Determination of the biological parameters required for managing the fisheries of four tuskfish species and western yellowfin bream

Fairclough, D. V., Hesp S. A., Potter, I. C. & N. G. Hall

MURDOCH
UNIVERSITY
PERTH, WESTERN AUSTRALIA

Australian Government
Fisheries Research and
Development Corporation

Project No. 2000/137

Fisheries Research and Development Corporation Report

FRDC project 2000/137

Determination of the biological parameters required for managing the fisheries of four tuskfish species and western yellowfin bream

Fairclough D.V.
Hesp S.A.
Potter I.C.
Hall N.G.

June 2004

Centre for Fish and Fisheries Research
Murdoch University
Murdoch, Western Australia 6150

June 2004
ISBN: 0-646-39851-2

Table of Contents

2000/137	Determination of the biological parameters required for managing the fisheries of four tuskfish species and western yellowfin bream

PRINCIPAL INVESTIGATOR:	Professor I. C. Potter
ADDRESS:	Centre for Fish & Fisheries Research Division of Science & Engineering Murdoch University South St., Murdoch WA 6150 Ph: 08 9360 2524 Fax: 08 9360 6303

OBJECTIVES:

1) To obtain the following data for western yellowfin bream, baldchin groper, blackspot tuskfish, blue tuskfish and bluespotted tuskfish, so that they can be used by the Department of Fisheries Western Australia for managing effectively and appropriately the fisheries for these species.
2) Age composition and growth rate.
3) Location and duration of spawning.
4) Fecundity.
5) Length and age at which fish change sex.
6) Length and age at maturity, taking into account the fact that the five species are all likely to be hermaphrodites.
7) The habitat occupied at each stage in the life cycle of each of these species.

Additional aims, that were not part of the original objectives, were as follows:

8) Estimate natural, total and fishing mortality for western yellowfin bream.
9) Conduct per recruit analyses for western yellowfin bream.
10) Determine the habitats occupied at each stage in the life cycle of a fifth species of tuskfish, the purple tuskfish *Choerodon cephalotes*.

NON-TECHNICAL SUMMARY:

OUTCOMES ACHIEVED TO DATE

Data have been collected on the biology of western yellowfin bream and four tuskfish species that are of the type and quality required by managers for developing appropriate plans for conserving the stocks of these five commercial and recreational species. Emphasis was thus placed on determining (1) the size and age at which each species reaches sexual maturity, (2) the size and age at which the first species, a protandrous hermaphrodite, changes from male to female and the other four species, which are protogynous hermaphrodites, change from female to male and (3) the proportions of individuals of each species that change sex. The marked interspecific variations in the above characteristics imply that each species should be considered independently when developing management plans. We are using the experience gained during this study to assist Dr Rod Lenanton, the chief supervising scientist for finfish at WA Fisheries, to produce a document on the importance of considering carefully the implications of hermaphroditism in managing fish species. During this study we developed an improved method for determining natural and total mortality in fish populations, which will be invaluable for managers of all fisheries for which there are appropriate data. The new method for estimating mortality has been provided to and discussed with Dr Lenanton.

The levels of commercial and recreational exploitation of certain species in Western Australia are high and continuing to increase. The sustainability of the stocks of these species, in the face of increasing fishing pressure, is dependent on establishing appropriate management plans that are based on sound and relevant biological data. The biology of the western yellowfin bream *Acanthopagrus latus* and four congeneric species of tuskfish, *Choerodon rubescens*, *C. schoenleinii*, *C. cauteroma* and *C. cyanodus*, were studied in Shark Bay, a large subtropical marine embayment in Western Australia and within which these species are fished recreationally and, in the first two cases, also commercially. The biology of *C. rubescens* was also studied in the Abrolhos Islands to the south of Shark Bay, where there is an important commercial fishery for this species.

Choerodon rubescens is found predominantly on reefs along the western boundary of Shark Bay, whereas the other tuskfish species are found mainly in the two gulfs of this large embayment. The western yellowfin bream lives in mangroves and along rocky shorelines, whereas the blackspot and blue tuskfish occupy mainly reefs and the bluespotted tuskfish lives in seagrass as a juvenile and mainly in and around reefs as an adult. The purple tuskfish lives in seagrass throughout its life.

Acanthopagrus latus was shown to be a protandrous hermaphrodite in Shark Bay, *i.e.* individual fish change from male to female, whereas all four tuskfish species are protogynous hermaphrodites, *i.e.* individual fish change from female to male. The males of the western yellowfin bream become sexually mature at ~245 mm and ~2 years of age and change to females at ~350 mm and 5 years of age.

The females of *C. cyanodus C. cauteroma* and *C. schoenleinii* attain maturity at ~130, 200 and 250 mm, respectively, and at ~2, 2 and 4 years of age, respectively. The individuals of these species change to males at ~220, 310 and 550 mm, respectively, and at ~4, 7 and 11 years of age, respectively. The females of *C. rubescens* in Shark Bay and the Abrolhos Islands attain maturity at similar lengths of ~282 and 291 mm, respectively, and at 3 and 4 years of age, respectively. However, the females change to males at a greater length in Shark Bay (545 mm) than the Abrolhos Islands (479 mm), but at about the same age (11-12 years). The sex ratios of the populations of the four tuskfish species in Shark Bay varied greatly from close to parity for *C. cyanodus* to 1 male : 153 females for *C. schoenleinii*.

Western yellowfin bream spawns during late winter and early spring, whereas each of the four species of tuskfish spawns mainly in spring and/or summer. *Acanthopagrus latus* has determinate fecundity, *i.e.* the number of eggs released by individual females during a spawning season is determined prior to the commencement of that season. Thus, the number of large eggs present in mature ovaries of *A. latus* in the period immediately prior to the commencement of spawning (mean = 2,000,000) corresponds to the potential annual fecundity of this species. In contrast, all four species of tuskfish have indeterminate fecundity, *i.e.* the number of eggs released by individual females during a spawning season is not determined prior to the commencement of that season. *Choerodon rubescens*, *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* spawn eggs in batches on numerous occasions during their spawning periods. The mean batch fecundities of these four species were 42,700, 37,400, 11,800 and 12,100, respectively.

Acanthopagrus latus attains lengths of about 110, 190, 330, 400 and 415 mm at the completion of the first, second, fifth, tenth and fifteenth years of life, respectively. The largest and oldest *A. latus* were 466 mm and 24 years, respectively. The maximum ages of the four species of tuskfish in Shark Bay ranged only from 12 to 16 years. However, 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). *Choerodon rubescens* grows more rapidly in Shark Bay than in the Abrolhos Islands, possibly reflecting greater food availability and/or lower densities in the former environment.

The length that *A. latus* typically becomes a male (245 mm) is similar to the minimum legal length for retention (MLL) of 250 mm. However, on average, this species does not typically change sex from male to female for a further 2.5 years beyond the age at which it reaches 250 mm. This implies that, if fishing pressure was to increase markedly, the females of this species, in particular, would presumably become severely depleted. Our analyses indicate that, in contrast to the past, when the number of commercial fishing licenses was greater, the current level of fishing pressure on *A. latus* is sustainable. Should the recreational fishing pressure on *A. latus* continue to increase, managers will need to either change the current MLL and/or employ other measures, *e.g.* reduce the bag limit. Since the MLL for *C. rubescens* and *C. schoenleinii* is less than the length at which these species change sex, similar approaches will need to be adopted for these species if they were to experience severe depletion from heavy fishing pressure. Since the sex ratios vary greatly among the four tuskfish species, their susceptibility to fishing pressure is likely to differ and thus that variability should be taken into account when developing plans for managing those species.

Natural and total mortality were estimated for *A. latus*. Since traditional life history methods for estimating natural mortality yielded very unrealistic estimates, we developed a new approach to overcome this problem. This yielded single integrated estimates for *M* and *Z*, which were realistic and more precise than those obtained using traditional approaches alone. The results are consistent with those reported earlier in that they likewise demonstrate that the stock is currently not overfished.

The biological data produced during this study now makes it possible to assess, in an ongoing manner, the status of the stocks for western yellowfin bream and four tuskfish species, as fishing pressure increases.

KEYWORDS: reproduction, hermaphroditism, protandry, protogyny, age composition, growth, mortality, habitat.

ACKNOWLEDGEMENTS

Gratitude is expressed to our colleagues at the Murdoch University Centre for Fish and Fisheries Research, who helped with sampling fish and, in particular, to William White, Simon de Lestang, Matthew Pember, Michael Travers, Daniel French and Peter Coulson.

Our thanks are also extended to several staff at the Western Australian Department of Fisheries, in particular, Kim Grey, who obtained samples of fish for us from Shark Bay and/or the Abrolhos Islands and to the staff at Festival Fish, Garden City Seafood Gallery and Seafresh Innaloo.

To Les and Glenys Fewster, Shark Bay Charter Service, and Robbie and Peter Morgan at the Monkey Mia Pearl Farm, for their help in obtaining samples. Also thank you to Gary, Brian and Johno from the Shark Bay Hotel and the Heritage Hotel.

To Kevin Crane and staff at CALM in Shark Bay and Paul Dickinson, Steep Point Ranger, and John Glesing (Shark Bay Salt) for their help and support.

To Rod Lenanton, Gavin Sarre, and Mike Moran from the Western Australian Department of Fisheries, and Professor Yvonne Sadovy from the University of Hong Kong for very helpful discussions regarding various aspects of our project.

Our thanks to the following people who gave their support for our project:
Mr D. Bathgate, Gascoyne development Commission: Chairman of the Working Group on the "Quality future for recreational fish in the Gascoyne".
Mr L. Fewster, Denham RRFAC, Shark Bay Charter Service operator and committee member
Mr D. Hoult, President, Denham Fishing Association
Mr K. Shadbolt, Denham RRFAC, President, Volunteer Marine Rescue Shark Bay Inc.
Mr P. Anning, Chief Executive Officer, Shire of Shark Bay
Dr C. Simpson, Habitat Manager for Marine Conservation Branch, Department of Conservation and Land Management
Dr C. Chalmers, Program Manager (Habitats), Fisheries WA
Mr A. Cribb, Program Manager (Recreational Fishing), Fisheries WA
Mr F. Prokop, Executive Director, Recfishwest

1.0 GENERAL INTRODUCTION

1.1 BACKGROUND

The levels of commercial and recreational exploitation of the fish stocks of certain species in the ecologically very important environment of Shark Bay, Western Australia, are high and continuing to increase. However, the amount of biological data that can be used for management purposes for most of those species is minimal. The ability to sustain stocks of such species, in the face of increasing fishing pressure, by setting in place appropriate management plans is dependent on acquiring strategic information on the biology of those species.

The Shark Bay fishery

Shark Bay, which is the only marine area in Western Australia that has been granted World Heritage status, supports very important commercial fisheries (Fisheries Department of WA, 1996; **Figure 1.1**). Furthermore, over 60,000 recreational fishers visit Shark Bay every year (Fisheries WA, 1999) and this number will inevitably continue to rise in future years. Some of the fish species that are commercially and recreationally fished in Shark Bay are also fished in waters to the north and south, including the Houtman-Abrolhos Islands **(Figure 1.1)**.

The marked rise in the number of recreational fishers in Western Australia 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). The most vulnerable species are those that remain within the bay throughout the whole of their life cycles and are subjected to commercial as well as recreational fishing pressure. Greater ease of access to remote areas such as Shark Bay and technological improvements in the methods of locating fish will obviously increase the pressure on the stocks of the most vulnerable and sought-after resident species in this embayment (Fisheries WA, 1999).

The decline during recent years in the abundance of pink snapper in Shark Bay, as a result of increased 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 size and bag limits elsewhere in Shark Bay were tightened. This change in regulations resulted in a diversion of fishing pressure towards other reef-dwelling species, such as the blue-lined emperor *Lethrinus laticaudus* (see FRDC project 99/152) and species of tuskfish, *i.e.* the baldchin groper *Choerodon rubescens*, the blackspot tuskfish *Choerodon schoenleinii*, the blue tuskfish *Choerodon cyanodus* and the bluespotted tuskfish *Choerodon cauteroma* (Fisheries WA, 1999;

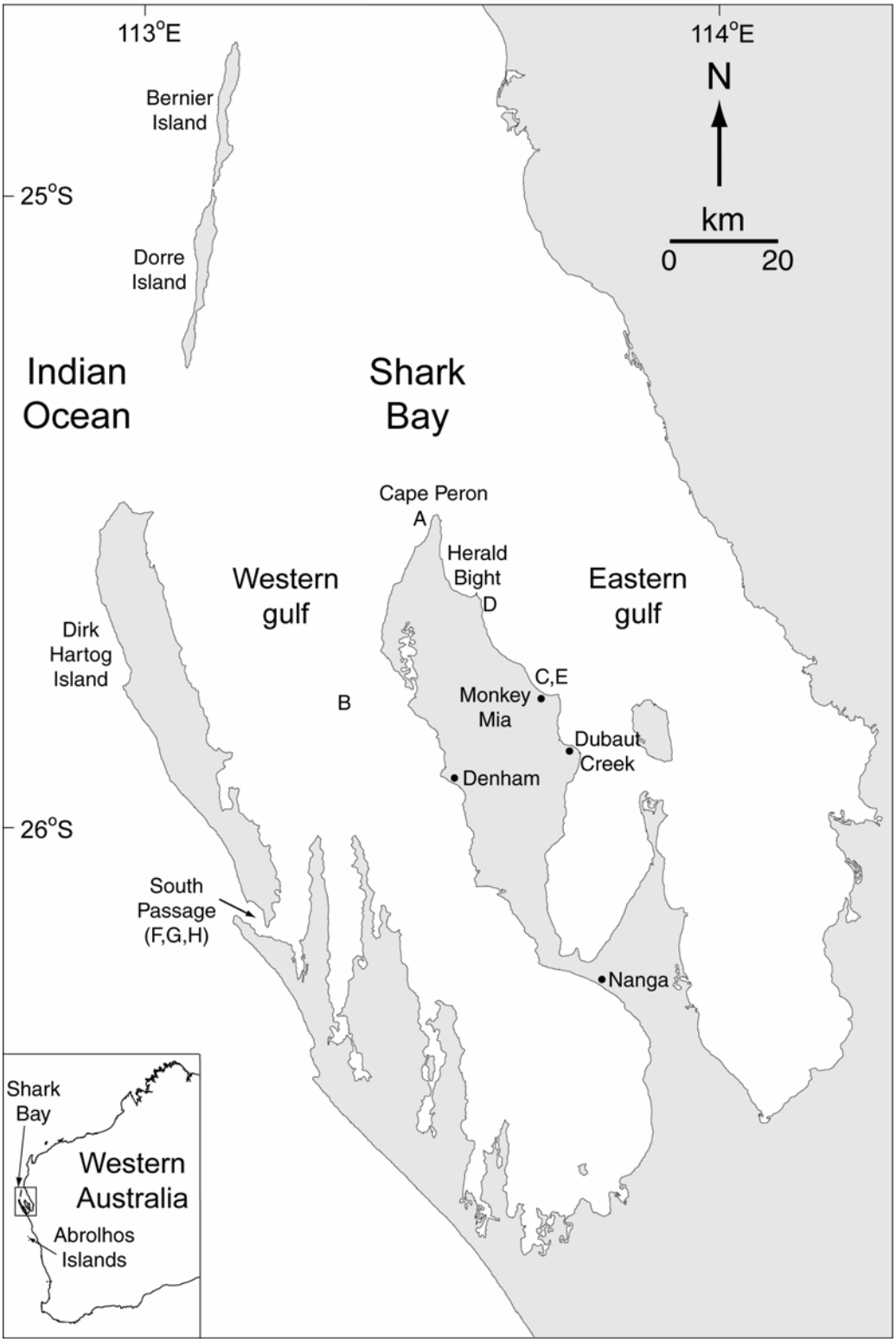

Figure 1.1. Map of Shark Bay, showing main sampling areas and underwater visual census sites (A-H). Descriptions for each of the site codes, A-H, are given in Chapter 7.2.1.

S. Ayvazian, Fisheries WA, pers. comm.). Juvenile tuskfish are also taken as bycatch during commercial prawn and scallop trawling and commercial haul netting for whiting and western yellowfin bream (Fisheries Department of WA, 1996; P. Unsworth, Fisheries WA, pers. comm.).

The five fish species which are the subject of the present study are the western yellowfin bream *Acanthopagrus latus*, the baldchin groper *C. rubescens*, the blackspot tuskfish *C. schoenleinii*, the blue tuskfish *C. cyanodus* and the bluespotted tuskfish *C. cauteroma*. The western yellowfin bream and the four species of tuskfish collectively contribute about 20 tonnes of high value product to the commercial catch in Shark Bay each year and there is potential for the fishery for the three largest tuskfish species to be expanded (R. Lenanton, Fisheries WA, pers. comm.). Current retail prices for whole yellowfin bream are about $10 per kg, while those for fillets of baldchin groper and other tuskfish, commonly referred to as “bluebone” and “baby groper” in fish markets, range from $30 to $40 per kg.

The western yellowfin bream forms an important component of the recreational fishery not only in Shark Bay, but also in Exmouth further north (R. Lenanton, Fisheries WA, pers. comm.). Tuskfish species have prime eating qualities and are highly sought after by recreational fishers within Shark Bay and also northwards and southwards of this embayment (Department of Conservation and Land Management (CALM), 1996; Fisheries Department of WA, 1996; Allen, 1997; Fisheries WA, 1999; Yearsley *et al*., 1999). The recognition by CALM that the baldchin groper and bluespotted tuskfish are key targets for line and spearfishers in Shark Bay led to the institution of sanctuary zones in the waters around Mary Anne Island, in the western gulf of Shark Bay, and in South Passage at the southern end of Dirk Hartog Island.

The management plan by Fisheries WA for recreational fisheries of the Gascoyne region highlights specifically the need for acquiring crucial biological data for the the baldchin groper and blackspot tuskfish to facilitate the development of management plans for these two species. Although there are some data on restricted aspects of the biology of these two species and the blue tuskfish, there is no such information for the bluespotted tuskfish or the western yellowfin bream anywhere in Australia (CALM, 1996; Fisheries WA, 1999).

The baldchin groper, blackspot, blue and blue spotted tuskfish are reported to reach total lengths of *ca* 65, 80, 60 and 43 cm, respectively (Allen, 1999). However, in Western Australia, all tuskfish species have been allocated the same minimum legal length (MLL), *i.e.* 40 cm, which reflects an absence of the types of crucial biological data, such as the size at which these species attain maturity, which are required for determining appropriate values for this variable. A MLL of 25 cm has been imposed for the western yellowfin bream, which reaches a maximum total length of 45 cm (Allen, 1999).

The establishment of a MLL or any other form of size limit for sparids, such as the western yellowfin bream, and for labrids, such as the four species of tuskfish, must take into account the fact that many members of these two families undergo sequential hermaphroditism (Buxton and Garratt, 1990; Policansky, 1982). In other words, as such species increase in size and age, they change either from functional males to functional females (protandrous hermaphroditism), as has been reported to be the case with *A. latus* in the Arabian Gulf and Japan (Abu-Hakima, 1984; Abol-Munafi and Umeda, 1994; Abou-Seedo *et al*., 2003), or from functional females to functional males (protogynous hermaphroditism), as has been reported for baldchin groper in the Houtman-Abrolhos Islands and blackspot tuskfish in Japan (Walker, 1983; Ebisawa *et al.* 1995; Nardi, 1999). Consequently, the MLL must be high enough to ensure that there is a sufficient number of mature individuals of each sex of the western yellowfin bream and the four tuskfish species for those populations to remain sustainable (see Buxton, 1992).

Although some research had been carried out previously on aspects of the biology of the baldchin groper in the Abrolhos Islands (Figure 1.1) by both Walker (1983) and Nardi (1999), the latter author recognised that further work was required on such fundamental aspects as validating that an annulus, *i.e.* growth zone, is formed in the otoliths each year and that the number of such annuli can thus be used to age this species. Furthermore, the length at maturity was determined from only a small number of fish and was based on the trends exhibited by gonadosomatic indices rather than on more reliable criteria, such as logistic regression analyses of the proportions of sexually mature fish in a wide range of sequential length classes. Although aspects of the reproductive biology of the blackspot tuskfish have been determined in Japan, the age and growth of this species have not been studied. Although there is some published information on the biology of yellowfin bream in the waters of Kuwait and Japan (*e.g.* Samuel and Mathews, 1987; Abu-Hakima, 1984; Abou-Seedo *et al*., 2003), no such data are available for Australia. Some basic biological information on the reproductive biology of the blue tuskfish was determined by Choat (1969) for this species on the Great Barrier Reef. However, the results were based on a very small sample size and aspects, such as length at sexual maturity and age and growth studies, were not studied. No biological information is available for the bluespotted tuskfish.

1.2 NEED

The Department of Fisheries WA has identified Shark Bay as a priority area for developing a formal management process for its fisheries and the habitats occupied by its commercial and

recreational fish species (Fisheries WA, 1999). Such management plans are needed to sustain the commercial and recreational fish stocks and biodiversity of the fish communities of the region, which are considered essential for maintaining the value of Shark Bay both socially and as a World Heritage area (Fisheries WA, 1996; Fisheries WA, 1999).

The development of appropriate plans for conserving western yellowfin bream, blackspot tuskfish, blue tuskfish and bluespotted tuskfish stocks in Shark Bay and the baldchin groper in both Shark Bay and the Abrolhos Islands requires the following biological data. (1) Reliable data on the age and size compositions, growth rates, lengths and ages at first maturity, fecundity and, for those species which are hermaphroditic, the proportions of each sex in each age and size class. (2) A thorough understanding of the types of habitat occupied at sequential stages in the life cycle so that critical habitats can be protected.

1.3 OBJECTIVES

1. To obtain, for western yellowfin bream, baldchin groper, blackspot tuskfish, blue tuskfish and bluespotted tuskfish, the following data for use by the Department of Fisheries Western Australia for managing effectively and appropriately the fisheries for these species.
2. Age composition and growth rate.
3. Location and duration of spawning.
4. Fecundity.
5. Length and age at which fish change sex.
6. Length and age at maturity, taking into account the fact that the five species are all likely to be hermaphrodites.
7. The habitats occupied at each stage in the life cycle of each of these species.

1.4 ADDITIONAL OBJECTIVES

1. Estimate total, natural and fishing mortality of western yellowfin bream.
2. Conduct per recruit analyses for western yellowfin bream.
3. Determine the habitats occupied at each stage in the life cycle of a fifth species of tuskfish, the purple tuskfish *Choerodon cephalotes*.

2.0 GENERAL MATERIALS AND METHODS

2.1 STUDY AREAS

Shark Bay

Shark Bay, which is one of only 14 World Heritage areas listed for Australia (Francesconi & Clayton, 1996; http://www.unesco.org/whc/heritage.htm), is located approximately 800 km north of the city of Perth. Seventy one percent of the total area of Shark Bay, *i.e*. 2.2 million hectares, comprises marine waters that constitute the largest marine embayment in Australia (Francesconi & Clayton, 1996). The embayment extends southward from the northern tip of Bernier Island ($24^{o}45'S$, $113^{o}10'E$) to the southernmost point of Freycinet Harbour ($26^{o}36'S$, $113^{o}41'E$) and longitudinally lies between *ca* 113^{o} and $114^{o}30'E$ (Anon., 1996). Shark Bay is one of only a few natural heritage areas to meet all of the four following criteria for World Heritage Listing (Francesconi & Clayton, 1996):

- an outstanding example representing the major stages of the earth's evolutionary history
- an outstanding example representing significant ongoing geological processes, biological evolution and human interaction with the natural environment
- contains unique, rare or superlative natural phenomena, formations or features of exceptional natural beauty
- contains 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.

The flora and fauna of Shark Bay is very diverse, which is due, in part, to its transitional location between tropical and temperate regions and thus its possession of a range of both tropical and temperate species. Furthermore, Shark Bay contains the largest and most diverse suite of seagrass meadows in the world (Walker, 1990) and these provide not only habitats for many species, but also influence the hydrology of the bay. This ultimately leads to highly elevated salinities in the inner reaches of the bay, which, in turn, have greatly affected the

distribution and diversity of its flora and fauna (Walker, 1990). A total of 323 fish species have been recorded in the bay, 83% of which are tropical, 11% subtropical and 6% warm temperate (Hutchins, 1991).

The Abrolhos Islands

The Abrolhos Islands is a complex of low lying reefs and islands at the edge of the continental shelf, located between 28°15'S amd 29°00'S, *ca* 60 km offshore from Geraldton on the mid-west coast of Western Australia (Fisheries Western Australia, 1998). In 1994, The Marine Parks and Reserves Selection Working Group considered the Abrolhos Islands to be the most significant area on the Western Australian coast, and the most worthy of reservation. The following attributes make this system of such high conservation value to the people of Western Australia. It contains:

1. highly significant populations of seabirds;
2. sub-species of reptiles and birds endemic to the islands;
3. a unique combination of tropical, temperate and Western Australian endemic marine species;
4. tropical corals which mix with temperate algae;
5. the southernmost living coral reefs in the Indian Ocean;
6. a high diversity of marine ecosystems; and
7. several rare species of fauna which live on the islands (Fisheries Western Australia, 1998).

The Abrolhos Islands supports several important commercial fisheries, including those for western rock lobster, scallops and finfish which, respectively, are worth $30-50, 0.3-9.5 and *ca* $1 million each year, respectively. There is a charter boat industry and an increasingly important recreational fishery, which operate in this area (Fisheries Western Australia, 1998).

The baldchin groper, *Cheorodon rubescens*, which is endemic to Western Australia, is an abundant finfish species in the Abrolhos Islands and is heavily-targeted by the commercial and recreational fishery (Fisheries Western Australia, 1998).

2.2 SAMPLING REGIME

Western yellowfin bream and the four species of tuskfish were obtained at bimonthly intervals from Shark Bay between July 2000 and January 2003, through rod and line angling, spearfishing and seine netting. Samples of all of the tuskfish species, except baldchin groper, that had been collected by trawling and retained from a previous study in Shark Bay (FRDC 97/137) were used to supplement the samples of these species collected during this project. Additional samples of western yellowfin bream from Shark Bay and baldchin groper from Shark Bay and the Abrolhos Islands were also obtained from wholesale fish markets. In addition, baldchin groper were collected from the Abrolhos Islands during the spawning period in 2002 by rod and line angling and spearfishing. Opportunistic samples were also obtained from Shark Bay by staff of the Department of Fisheries Western Australia. The details of the methods and regions in which juveniles and adults of each of the five species were collected are given in **Table 2.1**.

Table 2.1. Regime for sampling the different life cycle stages of the five species of fish studied in Shark Bay. **Figure 1.1** shows location of individual sampling sites.

Species	Life Stage	Habitats	Region	Method
Yellowfin bream	Juvenile	Mangroves	Dubaut Creek Herald Bight	21.5 m seine
	Adult	Shallow, nearshore sandstone rocky areas and reefs	Eastern and western gulfs	Rod and line
Baldchin groper	Juvenile	Weed-covered reefs	South Passage, Abrolhos Islands	Spearfishing
	Adult	Reefs	Oceanic waters around Dirk Hartog, Dorre and Bernier Islands. Abrolhos Islands	Rod and line/ spearfishing
Blackspot tuskfish	Juvenile	Seagrass/ reefs	Eastern and western gulfs	Trawling/ spearfishing
	Adult	Reefs	Eastern and western gulfs	Rod and line/ spearfishing
Blue tuskfish	Juvenile	Seagrass/ reefs	Eastern and western gulfs	Trawling/ rod and line/spearfishing
	Adult	Reefs	Eastern and western gulfs	Rod and line/ spearfishing
Bluespotted tuskfish	Juvenile	Seagrass/ reefs	Eastern and western gulfs	Trawingl/ rod and line/ spearfishing
	Adult	Reefs	Eastern and western gulfs	Rod and line/ spearfishing

The seine net used to sample the mangrove areas in Shark Bay was 21.5 m long and its wings and pocket consisted of 9 and 3 mm mesh, respectively. The 21.5 m seine net was stretched parallel to the beach in a water depth of *ca* 1-1.5 m and its ends then drawn inwards in a circle and on to the beach. The area covered by this seine net was *ca* 116 m^2. The otter trawl net had an effective fishing width of 2.6 m (mouth of net) and was 0.5 m high and 5 m long from net mouth to bunt end. The wings and bunt consisted of 56 and 25 mm mesh, respectively and the bridle length was 13 m.

2.3 ENVIRONMENTAL MEASUREMENTS

Water temperature and salinity at the bottom of the water column were recorded at each site on each sampling occasion.

2.4 FISH MEASUREMENTS

The total length (TL) and wet weight of each fish were recorded to the nearest 1 mm and 0.1 g, respectively, and the gonads of each fish were weighed to the nearest 0.01 g. The length-weight relationships were determined for the four species of tuskfish so that the weights of individual fish could be estimated when frames (filleted fish) of those species were obtained.

2.5 REPRODUCTIVE BIOLOGY

Gonadosomatic indices (GSI) were calculated using the following equation: W1/(W2-W1) x 100, where W1 = wet weight of the gonad and W2 = wet weight of the whole fish, *i.e.* W2-W1 = somatic weight. Each gonad that contained exclusively either ovarian or testicular tissue was allocated, on the basis of the macroscopic characteristics of the dominant tissue, to one of the following eight maturity stages, derived from the scheme of Laevastu (1965), *i.e.* I/II = immature/resting, III = developing, IV = maturing, V = mature, VI = spawning, VII = spent, VIII = recovering. Since it was often not possible to distinguish macroscopically between stages V and VI, the data for these two stages have been pooled.

Histological sections of the gonads of the five fish species were produced to (1) ensure that ovaries were assigned to their appropriate macroscopic stages of maturity, (2) determine whether each of these species had determinate or indeterminate fecundity, which is required to ascertain which technique is most appropriate for estimating fecundity, and (3) to elucidate whether these species are hermaphrodites and, if so, whether they are protandrous, protogynous or rudimentary hermaphrodites (*sensu* Buxton & Garrat, 1990; Sadovy and Shapiro, 1987). For histological sectioning, gonads were removed from at least 20 individuals in each month. The gonads were placed in Bouin's fixative for 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 characteristics of each macroscopic and

histological stage in the development of the ovaries of western yellowfin bream and the four species of tuskfish are presented in **Table 2.2**.

Table 2.2. Characteristics of the macroscopic stages, and each corresponding histological stage, in the development of ovaries of western yellowfin bream and the four species of tuskfish. Adapted from Laevastu (1965). Terminology for oocyte stages follows Wallace & Selman (1989).

Stage	Macroscopic characteristics	Histological characteristics
I/II *Virgin and Immature/resting	Small and transparent. Yellowish-orange in colour. Oocytes not visible through ovarian wall.	Ovigerous lamellae highly organised. Chromatin nucleolar oocytes dominate the complement of oocytes. Oogonia and perinucleolar oocytes sometimes present. Small previtellogenic oocytes present in all subsequent ovarian stages.
III - Developing	Slightly larger than at stage II. Pinkish colour. Oocytes visible through ovarian wall.	Chromatin nucleolar, perinucleolar and cortical alveolar oocytes present.
IV - Maturing	Larger than stage III, occupying about half of body cavity. Orange in colour (yellowfin bream) or creamy colour (tuskfish species). Large oocytes visible through ovarian wall.	Cortical alveolar and yolk granule oocytes abundant.
V/VI -Mature/spawning	Large, occupying about two thirds of body cavity. Extensive capillaries visible in ovarian wall. Hydrated oocytes sometimes visible through ovarian wall in stage VI ovaries.	Yolk granule oocytes abundant. Migratory nucleus oocytes, hydrated oocytes or post ovulatory follicles present in “spawning ovaries”.
VII - Spent	Smaller than V/VI and flaccid. Some large oocytes visible through ovarian wall.	Remnant yolk granule oocytes present, typically undergoing atresia. Some scar tissue present
VIII- Recovering	Small, flaccid and dark red.	Extensive scar tissue present. Ovarian lamellae disorganised.

* Stage I – Virgins of larger juveniles of *Acanthopagrus latus* contain substantial amounts of both testicular and ovarian tissue whereas those of juvenile tuskfish contain only ovarian tissue.

The circumferences of 100 oocytes in two mature (stage V/VI) ovaries of each species were measured to the nearest 0.01 µm to determine whether they have determinate or indeterminate fecundity (Hunter & Macewicz, 1985; Hunter *et al*., 1985). Measurements of the circumferences of oocytes, that had been sectioned through their nuclei, were made using computer imaging software (Leica IM1000), which obtained the image via a digital camera attached to a dissecting microscope and these were then used to calculate the diameters of those

oocytes. Note that since yellowfin bream were shown during this study to have determinate fecundity and the four species of tuskfish each have indeterminate fecundity, different methods were used to estimate their fecundities. These methods are described in chapters 3 and 5, respectively.

2.6 AGE AND GROWTH

The two sagittal otoliths of each fish were removed, cleaned, dried and stored in paper envelopes. A sample of 100 whole otoliths of *A. latus* and *C. cauteroma*, containing a range of numbers of opaque zones were placed in a small black dish, covered with methyl salicylate and examined microscopically under reflected light, employing a dissecting microscope. The numbers of opaque zones on those otoliths were compared with those recorded for the same otoliths after they had been sectioned. For sectioning, the otoliths were mounted in clear epoxy resin and cut into sections of *ca* 350 μm using a low speed diamond saw (Buehler). The sections were cut through the primordium at right angles to the longest axis of the otoliths. The resultant sections were cleaned and mounted on slides using DePX mounting medium, and examined using a dissecting microscope under reflected light. Since sectioning improved the resolution of the opaque zones in the otoliths of *A. latus* that contained > 8 opaque zones, it was decided to be conservative and section all otoliths of *A. latus* with ≥ 5 opaque zones. In the case of *C. cauteroma*, sectioning improved the resolution of opaque zones in otoliths of fish of all sizes. As the otoliths of each of the four species of tuskfish were similar in general appearance and size, all of the otoliths of these tuskfish species were sectioned.

Marginal increment analysis was employed to determine whether the opaque zones detectable in otoliths of each of the five 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. 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 a computer-imaging package (Leica IM1000). The marginal increment on 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 on otoliths with the same number of opaque zones in the corresponding calendar months of different years were grouped together.

Growth equations

The approximate time of peak spawning was estimated from the trends shown throughout the year by the gonadosomatic indices, gonadal maturity stages and pattern of oocyte development. This was considered to correspond to the birth date, which was then used, in conjunction with the time of year when the opaque zones (annuli) on the otoliths become 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 all individuals of each species, using non-linear regression in SPSS (SPSS Inc., 1999). The von Bertalanffy equation is $L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right]$, where L_t = the total length (mm) at age t (years), L_∞ = the mean of 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 the growth followed that predicted by the equation.

3.0 REPRODUCTIVE BIOLOGY OF *ACANTHOPAGRUS LATUS*

S. A. Hesp, I. C. Potter & N. G. Hall

3.1 INTRODUCTION

Like other sparids, *Acanthopagrus latus* possesses ovotestes, *i.e.* gonads which comprise paired bisexual gonads consisting of a medio-dorsal ovarian zone and a latero-ventral testicular zone, separated by a wall of connective tissue (D'Ancona, 1949; Besseau & Bruslé-Sicard, 1995). However, there is a divergence of opinion as to whether all of the individuals of *A. latus* are protandrous hermaphrodites or whether all or some individuals are essentially gonochorists (*cf.* Kinoshita, 1939; Abu-Hakima, 1984; Abol-Munafi & Umeda, 1994; Abou-Seedo *et al.*, 2003). Abol-Munafi & Umeda (1994) based their conclusion that *A. latus* was a protandrous hermaphrodite on the fact that the individuals in the population they studied shifted from exclusively males to very largely females as they increased in size. However, as sex-related bimodal size-frequency distributions can be produced by factors other than sequential hermaphroditism (Sadovy & Shapiro, 1987), this finding does not constitute definitive evidence of protandry. Indeed, Buxton & Garrett (1990) considered many of the reports that certain sparid species are protandrous to be questionable and that at least some of those species are rudimentary hermaphrodites, *i.e.* an individual progresses from a juvenile possessing gonads with both immature testicular and ovarian tissue into either a functional male with an ovotestis containing ovarian rudiments or a functional female with an ovotestis containing testicular rudiments.

Previous studies on the reproductive biology of *A. latus*, which have all been undertaken on populations in the northern hemisphere, have shown that the spawning period of this species varies markedly among regions (Hussain & Abdullah, 1977; Abu-Hakima, 1984; Abol-Munafi & Umeda, 1994; Chang *et al.*, 2002). The fecundity of *A. latus* in the wild has been estimated by Abu-Hakima (1984) and Abol-Munafi & Umeda (1994). The estimates of the first of those workers corresponded to the number of oocytes with a diameter ≥ 180 μm present in the mature

ovaries of five individuals of *A. latus*. Although this approach for determining the potential annual fecundity of a species is valid if that species has determinate fecundity (*sensu* Hunter *et al*., 1985), no attempt was made in that study to determine whether or not this was the case for *A. latus*. The estimates of Abol-Munafi & Umeda (1994) corresponded to the total number of oocytes in ovaries of *A. latus* caught during the spawning season. Since *A. latus* is reported by Abol-Munafi & Umeda (1994) to be a multiple spawner, regardless of whether or not this species has either determinate or indeterminate fecundity, their estimates would not correspond to the annual fecundity, *i.e.* the number of eggs released by individual females in a spawning season. There was thus an important need to determine whether or not *A. latus* has determinate or indeterminate fecundity and then use an appropriate technique to determine its potential annual fecundity in Shark Bay.

Successful fisheries management requires that the reproductive capacity of a stock is sustained above a threshold level that is sufficient to ensure that a high level of egg production is maintained and that recruitment is not jeopardised (Goodyear, 1993; Mace & Sissenwine, 1993; Mace, 2001). Since exploitation is often size selective, species that undergo an irreversible sex change, *i.e.* protandrous and protogynous hermaphrodites, may be particularly susceptible to recruitment overfishing unless specific measures, such as the introduction of appropriate minimum legal lengths for capture, are undertaken to ensure that sufficient numbers of both sexes are maintained (Buxton, 1992; Milton *et al.*, 1998). The development of reliable estimates for the optimal levels of exploitation for hermaphroditic species, such as those derived from per recruit models, requires a thorough understanding of the pattern of sex change exhibited by these species as individuals increase in size and/or age. Data on changes in sex were thus required for producing the type of per recruit analyses that were undertaken by Bannerot *et al.* (1987), Buxton (1992), and Punt *et al.* (1993) for protogynous species and by Milton *et al.* (1998), in essence, for a protandrous species.

The first aim of the present study was to examine, both macroscopically and histologically, the gonads of a wide size and age range of *A. latus* from Shark Bay in order to determine the changes undergone by the ovotestes during the life of this hermaphroditic sparid. Particular emphasis has been placed on ascertaining quantitatively how the prevalence of fish with different types of ovotestes in the different size classes changes throughout the year and in both sequential size and age classes during the spawning period. The latter data have then been used to ascertain the lengths and ages over which this species changes sex and to provide reliable data on sex ratios for use in stock assessment. The second aim was to determine the duration of the spawning period and whether *A. latus* has determinate or indeterminate fecundity *sensu* Hunter *et al.* (1985), *i.e.* whether or not the number of eggs released by individual females within a spawning period is determined prior to that period. The third aim was to determine the relationships between potential annual fecundity and both the total length and somatic weight of *A. latus*. The fourth aim was to determine the spawning biomass per recruit of male and female *A. latus* and egg production per recruit for the females by using an estimate derived for total mortality (Chapter 4) and a range of natural mortalities. Finally, the management implications of our results for *A. latus* are discussed.

3.2 MATERIALS AND METHODS

3.2.1 *Hermaphroditism of* Acanthopagrus latus

The gonads of a large number of *A. latus* that covered a wide size range were assigned, on the basis of a macroscopic investigation, to one of the following categories. (1) Very thin, strand-like and of indeterminate sex. These are found only in juveniles < *ca* 160 mm in total length, (2) ovotestes containing substantial amounts of both immature testicular and ovarian material, (3) ovotestes in which the testicular zone clearly predominates and (4) ovotestes in which the ovarian zone clearly predominates. Fish with gonads in categories 3 and 4 during the spawning period were considered to be males and females, respectively.

The patterns of change in prevalence of juveniles to functional males and then to functional females as *A. latus* increased in size, based on data collected just prior to and during the spawning period, were described using the following approach. The proportion of *A. latus* that were immature, *i.e.* juveniles, at the length L_a corresponding to age *a*, was calculated using the following equation:

$$p_{a,\text{juvenile}} = 1 - \frac{1}{1+\exp\left[-\log(19)\dfrac{L_a - L_{50,\text{male}}}{L_{95,\text{male}} - L_{50,\text{male}}}\right]}.$$

The proportion of functional female fish at this length (and age) was calculated as

$$p_{a,\text{female}} = \left(1 - p_{a,\text{juvenile}}\right)\frac{1}{1+\exp\left[-\log(19)\dfrac{L_a - L_{50,\text{female}}}{L_{95,\text{female}} - L_{50,\text{female}}}\right]}$$

and the proportion of functional males was described as $p_{a,\text{male}} = 1 - p_{a,\text{juvenile}} - p_{a,\text{female}}$. The parameters $L_{50,\text{male}}$, $L_{95,\text{male}}$, $L_{50,\text{female}}$ and $L_{95,\text{female}}$ represent the lengths at which 50 and 95% of juveniles and functional males become functional males and functional females, respectively. Natural logarithms are used in these equations. Note that, as used above and throughout this report, the logistic model, normally described as $p = \dfrac{1}{1+\exp\left[-(a+bL)\right]}$, has been reparameterised into the form: $p = \dfrac{1}{1+\exp\left[-\ln(19)\dfrac{(L-L_{50})}{(L_{95}-L_{50})}\right]}$, as the parameters L_{50} and L_{95} are likely to be more meaningful to the biologist than the parameters *a* and *b* of the normal logistic equation. Similar relationships were used to represent these proportions as functions of age, where

$$P_{a,\text{juvenile}} = 1 - \frac{1}{1+\exp\left[-\log(19)\dfrac{\exp(-K_{\text{male}}a) - \exp(-K_{\text{male}}a_{50,\text{male}})}{\exp(-K_{\text{male}}a_{95,\text{male}}) - \exp(-K_{\text{male}}a_{50,\text{male}})}\right]},$$

$$P_{a,\text{female}} = (1 - P_{a,\text{juvenile}}) \frac{1}{1 + \exp\left[-\log(19) \frac{\exp(-K_{\text{female}} a) - \exp(-K_{\text{female}} a_{50,\text{female}})}{\exp(-K_{\text{female}} a_{95,\text{female}}) - \exp(-K_{\text{female}} a_{50,\text{female}})} \right]}$$

and $P_{a,\text{male}} = 1 - P_{a,\text{juvenile}} - P_{a,\text{female}}$. The parameters $a_{50,\text{male}}$, $a_{95,\text{male}}$, $a_{50,\text{female}}$, and $a_{95,\text{female}}$ represent the ages at which 50 and 95% of the juveniles and functional males become functional males and functional females, respectively, while the parameters K_{male} and K_{female} determine the shapes of the curves that relate proportions to age. Estimates of these parameters were obtained by fitting these models to the number of fish within each category for each length or age class, using the maximum likelihood technique. Because relatively few fish were older than 6 years, the values for age classes 7-9, 10-12 and > 12 are shown later in **Figure 3.7** as pooled values.

3.2.2 *Potential annual fecundity*

Since, unlike the four species of tuskfish, *A latus* has determinate fecundity (see later), the potential annual fecundity of this species could be determined by estimating, just prior to the commencement of the spawning season, the number of eggs in the complement of the largest mode of oocytes in mature (stage V) ovaries. Accordingly, both of the mature ovotestes were removed from 24 *A. latus* that were caught at the beginning of the spawning season (mid-July - see results) in 2001 and placed in Gilson's fluid. Note that the amount of testicular material in these gonads was negligible. The ovotestes were shaken once weekly for approximately 6 months to facilitate the breakdown of ovarian connective tissue. The contents of the two ovotestes were then sieved through firstly a 600 μm mesh sieve to remove any remaining undissolved tissue and then through a 125 μm mesh sieve. This essentially facilitated the retention of just cortical alveolar and yolk granule oocytes, which were then weighed to the nearest 0.001 g. Three random subsamples of these oocytes were weighed (mean = *ca* 0.05 g) and a count made of the oocytes they each contained. The numbers of eggs in the three ovarian subsamples of known weight were then used, in conjunction with the total weight of all of the

oocytes, to estimate the total number of eggs in the ovaries of each fish. The relationships between the total number of eggs and both the total length and somatic weight of these 24 fish were determined by fitting linear regressions to the natural logarithms of the variables.

3.2.3 *Biomass and egg per recruit analysis*

The spawning stock biomasses per recruit (*SSB/R*) for female and male *A. latus* were calculated assuming knife-edge recruitment at 3 years (Chapter 4), constant total mortality for fully-recruited fish and a maximum age of 40 years, as $SSB/R_{\text{female}} = \sum_{a=3}^{40} p_{a,\text{female}} W_a \exp(-Z\ a)$ and $SSB/R_{\text{male}} = \sum_{a=3}^{40} p_{a,\text{male}} W_a \exp(-Z\ a)$, respectively, where the proportions of females and males at age *a* during the spawning period, $p_{a,\text{female}}$ and $p_{a,\text{male}}$, were determined from the functions that relate the proportions directly to age. The total body weight, W_a, at age *a* for each sex was determined from the length at age that was calculated from the von Bertalanffy growth equation (Chapter 4, L_∞ = 419 mm, k = 0.320 year^{-1} and t_0 = 0.081 years), employing the total body weight (g) to length (mm TL) relationship for *A. latus* in Shark Bay, which is $W = 0.0000174 L^{2.997}$. Eggs per recruit, E/R, were determined from the equation $E/R = \sum_{a=3}^{40} p_{a,\text{female}} F_a \exp(-Z\ a)$, using the fecundity F_a calculated from the length at age *a*, that was derived from the von Bertalanffy growth equation. Using an estimate of total mortality, *Z*, of 0.23 year^{-1}, which was determined from catch curve analysis (Chapter 4) and a range of alternative values for the instantaneous rate of natural mortality, the spawning potential ratio (SPR) was calculated by dividing the estimated value of the current level of E/R by the value of E/R calculated for the unfished stock (Goodyear, 1993).

