Biological parameters for managing the fisheries for Blue and King Threadfin Salmons, Estuary Rockcod, Malabar Grouper and Mangrove Jack in north-western Australia.

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Fisheries Research and Development Corporation Report

FRDC project 2002/003

Murdoch University
Perth, Western Australia
Centre for Fish and Fisheries Research
Australian Government
Fisheries Research and Development Corporation
Government of Western Australia
Department of Fisheries

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

December, 2005
ISBN: 86905-963-7

PROJECT TITLE

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PRINCIPAL INVESTIGATOR

Professor Ian C. Potter
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

The main objective of this study was to produce the biological data required for appropriate management of the Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack in waters off the Pilbara and Kimberley coasts. Unless otherwise stated, this involved determining the following for each species.

1. Size and age compositions, sex ratios and growth rates.
2. Sizes and ages at which the first four species change sex.
3. Sizes and ages at which females and males reach maturity.
4. Duration and location of spawning and whether multiple spawning occurs within a breeding season.
5. Batch fecundity and its relationship to body size.
6. Size compositions of fish caught by recreational, commercial, aboriginal and charter fishers.
7. A yield and spawning biomass-per-recruit assessment and evaluation of the effectiveness of different legal minimum and maximum sizes.

NON-TECHNICAL SUMMARY

OUTCOMES ACHIEVED TO DATE

Data have been collected on those crucial aspects of the biology of Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack that are required to develop appropriate management plans for conserving the stocks of these five commercially and recreationally important species. The following biological data have been obtained. (1) The size and age at which each species reaches sexual maturity. (2) The size and age at which the two species of threadfin change from male to female and the Estuary Rockcod and Malabar Grouper change from female to male. Note that, unlike the above four species, the Mangrove Jack is not hermaphroditic and thus does not change sex. (3) The habitats, size and age compositions, duration and location of spawning, and mortality of each species. As the two threadfin species are largely restricted to areas over bare substrate in nearshore waters, they are particularly accessible to fishers. Our results indicate that, currently, the Blue Threadfin is fully exploited and the King Threadfin is over-exploited, whereas the fisheries for the Estuary Rockcod, Malabar Grouper and Mangrove Jack are apparently sustainable at current fishing levels. However, our results emphasize that fishing mortality has a very marked adverse impact on the abundance of the ultimate sex of the four hermaphroditic species, and this needs to be considered when specifying legal lengths for retention. Managers also need to monitor the status of the stocks of Mangrove Jack which, because of its high value, is attracting an increasing amount of attention from the recreational, commercial and charter boat fishing sectors. Finally, the results of this study emphasize the pressing need to develop better methods for determining the natural mortality of fish species and thus being able to derive more robust estimates of fishing mortality.

The Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack are among the most important recreational and commercial fish species along the Pilbara and Kimberley coasts of north-western Australia. These species, and in particular the two species of threadfin, also hold particular cultural significance and are an important food source for local aboriginal communities. As exploitation of the above five species is continuing to increase, the sustainability of their stocks depends on establishing sound and appropriate management plans that are based on relevant and high quality biological data. The aim of this study was to provide these data.

The juveniles and adults of the Blue and King Threadfins complete their life cycles in sandy and muddy beach habitats in nearshore, shallow waters. The juveniles of Estuary Rockcod, Malabar Grouper and Mangrove Jack live in mangrove and nearshore rocky areas and move offshore to waters over reefs as they increase in size and age.

In north-western Australia, the King Threadfin grows far larger and lives for longer than the Blue Threadfin, a difference reflected in the maximum total lengths and ages we recorded for these two species, *i.e.* 1393 mm and 10 years *vs* 793 mm and 6 years, respectively. King Threadfin grow faster than Blue Threadfin, attaining lengths of 322, 520 and 945 mm *vs* 245, 400 and 635 mm, by the end of years 1, 2 and 5, respectively. Estuary Rockcod and Malabar Grouper grow at a similar rate during their first 10 years of life, reaching lengths of 282, 522 and 841 mm *vs* 287, 545 and 833 mm at 2, 5 and 10 years of age, respectively. However, the maximum length of 1156 mm and age of 21 years attained by Estuary Rockcod are less than the values of 1270 mm and 32 years we recorded for the Malabar Grouper. Mangrove Jack are long lived, with some individuals exceeding 50 years in age. This species grows to *ca* 400 and 550 mm in 5 and 10 years, respectively, after which it does not increase markedly in length.

Both threadfin species and the Mangrove Jack have protracted spawning periods of *ca* 6 months, with spawning peaking in spring and early summer, *i.e.* September to December. Although Estuary Rockcod and Malabar Grouper spawn for most of the year, spawning occurs predominantly between late spring and early autumn. All five species spawn on many occasions each year.

The Blue and King threadfins both mature first as males and all of the males later change to females, *i.e.* they are protandrous hermaphrodites. These species typically reach sexual maturity as males at the end of their first year of life when their lengths are *ca* 200 and 230 mm, respectively. Blue and King Threadfin typically change from male to female at *ca* 400 and 810 mm, respectively, when they are *ca* 2 and 4 years old, respectively.

Estuary Rockcod and Malabar Grouper mature first as females and, with increasing size and age, typically change to males, *i.e.* they are protogynous hermaphrodites. The females of Estuary Rockcod attain maturity at a smaller length (*ca* 575 mm) than those of Malabar Grouper (*ca* 800 mm). The change from females to males occurs at a smaller length in Estuary Rockcod (*ca* 925 mm) than in Malabar Grouper (*ca* 1100 mm). The youngest individuals of these two species to have changed sex to males were 8 and 13 years of age, respectively. The fastest growing fish are typically destined to change sex and the majority of the slowest growing fish remain as females. The females and males of Mangrove Jack typically attain maturity at lengths of 450-500 mm and 6-7 years of age.

Estimates of the current impacts of fishing indicate that the Blue Threadfin is fully exploited and that the King Threadfin is over-exploited. Managers also need to recognize that Blue and King Threadfin are restricted to readily accessible nearshore waters and that fishers take many individuals of these two species before they reach the size at which they typically change sex from male to female.

The fisheries for the Estuary Rockcod and Malabar Grouper are apparently sustainable at the current levels of fishing. However, because these species change sex from female to male, a precautionary approach should be adopted for managing these species as the abundance of their males can be impacted heavily at even relatively low levels of fishing. In principle, the reduction from 1200 to 1000 mm of the upper legal length for retention of Estuary Rockcod will help protect the males of this species. However, the effectiveness of this regulation will depend on the ability of these large males to survive being caught and released.

The fishery for Mangrove Jack also appears to be sustainable at the current level of fishing. However, managers will need to monitor the status of the stock of this species, which, because of its high value, will inevitably attract increasing attention from the recreational, commercial and charter boat sectors. As the current minimum legal lengths for Mangrove Jack, and the Estuary Cod and Malabar Grouper are far lower than the size at which these species typically attain maturity and these species have low natural mortality and thus low productivity, managers will need to consider increasing the MLLs for these species to ensure that their fisheries are sustainable as fishing pressure increases. However, at the same time, managers will need to take into account the fact that the introduction of such a policy would prohibit many recreational anglers from catching these species, as these anglers fish in nearshore waters where only the juveniles of Mangrove Jack, Estuary Cod and Malabar Grouper occur. Alternatively, managers might need to consider policies which reduce fishing effort.

The discussion of the implications of our results emphasizes the overwhelming need to obtain more reliable life cycle data for the wide range of other species that are used in the models for determining more precisely the natural mortality of individual fish species. Reliable estimates of natural mortality are necessary to obtain robust estimates of fishing mortality. Consequently, managers need to adopt a precautionary approach until such data become available.

Keywords: Polynemidae, Serranidae, Lutjanidae, reproduction, hermaphroditism, protandry, protogyny, age composition, growth, mortality, per recruit analysis, stock assessment, management implications.

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ACKNOWLEDGEMENTS

Gratitude is expressed to Mike and Steve Travers, Chris Marsh, Mark, Brenton and Susan Pember, Maska Law, Shawn Carman and Steve Young for their unstinting help with sampling in the field. We would also like to thank David Fairclough from Murdoch University for helpful discussions regarding hermaphroditic fish. We also gratefully acknowledge the assistance with sampling, histological assessment and otolith preparation provided by the following staff from the Fisheries Research Division, Department of Fisheries, Western Australia; Ben Rome, Mike Hammond, Ian Keay, Paul Lewis, Lee Higgins, Jan Richards, Amanda Nardi and Dr. Michael Mackie.

We would also like to thank Paul Shandler of Mt. Minnie Station, and Tamlin Little and other members of the Nickol Bay Sportfishing Club for providing samples caught recreationally in the Pilbara region of Western Australia. Thanks also to members of the Broome Fishing Club and other recreational fishers who provided samples. Many thanks are due for the regional support provided by Eric Loughton and Michael Dunne (Exmouth District Office, W.A. Department of Fisheries), and Troy and Greg from Bettsy's Seafood and Tackle in Exmouth.

The successful completion of this project was made possible by the significant and continuing support of commercial fishers and fish processors in the Pilbara and Kimberly trap, trawl and gillnet fisheries. In particular, gratitude is expressed to commercial gill net fishers Milton Comino and Graham Rogers and their employees at Roebuck Seafoods and to Bruce Gould for making large numbers of Threadfin available. The vast majority of Estuary cods and Mangrove Jack sampled during the project were provided by Perth processors. In particular, we thank Sam and Theresa Curulli at Curulli's Seafoods, Tony Miragliotta at Kailis Bros., Paul Paino at Sealanes, Paul Catalano at Catalano's Seafoods, Gavin Glaubert at Festival Seafoods, Peter and Alex at New West Seafoods and Toby Abbott from Shine Fisheries.

We are very grateful to the following people who supported the development of this project: Douglas Gibson – Onslow Professional Fishermans Association; Bob Masters – Kimberley Professional Fishermans Association; Milton Comino – Roebuck Seafoods (KGBMF); Gary Tuck – Kimberley Charter Boat Operators Association; Jeremy Elliot – Aboriginal Affairs Department; Ben Fraser – Aboriginal Fishing Strategy, Department of Fisheries W.A.; Jeff Gooding – Kimberley Development Commission; The Honourable Tom Stephens MLC; Monique Ellis - Bealwood Pty Ltd, (aquaculture); Stephen Gilders – Australian National Sportfishing Association; Frank Prokop – RecFishWest; Terry Fuller- Australian Anglers Association; Derren Greenhill - Broome Fishing Club; Tamlin Little - Nickol Bay Sportfishing Club; Derek Blackman -Regional Supervising Fisheries Officer (Broome), Department of Fisheries W.A.; Richard Stevens – WAFIC; Simon Bennison – WAFIC; Steve Bunts – Ranger, Cape Keraudren (Pardoo); 80-Mile Beach Caravan Park; Port Smith Caravan Park.

Finally, but by no means least, we are greatly indebted to Gordon Thomson for his endless patience in producing high quality histological slides of fish gonads.

1. GENERAL INTRODUCTION

1.1 BACKGROUND

The Blue and King Threadfins *Eleutheronema tetradactylum* and *Polydactylus macrochir* (previously *Polynemus sheridani*) and the Estuary Rockcod *Epinephelus coioides*, Malabar Grouper *Epinephelus malabaricus* and Mangrove Jack *Lutjanus argentimaculatus* are among the most important recreational and commercial fish species on the *ca* 3000 km of the Pilbara and Kimberley coasts (Department of Fisheries WA, unpublished creel census data and Commercial Catch and Effort Statistics - CAES). As a result of increases in tourism and population size, the number of recreational anglers fishing for the above five species along the Pilbara and Kimberley coasts presumably will continue to rise. These species also constitute the main food source of local aboriginal communities and play an important cultural role in the life of these communities.

