Distributions, relative abundances and reproductive biology of the deep-water crabs *Hypothalassia acerba* and *Chaceon bicolor* in southwestern Australia

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This thesis is presented for the Degree of Doctor of Philosophy from Murdoch University, School of Biological Sciences.
DECLARATION

I certify that I am the author of this thesis, and that it has not previously been submitted for the award of a degree.

Any assistance that I have received during my PhD candidature, including the writing of this thesis has been dutifully acknowledged. All sources of information have also been accurately acknowledged.

__________________
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Abstract

Three species of large crab are found in Western Australian waters, namely the champagne crab *Hypothalassia acerba*, the crystal crab *Chaceon bicolor* and the giant crab *Pseudocarcinus gigas*, all of which are fished commercially in these waters. This thesis reports the results of studies carried out on the biology of the first two species, for which there were previously very little information. The results increase our knowledge of the benthic fauna in deeper waters off the southwestern Australian coast and provide data that can be used by fisheries managers to develop plans for conserving the stocks of *H. acerba* and *C. bicolor*.

The champagne crab *Hypothalassia acerba* is found southwards of Kalbarri at ~ 27°S, 114°E on the west coast and eastwards to Eucla at ~ 32°S, 129°E on the south coast. There is a small commercial trap fishery for *H. acerba* on both the lower west and south coasts of Western Australia. However, on the west coast, *H. acerba* is managed as a single species fishery, whereas on the south coast it is a component of a multi-species fishery, which also includes the southern rock lobster *Jasus edwardsii* and *P. gigas*. On the west coast, the commercial catches of *H. acerba* increased sharply from ~ 1,500 kg in 1989 to reach maximum levels of 30-46,000 kg in 1997-99, reflecting a marked increase in fishing effort. However, it subsequently declined to essentially zero after 2000 due to effort shifting towards fishing for *C. bicolor*. Catches of *H. acerba* on the south coast peaked at 26-27,000 kg in 1997-98 but, in contrast to those on the west coast, remained relatively high in 2001 to 2003.

The crystal crab *Chaceon bicolor* occurs in water depths of ~ 450 to 1220 m around Australia and New Zealand. However the commercial fishery is almost entirely located between Carnarvon on the north-west coast at ~ 25°S, 113°E to approximately Windy Harbor at ~ 35°S, 116°E on the south coast. Commercial catches of *C. bicolor* in southwestern Australia, which came almost entirely from the lower west coast, rose from very low levels in
1997 to ~ 222,000 kg in 2001 and then remained close to this level in 2002 and 2003. These trends largely reflect an increase in fishing effort.

*Hypothalassia acerba* was sampled seasonally by setting traps at depths of 35, 90, 145, 200, 255, 310 and 365 m on the west and south coasts of Western Australia. Catch rates on the west and south coasts peaked sharply at depths of 200 and 145 m, respectively, but at similar temperatures of 16 - 17°C. The catches on those coasts contained 69 and 84% males, respectively. The carapace length of *H. acerba* declined significantly by 4 mm for each 100 m increase in depth. Males attained a greater maximum carapace length than females on both the west coast, *i.e.* 135 vs 113 mm, and south coast, *i.e.* 138 vs 120 mm. Furthermore, after adjustment to a common depth of 200 m, the mean carapace length of males was greater than females on both the west coast (96.6 vs 94.6 mm) and south coast (101.5 and 91.4 mm) and the latter difference was significant (*p* < 0.001). These results thus show that, for *H. acerba*, (1) the distribution is related to depth and temperature, (2) body size is inversely related to water depth and (3) males grow to a larger size and are more prevalent in catches than females. There was also evidence that the distribution of *H. acerba* changed slightly with season and that there was spatial partitioning by this species and other large deep water invertebrate predators.

The trends exhibited by reproductive variables demonstrate that *H. acerba* reproduces seasonally on the lower west coast, with ovaries maturing progressively between July and December and oviposition occurring between January and March. The characteristics of *H. acerba* on the south coast differed in the following ways from those on the lower west coast. (i) No ovigerous females and only two females with egg remnants were caught. (ii) Ovaries did not develop late yolk granule oocytes until females had reached a larger size. (iii) Investment in gonadal development was less. These results strongly suggest that conditions on the south coast are not as conducive for ovarian development and reproduction and indicate that females
migrate from the south to lower west coast for spawning. In contrast to *H. acerba, C. bicolor* reproduces throughout much or all of the year on the lower west coast, presumably reflecting its occupancy of far deeper waters where environmental conditions vary less during the year. Although the mean weights of ovigerous females of *H. acerba* and *C. bicolor* were not significantly different (*p > 0.05*), the mean fecundity of the former species (356,210) was significantly greater (*p < 0.001*) than that of the latter species (192,070). The relatively high fecundity of *H. acerba* may reflect adaptations by this species to optimise egg production during its relatively short breeding season.

The size at onset of sexual maturity (SOM) of the females of crustacean species, which is often used by fisheries managers for developing management plans for such species, is typically estimated using logistic regression analysis of the proportions of mature females in sequential size classes. The validity of this approach depends on the composition of the samples reflecting accurately that present in the environment. However, catches obtained by traps, a passive fishing method, typically contain disproportionately greater numbers of large crabs, whereas those obtained using active fishing methods, such as seine netting and otter trawling, will presumably represent far better the size composition of the population. Since *H. acerba* and *C. bicolor* could be caught in numbers only by using traps, comparisons between the influence of passive and active fishing methods were explored using the extensive data previously collected for *Portunus pelagicus* employing different sampling methods (de Lestang *et al.* 2003a,b). These data are analysed in order to demonstrate that the females of *P. pelagicus* caught by trapping were predominantly mature, whereas those obtained by seining and trawling contained numerous immature as well as mature females. The samples of females collected by trap are, therefore, clearly biased towards mature crabs. Consequently, for any size class, it would be predicted that the proportion of mature females in trap catches will be overestimated, thus shifting the logistic curve fitted to the proportions of mature crabs at each
size to the left, and thereby yielding an underestimate of the SOM. This conclusion is substantiated by the fact that the carapace width of female \textit{P. pelagicus}, at which 50\% of individuals reach maturity (SOM$_{50}$), was estimated to be markedly greater when using the proportion of mature females obtained by seine-netting and otter trawling collectively, \textit{i.e.} 101.1 mm, than by trapping, \textit{i.e.} 86.1 mm. From the above data for \textit{P. pelagicus}, it is considered likely that, through a greater vulnerability of mature females of these species to capture by traps, the respective SOM$_{50}$s derived for female \textit{H. acerba} and \textit{C. bicolor} from trap samples (\textit{i.e.} carapace lengths of 69.7 and 90.5 mm) will represent considerable underestimates of the true SOM$_{50}$s.

Many workers have assumed that the chelae of male crabs undergo a change in allometry at the pubertal moult and that this could thus be used as the basis for determining the size of those crabs at morphometric maturity. Since initial plots of the logarithms of propodus length and carapace width (CW) of the males of \textit{P. pelagicus} and carapace length (CL) of the males of \textit{H. acerba} and \textit{C. bicolor} revealed no conspicuous change in allometry, the question of whether the chelae of these species undergo such an allometric change was explored statistically. The Akaike and Bayesian Information Criteria were thus used to ascertain whether a linear, quadratic, broken stick or overlapping-lines model best represented the above logarithmic size data. Since the broken stick model provided the best fit for \textit{P. pelagicus}, the chelae of this species does undergo allometric change. This occurred at 80.0 mm CW, which is $\sim$ 8 mm less than the CW at physiological maturity. In contrast, my analyses provided no evidence that the chelae of either \textit{H. acerba} or \textit{C. bicolor} exhibited an inflection and thus morphometric maturity could not be determined for these two species from chela length. Thus, managers will have to use the SOM$_{50}$ for physiological maturity, which was estimated to be 68.1 and 94.3 mm CL for \textit{H. acerba} and \textit{C. bicolor}, respectively.
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Chapter 1

GENERAL INTRODUCTION
1.1 THE OFFSHORE ENVIRONMENT

The earth’s surface comprises 12 main continental plates, which rise from the ocean floor to above sea level (Gardner, 1991). The continental slope is defined as the area that links the coastlines of these continents to the deep-water environment. The upper region of the continental slope is referred to as the continental shelf and typically comprises a narrow band of varying width. This surrounds the continents and slopes gradually downwards to the shelf break, *i.e.* that point where the continental shelf increases markedly in steepness. Continental shelves comprise 7.3% of the total surface area of the world’s oceans (Zezina, 1997). The shelf breaks are generally situated at water depths of approximately 150 to 200 m, while the continental slope continues downwards to the deep ocean floor, *i.e.* the abyss at water depths of 3000 to 6000 m (Postma and Zilstra, 1988).

The bathyal zone extends from the edge of the continental shelf to the beginning of the abyss and occurs at water depths of between 200 and 3000 m. It encompasses areas along the slopes of not only continents, but also seamounts and underwater rises (Zezina, 1997). The bathyal zone occupies 17.8% of the total surface area of the world’s oceans (Zezina, 1997).

1.2 CHARACTERISTICS OF THE DEEP-WATER ENVIRONMENT OF AUSTRALIA

1.2.1 Geomorphology

The continental shelf of Australia is narrowest (approximately 20 km wide) off the coast of New South Wales, where the shelf edge ranges from 80 m to more than 200 m in water depth. It is widest, *i.e.* > 295 km off north-western Australia, where the shelf break is deepest, *i.e.* > 450 m (Prescott, 1979). The continental shelf off the west coast of Australia is generally approximately 50 - 100 km wide and the shelf break occurs at water depths of 163 to 170 m (Collins, 1988). The continental slope is steepest (up to 27°) off the south-west coast of
Western Australia where it extends to the ocean floor at depths in excess of 4000 m (Prescott, 1979).

Near Perth in Western Australia, the upper continental slope has an average gradient of 59 to 90 m km$^{-1}$ (between 3 and 5º), with terraces occurring at 200 to 212 m and 236 to 242 m (Collins, 1988). Furthermore, west of Rottnest Island, the Perth Canyon incises the shelf about two kilometres seaward of the 200 m isobath (Collins, 1988). The sediments of the continental shelf off southwestern Australia consist mainly of calcareous and organogenic clastics (foraminiferans, broken shells, algal debris etc.) and re-worked quartz sands (Carrigy and Fairbridge, 1955). As water depth increases, particularly on the slope and past the shelf break, the percentage of silt and clay increases (Carrigy and Fairbridge, 1955). At approximately 720 m, benthic sediments consist of spicular ooze, i.e. mainly shell fragments, with smaller amounts of sponge spicules, foraminiferans and small fragments of gastropod molluscs (Carrigy and Fairbridge, 1955). Although the Perth canyon may accelerate the sedimentation rate to the deep-water from the continental slope off Perth, this has not been documented.

1.2.2 Oceanography

Southwestern Australia is bounded by the Indian Ocean to the west and by the Southern Ocean to the south. The Indian Ocean was once regarded by some oceanographers as the most complex and least understood of the world’s oceans (Colborn, 1975). The first investigation of its oceanography was undertaken in equatorial waters in 1947 - 1948 by scientists on the Swedish vessel, the Albatross, and in 1955 - 1956 by those on the French vessels Norse I and Norse II (Colborn, 1975). The International Indian Ocean Expedition in 1960 - 1965 was the first large scale international oceanographic study of the entire Indian Ocean. Unlike other continental shelves with equatorial boundary currents, there is no upwelling of nutrient-rich, bottom water along Western Australia’s continental shelf (Lenanton et al., 1991). In addition,
the Rottnest and Dirk Hartog continental shelves off Western Australia are located in a relatively arid region and thus receive sedimentary run-off from only a few rivers, some of which flow for only a few weeks of the year (Carrrigy and Fairbridge, 1955). As a result of the influx of only small amounts of nutrients, and thus of limited phytoplankton and zooplankton production, the fish stocks of Western Australia’s continental shelf are relatively depauperate (Lenanton et al., 1991; Williams et al., 2001), compared with those of other shelves where there are upwellings and high rates of sedimentation from land run-off.

The Leeuwin Current

The dominant current over the continental slope along the west coast of Australia is the Leeuwin Current, the characteristics of which have been well documented (Cresswell and Golding, 1980; Godfrey and Ridgway, 1985; Thompson, 1987; Pearce and Griffiths, 1991; Cresswell and Peterson, 1993; Nof et al., 2002; Feng et al., 2003; Morrow et al., 2003; Cresswell and Griffin, 2004). The Leeuwin Current consists of a broad body of warm, low salinity tropical water originating off north-west Australia and flowing southwards at speeds of up to 0.4 m s\(^{-1}\) along the continental shelf, from the Abrolhos Islands, around Cape Leeuwin and across the Great Australian Bight (Hatcher, 1991). Eddies are a prominent feature of the Leeuwin Current, \textit{i.e.} masses of circulating water which spin off the margins of the main body of the Leeuwin Current seaward in a southerly direction (Legeckis and Cresswell, 1981; Pearce and Griffiths, 1991; Pearce and Pattiaratchi, 1999). These eddies can result in small upwellings of colder nutrient-rich water to the surface. The Leeuwin Current occurs throughout the year, but is strongest between May and September (Cresswell and Golding, 1980). At its strongest, the Leeuwin Current can penetrate to water depths of at least 350 m (Pearce and Griffiths, 1991). Previous research has documented that the Leeuwin Current influences the distribution of finfish, coral, echinoderms, molluscs, macrophytes, seagrasses and

*The Capes’ Current*

Between November and March, strong northward wind stresses slow the Leeuwin Current and drive the northerly Capes’ Current, causing the Leeuwin Current to move offshore. The seasonal reversal of the direction of water flow off the southwestern Australian coast was first documented by Rochford (1969). The Capes’ Current is a cool inshore coastal current that is strongest between Cape Naturaliste and Cape Leeuwin (Pearce and Pattiaratchi, 1999). It can influence waters as deep as 1000 m, but its surface velocity is reduced by half at a depth of 370 m (Andrews, 1977).

*The Ningaloo Current*

Off the north-west coast of Australia, the dominant current along the inner-continental shelf between September and mid April is the Ningaloo Current (Taylor and Pearce, 1999). Flowing northward, seaward of the Ningaloo reef, the Ningaloo Current is driven by the south-east trade winds and strong diurnal coastal south-westerly sea breezes (Taylor and Pearce, 1999).

1.2.3  *Biota of the continental shelf and slope of Western Australia*

The first survey of the demersal fish fauna assemblages off the southwestern coast of Australia, which took place in 1991, revealed that clear transitions between species assemblages occurred at 250 to 350 m and at 700 to 800m (Williams *et al.*, 2001). Furthermore, these transitions coincided with the lower limits of the Leeuwin Current and the upper extent of the Antarctic Intermediate Water, respectively (Williams *et al.*, 2001). Antarctic intermediate water is
thought to reach southwestern Australia either from south of 40° S or from the Southern Pacific Ocean (Williams et al., 2001). In addition, the Leeuwin Current is thought to be responsible for the higher diversity of tropical fauna found in offshore than inshore regions of southwestern Australia. This is due to a regular supply and subsequent survival of tropical larvae in the offshore locations (Hutchins, 1994).

The relatively low fish densities recorded during the study by Williams et al. (2001) were attributed to the low productivity caused by the absence of upwelling associated with the Leeuwin current. The exceptionally high species diversity was credited to the overlap between independently evolved temperate and tropical faunas (Williams et al., 2001). A total of 388 species from 108 families were recorded, which represents 9% of the world’s deep-water fish species (Williams et al., 2001).

The elevated temperatures found within the southward-flowing Leeuwin Current facilitate the extension of the southerly distribution of tropical marine fish, corals, echinoderms and molluscs (Cresswell and Golding, 1980; Legeckis and Cresswell, 1981; Lenanton et al., 1991; Morgan and Wells, 1991) and tropical seagrasses (Walker, 1991). The Leeuwin Current also helps maintain the clear water environment which sustains the macrophyte communities and seagrass beds (Lenanton et al., 1991). These, in turn, support the flora and fauna upon which, amongst others, species such as the western rock lobster *Panulirus cygnus* George feed (Lenanton et al., 1991).

The Leeuwin Current also plays an integral role in facilitating recruitment and settlement by the western rock lobster (Pearce and Phillips, 1988; Phillips et al., 1991), the production of pilchards (*Sardinops sagax*) (Lenanton et al., 1991), scallop settlement in Shark Bay (Lenanton et al., 1991), egg and larval dispersal of the Western Australian salmon, *Arripis truttaceus* and larvae of the Australian herring *Arripis georgianus* (Lenanton et al., 1991; Fairclough et al., 2000).
1.3 DEEP-WATER CRAB FISHERIES

1.3.1 History

Catch statistics indicate that crabs in deep waters first began to be targeted commercially in the Northern Hemisphere during the 1920s. At this time, the snow crab *Chionoecetes opilio* was being taken by seine fishers in water depths of 200 m to 1500 m off the southwestern coast of Japan (Sinoda, 1982) and the southern king crab *Lithodes santolla* was being caught using tangle nets in waters from the subtidal region down to 200 m off Chile and Argentina (Vinuesa et al., 1996). With stocks of *Chionoecetes opilio* in the Sea of Japan showing signs of over-exploitation as early as the mid 1960s (Colgate, 1982), exploratory fishing for alternative crab grounds was initiated in 1967 in the adjacent East Bering Sea by the Japanese and, to a lesser extent, by Soviet fishers (Otto, 1982). This led to the exploitation of stocks of the tanner crab *Chionoecetes bairdii* (Colgate, 1982). At this time, the trap fishery for crabs in Alaska was developing rapidly. Fishing effort was being fuelled by high catches of the red king crab *Paralithodes camtschaticus* in shallower waters within the Gulf of Alaska. However, stocks of *P. camtschaticus* started to decline in the late 1960s (Colgate, 1982) and as a result, fishers in Alaska started fishing in deeper waters for *C. bairdii*. Trap-fishing technology quickly spread to Japan and was used to fish *Chionoecetes japonicus*, *C. opilio* and *C. bairdii* (Sinoda, 1982).

The Japanese initiated the fishery for *Chaceon maritae* off the Namibian coast in 1973 and this still continues (Melville Smith et al., in press). There are also fisheries for the following geryonid species; *Chaceon quinquedens* on the Scotian shelf off Canada and the east coast of the United States, the golden crab *Chaceon fenneri* in the Gulf of Mexico, *Chaceon
affins in north-western Spain and Chaceon notialis off Uruguay (Linberg et al., 1989, Lockhart et al., 1990; Attrill et al., 1991; Defeo et al., 1991; López Abellán et al., 2002).

1.3.2 Exploited crabs in Western Australia

The blue swimmer crab Portunus pelagicus (Linnaeus) (Portunidae), the mud crab Scylla serrata (Forskål) (Portunidae), the champagne crab Hypothalassia acerba Koh and Ng (Eriphidae), the giant crab Pseudocarcinus gigas Lamarck (Xanthidae) and the crystal crab Chaceon bicolor Manning and Holthuis (Geryonidae) are fished commercially and/or recreationally in Western Australia (Anon, 2002). The last three species live at progressively deeper water depths from 70 m to over 800 m and are commonly referred to in Western Australia as deep-water crabs (Levings et al., 1996; Anon, 2002; Melville Smith et al., in press; K. Smith, unpublished data). Aspects of the biology of all of the common recreationally and commercially fished species that live in the shallower waters of Western Australia, and also of P. gigas in deeper waters, have been studied (Heasman et al., 1985; Hill, 1994; Knuckey, 1996; Levings et al., 1996; Gardner, 1997; Levings et al., 2001; Gardner and Williams, 2002; de Lestang et al., 2003a,b). However, there have been no comparable studies on the biology of either H. acerba or C. bicolor.

Pseudocarcinus gigas

The Xanthoidea, or “dark fingered crabs”, comprising 50 genera and 170 species within the Australian region alone, constitute the largest super-family of decapod crustaceans (Reid, 1970). Pseudocarcinus gigas is found southwards of the Perth canyon in southwestern Australia and eastwards across the full length of southern Australia, including Tasmania, and as far north on the east coast of Australia as ~ 31ºS (Kailola et al., 1993; Gardner, 1998b). The trap fishery for P. gigas is the most valuable of Australia’s deep-water crab fisheries (Levings
et al., 1996). The life cycle of *P. gigas* has been determined and larvae have been reared in the laboratory to megalopae stage (Gardner, 1996; Gardner and Northam, 1997). The implications to management of the size structure reproductive biology, egg production, size at sexual maturity, catch rates, seasonal variations in catch and effort and depth distribution of *P. gigas* have been discussed (Levings et al., 1996; Gardner, 1998a; Gardner and Williams, 2002).

**Hypothalassia acerba**

*Hypothalassia acerba* (Xanthidae: Eriphidae) (Figure 1.1a), commonly referred to as the spiny crab and more recently as the champagne crab, is the closest relative of *P. gigas* in Australian waters. Koh and Ng (2000) have recently distinguished this species from *Hypothalassia armata*, which is the only other member of the *Hypothalassia* and is restricted to the Pacific and not fished commercially. On the basis of catches obtained by commercial fishers, *Hypothalassia acerba* occurs from the mid-western coast of Australia off Kalbarri (27° S), southwards and eastwards as far as Eucla 129° E (Anon., 2002). The only published record of this species from outside this range is that for a single individual from at ~ 31 °S, 153 °E on the east coast of Australia (George, 1966).