3.3 RESULTS

3.3.1 *Macroscopic and histological observations of gonad tissues*

The gonads of *A. latus* < 90 mm TL are thin and strand like and consist almost entirely of connective tissue, the stroma cells of which are *ca* 50 μm in diameter and possess deeply-staining nuclei **(Figure 3.1a, 3.2)**. Gonial cells were first detected in the gonads of fish of 80 to 90 mm, **(Figure 3.2)**, while gonads with both identifiable testicular and ovarian tissue were first observed in a fish of 95 mm and could almost invariably be detected in fish > 110 mm **(Figure 3.2)**. The testicular zone of fish of 110 to 190 mm, *i.e.* < the length at which functional males were first found during the spawning period (see later), contains spermatogonia, spermatocytes and occasionally spermatids, which are located in crypts, while the ovarian zone contains immature oocytes, *i.e.* oogonia and chromatin nucleolar oocytes **(Figure 3.1b, 3.2)**.

During the middle of the non-spawning period, the gonads of fish > *ca* 190 mm in length, possess either substantial amounts of ovarian and testicular tissue or contain predominantly or exclusively ovarian tissue **(Figure 3.2)**. The testicular zone of the first type of ovotestis is flattened and reddish-grey to greyish-white, while its ovarian zone is rounded and translucent-orange. Macroscopically, such gonads are slightly larger but otherwise indistinguishable from those of juveniles of 110-190 mm **(Figure 3.2)**. The testicular zone contains either spermatogonia, spermatocytes and some spermatids in crypts **(Figure 3.1c,d)**, or substantial amounts of connective tissue and brown bodies and no crypts or evidence of spermatogenesis **(Figure 3.1e,f)**. In both types of ovotestis, the oocytes in the ovarian zone are still at an early previtellogenic stage **(Figure 3.2)**.

In the one to two months prior to the commencement of the spawning period, the testicular zones of some ovotestes are white, lobular and far larger than their ovarian zones **(Figure 3.3a)** and contain spermatocytes, spermatids and spermatozoa **(Figure 3.2, 3.3b)**. Fish with this type of gonad, which are destined to become functional males, are assumed to have

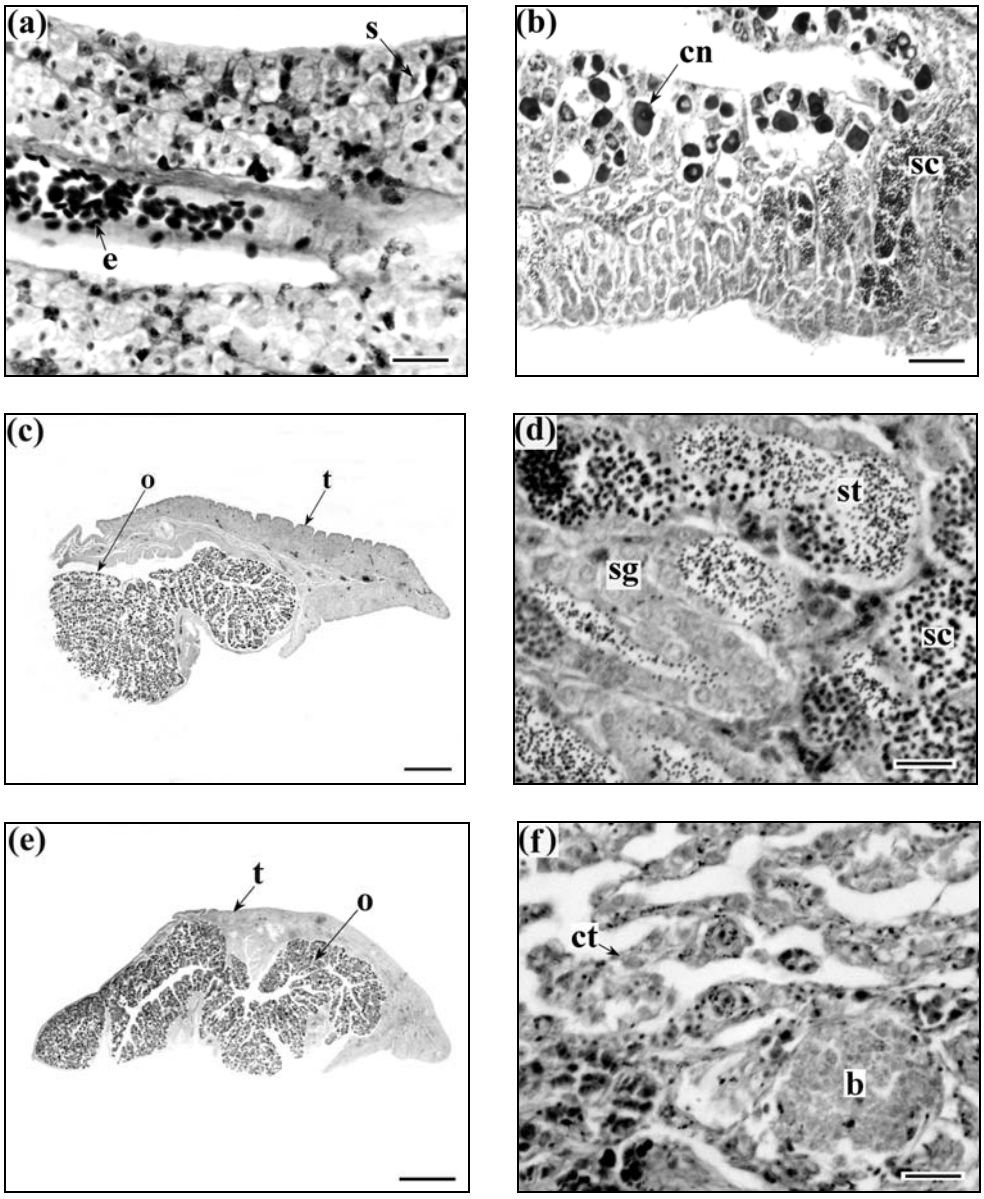

Figure 3.1. Histological sections of gonads of *Acanthopagrus latus*. Gonads of juvenile fish measuring (a) 84 mm and (b) 137 mm. Ovotestes of fish of (c) 380 mm and (e) 400 mm caught in the middle of the non-spawning period and which contained substantial amounts of testicular and ovarian tissue. (d) Spermatogenesis in the testicular zone of the ovotestis shown in (c). (f) Degeneration of the testicular zone of the ovotestis shown in (e). b, brown bodies; cn, chromatin nucleolar oocytes; ct, connective tissue; e, erythrocytes; o, ovarian zone; s, stroma cells; sc, spermatocytes; sg, spermatogonia; st, spermatids; t, testicular zone. Scale bars. a, d, f = 50 μm; b = 100 μm; c, e = 2000 μm.

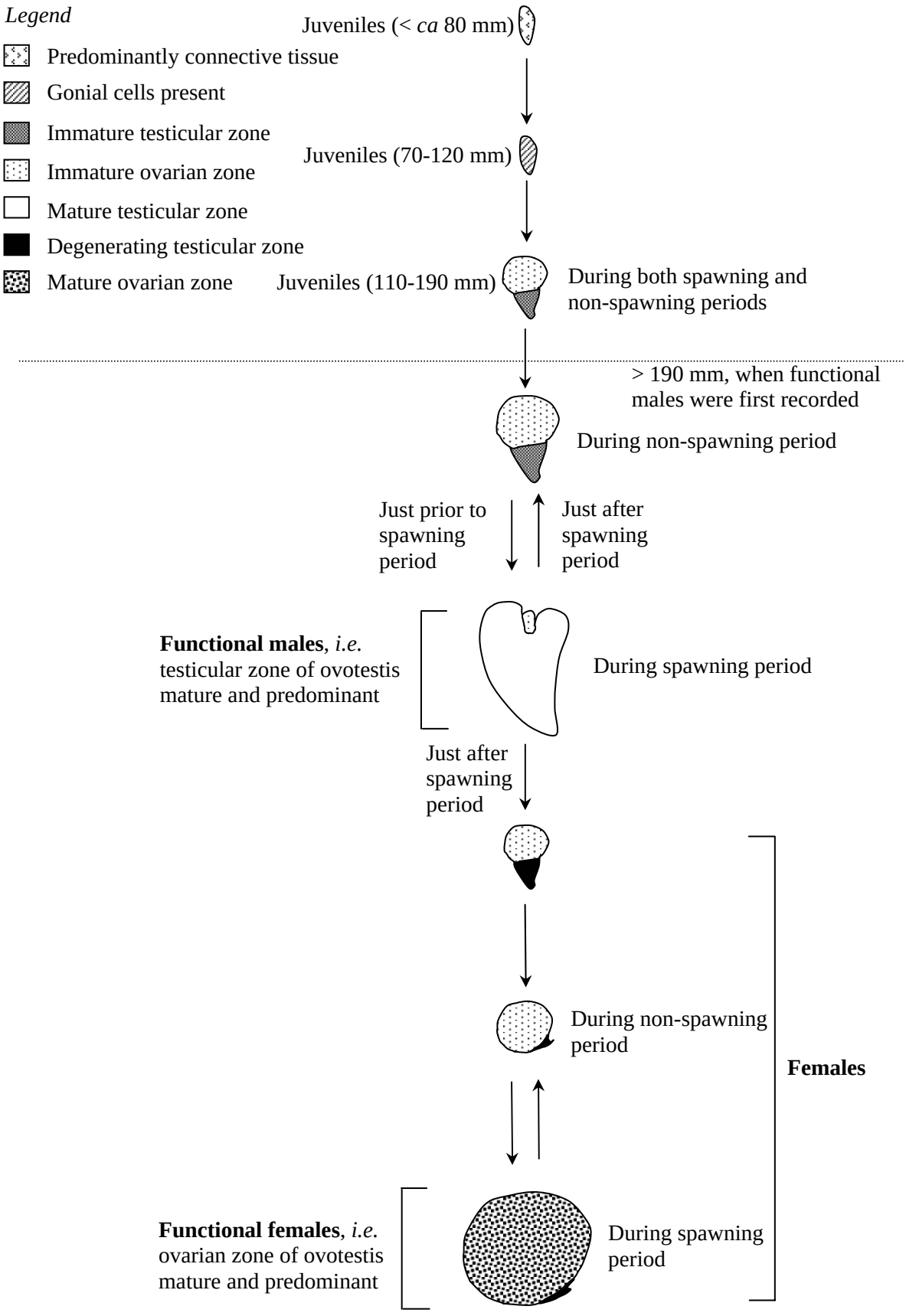

Figure 3.2. Schematic representation of the sequence of protandric events that occur during the life cycle of *Acanthopagrus latus*.

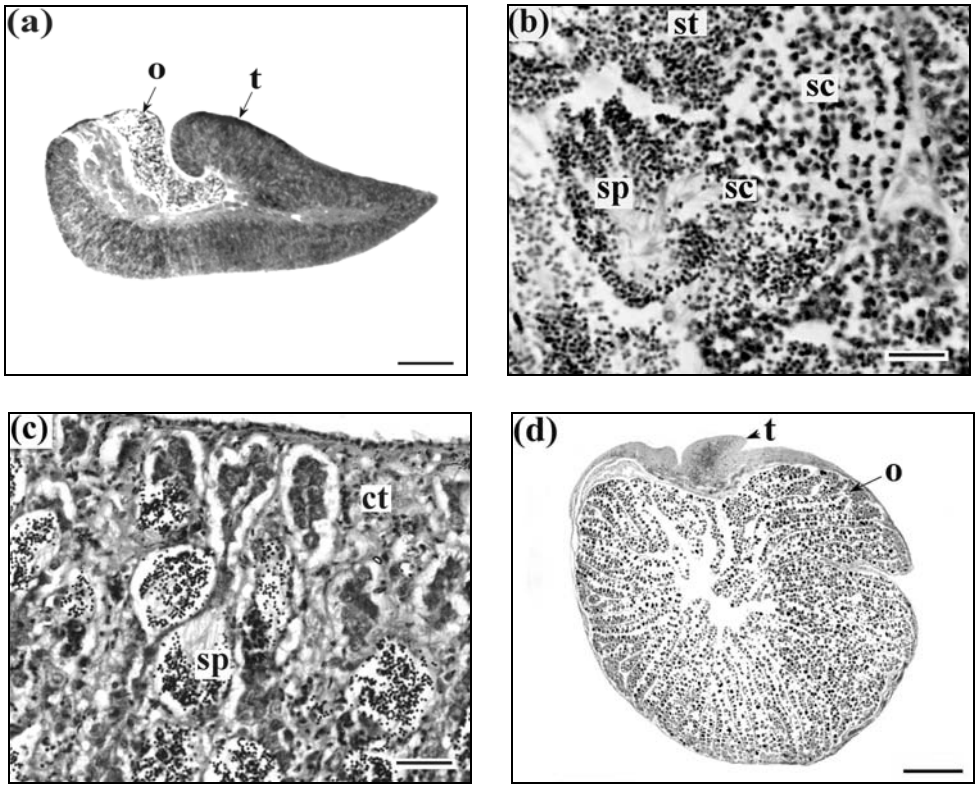

Figure 3.3. Histological sections of (a) an ovotestis of a 307 mm fish caught just prior to the commencement of the spawning period and in which the testicular zone predominates, (b) the testicular zone of the ovotestes shown in (a) with extensive spermatogenesis, (c) the testicular zone of an ovotestis of a 441 mm functional male at the end of the spawning period and (d) an ovotestis of a 257 mm fish caught during the non-spawning period. ct, connective tissue; o, ovarian zone; sc, spermatocytes; sp, spermatozoa; st, spermatids; t, testicular zone. Scale bars. a = 2000 μm; b, c = 100 μm; c = 1000 μm.

developed from fish, which, during the non-spawning period, possessed ovotestes containing substantial amounts of immature testicular tissue with gametes in the early stages of spermatogenesis and immature ovarian tissue with previtellogenic oocytes **(Figure 3.2)**.

During the spawning period, the crypts in the testicular zone of functional males break down and release their spermatozoa. Although a small amount of ovarian tissue is present in the gonads of functional males, the oocytes in this tissue never mature beyond the chromatin nucleolar stage. After spawning, the testicular zone of such gonads decreases in size and becomes dark red-grey and similar in size to the ovarian region. These gonads thus revert to a form of ovotestes that is similar to, but of larger size than that of juveniles of 110-190 mm **(Figure 3.2)**. The periphery of the testicular zone possesses crypts, some of which contain residual spermatids or spermatozoa **(Figure 3.3c)**. During the middle part of the non-spawning period, the testicular zones of these ovotestes contain substantial amounts of degenerating tissue and, as a consequence of their degeneration, have become far smaller than the ovarian zone **(Figure 3.2, 3.3d)**. Shortly prior to the commencement of the spawning period, the ovarian zone of all ovotestes with these signs of degenerating testicular tissue contain several stages in oocyte development, *i.e.* chromatin nucleolar, perinucleolar and some cortical alveolar oocytes **(Figure 3.2, 3.4a)**. Although the very small testicular zone consists mainly of connective tissue, some residual germ cells are present near its periphery **(Figure 3.4b)**. Fish with this type of ovotestis are clearly destined to become functional females in the next spawning season **(Figure 3.2)**. In functional ovaries, *i.e.* those with large numbers of yolk granule stage oocytes, the testicular zone is very small and no longer contains detectable germ cells **(Figure 3.4 c,d)**.

3.3.2 *Seasonal changes in gonadal categories with increasing length and age*

During summer (December to February), the gonads of *A. latus* possess either no macroscopically identifiable ovarian or testicular tissue, a condition found in fish < 160 mm **(Figure 3.5)**, or contain relatively substantial amounts of both immature ovarian and testicular

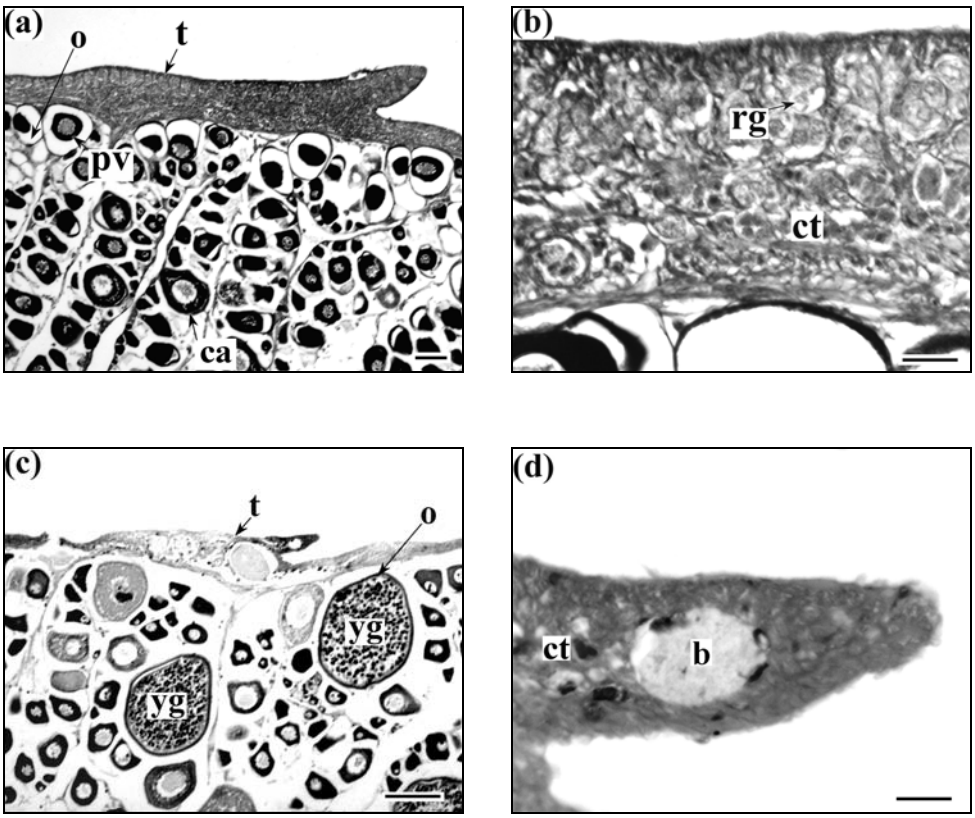

Figure 3.4. Histological sections of part of the ovotestes of fish of 242 mm (a and b) and 283 mm (c and d). The ovarian zones of the ovotestes shown in (a) and (c) were at stages III and IV, respectively, and the testicular zone shown in (d) had regressed further than that in (b). b, brown body; ca, cortical alveolar oocyte; ct, connective tissue; o, ovarian zone; pv, previtellogenic oocyte; rg, residual germ cell; t, testicular zone; yg, yolk granule oocyte. Scale bars. a, c = 100 μm; b, d = 50 μm.

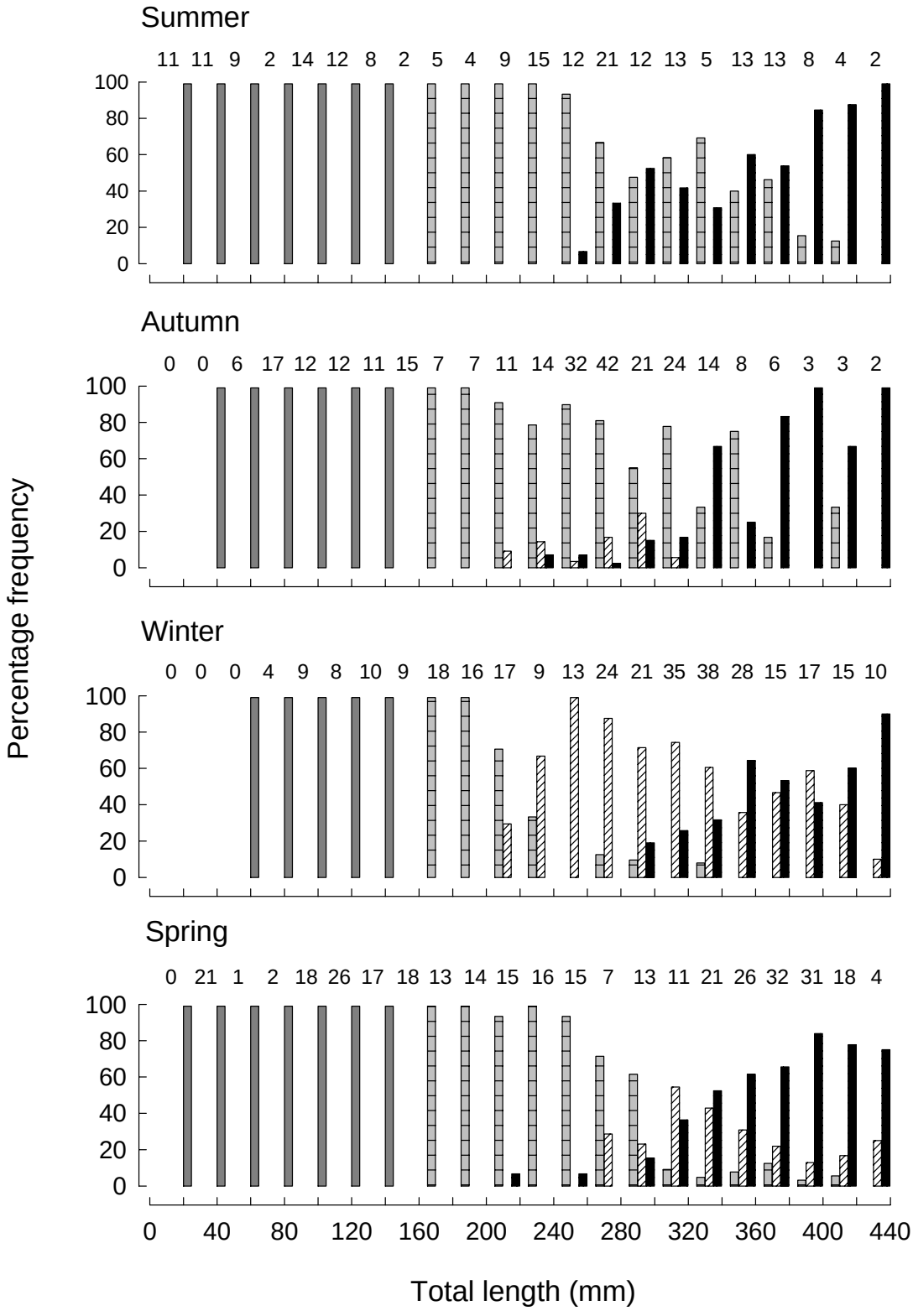

Figure 3.5. Seasonal frequencies of occurrence of different gonadal categories (1-4) in sequential 20 mm length classes of *Acanthopagrus latus* in each season. (1) indeterminate gonads of young juveniles (dark grey), (2) ovotestes containing substantial amounts of both immature testicular and ovarian material (light grey and horizontal lines), (3) ovotestes in which the testicular zone predominates (white and diagonal lines) and (4) ovotestes in which the ovarian zone predominates (black).

tissue or consist predominantly of ovarian tissue. The contributions made by fish with gonads containing both immature ovarian and testicular tissue declined from 100% in fish of 160-240 mm to 48% in those of 280-299 mm and 12% in those of 400-419 mm **(Figure 3.5)**. In contrast, the contributions made by fish with gonads containing predominantly ovarian tissue increased from 7% in fish of 240-259 mm to 54% in those of 360-379 mm and 100% in those of 420-439 mm.

In autumn, a fourth type of gonad was detected, in which the testicular zone is far larger than the ovarian zone and which, on the basis of the histological study reported earlier, belongs to fish presumably destined to become functional males **(Figure 3.2)**. The lengths of all of these fish lay between 200 and 319 mm **(Figure 3.5)**. The contributions made by the number of males increased greatly in winter, and rose sharply from 29% in the 200-219 mm length class to 100% in the 240-259 mm length class, before declining to 56% in the 320-339 mm length class and 10% in the 420-439 mm length class. In contrast, the number of fish with ovotestes containing substantial amounts of both immature testicular and ovarian tissue declined during winter, due to the intervening conversion of such fish into males **(Figure 3.2)**. The remainder of the fish with gonads with immature testicular and ovarian zones correspond to juveniles, a conclusion consistent with the fact that their lengths lay almost exclusively between 60 and 219 mm and thus largely less than all but the smallest functional males **(Figure 3.2)**. The overall contribution made by functional males decreased markedly in spring **(Figure 3.5)**. The continued and similar contribution made by fish with ovotestes containing predominantly ovarian tissue throughout the year implies that once a fish has become a functional female during the spawning period, it remains a female for the rest of its life **(Figure 3.2)**.

3.3.3 *Proportions of juveniles, males and females immediately prior to and during the spawning period*

In the weeks prior to and during the spawning period, the gonads of all *A. latus* < 190 mm were either undifferentiated or contained both immature testicular and ovarian tissue. The contributions made by fish with such gonads subsequently declined precipitously to zero at just above 300 mm **(Figure 3.6)**. In contrast, the contributions of males rose from zero at *ca* 190 mm to a maximum of *ca* 85% at *ca* 270 mm and then fell to zero at *ca* 470 mm, trends that are reflected in the 'parabolic curve' that describes these changes in contribution. Females were first found at lengths of *ca* 290 mm, after which their contribution increased in a logistic manner, eventually reaching over 95% in the largest fish **(Figure 3.6)**. The parameters describing the transition of fish from indeterminate to male and subsequently to female, *i.e.* $L_{50,\text{juvenile}}$, $L_{95,\text{juvenile}}$, $L_{50,\text{female}}$ and $L_{95,\text{female}}$, were 245, 310, 348 and 494 mm TL, respectively.

The above trends in the percentage contributions of juveniles, functional males and functional females just prior to and during the spawning season are parallelled by those they exhibit with the age of fish **(Figure 3.7)**. Thus, the functional male category dominated the 2+, 3+ and 4+ age classes, but then declined markedly in the 5+ and older age classes. In contrast, the proportion of functional females increased from relatively low values in the 2+, 3+ and 4+ age classes to become the dominant category in the 5+ and older age classes **(Figure 3.7)**. The parameters of the logistic curves relating the proportions of each sex to age, *i.e.* $a_{50,\text{male}}$, $a_{95,\text{male}}$, $a_{50,\text{female}}$, $a_{95,\text{female}}$, K_{male} and K_{female}, were 1.75, 3.70, 4.78 and 15.45 years and 0.658 and 0.160 year^{-1}, respectively. Note that, since the older age classes were not well represented and thus carry a reduced weight, the curves do not pass through the points for those age classes.

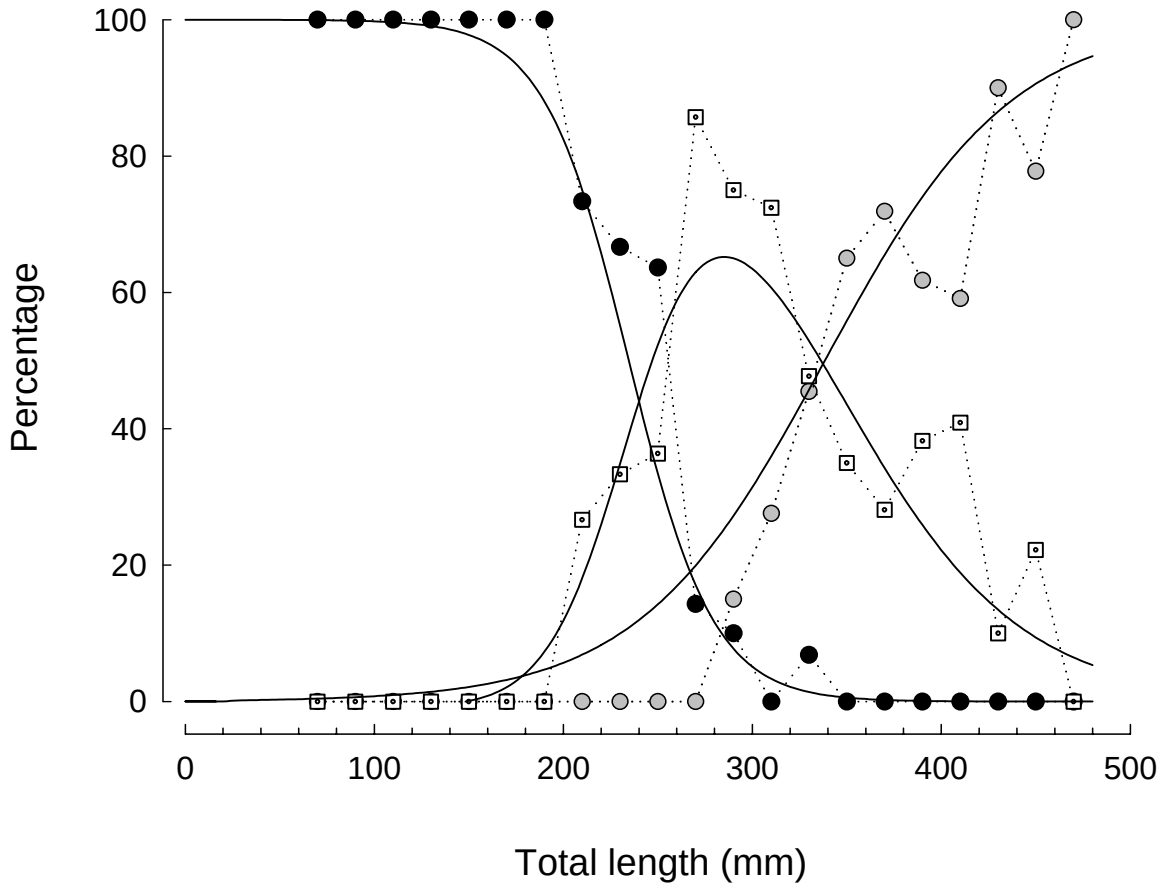

Figure 3.6. Models fitted to the observed frequencies of juveniles (black circles), functional males (white squares) and functional females (grey circles) in sequential 20 mm length classes of *Acanthopagrus latus* caught just prior to and during the spawning season. Sample sizes of fish < 200, 200-299, 300-399 and > 400 were 75, 99, 199 and 40, respectively.

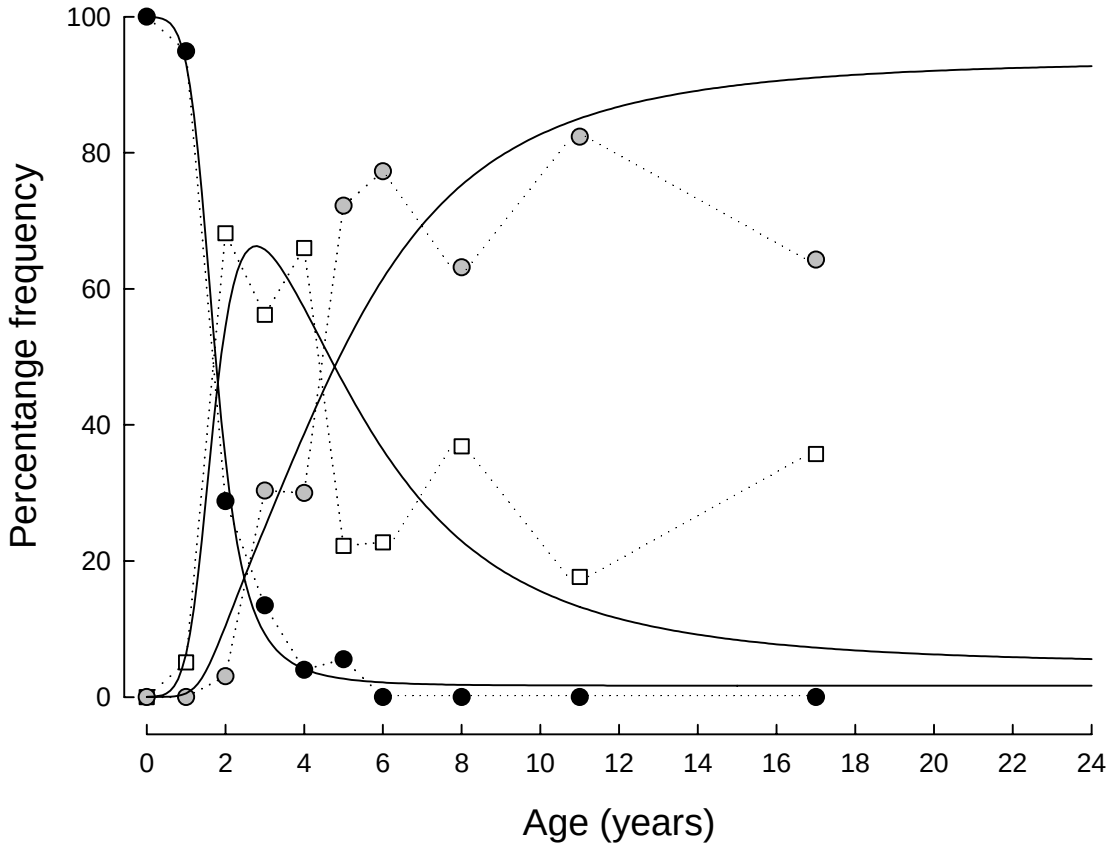

Figure 3.7. Models fitted to the observed frequencies of juveniles (black circles), functional males (white squares) and functional females (grey circles) in sequential age classes of *Acanthopagrus latus* caught just prior to and during the spawning season. Because relatively few fish were older than six years, the data for age classes 7-9 (n = 38), 10-12 (n = 17) and > 12 (n = 14) are shown as pooled values.

3.3.4 *Reproductive variables*

The mean monthly GSIs of females, *i.e.* fish with ovotestes containing almost exclusively ovarian tissue **(Figure 3.2)**, rose sharply between June and August and then fell precipitously during the ensuing two months **(Figure 3.8)**. The mean monthly GSIs of fish that did not possess ovotestes with the above characteristics and were > 245 mm, the length at which 50% of juveniles became males, and were thus considered to be presumptive or functional males, followed an essentially identical trend to that of females. The sharp rise and then marked decline in the mean monthly GSIs indicate that *A. latus* has a short spawning period.

The macroscopic characteristics of the different stages in the development of the ovarian tissue of females, together with the cytological characteristics of each of those stages, are presented in **Table 2.2**. The ovarian tissue of all females in March and April were at stages I/II, *i.e.* virgin or immature/resting **(Figure 3.9)**. Fish with ovaries at stages III (developing) and IV (maturing) were first found in May and those with ovaries at stages V-VI (mature or spawning) were first recorded in June and were collectively the most prevalent category in July and the sole category in August. Although the above trends suggest that spawning could commence as early as June, the fact that the mean monthly GSIs were still continuing to increase markedly between July and August implies that, by July, the gonads of many fish had still not reached full maturity, *i.e.* were not producing and releasing hydrated oocytes. This conclusion is consistent with the observation that, in contrast with the situation in August, the ovaries of very few fish in July contained hydrated oocytes or post-ovulatory follicles. Fish with stage VII (spent) ovaries were first found in September and, together with stage VIII (recovering) ovaries, collectively dominated the complement of ovaries recorded in that month. Furthermore, very few stage V/VI ovaries were found in fish caught during October **(Figure 3.9)**. The above trends imply that very little spawning occurs after September. Thus, spawning takes place predominantly during a relatively short period in late winter and early spring. Furthermore, since *A. latus* has determinate fecundity (see later), the large contribution, *i.e.* sometimes up to *ca* 50%, made by hydrated

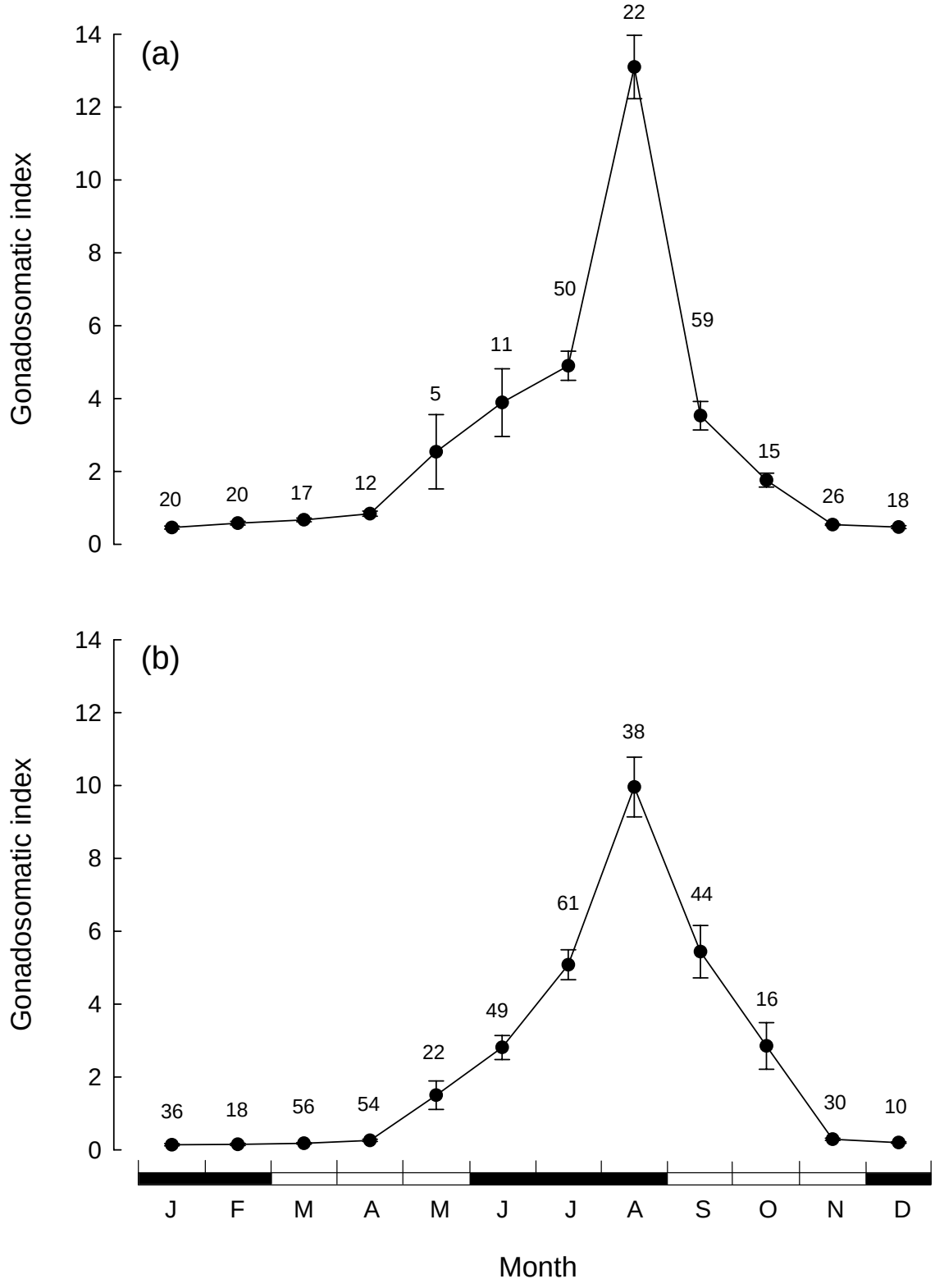

Figure 3.8. Mean monthly gonadosomatic indices ±1SE of (a) definitive females and (b) collectively for functional males and fish with gonads that contained relatively substantial amounts of female and male tissue and were > 245 mm. Number of fish used to derived each mean is shown.

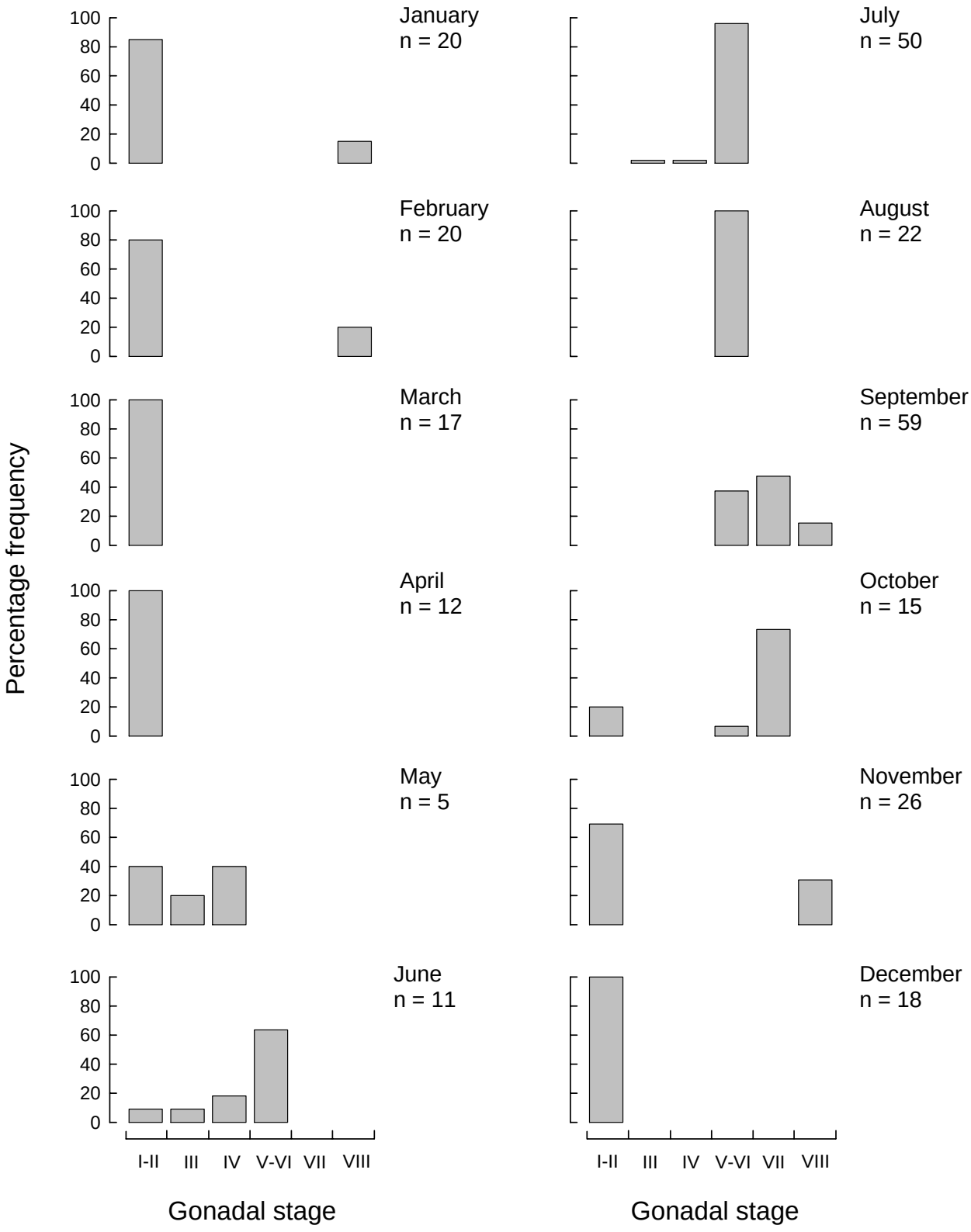

Figure 3.9. Monthly percentage frequency histograms for gonadal maturity stages of female *Acanthopagrus latus*. n = sample size.

oocytes to the suite of vitellogenic oocytes in ovaries with this category of oocyte, suggests that *A. latus* spawns on a limited number of occasions within this short period.

3.3.5 *Fecundity*

The distributions of the oocyte diameters in the mature (stage V) ovaries of the two mature females shown in **Figure 3.10** were markedly bimodal, as was the case with other such ovaries during the spawning period. The distribution of the diameters of the group of smallest oocytes, *i.e.* typically < 120 μm, which were predominantly at the chromatin nucleolar or perinucleolar stages, was strongly skewed to the left, with a modal class at 20-39 μm. In both ovaries, the largest oocytes, which were mainly yolk granule oocytes, were represented by a modal diameter class that lay between 380 and 419 μm. The presence of a gap between the diameters of the groups of small and large oocytes in mature females demonstrates that this species has determinate fecundity *sensu* Hunter *et al.* (1985). Thus, the number of large eggs in the ovaries of females caught immediately prior to the commencement of the spawning period was used to provide estimates of the potential annual fecundity of *A. latus*, *i.e.* the annual fecundity uncorrected for atretic losses. However, it should also be pointed out that the histological sections of mature ovaries of fish caught just prior to and during the spawning period contained very few atretic oocytes and therefore that the influence of atresia on our estimates for fecundity of *A. latus* is likely to be negligible. *i.e.* our estimates for those individuals of *A. latus* would have closely approximated their true annual fecundities. Furthermore, the fact that the ovaries of females with stage VI ovaries contained substantial numbers of both yolk granule oocytes with no signs of hydration and oocytes in an advanced stage of hydration, strongly indicates that *A. latus* is a multiple spawner *sensu* de Vlaming (1983), *i.e.* individual females release oocytes on more than one occasion during a spawning season, even though such spawning may occur on only a few occasions within that season.