Threadfins

The Blue and King Threadfins contribute over 60% to the total landings of the Kimberley Gill Net and Barramundi Managed Fishery (KGBMF), which is the major nearshore commercial fishery in the coastal waters of Western Australia north of Port Hedland at 20°10´S, 118°, 36´E (State of the Fisheries Report WA, 1999/2000). The management zone of the KGBMF covers almost 2000 km of coastline from Eighty Mile Beach at 19°S, 121.30°E, northwards to the Western Australia/Northern Territory border. There are also other commercial fishers who are licensed to catch these two species outside the boundaries of the KGBMF.

In 1999/2000, the total commercial catch of threadfin salmons in north-western Australia was 174 tonnes and valued at $1.65 million, which represents a very substantial contribution to the economy of the small and isolated communities of the Pilbara and Kimberley regions. The trends in commercial catch of the two threadfin species between 1988 and 2004 are presented in Chapter 3.

An analysis of catch statistics by R. Lenanton (Supervising Scientist for Finfish Research, Department of Fisheries Western Australia, unpublished data) demonstrated that more than 90% of the commercial catch of threadfins by the KGBMF and exemption holders operating along the Eighty Mile Beach section of the Pilbara is obtained from between 20°S, 120°E and 16.30°S, 123°E, with the greatest proportion of the catch of the managed fishery being taken in the southern part of that management zone. We have therefore focused much of our sampling for threadfins in that southern region.

The owners of local fish markets, such as those in Broome, are increasingly focusing on selling threadfin because they are experiencing difficulties in obtaining supplies of other species, such as red emperor and gold band snapper, which have become very highly sought after by the Perth market. The Perth and interstate markets have also become aware of the high quality of threadfin as a table fish and are therefore purchasing more of these species. Indeed, the purchase of threadfin salmon by these markets is now beginning to impact even on the Broome market, which often cannot obtain sufficient supplies to satisfy local demand. The Blue and King Threadfins are also the fish species most heavily targeted by shore-based recreational fishers along the Pilbara and Kimberley coasts (Williamson *et al*., in press). From the above, it is evident that the combined fishing effort for threadfins from both fishing sectors is increasing and must therefore be having at least some effect on the abundance of the stocks of these species.

Estuary Rockcod, Malabar Grouper and Mangrove Jack

Unlike the two threadfin species, the Estuary Rockcod, Malabar Grouper and Mangrove Jack are caught offshore as well as inshore. However, as with the first two species, the latter three species are well regarded as table fish, attracting excellent prices for commercial fishers.

Estuary Rockcod, Malabar Grouper and Mangrove Jack are caught commercially by the Northern Demersal Scalefish Managed Fishery (NDSF) and by the Pilbara Demersal Finfish Fisheries, which include the Pilbara Fish Trawl (Interim)

Managed Fishery, the Pilbara Trap Managed Fishery and a line fishery. The above fisheries are subject to management regulations that restrict fishing effort.

The commercial catches of the Estuary Rockcod and Malabar Grouper are not recorded separately in the CAES records of the Department of Fisheries WA. In Western Australia, the majority of the commercial catches of Mangrove Jack are landed by fishers operating north of the North West Cape (21°47'S, 114°09'E) (S. Newman, unpub. data). The trends in commercial catch of *L. argentimaculatus* between 1988 and 2004 are presented in Chapter 5.

In Western Australia, the highly-valued catches of the above three species are transported by road from the regional ports of Onslow, Point Samson, Port Hedland and Broome to markets in Perth, where they are marketed whole and usually fresh on ice. *Lutjanus argentimaculatus* is a prized angling and sport fish in Western Australia and, during a recent survey, was found to be one of the ten most abundant species landed by the recreational fishers of the Pilbara and West Kimberley region (Williamson *et al*., in press). During the latter survey, the recreational catch of this species over a 12 month period was estimated to be approximately 5 tonnes.

In a recreational fishing survey of anglers by the Department of Fisheries WA, the fish recorded as Estuary Rockcod (which constitutes Estuary Rockcod and Malabar Grouper, collectively) and the Mangrove Jack were both ranked among the ten most abundant taxa in the catches of both the inshore and offshore recreational fisheries of the Pilbara (P. Williamson, Department of Fisheries WA, pers. comm.).

Although still small, there is also a rapidly developing charter boat fishery in the Pilbara region which, in the future, may take significant numbers of the above three species. Some idea of the growth in this fishery is provided by the fact that the catches rose from just 3 tonnes in 1991 to 33 tonnes in 1996 and 47 tonnes in 1999 (State of the Fisheries Report WA, 1999/2000).

The aboriginal communities along the Pilbara and Kimberley coasts fish the Estuary Rockcod, Malabar Grouper and Mangrove Jack, and also threadfins, as a source of food. These communities are also showing an interest in developing a commercial enterprise in which visitors will be charged for fishing on their native lands. The recognition of the right for aboriginal people to continue to fish in a traditional but non-exclusive manner was recognised by the High Court of Australia with respect to the Croker Island community.

The aquaculture potential for Estuary Rockcod has been recognised by the Western Australian Government through their provision of funds to Ocean West Fisheries Pty Ltd for this purpose. This species, and also the other four species which are the subject of the current study, form the basis of successful aquaculture ventures elsewhere in the world (see Shiau & Lan, 1996; Emata *et al*., 1999; Ahmad *et al*., 2000; Lee & Ostrowski, 2001).

Although the catches of the Estuary Rockcod and Malabar Grouper are not recorded separately in the Catch and Effort Statistics (CAES) records of the Department of Fisheries WA, the combined data for those two species, together with the observations of experienced local commercial fishers, provide strong circumstantial evidence that the abundance of these species in traditional fishing areas has declined in recent years. There can be little doubt that, through the overall expansion of the fisheries for these species in north-western Australia, the fishing effort for the two species of threadfin, Estuary Rockcod, Malabar Grouper and Mangrove Jack will continue to increase in this region.

There are very limited biological data on the habitats, size and age compositions, growth, reproductive biology and mortality of Blue and King Threadfin, Estuary Rockcod, Malabar Grouper and Mangrove Jack in north-western Australia. Such data are crucial for developing appropriate plans for ensuring that the stocks of these increasingly-exploited populations can be sustained. In the context of their reproductive biology, it is important to confirm that, as is implied from the data for the same or similar species elsewhere, the two threadfin species are protandrous hermaphrodites and the Estuary Rockcod and Malabar Grouper are protogynous hermaphrodites in Western Australia. Details of the size and age at sex change and sex ratios of such hermaphroditic species are essential for developing appropriate management plans for these species. The implications of hermaphroditism for managing the two threadfin species and Estuary Rockcod and Malabar Grouper are provided in chapters 3 and 4.

Details of the biological data available for each species elsewhere are provided in the introductions to the relevant chapters.

1.2 NEED

Although the Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack are of high recreational and commercial importance in the Pilbara and Kimberley regions, there are essentially no biological data of the type required by the Department of Fisheries, Western Australia, for managing and thus conserving the stocks of these species in this region of north-western Australia. The continuing exploitation by commercial fishers, together with the increases in population size and tourism in north-western Australia that will inevitably lead to increases in recreational fishing pressure, means that there is an urgent need to acquire reliable biological data for developing effective and appropriate management plans for the above five species.

1.3 OBJECTIVES

The main objective was to produce the biological data required for appropriate management of the Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack in waters off the Pilbara and Kimberley coasts. Unless otherwise stated, this involved determining the following for each species:

1. Size and age compositions, sex ratios and growth rates.
2. Sizes and ages at which the first four species change sex.
3. Sizes and ages at which females and males reach maturity.
4. Duration and location of spawning and whether multiple spawning occurs within a breeding season.
5. Batch fecundity and its relationship to body size.
6. Size compositions of fish caught by recreational, commercial, aboriginal and charter fishers.
7. A yield and spawning biomass-per-recruit assessment and evaluation of the effectiveness of different legal minimum and maximum sizes.

2. GENERAL MATERIALS AND METHODS

2.1 SAMPLING REGIME

The Blue Threadfin *Eleutheronema tetradactylum*, the King Threadfin *Polydactylus macrochir*, the Estuary Rockcod *Epinephelus coioides*, the Malabar Grouper *Epinephelus malabaricus* and the Mangrove Jack *Lutjanus argentimaculatus* were collected from sites along the Pilbara and Kimberley coasts at approximately bimonthly intervals between July 2002 and January 2005. The samples of the two threadfin salmon species and, to a lesser extent, those of the other three species, were supplemented by samples obtained between December 2000 and June 2002 during another FRDC project (2000/132) entitled "Characterisation of the inshore fish assemblages of the Pilbara and Kimberley coasts." Details of the sampling regime of the current project are summarised in **Table 2.1**.

Table 2.1. Sampling regimes for juveniles and adults of the five fish species in Pilbara and Kimberley waters. Locations of sampling sites are shown in Figure 2.1.

Species	Life Stage	Habitat	Region	Method
Blue Salmon *Eleutheronema tetradactylum* **King Threadfin Salmon** *Polydactylus macrochir*	Juvenile	Nearshore sand Nearshore mud	Derby Anna Plains Eighty Mile Beach	Seine net Gill net
	Adult	Nearshore sand Nearshore mud Mangroves	Roebuck Bay Anna Plains Eighty Mile Beach Cape Keraudren Karratha	Gill net Recreational angling Recreational haul netting Commercial gill netting
Estuary Rockcod *Epinephelus coioides* **Malabar Grouper** *Epinephelus malabaricus* **Mangrove Jack** *Lutjanus argentimaculatus*	Juvenile	Intertidal pools Mangroves	Broome Port Smith Cape Keraudren Karratha Robe River Exmouth	Rotenone treatment Angling
	Adult	Inshore reefs Offshore reefs	Kimberley coast Pilbara coast	Research trap Commercial trap Commercial trawl