For several decades, *H. acerba* has been taken as “by-catch” by fishers targeting the valuable western rock lobster *P. cygnus*. Although some of these fishers regard the champagne crab as a nuisance and thus destroy them on capture (C. Neave, Deep-Water Crab Endorsement holder, pers. comm.), the potential commercial value of *H. acerba* was recognised in the 1980s and, as a consequence, a trap fishery was established on the lower west and south coasts of Western Australia. Live export of *H. acerba* commenced in 1989, with catches (total live weight) rising progressively to reach a peak of 76,381 kg in 1997/98 (Anon., 2002). The targetting of *H. acerba* off the lower west coast of Western Australia ceased in 2000, due to a combination of reduced catches and an increased interest in fishing for *C. bicolor* (C. Neave,
pers. comm.). However, *H. acerba* continues to be harvested off the southern coast by fishers who target giant crabs and southern rock lobsters *Jasus edwardsii*.

During the two years that champagne crabs were targeted commercially off the lower west coast between 1999 and 2000, they were fished within a narrow range of water depths of 150 and 300 m located between 30° 08’S, 114° 33’E (~ Jurien) and 32° 29’S, 114° 58’E (Mandurah) (Figure 2.1) (K. Smith, unpublished data). Although this species was caught incidentally in other years, it was not sold commercially in those years. Off the south coast, *H. acerba* is caught mainly in water depths of 70 to 210 m in waters from Cape Leeuwin east to at least Esperance (Anon., 2002; K. Smith, unpublished data). *Hypothalassia acerba* is considered by fishers to be most abundant over substrates of coral and/or broken rock.

The fishery for *H. acerba* on the south coast differed from that on the west coast, in that it was based on fishing vessels that also catch the more valuable giant crab *Pseudocarcinus gigas* and southern rock lobster *Jasus edwardsii*. Furthermore, less favourable weather conditions off the south coast mean that boats are not able to fish on as many days on this coast as on the west coast. When they do go to sea, they stay out of port for periods of up to a week. Therefore, although the fishery for *H. acerba* off the south coast has a longer history and continues to the present day, the catches of this species within my study period were lower than those on the west coast.

**Chaceon bicolor**

The Geryonidae contains 36 species, of which 33 belong to the genus *Chaceon*, two to the genus *Geryon* and one to the genus *Zariquieyon* (Dawson and Webber, 1991). Although *Chaceon bicolor* (Figure 1.1a) is widely distributed around Australia and in New Zealand waters, (Jones and Morgan, 2002) it is only fished commercially off southwestern Australia (Anon, 2002). In this region, it is fished from a latitude of ~ 22ºS, southwards and then
eastwards to about 129°E (Anon, 2002). This species is thus fished within the same geographical range as *H. acerba*.

### 1.4 RATIONALE AND BROAD AIMS FOR PRESENT STUDY

Worldwide, 8.4 million tonnes of Crustacea were harvested in 2001 (FISHSTAT 2001). In Western Australia, the western rock lobster fishery alone is worth 200 to 400 AU$ million p.a. (Anon., 2002). At the commencement of this study, significant interest in fishing for deep-water crabs was being expressed by fishers who wanted to catch deep-water crabs off southwestern Australia. Although the biology of *Pseudocarcinus gigas* had been studied in these waters, and particularly further east (Levings *et al.*, 1996), no work had been conducted on the biology of either *Hypothalassia acerba* or *Chaceon bicolor*.

The broad aims of this thesis are:

1. *Describe the commercial fisheries for Hypothalassia acerba and Chaceon bicolor.*
2. *Determine the relative abundances and size compositions of males and females of the champagne crab Hypothalassia acerba in different water depths and seasons on the lower west and south coasts of Western Australia.*
3. *Describe the reproductive biology of females of Hypothalassia acerba and Chaceon bicolor.*
4. *Determine the size at maturity of the females and males of Hypothalassia acerba and Chaceon bicolor.*
5. *Discuss the management implications of the results.*
Figure 1.1. (a) Male Hypothalassia acerba (above) and male Chaceon bicolor (below) and (b) the fishing vessel Barbarossa which was used on the lower west coast for the depth-stratified sampling regime (see Chapter 2).
Chapter 2

GENERAL MATERIALS AND METHODS
2.1 SAMPLING OF HYPOTHALASSIA ACERBA

The biological data reported for champagne crabs in Chapters 4 to 7 were obtained from three sampling regimes. The first sampling regime was designed specifically to obtain monthly data on the relative abundance and size composition of *H. acerba* in different water depths off the lower west and south coasts of Western Australia (Chapter 4). It is subsequently referred to as the depth-stratified sampling regime to distinguish it from the second sampling regime which involved obtaining data for *H. acerba* by examining crabs while onboard commercial fishing vessels during their normal fishing activities. The third sampling regime involved collecting or purchasing samples of commercial catches from fish markets.

### 2.1.1 Depth-stratified sampling regime

For the depth-stratified sampling regime, *Hypothalassia acerba* was sampled off the lower west coast of Western Australia at a latitude of ~ 30° 45′S and a longitude of ~ 114° 50′E and off its southern coast at a latitude of ~ 35° 15′S and a longitude of ~ 118° 30′E (Figure 2.1). Seven sites (water depths) were sampled on each sampling occasion on both coasts. The sites were selected so that they were located in areas where the mean water depths were 35, 90, 145, 200, 255, 310 and 365 m, respectively, *i.e.* the sites were equally spaced at depth intervals of 55 m. They were located at distances from the shore of ~ 21.6, 28.5, 34.1, 40.1, 40.8, 40.9 and 41.1 km off the lower west coast and of ~ 0.5, 28.2, 31.8, 32.1, 32.5, 32.7 and 33.1 km from the shore off the south coast.

The seven sites on the lower west coast and seven sites on the south coast were sampled in nine and four months, respectively, between January 2000 and April 2002, with each coast being sampled at least once in each calendar season (Table 2.1). Samples were collected from each site (water depth) on each sampling occasion using three lines of traps, with each line of 11 mm propylene rope having rectangular traps at each end separated by a circular trap in the
middle (see Figure 2.2a). The rectangular traps had a steel base and timber frame that was 960 mm long x 800 mm wide x 460 mm high and contained an entrance 270 mm in diameter x 170 mm in depth at the top. The trap bases consisted of parallel steel rods, 5 mm in diameter, situated 80 mm apart. The sides, top and ends of the traps were enclosed with wooden battens approximately 70 mm apart. The round traps were 880 mm in diameter x 450 mm in height and contained an entrance of 280 mm diameter x 200 mm deep at the top. Both of the trap types described above, which are typically employed to catch the western rock lobster *Panulirus cygnus* (George, 1962), are the same as those used by commercial fishers to catch champagne crabs.

In each water depth, the length of rope between the trap and the water surface was always ~ twice the water depth. A distance of 72 m separated the traps in each line (Figure 2.2b). Each line was set ~ 500 m apart. Escape gaps, a legal requirement of these commercial western rock lobster traps, were covered. Traps were baited with fish heads, such as those of the orange roughy *Hoplostethus atlanticus* Collett or the New Zealand hoki *Macryronus novaezelandiae* (Hector) which are commonly used to catch these crabs, and also with cattle hide or foreleg, which is more resistant to lice (isopods and amphipods) than the fish heads and thus last longer. A single inflatable fender and up to 5 cast alloy buoys were used to keep the surface rigs afloat (Figure 2.3a). Traps were typically set for five days.

In an attempt to catch greater numbers of small crabs off the lower west coast during May (autumn) and November (spring) 2001, the rectangular traps at each end of an additional equal number of lines were enclosed with welded galvanised aviary mesh with meshes of 12.7 x 25.4 mm (Figure 2.3b). The mesh, which was attached to the traps using cable ties, nails and staples, enclosed the whole of the traps, except for their entrance. Since the spaces between the canes used in the central circular trap were small, it was not considered necessary also to enclose these traps in aviary mesh. The additional lines of small mesh traps were used
to fish the same water depths, but ~ 2 km further south, effectively replicating the experiment in those two months. In all of the sampling conducted off the lower west coast after November 2001, the rectangular traps were enclosed with aviary mesh (see Table 2.1).

Table 2.1 Dates and seasons when traps were used to catch Hypothalassia acerba off the lower west and south coasts of Western Australia. n.c., not covered with aviary mesh; c, covered with aviary mesh.

<table>
<thead>
<tr>
<th>Date</th>
<th>Season</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>West coast</strong></td>
<td></td>
</tr>
<tr>
<td>17.02.00</td>
<td>Summer, n.c.</td>
</tr>
<tr>
<td>23.8.00</td>
<td>Winter, n.c.</td>
</tr>
<tr>
<td>18.9.00</td>
<td>Spring, n.c.</td>
</tr>
<tr>
<td>3.3.01</td>
<td>Autumn, n.c.</td>
</tr>
<tr>
<td>12.5.01</td>
<td>Autumn, n.c. and c.</td>
</tr>
<tr>
<td>6.11.01</td>
<td>Spring, n.c. and c</td>
</tr>
<tr>
<td>18.12.01</td>
<td>Summer, c</td>
</tr>
<tr>
<td>20.1.02</td>
<td>Summer, c</td>
</tr>
<tr>
<td>25.4.02</td>
<td>Autumn, c</td>
</tr>
<tr>
<td><strong>South coast</strong></td>
<td></td>
</tr>
<tr>
<td>19.3.00</td>
<td>Autumn, n.c.</td>
</tr>
<tr>
<td>17.6.00</td>
<td>Winter, n.c.</td>
</tr>
<tr>
<td>25.11.00</td>
<td>Spring, n.c.</td>
</tr>
<tr>
<td>22.2.02</td>
<td>Summer, n.c.</td>
</tr>
</tbody>
</table>

2.1.2 Onboard sampling of commercial catches of Hypothalassia acerba

Samples of Hypothalassia acerba were obtained onboard from the trap catches of commercial fishers operating off the lower west and south coasts of Western Australia between ~ 30° 10’S, 114° 30’E (~ west of Jurien) and 32° 30’S, 114° 60’E (west of Mandurah) and between ~ 34° 40’S, 115° 40’E (south of Augusta) and 34° 45’S, 119° 30’E (south of Bremer Bay), respectively (Figure 2.1). Off the lower west and south coasts, the water depths fished by commercial fishers during these monitoring cruises, ranged from 180 to 280 m and 70 to 240 m
respectively. These trips were undertaken at regular intervals off the lower west coast between July 1999 and December 2000 and off the south coast between July 1999 and February 2002.

### 2.1.3 Structure of traps used in the commercial fishery to catch Hypothalassia acerba

The single commercial fisher who targeted champagne crabs on the west coast consistently, used rectangular jarrah rock lobster traps of the type employed in the depth-stratified sampling regime described in Section 2.1.1. Note that other fishers, who were targeting western rock lobster on the west coast, were not allowed to retain for sale any incidental catches of champagne crabs.

Since there is no legislation specifying that a particular type of trap should be used by commercial fishers for catching champagne crabs, the trap types used on the south coast varied. Note that, on the south coast as opposed to the west coast, some fishers possessed licenses that enabled them to sell any catches of *H. acerba* that were obtained incidentally when they were fishing for other species such as the southern rock lobster *Jasus edwardsii* and the giant crab *Pseudocarcinus gigas*.

The three main types of trap used on the south coast included the circular cane stick traps of the type used in the depth-stratified sampling regime (Section 2.1.1). The first of the other two trap types was round-sided with flat tops (1400 mm base diameter, 350 mm high, 272 mm neck diameter), while the second was conical and beehive shaped (860 mm base diameter, 407 mm high, 272 mm neck diameter). Both of these latter traps were enclosed with either diamond-shaped stainless steel chicken wire or resilient synthetic netting. All three traps were weighted with ~ 40 kg of steel ballast.

For commercial fishing off both coasts, between two and twelve traps were strung together in lines, with varying distances of rope between the traps. Furthermore, soak time ranged from four days to several weeks, mainly due to variations in weather conditions. Traps
were usually baited with fresh or salted heads of fish species such as the orange roughy *Hoplostethus atlanticus* Collett or the New Zealand hoki *Coryphaenoides novaezelandiae* Hector. Cattle hide or foreleg was employed until its use was banned in January 2002.

### 2.1.4 Tagging of *Hypothalassia acerba*

Crabs were tagged using Hallprint TBA-1 double T-bar tags (Levings et al., 1996). The tags were inserted using a Paxar tagging gun on the right hand side medial epimeral suture line of the carapace, between the fourth and fifth coxa, with the t-bar lodged in the branchial cavity (Figure 2.4a). After tagging, crabs were returned immediately to the water in order to minimise their displacement due to drift. Crabs with missing appendages were not tagged.

### 2.1.5 Sampling of *Chaceon bicolor*

Sampling for *C. bicolor* aboard commercial fishing vessels was undertaken on four occasions during 2000 and, wherever possible, bimonthly between June 2001 and December 2003.

### 2.1.6 Structure of traps used in the commercial fishery to catch *Chaceon bicolor*

*Chaceon bicolor* is fished commercially using lines containing up to 100 plastic recreational western rock lobster traps, which are 675 mm long, 350 mm wide and 475 mm high and possess, at their top, an entrance of 170 mm diameter and 200 mm depth (Figure 2.4b). The traps are made of light-weight plastic to prevent them sinking into the soft substrate and are baited with heads of the New Zealand hoki or whole Australian salmon, *Arripis truttaceus* (Cuvier).
2.2 MEASUREMENTS

2.2.1 Water temperature

On each occasion that the depth-stratified sampling for *H. acerba* was implemented, the bottom water temperature at each site was recorded using StowAway TidbiT HTI-537 digital temperature loggers that were enclosed in protective wire mesh and attached to the inside top of one of the traps. When a logger occasionally malfunctioned, the temperature in that depth was not recorded on that sampling occasion. Bottom water temperature was recorded using the same devices, which were attached to commercial traps deployed to catch *C. bicolor*. The temperature was recorded to 0.1°C at 5 min intervals and the resultant values downloaded from these loggers to a computer and subsequently averaged for each sampling occasion at each sampling site.

2.2.2 Data recorded for crabs

In the field, the contents of each individual trap were recorded separately and a note made of the location, date and depth (m) at which all crabs were caught. The following characteristics of each crab were recorded. (1) The carapace length (CL) of each *H. acerba* and *C. bicolor*, *i.e.* the distance from the midpoint between the bases of the two anterior medial horns and the posterior margin of the carapace, was measured to the nearest 1 mm. This is the typical way of measuring body size in deep-water crabs (Levings et al., 1996; Gardner, 1997; Goshima and Kanazawa, 2000). It is preferable to using carapace width, *i.e.* the distance between the two lateral spines of the carapace, as those structures are particularly prone to wear. (2) In the case of females, pleopod condition was recorded as either clean with no sign of egg attachment, or as having either eggs (berried) or egg remnants attached. (3) For each female, a record was kept of the relative size and shape of the gonopores and whether mating abrasions were present around their gonopores. Most females of *C. bicolor* with a CL < 100 mm possessed
elliptical/closed gonopores (Figure 2.5a) indicating that they had not mated, a conclusion consistent with the absence of mating scars in the region of their gonopores (Figure 2.5b) (see also Melville Smith, 1987a; Haefner, 1977). Although the gonopores of female *H. acerba* did not exhibit such a conspicuous dichotomy in shape as those of *C. bicolor*, the individuals of this species with a CL < ~ 70 mm had relatively very small gonopores and, unlike many larger individuals, never bore mating scars in the region of their gonopores (Figure 2.6). The first and small group of *H. acerba* was thus considered not to have mated, which is consistent with the ovaries of all such individuals being at stage I (see Table 5.1, Chapter 5 for description of the characteristics of the different stages in ovarian development).
Figure 2.1. Map showing the region of southwestern Australia where *Hypothalassia acerba* and *Chaceon bicolor* were caught. Boxes show location of the depth-related sampling regime on the west and south coasts. Circles designate the location where the samples at the different depths were collected. Each sampling unit contained one rectangular trap at each end and a central circular trap (see bottom left hand corner).
Figure 2.2. (a) Round cane stick traps (above) and rectangular jarrah slat traps (below) used for the depth-stratified sampling regime and (b) warning ropes (blue) to which the traps were attached. The traps were separated by 72 m of ground rope (yellow).
Figure 2.3. (a) Inflatable buoy, one of which was attached to each line of traps and (b) rectangular jarrah trap enclosed with wire mesh.
Figure 2.4. (a) Female *Hypothalassia acerba* showing the t-bar anchor tag inserted within the epimeral suture line of the carapace and (b) commercial fishing trap used to catch *Chaceon bicolor*. (Photo courtesy of S. Norton).
Figure 2.5. (a) Abdomen of an immature female *Chaceon bicolor* showing elliptical/closed gonopores and (b) abdomen of a mature female *C. bicolor* showing open and circular gonopores and mating abrasions.
Figure 2.6. Abdomen of a mature female *Hypothalassia acerba* showing open and circular gonopores.
Chapter 3

THE FISHERIES FOR *HYPOTHALASSIA ACERBA* AND *CHACEON BICOLOR*
3.1 INTRODUCTION

The fishery for the champagne crab *Hypothalassia acerba* is concentrated on the lower west coast of Australia between Jurien in the north at 30° 08’S, 114° 30’E and Mandurah in the south at 32° 29’S and 115° 40’E, and on its south coast between Augusta in the west at 34° 20’S, 115° 10’E and Bremer Bay in the east at 34° 40’S, 119° 30’E (Chapter 1). Under deep-sea crab endorsements to fishers by the Western Australian Department of Fisheries, *H. acerba* was only fished commercially on the lower west coast between 1989 and 2000. Although that endorsement extended beyond 2000, the holders of this endorsement switched to targeting the crystal crab *Chaceon bicolor* in that year. The catches of *H. acerba* by fishers with deep-sea crab endorsements have been supplemented to a small degree by those of commercial rock lobster fishers. However, since 2000, the latter fishers have been permitted to retain only six *H. acerba* per vessel per day on the west coast during the western rock lobster season (Anon., 2004). In contrast to the situation on the west coast, the champagne crab has been fished commercially since 1991 on the south coast, where this species contributes to a multi-species fishery that also includes the giant crab *Pseudocarcinus gigas* and the southern rock lobster *Jasus edwardsii* (Anon., 2004).

*Chaceon bicolor* occurs in water depths of 450 to 1220 m, which is far greater than the depths of 90 to 310 m in which *H. acerba* is typically caught (Melville Smith *et al.*, in press; Chapter 4). The fisheries for *C. bicolor* off the lower west coast and south coast commenced in 1999 and 2002 respectively. Although *C. bicolor* is distributed around Australia and New Zealand, it is only commercially fished in Western Australian waters. However, several other species belonging to the Geryonidae are fished elsewhere in the world (*e.g.* Wigley *et al.*, 1975; Wenner *et al.*, 1987; Erdman and Blake, 1988; Melville Smith, 1988; Defeo *et al.*, 1991; López Abellán *et al.*, 2002). Although a deep-sea crab endorsement entitles fishers to harvest *C. bicolor* as well as *H. acerba*, the former species requires refrigerated water for it to be kept
alive and therefore tends to be fished independently of *H. acerba* by fishers who have vessels fitted with refrigerated tanks for holding *C. bicolor*.

The first aim of this chapter is to describe quantitatively the trends exhibited by catch (landed live weight), fishing effort (number of pot lifts) and catch per unit effort (CPUE) for *H. acerba* and *C. bicolor* on the lower west and south coasts since the commencement of the fisheries for these species, and to determine whether these three variables change throughout the year. The second aim was to determine whether the relative abundance and size of both the females and males of *H. acerba* and *C. bicolor* differed among the regions in which they were being fished. The third aim was to tag and release individuals of *H. acerba* in an attempt to obtain data on the movement and growth of this species.

### 3.2 MATERIALS AND METHODS

#### 3.2.1 Data on commercial catches

The monthly landed catches of each species by commercial fishers on both the lower west and south coasts between 1989 and 2003, together with the number of pot lifts, were extracted by M. Cliff and L. Bellchambers from the Catch and Effort Statistics (CAES) of the Department of Fisheries Western Australia. This data is derived from compulsory monthly logbook returns. Weights (in kg) represent estimates recorded by fishers while at sea.

#### 3.2.2 Onboard collection of data

**Hypothalassia acerba**

Data for *H. acerba* were collected onboard the boat of a commercial fisher operating in five Department of Fisheries 1° x 1° fishing blocks along the lower west coast and those of three commercial fishers working in five such fishing blocks on the south coast. The first two digits identifying these fishing blocks represent the location of the north-west corner of the block in degrees latitude and the second two numbers represent the last two of the three numbers of the
location of the north-west corner of the block in degrees longitude, e.g. longitude 114° is given as 14. Fishing blocks 3014, 3114 and 3115 were grouped to represent the northern region and blocks 3214 and 3215 the southern region of the lower west coast, while fishing blocks 3415, 3515 and 3516 were grouped to represent the western region and blocks 3517 and 3419 the eastern region of the south coast. The onboard trips were conducted at two to four month intervals between July 1999 and December 2000 on the lower west coast and less frequently between July 1999 and February 2002 on the south coast (see Chapter 2 for further details). Note that sampling on the south coast occurred less frequently because fishing on this coast was more sporadic and the time spent by fishers at sea was far greater. Whenever possible, a record was kept of the carapace length of each male and female *H. acerba* caught (see Chapter 2) and the latitude and longitude where each line of traps was laid.

**Chaceon bicolor**

The onboard collection of the same data for *C. bicolor*, as those recorded for *H. acerba* (see above), was restricted to the west coast as this species was not fished on the south coast during the present study. Catches of *C. bicolor* were grouped into two regions of the west coast, *i.e.* to the north and south of 28° 50’S (approximately Geraldton), which lies in the middle of the range of latitudes where sampling was undertaken. Onboard recording of *C. bicolor* was undertaken bimonthly between June 2001 and December 2003, with an additional four trips being undertaken in 2000.

