The biology of four tuskfish species (*Choerodon*: Labridae) in Western Australia

By

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This thesis is presented for the degree of Doctor of Philosophy at Murdoch University

2005
DECLARATION

I declare that the information contained in this thesis
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2005
Abstract

The biology of four species of *Choerodon* (Labridae), the blue tuskfish *C. cyanodus*, the bluespotted tuskfish *C. cauteroma*, the baldchin groper *C. rubescens* and the blackspot tuskfish *C. schoenleinii* was studied in Shark Bay in Western Australia. These species are fished commercially and/or recreationally in this large subtropical marine embayment, which is a world heritage area. The biology of *C. rubescens* was also studied in the Abrolhos Islands, which are located ~ 300 km to the south of Shark Bay, where this labrid is an important commercial and recreational fish species. The broad aims of this project were to determine the following for the above four *Choerodon* species in Shark Bay. (1) Whether they are protogynous hermaphrodites, as is the case with many labrids. (2) The biological variables required for developing management plans for these species, such as the timing of spawning, the lengths and ages at both maturity and sex change, size and age compositions and growth parameters, and (3) the habitat types occupied during their life cycles and also of the purple tuskfish *Choerodon cephalotes*. Finally, comparisons are made between the age and size compositions, growth and reproductive biology of *C. rubescens* in Shark Bay and the Abrolhos Islands. Where relevant, the underlying hypotheses for the individual studies conducted during this PhD are included in the following chapters.

A macroscopic and histological examination of the gonads of the full size range of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii*, together with an analysis of the length and age compositions of female, transitional (individuals changing sex) and male individuals, demonstrated that each of these species is a protogynous hermaphrodite, i.e. individuals change sex from female to male during their life cycle. The gonads of all small (< ca 100 mm) and young (< ca 1 year old) individuals of each species comprised solely ovarian tissue and thus the individuals of each species began life as a female. All individuals subsequently become sexually mature as females and then later in life some will change to males. Since this was found to be the only method of sex change in these species, they are termed monandric. Individuals that were changing sex contained “undelimited type 2” gonads *sensu* Sadovy and Shapiro (1987). These gonads contained both ovarian and testicular tissue that was intermixed and not separated by connective tissue. The males of each species possessed secondary testes, which retained structures of the ovary they had replaced, such as a membrane-lined ovarian lumen, lamellae and ovary wall. Furthermore, histological sections indicated that sperm were transported towards the outer walls of the testes, where the multiple
sperm sinuses present in that region were presumably responsible for transporting sperm to the cloaca, rather than to a singular sperm duct as is the case with gonochoristic species.

The typically large size and different colour of the males of *C. rubescens*, *C. schoenleinii* and *C. cauteroma* and the bias in the sex ratios of their adults towards females suggests that the males of each of these species are either haremic, *i.e.* permanently territorial, or form leks, *i.e.* are temporarily territorial during their spawning seasons. In these three species, the presence of ripe testes that are far smaller than ripe ovaries and the release by females of eggs in batches are consistent with a single male spawning with an individual female, as commonly occurs in haremic/lekking species. In contrast to the above species, *C. cyanodus* was not sexually dichromatic, the sex ratio was not biased towards either sex and the weight of ripe testes remained relatively constant as body weight increased. The latter implies that the relative investment of energy by males into testicular development during the spawning season declines with increasing fish size. Thus, the males of *C. cyanodus* may be opportunistic spawners when small, possibly spawning in groups, and may tend towards a haremic or lek mode of life when larger.

The respective lengths and ages at which 50% of the females of *C. cyanodus*, *C. cauteroma* and *C. schoenleinii* attained sexual maturity (*L*<sub>50m</sub>, *A*<sub>50m</sub>) in Shark Bay were *ca* 129, 196 and 253 mm and 2.3, 2.0 and 3.5 years of age. The corresponding *L*<sub>50m</sub> and *A*<sub>50m</sub> for *C. rubescens* in Shark Bay and the Abrolhos Islands were *ca* 274 and 279 mm, respectively, and 2.7 and 4.1 years of age, respectively. The respective lengths and ages at which 50% of the females of *C. cyanodus*, *C. cauteroma* and *C. schoenleinii* changed to males (*L*<sub>50c</sub>, *A*<sub>50c</sub>) in Shark Bay were 221, 310 and 556 mm and 4.1, 6.4 and 10.4 years of age. The length at which *C. rubescens* changed sex (*L*<sub>50c</sub>) was significantly greater in Shark Bay (545 mm) than in the Abrolhos Islands (479 mm), whereas the reverse pertained with respect to the age at sex change (*A*<sub>50c</sub>), *i.e.* 10.5 vs 11.9 years of age. Since some females were found in the oldest age classes of each species in Shark Bay and in the population of *C. rubescens* in the Abrolhos Islands, some of the females of each species do not apparently change sex.

The trends exhibited by the gonadosomatic indices of females and males and the stages of ovarian development in sequential months demonstrated that the spawning periods of each species varied. Thus, *C. rubescens* (in both Shark Bay and the Abrolhos Islands) and *C. cauteroma* spawn predominantly in spring, whereas spawning occurs in late spring/early summer in *C. schoenleinii* and in summer in *C. cyanodus*. As
C. schoenleinii, C. cyanodus and C. cauteroma occur predominantly within the inner gulfs of Shark Bay, the offset in the timing of their spawning periods would be likely to reduce any potential for competition between the larvae of those three species for resources.

The trends exhibited by the mean monthly marginal increments in sectioned otoliths with differing numbers of opaque zones demonstrated that, in each species, those opaque zones were laid down annually. Thus, the numbers of opaque zones in the sectioned otoliths of individuals of each species could be used, in conjunction with the birth date and time of year when those zones are delineated, to determine their approximate ages at capture. The maximum ages recorded for the four Choerodon species in Shark Bay ranged only from 12 to 16 years. However, in that environment, the maximum lengths of C. rubescens (649 mm) and C. schoenleinii (805 mm) were far greater than those of C. cauteroma (424 mm) and C. cyanodus (382 mm). In contrast to the situation with C. rubescens in Shark Bay, this species reached a substantially older maximum age (22 years), but slightly shorter length (629 mm), and grew at a slower rate in the Abrolhos Islands, possibly reflecting the influence of greater productivity in Shark Bay and/or greater densities of this species in the Abrolhos Islands.

Although a few C. rubescens and C. schoenleinii reach large sizes in Shark Bay, most of the individuals of these species were less than 400 mm, their minimum legal length (MLL) for capture. This raises the possibility that these two sought after species, i.e. the seventh and ninth most abundant species in the recreational fishery in Shark Bay, are subjected to substantial fishing pressure. Sampling for C. cyanodus was considered representative of the sites that this species occupies in Shark Bay and the sampling methods would have been likely to have captured the full size range of this tuskfish. Thus, the failure to catch any C. cyanodus greater than 400 mm indicates that, in Shark Bay, this species does not grow to the far greater lengths of about 600 mm reported for this species as a maximum by Allen (1999). Furthermore, the 400 mm MLL for this species in Western Australia precludes the retention by fishers of this species in this environment. Choerodon cauteroma was caught at lengths up to 424 mm, which is greater than the maximum of 360 mm reported for this species (Allen, 1999). Although there is no MLL for C. cauteroma, recreational fishers are restricted to a bag limit of four fish per person per day, as is the case with all other tuskfish species.

Since fishers target large fish preferentially and the largest size classes of each of the species of tuskfish are dominated by males, heavy fishing pressure has the potential to remove a large proportion of the males of the Choerodon species that are
fished in Shark Bay, *i.e.* *C. rubescens, C. schoenleinii* and *C. cauteroma,* and also of *C. rubescens* in the Abrolhos Islands. Since the ratio of females to males in catches of *C. rubescens* taken by the commercial fishery in the Abrolhos Islands are *ca* 1:1 and yet the typical adult sex ratio is heavily biased towards females (*ca* 14:1), that fishery is removing a substantial proportion of the males from the population. Protogynous hermaphroditic species are apparently able to respond to such pressure on the males by initiating a change in sex by the larger females. However, there is evidence from studies of other protogynous species that heavy size-selective fishing can lead to a reduction in the size and age at which a species changes sex and ultimately to a collapse in the stock.

The results of visual surveys, when taken in conjunction with the locations of the catches of each of the five *Choerodon* species, demonstrated that *C. rubescens* lives on reefs in “oceanic” waters along the western boundary of Shark Bay, whereas *C. schoenleinii, C. cyanodus, C. cauteroma* and *C. cephalotes* are found predominantly in the two inner gulfs of this large embayment. *Choerodon cephalotes* lives almost exclusively in seagrass beds, while *C. schoenleinii* and *C. cyanodus* occupy predominantly inner gulf reefs and rocky shorelines and *C. cauteroma* occurs in all of those three habitats. *Choerodon cauteroma* was the only species that underwent an obvious size-related shift during its life cycle, moving from seagrass to hard substrates, such as inner gulf reefs and rocky shorelines, as it reached adulthood.

The biological and habitat data produced during this thesis will provide fisheries and environmental managers with the types of information that will enable them to develop management plans for conserving tuskfish species and their habitats in Shark Bay. The biological data for *C. rubescens* in the Abrolhos Islands will be able likewise to be used to develop plans for conserving the stock of this species in waters in which it is heavily fished.
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Acknowledgements

In four years of doing a PhD you come across a very long list of helping hands. The biggest thanks go, of course, to my supervisor Professor Ian Potter, thank you so much for your support, guidance, encouragement and belief in me. Thank you for the opportunity to work with you. Hopefully this thesis is some reward for your time and investment in my work. It wouldn’t have been possible without you. Shame you didn’t make it to Shark Bay for a fishing trip or a transect amongst the tiger sharks! The study was funded by the Australian Fisheries Research and Development Corporation and Murdoch University.

Thanks to all the Murdoch crew who came on those Shark Bay adventures and put up with the wind and chop! A really, really big thanks to Simon de Lestang, William White, Alex Hesp, Matt Pember, Michael Travers, Dan French, Pete Coulson, Justin King, Thea Linke, Bryn Farmer, Steeg Hoeksema, Fiona Valesini and Dave Waayers. And the unwary volunteers: Tim, Ed, Brian, Shawny, Nathan, Alan and Dazza. Sime and Matty, being marooned on the Abrolhos Islands just wouldn’t have been the same without you two! I’ll never forget the squid stuffed with crayfish!!! Thanks for all your help guys. Mikey, thanks for all the tusk info and data and don’t forget that 3 will always be the magic number. Thanks also to Norm Hall for your mathematical and logical genius and for just keeping me going. Tim Meecham, well done mate, you caught the biggest (10kg) bluebone. Cheers for your help and the trip to Bernier. Thank you to Sonja Schubert for your help with the fecundity work. And a big thank you to Colleen Hubbard for the moral support when I needed it the most. Special thanks to Fi for all your help with the habitat chapter and taking me to the land of the bubble and to Hespy for your biological and editing craftsmanship. A huge thanks to Will for your sampling genius (!), the blackspot data wouldn’t have been so good without your efforts. To Lynnath Beckley, thanks for pushing me and to Yvonne Sadovy for introducing me to the broader purpose of fish research and inviting me to join the IUCN Specialist group for groupers and wrasses. Thank you also to Robert Warner for your helpful comments on the hermaphroditic side of things. Thanks to Barry Hutchins for your help and info on your work in Shark Bay. Thank you to William Eschmeyer, Theodore Pietsch and Martin Gomon for your help with the species descriptions and thanks also to Alan Pearce for the sea surface temperature data.

Thanks to all the helpers from the Department of Fisheries Western Australia who claim that fishing for baldies was just part of their job! Ian Keay, Roy Melville-Smith, Jason How, Jason Mant, Jim ‘Zorba’ Christianopoulos, Rick Allison, Gary Jackson, Jeff Norris, Brenton Chatfield, Justin King, Corey Wakefield, Kim Nardi, Steve Newman and Craig. Special thanks to Kim Grey of the Shark Bay fisheries office for your assistance, interesting stories and nights out! Keep strumming that guitar, you’ll make it one day mate! Hope this thesis helps you sleep at night!

To the fishers and people of Shark Bay that lent a hand and provided the frames and the stories. In particular Steve McCaskie of Fivestar fisheries, Geraldton, Jeremy and Gavin at Festival Fish and to Dean Thorburn and Lou of Seafresh. In Shark Bay itself, many many thanks to Les and Glenys Fewster of Shark Bay Charter Service for your time, support and the effort involved in getting us to Turtle Bay and back (!), to Brian and Johnno of the Shark Bay Hotel, Gary, Dave and Matt at the Heritage Hotel, to Elaine and Rob Crawford-Ferguson of Ray White Real Estate for putting us up (or putting up with us!), Kevin Crane and the staff at CALM Shark Bay, Robbie and Peter Morgan of the Monkey Mia Pearl Farm, Brad, Kath, Brett, Tammy and Skye of Tradewinds for feeding me, John and the staff at the Shell for filling us up and John Glesing of Shark Bay Salt. Thanks also to the many people who I shared a beer and story with in Shark Bay.

To my very special friends, Jason and Sandy How, for their friendship and love during some very topsy turvy times in my life! You guys were always there for me. Thank you.

To Sime. Thanks man. You’ve been there from the beginning and seen it through with me. Thanks for your ideas and inspiration and thanks for giving me so much help and trying to lift me when it wasn’t happening. I couldn’t have done it without you or your homebrew. Thanks heaps mate. Let’s have a beer!

Thank you to my Mum and Dad, who although I’m sure were somewhat bemused at my continuing desire to be at Uni, believed in me and my need to do what made me happy. Thank you for supporting me, for being there for all those years and for the roast dinners. Hopefully now you can see the light too!!

To my beautiful partner, Lyndsay. Thank you so much for being there, for putting up with me and for supporting me through this. You always believed in me and I could never have done it without you. I love you girl.
Chapter 1

1.0 Introduction
1.1 General characteristics of the Labridae

The Labridae (wrasses), which is the second largest teleost family, comprises 69 genera and *ca* 500 species (Allen, 1999; Eli, 2004). This family name was chosen in recognition of the labriform swimming technique of its species, *i.e.* the use of the pectoral fins as the main source of propulsion (Fig. 1.1a-c; Bellwood and Wainwright, 2001). Wrasses have a protrusible mouth with prominent, sometimes outward-jutting, canine teeth, which are used by many of their species to extract their benthic invertebrate prey, *e.g.* crustaceans, molluscs and echinoderms, from the substrate (Fig. 1.1c; 1.2a,b; Gomon, 1997; Allen, 1999; Pitkin, 2001). Although wrasses range in length from only about 5 cm in the case of species such as the midget wrasse *Pseudocheilonops ataenia* to as much as 230 cm with the humphead maori wrasse *Cheilinus undulatus*, the maximum length of many species in this family is less than 20 cm (Allen, 1999; Westneat, 2001).

The swimming style and wide diversity in shape, size and colour make labrids one of the most conspicuous reef-fish families. They are commonly found on the coral reefs of the tropical marine waters of the Indian, Pacific and Atlantic oceans (Allen, 1999; Jones, 1999). However, labrids are also well represented in warm temperate marine environments, such as those of Australia. Although they occur in waters up to 100 m in depth, they are more common in shallow waters, where they live in a range of habitats, including sand, rubble, seagrass, algae, rock and coral substrates (Allen, 1999; Westneat, 2001). Labrids are diurnally active, becoming inactive after sunset, when they occupy reef crevices, burrow into sand substrates or live in nests (Fig. 1.2c; Randall *et al.*, 1997; Nanami and Nishihira, 1999; Pitkin, 2001; Westneat, 2001; Takayanagi *et al.*, 2003).
Figure 1.1. Photographs of *Choerodon rubescens* showing the large pectoral fins that are used for propulsion.
Figure 1.2. Photographs of (a) front view of the head and teeth of *Choerodon cyanodus*, (b) lower jaw of *Choerodon rubescens* showing tusk-like teeth (Scale = 1 cm), and (c) *Choerodon schoenleinii* in a reef hole excavated for nocturnal occupancy.
1.2 Biology of the Labridae

Studies of members of the Labridae have shown these species to be either gonochorists or protogynous hermaphrodites (Reinboth, 1970; Policansky, 1982; Francis, 1992). However, only a few labrid species, *e.g.* *Symphodus ocellatus*, *Symphodus melops* and *Centrolabrus exoletus* are gonochoristic, *i.e.* remain as one sex throughout their life (Dipper and Pullin, 1979; Bentivegna and Benedetto, 1989). Two species of wrasse, the vieja *Bodianus echlancheri* and the purple wrasse *Notolabrus fucicola*, have been reported to be “secondary” gonochorists, *i.e.* the gonads of juveniles develop first as ovaries and subsequently some of these change permanently to testes before sexual maturity is attained (Hoffman, 1985; Barrett, 1995; Denny and Schiel, 2002). Protogynous hermaphroditism, *i.e.* where individuals change sex from female to male, is the dominant reproductive strategy of labrids (Policansky, 1982; Warner, 1984), and occurs in most genera, including, for example, *Anampses*, *Choerodon*, *Cirrhilabrus*, *Halichoeres*, *Nelabrichthys*, *Thalassoma* and *Xyrichthys* (Warner and Robertson, 1978; Nemtzov, 1985; Bentivegna and Rasotto, 1987; Kobayashi and Suzuki, 1990; Ebisawa et al., 1995; Gillanders, 1995; Leem et al., 1998; Andrew et al., 1996; Feddern, 1965).

Two main categories of protogynous hermaphroditism are recognised, *i.e.* monandry and diandry. In monandric protogynous hermaphrodites, *e.g.* *Nelabrichthys ornatus* and *Achoerodus viridis*, the males are derived exclusively from adult females and are termed secondary males (Sadovy and Shapiro, 1987; Gillanders, 1995; Andrew et al., 1996). However, in diandric protogynous hermaphrodites, *e.g.* *Thalassoma bifasciatum* and *Cheilinus undulatus*, the males are derived either from small juveniles that contain an undifferentiated gonad, which are termed primary males, or from adult females, as in monandric species, *i.e.* secondary males (Warner and Robertson, 1978; Sadovy and Shapiro, 1987; Shapiro and Rasotto, 1993; Donaldson and Sadovy, 2001).
Protogyny is a more common form of hermaphroditism in fishes than protandry, *i.e.* where sex change is from male to female, or simultaneous hermaphroditism, *i.e.* where individuals function as both female and male at the same time. Neither of the latter two forms of sex change have been recorded in the Labridae (Policansky, 1982).

Ghiselin (1969) suggested that the evolution of sex change in fishes enabled fish to take optimal advantage of their size, *i.e.* a change in sex would occur when a fish reached a particular size if it provided a reproductive advantage, and thus an individual could maximise its lifetime reproductive potential. Thus, for example, a change from male to female in the protandrous sparid, the western yellowfin bream *Acanthopagrus latus*, enables egg production to be concentrated in its largest fish, which can produce the largest number of eggs (Hesp *et al.*, 2004a). However, many studies of the reproductive behaviour of protogynous labrids have demonstrated that, while size may influence when an individual changes sex, various social factors may act in combination with size to trigger sex change. For example, some species are haremic, *e.g.* the cleaner wrasse *Labroides dimidiatus* and the Red Sea razorfish *Xyrichtys pentadactylus*. A haremic social group consists of one large male and several females, which are usually smaller (Robertson, 1972; Nemtzov, 1985; Sakai *et al.*, 2001; see also Muñoz and Warner, 2003). These species exhibit “sex-change suppression”, where the male aggressively dominates the females and thereby prevents them from changing sex. A male thus has the advantage of reproducing with several females and therefore ensuring that his genetic traits are passed on to the next generation (Ross, 1990). If the male is removed or dies, the largest female will change sex, thus conferring the reproductive advantage to this individual (Robertson, 1972; Nemtzov, 1985). Other triggers for sex change include, for example, when the ratio of females to males exceeds a certain minimum level, and thus leads to a reduction in the number of male-female interactions (Shapiro and Lubbock, 1980), or when the number of large fish, which are usually male,
becomes low and thereby provides the cue for a larger female to change sex, as occurs with the saddleback wrasse *Thalassoma duperrey* (Ross *et al*., 1983; Ross, 1990). Early sex change may occur when the largest female changes sex before the loss of the dominant male. This female becomes a ‘bachelor male’ and may later establish its own territory and harem (Ross, 1990). Several other examples of social factors influencing sex change in protogynous species have been documented, *e.g.* Warner (1988), Ross (1990), Muñoz and Warner (2003). The above types of sex change highlight the variability in labrid reproductive strategies and their ability to respond to many different social situations.

Some of the small species of labrids with maximum total lengths of less than 25 cm, *e.g.* the Mediterranean razorfish *Xyrichthys novacula*, the corkwing wrasse *Symphodus melops* and *Centrolabrus exoletus* live for less than ten years (Sayer *et al*., 1996; Cardinale *et al*., 1998). However, other small labrids, such as the goldsinny *Ctenolabrus rupestris* and the slightly larger purple wrasse *Notolabrus fucicola*, live for far longer, reaching 20 years of age, while the large eastern blue groper *Achoerodus viridis*, which reaches a maximum length of 100 cm, may live for 35 years (Gillanders, 1995; Sayer *et al*., 1995; Ewing *et al*., 2003).

### 1.3 The importance of labrids in fisheries

The small size and attractive colouring of many wrasse species, *e.g.* those belonging to the genera *Anampses*, *Coris* and *Thalassoma*, have made them very popular in the aquarium trade, while other small wrasses, *e.g.* the rock cook *Centrolabrus exoletus* and the goldsinny *Ctenolabrus rupestris*, are collected for use as “cleaner fish” for removing parasites from salmon in oceanic aquaculture cages in northern Europe (Björdal, 1991; Westneat, 2001; Treasurer, 1996; Kvenseth, 1996). Some of the larger wrasses, such as those of the *Bodianus*, *Cheilinus*, *Choerodon*,
Hemigymnus and Tautoga genera, for example, are considered excellent food fish and are thus sought after by commercial, artisanal and/or recreational fishers (Last et al., 1999; Westneat, 2001; Warner, 1975). Thus, in the western central Pacific, the annual catches of labrids between 1990 and 1995 ranged from 10,500 to 21,500 t (Westneat, 2001).

In the Indo-west Pacific, the use by commercial and artisanal fishers of destructive and indiscriminate fishing practices, such as poisons and explosives, has led to the widespread destruction of habitats that are important for labrids, particularly coral reefs (McManus, 1997; Spalding et al., 2001). A combination of a loss of habitat, the development of the live reef fish trade and heavy fishing pressure throughout its distribution, has resulted in the rapid decline of the stocks of species such as the humphead maori wrasse Cheilinus undulatus (Sadovy et al., 2003). This species is listed as “vulnerable” in the IUCN 1996 Red Data Book for endangered animals and fishing regulations have been tightened in many areas of its distribution, which, in Western Australia, includes total protection (Donaldson and Sadovy, 2001; Pogonoski et al., 2002; IUCN, 2003; Sadovy et al., 2003). Night-time spear fishing, or “dentou moguri” in Japan, which targets sought-after species of labrids, such as the blackspot tuskfish Choerodon schoenleinii, when they are known to be inactive, has led to overexploitation of this species in those waters (Ebisawa et al., 1995).

1.4 Labrids of Australia and their fisheries

Many different wrasse species with Indo-Pacific distributions occur in the tropical waters of northern Australia. These species belong to a variety of genera, e.g. Anampses, Bodianus, Cheilinus, Cirrhilabrus, Choerodon, Halichoeres and Thalassoma (Allen, 1999). Up to 130 tropical and temperate species have been recorded on the shallow reefs of Western Australia (Hutchins, 1994; 2001a). Some tropical wrasses, e.g.
*Thalassoma lunare* and *Coris picta*, are found in the warm temperate waters on the western and eastern coasts of Australia, respectively, reflecting the influence of the warm Leeuwin and East Australian currents, that originate in tropical waters adjacent to those two coastlines and which carry their eggs and larvae southwards along those two coastlines (Jones, 1999; Hutchins, 1991). Other species with subtropical distributions, e.g. the baldchin groper *Choerodon rubescens* and the seven banded wrasse *Thalassoma septemfasciata*, occur only on the west coast of Australia. Ninety species, including those of the *Notolabrus*, *Achoerodus* and *Pictilabrus* genera, are found only in the temperate waters of Australia (Jones, 1999; Hutchins, 1994; 2001b). Some of these temperate species are found only across southern Australia, e.g. the senator wrasse *Pictilabrus laticlavius* and the Maori wrasse *Ophthalmolepis lineolatus* (Jones, 1999).

Few wrasse species are targeted directly by commercial fishers in Australia. Most of the wrasses captured form part of multi-species line and trap fisheries, e.g. the venus tuskfish *Choerodon venustus* in Queensland and the baldchin groper *Choerodon rubescens* in Western Australia, or are taken as bycatch of other commercial fisheries, e.g. prawn trawl fisheries, such as the blackspot pigfish *Bodianus unimaculatus* (Last et al., 1999; Platten et al., 2002). Since commercial catches of most labrid species are generally low, they are often published in broad groups, e.g. “parrots” in Queensland and the Northern Territory, that also includes the true parrotfishes (Family: Scaridae), and “groper” or “other” in Western Australia and other states, (Penn, 2002; ABARE, 2003; J. Platten pers. comm.). However, some individual labrid species are the focus of rapidly-expanding commercial fisheries in Victoria, on the south coast of Australia, such as the live fish trade for the blue throat wrasse *Notolabrus tetricus* and the purple wrasse *Notolabrus fucicola*, the catches of which have increased dramatically from 0.84 t in 1990 to 810 t in 1997 (Anon., 2004; Cappo et al., 1998; Last et al., 1999; Smith et al., 2003). Previous overexploitation of the eastern blue groper *Achoerodus*
viridis led to a ban being placed on commercial fishing and recreational spearfishing of this species in New South Wales (Gillanders, 1995; 1999).

1.5 Commercial and recreational fisheries for labrids in Western Australia

A few labrid species are taken in Western Australia by commercial fishers, either as part of mixed species line or trap fisheries or as a bycatch of demersal gillnet and long-line fisheries, and by recreational line and spear fishers. The species include the western blue groper Achoerodus gouldii, the western king wrasse Coris auricularis, the western foxfish Bodianus frenchii and the saddleback pigfish Bodianus bilunulatus (Crowe et al., 1999; Anon., 2000). However, the most important species of wrasses in Western Australia are those belonging to the genus Choerodon, the tuskfishes, such as the baldchin groper Choerodon rubescens and the blackspot tuskfish Choerodon schoenleinii (Crowe et al., 1999; Anon., 2000; Penn et al., 2003). Tuskfish are sought after for their high quality white flesh and attract high prices of ca AUS$30-40 per kg for fillets in Perth (Last et al., 1999; Market Price in 2003).

Choerodon rubescens is taken mostly on the west and Gascoyne coasts of Western Australia, while other Choerodon species are taken on either the Gascoyne or north coasts (Fig. 1.3). Annual commercial catches of C. rubescens in the west coast region of Western Australia over the last 10 years have ranged between ca 30 and 40 t, with approximately 46% of this catch being taken from the Houtman-Abrolhos Islands region (subsequently referred to as the Abrolhos Islands, Fig. 1.3), where it is abundant (Walker, 1983; Nardi, 1999; Crowe et al., 1999; Penn, 2002). However, it may be over-exploited in this region (Crowe et al., 1999; Pogonoski et al., 2002; Penn et al., 2003). Choerodon rubescens is also caught commercially by fishers targeting pink snapper in oceanic waters around Shark Bay in the Gascoyne region (Fig. 1.3; Crowe et al., 1999). Commercial catches of other tuskfish, commonly referred to as bluebone groper, ranged
Figure 1.3. Map showing boundaries (blue lines) of managed fishing bioregions of Western Australia, i.e. North coast, Gascoyne coast, West coast and South coast (after Penn et al., 2003). Note that Australian fishing waters extend 200 nm (ca 370 km) outwards from the coast.
from *ca* 16 to 34 t per year between 1994/95 and 1998/99 (Anon., 2000). The colloquial name “bluebone” was given to tuskfish species in recognition of their bright blue ribs, dorsal spines and vertebrae, and is used interchangeably for all of the regularly-caught species, although it is most commonly used to refer specifically to blackspot tuskfish *Choerodon schoenleinii*. The other “bluebone” species include the blue tuskfish *Choerodon cyanodus* and bluespotted tuskfish *Choerodon cauteroma*, while the name groper is often used for the largest species, even though tuskfish are no relation to the true gropers, *i.e.* the Serranidae (Jones, 1999).