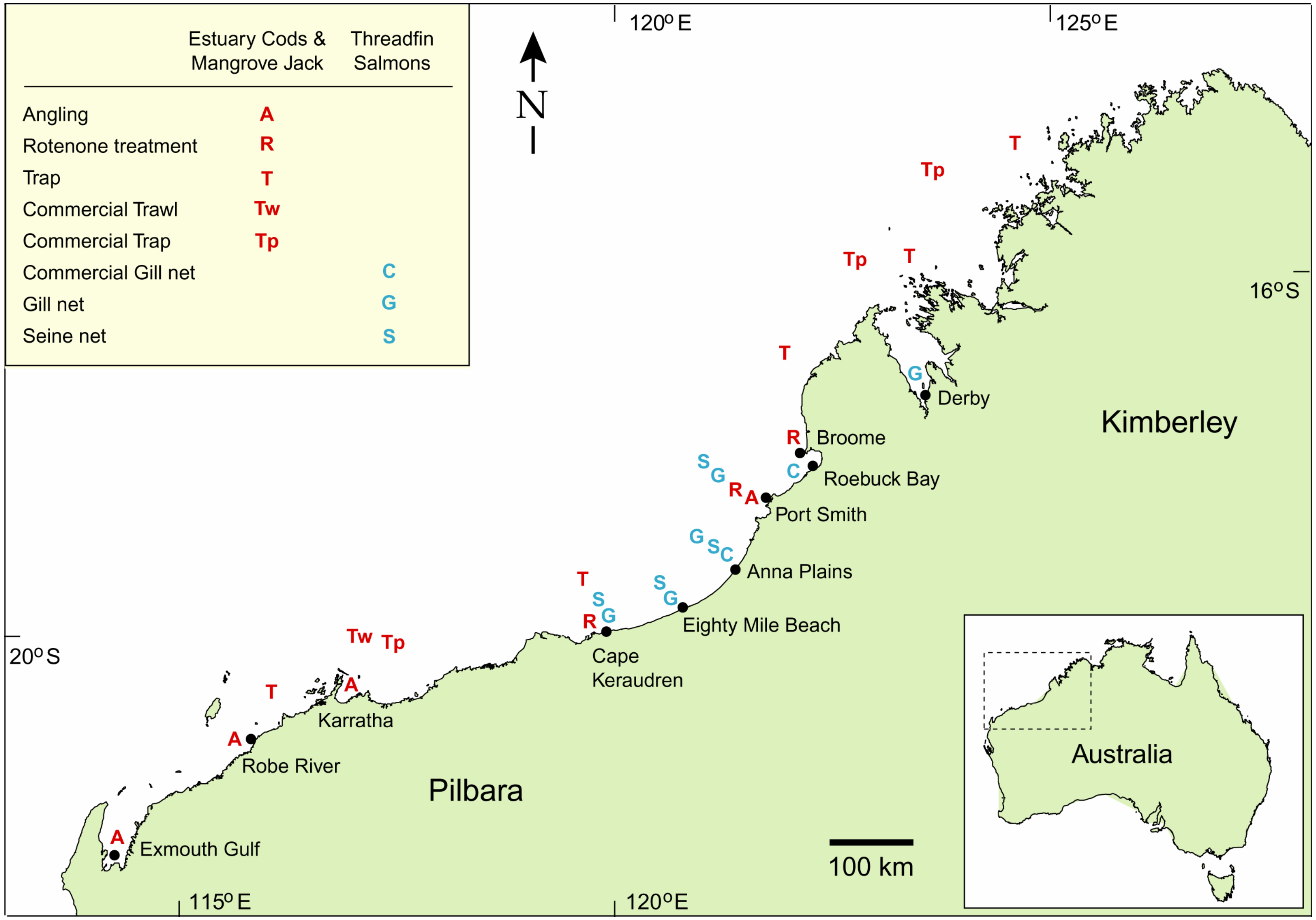

Figure 2.1: Map showing the location of the various sampling sites and the sampling methods used to catch Blue and King Threadfin, Estuary Rockcod, Malabar Grouper and Mangrove Jack.

Samples of *E. tetradactylum* and *P. macrochir* were collected by gill netting over bare sand habitats at Cape Keraudren, Eighty Mile Beach and Port Smith, and in mangroves at the first and last of these locations. The composite gill nets were 60 m long, 2 m high and consisted of six 10 m long monofilament panels, each with a different stretched mesh width of either 51, 76, 102, 127, 152 or 178 mm. When sampling over bare sand, the gill net was set parallel to the shoreline at low to mid tide and was fixed in place using fencing pickets. The net was located in a position that ensured it would be covered for *ca* 3h by the incoming tide. When sampling in mangrove areas, the gill net was extended parallel to the shoreline and attached to mangrove trunks in an area where it would likewise be covered for *ca* 3h at high tide. On each sampling trip, two gill nets were set at each habitat on two consecutive nights.

A 60.5 m seine net was also used to sample *E. tetradactylum* and *P. macrochir* over bare sand sites at Port Smith, Eighty Mile Beach and Cape Keraudren and a 21.5 m seine net was used to sample the juveniles of these species over mud and bare sand at Anna Plains and Eighty Mile Beach (**Figure 2.1**). The 60.5 m seine net consisted of two 29 m long wings, each made of 25 mm mesh, and a 2.5 m bunt consisting of 9 mm mesh. This net fished to a depth of 2.5 m and swept an area of 583 m^2. The 21.5 m seine net consisted of two 10 m long wings and a 1.5 m bunt. Each wing consisted of a 6 m panel of 9 mm mesh and a 4 m panel of 3 mm mesh, while the bunt was made of 3 mm mesh. The net fished to a depth of 1.5 m and covered an area of *ca* 116 m^2. Seine nets were either laid in a semi-circle or extended parallel to the shore and then rapidly dragged onshore. All sites were sampled on neap tides, when the tidal height was at or close to its maximum and water movement was minimal. For safety reasons, seine netting was only conducted during the day.

Samples of the two threadfin species were also obtained from recreational and commercial fishers. Recreational fishers catch these species by employing either rod and line angling or 30 m long monofilament haul nets comprising of 80 to 100 mm mesh. Commercial fishers target threadfin salmon using heavy gauge monofilament gill nets with mesh sizes of 140 to 165 mm. Although gill nets are typically only *ca* 60 m long, the use of such nets up to 1000 m long is permitted by the Department of

Fisheries, Western Australia. Gill nets are either set from boats in shallow (< 1 m) tidal waters (*i.e.* at Roebuck Bay, Broome) or staked or anchored perpendicular to the shoreline below the high water mark, so that they become inundated by the incoming spring tide (*i.e.* at Anna Plains, Eighty Mile Beach).

The juveniles of *E. coioides, E. malabaricus* and *L. argentimaculatus* were collected from intertidal pools at Gantheaume Point (Broome), Port Smith and Cape Keraudren by using rotenone. Three randomly-selected pools, which ranged from 10 to 20 m^2 in area and from 0.4 to 0.6 m in depth, were sampled at each of these three sampling locations on each sampling trip. Prior to its addition to each pool at low tide, powdered rotenone was mixed with water to form a paste and applied in a concentration of *ca* 200 g of dry rotenone powder 10 m^{-2} of pool area. Every effort was made to ensure that neighbouring pools did not become contaminated with this ichthyocide. This included the construction of barriers to prevent water moving out of the treated pool until it had become well diluted by the incoming tide. Ten minutes after their treatment with rotenone, the pools were sampled for fish using a long-handled scoop net constructed of 5.0 mm mesh.

The larger juveniles of both cod species and Mangrove Jack were collected by angling in nearshore habitats, including inshore reefs and mangrove creeks, whereas the adults of these three species were obtained by research trapping and from commercial trap and trawl fishers.

The fish traps used by the Kimberley trap fishers are constructed of 50 mm galvanised weldmesh and are subject to the regulation that the diagonal corners of each square of the mesh cannot be < 70 mm. The weldmesh is welded onto a supporting frame comprising galvanised steel rods or bars. The regulations also require that each trap has an internal volume that is ≤ 2.25 m^3. The fish traps are typically 1600 mm in length, 1500 mm in width and 900 mm in height. Each trap has a single opening of *ca* 100 mm by 900 mm, although the exact dimensions vary among vessels.

The vessels in the Pilbara trawl fishery tow a single net with two otter boards. The net consists of mesh that must exceed 100 mm and a headrope length that may not exceed 37 m. The regulations also require that the overall trawl gear (including sweeps, bridles, and headropes) do not exceed 274 m. The ground (or foot) rope of the net opening has rollers or bobbins attached which have a diameter that is less than 350 mm. These are placed about a third of a metre apart along the ground rope. The bottom rope is weighted so that the bobbins contact the sea floor to enable the bottom-dwelling species to be caught. The weighted ground rope, which is integral to the fishing process, has an impact on the bottom habitat. The duration of each trawl is 0.5 to 5 h with a modal time of 3 h. The net is retrieved on a net drum, with the catch being spilled on to the deck or alternatively below deck through a hopper.

Water temperature and salinity were measured at the bottom of the water column at each site on each sampling occasion using a YSI30 conductivity meter.

2.2 FISH MEASUREMENTS

The total length (TL) and fork length (FL) of all *E. tetradactylum* and *P. macrochir* and the TL and standard length (SL) of all *E. coioides, E. malabaricus* and *L. argentimaculatus* were measured to the nearest 1 mm. The fork length was measured for the first two species to enable comparisons to be made with values recorded for this variable in other polynemids. All fish < *ca* 6 kg were weighed to the nearest 0.1 g, while those > *ca* 6 kg were weighed to the nearest 1 g. The relationship between total weight and total length of each species was calculated so that the weight of an individual of any of those species could be estimated when only the frame (filleted fish) of that individual was available, as was sometimes the case with fish obtained from markets or recreational anglers.

2.3 REPRODUCTIVE BIOLOGY

The gonads of each fish were weighed to the nearest 0.01 g and used to calculate the gonadosomatic index (GSI) of each fish from the equation $W1/(W2-W1) \times 100$, where $W1$ = wet weight of the gonad and $W2$ = wet weight of the whole fish, *i.e.* $W2-W1$ = somatic weight. Each gonad was examined macroscopically and those that contained exclusively either ovarian or testicular tissue were allocated 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 = spent/recovering. Since it is often not possible to distinguish macroscopically between stages V and VI, the data for these two stages have been pooled. The stages in the development of ovaries and testes of the two threadfin species are described in Chapter 3. Since relatively few males were recorded for the two protogynous species, *i.e.* the Estuary Rockcod and Malabar Grouper, estimates of the duration of the spawning period has focused on the trends exhibited by the reproductive variables for the females of these species. Since the stages in the development of the gonads of Mangrove Jack were essentially the same as for the other four species, for this species, the reader is referred to the descriptions given in Chapters 3 and 4 for the other four species.

In each month, the mid-region of the gonads of at least 10 individuals of each species were placed in Bouin's fixative for *ca* 48 h, dehydrated in a series of increasing concentrations of ethanol, embedded in paraffin wax, cut into 6 µm thick transverse sections and stained with Mallory's trichrome. These histological sections were used 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 to ascertain the most appropriate technique for estimating fecundity, and (3) ensure that the fish were sexed correctly and (4) to confirm that the two threadfin species are protandrous hermaphrodites and that the Estuary Rockcod and Malabar Grouper are protogynous hermaphrodites (*sensu* Sadovy and Shapiro, 1987; Buxton & Garratt, 1990).

The L_{50} at maturity, *i.e.* length at which 50% of individuals attain maturity, was determined for male *E. tetradactylum* and *P. macrochir*, female *E. coioides* and *E. malabaricus* and both sexes of *L. argentimaculatus.* The above choices of sex for determining the L_{50} were based on the fact that our results confirmed that the first two species are protandrous hermaphrodites and the second two species are protogynous hermaphrodites, while the last species is a gonochorist (see later). The L_{50}s were calculated by using logistic regression analysis to determine the relationship with length of the probability that a fish, during the spawning season, possessed gonads at stages III to VIII and would thus have had the potential to spawn or have spawned during that period. The data were randomly re-sampled 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 derived using this re-sampling technique were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this re-sampling 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 = probability that a fish is 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. For the protandrous hermaphroditic *P. macrochir*, this re-sampling procedure was also used to determine the length at which 50% of individuals had completed sex change, but where P = the probability that a fish has changed sex to become a female. Since there were substantial numbers of transitional fish, *i.e.* undergoing sex change, for the second protandrous threadfin, *E. tetradactylum*, the same procedure was used to estimate the lengths at both the beginning and completion of sex change, where, in the latter case, P = the probability of a fish, at it's time of capture, of being either transitional between male and female or a female. In the case of the protogynous hermaphroditic Estuary Rockcod and Malabar Grouper, the L_{50}s at sex change were calculated by grouping the very few fish which, at their time of capture, were undergoing sex change, with the males, as it was considered likely that fish of the former category were capable of functioning as males (see Chapter 4 for rationale). In the case of the Estuary Rockcod, Malabar Grouper and Mangrove Jack, this re-sampling procedure has also been used to estimate the length and age at which 50% of individuals in the samples were caught in offshore waters.