**Mesh selectivity of Chaceon bicolor**

During onboard sampling, three recreational rock lobster traps, enclosed with plastic mesh of 20 mm × 20 mm, were randomly placed in each of two lines of ~ 100 non-meshed traps of the same type as those used by the commercial fishers who target *C. bicolor* (see Chapter 2.1.6).
On each sampling occasion, the carapace lengths of crabs caught in non-meshed and meshed traps were recorded. When the candidate was not present, commercial fishers were asked to record, whenever feasible, the sex and carapace length of crabs in meshed traps and in an equal number of non-meshed traps. The data recorded by the fishers were later forwarded to Murdoch University for inclusion in my analyses.

Note that the experiments carried out to explore the mesh selectivity of *H. acerba* are reported in Chapter 4 as the data derived from those experiments contributed to the total data set used to determine the depth distribution of this species.

### 3.2.3 Data analysis

**Hypothalassia acerba**

Plots of log$_{10}$ of the standard deviation against log$_{10}$ of the mean for both the CPUE (catch per pot lift) and the carapace lengths of *H. acerba* recorded on commercial vessels in each of the two regions on each coast showed that neither variable required transformation prior to subjection to analysis of variance (ANOVA) (see Clarke and Gorley (2001) for rationale for this approach).

The catches were subjected to ANOVA, with the number of crabs per pot lift as the dependent variable and sex and region as fixed factors. The carapace lengths were also subjected to ANOVA, with carapace length as the dependent variable, and sex and region as fixed factors. No attempt has been made to separate the data by season because it was not possible to obtain samples from each region in every season. Scheffé’s *a posteriori* test was used to compare the CPUE and mean carapace lengths for each of the four regions.

**Chaceon bicolor**

The catch and carapace length data for *C. bicolor* were analysed in the same way as for *H. acerba*. Note however that in this case the catch rates required log transformation.
3.3 RESULTS

3.3.1 Commercial catch and effort data for Hypothalassia acerba

The total landed catch of *H. acerba* in Western Australia rose from less than 1,500 kg in 1989 and 1990 to between 13,050 and 10,850 kg in 1991 to 1996 and then sharply to a peak of 72,975 kg in 1998, before declining progressively to 17,295 kg in 2003 (Figure 3.1a). The annual catches peaked on the west coast at 30,900 to 45,630 kg in 1997 to 1999 and on the south coast at 26,070 and 27,345 kg in 1997 and 1998, respectively (Figure 3.1b). However, catches on the west coast declined precipitously to essentially zero after 2000, whereas on the south coast they remained at between 10,790 and 21,560 kg between 2000 and 2003 (Figure 3.1b).

The total number of pot lifts per annum on both coasts collectively rose progressively from ~ 5,500 in 1989 and 1990 to 114,850 in 1994 and then declined to 48,220 in 1996, before rising again to reach a maximum in 1998 (Figure 3.2a). It subsequently remained at between 44,000 and 61,000 pot lifts in 1999 to 2003. The number of pot lifts per annum on the west and south coasts followed different trends. Thus, on the west coast, they peaked sharply at 73,000 and 94,000 in 1997 and 1998, respectively, and had declined to very low levels by 2001, whereas, on the south coast, they peaked at 90,510 in 1994 and were relatively high in 2001 to 2003 (Figure 3.2b).

The annual catch per unit effort (CPUE) for the whole fishery for *H. acerba*, as expressed by catch (kg) per pot lift, peaked in 1999 at 0.80, after which it declined progressively to 0.25 in 2003 (Figure 3.3a). Prior to 1991, the effort on both coasts was either low or zero (Figure 3.2b) and thus attention is not focused on the CPUEs for those years. On the west coast, the CPUEs remained at between 0.30 and 0.53 in all years between 1991 and 2000, except in 1995 and 1996 when they were 0.15 and 0.09, respectively, and in 1999 when they rose to a sharp peak at 1.25. The catch rates, and also the effort, on the west coast in 2001
to 2003 were negligible and thus are unlikely to provide reliable measures of relative abundance. The annual CPUE on the south coast rose to a maximum of 0.85 in 1997 and then declined to 0.27 in 2003 (Figure 3.3b).

Between 1992 and 1999, when the annual catches of *H. acerba* on the west coast of Australia were greatest, the mean monthly catches on that coast appeared to follow an annual cycle, increasing from low levels of 620 to 1,240 kg in March to June to maximum levels of 1,790 to 3,000 kg in August to January (Figure 3.4a). The mean monthly catches on the south coast for the years 1992 to 2003, when catches were substantial on that coast, followed a distinct annual cycle, declining from 2,390 kg in January to a minimum of 410 kg in August, and then rising steeply to 2,260 kg in December (Figure 3.4b).

The mean monthly number of pot lifts on the west coast followed a less seasonal cycle than that of total landed catch and only exceeded 4,000 in January and December (Figures 3.4a, 3.5a). The mean monthly number of pot lifts on the south coast followed similar trends to those exhibited by the mean monthly catches, declining from 8,085 in January to between 960 and 2,245 in May to October and then rising to 6,445 in December (Figure 3.5b).

The mean monthly CPUEs for *H. acerba* on the west coast rose progressively from low levels of <0.65 kg per pot lift in January to April to reach a maximum of 2.47 kg per pot lift in November, and then declined precipitously to 0.20 kg per pot lift in December (Figure 3.6a). The mean monthly CPUEs for *H. acerba* on the south coast rose from ~0.37 kg per pot lift in January to March to attain a peak of 1.08 kg per pot lift in July (Figure 3.6b).

### 3.3.2 Commercial catch and effort data for *Chaceon bicolor*

The total annual catch of *C. bicolor* in Western Australia rose progressively from a negligible level in 1997 to reach a maximum of 222,520 kg in 2001 and remained at above 193,280 kg in
2002 and 2003 (Figure 3.7a). The vast majority of the catch in each year came from the west coast (Figure 3.7b).

The annual number of pot lifts for *C. bicolor* followed a similar trend to that of landed catch, except that they peaked one year earlier, *i.e.* in 2000 rather than 2001 (Figure 3.8a). The maximum number of pot lifts per year on the west coast was 245,000.

The CPUE for *C. bicolor* in southwestern Australia rose progressively from 0.11 kg per pot in 1998 to 1.16 kg per pot in 2002 and 2003 (Figure 3.9a). Since the effort was very low on the south coast (Figure 3.8b), emphasis was not placed on the catch per unit effort for this coast (Figure 3.9b).

The mean monthly catches of *C. bicolor* show no conspicuous seasonal trends, with values ranging from minima of 12,775 to 14,485 kg in April, June and November to maxima of 8,895 to 20,240 kg in January, August, September and October (Figure 3.10a). The trends exhibited by the mean monthly number of pot lifts and, to a large extent, the mean monthly CPUE, essentially parallel those of the mean monthly catches (cf Figures 3.10a,b,c).

### 3.3.3 Analysis of catches and sizes of crabs derived from onboard sampling

**Hypothalassia acerba**

ANOVA demonstrated that the CPUEs of *H. acerba* differed significantly between sexes and among regions, with the mean square being far higher for sex than region (Table 3.1). The sex × region interaction was not significant (Table 3.1). The mean CPUE of males, *i.e.* ~ 2.5 per pot, was far greater than that of females, *i.e.* ~ 0.9 (Figure 3.11a).
Table 3.1  Mean squares and significance levels for ANOVA of catch per pot lift (CPUE) of male and female *Hypothalassia acerba* in northern and southern regions off the lower west coast and western and eastern regions off the south coast of Western Australia. Data were recorded onboard commercial vessels between 1999 and 2003. **$p < 0.01$, ***$p < 0.001$; d.f., degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>Mean Square</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (S)</td>
<td>286.4***</td>
<td>1</td>
</tr>
<tr>
<td>Region (R)</td>
<td>13.7**</td>
<td>3</td>
</tr>
<tr>
<td>$S \times R$</td>
<td>5.4</td>
<td>3</td>
</tr>
<tr>
<td>Residual</td>
<td>2.8</td>
<td>990</td>
</tr>
</tbody>
</table>

The mean number of crabs per pot in the four regions ranged from 2.1 in the southern region of the west coast to 1.4 in the western region of the south coast (*Figure 3.11b*). Scheffé’s *a posteriori* test showed that the mean CPUE in the southern region of the lower west coast was significantly greater ($p < 0.05$) than in its northern region.

**Chaceon bicolor**

ANOVA demonstrated that the CPUE for *C. bicolor* differed significantly between sexes ($p < 0.001$) and between regions ($p < 0.01$), with the mean square being greater for sex than for region (*Table 3.2*). The sex × region interaction was not significant ($p > 0.05$) (*Table 3.2*). The mean CPUE was greater for males than females, *i.e.* 1.4 vs 1.2 per pot (*Figure 3.12a*) and was greater in the northern region than southern region, *i.e.* 1.4 vs 1.3 per pot (*Figure 3.12b*).
Table 3.2  Mean squares and significance levels for ANOVA of catch per pot (CPUE) of male and female *Chaceon bicolor* in northern and southern regions off the lower west coast. Data were recorded onboard commercial vessels between 1999 and 2003. **p < 0.01, ***p < 0.001; d.f., degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>Mean Square</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (S)</td>
<td>13.0***</td>
<td>1</td>
</tr>
<tr>
<td>Region (R)</td>
<td>2.2**</td>
<td>1</td>
</tr>
<tr>
<td>S × R</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>Residual</td>
<td>0.2</td>
<td>5671</td>
</tr>
</tbody>
</table>

3.3.4 *Carapace lengths*  
*Hypothalassia acerba*  
ANOVA demonstrated that the carapace length of *H. acerba* was influenced significantly by both sex and region (*p < 0.001*), with the mean square for sex being slightly greater than that for region (Table 3.3). The region × sex interaction was not significant.

Table 3.3. Mean squares and significance levels for ANOVA of carapace lengths of male and female *Hypothalassia acerba* in northern and southern regions off the lower west coast and western and eastern regions off the south coast of Western Australia. Data were recorded onboard commercial vessels between 1999 and 2003. ***p < 0.001; d.f., degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>Mean Square</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (S)</td>
<td>2954.2***</td>
<td>1</td>
</tr>
<tr>
<td>Region(R)</td>
<td>2559.7***</td>
<td>3</td>
</tr>
<tr>
<td>S × R</td>
<td>104.8</td>
<td>3</td>
</tr>
<tr>
<td>Residual</td>
<td>146.2</td>
<td>1713</td>
</tr>
</tbody>
</table>
The mean carapace length of males (100.7 mm) was greater than that of females (95.2 mm) (Figure 3.13a,b). The mean carapace length of *H. acerba* ranged from 91 mm in the eastern region of the south coast to 103 mm in the western region of the south coast (Figure 3.13c). Scheffé’s *a posteriori* test showed that the mean carapace lengths of *H. acerba* differed significantly (*p* < 0.05) between each pair of regions, except for between the southern region of the west coast and the western region of the south coast.

Although the maximum carapace length of males (139 mm) was greater than that of females (120 mm) in the samples examined onboard commercial vessels on the lower west and south coasts, the modal carapace length classes of males and females were both 90 to 94 mm (Figure 3.13b).

**Chaceon bicolor**

The carapace lengths of *C. bicolor* differed significantly between the sexes and between the two regions (Table 3.4). The mean square was far greater for sex than for region, and the region × sex interaction was not significant (Table 3.4).

**Table 3.4** Mean squares and significance levels for ANOVA of carapace lengths of male and female *Chaceon bicolor* in northern and southern regions off the lower west coast of Western Australia. Data were recorded onboard commercial vessels between 1999 and 2003. ***p* < 0.001; d.f., degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>Mean Square</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (S)</td>
<td>72513.2***</td>
<td>1</td>
</tr>
<tr>
<td>Region (R)</td>
<td>6298.8***</td>
<td>1</td>
</tr>
<tr>
<td>S × R</td>
<td>28.1</td>
<td>1</td>
</tr>
<tr>
<td>Residual</td>
<td>323.7</td>
<td>13326</td>
</tr>
</tbody>
</table>
The mean carapace length of the males of *C. bicolor* (119.0 mm) was greater than that of its females (106.3 mm) (Figure 3.14a,b). Furthermore, males reach a larger maximum size (169 mm CL) than females (148 mm CL) (Figure 3.14b). In contrast to *H. acerba*, however, the modal size class of male *C. bicolor* (115 - 119 mm CL) was substantially greater than that of females (100 - 104 mm CL) (Figure 3.14b). Few crabs were caught with carapace lengths < 80 mm. The mean carapace length of *C. bicolor* was greater in the southern than in the northern region, *i.e.* 113 vs. 110 mm (Figure 3.14c).

### 3.3.5 Carapace lengths of Chaceon bicolor in non-meshed and meshed traps

In the case of the males of *C. bicolor*, the mean carapace lengths were greater in the catches obtained in meshed than non-meshed traps in each of the three seasons in which substantial numbers were caught in the non-meshed traps (Table 3.5). However in none of these seasons was the difference in size significant. The mean carapace length of females was significantly greater in the catches obtained in the non-meshed than meshed traps in summer (*p* < 0.05), the only season in which the catches of females in non-meshed traps was substantial (Table 3.5). However, even in this latter case, the difference between the carapace lengths in the two trap types was < 8 mm. It is thus concluded that the enclosure of traps in relatively fine mesh did not lead to an increase in the capture of small crabs. This point is highlighted by the fact that the percentage of the crabs caught < 80 mm CL in the meshed traps were only slightly greater than in the non-meshed traps, *i.e.* 3 vs 1%.
Table 3.5  Mean carapace lengths ± 95% CIs of male and female *Chaceon bicolor* caught in non-meshed vs meshed traps in four seasons between 2001 and 2003. *n*, sample size; NS = not significant at *p > 0.05*; *p* < 0.05.

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th></th>
<th></th>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>n</em></td>
<td><em>P</em></td>
<td>Size range (mm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>Non-mesh 119.6 ± 0.7 mm</td>
<td>2115</td>
<td>NS</td>
<td>34 - 169</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mesh 115.8 ± 5.3 mm</td>
<td>63</td>
<td></td>
<td>38 - 155</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td>Non-mesh 117.9 ± 1.1 mm</td>
<td>601</td>
<td>NS</td>
<td>59 - 160</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mesh 112.6 ± 8.8 mm</td>
<td>20</td>
<td></td>
<td>82 - 140</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>Non-mesh 116.2 ± 1.0 mm</td>
<td>785</td>
<td>NS</td>
<td>72 - 153</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mesh 114.8 ± 4.1 mm</td>
<td>45</td>
<td></td>
<td>88 - 143</td>
<td></td>
<td></td>
</tr>
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<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>Non-mesh 106.5 ± 0.7 mm</td>
<td>782</td>
<td>*</td>
<td>57 - 141</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mesh 98.8 ± 6.6 mm</td>
<td>47</td>
<td></td>
<td>35 - 128</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3.3.6 **Results from release of tagged Hypothalassia acerba**

Twenty eight of the 1,622 champagne crabs tagged and released off the lower west coast were recaptured. All of the nine tagged females and nineteen tagged males that were released and recaptured were mature. However, none of the females were ovigerous when either tagged, released or recaptured. All but four of the tagged females that were subsequently caught were recaptured within 50 km of their point of release. Two of the recaptured tagged crabs had moved ~ 200 km in a north-westerly direction and a further two had moved over 200 km in a south-westerly direction (Figure 3.15). These crabs had thus moved along the contour of the upper shelf break, which runs approximately parallel to the lower west Australian coastline.

None of the 28 recaptured crabs moulted, and this included one female that had been released back into the environment for over 12 months.

3.4 **DISCUSSION**

3.4.1 **Annual trends in catch statistics**

**Hypothalassia acerba**

The data shown in Figure 3.1 demonstrate very clearly how the overall catches of *Hypothalassia acerba* in Western Australia rose from very low levels in 1989 and 1990 to peak
at over 70,000 kg in 1998 and then declined sequentially in subsequent years to under 20,000 kg in 2002 and 2003. Those data also show that the fishery for *H. acerba* on the west coast became essentially non-existent in 2001 to 2003, due to the deep-water crab fishers on this coast shifting their effort almost exclusively to catching *Chaceon bicolor*.

The trends exhibited by the annual number of pot lifts for *H. acerba* in Western Australia demonstrate that the fishing effort in this state peaked in 1998, when the number of pot lifts was ~135,000, and has subsequently remained relatively constant at about half this level from 1999 to 2003. A decline in effort on the west coast in the last five years has been compensated for by an increase in effort on the south coast. The decline undergone each year since 1999 by the overall CPUE for Western Australia, as reflected in the trends exhibited by the annual catches per pot lift for the state, indicate that the relative abundance of *H. acerba* has declined during recent years. The decline in CPUE on the west coast reduced the financial viability of the fishery and contributed to the termination of fishing within a short period. Fishery managers should concern themselves with the increasing levels of fishing effort on the south coast.

The intra annual trends in landed catches of champagne crabs on the west coast show that CPUE declined alarmingly soon after this fishery established, indicating that the stocks were not capable of withstanding sustained fishing pressure. This rapid and marked decline in fishery yield should alert managers of the south coast fishery that this species is susceptible to overfishing. The comparative resilience of champagne crabs stocks to overfishing on the south coast may indicate that local depletion of stocks on the south coast is reduced because of the champagne crabs are one of several species targeted as part of the multi-species fishery. Comparisons of catch rates between the two coasts do not indicate that champagne crabs are more abundant on the south coast. Trends in landed catches of champagne crabs on the south
coast show a declining trend in recent years, which could precede a stock decline as shown on the west coast.

**Chaceon bicolor**

The data in Figure 3.7 emphasise that the commercial fishery for *C. bicolor* in Western Australia commenced later than that of *H. acerba*, but that catches rose sharply from negligible values in 1997 and 1998 to peak at 225,000 kg in 2001 and remained close to that level in 2001 to 2003. The rapid increase in the fishery was due to the development of a sudden and focused interest on *C. bicolor*, which led to the construction of vessels that were purpose-built for targeting this species (D. Hand, Deep-Water crab Endorsement holder, pers. comm.). The fisheries data also emphasize that the fishery has been based almost exclusively on the west coast. Although the progressive rise in CPUE between 1998 and 2002/3 suggest that the relative abundance of *C. bicolor* increased during this period, that upward trend is almost certainly attributable to a rapid increase in the knowledge by fishers of the best locations and best fishing methods for catching this species.

Trends in the commercial catch statistics of crystal crabs indicate that this species is in much higher abundance on the west compared to the south coast, and managers should consider this when reviewing license and trap allocations for the south coast fishery. Inter-annual trends in landed catches reflect the rapid development of knowledge and technology within the fishery, and catches have slowly declined since their peak in 2000 on the west coast and 2001 off the south coast. Resilient catches indicate the early stages of development of this fishery.

### 3.4.2 Monthly trends in catch statistics

**Hypothalassia acerba**
The monthly trends exhibited by the fishing effort for *H. acerba* on the south coast closely paralleled those of catch, with values being least in early winter to mid-spring. The relatively low fishing effort in the above period reflects, in part the adverse weather conditions at this time and, also in the case of the months between July and October, the closure of the fisheries for one of the other two species that comprise the multi-species fishery for large crustaceans on the south coast, *i.e.* the southern rock lobster *Jasus edwardsii*. The similarity in the trends exhibited by both catch and effort accounts for the fact that the catch per unit effort did not change markedly throughout the year.

In contrast to the situation with *H. acerba* on the south coast, the monthly trends displayed by effort for this species on the west coast did not parallel those of catch. Indeed, effort was least in September, October and November on this coast, which explains why the catch per unit effort was greatest in these months. Although caution must be exercised in drawing conclusions from these catch statistics for this new fishery, the consistency of the progressive rise in CPUE between summer and the following spring does suggest that the relative abundance, or more likely the catchability of *H. acerba*, is greatest in the spring months. The period when *H. acerba* are most catchable on the west coast corresponds with the period when the mature females with late vitellogenic oocytes are most prevalent and with the peak in the mean monthly relative gonad weights. This is when the energy requirements of crabs are likely to be the highest and therefore crabs might be most actively feeding during this time. Catchability declined in December when females are possibly extruding their eggs to their pleopods, and catchability remains low throughout January to April which is the period when most ovigerous females were caught.

Intra-annual trends in catchability indicate that fishers can maximise their catches by fishing for champagne crabs from May to November on the west coast and from May to July on the south coast.
**Chaceon bicolor**

The lack of a conspicuous seasonality in either the catch or fishing effort for *C. bicolor* on the west coast accounts for the CPUE for this species on this coast remaining remarkably constant throughout the year. This, in turn, implies that the relative abundance and catchability of *C. bicolor* on the west coast vary little during the year, which is likely to reflect the stability of the deep-water environment. Due to environmental conditions that are relatively constant throughout the year, the factors that affect catchability such as mating, spawning and moulting probably occur all the year round. The constant CPUE throughout the year for this fishery enable fishers to be active throughout the year.

### 3.4.3 **Catches and carapace lengths of Hypothalassia acerba and Chaceon bicolor**

The fact that the catches of females were significantly less than those of males in the case of both *H. acerba* and *C. bicolor* parallels the results recorded for the trap catches of other species of deep-water crabs such as *Chaceon affinis, Chaceon maritae, Chaceon notialis, Pseudocarcinus gigas, Chionoecetes bairdii, Chionoecetes tanneri* (Melville Smith, 1988; Defeo *et al.*, 1991; Levings *et al.*, 2001; López Abellán, *et al.*, 2002; Workman and Phillips, 2002; Rosenkranz, 2002). The dominance of males in trap catches has been attributed to such features as male aggression (Bovjberg, 1956) and trap avoidance by ovigerous females (Melville Smith, 1987). Although there were some regional differences in the CPUEs for both *H. acerba* and *C. bicolor*, the differences were not pronounced and the basis for these differences was not clear.

