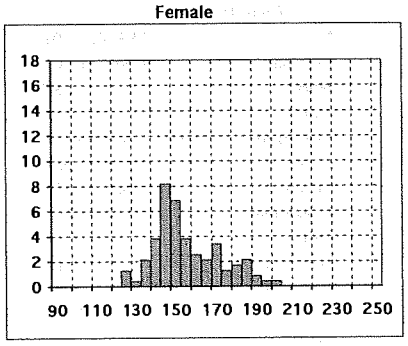
SPRING 1998

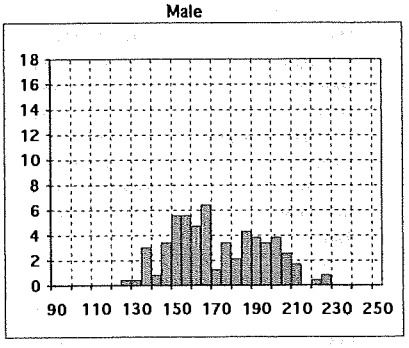


Sampling locations for western Victoria

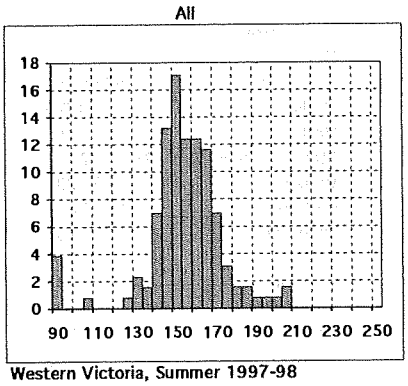
Scale:
1 centimeter = 20 miles

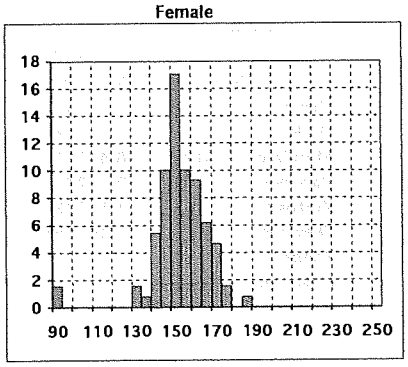


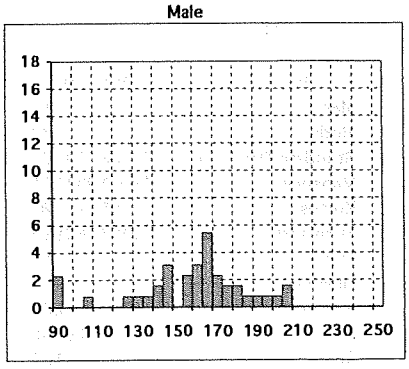




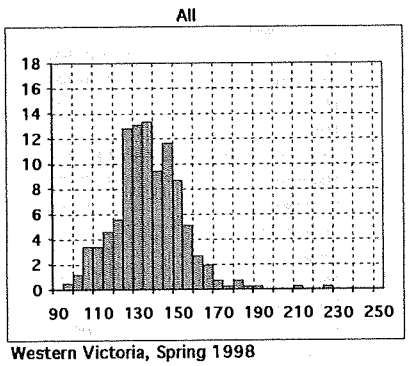
Western Victoria, Autumn 1996

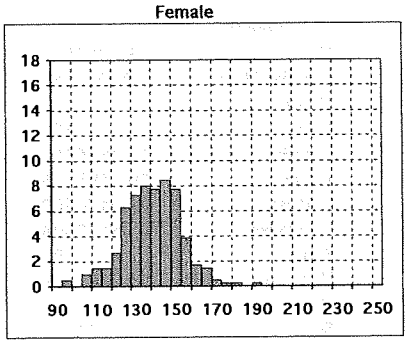


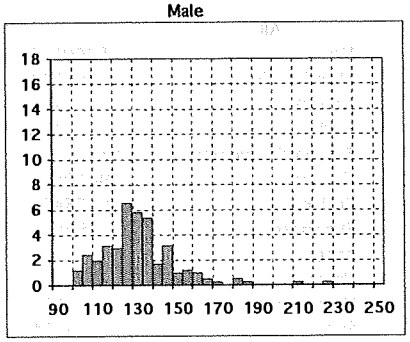




Western Victoria, Summer 1997-98







Western Victoria, Spring 1998

Appendix 2

Giant Crab

Catch and Effort proforma

Start a new page for each trip

Boat Number	Skippers name
Are you using Metres or Fathoms? Circle which unit is in use	

Please complete for each line hauled.						Count Legal Catch		Count Discarded Catch		
								Undersized		*Too big*
Date	Latitude	Longitude	Days Soak	Number of pots in line	Average depth	Male	Female	Male	Female	Male

Unloaded Date Processor

Were all crabs unloaded Y/N

If not how many kgs left? ....kgs

Write down price/kg and weight of each size group

	<3kg	3-5kg	> 5 kg
Price/kg			
Weight			

Your Observations

Source: A Levings, Deakin University Giant Crab Research Project

Appendix 3

Morphology of the mouthparts, gastric mill and digestive tract of the giant crab,
Heeron, T. and Mitchell, B. 1997.

Mar. Freshwater Res., 1997, **48**, 7–18

Morphology of the mouthparts, gastric mill and digestive tract of the giant crab, *Pseudocarcinus gigas* (Milne Edwards) (Decapoda: Oziidae)

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Abstract. Digestive tract histology, morphology of feeding appendages and gastric mill, and examination of gastric contents showed *P. gigas* to be carnivorous. The digestive tract showed typical decapod form and consisted of oesophagus, anterior and posterior gastric chambers, and midgut and hindgut segments. Dimorphic crushing-type chelipeds present food to the third maxillipeds. The mandibles and third maxillipeds tear the food; however, large fragments still reach the anterior gastric chamber. The mandibles are dimorphic, with the right mandible possessing a pointed beak-like structure. The ossicles of the gastric mill are blunt and used to grind and crush the ingested food. Dietary analysis showed predation on asteroid starfish and gastropod molluscs.

Introduction

The giant crab, *Pseudocarcinus gigas*, was first described by Jean-Baptiste Lamarck in 1818. Since that time, there has been little research on the biology and ecology of Australia's largest marine crustacean. *P. gigas* is a large (up to 14 kg) xanthoid characterized by a thick exoskeleton and heavy crushing-type chelae. Xanthoids typically have a lumbering, slow habit suggesting that live prey is slow-moving (Skilleter and Anderson 1986). *P. gigas* is distributed along the southern coastline of Australia, inhabiting the edge or upper slopes of the continental shelf at depths between 20 and 600 m (Levings and Mitchell 1994). The substratum in this region is predominantly sandy to silty.

Observations on the structure of the decapod digestive tract have focused mainly on commercially important species (Dall 1967; Rigdon and Mensik 1976; Bell and Lightner 1988). The digestive tract of brachyuran crabs has been described in only a few cases (Barker and Gibson 1978; Johnson 1980). The morphology of feeding structures can be used as a guide to dietary preferences and modes of feeding (Warner 1977; Skilleter and Anderson 1986; Woods 1993). The present study examined the chelipeds, mouthparts and gastric ossicles of *P. gigas* in relation to the gastric contents.

Materials and methods

P. gigas specimens were captured by deep-sea trawling methods from the waters of Bass Strait at depths between 300 and 420 m off Portland (38°20′S,141°35′E) in south-western Victoria, Australia. The crabs were killed immediately by freezing in ice aboard the trawling vessels, thereby arresting digestion. Animals required for histological examination were killed by inducing a chill coma but were not allowed to freeze solid.