In Western Australia, participation in recreational fishing has risen markedly in the last 15 years, with currently *ca* 640,000 fishers fishing for a total of 3.4 million fisher days year\(^{-1}\) (Penn, 2002; Penn *et al*., 2003). The combined “wrasse/tuskfish/gropers” group represents the ninth and fifth most important group of fishes, in terms of numbers caught by recreational and indigenous fishers, respectively, in that state (Henry and Lyle, 2003). Note that this group does not include the true groupers of the Serranidae family, which are recorded separately. In the west coast region of Western Australia (Fig. 1.3), the total annual catch of *C. rubescens* by recreational fishers is slightly less than the annual commercial catch, with, for example, *ca* 23 t being taken by recreational boat fishers in the 12 month period between September 1996 and August 1997 (Sumner and Williamson, 1999). The Abrolhos Islands is a major focus for recreational fishers in that region, who are targeting *C. rubescens* (Fig. 1.3; Nardi, 1998; Penn *et al*., 2003).

In the Gascoyne region, Shark Bay is an important location for recreational fishers, with approximately 40 – 60,000 recreational fishers visiting this region every year and fishing for *ca* 243,000 fisher days year\(^{-1}\) (Fig. 1.3; Shaw, 2000; Sumner *et al*., 2002). The marked rise in the number of recreational fishers during recent years, together with the ease with which fishing can be carried out in the relatively protected
waters of Shark Bay, make the most popular fish species in this large embayment susceptible to overfishing (Fisheries WA, 1999; Penn et al., 2003). Greater ease of access to remote areas, such as Shark Bay, and technological improvements in the methods of locating fish have increased the pressure on the stocks of the most vulnerable and sought-after species, such as reef fish, in this embayment (Fisheries WA, 1999; Sumner et al., 2002; Penn et al., 2003).

The decline during recent years in the abundance of the most important of the commercial and recreational fish species in Shark Bay, i.e. the pink snapper *Pagrus auratus*, mainly as a result of increasing recreational fishing pressure, became so extreme that a ban was placed on recreational fishing for this species in the eastern gulf of this embayment and the minimum legal size and catch limits elsewhere in Shark Bay were tightened (Penn et al., 2003). This change in regulations resulted in a diversion of fishing pressure towards other reef-dwelling species, such as the blue-lined emperor *Lethrinus laticaudus*, the estuary cod *Epinephelus coioides* and the four largest tuskfish in Shark Bay, i.e. *C. rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma*, with, for example, *C. rubescens* and *C. schoenleinii* being the seventh and ninth recreationally most important species in this embayment (Curnow and Harrison, 2001; Sumner et al., 2002; Penn et al., 2003; S. Ayvazian, pers. comm., Department of Fisheries W. A.). The importance of the above four tuskfish species to recreational fishers is reflected in the recent increase in the number of articles on these species in local fishing magazines (Shaw, 2000; Harrison, 2001; Sumner et al., 2002; Kershaw, 2003; Penn et al., 2003; Monks, 2004). Furthermore, there are often reports of recreational line and spear fishers targeting specific areas of Shark Bay repeatedly and removing substantial numbers of individual species, such as *C. rubescens* and *C. schoenleinii*, on consecutive days (P. Dickinson, pers. comm., Shark Bay Resources; K. Grey, pers. comm., Denham Department of Fisheries W. A.). Thus, a tightening of regulations on taking pink
snapper would inevitably have led to the catches of sought-after species, such as tuskfish, to have increased in recent years.

There is little information on the long-term catch rates of tuskfish species in the commercial or recreational fisheries in Shark Bay and essentially no biological data suitable for developing management plans for their stocks. However, a recently-published management plan by the Department of Fisheries W.A. for the recreational fisheries of the Gascoyne region highlights specifically the need for acquiring crucial biological data and information on key habitats for *C. rubescens* and *C. schoenleinii* to facilitate the development of management plans for these two species (Curnow and Harrison, 2001). Furthermore, a five year strategy for managing the fisheries of the west coast region of Western Australia also highlighted *C. rubescens* as a priority species for research and suggested that it could be used as an indicator of “fishing quality” (Harrison, 2001). Although other tuskfish species are targeted by fishers, there is still no specific mention in relevant fisheries reports of any requirement for their management.

### 1.6 The tuskfishes of Western Australia

The 26 described species of *Choerodon*, or tuskfish, belong to the Hypsigenyini tribe, which is characterised by a deep head and large sub-orbital space or cheek (Gomon, 1997; Westneat, 2001). The members of the *Choerodon* genus are so named because of their tusk-like teeth, with *Choerodon* literally meaning “pig tooth” (Fig. 1.2a, b; Gomon, 1997). The tuskfishes are broadly distributed throughout the tropical west Pacific or Indo-west Pacific regions, eleven of which have been recorded in Western Australia (Hutchins, 2001a). Some of the *Choerodon* species in Western Australia, *e.g.* the red-stripe tuskfish *Choerodon vitta*, the anchor tuskfish *Choerodon anchorago* and the wedge-tailed tuskfish *Choerodon sugillatum*, do not occur south of the north coast region (Fig. 1.3; Allen, 1999; Hutchins, 2001b; M. Travers unpubl. data). However, the
tropical purple tuskfish *Choerodon cephalotes* occurs as far south on the west coast of Australia as Shark Bay at *ca* 26ºS, while others, *i.e.* *C. schoenleinii*, *C. cyanodus* and *C. cauteroma*, have been recorded as far south as the Abrolhos Islands, although they are rare at that location (Fig. 1.3; Hutchins, 2001b; Black *et al.*, 1990; Travers and Potter, 2002). In Western Australia, most *Choerodon* species occupy reefs and/or sand, rubble or weed areas adjacent to reefs, however, *C. cephalotes* is also found in seagrass beds and is named the grass tuskfish in eastern Australia presumably for that reason (Grant, 1993; Allen, 1999; Hutchins, 2001b; Hutchins, 1995).

**The baldchin groper *Choerodon rubescens* (Günther, 1862)**

The baldchin groper *C. rubescens*, also colloquially termed baldy, bluebone groper and sometimes baldchin tuskfish, is endemic to Western Australia and is described as being “sub-tropical”, occurring on the west coast between Coral Bay (*ca* 23ºS) and Geographe Bay (*ca* 34ºS) (Fig. 1.3; Hutchins and Swainston, 1986; Hutchins, 2001b). Although the name “baldchin” is derived from its possession of a prominent white chin, it is distinguished from other tuskfish species, which may also have a pale chin, by its white pectoral peduncle (Fig. 1.4a). The species name *rubescens* refers to the pink to red coloration exhibited by some medium-sized fish (Fig. 1.4a). This species grows to *ca* 65 cm long and attains a maximum weight of *ca* 6.5 kg (Allen, 1999).

**The blackspot tuskfish *Choerodon schoenleinii* (Valenciennes, 1839)**

The blackspot tuskfish *Choerodon schoenleinii*, which is also known as bluebone groper or just bluebone in Australia, is a tropical species with a wide distribution throughout the Indo-west Pacific (Allen, 1999). This common name is derived from its possession of a prominent black spot at the base of the dorsal fin (Fig. 1.4b), while the species was named after Dr. Johannes Schönlein, who assisted
with its description (W. Eschmeyer, T. Pietsch, pers. comm.). Although blackspot
tuskfish are normally blue to green, individuals can change colour to match the substrate
over which they are swimming (Allen, 1999; D. Fairclough, pers. obs.). *Choerodon*
schoenleinii, which is the largest tuskfish species, can reach over 90 cm in length and ca 16 kg in weight (Grant, 1993; Randall et al., 1997).

The blue tuskfish *Choerodon cyanodus* (Richardson, 1843)

The blue tuskfish *Choerodon cyanodus* is also a tropical species and is suggested to occur throughout the Indo-west Pacific (Randall et al., 1990; Allen, 1999). However, other studies, *i.e.* Masuda et al. (1984), Monkolprasit et al. (1997), Allen and Adrim (2003), did not record this species in areas of Japan, Thailand and Indonesia, respectively, suggesting its distribution is more restricted. Although occasionally mistaken for the baldchin groper in Western Australia, because of its pale chin, it lacks the distinguishing white pectoral peduncle of *C. rubescens*. In addition, its tail contains orange and blue vermiculations and the region just below the posterior end of the dorsal fin often has a pale patch (Fig. 1.5a; Randall et al., 1997). The variability in the colouration of the body, particularly the presence or absence of the pale patch, may have led to some confusion in its identification and the description of another tuskfish species by Whitley (1945), *i.e.* *Choerodon paynei*, the type specimen of which was collected in Shark Bay, where *C. cyanodus* is found (B. Hutchins, pers. comm.; Hutchins, 2001b). It is worth noting that the white patch on specimens of *C. cyanodus* often fades when removed from the water (D. Fairclough, pers. obs). The blue tuskfish, which takes the name *cyanodus* from its possession of blue-green teeth, is reported to reach ca 60 cm in length and 7 kg in weight (Allen, 1999).

The bluespotted tuskfish *Choerodon cauteroma* (Gomon and Allen, 1987)

The bluespotted tuskfish *Choerodon cauteroma* is a tropical species endemic to Western Australia, occurring only in north-western Australian waters, between ca Cape
Figure 1.5. Photographs of (a) *Choerodon cyanodus* and (b) *Choerodon cauteroma*.

Leveque at *ca* 16.5°S and the Abrolhos Islands (Fig. 1.3; Allen, 1999; Hutchins, 2001). *Choerodon cauteroma* is pale to orange in colour, with bright blue spots on its scales (Fig. 1.5b). The name *cauteroma* is derived from the short dark band or “branding” that is located on its flank between the dorsal and pectoral fins. This species grows to *ca*
43 cm in length (B. Hutchins, pers. comm.), however, there are no published reports of either the maximum weight or the biology of this species.

Despite the substantially different reported total lengths of the baldchin groper and the blackspot, blue and bluespotted tuskfishes, each of these species has been allocated the same minimum legal length (MLL) of 40 cm in both the west coast and Gascoyne regions of Western Australia. This reflects an absence of the type of crucial biological data, such as the length at which 50% of fish of each of these species attain sexual maturity, typically used for assigning MLLs (Anon., 2003a, b; Hill, 1990; Winstanley, 1990). Furthermore, there is no information on the age at maturity, age compositions or growth of each species, derived using validated ageing techniques, that can be used in assessments of natural and fishing mortality, length- or age-structured models and to provide indications of their generation times. Current regulations restrict recreational fishers to retaining a maximum of four tuskfish per person per day (Anon., 2003a, b, c).

1.7 Aims of the study

The data produced by many studies on commercially and/or recreationally important fish species are inadequate in terms of the reporting of the techniques used and of how the results can be interpreted and applied in fisheries management (Sadovy, 1996b). Sadovy (1996b) highlights the fact that, in relation to studies of reproductive biology, there is often a lack of information on, for example, “…the type of sexual maturation assessed (i.e. minimum or 50%)”, “…what was intended by the term ‘mature’ or ‘maturing’…”, or what sizes or ages of fish, e.g. juveniles or adults, were included in sex ratio calculations. In addition, Campana (2001) has recently reiterated the requirement for validation in ageing studies, which, despite the call for this
requirement by Beamish and McFarlane in 1983, is still overlooked or poorly conducted in many studies of teleosts.

The broad aims of this study are as follows. (1) Provide information on key aspects of the reproductive biology and determine the size and age compositions and growth of *Choerodon rubescens, Choerodon schoenleinii, Choerodon cyanodus* and *Choerodon cauteroma* in Shark Bay. (2) Compare the data for *C. rubescens* in Shark Bay with those determined during the same period for this species in the Abrolhos Islands, 300 km to the south. (3) Determine the relative importance of different habitats during the life cycles of the above four tuskfish species and another species of tuskfish, the purple tuskfish *Choerodon cephalotes*, in Shark Bay. Where appropriate, specific hypotheses are set out in the aims of the chapter dealing with the individual components of this thesis. The data collected will be of the type required for the development of appropriate management plans for each of these species.
Chapter 2

2.0 Study regions and general materials and methods
2.1 Shark Bay World Heritage Area

The Shark Bay World Heritage Area, which is located approximately 700 km to the north of Perth in Western Australia (Fig. 2.1), covers an area of \(2.2 \times 10^6\) ha, of which \(71\%\) comprises marine waters (Anon., 1996). It encompasses the waters southwards from Carnarvon and the northern end of Bernier Island to the southern extremities of the eastern and western gulfs (Fig. 2.1). It also includes waters up to three nautical miles offshore from the western coastlines of the Bernier, Dorre and Dirk Hartog Islands and Edel Land Peninsula southwards to 27°16’S (Fig. 2.1; Anon., 2001). Although the inner gulf waters are shallow, averaging 9 m in depth, they reach depths of up to 29 m (Marsh, 1990). The waters to the west of Bernier, Dorre and Dirk Hartog Islands and Edel Land Peninsula deepen rapidly towards the edge of the continental shelf.

Shark Bay was listed as a World Heritage Area in 1991 because inter alia it possesses “… important and significant habitats where threatened species of plants and animals of outstanding universal value from the point of view of science and conservation still survive” (Anon., 2001). Thus, for example, Shark Bay has the largest and most diverse seagrass meadows in the world, covering an area of \(4000\) km\(^2\) and containing 12 species and constituting the dominant marine habitat in this embayment (Walker, 1990). The seagrasses include temperate species, such as *Amphibolis antarctica* and *Posidonia australis*, and tropical species, such as *Syringodium isoetifolium* and *Halophila decipiens* (Walker, 1990; Huisman, 2000). Although Shark Bay does not contain any true coral reefs, it does house 80 species of hermatypic corals, which occur in scattered coral communities, principally in those areas around Bernier, Dorre and Dirk Hartog Islands that are least exposed to wave action (Marsh, 1990). The coral fauna is more depauperate than that of both Ningaloo Reef to the north and the Abrolhos Islands to the south (Marsh, 1990). Other marine habitats include small bare
Figure 2.1. Map of the Shark Bay World Heritage Area (approximate boundary indicated by dashed line), showing areas sampled by line and spearfishing (●) during the present study and by trawling (○, after Travers and Potter, 2002). Inset: Location of Shark Bay and the Abrolhos Islands in Western Australia.
rock or algal–covered reefs, rubble areas, submerged unvegetated sand areas, tidal sand flats, mangrove habitats, lagoons and hypersaline regions (Anon., 1996).

Since Shark Bay receives little freshwater input and is connected to the ocean only by three main channels, water movement within this embayment is limited (Fig. 2.2; Marsh, 1990; Burling et al., 2003). Tidal flow into and out of the bay and the prevailing winds are the dominant influences on circulation and water exchange in the inner waters of the bay (Logan and Cebulski, 1970; Burling et al., 2003). The limited circulation, coupled with the shallowness of the bay and the aridity of the local environment, lead to high rates of evaporation and thus to salinity rising with increasing distance from the ocean (Fig. 2.2). Thus, for example, the waters of the western gulf and northern part of the eastern gulf of Shark Bay are predominantly metahaline, i.e. 40-56‰, while the southern reaches of the eastern gulf are hypersaline, i.e. 57-70‰, waters, in the northern end of this gulf, respectively (Fig. 2.2; Logan and Cebulski, 1970; Burling et al., 2003). The high salinities found in regions of the bay influence the diversity of the biota of those regions (Anon., 1996) (Fig. 2.2). For example, Lenanton (1977) demonstrated that the fauna of the hypersaline Hamelin Pool (Fig. 2.2), at the southern end of the eastern gulf of Shark Bay, contained only six teleost species and a low overall abundance of fish. Furthermore, the two dominant seagrass species in Shark Bay, i.e. *A. antarctica* and *P. australis*, are found predominantly in areas where salinities are less than 60 and 50‰, respectively, and coral communities are restricted mostly to areas where salinities are *ca* 35‰, i.e. full strength sea water (Fig. 2.2) (Walker, 1990). The limitation imposed by high salinities on the distributions of seagrasses and corals in Shark Bay must inevitably restrict the distributions of those fauna that require these habitats.

Although Shark Bay is located in a region where tropical and temperate marine fauna overlap, the majority of the species found in that embayment have a tropical
Figure 2.2. Satellite photo of Shark Bay, showing oceanic (ca 35‰), metahaline (40-56‰) and hypersaline (57-70‰) waters and the approximate salinoclines between these regions (dashed lines) after Logan and Cebulski (1970), and the main channels connecting Shark Bay with the Indian Ocean, indicated by the arrows (Satellite image courtesy www.visibleearth.nasa.gov).
affinity (Wells, 1980; Wilson and Allen, 1980; Anon., 1996). Thus, for example, 86% of the 218 species of molluscan bivalve and 91% of the 232 species of decapod crustacean have a tropical distribution (Jones, 1990; Slack-Smith, 1990). Furthermore, surveys of a range of habitats in South Passage (Fig. 2.1) by Hutchins (1990) demonstrated that 83% of the 323 fish species recorded were of tropical origin, while 11% were subtropical and 6% warm temperate. In addition, Black et al. (1990) found that tropical teleost species comprised 70% of the fish fauna in the seagrass and unvegetated habitats at Monkey Mia in the eastern gulf of Shark Bay (Fig. 2.1). Similarly, 79% of the teleost species caught by Travers (1999) in seagrass and unvegetated habitats further offshore in the eastern and western gulfs of Shark Bay have tropical affinities. In addition, 75% of the teleost species collected in nearshore, shallow unvegetated habitats in both the eastern and western gulfs by Pember (1999) are tropical. The dominance of tropical fauna in Shark Bay is attributable to the larvae of tropical species being transported southwards into this embayment by the prevailing Leeuwin Current that flows close to the coast in this region (Legeckis and Cresswell, 1981; Jones, 1990; Slack-Smith, 1990; Hutchins, 1990).

2.2 Abrolhos Islands

The Abrolhos Islands are located ca 400 km north of Perth and ca 70 km offshore (Fig. 2.1). They contain 122 low-lying islands and reefs that are located at the edge of the continental shelf between 28°15’S and 29°00’S and are arranged in three major groups, i.e. the Wallaby, Easter and Pelsaert groups (Nardi, 1998). The islands lie in the path of the southwards-flowing low salinity and warm Leeuwin Current, which is usually > 24°C at its origin off the north-west coast of Australia (Cresswell, 1991; Pearce, 1997). The islands, which have long been recognised as having high conservation value, contain the southernmost coral reefs in the Indian Ocean (Hatcher,
1991; Nardi, 1998). They house 211 species of hermatypic and ahermatypic corals, 260 species of tropical and temperate algae and ten temperate seagrass species. A total of 389 fish species, 492 species of crustaceans and molluscs and 172 species of echinoderms have been recorded in the Abrolhos Islands (Veron and Marsh, 1988; Collins et al., 1991; Marsh, 1994; Brearley, 1997; Huisman, 1997; Hutchins, 1997; Wells and Bryce, 1997; Webster et al., 2002). The commercially and recreationally important Western Australian species, the western rock lobster *Panulirus cygnus*, the baldchin groper *Choerodon rubescens* and the West Australian dhufish *Glaucosoma hebraicum*, constitute a major component of the fisheries in this region (Nardi, 1998; Penn, 2002).

2.3 Sampling regime in Shark Bay


Monkey Mia, Herald Bight, Denham and Nanga (Fig. 2.1) were sampled for tuskfish bimonthly between March 1999 and January 2000 using a small otter trawl net, which had an effective fishing width of 2.6 m (ca 2/3 length of head rope) and was 0.5 m high and 5 m long from net mouth to cod end. The wings and cod end consisted of 56 and 25 mm mesh, respectively. The bridle length was 13 m and the warp length was varied with water depth according to the equation: warp length = water depth × 4. Four replicate trawls were conducted in both vegetated habitats, *i.e.* consisting of the seagrass species *Posidonia australis* and *Amphibolis antarctica*, and unvegetated (bare sand) habitats in nearshore, shallow (< 4 m deep) waters at each of the four sites. Four replicate trawls were also conducted on each sampling occasion at each site in offshore, deeper waters (6 - 12 m). The two offshore, deeper sites at Monkey Mia and Herald Bight were unvegetated, while those at Denham and Nanga contained dense beds of *P. australis* and *A. antarctica*, respectively. All trawls were conducted during the day at
a speed of \( ca \ 3 - 4 \) km h\(^{-1}\) and for a distance of \( ca \ 150 \) m. The precise distance trawled during each replicate was measured using a Garmin GPS Map 185 global positioning system, which, together with the width of the mouth of the net, enabled the area of substrate trawled to be determined.

**2000-2003**

A wide size range of *C. rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* were obtained bimonthly between July 2000 and January 2003 from rock and coral habitats in the eastern and western gulfs and/or the more oceanic regions, *e.g.* South Passage, of Shark Bay (Fig. 2.1, Table 2.1). Note that *C. cephalotes* was caught predominantly during otter trawling, as described above. Sampling was undertaken using rod and line fishing and spearfishing at as many different locations as possible in both shallow (< \( ca \) 5 m) and deeper (to \( ca \) 25 m) waters, in order that the resultant data could be used to produce a sound description of the biology of each of the above species in Shark Bay as a whole. Samples of tuskfish were also obtained from staff of the Department of Fisheries Western Australia, who were working in Shark Bay, and further samples of *C. rubescens* were purchased from wholesale fish markets. The details of the habitats and regions of Shark Bay and the methods by which juveniles and adults of each of the four species were collected are given in Table 2.1.

**2.4 Sampling regime in the Abrolhos Islands**

Samples of *C. rubescens*, which had been collected between July 2000 and June 2002 by commercial fishers from waters around the Abrolhos Islands, were purchased from wholesale and retail fish markets in each calendar month of the year. These fish were usually collected in water depths of 30 to 100 m. In addition, a wide range of sizes and life cycle stages of *C. rubescens* were collected by rod and line fishing and
spearfishing during the spawning period in 2002 (see Results). Additional opportunistic samples were obtained from staff of the Department of Fisheries Western Australia, who were working at the Abrolhos Islands. Details of the habitats sampled and the methods of sampling the Abrolhos Islands are given in Table 2.1.

2.5 Environmental and fish measurements

Water temperature (°C) and salinity were recorded in the water column at each site on each sampling occasion using a Yellow Springs Instruments YSI-30 salinity and conductivity meter. The water depth at each site was also recorded. The total length (TL) and wet weight (W) of each retained fish of each species were recorded to the nearest 1 mm and 0.1 g, respectively.
Table 2.1. Period and methods of sampling the different life cycle stages of the five species of tuskfish in Shark Bay and the Abrolhos Islands and the locations and habitats from which those species were obtained. Figure 2.1 shows location of sampling locations in Shark Bay.

<table>
<thead>
<tr>
<th>Species</th>
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<th>Life cycle stage</th>
<th>Location</th>
<th>Habitat</th>
</tr>
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<tr>
<td>Choerodon rubescens</td>
<td>2000-2003 Rod and line fishing/ spearfishing</td>
<td>Juvenile</td>
<td>South Passage, Shark Bay; Abrolhos Islands.</td>
<td>Limestone reefs with coral communities and/or light to moderate algal-cover.</td>
</tr>
<tr>
<td></td>
<td>2000-2003 Commercial line fishing/ rod and line fishing/ spearfishing</td>
<td>Adult</td>
<td>Oceanic waters of Shark Bay, around Dirk Hartog, Dorre and Bernier Islands; Abrolhos Islands.</td>
<td>Limestone reefs with coral communities and/or light to moderate algal-cover.</td>
</tr>
<tr>
<td>Choerodon schoenleinii, Choerodon cyanodus, Choerodon cauteroma, Choerodon cephalotes</td>
<td>1999-2000 Trawling/ rod and line fishing/ spearfishing</td>
<td>Juvenile</td>
<td>Eastern and western gulfs and oceanic waters of Shark Bay.</td>
<td>Seagrass beds, limestone reefs with coral communities and/or light to moderate algal-cover.</td>
</tr>
<tr>
<td></td>
<td>2000-2003 Rod and line fishing/ spearfishing</td>
<td>Adult</td>
<td>Eastern and western gulfs and oceanic waters of Shark Bay.</td>
<td>Limestone reefs with coral communities and/or light to moderate algal-cover.</td>
</tr>
</tbody>
</table>
Chapter 3

3.0 Reproductive biology of *Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens* and *Choerodon schoenleinii* in Shark Bay
3.1 Introduction

Reliable data on the reproductive biology of fish species are essential for effectively managing the fisheries for those species. For example, knowledge of the spawning period of a species can facilitate the protection of its stocks by imposing bans on their capture when they are spawning or through the permanent or semi-permanent closure to fishing of areas in which spawning aggregations occur (Sadovy, 1996b; Jennings et al., 2001; Jones et al., 2002). Such knowledge is also required to enable the acquisition of data from that time of year for determining the length at maturity of a species, which is commonly used in setting an appropriate minimum legal length for capture (Beverton and Holt, 1957; Sadovy, 1996b; Hill, 1990; Winstanley, 1990).

Furthermore, elucidation of whether a species is a single or multiple spawner and the estimation of its fecundity is dependent on data derived from samples collected during its spawning period (de Vlaming, 1983; Hunter et al., 1992).

Management of hermaphroditic species requires information on the type(s) of hermaphroditism exhibited, such as protogyny or protandry, and at what size and/or age that sex change occurs (Bannerot et al., 1987; Sadovy, 1996b). Data on the sex ratios of a hermaphroditic species provide information on whether the populations of that species are biased towards one sex, as is usually the case for protogynous and protandrous hermaphrodites (Choat and Robertson, 1975; Sadovy, 1996b) and thus whether maximum size limits for capture, for example, could be used to protect the large fish of such species, which are likely to be of one sex (Levin and Grimes, 2002). Such limits are in place for the protandrous barramundi *Lates calcarifer* and protogynous serranids in Western Australia (Anon., 2002; Anon., 2003c). Since fishing effort is usually directed at large fish, heavy sex-selective fishing pressure could have deleterious effects on a population if that sex occurs in low abundance (Bannerot et al., 1987; Buxton, 1993; Sadovy, 1996b; Vincent and Sadovy, 1998).
Several criteria must be met before a species can be unequivocally regarded as an hermaphrodite. A species can only be considered to be a functional hermaphrodite if a substantial proportion of its individuals function as first one sex and then the other sex at some stage during their life (Sadovy and Shapiro, 1987). Although bimodality in length-frequency distributions of the two sexes indicates that a species may be a protogynous or protandrous hermaphrodite, such bimodality can be produced by other factors, *e.g.* differences in growth rates, mortality or migration (Sadovy and Shapiro, 1987). Thus, it is necessary to examine the gonads of such species histologically to confirm whether any marked bimodality in the length-frequency distributions is a result of that species undergoing a change in sex with increasing body size (Reinboth, 1970; Sadovy and Shapiro, 1987).