The mean carapace lengths of the males of both *H. acerba* and *C. bicolor* were significantly greater than those of their females, as is the case with several other species of deep-water crab (Melville Smith, 1988; Levings *et al.*, 1996; López Abellán, *et al.*, 2002). However, the modal carapace length classes of males and females of *H. acerba* are the same,
*i.e.* 90 to 94 mm, whereas that of the males of *C. bicolor*, *i.e.* 115 to 119 mm, is considerably greater than that of the females, *i.e.* 100 to 104 mm. The differences between the sizes of the two sexes are thus greater in *C. bicolor* than *H. acerba.*
Figure 3.1. (a) Total landed catch of *Hypothalassia acerba* in southwestern Australia and (b) landed catch of this species on the lower west and south coasts of Western Australia separately. Data were extracted from the catch and effort statistics of the Department of Fisheries Western Australia and encompass the years between 1989 and 2003.
Figure 3.2. (a) Total number of pot lifts for *Hypothalassia acerba* in southwestern Australia and (b) number of pot lifts for this species on the lower west and south coasts of Western Australia separately. Data were extracted from the catch and effort statistics of the Department of Fisheries Western Australia and encompass the years between 1989 and 2003.
Figure 3.3. (a) Total catch per pot lift of *Hypothalassia acerba* in southwestern Australia and (b) total catch per pot lift of this species on the lower west and south coasts of Western Australia separately. Data were extracted from the catch and effort statistics of the Department of Fisheries Western Australia and encompass the years between 1989 and 2003.
Figure 3.4. Mean monthly landed weight of *Hypothalassia acerba* ± 95% CIs on (a) the lower west coast in the years 1992 - 1999 and (b) the south coast in the years 1992 - 2003.
Figure 3.5. Mean monthly number of pot lifts for *Hypothalassia acerba* ± 95% CIs on (a) the lower west coast in the years 1992 - 1999 and (b) the south coast in the years 1992 - 2003.
Figure 3.6. Mean monthly CPUEs of *Hypothalassia acerba* ± 95% CIs on (a) the lower west coast between 1992 and 1999 and (b) the south coast between 1992 and 2003.
Figure 3.7. (a) Total landed catch of *Chaceon bicolor* in southwestern Australia and (b) landed catch of this species on the lower west and south coasts of Western Australia separately. Data extracted from the catch and effort statistics of the Department of Fisheries Western Australia for the years between 1999 and 2003.
Figure 3.8. (a) Total number of pot lifts for *Chaceon bicolor* in southwestern Australia and (b) number of pot lifts for this species on the lower west and south coasts of Western Australia separately between 1994 and 2003. Data extracted from the catch and effort statistics of the Department of Fisheries Western Australia.
Figure 3.9. Total catch per pot lift of *Chaceon bicolor* in southwestern Australia and (b) total catch per pot lift of this species on the lower west and south coasts separately for the years between 1994 and 2003. Data extracted from the catch and effort statistics of the Department of Fisheries Western Australia.
Figure 3.10. (a) Mean monthly landed weight of *Chaceon bicolor* ± 95 % CIs on the lower west coast and (b) mean monthly number of pot lifts ± 95 % CIs on the lower west coast and (c) mean monthly landed weight per pot lift ± 95 % CIs on the lower west coast. Data were for the years between 2000 and 2003.
Figure 3.11. (a) Mean numbers of male and female Hypothalassia acerba per pot lift ± 95% CIs and (b) mean numbers of Hypothalassia acerba per pot lift ± 95% CIs in each region.
Figure 3.12. Mean numbers of *Chaceon bicolor* per pot lift \( \pm 95\% \) CIs for (a) males and females and (b) the northern and southern regions of the west coast.
Figure 3.13.  (a) Mean carapace lengths of male and female *Hypothalassia acerba* ± 95% CIs and (b) Carapace length - frequency distributions and mean carapace lengths for male and female *Hypothalassia acerba* caught by commercial fishers off the lower west and south coasts of Western Australia and c) mean carapace lengths of *Hypothalassia acerba* ± 95% CIs in each region.
Figure 3.14. (a) Mean carapace lengths of male and female *Chaceon bicolor* ± 95% CIs and (b) Carapace length - frequency distributions and mean carapace lengths for male and female *Chaceon bicolor* caught by commercial fishers off the lower west coast of Western Australia and (c) mean carapace lengths of *Chaceon bicolor* ± 95% CIs for each region.
Figure 3.15. Distances in km of the location of recaptured tagged *Hypothalassia acerba* from the point of their release.
RELATIVE ABUNDANCES AND SIZE
COMPOSITIONS OF HYPOTHALASSIA ACERBA
ON TWO COASTS AND IN DIFFERENT WATER
DEPTHS AND SEASONS
4.1 INTRODUCTION

The champagne crab *Hypothalassia acerba*, together with the western rock lobster *Panulirus cygnus*, the southern rock lobster *Jasus edwardsii*, the giant crab *Pseudocarcinus gigas* and the crystal crab *Chaceon bicolor*, are the main large benthic, crustacean predators in water depths greater than 20 m off the southwestern Australian coast (George, 1962; Kailola *et al*., 1993; Levings *et al*., 1996, 2001; Koh and Ng, 2000; Jones and Morgan, 2002).

The acquisition of appropriate biological data is crucial for managing deep-water crab species as they typically grow slowly and are long lived and are thus susceptible to becoming the subject of boom-and-bust fisheries (Hastie, 1995). Prior to the present study, no data on features such as distribution patterns, size compositions and sex ratios were available for *H. acerba*, or for any other species of the family Eriphidae except those provided in reports on the giant crab *Pseudocarcinus gigas* by Gardner (1998) and Levings *et al*., 2001.

However, such data are available for a number of deep-water crab species elsewhere in the world, and particularly for certain species belonging to the Geryonidae and Lithodidae. The distribution of several of these species is known to be related to water depth, temperature and/or substrate type (Melville Smith and Bailey, 1989; Hastie, 1995; Comeau *et al*., 1998) and the males tend to be more abundant in catches and grow to a larger size than the females (Lux *et al*., 1982; Melville Smith, 1988; Attrill *et al*., 1991; López Abellán *et al*., 2002). Furthermore, body size has been shown to be inversely correlated with water depth in certain deep-water geryonid species, implying that the individuals of these species are recruited into deeper water and subsequently move shorewards as they increase in size (Beyers and Wilke, 1980; Attrill *et al*., 1990; Lockhart *et al*., 1990). In some species, such movements are apparently more pronounced amongst females than males, occur seasonally and/or are related to such factors as temperature and/or reproductive state (Melville Smith, 1987b; Lockhart *et al*., 1990; Defeo *et al*., 1991; Hastie, 1995). Moreover, differences between the compositions of the invertebrate fauna living on the shells of males and females of *Chionoecetes opilio* imply
that, when not pairing, the two sexes of this species tend to occupy different niches off Newfoundland (Hooper, 1986). There is also evidence that the spatial resources in deep-water waters are partitioned among two congeneric species of deep-water crab in the Gulf of Mexico, with *Chaceon quinquedens* being more abundant in shallower waters and *Chaceon fenneri* being more numerous in deeper waters (Lockhart *et al.*, 1990; Hastie, 1995).

During the present study, we collected *H. acerba* during each season from seven water depths located at depth intervals of 55 m between 35 and 310 m on both the lower west and south coasts of Western Australia in order to test the following hypotheses. (1) *Hypothalassia acerba* will occur predominantly in a range of water depths that differ from those in which the other main large benthic invertebrate carnivores are predominantly found and thus reduce the likelihood of competition for resources amongst those species. (2) Since bottom water temperature declines with increasing water depth and overall is higher at corresponding depths on the lower west coast than south coast, the relative abundance of this species would be likely to peak at a deeper water depth on the lower west than south coast if temperature influences the distribution of *H. acerba*. (3) The distribution by depth will change seasonally in response to changes in bottom water temperature. The study also focuses on determining whether, as with certain representatives of two other families of deep-water crabs, the following apply on both coasts. The males will be relatively more abundant and attain a greater size than females, the body size will be inversely correlated with water depth and there will be a certain degree of habitat segregation between the sexes. Since the “western rock lobster” traps used in my study caught few small *H. acerba*, as is often the case with the traps employed to catch deep-water crabs (*e.g.* Lux *et al.*, 1982; López Abellán *et al.*, 2002), the question of whether the enclosure of these traps with a fine mesh would increase the catches of small crabs was also examined.
4.2 MATERIALS AND METHODS

4.2.1 Sampling regime

The data used to determine the relative abundance of *Hypothalassia acerba* in different water depths were derived from the depth-stratified sampling regime, which was undertaken once per calendar season on both the lower west and south coasts using traps that were not enclosed in mesh (Chapter 2).

The data used to describe the relationships between carapace length and water depth, coast and season were derived collectively from the sampling described above, but in this case they included the data collected using traps enclosed in small mesh. Refer to chapter 2 for a full description of the sampling regime.

4.2.2 Data analysis

Plots of $\log_{10}$ (mean) against $\log_{10}$ (standard deviation) showed that, prior to subjecting catch rates to Analysis of Variance (ANOVA), they required square root transformation (see Clarke and Gorley (2001) for rationale for this approach). These two values ($\text{mean}$ and $\text{s.d.}$) were calculated from the catches per line of three traps in each water depth on each coast in each season. The transformed values for catch for each sex for each line of traps in each water depth on each coast in each season were subjected to ANOVA, with each factor being fixed. Note that since no crabs were caught at depths of either 35 or 365 m on either coast, these zero values were not employed in the ANOVA. Since the four-way interaction between coast, depth, sex and season was not significant ($p > 0.05$), this term was removed from the model and the data reanalysed. Results from the ANOVA were back-transformed before plotting.

The distribution of crabs with respect to bottom water temperature was explored by fitting a nonlinear regression model that related the catch $C(T)$ by all three lines of traps to the
bottom water temperature $T \, ^\circ\text{C}$ recorded at the corresponding depth at which the traps were placed. The base model used, \textit{i.e.}

$$C(T) = a + b \exp\left[ -c(T - d)^2 \right],$$

was intended to represent catches for the sampling unit that were proportional to a common base level of catch, $a$ (where $a \geq 0$), over all temperatures, augmented by a “normal distribution” of increased catches of crabs centred at a mean temperature of $d \, ^\circ\text{C}$. The parameters $a$, $b$, $c$ and $d$ were estimated by minimizing the weighted sum of squared deviations between transformed values of the observed and predicted catches, where each weight was calculated as the inverse of the predicted catch and a penalty function was used to ensure that $a \geq 0$. A likelihood ratio test was used to determine whether the above model provided a better description of the distribution of crabs than the simpler model $C(T) = a$, \textit{i.e.} a distribution of crabs that was independent of water temperature. Likelihood ratio tests were also used to test whether the value of $a$ in the base model differed significantly from zero and/or whether there were differences between the mean temperatures of the ‘normal distributions’ for the curves for the south and west coasts and, on the west coast, between those for the meshed and non-meshed traps.

The logarithms of the standard deviations of the carapace lengths for each sex on each sampling occasion on both coasts were plotted against the logarithms of the mean values for those carapace lengths. This demonstrated that the carapace lengths did not require transformation prior to subjection to analysis of covariance (ANCOVA). This latter analysis, which employed the General Linear Model (GLM) procedure within SPSS Version 10 (SPSS Inc., Chicago, Illinois, USA) and assumed a normal distribution of observation errors, was undertaken to ascertain whether there was a significant linear relationship between carapace length and water depth and whether this relationship was influenced by sex, coast and/or
season. If the covariate in an ANCOVA is found to be significant, the absolute value of the dependent variable is dependent upon the value of the covariate and values of the dependent variable for the other factors must be adjusted to a standard value of this covariate before they are compared. In the SPSS analysis of the data for *H. acerba*, a water depth of 200 m was specified as the standard depth at which the comparison among other factors was to be made if the covariate, depth, was found to be significant. Likewise, if the other factors (or their interactions) are found in the ANCOVA to be significant, a plot of the values of the dependent variable against the values of the covariate will reflect both the linear trend associated with the covariate and the effects of the other significant factors and interactions. To remove these effects and thereby illustrate more clearly the relationship between the dependent variable and the covariate, the values of the effects of the significant factors and interactions, as calculated in the ANCOVA, were subtracted from the corresponding values of the dependent variable to transform the data to values that would be approximately “equivalent” to those recorded at the reference levels of the factors, *i.e.* females of *H. acerba* on the south coast during spring. The means and 95% confidence intervals of the transformed data were calculated and plotted against the values predicted for the corresponding depths for females on the south coast during spring.

A fully saturated statistical model was fitted to the carapace lengths, with sex, coast and season as factors and depth as a covariate. Higher order interactions that were not significant (*p > 0.05*) were then successively removed, with the term having the greatest *p*-value being selected as the next term to be eliminated. Next, lower-order interaction terms that were not significant were examined to determine whether they might also be removed to reduce the model further. Such lower-order terms were retained if they contained constituent variables that were included in the remaining significant higher-order interaction terms. The value for the Bayesian Information Criterion (BIC) was calculated for the resulting model as
\[ BIC = n \log_e \left( \frac{SS_e}{n} \right) + p \log_e (n), \]

where \( SS_e \) is the sum of squares of the errors, \( n \) is the number of observations, \( p \) is the number of parameters that were estimated by the GLM procedure and \( \log_e \) is the natural logarithm (Schwarz, 1978). The highest-order interaction terms in the model were then removed and the BIC recalculated. If the latter value was less than the corresponding value for the preceding model, it was concluded that this latter model was the more appropriate description. In this case, the simpler model was accepted and re-examined to determine whether further non-significant terms could be removed, using the same procedure as described above.

4.3 RESULTS

4.3.1 Water temperature

Water temperatures declined with increasing water depth on both the west and south coasts (Figure 4.1). However, at each depth for which there were comparable data, the temperatures were appreciably greater on the west than south coast in both summer and spring, but not in autumn or winter. Temperatures in depths \( \leq 255 \) m were greater in summer and autumn than in winter and spring on the west coast, whereas they were greater in autumn and winter than in spring and summer on the south coast (Figure 4.1).

4.3.2 Relative abundance of crabs in different water depths and temperature

ANOVA demonstrated that the catch rates of crabs differed significantly between sexes and among water depths and seasons (Table 4.1). However, the mean squares and significance levels were far greater for water depth and sex than for season. All of the two-way interactions except sex × season and the three-way interactions sex × coast × water depths and coast × depth × season were significant (Table 4.1).
On both the west and south coasts, the mean catch rates were greater for males than females in those water depths in which the majority of crabs were caught, *i.e.* 200 and 255 m on the west coast and 90, 145 and 200 m on the south coast (Figure 4.2). These depth-related differences in the abundances of crabs on the west and south coasts, together with the fact that males were proportionately more abundant on the south coast, explain the sex × coast × depth interaction for catch rates (Table 4.1).

Table 4.1. Mean squares and significance levels for ANOVA of catch rates of female and male *Hypothalassia acerba* recorded in the seven water depths sampled on the lower west and south coasts of Western Australia during the four seasons of the year. *p < 0.05 **p < 0.01 ***p < 0.001

<table>
<thead>
<tr>
<th></th>
<th>Mean squares</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (S)</td>
<td>16.4***</td>
<td>1</td>
</tr>
<tr>
<td>Coast (C)</td>
<td>2.5</td>
<td>1</td>
</tr>
<tr>
<td>Depth (D)</td>
<td>23.6***</td>
<td>4</td>
</tr>
<tr>
<td>Season (T)</td>
<td>3.1**</td>
<td>3</td>
</tr>
<tr>
<td>S × C</td>
<td>7.4**</td>
<td>1</td>
</tr>
<tr>
<td>S × D</td>
<td>2.4*</td>
<td>4</td>
</tr>
<tr>
<td>S × T</td>
<td>0.2</td>
<td>3</td>
</tr>
<tr>
<td>C × D</td>
<td>26.3***</td>
<td>4</td>
</tr>
<tr>
<td>C × T</td>
<td>7.1***</td>
<td>3</td>
</tr>
<tr>
<td>D × T</td>
<td>7.0***</td>
<td>12</td>
</tr>
<tr>
<td>S × C × D</td>
<td>4.3***</td>
<td>4</td>
</tr>
<tr>
<td>S × C × T</td>
<td>1.2</td>
<td>3</td>
</tr>
<tr>
<td>C × D × T</td>
<td>3.5***</td>
<td>10</td>
</tr>
<tr>
<td>S × D × T</td>
<td>0.8</td>
<td>12</td>
</tr>
<tr>
<td>Residual</td>
<td>0.8</td>
<td>54</td>
</tr>
</tbody>
</table>

The catch rates of crabs on the west coast peaked at a water depth of 200 m in summer, autumn and winter and at 255 m in spring (Figure 4.3). In contrast, on the south coast, catch rates peaked at 90 or 145 m in summer, autumn and spring and at 255 m in winter. These differences explain the coast × depth × season interaction (Table 4.1).

Comparison of the fitted model with one that assumed a distribution of catch rates independent of temperature revealed that, on the south coast, catch rates were not significantly
influenced by temperature ($p > 0.05$). However, on the west coast, catch rates of champagne crabs were influenced markedly and significantly ($p < 0.001$) by bottom water temperatures (Figure 4.4). While the value of the parameter $a$ did not differ significantly from zero for either trap type on the latter coast ($p > 0.05$), the mean temperatures of the ‘normal distributions’ fitted to the numbers of crabs caught using non-meshed and meshed traps, *i.e.* 17.1 and 16.1°C, respectively, differed significantly ($p < 0.01$). Although the temperature distribution of the catches of the non-meshed traps on the south coast were not demonstrated to be significantly influenced by temperature, it should be noted that the mean temperature associated with the ‘normal distribution’ in the curve fitted to these catches was 16.4°C and did not differ significantly from that for non-meshed traps on the west coast ($p > 0.05$). It is thus concluded that the mean temperature occupied by *H. acerba* of the size range caught by traps on both coasts lies between 16.1 and 17.1°C.

### 4.3.3 Relationship between carapace length and water depth, coast and season

The carapace lengths of male and female *H. acerba* caught during the study ranged from 50 to 135 mm and from 51 to 113 mm, respectively on the west coast and from 62 to 138 mm and from 69 to 120 mm, respectively, on the south coast (Figure 4.5). The size distribution of the females was skewed markedly to the left of males on the south coast but not on the west coast.

As the four-way interaction between the carapace lengths of crabs and sex, coast, depth and season was not significant ($p > 0.05$) in the ANCOVA to which these data were subjected, the analysis was repeated but excluding this interaction term. Season × depth × sex was the only three-way interaction term that was significant ($p < 0.05$). However, the value for the BIC for this model, *i.e.* 5628, was greater than that for the model that excluded this three-way interaction term, *i.e.* 5616. Thus, this three-way interaction term was removed from the ANCOVA, together with non-significant two-way interaction terms.
Carapace length was significantly influenced by water depth and the relationship between these two variables did not exhibit a significant interaction with either sex, coast or season (Table 4.2). Thus, on average, the carapace length declined by 4 mm for every 100 m increase in water depth (Figure 4.6a). Sex × coast and coast × season were the only significant two-way interaction terms (Table 4.2). After adjustment of the data to a standard depth of 200 m, the mean carapace lengths of males and females were 96.6 and 94.6 mm, respectively, on the west coast, and 101.5 and 91.4 mm, respectively, on the south coast (Figure 4.6b), the latter difference being significant ($p < 0.001$). Although the mean carapace length of males on the south coast was significantly greater than that of males on the west coast ($p < 0.001$), no such significant difference was found between the mean carapace lengths of females on the two coasts ($p > 0.05$).

Table 4.2  Mean squares and significance levels for ANCOVA of carapace lengths of female and male *Hypothalassia acerba* caught in the seven water depths sampled on the lower west and south coasts of Western Australia during the four seasons of the year. Depth was treated as a covariate. ***$p < 0.001$

<table>
<thead>
<tr>
<th></th>
<th>Mean squares</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (S)</td>
<td>5906.0***</td>
<td>1</td>
</tr>
<tr>
<td>Coast (C)</td>
<td>82.0***</td>
<td>1</td>
</tr>
<tr>
<td>Depth (D)</td>
<td>2899.7***</td>
<td>1</td>
</tr>
<tr>
<td>Season (T)</td>
<td>882.4***</td>
<td>3</td>
</tr>
<tr>
<td>S × C</td>
<td>2684.4***</td>
<td>1</td>
</tr>
<tr>
<td>C × T</td>
<td>1251.4***</td>
<td>3</td>
</tr>
<tr>
<td>Residual</td>
<td>141.0</td>
<td>4</td>
</tr>
</tbody>
</table>

The mean carapace lengths of crabs caught during summer and winter off the south coast were greater than those of crabs caught during these corresponding seasons off the west coast, whereas the reverse pertained in autumn and spring (Figure 4.6c). During winter, the
mean carapace length of crabs caught off the south coast was significantly greater than that of crabs caught during autumn and spring off that coast ($p < 0.001$).

### 4.3.4 Sex ratios

Males dominated the catches obtained from all water depths collectively in each season on both the west and south coasts (Table 4.3). However, in each season, the prevalence of males was not as great on the west coast as on the south coast, with the seasonal percentage contributions made by males to the catches of crabs in each season ranging from 64.8 to 76.9% on the west coast compared with 76.0 to 88.8% on the south coast. The overall percentages of males on the west and south coasts were 69.2 and 84.0%, respectively (Table 4.3).

#### Table 4.3. Percentage of females and males of *Hypothalassia acerba* caught in traps in each season and overall on the lower west coast and south coasts of Western Australia. $n =$ number of crabs.