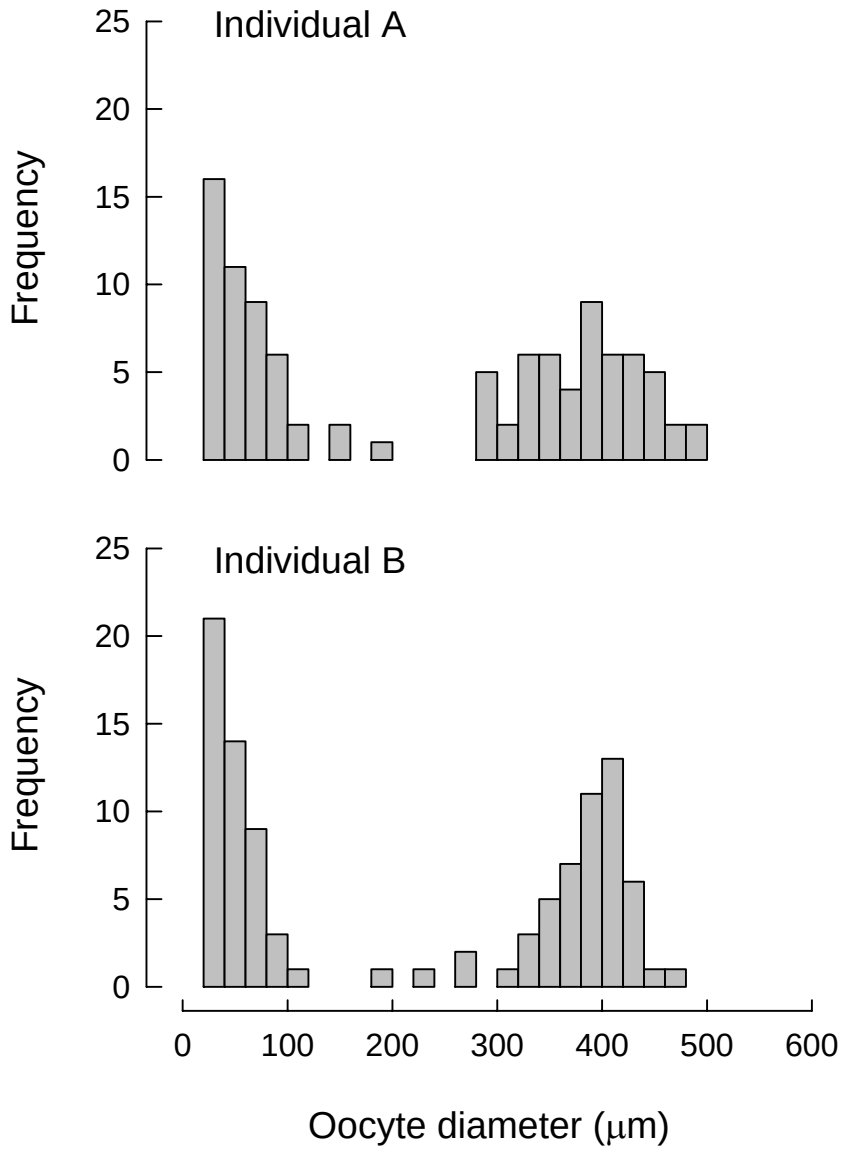

Figure 3.10. Ooctye diameter frequencies for two mature (stage V) female *Acanthopagrus latus.*

The relationships between the natural logarithms of potential annual fecundity and the total length **(Figure 3.11a)** and somatic weight of *A. latus* **(Figure 3.11b)** are described as follows:

(1) $\log F = 4.080 \log L - 9.651$ (R^2 = 0.54, n = 24)

(2) $\log F = 1.328 \log W + 5.528$ (R^2 = 0.66, n = 24),

where F = annual fecundity, L = total length (mm), W = somatic weight (g) and R^2 = the coefficient of determination.

The potential annual fecundities of *A. latus* predicted by the exponential equations for female *A. latus* with lengths of 300, 350, 400 and 450 mm are 959 410, 1 662 900, 2 882 220 and 4 995 620 eggs respectively, and for female *A. latus* with somatic weights of 500, 1 000, 1 500 and 2 000 g, are 1 076 000, 2 062 000, 3 9580 000 and 7 566 000 eggs. The mean fecundity ±1SE for the 24 fish was 1 935 000 ± 281 000. The fecundity ranged between 764 000 for a fish of 331mm and 600 g (total body weight), and 7 910 000 eggs for a fish of 450 mm and 2 050 g (total body weight), respectively.

3.3.6 *Spawning biomass per recruit*

The spawning biomass per recruit (SSB/R) analysis indicated that, with a total mortality (Z) of 0.23 year^{-1}, determined from catch curve analysis (Chapter 4), the spawning biomass of females currently exceeds that of males by 122%, *i.e.* 2 350 vs 1 060 g recruit^{-1}. If the levels of natural mortality were 0.1, 0.15 and 0.2 year^{-1}, the egg production per recruit by the females would correspond to SPRs of 0.29, 0.51 and 0.80, respectively.

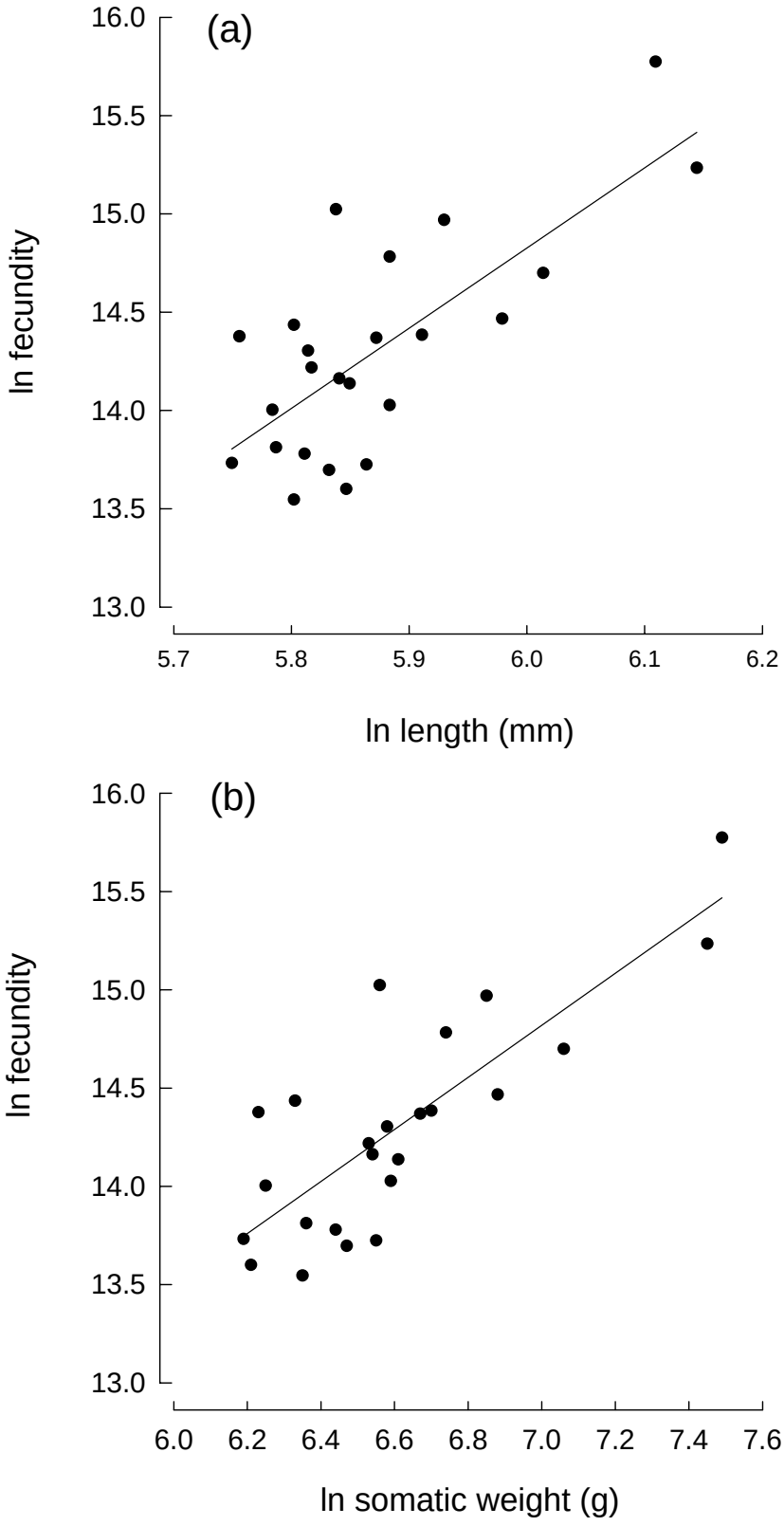

Figure 3.11. Relationship between potential annual fecundity and (a) total length and (b) somatic weight of *Acanthopagrus latus*.

3.4 DISCUSSION

3.4.1 Acanthopagrus latus *is a protandrous hermaphrodite*

Analysis of the trends exhibited by microscopic and macroscopic changes to the gonads over the full size and age range of *Acanthopagrus latus* in Shark Bay, and during both the non-spawning and spawning periods, clearly demonstrates that this sparid is a protandrous hermaphrodite in this large embayment. These trends have also enabled us to elucidate the precise sequence of changes that occur in the ovotestes of *A. latus* from early in life, when they consist almost exclusively of connective tissue, through to late in life when essentially all individuals are females **(Figure 3.2)**. Furthermore, the data on the changes in the percentages of the two sexes with increasing body size and age, using data for the period immediately prior to and during the spawning period, also demonstrate that all males are almost certainly destined to become females.

The problems inherent in using differences in the size distributions of males and females as evidence that a species is either a protandrous or protogynous hermaphrodite have been pointed out by Sadovy & Shapiro (1987), and were negated in the present study by the adoption of a rigorous and comprehensive sampling regime and methods for analysing the data. For example, (1) it is highly unlikely that the sex-related bimodality in the size distributions of *A. latus* in Shark Bay were due to the larger males of this species moving offshore since our fish were obtained from the full range of depths (0.5 m to 5 m) in which this species is caught by commercial and recreational fishers using a range of fishing methods. (2) It is also highly unlikely that the very conspicuous sex-related differences in length were due to selective fishing since substantial numbers of fish were obtained by each of three different sampling methods, *i.e.* seine netting, haul netting and rod and line fishing. (3) Furthermore, these differences were not due to differences in mortality rates between the sexes rather than to the influence of protandry, since only males were represented among the smaller and younger of the mature-sized fish during the spawning period. (4) Moreover, because the changes in the contributions made by

each sex with increasing age parallel those that occur with increasing size, the differences in the lengths of the two sexes cannot be attributed to differences between the growth rates of males and females. Although *A. latus*, and also *Acanthopagrus australis* and *Acanthopagrus berda*, which are likewise found in Australia (Pollock 1985, Tobin *et al.* 1997), are protandrous hermaphrodites, another Australian congeneric, *i.e. Acanthopagrus butcheri*, is a rudimentary hermaphrodite (Sarre & Potter 1999, Sarre 1999).

Our scheme for the sequential changes undergone during life by the gonads of *A. latus* in Shark Bay **(Figure 3.2)** contrasts markedly with that of Abol-Munafi & Umeda (1994), who concluded that, as *A. latus* increases in size, the ovarian zone of its ovotestes gradually enlarges at the expense of its testicular zone and that, as a consequence, the males become gradually transformed into females. Although the protandric changes undergone by *A. latus* may vary among populations, it seems far more likely that the conclusion drawn by Abol-Munafi & Umeda (1994) represents a failure to recognise that the ovotestes of males revert to a form similar to that of a large juvenile after spawning and thus, at that time, could not be distinguished as belonging to either a male or female. Furthermore, the fact that the prevalence of the females of *A. latus* in Shark Bay rose progressively to *ca* 100% with increasing length and age also contrasts with the conclusions of Abu-Hakima (1984) and Abou-Seedo *et al.* (2003) that many individuals of this species do not change sex. It appears highly relevant that those latter workers reached this conclusion without analysing the ways in which the prevalence of females changed over the full size and age range of their populations.

Our scheme for the pattern of gonadal changes in *A. latus* is similar to that of Pollock (1985) for the protandrous *A. australis* in eastern Australia. However, in contrast to Pollock (1985), we conclude that it is very unlikely that any fish develop directly from an immature juvenile into a female. This conclusion is based largely on the fact that, during the spawning period, the vast majority of the fish of *ca* 270 mm in length were males and no female fish were caught at this or lesser lengths. This conclusion is given further weight by the fact that, since a

single smooth curve could be used to describe the growth of the individuals in the population of *A. latus* in Shark Bay (Chapter 4), the sex-related bimodality in the lengths of individuals in this population could not have been due to differences in the rate of growth of the two sexes. Moreover, in view of the very strong protandric trends exhibited overall by *A. latus*, it appears reasonable to propose that the few fish that still possessed immature juvenile gonads when they had reached lengths of *ca* 290 mm, the size at which females were first found, would have been destined to become males **(Figure 3.6)**.

3.4.2 *Aspects of spawning and estimates of fecundity*

Since *A. latus* spawns in Shark Bay in late winter and early spring, the larvae are produced at a time when water temperatures in that embayment are starting to increase progressively from their winter minima (see **Figure 7.1**). This therefore provides the juveniles of *A. latus* with a protracted first growing season and therefore increases their chances of survival (see Conover, 1992; Cushing, 1990). The spawning period of *A. latus* is similar to that of another sparid in Shark Bay, namely the tarwhine *Rhabdosargus sarba* (Hesp & Potter, in press).

Since *A. latus* has determinate fecundity, the standing stock of large oocytes in functional females with mature ovaries in July represents the potential annual fecundity of this species in Shark Bay. The fecundities estimated in the present study are consistent with those derived for five females in the Arabian Gulf by Abu-Hakima (1984) on the basis of the number of oocytes with a diameter ≥ 180 μm, an approach that would have essentially only included cortical alveolar and yolk granule oocytes and, if they were present in their fish, also hydrated oocytes. However, our estimates and those of Abu-Hakima (1984) are far lower than those of Abol-Munafi and Umeda (1994), differences which can be attributed to those latter workers having counted all of the oocytes in the ovary and having thus included oocytes in earlier stages of

development. Our conclusion that *A. latus* is a multiple spawner conflicts with that of Abu-Hakima (1984), but agrees with that of Abol-Munafi & Umeda (1994).

3.4.3 *Implications for management*

The current minimum legal total length for *A. latus* in Western Australia is 250 mm, which is very similar to the length at which 50% of the fish first become identifiable as functional males during the spawning season, *i.e.* 245 mm. Since this species requires a further 2½ years to reach 348 mm (Chapter 4), the length at which 50% of the males will become females, it can legally be fished during this protracted period. Following his consideration of the implications of the results of sex changes on yield-per-recruit models for two protogynous species, Buxton (1992) proposed that the minimum legal length (MLL) for these species should be greater than the length at which they change from female to male. Since mortality due to fishing will have a greater impact on the females than the males of a protandrous species, it is even more valid to impose a MLL that is greater than the typical length at which sex change occurs in protandrous species such as *A. latus*. Indeed, if the current MLL for *A. latus* is maintained, the pressure from an ever-increasing number of recreational fishers could have a severe impact on the spawning biomass of the females of this species. Such a view would be consistent with the conclusion of the Western Australian Department of Fisheries that, prior to the implementation of management changes that reduced the number of commercial fishing licenses, commercial fishers were apparently having a detrimental impact on the stock of this species in Shark Bay (Shaw, 2000).

In the context of management, it is particularly relevant that *A. latus* forms spawning aggregations which are then targeted by fishers. Thus, if necessary, a reduction in fishing pressure on this species could also be achieved by placing restrictions on the capture of *A. latus* during the spawning season, which occupies a relatively short period.

Although the calculated spawning potential ratios (SPR) suggest that the current spawning female biomass is greater than 20% of the unfished spawning biomass for the range of likely natural mortalities for this species, *i.e.* 0.1 to 0.2 year^{-1}, it should be noted that, if the level of natural mortality is 0.1 year^{-1}, the SPR for female *A. latus* is currently only 0.29, which is approaching the limit reference point that is often used for other species (Goodyear, 1993). The current ratio of female to male spawning biomass per recruit, 2.21, and the current level of female spawning biomass per recruit, 2 350 g recruit^{-1}, based on the estimate of the current instantaneous rate of total mortality, 0.23 year^{-1} (Chapter 4) are benchmarks against which future values might be assessed if recreational fishing pressure continues to grow.

This chapter has been accepted for publication as follows:

Hesp. S. A., Potter, I. C. & Hall, N. G. in press. Reproductive biology and protandrous hermaphroditism of *Acanthopagrus latus*. *Environmental Biology of Fishes*.

4.0 AGE AND SIZE COMPOSITIONS, GROWTH, MORTALITY AND HABITATS OF *ACANTHOPAGRUS LATUS*

N. G. Hall, S. A. Hesp & I. C. Potter

4.1 INTRODUCTION

The age composition and growth of *A. latus* in the Arabian Gulf were determined by Samuel & Mathews (1987), using data derived from the number of opaque zones in otoliths, which had been cracked and burnt. However, no attempt was made during that study to validate that this method was appropriate for ageing this species, a procedure now regarded as a prerequisite before such counts can be used with confidence to estimate the ages of individual fish (Campana, 2001). Catch curve analyses by Samuel & Mathews (1987) strongly indicated that the total mortality of *A. latus* in the Arabian Gulf during the early 1980s was high. However, the estimate of the instantaneous coefficient of natural mortality, *M*, obtained by Samuel & Mathews (1987) using the equation of Pauly (1980), was far greater than their estimate of the instantaneous coefficient of total mortality, *Z*. Since the same anomalous results were recorded for three other *Acanthopagrus* species, Samuel & Mathews (1987) concluded that the Pauly equation was inappropriate for estimating the natural mortality of these four sparid species.

Estimates of natural mortality have often been derived from empirical equations, such as those of Pauly (1980) and Ralston (1987), which had been developed using data for a large number of species from several different regions. The data employed to develop the regression equations of Pauly (1980) and Ralston (1987) were water temperature, the growth coefficient, *k*, and asymptotic length, $L_{\infty,}$ in the von Bertalanffy growth equation, in the case of the former equation, and solely the above growth coefficient in the latter equation. In contrast, Hoenig (1983) derived equations for total mortality, based on the assumption that the estimated total mortalities are related to the maximum observed ages for the range of stocks that he used. Since Hoenig's (1983) regression equation for total mortality for fish employed data for a range of

lightly-fished stocks, it yielded values that would be similar to natural mortality in such stocks, but not in those that are heavily-exploited.

As pointed out by Vetter (1988), each of the above equations provides a single and very imprecise point estimate for mortality. Furthermore, the growth data employed by Pauly (1980) and Ralston (1987) and the age data used by Hoenig (1983) for constructing their equations were obtained prior to the time when it became mandatory to validate the procedure employed for ageing fish for growth studies (Beamish & McFarlane, 1983; Campana, 2001). Moreover, other studies have often found that the individual values derived for natural mortality using the equations of Pauly, Ralston and Hoenig, varied markedly (*e.g.* Burton, 2001). Since fishing mortality represents the difference between total and natural mortality, it is obviously important to obtain a reliable estimate of both of these types of mortality and, as has been stressed by Pascual & Iribarne (1993) and Cubillos *et al.* (1999), to assess the level of precision associated with these point estimates.

During the present study, lengths at age for individuals of *A. latus* in Shark Bay were obtained employing a validated ageing procedure, and used to determine the age compositions and growth of this species in this large marine embayment. The von Bertalanffy growth parameters derived from the present study were inserted into the empirical equations of Pauly (1980) and Ralston (1987) for determining natural mortality, *M*. Estimates for total mortality, *Z*, were then derived by inserting the maximum age of *A. latus* in commercial fish catches from Shark Bay into the equations of Hoenig (1983). Further estimates of *Z* were obtained by employing simulation to compute the approximate probability density function for *Z* associated with this maximum age and by subjecting the age composition data to relative abundance analysis. However, the resultant estimates of *M* for *A. latus* in Shark Bay were far greater than all of those for *Z* (see results). Therefore, a Bayesian approach was used, which, through incorporating all of the available information relating to mortality, yields more realistic and

consistent estimates for the very important parameters *M* and *Z* than were produced by the empirical equations on their own. This approach involved combining the likelihood distributions associated with each of the separate estimates of *M* and *Z* to derive single likelihood distributions for each of these two mortality variables. The Bayesian approach used in the present study is equally applicable for determining natural and total mortality of other fish species for which there are multiple and often inconsistent estimates of these parameters.

4.2 MATERIALS AND METHODS

An independent reader (Dr G. A. Sarre, Murdoch University) counted the opaque zones that he observed in 100 sectioned otoliths removed from a wide size range of *A. latus*. Ninety percent of the counts were the same as those made by S. A. Hesp. In six of the ten cases where there were discrepancies, it was mutually agreed, after re-examination of the otoliths, that the independent reader had not detected the outermost opaque zone on those otoliths. Both readers agreed that some of the opaque zones in the other four otoliths could not be readily distinguished. Hence, these otoliths, and the small number of other otoliths for which it was not possible clearly to detect each of the opaque zones, were not employed for ageing.

4.2.1 *Natural mortality*

Pauly's (1980) regression model was refitted to the data for the 175 fish stocks used in his study in order to provide the additional information required for calculating the confidence limits for an estimate of natural mortality, *M*, derived from that regression equation. This model took the following form,

$$\log_e M = -0.0152 - 0.279 \log_e L_\infty + 0.6543 \log_e k + 0.4634 \log_e T ,$$

where T = mean annual surface water temperature ($^\circ$C) and L_∞ and k are the von Bertalanffy growth parameters. Since the length measurements used by Pauly were recorded as total length

in cm, this policy was adopted for this mortality equation. A point estimate of *M* was then determined for *A. latus* in Shark Bay by inserting into this regression model the estimates of L_∞ and *k*, derived from the above growth equation, and the mean annual surface water temperature of 22.5°C at Denham in Shark Bay, which was derived from data obtained by the Australian Oceanographic Data Centre (http://www.AODC.gov.au).

The likelihood distribution of *M* for *A. latus* in Shark Bay was also estimated from the refitted regression equation and the associated variance-covariance matrix for the parameter estimates. For this calculation, it was assumed that the predicted value of $\log_e M$ for *A. latus*, which was determined from the regression equation, has a Student's *t*-distribution with 171 degrees of freedom and a mean and standard error for the prediction, which were calculated from the values for the independent variables (for formulae see Sokal & Rohlf, 1995, p. 633). If $f(\log_e M)$ is the probability density function of $\log_e M$, then the probability density function of *M* is $g(M) = f(\log_e M)/M$. Accordingly, the likelihood associated with each value of *M* was calculated by dividing by *M* the likelihood of $\log_e M$, as determined from the *t*-distribution derived from the regression equation. Estimates of the confidence limits for *M* were calculated from the resulting likelihood distribution for *M*.

An estimate of *M* and its confidence limits were also calculated by refitting Ralston's (1987) data to his regression equation, *i.e.* $M = 0.0189 + 2.06\,k$, where *k* is the von Bertalanffy growth coefficient.

4.2.2 *Total mortality*

Hoenig's (1983) regression model was refitted to the data for the 82 fish stocks used in his study (provided in Hoenig, 1982) to provide the additional information required for calculating the confidence limits for the estimates of total mortality, *Z*. The model took the form, $\log_e Z = 1.46 - 1.01\log_e t_{max}$, where *Z* = total mortality (year^{-1}) and t_{max} = the maximum

observed age. An estimate of *Z* for *A. latus* in Shark Bay was calculated by inserting the maximum age observed in the sample of 291 fish collected from the commercial catches of *A. latus* in Shark Bay into this equation. These catches were used for this purpose since commercial fishers operate throughout Shark Bay and were therefore likely to obtain a more representative sample than were collected by sampling using seine netting and rod and line angling in more restricted areas.

The values for *Z*, predicted using Hoenig's regression equation for fish, are assumed to have a Student's *t*-distribution, 80 degrees of freedom and a mean and standard error calculated from the independent variable, longevity. If $f(\log_e Z)$ is the probability density function of $\log_e Z$, the probability density function of *Z* is $g(Z) = f(\log_e Z)/Z$. Thus, the likelihood associated with *Z* for *A. latus* in Shark Bay was calculated by dividing by *Z* the likelihood of $\log_e Z$, as determined from the *t*-distribution derived from the refitted regression equation. Estimates of the confidence limits for *Z* were calculated from the resulting likelihood distribution for *Z*.

A further point estimate of *Z*, which adjusts for sample size, was obtained by substituting the observed maximum age for $E(t_{max})$ for the sample from the commercial catches of *A. latus* from Shark Bay in the following equation of Hoenig (1983), *i.e.* $E(t_{max}) = \frac{1}{Z}\sum_{i=1}^{n}\frac{1}{i} + t_c$, where *n* = sample size and t_c = first age fully represented in the catches.

An approximation to the probability density function for *Z*, that is associated with the maximum age recorded in a random sample of a specified sample size, was obtained using simulation. For this purpose, it was assumed that the sample was taken from fish that had reached the age at which they became fully vulnerable to fishing gear, *i.e.* 3 years, and that total mortality, *Z*, was constant above this age. The sample size, which was employed for this simulation, was the number of fish that were ≥ 3 years old in the sample of 291 fish collected

from the commercial catches of *A. latus* in Shark Bay. The simulation was run 100,000 times to develop an approximation to the probability density function for the maximum age recorded in a random sample of the specified sample size for each of a large number of discrete values of *Z*, ranging from 0.05 to 10 year^{-1} at 0.01 intervals and covering the full range of feasible values for *Z*. These results were then used to determine the likelihood distribution for *Z* for *A. latus* in Shark Bay, by applying Bayes' theorem and assuming a uniform prior probability distribution function for *Z*. That is, $P(Z_j \mid t_{\max}) = \frac{P(t_{\max} \mid Z_j)P(Z_j)}{\sum_k P(t_{\max} \mid Z_k)P(Z_k)}$, where $P(Z)$ is the prior probability for *Z* and Z_j is the *j*'th value of the set of discrete values of *Z* that are considered in this analysis and which cover the full range of possible values for this variable.

An estimate of Z was also obtained by analysing the catch curves derived from the commercial samples of *A. latus* in Shark Bay. Since a major assumption of catch curve analysis is that the sample is taken randomly from the fully-recruited age classes (Ricker, 1975), the data used to construct our catch curves for *A. latus* were restricted to those on the descending limbs of the catch curves.

Relative abundance analysis, developed by Deriso *et al.* (1985) as a natural extension of catch curve analysis, was used to analyse the age composition data. This approach to analysing catch curves avoids the assumption that recruitment is constant and overcomes the problem of applying a log transformation to the frequencies for older age classes with zero fish. For a fish stock that experiences a constant level of total mortality, *Z*, from the age of full recruitment, $a=t_c$ years, the estimated proportion, $\hat{p}_{a,t}$, at age *a* in year *t* is $\hat{p}_{a,t} = \frac{R_{t-a}\exp[-(a-t_c)Z]}{\sum_{j=t_c}^{A} R_{t-j}\exp[-(j-t_c)Z]}$, where *A* is the maximum observed age. R_y is the level of recruitment for year class *y*, where recruitment represents the fish that reach the age of full recruitment t_c, relative to the average level, *i.e.* $\overline{R_y} = 1$. It is assumed that the age composition for fish of ages $t_c \le a \le A$ observed in year *t*,

represents a random sample from a multinomial distribution with uniform selectivity from the age of full recruitment. Thus, ignoring constants, the log-likelihood, λ, of the age compositions observed in the various years may be calculated as $\lambda = \sum_{t} \sum_{a=t_c}^{A} n_{a,t} \log[\hat{p}_{a,t}]$, where $n_{a,t}$ is the observed number of fish of age *a* in year *t*. The parameters of the model were estimated for *A. latus* in Shark Bay using AD Model Builder (Fournier, 1994) to maximise the log-likelihood, firstly with the relative levels of recruitment being constrained to the average level, $\overline{R_y} = 1$. The relative levels of recruitment were then, one by one, successively introduced as parameters to be estimated by the model. At each stage of this stepwise procedure, the parameter that was finally selected for inclusion in the model was the one that produced the greatest increase in the log-likelihood. Parameters were only added to the model if they resulted in a statistically significant improvement to the fit of the model to the data, as determined using a likelihood ratio test (*e.g.* Kimura, 1980), while the remaining levels of recruitment continued to be constrained to the average level. Estimates of the profile likelihood distributions of *Z* for *A. latus* in Shark Bay were also obtained for this analysis using AD Model Builder.

4.2.3 *Integrating the separate mortality estimates*

Three independent estimates of *Z* had been calculated for *A. latus* in Shark Bay, using the methods described above, namely those obtained from Hoenig's (1983) equation, the simulation method and the relative abundance analysis, which assumes that recruitment is variable. The two estimates of *Z* calculated for *A. latus*, using the relative abundance analysis, are not independent as they are derived from the same data. Since the variable recruitment hypothesis imposes less stringent conditions on the data, it is likely to yield a more reliable estimate than that which assumes constant recruitment. Although Hoenig's regression equation and the calculation of *Z* from the approximate probability density functions derived from simulation both use the

longevity of *A. latus* in Shark Bay, the former method employs information contained in the set of data from the range of species and stocks to which Hoenig fitted his regression equation. Thus, the information used to develop these two estimates may be assumed to be independent. For the first set of data considered in the analysis, D_1, *i.e.* the longevity of *A. latus* in Shark Bay and the data to which Hoenig's (1983) fish equation was fitted, it is assumed that the prior probabilities for Z are uniformly distributed. Therefore, from Bayes' (1763) theorem, $P(Z_j \mid D_1) = \frac{P(D_1 \mid Z_j)P(Z_j)}{\sum_k P(D_1 \mid Z_k)P(Z_k)}$. For the second set of data, D_2, *i.e.* the longevity of *A. latus* in Shark Bay and the sample size from which this longevity was obtained (as used in the simulation study), the prior probabilities for Z may now be taken as $P(Z \mid D_1)$. Hence, from Bayes' theorem, $P(Z_j \mid D_1, D_2) = \frac{P(D_2 \mid Z_j)P(Z_j \mid D_1)}{\sum_k P(D_2 \mid Z_k)P(Z_k \mid D_1)}$. Similarly, the same approach may be applied for the age composition data that were used in the relative abundance analysis, and subsequently any other data sets that are collected. Thus, for the n'th set of data, D_n, $P(Z_j \mid D_1, D_2, \ldots, D_n) = \frac{P(D_n \mid Z_j)P(Z_j \mid D_1, D_2, \ldots, D_{n-1})}{\sum_k P(D_n \mid Z_k)P(Z_k \mid D_1, D_2, \ldots, D_{n-1})}$. Accordingly, the information concerning Z that is contained in the separate data sets is combined by forming the product of the likelihoods for each value of Z derived from each data set and then normalising the resulting products.

The likelihood of the natural mortality M was calculated from the likelihood for Z by assuming that, for each value of Z, there is a uniform probability that $M<Z$. Thus, if $F(Z)$ represents the cumulative likelihood of Z and $\bar{Z}$ is the expected value of Z, the likelihood of M may be calculated as $(1-F(Z))/\bar{Z}$. The resulting likelihood distribution for M was then combined with that for the estimate of M derived from Pauly's (1980) equation by forming their product at each corresponding value of M and normalising the resultant products. Because there was considerable overlap in the data used by Ralston (1987) to develop his regression equation and

those used by Pauly (1980), the likelihood distribution calculated for *M* using the Ralston equation was not used in the derivation of the combined likelihood distribution for *M*.

4.3 RESULTS

4.3.1 *Comparisons between the number of opaque zones on whole and sectioned otoliths*

Although the same number of opaque zones were observed on the otoliths of *A. latus* prior to and after they had been sectioned when the number of such zones was seven or less, this was frequently not so when otoliths contained a greater number of opaque zones. In the latter cases, the number of opaque zones that could be observed on whole otoliths was less than those that were visible on sectioned otoliths. Furthermore, as the number of opaque zones increased, the frequency and extent of the discrepancies increased from 44% and 1, respectively, when the number of zones visible on the otolith after sectioning lay between 8 and 11, to 92% and 5, respectively, when their number lay between 12 and 15, respectively.

4.3.2 *Validation that opaque zones are formed annually*

The mean monthly marginal increments on otoliths of *A. latus* with two opaque zones rose from *ca* 0.5 in July to reach a maximum of *ca* 0.6 in October, before declining to *ca* 0.4 in November and a minimum of *ca* 0.2 in December and then rising in the ensuing months **(Figure 4.1)**. Essentially the same trend was followed by the mean monthly marginal increments on otoliths with a greater number of opaque zones. Although none of the fish caught in January to April contained otoliths with a single opaque zone, the trends exhibited by the mean monthly marginal increments for the other months of the year were consistent with those exhibited by otoliths with a greater number of opaque zones **(Figure 4.1)**.

Since, irrespective of the number of opaque zones in the otolith, the mean monthly marginal increment rose and declined only once during the year, a single opaque zone is laid down in the otoliths of *A. latus* each year. As the mean monthly marginal increment typically

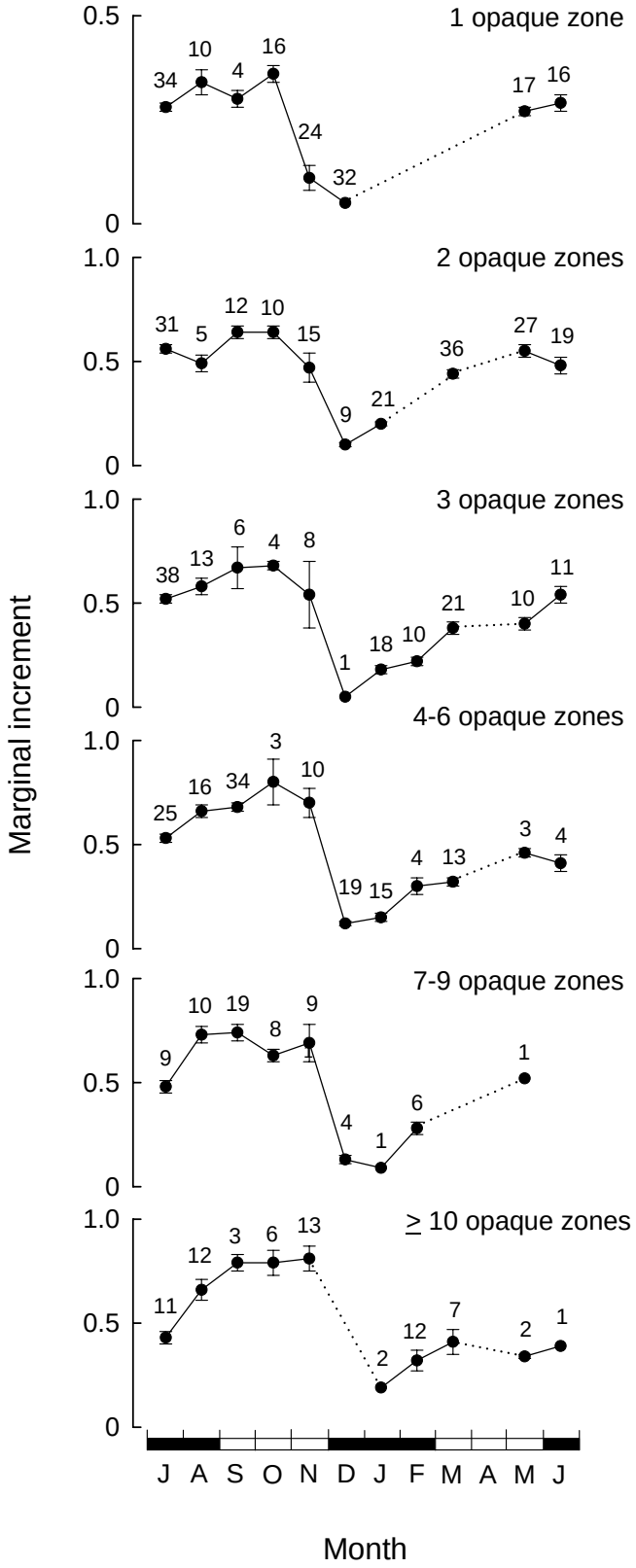

Figure 4.1. Mean monthly marginal increments ± 1SE for sagittal otoliths of *Acanthopagrus latus*. Sample sizes are shown above each mean. On the x axis, black rectangles refer to winter and summer months and open rectangles to spring and autumn months.

peaks in October or November and subsequently declines to its lowest level in December or January, the new opaque zone usually becomes delineated between the middle of spring and early summer.

4.3.3 *Length-frequency distributions of the different age classes*

As the trends exhibited during the year by the GSIs, stages in gonadal maturation and pattern of oocyte development of *A. latus* demonstrated that the spawning of *A. latus* in Shark Bay peaked in late August/early September (Chapter 3), this species was assigned a birth date of 1 September. 0+ *A. latus* were first caught in November, when their lengths ranged from 23 to 40 mm **(Figure 4.2)**. The modal length class reached 60-79 mm by March and 100-119 mm by June. The length distributions of the 0+ age class overlapped that of the 1+ age class in May, and the same situation applied to each pair of successive age classes. However, the length distributions of each of the older age classes produced a distinct modal class in some months. This applied, for example, to the 1+ age class in October, December and July, to the 2+ age class in October and January and to the 3+ age class in July **(Figure 4.2)**.

4.3.4 *Length-frequency distributions in different habitats*

Whilst the vast majority of juvenile *A. latus*, *i.e.* < 200mm TL, were caught in sandy areas amongst mangroves, virtually all fish > 260 mm were caught in waters along rocky shorelines **(Figure 4.3)**, thus strongly suggesting that the juveniles of this species use mangroves as a nursery area and the adults occupy mainly rocky shorelines. Further detailed information relating to the habitats occupied by the different life cycle stages of *A. latus* is given in Chapter 7.

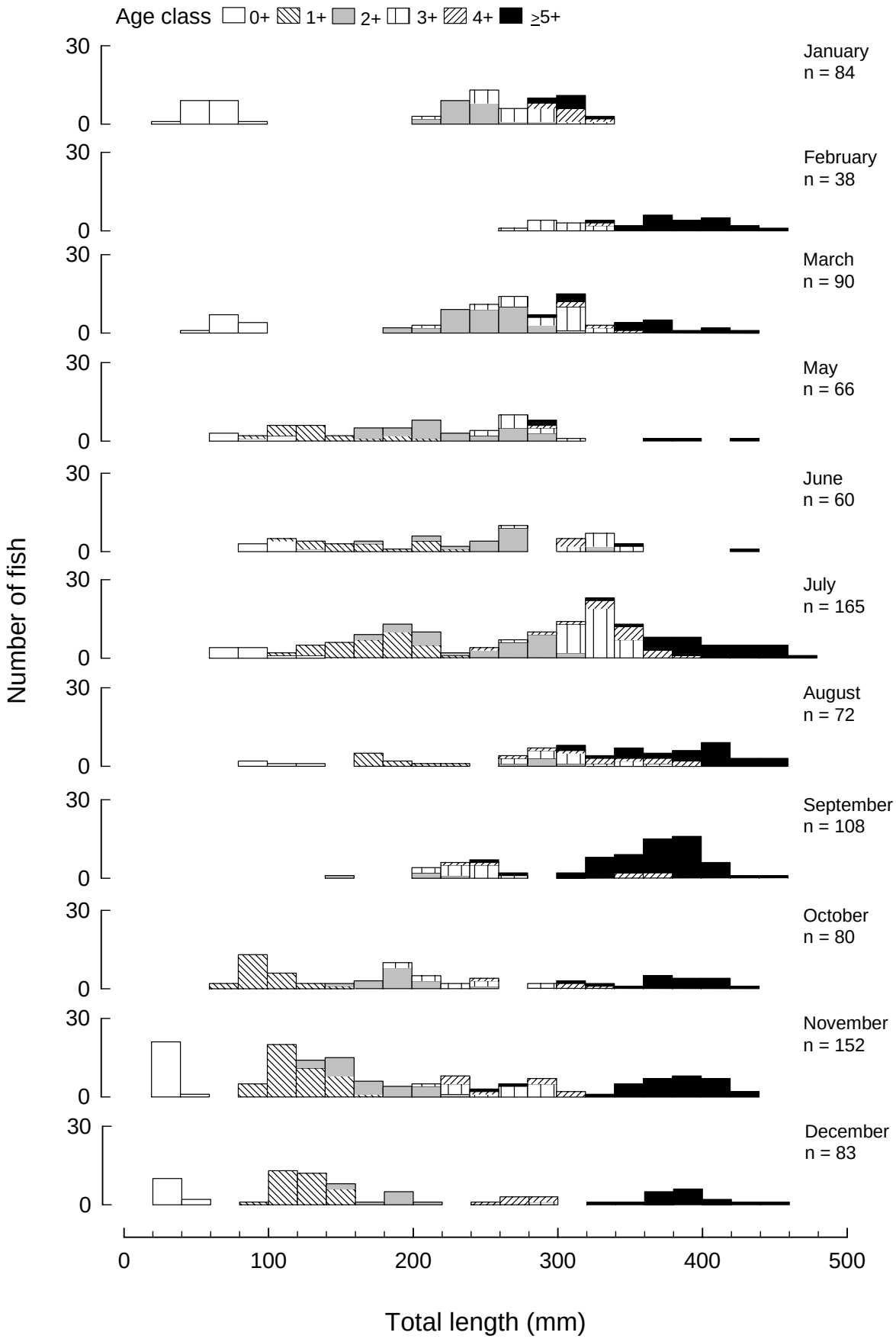

Figure 4.2. Length-frequency distributions for different age classes of *Acanthopagrus latus*. n = number of fish aged.

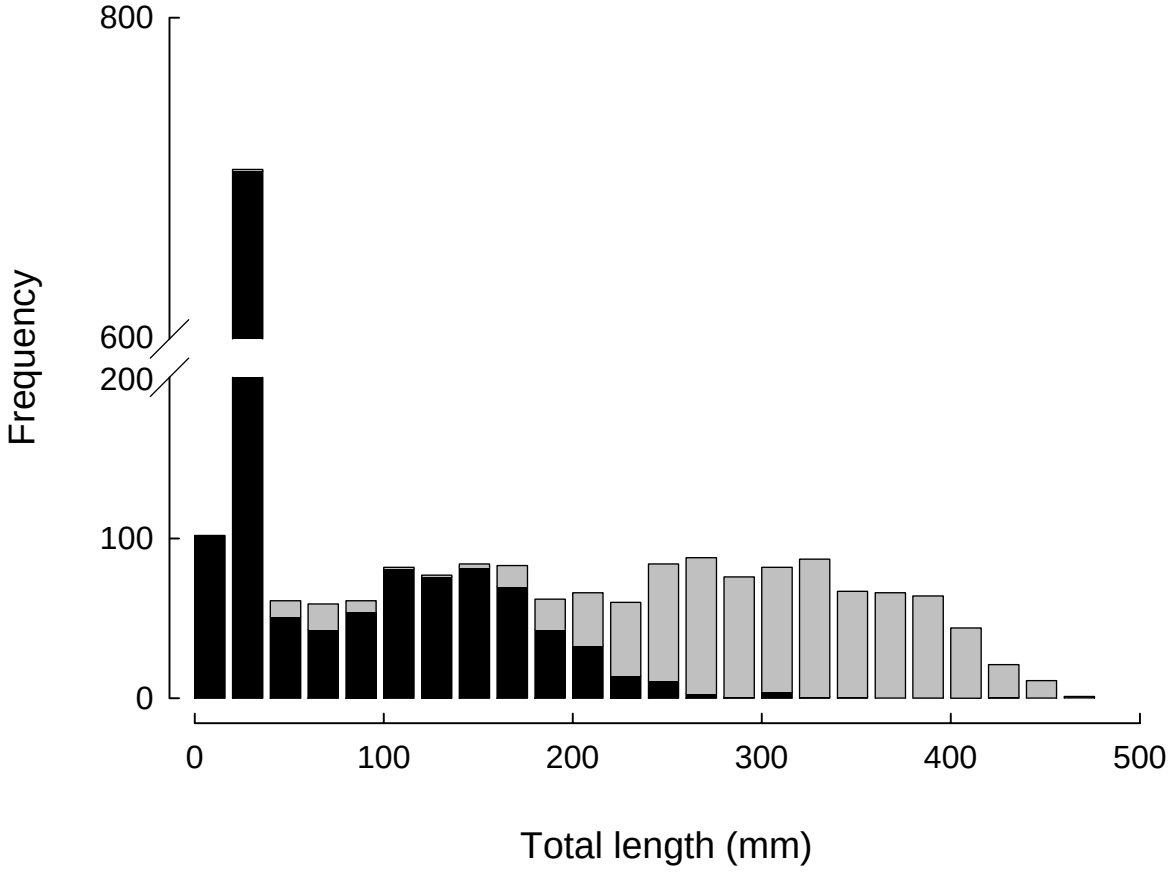

Figure 4.3. Length-frequency distributions for *Acanthopagrus latus* collected from mangrove areas (black) and rocky shorelines and reefs (grey) in Shark Bay.

4.3.5 *Growth of* Acanthopagrus latus

Since the coefficient of determination for the composite curve was as high as 0.921 and the age at zero length (t_0) was close to zero, *i.e.* 0.081 years, the lengths at age of all individuals of *A. latus*, irrespective of whether fish are of indeterminate sex or males or females, are described well by a single von Bertalanffy growth curve **(Figure 4.4, Table 4.1)**. The von Bertalanffy curve demonstrates that, by ages 1 to 5, the individuals of *A. latus* had, on average, reached lengths of 107, 192, 254, 299 and 332 mm, respectively, and that by 10 and 15 years, they had attained lengths of 401 and 415 mm, respectively **(Figure 4.4)**. The maximum recorded length and age for *A. latus* was 466 mm and 24.9 years, respectively. The age at which *A. latus* reached the minimum legal length for capture (MLL) of 250 mm was *ca* 2.9 years. The regression equation relating the total length in mm (L) and weight in g (W) of *A. latus* was $\log_e W = 2.997 \log_e L - 10.972$ (n = 942, $R^2 = 0.997$).