Sadovy and Shapiro (1987) pointed out that, for protogynous species, an histological study will demonstrate that the gonads of a fish are transitional, *i.e.* it is changing sex, when they contain proliferating sperm cells and degenerating oocytes. Protogynous species can be classified as either monandric protogynous hermaphrodites or diandric protogynous hermaphrodites and can be distinguished by a thorough histological examination of the testes of their males (Reinboth, 1967; 1970; *cf.* Shapiro and Rasotto, 1993). Monandric protogynous hermaphrodites have only one type of male, *i.e.* secondary males, which are derived from functional adult females via sex change. The testes of these secondary males possess a membrane-lined ovarian lumen and, when ripe, contain sperm sinuses in their outer walls. Diandric protogynous hermaphrodites have two types of males, *i.e.* primary and secondary males. Primary males develop from larval juveniles and contain testes that have a single sperm duct and do not contain a membrane-lined lumen or sperm sinuses, while the testes of the secondary males have the same characteristics as those of monandric protogynous hermaphrodites (Reinboth, 1970; Sadovy and Shapiro, 1987).
Information on the biology of the blue tuskfish *Choerodon cyanodus* is restricted to that derived by Choat (1969) from catches of a small number of individuals of this species on the Great Barrier Reef in eastern Australia. As one of the four males collected by Choat (1969) was identified as a primary male from an histological analysis of its testes, *i.e.* its testes presumably had a singular sperm duct, but did not contain a lumen (Sadovy and Shapiro, 1987), he concluded that *C. cyanodus* is a diandric protogynous hermaphrodite. Since four of the females collected in August contained resting ovaries and four of the females from January and February were undergoing gonadal development, this species presumably spawns in summer on the Great Barrier Reef (Choat, 1969).

Nardi (1999) demonstrated, through an histological examination of the gonads of a wide size range of individuals, that the baldchin groper *Choerodon rubescens* is a protogynous hermaphrodite in the Abrolhos Islands. However, he suggested that further work was required to determine whether this species is monandric or diandric. Based on fish abundance surveys and visual observations of the behaviour of individuals during their spawning period in the Abrolhos Islands, Nardi (1999) suggested that *C. rubescens* forms spawning aggregations and that its males maintain a harem at spawning time. The minimum length of *C. rubescens* at maturity was regarded by Nardi (1999) as corresponding to the length of the smallest fish, *i.e.* 290 mm, that had a relatively large gonadosomatic index, in a small sample of fish that were collected during the spawning period and covered a wide length range. No attempt was made to apply logistic regression analysis to the proportions of sexually mature fish at each length to determine the length at which 50% of individuals of each sex reach maturity. Furthermore, no estimates have been made of either the age at maturity or fecundity of *C. rubescens*. Nardi (1999) demonstrated, from the distribution of the diameters of oocytes in ovaries of individual females collected during the spawning period, that
oocyte development in *C. rubescens* was asynchronous and thus suggested that this species is a multiple spawner.

The blackspot tuskfish *Choerodon schoenleinii* was shown by Ebisawa *et al.* (1995), through the use of histological studies of the gonads of fish of a wide length range, to be a monandric protogynous hermaphrodite in Japan and that transitional individuals contained “undelimited type 2” gonads, as described by Sadovy and Shapiro (1987). These transitional gonads comprise both ovarian and testicular tissue, which are intermixed and not separated by connective tissue. Since the ovaries of some female *C. schoenleinii* contained hydrated oocytes between late autumn and early summer, this species spawns over many months in Japan. Using a similar approach to that of Nardi (1999), *i.e.* using the relationship between body length and gonadosomatic index of individual fish during the spawning season, Ebisawa *et al.* (1995) suggested that *C. schoenleinii* starts to mature at ca 240 mm. The reproductive biology of the bluespotted tuskfish *Choerodon cauteroma* has not been studied.

The first aim of this chapter was to test the hypothesis that, as is often the case with labrids, *C. cyanodus, C. cauteroma, C. rubescens* and *C. schoenleinii* are all protogynous hermaphrodites in Shark Bay and that, if this is proved correct, determine whether each is monandric or diandric. The second aim was to determine the likely spawning strategy of each of these species in Shark Bay based on the size compositions of its females and males, sexual dichromatism, sex ratios and gonad weights and length and age at maturity and sex change, and also the timing and locations of spawning. Focus has also been placed on ascertaining whether they each have determinate or indeterminate fecundity *sensu* Hunter *et al.* (1992), *i.e.* whether or not the number of eggs that are capable of being released by individuals females is determined prior to the onset of the spawning period, and thus whether they are multiple spawners, *i.e.* individual females release eggs on more than one occasion.
3.2 Materials and Methods

The gonads of each individual of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* were removed and weighed to the nearest 0.01 g. On the basis of their macroscopic characteristics, the gonads of each fish that apparently contained exclusively either ovarian or testicular tissue was allocated to one of the following six maturity stages, which were modified from the scheme of Laevastu (1965): I = virgin/resting, II = developing, III = ripe, IV = spawning, V = spent, VI = recovering (Table 3.1, Results). However, it was often not possible to distinguish macroscopically between gonads at stages III and IV in the case of either ovaries or testes (see Table 3.1, Results). Thus, since several of the ovaries and testes at these two stages were not sectioned histologically, the data on the numbers of stage III and IV gonads in individual months were pooled in the case of both ovaries and testes.

In a few fish of intermediate size between the “average” sizes of females and males, the gonads, at the macroscopic level, did not have the appearance of either typical ovaries or testes. These gonads were shown by histology to contain both ovarian and testicular material and have thus been considered to represent a transitional stage between ovary and testis (see Results).

The gonads of at least 20 individuals of each species, covering a wide size range and including small juveniles and large adults from each calendar month, together with the gonads of all fish identified macroscopically as transitional, were placed in Bouin’s fixative for 24 - 48 h and dehydrated in a series of increasing concentrations of ethanol. The mid-regions of each gonad and, in some cases, also of their anterior and posterior portions, were embedded in paraffin wax, cut into 6 µm thick transverse sections and stained with Mallory’s trichrome. The histological characteristics of each macroscopic stage in the development of the ovaries of the four species of tuskfish are recorded in Table 3.2 in the Results.
The circumferences of 100 oocytes (sectioned through their nuclei) in stage IV ovaries of two individuals of each species, were measured to the nearest 0.01 µm (Hunter and Macewicz, 1985; Hunter et al., 1985). Measurements were made using Leica IM1000 computer imaging software, which obtained an image via a Leica DC300 digital camera attached to a Leica Mz7.5 dissecting microscope. The circumferences were then used to calculate the diameters of the oocytes.

The gonadosomatic index (GSI) of individual fish was calculated from the equation \(\frac{W_1}{W_2 - W_1} \times 100\), where \(W_1\) = wet weight of the gonad and \(W_2\) = wet weight of the whole fish and thus \(W_2 - W_1\) = somatic weight. Since all four species of tuskfish were shown to be protogynous hermaphrodites (see results), GSIs were calculated for females \(\geq L_{50m}\), i.e. the length at which 50% of females reach sexual maturity, and for all male fish. For the same reasons, the lengths and ages at sexual maturity were determined only for their females (see below).

**Lengths and ages at sexual maturity**

During the main spawning periods of each of the four species of tuskfish, which were considered to represent those months where \(\geq 50\%\) of females of each species contained ovaries that were at stages II-VI (see Fig. 3.15), each female was classified, for the purposes of determining the lengths and ages at sexual maturity, as either sexually immature or sexually mature, based on the stage of development of its ovaries. Those females that were either virgins or contained ovaries that were resting, i.e. stage I, were considered sexually immature, while those with ovaries that were developing, i.e. stage II, were destined to become ripe and spawn in that spawning season and were thus considered to be sexually mature (see Fig. 3.15). Those females containing ovaries that were either ripe, spawning, spent or recovering, i.e. stages III-VI, were also considered sexually mature. The lengths \((L_{50m})\) and ages \((A_{50m})\) of females at sexual maturity were
determined using a modified form of the logistic equation. The logistic model, normally described as \( P = \frac{1}{1 + \exp[-(a + bL)]} \), has been reparameterised into the form

\[ P_L = \frac{P_{\text{max}}}{1 + \exp[-\ln(19)(L-L_{50m})/(L_{95m}-L_{50m})]}, \]

as the parameters \( L_{50m} \) and \( L_{95m} \) are likely to be more meaningful to the biologist than the parameters \( a \) and \( b \) of the normal logistic equation. \( P_L \) = the predicted proportion of mature females at a particular total length \( L \), \( P_{\text{max}} \) is the average maximum proportion of mature females and is restricted to values between 0 and 1, \( L_{50m} \) and \( L_{95m} \) = the corresponding lengths at which 0.5 and 0.95 of the \( P_{\text{max}} \) are reached (referred to as the lengths at which 50 and 95% of female fish are sexually mature), respectively, and \( \ln = \) the natural logarithm. Note that length (\( L \)) is substituted with age (\( A \)) in the modified logistic equation for determining the \( A_{50m} \) and the procedure for determining the ages of individual fish is described in Chapter 4.

The data for the lengths of the individuals of each species and their corresponding maturity status, i.e. sexually immature or sexually mature, were randomly resampled and analysed to create 1000 sets of bootstrap estimates for the parameters of the logistic regression and estimates of the probability of maturity within the range of recorded lengths. The 95% confidence limits of the \( L_{50m} \)s and \( L_{95m} \)s were derived using this resampling technique, taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling analysis. The point estimates of each parameter and of each probability of maturity at the specified length were taken as the medians of the bootstrap estimates.

**Lengths and ages at sex change**

The prevalences of females, transitional individuals and males in the total catches of each tuskfish species were used to determine the length and age at which each species changes sex, i.e. \( L_{50c} \) and \( A_{50c} \). For the purposes of determining the \( L_{50c} \) and \( A_{50c} \), the small number of transitional individuals were considered to have already
changed sex from female to male and thus the data for their numbers and those of males were pooled. Since the proportion of individuals that had changed sex eventually reached 1 in the upper length and upper age classes of each species, the following form of the logistic equation was employed: \( P_L = \frac{1}{1 + e^{[-\ln(19)(L-L_{50c})/(L_{95c} - L_{50c})]}} \), where \( P_L \) = the predicted proportion of individuals that have changed sex at a particular length \( L \), \( L_{50c} \) and \( L_{95c} \) = the corresponding lengths at which 0.5 and 0.95 of the individuals in the population have changed sex (referred to as the lengths at which 50 and 95% of fish have changed sex), respectively, and \( \ln \) = the natural logarithm. Length \( (L) \) is substituted by age \( (A) \) in this equation for determining age at sex change \( (A_{50c}) \). The logistic regression analysis was carried out using the same method as that described above for length and age at maturity.

3.3 Results

**Macroscopic and histological characteristics of gonads**

At a macroscopic level, the morphological characteristics of the vast majority of the paired gonadal lobes of *Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens* and *Choerodon schoenleinii* could be clearly classified as either ovaries or testes (Table 3.1). An histological examination of a large subsample of those gonads demonstrated that, apart from a very few recovering (stage VI) gonads, such macroscopic classification was valid. Those few recovering gonads that contained both ovarian and testicular tissue were thus assumed to belong to fish that were at the beginning or end of sex change. The gonads of a few fish were flattened, flaccid, red to brown in colour and contained a variable number of white longitudinal striations, and occupied approximately one half to two thirds of the length of the body cavity, and thus could not be readily classified as either ovaries or testes. Histological studies demonstrated that these gonads contained substantial amounts of both ovarian and
testicular tissue and they were thus classified as transitional (see later). Fish with this type of gonad were assumed to be changing sex.

The macroscopic and histological characteristics of the ovarian lobes at each of the six macroscopic stages of development, as described in Tables 3.1 and 3.2, were essentially the same for each of the four species of tuskfish. The gonads of small individuals of the four tuskfish species, *i.e.* ca 40–70 mm in length, were always at stage I (Table 3.1). These gonads consisted solely of ovarian tissue that comprised developing oogonia and chromatin nucleolar oocytes (Fig. 3.1a). The gonads of larger juveniles (virgins) and the resting ovaries of adult females, *i.e.* stage I, had similar macroscopic and histological characteristics, both containing chromatin nucleolar and perinucleolar oocytes, with oogonia sometimes being visible (Tables 3.1, 3.2; Fig. 3.1b). An examination of histological sections of what were macroscopically designated as developing, ripe, spawning, spent and recovering ovaries, *i.e.* ovaries at stages II–VI, demonstrated that they contained only ovarian tissue (Tables 3.1, 3.2). Stage IV ovaries could only be separated macroscopically from stage III ovaries when hydrated oocytes were visible through the ovarian wall. When hydrated oocytes were not visible, stage IV ovaries could only be distinguished from stage III ovaries by examining histological sections, which, in stage IV ovaries, revealed the presence of either migratory nucleus oocytes and/or post-ovulatory follicles, which provides evidence of approaching or recent spawning (Tables 3.1, 3.2; Hunter and Goldberg, 1980; Hunter *et al.*, 1986; Mayer *et al.*, 1988).

Although no transitional *C. cyanodus* or *C. rubescens*, *i.e.* individuals that were presumably changing sex, were caught in Shark Bay, the macroscopic and histological characteristics of the transitional gonads of the *C. cauteroma* and *C. schoenleinii* collected from Shark Bay and of *C. rubescens* from the Abrolhos Islands were essentially the same. Some of the transitional gonads contained predominantly ovarian
tissue, that consisted mainly of chromatin nucleolar and perinucleolar oocytes, and a few small areas of testicular tissue, comprising spermatogonia, spermatocytes and, in

Table 3.1. Characteristics of the macroscopic stages in the development of the ovaries and testes of Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens and Choerodon schoenleinii. Scheme adapted from Laevastu (1965).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Ovaries</th>
<th>Testes</th>
</tr>
</thead>
<tbody>
<tr>
<td>I - Virgin/*resting * “virgin” only applicable to females</td>
<td>Ovaries occupy up to one half length of body cavity. String-like in very small juveniles to essentially rounded in larger juveniles and resting ovaries. Translucent, pale yellow to pink in colour. Very small oocytes visible through ovary wall of larger stage I ovaries under low power magnification.</td>
<td>Testes occupy one third to half length of body cavity. Essentially flat, although may be triangular in cross-section towards cloaca, translucent, pinkish in colour.</td>
</tr>
<tr>
<td>II - Developing</td>
<td>Ovaries one third to two thirds length of body cavity and rounded. Translucent, pinkish and with some small white oocytes visible through ovary wall to essentially opaque, pinkish to cream in colour, granular in appearance and many white oocytes visible through ovary wall.</td>
<td>Testes one third to half length of body cavity. Flat to partially swollen, tapering towards anterior end. Partially translucent with some cream coloured areas to opaque and cream in colour in more developed testes.</td>
</tr>
<tr>
<td>III - Ripe</td>
<td>Ovaries occupy two thirds to full length of body cavity. Rounded and full, opaque and cream to yellow in colour. Granular appearance with many tightly-packed large white to yellow oocytes visible to the naked eye.</td>
<td>Testes one to two thirds length of body cavity. Swollen, full in appearance, almost triangular in shape at posterior end and tapering towards anterior end. Opaque and cream to white in colour.</td>
</tr>
<tr>
<td>IV - Spawning</td>
<td>Ovaries occupy two thirds to full length of body cavity. Rounded or may be slightly flaccid, opaque and cream to yellow in colour or becoming slightly reddish. Granular appearance with hydrated oocytes and large white to yellow eggs visible through ovary wall. May also contain spaces between oocytes.</td>
<td>Testes one to two thirds length of body cavity. Swollen, full in appearance, almost triangular in shape at posterior end and tapering toward anterior end. Opaque and cream to white in colour. Sperm rarely extruded under pressure. May have brown tinges at anterior ends.</td>
</tr>
<tr>
<td>V - Spent</td>
<td>Ovaries two thirds to full length of body cavity. Ovary reddish with brown tinges at anterior ends, flaccid, but not completely empty. Many to some opaque white to yellow oocytes may be visible through ovary wall.</td>
<td>Testes one to two thirds length of body cavity. Flaccid, cream to reddish in colour, brown tinges at anterior ends of lobes.</td>
</tr>
<tr>
<td>VI - Recovering</td>
<td>Ovaries half to two thirds length of body cavity. Flaccid, reddish to brown in colour. A few large opaque eggs sometimes visible through the ovary wall.</td>
<td>Testes one to two thirds length of body cavity. Flaccid, essentially flat and red to brown in colour.</td>
</tr>
</tbody>
</table>

Table 3.2 (overleaf). Histological characteristics of the macroscopic stages in the development of the ovaries of Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens and Choerodon schoenleinii. Terminology for oocyte stages follows Wallace and Selman (1981).
<table>
<thead>
<tr>
<th>Macroscopic Stage</th>
<th>Histological section</th>
<th>Histological characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>I - Virgin/ resting</td>
<td><img src="image1.png" alt="Image" /></td>
<td>Ovarian lamellae highly organised. Only oogonia, chromatin nucleolar (cn) and perinucleolar (p) oocytes present. Scale = 100 µm.</td>
</tr>
<tr>
<td>II - Developing</td>
<td><img src="image2.png" alt="Image" /></td>
<td>Highly organised lamellae. Oogonia, chromatin nucleolar, perinucleolar (p) and cortical alveolar (ca) oocytes present. Contains few to many cortical alveolar oocytes at all stages of development. Late stage II ovaries contain some yolk granule oocytes. Scale = 150 µm.</td>
</tr>
<tr>
<td>III - Ripe</td>
<td><img src="image3.png" alt="Image" /></td>
<td>Previtellogenic and vitellogenic oocytes present. Yolk granule (y) and cortical alveolar oocytes (ca) abundant. Scale = 400 µm.</td>
</tr>
<tr>
<td>IV - Spawning</td>
<td><img src="image4.png" alt="Image" /></td>
<td>Yolk granule (y) and cortical alveolar (ca) oocytes abundant in early stage IV to few in late stage IV. Migratory nucleus oocytes and/or hydrated oocytes (h) and/or post ovulatory follicles present. Scale = 300 µm.</td>
</tr>
<tr>
<td>V - Spent</td>
<td><img src="image5.png" alt="Image" /></td>
<td>Ovary disorganised, containing chromatin nucleolar (cn) and perinucleolar oocytes (p) and remnant cortical alveolar (ca) and/or yolk granule (y) oocytes undergoing atresia. Scale = 150 µm.</td>
</tr>
<tr>
<td>VI - Recovering</td>
<td><img src="image6.png" alt="Image" /></td>
<td>Ovarian lamellae disorganised. Contains predominantly chromatin nucleolar and perinucleolar oocytes (p). Connective tissue (t) and/or few remnant cortical alveolar and/or yolk granule oocytes in late stages of atresia (a) present. Scale = 150 µm.</td>
</tr>
</tbody>
</table>
Figure 3.1. Histological sections of gonads representing (a, b) females, (c, d) transitional individuals and (e) males of the four species of tuskfish at low (left column) and high (right column) magnification, showing development from (a) small juvenile ovaries to (b) larger juvenile or resting adult ovaries and (c–e) subsequent gonadal changes from early transitional gonad to resting male secondary testes. Low magnification scale bars: (a) 250 mm; (b, c) 1 mm; (d, e) 500 mm; high magnification scales bars: (a, d, e) 20 mm; (b, c) 50 mm. c, chromatin nucleolar oocyte; d, degenerating oocyte; g, oogonia; l, lumen, o, ovarian tissue; p, perinucleolar oocyte; sc, spermatocyte; sg, spermatogonia; st, spermatid; t, testicular tissue.
some cases, spermatids, that were each typically arranged in crypts (Fig. 3.1c).

Although many of the oocytes in those gonads did not appear to be degenerating, the presence of some testicular tissue suggests that these gonads were in the early stages of changing from ovaries to testes. Some of the other transitional gonads contained substantial amounts of ovarian and testicular tissue, the former consisting predominantly of degenerating chromatin nucleolar and perinucleolar oocytes and the latter of spermatogonia and spermatocytes and sometimes spermatids (Fig. 3.1d). These gonads were thus at an intermediate stage of changing to testes. Finally, some transitional gonads contained predominantly testicular tissue, comprising mainly spermatogonia and spermatocytes and sometimes also spermatids, and a few to several scattered degenerating chromatin nucleolar and perinucleolar oocytes. These gonads are assumed to represent an advanced stage of transition from ovaries to testes (not shown).

Transitional gonads at the early, intermediate and advanced stages of changing from ovaries to testes always retained the membrane-lined ovarian lumen (Fig. 3.1c,d). Neither cortical alveolar nor vitellogenic oocytes, that were atretic or non-atretic, were observed in transitional gonads.

Histological sections of the testes of a subsample of 37 male *C. cyanodus*, 36 male *C. cauteroma*, 8 male *C. rubescens* and all of the seven male *C. schoenleinii* caught demonstrated that those testes retained the lamellae, membrane-lined lumen and wall of the ovary after they had changed from ovaries to testes (Fig. 3.1e). Resting testes, *i.e.* stage I, contained spermatogonia, spermatocytes and sometimes spermatids that each generally occurred in small crypts (Fig. 3.1e, Table 3.1), while developing testes, *i.e.* stage II, always contained the above three sperm cell types. Histological sections of stage III and IV testes demonstrated that, by these stages, the lumen had become greatly reduced in size and the lamellae of the testes were tightly packed into large segments (Fig. 3.2a). Stage III testes contained predominantly spermatocytes,
spermatids and spermatozoa that were located in crypts and often surrounded by connective tissue (Fig. 3.2b,c). Spermatogonia were either rare or absent in these testes. In males with stage IV testes, large aggregations of spermatids and/or spermatozoa were often visible, generally towards the centre of the segments of the testes and also in
sperm sinuses in the outer wall of the testes (Fig. 3.2d). The connective tissue surrounding many of the crypts was no longer visible and had presumably broken down, thus allowing sperm to be transported towards the sinuses in the testis wall (Fig. 3.2d-f). Sperm were never observed in the central lumen of the testes.

**Relationship between lengths and ages at maturity and sex change**

Length-frequency distributions for each of the four species of tuskfish demonstrated that the lengths of all but two males of both *C. cyanodus* and *C. cauteroma* and those of all males of *C. rubescens* and *C. schoenleinii* were greater in length than their $L_{95m}$ (see later; Figs 3.3a-3.6a). The minimum and maximum lengths of female *C. cyanodus* (39 and 315 mm), *C. cauteroma* (58 and 372 mm), *C. rubescens* (70 and 574 mm) and *C. schoenleinii* (72 and 626 mm) fell below those of their males, *i.e.* 138 and 382 mm, 219 and 424 mm, 500 and 649 mm, 521 and 805 mm for each of the four species, respectively (Figs 3.3a-3.6a).

The age-frequency distributions of *C. cauteroma*, *C. rubescens* and *C. schoenleinii* demonstrated that the males of each of those species were greater in age than their respective $A_{95m}$ (see later; Figs 3.4b-3.6b). The age ranges of the females of those three species were 0.2-10.6, 0.4-12.2 and 0.3-10.6 years old, respectively, while those of their males were 3.4-14.8, 7.8-16.4 and 6.9-16.2 years old, respectively. However, the ages of ca 27% of the males of *C. cyanodus* were less than the $A_{95m}$ (4.4 years old; see later) of that species (Fig. 3.3b). The age ranges of the females and males of *C. cyanodus* were 0.5-8.2 and 2.4-12.5 years, respectively.

**Sexual dichromatism**

*Choerodon cyanodus* did not display any sexual dichromatism, *i.e.* change in colour, after it changed from female to male (Fig. 3.7a). The characteristic colour
Figure 3.3. *Choerodon cyanodus*. (a) Length and (b) age distributions for immature (■) and mature (□) females during the spawning period (above reference line) and for all females (■) and males (□) (below reference line) and lengths and ages at 50 and 95% sexual maturity ($L_{50m}$, $A_{50m}$) and sex change ($L_{50c}$, $A_{50c}$) ± 95% CI (represented by red line and surrounding blue shading) derived from logistic regression analysis.
Figure 3.4. *Choerodon cauteroma*. (a) Length and (b) age distributions for immature (●) and mature (●) females during the spawning period (above reference line) and for all females (■), transitional individuals (■) and males (■) (below reference line) and lengths and ages at 50 and 95% sexual maturity ($L_{50m}$, $A_{50m}$) and sex change ($L_{50c}$, $A_{50c}$) ± 95% CI (represented by red line and surrounding blue shading) derived from logistic regression analysis.
Figure 3.5. Choerodon rubescens. (a) Length and (b) age distributions for immature (□) and mature (■) females during the spawning period (above reference line) and for all females ( □ ), and males (■) (below reference line) and lengths and ages at 50 and 95% sexual maturity ($L_{50m}$, $A_{50m}$) and sex change ($L_{50c}$, $A_{50c}$) ± 95% CI (represented by red line and surrounding blue shading) derived from logistic regression analysis.
Figure 3.6. *Choerodon schoenleinii*. (a) Length and (b) age distributions for immature (■) and mature (□) females during the spawning period (above reference line) and for all females (▲), transitional individuals (■) and males (□) (below reference line) and lengths and ages at 50 and 95% sexual maturity ($L_{50m}$, $A_{50m}$) and sex change ($L_{50c}$, $A_{50c}$) ± 95% CI (represented by red line and surrounding blue shading) derived from logistic regression analysis.
Figure 3.7. Photographs of males (above) and females (below) of (a) *Choerodon cyanodus* and (b) *Choerodon cauteroma.*
patterns of this species, such as the white patch just below the posterior end of the
dorsal fin and the dark bands across its back, were displayed to varying degrees and that
variation was not related to the sex of the individual. The other three species of tuskfish
exhibited varying degrees of sexual dichromatism. *Choerodon cauteroma* exhibited the
most marked change in colour, with the females being moderate to bright orange overall
and the males usually being pale cream to grey and with the blue striping on the caudal
fin and brown bands between the cheek and pectoral fin being more distinct (Fig. 3.7b).
Female *C. rubescens* ranged in colour from a dark brown to a greyish-brown and the
males were usually a pale grey-brown (Fig. 3.8a). Some medium-sized female fish that
were caught in deep water, *i.e.* > ca 20 m, were pale pink to bright orange in colour
(Fig. 3.8b). The females of *C. schoenleinii* ranged in colour from an orange to brown or
green mottled colour as a small juvenile to an overall blue-green or dark brown in larger
females (Fig. 3.9a, b). Male *C. schoenleinii* ranged in colour from a bright blue-green to
a pale cream. The overall colour of the four tuskfish species often changed to match the
overall colour of the substrate over which they were observed.
Figure 3.8. Photographs of (a) female (above) and male (below) *Choerodon rubescens* and (b) pink and brown colour variations of female *C. rubescens*. 
Figure 3.9. Photographs of (a) a juvenile and (b) an adult female *Choerodon schoenleinii*. 
Sex ratios

The ratio of females to males in samples of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* collected by all methods and specifically of those collected by line fishing and which were $\geq L_{50m}$ varied greatly among these species (Table 3.3). The ratio was equal to or close to parity for *C. cyanodus*, but favoured females in the case of each of the other three species and particularly *C. schoenleinii*.

The ratios of females to males of 9.6:1 for *C. rubescens* and of 153:1 for *C. schoenleinii* that were $\geq$ their respective $L_{50m}$s favoured females far more greatly than the corresponding sex ratios of 5.6:1 and 31.1:1 recorded for individuals of these two species that were caught by rod and line angling and were $\geq$ their minimum legal length (MLL) of 400 mm (Table 3.3).

<table>
<thead>
<tr>
<th></th>
<th>Choerodon cyanodus</th>
<th>Choerodon cauteroma</th>
<th>Choerodon rubescens</th>
<th>Choerodon schoenleinii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall (all methods)</td>
<td>1.0:1 (805)</td>
<td>2.8:1 (955)</td>
<td>12.3:1 (453)</td>
<td>93:1 (658)</td>
</tr>
<tr>
<td>Adults, <em>i.e.</em> $\geq L_{50m}$ (all line fishing methods)</td>
<td>0.8:1 (671)</td>
<td>1.9:1 (653)</td>
<td>9.6:1 (349)</td>
<td>153:1 (308)</td>
</tr>
<tr>
<td>$\geq$ MLL (400 mm) rod and line sampling</td>
<td>None caught above MLL</td>
<td>No MLL</td>
<td>5.6:1 (139)</td>
<td>31:1 (63)</td>
</tr>
<tr>
<td>$\geq$ MLL (400 mm) commercial line fishing</td>
<td>Not commercially fished in Shark Bay</td>
<td>Not commercially fished in Shark Bay</td>
<td>1:1 (24)</td>
<td>Not commercially fished in Shark Bay</td>
</tr>
</tbody>
</table>

Table 3.3. Ratio of females to males in samples of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* from Shark Bay. Sample sizes shown in parentheses.
Lengths and ages at maturity

The months during which ≥ 50% of the ovaries of female \( C. \) cyanodus, \( C. \) cauteroma, \( C. \) rubescens and \( C. \) schoenleinii were at stages II-VI, and for which the data could thus be used to determine the lengths and ages at sexual maturity, were November to February, May to November, August to December and October to November, respectively (see Fig. 3.13). The minimum lengths at which sexually mature females, \textit{i.e.} females that contained ovaries at stages II-VI during the spawning period, of \( C. \) cyanodus, \( C. \) cauteroma, \( C. \) rubescens and \( C. \) schoenleinii were recorded during their spawning periods were 106, 182, 230 and 245 mm, respectively. The lengths at which 50% of the females of \( C. \) cyanodus, \( C. \) cauteroma, \( C. \) rubescens and \( C. \) schoenleinii reached sexual maturity, \textit{i.e.} their \( L_{50m} \)s, were 129, 196, 274 and 253 mm, respectively (Fig. 3.10a-d, Table 3.4).