To determine whether each of the five species has determinate or indeterminate fecundity, the diameters of 200 oocytes in histological sections of stage VI ovaries of two fish caught during the spawning period were measured to the nearest 10 μm and the stage of each of those oocytes recorded. Measurements were restricted to oocytes in which a nucleus was visible in their centre to ensure that the oocytes had been sectioned through their centre. This approach could not be used to measure the oocyte diameters of migratory nucleus or hydrated oocytes in histological sections because the nucleus of these oocytes migrates towards the periphery of the cytoplasm and then undergoes germinal vesicle breakdown.

Since all five species were shown to have indeterminate fecundity (see later), 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 annual fecundity of any of these species (see Hunter *et al.*, 1985). The ability to estimate the annual fecundity of species with indeterminate fecundity requires data on both spawning frequency and batch fecundity. Due to the remoteness of the Pilbara and Kimberley coasts, it was not logistically possible to determine the spawning frequency for any of the five species and thus derive estimates of annual fecundity. However, batch fecundities were able to be calculated for Mangrove Jack as a number of individuals of this species were caught with ovaries containing hydrated oocytes. For this purpose, one of the ovarian lobes containing hydrated oocytes was preserved in 10% neutrally-buffered formalin. The formalin-preserved ovarian lobe was dried with blotting paper and *ca* 180-200 mg of tissue was removed from each of its anterior, middle and posterior regions and weighed to the nearest 1 mg. These pieces of tissue were placed on separate slides, covered with 30% glycerol and examined under a dissecting microscope. The oocytes were then teased apart and the number of hydrated oocytes recorded. The number of hydrated oocytes in each of the three pieces of ovarian tissue of known weight were then used, in conjunction with the weight of both ovarian lobes, to estimate the total number of hydrated oocytes (= batch fecundity) that would have been present in the pair of ovarian lobes of each fish.

2.4 AGE AND GROWTH

The two sagittal otoliths of each individual of each species were removed, cleaned, dried and stored in paper envelopes. Whole otoliths were placed in methyl salicylate and examined under reflected light against a black background using a dissecting microscope. For each species, the number of opaque zones in whole otoliths of 100 fish was compared with those recorded for the same otoliths after they had been sectioned. For sectioning, one of the otoliths of each fish was mounted in clear epoxy resin and cut along the same plane into *ca* 300 µm thick sections using a low speed diamond saw (Buehler). The sections were cleaned and mounted on slides using DePX mounting medium and examined under reflected light, employing a dissecting microscope attached to a video camera (Leica DC 300). The image was analysed using the Leica computer imaging package IM1000. The 100 otoliths were chosen so that overall they contained a wide range in the numbers of opaque zones. Since sectioning did not improve the resolution of the opaque zones in any of the otoliths of *E. tetradactylum* and *P. macrochir*, whole otoliths were used for ageing these species (**Plate 2.1**). However, as opaque zones were typically more easily discernible in the sectioned than whole otoliths of *E. coioides*, *E. malabaricus* and *L. argentimaculatus*, sectioned otoliths were used for ageing these three species. The opaque zones in all otoliths were counted without knowledge of the size or time of capture of the fish from which the otolith had been removed.

Marginal increment analysis was used to validate that a single opaque zone is formed annually in the otoliths of each of the five species. For this purpose, the marginal increment, *i.e.* the distance between the outer edge of the single or outermost opaque zone and the edge of the otolith (L_1 in **Plate 2.2**), was measured and expressed in one of the following ways. 1) As a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one such zone was present (L_2 in **Plate 2.2**) or 2) as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present (L_2 in **Plate 2.3**). All measurements were made perpendicular to the opaque zones and along the long posterior axis of whole otoliths and close to the sulcus in the case of sectioned otoliths. The marginal increments were measured without knowledge of the date of capture or length of the fish from which that otolith had been removed. The data for otoliths with corresponding numbers of opaque zones in corresponding months of the year were pooled.

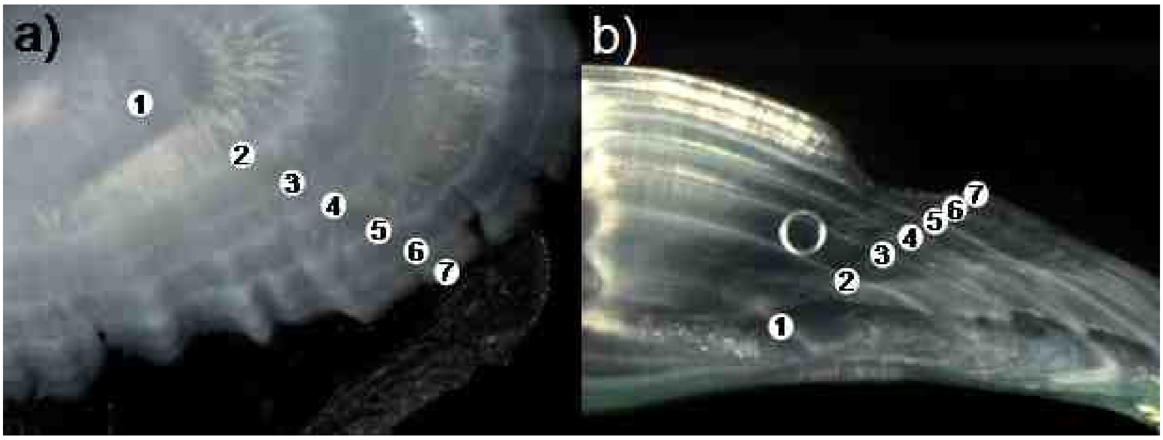

Plate 2.1. a) A whole otolith of a 1143 mm (TL) *Polydactylus macrochir* and b) the same otolith after sectioning. Seven zones are visible prior to and after sectioning of the otolith

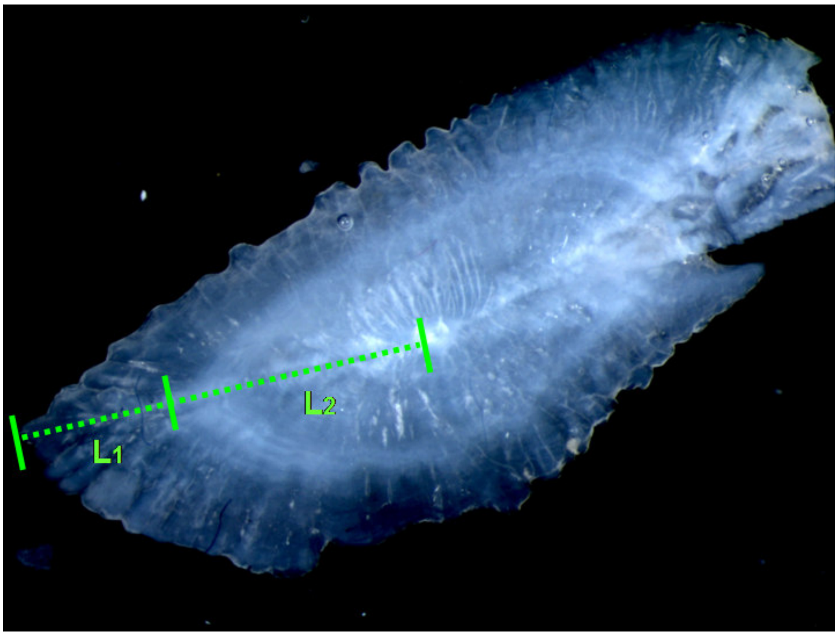

Plate 2.2. A whole otolith of *Eleutheronema tetradactylum* (383 mm TL) showing the measurements used for marginal increment analysis when only one opaque zone was present. L_1 = distance between the opaque zone and the otolith edge, *i.e.* the marginal increment; L_2 = distance between the primordium and the outer edge of the opaque zone.

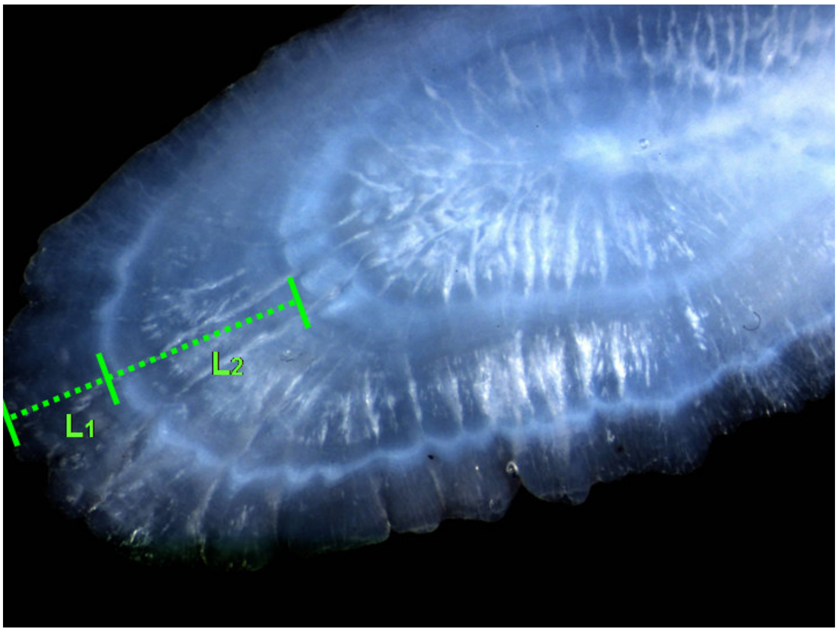

Plate 2.3. A whole otolith of *Polydactylus macrochir* (827 mm TL) showing the measurements used for marginal increment analysis when more than one opaque zone was present. L_1 = distance between the outer edge of the outermost opaque zone and the otolith edge, *i.e.* the marginal increment; L_2 = distance between the outer edges of the penultimate and ultimate opaque zones.

The middle of the spawning period of each species, determined from the trends throughout the year in mean monthly GSIs, gonadal maturity stages and pattern of oocyte development, was assigned as the birth date of each species. Monthly samples of small fish which, from length-frequency distributions, were determined to belong to the 0+ age class were used to confirm that the first opaque zone was laid down in the first winter of life. The age of each individual of each species on their date of capture was determined using the assigned birth date of the species, the number of opaque zones in their otoliths and the time of year when the opaque zone becomes delineated from the edge of the otolith.

Since *E. tetradactylum*, *P. macrochir*, *E. coioides* and *E. malabaricus* undergo a change of sex with increasing age (see later), a single von Bertalanffy growth curve was fitted to the lengths at age of the individuals of these species. In the case of *L. argentimaculatus,* which is gonochoristic (see later), growth curves were fitted to the lengths at age of both males and females. The von Bertalanffy growth equation is $L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$, where L_t is the predicted total length at age *t* years, L_∞ is the asymptotic length predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age at which fish would have zero length. The von Bertalanffy growth curves were fitted by minimizing the sum of squares, using SOLVER in Microsoft Excel™. The data were randomly resampled and analysed to create 1000 sets of bootstrap estimates for the parameters of the von Bertalanffy growth equation. The point estimate for each parameter was taken as the median of the 1000 bootstrap estimates. The 95% confidence limits for the von Bertalanffy growth parameters were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values.

A likelihood-ratio test was used to compare the growth curves for *E. tetradactylum* and *P. macrochir*, for *E. coioides* and *E. malabaricus*, and to compare those of the females and males of *L. argentimaculatus*. The hypothesis of a common growth curve for the two sexes (or two species) was rejected at the $\alpha = 0.05$ level of significance if the test statistic, calculated as twice the difference between the log-likelihoods obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex (or species) exceeded $\chi_{\alpha}^{2}(q)$, where q is the difference between the numbers of parameters, *i.e.* 3, in the two approaches (*e.g.* Cerrato, 1990).