<table>
<thead>
<tr>
<th>Season</th>
<th>West coast</th>
<th></th>
<th>South coast</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males %</td>
<td>Females %</td>
<td>Males %</td>
<td>Females %</td>
</tr>
<tr>
<td>Summer</td>
<td>76.9</td>
<td>23.1</td>
<td>87.2</td>
<td>12.8</td>
</tr>
<tr>
<td>Autumn</td>
<td>64.8</td>
<td>35.2</td>
<td>79.0</td>
<td>21.0</td>
</tr>
<tr>
<td>Winter</td>
<td>70.2</td>
<td>29.8</td>
<td>88.8</td>
<td>11.2</td>
</tr>
<tr>
<td>Spring</td>
<td>68.8</td>
<td>31.2</td>
<td>76.0</td>
<td>24.0</td>
</tr>
<tr>
<td>Overall</td>
<td>69.2</td>
<td>30.8</td>
<td>84.0</td>
<td>16.0</td>
</tr>
</tbody>
</table>

#### 4.3.5 Results of enclosing traps with mesh

On the two occasions when crabs were caught in non-meshed and meshed traps, the mean carapace length of both male and female crabs obtained using meshed traps was significantly different ($p < 0.05$) from that of the corresponding sex collected using the same type of trap but without mesh (Figure 4.7). However, the differences in the mean carapace lengths of the crabs
caught in meshed and non-meshed traps differed by only between 3.9 and 6.9 mm in each of the four comparisons. Furthermore, the number of crabs that were caught with carapace lengths of less than 75 mm still remained low.

4.4 DISCUSSION

4.4.1 Relationship between catch rates and water depth

The sampling regime used in this study was designed to collect *Hypothalassia acerba* from the range of water depths in which preliminary studies had indicated that this species occurred on the lower west and south coasts of Western Australia. Furthermore, particular attention was paid to ensuring that the seven sampling sites were aligned perpendicular to the shoreline and were located sequentially at even depth intervals of 55 m from the shallowest site at 35 m to the deepest site at 365 m. The sampling of seven sites (water depths) on both coasts in each season thus produced results that enabled conclusions to be drawn regarding aspects of the spatial and size distributions and sex ratios of *H. acerba*. This species of deep-water crab was not caught in the shallowest depth and was rarely caught in the deepest waters in any season on either coast, and the catch rates at the intermediate depths rose progressively and then declined sequentially. This demonstrates that my sampling regime essentially encompassed the full range of depths at which at least all but the smaller members of this species occur in the sites sampled. Furthermore, the depths at which *H. acerba* were predominantly caught on both the west and south coasts are entirely consistent with those in which commercial fishers obtained their catches (R. Melville Smith, Department of Fisheries W.A., pers. comm.). The very strong relationship between catch rate and water depth is further illustrated by my finding that, in the case of the most abundant sex, *i.e.* males, the catches peaked sharply at 200 m on the west coast and at 145 m on the south coast. Furthermore, the catches of males at 200 and 255 m collectively on the west coast and at 90, 145 and 200 m collectively on the south coast contributed 90 and 92%, respectively, to the total catches of this sex on these two coasts.
Although the females of *H. acerba* were less abundant than their males on both the west and south coasts, my data still clearly demonstrate that the trends exhibited by the abundance of females with water depth were the same as those for males on both coasts. Thus, the catches of females likewise peaked at 200 m on the west coast and at 145 m on the south coast. The presence of the same pattern of distribution of the two sexes of *H. acerba* in all seasons contrasts with the situation with certain other deep-water crabs species in which, when unpaired, the sexes tend to occupy different water depths (Beyers and Wilkie, 1980; Melville Smith, 1987; Lockhart *et al.*, 1990; Defeo *et al.*, 1991). For example, the females of *Geryon maritae*, *Chaceon fenneri*, *Chaceon notialis*, and *Chionoecetes opilio* were relatively more prevalent than males in shallower waters (Melville Smith, 1987, 1988; Lockhart *et al.*, 1990; Defeo *et al.*, 1991).

Comparisons of my results with those for other species of deep-water crabs suggest that *H. acerba* is restricted to a particularly narrow range of water depths for such species. For example, *Chaceon notialis* was caught in water depths of 300 to 900 m in the Argentinian-Uruguayan fishing zone and, in summer, the catch per unit of effort (CPUE) was still increasing at the upper end of this range in water depths (Defeo *et al.*, 1991). Although the catch rates of *Chaceon affinis* peaked at 800 - 900 m water depth, this species was caught in water depths of 500 to 1200 m and, from the data presented, presumably well beyond that latter depth (López Abellán *et al.*, 2002). *Geryon quinquedens* and *Geryon maritae* are also found in a wide range of water depths, *i.e.* from 275 to 1000 m off southern New England and from 270 to 924 m off Namibia (Lux *et al.*, 1982; Melville Smith and Bailey, 1989).

Since *H. acerba* appears to be largely restricted to water depths within the relatively narrow ranges of 145 to 310 m on the west coast and of 90 to 200 m on the south coast, it is relevant that other major large benthic crustaceans in this region are most abundant in water depths to either side of those in which *H. acerba* occurs. Thus, on the west coast, the western
rock lobster *P. cygnis* is most common in depths up to 90 m (George, 1962), while off the south coast the southern rock lobster *J. edwardsii* is also most frequently caught in waters less than 90 m (Anon., 2002). The snow crab *Chaceon bicolor* is most abundant in depths exceeding 600 m on the west coast and 500 m on the south coast (K. Smith and R. Melville Smith, unpublished data), where my unpublished sediment analyses showed that the silt/clay fraction in the substrate was far greater than in the shallower waters where the champagne crab is found, *i.e.* 32 vs 5\%.

Furthermore, on the south coast, *P. gigas* also occurs mainly in water depths that, from Levings *et al.* (1996, 2001) and Gardner (1996), lie at the upper end of the range of that in which *H. acerba* lives. The distribution patterns of these decapod species thus provide evidence of spatial partitioning among these major components of the benthic communities on the two coasts, thereby parallelling the type of partial partitioning by depth exhibited by *Chaceon fenneri* and *Chaceon quinquedens* in the Gulf of Mexico (Lockhart *et al.*, 1990).

### 4.4.2 Relationship between catch rates and water temperature

Since the density of *H. acerba* is related to water depth on both the west and south coasts and water temperature decreases with increasing water depth, it seems highly likely that the relative abundance of this species will also be influenced by water temperature. Such a conclusion is consistent with the fact that, while the overall catches of *H. acerba* peaked at a shallower water depth on the south coast (145 m) than lower west coast (200 m), those peaks in abundance corresponded to a similar water temperature, *i.e.* 16.1 to 17.1 °C. Thus, by typically occurring in a shallower water depth on the south coast, *H. acerba* is located in the same temperature as would be the case on the west coast. It is thus not surprising that the distribution of catch rate of *H. acerba* by depth on the two coasts was most similar in winter when the water temperatures at the corresponding depths on the two coasts were most similar.
Although *H. acerba* was caught in water temperatures ranging from 11.9 to 21.9°C on the west coast and from 11.2 to 20.6°C on the south coast, over 85% of the individuals of this species were caught in temperatures of 15.8 to 18.2°C on the west coast and over 95% were collected at temperatures between 13.1 and 18.7 °C on the south coast. Furthermore, the water temperature at which the catches of *H. acerba* peak lies between 16.1 and 17.1°C on both coasts, which is ~6 to 10°C higher than those recorded for five *Chaceon* species, which live in deeper water (see Hastie, 1995).

### 4.4.3 Trap selectivity

Our failure to catch small *H. acerba* in traps parallels the situation recorded for several other species of decapod (Melville Smith, 1986; Miller, 1990). Furthermore, the mean size of crabs caught by the rectangular traps was only slightly reduced when these traps were enclosed in aviary mesh. This may reflect either trap shyness by small *H. acerba* or their exclusion from traps through the aggression of larger individuals or possibly their occupation of different water depths. The greater prevalence of males than females in my catches, and those of commercial fishers operating over a wide geographical area (K. Smith, unpublished data) may reflect females being less vulnerable to traps, as is the case in some other species of decapod (see Miller, 1990). Furthermore, the fact that only seven ovigerous *H. acerba* were caught during the present study, which is again consistent with the results for some other decapod species (Miller, 1990) and presumably reflects a tendency for the berried females of this species not to enter traps, also helps account for the predominance of males in my catches of *H. acerba*.

This chapter has been accepted for publication as follows: Smith, K.D, Hall, N.G. and Potter, I.C. (2004). Relative abundances and size compositions of male and female champagne crabs,
Figure 4.1. Mean bottom water temperatures ± 95% CIs in the water depths where *Hypothalassia acerba* was sampled off the lower west and south coasts of Western Australia in each season.
Figure 4.2. Mean numbers of male and female *Hypothalassia acerba* ± 95% CIs caught in trap lines in different water depths off the lower west (top) and south coasts (bottom) of Western Australia.
Figure 4.3. Mean numbers of *Hypothalassia acerba* ± 95% CIs caught in trap lines in different water depths off the lower west and south coasts of Western Australia in each season.
Figure 4.4. Distribution of numbers of champagne crabs caught at various bottom water temperatures in non-meshed and meshed traps off the lower west (above) and south (below) coasts of Western Australia.
Figure 4.5. Frequency distributions for the carapace lengths of male and female *Hypothalassia acerba* caught using non-meshed traps off the lower west and south coasts of Western Australia.
Figure 4.6.  (a) Mean carapace lengths ± 95% CIs for Hypothalassia acerba caught in different water depths off Western Australia. The mean carapace lengths have been calculated after adjusting the data to represent the equivalent lengths that, after adjustment, would have been obtained for females on the south coast during spring. Mean carapace lengths ± 95% CIs of (b) male and female H. acerba caught off the lower west and south coasts of Western Australia and of (c) both sexes collectively off the lower west and south coasts of Western Australia in each season. The data in Figs 3.5b and 3.5c have been adjusted to a standard depth of 200 m.
Figure 4.7. Frequency distributions for the carapace lengths of male and female Hypothalassia acerba caught off the lower west and south coasts of Western Australia using meshed and non-meshed traps in May (top) and November (bottom). Sample sizes (n) and mean ± 95% CIs are given on Figure.
Chapter 5

COMPARISONS BETWEEN THE
REPRODUCTIVE BIOLOGY OF THE FEMALES
OF *HYPOTHALASSIA ACERBA* AND *CHACEON BICOLOR*
5.1 INTRODUCTION

Three species of deep-water crab are fished commercially in Western Australian waters, namely the champagne crab *Hypothalasia acerba* Koh and Ng, the crystal crab *Chaceon bicolor* Manning and Holthuis and the giant crab *Pseudocarcinus gigas* Lamarck (Anon., 2002). On the basis of catches obtained by commercial fishers, the distribution of *H. acerba* ranges from a latitude at least as far north as about 27ºS on the west coast, southwards and then eastwards along the south coast to a longitude of at least 129ºE (Anon., 2002). Although *C. bicolor* occurs in the same geographical region as *H. acerba*, its distribution in Western Australia extends further north to latitude of ~ 22ºS (Melville Smith *et al.*, in press). In contrast, the distribution of *P. gigas* is essentially restricted to the south coast in Western Australia and extends eastwards across the full length of Australia, including Tasmania, and then northwards on the east coast to about 31ºS (Kailola *et al.*, 1993; Gardner, 1998).

Recent depth-stratified sampling off the southwestern Australian coast has demonstrated that *H. acerba* occurs predominantly in waters where temperatures lie between 13 and 20 ºC and the depths range from 200 to 255 m on the lower west coast and from 90 to 200 m on the south coast (Smith *et al.*, 2004a). Temperatures recorded during commercial fishing for *C. bicolor* show that, on the lower west coast of Australia, this species typically occurs in waters of 4 to 6.5 ºC (K. Smith unpublished data) and at water depths of 450 to 1,220 m (Melville Smith *et al.*, in press) and is thus located further offshore than *H. acerba*. *P. gigas* is found in waters of 11 to 17 ºC and at depths of 120 to 340 m (Levings *et al.*, 1996).

The commercial fisheries for *H. acerba* and *C. bicolor* in Western Australia started to develop during the late 1990s (Anon., 2002). However, in contrast to the situation with *P. gigas* (see Levings *et al.*, 1996, 2001; Gardner, 1997; Gardner and Williams, 2002), no biological studies have been conducted on the spawning period and location and fecundity of either of these two species.
The stages in development of the ovaries of several species of deep-water crabs belonging to the Geryonidae, e.g. *Chaceon quinquedens* (Smith), *Chaceon maritae* (Manning and Holthuis) and *Chaceon affinis* (Milne Edwards and Bouvier), have been described on the basis of their macroscopic appearance and, in some cases, also on the stages of maturation of their oocytes as determined from histological sections (Haefner, 1977; Melville Smith, 1987a; Fernández-Vergas *et al.*, 2000; López Abellán *et al.*, 2002). No such combined macroscopical and histological studies have been carried out on any deep-water species of the Eriphidae, the family to which *H. acerba* belongs. Although some deep-water crab species, such as *Chaceon fenneri* (Manning and Holthuis), have an annual reproductive cycle (see Hastie, 1995), no clear seasonal fluctuations in reproductive patterns were detected with *C. maritae* (Melville Smith, 1987a) and *C. quinquedens* (Wigley *et al.*, 1975; Haefner, 1978). It was proposed by Melville Smith (1987a) that the lack of a distinct reproductive cycle in *C. maritae* was attributable to the absence, in the deep waters in which this species is found, of changes in day length and temperature and other potential environmental reproductive triggers.

The aims of the present study were as follows. (1) Describe, on the basis of their macroscopic appearance, the sequential stages in the development of the ovaries of *H. acerba* and use histological sections to determine the stages of maturation of the oocytes in ovaries at each of those stages. Attention was paid to elucidating whether the criteria developed for categorizing the ovarian stages of *H. acerba* were the same as those we developed concomitantly for *C. bicolor* and those described for other species of deep-water crab. (2) Use the trends exhibited throughout the year by the monthly prevalences of female crabs with ovaries at different stages in development and of females bearing either eggs or egg remnants, together with those of the mean monthly gonad weights of females, to determine the timing of reproduction in these two species. Particular emphasis is placed on testing the hypothesis that, as *H. acerba* lives in far shallower waters than *C. bicolor*, and thus lives in an environment that
undergoes a greater degree of seasonal change and particularly in water temperature, it is far more likely to reproduce seasonally. (3) Determine the fecundities of *H. acerba* and *C. bicolor* and their relationships to the body size and body weight of these species. (4) Establish whether aspects of the reproductive biology of *H. acerba* on the lower west and southern coasts of Western Australia exhibit similar patterns. Since preliminary analyses indicated that *H. acerba* invests less in gonadal development on the south than west coasts, we examined whether the relative ovarian weights and diameters of the mature oocytes of females on the two coasts differed.

5.2 MATERIALS AND METHODS

5.2.1 *Collection of samples*

The reader is referred to Chapter 2 for details of the depth-related sampling regime and the onboard sampling which together yielded the *H. acerba* and *C. bicolor* used for the present study.

5.2.2 *Laboratory processing*

The reader is referred to Chapter 2 for description of measurements made on *H. acerba* and *C. bicolor* and the criteria used to designate female crabs as either immature or mature.

The ovary of each female was removed and allocated to a numerical developmental stage on the basis of macroscopic criteria (see Results). The stages in development of the testes and vas deferens were recorded during another study aimed at determining the size at maturity of the males of these two species (Chapter 7).

The ovary of each female of *H. acerba* and *C. bicolor* was weighed to the nearest 0.1 g. The mean monthly ovarian weights (± 95% CIs) at standardised carapace lengths were determined for *H. acerba* on the lower west and south coasts and for *C. bicolor* on the former
coast using analysis of covariance (ANCOVA) of the natural logarithm of the gonad weight as the dependant variable, month as a fixed factor and the natural logarithm of the carapace length as a covariate. Note that the standardised carapace length was calculated separately for the lower west and south coast assemblages of *H. acerba* and the lower west coast assemblage of *C. bicolor*. These constant carapace lengths were a default value calculated by the ANCOVA. ANCOVA was also used in the above manner to calculate the mean gonad weight (± 95% CIs) for *H. acerba* with ovaries containing previtellogenic, early vitellogenic and late vitellogenic oocytes on the lower west and south coasts. The standardised carapace length was calculated separately for each of these three developmental stages, but was common for a given stage on the two coasts. Data for the small individuals that were considered not to have mated were not used when calculating the monthly prevalences of females with ovaries at different stages in development, the mean monthly gonad weights for females at a standardized carapace length, and the mean gonad weights for west and south coast *H. acerba* with ovaries at different stages in development (see Figures 5.2-5.5 in Results).

The method of Melville Smith (1987a) was used for determining the batch fecundity of *H. acerba* and *C. bicolor*. Thus, alternate pleopods were removed from the abdomen of each ovigerous female and soaked for 1 to 4 h in 0.5 M NaOH to facilitate the separation of eggs from the pleopod setae. All of the eggs removed from each crab were pooled, oven dried at 70°C for 24 h and then weighed to the nearest 0.001 g. Subsamples of ~ 0.1 g of eggs (= ~ 300 eggs) were then weighed and counted, and the average weight of a single egg in each subsample was calculated. When estimates of the weight of a single egg in three subsamples differed by < 5%, the mean of those weight estimates was then used, in conjunction with twice the weight of all eggs removed (in order to adjust for having removed half the pleopods), to estimate the fecundity of the crab.
The right posterior side of the ovary was removed from up to 20 females of both species in each season, ensuring that these subsamples covered the full size range of those species in the total catch in each season. The ovarian material was fixed in 4% glutaraldehyde in a 0.025 M phosphate buffer solution (pH 7.0), dehydrated in a series of increasing concentrations of ethanols, embedded in paraffin wax, sectioned transversely at 6 μm and stained with Mallory’s trichrome. The ovarian material was fixed in glutaraldehyde since it was not fixed well by traditional fixatives used for light microscopy such as Bouin’s and 10% formalin. The smallest and largest diameters of oocytes of *H. acerba* and *C. bicolor* at different developmental stages sectioned through their nuclei were measured to the nearest 5 μm. The smallest and largest diameters of each oocyte were then averaged.

In addition to the above laboratory processing of crabs, the candidate also recorded, when on board fishing vessels, the total number of mature female crabs caught and the percentage of both ovigerous females and of females with egg remnants attached to their pleopods. Note that, due to inclement weather, the commercial fisher with whom we mainly worked did not operate in September in the deep waters off the lower west coast of Australia where *C. bicolor* is found and thus there are no data on the above variables for that month.

5.3 RESULTS

5.3.1 Ovarian maturation stages

On the basis of their macroscopic appearance, the ovaries of the females of *Hypothalassia acerba* and *Chaceon bicolor* each followed essentially the same pattern of development (*Table 5.1*). Thus, for both species, six sequential stages were recognised (*Table 5.1; Figure 5.1*). As
Table 5.1. Macroscopic and microscopic characteristics of sequential stages in ovarian development of Hypothalassia acerba and Chaceon bicolor. Range in oocyte diameters at each stage of development are provided. Scheme has been adapted from that of Haefner (1977).

<table>
<thead>
<tr>
<th>Ovarian stage</th>
<th>Macroscopic description</th>
<th>Histological description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I</td>
<td>Virgin/immature resting</td>
<td>Ovaries small but generally visible macroscopically, thin and ‘H’ shaped. (Shape is maintained for all latter stages except stage IV). Oocytes not visible through ovarian wall. Colour varies from pale grey to ivory.</td>
</tr>
<tr>
<td>Stage II</td>
<td>Developing</td>
<td>Ovaries always visible macroscopically, larger than stage I and slightly dorso-ventrally compressed. Ovaries beginning to displace hepatopancreas. Oocytes not visible through ovarian wall. Colour varies from ivory to white.</td>
</tr>
<tr>
<td>Stage III</td>
<td>Maturing</td>
<td>Ovaries larger than at stage II and outer membrane has wrinkled appearance. Oocytes not visible through ovarian wall. Ovaries are pale pink in H. acerba while range from very pale yellow to yellowish orange in C. bicolor.</td>
</tr>
<tr>
<td>Stage IV</td>
<td>Mature</td>
<td>Ovaries larger than at stage III and consequently are no longer ‘H-shaped’. Ovarian wall more folded. Oocytes visible through ovarian wall. Ovaries pink to red in H. acerba and brown to purple in C. bicolor.</td>
</tr>
<tr>
<td>Stage V</td>
<td>Recently spent</td>
<td>Ovaries similar in appearance to stage II, but more flaccid and yellowish-grey in colour.</td>
</tr>
<tr>
<td>Stage VI</td>
<td>Spent-recovering</td>
<td>Same as stage V.</td>
</tr>
</tbody>
</table>
they progress from stages I to IV, the ovaries increase progressively in size and change colour (Figures 5.1a-d). However, the colours of the ovaries of the two species at stages III and IV differ. In both species, ovaries at stages V and VI are flaccid and could not be separated macroscopically.

At a histological level, cortical alveolar oocytes first appeared in stage II ovaries of *H. acerba* (Figures 5.1a,b), and the presence of early and late yolk granule oocytes characterised stage III (Figure 5.1c) and IV ovaries (Figure 5.1d), respectively. Ovaries of recently-spent females (stage V) of *H. acerba* contained some atretic oocytes (Figure 5.1e), while those of spent-recovering (stage VI) females possessed no such oocytes but did contain numerous early previtellogenic oocytes (Figure 1f). The histological characteristics of the ovaries of *C. bicolor* are essentially the same as those shown for *H. acerba* in Figures 5.1a-f. However, the mean diameters of the mature oocytes, as measured in stage IV ovaries, are significantly greater (*p* < 0.001) for *C. bicolor* than *H. acerba*.

Comparisons of the macroscopic and microscopic characteristics of my ovarian stages for *H. acerba* and *C. bicolor* with those of Haefner (1977) demonstrate that the ovaries of the former two species undergo the same pattern of development as *Chaceon quinquedens*. However, the maximum diameter of the oocytes in my stage I (70 μm) is far less than that recorded by Haefner (1977) for his first stage for *C. quinquedens* (172 μm) and yolk granule oocytes are already present in his stage II whereas they do not appear until stage III of my categorization for *H. acerba* and *C. bicolor*. In essence, Haefner (1977) did not recognise the presence of the early stage I have termed virgin/immature resting. However, that stage was recognised by de Lestang *et al.* (2003) in their description of ovarian development in *Portunus pelagicus* (Linnaeus) in inshore waters in Western Australia. Furthermore, unlike the study of Haefner (1977), my histological staging criteria distinguish recently-spent ovaries from spent-
recovering ovaries, which is useful for obtaining an idea of how recently ovulation had occurred.