The youngest sexually mature females of \( C. \) cyanodus, \( C. \) cauteroma, \( C. \) rubescens and \( C. \) schoenleinii were one, two, two and three years old, respectively (Fig. 3.10a-d). The ages at sexual maturity (\( A_{50m} \)) of these four species were 2.3, 2.0, 2.7 and 3.5 years old, respectively (Fig. 3.10a-d; Table 3.5).

Lengths and ages at and the timing of sex change

Transitional individuals of \( C. \) cauteroma and \( C. \) schoenleinii, but not of \( C. \) cyanodus and \( C. \) rubescens, were caught in Shark Bay. The eight transitional individuals of \( C. \) cauteroma ranged from 266 to 338 mm in length and from 5.7 to 8.1 years in age and thus belonged to the intermediate size and age classes of this species. Five of the transitional \( C. \) cauteroma were caught in either July or August and a further one in each of September, October and November. The single transitional \( C. \) schoenleinii, which was 526 mm in length and 7.4 years old, was caught in April.
Figure 3.10. The proportions of sexually mature females (○) in each length and age class for (a) *Choerodon cyanodus*, (b) *Choerodon cauteroma*, (c) *Choerodon rubescens* and (d) *Choerodon schoenleinii* during their spawning periods, with the curve predicted using logistic regression analysis of the length (left-hand side) or age (right-hand side) and status (immature or mature) of individual fish. Points for $L_{50m}$ and $A_{50m}$ ± 95% C.I.s shown (●). Sample sizes (n) shown on each figure.
The smallest males of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* in the samples from Shark Bay were 138, 219, 500 and 521 mm, respectively. The proportions of males of *C. cyanodus* and *C. cauteroma* in individual length classes increased progressively until they each reached one in their upper length classes of 320-329 and 380-389 mm, respectively, while those of *C. rubescens* increased more rapidly to reach one by the 580-599 mm length class (Fig. 3.11a-c). The *L*\textsubscript{50c} of *C. cyanodus*, *C. cauteroma* and *C. rubescens* were 221, 310 and 545 mm, respectively (Fig. 3.11a-d, Table 3.4). The small number of males of *C. schoenleinii*, ranged in length from 521 to 805 mm and the *L*\textsubscript{50c} was 556 mm (Fig. 3.11d).

The proportion of males in the individual age classes of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* increased from their first occurrence in their 2, 3, 6 and 7+ age classes, respectively, to one in their 9, 11, 13 and 12+ age classes, respectively (Fig. 3.11a-d). The *A*\textsubscript{50c} of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* were 4.2, 6.4, 10.5 and 10.4 years, respectively (Figs 3.11a-d; Table 3.5).
Figure 3.11. The proportions of transitional and male individuals (pooled) (●) in each length and age class for (a) *Choerodon cyanodus*, (b) *Choerodon cauteroma*, (c) *Choerodon rubescens* and (d) *Choerodon schoenleinii*, with the curve predicted using logistic regression analysis of the length (left-hand side) or age (right-hand side) and status (female or transitional and male pooled) of individual fish. Points for $L_{50c}$ and $A_{50c}$ ± 95% C.I.s shown (●). $n_f$ = number of females and $n_m$ = number of males and transitional individuals pooled.
Table 3.4. Lengths at sexual maturity ($L_{50m}$, $L_{95m}$, ± 95% CI; $P_{max}$ values ± 95% CI shown in parentheses below values for the $L_{50m}$) of females during the spawning periods and lengths at sex change ($L_{50c}$, $L_{95c}$, ± 95% CI) of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* in Shark Bay.

<table>
<thead>
<tr>
<th></th>
<th>Maturity</th>
<th>Sex change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$L_{50m}$ (mm)</td>
<td>Lower 95% CI (mm)</td>
</tr>
<tr>
<td><em>Choerodon cyanodus</em></td>
<td>128.7 (0.79)</td>
<td>110.2 (0.71)</td>
</tr>
<tr>
<td><em>Choerodon cauteroma</em></td>
<td>196.4 (0.78)</td>
<td>167.1 (0.70)</td>
</tr>
<tr>
<td><em>Choerodon rubescens</em></td>
<td>273.7 (0.94)</td>
<td>243.8 (0.86)</td>
</tr>
<tr>
<td><em>Choerodon schoenleinii</em></td>
<td>252.6 (0.46)</td>
<td>239.4 (0.39)</td>
</tr>
</tbody>
</table>
Table 3.5. Ages at sexual maturity ($A_{50m}, A_{95m}, \pm 95\% CI; P_{max}$ values ± 95% CI shown in parentheses) of females during the spawning periods and ages at sex change ($A_{50c}, A_{95c}, \pm 95\% CI$) of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* in Shark Bay.

<table>
<thead>
<tr>
<th></th>
<th>Maturity</th>
<th>Sex change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$A_{50m}$ (years)</td>
<td>Lower 95% CI (years)</td>
</tr>
<tr>
<td><em>Choerodon cyanodus</em></td>
<td>2.32 (0.99)</td>
<td>1.90 (0.84)</td>
</tr>
<tr>
<td><em>Choerodon cauteroma</em></td>
<td>2.01 (0.75)</td>
<td>1.89 (0.70)</td>
</tr>
<tr>
<td><em>Choerodon rubescens</em></td>
<td>2.70 (0.95)</td>
<td>2.28 (0.89)</td>
</tr>
<tr>
<td><em>Choerodon schoenleinii</em></td>
<td>3.45 (0.51)</td>
<td>3.06 (0.42)</td>
</tr>
</tbody>
</table>
Comparison of weights of ovaries and testes

The weights of ripe ovaries, \textit{i.e.} stage III, of individual females of each of the four species of tuskfish demonstrated a significant positive relationship with fish weight (Fig. 3.12a-d; Table 3.6). The positive relationships between the weights of stage III, \textit{i.e.} ripe, testes and total weights of individual males of \textit{C. cauteroma} and \textit{C. rubescens} were also significant (Fig. 3.12b, c; Table 3.6). Although the slope for the relationship between testes weight and body weight of \textit{C. schoenleinii} was not significantly different from zero (Table 3.6), only a few males of this species were obtained and their testes weights tended to increase with increasing fish length (Fig. 3.12d). The weights of the testes of individual males of \textit{C. cyanodus} did not change conspicuously with increasing fish weight and the slope of the relationship was not significantly different from zero. Furthermore, the very low $R^2$ demonstrated a poor relationship between testes weight and fish weight and the weights of the stage III testes of three male \textit{C. cyanodus} were far larger than those of all other males (Fig. 3.12a).

Water temperatures

Mean monthly water temperatures declined from their maxima of 27.5°C in late summer in both the eastern and western gulfs of Shark Bay to their minima of 15.8°C in the eastern gulf and 18.8°C in the western gulf in late winter (Fig. 3.13). Although mean monthly water temperatures followed a similar trend in the waters of South Passage, it was not as pronounced as those for the inner gulfs of Shark Bay. Thus, they ranged from a minimum of 21.1°C to a maximum of 24.9°C in early spring and late summer, respectively (Fig. 3.13).
Figure 3.12. Relationships between total weight and stage III ovaries (left-hand side) and stage III testes (right-hand side) for (a) *Choerodon cyanodus*, (b) *Choerodon cauteroma*, (c) *Choerodon rubescens* and (d) *Choerodon schoenleinii*. 
Table 3.6. Parameters (± 95% confidence intervals) for the linear regressions fitted to total weight of females against stage III ovary weight and total weight of males against stage III testes weight for *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii*. *p* value: * < 0.05; *** < 0.001.

<table>
<thead>
<tr>
<th>Females</th>
<th>Parameters</th>
<th>$a$</th>
<th>95% CI</th>
<th>$b$</th>
<th>95% CI</th>
<th>$R^2/p$ value</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choerodon cyanodus</td>
<td>0.011 (0.0004, 0.210)</td>
<td>2.353 (0.180, 4.527)</td>
<td>0.13*</td>
<td>33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Choerodon cauteroma</td>
<td>0.025 (0.016, 0.033)</td>
<td>-2.035 (-5.548, 1.478)</td>
<td>0.46***</td>
<td>45</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Choerodon rubescens</td>
<td>0.018 (0.015, 0.021)</td>
<td>5.306 (-0.208, 10.82)</td>
<td>0.46***</td>
<td>151</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Choerodon schoenleinii</td>
<td>0.023 (0.016, 0.030)</td>
<td>-4.652 (-13.62, 4.323)</td>
<td>0.62***</td>
<td>28</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Males</th>
<th>Parameters</th>
<th>$a$</th>
<th>95% CI</th>
<th>$b$</th>
<th>95% CI</th>
<th>$R^2/p$ value</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choerodon cyanodus</td>
<td>0.0011 (-0.0011, 0.0032)</td>
<td>1.412 (0.632, 2.192)</td>
<td>0.01</td>
<td>98</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Choerodon cauteroma</td>
<td>0.0024 (0.0012, 0.0036)</td>
<td>0.092 (-1.042, 1.227)</td>
<td>0.40***</td>
<td>27</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Choerodon rubescens</td>
<td>0.0025 (0.0015, 0.0034)</td>
<td>-2.154 (-5.668, 1.359)</td>
<td>0.48***</td>
<td>32</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Choerodon schoenleinii</td>
<td>0.0042 (-0.0033, 0.012)</td>
<td>-4.255 (-40.78, 32.27)</td>
<td>0.38</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 3.13. Mean monthly water temperatures ± 1 S.E. recorded at all sites sampled on each sampling occasion in the eastern (■) and western gulfs (□) of Shark Bay and in the oceanic waters (□) along the western boundary of Shark Bay. Data for each month of the year are pooled from 2000 to 2003.
Spawning periods of the four tuskfish species

Gonadosomatic indices

The mean monthly gonadosomatic indices (GSI) of female C. cauteroma, C. rubescens, C. schoenleinii and C. cyanodus ≥ L50m reached their maxima in sequentially later months, i.e. October, November, November and January, respectively (Fig. 3.14a-d). The mean monthly GSIs for female C. cauteroma rose from 1.5 in July to reach a peak of 3.4 in October and then declined precipitously to 0.4 in December and remained low during the following two months, before undergoing a modest rise (Fig. 3.14a). The mean monthly GSIs of the males of C. cauteroma rose earlier and remained high for longer than those of their females. They thus increased from 0.04 in February to 0.17 in June and then remained at between 0.16 and 0.20 from July to October, before declining progressively to 0.05 in January (Fig. 3.14a).

The mean monthly GSIs of female C. rubescens in Shark Bay rose sharply from 0.6 in July to 2.3 in September and then to a maximum of 2.7 in November, after which they declined precipitously to 1.1 in December and 0.8 in January and remained low, i.e. < 0.5, between February and June (Fig. 3.14b). The mean monthly GSIs of male C. rubescens rose from 0.09 in August to 0.19 in October, before declining steadily to 0.06 in January and then remaining at < 0.10 from February to June (Fig. 3.14b).

The mean monthly GSIs of female C. schoenleinii followed a similar trend to that of C. rubescens, and thus rose from a low of 0.3 in August to a maximum of 1.1 in November and then returned to 0.3 in January and subsequently remained below this level from February to June (Fig. 3.14c). Although few male C. schoenleinii were caught, the decline in the mean monthly GSIs of males from 0.49 in September to ≤ 0.21 in December, May and June follows a similar trend to that of the females of this species (Fig. 3.14c).
Figure 3.14. Mean monthly gonadosomatic indices ± 1 S.E. for females and males of (a) Choerodon cauteroma, (b) Choerodon rubescens, (c) Choerodon schoenleinii and (d) Choerodon cyanodus in Shark Bay using data for individuals ≥ their respective $L_{50}$ at sexual maturity. Sample sizes for each mean are shown above each mean.
The mean monthly GSIs of female *C. cyanodus* rose from 0.7 in October to 2.6 in December and then to 2.8 in January, after which they declined precipitously to 1.4 in February and 0.4 in March and subsequently remained below 0.7 from April to September (Fig. 3.14d). The mean monthly GSIs of male *C. cyanodus* followed similar trends to those of their females. After reaching a maximum of 0.74 in December, they fell precipitously to 0.46 in January, 0.37 in February and 0.15 in March and then remained at < 0.17 from April to October (Fig. 3.14d).

**Stages of development in ovaries**

Female *C. cauteroma*, that were ≥ *L*<sub>50m</sub> at sexual maturity and possessed developing ovaries, *i.e.* stage II, were first recorded in March (Fig. 3.15a; Table 3.2). Many of the female *C. cauteroma* collected from April to October contained ovaries that were either at the developing, mature or spawning stages, *i.e.* stages II or III/IV (Fig. 3.15a). Females with stage III/IV ovaries were most prevalent in September and October, when they represented 68% of all females with lengths ≥ *L*<sub>50m</sub> in both of those months (Fig. 3.15a). Although the ovaries of some female *C. cauteroma* in November were still mature or in spawning condition or spent, *i.e.* stages III/IV or V, a substantial number were recovering, *i.e.* stage VI (31%), and by January the ovaries of all females were either at stage VI or I (Fig. 3.15a).

The majority or all of the females of *C. rubescens*, that were caught between February and June and were ≥ *L*<sub>50m</sub> in length, possessed stage I ovaries (Fig. 3.15b). Females with ovaries at stages II and III/IV were first collected in May and July, respectively. The ovaries of the vast majority of female *C. rubescens* sampled between September and November were either at the mature or spawning stages, *i.e.* stages III/IV (Fig. 3.15b). Although the ovaries of some of the females of *C. rubescens* in December and January were at stage III/IV, 52 and 21% of the females in those months,
Figure 3.15. Monthly percentage frequencies of occurrence of sequential stages in gonadal development in females of (a) Choerodon cauteroma, (b) Choerodon rubescens, (c) Choerodon schoenleinii and (d) Choerodon cyanodus that were caught in Shark Bay between January 2000 and January 2003 and were > their respective $L_{50m}$. Data for corresponding months in the different years have been pooled. Sample sizes are shown for each month on each figure.
respectively, contained either stage V or VI ovaries. By February, the ovaries of all females were either at stage VI or I (Fig. 3.15b).

The ovaries of all female *C. schoenleinii* that were $\geq L_{50m}$ in length and were caught between February and August were at stage I (Fig. 3.15c). Fish with ovaries at stages II and III/IV were first recorded in September and were found until December, while stage III/IV ovaries were most abundant in fish caught in November (32%) and some (ca 16%) were also recorded in December. By January, the ovaries of all female *C. schoenleinii* with lengths $\geq L_{50m}$ were at either stage VI or I (Fig. 3.15c).

The females of *C. cyanodus* $\geq L_{50m}$, that were caught between March and September, contained ovaries that were predominantly or exclusively at stage I (Fig. 3.15d). Females with ovaries at stage III/IV were first recorded in November and such females dominated the catches in December (58%) and January (60%) (Fig. 3.15d). Although, in February, some females with ovaries at stages II, III/IV or V were recorded and 36% were at stage VI, the ovaries of all female *C. cyanodus* were at either stage VI or I by March (Fig. 3.15d).

**Oocyte diameter frequencies**

A comparison of histological sections taken from the anterior, middle and posterior regions of the ovaries of a subsample of females with ovaries at different stages of development, *i.e.* stages II, III and IV (Table 3.2), demonstrated that the pattern of development and maturation of oocytes was the same in each of those regions. Thus, to determine whether each of the four species of tuskfish had determinate or indeterminate fecundity, oocyte diameters were calculated from measurements taken in the middle region of two stage IV ovaries (identified using histology, Table 3.2), which was considered to represent the ovary as a whole. The distributions of the diameters of the chromatin nucleolar, perinucleolar, cortical alveolar and yolk granule
oocytes in the ovaries of two stage IV ovaries of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* essentially formed a continuum and thus each of these species has indeterminate fecundity (Fig. 3.16). This implies that the individual females of each species will spawn on more than one occasion during the spawning period as confirmed by the presence in stage IV ovaries of vitellogenic oocytes, together with either hydrating oocytes and/or post-ovulatory follicles.

### 3.4 Discussion

**Evidence for protogynous hermaphroditism**

The question arises as to whether each of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* are monandric or diandric protogynous hermaphrodites. Monandric protogynous hermaphroditism is characterised by the males having only one developmental pathway, *i.e.* they are derived from adult females via sex change. It is thus relevant that histological sections showed that the gonads of the small 0+ individuals, *i.e.* < 100 mm, of each species contained solely ovarian tissue. This demonstrates that each of these species begins life as a female. By definition, individuals of monandric protogynous hermaphrodites subsequently reach sexual maturity as females and some of those will later change from adult females to males, which are referred to as secondary males (Reinboth, 1970; Sadovy and Shapiro, 1987). Histological sections of subsamples of the testes of the full size range of males of each of the four species of tuskfish demonstrated that their testes contained the essential characteristics of secondary males (Reinboth, 1970; Sadovy and Shapiro, 1987). They thus retained the membrane-lined ovarian lumen, lamellar organisation and ovarian wall of their ovaries. Furthermore, an histological examination of stage III and IV testes found mature sperm in sperm sinuses in the outer wall of the testes, which would thus be used to facilitate the transport of sperm towards the cloaca.
during spawning and which is a characteristic of the secondary males of monandric protogynous hermaphrodites. This view was supported by the fact that the lumen of these testes never contained sperm cells, thus it was not used in sperm transport (Sadovy and Shapiro, 1987).

The conclusion that *C. rubescens* and *C. schoenleinii* are monandric protogynous hermaphrodites in Shark Bay agrees with the conclusions of Nardi (1999) for *C. rubescens* in the Abrolhos Islands and of Ebisawa *et al.* (1995) for *C. schoenleinii* in Japan. Monandry is also known to occur in many other labrid species, *e.g.* *Achoerodus viridis*, *Bodianus rufus*, *Cirrhilabrus temmincki*, *Nelabrichthys ornatus* and *Xyrichtys novacula* (Hoffman, 1980; Bentivegna and Rasotto, 1987; Kobayashi and Suzuki, 1990; Gillanders, 1995; Andrew *et al.*, 1996; Candi *et al.*, 2004).

Choat (1969) concluded that *C. cyanodus* was a diandric protogynous hermaphrodite on the Great Barrier Reef based on his analysis of the lengths and histology of the testes of four males. That author found that one of the male *C. cyanodus*, which was small in length, was a primary male, while the other males, which were much larger, were secondary males. This contrasts with the findings for this species in Shark Bay.

The gonads of transitional individuals of *C. cauteroma*, *C. rubescens* and *C. schoenleinii* contained degenerating chromatin nucleolar and perinucleolar oocytes and testicular tissue that were intermixed. The gonads of those individuals thus belong to the “undelimited type 2” category as described by Sadovy and Shapiro (1987). This parallels the findings of Ebisawa *et al.* (1995) for *C. schoenleinii* in Japan and of Nardi (1999) for *C. rubescens* in the Abrolhos Islands and also of Platten (2003) for the congeneric *Choerodon venustus* in eastern Australia. An “undelimited type 2” transitional gonad is also typical of several other protogynous labrids, *e.g.* *Nelabrichthys ornatus*, *Semicossyphus pulcher*, *Thalassoma duperrey* and *Thalassoma*
*bifasciatum* (Warner, 1975; Nakamura *et al*., 1989; Shapiro and Rasotto, 1993; Andrew *et al*., 1996). Although no transitional individuals of *C. cyanodus* were found in Shark Bay, the individuals of this congeneric *Choerodon* species would also presumably contain “undelimited type 2” transitional gonads when undergoing sex change. The paucity or absence of transitional individuals of each of the four species of tuskfish in samples which were of a substantial size, indicates that sex change takes place rapidly, a conclusion consistent with that of Reinboth (1980) for protogynous wrasses in general.

The conclusion that the four species of tuskfish are monandric, is supported by the fact that all but a few of the males of *C. cyanodus* and *C. cauteroma* and all of the males of *C. rubescens* and *C. schoenleinii* belonged to their upper size and age classes and were greater in length and age than their $L_{95m}$ and $A_{95m}$, respectively, *i.e.* the sizes and ages at which 95% of females reached maturity. Furthermore, the fact that those small males of *C. cyanodus* and *C. cauteroma* were greater in length than the $L_{50m}$ of their females strongly suggests that all *C. cyanodus* and *C. cauteroma* mature first as females and only later change sex to males, as is clearly the case for *C. rubescens* and *C. schoenleinii*.

It appears highly likely that those very few secondary males of *C. cyanodus* and *C. cauteroma* with lengths less than the length at which 95% of females mature would have matured as a female at a small size and then later changed sex while still at a small size, *i.e.* below the $L_{95m}$. However, the possibility that one or a few fish could have changed sex without having previously matured as a female cannot be ignored. Such males were referred to by Warner and Robertson (1978) as “pre-maturational secondary males”. Prematurational secondary males contain testes which have the same characteristics as secondary males which are derived from adult females, *i.e.* a membrane-lined lumen, lamellar structure, ovarian wall and sperm sinuses, but they occur at sizes which are less than the typical length at maturity of females. These males
have been recorded previously in the scarids *Sparisoma rubripinne, Sparisoma chrysopterum* and *Sparisoma viride*, the serranids *Epinephelus andersoni* and *Cephalopholis boenak* and the labrids *Halichoeres radiatus* and *Cirrhilabrus temmincki* (Robertson and Warner, 1978; Warner and Robertson, 1978; Kobayashi and Suzuki, 1990; Chan and Sadovy, 2002; Fennessy and Sadovy, 2002). In the case of the two serranids, the authors concluded that those species were diandric, which is a term usually reserved for species that have both primary and secondary males (Reinboth, 1970), rather than pre-maturational and secondary males. Since the few males of *C. cyanodus* and *C. cauteroma* that were < L95m in length contained secondary testes, they represented a very small minority of all males and probably changed sex at a small size after first maturing as a female. Thus, it is appropriate to consider these two species to be monandric in Shark Bay rather than diandric.

**Biological evidence for different spawning strategies**

The differences in the length ranges of females and males and the numbers of the two sexes of the four species of tuskfish indicates that these species have different reproductive strategies. The large size and sexually dichromatic colour of the vast majority of the males of *C. cauteroma*, and of all males of *C. rubescens* and *C. schoenleinii*, coupled with the female-biased sex ratios of their adults (very strong bias in the case of the latter two species), suggests that their males are either haremic, *i.e.* permanently territorial, or form leks during their spawning periods, *i.e.* are temporarily territorial (Warner and Robertson, 1978; Hoffman, 1985). Since Nardi (1999) observed the males of *C. rubescens* herding females during the spawning season at the Abrolhos Islands, he suggested that they are haremic. The males of several other labrids, *e.g.* *Bodianus rufus, Labroides dimidiatus* and *Xyrichtys pentadactylus*, have been described as haremic (Warner and Robertson, 1978; Hoffman, 1985; Nemtzov,
1985; Andrew et al., 1996). The sexual dichromatism of *C. cauteroma*, *C. rubescens* and *C. schoenleinii* allows the opposite sex to be easily identified, and the large size of the males allows them to aggressively control a harem of females and/or defend a territory from other males (Choat and Robertson, 1975; Warner, 1984; Hoffman, 1985). The smaller size of the ripe testes of individual males of those three species than of the typically large ripe testes of gonochoristic species, coupled with the fact that females release eggs in batches, suggests that an individual male and female will spawn together as a pair, *i.e.* they are pair spawners, as has been demonstrated to occur with *Xyrichthys novacula*, *N. ornatus* and implied for *B. rufus* and *Clepticus parrae* (Robertson and Choat, 1974; Warner and Robertson, 1978; Choat and Robertson, 1975; Marconato et al., 1995; Andrew et al., 1996). Thus, the pair-spawning males of hermaphroditic species only need to release a relatively small amount of sperm at any one time, in order to fertilise a single batch of eggs of one female (Warner and Robertson, 1978). Large ripe testes are common in males of species that spawn in groups, such as the primary males of diandric protogynous hermaphrodites, *e.g.* *Thalassoma bifasciatum* and *Thalassoma duperrey*, and the males of gonochorists, *e.g.* *Arripis georgiana* and *Sillago vittata*, and rudimentary or protandrous hermaphrodites, *e.g.* *Acanthopagrus butcheri* and *Acanthopagrus latus* (Warner et al., 1975; Ross, 1984; Sarre and Potter, 1999; Fairclough et al., 2000a; Hyndes et al., 1996; Hesp et al., 2004a).

The sex ratio of the adults of *C. cauteroma* was not as strongly biased towards females as those of *C. rubescens* and *C. schoenleinii*, which suggests that individual males of *C. cauteroma* may control smaller harems than those of the former two species. However, the greater number of males of *C. cauteroma* in catches may have been due, in part, to biases associated with the dominant method of capture, *i.e.* line fishing, since that method can result in the capture of larger fish (see *e.g.* Løkkeborg and Bjordal, 1992; Welch, 2002).
The data for *C. cyanodus* indicate that this species has a different spawning strategy. The sex ratios of *C. cyanodus* were not biased towards either sex and their males were not sexually dichromatic. Hence, the females and males of this species are not visually distinguishable from each other, as is also the case for this species on the Great Barrier Reef (Choat, 1969). Furthermore, the ripe testes of male *C. cyanodus* did not tend to increase with increasing fish size, as they did for the other three tuskfish species. This indicates that investment in the development of testes, relative to body size, effectively decreased with increasing size. Thus, large male *C. cyanodus* may direct more energy towards maintaining a harem and defending territories or spawning sites than small males and be pair spawners, while small males with relatively larger testes are more likely to be opportunistic spawners, spawning in groups (Choat and Robertson, 1975; Warner and Robertson, 1978). The relatively very large testes found in three males suggests that these males may engage in “sneaking”, *i.e.* where they rush in to release their sperm amongst the eggs and sperm of a spawning pair of *C. cyanodus*, which is more typical of diandric species, *e.g.* *Thalassoma bifasciatum* (Warner et al., 1975; Warner and Robertson, 1978). The resemblance of females and males increases the chances of successful spawning for the smaller males in group spawning or “sneaking” situations (Choat and Robertson, 1975; Warner et al., 1975; Warner and Robertson, 1978).

**Comparison of lengths and ages at sexual maturity and sex change**

The $L_{50m}$s for *C. cyanodus* (129 mm) and *C. cauteroma* (196 mm), species which attained maximum lengths of 382 and 424 mm, respectively, were less than those for *C. rubescens* (274 mm) and *C. schoenleinii* (253 mm), which reached far greater lengths, *i.e.* 649 and 805 mm, respectively. Furthermore, the first two species changed sex at a much smaller length ($L_{50c} = 221$ and 310 mm) than the second two species ($L_{50c}$...
= 545 and 556 mm). Although the $L_{50m}$s for *C. cyanodus* and *C. cauteroma* were less than those for *C. rubescens* and *C. schoenleinii*, the $A_{50m}$s for the former two species (2.3 and 2.0 years) were only slightly less than those of the latter two species (2.7 and 3.5 years). However, the $A_{50c}$s for the first two species (4.2 and 6.4 years) were much less than those for the latter two species (10.5 and 10.4 years). These differences in the age at sex change occur despite the fact that, in Shark Bay, the maximum age for the above species ranged only from 12 to 16 years (see Chapter 4). While some females of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* had changed sex to males by their 3rd, 4th, 7th and 8th years, respectively, a few females were recorded in the upper age classes of each of those species, suggesting that those females might never change sex. This may be caused by the lack of one or more suitable cues for sex change during their life, such as the loss of a dominant male (Robertson, 1972; Sakai *et al.*, 2001), the reduction of the number of males in a population below a threshold (Shapiro and Lubbock, 1980), the changes in encounter rates with female and male conspecifics, *i.e.* density dependence (Lutnesky, 1994), or the reproductive advantage of remaining as a large female, and thus being able to produce a large number of eggs, being greater than that of changing sex to a male, and thus the opportunity to fertilise the eggs of multiple females in a spawning season (Ghiselin, 1969; Muñoz and Warner, 2003).