2.5 MORTALITY

The instantaneous coefficients for total mortality, *Z*, and natural mortality, *M*, for each species were estimated using the approach of Hall *et al.* (2004), which was developed during a previous FRDC project (2000/137). This method combines the various estimates of mortality and takes into account the fact that *M* should not exceed *Z*. The following is a summary of the methods for deriving each of the individual mortality estimates and of the method of Hall *et al.* (2004) for combining the various results.

An estimate of the instantaneous coefficient of total mortality, *Z*, was determined for each species using relative abundance (catch-curve) analysis (Deriso *et al.*, 1985). The age at full recruitment to the exploited stock of each of the five species was determined by developing an age-frequency histogram for each of those species. The mortality estimates were derived from the age classes that were located on the descending limb of the age-frequency distribution to the fishery (Ricker, 1975). The catch curves for each species were analysed using the assumptions that Z and the levels of annual recruitment are constant and that the age composition of fully-recruited fish represents a random sample from a multinominal distribution with uniform selectivity from the age of full recruitment (Hall *et al.*, 2004). The value of Z was estimated by maximising the log-likelihood using the SOLVER routine in Microsoft Excel™. The data for each species were randomly resampled with replacement and the resulting samples were analysed to create 10,000 sets of bootstrap estimates. The point estimate of Z was taken as the median of the 10,000 bootstrap estimates. The 95% confidence limits were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values.

A second estimate of Z was obtained for each of the five species using the relationship between total mortality and maximum age, as described by the equation of Hoenig (1983) for fish. This relationship was refitted to the data given for the 82 fish stocks provided in Hoenig (1982). For each species, the maximum recorded age was then inserted into the Statistical Package for the Social Sciences (SPSS Inc., Chicago III) to obtain point estimates and associated 95% confidence limits, thereby taking into account the uncertainty of the parameter estimates and the variation of the data around the regression line.

A third estimate of Z was determined for each of the five species using the simulation approach described by Hall *et al*. (2004). To provide more precise estimates for Z when using the simulation approach, the routine was modified slightly from that described by Hall *et al.* (2004) so that it employed, within each of the samples, the number of fish that were as old or older than a specified age, rather than the age associated with the oldest of those fish. The specified ages for *E. tetradactylum*, *P. macrochir*, *E. coioides*, *E. malabaricus* and for *L. argentimaculatus* in both the Pilbara and Kimberley regions, were 4, 7, 14, 16 and 46 and 40 years, respectively, and the number of fish above those ages were 9, 7, 5, 5 and 6 and 4 individuals, respectively. The three estimates of Z derived for each species were then combined, using the Bayesian approach of Hall *et al.* (2004).

Estimates of natural mortality M for each of the five species were calculated from the relationship between natural mortality, growth and water temperature as described by Pauly (1980). This relationship was refitted to Pauly's data for 175 fish stocks using SPSS. The values of k (year^{-1}) and L_∞ (cm TL) in the growth curves derived for each species, and mean annual surface water temperature, T, were then inserted into SPSS to obtain point estimates and associated 95% confidence limits for M. The mean annual surface water temperature used for each species was 26.9 °C, which is the mean temperature derived from data recorded by the Australian Oceanographic Data Centre http://www.AODC.gov.au for the region between Karratha and Broome.

The Bayesian approach of Hall *et al*. (2004) was used to determine, for each species, the likelihood for M, calculated using the combined likelihood for Z. The calculation assumed that, for each value of Z, there is a uniform probability that $M < Z$ (Hall *et al.*, 2004). The resulting likelihood for M was then combined with the estimate for M derived from the Pauly (1980) equation.

A Monte Carlo resampling approach was used to derive estimates of F for each species. Estimates of Z and M were randomly resampled, with replacement, from their respective probability distributions (*i.e.* combined Z estimate and Pauly (1980) estimate for M), but were rejected when corresponding values for M were greater than for Z. These values were used to produce 5000 estimates for F, determined using the equation $F = Z - M$. The point estimate of F and associated 95% confidence limits were taken as the median value and the 2.5 and 97.5 percentiles of the 5000 estimates derived from the re-sampling analysis.

2.6 YIELD AND SPAWNING BIOMASS PER RECRUIT

The yield per recruit (YPR) and spawning stock biomass per recruit (SSB/R) for each species were calculated assuming knife-edge recruitment at the age of full recruitment t_c, constant total mortality for fully-recruited fish and a maximum age of 50 years. Yield per recruit was calculated as $YPR = \sum_{a=t_c}^{50} \frac{F}{Z}(1 - e^{-Z})W_a \exp(-Za)$, where F refers to the estimated current level of fishing mortality and where W_a, the total body weight at age a, was determined from the predicted length at age determined using the von Bertalanffy growth curve for that species and employing the relationship between total body weight (g) and length (mm) for each of the five species. The values for the fishing mortality that maximises YPR, F_{max}, and that at which the derivative of YPR with respect to F is one tenth of that at the origin, $F_{0.1}$, were estimated numerically in Excel™. These two values were used as the biological reference points for fishing mortality for each species against which the estimate of the current level of fishing mortality was compared (Hilborn and Walters; 1992, Haddon, 2001).

The SSB/R for the females and males of each species was calculated as $SSB/R = \sum_{a=t_c}^{50} W_a P_{sex,a} P_{mat,a} \exp(-Za)$. W_a, the total body weight at age a, was determined from the length at age predicted using the von Bertalanffy growth curve and employing the total body weight (g) to length (mm TL) relationship. In the case of the hermaphroditic species, $P_{sex,a}$, the proportion of that sex at age a, was determined using the logistic function relating the proportion at each length of that sex and the von Bertalanffy growth equation for that species. For the protandrous species, $P_{sex,a}$ for males was calculated as 1 minus the proportion of fish that had changed sex from male to female. Similarly, for protogynous species, $P_{sex,a}$ for females was calculated as 1 minus the proportion of fish that had changed sex from female to male. For the gonochoristic *L. argentimaculatus*, $P_{sex,a}$ was always assumed to equal 0.5. For all species, the calculation for the proportion of mature fish at age a, *i.e.* $P_{mat,a}$, was determined using the logistic function relating the proportion of mature fish to length, and the length at age predicted using the von Bertalanffy growth function.

Estimates for the current levels of YPR and SSB/R were determined for each of the 5000 values generated for F derived from the Monte Carlo re-sampling procedure. The point estimates and associated 95% confidence limits for the current level of YPR and SSB/R for each species were taken as the median and 2. 5 and 97.5 percentiles of the resulting YPR and SSB/R values. The spawning potential ratio, SPR, was calculated as the ratio of SSB/R at a specified level of fishing mortality to that estimated for an unfished population (Goodyear, 1993).

3. BIOLOGY OF THE BLUE THREADFIN *ELEUTHERONEMA TETRADACTYLUM* AND THE KING THREADFIN *POLYDACTYLUS MACROCHIR.*

3.1 INTRODUCTION

The Polynemidae (threadfins) is a percoid family that comprises approximately 40 species which are found in coastal marine waters, estuaries or rivers in the tropics (Feltes, 1991; Motomura, 2004a, b). They typically live in shallow, turbid inshore waters, where they often occur in large numbers, and several species attain a relatively large size (Mukhopadhyay *et al.*, 1995; Motomura, *et al.*, 2002; Motomura, 2004b). Threadfin species are highly regarded for their eating qualities and form the basis of important commercial, recreational and subsistence fisheries. Although they typically grow rapidly (Gopalakrishnan, 1972; Kagwade, 1973) and reach maturity early in life (Dentzau & Chittenden, 1990; Szyper *et al.*, 1991), the yields of some threadfin species in certain regions have declined so markedly in recent years that the commercial fisheries for those stocks have virtually collapsed (Abohweyere, 1989; Szyper *et al.*, 1991; Bensam & Menon, 1994).

The susceptibility of certain threadfin species to fishing pressure has been attributed mainly to the consequence of their being protandrous hermaphrodites, *i.e.* maturing first as males and then changing sex to females with increasing size and age (Bensam & Menon, 1994; Friedlander & Ziemann, 2003; Poepoe *et al.*, 2003). This conclusion is based on the fact that, as fishing pressure is typically biased toward the larger individuals in a population, it is the females of protandrous species that will be subjected to the greatest fishing mortality (Milton *et al.*, 1998; Blaber *et al.*, 1999). Heavy fishing pressure on such species will thus have a particularly severe effect on the total production of eggs by the population and thus potentially lead to recruitment overfishing (Blaber *et al.*, 1996, 1999; Friedlander & Ziemann, 2003; Ley & Halliday, 2004). For this reason, it is crucially important that the development of management plans for sustaining the stocks of such species is based on a thorough understanding of the sizes and ages over which sex change occurs and thus of the implications of such changes (Buxton, 1992; Hesp *et al*., 2004a; Blaber *et al*., 2005).

Blue and King Threadfins live in shallow, turbid nearshore and estuarine waters and have a common tropical distribution in northern Australia, occurring from approximately the Ashburton River in Western Australia at *ca* 21°S 115°E to near the border of Queensland and New South Wales at *ca* 28°S 153°E. Although *P. macrochir* is only otherwise found in southern Papua New Guinea, *E. tetradactylum* occurs northwards from Australia to China and Japan and the Persian Gulf in the west (Feltes, 1999; Motomura *et al*., 2000; 2002).

Although the majority of threadfin species are apparently protandrous hermaphrodites, a few are gonochoristic (*cf*; Hida, 1967; Kagwade, 1970; Dorairaj, 1973; Santerre & May, 1977; Dentzau & Chittenden, 1990). Furthermore, there is evidence that *E. tetradactylum* is hermaphroditic in certain regions and gonochoristic in others. For example, it is protandrous in eastern Australia (Stanger, 1974; Russell, 1988; McPherson, 1997), but gonochoristic in India (Patnaik, 1967, 1970; Gopalakrishnan, 1972) and apparently also in Singapore (Chao *et al*., 1994). Moreover, *E. tetradactylum* attains far greater total lengths in Indian waters, *i.e.* 1800-2000 mm (Gopalakrishnan, 1972; Krishhnamurthy & Jeyaseelan, 1981; Feltes, 1999) than in Australian waters, *i.e. ca* 1000 mm (Kailola, 1993).

Polydactylus macrochir has been shown to be a protandrous hermaphrodite in the coastal waters of Queensland and the Northern Territory (Garrett, 1992; R. Griffin unpubl. data, cited in Kailola, 1993; McPherson, 1997). However, there is evidence that the size and age at which this species attains maturity as a male and changes from male to female differs considerably among populations and that the spawning period varies with latitude (N.T. Fisheries, unpublished data; Garrett, 1992; McPherson, 1997). Moreover, estimates of the fork lengths at which the males of this species reach maturity in the eastern part of the Gulf of Carpentaria ranged from as low as *ca* 280 mm (McPherson, 1997) to as high as 600-800 mm (Garrett, 1992). The possibility that at least some of the variations among the biological characteristics of *P. macrochir*, and also of *E. tetradactylum*, may be due to genetic differences among populations, is consistent with the results of allozyme and mitochondrial DNA studies carried out by Keenan (1997) and Chenoweth & Hughes (2003), respectively.