In all, 54 animals (21 males and 33 females) in the size range of 156–295 mm carapace width were examined. The chelipeds, mouthparts and gastric mill were removed from six of the largest specimens and preserved in 4% neutral buffered formaldehyde for at least 24 h. Each structure was photographed and the colour plates were scanned into a computer so that line drawings could be produced with a graphics program.

The foregut of each crab was removed and the contents were preserved in 4% neutral buffered formaldehyde for dietary analysis. After fixation the stomach contents were washed in a fine sieve and transferred to water-filled Petri dishes for microscopic examination.

The digestive tract was removed whole, opened and emptied of its contents and then fixed in 4% neutral buffered formaldehyde for 48 h. After fixation the digestive tract was macroscopically examined, measured and described with representative sections taken from the oesophagus, anterior chamber, posterior chamber, midgut and hindgut. These blocks underwent routine histological processing and subsequent embedding in paraffin wax and were sectioned at a thickness of 3 μm with a Leitz hand microtome.

One section from each block was stained with haematoxylin and eosin (H&E) in an automated staining machine. These slides were assessed and basic structural anatomy of the sections was described. Sections that contained glandular tissue were stained by the periodic acid–Schiff reaction (PAS) for neutral mucins, the alcian blue method for acid mucins, and a combined alcian blue–PAS method. All staining techniques were adapted from Bancroft and Stevens (1982). Photomicrographs of representative areas from each section were taken at magnifications ranging from ×8 to ×20. The terminology used to describe the histological structures found in the digestive tract of *P. gigas* is based on previous work by Bell and Lightner (1988) in the penaeid shrimp *Penaeus stylirostris*.

Captive giant crabs were observed during feeding, and the behaviour and action of the chelipeds and mouthparts were noted.

Results

Structure and function of chelipeds

The chelipeds of *P. gigas* are dimorphic, with the right one being significantly larger than the left in both sexes ($P < 0{\cdot}001$ in females, $P = 0{\cdot}02$ in males). The right and left chelipeds of males are significantly larger ($P < 0{\cdot}001$ and $P < 0{\cdot}001$ respectively) (Fig. 1) than the right and left chelipeds of females of the same carapace length. Both chelipeds have a series of longitudinal denticles that line the inner aspect of the dactylus and propodus. As the crab grows larger the chelipeds develop larger molariform pegs on the propodus. The dactylus and propodus also increase in length and tend to curve towards the body.

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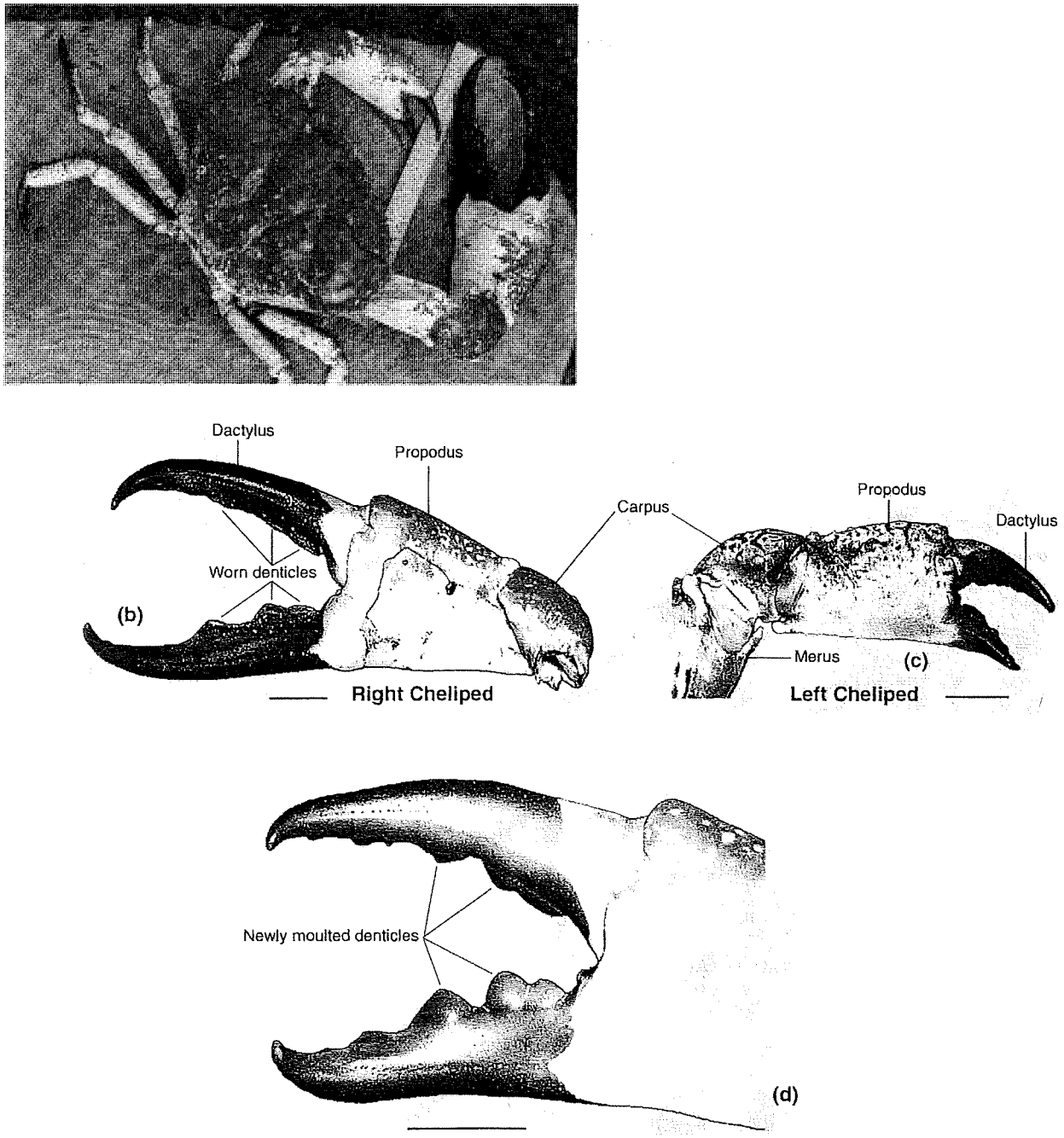

Fig. 1. Chelipeds of *P. gigas*. *(a)* Top view of *P. gigas* male, showing dimorphism of the chelipeds. The right cheliped is always the larger. The wooden rule measures 40 cm. *(b, c)* Dimorphic chelae of *P. gigas* male (carapace width 295 mm, carapace length 215 mm), medial view. *(d)* Close-up view of the right cheliped from a newly moulted individual, showing non-worn denticles. Scale bars, 50 mm.