The percentage of females of each of the four tuskfish species that were $\geq$ their respective $L_{50m}$s and were considered to be sexually mature, *i.e.* contained ovaries at stages II-VI, was rarely 100% at any individual location in Shark Bay. This may reflect variations in the timing of the main spawning periods of each species at individual sites. However, in the case of *C. schoenleinii*, only 45% of those females that were collected between September and December, *i.e.* its main spawning period, and were $\geq L_{50m}$ contained ovaries at stages II-VI. Furthermore, the percentage of females that contained ovaries at stages II-VI in any length or age class during the spawning period was rarely
50%. Thus, only approximately half of the females with lengths ≥ the $L_{50m}$ took part in spawning in any one year. This was not caused by any size-specific differences in the timing of gonadal maturation, as was demonstrated for the labrids *Notolabrus fucicola*, *Notolabrus celidotus*, *Pseudolabrus miles* and *Suezichthys aylingi* (Jones, 1980; Jones, and Thompson, 1980; Denny and Schiel, 2002), since female *C. schoenleinii* of the full adult size range contained ovaries at stages II-VI in each month between September and December.

The presence of only a small proportion of females with maturing ovaries during the spawning period has previously been recorded for the groupers *Epinephelus andersoni*, *Mycteroperca microlepis* and *Epinephelus marginatus* (Chauvet, 1991; Koenig *et al.*, 1996; Fennessy and Sadovy, 2002) and the sparids *Acanthopagrus australis* and *Chrysoblephus puniceus* (Pollock, 1984; Garratt, 1993). This was suggested to be related to an edge of range effect in *M. microlepis* and *A. australis* and possibly also *E. andersoni*, whereby environmental conditions are unsuitable for gonadal recrudescence and spawning, and due to the emigration to spawning areas of mature females of *E. marginatus* and *C. puniceus*. An edge of range effect would be more likely in the case of *C. schoenleinii*, since Shark Bay is essentially the most southerly location where this species is found in substantial numbers in Western Australia (Hutchins, 2001b; Chapter 6). However, any edge of range effect did not influence the spawning of either *C. cyanodus* or *C. cauteroma*, which are also effectively at the southerly limit of their range in Shark Bay. Since ripe, spawning and recovering females and ripe males were collected at several different sites in Shark Bay, demonstrating that spawning occurred at each of those sites, individuals do not migrate to one specific location to spawn.
Spawning periods and location

The trends exhibited by the mean monthly GSIs and the prevalence of the various gonad stages in sequential months demonstrated that the spawning periods of each of the four tuskfish species in Shark Bay differed. Thus, *C. cauteroma* and *C. rubescens* spawn mainly during spring, *C. schoenleinii* in late spring/early summer and *C. cyanodus* during summer. Since water temperature is likely to be one of the major “triggers” for gonadal development and spawning (Lam, 1983), the progressive shift to a later time in the main spawning period of the above species suggests that *C. cyanodus* has a higher threshold temperature for spawning than *C. cauteroma* and *C. rubescens*. Variations in the timing of the main spawning periods of *C. cauteroma*, *C. schoenleinii* and *C. cyanodus*, which co-occur in the same regions of Shark Bay, would have the advantage of facilitating recruitment into nursery areas by these species at slightly different times and thereby reduce the potential for competition between the larvae of those species for resources.

The spawning period of *C. schoenleinii* in Shark Bay, *i.e.* spring and summer, is similar to that of this species in Japan (Ebisawa *et al.*, 1995) and the spawning period of *C. cyanodus* in Shark Bay is similar to that suggested by Choat (1969) for this species in Queensland. *Choerodon rubescens* spawns in Shark Bay at essentially the same time of year as in the Abrolhos Islands *ca* 300 km further south, *i.e.* during spring and summer (Nardi, 1999, Chapter 5). The spawning by all four species of tuskfish at some time between early spring and late summer parallels those of many other species of labrids, *e.g.* *Cirrhilabrus temmincki*, *Labroides dimidiatus* and *Xyrichtys novacula* (Kobayashi and Suzuki, 1990; Cardinale *et al.*, 1998; Sakai and Kohda, 2001).

Although *C. cauteroma* spawned mainly in spring, a few ripe and spawning females were also caught in the preceding months and as early as April. However, those ripe and spawning females obtained in the earlier months were caught around the
southern or northern extremities of Dirk Hartog Island, at the western border of Shark Bay (Fig. 2.1), where, due to the influence of oceanic water, the water temperatures during that period of the year were far greater than the eastern and western gulfs of Shark Bay (Fig. 3.13). In contrast to the situation in the predominantly shallow waters of the inner gulfs of Shark Bay, the water temperature at those deeper and more oceanic locations around Dirk Hartog Island doesn’t vary greatly during the year. This could account for the fact that *C. rubescens*, which was caught only around Dirk Hartog, Dorre and Bernier Islands, spawns over a longer period than the other three tuskfish species within the inner gulfs.

Relative abundances of the four species of tuskfish, derived from underwater visual surveys during their reproductive and non-reproductive periods, did not provide any evidence of spawning aggregations. A spawning aggregation, according to the definition of Domeier and Colin (1997), requires proof of spawning at a particular location and at least a three-fold increase in the density of fish in comparison to the non-reproductive period at that location. Since densities of the four tuskfish species at individual reef sites were generally low and at least a three-fold increase in density was not recorded for any of the four species of tuskfish where evidence of spawning was recorded, this provides strong evidence that these species do not form spawning aggregations.

All of the tuskfish obtained for this study were collected during the day, since labrids are inactive at night (Randall *et al.*, 1997). Since new post-ovulatory follicles (see Hunter and Macewicz, 1985) were never recorded in the ovaries of individual females during the day but that hydrated oocytes were recorded in the ovaries of females at that time and the hydration period is typically less than 12 hours (Lisovenko and Adrianov, 1991; McBride *et al.*, 2003; Hesp *et al.*, 2004c), it is probable that each of the four species of tuskfish spawn at dusk, as occurs in several other wrasse species.
(see e.g. Colin and Bell, 1991; Donaldson, 1995; Sancho et al., 2000). Although surveys were not conducted at dusk, it is unlikely that numbers of each species would have increased dramatically from the time of surveys until dusk, since many of the reef patches surveyed in Shark Bay are highly fragmented and thus it would be unlikely that individuals would travel long distances in such a short time to spawn (Huisman et al., 1990). While C. cyanodus, C. cauteroma and C. schoenleinii in Shark Bay may not aggregate to spawn, C. rubescens was found in areas where there was high connectivity between reefs, thus allowing for easier movement between sites. However, the lack of large numbers recorded during surveys at any one area during the spawning period, despite the potential for migration between sites, suggests that this species does not aggregate to spawn at any one location in Shark Bay. This contrasts with the findings of Nardi (1999) for this species in the Abrolhos Islands, who found up to 100 fish in an area during the spawning period and suggested that it does aggregate to spawn.

Management implications

The management implications of the reproductive biology of each of the four tuskfish species presented in this chapter are discussed in the conclusions.
CHAPTER 4

4.0 Size and age compositions and growth of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* in Shark Bay
4.1 Introduction

Data on population demographics, such as size and age composition, growth parameters and mortality, are important for producing models that can be used to assess and predict the impacts of commercial and recreational fishing (Beverton and Holt, 1957; Appledoorn, 1996; Choat and Robertson, 2002). Since labrids are typically small, they generally contribute less to reef fisheries than, for example, members of the Lutjanidae, Serranidae and Carangidae (Munro, 1996; Munday and Jones, 1998; Maypa et al., 2002). However, as the populations of preferred species decline, fishers are essentially moving down the food web and starting to remove species at lower trophic levels. This is leading to the development of new fisheries, as different species, such as those of the Labridae, are targeted (Russ, 1991; Sadovy, 1996b; Pauly et al., 1998; Pauly et al., 2002; Smith et al., 2003). Many studies of labrids have focused on determining aspects of their reproductive biology and behaviour, e.g. Hoffman, 1985; Warner and Swearer, 1991; Warner and Schultz, 1992; Shapiro and Rasotto, 1993; Ebisawa et al., 1995; Warner, 1998 and Sakai et al., 2001. However, there is relatively little published information on the age compositions and growth of important labrid species, including those that are found in Western Australia. Of the published ageing studies, the growth zones on a range of hard structures of fish, including dorsal spines, opercula, scales and otoliths, have been used to estimate the ages of different species of labrid, see e.g. Warner, 1975; Dipper et al., 1977; Jones, 1980; Hashimoto et al., 1991; Kimura et al., 1992; Hostetter and Munroe, 1993; Gillanders, 1995; Shung, 1995; Sayer et al., 1995; Platten et al., 2002; Pallaoro and Jardas, 2003 and Ewing et al., 2003.

Validation that the growth zones on hard structures are formed annually and that those zones can thus be used in estimating the ages of individual fish, is crucial in these types of study (Beamish and McFarlane, 1983; Campana, 2001). A commonly used technique in validation studies is marginal increment analysis. The marginal increment,
i.e. the distance between the edge of the otolith and the last completed growth zone (annulus), is measured and expressed as a proportion of the distance between the primordium and the outer edge of the annulus, when only one such growth zone is present, or the distance between the outer edges of the last two annuli, when more than one growth zone is present. If an annulus is formed annually, then the mean marginal increments in each month (or season) will demonstrate a sinusoidal trend during the year (Campana, 2001). Determination of the timing of formation of the first increment (annulus) and the age of fish at that time is also a necessary component of any validation study and requires examination of the otoliths of fish in their early life (Campana, 2001). The absolute age of a fish at that time is based on the time difference between birth (usually inferred from the time of peak spawning) and the delineation of the first annulus. It is also important to recognise that it is often necessary to section otoliths to reveal all of their growth zones (Hyndes et al., 1992), particularly in long-lived species, such as the West Australian dhufish *Glaucosoma hebraicum* and the eastern blue groper *Achoerodus viridis* (Gillanders, 1995; Hesp et al., 2002).

In the studies listed above of the age and growth of different labrid species and, for which, growth zones were validated as being formed annually in their hard structures, such validation was based on marginal increment analysis. However, the requisite measurements were often made on hard structures containing only a limited range of the numbers of zones and those studies pooled the measurements of the marginal increments for all otoliths in each month. Campana (2001) stated that marginal increment analysis should employ data from both the young and older individuals of a species, in order to demonstrate that growth zones are formed annually throughout the life of a species. The study by Ewing *et al.* (2003) of the purple wrasse *Notolabrus fucicola* is apparently the only one that has comprehensively validated that growth zones are formed annually in the hard structures of a labrid throughout its life, through
determining when the first opaque annuli is delineated and measuring the marginal increment on sectioned otoliths containing the full range of the numbers of opaque zones for that species.

Individuals in the population of *Choerodon rubescens* in the Abrolhos Islands have been “aged” using the number of opaque zones in sectioned otoliths (Nardi, 1999). However, that author recognised that his marginal increment analysis was based on otoliths that did not encompass those with less than five opaque zones and did not provide conclusive evidence that the opaque zones in those otoliths were formed annually. The size and “age” distributions of female and male *C. rubescens* in the Abrolhos Islands were found by Nardi (1999) to differ markedly, with the larger size and older age classes being dominated by males. Nardi (1999) recorded *C. rubescens* up to ca 64 cm long and estimated that this species could live for at least 20 years in that region.

There is no published information on the age compositions of *Choerodon schoenleinii*, a species which reaches lengths of 90 cm (Allen, 1999). However, the studies of Kanashiro (1998) on the early life history of *C. schoenleinii* in Japan demonstrated that the small juveniles of this species, which settled in seagrass beds and remained there for a few months, grew rapidly in that habitat. Ebisawa *et al.* (1995) collected *C. schoenleinii* in Japan that ranged from 150 to 649 mm in length among females and from 400-799 mm among males. Individuals of *C. schoenleinii* that were transitional, *i.e.* changing sex, were of intermediate lengths, ranging from 450 to 649 mm. There is no information available on the age compositions or growth of *Choerodon cyanodus* or *Choerodon cauteroma*, which reach maximum lengths of 60 and *ca* 43 cm, respectively (Allen, 1999; B. Hutchins, pers. comm.). In his samples of *C. cyanodus* from the Great Barrier Reef, which ranged from 98-405 mm in length,
Choat (1969) found females to be confined to the smaller size classes, while the males ranged widely in length.

The aims of the work described in this chapter were to determine the size and age compositions and growth of *C. cyanodus*, *C. cauteroma*, *C. rubescens* and *C. schoenleinii* in the subtropical environment of Shark Bay. An analysis of the number of growth zones on whole and sectioned otoliths was carried out to ascertain whether it was necessary to section the otoliths of each of these species to obtain reliable counts of growth zones in those otoliths. Marginal increment analysis was used to validate that the growth zones are formed annually in the otoliths of each of these species and can thus be used to determine the ages at capture of individual fish. The relationships between total length and total weight for each species of tuskfish were determined to allow the total weights of individual fish to be estimated when only frames were obtained and also to enable fisheries managers, in the future, to calculate from length data, biomass of recreational and/or commercial fisheries.

### 4.2 Materials and methods

**Otolith preparation and precision of annulus counts**

The two sagittal otoliths of each individual of *Choerodon cyanodus*, *Choerodon cauteroma*, *Choerodon rubescens* and *Choerodon schoenleinii* were removed, cleaned, dried and stored in paper envelopes. The number of opaque zones in each of 100 otoliths covering a wide size range of *C. cauteroma* were compared prior to and after those otoliths had been sectioned. For counting the growth zones in whole otoliths, each otolith was placed in a small black dish, covered with methyl salicylate and examined under a dissecting microscope using reflected light. For sectioning, the otoliths were mounted in clear epoxy resin and cut into *ca* 300 µm sections using an Isomet low speed diamond saw. The sections were cut through the primordium at right angles to the
longest axis of the otoliths. The resultant sections were ground using fine wet and dry
carborundum paper (Grade 1200), cleaned and mounted on slides using DePX mounting
medium and examined on a black background under a dissecting microscope with
reflected light. The number of opaque annuli observed in each sectioned otolith was
recorded. The otoliths of each tuskfish species were small and increased in thickness
with increasing size of fish, making it difficult to count the growth zones without
sectioning, particularly in the case of those in large fish (Fig. 4.1). Since sectioning
improved the resolution of the opaque zones in the otoliths of *C. cauteroma* of all sizes,
all of the otoliths of each species were sectioned. The opaque zones in the sectioned
otoliths of each individual were counted on two occasions without knowledge of the
date of capture or size of individual fish. Any discrepancies in the numbers of zones
recorded for an otolith were investigated and in the few cases where the readability of
the otolith was poor, these were not included in any analysis of age compositions or
growth.

The zones on a random subsample of 100 sectioned otoliths covering a wide size
range of each of the four species of tuskfish were counted by a second experienced
reader, without knowledge of the date of capture or size of the fish. The counts of the
author and the second reader differed in only one case for *C. cauteroma* and
*C. schoenleinii* and then by only one zone and in two cases for *C. rubescens* and
*C. cyanodus*, again only by one zone. During a concurrent examination and discussion
of the pattern of distribution of the zones on those otoliths, for which there were
discrepancies, it became apparent that the second reader had failed to detect the recently
delineated outermost opaque zone in the otolith of the individual *C. cauteroma*, while
the author or second reader had failed to count a partially obscured innermost opaque
zone for *C. schoenleinii*, *C. rubescens* and *C. cyanodus.*
Figure 4.1. The whole and corresponding sectioned otoliths of a (a, b) 256 mm *Choerodon cauteroma* with two delineated opaque zones and of a (c, d) 298 mm *Choerodon cauteroma* with ten delineated opaque zones. Numbers in (b) and (d) indicate positions of opaque zones (Scale bar: a, c = 1 mm; b, d = 500 µm).
Validation procedures

Marginal increment analysis was employed to determine whether the opaque zones detectable in otoliths of each of the four species were formed annually. For this purpose, measurements were made of the distance between the primordium and the outer edge of both the otolith and the single opaque zone, when only one such zone was present, and of the distances between the outer edge of the otolith and each of the two outermost opaque zones, when two or more opaque zones were present (Fig. 4.2). These measurements, which were made perpendicular to the opaque zones and without knowledge of the date of capture of the fish from which that otolith had been removed, were recorded to the nearest 0.01 mm using the Leica microscope and computer-imaging package described in Chapter 3. The marginal increment in each otolith, i.e. the distance between the single or outermost opaque zone and the edge of that otolith, was expressed as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, and as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. The marginal increments in otoliths with the same number of opaque zones in the corresponding calendar months of different years were pooled.

Analysis of growth

The approximate time of peak spawning, which was considered to correspond to the birth date and was estimated from the trends shown throughout the year by the gonadosomatic indices and gonadal maturity stages, occurred in October for C. cauteroma, November for C. rubescens and C. schoenleinii and January for C. cyanodus (Chapter 3). Thus, these species were assigned birth dates of 1 November, 1 December, 1 December and 1 February, respectively. This birth date was then used, in conjunction with the time of year when the opaque zones (annuli) in the otoliths become
**Figure 4.2.** Sectioned otoliths of *Choerodon cauterota* showing locations of measurements taken for marginal increment analysis (orange and blue) in the case of a fish with (a) one opaque annulus and (b) greater than one opaque annulus. Scale bar = 250 µm.
delineated, to determine the age of individual fish on their date of capture. A single von Bertalanffy growth curve was fitted to the lengths at age of the individuals of each species, using non-linear regression in SPSS (SPSS Inc., 1999). The von Bertalanffy equation is 

\[ L_t = L_\infty (1 - e^{-kt}) \]

where \( L_t \) = the total length (mm) at age \( t \) (years), \( L_\infty \) = the asymptotic length (mm) predicted by the equation, \( k \) = the growth coefficient (year\(^{-1}\)) and \( t_0 \) = the hypothetical age (years) at which fish would have zero length, if growth followed that predicted by the equation.

### 4.3 Results

**Length-weight relationships**

The parameters for the relationships between ln total length (\( TL \)) (mm) and ln wet weight (\( W \)) (g) for the four species of tuskfish are shown in Table 4.1. The total length of individuals of each species, that had been filleted were thus able to be used to estimate their total weight prior to filleting. This is achieved by inserting the length into the equation: 

\[ \ln W = a \ln TL + b \]

using the constants \( a \) and \( b \) in Table 4.1. The predicted \( \ln W \) is then back-transformed to determine actual weight and multiplied by the correction factor: \( \exp(\text{mean of squared residuals}/2) \), in order to take into account the bias associated with the log transformation and thereby produce a more reliable estimate of the expected value of \( W \) at each value of \( TL \) (Beauchamp and Olson, 1973).

**Validation results**

The smallest individuals of \( C. \) cyanodus, \( C. \) cauteroma, \( C. \) rubescens and \( C. \) schoenleinii were first collected in July, January, April and March, respectively. The otoliths of these fish, which had mean lengths of 46, 78, 70 and 100 mm, respectively, exhibited no annuli and neither did those of the corresponding cohorts in the immediately ensuing months. The first annulus in the otoliths of some fish in the
Table 4.1. Parameters (± 95% confidence intervals) for the linear regressions fitted to ln total length (TL, mm) against ln total weight (W, g), according to the equation lnW = a lnTL + b, of Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens and Choerodon schoenleinii. ANOVA p value *** < 0.001.

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameters</th>
<th>Mean of squared residuals</th>
<th>$R^2$</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choerodon cyanodus</td>
<td>3.061 (3.044, 3.078)</td>
<td>-11.129 (-11.221, -11.037)</td>
<td>0.00609***</td>
<td>0.994</td>
</tr>
<tr>
<td>Choerodon cauteroma</td>
<td>3.007 (2.997, 3.017)</td>
<td>-10.836 (-10.892, -10.780)</td>
<td>0.00522***</td>
<td>0.997</td>
</tr>
<tr>
<td>Choerodon rubescens</td>
<td>2.980 (2.965, 2.995)</td>
<td>-10.581 (-10.668, -10.494)</td>
<td>0.00333***</td>
<td>0.998</td>
</tr>
<tr>
<td>Choerodon schoenleinii</td>
<td>2.945 (2.927, 2.962)</td>
<td>-10.465 (-10.564, -10.366)</td>
<td>0.00462***</td>
<td>0.995</td>
</tr>
</tbody>
</table>

corresponding cohort (see Fig 4.2a) of each of the four species became delineated in September, September, January and September, respectively, when, based on the birth dates for each species, those fish were approximately 7, 10, 13 and 9 months old, respectively. The first annulus in the otoliths of the majority of the individuals of this cohort of C. cyanodus, C. cauteroma, C. rubescens and C. schoenleinii had become delineated by January, November, March and February, respectively, when those fish were approximately 11, 12, 15 and 14 months old, respectively.

The mean monthly marginal increments in the otoliths of C. cyanodus with one opaque zone rose from a minimum of 0.08 in September, i.e. early spring, to a maximum of 0.27 in May, i.e. late autumn, and subsequently declined (Fig. 4.3). The mean monthly marginal increments of C. cyanodus with 2–3, 4–5 and ≥ 6 opaque zones in their otoliths rose from their minima of ca 0.2–0.3 in January, i.e. mid-summer, to their maxima of ca 0.8 in August, i.e. late winter, and then declined (Fig. 4.3). The mean monthly marginal increments for C. cauteroma with different numbers of opaque zones rose from their minima in mid- to late spring or early to mid-summer to their maxima in mid- to late winter and then declined (Fig. 4.4). The mean monthly marginal increments for C. rubescens with different numbers of opaque zones rose from their
Figure 4.3. Mean monthly marginal increments ± 1 SE in sectioned otoliths of *Choerodon cyanodus* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean. In this Fig. and Figs 4.4-4.6, the closed rectangles on the x-axis refer to the winter and summer months and the open rectangles to the spring and autumn months.
Figure 4.4. Mean monthly marginal increments ± 1 SE in sectioned otoliths of Choerodon cauteroma collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.
minima in mid- to late summer or early autumn to reach their maxima in late spring or early summer, which was then followed by a conspicuous decline (Fig. 4.5). The mean monthly marginal increments in the otoliths of *C. schoenleinii* with one opaque zone rose from its minima in mid-summer to its maxima in late spring (Fig. 4.6). The mean monthly marginal increments for *C. schoenleinii* with 2-3, 4-5 and ≥ 6 opaque zones followed similar seasonal trends. They thus rose from their minima in late spring or early summer to their maxima in mid-winter (Fig. 4.6).

The fact that, irrespective of the numbers of opaque zones, the mean monthly marginal increments in the sectioned otoliths of all four species of tuskfish exhibited a marked decline only once during the year and then rose progressively over subsequent months demonstrates that a single opaque zone is formed in the otoliths of each species annually (Figs 4.3-4.6). Thus, the number of opaque zones (annuli) in sectioned otoliths can be used to determine the ages of individuals of each of the four species of tuskfish.

**Length and age compositions of the four tuskfish species**

Female *C. cyanodus* and *C. cauteroma* ranged in length from 39 to 315 mm and from 58 to 372 mm, respectively, and from 0 to 8 and from 0 to 10 years old, respectively (Fig. 4.7a,b). The males of these two species ranged in length from 138 to 382 mm and from 219 to 424 mm, respectively, and from 2 to 12 and from 3 to 14 years old, respectively (Fig. 4.7a,b). The eight transitional *C. cauteroma* ranged in length from 266 to 338 mm and belonged to the 5 to 8+ age classes (Fig. 4.7b). None of the individuals of *C. cyanodus* were transitional, i.e. possessed gonads that contained both ovarian and testicular tissue.

The females and males of *C. rubescens* ranged in length from 70 to 574 mm and from 500 to 649 mm, respectively (Fig. 4.7c). The females of *C. rubescens* belonged to the 0 to 12+ age classes, while the males belonged to the 6 to 16+ age classes,
Figure 4.5. Mean monthly marginal increments ± 1 SE in sectioned otoliths of *Choerodon rubescens* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.
Figure 4.6. Mean monthly marginal increments ± 1 SE in sectioned otoliths of *Choerodon schoenleinii* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.
Figure 4.7. Length and age frequency compositions of female ( ), transitional (■) and male ( )
(a) Choerodon cyanodus, (b) Choerodon cauteroma, (c) Choerodon rubescens and (d) Choerodon
schoenleinii collected in Shark Bay.
respectively (Fig. 4.7c). No transitional individuals of *C. rubescens* were collected in Shark Bay. Female *C. schoenleinii* ranged in length and age from 72 to 626 mm and from 0 to 10 years in age (Fig. 4.7d). The seven males of that species, which were all large, ranged in length and age from 521 to 805 mm and 7 to 16 years, respectively. The single transitional *C. schoenleinii* was 526 mm in length and 7 years old (Fig. 4.7d).

**Growth patterns**

In the age classes of *C. cyanodus* and *C. cauteroma*, for which there were sufficient numbers of fish of both sexes, the mean lengths of the males were greater than those of their females (Fig. 4.8). This was also the case for the few male *C. rubescens* and *C. schoenleinii* (Fig. 4.9). von Bertalanffy growth curves provided a good fit to the lengths at age of individuals of each of the four species of tuskfish, as reflected in the high $R^2$ values derived from the non-linear regression analysis (Figs 4.10, 4.11; Table 4.2). The asymptotic lengths ($L_\infty$) of 289 mm for *C. cyanodus* and 330 mm for *C. cauteroma* were far lower than the 640 mm for *C. rubescens* and 734 mm for *C. schoenleinii* (Table 4.2). In contrast, the values for $k$ were far greater for the first two species (0.38 and 0.35 year$^{-1}$) than for the latter two species (0.16 and 0.11 year$^{-1}$) (Table 4.2).
Figure 4.8. Mean lengths ± 1 S.E. of females (□) and males (■) in each age class of *Choerodon cyanodus* and *Choerodon cauteroma*. Sample sizes for females and males are shown at the bottom and top of each graph, respectively.
Figure 4.9. Mean lengths ± 1 S.E. of females (□) and males (■) in each age class of *Choerodon rubescens* and *Choerodon schoenleinii*. Sample sizes for females and males are shown at the bottom and top of each graph, respectively.
Figure 4.10. von Bertalanffy growth curves fitted to the lengths at age of female ( ), transitional ( ) and male ( ) Choerodon cyanodus and Choerodon cauteroma collected in Shark Bay. Sample sizes (n) shown on each figure.
Figure 4.11. von Bertalanffy growth curves fitted to the lengths at age of female (■), transitional (■) and male (□) Choerodon rubescens and Choerodon schoenleinii and all four Choerodon species in Shark Bay. Sample sizes (n) shown on each figure.
Table 4.2. Parameters for the von Bertalanffy growth curves (±95 % confidence intervals) fitted to the lengths at age of *Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens* and *Choerodon schoenleinii* in Shark Bay.