4.3.6 *Mortality estimates and year class strengths*

The point estimates for the instantaneous coefficient of natural mortality, M, for *A. latus*, calculated using the equations of Pauly (1980) and Ralston (1987), were both 0.70 year^{-1} **(Table 4.2)**. The confidence intervals derived from these regression equations were very broad, particularly in the case of the Pauly equation **(Table 4.2)**.

The value of 0.18 year^{-1} derived for total mortality, Z, using the regression equation refitted to Hoenig's (1983) fish data, which related the expected maximum age to Z for lightly-exploited fish stocks, was far lower than the point estimates for M that were calculated from the Pauly and Ralston equations **(Table 4.2)**. The same generalisation was true for the estimate of 0.30 year^{-1} for Z obtained using Hoenig's (1983) equation, which contained an adjustment for sample size. The estimate of $Z = 0.30$ year^{-1}, obtained from the simulation study, was identical to that calculated using this last equation, as calculated using the relative abundance analysis

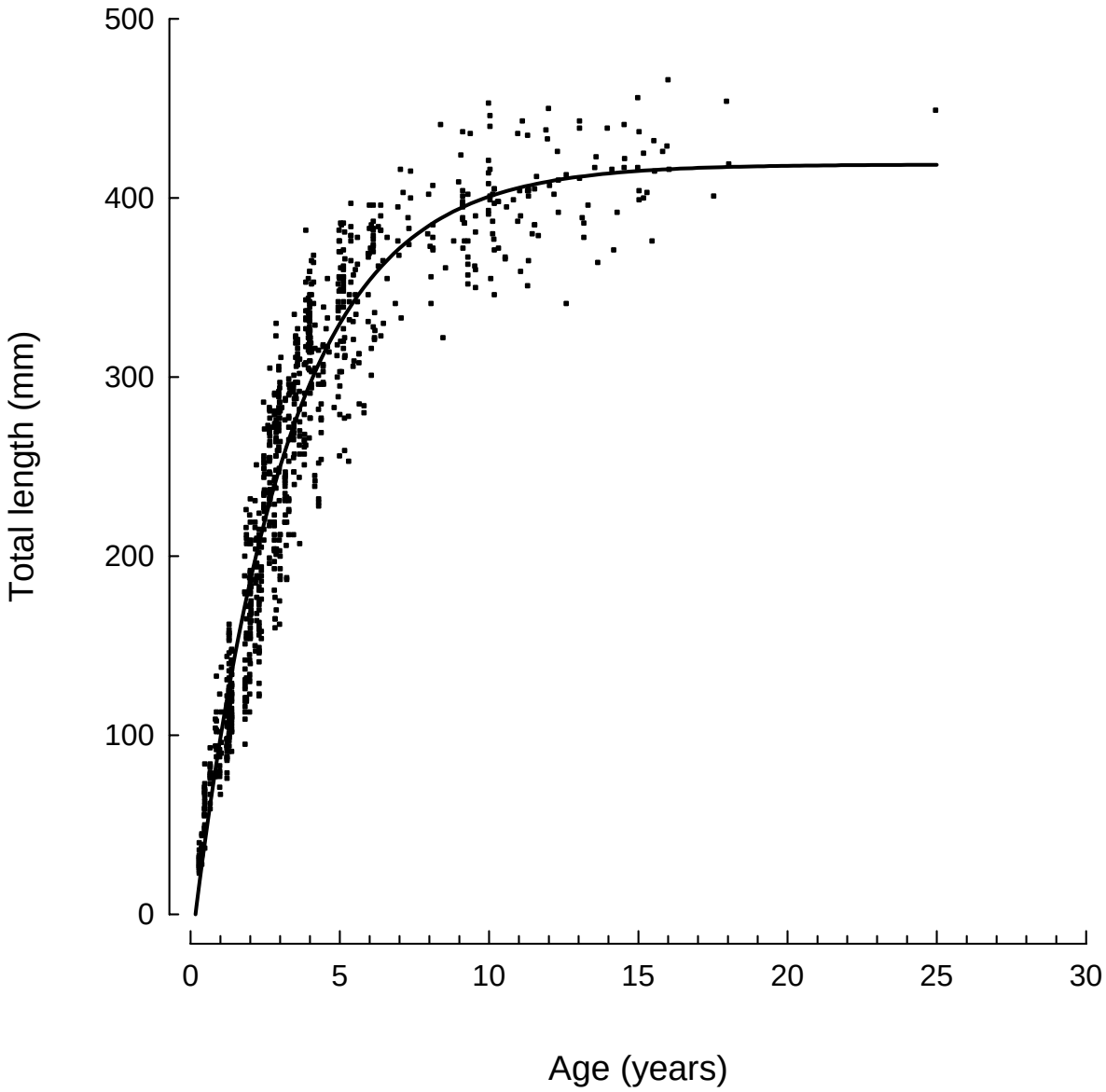

Figure 4.4. von Bertalanffy growth curve for *Acanthopagrus latus* determined using the lengths at age of 922 fish.

Table 4.1. von Bertalanffy growth parameters derived from lengths at age for *Acanthopagrus latus*, including 95% confidence limits, the coefficient of determination (R^2) and number of fish aged (*n*).

	von Bertalanffy growth parameters				
	L_∞ (mm)	k (year^{-1})	t_0 (years)	R^2	*n*
Estimate	419	0.320	0.081	0.921	922
Lower	412	0.304	0.027		
Upper	425	0.335	0.136		

(Table 4.2). The confidence intervals for all of these estimates of *Z* were much tighter than those determined for *M* using the refitted Pauly or Ralston equations **(Table 4.2)**.

The strength of the different age classes in the fishery in 1999 and 2000, varied markedly **(Figure 4.5)**. Therefore, while the 1985 and 1990 year classes were strong in both 1999 and 2000, the recruitment in those years were as much as 2.6 (SE ± 0.8) and 3.2 (SE ± 0.5) times greater than the average, respectively. The 1989 and 1995 year classes were also strong, with recruitment being 1.8 (SE ± 0.4) and 1.8 (SE ± 0.3) times the average, respectively.

The application of a relative abundance analysis, which assumed that recruitment is constant, yielded an estimate for *Z* for *A. latus* of 0.20 year^{-1}, which was thus approximately the same as that produced by the refitted version of Hoenig's (1983) equation for fish, whilst a relative abundance analysis, which did not require that assumption, yielded a slightly higher estimate for *Z*, *i.e.* 0.23 year^{-1} **(Table 4.2)**. However, the confidence intervals for the estimates of *Z* obtained by both of these analyses were far narrower than those obtained using the refitted Hoenig (1983) equation.

The likelihood distribution for the estimates of *Z*, derived using the equation that was refitted to Hoenig's (1983) data, provided more conservative estimates of total mortality than

Table 4.2. Mortality (year^{-1}) of *Acanthopagrus latus* in Shark Bay calculated using different life history models, estimation of longevity based on simulation or relative abundance analyses. N = no value could be obtained, *M* = natural mortality, *Z* = total mortality.

Method of analysis	*M* or *Z*	Estimate	Lower 95%	Upper 95%
Refitted Hoenig (1983) fish equation	Z	0.18	0.05	0.38
Hoenig (1983), adjusted for sample size	Z	0.30	N	N
Relative abundance analysis, constant recruitment	Z	0.20	0.17	0.23
Relative abundance analysis, variable recruitment	Z	0.23	0.18	0.27
Estimation based on simulation and maximum age	Z	0.30	0.21	0.46
Combined estimate of *Z* from Bayesian approach	Z	0.23	0.21	0.26
Refitted Pauly (1980)	M	0.70	0.16	1.54
Refitted Ralston (1987)	M	0.70	0.38	0.96
Combined estimate of *M* from Bayesian approach	M	0.19	0.10	0.25

those that were derived from the relative abundance analyses, while the distribution derived from the simulation study produced much higher estimates of *Z* **(Table 4.2; Figure 4.6a)**. The overall likelihood distribution for *Z* was determined by combining the separate likelihood distributions for the various estimates of *Z* **(Figure 4.6b)**, but excluding that for the relative abundance estimate assuming constant recruitment. This resultant likelihood distribution was dominated by the relative abundance estimate assuming variable recruitment **(***cf.* **Figure 4.6a,b)**. The resulting likelihood distribution for *M*, which was determined from this combined likelihood distribution for *Z* and the requirement that $M \leq Z$, is shown in **Figure 4.7a**, together with the broad likelihood distribution for *M* that was calculated from the refitted Pauly equation. The resultant likelihood distribution for *M*, which combines the likelihood distributions of the various estimates for *Z* and *M*, but excluding that for the relative abundance estimate assuming constant recruitment, is shown in **Figure 4.6b**. Based on these resultant likelihood distributions, the values for *M* and *Z* of *A. latus* in Shark Bay and their confidence limits are estimated to be 0.19 (0.10 to 0.25) year^{-1} and 0.23 (0.21 to 0.26) year^{-1}, respectively.

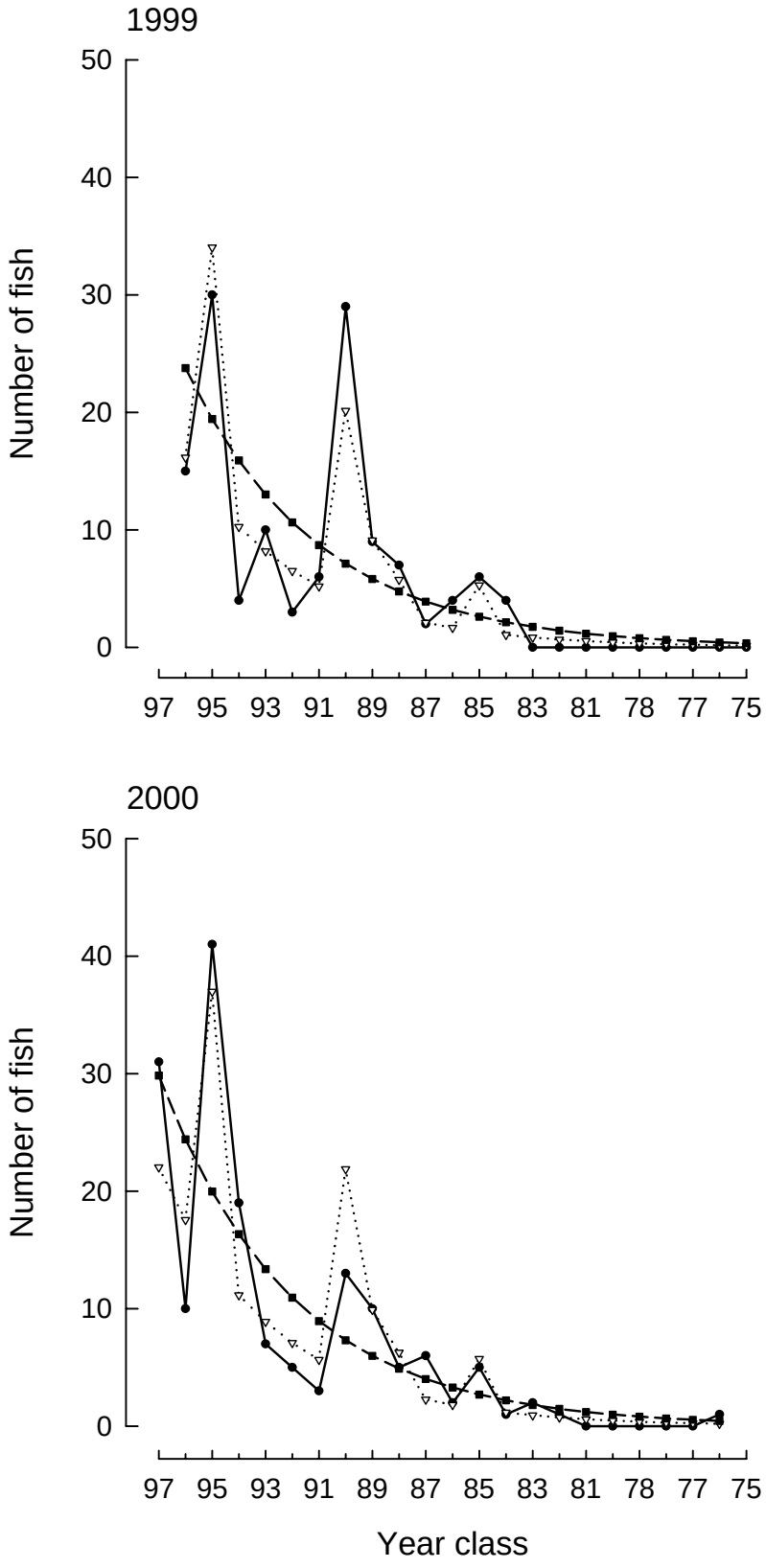

Figure 4.5. Numbers of individuals of the 1975 to 1997 year-classes of *Acanthopagrus latus* in samples collected by commercial fishers in 1999 and 2000. Relative abundance analyses were used to fit lines to the observed frequency of abundance of fish in each year-class, assuming that recruitment is either constant (dashed line) or variable (dotted line).

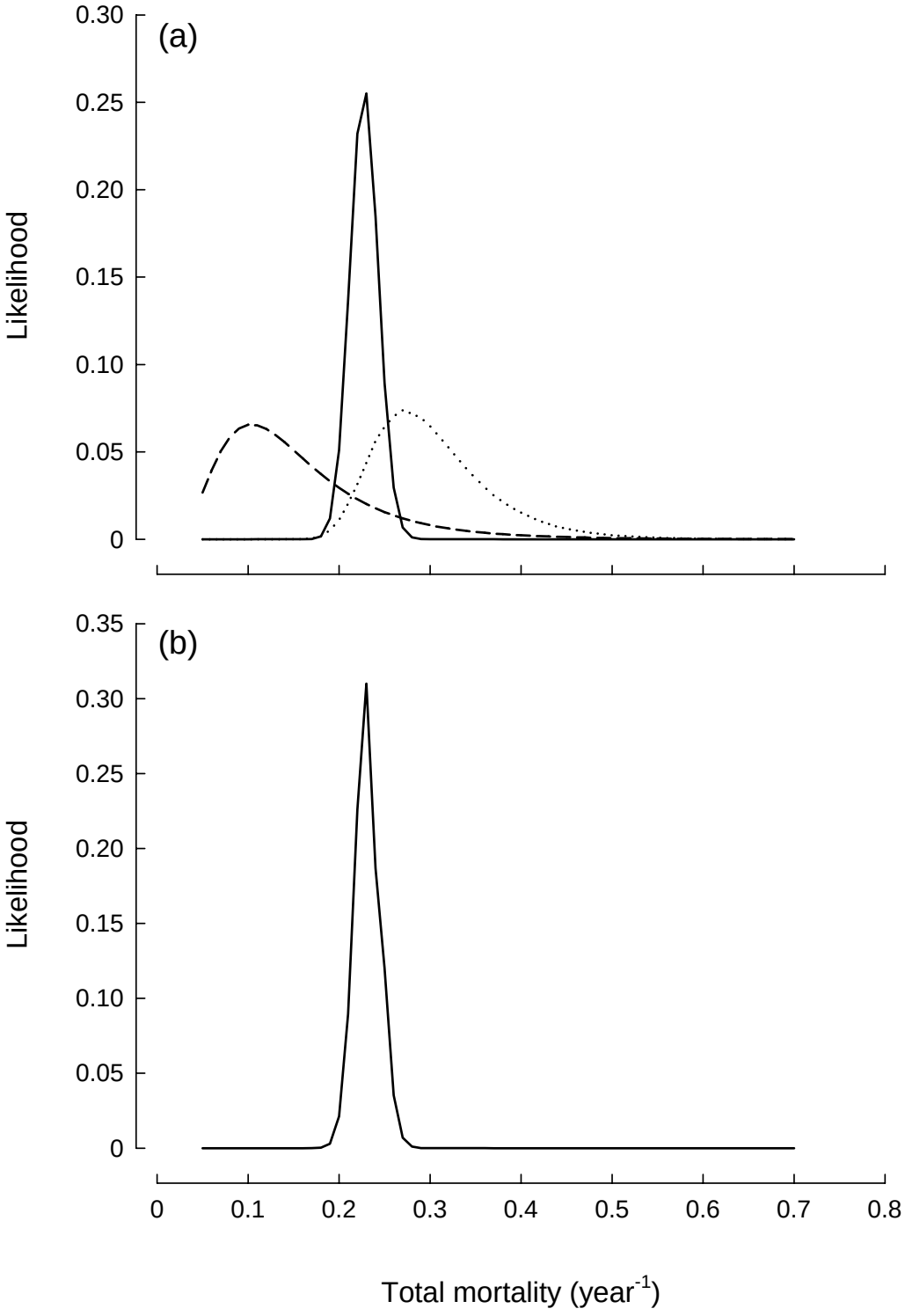

Figure 4.6. (a) Estimated likelihood distributions for total mortality, *Z*, of *Acanthopagrus latus*, derived using Hoenig's (1983) regression equation for fish (dashed line), relative abundance analysis assuming variable recruitment (solid line) and a simulation method based on maximum age and sample size (dotted line). (b) The combined likelihood distribution for *Z* for *Acanthopagrus latus* derived from the separate likelihood distributions shown in (a).

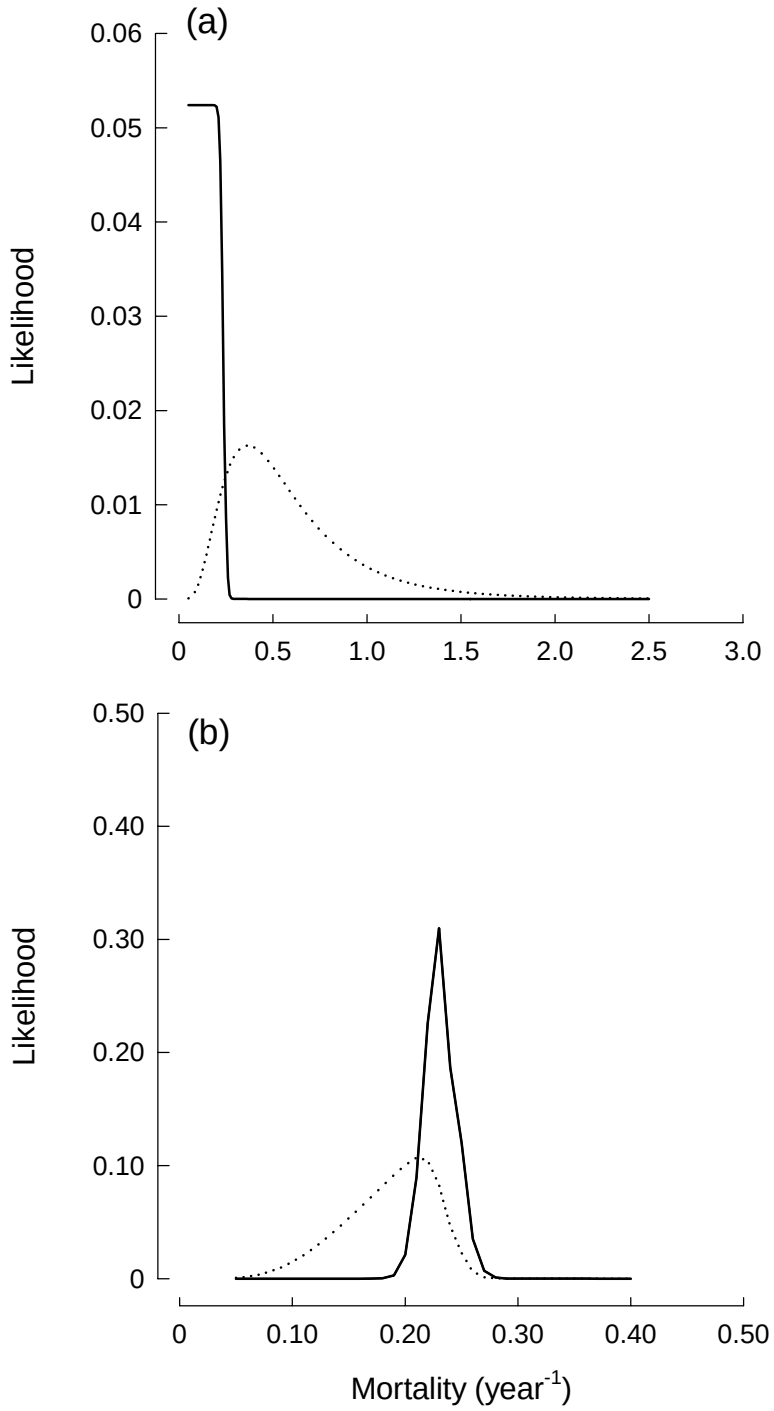

Figure 4.7. (a) Likelihood distributions derived for *M* for *Acanthopagrus latus* from Pauly's (1980) equation (dotted line) and the likelihood distribution for *M* (solid line), assuming that it is less than the combined estimate for *Z* that was derived from Hoenig's (1983) regression equation, simulation-derived estimates of the likelihood distributions of the maximum age and the relative abundance analysis. (b) Combined likelihood distributions for *Z* (solid line) and *M* (dotted line) for *Acanthopagrus latus*, representing the combined likelihood distribution for estimates of *Z* determined from Hoenig's (1983) regression equation, simulation-derived estimates of the likelihood distributions of the maximum age and the relative abundance analysis, and the likelihood distribution of *M* derived from Pauly's (1980) method, combined with the likelihood distribution of *M* based on the combined likelihood distribution for *Z*.

4.4 DISCUSSION

4.4.1 *Age and growth of* Acanthopagrus latus

The trends exhibited during the year by the mean monthly marginal increments on the otoliths of *A. latus* demonstrated that, as is typically the case with other teleosts in south-western Australia (*e.g.* Hyndes *et al.*, 1992b, 1996b, 1998; Fairclough *et al*., 2000; Sarre & Potter, 2000; Hesp *et al*., 2002), a single annulus is formed in the otoliths of this sparid each year and that their number could therefore be used for ageing individual fish. This strongly suggests that the corresponding growth zones in the otoliths of *A. latus* in Kuwait (Samuel & Mathews, 1987) were likewise formed annually and that the estimates of age derived by those workers from their counts of these zones were also valid.

The L_∞ in the von Bertalanffy growth equation for *A. latus* in Shark Bay at 22° 50′ S, *i.e.* 419 mm TL, was only slightly greater than that recorded by Samuel & Mathews (1987), *i.e.* 405 mm, for the same species in the very different environment of the Arabian Gulf, which is located at 29° N. Although the value obtained in the present study for *k* was also slightly greater, *i.e.* 0.32 vs 0.26, that for t_0 was far closer to zero, *i.e.* 0.08 *vs* –0.96. The fact that the t_0 obtained by Samuel & Mathews (1987) approached –1 can be attributed, at least in part, to the paucity of fish < 100 mm total length and thus of a length that could constrain the bottom end of the growth curve.

The values for the L_∞ of *A. latus* in Shark Bay and the Arabian Gulf are similar to those recorded for *Acanthopagrus bifasciatus* and *Acanthopagrus berda* in the latter water body (Samuel & Mathews, 1987) and of *Acanthopagrus butcheri* in four estuaries and a coastal lagoon at distances in excess of 800 km further south of Shark Bay and thus in a far more temperate and very different environment (Sarre & Potter, 2000). Although the value for *k* for *A. bifasciatus* in the Arabian Gulf, *i.e.* 0.19, was lower than those recorded for the above populations, this can be attributed, at least in part, to the highly negative and thus anomolous value of –2.24 for t_0 for this species (Samuel & Mathews, 1987). While the value for *k* for *A. butcheri* in another south-

western Australian estuary, the Moore River Estuary, was far lower than those recorded in the above populations, *i.e.* 0.11, this estuary is highly atypical in that salinities remain at very low levels throughout the year (Young *et al.*, 1997) and such conditions have been shown, in aquaculture studies, not to be conducive to a rapid growth of juvenile black bream (Partridge & Jenkins, 2002). Furthermore, the maximum age recorded for all but one of the above ten populations of *Acanthopagrus* species was at least 14 years. From the above, the values for L_∞, k and t_{max} for *Acanthopagrus* species each apparently typically lie within a relatively narrow range, even when the species live in very different regions.

4.4.2 *Estimates of mortality*

The estimates of *M* calculated for *A. latus* during the present study using the refitted equations of Pauly (1980) and Ralston (1987) were both far greater than those calculated for *Z* for this species using the two Hoenig (1983) equations, the simulation study and our two relative abundance analyses. This type of inconsistency parallels that found by Samuel and Mathews (1987), in that the estimates they derived for *M* for *A. latus* and three other *Acanthopagrus* species in the Arabian Gulf using the Pauly (1980) equation were also considerably greater than those derived for *Z* using catch curve analysis. However, natural mortality cannot, of course, exceed total mortality. Since the estimates obtained for *Z* in the present study derived using both of the Hoenig (1983) equations, simulation and relative abundance analyses are consistent and based on sound data, the high point estimates obtained for the natural mortality of *A. latus* using the refitted equations of Pauly (1980) and Ralston (1983) are erroneously elevated. Although the value for t_{max} for a species is strongly influenced by sample size and can therefore affect the resulting value of Z derived from Hoenig's (1983) fish equation, this influence has been taken into account through using the simulation method described in this chapter.

The substitution of the estimate of 0.70 year^{-1} for *M* for *A. latus*, derived from Pauly's (1980) equation into Hoenig's (1983) equation, which relates the expected maximum age to

sample size, yields an expected age of 12 years for an unfished population with an hypothetical sample of 291 fish, *i.e.* the number of fish in the sample from commercial catches of *A. latus* in Shark Bay. However, the maximum recorded age for this population in Shark Bay was 24 years, with a substantial number of fish exceeding 15 years of age. Thus, the mortality of *A. latus* lies well outside the norm for the mortalities of the species used by Pauly (1980) for estimating mortalities.

By using a Bayesian approach to combine the likelihood distributions associated with each of the various estimates of *Z* and *M*, the inconsistencies between those estimates (see **Table 4.2**) can be reconciled through the production of single integrated estimates of both of these mortality variables. The likelihood distribution that has been calculated from each of the empirical equations is derived from the uncertainty associated with the parameter estimates from the regression equation, as was used by Cubillos *et al*. (1999), but also takes into account the correlations between the parameter estimates and the variability of values of the dependant variable about the regression line. The resultant likelihood distribution for *Z* was dominated by the likelihood distribution of the relative abundance analysis assuming variable recruitment, which produced far more precise estimates of *Z* than were obtained using either the refitted Hoenig equation or the simulation study (*cf.* **Figure 4.16a,b**). Thus, assuming the resulting estimates of *Z* are correct, the only feasible values of *M* for *A. latus* are clearly those that fall within the lower tail of the likelihood distribution derived from the refitted Pauly equation **(Figure 4.7a)**.

The estimate obtained in the present study of 0.23 $year^{-1}$ for *Z* for *A. latus* in Shark Bay, derived from the combination of likelihood distributions, was far lower than the 0.60 $year^{-1}$ calculated by Samuel & Mathews (1987) for the same species in the Arabian Gulf. This implies that the fishing pressure on *A. latus* is currently far lower in Shark Bay than it was in the Kuwaiti waters of the Arabian Gulf during the 1970s and 1980s, when that species was known to have been heavily fished. In the case of the population of *A. latus* in Shark Bay, the estimate of

0.19 year^{-1} calculated for *M* from the combination of likelihood distributions is close to the current estimate of 0.23 year^{-1} for *Z*. Indeed, the value of only 0.04 year^{-1} for fishing mortality, *F*, calculated as $F = Z - M$, implies that just under 4% of the fish over three years of age are taken by the fishery each year. Thus, while the population of *A. latus* used to be heavily targeted by commercial fishers in Shark Bay to the point of apparently being over-exploited, the position has now apparently been improved by the reduction in the number of fishing units from 17 to 9 (Shaw, 2000).

This study has demonstrated that the use of a range of traditional techniques to estimate mortality in *A. latus*, such as empirical equations and relative abundance analysis, as well as simulation, invariably yielded far lower values for total mortality than for natural mortality, which clearly cannot be the case. However, the analyses also showed that, as a result of a lack of precision and variability in the underlying data, the probability distributions for most of the various estimates of *M* and *Z* for *A. latus* are so broad that they overlap. Therefore, during the present study, a Bayesian approach was adopted to develop a method in which the information content used to develop the life history based equations for estimating mortality in fish species is integrated and combined with data that was obtained during the present study for *A. latus*. This approach has produced far more precise and consistent estimates of both *Z* and *M*. Precisely the same approach can be used to improve the quality of the estimates for *Z* and *M* in other fish species.

This chapter has been accepted for publication as follows:

Hall, N. G., Hesp. S. A., & Potter, I. C. in press. A Bayesian approach for overcoming inconsistencies in mortality estimates, using, as an example, data for *Acanthopagrus latus*. *Canadian Journal of Fisheries and Aquatic Sciences*.

5.0 REPRODUCTIVE BIOLOGY OF THE FOUR TUSKFISH SPECIES

D. V. Fairclough & I. C. Potter

5.1 INTRODUCTION

Many wrasses (Labridae) are protogynous hermaphrodites, *i.e.* change sex from females to terminal males. This includes species such as *Achoerodus viridus*, *Pseudolabrus celidotus* and *Nelabrichthys ornatus* and species of tuskfish, *e.g. Choerodon rubescens* in Western Australia, *Choerodon venustus* in Queensland and *Choerodon schoenleinii* and *Choerodon azurio* in Japan (Jones, 1980; Policansky, 1982; Nakazono & Kusen, 1991; Gillanders, 1995; Andrew *et al.*, 1996; Ebisawa *et al.*, 1995; Nardi, 1999; Platten *et al.*, 2002). There are two main categories of protogynous hermaphroditism that are distinguished on the basis of the types of their males, namely monandry and diandry. In monandric species, *e.g. Nelabrichthys ornatus*, the males are derived exclusively from adult females and have therefore been termed secondary males (Sadovy & Shapiro, 1987; Andrew *et al*., 1996). However, in diandric species, *e.g. Thalassoma bifasciatum* and *Cheilinus undulatus*, the males can be either derived directly from adult females, as in monandric species, or develop from small juveniles that contain an undifferentiated gonad (Warner & Robertson, 1978; Sadovy & Shapiro, 1987; Shapiro & Rasotto, 1993; Donaldson & Sadovy, 2001).

As pointed out in Chapter 3, several criteria must be met before a species can be unequivocally regarded as a protandrous or protogynous hermaphrodite. Although bimodality in the length-frequency distributions according to sex can provide evidence that a species is a sequential hermaphrodite, such bimodality can be caused by other factors, *e.g.* differences in growth rates, mortality or migration (Sadovy & Shapiro, 1987). Thus, it is necessary to examine the gonads of such species histologically to determine the status of the gonadal tissues and thus be able to confirm whether or not 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 & Shapiro, 1987). Sadovy & Shapiro (1987) have pointed out that, for protogynous species, an histological study will demonstrate that the gonads of transitional individuals contain proliferating sperm cells and degenerating oocytes, and the testes of males contain a membrane-lined ovarian lumen and sperm sinuses in the gonadal wall.

The spawning behaviour, details of sex change and social structure have been described for several species of protogynous labrids, *e.g. Thalassoma bifasciatum* and *Bodianus* spp. (Hoffman, 1985; Warner & Swearer, 1991; Warner & Schultz, 1992; Shapiro & Rasotto, 1993; Warner, 1998). However, although the Labridae is the second largest teleost family and many of its species are targeted by fishers, relatively few studies have focused on obtaining data for those biological parameters, such as length and age at maturity and fecundity, that are crucial for managing fish stocks (Choat & Robertson, 2002).

On the basis of analysis of length and age compositions and histology of the gonads of a population of *C. rubescens* in the Abrolhos Islands, Nardi (1999) concluded that this species is a monandric protogynous hermaphrodite. The trends exhibited by the gonadosomatic indices (GSI) and gonadal maturity stages of females indicated that, in the Abrolhos Islands, *C. rubescens* spawns mainly in spring and early summer (Nardi, 1999). The minimum length at maturity of this species was estimated by Nardi (1999) to be *ca* 290 mm (TL). However, this estimate was based on GSI data for fish of different sizes during the spawning season, rather than through using logistic regression analysis of the proportions of mature females in sequential size classes, which would have been more likely to have yielded a more accurate estimate. The fact that the diameters of the early previtellogenic, cortical alveolar and yolk granule oocytes in the ovaries of a sample of spawning females of *C. rubescens* formed a continuous distribution were taken by Nardi (1999) as indicating that this species is a multiple spawner (de Vlaming, 1983). Batch or annual fecundity have not been determined.

Choerodon schoenleinii has been shown to be a monandric protogynous hermaphrodite in Japan, where this species is commercially important (Ebisawa *et al.*, 1995). The smaller fish

were all females, whereas males, which were not abundant, were found only amongst the largest fish. Since the gonads of transitional individuals contained degenerating previtellogenic oocytes and proliferating testicular tissue and the testes had the structural characteristics of secondary males, this species is a protogynous hermaphrodite (Ebisawa *et al.* 1995). The latter worker found that the ovaries of some females of *C. schoenleinii* contained hydrated oocytes between late autumn and early summer and thus, this species spawns over many months in Japan (Ebisawa *et al.*, 1995). Individuals that were changing sex were found mainly in the months between spawning periods. The data of Ebisawa *et al.* (1995) suggested that *C. schoenleinii* starts to mature at *ca* 240 mm and is a multiple spawner.

Information on the biology of the blue tuskfish *Choerodon cyanodus* is restricted to that derived from catches of a small number of this species on the Great Barrier Reef (Choat, 1969). Since four of the females collected in August contained resting ovaries and four of the females from January and February were undergoing gonadal maturation, this species presumably spawns in summer. One of the four males that Choat (1969) collected contained primary testes and thus he suggested that *C. cyanodus* could be a diandric protogynous hermaphrodite. The reproductive biology of *C. cauteroma* has not been studied.

The first aim of this component of the project was to confirm that, as is typically the case with labrids, *C. rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* are each protogynous hermaphrodites in Shark Bay and, if so, which type of protogyny they exhibit. The second aim was to determine, for each of these species, their sex ratios, the duration of their spawning periods and time of peak spawning, the lengths and ages at which they reach maturity and change sex, whether or not they have determinate or indeterminate fecundity and an appropriate measure of fecundity. The data collected for *C. rubescens* in Shark Bay are compared with those obtained for this species in the Abrolhos Islands (see **Figure 1.1**).

5.2 MATERIALS AND METHODS

Details of the sampling localities and regime, the length and weight measurements (including gonad weights), the scheme for staging gonads (stages I-VIII), the gonadosomatic index, the histological studies of gonads and the methods for ageing fish were given in Chapter 2.

5.2.1 *Hermaphroditism of the four species of tuskfish*

On the basis of a macroscopic examination of their gonads, each individual of each of the four tuskfish species (*Choerodon rubescens*, *Choerodon schoenleinii*, *Choerodon cyanodus* and *Choerodon cauteroma*) was recorded as either female, transitional or male. Female and male fish were those with gonads containing solely ovarian and only testicular tissue, respectively, whilst transitional fish were those with gonads containing both ovarian and testicular tissue, *i.e.* they were assumed to be undergoing sex change. Transitional fish were identifiable through having gonads that macroscopically were elongate, flaccid and reddish to brownish in colour and were shown through histology to contain both ovarian and testicular tissue.

Sectioning of the gonads of 207 fish in which the gonads, on the basis of their macroscopic appearance, appeared to contain solely immature ovarian tissue, were only found in one case to contain both ovarian and testicular tissue. In that case, the gonads contained predominantly ovarian tissue and were thus assumed to be in the very early stages of changing from female to male.

Since all four species of tuskfish were shown to be protogynous hermaphrodites (see results), gonadosomatic indices were calculated for females $\geq L_{50}$, *i.e*. the length at which 50% of females first reach maturity, and for all male fish (see Chapter 2.4).

5.2.2 *Lengths and ages at sexual maturity and sex change*

The percentage contributions made to the total numbers of female *C. rubescens* by the number of females at each length which, during the spawning season, possessed gonads at stages III to VIII and were thus likely to have spawned during that period, were subjected to logistic regression analysis. This procedure was carried out separately on samples collected from Shark Bay and the Abrolhos Islands to determine the lengths at which 50 and 95% of females reach maturity in both of those regions. The data for *C. rubescens* 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_{50}s and L_{95}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. The form of the logistic equation is $P = 1/\{1+\exp[-\ln(19)(L-L_{50})/(L_{95}-L_{50})]\}$, where P = proportion mature, L = total length, L_{50} and L_{95} = the lengths at which 50 and 95% of female fish reach sexual maturity, respectively, and ln = the natural logarithm. The same resampling technique was used to determine the L_{50}s and L_{95}s for female *C. schoenleinii*, *C. cauteroma* and *C. cyanodus*. However, since the prevalences of females with ovaries at stages III-VIII for these species never reached 100% in the larger size classes, the additional parameter, $P_{\max}$, was incorporated into the logistic regression equation to allow for that fact, as follows $P = P_{max}/\{1+\exp[-\ln(19)(L-L_{50})/(L_{95}-L_{50})]\}$.

The lengths and ages at which 50% of *C. rubescens* in Shark Bay and the Abrolhos Islands and of *C. cauteroma* and *C. cyanodus* in Shark Bay changed sex were estimated using the form of the logistic equation without the additional parameter P_{max} and the same resampling procedure. Since only a small number of male *C. schoenleinii* were obtained during the study, logistic regression analysis could not be used to estimate reliably the length or age at which 50% of individuals in the population in Shark Bay change sex.

A likelihood ratio test was used to compare the lengths at maturity and lengths and ages at sex change for *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-likelihoods 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 $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two logistic curves (Kimura, 1980).

5.2.3 *Fecundity*

Both of the ovarian lobes of individuals in a subsample of each tuskfish species in which hydrated oocytes were macroscopically visible through the ovarian wall were removed 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 2.4) 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.* < 12 h old, were identified using the descriptions provided by Hunter & Macewicz (1985) for this structure in ovaries of the northern anchovy *Engraulis mordax* and which applies equally 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 & Acha, 2000; Hesp, 2003). 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 one of four sequential stages according to the extent to which they had been resorbed, *i.e.* α, β, γ

and δ-stages as described by Hunter & Macewicz (1985). Since the first two stages are far more readily identified in ovaries, attention was focused on these stages, as is typically the case in this type of study (*e.g.* Hunter *et al.*, 1986; Karlou-Riga & Economidis, 1997; Nichol & Acuna, 2001).

Ovaries were then classified into one of four numerical stages according to the degree of resorption of oocytes (Hunter & 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 contain oocytes in β stage atresia and are considered to be postspawning. During the present study, atretic state 1 ovaries were further divided into three categories on the basis of the percentage of α atretic yolk granule oocytes in histological sections, namely early (< 10%), mid (10-35%) and late (35-50%) atretic state 1, an approach similar to that adopted by Farley & Davis (1998). Ovaries in atretic state 0 and early atretic state 1 were considered to be in an active reproduction mode and were therefore used for estimating the batch fecundity of individuals of the four tuskfish species employing the hydrated ooycte method of Hunter *et al.* (1985).

The second of the ovarian lobes of each of these fish that was preserved in 10% neutrally-buffered formalin was removed and 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. A likelihood ratio test (see earlier) was used to test whether linear regressions fitted to the data for the natural logarithm (ln) of batch fecundity *vs* ln total length for *C. rubescens* in Shark Bay and the

Abrolhos Islands were significantly different, and thus whether the data for these two regions could be pooled.

5.3 RESULTS

5.3.1 *Histological evidence for hermaphroditism*

The gonads of all of the individuals of *C. rubescens* that were caught in Shark Bay and the Abrolhos Islands and were < 350 mm and some larger individuals consisted entirely of ovarian tissue. Histological studies showed that the gonads of fish < 100 mm in length contained only oogonia and chromatin nucleolar oocytes and that those of fish with lengths of 100 to 200 mm typically also contained perinucleolar oocytes **(Figure 5.1a,b)**. Thus, testicular tissue was never present in the gonads of small *C. rubescens*.

All of the five transitional *C. rubescens* that were caught, *i.e.* those with gonads containing both ovarian and testicular tissue, ranged from 395 to 514 mm in length and from 9.9 to 12.3 years in age and were collected between late October and mid-March. The gonads of three of these transitional fish contained substantial amounts of ovarian and testicular tissue **(Figure 5.1c)**. The oocytes in the ovarian tissue, all of which were previtellogenic and some of which were degenerating, occurred either singly or in small clusters **(Figure 5.1d)**. The testicular tissue comprised spermatogonia and spermatocytes, and in some cases also spermatids **(Figure 5.1e)**.

The lamellae of the gonads of one of the other transitional fish contained previtellogenic oocytes and only a few small areas of testicular tissue **(Figure 5.1f)**. Although those oocytes showed no obvious signs of degeneration, the presence of some testicular tissue suggests that this fish was in the early stages of changing from female to male.

Histological sections of the gonads of a subsample of 41 *C. rubescens* from Shark Bay and the Abrolhos Islands that possessed solely testicular tissue demonstrated that these testes retained their ovarian lumen after the fish had changed from female to male **(Figure 5.1g)**. The

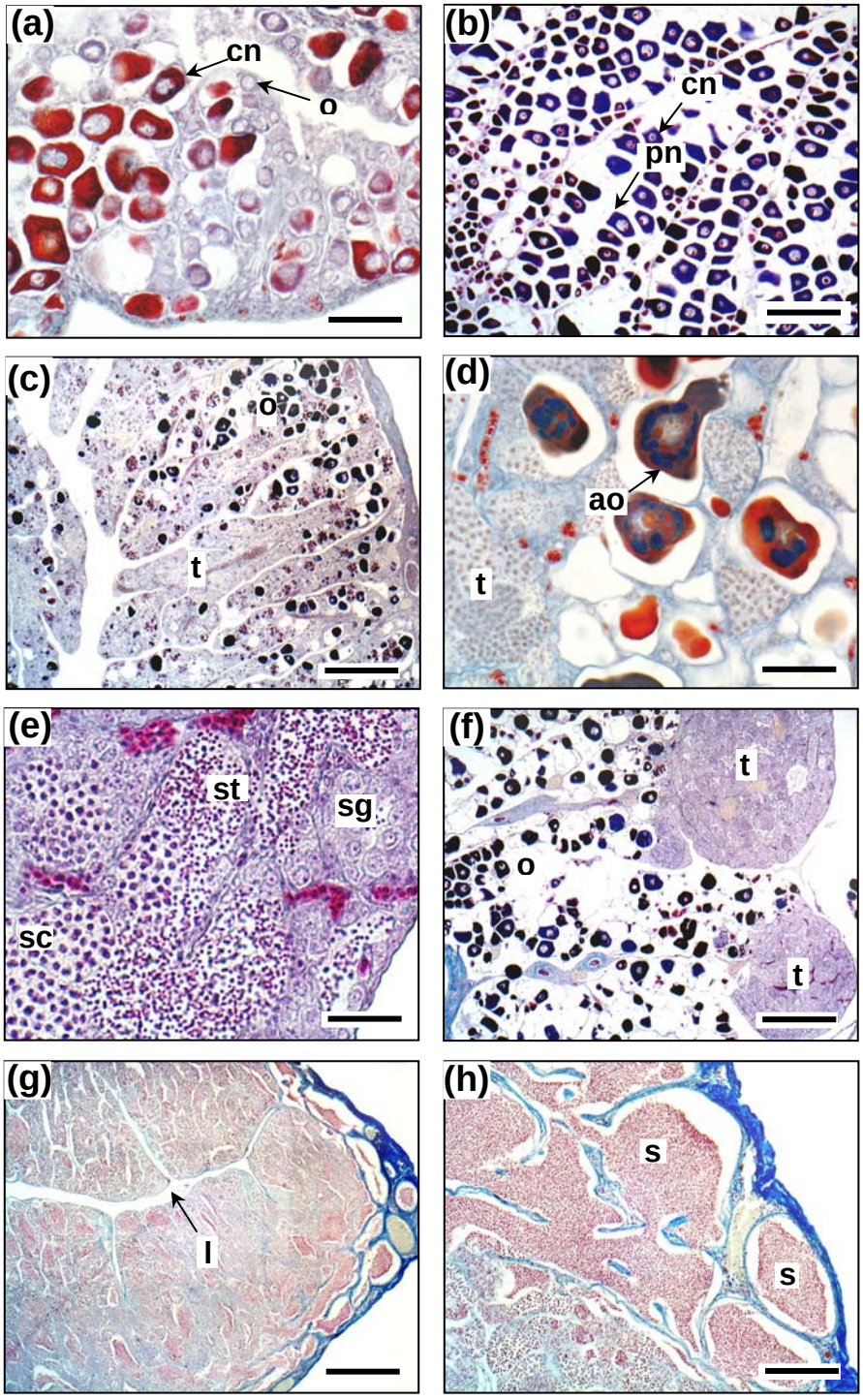

Figure 5.1 Histological sections of gonads of *Choerodon rubescens*. Juvenile fish of 82 mm (a) and 130 mm (b) in length. Transitional individuals containing both ovarian and testicular tissue (c), degenerating oocytes (d), testicular tissue (e), and small areas of testicular tissue in a transitional fish in the early stages of sex change. Mature (stage V/VI) secondary male (g, h). cn, chromatin nucleolar; do, degenerating oocyte; l, lumen; o, ovarian tissue; pn, perinucleolar oocyte; s, sperm sinuses; sc, spermatocytes; sg, spermatogonia; st, spermatids; t, testicular tissue. Scale bars: (e) = 25 µm, (a) = 50 µm, (d) = 100 µm, (h) = 200 µm, (b) = 250µm, (c, f, g) = 300 µm.

spermatids and spermatozoa of mature males, *i.e.* with gonads at stages V-VI, were located in sperm sinuses in the outer wall of the testes. The presence of large areas of mature sperm cells in the gonads of these fish has led to the lumen of the former ovary having become greatly reduced in size **(Figure 5.1h)**.