The overall aim of the present study was to obtain, for the first time, sound quantitative data on crucial aspects of the biology of *E. tetradactylum* and *P. macrochir* in Western Australia. The individual aims, which were the same for both species, were as follows. 1. Describe the trends exhibited by commercial catch data since the late 1980s. 2. Confirm that, as elsewhere in Australia, these species are protandrous hermaphrodites, in Western Australia. 3. Determine the length and age at which maturity is attained and sex change occurs. 4. Determine the timing and duration of the spawning period and whether fecundity is determinate or indeterminate and if spawning occurs on several occasions during a spawning period. 5. Determine the size and age compositions and growth characteristics. 6. Estimate total, natural and fishing mortality. 7. Estimate the current level of yield per recruit, spawning biomass per recruit and spawning potential ratio.

3.2 MATERIALS AND METHODS

Unless otherwise recorded below, the methods used in this study of *Eleutheronema tetradactylum* and *Polydactylus macrochir* are those described in the General Materials and Methods (Chapter 2).

3.2.1 Reproductive studies

The subsequent results and discussion provide overwhelming evidence that, as elsewhere in Australia, *E. tetradactylum* and *P. macrochir* are protandrous hermaphrodites in Western Australian waters. Thus, when both testicular and ovarian tissues were observed in the gonad of a fish, that fish was recorded as transitional between male and female. The gonads of each transitional fish were removed and weighed and their testicular and ovarian components each assigned a maturation stage (see Chapter 2). The mid-region of each transitional gonad was cut transversely and the cross-sectional areas of its testicular and ovarian components were then estimated subjectively. This enabled the approximate percentage contributions of each of those components to be calculated. N.B. Preliminary studies demonstrated that, in transitional gonads, the proportions of each component were similar throughout the length of both gonadal lobes. The proportions of testicular and ovarian components in each gonad of transitional fish were used, in conjunction with the total weight of that gonad and of the fish, to obtain approximate GSI values for both components.

The lengths and ages at the attainment of maturity and lengths at the initiation and completion of sex change of *E. tetradactylum* and of sex change in *P. macrochir* were derived (see Chapter 2) using data obtained for fish collected by our seine netting and composite gill netting and by recreational fishers.

3.2.2 Catch rates and densities

The number of *E. tetradactylum* and *P. macrochir* in each replicate gill net and seine net sample were converted to a catch rate, *i.e.* number of individuals caught $3h^{-1}$, and a density, *i.e.* number of individuals 100 m^{-2}, respectively. An examination of the relationship between the mean and standard deviation for catch rates and densities showed that, prior to subjection to analysis of variance (ANOVA), both of these variables should be $\log_{10}$ (n+1) transformed (see Clarke & Gorley (2001) for rationale for this approach).

The transformed catch rates in the replicate samples of both *E. tetradactylum* and *P. macrochir* over bare sand at Port Smith, Eighty Mile Beach and Cape Keraudren in each season were subjected to two-way ANOVA to determine whether catch rates in this type of habitat differed among these three regions and seasons. Next, the transformed catch rates over bare sand and in mangroves at Port Smith and Cape Keraudren were subjected to three-way ANOVA to determine whether catch rates differed among regions and seasons and between sand and mangrove habitats in these two regions. N.B. Mangroves are not found at Eighty Mile Beach and the data for summer were not included in these analyses as poor weather conditions prevented the collection of gill net samples from Cape Keraudren during this season. When ANOVA showed that the values for one or more of the main effects were significantly different and there were no significant interactions between those effects, Scheffé's *a posteriori* test was used to determine which values were significantly different. When there was a significant interaction between the main effects, the back-transformed mean values for these effects were plotted to explore the basis for the interaction.

In the case of *E. tetradactylum*, estimates of total mortality (*Z*), natural mortality (*M*) and fishing mortality (*F*) were derived using data that we collected directly from the large catches obtained by recreational anglers fishing between Dampier and Broome. These catches were considered to represent best the population of *E. tetradactylum* in this region. However, as recreational catches of *P. macrochir* sampled during this study were not substantial, the length data for the fish in those catches were supplemented by those recorded by other workers as part of a recreational tagging program (WESTAG). The ages of fish in the latter database were derived from their lengths using the inverse of the von Bertalanffy growth equation for this species. The data for the study of *P. macrochir* were collected in the region between Dampier and Port Headland.

3.3 RESULTS

3.3.1 Trends exhibited by catch statistics

The total catch of *E. tetradactylum* in the Pilbara and Kimberley regions typically ranged between 22 and 44 tonnes between 1988 and 1997 and then declined markedly to *ca* 10 tonnes between 2000 and 2002, before recovering to *ca* 20 tonnes in 2004 (**Figure 3.1**). In general, the catches in the Pilbara and Kimberley followed similar relative trends between 1988 and 2004. In contrast to the situation with *E. tetradactylum*, the total catches of *P. macrochir* were generally relatively low between 1988 and 1995, *i.e.* < 30 tonnes, but then rose markedly and remained at > 100 tonnes between 1997 and 2004 (**Figure 3.1**). The annual catches of *P. macrochir* in the Pilbara and Kimberley were relatively similar.

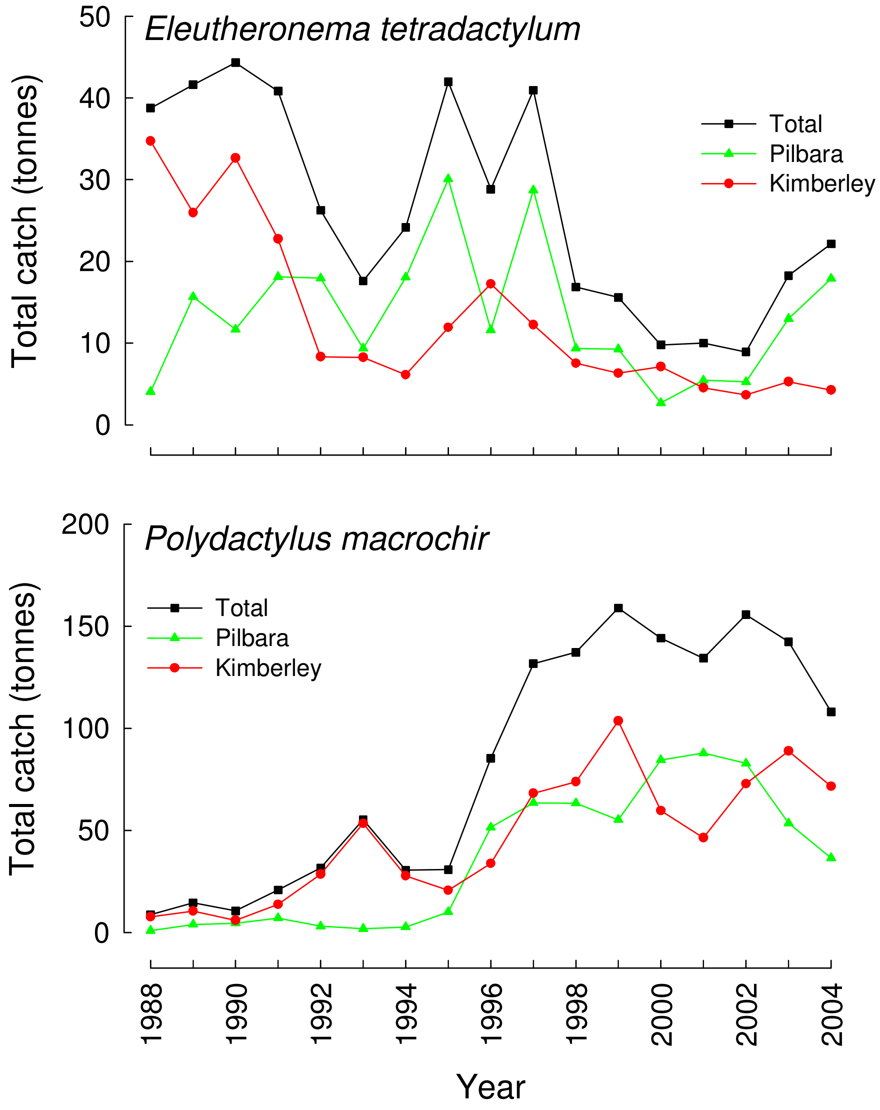

Figure 3.1. Commercial catch (tonnes) of Blue Threadfin *Eleutheronema tetradactylum* and King Threadfin *Polydactylus macrochir* in north-western Australia in each year between 1988 and 2004.

3.3.2 Characteristics of testes, ovaries and transitional gonads

The vast majority of the paired gonads of the 1348 *Eleutheronema tetradactylum* (85.3%) and the 1662 *Polydactylus macrochir* (96.0%) that were examined were able to be designated macroscopically as comprising of either testicular or ovarian tissue and to be assigned a maturity stage. Thus, the individuals of each of these two species with such well defined gonads could typically be identified as male or female and assessed as to their reproductive status. The macroscopic characteristics of the different stages in the development and maturation of the definitive testes and ovaries of *E. tetradactylum* and *P. macrochir* together with the cytological characteristics of each of those stages, are presented in **Tables 3.1 and 3.2** and illustrated in **Figures 3.2 and 3.3.** Histological sections of the gonads of a random subsample of approximately 20 such fish in each month were used to confirm that these fish contained exclusively either testicular or ovarian tissue. However, some of the other individuals of *E. tetradactylum* (14.7%) and *P. macrochir* (4.0%) clearly contained both testicular and ovarian tissue, the ratios of which varied markedly. In a minority of these cases, the minor component was barely detectable, *i.e*. contributed < 5% of the gonad, or the gonads did not have the typical appearance of a testis or an ovary, *i.e.* was atypically pink and possessed a thin white strand on its dorsal surface. The gonads in which the minor component contributed < 5% or there was some doubt as to whether there was a second component were subjected to histology. The resultant histological sections demonstrated that all samples of this type of gonad contained both testicular and ovarian material.

Table 3.1. Characteristics of the macroscopic stages in the development of the testes of *Eleutheronema tetradactylum* and *Polydactylus macrochir*, together with their corresponding histological characteristics.

Stage	Macroscopic characteristics	Histological characteristics
I/II Virgin and Immature / resting	Testes very small, grey and strand-like (stage I) to white and ribbon-like (stage II).	Dominated by large amounts of connective tissue. Stage II testes have numerous crypts containing spermatocytes, spermatids and some spermatozoa which are present in all subsequent testicular stages.
III Developing	Testes white. Occupy approximately half the length of the ventral cavity.	Large amounts of connective tissue still obvious, crypts containing spermatozoa proliferating, spermatids and spermatozoa congregate near the centre of the testes in sperm sinuses close to the now obvious sperm duct.
IV Maturing	No milt appears when pressure is applied to the trunk of males. Occupy greater than half of the length of the ventral cavity.	Sperm duct well developed and usually full of spermatids and spermatozoa. Sperm sinuses are well developed close to sperm duct and typically occupy up to half the area of testis.
V/VI Mature / spawning	Gonads 1/3 to filling ventral cavity. Milt appears from testes with firm pressure to trunk.	Sperm duct and the majority of testis full of spermatids and spermatozoa. Often difficult to distinguish between sperm duct and sinuses. Crypts of spermatozoa are usually confined to the outer perimeter of the testis.
VII Spent	Gonads smaller than stage V or VI. Testes flaccid though not fully empty.	Large numbers of spermatids and spermatozoa are still obvious in sperm sinuses and duct. However, large spaces empty of sperm are also present within the connective tissue.
VIII Recovering	Testes red to brown, small and flaccid.	Testes dominated by connective tissue containing large spaces and containing no sperm. Fewer crypts containing spermatozoa tha in other stages.