<table>
<thead>
<tr>
<th>Species</th>
<th>$L_\infty$ (mm)</th>
<th>$k$ (year$^{-1}$)</th>
<th>$t_0$ (years)</th>
<th>$R^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Choerodon cyanodus</em></td>
<td>289.3</td>
<td>0.349</td>
<td>-0.149</td>
<td>0.671</td>
<td>746</td>
</tr>
<tr>
<td>Lower</td>
<td>278.2</td>
<td>0.302</td>
<td>-0.347</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>300.5</td>
<td>0.397</td>
<td>0.472</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Choerodon cauteroma</em></td>
<td>330.2</td>
<td>0.383</td>
<td>-0.185</td>
<td>0.832</td>
<td>935</td>
</tr>
<tr>
<td>Lower</td>
<td>323.0</td>
<td>0.351</td>
<td>-0.279</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>337.4</td>
<td>0.416</td>
<td>-0.091</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Choerodon rubescens</em></td>
<td>639.7</td>
<td>0.157</td>
<td>-0.82</td>
<td>0.924</td>
<td>447</td>
</tr>
<tr>
<td>Lower</td>
<td>613.6</td>
<td>0.142</td>
<td>-1.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>665.7</td>
<td>0.174</td>
<td>-0.617</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Choerodon schoenleinii</em></td>
<td>733.5</td>
<td>0.111</td>
<td>-0.720</td>
<td>0.740</td>
<td>572</td>
</tr>
<tr>
<td>Lower</td>
<td>609.2</td>
<td>0.077</td>
<td>-1.138</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>857.8</td>
<td>0.146</td>
<td>-0.301</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4.4 Discussion

Validation

Examination of the otoliths of small *Choerodon cyanodus, Choerodon cauteroma, Choerodon rubescens* and *Choerodon schoenleinii* in each month demonstrated that the first opaque annuli in the otoliths of each of these species was delineated by the time the individuals were approximately 11, 12, 15 and 14 months old, respectively. Marginal increment analysis demonstrated that a single opaque zone is formed annually in the otoliths of each species in Shark Bay. Thus, the numbers of opaque zones in the otoliths of the individuals of each species can be used, in conjunction with the birth date and timing of delineation of opaque zones in the otoliths of the species in question, to determine the ages at capture of those individuals. The opaque zones became delineated during late spring or summer, which parallels the situation with the otoliths of the bluethroat wrasse *Notolabrus tetricus* and purple
wrasse *Notolabrus fucicola* in southern Australia (Ewing *et al.*, 2003; Smith *et al.*, 2003), the eastern blue groper *Achoerodus viridis* in south-eastern Australia (Gillanders, 1995) and other teleost species in Western Australia, *e.g.* West Australian dhufish *Glaucosoma hebraicum* and Australian herring *Arripis georgiana* (Fairclough *et al.*, 2000b; Hesp *et al.*, 2002).

**Length and age compositions**

The maximum length of *C. rubescens* recorded during this study, *i.e.* 649 mm, was similar to that of ca 640 mm obtained by Nardi (1999) from the Abrolhos Islands and the maximum size of 650 mm reported for this species by Allen (1999). However, the number of *C. rubescens* caught in Shark Bay declined markedly above 440 mm in length, which is just above the minimum legal length (MLL) of 400 mm for this species in Western Australia. This corresponds to a similarly dramatic decline in the numbers of *C. rubescens* greater than six years of age. This is presumably due to the fact that most of the *C. rubescens* were caught in a relatively small geographical area, *i.e.* South Passage and the areas immediately outside the passage (see Fig. 2.1), and this area is subjected to heavy recreational fishing pressure, particularly during autumn and winter, when weather conditions are optimal for angling and spearfishing (Sumner *et al.*, 2002). The decrease in the numbers of *C. rubescens* above 440 mm and six years of age may also reflect a size-related movement into the deeper waters, *i.e.* > 20 m deep, that are located on the oceanic (western) side of South Passage. Such movements are exhibited by many other demersal species, *e.g.* King George whiting *Sillaginodes punctata*, tarwhine *Rhabdosargus sarba* and labrids, such as the eastern blue groper *Achoerodus viridis* and the humphead wrasse *Cheilinus undulatus* (Gillanders, 1997; Hyndes *et al.*, 1998; Hesp *et al.*, 2004b; Sadovy *et al.*, 2003). Evidence for such a movement in *C. rubescens* is provided by the fact that commercial fishers collected a substantial
number of larger and older fish in deeper waters of the Abrolhos Islands and this was also true for a sample of commercially-caught fish from Shark Bay (see Chapter 5).

The maximum length of *C. schoenleinii* recorded in Shark Bay, *i.e.* 805 mm, was similar to the 800 and *ca* 790 mm reported by Allen (1999) and by Ebisawa *et al.* (1995) in Japan, respectively. Individuals of *C. schoenleinii* weighing up to 16 kg have been recorded by Grant (1993) in eastern Australia, which, from the length-weight relationship for this species in Shark Bay, would have corresponded to a length of *ca* 937 mm. Although *C. schoenleinii* with lengths of up to 805 mm were collected in Shark Bay, the number of fish in the catches of this species that were greater than its MLL of 400 mm was relatively low. Since sampling took place at many different locations throughout Shark Bay and the largest individuals of *C. schoenleinii* were taken from sites visited relatively regularly and which were often in shallow water, the size range of *C. schoenleinii* is not due to either the concentration of sampling effort in particular areas or a size or age-related movement into deeper water. *Choerodon schoenleinii* represents the ninth most important species in terms of numbers taken by recreational fishers in Shark Bay and thus the size composition may be influenced by its subjection to substantial fishing pressure (Sumner *et al.*, 2002). Furthermore, observations made during boat ramp surveys conducted by the Department of Fisheries Western Australia (K. Grey, pers. comm.) indicated that fishers commonly target specific reefs, take their catch limit on one day and then return to that location on the following day. Since many reef species typically exhibit site fidelity throughout their life, they are particularly susceptible to this type of fishing pressure (Coleman *et al.*, 1999). Ebisawa *et al.* (1995) found relatively low numbers of large individuals in the commercial catches of this species in Japan, with the majority of fish ranging in length from 20 to 35 cm, and they thus concluded that this species was overexploited.
The maximum length of 424 mm recorded for *C. cauteroma* in our catches in Shark Bay is substantially greater than the maximum of 360 mm listed for this species by Allen (1999), but similar to the 430 mm reported by B. Hutchins (pers. comm.) from the northern coastline of Western Australia. Since very few individuals > 400 mm in length were collected in Shark Bay, the majority of this species are smaller than the recently-introduced MLL of 400 mm for all tuskfish species in the Gascoyne fisheries bioregion (see Fig. 1.1). Retention of this species by recreational fishers is not restricted by an MLL. However, fishers are limited to four tuskfish per person per day.

Although *C. cyanodus* is reported to reach a maximum length of 600 mm (Allen, 1999), all of the individuals of this species caught in Shark Bay during the present study were less than 400 mm in length and the majority were less than 300 mm and thus well below its current MLL of 400 mm. Since the von Bertalanffy growth curve for this species in Shark Bay is markedly asymptotic and the samples collected were obtained from a sampling regime that encompassed a large number of sites and employed a variety of methods of capture, *e.g.* line and spear fishing, those samples thus presumably included representatives of the largest individuals in Shark Bay. The length range of *C. cyanodus* in Shark Bay is similar to that reported by Choat (1969) for this species at Heron Island on the Great Barrier Reef and by Travers (unpublished data) on the Pilbara/Kimberley coastline of Western Australia. However, Grant (1993) reports that the weights of individuals in the catches of *C. cyanodus* in Queensland are generally about 1.8 kg, which, on the basis of the length-weight relationship for this species in Shark Bay, would correspond to a length of *ca* 440 mm and thus this species presumably often reaches greater lengths in that region than in Shark Bay. Although the Australian Anglers Association records note that a 4.5 kg individual of *C. cyanodus* was collected in Shark Bay, this was probably a misidentified species (Anon., 2003d).
Growth

The maximum lengths recorded for *C. cyanodus* (382 mm) and *C. cauteroma* (424 mm) in Shark Bay were far less than those of *C. rubescens* (649 mm) and *C. schoenleinii* (805 mm). This is reflected in the $L_{\infty}$s of 289 and 330 mm, that were derived for the first two species, being less than those for the second two species, *i.e.* 640 and 734 mm. The difference in size is remarkable, considering the fact that the maximum ages attained by the four species of tuskfish in Shark Bay ranged only from 12 to 16 years, and that the majority of individuals of each species were less than *ca* 7 years of age. However, this difference can be explained by the fact that the rates of growth ($k$) of the two smaller species, *i.e.* *C. cyanodus* (0.35 year$^{-1}$) and *C. cauteroma* (0.38 year$^{-1}$), which were similar, were much greater than those of the two larger species, *i.e.* *C. rubescens* (0.16 year$^{-1}$) and *C. schoenleinii* (0.11 year$^{-1}$). Choat *et al.* (1996) found a similarly wide variation in growth among several congeneric *Scarus* species of the closely-related Scaridae family. However, the *Scarus* species that exhibited a markedly asymptotic pattern of growth generally had longer life spans than those with more continuous growth (Choat *et al.*, 1996). This contrasts with the four *Choerodon* species, which each had similar maximum ages in Shark Bay, despite having different growth parameters.

The tendency for the growth curves of *C. cyanodus* and *C. cauteroma* to asymptote at shorter lengths than those of *C. rubescens* and *C. schoenleinii* is paralleled by the attainment of maturity at smaller lengths ($L_{50m}$), *i.e.* 129 and 196 mm, respectively, vs 274 and 253 mm, respectively. Thus, while each species exhibits similar growth during the first two years of life, the somatic growth of the first two species then starts to slow down. This may be influenced, in part, by the fact that *ca* 40 and 27% of the females of the former two species have commenced investing in gonadal development for the first time at the end of their second year of life, whereas the
majority of individuals of the second two species continue to undergo a substantial increase in somatic growth for at least one more year before sexual maturation occurs (Wootton, 1990). This reflects the variations in reproductive strategies that have evolved in different species and have enabled their reproductive potential to be maximised (Jennings et al., 2001; Robertson, 1991; Beverton, 1992). The difference in growth rates may also be influenced by how the individuals of each species cope with a range of factors, such as hypersalinity, extreme water temperature range, the types and availability of food in Shark Bay and conspecific densities (Beverton and Holt, 1957; Wootton, 1990). It is noteworthy that *C. rubescens* is found only in the western and northern oceanic reaches of Shark Bay, where the temperature range is not as great as within the two gulfs of this embayment and where the salinity is relatively constant (see Fig. 6.2). This species may thus be exposed to more favourable conditions for growth and different food sources. However, *C. schoenleinii*, which also grows rapidly, occurs predominantly within the embayment, and thus clearly copes well with the conditions it is exposed to.

Although the von Bertalanffy growth curves provided a good description of the lengths at age of the populations of each of the four tuskfish species in Shark Bay, the mean lengths of the males in the individual age classes of each species were generally greater than those of their females, a situation also found for the congeneric *Choerodon venustus* by Platten (2003). This implies that the individuals which grew most rapidly initially were more likely to become males. Such a situation has been proposed to occur with other protogynous species, *e.g.* the serranid *Plectropomus maculatus* and the scarid *Scarus frenatus* (Adams and Williams, 2001; Munday et al., 2004) and implies that larger size is required in order to be a successful male. Other studies of the growth of protogynous hermaphrodites, *e.g.* several scarids, the sandperch *Parapercis cylindrica*, the sparid *Chrysoblephus puniceus* and the saddleback wrasse *Thalassoma duperrey*
(Ross, 1987; Garratt *et al.*, 1993; Choat *et al.*, 1996; Walker and McCormick, 2004), have demonstrated or suggested that accelerated growth occurs in conjunction with sex change, *i.e.* there is a transitional growth spurt. On the basis of increased widths of growth zones on the opercula of *C. venustus* relative to the widths of previous zones, Platten (2003) suggested that this may also have occurred in the males of that species. However, that author recognised that it was difficult to prove the true reasons for the variations in width.

**Management implications**

The management implications of the size and age compositions and growth patterns of each of the four tuskfish species presented in this chapter are discussed in the conclusions.
Chapter 5

5.0 Comparisons between the biology of the baldchin groper *Choerodon rubescens* in Shark Bay and the Abrolhos Islands
5.1 Introduction

Life history parameters of individual species, including size and age at maturation, growth rates and mortality, may be influenced by demographic and environmental factors, such as population density, food availability and water temperature (Conover, 1992; Pollock, 1995; Barrett, 1999; Fromentin et al., 2001; Jennings et al., 2001; Pauly, 1980; Choat and Robertson, 2002; Vøllestad et al., 2002). Latitudinal variations in water temperature have been shown to influence the growth rates of the cod *Gadus morhua* and the Atlantic silverside *Menidia menidia* and yet have little effect on the growth rates of the stoplight parrotfish *Sparisoma viride* (Conover and Present, 1990; Choat et al., 2003; Vinje et al., 2003). The biological characteristics of a species may also vary across short distances, *e.g.* tens of kilometres (Gust et al., 2002; Gust, 2004). Variations in the biological parameters of different stocks of a species, such as growth rate and length at maturity, which is commonly used as a guide to establishing minimum legal lengths for retention, may have implications for the management of those stocks (Clark, 1991; Brodziak and Mikus, 2000; Hannah et al., 2002; Hill, 1990; Winstanley, 1990). Since *Choerodon rubescens* is an important commercial and/or recreational species across much of its geographic range in Western Australia, the development of effective management plans for sustaining the stocks of this species must take into account any biological differences that occur across this range.

Although Shark Bay (26°S) is approximately 300 km and 2.5° north of the Abrolhos Islands, both locations lie in the path of the warm Leeuwin Current, which flows southwards along the Western Australian coastline and helps account for the water temperatures at the two locations following similar seasonal trends (Pearce, 1991; Pearce et al., 1999). However, the mean monthly sea surface temperature is consistently between ca 0.5 and 2°C greater in South Passage in Shark Bay than that at Rat Island in
the Abrolhos Islands (Pearce et al., 1999). It is therefore hypothesised that, since water
temperature is frequently a cue for spawning activity (Lam, 1983), spawning will occur
slightly earlier in Shark Bay than in the Abrolhos Islands, but at a similar time of the
year. It is also hypothesised that, due to the very high productivity of the waters of
Shark Bay, as evidenced by the presence of large areas of dense seagrass (Walker,
1990), the growth of *C. rubescens* in these waters will be relatively rapid and greater
than in the less productive waters of the Abrolhos Islands. Thus, if maturity is related to
body size, it might be attained at an earlier age in Shark Bay than the Abrolhos Islands.
In Shark Bay, *C. rubescens* has indeterminate fecundity *sensu* Hunter et al. (1992) (see
Chapter 3) and thus individual females release multiple batches of eggs during a
spawning period. Since annual fecundity cannot thus be calculated from counts of all of
the oocytes in an ovary immediately prior to the spawning season and it was not feasible
to attain a series of samples during consecutive days for estimating the spawning
frequency of *C. rubescens*, only batch fecundities could be calculated for Shark Bay and
the Abrolhos Islands (Hunter and Macewicz, 1985).

Histological examination of the gonads confirmed that *C. rubescens* is a
monandric protogynous hermaphrodite in the Abrolhos Islands, as was demonstrated for
this species in Shark Bay (Chapter 3). Since heavy fishing pressure may affect the size
and age at which populations of a species change sex, e.g. Platten et al., (2002), the size
and age at which *C. rubescens* changes sex in the Abrolhos Islands, where fishing
pressure is greatest, will be less than in Shark Bay. Other demographic factors,
including the way the size and age compositions vary with water depth and the sex
ratios of the overall populations, adult populations and of fish above the minimum legal
length, obtained using different methods of capture in both regions, are also compared.
5.2 Materials and methods

Reproductive biology

Reproductive variables

The laboratory procedures used for macroscopic and histological analysis of the gonads of *C. rubescens* obtained from the Abrolhos Islands follow those described in Chapter 3. The length-weight relationship for *C. rubescens*: $\ln TW = 3.024\ln TL - 10.891$, derived from fish caught in the Abrolhos Islands, was used to estimate, for those fish obtained from the Abrolhos Islands via fish markets, the total wet weight they would have had prior to filleting. The estimated total weight of each fish could then be used in conjunction with its gonad weight to calculate its gonadosomatic index (see Chapter 3).

Length and age at sexual maturity

The lengths and ages of *C. rubescens* at sexual maturity and at sex change in the Abrolhos Islands were determined using the logistic regression analysis methods described in Chapter 3. A likelihood ratio test was used to compare both the lengths and ages at maturity, the lengths at sex change and the ages at sex change of *C. rubescens* in Shark Bay and the Abrolhos Islands. The null hypothesis that the data for both regions could be described by a common logistic curve, was compared with the alternative hypothesis that the data for each region would be better described by separate logistic curves. The test statistic was calculated as twice the difference between the log-likelihood obtained by fitting a common logistic curve to the data for both regions and by fitting separate logistic curves to the data for each region. The null hypothesis was rejected at the $\alpha = 0.05$ level of significance if the test statistic exceeded $\chi^2(q)$, where $q$ is the difference between the numbers of parameters in the common curve and the separate curves (Kimura, 1980).
Fecundity

Both of the ovarian lobes of individuals in a subsample of *C. rubescens* from Shark Bay and the Abrolhos Islands in which hydrated oocytes were macroscopically visible through the ovarian wall, *i.e.* stage IV (Chapter 3), were removed, weighed and placed in separate labeled vials containing 10% buffered formalin. The mid-region of one of the ovarian lobes of each of these fish was sectioned (see Chapter 3) and the resultant histological sections examined to determine whether they contained migratory nucleus stage oocytes or newly formed post-ovulatory follicles (POFs). Newly-formed POFs, *i.e.* < 6 h old, were identified using the descriptions provided by Hunter and Macewicz (1985) for this structure in ovaries of the northern anchovy *Engraulis mordax* and which applies similarly to many other marine teleosts, *e.g.* skipjack tuna *Katsuwonus pelamis*, the Brazilian menhaden *Brevoortia aurea* and the tarwhine *Rhabdosargus sarba* (Hunter *et al.*, 1986; Macchi and Acha, 2000; Hesp *et al.*, 2004c). Ovaries that contained either migratory nucleus stage oocytes or new POFs were not used for estimating batch fecundity (Hunter *et al.*, 1992).

In the histological sections of the remaining ovaries, atretic oocytes were separated into either the α or β stages of atresia, as described by Hunter and Macewicz (1985). Ovaries were then classified into one of four numerical stages according to the proportions of their α or β stage oocytes (Hunter and Macewicz, 1985). Ovaries in atretic state 0 contain yolk granule oocytes that are not exhibiting α atresia. Atretic state 1 and 2 ovaries have less than and greater than 50% of their yolk granule oocytes in the α stage of atresia, respectively. Ovaries in atretic state 3 have no yolk granule oocytes, but do contain oocytes in β stage atresia and are considered to be post-spawning. Ovaries in atretic state 0 and early atretic state 1, *i.e.* < 10% of yolk granule oocytes undergoing atresia, were considered to be in an “active reproduction mode” and were
therefore used for estimating the batch fecundity of the individuals of *C. rubescens* employing the hydrated oocyte method of Hunter *et al.* (1985).

The second of the ovarian lobes of each of these fish, that had been preserved in 10% neutrally-buffered formalin, was dried with blotting paper. A sample of ca 300 mg of tissue was removed from each of the anterior, middle and posterior regions of each ovary, placed on a microscope slide and covered with a few drops of 30% glycerol for ca 10 minutes and then by several more drops of glycerol. The tissue sample was teased apart under a dissecting microscope and the number of hydrated oocytes recorded. The number of hydrated oocytes in each of the three subsamples, in conjunction with the weight of the subsamples and the total weight of the ovary, were used to estimate the batch fecundity for each fish.

**Ageing methods and growth analysis**

The methods used to prepare otoliths and determine the ages of individual fish collected from the Abrolhos Islands and to analyse their growth, using the von Bertalanffy growth equation, are the same as those described in Chapter 4. Since spawning peaked at a similar time in the Abrolhos Islands as in Shark Bay (see Results), the same birth date of 1 December was assigned to *C. rubescens* for the former region. The parameters for the von Bertalanffy growth curves in each region were compared using a likelihood ratio test (see earlier).

**5.3 Results**

**Water temperatures and reproductive variables**

The mean water temperatures in each month in the oceanic waters of Shark Bay, were greater than the sea surface temperatures recorded by Pearce *et al.* (1999) for the corresponding months in the Abrolhos Islands (Fig. 5.1), except in December, when
they were 0.2°C less in the former region. Note that the high water temperature recorded in February in Shark Bay, was caused by warm water from within the western gulf passing through South Passage during an outgoing tide.

The mean monthly gonadosomatic index (GSI) of female *C. rubescens* ≥ the length at sexual maturity, *i.e.* $L_{50m}$ (see later), in Shark Bay rose sharply from 0.6 in July to 2.3 in September and then to a maximum of 2.7 in November, after which it declined precipitously to 1.1 in December and 0.8 in January and remained low, *i.e.* < 0.5, between February and June (Fig. 5.2a). The mean monthly GSI for female *C. rubescens* ≥ $L_{50m}$ (see later) in the Abrolhos Islands rose progressively from 0.3 in July to reach a maximum of 2.8 in November and then fell precipitously to 0.7 in December and
remained at low values of 0.2 to 0.3 from January to June (Fig. 5.2b). The mean monthly GSI of male *C. rubescens* in Shark Bay rose from 0.09 in August to 0.19 in October, before declining steadily to 0.06 in January and then remaining below 0.08 from February to April (Fig. 5.2a). In the Abrolhos Islands, the mean monthly GSI for male *C. rubescens* rose from 0.07 in July to 0.14 in August and remained elevated at between 0.12 and 0.17 until January, before declining and remaining below 0.1 from February to June (Fig. 5.2b).
Female *C. rubescens* that were ≥ *L*\textsubscript{50m} and possessed resting ovaries, *i.e.* stage I, were most abundant between February and July in Shark Bay and between April and June in the Abrolhos Islands (Fig. 5.3a, b). Females with developing ovaries, *i.e.* stage II, were first collected in May in Shark Bay and in June in the Abrolhos Islands (Fig. 5.3a, b). The ovaries of the vast majority of female *C. rubescens* sampled in both regions between September and November were either at the ripe or spawning stages, *i.e.* stages III-IV (Fig. 5.3a, b). Note that since it was not always possible to distinguish between stages III and IV macroscopically and not all ovaries were sectioned histologically, those two stages have been pooled for the purposes of analysis. Although some of the female *C. rubescens* caught in Shark Bay in December and January contained ovaries at stages III-IV, 52 and 21% of the females in those months, respectively, contained either spent or recovering ovaries, *i.e.* stages V or VI. By February, the ovaries of all females in that region were either recovering or resting, *i.e.* stage VI or I (Fig. 5.3a). The small number of female *C. rubescens* collected from the Abrolhos Islands in December and January contained either mature, recovering or resting ovaries. However, by February, the ovaries of all females were either recovering or resting (Fig. 5.3b).

**Fecundity**

The minimum, maximum and mean batch fecundities for *C. rubescens* in Shark Bay and the Abrolhos Islands are shown in Table 5.1. The relationships between ln batch fecundity (*BF*) and ln total length (*TL*) and between batch fecundity and total weight (*W*) for the populations in Shark Bay and the Abrolhos Islands (Fig. 5.4a, b) each had a positive slope that was significantly different from zero (ANOVA, *p* < 0.001). The parameters for each of those relationships are listed in Table 5.2.
Figure 5.3. Monthly percentage frequencies of occurrence of sequential stages in gonadal development of female *Choerodon rubescens* > *L*$_{50}$ at sexual maturity in (a) Shark Bay and (b) the Abrolhos Islands, derived from samples collected between July 2000 and January 2003. Data for the corresponding months in different years have been pooled. Sample sizes for each month are shown on each figure.
Figure 5.4. In batch fecundity vs ln total length (mm) (left-hand side) and batch fecundity vs total weight (g) (right-hand side) for *Choerodon rubescens* in (a) Shark Bay, (b) the Abrolhos Islands and (c) both regions (white circles and solid line = Shark Bay, grey circles and dashed line = Abrolhos Islands).
Table 5.1. Minimum, maximum and mean batch fecundities ($BF$), and the corresponding total lengths ($TL$) in mm and wet weights ($W$) in g for *Choerodon rubescens* in Shark Bay and the Abrolhos Islands.

<table>
<thead>
<tr>
<th>Location</th>
<th>$BF$ Sample size</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shark Bay</td>
<td>17</td>
<td>12100</td>
<td>90000</td>
<td>52700</td>
</tr>
<tr>
<td>$TL$</td>
<td>260</td>
<td>482</td>
<td>386</td>
<td></td>
</tr>
<tr>
<td>$W$</td>
<td>390</td>
<td>1817</td>
<td>1334</td>
<td></td>
</tr>
<tr>
<td>Abrolhos Islands</td>
<td>27</td>
<td>4298</td>
<td>128170</td>
<td>41635</td>
</tr>
<tr>
<td>$TL$</td>
<td>284</td>
<td>492</td>
<td>383</td>
<td></td>
</tr>
<tr>
<td>$W$</td>
<td>509</td>
<td>2551</td>
<td>1324</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.2. Parameters ($\pm$ 95% confidence intervals in parentheses) for the linear regressions fitted to data for ln batch fecundity ($BF$) vs ln total length ($TL$, mm), according to the equation $\ln BF = a \ln TL + b$, and for batch fecundity vs total weight ($W$), according to the equation $BF = aW + b$, for *Choerodon rubescens* in Shark Bay and the Abrolhos Islands. Note: Mean of squared residuals is not required for batch fecundity vs total weight relationship.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Location</th>
<th>a</th>
<th>b</th>
<th>Mean of squared residuals</th>
<th>$R^2$</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>ln Total length</td>
<td>Shark Bay</td>
<td>3.237 (2.176, 4.298)</td>
<td>-8.486 (-14.799, -2.173)</td>
<td>0.0741</td>
<td>0.738</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Abrolhos Islands</td>
<td>5.050 (4.037, 6.063)</td>
<td>-19.614 (-25.633, -13.595)</td>
<td>0.1270</td>
<td>0.808</td>
<td>27</td>
</tr>
<tr>
<td>Total weight</td>
<td>Shark Bay</td>
<td>37.02 (20.78, 53.25)</td>
<td>3276.49 (-19649, 26202)</td>
<td>-</td>
<td>0.61</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Abrolhos Islands</td>
<td>48.11 (38.92, 57.30)</td>
<td>-21599 (-34660, -8537)</td>
<td>-</td>
<td>0.823</td>
<td>27</td>
</tr>
</tbody>
</table>

Any estimated batch fecundities derived, in the future, using the length of a fish and the regression equations for ln batch fecundity vs ln total length, once back-transformed, must then be multiplied by the correction factor: $\exp(\text{mean of squared residuals}/2)$ as described in Chapter 4.3 (Beauchamp and Olson, 1973). The relationships for ln batch fecundity vs ln total length and for batch fecundity vs total weight for Shark Bay and the Abrolhos Islands were different (Fig. 5.4c). However, since only small sample sizes were obtained for each region, the use of ANCOVA to compare regression equations...
between regions may result in an increased risk of a type I error and thus an incorrect conclusion that the two regressions are significantly different.