Histological studies demonstrated that the pattern of sex change of *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* is similar to that of *C. rubescens*. Thus, the gonads of small and young *C. schoenleinii* (100-299 mm, 0-4 years old, sample size (n) = 26), *C. cauteroma* (76-220 mm, 0-3.7 years old, n = 20) and *C. cyanodus* (67-150 mm, 0-3 years old, n = 23) contained only ovarian tissue. The gonads of one large *C. schoenleinii* and eight *C. cauteroma* contained both ovarian and testicular tissue. No such transitional *C. cyanodus* were caught. The lengths and ages of the single transitional *C. schoenleinii* and eight transitional *C. cauteroma* were 526 and 266-338 mm, and 7.4 and 5.7-8.1 years old, respectively. The transitional *C. schoenleinii* was collected in April, while five of the transitional *C. cauteroma* were caught in either July or August and a further one in each of September, October and November. As was the case with *C. rubescens*, the oocytes in the transitional gonads of *C. schoenleinii* and *C. cauteroma* were all at the previtellogenic stage and some of these were undergoing degeneration **(Figure 5.1c,d)**.

Histological examination of the testes of all of the males of *C. schoenleinii* (n = 7) and subsamples of male *C. cauteroma* (n = 36) and *C. cyanodus* (n = 37) demonstrated that, after sex change, the gonads retain their original ovarian lumen **(Figure 5.1g)**. Furthermore, as in *C. rubescens*, those testes that were at stages V-VI contained sperm sinuses within their walls **(Figure 5.1h)**.

5.3.2 *Sex ratios*

In both Shark Bay and the Abrolhos Islands, the number of females of *C. rubescens* was always greater than males in (1) catches using all methods, *i.e.* rod and line fishing, commercial hand-line fishing and spearfishing, (2) catches using both rod and line and commercial hand line

fishing, (3) catches of fish ≥ L_{50} obtained by rod and line and commercial hand line fishing, and (4) catches of fish ≥ 400 mm, *i.e.* the minimum legal length (MLL), obtained using only line fishing methods **(Table 5.1)**. In each of the above four cases, chi-squared goodness of fit tests demonstrated that the sex ratios differed significantly from parity ($p < 0.05$). However, samples of fish ≥ the MLL (400 mm) obtained using solely commercial line fishing were not significantly different from parity in either region ($p > 0.05$) **(Table 5.1)**.

Table 5.1. Ratio of females to males in samples of *Choerodon rubescens* from Shark Bay and the Abrolhos Islands and *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* in Shark Bay.

	Sex ratio			
	Overall (all methods)	**Overall (all line fishing methods)**	**≥ L_{50} (all line fishing methods)**	**≥ MLL (400 mm)** *** commercial line fishing** **** rod and line sampling**
Choerodon rubescens	12.3:1	10.0:1	9.6:1	1:1*
Shark Bay				10:1**
Choerodon rubescens	1.7:1	1.6:1	1.5:1	0.93:1*
Abrolhos Islands				8.9:1**
Choerodon schoenleinii	85:1	153.0:1	133.0:1	18:1**
Choerodon cauteroma	2.8:1	2.1:1	2.0:1	NA
Choerodon cyanodus	1.0:1	0.8:1	0.8:1	NA

The ratio of females to males of *C. rubescens* in the first three of the above categories of catches was significantly greater in Shark Bay than in the Abrolhos Islands ($p < 0.05$). However, although the ratio of females to males was greater in Shark Bay than the Abrolhos Islands in the above fourth and fifth categories of catches, those differences were not significant ($p > 0.05$) **(Table 5.1)**.

The overall ratios of females to males of *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* in Shark Bay collected by all methods used, *i.e.* rod and line fishing, spearfishing and trawling,

were 85♀:1♂, 2.8♀:1♂ and 1♀:1♂, respectively **(Table 5.1)**. The ratios of females to males of *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* in each of the different categories of catches varied greatly, with females being by far the most prevalent in those of the first species and the least prevalent by far in those of the last species **(Table 5.1)**. The sex ratio of the small number of *C. schoenleinii* caught above the MLL for this species (400 mm), all of which were caught by line, was 17.5♀:1♂. Very few *C. cauteroma* and no *C. cyanodus* were collected above their MLL, which was the same as that for *C. schoenleinii* **(Table 5.1)**. All of the sex ratios shown for *C. schoenleinii* and *C. cauteroma* in **Table 5.1** were significantly different from parity ($p < 0.05$), but this was not the case with those for *C. cyanodus* ($p > 0.05$) **(Table 5.1)**.

5.3.3 *Reproductive variables*

Choerodon rubescens in Shark Bay and the Abrolhos Islands

The mean monthly gonadosomatic index (GSI) 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 it declined precipitously to 1.1 in December and 0.8 in January and remained low, *i.e.* < 0.5, between February and June **(Figure 5.2)**. The mean monthly GSI for female *C. rubescens* 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 **(Figure 5.2)**. The mean monthly GSIs 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 **(Figure 5.2)**. 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 **(Figure 5.2)**.

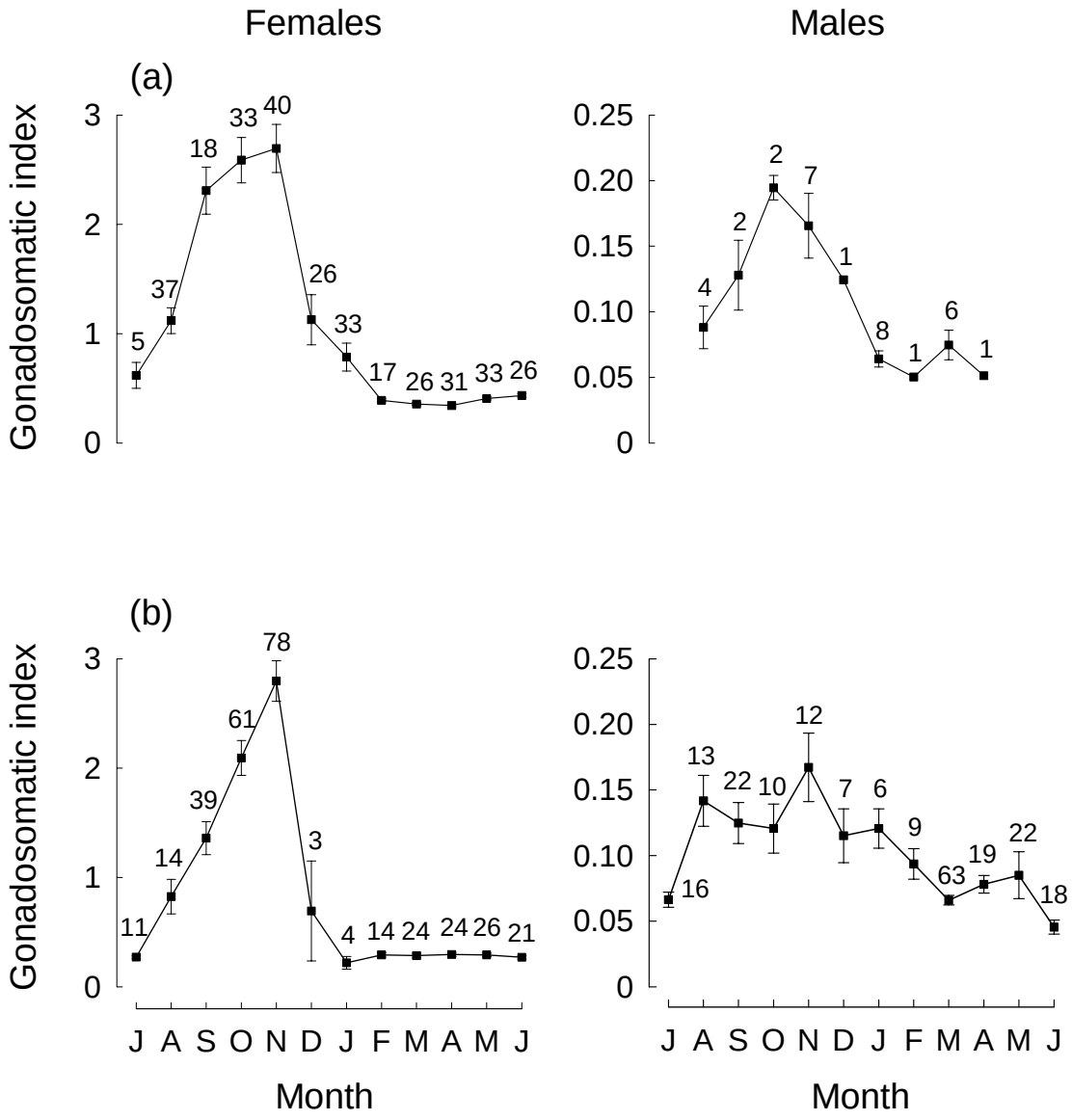

Figure 5.2. Mean monthly gonadosomatic indices ±1SE for *Choerodon rubescens* ≥L_{50} at sexual maturity in (a) Shark Bay and (b) the Abrolhos Islands derived from catches obtained between July 2000 and January 2003. Data for corresponding months in each calendar year have been pooled. Sample sizes are shown above each mean.

Female *C. rubescens* that were ≥ L_{50} at maturity and possessed resting ovaries, *i.e.* stage II, were most abundant between February and July in Shark Bay and between April and June in the Abrolhos Islands **(Figure 5.3)**. Females with developing ovaries, *i.e.* stages III - IV, were first collected in May in Shark Bay and June in the Abrolhos Islands **(Figure 5.3)**. The ovaries of the vast majority of female *C. rubescens* sampled in both regions between September and November were either at the mature or spawning stages, *i.e.* stages V-VI **(Figure 5.3)**. Although some of the female *C. rubescens* caught in Shark Bay in December and January contained ovaries at stages V-VI, 52 and 21% of the females in those months, respectively, contained either spent or recovering ovaries, *i.e.* stages VII or VIII. By February, the ovaries of all females were either recovering or resting, *i.e.* stage VIII or II **(Figure 5.3)**. The small number of female *C. rubescens* collected from the Abrolhos Islands in December and January contained either mature, recovering or resting ovaries **(Figure 5.3)**. The above trends demonstrate that at least the vast majority of females with ovaries at stages III-VIII during the spawning season will become fully mature and spawn or have spawned during that spawning season.

Choerodon cauteroma, *Choerodon schoenleinii* and *Choerodon cyanodus* in Shark Bay

The mean monthly GSIs for females of *C. cauteroma* rose progressively 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 at low values during the ensuing two months, before undergoing a modest rise. **(Figure 5.4)**. The sharp peak in the mean monthly GSI for females of *C. cauteroma* thus coincided with the middle of the three months of similarly high mean monthly GSIs for *C. rubescens*. The mean monthly GSIs of females of *C. schoenleinii* and *C. cyanodus* followed similar trends to those of *C. cauteroma*, except that they peaked slightly later in these species, *i.e.* November and January, respectively **(Figure 5.4)**.

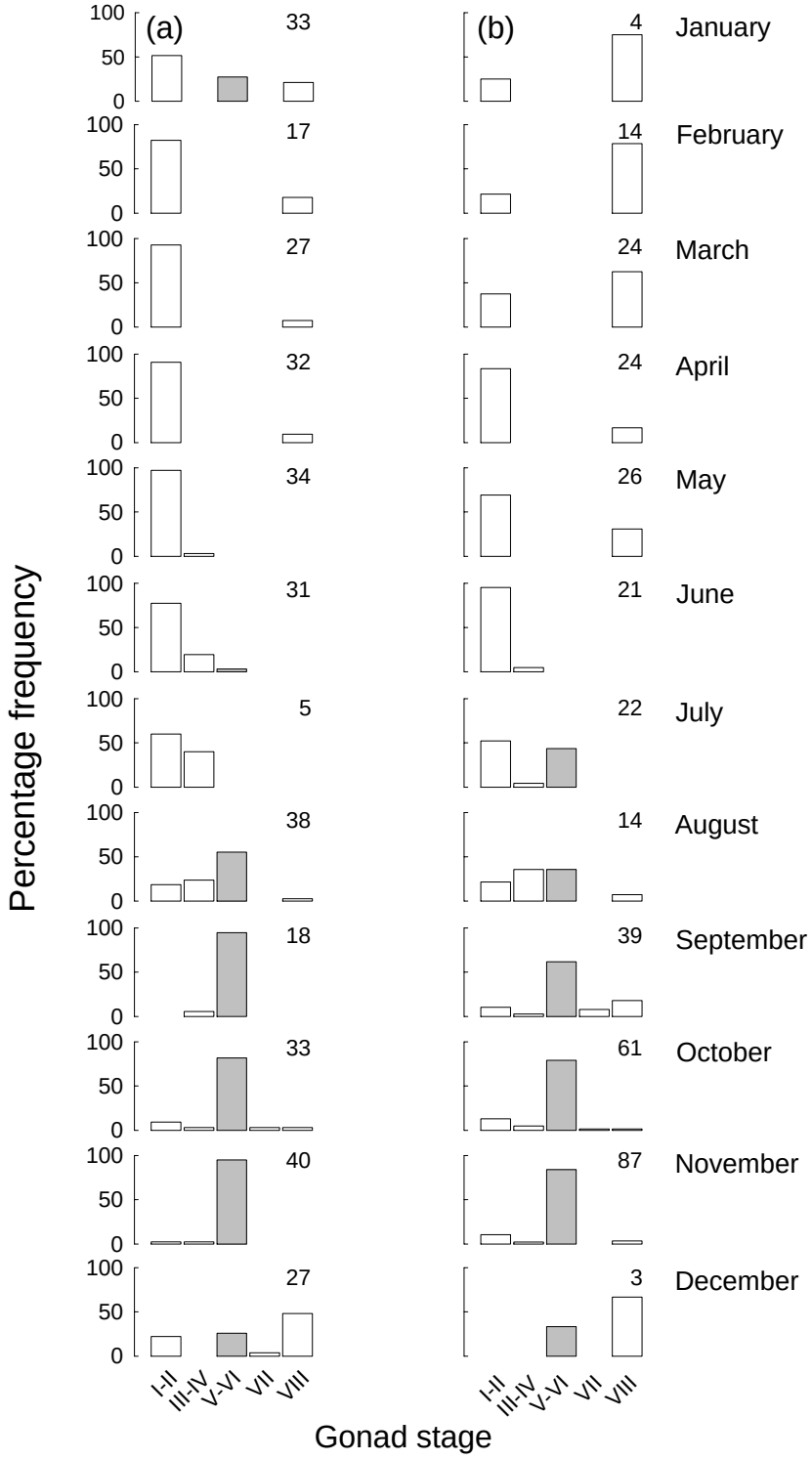

Figure 5.3. Monthly percentage frequency of occurrence of sequential stages in gonadal development of female *Choerodon rubescens* $\geq L_{50}$ at sexual maturity in (a) Shark Bay and (b) the Abrolhos Islands derived from samples collected between July 2000 and January 2003. Data for corresponding months in different years have been pooled. Sample sizes are shown for each month on each figure.

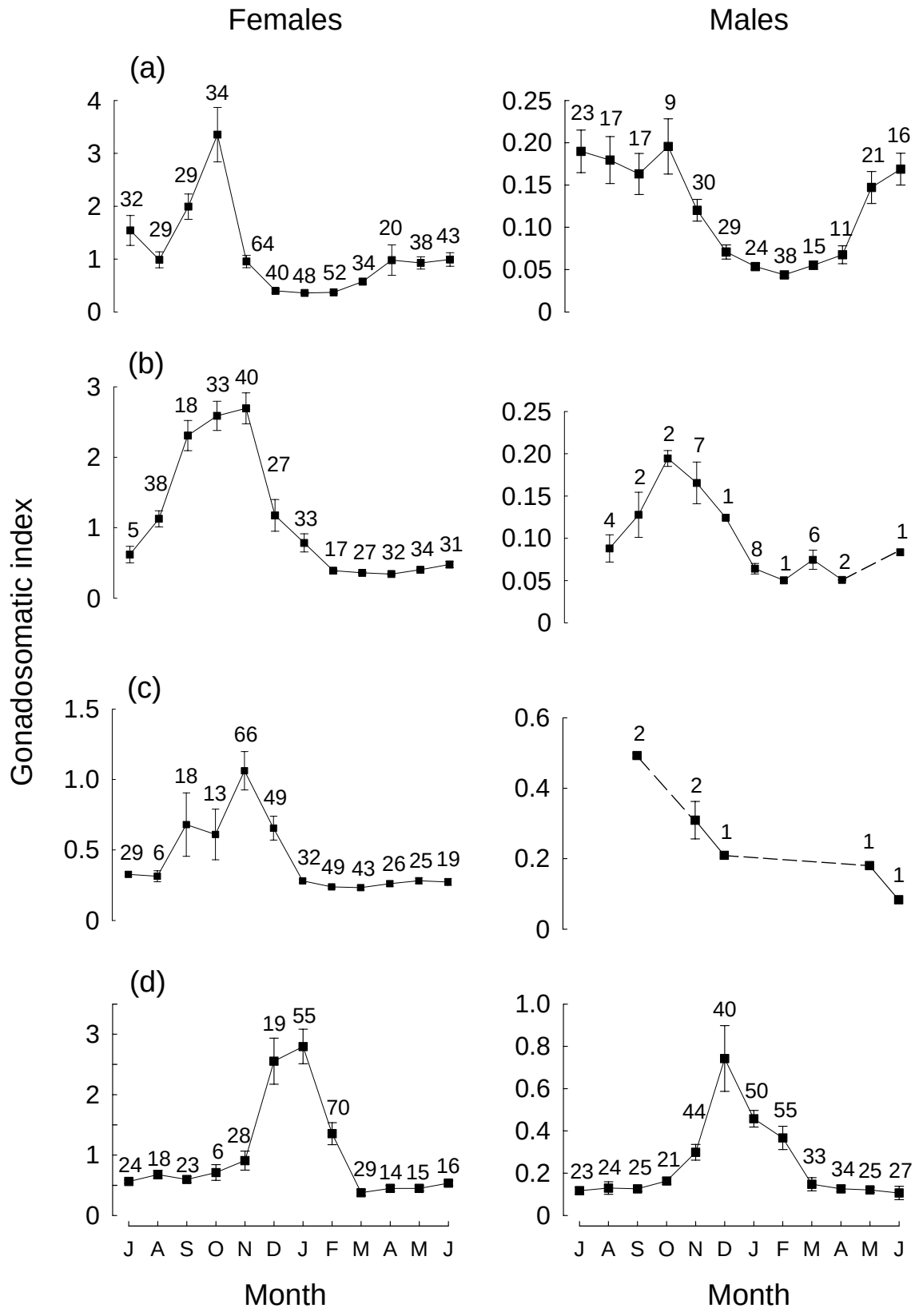

Figure 5.4. Mean monthly gonadosomatic indices ±1SE for (a) *Choerodon cauteroma*, (b) *Choerodon rubescens*, (c) *Choerodon schoenleinii* and (d) *Choerodon cyanodus* ≥ their respective L_{50}s at first maturity derived from catches obtained between July 2000 and January 2003 in Shark Bay. Sample sizes for each month are shown above each mean.

The mean monthly GSIs of the males of *C. cauteroma* rose earlier and remained higher 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 **(Figure 5.4)**. Although only a small number of male *C. schoenleinii* were caught, the decline in the mean monthly GSI from 0.5 in September to ≤ 0.21 in December, May and June follows a similar trend to those of the females of this species **(Figure 5.4)**. The mean monthly GSIs for male *C. cyanodus* followed essentially the same trends as those of their females **(Figure 5.4)**.

Female *C. cauteroma* with stages III-IV ovaries were first recorded in March **(Figure 5.5)**. Many of the female *C. cauteroma* collected from April to October contained ovaries that were either at stages III-IV or V-VI. Females with stages V-VI ovaries were most prevalent in September and October, when they represented 68% of all females ≥ L_{50} that were caught in each month **(Figure 5.5)**. While some of the ovaries of female *C. cauteroma* in November were still mature, spawning or spent, *i.e.* stages V-VI or VII, a substantial number were recovering, *i.e.* stage VIII (31%), and by January the ovaries of all females were at either stage VIII or II **(Figure 5.5)**.

Female *C. schoenleinii* ≥ L_{50} contained exclusively stage II ovaries between February and August. Stages III, IV and V ovaries in female *C. schoenleinii* first occurred in September and were recorded until December **(Figure 5.5)**. Stages V-VI ovaries were most abundant in catches in November (32%) and some (*ca* 16%) were also recorded in December. By January, all female *C. schoenleinii* ≥ L_{50} were at either stage VIII or II **(Figure 5.5)**.

The numbers of ovaries at stages III-IV of female *C. cyanodus* were low between July and October **(Figure 5.5)**. Ovaries at stages V-VI were first recorded in November and dominated the catches in December (58%) and January (60%) **(Figure 5.5)**. While some females with stages III-IV, V-VI and VII ovaries were recorded in February, a substantial number (36%)

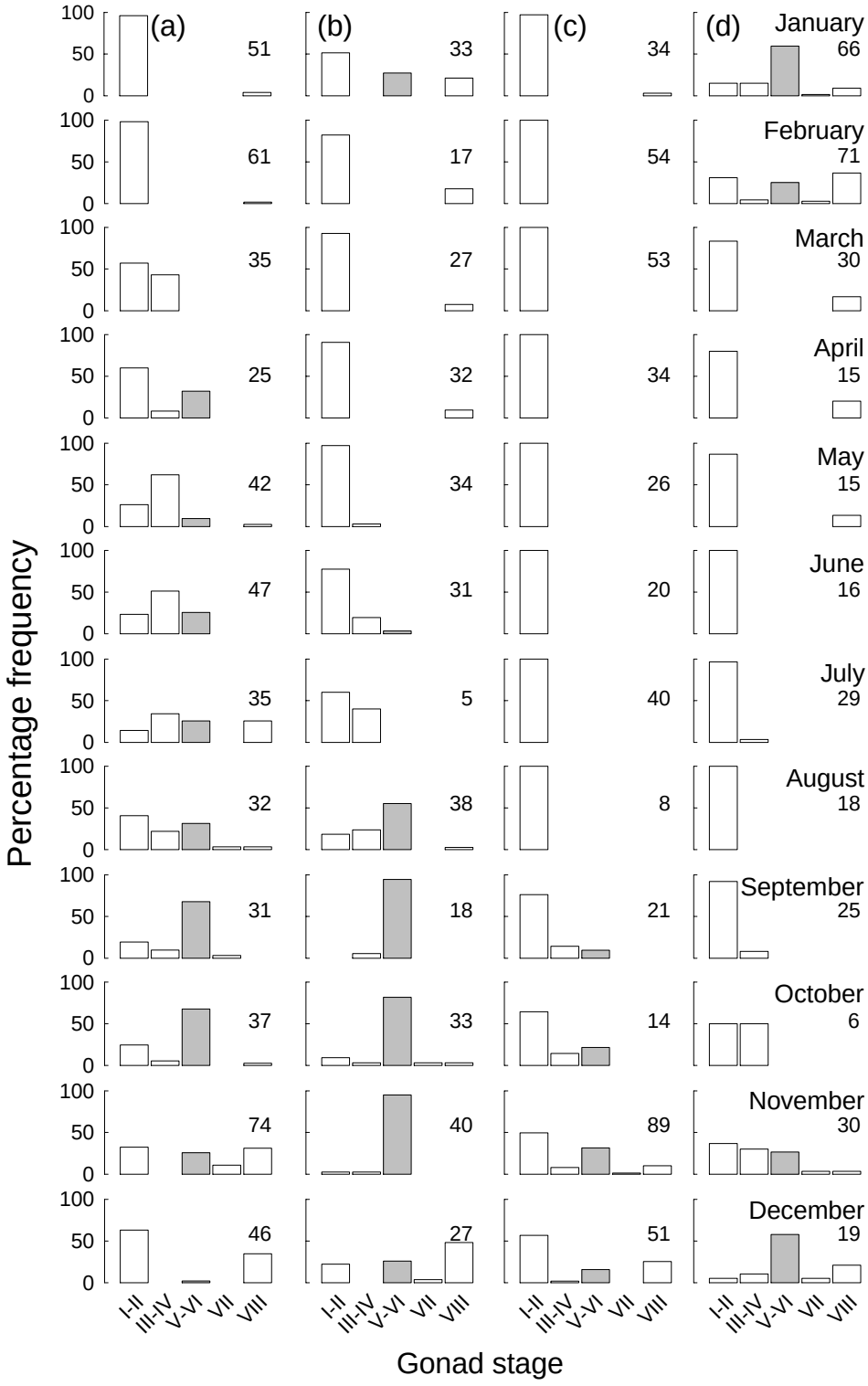

Figure 5.5. Monthly percentage frequencies of occurrence of sequential stages in gonadal development of female (a) *Choerodon cauteroma*, (b) *Choerodon rubescens*, (c) *Choerodon schoenleinii* and (d) *Choerodon cyanodus* $\geq L_{50}$ at sexual maturity derived from samples that were obtained in Shark Bay between July 2000 and January 2003. Data for corresponding months in the different years have been pooled. Sample sizes are shown for each month on each figure.

were at stage VIII, *i.e.* recovering, and by March the ovaries of all female *C. cyanodus* were at either stages VIII or II **(Figure 5.5)**.

5.3.4 *Lengths and ages at maturity and sex change*

Length and age at maturity of *Choerodon rubescens*

Female *C. rubescens* that were caught during the spawning season and contained ovaries at stages III-VIII were first recorded in the 220-239 mm length class in both Shark Bay and the Abrolhos Islands **(Figure 5.6a,b)**. Note that the possession by females of gonads at these stages strongly indicated that, by the end of the spawning period, such fish were destined to have spawned in that period and could thus be used to estimate the L_{50} of the females of this species at maturity. The L_{50} of females in Shark Bay (282 mm) did not differ significantly ($p > 0.05$) from that of females in the Abrolhos Islands (291 mm). The youngest mature females of *C. rubescens* caught in Shark Bay and the Abrolhos Islands were two and three years old, respectively, and *ca* 75% of females in these two regions were mature by four and five years of age, respectively **(Figure 5.6 a,b)**.

Length and age at sex change of *Choerodon rubescens*

Male *C. rubescens* were first recorded in the 500-519 mm length class in Shark Bay and in the 360-379 mm length class in the Abrolhos Islands **(Figure 5.6c,d)**. The majority or all fish were male in both regions by the 580-599 mm length class. The lengths at which 50 and 95% of fish (L_{50}, L_{95}) were either transitional, *i.e.* possessed gonads containing both ovarian and testicular tissue and were thus considered to have been undergoing sex change at their time of capture, or male, *i.e.* whose gonads contained only testicular tissue and thus had changed sex, were 545 and 589 mm, respectively, for Shark Bay, and 479 mm and 595 mm, respectively, for the Abrolhos Islands **(Figure 5.6c,d)**. Likelihood ratio tests demonstrated that the L_{50}s at sex change in Shark Bay and the Abrolhos Islands were significantly different ($p < 0.05$), but that the L_{95}s were not

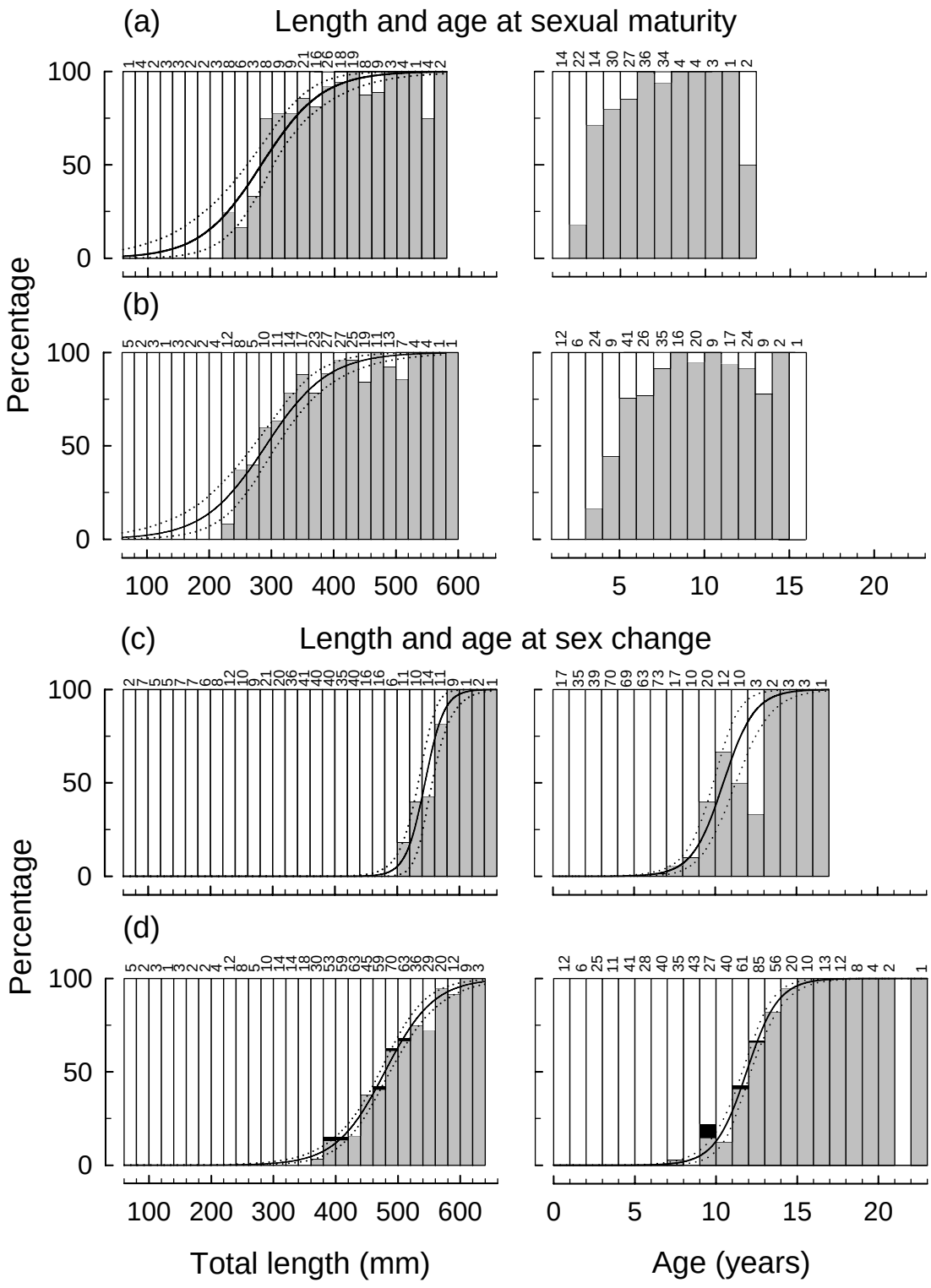

Figure 5.6. Length and age distributions of immature (white) and mature (grey) female *Choerodon rubescens* in (a) Shark Bay and (b) the Abrolhos Islands with logistic curves (± 95% CIs) fitted to the percentage of mature females in each length class, and of female (white), transitional (black) and male (grey) *C. rubescens* in (c) Shark Bay and (d) the Abrolhos Islands, with logistic curves (± 95% CIs) fitted to the percentage of transitional and male fish at each length and age.

($p > 0.05$). Males were first recorded in the 6+ age class in Shark Bay and the 7+ age class in the Abrolhos Islands **(Figure 5.6c,d)**. The majority or all *C. rubescens* in both regions had become male by the age of 13 years **(Figure 5.6c,d)**. Likelihood ratio tests demonstrated that, while the A_{50}s at sex change, *i.e.* the estimated ages at which 50% of *C. rubescens* had changed sex to males, for Shark Bay (10.5 years) and the Abrolhos Islands (11.9 years) were significantly different, the A_{95}s were not (13.3 *vs* 14.7 years).

Lengths and ages at maturity of *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* in Shark Bay.

The percentages of female *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* caught during their spawning periods in Shark Bay, that were ≥ their L_{50}s at maturity (see below) and contained gonads at stages III-VIII, varied markedly between individual sites **(Figure 5.7)**. Thus, at some sites, all females of each of these three species ≥ their L_{50} at maturity contained gonads that were at stages III-VIII, while at all other sites, females that were ≥ L_{50} and contained gonads at these stages comprised as low as 21% of fish caught **(Figure 5.7)**.

Female *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* collected during their spawning periods in Shark Bay with gonads at stages III-VIII were first recorded in the 240-259, 180-199 and 100-119 mm length classes, respectively **(Figure 5.8b,c,d)**. However, in the case of each of these species, those females never comprised 100% of fish in any length class. For this reason, an additional parameter, P_{max}, was incorporated into the logistic regression equation to analyse the data for the lengths at sexual maturity of each of these species. Female *C. schoenleinii* with ovaries at stages III-VIII comprised between 15 and 83% of fish in length classes between 240 and 459 mm **(Figure 5.8b)**. *Choerodon cauteroma* and *C. cyanodus* with ovaries at stages III-VIII represented 48-84% of females from 180 to 359 mm and 71-85% of females from 140-279 mm, respectively **(Figure 5.8c,d)**. Logistic regressions fitted to the proportions of females of

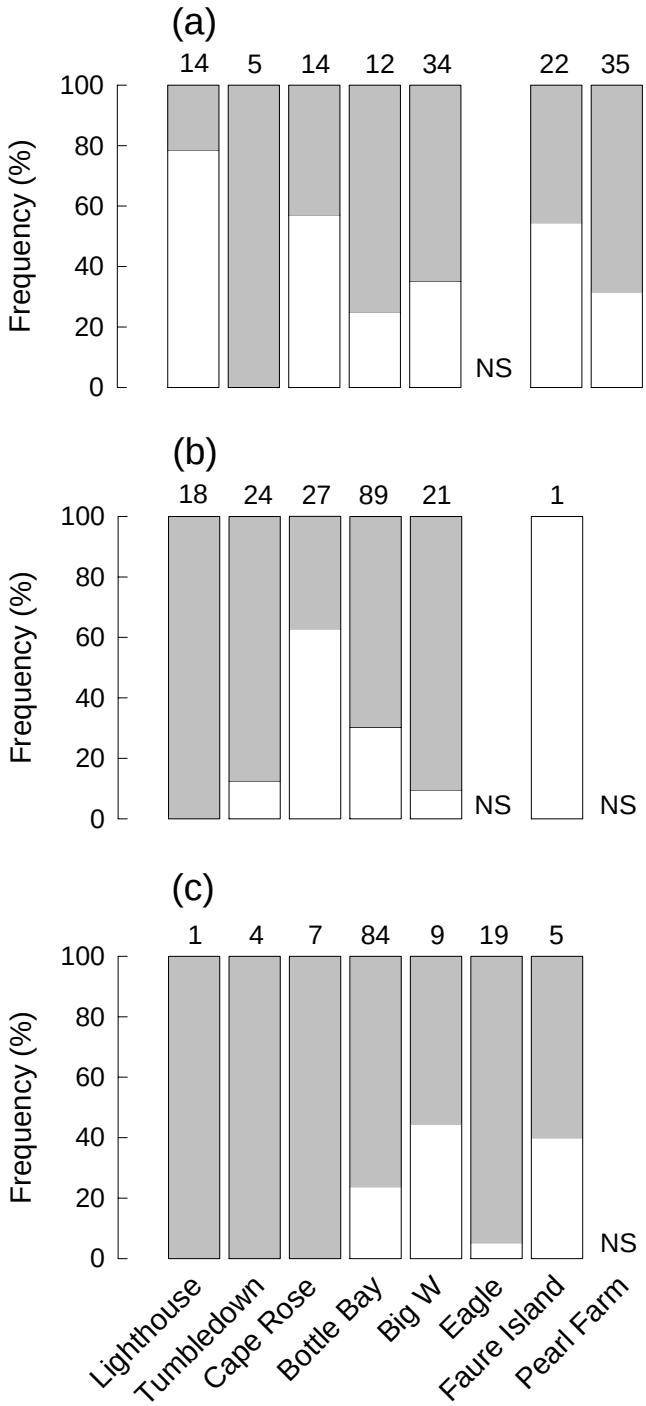

Figure 5.7. Percentage frequency of female (a) *Choerodon schoenleinii*, (b) *Choerodon cauteroma* and (c) *Choerodon cyanodus* ≥ their respective L_{50}s that contained ovaries that were at stage II (white) and stages III-VIII (grey) and were collected at different sites during their spawning periods. NS = no sample.

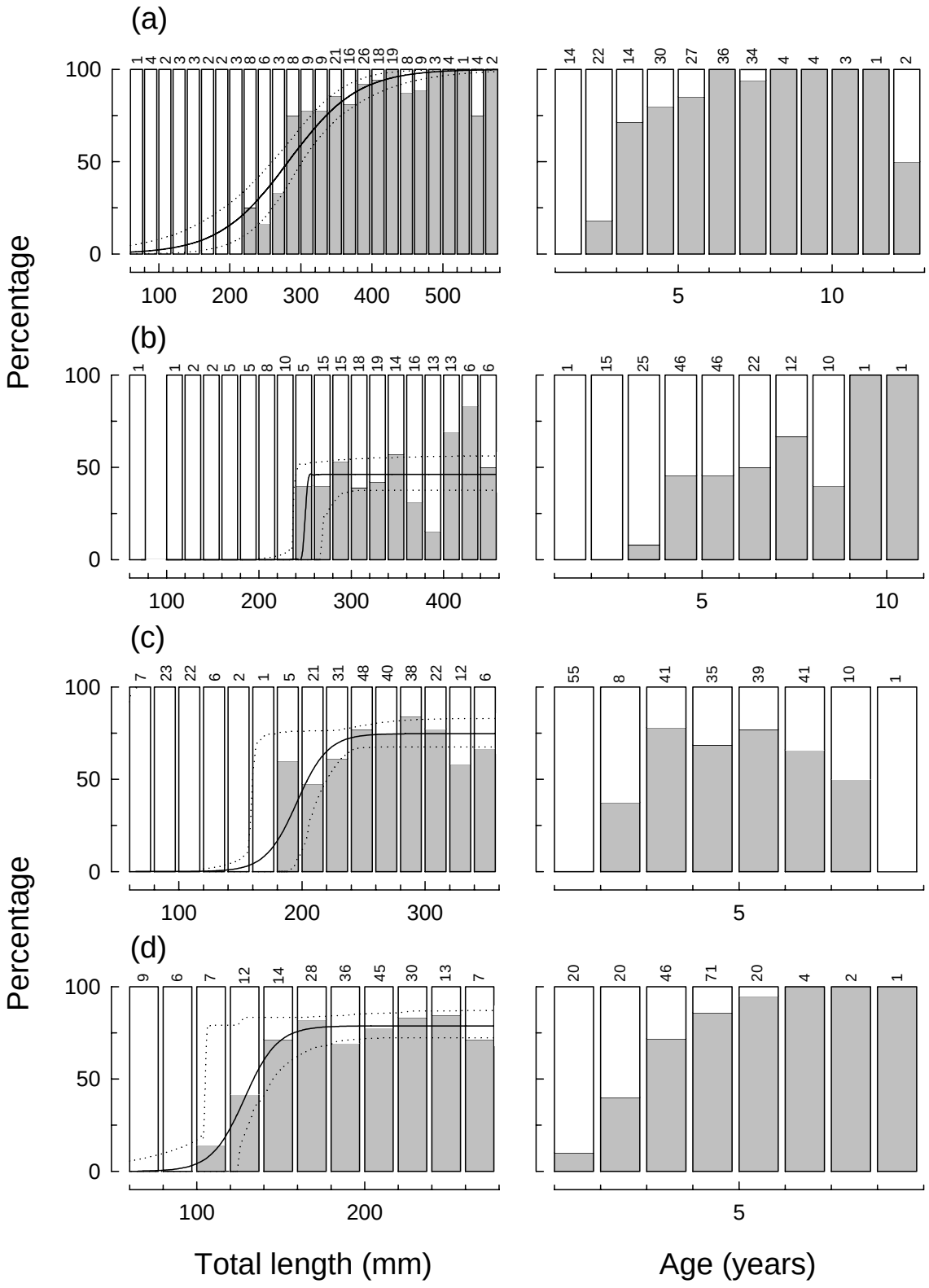

Figure 5.8. Length and age distributions of immature (white) and mature (grey) female (a) *Choerodon rubescens*, (b) *Choerodon schoenleinii*, (c) *Choerodon cauteroma* and (d) *Choerodon cyanodus* during their spawning period in Shark Bay with logisitic curves (± 95% CIs) fitted to the percentage of mature females at each length.

C. schoenleinii, *C. cauteroma* and *C. cyanodus* with ovaries at stages III-VIII yeilded L_{50}s of 250 mm (P_{max} = 0.46, 95% CI: 0.38-0.56), 196 mm (P_{max} = 0.75, 95% CI: 0.67-0.83) and 128 mm (P_{max} = 0.79, 95% CI: 0.72-0.88), respectively.

The youngest females of *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* with gonads at stages III-VIII were three, two and one years old, respectively **(Figure 5.8b,c,d)**. While such females comprised 100% of female *C. schoenleinii* in the upper age classes, the sample sizes were low, and thus, in the more abundant age classes, *i.e.* ≤ 8 years, the percentage of these females was always much lower, *i.e.* ≤ 67% **(Figure 5.8b)**. *Choerodon cauteroma* from 2 to 7 years of age that contained ovaries at stages III-VIII represented between 38 and 78% of females, but never represented 100% of females in any age class **(Figure 5.8c)**. The percentage of such females of *C. cyanodus* in each age class increased steadily from 10% of 1 year olds to 100% of fish ≥ 6 years old **(Figure 5.8d)**.

Length and age at sex change of *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* in Shark Bay.

The single transitional *C. schoenleinii* with gonads containing both sperm cells and previtellogenic oocytes and which was thus presumably in the process of changing sex was 526 mm in length and 7.4 years old **(Figure 5.9b)**. Male *C. schoenleinii* were first recorded in the 520-539 mm length class and the 7+ age class and subsequently increased in prevalence above this size and age. The largest male *C. schoenleinii* was 805 mm in length and 16.4 years old **(Figure 5.9b)**. Small sample sizes of transitional and male *C. schoenleinii* prevented the use of logistic regression analysis to determine values for the L_{50}s and A_{50}s for the length and age at which this species changes sex. The percentage of transitional or male *C. cauteroma* increased steadily from 2% of fish in the 200-219 mm length class to 100% by the 380-399 mm length class and from 4% in the 3+ age class to 100% by the 11+ age class **(Figure 5.9c)**. Logistic

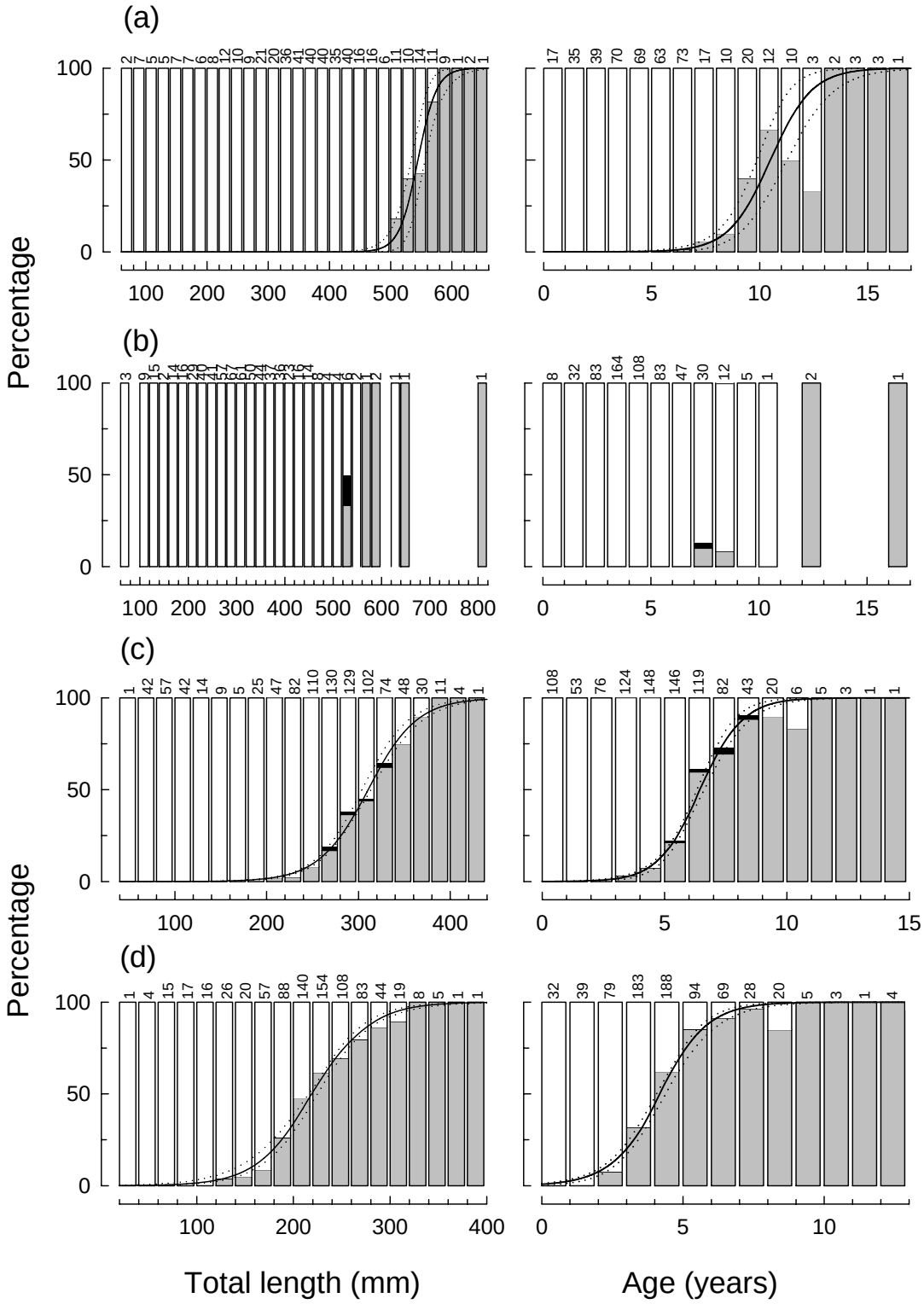

Figure 5.9. Length and age distributions of female (white), transitional (black), and male (grey) (a) *Choerodon rubescens*, (b) *Choerodon schoenleinii*, (c) *Choerodon cauteroma*, and (d) *Choerodon cyanodus* in Shark bay with logistic curves (± 95% CIs) fitted to the percentage of transitional and male fish at each length and age.

regressions fitted to the lengths and ages of transitional and male *C. cauteroma* produced an L_{50} and A_{50} of 310 mm and 6.4 years, respectively **(Table 5.2)**.