When crabs in the tanks were presented with squid (*Loligo* sp.), food-seeking behaviour was initiated. When a crab located the food, using its outstretched walking pereiopods, it surrounded the food with its entire body and legs. The chelipeds were used to present the food to the third maxillipeds, which then gripped the food. The cheliped holding the food item was then pulled away from the mouth, thus tearing pieces from the food. The smaller fragments retained by the third maxillipeds were then processed by the mouthparts. Females used both chelipeds in a similar manner while feeding. Owing to the size of the right cheliped of the males, these were not used extensively for feeding. If food was gathered by this large cheliped, it was immediately transferred to the smaller left cheliped, which

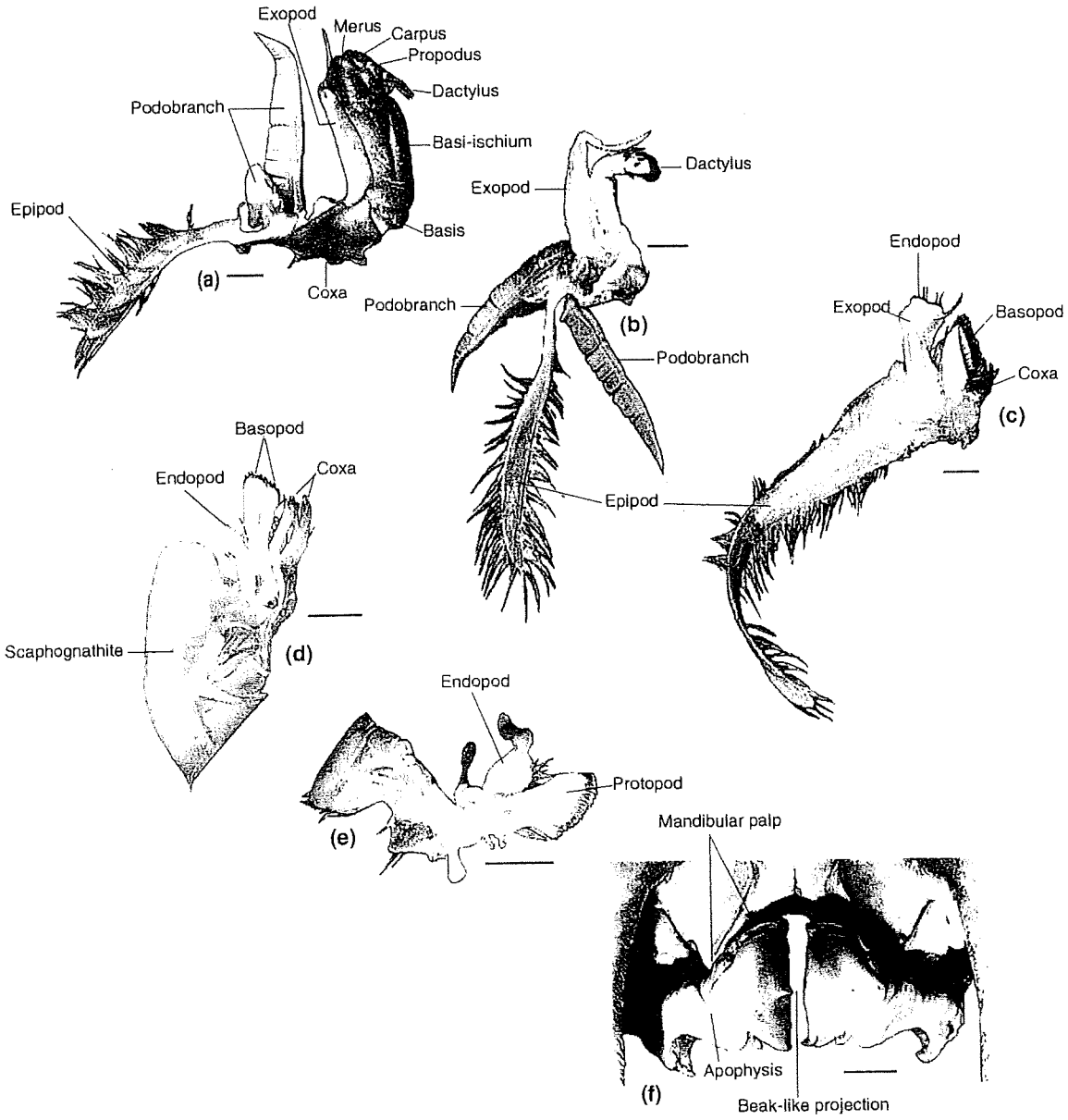

Fig. 2. Mouthparts of *P. gigas*. All mouthparts are right side, aboral view. *(a)* Third maxilliped. *(b)* Second maxilliped. *(c)* First maxilliped. *(d)* Maxilla. *(e)* Maxillule. *(f)* Mandibles *in situ*. Scale bars, 10 mm.

then proceeded to pass it to the third maxillipeds. The right cheliped appeared to be used predominantly to fend off other crabs if they strayed too close while feeding.

Structure and function of mouthparts

The general structure of the mouthparts is same as that of most decapod crustaceans described in the literature (Barnes 1968; Warner 1977; Barker and Gibson 1978; Phillips *et al.* 1980; McLaughlin 1983; Skilleter and Anderson 1986; Dorit *et al.* 1991). The mouthparts are identical in morphology in both sexes (Fig. 2).

Third maxillipeds. The description of the mouthparts is based on the terminology of Barker and Gibson (1978) and Skilleter and Anderson (1986). In the giant crab the basi-ischium is dorsoventrally flattened and the two third maxillipeds form a complete cover over the more internal mouthparts (Fig. 3). The entire aboral surface of the third maxilliped is covered by short golden setae. Longer setae are present on the dactylus and the medial edge of the merus and ischium (Fig. 2*a*). The medial edge of the ischium also bears very small cristae dentatae. A dense row of short golden setae along the medial edge of the ischium obscures

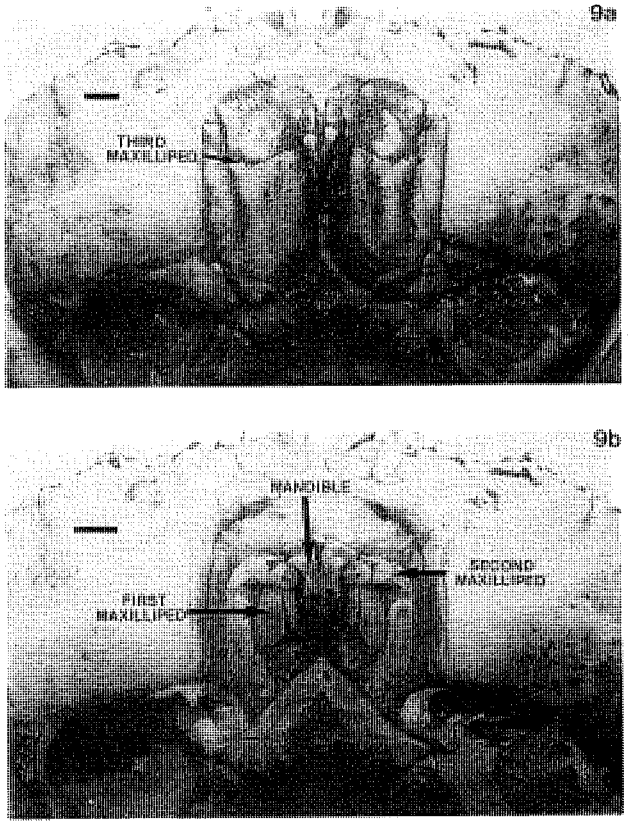

Fig. 3. Oral region of *P. gigas*. *(a)* The dorsoventrally flattened third maxillipeds completely cover the oral cavity. *(b)* The more internal mouthparts are exposed after the third maxillipeds have been removed. Scale bars, 10 mm.

the cristae dentatae in the aboral view. The oral surface of the ischium is devoid of setae with the exception of several individually isolated projections near the crista dentata that may be used for chemoreception.

During feeding the third maxillipeds hold food while the chelipeds tear pieces from the food. The smaller pieces of food are then transferred to the second maxillipeds.

Podobranchs and an epipod (gill cleaner) are attached to each third maxilliped and have a respiratory function. There is one large and one smaller podobranch attached to the coxa. The medial edges of the large dorsoventrally flattened epipod are lined by long golden setae that reached a maximum length of 20 mm in the specimen examined.

Second maxillipeds. The structure of the second maxilliped is similar to that of the third maxilliped (Fig. 2*b*). The exopod bears no setae, unlike the dactylus and propodus of the merus, which have short, thick, golden setae. These setae are inflexible and claw-like in nature, curving slightly towards the mouth. They are used to accept food from the third maxillipeds during feeding. The dactylus has two spots of dark-brown pigmentation on the aboral surface at the sites of origin of two small tufts of softer setae.