5.3.2 Monthly trends in reproductive indices

On the lower west coast, the prevalence of female *H. acerba* with ovaries containing late vitellogenic oocytes was greatest in September to February, during which months their contributions ranged from 58 to 76%, and was least in March to June when their monthly contributions ranged from 11 to 50% (Figure 5.2a). The prevalence of female crabs with ovaries containing only previtellogenic oocytes was less than 12% in each month from September to February and in April and only exceeded 30% in March and August. Small numbers of spent females were collected between January and March and in May. The mean monthly gonad weight of *H. acerba*, standardized to a constant carapace length of 94.7 mm, rose progressively from 11.5 g in July to between 25.2 and 28.6 g in October to December and then declined sequentially to between 4.9 and 8.3 g in March to May (Figure 5.2b). The prevalence of female *H. acerba* bearing egg remnants declined sequentially from 12% in July to zero or close to zero in October to January before rising progressively to 21% in May. Small numbers of ovigerous females were caught in February, March and May (Figure 5.2c) and a commercial fisher provided six ovigerous females and two females with egg remnants which he had caught in January 2000.

On the south coast, the prevalence of female *H. acerba* containing late vitellogenic oocytes and the mean monthly gonad weights, standardized to a common carapace length of 95.2 mm, peaked in September (Figures 5.3a-b). The prevalence of *H. acerba* with ovaries containing late vitellogenic oocytes never exceeded 47% in any month other than September and the prevalence of ovaries with previtellogenic oocytes exceeded 50% in five months.
Samples from the south coast yielded no ovigerous females and only two females bearing egg remnants, both of which were caught in August.

The prevalences of females of *C. bicolor* with ovaries containing late vitellogenic oocytes were greater in July to December than in January to April and in June (Figure 5.4a). The mean monthly gonad weights, standardised to a constant carapace length of 110.0 mm, peaked at 42.2 g in September and 43.1 g in December before declining to 11.6 g in February, increasing to 37.1 g in May and then declining to 8.8 g in June (Figure 5.4b). Ovigerous females were caught in each of the 11 calendar months in which samples were obtained and females bearing egg remnants were found in six of those months (Figure 5.4c).

The mean gonad weight ± 95% CIs, standardized to a constant carapace length, did not differ significantly (*p > 0.05*) between the assemblages on the lower west and south coasts when the females contained ovaries with either previtellogenic or early vitellogenic eggs (Figure 5.5). In contrast, the mean gonad weight ± 95% CIs for females of *H. acerba* with ovaries containing late vitellogenic oocytes was significantly greater (*p < 0.001*) for the assemblage on the lower west coast, 26.4 ± 1.71 g, than that on the south coast, 16.0 ± 1.85 g (Figure 5.5).

The relationships between gonad weight (*W*) and carapace length (*CL*) of west coast and south coast females of *H. acerba* with ovaries containing late vitellogenic oocytes (Figure 5.6) are described by the following equations.

West coast: \( \ln(W) = 2.561 \ln(CL) - 8.130; \ p < 0.001, \ R^2 = 0.240, \ n = 228 \)

South coast: \( \ln(W) = 6.430 \ln(CL) - 26.311; \ p < 0.001, \ R^2 = 0.442, \ n = 34 \)

Although none of the females of *H. acerba* from the south coast, which had CLs < 90 mm, contained ovaries with late vitellogenic oocytes, many females of *H. acerba* from the lower west coast with CLs of 75 to 90 mm possessed ovaries with oocytes at this advanced stage. The use of ANCOVA demonstrated that, in the case of *H. acerba* for a
standardised selected carapace length, the mean gonad weight of crabs was significantly greater on the lower west coast than south coast ($p < 0.001$).

To enable predictions of $W$ from $CL$ for $H. acerba$, the regression equations relating these two variables are provided below,

West coast: $\ln(W) = 2.809 \ln(CL) - 6.400; p < 0.001, R^2 = 0.946, n = 581$

South coast: $\ln(W)= 2.768 \ln(CL) - 6.128; p < 0.001, R^2 = 0.893, n = 185$

The mean lengths (± 95% CIs) of females from the lower west (93.8 ± 2.02 mm) and south coasts (93.0 ± 1.39 mm) were not significantly different ($p > 0.05$) when the individuals contained previtellogenic oocytes, whereas the corresponding values of 94.7 ± 0.91 mm and 99.1 ± 1.37 mm for females with late vitellogenic oocytes on those two coasts were significantly different ($p < 0.001$). These differences are reflected in the fact that the distributions of the carapace lengths of female $H. acerba$ on the south coast were located (skewed) more to the right than those on the lower west coast in the case of females with late vitellogenic oocytes, whereas this was not so with females with previtellogenic oocytes (Figures 5.7a,b).

The mean diameters (± 95% CIs) of late vitellogenic oocytes of $H. acerba$ from the lower west coast (357.7 ± 10.79 µm, $n = 342$) and south coast (370.3 ± 8.16 µm, $n = 134$) were not significantly different ($p > 0.05$).

The fecundities of $H. acerba$ ranged from 202,295 to 488,758 for crabs with CLs of 90 and 102 mm, respectively. The minimum and maximum fecundities for $C. bicolor$ were 15,592 and 288,512 respectively, for crabs with CLs of 98 and 133 mm respectively. The mean fecundities (± 95% CIs) of $H. acerba$, i.e. 356,210 (± 64,297) and $C. bicolor$, i.e. 192,070 (± 33,640), were significantly different ($p < 0.001$). Although the mean body weights (± 95% CIs) of the ovigerous females of $H. acerba$ used for the above fecundity estimates, i.e. 587.4 (± 96.5 g) were substantially less than that of $C. bicolor$, i.e. 651.9 (± 61.3 g), those means were
not significantly different ($p > 0.05$). The relationships between fecundity ($F$) and the carapace length ($CL$) and wet weight ($W$) of the two species are shown in Figures 5.8a-d and are described by the following regression equations.

**Hypothalassia acerba**

\[
\ln F = 3.44\ln(CL) + 1.235, \ p < 0.05, \ R^2 = 0.486, \ n = 10
\]

\[
F = 0.005W + 0.608, \ p < 0.05, \ R^2 = 0.569, \ n = 10
\]

**Chaceon bicolor**

\[
\ln F = 2.957\ln(CL) + 1.686, \ p < 0.05, \ R^2 = 0.127, \ n = 40
\]

\[
F = 0.003W + 0.1572, \ p < 0.05, \ R^2 = 0.260, \ n = 40
\]

5.4 DISCUSSION

5.4.1 **Comparisons between Hypothalassia acerba on the west and south coasts**

The trends exhibited by the three reproductive variables recorded for the females of *Hypothalassia acerba* on the lower west coast of Australia were consistent with each other and clearly imply that reproduction in this deep-water species is highly seasonal. Thus, the increase in the prevalence of females with ovaries containing late vitellogenic oocytes between July and October and subsequent levelling off to December was paralleled by a progressive rise and then levelling off in the mean monthly relative gonad weights. Likewise, the subsequent decline in the prevalence of females with this category of advanced ovary between December and March was accompanied by a pronounced decline in the mean monthly relative gonad weights. Furthermore, spent females were found in the relatively short period of January to March, which yielded most of the ovigerous females obtained during this study. It is also highly relevant that the prevalence of female *H. acerba* bearing egg remnants rose progressively from zero or very low levels in October to January to peak in May and subsequently declined sequentially to zero between July and October. The consistent trends
exhibited by the monthly data for the three reproductive variables strongly suggest that oviposition occurs mainly in January to March.

The patterns exhibited by the reproductive variables for female *H. acerba* on the south coast of Western Australia differed markedly from those displayed by this species on the lower west coast. Thus, on the south coast, the prevalence of females with late vitellogenic oocytes and the mean monthly relative gonad weights both peaked in September rather than December and the overall prevalence of females with ovaries containing previtellogenic oocytes was far higher. Moreover, no ovigerous female crabs and only two females with egg remnants were collected on the south coast. This strongly suggests that very little reproduction occurs on the south coast.

The possibility that the lack of capture of ovigerous females of *H. acerba* on the south coast is due to females moving inshore prior to oviposition, as occurs, for example, with *Chaceon affinis*, *Chaceon quinquedens*, *Chaceon maritae* and *Chionoecetes opilio* (Fabricus) (Haefner, 1978; Hastie, 1995; Melville Smith, 1987a, Comeau *et al.*, 1998, López Abellan *et al.*, 2002) appears unlikely. This conclusion is based on the results of my stratified sampling in sequential water depth intervals from 35 to 365 m, which showed that the females and males of *H. acerba* were both very largely concentrated in a relatively narrow range of water depths of 200 to 255 m off the lower west coast and of 90 to 200 m off the south coast, and that no crabs were caught in water depths of 35 m (Smith *et al.*, 2004a). However, it is relevant that, although the catches of *H. acerba* on both coasts contained a greater number of males than females, that difference was substantially greater on the south coast (Smith *et al.*, 2004a). The above data on *H. acerba* suggest that, at some stage prior to oviposition, the females of *H. acerba* on the south coast typically migrate westwards and then northwards on the lower west coast where they extrude their eggs.
The hypothesis that the females of large and maturing *H. acerba* undergo considerable migratory movements is consistent with the observation that such movements are undertaken, in particular, by mature females of some other species of deep-water crabs, *e.g.* *Chaceon fenneri*, *C. quinquedens* and *C. maritae* (Melville Smith, 1987b; Lockhart et al., 1990). Some species of lobster also move substantial distances, including the western rock lobster *Panulirus cygnus* George along the west coast of Australia (Phillips, 1983; Melville Smith and Cheng, 2002). In decapods, these types of movements are often related to reproduction and enable those species to return to their spawning locations as mature adults after they have been transported as larvae or juveniles away from the areas of spawning (*e.g.* Bennett and Brown, 1983; Moore and Macfarlane, 1984; Stewart and Kennelly, 1988; Groeneveld and Branch, 2002). In the context of possible larval movement in southwestern Australia, it is relevant that the important Leeuwin Current flows southwards along the lower west coast of Australia and then eastwards along the south coast and extends to a depth of 350 m (Pearce and Griffiths, 1991). It is thus proposed that the larvae of *H. acerba* are planktonic, as has been shown by Gardner (1998) to be the case with those of the confamilial *Pseudocarcinus gigas*, and would thus be likely to be transported by this major current from the areas on the lower west coast where spawning occurs. The likelihood of such transport would be enhanced by the fact that the larvae of *H. acerba* on the west coast are released in autumn, when the Leeuwin Current is strongest (Phillips et al., 1991).

### 5.4.2 Comparisons between Hypothalassia acerba and Chaceon bicolor

The trends exhibited by the reproductive variables for *Chaceon bicolor* were far less seasonal than those displayed by *H. acerba*. Thus, although the prevalence of females of *C. bicolor* with ovaries containing late vitellogenic oocytes was high in October to December, it was also relatively high in August and May and, while the mean monthly relative gonad weight declined
between December and February, it remained high from July to December. More importantly, however, *C. bicolor* with spent/spent-recovering ovaries were caught in eight months and in each season of the year, thereby indicating that oviposition occurs in most months of the year. This conclusion is consistent with the fact that ovigerous females of *C. bicolor* were caught in each of the eleven months for which samples were obtained for deriving this variable and that, unlike the situation with *H. acerba*, the prevalence of such females did not exhibit a clear pattern of change during the year. The finding that, unlike the situation with *H. acerba*, and also *P. gigas*, which live in similar water depths (Levings et al., 1996), *C. bicolor* clearly does not reproduce within a restricted part of the year is consistent with *C. bicolor* occupying far greater depths and thus living in an environment that undergoes little seasonal change. The lack of conspicuous seasonality in the reproduction of *C. bicolor* parallels that found by Melville Smith (1987a) for *Chaceon maritae*, which likewise lives in deep water. It is also consistent with the fact that the physiological processes of the majority of organisms living in deep waters do not exhibit seasonality (Tyler, 1988).

### 5.4.3 Investment in gonadal development by Hypothalassia acerba

It was particularly noteworthy that the mean relative gonad weights of females with late vitellogenic oocytes were far greater for the assemblage on the west coast than for that on the south coast, especially as this did not apply to females with oocytes in earlier stages of development. This strongly indicates that the females of *H. acerba* on the west coast invest relatively less energy in ovarian development than those on the south coast. Furthermore, the lack of a significant difference between the size of the late vitellogenic oocytes of females on the south and lower west coasts implies that any differences in energy allocation to ovarian development on the two coasts is not reflected in differences in an allocation to individual oocytes. From the above data and comparisons, it appears reasonable also to assume that the
number of eggs per batch produced by females of *H. acerba* that originated on the south coast are likely to be less than those of the individuals that spent at least most of their life on the west coast.

It is also evident from the data shown in Figure 5.6 that the females of *H. acerba* on the south coast do not start producing mature (late vitellogenic) oocytes until they have reached a substantially larger size than those on the west coast. This implies that, with respect to size, the attainment of maturity by the females of *H. acerba* is delayed on the south coast compared with the west coast (69 mm CL).

In summary, my results provide good circumstantial evidence that conditions are less conducive for gonadal development and reproduction by *H. acerba* on the south than lower west coast of Western Australia. Furthermore, they also suggest that maturing females of *H. acerba* migrate from the south coast, which is at the southern and cool end of the distribution of this species, to the west coast for spawning. Reproduction on the lower west coast was shown to occur seasonally in *H. acerba*, but throughout at least much of the year with *C. bicolor*, which occurs in far deeper water and thus where environmental conditions remain more constant during the year. The seasonality of reproduction by *H. acerba* is accompanied by producing, at any one time, a greater number of eggs per given body weight than does *C. bicolor*.

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Figure 5.1. Histological sections of ovaries of *H. acerba* at (a) stage I, (b) stage II, (c) stage III, (d) stage IV, (e) stage V (recently-spent) and (f) stage VI spent-recovering. a, atretic oocyte; ca, cortical alveolar oocyte; ct, connective tissue; eyg, early yolk granule; o, oogonia; lyg, late yolk granule; pv, previtellogenic oocyte. Scale bar = 200 µm.
Figure 5.2. Monthly data for female *Hypothalassia acerba* on lower west coast of Australia. (a) Frequency of occurrence of crabs at different stages of development and (b) mean gonad weights ± 95 CIs standardised to a constant carapace length of 94.7 mm, as selected by ANCOVA and (c) frequency of occurrence of crabs with eggs and egg remnants. In this Fig. and Figs 3 and 4, the sample sizes for each month in (b) are the same as those given in (a).
Figure 5.3. Monthly data for female *Hypothalassia acerba* on the south coast of Australia. (a) Frequency of occurrence of crabs at different stages of development and (b) mean gonad weights ± 95 CIs standardised to a constant carapace length of 95.2 mm, as selected by ANCOVA.
Figure 5.4. Monthly data for female *Chaecon acerba* on the lower west coast of Australia. (a) Frequency of occurrence of crabs at different stages of development and (b) mean gonad weights ± 95% CIs standardised to a constant carapace length of 110.0 mm, as selected by ANCOVA and (c) frequency of occurrence of crabs with eggs and egg remnants.
Figure 5.5. Mean gonad weights ± 95% CIs for female *Hypothalassia acerba* caught off the lower west versus south coasts and containing ovaries predominantly previtellogenic, early vitellogenic and late oocytes. The gonad weights of each of the ovarian categories on both coasts were standardised to constant carapace lengths as selected by ANCOVA.
Figure 5.6. Relationship between the weights of ovaries containing late vitellogenic oocytes and carapace lengths for *Hypothalassia acerba* from both the lower west and south coasts of Western Australia.
Figure 5.7. Carapace length - frequency distributions for female *Hypothalassia acerba* with ovaries containing (a) previtellogenic and (b) late vitellogenic oocytes off the lower west and south coasts of Western Australia.
Figure 5.8. Relationships between fecundity and carapace length and body weight for *Hypothalassia acerba* and *Chaceon bicolor*.
Chapter 6

POTENTIAL BIAS IN ESTIMATES OF THE SIZE OF MATURITY OF CRABS DERIVED FROM TRAP SAMPLES
6.1 INTRODUCTION

The age at which fish and crustaceans are first caught should be at least as great as the age at first maturity if recruitment overfishing is to be avoided (Caddy and Mahon, 1995). Therefore, the size at which the individuals of a decapod species typically reach the onset of sexual maturity (SOM) is frequently used by fisheries managers as the basis for assigning a minimum legal size for the retention of that species (Watson, 1970). The criteria used to designate whether a female decapod is mature vary among species, and often reflect differences in the secondary sexual characteristics of those species. For example, because the abdomen of female portunid crabs becomes relatively wider and more loosely attached at the pubertal moult, this characteristic provides a sound criterion for assessing whether a female of this family has reached maturity (e.g. Van Engel, 1958; Somerton, 1981; de Lestang et al., 2003a), whereas the shape of the gonopores (Melville Smith, 1987), or the presence of eggs under the abdomen (Levings et al., 2001), have been employed for this purpose with the females of some deep-water species of crabs.

The size at which 50% of the females of the stock of a crab species reach the onset of sexual maturity (SOM50) is usually estimated by subjecting the proportions of mature females in sequential size classes to logistic regression analysis (e.g. Fisher, 1999; Muino et al., 1999; de Lestang et al., 2003a). The validity of this approach depends on both the immature and mature individuals of the stock in question having been sampled in an unbiased manner. As many crab fisheries employ only baited traps, scientists have often used the data obtained from the resulting catches to estimate the SOM50 (Brown and Powell, 1972; Melville Smith, 1987; Abbe, 2002; Gardner and Williams, 2002). However, traps yield samples that are biased in terms of both the size and sex composition of the population (Williams and Hill, 1982; Zhou and Shirley, 1997; Jury et al., 2001).
Trap selectivity for decapod species typically occurs as a result of the larger individuals being more aggressive, thereby restricting the likelihood of smaller animals entering the trap (e.g. Bovbjerg, 1956; Rodhouse, 1984). In addition, the greater number of males than females typically found in the trap catches of decapods (Carroll and Winn, 1989; Potter and de Lestang, 2000) almost certainly reflects the greater aggression of males. Moreover, behavioural studies strongly indicate that, in the case of the portunid Callinectes sapidus, females are more likely to enter traps containing males once they have become mature (Jivoff and Hines, 1998). Hence, trap catches of the females of this species will almost certainly contain a disproportionately greater number of mature than immature females. Therefore, subjection of the proportions of trap-caught mature females of C. sapidus in successive size classes to logistic regression analysis would presumably underestimate the SOM. Similar biases in the estimates of SOM would be expected to result from analyses of trap catches of other crab species if there is likewise a greater likelihood of the capture of the mature females of those species than their immature females of the same size.

The commercial fishery for the blue swimmer crab (Portunus pelagicus) in Western Australia is the largest for this portunid in Australia, a total catch of 673 t being taken in 1999/2000, yielding a wholesale value of approximately $A3 million (Anon., 2002). The SOM of female P. pelagicus in Shark Bay, the location of the largest fishery for this portunid in Western Australia, has been estimated using data from samples obtained by baited traps, seine-netting and otter trawling collectively (de Lestang et al., 2003a). However, because of trap selectivity, the samples of P. pelagicus collected by baited traps in Shark Bay may have contained an atypically high proportion of mature females and, consequently, a logistic regression analysis using data from trap catches may have underestimated the SOM of the females there. In contrast, the size composition of samples of P. pelagicus collected by seine-netting and otter trawling would be far more representative of the population in Shark Bay.
The champagne crab (*Hypothalassia acerba*) and the crystal crab (*Chaceon bicolor*) are fished commercially using baited traps in water depths of ~150 to 360 m and 600 to 800 m, respectively, off the west and south coasts of Western Australia (Smith *et al*., in press; unpublished data). Although estimates of the SOMs can be derived from the trap catches of the females of these populations, no data are available from catches obtained using other fishing gear that could be used to determine whether vulnerability to capture by traps was greater among the mature females of these species.

This study aimed to determine whether the SOM\textsubscript{50} estimated for female *P. pelagicus* in Shark Bay was significantly lower when data derived from trapping were used in preference to data from seine-netting and otter trawling collectively. If this was the case, it would demonstrate that, as with *C. sapidus*, the mature female *P. pelagicus* are more vulnerable to capture by traps than the immature females of the same size. Consequently, a SOM\textsubscript{50} derived from trap catches will be an underestimate for species such as *P. pelagicus* and *C. sapidus*. However, the only method used for catching *H. acerba* and *C. bicolor* in Western Australia is trapping. Although it is recognized that the SOM\textsubscript{50}s derived from these trap catches may represent underestimates, we derived such values so that fisheries managers have data that, with discretion, can be used for determining, for example, the minimum legal size for capture of these species.

6.2 MATERIAL AND METHODS

6.2.1 Sampling and measurement of crabs

The data for *P. pelagicus* used in this study were extracted from the database constructed for the samples of this species collected in Shark Bay (26°S, 113.5°E), at bimonthly intervals between July 1998 and May 2000 (de Lestang *et al*., 2003a,b). Samples were collected with a seine-net 21.5 m long with a bunt made of 3 mm mesh, a small otter trawl with a net containing a codend constructed of 25 mm mesh, and a series of crab traps consisting of either 12 or
76 mm mesh (for further details see Potter and de Lestang, 2000). The crab traps were the same as those used by most professional fishers in Western Australia and measured ~ 630 mm high x 1000 mm in diameter. They were joined together in four lines of four, separated by a distance of 15 m. The traps were baited with fish, usually *Sardinops neopolichardus*, and set for ~ 24 h. The carapace width (CW) of each female *P. pelagicus*, i.e. the distance between the tips of the two lateral spines of the carapace, was measured to the nearest 1 mm.