A similar pattern to that just described for *C. cauteroma* was exhibited by the length and age classes of *C. cyanodus*, with the percentage of males in each length class increasing steadily from 4% in the 120-139 mm length class to 100% by the 320-339 mm length class **(Figure 5.9d)**. Note that no transitional individuals of *C. cyanodus* were collected. The percentage contribution made by males of *C. cyanodus* in each age class increased from 5% in the 2+ age class to 100% by the 9+ age class **(Figure 5.9d)**. The L_{50} and A_{50}, derived from logistic regression analysis of this data, were 221 mm and 4.2 years, respectively **(Table 5.2)**.

Table 5.2 Lengths at sexual maturity (L_{50}, L_{95}, ±95% CI) of females and lengths at sex change (L_{50}, L_{95}, ±95% CI) of all *Choerodon rubescens* in Shark Bay and the Abrolhos Islands and of *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* in Shark Bay.

	Maturity						Sex change					
	L_{50} (mm)	**Lower 95% CI (mm)**	**Upper 95% CI (mm)**	**L_{95} (mm)**	**Lower 95% CI (mm)**	**Upper 95% CI (mm)**	**L_{50} (mm)**	**Lower 95% CI (mm)**	**Upper 95% CI (mm)**	**L_{95} (mm)**	**Lower 95% CI (mm)**	**Upper 95% CI (mm)**
***Choerodon rubescens* Shark Bay**	282.2	259.7	301.7	424.0	385.6	474.9	544.6	532.6	556.1	589.3	570.1	609.6
***Choerodon rubescens* Abrolhos Islands**	290.9	271.1	308.6	438.6	404.5	480.4	478.7	470.1	487.3	595.2	576.3	618.6
Choerodon schoenleinii	250.1	237.2	273.7	253.9	238.5	314.2	-	-	-	-	-	-
Choerodon cauteroma	195.7	158.6	212.3	232.9	162.1	264.5	310.1	305.3	315.4	386.8	374.6	401.2
Choerodon cyanodus	128.4	105.0	143.9	157.1	106	196.4	220.6	215.8	225.7	307.4	293.8	322.9

5.3.5 *Fecundity*

The diameters of previtellogenic, cortical alveolar and yolk granule oocytes, in the ovaries of two spawning, *i.e.* stage VI, females of *C. rubescens*, *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* essentially formed a continuum **(Figure 5.10)**. Note that, when present, the migratory nucleus and hydrated oocytes in these ovaries were not measured. Thus, each of the four species of tuskfish has indeterminate annual fecundity *sensu* Hunter *et al*. (1985) **(Figure 5.10)**.

As a likelihood ratio test demonstrated that the linear regressions fitted to the natural logarithms of the batch fecundities *vs* total length for individuals of *C. rubescens* in Shark Bay and the Abrolhos Islands were not significantly different ($p > 0.05$), the batch fecundities for the individuals in both regions were pooled. The relationship between batch fecundity (*BF*) and total length (*TL*) for *C. rubescens* derived from those pooled data is $BF = 1.4297\times10^{-7}TL^{4.4242}$ ($R^2 = 0.72$; **Figure 5.11a**). The relationship for batch fecundity (*BF*) *vs* wet weight (*W*) for pooled data for *C. rubescens* in the two regions is $BF = 44.987W\text{-}13632$ ($R^2 = 0.73$; **Figure 5.11b**). Minimum, maximum and mean batch fecundities for *C. rubescens* in Shark Bay and the Abrolhos Islands and for *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* in Shark Bay are shown in **Table 5.3**. Regression analyses were not carried out for *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* as few fish were caught with ovaries containing hydrated oocytes **(Figure 5.11b-d)**.

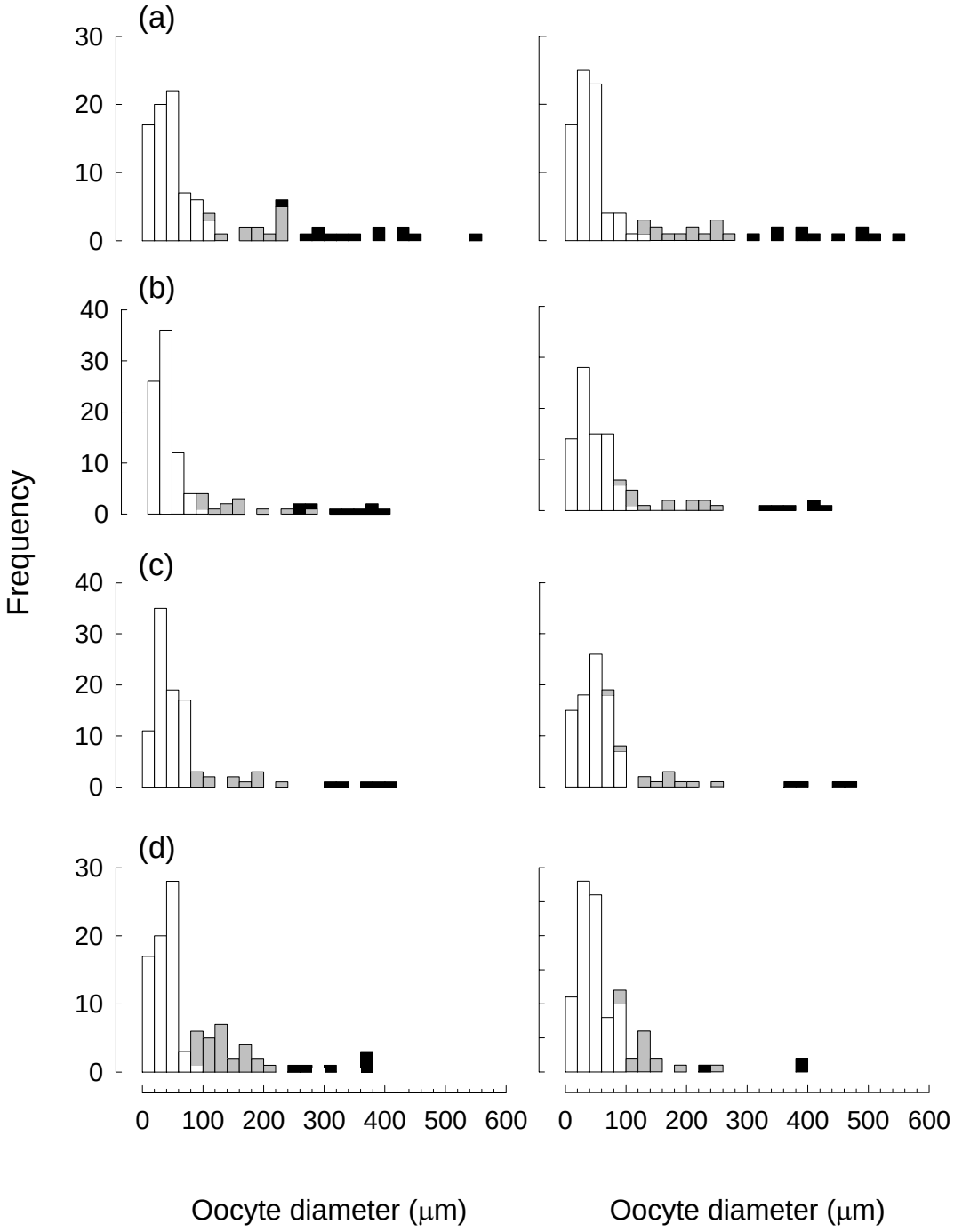

Figure 5.10. Oocyte diameter frequency distributions of spawning (stage V/VI) female (a) *Choerodon rubescens*, (b) *Choerodon schoenleinii*, (c) *Choerodon cyanodus* and (d) *Choerodon cauteroma*. Previtellogenic oocytes (white), cortical alveolar oocytes (grey), yolk granule oocytes (black).

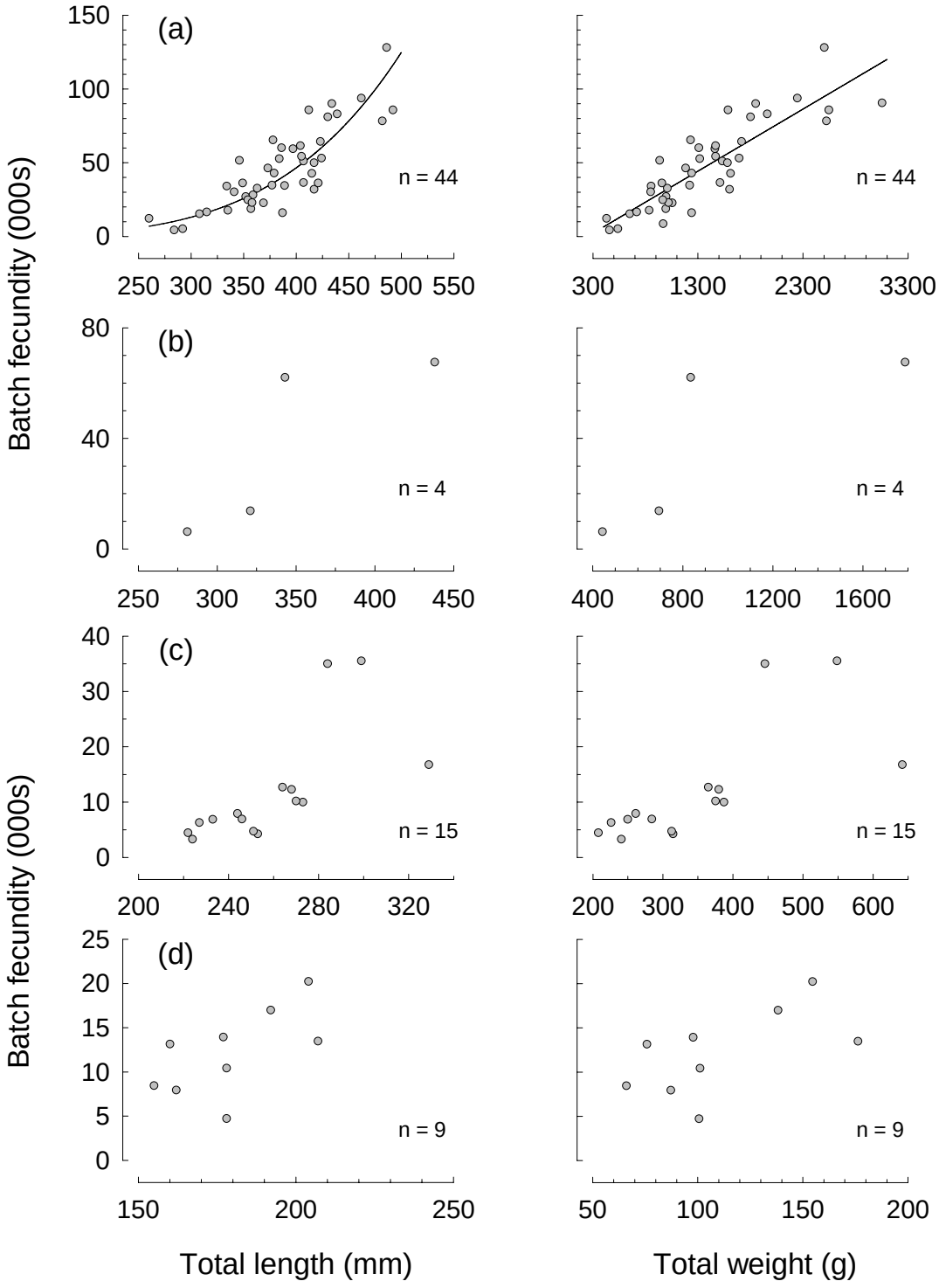

Figure 5.11. Relationships for batch fecundity with total length and total weight for (a) *Choerodon rubescens*, (b) *Cheorodon schoenleinii*, (c) *Choerodon cauteroma* and (d) *Choerodon cyanodus*.

Table 5.3. Minimum, maximum and mean batch fecundities (BF), and the total lengths (TL) in mm and wet weights (W) in g for *Choerodon rubescens* in Shark Bay and the Abrolhos Islands and for *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* in Shark Bay.

		Sample size	***Minimum***	***Maximum***	***Mean***
Choerodon rubescens Shark Bay	BF	44	4300	128200	45900
	TL		260	492	384
	W		429	2503	1323
Choerodon rubescens Abrolhos Islands	BF	29	4298	128170	39495
	TL		284	492	383
	W		458	2503	1306
Choerodon schoenleinii	BF	4	6242	67543.6	37397
	TL		281	438	346
	W		443	1787	940
Choerodon cauteroma	BF	15	3268	35538	11806
	TL		224	299	259
	W		246	580	361
Choerodon cyanodus	BF	9	4722	20232	12146
	TL		178	204	179
	W		104	165	118

5.4 DISCUSSION

5.4.1 *Evidence for hermaphroditism*

Initial analyses demonstrated that the length- and age-frequency distributions of *C. rubescens* in Shark Bay and the Abrolhos Islands and of *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* in Shark Bay were bimodal in terms of sex. For each of those species, the smaller and younger fish were females, while males were found only among the larger and older fish. This strongly indicates that each of these species is a protogynous hermaphrodite.

An histological examination of the gonads of fish covering the full size and age range of each of the four tuskfish species confirmed that the gonads of these species possessed the essential characteristics of protogynous hermaphrodites (Sadovy & Shapiro, 1987). Thus, the gonads of the smaller and younger individuals of all four species contained solely ovarian tissue and those of the transitional individuals of *C. rubescens*, *C. schoenleinii* and *C. cauteroma* contained degenerating previtellogenic oocytes and proliferating testicular tissue. Furthermore, the gonads of the males of these three species, and of those of *C. cyanodus* for which transitional individuals were not caught, were secondary *sensu* Sadovy & Shapiro (1987). These testes thus retained the ovarian lumen, lamellar structure and ovarian wall of their previously functional ovaries and, in the case of mature males, contained numerous sperm sinuses in their outer wall. The four tuskfish species can therefore be considered to be monandric protogynous hermaphrodites, a conclusion reached previously for *C. rubescens* in the Abrolhos Islands (Nardi, 1999) and *C. schoenleinii* in Japan (Ebisawa *et al*., 1995). The congeneric *Choerodon venustus* is also believed to be a monandric protogynous hermaphrodite in Queensland (Platten *et al.*, 2002). This type of hermaphroditism is known to occur in many other labrid species, *e.g. Achoerodus viridis*, *Cirrhilabrus temmincki*, *Nelabrichthys ornatus* and *Xyrichthys novacula* (Bentivegna & Rasotto, 1987; Kobayashi & Suzuki, 1990; Gillanders, 1995; Andrew *et al.*, 1996).

One of the four males of *C. cyanodus* collected by Choat (1969) on the Great Barrier Reef was identified, on the basis of the histological characteristics of its gonads, as a primary rather than a secondary male, as was the case with the other three males. Although this finding implies that *C. cyanodus* is diandric on the Great Barrier Reef, this is very unlikely to be the case with this species in Shark Bay. This conclusion is based on the fact that all of the 37 males of *C. cyanodus*, that were caught in that embayment and whose testes were examined histologically, were secondary.

5.4.2 *Spawning periods*

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 maturation 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" than *C. cauteroma* and *C. rubescens* in terms of this trigger. 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 the recruitment into the nursery areas by these species at slightly different times and thereby leading to a reduction in the potential for competition for space and food during that critical early stage in the life cycle.

The spawning by *C. schoenleinii* in Shark Bay during spring and/or summer occurs at a similar time to that of this species in Japan (Ebisawa *et al.*, 1995) and the spawning period of *C. cyanodus* in this embayment is similar to that suggested by Choat (1969), on the basis of limited data, for this species in Queensland. The spawning period of *C. rubescens* in Shark Bay,

i.e. during spring and summer, is essentially the same as that of this species in the Abrolhos Islands *ca* 350 km further south. 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*, *Xyrichtys novacula* (Kobayashi & Suzuki, 1990; Cardinale *et al.*, 1998; Sakai & Kohda, 2001).

Although *C. cauteroma* spawned mainly in spring, a few mature/spawning (stage V/VI) fish were also caught in the preceding months and as early as April. However, the mature/spawning fish obtained in the earlier months were caught around the southern or northern extremities of Dirk Hartog Island **(Figure 1.1)**, where, due to the influence of oceanic water, the water temperatures during that period of the year were far greater than within the eastern and western gulfs of Shark Bay **(Figure 7.1)**.

In contrast to the situation in the inner gulfs, the water temperature 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 those individuals of the other three tuskfish species within the inner gulfs.

5.4.3 *Lengths and ages at maturity*

Since all four species of tuskfish are monandric protogynous hermaphrodites, they each become sexually mature as females before changing sex to become males. Furthermore, since all males are adults, they have the potential to spawn during each spawning period. The L_{50}s for the females at maturity were greater for *C. rubescens* (282 mm) and *C. schoenleinii* (250 mm), which reached far greater lengths, *i.e.* 649 and 805 mm, respectively, than for *C. cauteroma* (190 mm) and *C. cyanodus* (128 mm), which only attained lengths of 424 and 382 mm, respectively. Furthermore, the first two species changed sex at a greater length (L_{50} = 545 and *ca* 550 mm) than the second two species (L_{50} = 310 and 221 mm). The above differences in the

length at maturity and sex change of the above two pairs of species are paralleled by those differences for the age at maturity and sex change. Thus, on the basis of values derived from the inverse von Bertalanffy growth equation (see Stergiou, 1999), the A_{50}s at maturity were greater for *C. rubescens* (2.9 years) and *C. schoenleinii* (3.0 years) than for *C. cauteroma* (2.2 years) and *C. cyanodus* (1.5 years), and the A_{50}s at sex change for the first two species (11.3 and 11.7 years) were far greater than those for the latter two species (7.1 and 4.0 years). It should be noted that these differences occur despite the fact that, in Shark Bay, the maximum age for the above species ranged only from 12 to 16 years.

The above interspecific differences in the age at sex change are reflected in differences in the sex ratios. For example, the overall ratios of females to males were far higher for *C. rubescens* (12:1) and *C. schoenleinii* (85:1) than for *C. cauteroma* (3:1) and *C. cyanodus* (1:1). This implies that many of the females of the first two species do not become males. It also suggests that the males of the first two species, in particular, probably have harems, as has been shown to occur with a number of other labrid species, *e.g. Labroides dimidiatus* and *Xyrichtys pentadactylus* (Nemtzov, 1985; Sakai *et al.*, 2001).

5.4.4 *Comparisons between* Choerodon rubescens *in Shark Bay and the Abrolhos Islands*

Our data demonstrated that *C. rubescens* reached maturity at a similar size in the Abrolhos Islands (L_{50} = 291 mm) as in Shark Bay (L_{50} = 282 mm), which strongly suggests that the attainment of maturity is size-related. Such a view is consistent with the fact that, presumably as a result of a faster growth rate, *C. rubescens* reaches maturity a year earlier in Shark Bay than in the Abrolhos Islands. The strong indications that a faster growth rate is accompanied by the attainment of maturity at an earlier age with *C. rubescens* parallels the situation recorded for the tarwhine *Rhabdosargus sarba* in different environments in Western Australia (Hesp & Potter, 2003).

In contrast to the situation with the attainment of maturity, *C. rubescens* changes sex at a similar age (11 years) in Shark Bay as the Abrolhos Islands, but at a larger size, *i.e.* 545 and 479, respectively. Although this implies that sex change is age and not size-related, it should be recognised that the size at sex change of *C. rubescens* in both Shark Bay and the Abrolhos Islands is approximately 80% of the L_∞ (640 and 535 mm, respectively), thereby essentially paralleling the situation found with a number of other species (Allsop & West, 2003).

The sex ratios for *C. rubescens* that were above the MLL for this species (400 mm) and were collected by rod and line fishing in waters less than 30 m deep yielded a greater proportion of females than males in both Shark Bay (10♀:1♂) and the Abrolhos Islands (9♀:1♂). However, the sex ratio in catches from commercial hand-lining in waters > 30 m deep were approximately parity in both regions. Since the proportion of males increased with depth, this implies that the individuals of this species move into deeper waters as they increase in size. Such a size-related movement would parallel that exhibited by another protogynous species *Achoerodus viridis*, in eastern Australia (Gillanders, 1995; 1997).

5.4.5 *Fecundity*

The four species of tuskfish have indeterminate fecundity and thus differ in this respect from *A. latus* (Chapter 3). Thus, in these species, the number of large "eggs" present in the mature ovaries of fish caught just prior to the commencement of the spawning period does not correspond to the potential annual fecundity of those species (see Hunter *et al.*, 1985). Since it was logistically impossible to determine, in an environment as remote as Shark Bay, the frequency of spawning by the four tuskfish species during their spawning periods, the batch fecundities that were obtained for each species could not be used to derive a reliable estimate of the potential annual fecundity of those four fish species.

The data on batch fecundity for *C. rubescens*, which was the most comprehensive of any tuskfish species, clearly demonstrated that this variable is positively correlated with both the total length and total weight of those species. The mean number of eggs produced in a single batch by *C. rubescens* was 42,700 and was as high as 128,200 in a fish weighing 2,500 g.

5.4.6 *Management implications*

The management implications of the reproductive data presented in this chapter are considered in the next chapter in the context of those associated with the length and age compositions, sex ratios and growth.

6.0 AGE COMPOSITIONS AND GROWTH OF THE FOUR TUSKFISH SPECIES

D. V. Fairclough & I. C. Potter

6.1 INTRODUCTION

Many studies have focused on determining aspects of the reproductive biology of labrids (*e.g.* Hoffman, 1985; Warner & Swearer, 1991; Warner & Schultz, 1992; Shapiro & Rasotto, 1993; Ebisawa *et al*., 1995; Warner, 1998). In contrast, relatively few studies have concentrated on obtaining sound data for the age compositions and growth rates of protogynous labrids (Choat & Robertson, 2002).

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, Nardi (1999) recognised that his marginal increment analysis did not provide conclusive evidence that the opaque zones in those otoliths had been formed annually, which is now considered essential for studies of the age compositions and growth of fish (Campana, 2001). 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.

There is no information on the age compositions and growth rates of *C. schoenleinii*, *C. cyanodus* and *C. cauteroma*. Ebisawa *et al.* (1995) demonstrated that the females of *C. schoenleinii* in Japan were found in fish of 150-649 mm, while their males were found only amongst the larger fish, *i.e.* 400-799 mm. Transitional individuals of *C. schoenleinii* ranged from 450 to 649 mm in length. In his samples of *C. cyanodus* from the Great Barrier Reef, which ranged from 98-405 mm in length, Choat (1969) found that females were confined to the smaller size classes, while the males ranged widely in length. No studies have been carried out on the age compositions or growth rates of *C. cauteroma*, a species which attains a maximum length of about 36 cm (Allen, 1999).

The first aim of this component of the project was to validate that the opaque zones in the otoliths of *C. rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* are formed annually and to determine the size and age compositions and growth rates of these species in Shark Bay. The second aim was to compare the size and age compositions and growth rates for *C. rubescens* in Shark Bay with those recorded concurrently for this species in the Abrolhos Islands.

6.2 MATERIALS AND METHODS

Details of the sampling localities and regime, the length and weight measurements, the validation of the methods used for ageing fish and the von Bertalanffy growth equation were given in Chapter 2, while details of the likelihood ratio test (which was used in this chapter for comparing the growth curves of *Choerodon rubescens* in Shark Bay and the Abrolhos Islands) were given in Chapter 5, section 5.2.

6.3 RESULTS

6.3.1 *Length-weight relationships*

The relationships between the total length (*TL*) and wet weight (*W*) of each tuskfish species are as follows:

Choerodon rubescens $W = 2.23997\times10^{-5} \times TL^{2.99871}$ ($R^2 = 0.9972$, n = 545);

Choerodon schoenleinii $W = 2.85230\times10^{-5} \times TL^{2.94451}$ ($R^2 = 0.9948$, n = 581);

Choerodon cauteroma $W = 1.96817\times10^{-5} \times TL^{3.00722}$ ($R^2 = 0.9970$, n = 1011); and

Choerodon cyanodus $W = 1.50215\times10^{-5} \times TL^{3.05629}$ ($R^2 = 0.9931$, n = 858).

6.3.2 *Validation of annual growth zone formation in otoliths and determination of birth dates*

The mean monthly marginal increments on the otoliths of *C. rubescens*, *C. cauteroma* and *C. cyanodus* with different numbers of opaque zones rose from their minima in mid to late summer to reach their maxima between winter and early summer and then underwent a conspicuous decline **(Figure 6.1-6.3)**. Although the mean monthly marginal increments for *C. schoenleinii* followed similar pronounced seasonal trends, they fell to their minima slightly earlier, *i.e.* late spring **(Figure 6.4)**. The fact that the mean monthly marginal increments for 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 **(Figure 6.1-6.4)**. Thus, the number of opaque zones (annuli) can be used to age each of the four species of tuskfish.

The trends exhibited by gonadosomatic indices, gonadal maturity stages and the patterns of oocyte development in each of the four species of tuskfish demonstrated that spawning peaked in October for *C. cauteroma*, November for *C. rubescens* and *C. schoenleinii* and January for *C. cyanodus* (Chapter 5.3.3). Thus, these species were assigned birth dates of 1 November, 1 December, 1 December and 1 February, respectively.

6.3.3 *Length and age compositions of* **Choerodon rubescens**

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 **(Figure 6.5a,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 **(Figure 6.5a,b)**. The females of *C. rubescens* in Shark Bay and the Abrolhos Islands 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

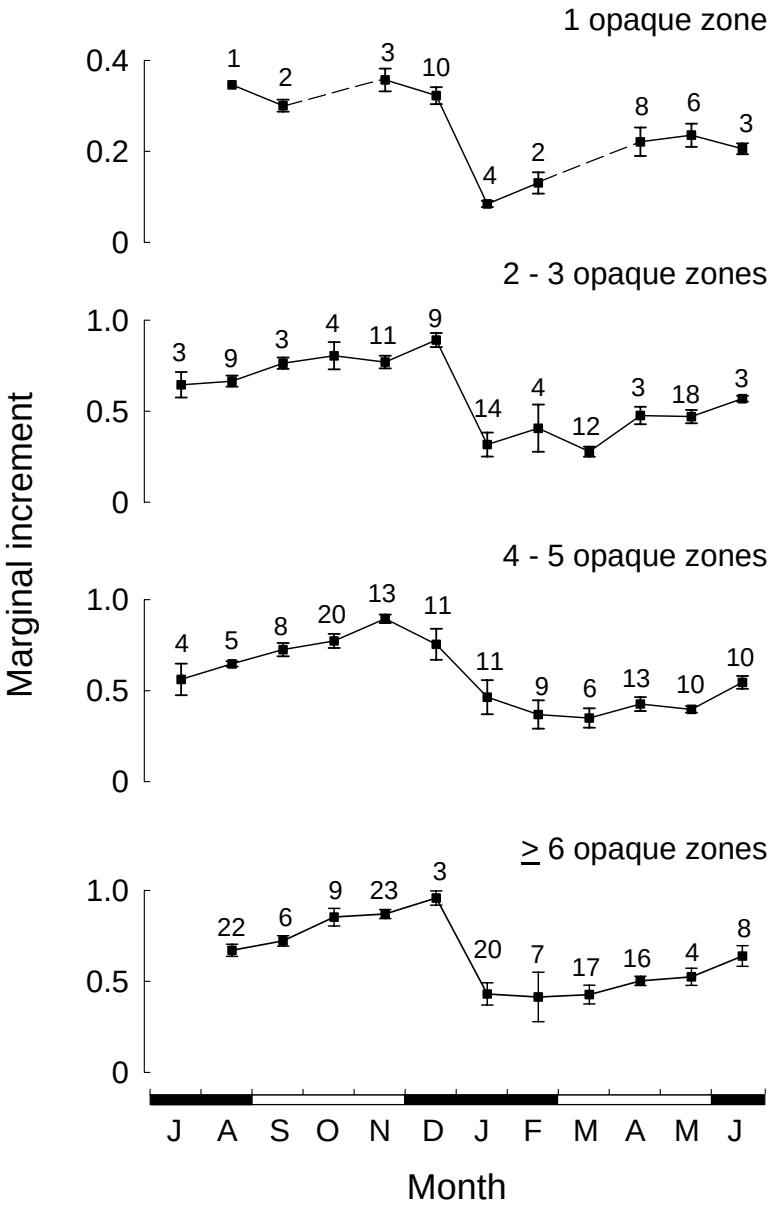

Figure 6.1. Mean monthly marginal increments ±1SE for *Choerodon rubescens* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.

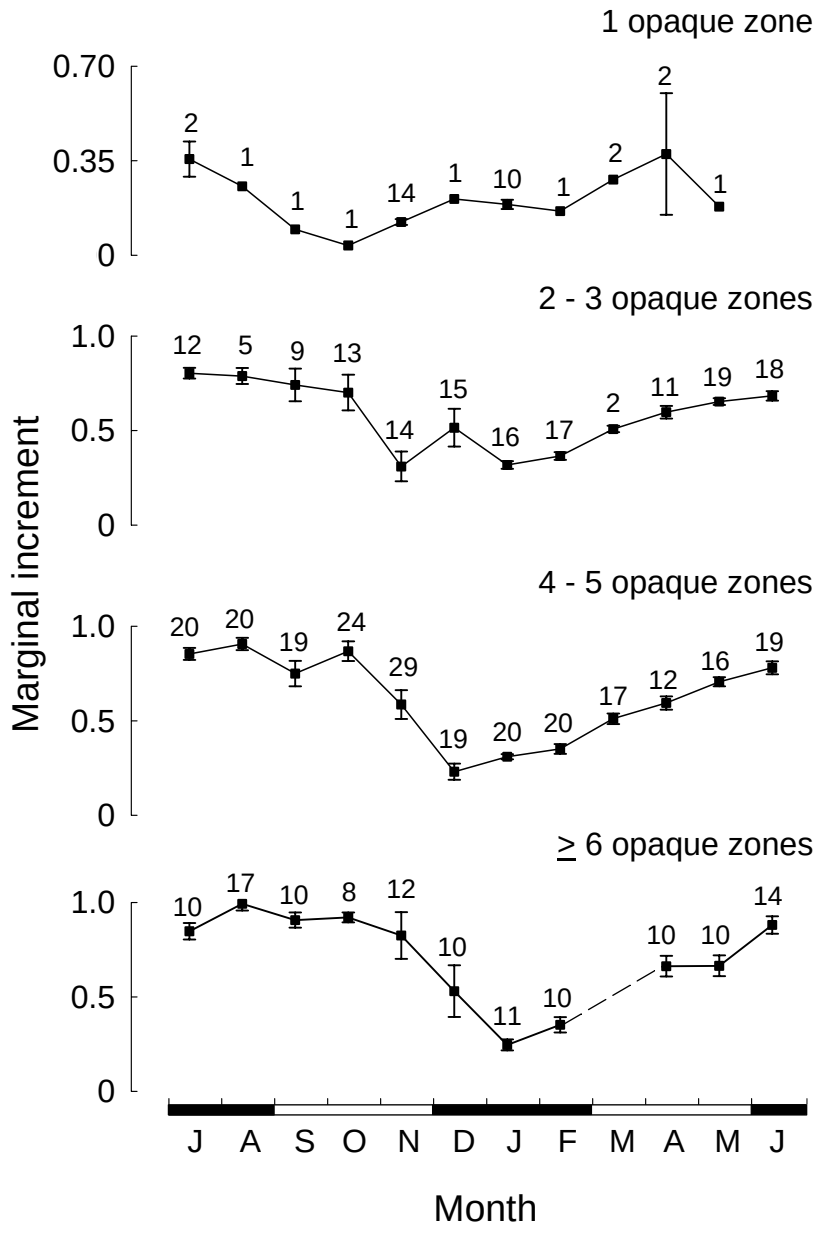

Figure 6.2. Mean monthly marginal increments ±1SE for *Choerodon cauteroma* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.

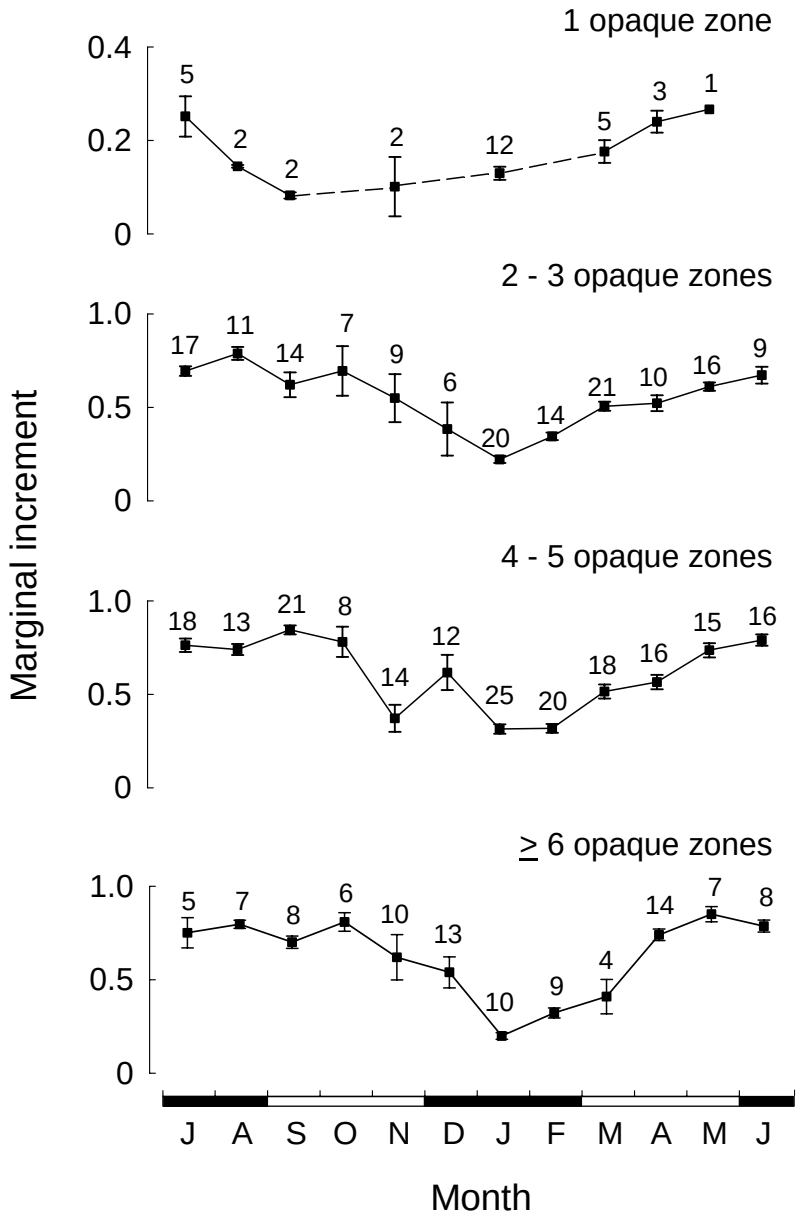

Figure 6.3. Mean monthly marginal increments ±1SE for *Choerodon cyanodus* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.

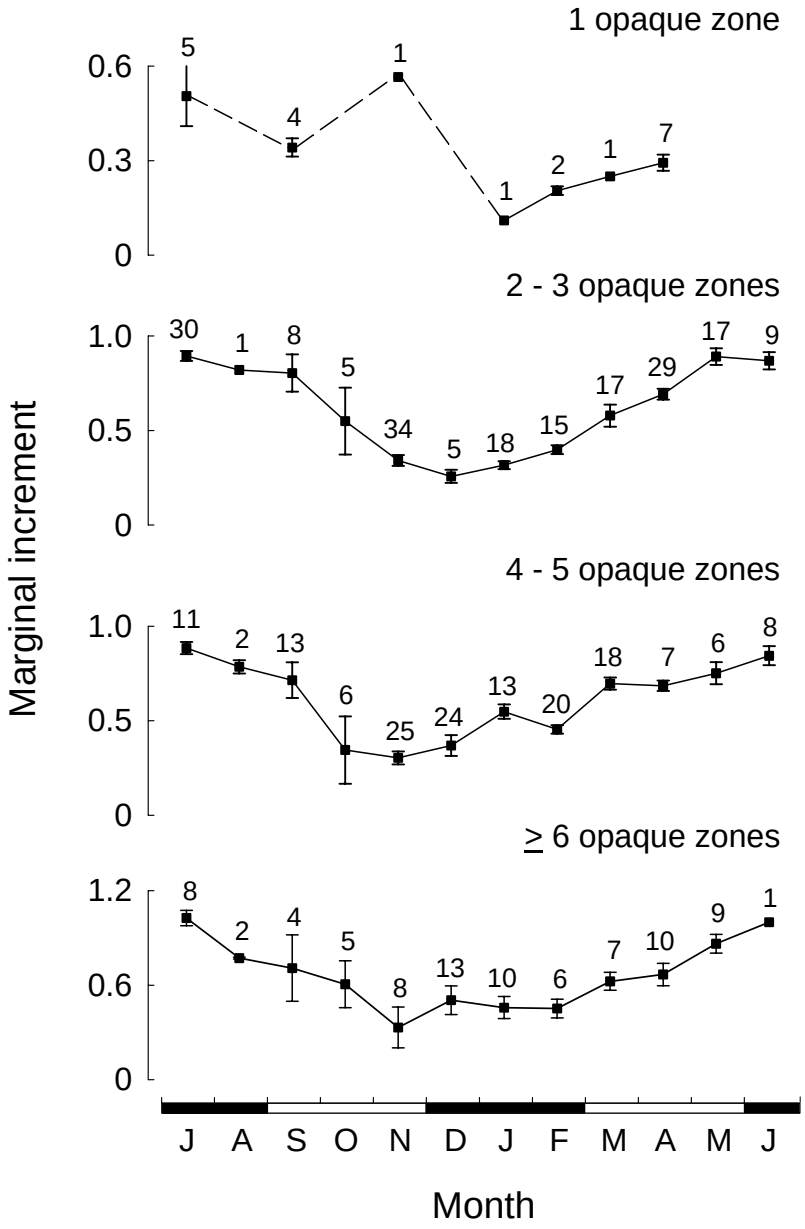

Figure 6.4. Mean monthly marginal increments ±1SE for *Choerodon schoenleinii* collected in Shark Bay between July 2000 and January 2003. Sample sizes are shown above each mean.

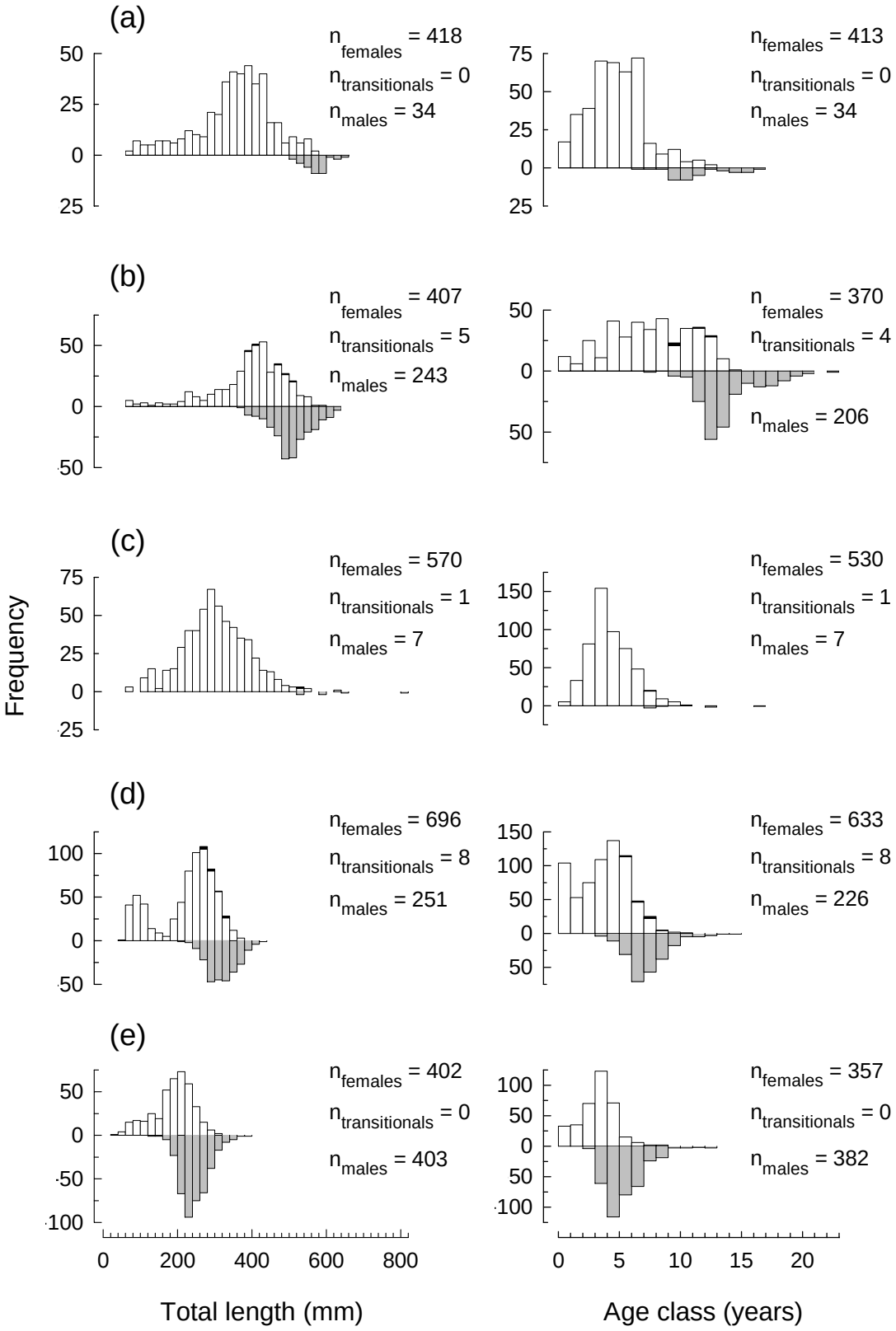

Figure 6.5. Length and age frequency compositions of female (white), transitional (black) and male (grey) *Choerodon rubescens* collected in (a) Shark Bay and (b) the Abrolhos Islands, and (c) *Choerodon schoenleinii*, (d) *Choerodon cauteroma* and (e) *Choerodon cyanodus* collected in Shark Bay.

(Figure 6.5a,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.

The length range of *C. rubescens* collected in shallow waters (< 30 m) in Shark Bay, 70 to 625 mm, and the Abrolhos Islands, 63 to 601 mm, were similar **(Figure 6.6)**. The individuals of *C. rubescens*, that were purchased from wholesale fish markets and had been caught in waters of 30-100 m in Shark Bay and the Abrolhos Islands, ranged in length from 415 to 649 mm and 366 to 629 mm, respectively **(Figure 6.6)**. 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 23+ years, respectively, in the Abrolhos Islands **(Figure 6.6)**.

6.3.4 *Length and age compositions of* Choerodon schoenleinii*,* Choerodon cauteroma *and* Choerodon cyanodus

Female *C. schoenleinii* ranged in length and age from 72 to 626 mm and 0 to 10 years **(Figure 6.5c).** The seven male individuals of this species caught in Shark Bay were all relatively large and old, ranging in length and age from 521 to 805 mm and 7 to 16 years. The single transitional *C. schoenleinii* was 526 mm in length and 7 years old **(Figure 6.5c)**. Female *C. cauteroma* and *C. cyanodus* ranged in length from 58 to 372 mm and 39 to 315 mm, respectively, and were 0 to 10 and 0 to 8 years old, respectively **(Figure 6.5d,e)**. The males of these two species ranged in length from 219 to 424 mm and 138 to 382 mm, respectively, and were 3 to 14 and 2 to 12 years old, respectively **(Figure 6.5d,e)**. The eight transitional *C. cauteroma* ranged in length from 266 to 338 mm and belonged to the 5 to 8+ age classes **(Figure 6.5d)**. None of the individuals of *C. cyanodus* possessed gonads that contained both ovarian and testicular tissue.