The second maxilliped also bears two large podobranchs and an epipod; the dorsal podobranch is larger than the ventral one. The epipod extends from the distal end of the coxa and its medial edge is lined by long setae similar to those of the third maxilliped.

First maxillipeds. The first maxilliped bears an epipod similar to those attached to the coxa of the other maxillipeds (Fig. 2*c*). However, it differs markedly in size, being almost twice as long and wide as the epipods on the other maxillipeds. The setae lining the medial edges are denser than those of the other two maxillipeds. The endopod has a sparse row of golden setae on its transverse ridge. The basopod bears two rows of short, stiff setae along its medial edge, one row being found slightly anterior to the medial edge. These setae are similar to those found on the dactylus and propodus of the second maxilliped but are slightly more flexible. The coxa bears longer, more flexible setae that form a dense tuft below the basopod. There is no podobranch associated with the coxa of the first maxilliped. The first maxillipeds also assist in manipulating food fragments.

Maxillae and maxillules. The maxilla is notable for its large dorsoventrally flattened scaphognathite (Fig. 2*d*). The basal endites are lined by short golden setae. The endopods of the maxillule bear short golden setae along their medial edge. The medial edge of the larger lobe of the maxillule is lined by short, inflexible setae (Fig. 2*e*). This lobe brushes the aboral surface of the mandible. These structures help push food into the buccal cavity once it has been processed by the mandibles and the maxillipeds.

Mandibles. The mandibles of the giant crab are dimorphic (Fig. 2*f*). The right mandible overlaps the left mandible and has a pointed beak-like process on the aboral surface that is absent on the left mandible. This feature was present in all animals examined. The medial edge of the mandibles is curved, sharp and darkly coloured. On the oral surface the mandibles possess a tooth-like structure near the ventral edge. These structures assist the mandibles in gripping food items. The mandibular palps arise dorsally from the apophysis of each mandible and lie in a depression in the posterior surface. The palps bear flexible, short, dense, golden setae that lie along the lateral edge. During feeding the mandibles crush food fragments that are transferred to them by the maxillipeds.

Digestive tract morphology and histology

Decapod crustaceans share a common digestive tract morphology consisting of three main parts: the foregut, the midgut and the hindgut. Both the foregut and the hindgut are ectodermal in origin and are lined by non-calcified cuticle.

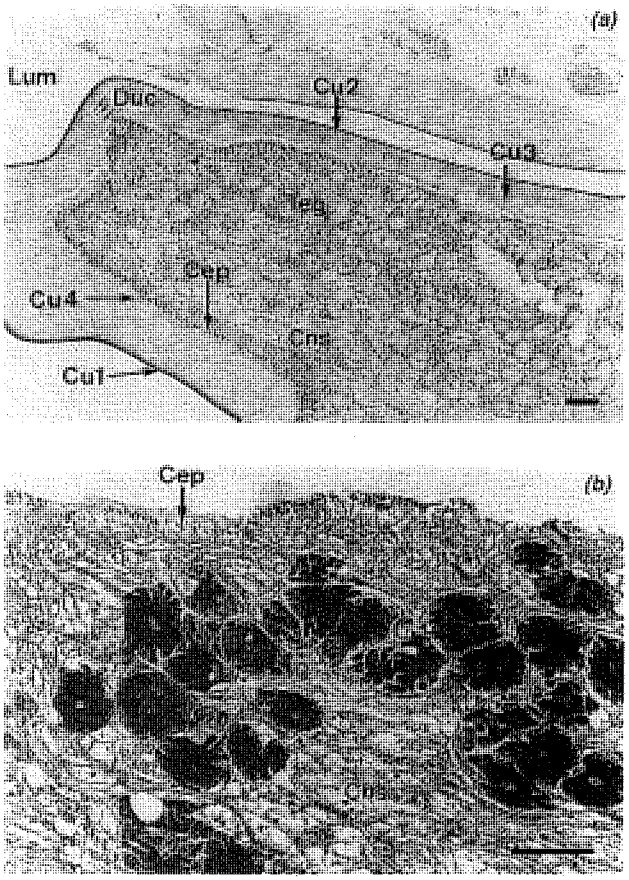

Fig. 4. *(a)* Oesophagus of *P. gigas*, showing the four-layered cuticle and tegumental glands (H&E staining). *(b)* Oesophageal tegumental glands (PAS staining). The cuticle has become detached during the staining process. Cep, cuboidal epithelium; Cns, spongy connective tissue; Cu1, epicuticle; Cu2, exocuticle; Cu3, endocuticle; Cu4, membranous layer; Duc, oesophageal ducts; Lum, intestinal lumen; Teg, tegumental glands. Scale bars, 10 μm.

The shorter midgut is endodermally derived and lacks a cuticle. This is the region in which assimilation takes place (Warner 1977; Dall and Moriarty 1983).

Foregut. The foregut is made up of a short oesophagus and a gastric chamber divided into two parts. The mouth lies posterior to the mandibles. The fleshy lips that surround the mouth comprise glandular tissue. The oesophagus begins behind the mouth and connects dorsally to the anterior chamber. This chamber is involved in the grinding of food and primary digestion.

Oesophagus. The histology of the oesophagus is depicted in Fig. 4. Tegumental glands, similar in morphology to those in the lips, line the oesophagus. The oesophagus examined had a maximum diameter of 8.4 mm and was 32·0 mm in total length (12·6% of total digestive tract length, 23·1% of total body length). The oesophagus is lined by a four-layered non-calcified chitinous cuticle. In H&E-stained sections the epicuticle (outermost layer) stains intensely blue and is strongly PAS-positive, whereas the exocuticle (second layer) and the endocuticle (third layer) stain light blue. The innermost or membranous layer is weakly basophilic, similar to the two layers immediately above it. The cuticle is smooth, does not show folding, and is generally uniform in thickness. A simple cuboidal epithelial cell layer underlies the cuticle. The cells have central nuclei and the cytoplasm contains neutral mucin. Supporting the cuticle and cuticular epithelium is a thick layer of spongy connective tissue that contains numerous mucus-secreting tegumental glands, the cells of which have basal nuclei. These glandular elements stain positively with PAS and alcian blue, indicating that they contain both neutral and acid mucins. In several places in the exocuticle there are small, oval lucent areas that represent ductal structures cut obliquely. These presumably connect the tegumental glands to the surface, although a direct communication was not identified in these sections.

Bundles of striated muscle are present within the connective tissue, there being a circular layer and, below this, a longitudinal layer of muscle bundles.

Anterior chamber. The maximum dimensions of the dissected gastric chamber were: length, 40.0 mm; width, 50.4 mm; height, 45.4 mm. This structure accounted for 15.7% of total digestive tract length and 28.8% of total body length. The anterior chamber wall is translucent, with the ossicles of the gastric mill being visible through the wall.

The anterior chamber (Fig. 5) is lined by a non-calcified cuticle that is divided into four layers as in the oesophagus. The thickness of each layer is, however, different from that of the oesophagus, with the exocuticle being thicker in the chamber. A simple cuboidal epithelial layer with central nuclei, similar to that seen in the oesophagus, is present in both the anterior and posterior chambers. There are no mucus glands present in the gastric chamber sections.

The proximal region of the anterior chamber is very similar to the oesophagus. At the base of the connective tissue, haemapoietic tissue is present. This is bounded by a thin basement membrane that encloses the young haematocytes. The circulatory vessels are endothelially lined and bundles of striated muscle are present within the connective tissue. The cuticle in the mid-chamber region is thick and convoluted and there are setae projecting from it into the lumen at irregular intervals. Bundles of striated muscle are present in this region. The gastric mill region has the same basic structure as the rest of the chamber. The cuticle is somewhat thickened and irregular. In the distal region, near the junction between the anterior and posterior chambers, finger-like projections extend into the lumen. A single layer of cuboidal structures resembling chondrocytes in mammals is present in the exocuticle.