**Sex ratios**

The sex ratios of *C. rubescens* collected using all methods were significantly different from parity in both Shark Bay and the Abrolhos Islands (*p* < 0.05, $\chi^2$ goodness of fit test; Table 5.3), with the proportion of females to males being greatest in Shark Bay. Sex ratios for adult *C. rubescens*, *i.e.* those fish that were $\geq$ the length at sexual maturity ($L_{50m}$) and were thus likely to be capable of reproduction, were determined using just the catches from rod and line fishing, since that was the only method used in both regions for collecting the full size range of fish and which could thus provide comparable data for the two regions. The ratio of females to males in this category was *ca* 14:1 (*p* < 0.05; Table 5.3). In Shark Bay and the Abrolhos Islands, the ratios of females to males in commercial catches of *C. rubescens* that were thus $\geq$ the MLL did not differ significantly from parity (*p* > 0.05; Table 5.3). However, this was not the case for fish $\geq$ the MLL that were caught by rod and line sampling and which would thus represent ratios similar to those that would be obtained from catches in the recreational fishery (*p* < 0.05). The ratios in this case were strongly in favour of females in both environments (Table 5.3)

**Lengths and ages at maturity**

As demonstrated for the females of *C. rubescens* in Shark Bay, the possession by females in the Abrolhos Islands, of gonads at stages II-VI and the trends exhibited by the maturity stages of females during the year strongly indicated that, by the end of the spawning period, such fish were destined to have spawned in that period and could thus
Table 5.3. Ratios of females to males of *Choerodon rubescens* in samples from Shark Bay and the Abrolhos Islands. Sample sizes shown in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Overall (all methods)</th>
<th>Adults, <em>i.e.</em> ≥ L&lt;sub&gt;50m&lt;/sub&gt; (rod and line sampling)</th>
<th>≥ MLL (400 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>*commercial line fishing</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><strong>rod and line sampling</strong></td>
</tr>
<tr>
<td><strong>Shark Bay</strong></td>
<td>12.3:1 (452)</td>
<td>14.4:1 (323)</td>
<td>1:1* (24)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5.6:1** (139)</td>
</tr>
<tr>
<td><strong>Abrolhos Islands</strong></td>
<td>1.7:1 (650)</td>
<td>14.4:1 (139)</td>
<td>0.93:1* (450)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>8.9:1** (89)</td>
</tr>
</tbody>
</table>

be used to estimate the length at which 50%, *i.e.* L<sub>50m</sub>, of the females of *C. rubescens* in the Abrolhos Islands, reach maturity. The minimum lengths at which sexually mature females of *C. rubescens*, *i.e.* females with ovaries at stages II-VI during the spawning period, in Shark Bay and the Abrolhos Islands were 230 and 229 mm, respectively (Fig. 5.5a, b). A likelihood ratio test demonstrated that the L<sub>50m</sub>s in Shark Bay (274 mm) and the Abrolhos Islands (279 mm), derived using logistic regression analysis were not significantly different (*p* > 0.05) and neither were their L<sub>95m</sub>s, *i.e.* 355 and 352 mm (Fig. 5.5a, b; Table 5.4). The youngest mature females of *C. rubescens* caught in Shark Bay and the Abrolhos Islands were two and three years old, respectively, and both the A<sub>50m</sub>s (2.7 and 4.1 years) and A<sub>95m</sub>s (4.4 and 6.2 years) in those two regions were significantly different (*p* < 0.05) (Fig. 5.5 a, b; Table 5.4).

**Length and age compositions and lengths and ages at sex change**

The length range of the females of *C. rubescens* caught in Shark Bay, 70 to 574 mm, was very similar to that recorded in samples of this sex in the Abrolhos Islands, 63 to 592 mm (Fig. 5.6a, b). In contrast, the length range of males in Shark Bay, 500 to 649 mm, was far narrower than in the Abrolhos Islands, 366 to 633 mm (Fig. 5.6a, b). The females of *C. rubescens* in Shark Bay and the Abrolhos Islands
Figure 5.5. The proportions of sexually mature females (○) in each length and age class for *Choerodon rubescens* during its spawning period in (a) Shark Bay and (b) the Abrolhos Islands, with the curve predicted using logistic regression analysis of the length (left-hand side) or age (right-hand side) and status (immature or mature) of individual fish ($L_{50m}$ and $A_{50m}$ ± 95% C.I.s shown (○); n = sample size). The proportions of transitional and male individuals pooled (□) in each length and age class for *Choerodon rubescens* in (c) Shark Bay and (d) the Abrolhos Islands, with the curve predicted using logistic regression analysis of the length (left-hand side) or age (right-hand side) and status (female or transitional and male pooled) of individual fish ($L_{50t}$ and $A_{50t}$ ± 95% C.I.s shown (□); $n_f$ = number of females and $n_m$ = number of males and transitional individuals pooled).
Figure 5.6. Length and age frequency compositions of female ( ), transitional ( ) and male ( ) *Choerodon rubescens* collected in (a) Shark Bay and (b) the Abrolhos Islands. Sample sizes of each sex and of transitional individuals shown on each figure.
belonged to the 0 to 12+ and 0 to 14+ age classes, respectively, while males belonged to the 6 to 16+ and 7 to 22+ age classes, respectively (Fig. 5.6a, b). The few transitional individuals of *C. rubescens*, which were all collected from the Abrolhos Islands, ranged in length from 395 to 514 mm and belonged to the 9 to 12+ age classes (Fig. 5.6b).

The lengths at which 50 and 95% of fish (\( L_{50c}, L_{95c} \)) were either transitional or male, *i.e.* were presumably changing or had changed sex, were 545 and 589 mm, respectively, for Shark Bay, and 479 and 595 mm, respectively, for the Abrolhos Islands (Fig. 5.5c, d; Table 5.4). Likelihood ratio tests demonstrated that the \( L_{50c} \)s in Shark Bay and the Abrolhos Islands were significantly different \((p < 0.05)\), but that the \( L_{95c} \)s were not \((p > 0.05)\). Likelihood ratio tests demonstrated that, while the \( A_{50c} \)s at sex change, *i.e.* the estimated ages at which 50% of *C. rubescens* had changed sex to males, were significantly different in Shark Bay (10.5 years) from the Abrolhos Islands (11.9 years), the corresponding \( A_{95c} \)s were not significantly different (13.3 and 14.8 years) (Fig. 5.5c, d; Table 5.4).

**Length and age compositions at different depths**

The length range of *C. rubescens* collected in shallow waters (< 20 m) in Shark Bay, 70 to 625 mm, and the Abrolhos Islands, 63 to 601 mm, were similar (Fig. 5.7a, b). The individuals of *C. rubescens*, that were purchased from wholesale fish markets and had been caught in waters of > 20 m in oceanic waters along the western boundary of Shark Bay and the Abrolhos Islands, ranged in length from 415 to 649 mm and from 366 to 629 mm, respectively (Fig. 5.7c, d). Fish collected in shallow and deeper waters ranged in age from 0 to 11+ and 7 to 16+ years, respectively, in Shark Bay, and from 0 to 13+ and 5 to 22+ years, respectively, in the Abrolhos Islands (Fig. 5.7a-d).
Figure 5.7. Length and age frequency compositions of female (◇), transitional (◼) and male (◻) Choerodon rubescens collected using line and spearfishing in shallow waters (< 20 m) in (a) Shark Bay and (b) the Abrolhos Islands and by commercial line fishing in deeper waters (> 20 m) in (c) Shark Bay and (d) the Abrolhos Islands. Sample sizes of each sex and of transitional individuals shown on each figure.
Table 5.4. Lengths and ages at sexual maturity ($L_{50m}$, $L_{95m}$, $A_{50m}$, $A_{95m}$ ± 95% CI; $P_{max}$ values ± 95% CI shown in parentheses below values for the $L_{50m}$ and $A_{50m}$) of females during the spawning periods and lengths and ages at sex change ($L_{50c}$, $L_{95c}$, $A_{50c}$, $A_{95c}$ ± 95% CI) of *Choerodon rubescens* in Shark Bay and the Abrolhos Islands.

<table>
<thead>
<tr>
<th></th>
<th>$L_{50m}$</th>
<th>Lower 95% CI</th>
<th>$L_{95m}$</th>
<th>Lower 95% CI</th>
<th>$L_{50c}$</th>
<th>Lower 95% CI</th>
<th>$L_{95c}$</th>
<th>Lower 95% CI</th>
<th>$P_{max}$ value ± 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shark Bay</strong></td>
<td>273.7 (0.94)</td>
<td>243.8 (0.86)</td>
<td>295.6 (1.00)</td>
<td>354.5</td>
<td>261.7</td>
<td>419.3</td>
<td>544.5</td>
<td>533.8</td>
<td>556.1</td>
</tr>
<tr>
<td><strong>Abrolhos Islands</strong></td>
<td>279.0 (0.93)</td>
<td>255.6 (0.88)</td>
<td>301.6 (0.98)</td>
<td>352.3</td>
<td>289.3</td>
<td>408.3</td>
<td>478.9</td>
<td>470.8</td>
<td>48.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>$A_{50m}$</th>
<th>Lower 95% CI</th>
<th>$A_{95m}$</th>
<th>Lower 95% CI</th>
<th>$A_{50c}$</th>
<th>Lower 95% CI</th>
<th>$A_{95c}$</th>
<th>Lower 95% CI</th>
<th>$A_{P_{max}}$ (years) ± 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shark Bay</strong></td>
<td>2.70 (0.95)</td>
<td>2.28 (0.89)</td>
<td>3.20 (1.00)</td>
<td>4.42</td>
<td>3.33</td>
<td>5.60</td>
<td>10.49</td>
<td>9.87</td>
<td>11.27</td>
</tr>
<tr>
<td><strong>Abrolhos Islands</strong></td>
<td>4.06 (0.92)</td>
<td>3.58 (0.88)</td>
<td>4.50 (0.97)</td>
<td>6.18</td>
<td>4.76</td>
<td>7.01</td>
<td>11.88</td>
<td>11.62</td>
<td>12.14</td>
</tr>
</tbody>
</table>
Growth

von Bertalanffy growth curves provided good fits to the lengths at age of individuals of *C. rubescens* in both Shark Bay and the Abrolhos Islands, as indicated by the high $R^2$ values (Fig. 5.8a, b; Table 5.5). The asymptotic length ($L_\infty$) was greater for the Shark Bay population (640 mm) than the Abrolhos Islands population (535 mm), whereas the reverse applied to the growth coefficient ($k$), *i.e.* 0.16 vs 0.19 year$^{-1}$ (Table 5.5). Likelihood ratio tests demonstrated that the von Bertalanffy growth curve for the population in Shark Bay was significantly different from that of the Abrolhos Islands ($p < 0.05$, Fig. 5.8c). Furthermore, when tested individually, the parameters $L_\infty$ and $k$ of the von Bertalanffy growth curve for the population in Shark Bay, were each significantly different from those of the growth curve for the population in the Abrolhos Islands ($p < 0.05$) (Fig. 5.8, Table 5.5).

The mean lengths of females and males of *C. rubescens* in each age class in Shark Bay were always greater than those of the females and males, respectively, in the corresponding age classes in the Abrolhos Islands (Fig. 5.9). The mean lengths of the males of *C. rubescens* were greater than those of their females in corresponding age classes in both Shark Bay and the Abrolhos Islands (Fig. 5.9).

**Table 5.5.** Parameters for the von Bertalanffy growth curve ($\pm$ 95% confidence intervals in parentheses) fitted to the lengths at age of *Choerodon rubescens* in Shark Bay and the Abrolhos Islands.

<table>
<thead>
<tr>
<th>von Bertalanffy parameters</th>
<th>$L_\infty$ (mm)</th>
<th>$k$ (year$^{-1}$)</th>
<th>$t_0$ (years)</th>
<th>$R^2$</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Shark Bay</em></td>
<td>639.7 (613.6, 665.7)</td>
<td>0.157 (0.142, 0.174)</td>
<td>-0.82 (-1.001, -0.617)</td>
<td>0.924</td>
<td>447</td>
</tr>
<tr>
<td><em>Abrolhos Islands</em></td>
<td>534.7 (521.1, 548.3)</td>
<td>0.192 (0.172, 0.214)</td>
<td>-0.162 (-0.481, 0.156)</td>
<td>0.789</td>
<td>580</td>
</tr>
</tbody>
</table>
Figure 5.8. von Bertalanffy growth curves fitted to the lengths at age of female (○), transitional (●) and male (□) *Choerodon rubescens* collected in (a) Shark Bay, (b) the Abrolhos Islands and (c) both regions.
Figure 5.9. Mean lengths of female (○) and male (□) *Choerodon rubescens* in Shark Bay and of female (●) and male (■) *C. rubescens* in the Abrolhos Islands. Sample sizes for females and males are shown at the bottom and top of each graph, respectively, for Shark Bay (SB) and the Abrolhos Islands (AI).
5.4 Discussion

Timing of the spawning period

Lam (1983) has proposed that increasing water temperatures and photoperiod often initiate gonadal recrudescence in teleost fish. Since recrudescence of the ovaries of *Choerodon rubescens* commenced in late autumn (May) in Shark Bay and early winter (June) in the Abrolhos Islands, it was initiated when water temperatures were still falling and photoperiod had essentially declined to its minimum level (Pearce et al., 1999, Anon., 2003e). Thus, gonadal recrudescence in *C. rubescens* does not coincide with an increase in water temperature, as occurs with many other species that spawn in the spring or early summer (Lam, 1983). However, gonadal development was particularly rapid between July and September, when photoperiod was increasing and water temperatures had either reached their minimum or had just started to rise (Fig. 5.1). Thus, at least in the case of *C. rubescens*, photoperiod would appear to be the most likely environmental candidate for stimulating gonadal recrudescence.

*Choerodon rubescens* spawns at essentially the same time of year in the Abrolhos Islands as in Shark Bay, *i.e.* from late winter to early summer. Since, in both regions, the prevalence of female *C. rubescens* with ovaries that were either ripe or in spawning condition was greatest in spring, *i.e.* September to November, spawning occurred mainly when water temperatures in those regions had started to increase from their winter minima (Fig. 5.1). However, spawning occurs at very similar times in Shark Bay as in the Abrolhos Islands, even though the water temperatures in the spring are substantially lower in the latter environment (Fig. 5.1). Thus, although there is circumstantial evidence that increasing water temperatures play a role in stimulating spawning activity, as is the case with many other teleosts (Lam, 1983), it would appear that it is the rise in temperature rather than the actual temperature that stimulates spawning. The production of larvae predominantly in the spring provides the 0+
juveniles of *C. rubescens* with a long growing season, which would enhance the likelihood of their survival, an advantage also proposed for other species, *e.g.* Conover and Present (1990), Conover (1992).

**Relationships between growth and the length and age at maturity**

The growth rate, $L_\infty$, and maximum age of *C. rubescens* in Shark Bay and the Abrolhos Islands differed. Thus, while individuals typically reach a larger size at any given age in Shark Bay than in the Abrolhos Islands, they do not apparently live as long in the former environment, *i.e.* maximum age is 16 vs 22 years. The faster growth rate of *C. rubescens* in Shark Bay than in the Abrolhos Islands is likely to reflect, at least in part, differences in the productivity of the two environments. It would appear particularly relevant that Shark Bay is highly productive, as is illustrated by the presence of large beds of dense seagrass (Walker, 1990). Thus, during each tidal cycle, the areas occupied by *C. rubescens* receive water from the shallow and highly productive inner gulfs of that embayment (Burling *et al.*, 2003), which, in turn, would lead to an increase in the density of the benthic macroinvertebrates that constitute the prey of this fish species (Elaine Lek, Murdoch University, pers. comm.).

The possibility cannot be excluded that the slower growth rate of *C. rubescens* in the Abrolhos Islands than in Shark Bay may be partly due to a density-dependent effect (Jones and McCormick, 2002). Thus, surveys conducted by Hutchins (2001b) throughout the distribution of baldchin groper, demonstrated that the abundance of this species is greatest in the Abrolhos Islands, which helps account for the fact that the waters of this region support the largest catches of *C. rubescens* (Crowe *et al.*, 1999). It is also relevant that experimental manipulations of the densities of the labrids *Tautogolabrus adspersus* and *Pseudolabrus celidotus* and of the pomacentrid *Pomacentrus amboinensis* led to the growth rate of each of these species being least.
when the densities were greatest (Jones, 1980; Jones, 1987; Tupper and Boutilier, 1995).

*Choerodon rubescens* reached maturity at a similar size in Shark Bay \((L_{50m} = 274\ mm)\) and the Abrolhos Islands \((L_{50m} = 279\ mm)\), which strongly suggests that the attainment of maturity by this species is size-related. The similarity in the size at maturity in the two populations, allied with the faster growth rate in Shark Bay, accounts for the fact that *C. rubescens* typically reaches maturity substantially earlier in that environment, as reflected in the respective \(A_{50m}\)s of 2.7 vs 4.1 years. The attainment of maturity at different ages at different locations parallels the situation recorded for the tarwhine *Rhabdosargus sarba* in Shark Bay and marine waters much further south at 32°S in Western Australia (Hesp and Potter, 2003) and for the labrids *Pseudolabrus celidotus* and *Semicossyphus pulcher* elsewhere (Jones, 1980; Cowen, 1990). They thus provide examples of the ways in which the age at maturation is modified in response to differences in growth rate (Stearns, 1992; Pollock, 1995; Morita and Morita, 2002).

### Size and age at sex change, sex ratios and the impacts of fishing

The attainment of maturity by *C. rubescens* approximately one year earlier in Shark Bay than in the Abrolhos Islands, apparently due to the effect of having a faster growth rate, is paralleled by the younger age at which, in the former region, the individuals first begin to change sex, *i.e.* 6 vs 7 years, and 50% have changed sex \(\left(A_{50c}\right)\), *i.e.* 10.5 vs 11.9 years. Thus, the younger age at which *C. rubescens* changes sex in Shark Bay than in the Abrolhos Islands apparently also reflects, to a large extent, the influence of a faster growth rate. Furthermore, the far larger size at sex change \(\left(L_{50c}\right)\) in Shark Bay (545 mm) than the Abrolhos Islands (479 mm) is associated with a greater \(L_{\infty}\) in the former region, *i.e.* 640 vs 535 mm. However, the length at sex change in the two regions represents similar percentage values of the maximum size of fish recorded
for each region, i.e. 84 and 76%, respectively, thereby essentially paralleling the situation found with a number of other species (Allsop and West, 2003).

Since rod and line angling caught the full size range of *C. rubescens*, and if it is assumed that both sexes are equally susceptible to this form of fishing, the ratio of 14♀:1♂ that was recorded in the samples of adults obtained from both Shark Bay and the Abrolhos Islands would approximate to the sex ratio of adult fish found in those two water bodies. Thus, sex ratios close to parity in samples obtained from commercial fishers in both Shark Bay and the Abrolhos Islands implies that commercial fishing has the potential to remove a relatively large number of the males in the population (see e.g. Alonzo and Mangel, 2004) and particularly those of the largest size, which have the greatest commercial value. Under such circumstances, there would be strong selection pressures for sex change to occur at a smaller size (e.g. Buxton, 1993; Huntsman *et al.*, 1999; Hawkins and Roberts, 2003). Indeed Platten *et al.* (2002) have demonstrated that heavy fishing pressure on *Choerodon venustus* at one location on the Great Barrier Reef has led to this species changing sex at a smaller size and younger age at this location than in other lightly fished or protected locations. Although *C. rubescens* began to change sex at a far smaller size in the Abrolhos Islands (366 mm), where fishing pressure is greatest, than in Shark Bay (500 mm), the $A_{50c}$ at sex change is greater in the former region. There is thus circumstantial evidence that fishing pressure has not led to a reduction in the age at sex change, as in *C. venustus*. However, continued heavy fishing pressure may ultimately result in a decrease in both the size and age at which this species changes sex in the Abrolhos Islands.
Chapter 6

6.0 Distribution and habitat partitioning of *Choerodon* species in Shark Bay
6.1 Introduction

Successful management of the stocks of a fish species requires data not only on aspects of its biology, such as size and age compositions, growth and reproduction, but also on the habitats occupied by that species and whether they change during the life cycle. The information on the habitats of a species can then be used to determine, for example, the most appropriate areas for closure to fishing, with a view to protecting the stocks of that species (Bohnsack, 1998; Agardy, 2000; Halpern and Warner, 2002).

The approaches used to determine the relative abundances of certain fish species, such as those involving the catches obtained by trawling, seine netting, trapping and line fishing, frequently have limitations due to the fact that those species exhibit either net avoidance, trap shyness or rarely take bait (Harmelin-Vivien and Francour, 1992; Appledoorn, 1996; Wassenberg et al., 1997; Connell et al., 1998). Furthermore, most sampling methods can only be used in certain habitat types, e.g. trawling can be employed to sample seagrass and bare sand, but not reefs. Since it is necessary to use several methods to obtain samples of those species that occupy diverse habitat types at different stages in their life cycles, comparisons between the abundances derived from the use of those various methods must be made with caution. For the above reasons, underwater visual census techniques, which can be employed in a wide range of habitats, are now widely used to determine the relative abundances of those fish species that occupy different habitats during their life cycle (e.g. Gillanders, 1997; Jenkins and Wheatley, 1998; Guidetti, 2000; Nagelkerken et al., 2000, 2001). These visual techniques also have the great advantage of avoiding fish mortality and habitat damage (English et al., 1997; Watson and Quinn, 1997).

The large subtropical embayment of Shark Bay contains a diverse range of habitat types, which include unvegetated sand, seagrass, mangroves, intertidal rocky shorelines, rocky reefs and coral patches (Marsh, 1990; Anon., 1996). However, data on
the abundance of the most important fish species in this environment have been based either on studies of a restricted number of habitat types in the inner gulfs, *e.g.* seagrass and sand (Black *et al.*, 1990; Travers and Potter, 2002), or on surveys of different habitat types in South Passage and around Bernier and Dorre Islands (Hutchins, 1990; Hutchins, 1995) (Fig. 6.1). Thus, the allocation of no-take sanctuary zones for fish in Shark Bay by the Department of Conservation and Land Management (Anon., 1996) had to be made in the absence of sound quantitative data on the types of habitat occupied by the most important species at different stages in their life cycle.

Labrids are very well represented in Shark Bay (Hutchins, 1990; Hutchins, 1995), with members of the *Choerodon* genus, and particularly *C. rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma*, being found to be relatively abundant in this environment during the present study. Although there are broad accounts of the types of habitat occupied by the above *Choerodon* species throughout their distributions (Allen, 1999; Randall *et al.*, 1997), there has been no previous attempt to determine quantitatively the range of habitat types occupied by the various stages in the life cycle of these species in any environment.

The aim of this component of the study was to test the hypothesis that, in Shark Bay, the abundant *Choerodon* species will tend to occupy different habitat types and will shift habitat type at some stage in their life cycles, *i.e.* as they reach adulthood. Such habitat partitioning would reduce the potential for both inter- and intraspecific competition for spatial resources in Shark Bay by these abundant species.
6.2 Materials and methods

Overall distribution

Data collected during the present and previous studies through trawling, seine netting, angling and spear fishing and opportunistic underwater observations from a large number of sites in the two inner gulfs and oceanic regions of Shark Bay (Fig. 6.1), were collated to obtain a broad picture of how the four abundant *Choerodon* species, and the other representative of this genus (*Choerodon cephalotes*) in Shark Bay, were distributed in that large embayment. The earlier data for seagrass and bare sand sites at Monkey Mia, Herald Bight, Denham and Nanga were derived from the seine net samples of Pember (1999) and trawl samples of Travers and Potter (2002), while those for seine net sites in mangrove areas at Herald Bight and Dubaut Creek were derived from King (2003) (Fig. 6.1).

Visual surveys

Underwater visual surveys of the five *Choerodon* species found in Shark Bay were conducted at fourteen sites in five habitat types, *i.e.* inner gulf reefs, inner gulf rocky shorelines, inner gulf seagrass, inner gulf bare sand and reefs in oceanic locations of this embayment (Fig. 6.1; Table 6.1). Note that underwater visual surveys were not employed in mangroves, as this would have been virtually impossible and, in any case, *Choerodon* species were not found during extensive seine netting of this habitat type (King, 2003). The water depths at each of the 14 sites and the number of times (seasons) they were surveyed, including the number of replicate transects on each sampling occasion, are given in Table 6.1. The surveys were conducted using a 50 m long × 5 m wide transect (English et al., 1997). The length of each transect was measured by placing a weight on the substrate and unravelling an attached 50 m rope as the diver swam along the transect, to minimise the likelihood of disturbing fish prior to counting.
Figure 6.1. Map of Shark Bay showing sites sampled by line and spearfishing (○), trawling and seine netting (●) and underwater visual survey sites (1-14, ○). Note that dashed circles represent groupings of sites presented in Table 6.2.
The transects over bare sand (sites 3 and 8), *Posidonia coriacea* seagrass (sites 9 and 10) and reefs (sites 11-14) were arranged parallel to each other and were located at least 20 m apart. However, because of the narrowness of the sites at the rocky shoreline (sites 2, 4 and 7) and reef habitats (sites 1, 5 and 6), the transects at those sites were longitudinally arranged, with the opposing ends of successive transects being separated by at least 10 m. The number of individuals observed of each tuskfish species along each transect were counted and each individual was allocated by eye to its appropriate 50 mm (TL) length class. The author conducted all surveys to ensure consistency of survey technique, identification of species and fish measurements. In all but the first few samples, each fish was recorded as a juvenile or adult using its length in the following manner:
(1) The individuals of *C. rubescens*, *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* were regarded as having changed from juvenile to adult when their lengths were greater than those of the approximate $L_{50\text{m}}$ at sexual maturity, *i.e.* 300, 250, 200 and 150 mm, respectively (see Chapter 3).

(2) Since only 95 *C. cephalotes* were caught by line and spear fishing during the present study and during the previous trawling study (Travers and Potter, 2002), the length at sexual maturity of this species could not be reliably determined using logistic regression analysis. Thus, adopting a conservative approach, this species was regarded as becoming adult when it was ≥ 150 mm, which is 20 mm above the length at which some of the females of this species contained gonads beyond stage I (see Chapter 3).

Analyses

*Species composition in different habitat types*

The number of individuals of each species observed in each transect at each site on each sampling occasion was converted to a density (fish 100m$^{-2}$). The mean densities of each of the five *Choerodon* species at each site over inner gulf reefs, rocky shorelines, seagrass and oceanic reefs on each sampling occasion were square-root transformed and then used to construct a Bray-Curtis similarity matrix employing the PRIMER v 5.2 package (Clarke and Gorley, 2001). The matrix was then subjected to non-metric multidimensional scaling ordination (MDS). Since no *Choerodon* species were observed at either of the two sites representing the unvegetated sand habitat (sites 3 and 8), or at one of the sites representing the rocky shoreline habitat (site 2), these sites were not included in the above analyses.

One-way analysis of similarities (ANOSIM) was employed to test whether the compositions of *Choerodon* species in the different habitat types were significantly
different (Clarke, 1993). The null hypothesis that there was no significant difference between habitat types was rejected when the significance level ($p$) was $> 5\%$. The associated $R$-statistic values in the ANOSIM test ranges largely between 0, \textit{i.e.} all samples in all habitat types are similar in composition, and 1, \textit{i.e.} all samples in each habitat type are more similar to each other than to any sample from any other habitat type (Clarke, 1993). When ANOSIM detected a significant difference between habitat types, Similarity Percentages (SIMPER) was used to determine which species typified and distinguished the samples observed in each habitat type (Clarke, 1993).

\textbf{Habitat preference of juvenile and adult life cycle stages}

To investigate the extent to which the juveniles and adults of \textit{C. rubescens}, \textit{C. schoenleinii}, \textit{C. cauteroma} and \textit{C. cyanodus} occupied different habitat types, the number of individuals of each life cycle stage of each of those species in each replicate sample was converted to a density (fish 100 m$^{-2}$), which was then square-root transformed. The transformed data for each species were used to construct separate Bray-Curtis similarity matrices, which were then each subjected to MDS ordination (Clarke and Gorley, 2001). Circles of differing magnitude, reflecting the relative densities of both life cycle stages in each replicate, were then superimposed on the samples in each of the resultant plots. Note that the data for the densities of the juveniles and adults of \textit{C. cephalotes} could not be used to construct a Bray-Curtis similarity matrix, since both of the life cycle stages of that species occurred almost exclusively at one site within one habitat type, \textit{i.e.} seagrass. One-way ANOSIM was employed to test whether the life cycle stage composition of \textit{C. schoenleinii}, \textit{C. cyanodus} and \textit{C. cauteroma} differed between habitat types (Clarke, 1993). When the results of those tests were significant, SIMPER was used to determine which life cycle stage of each of those species typified and distinguished between each habitat type (Clarke, 1993).
data for *C. rubescens* and *C. cephalotes* were not subjected to ANOSIM and SIMPER since these two species were recorded in only one habitat type.

### 6.3 Results

**Overall distribution of *Choerodon* species**

The mean monthly salinities at the “sampling” sites in the eastern and western gulfs ranged from 38.5 to 41.5‰ and from 36.4 to 42.1‰, respectively (Fig. 6.2). In contrast, in the “oceanic” waters along the western side of Shark Bay and in South Passage, they lay between 33.6 and 34.8‰ in all months except August (Fig. 6.2).