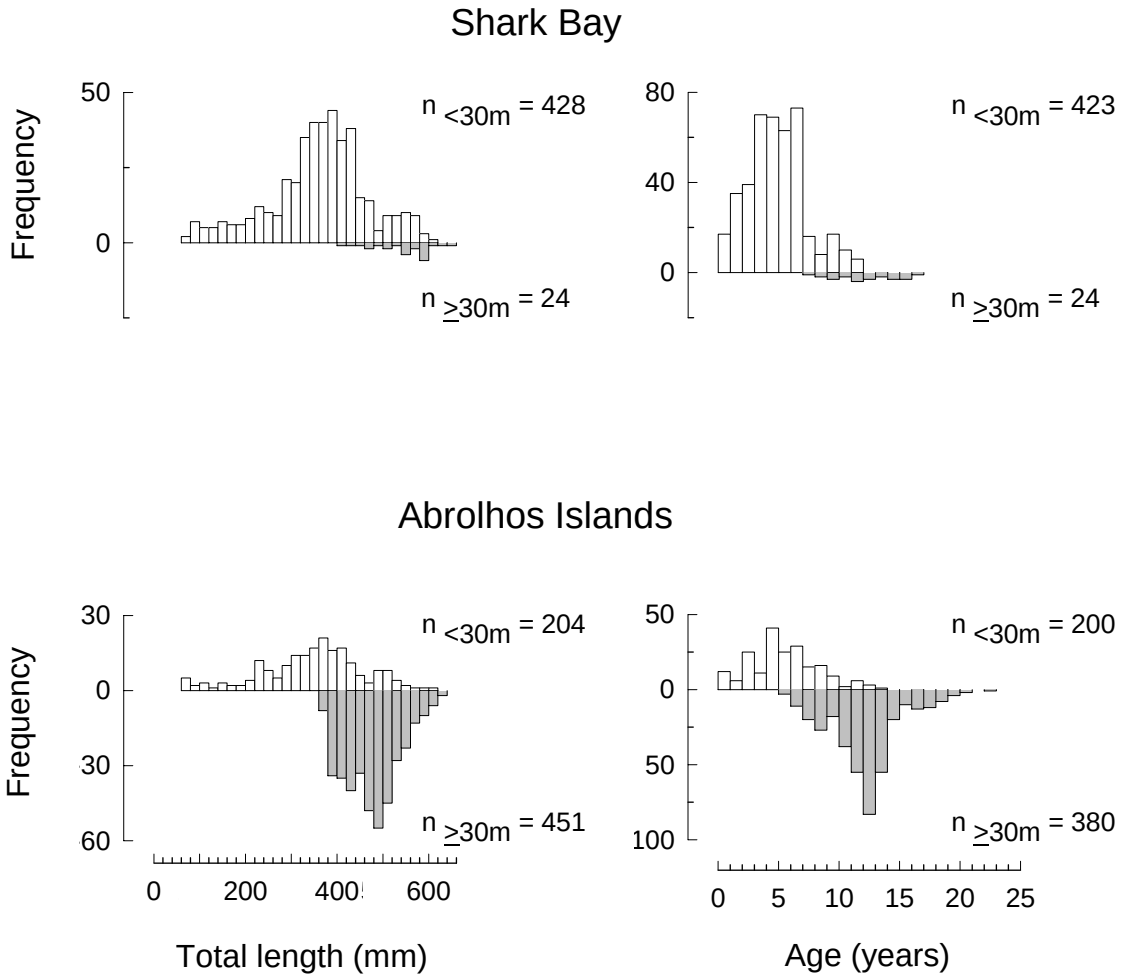

Figure 6.6. Length and age frequency compositions of *Choerodon rubescens* collected in shallow (white) and deep (grey) water in Shark Bay and the Abrolhos Islands.

6.3.5 *von Bertalanffy growth curves*

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 **(Figure 6.7, Table 6.1)**. The lengths at each age of *C. rubescens*, estimated from the von Bertalanffy growth curves, were always greater for the population in Shark Bay than for that in the Abrolhos Islands. A likelihood ratio test demonstrated that the curves for these two populations were significantly different ($p < 0.05$) **(Figure 6.7, Table 6.1)**. The asymptotic length (L_∞) 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), for which the respective values were 0.16 and 0.19 year^{-1} **(Table 6.1)**. von Bertalanffy growth curves also provided a good fit to the lengths at age of the other three species of tuskfish. In Shark Bay, the L_∞s of 640 and 734 for *C. rubescens* and *C. schoenleinii*, respectively, were far greater than those of 330 and 289 mm for *C. cauteroma* and *C. cyanodus*, respectively **(Figure 6.8, Table 6.1)**. In contrast, the values for k for the first two species (0.16 and 0.11 year^{-1}) were much lower than those for the latter two species (0.38 and 0.35 year^{-1}) **(Table 6.1)**.

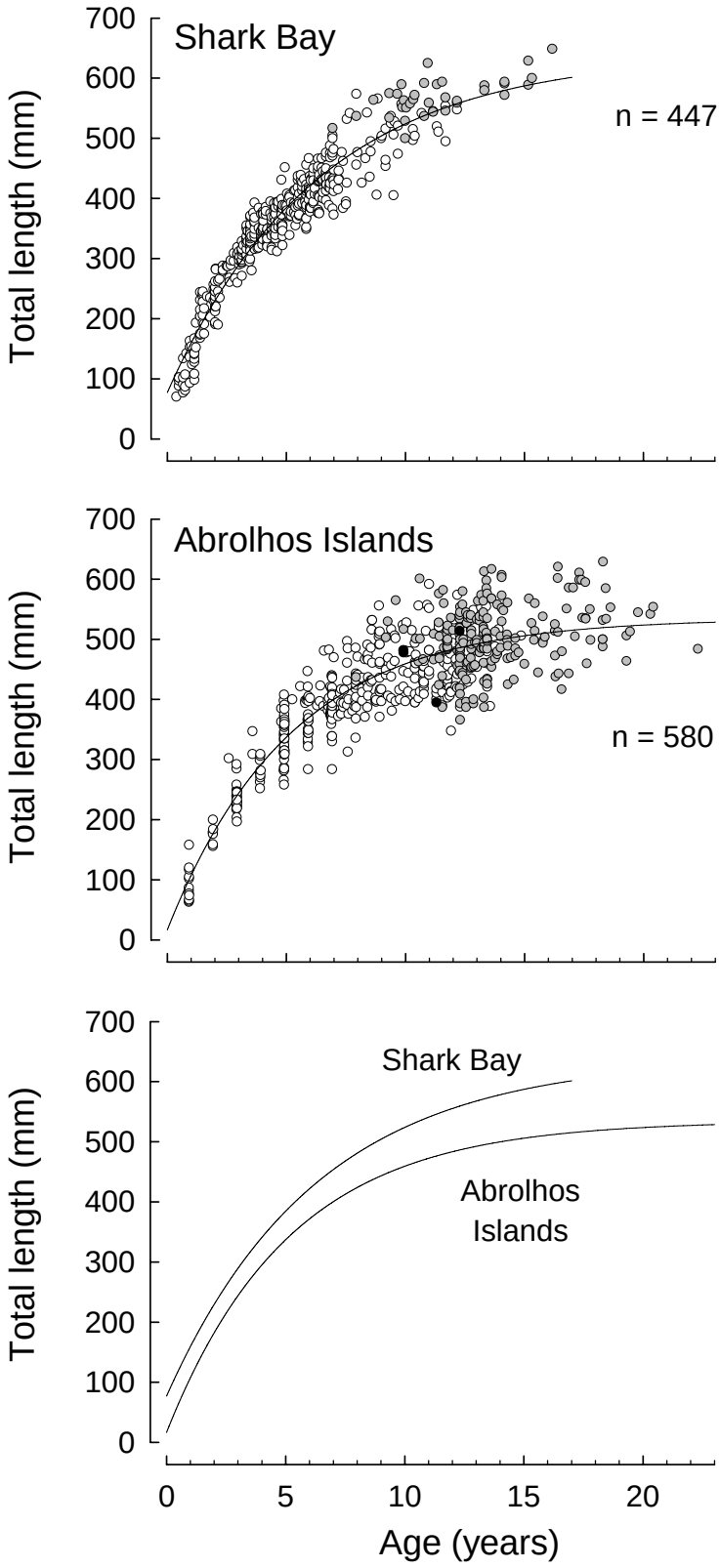

Figure 6.7. von Bertalanffy growth curves fitted to the lengths at age of female (white), transitional (black) and male (grey) *Choerodon rubescens* collected in Shark Bay and the Abrolhos Islands.

Table 6.1. Parameters for the von Bertalanffy growth curves and their 95 % confidence intervals fitted to the lengths at age of *Choerodon rubescens* in Shark Bay and the Abrolhos Islands, and of *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* in Shark Bay.

	von Bertalanffy parameters				
Species	L_∞ **(mm)**	k **(year^{-1})**	t_0 **(years)**	R^2	n
***Choerodon rubescens* Shark Bay**	**639.7**	**0.157**	**-0.82**	**0.924**	**447**
Lower	613.6	0.142	-1.001		
Upper	665.7	0.174	-0.617		
***Choerodon rubescens* Abrolhos Islands**	**534.7**	**0.192**	**-0.162**	**0.789**	**580**
Lower	521.1	0.172	-0.481		
Upper	548.3	0.214	0.156		
Choerodon schoenleinii	**733.5**	**0.111**	**-0.720**	**0.740**	**572**
Lower	609.2	0.077	-1.138		
Upper	857.8	0.146	-0.301		
Choerodon cauteroma	**330.2**	**0.383**	**-0.185**	**0.832**	**935**
Lower	323.0	0.351	-0.279		
Upper	337.4	0.416	-0.091		
Choerodon cyanodus	**289.3**	**0.349**	**-0.149**	**0.671**	**746**
Lower	278.2	0.302	-0.347		
Upper	300.5	0.397	0.472		

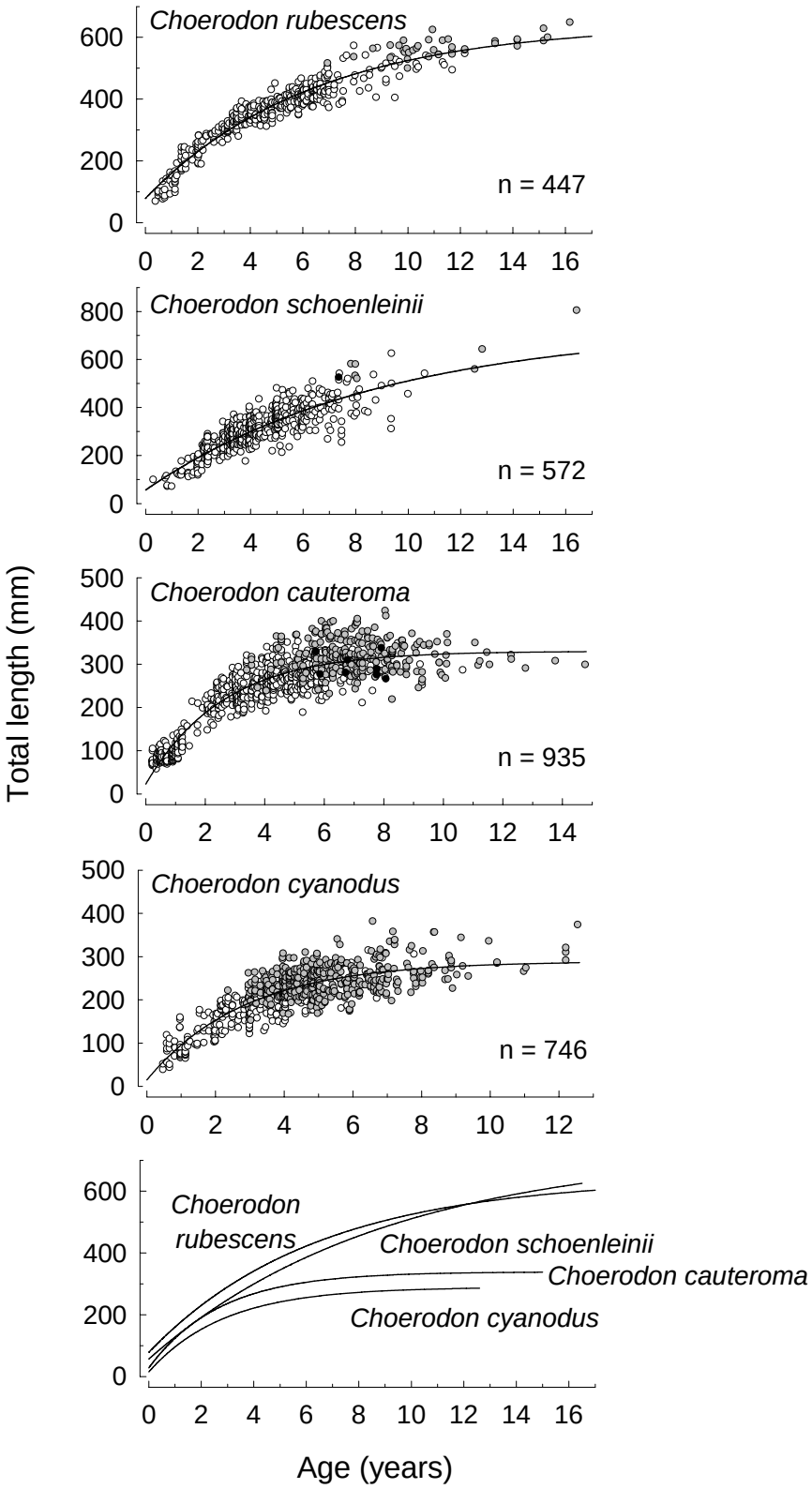

Figure 6.8. von Bertalanffy growth curves fitted to the lengths at age of female (white), transitional (black) and male (grey) *Choerodon rubescens*, *Choerodon schoenleinii*, *Choerodon cauteroma* and *Choerodon cyanodus* collected in Shark Bay.

6.4 DISCUSSION

6.4.1 *Validation of the ageing method*

Marginal increment analysis demonstrated that, as with *Acanthopagrus latus*, a single opaque zone is formed annually in the otoliths of each of the four species of tuskfish. Thus, the numbers of opaque zones in otoliths can be used to age the individuals of these species. The opaque zones typically became delineated during late spring or summer, which parallels the situation with the otoliths of *A. latus* in Shark Bay and many other species in Western Australia, *e.g.* West Australian dhufish *Glaucosoma hebraicum* and Australian herring *Arripis georgiana* (Chapter 4; Fairclough *et al.*, 2000; Hesp *et al.*, 2002).

6.4.2 *Length and age compositions and growth of the four tuskfish species in Shark Bay*

Some species of *Choerodon* reach a substantial size and are valued for their qualities as an angling fish and as a food source. This is the case with the four largest tuskfish species in Western Australia and also *C. schoenleinii*, *C. cyanodus* and the venus tuskfish *Choerodon venustus* in Queensland (Grant, 1993; Platten *et al*., 2002). In Shark Bay, *C. rubescens* (649 mm) and *C. schoenleinii* (805 mm) reached far greater lengths than *C. cauteroma* (424 mm) and *C. cyanodus* (382 mm). These differences are reflected in far greater L_{∞}s, *i.e.* 640 and 734 mm *vs* 330 and 289 mm, respectively. The above maximum lengths of *C. rubescens* and *C. schoenleinii* are very similar to the maximum lengths of 650 and 800 mm recorded by Allen (1999) for these two species, respectively. Individuals of *C. schoenleinii* weighing up to 16 kg have been caught in Queensland, which, from the length-weight relationship for that species, would have corresponded to a length of approximately 935 mm (Grant, 1993). The largest *C. schoenleinii* collected during the present study is similar to the maximum length of *ca* 790 mm recorded by Ebisawa *et al.* (1995) for this species in Japan.

The number of *C. rubescens* caught in Shark Bay declined markedly above a length of 400 mm, the MLL for this species in Western Australia. This may be related to the fact that South Passage, where most of the *C. rubescens* were caught, is a relatively small area and is subjected to heavy fishing pressure, particularly during autumn and winter when weather conditions are optimal for angling. It may also be relevant that, even though *C. schoenleinii* reaches lengths of 805 mm in Shark Bay, the number in the catches of this species that were greater than the MLL of 400 mm was low. Thus, *C. schoenleinii* in Shark Bay may also be subjected to heavy fishing pressure. Ebisawa *et al.* (1995) found relatively low numbers of the large individuals in commercial catches obtained in Japan and concluded that this species was being overexploited.

The maximum length of 424 mm recorded in our catches of *C. cauteroma* in Shark Bay is substantially greater than the maximum of 360 mm listed for this species by Allen (1999). 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 and the majority of these were less than 300 mm, and thus well below the current MLL of 400 mm. The length range of *C. cyanodus* we recorded is similar to that reported by Choat (1969) for this species at Heron Island on the Great Barrier Reef. 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 about 440 mm and thus greater than the maximum length of 382 mm recorded for this species in Shark Bay.

The maximum ages attained by the four species of tuskfish in Shark Bay ranged only from 12 to 16 years. However, although the patterns of growth exhibited by *C. rubescens* and *C. schoenleinii* were similar, they differed markedly from those of *C. cauteroma* and *C. cyanodus*, which were similar. These differences are reflected in the fact that the values for *k*

in the von Bertalanffy growth equation of 0.16 and 0.11 year^{-1} for the first two species, respectively, were far less than those of 0.38 and 0.35 year^{-1} for the second two species, respectively. The difference between the growth curves is also reflected in the greater L_{∞}s derived for the first two species, *i.e.* 640 and 734 mm, than for the second two species, *i.e.* 330 and 289 mm. The tendency for the growth curves of *C. cauteroma* and *C. cyanodus* to asymptote at a shorter length than those of *C. rubescens* and *C. schoenleinii* is correlated with the attainment of maturity at a smaller length (L_{50}) in the first two species, *i.e.* 196 and 128 mm, respectively, than the second two species, *i.e.* 282 and 250 mm, respectively. Thus, while each species exhibits similar growth during the first three years of life, the somatic growth of the first two species then starts to slow down as those species commence investing substantially in gonadal development, whereas the second two species continue to undergo a substantial increase in somatic growth. This reflects the variation in reproductive strategies that have evolved in different species in order to maximise their reproductive potential (Jennings *et al.*, 2001).

6.4.3 *Choerodon rubescens in Shark Bay and the Abrolhos Islands*

The von Bertalanffy growth equations for *C. rubescens* in Shark Bay and the Abrolhos Islands were significantly different, mainly reflecting a large difference in the L_{∞}s for the populations in the two regions, *i.e.* 640 *vs* 535 mm, respectively. This difference is reflected in greater lengths at age for all of the younger age classes as derived from the von Bertalanffy growth equation. The above comparisons imply that *C. rubescens* grows more rapidly in Shark Bay than the Abrolhos Islands. It thus appears relevant that the assemblage of *C. rubescens* sampled in Shark Bay was located in an area that, during each tidal cycle, receives water from the inner gulfs of that embayment, and which would thus presumably be more productive than the oceanic waters surrounding the Abrolhos Islands (Burling *et al.*, 2003).

Although *C. rubescens* reached similar maximum lengths in Shark Bay (649 mm) and the Abrolhos Islands (629 mm), a smaller number of individuals above the MLL of 400 mm were obtained from Shark Bay than the Abrolhos Islands. Furthermore, the number of fish caught over 15 years of age was also less in Shark Bay than the Abrolhos Islands. The above differences may reflect the fact that *C. rubescens* is very heavily targeted in South Passage, the location where the majority of the samples of this species were obtained in Shark Bay. Moreover, since the Abrolhos Islands occupies a far greater area than South Passage, the overall fishing pressure on this species would tend to be less concentrated in the waters surrounding those islands.

6.4.4 *Management implications*

The length and age frequency distributions for each of the four species of tuskfish demonstrated that males were represented only amongst the larger and older fish. Thus, since fishers preferentially target large fish, the proportion of males that they catch is substantially higher than in the population as a whole **(see Table 5.1)**, particularly in the case of *C. rubescens*, which is the tuskfish species most heavily targeted by commercial and recreational fishers. The use of too stringent a minimum size limit for management purposes may therefore result, if fishing pressure is high, in a marked reduction in the number of males in the population (Bannerot *et al.*, 1987; Sadovy, 1996). Indeed, Coleman *et al*. (1999) have pointed out that the complex life history and behaviour of protogynous species explain why the management approaches employed have entirely failed to stem the effects of commercial and recreational fishing pressure on an important group of reef fishes in the United States.

Many hermaphroditic species change sex on the basis of social cues, *e.g.* the loss of a male from a social group (*e.g.* Nemtzov, 1985; Sakai e*t al*., 2001). Furthermore, with sustained and heavy fishing pressure, some protogynous species may change sex at a shorter length than

normal in response to the removal of substantial numbers of their males and thus in an attempt to maintain an appropriate sex ratio (Shapiro & Lubbock, 1980; Warner, 1988; Darwall *et al.*, 1992). Thus, for example, in the case of *Choerodon venustus*, Platten *et al.* (2002) found that, while the individuals of this species changed sex at essentially the same size and age at two different locations, those from a third location, where fishing pressure was far greater, changed sex at a smaller size and younger age. Furthermore, fish from the third location did not attain the same lengths as in the other two localities (Platten *et al.*, 2002). Thus, even in cases where protogynous species are able to adapt to increased fishing pressure by changing sex at a smaller length and age, fishing pressure can lead to an undesirable shift in the size and age composition.

7.0 HABITAT PARTITIONING AMONGST *ACANTHOPAGRUS LATUS* AND FIVE SPECIES OF *CHOERODON* IN SHARK BAY

D. V. Fairclough & I. C. Potter

7.1 INTRODUCTION

Successful management of the stocks of a marine fish species requires not only data on crucial aspects of the biology of a species, such as size and age compositions, growth and reproductive biology, but also reliable information on the habitats occupied by that species and how they change during its life cycle. The latter information can be used, for example, to establish closed fishing areas to protect stocks (Bohnsack, 1998; Agardy, 2000; Halpern & Warner, 2002).

The relative abundances of a species in the habitats that it occupies during its life cycle provide information on which habitat types most require protection to ensure the sustainability of the stock(s) of that species. However, many of the methods used to determine the relative abundances of different species, *e.g.* those derived from the catches obtained by trawl and seine netting, trapping and line fishing, have limitations, due to the problems posed by the fact that, for example, some species of fish exhibit net avoidance, trap shyness or are not prone to take bait. Furthermore, while most sampling methods, *e.g.* trawling, can be used in particular habitats, such as in seagrass and over bare sand, they cannot be employed in other habitats, *e.g.* reefs. Moreover, since it is sometimes necessary to use several methods to obtain samples of all of the different life cycle stages of a species from the various habitat types occupied by that species, it is difficult to make valid comparisons between the different estimates of relative abundances of species obtained by those different methods. For the above reasons, underwater visual census techniques are now widely used for comparing the relative abundances of a fish species that occurs in different habitats at different stages in its life cycle (*e.g.* Gillanders, 1997; Jenkins & Wheatley, 1998; Nagelkerken *et al.*, 2000). Moreover, these techniques have a great

advantage in that they do not involve killing fish and do not result in damage to the habitat (English *et al.*, 1997; Watson & Quinn, 1997).

The western yellowfin bream *Acanthopagrus latus* and the various tuskfish species (*Choerodon* spp.) are known to occupy areas on and around reefs (Allen, 1999). This has been shown to apply to the baldchin groper *Choerodon rubescens* in both the protected and unprotected fishing areas of the Abrolhos Islands (Nardi, 1999). However, the juveniles of many reef species are found in environments, such as seagrass beds and mangroves, that provide protection from predators and a reliable source of food (Pollard, 1984; Gillanders, 1997; Cocheret de la Morinière *et al.*, 2003). For example, seagrass beds are occupied by substantial numbers of small blackspot tuskfish, *Choerodon schoenleinii*, in Japan (Kanashiro, 1998) and by juveniles of the bluespotted tuskfish, *Choerodon cauteroma*, in Shark Bay (Travers and Potter, 2002). *Acanthopagrus latus* is found in mangroves in the Dampier region of north-western Australia (Blaber *et al.*, 1985). However, none of the above studies made any attempt to compare the relative abundances of these species in different habitats at different stages of their life cycle.

The diverse range of habitats present in Shark Bay include bare sand, seagrass, mangroves, intertidal rocky areas, rocky reefs and coral areas (Marsh, 1990; Anon., 1996). Although some areas of Shark Bay have been declared no-take sanctuary zones by the Department of Conservation and Land Management (CALM) (Anon., 1996), that authority had to make those designations in the absence of sound quantitative data on the types of habitat occupied by the most important species in that large marine embayment. Reliable information on which habitats are important during the life cycles of *A. latus*, *C. rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* is crucial for the development of appropriate management plans for the fisheries of these important species in Shark Bay. The main aims of this component of the FRDC project were to determine the following:

(1) The broad distribution of the western yellowfin bream and each of the above four species of tuskfish within Shark Bay. Since a fifth tuskfish species, *Choerodon cephalotes*, occurs in Shark Bay, data were also collected on its distribution in this embayment.

(2) The type of habitats occupied in Shark Bay by the different stages in the life cycle of the above sparid and five species of labrid.

7.2 MATERIALS AND METHODS

7.2.1 *Visual survey regime*

Underwater visual surveys were conducted using a 50 × 5 m transect (English *et al.*, 1997). Transects were laid out using a 50 m long rope, which was unraveled as the diver swam, thereby minimising the likelihood of disturbing fish prior to counting. The list of habitat types and water depths at each of the eight sampling sites (A-H in **Figure 1.1**), the number of times each site was sampled, including the number of replicates, and the location of each site within Shark Bay are given in **Table 7.1**.

The transects over bare sand and seagrass (*Posidonia australis*) at site A and over reefs at sites B, G and H were laid out approximately parallel to each other and at least 20 m apart. However, because of the narrowness of the rocky shoreline habitats at sites A, C and D and the reef habitats at sites A, E and F, the transects were laid out longitudinally, with the opposing ends of successive transects being separated by at least 10 m. The same diver conducted all surveys to ensure consistency. All of the individuals of the western yellowfin bream and each of the five tuskfish species that were observed were counted and the individuals of each species separated by eye into juvenile and adult length classes based on the following criteria:

(1) Since western yellowfin bream first become males, and thus begin to mature for the first time at *ca* 200 mm (see Chapter 3.3), the individuals of this species were separated into those less than (juveniles) and greater than (adults) this length.

(2) The individuals of *Choerodon rubescens*, *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* were separated into those less than (juveniles) and greater than (adults) the length at which they mature, *i.e. ca* 300, 250, 150 and 200 mm, respectively (see Chapter 5.3).

(3) Since few *C. cephalotes* were caught, it was not possible to determine a length at maturity using logistic regression analysis. However, analysis of the gonads of the females of this species demonstrated that, in certain months, some of these females contained ovaries at stages III, IV and VIII (see **Table 2.2**) and these fish were all ≥ 130 mm. Thus, the individuals of this species were separated into two categories based on a conservative estimate of their length at maturity, *i.e.* < (juveniles) or ≥ (adults) 150 mm.

Table 7.1 Location, site, habitat type, depth, number of sampling occasions (seasons) and number of replicates employed for the visual surveys in Shark Bay. Locations and sites are illustrated in Figure 1.1.

Location	Site	Habitat type	Depth (m)	No. of sampling occasions	No. of replicates/ sampling occasion
Inner gulfs	A	Reef (1)	1-3	8	4
		Reef (2)	2-4	4	4
		Rocky shoreline	<2	4	3
		Sand	2-3	4	4
		Seagrass (1)	5-6	4	4
		Seagrass (2)	5-6	4	4
	B	Reef	1-3	5	4
	C	Rocky shoreline	<1	5	4
	D	Rocky shoreline	<1	5	4
	E	Reef	1-2	5	4
South Passage (oceanic reefs)	F	Reef	2-5	5	4
	G	Reef	1-2	5	6
	H	Reef	8-12	5	4

7.2.2 *Analyses*

Where necessary, a Student's t-test or one-way ANOVA was used to determine whether the densities of a particular fish species differed between habitat types. The results of the plots of the natural logarithms of the standard deviation against the natural logarithms of the mean for the densities of each species at each site on each sampling occasion demonstrated that, prior to subjection to ANOVA, these densities required square root transformation.

The mean densities of the two size groups of the various fish species at each site on each sampling occasion were subjected to non-metric multidimensional scaling (MDS) using the PRIMER v 5.5 package (Clarke & Gorley, 2001). Prior to ordination, the densities were square root transformed and a similarity matrix was then constructed using the Bray-Curtis similarity coefficient. One-way analysis of similarities (ANOSIM) was used to test whether the species composition (using firstly pooled data for all size classes and then separated by size class) in each habitat type in which fish were observed (rocky shorelines, seagrass, inner gulf reefs and

"oceanic" reefs) were significantly different (Clarke, 1993). Similarity percentages (SIMPER) were used to determine which species typified the samples observed in each habitat type (Clarke, 1993). Multivariate dispersion (MVDISP) was employed to ascertain the degree to which the samples in the different habitat types were dispersed on the ordination plot (Somerfield & Clarke, 1997). In the case of the ordination plot for each species, circles of varying magnitude have been superimposed on the points for the samples for the sites in which that species was observed in order to illustrate the relative densities of both the juveniles and the adults at those sites.

7.3 RESULTS

7.3.1 *Water temperatures and salinities*

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 **(Figure 7.1)**. Although mean monthly water temperatures followed a similar trend in South Passage, it was not as pronounced as those for the inner gulfs of Shark Bay, with temperatures at the former area ranging from a minimum of 21.1°C to a maximum of 24.9°C in early spring and late summer, respectively **(Figure 7.1)**.

Mean monthly salinities in the eastern and western gulfs ranged from 38.5 to 41.5‰ and from 36.4 to 42.1‰, respectively **(Figure 7.1)**. Mean salinity in the waters of South Passage lay between 33.6 and 34.8‰ in all months except August, when it was 37.3‰, and thus, in any month, it was always less than those in either of the gulfs **(Figure 7.1)**.

7.3.2 *Overall distribution of each species in Shark Bay*

The catches obtained from various habitats by extensive trawling (Travers & Potter, 2002), seine netting (Pember, 1999; King, 2003) and rod and line angling during the present study (see

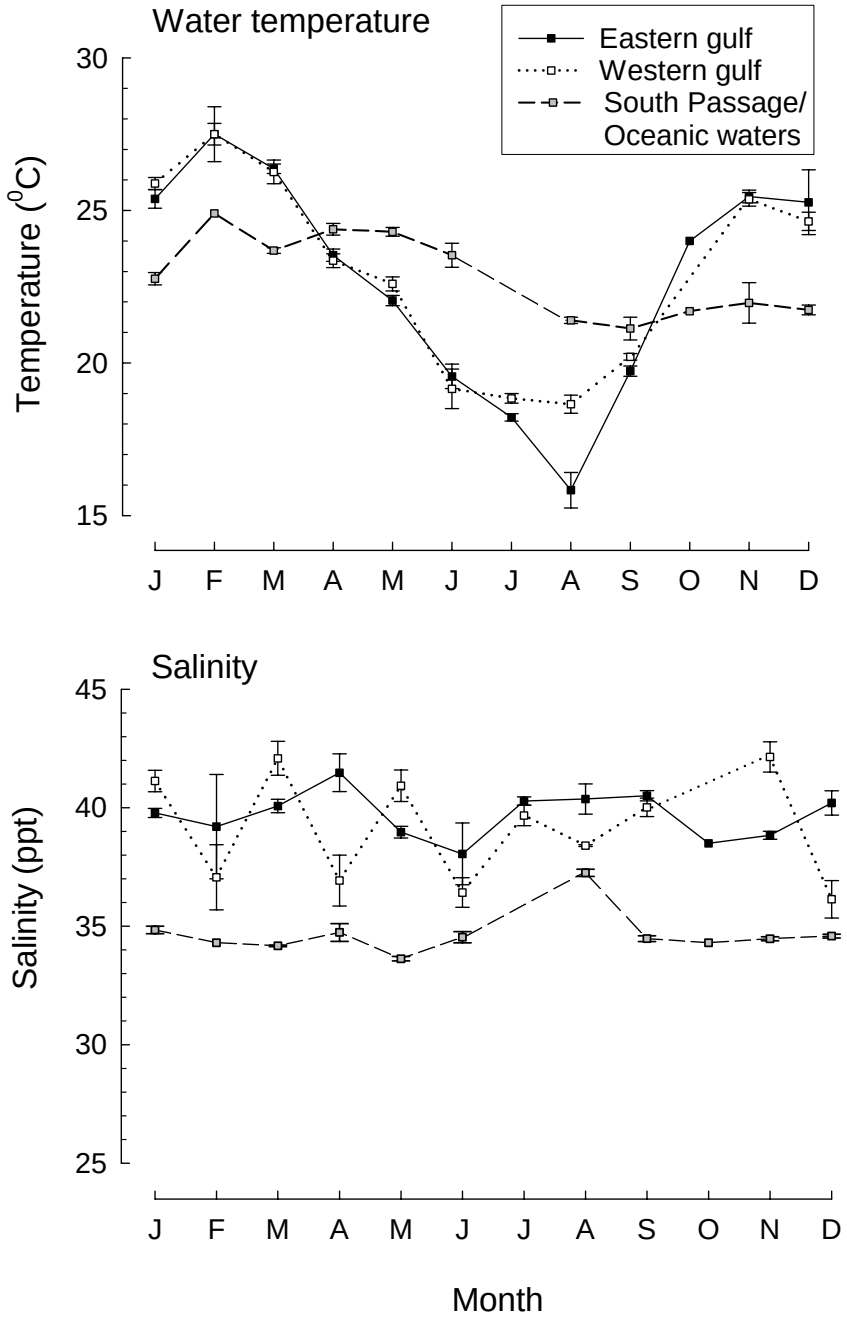

Figure 7.1. Mean monthly water temperatures and salinities recorded at all sites sampled on each sampling occasion in the eastern and western gulfs of Shark Bay, and in South Passage and the oceanic waters sampled along the western boundary of Shark Bay. Data for each month of the year are pooled from 2000 to 2003.

earlier chapters) were considered in conjunction with data from underwater visual surveys in the eastern and western gulfs and in the more "oceanic" waters of Shark Bay, *i.e.* South Passage. These comparisons provide overwhelming evidence that *A. latus*, *C. schoenleinii*, *C. cyanodus*, *C. cauteroma* and *C. cephalotes* live mainly in the inner gulfs, whereas *C. rubescens* lives in "oceanic" regions. Indeed, the last species was collected or observed during visual surveys only in South Passage and in regions along the west coast of Dirk Hartog Island and around Bernier and Dorre Islands in the very northern part of Shark Bay **(Figure 1.1)**.

None of the six species were observed over bare sand. *Acanthopagrus latus* was recorded predominantly over rocky substrates along shorelines, *C. schoenleinii* mainly over inner gulf reefs and *C. cephalotes* almost exclusively over seagrass, and *C. rubescens* was observed only on oceanic reefs **(Figure 7.2)**. In contrast, substantial numbers of *C. cyanodus* were observed along rocky shorelines and over inner gulf reefs, while appreciable numbers of *C. cauteroma* were recorded not only in both of these habitat types, but also, in particular, over seagrass.

The mean density of *A. latus* was far greater along rocky shorelines, *i.e.* 11.2 fish $100m^{-2}$, than over inner gulf reefs, *i.e.* 0.6 fish $100m^{-2}$, and that of *C. rubescens* over oceanic reefs was 1.5 fish $100m^{-2}$ **(Figure 7.2)**. Although a few *C. schoenleinii* were observed on rocky shorelines (0.5 fish $100m^{-2}$), the mean density of this species was significantly greater on inner gulf reefs (2.8 fish $100m^{-2}$; $p < 0.05$; **Figure 7.2**). The mean densities of *C. cyanodus* along rocky shorelines (1.1 fish $100m^{-2}$) and on inner gulf reefs (0.7 fish $100m^{-2}$), which were not significantly different ($p > 0.05$), were both significantly greater than over seagrass (0.2 fish $100m^{-2}$; $p < 0.05$). The mean densities of *C. cauteroma* in each of the four habitats were significantly different. The densities of this species were greatest in seagrass (3.5 fish $100m^{-2}$)

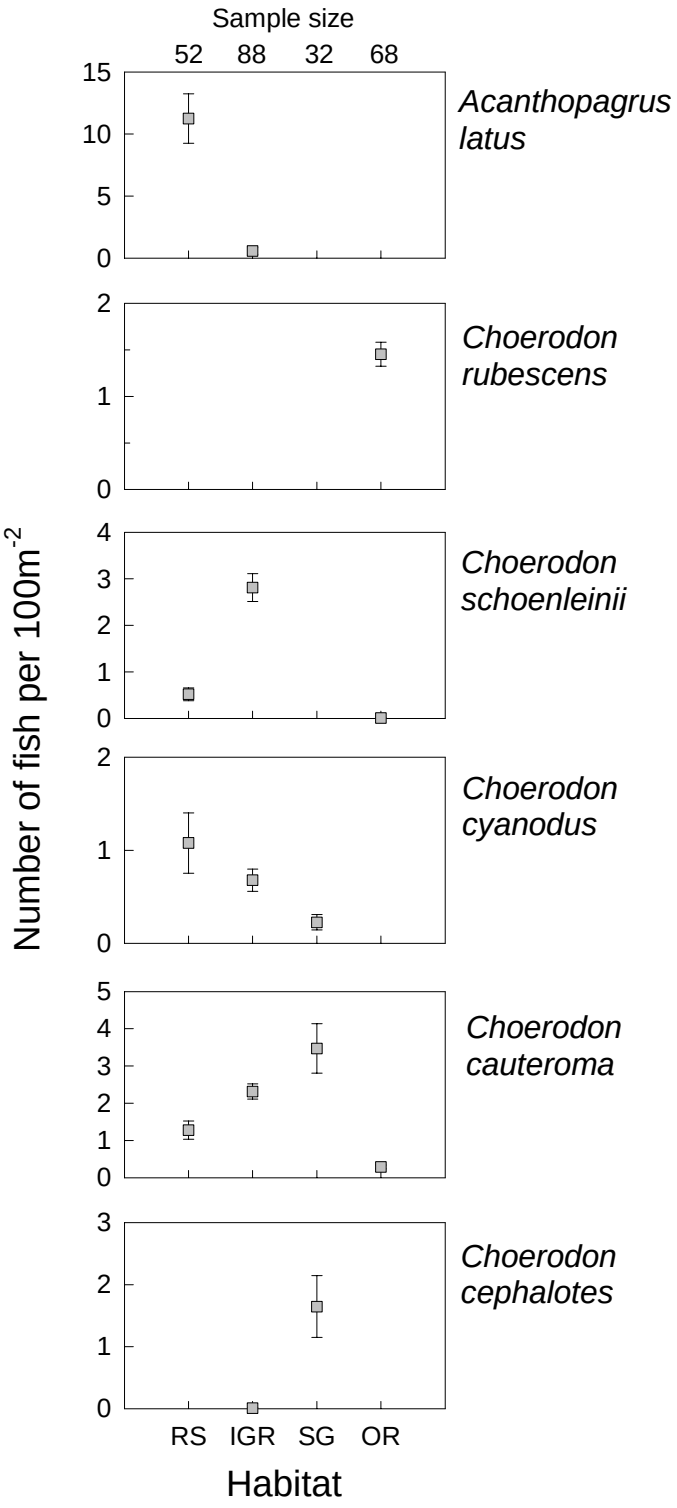

Figure 7.2. Mean density ± 1 SE of *Acanthopagrus latus*, *Choerodon rubescens*, *Choerodon schoenleinii*, *Choerodon cyanodus*, *Choerodon cauteroma* and *Choerodon cephalotes* over rocky shorelines (RS), inner gulf reefs (IGR), seagrass (SG) and oceanic reefs (OR) during underwater visual surveys. Sample size equals total number of replicate transects conducted over each habitat.

and on inner gulf reefs (2.3 fish $100m^{-2}$). The density of *C. cephalotes* on seagrass was 1.6 fish $100m^{-2}$ **(Figure 7.2)**.

Following MDS ordination of the mean densities determined from the pooled data for all size classes of western yellowfin bream and each of the five tuskfish species at each site on each sampling occasion, the samples for both inner gulf and "oceanic" reefs and over seagrass formed groups that exhibited no overlap **(Figure 7.3)**. Furthermore, the majority of the samples for rocky shorelines constituted a distinct group on the left-hand side of the plot **(Figure 7.3)**. The results of MVDISP demonstrated that the points for the samples for rocky shorelines were more widely dispersed (1.497) than for the inner gulf reefs (0.958), oceanic reefs (0.642) or seagrass (1.076).

ANOSIM demonstrated that the species composition differed significantly among rocky shoreline, seagrass, inner gulf reef and oceanic reef habitats (p = 0.1%; Global R statistic = 0.766). Pairwise comparisons showed that 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). The R statistic values ranged from 0.440 and 0.473 for the faunas along rocky shorelines *vs* seagrass and inner gulf reefs to 0.997 both for "oceanic" reefs *vs* inner gulf reefs and seagrass. SIMPER demonstrated that *A. latus* typified the species composition of the rocky shorelines, while *C. cauteroma* and *C. cephalotes* typified seagrass, *C. schoenleinii* and *C. cauteroma* typified the inner gulf reefs and *C. rubescens* typified oceanic reefs.

7.3.3 *Relationships between life cycle stages and habitat type*

Following MDS ordination of the mean densities of the juveniles and adults of *A. latus* in the different habitats, the samples of the juveniles on the ordination plot were located well above and/or to the left of those of the adults of this species **(Figure 7.4a)**. The rocky shoreline habitats that were occupied mainly by juveniles did not have any mangroves nearby, whereas

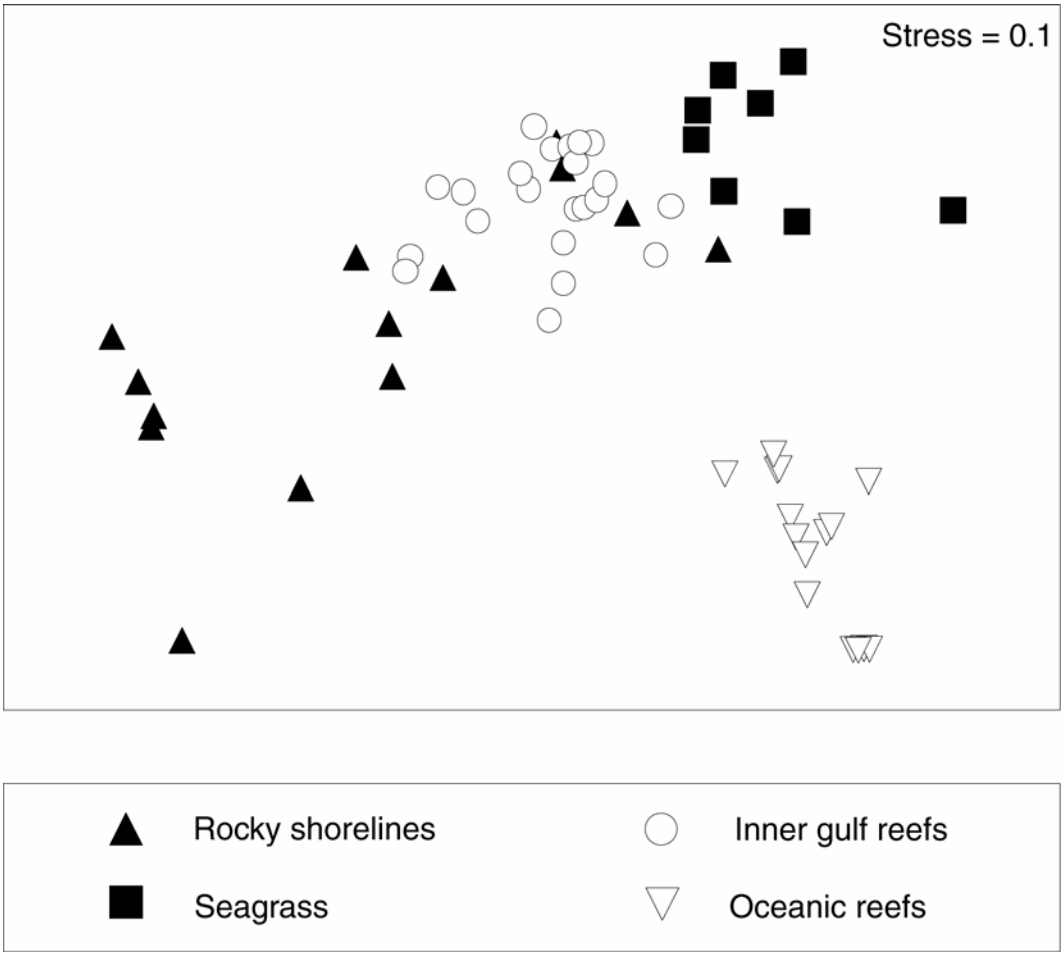

Figure 7.3. Non-metric multidimensional scaling ordination of the mean densities of the western yellowfin bream and five tuskfish species on rocky shorelines, inner gulf reefs, seagrass and oceanic reefs on each sampling occasion.