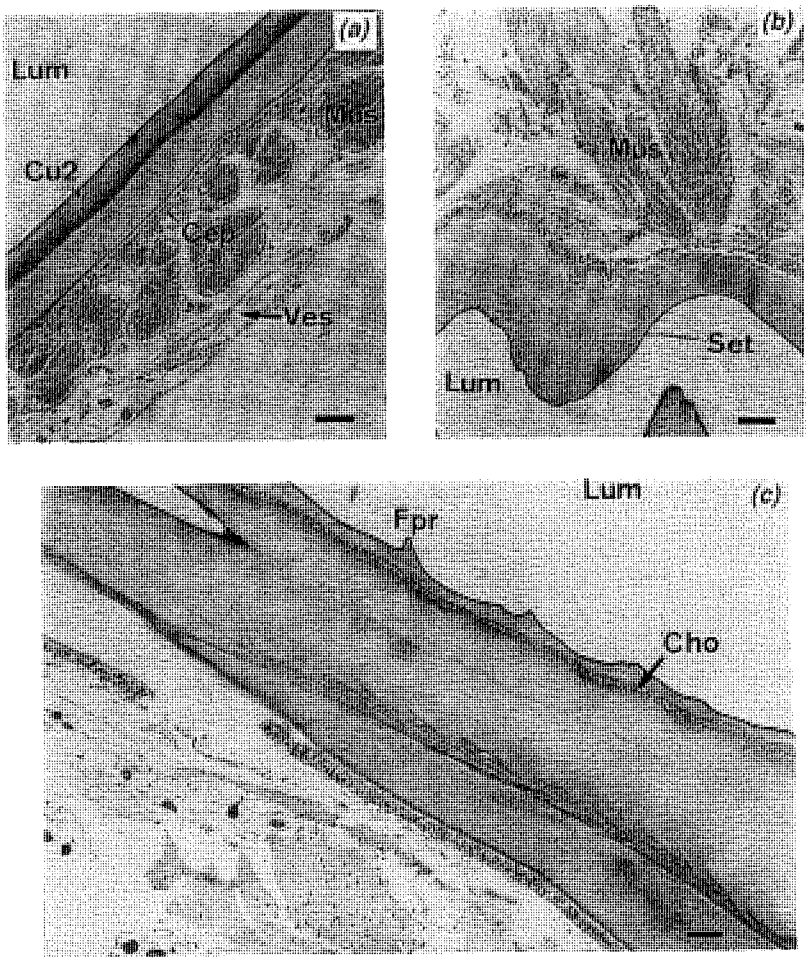

Fig. 5. *(a)* Proximal region of the anterior chamber of *P. gigas* (H&E staining). *(b)* Middle region of the anterior chamber, showing the thicker cuticle and a single setal element (H&E staining). *(c)* Gastric mill region (H&E staining). Cep, cuboidal epithelium; Cho, chondrocyte-like cells; Cu2, exocuticle; Fpr, finger-like projections; Lum, intestinal lumen; Mus, striated muscle; Set, gastric seta; Ves, circulatory vessel. Scale bars, 10 μm.

Gastric mill ossicles. *P. gigas* has three large gastric ossicles: one dorsal tooth (urocardiac ossicle) and two lateral teeth (zygocardiac ossicles) (Fig. 6). These ossicles are golden brown and have structural characteristics that resemble those described in other carnivorous crabs (Warner 1977; Skilleter and Anderson 1986; Creswell and Marsden 1990). Individual muscle bundles are connected to each ossicle, allowing independent movement.

The dorsal tooth is a rounded, smooth projection that grinds against the molar surface of the two lateral teeth. The dorsal tooth carries two pairs of small setose brushes, one pair laterally and one pair dorsally. The setae are short and present as single ridges only. The molar process of each lateral tooth is relatively flattened anteriorly and has 14 narrow vertical ridges posteriorly.

On the ventral surface of the gastric mill region there is a hardened plate that has setae on its lateral and dorsal edges. The accessory teeth described in some other decapods appear to be absent in the gastric mill of *P. gigas*. The chamber lining around the gastric mill has areas densely covered by setae.

Posterior chamber. Once processed, food passes into the posterior chamber via a connecting valve that prevents food from returning to the anterior chamber. Food that has been ground by the gastric mill is filtered and sorted in this chamber. The posterior chamber is lined by a non-calcified cuticle whose thickness is similar to that in the mid region of the anterior chamber. The structure of the rest of the wall is also similar to the wall of the anterior chamber. The gastric sieve (Fig. 7) is a triangular structure located within the posterior chamber. Evenly spaced setae project from it, allowing the passage of only liquid and fine particles. The ends of the setae appear to be ciliated. The finer particles and

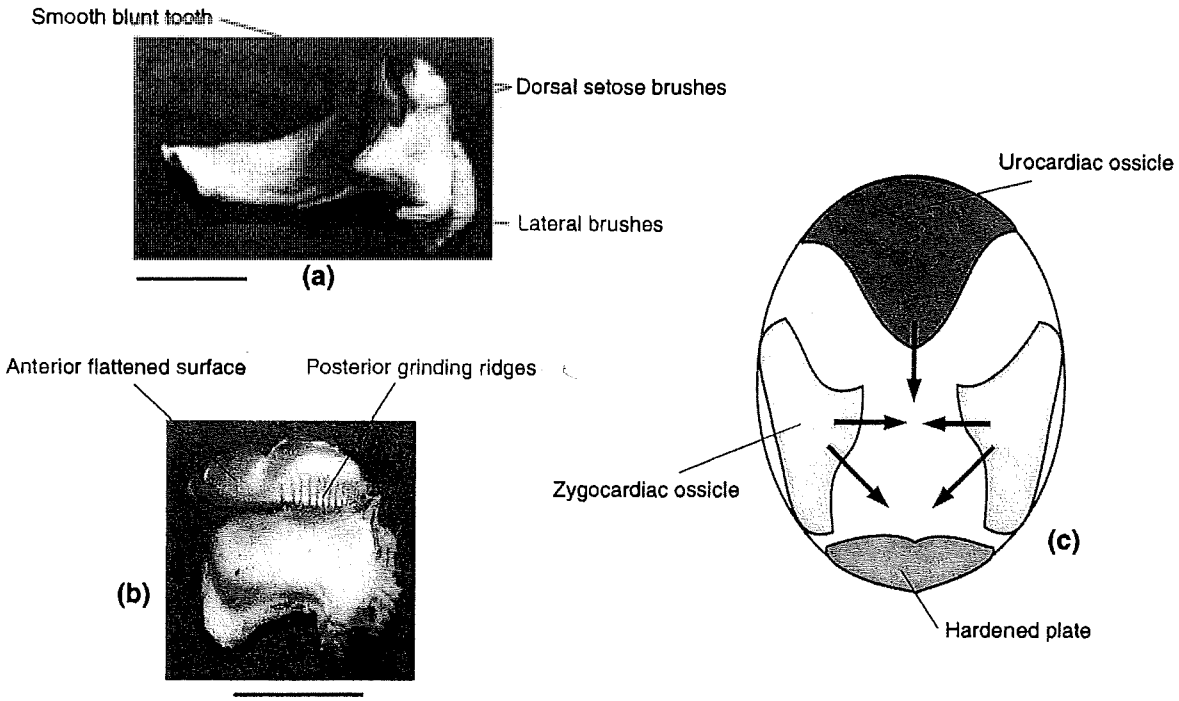

Fig. 6. Gastric ossicles of *P. gigas*. *(a)* Lateral view of the urocardiac ossicle, showing the smooth, blunt tooth and the setose brushes. *(b)* Lateral view of the right zygocardiac ossicle, showing the anterior flattened surface and the posterior grinding ridges. Scale bars, 10 mm. *(c)* Schematic diagram showing the position of the gastric mill ossicles and their relative action as seen from the anterior aspect.

juices then enter the filter-press, via the longitudinal inter-setal grooves, for direct absorption by the digestive gland. The pores of the filter-press are uniform in size and almost equidistant from each other. Larger particles and indigestible matter pass through the distal region of this chamber into the midgut.