The *H. acerba* and *C. bicolor* used in this study were derived from the depth-stratified sampling regime and from commercial catches as described in Chapter 2. That chapter also describes the measurements made on these two species of crab.

As the morphology and tightness of the abdominal flap of the immature and mature females of both *H. acerba* and *C. bicolor* do not differ markedly, abdominal flap characteristics could not be used to determine the maturity status of the females of those deep-water crabs. Moreover, as the morphology of the gonopores of immature and mature females of *H. acerba* does not differ markedly, which contrasts with the situation in some other species of deep-water crab (Melville Smith, 1987), this structure could not be used to determine the maturity status of the champagne crab. Therefore, female *H. acerba* were classified as having reached maturity when their ovaries were relatively large and pale yellow to pink (and shown by histology to contain yolk granule oocytes), rather than being either inconspicuous or thin and white (and shown by histology to contain oogonia and primary oocytes). As the gonopores of female *C. bicolor* are elliptical and compressed in immature individuals, and circular and open in mature individuals, it was possible to use this criterion to determine whether an individual crab was immature or mature.
6.2.2 Data analysis

The SOM$_{50}$s of female *P. pelagicus* taken by trap, and by seining and trawling collectively, were estimated using logistic regression analysis of the proportions mature at each CW. The probability that the $j^{th}$ crab is mature ($P_j$) is

$$P_j = \frac{1}{1 + \exp \left[ -\ln(19) \right] \left( \text{CW}_j - \text{SOM}_{50} \right) / \left( \text{SOM}_{95} - \text{SOM}_{50} \right)}$$

where $\text{CW}_j$ is the CW of that crab, SOM$_{50}$ and SOM$_{95}$ the CWs at which 50 and 95% of the assemblage reach maturity, and $\ln$ is the natural logarithm of the specified value. This equation represents a simple reparameterization of the logistic equation, which employs the parameters SOM$_{50}$ and SOM$_{95}$ that may be more readily interpreted than the traditional parameters of this equation. The SOM$_{50}$ and SOM$_{95}$ were determined through use of a computer program that maximizes log-likelihood, and employs AD Model Builder (Fournier, 2000). The confidence limits of these parameters and of the estimated percentages of mature crabs at different CWs were determined from likelihood profile distributions calculated using AD Model Builder. Similarly, estimates of the SOM$_{50}$s were derived for trap-caught females of both *H. acerba* and *C. bicolor*. Note that, in the case of each of these latter species, CW is replaced by CL in the above equations.

A likelihood-ratio test (see Cerrato, 1990) was used to determine whether the SOM$_{50}$s of *P. pelagicus* estimated from samples caught by trap, and by seining and trawling collectively, were significantly different.

6.3 RESULTS

6.3.1 Size composition

The 272 female *P. pelagicus* caught in traps in Shark Bay, of which only 2.9% were immature, ranged from 74 to 178 mm CW (Figure 6.1a). In contrast, the size range of the 238 female *P. pelagicus* caught by seining and trawling collectively, of which as many as 57% were immature, ranged from 12 to 160 mm CW (Figure 6.1a). The mean CWs of mature females
collected by trapping (127.5 mm), and by seining and trawling collectively (125.5 mm), were not significantly different ($p > 0.05$).

The CLs of the 598 female *H. acerba* and the 2,981 female *C. bicolor* caught by traps ranged from 50 to 114 mm and from 34 to 148 mm, respectively (Figure 6.2). The size distributions of both of these species were essentially unimodal, peaking at ~95 and ~110 mm CL, respectively. The number of immature individuals in the samples of female *H. acerba* and *C. bicolor* were 20 and 186, respectively, thus contributing only 3.3 and 6.2% to the total catch of the females of these two species (Figure 6.2).

### 6.3.2 Size at maturity

A logistic regression analysis of the proportions of mature female *P. pelagicus* in sequential CWs in trap samples yielded a SOM$_{50}$ of 86.1 mm, with lower and upper 95% confidence limits of 59.7 and 97.2 mm, respectively (Figure 6.3a). A far greater SOM$_{50}$, *i.e.* 101.1 mm, and a far narrower 95% confidence interval, *i.e.* 96.1 to 105.4 mm, were obtained when subjecting the proportions of mature crabs in seine and trawl samples to the same analysis (Figure 6.3b). The above two SOM$_{50}$s were significantly different ($p < 0.001$). As the mean CW of ovigerous female *P. pelagicus* in trap catches did not differ significantly ($p > 0.05$) from that recorded in seine and trawl catches collectively, the size frequency data for these methods were pooled. The CWs of ovigerous females caught in Shark Bay ranged from 104 to 157 mm, with a mean and 95% confidence limits of $131.3 \pm 3.4$ mm (Figure 6.3c).

Logistic regression analyses of the proportions of mature females of *H. acerba* in sequential CLs in samples collected by traps yielded a SOM$_{50}$ of 69.7 mm (Figure 6.4a). The CLs of ovigerous females and females with egg remnants collectively ranged from 75 to 114 mm, producing a mean and 95% confidence limits of $96.6 \pm 3.0$ mm (Figure 6.4b). Subjection of the proportions of the mature females of *C. bicolor* in trap catches to logistic
regression analysis yielded a SOM$_{50}$ of 90.5 mm (Figure 6.5a). The CLs of ovigerous females and females with egg remnants collectively ranged from 91 to 140 mm, with a mean and 95% confidence limits of 108.2 ± 1.0 mm (Figure 6.5b).

6.4 DISCUSSION

The proportion of small female $P. pelagicus$ obtained by trapping in Shark Bay is far less than that obtained by seine-netting or otter trawling in the same environment. Indeed, the percentage contribution made by female $P. pelagicus$ with a CW $< 100$ mm to the total catch of females was only 3.3% in trap catches, whereas it exceeded 57.6% in the combined catches obtained by seine-netting and otter trawling. The proportion of large female crabs that entered traps was also high in the case of the two species of deep-water crabs. Therefore, the proportions of female $H. acerba < 70$ mm CL and of $C. bicolor < 90$ mm CL among all females of each of those species were only 3.3 and 4.4%, respectively. It should be noted that the numbers of small deep-water crabs caught were low, even when the traps were enclosed in a smaller mesh or plastic covering and had their entrances narrowed.

The size composition data for $P. pelagicus$ for Shark Bay, and also for the Leschenault Estuary much farther south (Potter and de Lestang, 2000, unpublished data), demonstrate that, in contrast to mature females, few immature females of this species enter traps. This finding is consistent with the implications of the results of behavioural studies on $Callinectes sapidus$ by Jivoff and Hines (1998), which indicated that an immature female of this portunid would be more likely to avoid any male(s) of this species present in traps than would a mature female. Furthermore, male American lobster ($Homarus americanus$) do not allow the immature females of the same species to occupy their shelter (Salmon, 1983). If the proportion of mature females in any size category is greater in trap samples than in the environment, the SOM$_{50}$ derived from such samples would underestimate this parameter as a result of the sample being biased towards those mature individuals. This conclusion is strongly supported by the fact that
the estimated SOM\textsubscript{50} of female \textit{P. pelagicus}, based on data from trapping (86.1 mm CW), was significantly less than that of 101.1 mm CW estimated with the data derived from seine-netting and otter trawling, which would have caught a far more representative sample of the population. The CW of the smallest ovigerous female \textit{P. pelagicus}, 104.0 mm, was substantially greater than the SOM\textsubscript{50} of 86.1 mm, estimated from the proportions of mature females in trap catches, which, as argued above, is an underestimate.

As with \textit{P. pelagicus}, the estimates of SOM\textsubscript{50} for \textit{H. acerba} and \textit{C. bicolor}, 69.7 and 90.5 mm, respectively, calculated using the proportions of mature females in trap catches, were lower than the sizes of the smallest ovigerous females. Catches of those species obtained using active fishing methods are not available, so precluding investigation of the possibility that the vulnerability of the females of these species might be greater for mature than for immature crabs. Until this hypothesis can be tested for each species, the values of the SOM\textsubscript{50}s for \textit{H. acerba} and \textit{C. bicolor} calculated from trap catches should be considered lower “bounds” of the true SOM\textsubscript{50}s rather than accurate estimates of these crucial reproductive parameters.

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Figure 6.1. Size compositions of immature and mature female *Portunus pelagicus* caught in (a) traps and (b) seine-nets and otter trawls collectively, in Shark Bay, Western Australia.
Figure 6.2. Size compositions of immature and mature females of (a) Hypothalassia acerba and (b) Chaceon bicolor in samples collected by traps on the lower west coast of Australia.
Figure 6.3. Logistic regression analysis of the proportions of mature female *Portunus pelagicus* caught in (a) traps and (b) seine and otter trawl nets collectively. (c) Size composition of ovigerous female *P. pelagicus* caught using all three sampling methods. The estimates of the SOM$_{50}$s and 95% confidence limits are denoted by the arrows and dashed lines, respectively. Values for the SOM$_{50}$s and 95% confidence limits are also presented.
Figure 6.4. (a) Logistic regression analysis of the proportions of mature female *Hypothalassia acerba* caught in traps. (b) Size composition of ovigerous female *H. acerba*. The estimate of the SOM$_{50}$ and 95% confidence limits are denoted by the arrows and dashed lines, respectively. Values for the SOM$_{50}$ and 95% confidence limits are also presented.
Figure 6.5. (a) Logistic regression analysis of the proportions of mature female *Chaceon bicolor* caught in traps. (b) Size composition of ovigerous females of *C. bicolor*. The estimate of the SOM$_{50}$ and 95% confidence limits are denoted by the arrows and dashed lines, respectively. Values for the SOM$_{50}$ and 95% confidence limits are also presented.
Chapter 7

DO THE CHELAE OF THE MALES OF THREE CRAB SPECIES UNDERGO ALLOMETRIC CHANGES THAT CAN BE USED TO DETERMINE MORPHOMETRIC MATURITY?
7.1 INTRODUCTION

The size at which the individuals in fished stocks become mature is one of the most important parameters used by managers to develop plans for ensuring the sustainability of those stocks. Indeed, concerns that the reduced number of males found in crab fisheries, that exploit only or predominantly males, might influence the sustainability of the stocks of certain species have highlighted the need for information on the sizes at which the males of those species attain maturity (Conan and Comeau, 1986; Ennis et al., 1988; Gardner and Williams, 2002).

Studies aimed at determining the size at maturity of male crabs have used data on whether individual crabs have become functionally, physiologically and/or morphometrically mature (e.g. Goshima et al., 2000; Conan et al., 2001; Comeau and Conan, 1992; Gardner and Williams, 2002; de Lestang et al., 2003a). Evidence of functional maturity is derived from observations that copulation has occurred (Goshima et al., 2000; Gardner and Williams, 2002), whereas demonstration that males are physiologically mature is provided by their production of spermatophores (Warner, 1977; Melville Smith, 1987). The attainment of morphometric maturity by a male crab is identified by determining whether certain body parts, e.g. chelae, undergo a conspicuous change at the pubertal moult (Somerton, 1981; Comeau and Conan, 1992; Gardner and Williams, 2002).

A male crab must become both functionally and physiologically mature before it can reproduce and the ability to mate may depend on the crab having become morphometrically mature. In an aquarium study involving males of *Chionoecetes opilio* with carapace widths (CWs) in excess of the size at physiological maturity and mature females, precopulatory pairing behaviour was found to be initiated only by the larger of the males that had become morphometrically mature, i.e. > ~ 95 mm CW (Conan and Comeau, 1986). It was thus concluded that, although physiological maturity is attained by the males of *C. opilio* before they reach a CW of ~ 60 mm, functional maturity is not attained until individuals have moulted.
to become morphometrically mature and attained a CW of ~ 95 mm. However, Paul (1992) has queried why physiologically mature males would produce sperm if they were not to be used immediately. Subsequently, Sainte-Marie et al. (1995) found that males of *C. opilio* from the Gulf of Saint Lawrence became physiologically mature at a CW of only 38.5 mm and that, in non-competitive aquarium studies, males that were physiologically mature but morphometrically immature were functionally mature, *i.e.* mated successfully.

The changes undergone in the allometry of a body part (i.e. a disproportionate relationship between size of a body part and size of the whole body), of a male crab may not be sufficiently well defined to be able to be used with confidence for estimating the size at which morphometric maturity is attained (Clayton, 1990; Goshima *et al.*, 2000). For example, in some decapod species, the changes in the “level of allometry” *sensu* Hartnoll (1978) are gradual and the logarithms of the measurements appear to follow a curvilinear trend. Consequently, the straight lines that are fitted to the presumed juvenile and adult data may be artefactual and cannot thus provide a reliable means for distinguishing between pre- and post-pubertal moult animals (Conan *et al.*, 2001). Indeed, Somerton (1980) has pointed out that it is essential to test whether a difference between the patterns of growth of that body part in juveniles and adults can be detected.

Somerton (1980) fitted separate, overlapping lines, rather than a single straight line, to the logarithms of the dimensions of various body parts of juvenile and adult crabs and used a *F*-test to determine whether the difference between the sums of squares of those two models was statistically significant. However, the objective function calculated by Somerton (1980), using his iterative approach to fit separate overlapping lines, relies on the allocation of intermediate points to one or other of the straight lines, based on the value of the dependent variable and the predicted values of the lines at that body size. It was thus inappropriate to employ statistical tests, such as the *F*-test, to compare his models of differing complexity using
the value of this objective function and that obtained from a traditional regression model. However, several studies on the maturity of male crabs, including one on *P. pelagicus* (de Lestang *et al.*, 2003a), have used an overlapping-lines model without validating that it was appropriate.

In Western Australia, the blue swimmer crab *Portunus pelagicus* is fished in estuaries and protected coastal waters, whereas the champagne crab *Hypothalassia acerba* and the crystal crab *Chaceon bicolor* are fished predominantly in water depths of 90 to 310 m and 450 to 1220 m, respectively (de Lestang *et al.*, 2003b; Smith *et al.*, 2004a; Melville Smith *et al.*, in press). The main aim of the current study was to determine statistically whether the allometry of the chelae of the males of *P. pelagicus*, *H. acerba* and *C. bicolor* underwent a change that could be assumed to reflect a morphological transition from an immature to a mature state. The Akaike and Bayesian Information Criteria were thus used to explore which of a linear, quadratic, broken stick or overlapping-lines model was the most appropriate for representing the relationship between the natural logarithms of the length of the dorsal propodus and body size of the male crabs of each species (Akaike, 1973; Schwartz, 1978). A linear model would imply that allometry does not change as body size increases, whereas a quadratic model would indicate that the pattern of growth changes continuously with increasing body size and the broken stick or overlapping-lines models would imply that there is a distinct change in allometry during growth. If there was found to be a change in allometry, the resulting estimate of the body size at which this change occurred was compared with the size at which the animal becomes physiologically mature. This required the determination of the size at which physiological maturity is attained by the males of *H. acerba* and *C. bicolor* to provide data, which would complement that already derived for this variable for *P. pelagicus* (de Lestang *et al.*, 2003a).
7.2 MATERIAL AND METHODS

7.2.1 Collection of crabs

Male *P. pelagicus*, with CWs ranging from 21 to 154 mm, were collected from Cockburn Sound (32°12’S, 115°48’E) at monthly intervals between February 1997 and March 2000. The crabs were caught using a 21.5 m seine net with a bunt made of 3 mm mesh and a small otter trawl net with a cod end constructed of 25 mm mesh (see de Lestang et al., 2003a).

The *H. acerba* and *C. bicolor* used for this study were collected during the depth-stratified sampling regime and sampling onboard commercial fishing boats (for details, see Chapter 2).

7.2.2 Measurements

The carapace width of each male *P. pelagicus*, *i.e.* distance between the tips of the two lateral spines of the carapace, and the carapace length of each male *H. acerba* and *C. bicolor*, *i.e.* distance across the gastric region from the midpoint between the bases of the two anterior medial spines and the posterior margin of the carapace, were each measured to the nearest 1 mm. Carapace length rather than carapace width is typically measured in deep-water crabs (*e.g.* Levings et al., 1996; Gardner, 1997; Goshima et al., 2000) as it overcomes the problems of using the distance between the two lateral spines of the carapace, which are particularly prone to wear. For all three species, the length of the dorsal propodus from the proximal edge of the depression below the upper articulation knob to the proximal edge of the depression at the articulation with the moveable finger of the molariform cheliped of each male was measured to the nearest 0.1 mm using vernier calipers. The choice of chela propodus length to provide data aimed at determining whether or not changes in allometry occur was based, in part, on the demonstration by Gardner and Williams (2002) that this was the most suitable of...
several variables for assessing morphometric changes in the giant crab *Pseudocarcinus gigas*. The latter species belongs to the same family (Eriphiidae) as *H. acerba*.

### 7.2.3 Relationship between propodus length and body size

The natural logarithms of the lengths of the dorsal propodus of the males of each species were plotted against the natural logarithms of body size, *i.e.* carapace length or width. In each case, the trend exhibited by the points with increasing body size appeared continuous and without marked disjunction. This suggests that the data for each species might be adequately described by a linear or quadratic regression or a broken-stick regression, *i.e.* a piecewise linear function that is continuous at the point of intersection, or a model comprising two overlapping lines in combination with a logistic function. The logistic function determines the probability that an observation is drawn from the distribution of points around either the first or the second of these overlapping lines. The straight line implies that there is no change in the level of allometry, whereas the quadratic model represents a continuous and smooth change in the level of allometry as body size increases. The broken stick and overlapping-lines models represent two distinct and constant levels of allometry, reflecting the different patterns of growth of morphometrically immature and mature crabs. For the broken stick model, the change occurs when the animals attain the length corresponding to the point at which the two lines intersect. For the model using overlapping lines, the change is gradual and its rate is determined by the parameters of the logistic curve that determine the proportion of the mixture of points associated with each of the overlapping lines. The linear and quadratic models are written as

\[
\ln DP = a + b \ln S \quad \text{and} \quad \ln DP = a + b \ln S + c(\ln S)^2,
\]

respectively, and the broken-stick model as

\[
\ln DP = \begin{cases} 
  d + e \ln S & \text{if } \ln S \leq X \\
  d + eX + f(\ln S - X) & \text{otherwise}
\end{cases}
\]
The overlapping-lines model is
\[
\ln DP = (1 - P_S)(a' + b' \ln S) + P_S(c' + d' \ln S),
\]
where
\[
P_S = \left\{1 + \exp[-\ln(19)(S - S_{50})/(S_{95} - S_{50})]\right\}^{-1}.
\]
In these equations, \(DP\) = length of the dorsal propodus, \(S\) = body size (i.e. CL or CW), \(a, b\) (and \(c\)) = parameters of the linear (and quadratic) model(s), \(d\) and \(e\) = intercept and slope, respectively, of the first line, and \(f\) = slope of the second line of the broken-stick model, \(X = \) value of \(\ln S\) at the point of intersection of the two straight lines that form the broken stick, \(a'\) and \(b'\) = intercept and slope, respectively, of the first of the overlapping lines, \(c'\) and \(d'\) = intercept and slope of the second of the overlapping lines, \(P_S\) = probability that a crab with body size \(S\) is associated with the second of the overlapping lines, \(S_{50}\) and \(S_{95}\) = body sizes at which 50 and 95%, respectively, of crabs are associated with the second of the overlapping lines, and \(\ln\) = natural logarithm of the associated variable.

It was assumed that observation errors \(\varepsilon\) were independent, identically distributed random variates drawn from a normal distribution, i.e. where \(\varepsilon \sim N(0, \sigma^2)\). Ignoring constants, the log-likelihood was calculated as \(\lambda = -n \ln \left(\frac{SS}{n}\right)\), where \(n\) is the number of observations and \(SS\) is the sum of squared deviations of the observed value of \(\ln DP\) from the value predicted using each model. The models were fitted to the data for each species using Solver in Microsoft Excel, and maximising the log-likelihood for each model to estimate the two parameters of the linear model, \(a\) and \(b\), the three parameters of the quadratic model, \(a, b\) and \(c\), the four parameters of the broken-stick model, \(d, e, f\) and \(X\) and the six parameters of the overlapping-lines model, \(a', b', c', d', S_{50}\) and \(S_{95}\). 95% confidence intervals for each parameter in each model were estimated as the 2.5 and 97.5 percentiles of 200 estimates of each of the parameters that were obtained by random resampling, with replacement, of the data
for each species and then refitting each model to the resulting set of data. When fitting the overlapping-lines model, a penalty function was used to ensure that, for crabs with a body size less than a specified minimum or greater than a specified maximum, the values of $S_{50}$ and $S_{95}$ were such that $(1 - P_s) > 0.99$ or $P_s > 0.99$, respectively. This emulates the approach used by Somerton (1980) whereby crabs with sizes below or above some intermediate size range were assumed to be immature or mature, respectively. For *P. pelagicus*, the values of these specified minimum and maximum body sizes were set at 60 and 110 mm CW, respectively, as these were the values used by de Lestang *et al.* (2003a). For *H. acerba* and *C. bicolor*, the values specifying this intermediate size range, *i.e.* 67 to 110 mm CL and 81 to 134 mm CL, respectively, were selected from plots of the data for each species and appeared to bracket the range likely to contain the point of inflection of the lines, if such a point exists.