Table 3.2. Characteristics of the macroscopic stages in the development of the ovaries of *Eleutheronema tetradactylum* and *Polydactylus macrochir*, together with their corresponding histological characteristics. Macroscopic criteria 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. Oocytes visible through ovarian wall.	Chromatin nucleolar, perinucleolar and cortical alveolar oocytes present.
IV Maturing	Larger than stage III, occupying about half of the body cavity. Creamy orange in colour. Large oocytes visible through ovarian wall.	Cortical alveolar and yolk granule oocytes abundant.
V/VI Mature / spawning	Large, occupying about half to two thirds of body cavity. Extensive capillaries visible in ovarian wall. Hydrated oocytes sometimes visible through ovarian wall in stage VI ovaries. Ovaries of *P. macrochir* typically with lateral undulations anteriorly.	Yolk granule oocytes abundant. Migratory nucleus oocytes, hydrated oocytes and/or post-ovulatory follicles present in stage VI 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 connective tissue present throughout ovaries.
VIII Recovering	Small, flaccid and dark red. Inconsistencies in wall thickness of *P. macrochir* ovaries gives a concertina appearance.	Extensive connective tissue present. Ovarian lamellae disorganised. No remnant yolk granule oocytes.

The results provide overwhelming evidence that, as elsewhere in Australia, *E. tetradactylum* and *P. macrochir* in Western Australian waters are protandrous hermaphrodites. Furthermore, histological sections demonstrated that the development and maturation of the testes and ovaries and the reorganisation of the gonad during its change from testis to ovary are essentially the same in both *E. tetradactylum* and *P. macrochir*.

Fish with gonads with both testicular and ovarian components, and which are thus assumed to be changing from male to female, are, for convenience, subsequently referred to as transitional individuals. In these transitional individuals, the testicular tissue is located along the dorsal and inner lateral regions of the paired gonads, whereas

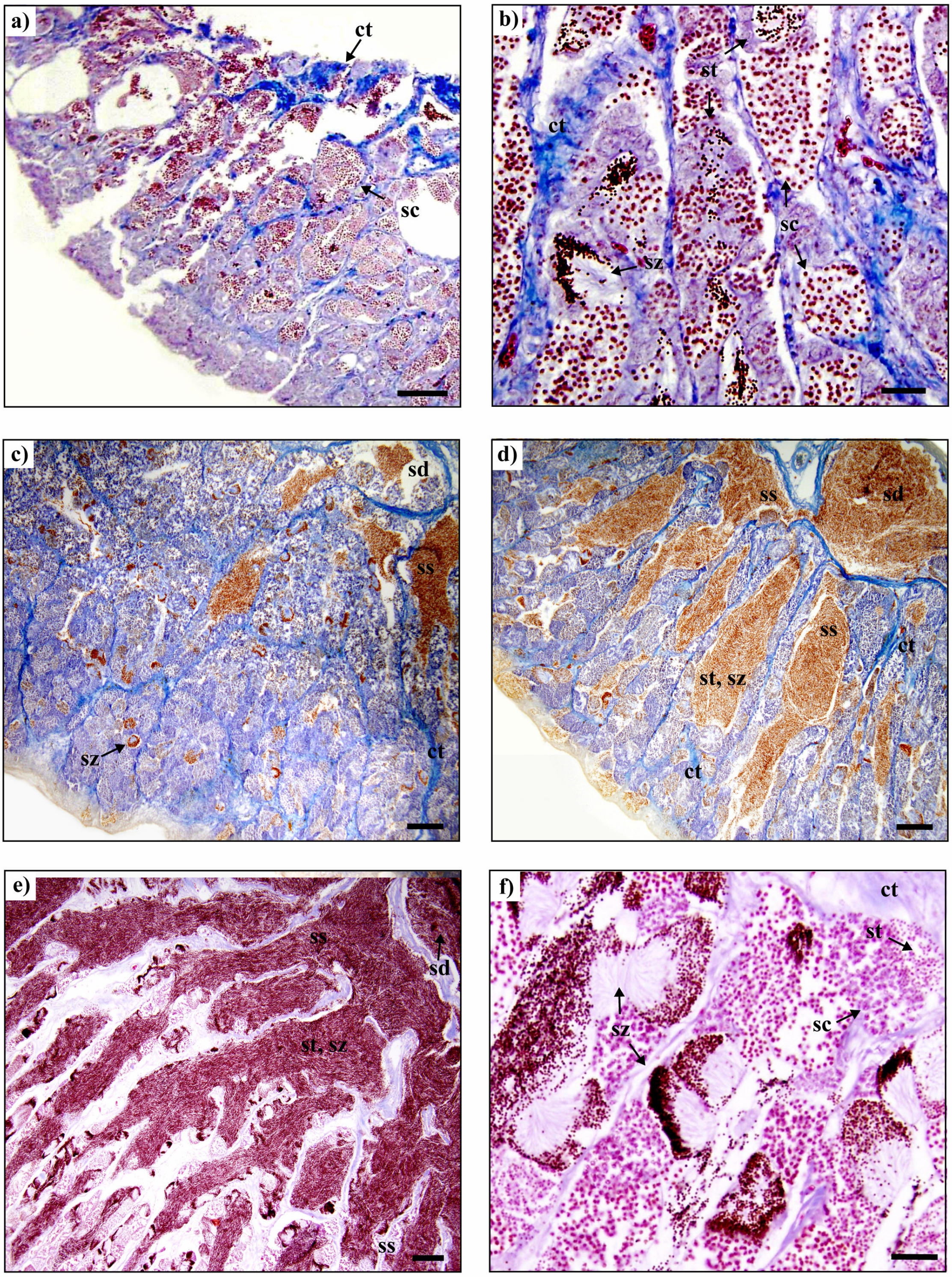

Figure 3.2. Histological sections showing selected stages in the development of the testes of the males of (c-d) *Eleutheronema tetradactylum* and (a-b, e-f) *Polydactylus macrochir*. (a-b) resting (stage II) (Aug; 626 mm TL) with minimal sperm development, (c) early developing (stage III) (Sept; 311 mm TL), (d) maturing (stage IV) (Sept; 243 mm TL) and (e-f) mature (stage V) (Oct; 383 mm TL). ct, connective tissue; sc, spermatocytes; sd, sperm duct; ss, sperm sinuses; st, spermatids; sz, spermatozoa. Scale bars (a, c-e) 100 µm; (b, f) 25 µm.

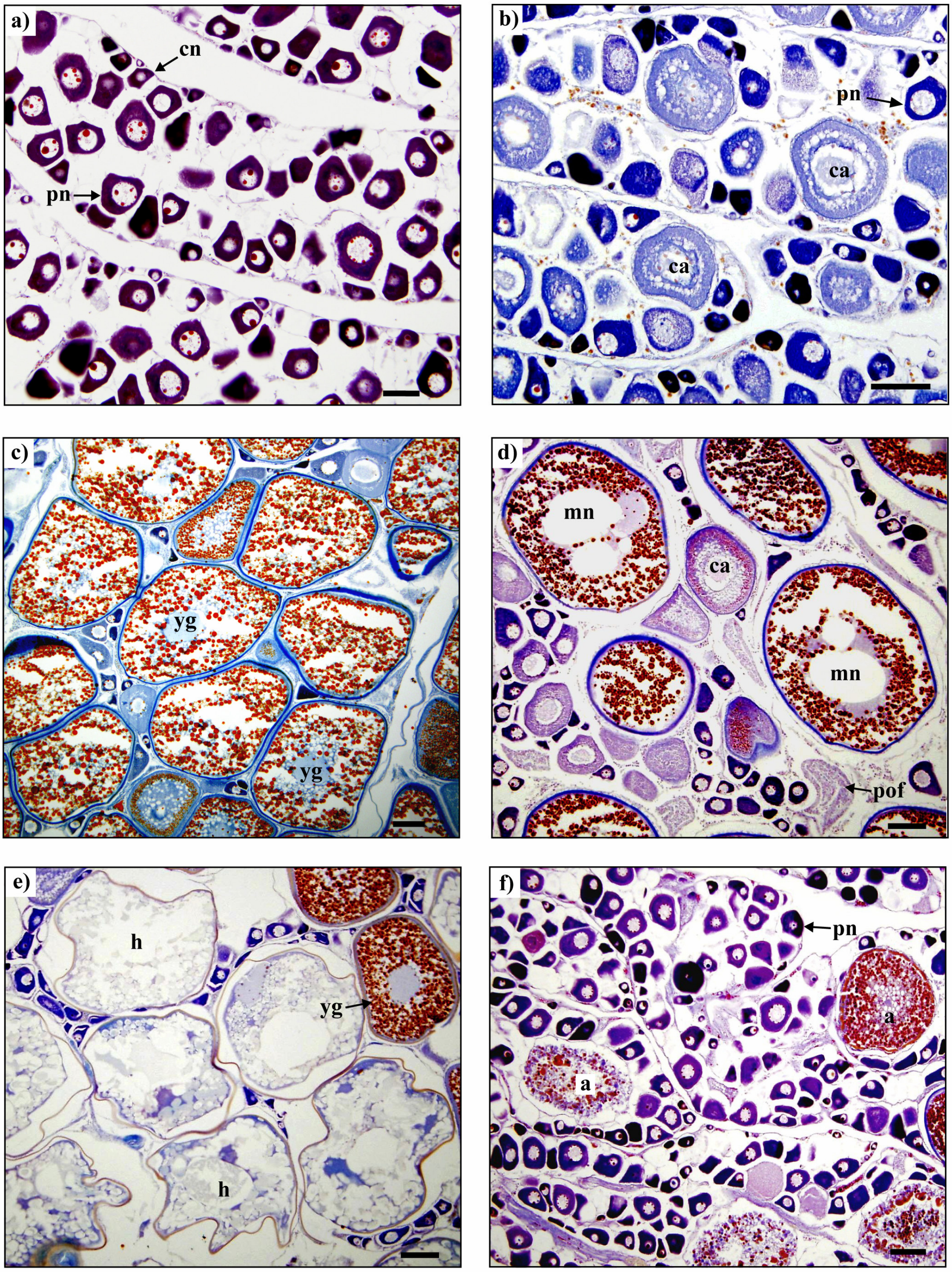

Figure 3.3. Histological sections showing selected stages in the development of the ovaries of (b-e) *Eleutheronema tetradactylum* and (a, f) *Polydactylus macrochir*.(a) resting (stage II) (Jun; 941 mm TL), (b) early developing (stage III) (Sept; 410 mm TL), (c) mature (stage V) (Sept; 525 mm TL), (d-e) spawning (stage VI) (Oct; 420 mm TL; Dec; 568 mm TL) and (f) recovering (stage VIII) (Feb; 568 mm TL). a, atretic oocyte; ca, cortical alveolar oocyte; cn, chromatin nucleolar oocyte; h, hydrated oocyte; mn, migratory nucleus oocyte; pn, perinucleolar oocyte; pof, post-ovulatory follicle; yg, yolk granule oocyte. Scale bars (a) 50 μm; (b-f) 100 μm.

the ovarian tissue occupies the ventral and outer regions (**Figure 3.4**). The testicular and ovarian components are separated by connective tissue. In transitional fish, the structure of each gonad and the ratio of testicular to ovarian tissue is essentially the same along the full length of each gonad.