Midgut. The midgut (Fig. 8) opens directly behind the posterior chamber. The duct of the digestive gland (hepatopancreas) opens ventrally into the midgut. It is here that enzymatic digestion is begun and absorption of food by the digestive gland occurs. The midgut of the specimen examined was 3·6 mm in diameter and 60 mm in length (23·6% of total digestive tract length, 43·3% of total body length). The midgut lumen is not lined by a cuticle, as is the rest of the digestive tract. It is lined by a layer of pseudostratified columnar epithelial cells. There is condensation of PAS-positive material along the luminal border of the epithelial cells, with a small amount of non-PAS-positive material in a more luminal location, suggesting that these cells have a brush border. The basement membrane is thick and convoluted and there is a vertically laminated structure immediately below it that is similar in appearance to the circular muscle layer described in the penaeid shrimp (Bell and Lightner 1988). Haemapoietic cells are found in the haemolymphatic space between the vertically laminated muscle layer and the basement membrane and in places are seen extending through the muscle layer to form a layer beneath it. Dense connective tissue supports the epithelium. No bundles of striated muscle are seen in the connective tissue.

Hindgut. At the midgut–hindgut junction the pseudostratified columnar epithelium of the midgut becomes covered by the non-calcified cuticle of the hindgut proper. Just proximal to the junction (Fig. 9), large numbers of tegumental glands lie below the epithelium, forming a circular ring of mucus-secreting glands around the gut. Ducts are seen in cross-section in the cuticle that are similar to those seen in the oesophagus. Although the ducts are not seen directly communicating with the tegumental glands, it can be assumed that this is the means by which mucus passes from the glands to the surface. These glands secrete the muco-peritrophic membrane that encloses the faeces, producing the characteristically long faecal pellets observed in decapods. The midgut-hindgut junction of the specimen examined measured 6.8 mm in diameter. According to the staining for mucins, two types of cells are present at the site that produces the muco-peritrophic membrane. The group of glands immediately below the epithelium are alcian-blue-positive, indicating the presence of acid mucins. The other glands, which lie beneath the first group, stain with both PAS and alcian blue, indicating that they contain a mixture of both neutral and acid mucins.

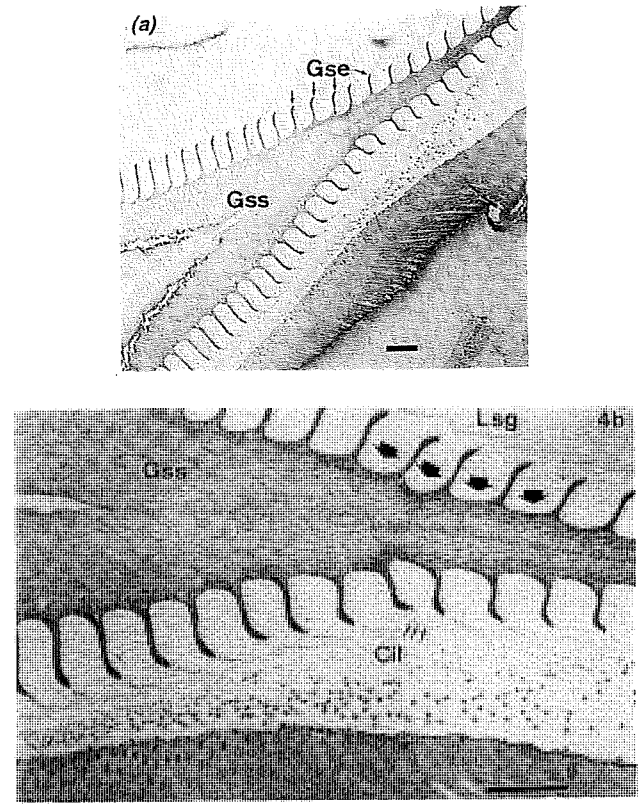

Fig. 7. *(a)* Gastric sieve of *P. gigas*, showing the triangular form of this structure. The inter-setal grooves lie between the evenly spaced setal elements (H&E staining). *(b)* Magnified view of gastric sieve, showing the ciliated ends of the gastric sieve setae (H&E staining). Cil, ciliated ends of gastric sieve setae; Gse, gastric sieve setae; Gss, gastric sieve; Lsg, longitudinal inter-setal grooves. Scale bars, 10 μm.

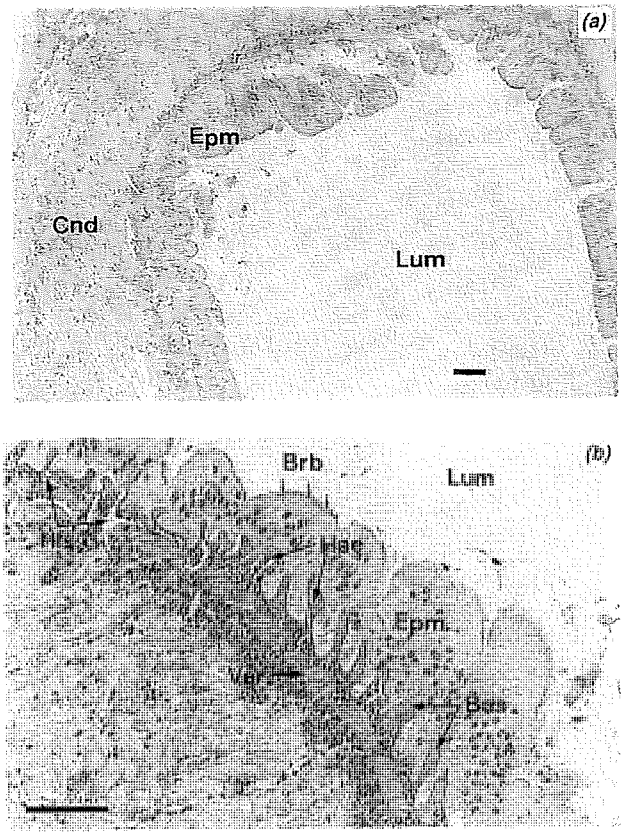

Fig. 8. *(a)* Midgut of *P. gigas*, showing the pseudostratified columnar epithelium, which is not lined by a cuticle (H&E staining). *(b)* Magnified view of midgut, showing the brush border of the epithelial cells and the thickened basement membrane with underlying haemapoietic cells (PAS staining). Bas, basement membrane; Brb, microvillous brush border; Cnd, dense connective tissue; Epm, pseudostratified columnar epithelium; Hae, haemapoietic cells; Hls, haemolymphatic space; Lum, intestinal lumen; Ver, vertically laminated muscle bundles. Scale bars, 10 μm.