The samples obtained from many sites within the inner gulfs and oceanic waters of Shark Bay using different methods, *i.e.* trawling (Travers and Potter, 2002), seine netting (Pember, 1999; King, 2003) and rod and line fishing, together with observations made during spot dives in the course of the present study (Fig. 6.1), enabled the following broad conclusions to be drawn. *Choerodon rubescens* was collected or observed only in the oceanic regions of Shark Bay, *i.e.* at sites in South Passage and along the west coast and northern end of Dirk Hartog Island and around Bernier and Dorre Islands in the very northern part of Shark Bay (Table 6.2). In contrast, *Choerodon schoenleinii*, *C. cyanodus*, *C. cauteroma* and *C. cephalotes* live predominantly at inner gulf sites and at sites on the eastern sides of Bernier and Dorre Islands (Table 6.2). None of the five species was collected or observed over bare sand or at the rocky shoreline at site 2.

MDS ordination of the mean densities of each of the five tuskfish species in each of the four habitat types over which they were observed, showed that the samples from seagrass, and particularly those from oceanic reefs formed distinct and discrete groups on the resultant ordination plot (Fig. 6.3). The majority of the samples from
Figure 6.2. Mean monthly salinities ± 1 S.E. recorded at all sites sampled on each sampling occasion in the eastern (■) and western gulfs (□) of Shark Bay and in the oceanic waters (▲) along the western boundary of Shark Bay. Data for each month of the year are pooled from 2000 to 2003.

Figure 6.3. Non-metric multidimensional scaling ordination plot of the mean densities of the five Choerodon species at each site over inner gulf reefs, rocky shorelines, seagrass and oceanic reefs on each sampling occasion.
inner gulf reefs formed a relatively tight group that lay close to the relatively well-dispersed group of samples from rocky shorelines (Fig. 6.3).

ANOSIM demonstrated that the species composition of the four habitat types were significantly different overall ($p = 0.1\%$, Global R-statistic = 0.808). Pairwise comparisons showed that, although the species composition in each habitat type was significantly different from that in each of the other habitat types ($p = 0.1\%$ in all cases except inner gulf reefs vs rocky shorelines when $p = 4.2\%$), the differences in species composition were greatest in the case of oceanic reefs vs each of the other three habitat types, with the associated R-statistic values each being close to 1. The compositions in seagrass differed more markedly from those in inner gulf reefs than rocky shorelines ($R$-statistic = 0.832 and 0.559, respectively). The $R$-statistic value for the comparison between inner gulf reefs and rocky shorelines was only 0.197.

SIMPER demonstrated that *C. schoenleinii*, *C. cyanodus*, *C. cephalotes* and *C. rubescens* typified the inner gulf reef, rocky shoreline, seagrass and oceanic reefs, respectively (Table 6.3). *Choerodon cauteroma* also typified the fauna in the first three habitat types and the distinguishing component of the SIMPER analyses did not indicate that this species had a particular preference for any one of those habitat types.

*Choerodon rubescens* was observed at each of the three oceanic reef sites, but not at any of the sites representing the other three habitat types (Fig. 6.4). The mean densities of this species at the three oceanic reef sites ranged from 1.0 to 2.1 fish 100m$^{-2}$. Although *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* were all observed at each of the four inner gulf reefs, the relative densities of those species at those sites varied markedly. Thus, the maximum mean density in fish 100m$^{-2}$ was 6.2 for *C. schoenleinii* 100m$^{-2}$ at site 1, compared with 2.3 for *C. cyanodus* 100m$^{-2}$ at site 4 and 3.5 for *C. cauteroma* at site 3 (Fig. 6.4). *Choerodon schoenleinii*, *C. cyanodus* and *C. cauteroma* were each observed at the same two of the three rocky shoreline sites, and the maximum mean
Table 6.2. Total number of sampling occasions or replicates (in the case of seining and trawling) and the number of fish collected at sites in the eastern and western gulfs of Shark Bay and in oceanic waters around Bernier, Dorre and Dirk Hartog (DHI) Islands. Note: number of individual reef sites at each main site shown in parentheses. Sampling trips conducted to Bernier and Dorre Islands and to reef sites at Nanga were predominantly for visual observation.

<table>
<thead>
<tr>
<th>Location</th>
<th>Site</th>
<th>Habitat type</th>
<th>Method</th>
<th>Number of sampling occasions/replicates</th>
<th>Choerodon rubescens</th>
<th>Choerodon schoenleinii</th>
<th>Choerodon cyanodus</th>
<th>Choerodon cauteroma</th>
<th>Choerodon cephalotes</th>
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<td>7</td>
<td>18</td>
<td>1</td>
<td>-</td>
<td>2</td>
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</table>
Table 6.3. *Choerodon* species detected by SIMPER as most important for typifying (shaded grey) the (1) inner gulf reefs, (2) rocky shorelines, (3) seagrass and (4) oceanic reefs and as most important for distinguishing each pair of habitat types (see white cells containing species arranged in descending order of importance). The habitat type at which distinguishing species were most abundant is also provided in each case for each pairwise comparison (see superscripts).

<table>
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<tr>
<td>1</td>
<td><em>C. schoenleinii</em></td>
<td><em>C. cauteroma</em></td>
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<tr>
<td>2</td>
<td><em>C. schoenleinii</em></td>
<td>(1) <em>C. cauteroma</em></td>
<td><em>C. cyanodus</em></td>
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<td>3</td>
<td><em>C. schoenleinii</em></td>
<td>(1) <em>C. cephalotes</em></td>
<td>(3) <em>C. cauteroma</em></td>
<td>(3) <em>C. cephalotes</em></td>
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<td>4</td>
<td><em>C. rubescens</em></td>
<td>(4) <em>C. rubescens</em></td>
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<td>(2) <em>C. cauteroma</em></td>
<td>(3) <em>C. cephalotes</em></td>
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Density of *C. cyanodus* at one of those sites, *i.e.* 2.5 fish 100m$^{-2}$, was similar to the density recorded at the fourth of the inner gulf reef sites. Although *C. cyanodus* and *C. cauteroma* were both observed in the two seagrass sites, the mean densities of 3.6 and 3.4 fish 100m$^{-2}$ for the latter species at these sites were far greater than those of the former species, *i.e.* 0.1 and 0.3 fish 100m$^{-2}$ (Fig. 6.4). Small numbers of *C. cauteroma* were observed at each of the three oceanic reef sites. *Choerodon cephalotes* was abundant only at one of the seagrass sites, where its mean density was 3.1 fish 100m$^{-2}$ (Fig. 6.4).

**Relationships between life cycle stages and habitat type**

The MDS ordination plot of the densities of the juveniles and adults of *C. rubescens* emphasises that the juveniles and adults of *C. rubescens* are both found exclusively on oceanic reefs and that they co-occur, but in varying proportions, at the sites representing that habitat type (Fig. 6.5a, b). Since the adults and juveniles...
Figure 6.4. Mean density ± 1 S.E. of Choerodon rubescens, Choerodon schoenleinii, Choerodon cyanodus, Choerodon cauteroma and Choerodon cephalotes at each site over inner gulf reefs ( □ ), rocky shorelines ( □ ), seagrass ( □ ) and oceanic reefs ( ■ ) during underwater visual surveys. Total number of replicate transects at each site shown at top. Zero values left blank.
of this species were recorded in only one habitat type, analysis using ANOSIM and SIMPER were not required.

MDS ordination and overlaying of the densities of the juveniles and adults of *C. schoenleinii* demonstrated that, while the adults of this species occurred over both inner gulf reefs and, to a lesser extent, rocky shorelines, their juveniles occurred almost entirely in the first of these habitat types (Fig. 6.6a, b). The results of ANOSIM showed that the composition of the life cycle stages of this species differed significantly between habitats (*p* = 0.1%; *R*-statistic = 0.370). The SIMPER results demonstrated that this significant difference was due to the fact that, although juveniles and adults were both found on inner gulf reefs, the adults were more abundant and occurred more consistently in that habitat. The MDS ordination plot of the densities of the juveniles and adults of *C. cauteroma* showed that, while the adults of this species occurred over inner gulf reefs and rocky shorelines and, to a lesser extent, seagrass, their juveniles were restricted almost entirely to seagrass (Fig. 6.7a, b). ANOSIM provided formal evidence that the difference in the spatial distribution of the life cycle stages of this species was significant (*p* = 0.1%, *R*-statistic = 0.194). Furthermore, SIMPER demonstrated that the adults of this species occurred in the greatest densities and most consistently on inner gulf reefs and rocky shorelines, while the juveniles were far more abundant and occurred more regularly than adults over seagrass habitats. MDS ordination and overlaying of the densities of the juveniles and adults of *C. cyanodus* on the resultant plot showed that neither of the life cycle stages of this species exhibited a strong preference for the inner gulf reefs, rocky shorelines or seagrass habitats (Fig. 6.8a, b). This accounts for the fact that ANOSIM failed to detect a significant difference in the compositions of the two life cycle stages among habitat types (*p* = 71.1%).
Figure 6.5. Non-metric multidimensional scaling ordination plot of the densities of the (a) juveniles and (b) adults of *Choerodon rubescens* in each replicate, as indicated by the magnitude of the size of the circles, on (1) inner gulf reefs, (2) rocky shorelines, (3) seagrass and (4) oceanic reefs. Arrows indicate where individual replicates overlap.
Figure 6.6. Non-metric multidimensional scaling ordination plot of the densities of the (a) juveniles and (b) adults of *Choerodon schoenleinii* in each replicate, as indicated by the magnitude of the size of the circles, on (1) inner gulf reefs, (2) rocky shorelines, (3) seagrass and (4) oceanic reefs. Arrows indicate where individual replicates overlap.
Figure 6.7. Non-metric multidimensional scaling ordination plot of the densities of the (a) juveniles and (b) adults of *Choerodon cauteroma* in each replicate, as indicated by the magnitude of the size of the circles, on (1) inner gulf reefs, (2) rocky shorelines, (3) seagrass and (4) oceanic reefs. Arrows indicate where individual replicates overlap.
Figure 6.8. Non-metric multidimensional scaling ordination plot of the densities of the (a) juveniles and (b) adults of *Choerodon cyanodus* in each replicate, as indicated by the magnitude of the size of the circles, on (1) inner gulf reefs, (2) rocky shorelines, (3) seagrass and (4) oceanic reefs. Arrows indicate where individual replicates overlap.
6.4 Discussion

The distributions of each of the five *Choerodon* species amongst different habitat types in Shark Bay, as revealed by visual surveys of 14 sites encompassing five habitat types, are consistent with the locations where these species had been collected during previous trawling and seine netting in this environment (Pember, 1999; Travers and Potter, 2002; King, 2003) and had been caught by line and spear fishing and/or observed when diving during the present study.

During the visual surveys, *Choerodon rubescens* was observed only over oceanic reefs in South Passage, which is one of the three main entrance channels to Shark Bay (Fig. 6.1). Furthermore, this species occurred only in those samples that were collected from this channel, as well as on reefs along the western coastlines of Dirk Hartog, Bernier and Dorre Islands, and which were used to obtain biological data for this species (Chapters 2-4; Table 6.2). Although substantial numbers of the juveniles, as well as the adults of *C. rubescens*, were observed over oceanic reefs, none of the juveniles were < 100 mm in length. Sampling that focused on obtaining small 0+ recruits indicates that this species initially occupies adjacent algal habitats in oceanic waters (Fig. 6.9) before moving to oceanic reefs when it is nearing the end of its first year of life (Fig. 6.9). Another labrid, *Pseudolabrus celidotus*, also uses macroalgal habitats as a nursery (Jones, 1984).

The implication that *C. rubescens* has a strong preference for waters which are directly exposed to the Indian Ocean and remain close to full strength salinity (35‰), is consistent with the locations where Hutchins (1990, 1995) recorded this species during his visual surveys. The maintenance of the salinity at about 35‰ and exposure to substantial wave action in the areas occupied by *C. rubescens* contrasts with the situation in the inner gulfs, in which the waters typically range from
metahaline to hypersaline and are not exposed to heavy seas (see Fig. 2.2; Logan and Cebulski, 1970; Burling et al., 2003).

**Figure 6.9.** Photographs of oceanic (a) algal habitat occupied by small (< 100 mm) juvenile *Choerodon rubescens* and (b) reef habitat occupied by larger juvenile and adult *C. rubescens*.

In contrast to *C. rubescens*, each of the other four *Choerodon* species occurs either exclusively or predominantly in habitats within the main body of the embayment. Thus, *C. cephalotes* lives almost entirely in seagrass, while *C. schoenleinii* and *C. cyanodus* occupy mostly inner gulf reefs and rocky shorelines and *C. cauteroma* occurs in all three of those habitats. Although *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* were all observed at each of the reef sites in the inner gulfs, the sites at which these species were most abundant varied. Thus, *C. schoenleinii* was observed most frequently at site 1, *C. cyanodus* at site 11 and *C. cauteroma* at sites 5 and 6. The variability in the densities among the four reef sites may reflect, in part, the preference for particular habitats, since site 11 consisted of coral, while sites 1, 5 and 6 comprised flat limestone. It may also reflect a tendency for reef species often to be territorial or have a home range (e.g. Zeller, 1997; Gonçalves and Almada, 1998; Chapman and Kramer, 2000; Zekeria et al., 2002). The occurrence of *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* at two of the three rocky shorelines (sites 4 and 7) implies that this habitat type provides an
alternative habitat to reefs for these species. Since none of the *Choerodon* species were observed at rocky shoreline site 2, it may be relevant that this site was essentially flat and thus did not provide the type of structural rugosity that these species commonly use as refugia (pers. obs.; *e.g.* Nanami and Nishihira, 1999; Mumby and Wabnitz, 2002).

*Choerodon cauteroma* was the only species that was shown by the results of the visual surveys to undergo an obvious shift in habitat type between its juvenile and adult life cycle stages. Thus, while the juveniles of this species were found almost entirely over seagrass, the adults occupied predominantly inner gulf reefs and rocky shorelines. These results are consistent with the fact that the numbers of the juveniles of this species caught during extensive trawling of seagrass beds in Shark Bay were sufficiently high to rank this species ninth in terms of abundance among 83 species recorded in those meadows (Travers and Potter, 2002). The use of seagrass by *C. cauteroma* as a nursery area parallels the situation found with a number of other species that spend the adult part of their life over reefs, including another labrid, *i.e.* *Achoerodus viridis* (Gillanders, 1997; Guidetti, 2000; Nagelkerken *et al.*, 2001; Gilllanders *et al.*, 2003).

The densities of the juveniles and adults of *C. schoenleinii* differed significantly in the types of habitat they occupied during those life cycle stages. However, these results were not attributable to an obvious shift in habitat type, *i.e.* juveniles and adults both occurred largely over inner gulf reefs, but were due more to the adults of this species occurring in higher numbers and more consistently in that habitat type than the juveniles. Substantial numbers of the larvae and small individuals (< 130 mm) of *C. schoenleinii* were caught by Kanashiro (1998) in seagrass in Japanese waters, while the larger individuals of this species occur over
reefs in those waters (Ebisawa et al., 1995). Such results contrast with those found in this embayment, where this species was never observed in seagrass and was caught only in very low numbers during trawling of seagrass (Travers and Potter, 2002).

In contrast to the other Choerodon species in Shark Bay, the juveniles and adults of C. cephalotes were both observed predominantly in seagrass. However, this species was more abundant at the site that consisted of seagrass and sand patches than at the dense seagrass site, which agrees with the results of visual surveys carried out on two occasions at other sites in patchy and dense seagrass. Despite the fact that the large seagrass meadows abut large areas of unvegetated sand in Shark Bay, none of the five tuskfish species were observed or caught over bare sand.

The results of the visual surveys reported in this chapter emphasise that the compositions of the Choerodon species in Shark Bay vary significantly among each of the four habitat types in which these species occur. The compositions over oceanic reefs and over seagrass were particularly discrete, while those over inner gulf reefs and along rocky shorelines were less distinct from each other. Choerodon rubescens was found only in one habitat type, while C. cauteroma was observed in all four habitat types and C. schoenleinii and C. cyanodus were observed in three habitat types. In addition, the juveniles and adults of C. cauteroma typically occupy very different habitat types. The above results demonstrate that there is a considerable amount of partitioning of Choerodon species among habitat types in Shark Bay and that this partitioning can extend to different life cycle stages. These variations in distribution patterns would reduce the likelihood of inter- and intraspecific competition for spatial resources by the abundant members of an important labrid genus in that embayment.
Chapter 7

7.0 Conclusions
Declining fish stocks are a worldwide problem (Jackson et al., 2001; Pauly et al., 2002). There are many examples of where heavy fishing pressure, lack of data, poor quality research and/or inappropriate management or lack of management has led to the decline of fish stocks, e.g. Myers et al., 1997; Jackson et al., 2001; Pauly et al., 2002; Myers and Worm, 2003 and Sadovy and Cheung, 2003. Although Western Australia has a relatively small population and an extensive coastline, many of its existing fisheries are already considered fully exploited (Penn et al., 2003). However, since the population of this state is growing and becoming more widely distributed along the coastline, the demand on fish stocks will inevitably increase. Furthermore, although Western Australia is considered to have well-managed fisheries, there are still many species for which there are no basic biological data of the type required for developing appropriate management plans for conserving their stocks. Thus, the major aims of the present study were to provide the relevant biological data for some of the key labrid species in Western Australia.

Traditional considerations and current management practices for the four Choerodon species

Although C. cyanodus, C. cauteroma, C. schoenleinii and C. rubescens ranged markedly in maximum length in Shark Bay, i.e. 382 to 805 mm, their lifespans ranged only from 12 to 16 years. Furthermore, each of the four species matured at young and similar ages in Shark Bay, i.e. $A_{50w}$ ranged only from ca 2 to 3.5 years, and thus all have relatively short generation times. Choerodon rubescens matures approximately one year later in the Abrolhos Islands, i.e. $A_{50w}$ of ca 4 years of age, than in Shark Bay, and thus the generation time in the former environment is slightly longer. The short generation times would potentially make these species less
susceptible to overfishing than longer-lived and later-maturing species, e.g. some serranids (Huntsman et al., 1999; Coleman et al., 1999, 2000).

The MLL of 400 mm for *C. rubescens* and *C. schoenleinii* is far less than their maximum lengths of *ca* 650 and 900 mm, respectively, but greater than the *L*₅₀ₙₘₖ in Shark Bay, *i.e.* 274 and 253 mm, respectively. On the basis of data on their ages at maturity and growth rates, the females of those two species can spawn, on average, during approximately two and three spawning seasons, respectively, before they can be retained by fishers at a length of 400 mm. *Choerodon rubescens* matures at a similar length in the Abrolhos Islands (279 mm) as in Shark Bay and thus also well below the MLL for this species. However, since the growth of *C. rubescens* is slower in the Abrolhos Islands, sexual maturation is delayed in this region and, on the basis of the von Bertalanffy growth curve, individuals do not become susceptible to fishing until three years after maturation. Although *Choerodon cyanodus* is reported to reach 600 mm in length (Allen, 1999), it was never caught in Shark Bay above its current minimum legal length (MLL) for retention of 400 mm. The current legislation thus protects this species from retention by fishers. *Choerodon cauteroma* is also a relatively small species, rarely reaching 400 mm, but currently has no MLL, which thus allows the capture of fish of any size. However, recreational fishers are restricted to a catch limit of four fish per person per day of this as well as all other *Choerodon* species. Although there are no catch restrictions for *Choerodon* species by commercial fishers in Shark Bay, the commercial fishery for the members of this genus in this large embayment is very small (Crowe et al., 1999).

Since the fishery for the four *Choerodon* species in Shark Bay is predominantly a recreational fishery, and the main recreational fishing season occurs during the autumn and winter when the strong prevailing winds are weakest, *i.e.*
April to August, these species are typically exploited for only half of the year and this is outside their main spawning period, *i.e.* September to February. Thus, spawning fish would not typically be captured by fishers in large numbers. Furthermore, as visual surveys did not reveal any substantial increases in the numbers of any of the four species at individual reef sites during their spawning seasons, it is unlikely that these species aggregate to spawn at sites in that embayment. Such aggregations do occur in other species and, in the case of some serranid species, *e.g.* *Epinephelus striatus*, resultant overfishing have led to detrimental effects on their stocks (Domeier and Colin, 1997; Sadovy and Eklund, 1999). As commercial fishers regularly target *C. rubescens* in the Abrolhos Islands throughout the year, fishing pressure is much greater on this species in that location (Crowe *et al.*, 1999). Furthermore, Nardi (1999) suggested, based on his observations, that this species did aggregate in shallow areas during the spawning season. However, a recently introduced ban on the capture of *C. rubescens* between November and January in the “Fish habitat protection area”, an area surrounding the Abrolhos Islands, will assist in protecting those spawning fish.

**Implications of protogynous hermaphroditism for management**

A substantial amount of research has been carried out on hermaphroditic species, such as those of the Serranidae, Scaridae, Sparidae and Labridae. However, until recently, few studies have focused on acquiring data on the biological parameters that are required for developing management plans for the commercially and/or recreationally important hermaphroditic species in Western Australia (Mackie, 2000; Hesp *et al.*, 2004a).
Choerodon rubescens, C. schoenleinii, C. cyanodus and C. cauteroma are monandric protogynous hermaphrodites in Shark Bay and the same is true of C. rubescens in the Abrolhos Islands. Thus, their males are derived from adult females via sex change. This accounts for the fact that all of the males of C. rubescens and C. schoenleinii, and the majority of those of C. cyanodus and C. cauteroma, were found amongst the larger size and older age classes of those species. In the case of the two most targeted species, i.e. C. rubescens and C. schoenleinii, the sex ratios of adult fish, based on the catches by line of fish ≥ their $L_{50m}$, were biased towards females. Since fishers preferentially target large fish and the retention of fish is restricted to the upper size classes of those two species by the presence of a MLL of 400 mm, the proportion of males taken in catches will be substantially higher than that present in the population (Bannerot et al., 1987; Sadovy, 1996b; Alonzo and Mangel, 2004). In the case of C. rubescens in the Abrolhos Islands, the ratio of females to males in commercial catches, which comprised only larger fish, was 1:1 and thus far less than the ratio of adult fish in line catches, i.e. 14:1. The removal of large numbers of males from a population through heavy fishing pressure may impact on the spawning success of that population (Petersen and Warner, 2002). The potential to remove a disproportionately large number of males may not be as great an issue with C. cauteroma in Shark Bay, since fishers are not restricted by a MLL. Furthermore, many fishers believe that the individuals of this species that they catch are small individuals of C. schoenleinii and since they are predominantly smaller than the MLL for C. schoenleinii of 400 mm, they thus usually return those fish to the water.

Many protogynous hermaphrodites change sex in response to social cues. For example, the largest female in a harem will change sex when the dominant male is
removed or dies (e.g. Robertson, 1972; Nemtzov, 1985; Sakai et al., 2001). Since fishers typically target the largest fish, which are likely to be males, Bannerot et al. (1987) suggested that the above social behaviour should make protogynous hermaphrodites less vulnerable to exploitation. However, in response to heavy fishing pressure, and thus the removal of substantial numbers of large males, some protogynous species may begin to change sex at a shorter length than normal and thereby maintain an appropriate sex ratio (Shapiro and Lubbock, 1980; Warner, 1988; Darwall et al., 1992; Platten et al., 2002; Hawkins and Roberts, 2003). Thus, even though protogynous species may be able to adapt to increased fishing pressure by changing sex at a smaller length and younger age, fishing pressure can lead to an undesirable downward shift in the size and age compositions and thus to a reduction in the value of the fishery (e.g. Dulvy et al. 2004).

Since most management plans have been developed on the basis of gonochoristic species, they may not always be appropriate for hermaphroditic species. Indeed, Coleman et al. (1999) have pointed out that the complex life history and behaviour of many reef fishes explain why the adoption of the typical management approaches employed in the United States have “entirely failed to stem the effects of commercial and recreational fishing pressure on this important group”. Thus, in the case of protogynous hermaphrodites, such as the four Choerodon species, it is important to consider their reproductive behaviour in conjunction with aspects of their biology, e.g. length and age at maturity and sex change, size and age compositions, growth and mortality, when developing new or changing existing management plans. Vincent and Sadovy (1998) stated that without considering behaviour “one is in danger of interpreting the impact of extraction in numerical terms alone, rather than through a recognition of demographic effects”. The complex
life histories of hermaphroditic species may require the use of a combination of management measures, such as MLLs, bag limits (for recreational fishers), maximum size limits, which may be based on the length at which 50% of females change sex ($L_{50c}$) and also possibly the introduction of marine reserves, which protect species from capture in certain areas and may provide a source of recruitment for surrounding stocks (Buxton, 1993; Russ, 2002). Although maximum size limits based on the $L_{50c}$ may not be desirable from a fisher’s point of view, since they preclude the retention of the larger fish, they have the advantage of protecting not only the large males but also the largest females, which, due to their large body size and high fecundity are particularly important for replenishing stocks. However, the implementation of maximum size limits may not always be effective, since tuskfish that occur in waters deeper than $ca$ 10 m usually suffer barotrauma when brought to the surface.

Habitat partitioning

The results of this study demonstrated a substantial degree of habitat and thus resource partitioning amongst the five tuskfish species found in Shark Bay. Thus, *C. rubescens* and *C. cephalotes* are restricted to oceanic waters and essentially inner gulf seagrass beds, respectively, while *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* co-occurred in varying abundance on inner gulf reefs and rocky shorelines. *Choerodon cauteroma* was the only species that clearly demonstrated a size-related shift in habitat use, moving from seagrass to predominantly inner gulf reefs and rocky shorelines as it reached adulthood. This information on the types of habitats occupied in Shark Bay by the five tuskfish species during their life cycle provides valuable information as to where, in the future, any sanctuary zones that
prevent fishing should be located within this World Heritage Area. It would also be relevant for assessing the existing “no-take” sanctuary zones in Shark Bay, particularly in the case of the two most targeted species, *C. rubescens* and *C. schoenleinii*.

Many reef species exhibit site fidelity and thus remain on one reef throughout their life (Coleman *et al.*, 1999). As many of the inner gulf reefs are isolated from each other and are small in area, movement between reefs by individuals of those species that occur predominantly in the two gulfs may be restricted. Since a large number of the reefs in Shark Bay occur in shallow water (< 10 m) and are close to the shoreline, they are easily accessible to fishers. Thus, the main risk associated with fishing on reefs within the gulfs is that, since heavy fishing pressure on any one reef has the potential to remove substantial numbers of resident fish, this may be detrimental to the assemblage in an area. Furthermore, the distance between individual reefs may also restrict the replenishment of stocks on a particular reef by pelagic larvae that have been spawned elsewhere.

**A broader perspective**

The information obtained in this study on the biology of and habitats occupied by *Choerodon* species in Western Australia is important for developing appropriate management plans for these species in that region. These data should also be considered in a broader context when developing such plans. Since *C. rubescens* and *C. cauteroma* are endemic to Western Australia and thus have restricted distributions, heavy fishing pressure may be detrimental to the stocks of those species if management plans are inappropriate. This may ultimately result in the loss of genetic diversity. Although *C. schoenleinii* and *C. cyanodus* have much
broader distributions across the Indo-west Pacific, their stocks across a large part of their distribution are at risk due to poor management and inappropriate fishing, *i.e.* the destruction of fisheries resources through the use of inappropriate fishing techniques, such as poisons and dynamite, typically by poor fisherman (Pauly *et al.*, 1989; McManus, 1997). Thus, the stocks of those two species in Australia may currently represent last major strongholds for these species. Hence the assessment of the level of threats to a species on a global scale by the World Conservation Union (IUCN) is an important part of species management and, in situations where species are at risk globally, further highlights the need for effective management plans to be developed in order to protect the remaining stocks of a species on a local scale (see http://www.redlist.org/; http://www.hku.hk/ecology/GroupersWrasses/iucnsg/).
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