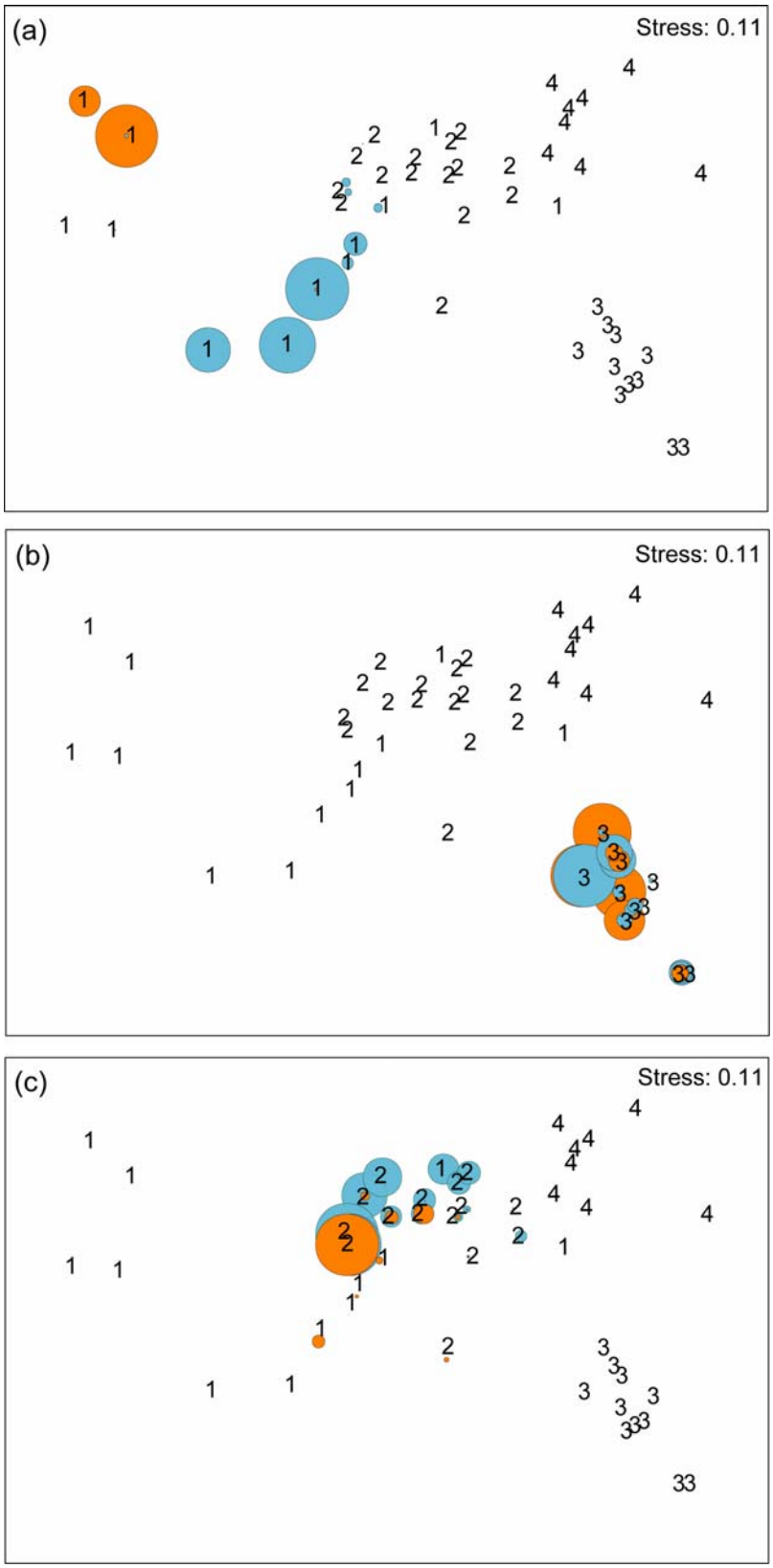

Figure 7.4. Non-metric multidimensional scaling of the mean densities, indicated by the magnitude of the size of the circles, of the juveniles (orange) and adults (blue) of (a) *Acanthopagrus latus*, (b) *Choerodon rubescens* and (c) *Choerodon schoenleinii* on rocky shorelines (1), inner gulf reefs (2), oceanic reefs (3) and seagrass (4).

the rocky shoreline where adults were found did contain areas nearby in which there were mangroves. SIMPER demonstrated that the adults of this species typified this habitat. Juveniles and/or adults of *C. rubescens* were observed at all of the oceanic reef sites and at no other site **(Figure 7.4b)**, as is also demonstrated by the data shown in **Figure 7.2**. Juveniles and/or adults of *C. schoenleinii* were found at the majority of the inner gulf reefs and very occasionally along rocky shorelines, but almost invariably in very reduced numbers **(Figure 7.4c)**. As with *C. schoenleinii*, neither the adults nor juveniles of *C. cyanodus* showed any obvious tendency to occupy predominantly either the rocky shorelines or inner gulf reefs, the two habitats at which all but a very few of this species were observed **(Figure 7.5a)**. The vast majority of the juveniles of *C. cauteroma* were observed in seagrass, whereas the adults of this species were found predominantly either on inner gulf reefs or along rocky shorelines. *Choerodon cauteroma* was the only species other than *C. rubescens* that was observed on oceanic reefs and all of those individuals were adults **(Figure 7.5b)**. Juvenile and/or adult *C. cephalotes* were recorded at most of the seagrass sites **(Figure 7.5c)**.

7.4 DISCUSSION

7.4.1 *Distribution of species within Shark Bay*

The broad distributions determined for *A. latus*, *C. rubescens*, *C. schoenleinii*, *C. cyanodus*, *C. cauteroma* and *C. cephalotes* in the western and eastern gulfs of Shark Bay and in South Passage by using visual surveys are consistent with the locations where these species have been caught during previous studies by trawling and seine netting (Pember, 1999; Travers & Potter, 2002) and during the present study by line fishing. Thus, *C. rubescens* was the only one of the above species that was never collected from the many sites in the inner gulfs that were sampled and subjected to visual census in Shark Bay. Furthermore, this species was the only one that

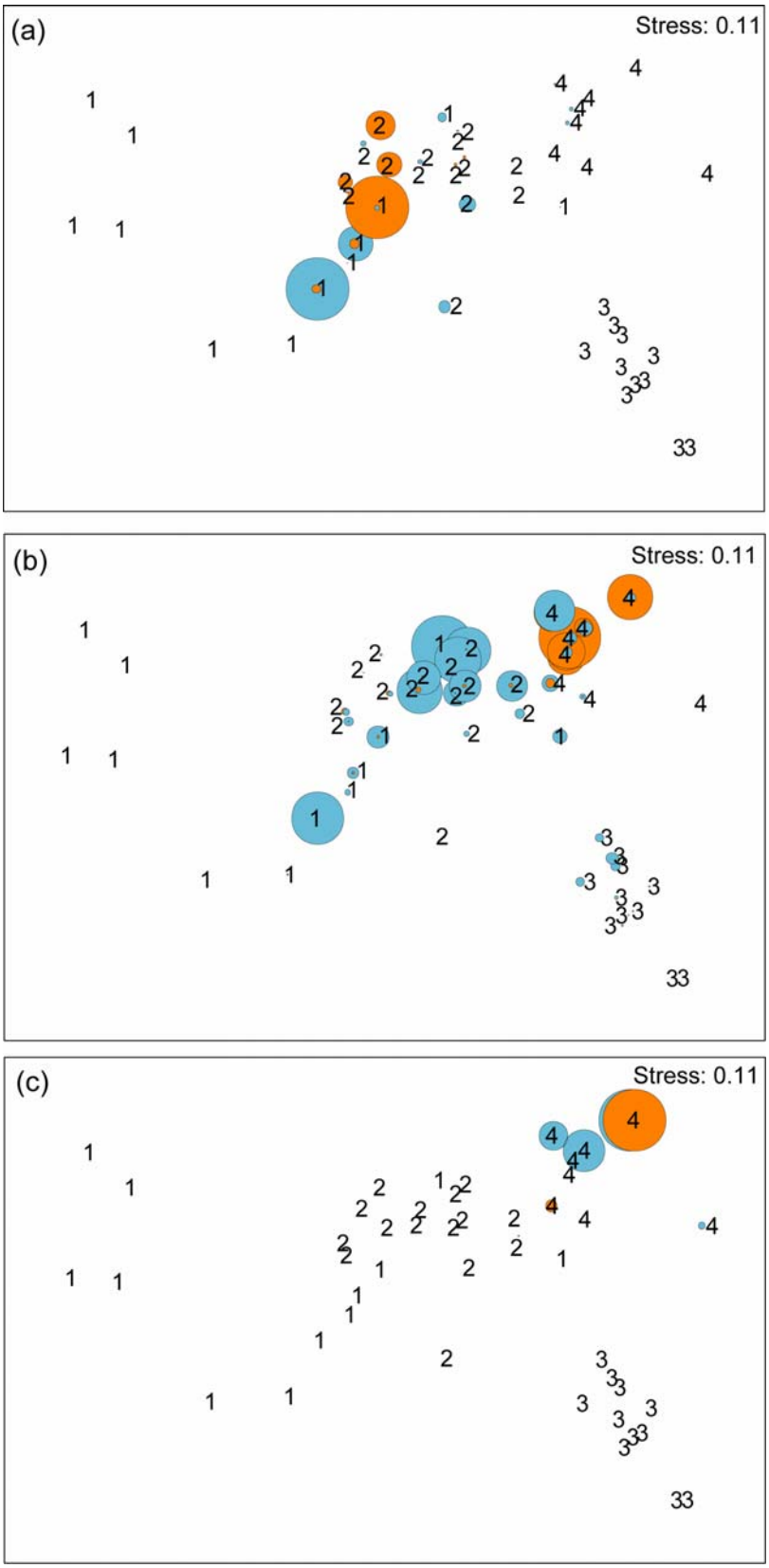

Figure 7.5. Non-metric multidimensional scaling of the mean densities, indicated by the magnitude of the size of the circles, of the juveniles (orange) and adults (blue) of (a) *Choerodon cyanodus*, (b) *Choerodon cauteroma* and (c) *Choerodon cephalotes* on rocky shorelines (1), inner gulf reefs (2), oceanic reefs (3) and seagrass (4).

was abundant in South Passage and along the western coastlines of Dirk Hartog, Bernier and Dorre Islands (Hutchins, 1990; Hutchins *et al.*, 1995 **(Figure 1.1)**. It thus appears highly relevant that the distribution of *C. rubescens* is confined to areas that are exposed directly to the waters of the Indian Ocean (**Figure 1.1**; Burling *et al*., 2003; Hutchins *et al.*, 1995; Logan & Cebulski, 1970).

Although *A. latus*, *C. schoenleinii*, *C. cyanodus*, *C. cauteroma* and *C. cephalotes* each occur in the waters of both the western and eastern gulfs of Shark Bay, the different types of habitat found in those waters are partitioned to a substantial degree amongst those species. Thus, *A. latus* is found predominantly along rocky shorelines and in mangrove habitats, whereas *C. schoenleinii* occurs mainly over inner gulf reefs and *C. cephalotes* lives predominantly in seagrass. In contrast, *C. cyanodus* is relatively abundant in two habitat types, *i.e.* along rocky shorelines and over inner gulf reefs, and *C. cauteroma* occurs in reasonable numbers in both of these habitat types and in even greater numbers in seagrass.

7.4.2 *Distributions of juveniles and adults of the different species*

Despite the large areas of bare sand in Shark Bay, neither *A. latus* nor any of the five tuskfish species were observed in these unvegetated areas. *Choerodon cauteroma* was the only species of tuskfish in which their juveniles and adults showed a pronounced tendency to occupy a different type of habitat. Thus, the juveniles of this species were found almost exclusively in seagrass, whereas the adults occurred predominantly on inner gulf reefs and along rocky shorelines. The results of the visual census for the juveniles of *C. cauteroma* are entirely consistent with the fact that the numbers of this species that were caught in seagrass during trawling were sufficiently high to rank this species ninth among 83 species in terms of abundance (Travers & Potter, 2002). The use by *C. cauteroma* of seagrass predominantly as a nursery area parallels the situation with a number of other species that spend the adult part of

their life over reefs, including another labrid, *i.e. Achoerodus viridis* (Gillanders *et al.*, 1997, 2003; Guidetti, 2000; Nagelkerken *et al.*, 2001).

Although essentially all of the juvenile *A. latus* caught during our study (see **Figure 4.3**) and in a previous study in Shark Bay by King (2003) were obtained by seine netting in mangrove areas, visual surveys demonstrated that juveniles of this species also occur along rocky shorelines. Note that visual surveys were not conducted in mangrove areas (see section 7.2.1). The points that represent the juveniles and adults of *A. latus* on the ordination plot (**Figure 7.4)** were clearly separated. The separation between these points are most likely due to the fact that juvenile *A. latus* were only observed during visual surveys that were conducted at rocky shoreline sites where there were no mangroves nearby. The absence of the juveniles of *A. latus* from those sites is thus almost certainly due to the fact that mangroves are a "preferred" habitat for young western yellowfin bream. Furthermore, large numbers of juvenile *A. latus* were caught by Blaber *et al.* (1985) in mangroves in the Dampier region of north-western Australia.

Choerodon schoenleinii was not found on the seagrass beds that were surveyed visually during the present study, which is consistent with the results of extensive trawling in seagrass meadows in Shark Bay (Travers and Potter, 2002). However, this contrasts with the situation recorded in Japanese waters by Kanashiro (1998), who found substantial numbers of the larvae and small individuals (<130 mm) of this species in seagrass. The larger individuals of *C. schoenleinii* were found over reefs in those latter waters (Ebisawa *et al.*, 1995). It is thus concluded that, in contrast to the situation in Japanese waters, this species spends at least the vast majority of its life over reefs in Shark Bay.

8.0 REFERENCES

Abol-Munafi, A. B. & Umeda, S. 1994. The gonadal cycle of the yellowfin porgy, *Acanthopagrus latus* (Houttuyn) reared in the net cage at Tosa Bay, Japan. Suisanzoshoku **42**: 135-144.

Abou-Seedo, F. S., Dadzie, S. & Al-Kanaan, K. A. (2003). Sexuality, sex change and maturation patterns in the yellowfin seabream, *Acanthopagrus latus* (Teleostei: Sparidae) (Houttuyn, 1982). J. App. Ichthyol. **19**: 65-73.

Abu-Hakima, R. 1984. Some aspects of the reproductive biology of *Acanthopagrus* spp. (Family:Sparidae). J. Fish Biol. **25**: 515-526.

Agardy, T. 2000. Information needs for marine protected areas: scientific and societal. Bull. Mar. Sci. **66**: 875-888.

Allen, G. 1999. *Marine fishes of tropical Australia and south-east Asia: A field guide for anglers and divers.* Western Australian Museum, Perth, Australia.

Allsop, D. J. & West, S. A. 2003. Constant relative age and size at sex change for sequentially hermaphroditic fish. J. Evol. Biol. **16**: 921-929.

Andrew, T. G., Buxton, C. D. & Hecht, T. 1996. Aspects of the reproductive biology of the concha wrasse, *Nelabrichthys ornatus*, at Tristan da Cunha. Env. Biol. Fish. **46**: 139-149.

Anon. 1996. *Shark Bay Marine Reserves Management Plan (1996-2000).* Department of Conservation and Land Management, Perth.

Bannerot, S., Fox Jr., W. W. & Powers, J. E. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and the Carribean. pp. 561-603. *In* J. J. Polovina & S. Ralston (eds). *Tropical snappers and groupers, biology and fisheries management*. Westview Press, Boulder.

Bayes, T. 1763. An essay toward solving a problem in the doctrine of chances. Phil. Trans. Roy. Soc. Lond. **53**: 370-418; reprinted in 1958 in Biometrika **45**: 293-315.

Beamish, R. J. & McFarlane, G. A. 1983. The forgotten requirements for age validation in fisheries biology. Trans. Am. Fish. Soc. **112**: 735-743.

Bentivegna, F. & Rasotto, M. B. 1987. Protogynous hermpahroditism in *Xyrichthys novacula* (L.1758). Cybium **11**:75-78.

Besseau, L. & Bruslé-Sicard, S. 1995. Plasticity of gonad development in hermaphroditic sparids: ovotestis ontogeny in a protandric species, *Lithognathus mormyrus*. Env. Biol. Fish. **43**: 255-267.

Blaber, S. J. M., Young, J. W. & Dunning, M. C. 1985. Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of north-western Australia. Aust. J. Mar. Freshwat. Res. **36**: 247-266.

Bohnsack, J. A. 1998. Application of marine reserves to reef fisheries management. Aust. J. Ecol. **23**: 298-304.

Burling, M. C., Pattiaratchi, C. B. & Ivey, G. N. 2003. The tidal regime of Shark Bay, Western Australia. Est. Coast. Shelf Sci. **57**: 725-735.

Burton, M. L. 2001. Age, growth and mortality of gray snapper, *Lutjanus griseus*, from the east coast of Florida. Fish. Bull. **99**: 254-265.

Buxton, C. D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. Fish. Res. **15**: 1-16.

Buxton, C. D. & Garratt, P. A. 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). Env. Biol. Fish. **28**: 113-124.

Campana, S. E. 2001. Review paper. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**: 197-242.

Cardinale, M., Colloca, F. & Ardizzone, G. D. 1998. Growth and reproduction of *Xyrichtys novacula* (Pisces: Labridae) in the Mediterranean Sea. Scientia Marina, **62**: 193-201.

Chang, C.-W., Hsu, C.-C., Wang, Y.-T. & Tzeng, W.-N. 2002. Early life history of *Acanthopagrus latus* and *A. schlegeli* (Sparidae) on the western coast of Taiwan: temporal and spatial partitioning of recruitment. Mar. Freshwater Res. **53**: 411-417.

Choat, J. H. 1969. *Studies on the biology of labroid fishes (Labridae and Scaridae) at Heron Island, Great Barrier Reef.* PhD thesis, University of Queensland.

Choat, J. H. & Robertson, D. R. 2002. Age-based studies. pp. 57-80 *In*. Coral Reef Fishes. Dynamics and diversity in a complex ecosystem. P. F. Sale (ed.). Academic Press, San Diego.

Clarke K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. **18**:117-143.

Clarke, K. R. & Gorley, R. N. 2001. *Primer v5.5: User Manual/Tutorial.* Primer-E, Plymouth.

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., Hemminga, M. A., Huiskes, A. H. L. & van der Velde, G. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. Mar. Ecol. Prog. Ser. **246**: 279-289.

Coleman, F. C., C. C. Koenig, A. M. Eklund, & C. Grimes. 1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. pp. 233-242 *In*. Life in the slow lane: ecology and conservation of long-lived marine animals. J. A. Musick (ed.). Am. Fish. Soc. Symp. **23**.

Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. J. Fish Biol. **41**: 161-178.

Cubillos, L. A., Alarcón, R. & Brante, A. 1999. Empirical estimates of natural mortality for the Chilean hake (*Merluccius gayi*): evaluation of precision. Fish. Res. **42**: 147-153.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. **26**: 249-293.

D'Ancona, U. 1949. Ermafroditismo ed intersessualita nei Telestei. Exper. **5**: 381-389.

Darwall, W. R. T., Costello, M. J., Donnelly, R. & Lysaght, S. 1992. Implications of life-history strategies for a new wrasse fishery. J. Fish Biol. **41** (Supplement B): 111-123.

Deriso, R. B., Quinn II, T. J. & Neal, P. R. 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. **42**: 815-824.

de Vlaming, V. L. 1983. Oocyte development patterns and hormonal involvements among teleosts. pp. 176-199. *In:* J. C. Rankin, T. J. Pitcher & R. T. Duggan (eds) Control processes in fish physiology, Croom Helm, Beckenham.

Donaldson, T. J. & Sadovy, Y. 2001. Threatened fishes of the world: *Cheilinus undulatus* Rüppell, 1835 (Labridae). Env. Biol. Fish. **62**: 428.

Ebisawa, A., Kanashiro, K. Kyan, T. & Motonaga, F. 1995. Aspects of reproduction and sexuality in the black-spot tuskfish, *Choerodon schoenleinii*. Japan. J. Ichthyol. **42(2)**: 121-130.

English, S., Wilkinson, C. & Baker, V. (eds). 1997. *Survey manual for tropical marine resources*. Australian Institute of Marine Science, Townsville.

Fairclough, D. V., Dimmlich, W. F. & Potter, I. C. 2000. Length and age compositions and growth rates of the Australian herring *Arripis georgiana* in different regions. Mar. Freshw. Res. **51**: 631-40.

Farley, J. H. & Davis, T. L. O. 1998. Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*. Fish. Bull. **96**: 223-236.

Fisheries Department of Western Australia. 1996. *Shark Bay World Heritage Property. Management Paper for Fish Resources.* Fisheries Management Paper No. 91.

Fisheries Western Australia. 1998. *Management of the Houtman Abrolhos System*. Fisheries Management Paper No. 117.

Fisheries Western Australia. 1999. *A quality future for recreational fishing in the Gascoyne*. Fisheries Management Paper No 124.

Fournier, D. A. 1994. AUTODIF, A C++ array language extension with automatic differentiation for use in nonlinear modelling and statistics. Otter Research Ltd. Sidney, Canada.

Francesconi, K. & Clayton, D. 1996. Shark Bay World Heritage Property. Management paper for fish resources. Fisheries Management Paper No. 91. Fisheries Department of Western Australia. Perth.

Gillanders, B. M. 1995. Reproductive biology of the protogynous hermaphrodite *Achoerodus viridus* (Labridae) from south-eastern Australia. Mar. Freshwater. Res. **46**: 999-1008.

Gillanders, B.M. 1997. Patterns of abundance and size structure in the blue groper, *Achoerodus viridis* (Pisces, Labridae): evidence of links between estuaries and coastal reefs. *Environmental Biology of Fishes* **49**: 153-173.

Gillanders, B. M., Able, K. W., Brown, J. A., Eggleston, D. B. & Sheridan, P. F. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser. **247**: 281-295.

Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management. Foundation and current use. Can. Spec. Publ. Fish. Aquat. Sci. **120**: 67-81.

Grant, E. 1993. *Grant's guide to fishes.* E. M. Grant. Scarborough, Queensland. Australia.

Guidetti, P. 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic sea. Est. Coast. Shelf Sci. **50**: 515-529.

Gunderson, D. R., Zimmermann, M., Nichol, D. G. & Pearson, K. 2003. Indirect estimates of natural mortality rate for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*). Fish. Bull. **101**:175-182.

Halpern, B.S. & Warner, R.R. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**: 361-366.

Hesp, S. A. 2003. *Biology of two species of sparid on the west coast of Australia*. PhD Thesis. Murdoch University. Western Australia.

Hesp, S. A. & Potter, I. C. 2003. Reproductive biology of the tarwhine *Rhabdosargus sarba* (Sparidae) in three different environments on the west coast of Australia. J. Mar. Biol. Ass. U.K. **83**:1333-1346.

Hesp, S. A., Potter, I. C. & Hall, N. G. 2002. Age and size compositions, growth rate, reproductive biology and habitats of the West Australian Dhufish, *Glaucosoma*

hebraicum, and their relevance to the management of this species. Fish. Bull. **100**: 214-227.

Hilborn, R. & Walters C. J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hoenig, J. M. 1982. A compilation of mortality and longevity estimates for fish, molluscs, and cetaceans, with a bibliography of comparative life history studies. GSO Technical Report Reference No. 82-2.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. **82**: 898-903.

Hoffman, S. G. 1985. Effects of size and sex on the social organization of reef-associated hogfishes, *Bodianus* spp. Env. Biol. Fish. **14**: 185-197.

Hunter, J.R. & Macewicz, B.J. 1985. Measurement of spawning frequency in multiple spawning fishes. pp 67-78. *In* An egg production method for estimating spawning biomass of pelagic fish. Application to the northern anchovy, *Engraulis mordax*. R. Lasker (ed.). NOAA Tech. Rep. NMFS 36.

Hunter, J. R., Lo, N. C. H. & Leong, R. J. H. 1985. Batch fecundity in multiple spawning fishes. pp. 79-94. *In:* R. Lasker (ed.). An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy (*Engraulis mordax*), U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., Macewicz, B. J. & Sibert, J. R. 1986. The spawning frequency of skipjack tuna *Katsuwonus pelamis*, from the South Pacific. Fish. Bull. **84**: 895-903.

Hunter, J. R., B. J. Macewicz, L. N. Chyan-huei, and C. A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. **99**: 101-128.

Hussain, N. A. & Abdullah, M. A. S. 1977. The length-weight relationship, spawning season and food habits of six commercial fishes in Kuwait waters. Indian J. Fish. **24**: 181-194.

Hutchins, J. B. 1990. Fish Survey of South Passage, Shark Bay, Western Australia. In *Research in Shark Bay. Report of the France-Australe Bicentenary Expedition Committee*. P.F. Berry, S.D. Bradshaw and B.R. Wilson (Eds). Western Australian Museum, Perth. Pp 263-278.

Hutchins, J. B. 1991. Dispersal of tropical fishes to temperate seas in the southern hemisphere. *Journal of the Royal Society of Western Australia* **74**, 79-84.

Hutchins, J. B., Slacksmith, S. M., Marsh, L. M., Jones, D. S., Bryce, C. W., Hewitt, M. A. & Hill, A. 1995. *Marine Biological Survey of Bernier and Dorre Islands, Shark Bay.*

Unpublished report prepared for the Ocean Rescue 2000 Program. Western Australian Museum and Western Australian Department of Conservation and Land Management, Perth.

Hyndes, G. A., Loneragan, N. R. & Potter, I. C. 1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. Fish. Bull. **90**: 276-284.

Hyndes, G. A., Potter, I. C. & Hesp, S. A. 1996. Relationships between the movements, growth, age structures and reproductive biology of the teleosts *Sillago burrus* and *S. vittata* in temperate marine waters. Mar. Biol. **126**: 549-558.

Hyndes, G. A., Platell, M. E., Potter, I. C. & Lenanton, R. C. J. 1998. Age composition, growth, reproductive biology, and recruitment of King George Whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia. Fish. Bull. **96**: 258-270.

Jenkins, G. P. & Wheatley, M. J. 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. J. Exp. Mar. Biol. Ecol. **221**: 147-172.

Jennings, S., Kaiser, M. J. & Reynolds, J. D. 2001. *Marine Fisheries Ecology*. Blackwell-Science, Oxford.

Jones, G. P. 1980. Growth and reproduction in the protogynous hermaphrodite *Pseudolabrus celidotus* (Pisces, Labridae) in New Zealand. Copeia **1980**: 660-675.

Kanashiro, K. 1998. Morphology, and changes of distribution and food habits with growth, of late larvae and juveniles of black-spot tuskfish, *Choerodon schoenleinii* (Labridae), settled on seagrass beds of Okinawa Island, the Ryukyus. Nippon Suisan Gakkaishi **64(3)**: 427-434.

Kobayashi, K. & Suzuki, K. 1990. Gonadogenesis and sex succession in the protogynous wrasse, *Cirrhilabrus temmincki*, in Suruga Bay, Central Japan. Japan J. Ichthyol. **37**: 256-264.

Karlou-Riga C. & Economidis, P. S. 1997. Spawning frequency and batch fecundity of horse mackerel, *Trachurus trachurus* (L.) in the Saronikos Gulf (Greece). J. App. Ichthyol. **6**: 20-25.

Kimura, D. K. 1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. **77**: 765-776.

King, J. 2003. The fish fauna of two mangrove systems in the Eastern Gulf of Shark Bay, Western Australia. Honours thesis. Murdoch University, Perth.

Kinoshita, Y. 1939. Studies on the sexuality of genus *Sparus* (Teleostei). Journal of Science. Hiroshima University Series B Division 1. Zoology **7**: 25-37.

Laevastu, T. 1965. Manual of methods in fisheries biology. FAO, Rome.

Lam, T. J. (1983). Environmental influences on gonadal activity in fish. pp. 65-116. *In.* Fish Physiology. Hoar, W. S. & D. J. Randall (eds). Academic Press. London.

Logan, B. W. & Cebulski, D. E. 1970. Sedimentary environments of Shark Bay, Western Australia. In Carbonate sedimentation and environments, Shark Bay, Western Australia. American Association of Petroleum Geologists, Memoirs **13**:1-37.

Mace, P. M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish and Fisheries **2**: 2-32.

Mace, P. M. & Sissenwine, M. P. 1993. How much spawning per recruit is enough? *In.* S. J. Smith, J. J. Hunt & D. Rivard (eds). pp. 101-118. Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. **120**: 101-118.

Macci, G. J. & Acha, E. M. 1999. Spawning frequency and batch fecundity of Brazilian menhaden, *Brevoortia aurea*, in the Río de la Plata estuary off Argentina and Uruguay. Fish. Bull. **98**: 283-289.

Marsh, L. M. (1989). Hermatypic corals of Shark Bay, Western Australia. pp. 115-128. *In.* Research In Shark Bay, Report of the Frances-Australe Bicentenary Expedition Committee. Berry, P. F., Bradshaw, S. D. & B. R. Wilson (eds). Western Australian Museum, Perth.

Milton, D. A., Die, D., Tenakanae, C. & Swales, S. 1998. Selectivity for barramundi (*Lates calcarifer*) in the Fly River, Papua New Guinea: implications for managing gill-net fisheries on protandrous fishes. Mar. Freshwat. Res. **49**: 499-506.

Nagelkerken, I., Kleijnen, S., Klop, T., van den Brand, R. A.C. J., Cocheret de la Morinière, E. and van der Velde, G. 2001. Mar. Ecol. Prog. Ser. **214**: 225-235.

Nagelkerken, I., van der Velde, G., Gorissen M. W., Meijer, G. J., van't Hof, T & den Hartog, C. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual survey technique. Est. Coast. Shelf Sci. **51**: 31-44.

Nakazono, A. & Kusen, J. D. 1991. Protogynous hermaphroditism in the wrasse *Choerodon azurio*. Nippon Suisan Gakkaishi **57(3)**: 417-420.

Nardi, K. 1999. *The life-history and the effect of protected areas on the baldchin groper (Pisces: Labridae) at the Houtman Abrolhos Islands, Western Australia*. MSc. Thesis, James Cook University, Townsville.

Nemtzov, S.C. 1985. Social control of sex change in the Red Sea razorfish *Xyrichtys pentadactylus* (Teleostei, Labridae). Env. Biol. Fish. **14**: 199-211.

Nichol, D. G. & Acuna, E. I. 2001. Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering sea. Fish. Bull. **99:** 108-122.

Partridge, G. J. & Jenkins, G. I. (2002). The effect of salinity on growth and survival of juvenile black bream (*Acanthopagrus butcheri*). Aquaculture **210**: 219-230.

Pascual, M. A. & Iribarne, O. O. 1993. How good are empirical predictions of natural mortality? Fish. Res. **16**: 17-24.

Pauly, D. 1980. On the interrelationships between *M*, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. int. Explor. Mer. **39**: 175-192.

Pember, M. B. 1999. Characteristics of the fish fauna of nearshore sandy habitats in Shark Bay, Western Australia. Honours thesis, Murdoch University, Perth.

Platten, J. R., Tibbets, I. R. & Sheaves, M. J. 2002. The influence of increased line-fishing mortality on the sex ratio and age of sex reversal of the venus tusk fish. J. Fish Biol. **60**: 301-318.

Policansky, D. 1982. Sex change in plants and animals. Ann. Rev. Ecol. Syst. **13**: 471-495.

Pollard, D.A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquat. Bot. **18**: 3-42.

Pollock, B. R. 1985. The reproductive cycle of yellowfin bream, *Acanthopagrus australis* (Günther), with particular reference to protandrous sex inversion. J. Fish Biol. **26**: 301-311.

Punt, A. E., Garratt, P. A. & Govender, A. 1993. On an approach for applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysoblephus puniceus* (Pisces: Sparidae). S. Afr. J. Mar. Sci. **13**: 109-119.

Ralston, S. 1987. Mortality rates of snappers and groupers. pp. 375-404. *In* Tropical snappers and groupers. Biology and fisheries management. J. J. Polovina & S. Ralston (eds). Westview Press, Colorado.

Reinboth, R. 1970. Intersexuality in fishes. *Memoirs of the Society for Endocrinology* **18**: 515-543.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. **191**: 382 pp.

Sadovy, Y. 1996. Reproduction of reef fishery species. pp. 15-59. *In.* Reef fisheries. N. V. C. Polunin C. & M. Roberts (eds). Chapman and Hall, London.

Sadovy, Y. & Shapiro, D. Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia **1987**: 136-156.

Samuel, M. & Mathews, C. P. 1987. Growth and mortality of four *Acanthopagrus* species. Kuwait Bull. Mar. Sci. 1987: 159-171.

Sarre, G. A. 1999. Hermaphroditism of *Acanthopagrus butcheri* in the Swan River Estuary (Chapter 6). *In:* Age composition, growth rates, reproductive biology and diets of the black bream *Acanthopagrus butcheri* in four estuaries and a coastal saline lake in south-western Australia. PhD thesis. Murdoch University, Western Australia.

Sarre, G. A. & Potter, I. C. 1999. Comparisons between the reproductive biology of black bream *Acanthopagrus butcheri* (Teleostei: Sparidae) in four estuaries with widely differing characteristics. Int. J. Salt Lake Res. **8**: 179-210.

Sarre, G. A. & Potter, I. C. 2000. Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors. Fish. Bull. **98**: 785-799.

Shapiro, D. Y. & Lubbock, R. 1980. Group sex ratio and sex reversal. J. Theor. Biol. **82**: 411-426.

Shapiro, D. Y. & Rasotto, M. B. 1993. Sex differentiation and gonadal development in the diandric, protogynous wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). J. Zool. Lond. **230**: 231-245.

Shaw, J. 2000. Fisheries environmental management review. Gascoyne. Fisheries Environmental Management Review No. 1, Department of Fisheries, Western Australia.

Sakai, Y. & Kohda, M. 2001. Spawning timing of the cleaner wrasse, *Labroides dimidiatus,* on a warm temperate rocky shore. Ichthyol. Res. **48**:23-30.

Sakai, Y., Kohda, M. and Kuwamura, T. 2001. Effect of changing harem on timing of sex change in female cleaner fish *Labroides dimidiatus*. Anim Behav **62**: 251-257.

Sokal, R. R. & Rohlf, F. J. 1995. Biometry. 3rd ed. Freeman, San Francisco.

Somerfield, P. J. & Clarke, K. R. 1997. A comparison of some methods commonly used for the collection of sublittoral sediments and their associated fauna. Mar. Environ. Res. **43**: 145-156.

SPSS Inc. 1999. SPSS-X 10.0. SPSS Inc, Chicago.

Stergiou, K. 1999. Intraspecific variations in size- and age-at-maturity for red bandfish, *Cepola macrophthalma*. Env. Biol. Fish. **54**: 151-160.

Tobin, A. J., Sheaves, M. J. & Molony, B. W. 1997. Evidence of protandrous hermaphroditism in the tropical sparid *Acanthopagrus berda*. J. Fish Biol. **50**: 22-33.

Travers, M. J. & Potter, I. C. 2002. Factors influencing the characteristics of fish assemblages in a large subtropical marine embayment. J. Fish Biol. **61**: 764-784.

Vetter, E. F. 1988. Estimation of *M* in fish stocks: a review. Fish. Bull. **86**: 25-43.

Walker, M. H. 1983. Aspects of the life history of baldchin groper trapped at the Abrolhos Islands. FINS **16**: 4-7.

Walker, D. I. 1990. Seagrass in Shark Bay, Western Australia. pp. 101-107. *In*. Research in Shark Bay, Report of the Frances-Australe Bicentenary Expedition Committee. Berry, P. F., Bradshaw, S. D. & B. R. Wilson (eds). Western Australian Museum. Perth.

Wallace, R. A. and Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Sci. Zool. **21**: 325-343.

Watson, R.A. & Quinn, T.J. 1997. Performance of transect and point count underwater visual census methods. Ecol. Model. **104**: 103-112.

Warner, R.R. 1988. Sex change in fishes: hypothesis, evidence, and objections. Env. Biol. Fish. **22**: 81-90.

Warner, R. R. 1998. The role of extreme iteroparity and risk avoidance in the evolution of mating systems. J. Fish Biol. **53** (Supplement A): 82-93.

Warner, R. R. and D. R. Robertson. 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The wrasses (Labridae). Smithson. Contrib. Zool., 254.

Warner, R. R. & Swearer, S. 1991. Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatium* (Pisces: Labridae). Biol. Bull. **181**: 199-201.

Warner, R. R. & Schultz, E. T. 1992. Sexual selection and male characteristics in the bluehead wrasse *Thalassoma bifasciatum*: Mating site acquisition, mating site defense, and female choice. Evol. **46(5)**: 1421-1442.

Yearsley, G. K., Last, P. R. & Ward, R. D. (eds). 1999. *Australian seafood handbook: an identification guide to domestic species*. CSIRO Marine Research, Australia.

Young, G. C., Potter, I. C., Hyndes, G. A. & de Lestang, S. 1997. The ichthyofauna of an intermittently open estuary: Implications of bar breaching and low salinities on faunal composition. Est. Coast. Shelf Sci. **45**: 53-68.

9.0 BENEFITS

The biological data produced during this study now makes it possible for managers and/or fisheries scientists to undertake the following:

a. Assess, in an ongoing manner, the status of the stocks for western yellowfin bream and four tuskfish species in Shark Bay, one of only fourteen World Heritage Areas in Australia.

b. Determine, for the first time, the most effective strategy(ies) for managing these recreational and commercial fisheries in Shark Bay.

c. Develop appropriate methods for allocating the fisheries resources for the above five species amongst recreational and commercial fishers in Shark Bay.

d. Develop appropriate plans for managing the fisheries for the baldchin groper in the Abrolhos Islands, where it is an important commercial and recreational species.

The realisation of the opportunities that flow from these biological data is dependent on their acceptance by the minister and their adoption by the Western Australian Department of Fisheries. The data have thus been provided to the department in a form that can readily be used by fisheries managers.

The provision of the biological data also to WAFIC, Recfishwest, CALM, Gascoyne Development Commission, Denham RRFAC, Denham Fishing Association, Volunteer Marine Rescue Shark Bay Inc., Shire of Shark Bay and the West Coast Recreational Fishing Advisory Committee will inform the members of those bodies of their implications in the context of plans to conserve the resources for those five important species.

10.0 FURTHER DEVELOPMENT

Once the final report has been accepted by the FRDC, it will be provided to the Western Australian Department of Fisheries so that, when developing management plans, fisheries managers are able to take into account highly relevant biological data on the western yellowfin

bream and four species of tuskfish that are fished commercially and/or recreationally in Shark Bay. The report will also be provided to WAFIC, Recfishwest, CALM, Denham RRFAC, Denham Fishing Association, Volunteer Marine Rescue Shark Bay Inc., Shire of Shark Bay and West Coast Recreational Fishing Advisory Committee to ensure that all of the members of these bodies are made aware of the biology of the above five species and their implications for sustainable management of these resources.

A poster will be prepared on both the western yellowfin bream and the four species of tuskfish that will outline the main findings of this study. Copies of these posters will be supplied to the relevant Fisheries and CALM offices and fishing associations.

Papers on the biology of western yellowfin bream have already been accepted for publication in international journals, namely *Canadian Journal of Fisheries and Aquatic Sciences* and *Environmental Biology of Fishes*. Further details of these papers are listed at the end of Chapters 3 and 4. We will also be submitting the results of the work conducted on the four tuskfish species for publication in international journals in 2004. Furthermore, we will present the findings of this project in local magazines such as *Western Angler*, *Western Fisheries* and *PROWEST* in order that the recreational and commercial fishing communities are aware of the results of our study and their implications.

The data produced during this study now provide the quantitative basis required to develop appropriate stock assessment models for the above five species.

One of the main investigators in this study (D. Fairclough) has accepted an invitation to join the IUCN specialist group for groupers and wrasses and is providing biological data on tuskfish to the convener of that group, Professor Y. Sadovy.

11.0 PLANNED OUTCOMES

Prior to this study, the biological data on these species were extremely sparse. During this project, we have obtained the type of reliable quantitative data for important biological parameters for western yellowfin bream and four species of tuskfish that are required by fisheries managers for developing appropriate management plans for these species. The same type of information has been obtained for baldchin groper in the Abrolhos Islands, where this species forms an important component of the commercial wetline and recreational fisheries and which, like the Shark Bay World Heritage area, is an area of high conservation value. The results of this study contribute greatly to our overall understanding of these species and the habitats in which they occur and will thus be invaluable for helping conserve the biological resources of these two areas.

The results of this study have highlighted the need for managers in Western Australia to recognise the problems that protandrous and protogynous hermaphroditic species pose for developing plans aimed at conserving those species. They demonstrate very clearly the need to consider a number of factors and possible management options for such species and that the use of minimum legal lengths on their own are likely to be less than ideal to counteract the effects of high fishing pressure.

In the context of minimum legal lengths (MLL), it is highly relevant that, in the absence of biological data in the past, the same MLL of 400 mm is imposed for tuskfish species in Western Australia. However, the present study has shown that the maximum length attained by these species varies markedly and two of the species of tuskfish, *Choerodon cyanodus* and *Choerodon cauteroma* rarely reach this length. Thus managers must now reconsider which minimum legal length is appropriate for each species.

The fact that this study has demonstrated that the different types of habitat are partitioned among the five species that were the subject of the current study will now enable

managers to identify far more precisely areas that, if appropriate, could be closed to fishing in order to facilitate the conservation of a particular species or several species in Shark Bay.

12.0 GENERAL CONCLUSIONS

Sound quantitative data have been obtained for all of the objectives listed in the original application. In addition to meeting these objectives, we also developed a new approach for estimating total, natural and fishing mortality for *A. latus* using Bayesian statistics and carried out yield per recruit analyses for this species.

During this study, we investigated aspects of the biology of one species of sparid, *Acanthopagrus latus*, and four congeneric species of labrid (*Choerodon* spp.) in the large sub-tropical Shark Bay and also the biology of one of those labrids (*Choerodon rubescens*) in the Abrolhos Islands, which are located *ca* 300 km further south. The major findings are as follows:

- *Acanthopagrus latus* and each of the tuskfish species except *C. rubescens* occur within the inner gulfs of Shark Bay. *Choerodon rubescens* is found mainly in oceanic waters at the entrances to Shark Bay and along the outer coast of this embayment.
- The juveniles of *A. latus* typically live in mangrove habitats, whereas the adults of this species are found mainly along rocky shorelines. The adults of all of the above four species of tuskfish live predominantly over reefs and/or along rocky shorelines. Although the juveniles of these species are also found over reefs, the juveniles of one species (*C. cauteroma*) and the juveniles and adults of a fifth tuskfish species (*C. cephalotes*) are most abundant and exclusively found in seagrass, respectively.
- Detailed macroscopic and histological examination of the gonads of a wide size range of each species, together with a quantification of how the prevalences of the different types of gonad change with size and age and, in the case of *A. latus*, also during the year, demonstrated that *A. latus* is a protandrous hermaphrodite, *i.e.* males change to females with increasing age, whereas all four species of tuskfish are protogynous hermaphrodites, *i.e.* females change to males with increasing age.
- The size and age at which individuals of *A. latus* become identifiable as males (L_{50} = 245 mm, *ca* 2 years) are the same as that at which they become mature. The L_{50}s for the lengths at maturity for *C. rubescens* (in Shark Bay), *C. schoenleinii*, *C. cyanodus* and *C. cauteroma* were 282, 250, 196 and 128 mm, respectively. These four species typically attain maturity at a similar age (2-4 years).

- *Choerodon rubescens* attains maturity at a similar size (282 *vs* 291 mm) but at an older age in the Abrolhos Islands (L_{50} = 4 years) than in Shark Bay (L_{50} = 3 years).
- The L_{50}s for the lengths and ages at which *C. cyanodus*, *C. cauteroma* and *C. schoenleinii* change sex were 220, 310 and *ca* 550 mm, respectively, and 4, 7 and 11-12 years of age, respectively.
- *Choerodon rubescens* changed sex at a similar age (11-12 years) but at different lengths in Shark Bay (L_{50} = 545 mm) and the Abrolhos Islands (L_{50} = 479 mm).
- *Acanthopagrus latus* spawns during late winter/early spring and has determinate fecundity. The potential annual fecundities of 24 *A. latus* ranged from 764,000 in a 600 g fish to 7,910,000 in a 2,050 g fish and produced a mean ±1SE of 1,935,000 ± 281,000.
- The four species of tuskfish each spawn mainly during spring and/or summer and have indeterminate fecundity. The mean batch fecundities of *C. rubescens*, *C. schoenleinii*, *C. cauteroma* and *C. cyanodus* were 42,700, 37,400, 11,800 and 12,100, respectively.
- The maximum lengths recorded for *A. latus*, *C. cyanodus*, *C. cauteroma*, *C. schoenleinii* and *C. rubescens* were 466, 382, 424, 805 and 649 mm, respectively. The maximum recorded age was greater for *A. latus* (24 years) than for all four tuskfish species in Shark Bay (12-16 years). However, *C. rubescens* as old as 22 years were caught in the Abrolhos Islands.
- *Choerodon rubescens* grows more rapidly in Shark Bay than the Abrolhos Islands.
- The total length at which *A. latus* typically become identifiable as males (245 mm) is very similar to the current minimum legal length (MLL) of 250 mm, which corresponds to an age of 2.5 years less than that at which 50% of males become females. This implies that, if fishing pressure were to increase markedly, the females of this species would be likely to become very severely depleted which, in turn, would have a detrimental impact on the overall population.
- Per recruit analyses (spawning biomass and egg per recruit), calculated over a range of alternative values for natural mortality for *A. latus* in Shark Bay, indicated that, in apparent contrast to the situation in the past when the number of fishing licenses was greater, the current level of fishing pressure on this species is sustainable.
- The estimates derived for total and natural mortality of *A. latus*, using our new Bayesian approach, support the conclusion that the stock of this species is currently not being overfished in Shark Bay.
- Our Bayesian approach provides more realistic and precise estimates for natural mortality and can be applied to any other species for which there are appropriate biological data.

13.0 APPENDICES

APPENDIX 1

INTELLECTUAL PROPERTY

The value of the intellectual property will be 49.16% based on PART C of the FRDC project proposal.

STAFF

Prof. Ian Potter

Mr. David Fairclough

Dr. Alex Hesp

Assoc. Prof. Norm Hall

Mr. Daniel French