The hindgut proper (Fig. 10) is the posterior continuation of the midgut, extending distally until it reaches the anus. It is lined by a non-calcified cuticle and in the specimen examined measured 122 mm in length (48·0% of total digestive tract length, 88·1% of total body length) and 3·7 mm in diameter. Longitudinal folds consisting of bundles of striated muscle are present throughout the length of the hindgut. The cuticle is uniform in thickness, similar to the appearance in the oesophagus. The exocuticle is strongly PAS-positive. A simple columnar epithelial cell layer subtends the cuticle, and spongy connective tissue supports the epithelium and cuticle. No mucus glands are present in the proximal region of the hindgut, but occasional mucus glands that are both PAS- and alcian-blue-positive are seen in the distal region of the hindgut, indicating the presence of both neutral and acid mucins respectively.

The longitudinal folds present in the hindgut of the giant crab extend to the anus. The maximum anal diameter in the specimen examined was 9·0 mm. Circular muscle bundles are seen surrounding the anus. Spongy connective tissue is found above and below this muscle layer. Scattered longitudinal muscle bundles are seen, deeper than the circular muscle. No glandular tissue is present in the anus. Vascular structures similar to those seen in other regions of the digestive tract are present.

Diet

Owing to the action of the gastric mill, food fragments could not be identified to species level. Some food items occurred more frequently than others, although some less frequent food items were present in larger volumes (Table 1). A more detailed analysis of the diet of *P. gigas* in this study can be found in Levings *et al.* (in press).

Organisms found in the gastric chamber of *P. gigas* were classified into the following seven categories of food items:

(1) Anomura. This group contained fragments of hermit crab (Paguroidea), including pieces of carapace, walking legs and mouthparts.

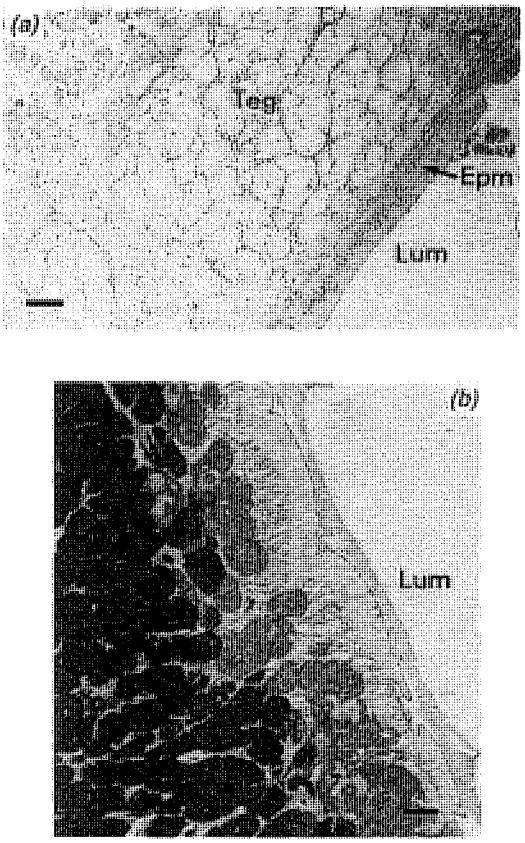

Fig. 9. *(a)* Midgut–hindgut junction of *P. gigas*, showing a large group of tegumental glands (H&E staining). *(b)* Differentially stained tegumental glands. The paler coloured glands contain acid mucins, whereas the more darkly coloured glands contain a combination of both acidic and neutral mucins (alcian blue–PAS staining). Epm, pseudostratified columnar epithelium; Lum, intestinal lumen; Teg, tegumental glands. Scale bars, 10 μm.

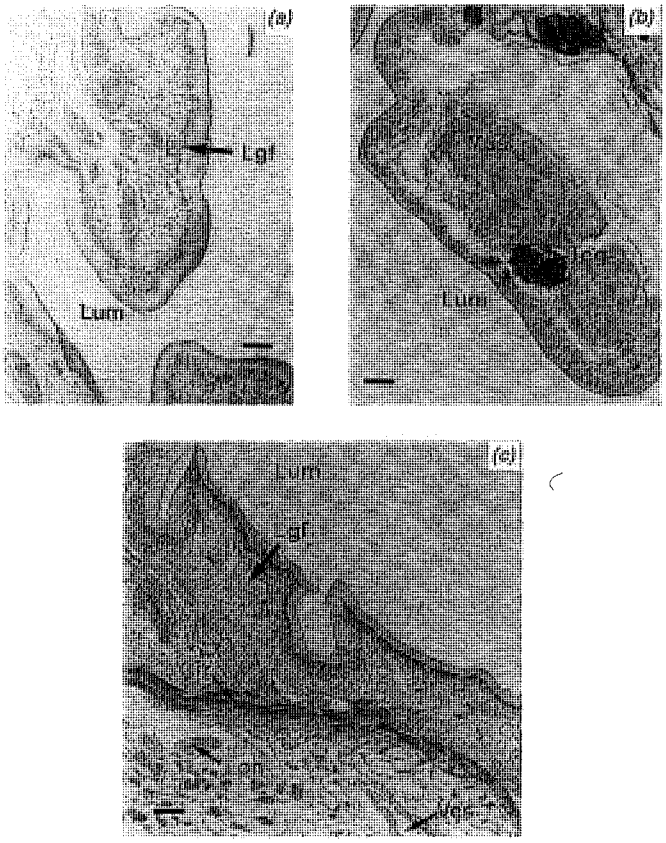

Fig. 10. *(a)* The hindgut of *P. gigas* is lined by cuticle and shows longitudinal folding (H&E staining). *(b)* Occasional tegumental glands are seen in the distal region of the hindgut (PAS staining). *(c)* The anus of *P. gigas* shows a circular ring of muscle tissue (H&E staining). Cir, circular muscle bundle; Lgf, longitudinal folds; Lon, longitudinal muscle bundle; Lum, intestinal lumen; Mus, striated muscle; Teg, tegumental gland; Ves, circulatory vessel. Scale bars, 10 μm.

(2) Asteroidea. This category contained only one species of starfish. This species could not be identified. It was recognized from skeletal ossicles and plates.

(3) Brachyura. This category consisted of both spider crabs (Majidae) and other giant crabs (*P. gigas*). These items included fragments of carapace, parts of walking legs and mouthparts. The fragments in this category were heavily masticated but still recognizable.

(4) Carrion. This food category contained items that were most likely ingested during scavenging. Included in it were equine or bovine hair and down feathers of unknown origin. No proteinaceous material was seen associated with these structures. This may indicate that the tissue had been processed before the gastric chamber was examined or that these items were ingested whole without any flesh attached.

(5) Gastropoda. This group consisted of two species of gastropod. A white-shelled species was present as shell fragments, making identification impossible. The other species present was represented by flat, brown operculi. These were always found intact but could not be identified. The two types of molluscs were considered to be separate species as parts of either could be found in a chamber in the absence of the other.

Table 1. Percentage occurrence and mean percentage volume of the seven categories of food items found in the gastric chamber of *P. gigas*

Category	Occurrence (%)	Mean volume (%)
Anomura	9·1	12·0
Asteroidea	31·8	33·3
Brachyura	13·6	4·3
Carrion	9·1	15·0
Gastropoda	40·1	7·6
Osteichthyes	13·6	25·0
Unidentified	40·1	33·7

(6) Osteichthyes. This group consisted of fragments of teleost fish. The scales, aural otoliths and skeletal elements were all identifiable, but the species to which they belonged could not be determined. These fragments were probably consumed as carrion, as the size of these fish suggests that they would be too fast-moving to be captured by the crab.

(7) Unidentifiable proteinaceous material. This category consisted of material that appeared similar under the microscope in all the gastric chambers in which it was present. It could not, however, be identified. It may represent the remains of a soft-bodied organism such as a cnidarian, but this could not be established.

The contents of *P. gigas* gastric chambers did not contain any evidence of sediments or other material that might have been inadvertently ingested during benthic feeding. Plant material was also absent from all chambers.