As the four models are not nested, they cannot be compared using the likelihood-ratio test to determine the most appropriate and parsimonious model, *i.e.* that possessing the fewest parameters, but which is consistent with the data. Accordingly, the selection of the most appropriate model to describe the data for each species was based on the Akaike and Bayesian information criteria, *i.e.* AIC and BIC, which were calculated as

$$
AIC = -2\lambda + 2k \\
BIC = -2\lambda + k \ln n
$$

where $k$ is the number of parameters, *i.e.* 2 for the linear, 3 for the quadratic, 4 for the broken stick regression and 6 for the overlapping-lines model (Akaike, 1973; Schwartz, 1978). The model with the smallest value for the information criterion was accepted as providing the best, most parsimonious fit to the data for that species and for that information criterion.
7.2.4 Probability of selecting an incorrect model

The parameters that were estimated when the linear model was fitted to each set of randomly resampled data for each of *P. pelagicus*, *H. acerba* and *C. bicolor*, and the resulting standard deviation of the observation errors were then used to generate a synthetic value of the logarithm of dorsal propodus length for each recorded body size. For this, a random normal variate with a mean of zero and standard deviation of 1 was generated. This was multiplied by the standard deviation of the observation errors to produce a random “observation error”, which was then added to the value predicted using the linear model and the recorded body size to produce a randomly-generated value of the logarithm of dorsal propodus length for the crab. The resulting data are thus formed from the linear model fitted to the resampled data, *i.e.* to data randomly drawn from the population from which the original data set was obtained. Linear, quadratic, broken-stick and overlapping-lines models were then fitted to the synthetic data and, for each of the AIC and BIC, the best, most parsimonious model was selected as that with the lowest value of that information criterion. This process of generating a synthetic set of data, fitting the three models and selecting the more appropriate model was repeated using each set of results obtained from refitting the linear model to each of the resampled data sets. The probability of erroneously selecting either the quadratic, broken-stick or overlapping-lines model as the best model was calculated as the proportion of these 200 runs for which each of these models was selected as the best model, *i.e.* the correct conclusion that there was no change in the level of allometry was rejected.

The same process was then repeated for each species, using the parameter estimates obtained when fitting the quadratic, then the broken-stick, and finally the overlapping-lines, models to generate the random data to which the other models were fitted and to determine whether or not the model that matched that used to generate the synthetic data was correctly selected using the AIC and the BIC.
I have considered four hypotheses concerning the relationship between the logarithms of the length of the dorsal propodus and of body size, \( i.e. H_1 \) - the relationship is linear, \( H_2 \) - the relationship is quadratic, \( H_3 \) - the relationship is a broken stick or \( H_4 \) - the relationship is one that is formed by overlapping lines. The conclusion from my analysis is that most appropriate relationship for describing the data is either \( D_1 \) - linear, \( D_2 \) - quadratic, \( D_3 \) - a broken stick, or \( D_4 \) - one that is formed by overlapping lines.

The results obtained from the simulations described in the preceding paragraphs were used to calculate the probability of each conclusion, \( D \), given that the relationship used to generate the synthetic data was known to be of each specific form. This has been denoted as \( P_{\text{AIC}}(D \mid H) \) or \( P_{\text{BIC}}(D \mid H) \). Thus, for example, \( P_{\text{BIC}}(D = D_1 \mid H_3) \) is estimated as the proportion of data sets that were generated using the broken stick relationship in which, employing the BIC, it was concluded that the relationship was linear.

A Bayesian approach was employed to assign probabilities to each of the hypotheses regarding the form of the relationship between the logarithms of the length of the dorsal propodus and the body size. It was assumed that, prior to the study, the four hypotheses were equally likely, \( i.e. P(H) = 0.25 \) for each hypothesis, \( H \). The posterior probabilities of these hypotheses were then calculated as

\[
P(H_j) = \frac{P(D \mid H_j)p(H_j)}{\sum_k P(D \mid H_k)p(H_k)}.
\]

### 7.2.5 Physiological maturity

Collected individuals of \( P. \ pelagicus \), \( H. \ acerba \) and \( C. \ bicolor \) were transported to the laboratory where they were euthanased in a bath of seawater and clove oil. The gonads of these crabs in a randomly-selected subset of the males of each species, which could be readily
distinguished from females by the shape of their abdomen, were examined macroscopically and classified as immature or mature using the following criteria. They were recorded as immature if either the reproductive tract, i.e. the testes and/or vas deferens, was not visible or if the middle and posterior vas deferens were present but were thin and either straight or loosely convoluted, and were classified as mature when the middle and posterior regions of the vas deferens were enlarged and highly convoluted (Ryan, 1967; de Lestang et al., 2003a). Note that, when examined microscopically, segments of the anterior vas deferens of large subsamples of each species always contained spermatophores in individuals designated as mature, but that this was never the case with immature crabs.

7.2.6 Size at physiological maturity

The sizes by which 50% of the males of *P. pelagicus*, *H. acerba* and *C. bicolor* have become physiologically mature was calculated by logistic regression analysis, using the equation

\[ p_j = \left\{1 + \exp\left[-\ln(19)\left(CL_j - CL_{50}\right) \left(CL_{95} - CL_{50}\right)\right]\right\}^{-1}, \]

\( p_j \) to calculate the probability that a male crab of carapace length \( CL_j \) is mature and where \( CL_{50} \) and \( CL_{95} \) are the carapace lengths at which 50 and 95% of the males are expected to be mature. This equation is a reparameterised version of the logistic model, in which the traditional parameters are replaced with the parameters \( CL_{50} \) and \( CL_{95} \). The model was fitted by maximum likelihood using a nonlinear subroutine in SPSS™.

7.3 RESULTS

7.3.1 Relationship between propodus length and body size

Comparison of the values of the AIC and BIC, calculated by fitting each model to the logarithms of \( DP \) and \( CW \) for the males of *P. pelagicus*, demonstrated that the relationship
between these measures was described better by a broken stick regression than by either a linear, quadratic or overlapping-lines model (Table 7.1, Figure 7.1).

Table 7.1. Estimates of the parameters (and 95% confidence limits) for the linear, quadratic, broken stick and overlapping-lines models fitted to the logarithms of the lengths of dorsal propodus versus logarithms of body sizes for *P. pelagicus*, *H. acerba* and *C. bicolor*, and values of the log-likelihood ($\lambda$) and of the Akaike (AIC) and Bayesian (BIC) Information Criteria.

<table>
<thead>
<tr>
<th></th>
<th><em>P. pelagicus</em></th>
<th></th>
<th></th>
<th><em>H. acerba</em></th>
<th></th>
<th></th>
<th><em>C. bicolor</em></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>Lower</td>
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<td></td>
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<td></td>
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<td>-3.029</td>
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<tr>
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<td>1.396</td>
<td>1.539</td>
<td>1.507</td>
<td>1.576</td>
<td>1.128</td>
<td>1.147</td>
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<td>2314</td>
<td>1018</td>
<td>988</td>
<td>1058</td>
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<td>0.161</td>
<td>0.259</td>
<td>-0.030</td>
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<td>0.092</td>
<td>0.035</td>
<td>0.161</td>
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<td>2340</td>
<td>2461</td>
<td>1019</td>
<td>989</td>
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<td>1694</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>$d$</td>
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<td>-3.143</td>
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<td>$S_{50}$</td>
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<td>85.891</td>
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<td>$S_{95}$</td>
<td>77.304</td>
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</tbody>
</table>

However, the use of the AIC suggested that, for the males of both *H. acerba* and *C. bicolor*, the overlapping-lines model provided the best description of the relationship between the
logarithms of $DP$ and $CL$, whereas the use of the BIC indicated that the linear model was more appropriate (Table 7.1).

7.3.2 The probability of selecting an incorrect model form

The percentages of synthetic data sets for which each model was correctly or incorrectly identified by the AIC or BIC as providing the best description of the relationship between the $\ln(DP)$ and $\ln(CW)$ or $\ln(CL)$ are presented in Table 7.2. These data were then used to generate the posterior probabilities shown in Table 7.3, the implications of which are considered in the discussion.

7.3.3 Size at physiological maturity

The estimates of $CW_{50}$ and $CW_{95}$ for *Portunus pelagicus*, based on the percentages of male crabs with mature gonads, were 88.4 (95% confidence interval 87.8 - 89.1) and 99.9 (95% CI 98.2 - 101.6) mm, respectively (de Lestang *et al.*, 2003a) (Figure 7.2). Males of *H. acerba* attain physiological maturity at a carapace length of 68.1 (95% CI 67.8 - 68.3) mm, and 95% are physiologically mature when they have reached a carapace length of 72.0 (95% CI 71.2 - 72.7) mm. For male *C. bicolor*, the estimates of $CL_{50}$ and $CL_{95}$ were 94.3 (95% CI 93.7 - 94.9) and 99.9 (95% CI 98.2 - 101.6) mm CL, respectively (Figure 7.2).

7.4 DISCUSSION

7.4.1 Morphometric and physiological maturity of *Portunus pelagicus*

Our results show that, irrespective of whether the selection of model form was based on AIC or BIC, the relationship between the logarithms of the dorsal propodus and carapace width of *P. pelagicus* was described better using the broken stick approach rather than either linear, quadratic or overlapping-lines models. Although the posterior probabilities estimated for the broken stick and overlapping-lines models for this species differed only slightly, but were both
Table 2. Percentage of data sets in which, using either the Akaike (AIC) or Bayesian (BIC) Information Criterion, each model was selected as the model of appropriate complexity that best described the 200 sets of synthetic random data generated using each of the linear, quadratic, broken stick and overlapping-lines models. The correct classification is identified by the shading.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model used to generate synthetic data</th>
<th>Linear</th>
<th>Quadratic</th>
<th>Broken stick</th>
<th>Overlap</th>
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</thead>
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<tr>
<td></td>
<td>Selected model</td>
<td>AIC</td>
<td>BIC</td>
<td>AIC</td>
<td>BIC</td>
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<tr>
<td><em>P. pelagicus</em></td>
<td>Linear</td>
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<td>98.5</td>
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<tr>
<td></td>
<td>Quadratic</td>
<td>9.0</td>
<td>1.0</td>
<td>99.0</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Broken stick</td>
<td>21.0</td>
<td>0.5</td>
<td>1.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Overlap</td>
<td>5.5</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>H. acerba</em></td>
<td>Linear</td>
<td>62.5</td>
<td>98.5</td>
<td>44.0</td>
<td>87.0</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>10.5</td>
<td>1.0</td>
<td>21.0</td>
<td>11.5</td>
</tr>
<tr>
<td></td>
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<td>0.5</td>
<td>25.5</td>
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<tr>
<td></td>
<td>Overlap</td>
<td>7.5</td>
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<td>9.5</td>
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<tr>
<td><em>C. bicolor</em></td>
<td>Linear</td>
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<td></td>
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<tr>
<td></td>
<td>Overlap</td>
<td>9.5</td>
<td>0.0</td>
<td>7.0</td>
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</tbody>
</table>
Table 3. Posterior probabilities of the model forms describing the allometric data for each species calculated from the fact that, using both the Akaike (AIC) and the Bayesian (BIC) Information Criterion, the broken stick model was selected as the most appropriate model to represent the allometric data for *P. pelagicus*, and that, using the AIC, the overlapping-lines model was selected as the most appropriate model to describe the data for *H. acerba* and *C. bicolor* whereas the linear model was chosen when the BIC was employed.

<table>
<thead>
<tr>
<th>Model form</th>
<th>Posterior probability of each model form for each species</th>
</tr>
</thead>
<tbody>
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<tr>
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<tr>
<td>Overlapping-lines</td>
<td>0.401</td>
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</table>

higher than those of either the linear or quadratic models, the broken stick is less complex than the overlapping-lines model (four as opposed to six parameters) and is thus the better and more appropriate model.

From my use of the broken stick approach, it is concluded that the growth of the largest cheliped of male *P. pelagicus* clearly undergoes an inflection when individuals reach a carapace width of about 80.0 mm (95% confidence limits 77.0 to 88.2 mm). This value is ~6 mm less than that derived previously by de Lestang et al. (2003a), *i.e.* 86.2 mm CW, when subjecting the same data to Somerton’s (1980) overlapping-lines method. However, in this context, it is relevant that the parameter estimates of the overlapping-lines model for *P. pelagicus* have been found to be very sensitive to the values selected as the upper and lower “limits” of the body sizes associated with morphometrically immature or mature individuals. Thus, the estimate derived from the previous study is unlikely to have been precise.
The males of *P. pelagicus* become physiologically mature at 88.4 mm CW (de Lestang *et al.*, 2003a), and thus ~ 8 mm after they have attained morphometric maturity. Thus, the males of this species would appear, at least on the basis of cheliped measurements, to have developed the potential to mate just prior to the time when their gonads become fully mature. From a management perspective, it would be appropriate to base management strategies and assessment on the size at which *P. pelagicus* has attained both morphometric and physiological maturity, *i.e.* 88.4 mm CW.

### 7.4.1 Morphometric and physiological maturity of *Hypothalassia acerba* and *Chaceon bicolor*

The values estimated for the AIC and BIC for the males of *H. acerba* and *C. bicolor* gave no consistent indication of which of the four models provides the best description of the relationship between the logarithms of the length of the dorsal propodus and CL. For both species, the value of the AIC suggested that the overlapping-lines model was best, whereas the value of the BIC indicated that the linear model was best. Since the values of the posterior probabilities that were estimated for each model showed the same inconsistency, there is no conspicuous change in the level of allometry of the males of either *H. acerba* or *C. bicolor*, that could be related to the attainment of morphometric maturity.

The absence of both distinct changes in the patterns of allometry of the chelae of the males of *H. acerba* and *C. bicolor* and direct information on the sizes at which these deep-water crabs are capable of mating, *i.e.* functional maturity, leaves only the size of physiological maturity as a basis for assessing the “reproductive” status of their stocks and as a measure of reproductive potential for developing management plans for these species. Thus, since *H. acerba* and *C. bicolor* become physiologically mature at 68.1 and 94.3 mm CL, respectively, it
would be appropriate for managers to consider these lengths when reviewing management plans involving the use of a minimum legal size.

It should be noted that *Chionoectes sp.* undergo a pattern of alometric change that is not described in this study because it does not apply to either of the species in question. Crabs belonging to *Chionoectes* undergo three allometric stages in their life history, immature, juvenile and morphometrically mature. The transition between immature and juvenile allometry is the type qualified as “broken stick” in the present study. The transition between juvenile and morphometrically mature does not fit any of the model allometric patterns described here, as morphometric maturity in *Chionocetes sp.* is reached at the onset of a terminal moult (Conan and Comeau, 1986).

This paper has been submitted for publication as follows: Hall, N.G., Smith, K.D., de Lestang, S. and Potter, I.C. (submitted). Do the chelae of the males of three crab species undergo allometric changes that can be used to determine morphometric maturity. *ICES Journal of Marine Science.*
Figure 7.1. Alternative model forms (linear, quadratic, broken stick and overlapping-lines) fitted to the relationship between the natural log of the length of the dorsal propodus of the largest cheliped and the natural log of the carapace width of *Portunus pelagicus* and the natural log of the carapace length for *Hypothalassia acerba* and *Chaceon bicolor*. 
Figure 7.2. Logistic regressions fitted to the proportions of males of (a) *Portunus pelagicus* (b) *Hypothalassia acerba* and (c) *Chaceon bicolor* which at each size possessed mature gonads.
Chapter 8

GENERAL DISCUSSION
This thesis provides a description of the catch, effort and catch per unit for *Hypothalassia acerba* and *Chaceon acerba* since the inception of the fisheries for those species on the lower west and south coasts of Western Australia. Particular emphasis has been placed on the way in which these variables have changed over those fishing periods and during the year. Attention was also focused on providing sound quantitative data on the biology of those two species and, most specifically, their distributions and the factors influencing those distributions and also those key aspects of their reproductive biology that are particularly relevant to management. The major findings are as follows.

- The fishery for *Hypothalassia acerba* in southwestern Australia commenced in the early 1990s and peaked in 1998, with catches of ~73,000 kg. The catches subsequently declined due to fishers on the lower west coast switching their effort to catching *Chaceon acerba*. A decline in effort for *H. acerba* on the lower west coast was partially compensated for by an increase in effort on the south coast.

- The catch per unit effort for *H. acerba* has declined in recent years, suggesting that fishing might have had a detrimental influence on the stocks of this species.

- The catches of *H. acerba* on the south coast underwent a cyclical change during the year, declining to minimal levels between late autumn and mid-spring, largely reflecting a decline in effort due to the harsh weather conditions that prevail in that period.

- The catch per unit effort of *H. acerba* on the lower west coast rose progressively from April to November, suggesting that this species gradually became more abundant and/or accessible to fishing in that period.

- The fishery for *C. bicolor*, which has been almost entirely based on the lower west coast, essentially commenced in 1997. Catches subsequently rose to reach a peak of 222,500 kg in 2000 and remained close to this level in the ensuing years.
The sharp rise in the annual CPUE during the early years of the fishery probably reflects an increasing knowledge by fishers of the best areas to fish.

The commercial catches of the males of both *H. acerba* and *C. bicolor* outnumbered those of their females.

The size of the males caught by traps was greater than that of females in the case of both *H. acerba* and even more particularly *C. bicolor*, i.e. selectivity was low for small crabs.

Traps did not catch many individuals of either *H. acerba* or *C. bicolor* which had a carapace length < 80 mm, even when the traps were covered in a fine mesh.

The catch rates of *H. acerba* peaked in water depths of 200 m on the lower west coast and at 145 m on the south coast and in temperatures of ~ 16 - 17ºC on both coasts.

The size (carapace length) of *H. acerba* decreased slightly with increasing water depth.

*Hypothalassia acerba* reproduces seasonally on the lower west coast, with egg extrusion occurring mainly in summer and early autumn. Since *H. acerba* does not typically appear to reproduce on the south coast, it is proposed that, maturing females migrate to the lower west coast.

In contrast to *H. acerba*, *C. bicolor* reproduces throughout at least most of the year. This continuity of reproduction probably reflects the occupancy by this species of deeper waters than *H. acerba* and thus an environment that undergoes less conspicuous seasonal changes.

Although the mean body weights of ovigerous females of *H. acerba* (587 g) and *C. bicolor* (652 g) were not significantly different (*p > 0.05*), the fecundities of these two species, *i.e.* 356,210 and 192,979, respectively, were significantly different. The relatively high fecundity of *H. acerba* may reflect an adaptation of this seasonal spawning species to optimise egg production.
• The passive sampling method of trapping was the only method available for catching *H. acerba* and *C. bicolor*. Thus data collected for *Portunus pelagicus* using both the above passive fishing method and the active fishing methods of seine netting and trawling were used to determine whether they yielded comparable data for estimating the size at maturity of female crabs. The trap caught samples contained predominantly mature crabs and were thus biased, leading to an underestimate of the size at maturity. It is reasonable to assume that the estimates of maturity of *H. acerba* and *C. bicolor* using data derived from trap-caught samples are likewise underestimates.

• The chelae of the males of *H. acerba* and *C. bicolor* were shown not to undergo a detectable change in allometric growth at the pubertal moult. Thus, it is inappropriate to use the traditional method, which is based on this assumption, to determine the size at morphological maturity of the males of these species.

The implications of these results will require managers to consider the following when they are reviewing plans for the management of *H. acerba* and *C. bicolor*.

1. Restriction of both *H. acerba* and *C. bicolor* to a narrow depth range makes these species particularly subject to depletion through focussed fishing.

2. Protection should be considered for the assemblage of *H. acerba* on the south coast as there is strong evidence that the females in these waters do not typically reach maturity and apparently move to the west coast for breeding.

3. Estimates of the size at physiological (gonadal) maturity of females, based on the use of logistic regression of analysis of the proportions of mature crabs in trap catches, are likely to be artificially low. This is due to a probable bias of trap catches towards large, mature female crabs.
4. Estimates of the size at maturity of males should be based on physiological (gonadal) maturity. This is because there was no apparent allometric change in the growth of chela that could be attributed to the attainment of morphometric maturity.

5. Values selected by managers as the minimum legal sizes for retention of *H. acerba* and *C. bicolor* are likely to be based on the sizes at physiological maturity of males and females of these species. However, since these estimates of the sizes at physiological maturity of males and females are likely to be low, an adaptive approach will be required to ensure that the numbers of mature crabs are maintained at a level sufficient to sustain the stocks.

6. As the *H. acerba* and *C. bicolor* that are caught in traps appear to have approximately attained their asymptotic body size, yield per recruit will be an asymptotic function of fishing effort (of a form determined by the Baranov catch equation). Similarly, spawning biomass per recruit will decline exponentially with fishing effort. Since natural mortality cannot be estimated, it is impossible to estimate the value of fishing mortality from the available data. However, any decline in spawning biomass per recruit with fishing effort would imply that catch per unit of effort (CPUE) will need to be sustained above some reference value determined from either the virgin CPUE or from historical levels of CPUE. Thus, decision rules for the fishery will need to be based on CPUE rather than being model-derived estimates of fishing mortality or biomass.

7. If CPUE is to be used as the primary indicator for fisheries management decisions, factors that increase the efficiency of fishing effort will need to be carefully monitored. The potential for spatial depletion also exists and CPUE will need to be estimated appropriately.
Although there are no data on growth or mortality, evidence from other deep sea crab species suggest that *Hypothalassia acerba* and *Chaceon acerba* are likely to be slow growing and long-lived. Thus, minimum legal size regulations are very likely to be inadequate unless they are accompanied by management strategies that ensure that the stocks of mature crabs are sustained at adequate levels. Since such slow growing and long-lived species are likely to be prone to becoming part of boom and bust fisheries, there is a need for constant monitoring to ascertain whether, at any stage, their catch statistics are deviating from those recorded during more recent years and thus provide evidence that the abundance of the stocks are declining. There is a strong need to consider the specification of appropriate limit and target reference points for the estimates of catch per unit of effort and for the implementation of appropriate decision rules, based on current estimates of catch per unit of effort, that will ensure that the stocks of *H. acerba* and *C. bicolor* are conserved. The decision rules should ensure that, as catch per unit of effort approaches the limit reference point for this variable, exploitation is reduced appropriately.
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