Discussion

Structure and function of chelipeds

The chelipeds of *P. gigas* are the largest chelipeds of any known decapod crustacean (Hale 1927). The dimorphism is similar to that in another xanthoid crab, *Ozius truncatus*, in which the right cheliped is also larger than the left (Skilleter and Anderson 1986). The larger cheliped of the male giant crab is reportedly used for territorial protection and during copulation, when it is used to hold the female close to the male while sperm is being transferred (Levings, personal communication).

The morphology of feeding structures can to some extent elucidate the mode of feeding and dietary preferences of a crab (Warner 1977; Skilleter and Anderson 1986). The shape and size of the chelipeds determine how the crab will manipulate and process food (Vermeij 1977). The chelipeds of carnivorous crabs have evolved into either crushing or cutting forms (Warner 1977), the form of the cheliped and the structure of the denticles being the chief distinguishing features. *P. gigas* possesses chelipeds of the crushing type that are very large and have large hardened triangular denticles on the inside margins of the dactylus and propodus. Similar denticles have been noted in other carnivorous crab species that feed on molluscs and other hard food items (Vermeij 1977; Williams 1978; Zipser and Vermeij 1978; Grahame 1983; McLaughlin 1983; Lowell 1986; Schram 1986; Skilleter and Anderson 1986).

The males of the genus *Uca* exhibit strong sexual dimorphism, with the right cheliped becoming hypertrophied for use in mating rituals and territorial displays; only the minor cheliped is used for feeding, and the feeding period per day must be increased to compensate for the functional loss of one feeding cheliped (Grahame 1983). This is more extreme than in the males of *P. gigas*, in which the larger cheliped can be used to gather food and the smaller cheliped presents the food item to the mouthparts and helps to tear pieces from it. Females, which have two smaller chelipeds, are able to process their food much more quickly. As the chelipeds of either sex enlarge through normal growth, the crab loses the ability to close them completely without leaving a gap between the denticles. This is due to the growth and curvature of the distal ends of the dactylus and propodus. This means that larger food items that can be held and crushed by the chelipeds must be sought as the animal grows.

Structure and function of mouthparts

The mouthparts of *P. gigas* show adaptations for a carnivorous diet. The third maxillipeds have small cristae dentatae that aid in gripping food presented to them by the chelipeds. Similar structures used for gripping large food items have been observed in the carnivorous crab *O. truncatus* (Skilleter and Anderson 1986) and the portunids (Borradaile 1922; Caine 1974; Williams 1978). The stiff setae of the second maxillipeds may play a role in removing food fragments from the setae on the basipod and coxa of the first maxilliped.

Descriptions of the morphology of the mandibles of other brachyuran species (Williams 1978; McLaughlin 1983; Skilleter and Anderson 1986) make no reference to a beak-like projection on the aboral surface of the right mandible or to a molariform structure on the oral surface of both mandibles. *P. gigas* may use these structures to help grip, tear, puncture and crush food items, including mollusc shells that the chelipeds are still able to pick up but can no longer crush owing to the small size of the food item. This may be particularly important for the males, with the right cheliped so hypertrophied that closure of the dactylus and propodus is incomplete. This would affect the size of items that *P. gigas* could effectively crush and prey upon.

Digestive tract morphology and histology

Histological examinations of the crustacean digestive tract have focused mainly upon the structure and function of the digestive gland (Momin and Rangneker 1975; Al-Mohanna and Nott 1987). Where the whole animal or digestive tract has been sectioned and examined, the emphasis has been largely on penaeid shrimps (Dall 1967; Rigdon and Mensik 1976; Bell and Lightner 1988), with less investigation of the structure and function of the digestive tract of crabs (Barker and Gibson 1978; Johnson 1980). The histology of the digestive tract in *P. gigas* appears to be very similar to that described in other crustaceans.

Food is transported through the oesophagus by peristaltic movements from the contraction of muscles that line the oesophageal wall (Vonk 1960). This musculature is similar to that described in *Scylla serrata* (Barker and Gibson 1978). The mucus-secreting tegumental glands that line the wall of the oesophagus aid in lubrication of food fragments during their passage through the oesophagus (Johnson 1980).

The cuticle that lines the oesophagus, gastric chamber and hindgut is divided into four layers with an underlying epithelial layer. A similar structure has been described in the penaeid shrimp, *Penaeus stylirostris* (Bell and Lightner 1988). It is non-calcified, which allows it to be flexible enough to withstand peristaltic contractions while being strong enough to provide protection against hard and sharp food fragments.

The anterior chamber is lined by a thicker cuticle than the oesophagus, possibly reflecting both the grinding and storage functions of this region. There are no tegumental glands present in the chamber wall. The cuticular lining of the gastric mill contains cartilage-like cells in the exocuticle, reflecting the greater structural integrity necessary in this region. The finger-like projections near the junction of the anterior and posterior chambers may aid in preventing reflux of processed food items back into the anterior chamber.

Despite processing by the mandibles and maxillipeds, the food fragments entering the anterior gastric chamber are still relatively large. The gastric mill ossicles of *P. gigas* are blunt and have few ridges associated with them, indicating that their function is one of pulverization. A similar functional morphology exists in another xanthoid, *O. truncatus* (Skilleter and Anderson 1986).

The structure of the gastric sieve and filter-press supports a role in filtering fine food particles (Bell and Lightner 1988). The morphology of the gastric sieve suggests that food passed into it is divided, some being directed towards the midgut and some towards the digestive gland ducts. It is not clear from the histology whether this is purely a random division of the material presented to it or whether the sieve discriminates between different elements of the food matter and preferentially passes some elements one way and other elements the other way.

The midgut is the only part of the digestive tract that is involved in the active absorption of food particles from its lumen (Dall and Moriarty 1983). This is reflected in the fact that it is not lined by cuticle, which would prevent nutrient movement across it. The lumen is lined by a pseudocolumnar epithelium that has a brush or microvillous border. This increases the absorptive surface area of the midgut. Similar brush borders have been previously described in other decapods (Barker and Gibson 1978; Dall and Moriarty 1983; Bell and Lightner 1988). The abundance of the haemolymphatic spaces below the basement membrane suggests that the nutrients are assimilated via the epithelial cells of the midgut and then transported by the haemolymphatic system to other parts of the body.

The midgut–hindgut junction contains numerous tegumental glands. The two different types of mucus-secreting cells present in this region are related to the production and subsequent lubrication of the muco-peritrophic membrane. It is not possible from the histology alone to be certain if both types of glands contribute to both the production and lubrication functions or whether each is responsible for only one of these functions. However, a similar combination of tegumental glands secreting acid and neutral mucin is found in the oesophagus, where these glands produce mucins for lubrication.

The longitudinal ridges of the hindgut of decapods help expel the muco-peritrophic membrane and its contents by grasping it and rhythmically moving it along the hindgut (Dall and Moriarty 1983). The ridges observed in *P. gigas* serve a similar function, with the musculature of the hindgut helping to propel the faeces out through the anus by peristaltic movements. The scattered mucus glands seen in the distal hindgut most likely play a lubricatory function. The circular ring of muscle seen at the anus may function as a sphincter.

Diet

The contents of the anterior chamber of *P. gigas* were consistent with the hypothesis that the slow-moving *P. gigas* is a benthic predator and scavenger. Identification to species level was mostly not possible. The crabs clearly scavenge fish cast off after trawling operations, which are prevalent in the study area. Similar observations have been made in other brachyuran crabs that inhabit areas subject to commercial fishing (Wassenberg and Hill 1987; Cartes 1993).

The digestive tract histology of the giant crab is similar in many respects to that seen in other decapod crustaceans. Although the histology of the digestive tract throws some light on the manner in which food is processed, it is not useful as a guide to diet.

Acknowledgments

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