Gonads in the early stages of transition from testis to ovary are white and similar in shape to that of a typical male (**Figure 3.4a**). The testicular region at this early stage of transition retains the characteristic of a typical testis and thus contains a range of stages in spermatogenesis from primary spermatocytes to spermatozoa (**Figure 3.4a, b**). The development of ovarian tissue commences with a proliferation of blood vessels and the formation of a prominent lumen along the inner wall of the gonad. Previtellogenic oocytes develop in the connective tissue that lines the luminal spaces which represent extensions of the above-mentioned prominent lumen (**Figure 3.4b**). As the transition proceeds, the testicular and ovarian components of the gonad become demarcated through the development of intervening connective tissue (**Figure 3.4c**). Although the ovarian tissue is now enlarged, the testicular tissue still contains spermatids and spermatozoa (**Figure 3.4d**). By the end of the transition of the gonad, the testicular component has become so reduced that it occupies only a short length of the dorsal surface of the gonad (**Figure 3.4e**). Many of the crypts in the testicular region are now empty and the remnant sperm are pycnotic, staining more darkly than those in the gonads of mature males, and are not tightly packed (**Figure 3.4f**). At this late stage in transition, the gonad has assumed the appearance of a typical ovary with evaginations of the prominent lumen extending throughout this structure (**Figure 3.4e**). Most of the oocytes are at an early previtellogenic stage.

3.3.3 Size and age at maturity of males

During the spawning period, all of the males of *E. tetradactylum* < 196 mm were immature, whereas all of those > 249 mm were mature (**Figure 3.5**). The L_{50} for length at maturity was 201.1 mm (**Table 3.3**). All of the males of *P. macrochir* < 202 mm were immature and all of those > 412 mm were mature and the L_{50} for maturity was 229.0 mm (**Table 3.3, Figure 3.6**). The majority of the males of *E. tetradactylum*

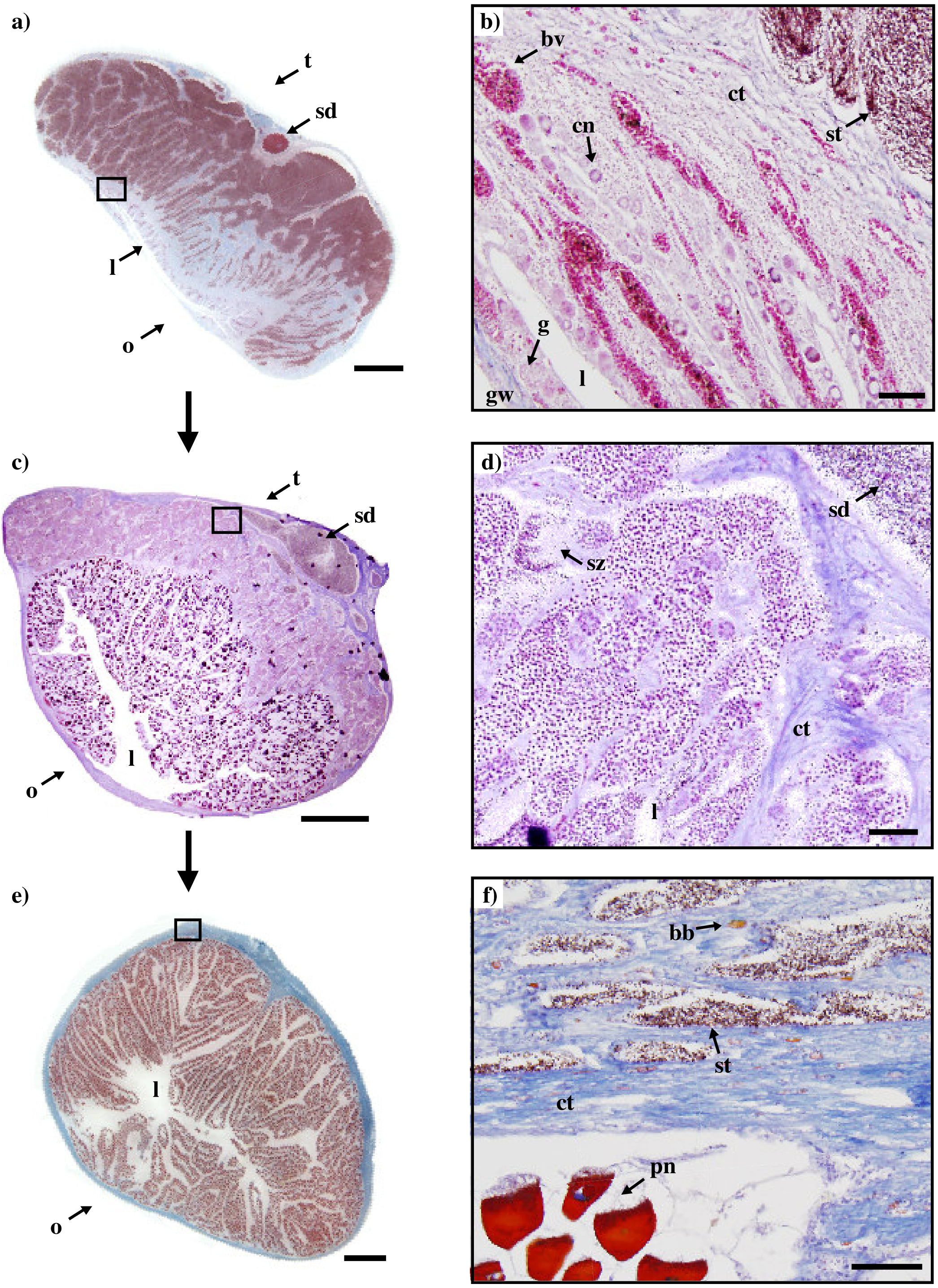

Figure 3.4. Transverse sections through the mid-region of ovotestes from (a-b) T1 - early transitional (437 mm TL), (c-d) T2 - mid transitional (313 mm TL) and (e-f) T3 - late transitional (516 mm TL) *P. macrochir* illustrating the mode of protandrous sex change including the proliferation of previtellogenic oocytes and the degeneration of testicular tissue. bv, blood vessel; cn, chromatin nucleolar oocyte; ct, connective tissue; g, oogonia; gw, gonad wall; l, ovarian lumen; o, ovary; pn, perinucleolar oocyte; sd, sperm duct; st, spermatid; sz, spermatozoa; t, testis; Scale bars (a, c) 500 μm; (b, d, f) 50 μm; (e) 1 mm.

Table 3.3. L_{50}s and L_{95}s (±95% CIs) derived from the logistic regression analysis describing the relationship between the total length and probability that an individual male of *Eleutheronema tetradactylum* and *Polydactylus macrochir* is mature.

Species	Total length at first maturity (mm)					
	L_{50}	Lower 95% CI	Upper 95% CI	L_{95}	Lower 95% CI	Upper 95% CI
Eleutheronema tetradactylum	201.1	187.2	223.7	236.7	187.9	272.7
Polydactylus macrochir	229.0	210.9	247.2	354.4	323.0	384.9

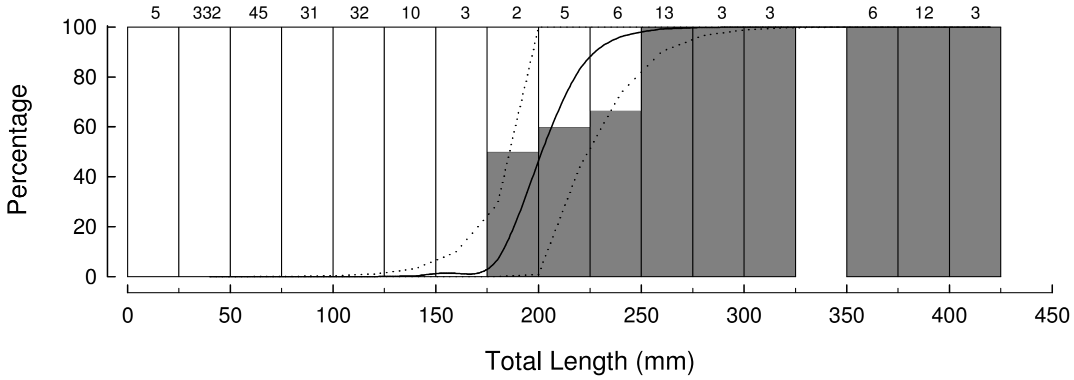

Figure 3.5. Percentage frequency of occurrence of immature (white) and mature (grey) males of *Eleutheronema tetradactylum* in each 25 mm length class during the spawning period. The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and probability that an individual was mature. Numbers above bars are sample sizes for each length category.

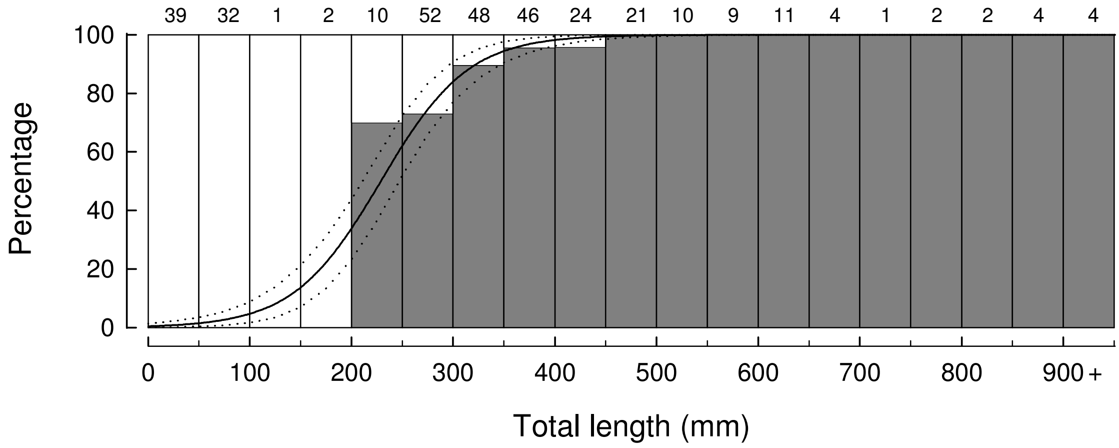

Figure 3.6. Percentage frequency of occurrence of immature (white) and mature (grey) males of *Polydactylus macrochir* in each 50 mm length class during the spawning period. The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and probability that an individual was mature. Numbers above bars are sample sizes for each length category.

(72.2%) and *P. macrochir* (84.2%) reached maturity at the end of their first year of life and all individuals of both species were mature at two years of age and older.

3.3.4 Length distributions and size and age at sex change

The lengths of *E. tetradactylum* collected using all sampling methods ranged from 20 to 793 mm, with the lengths of males, *i.e.* 20 to 413 mm, $\bar{x}$ = 119 mm, showing limited overlap with those of females, 330 to 793 mm, $\bar{x}$ = 486 mm. The length range of the transitional fish, *i.e.* 279 to 455 mm, $\bar{x}$ = 370 mm, lay at the upper end of that for males and at the lower end of that for females.

The logistic curve relating total length to the proportions of transitional individuals and females, collectively, at each length, derived from logistic regression analysis, yielded a L_{50} of 325.9 mm (**Figure 3.7**). This corresponds to the length at which 50% of *E. tetradactylum* have initiated the change from male to female. A logistic curve relating total length to the proportions of just females at each length, derived from logistic regression analysis, yielded a L_{50} of 401.9 mm (**Table 3.4, Figure 3.7**). This corresponds to the length at which 50% of *E. tetradactylum* have changed from male to female. All fish in their first year of life were males and virtually

Table 3.4. L_{50}s and L_{95}s (±95% CIs) derived from the logistic regression analysis describing the relationship between the total length and probability that an individual of *Eleutheronema tetradactylum* and *Polydactylus macrochir* has completed the change of sex to female.

	Total length at sex change (mm)					
Species	L_{50}	Lower 95% CI	Upper 95% CI	L_{95}	Lower 95% CI	Upper 95% CI
Eleutheronema tetradactylum	401.9	395.3	408.2	459.8	448.0	472.6
Polydactylus macrochir	814.3	766.3	876.6	1178.5	1073.0	1296.4

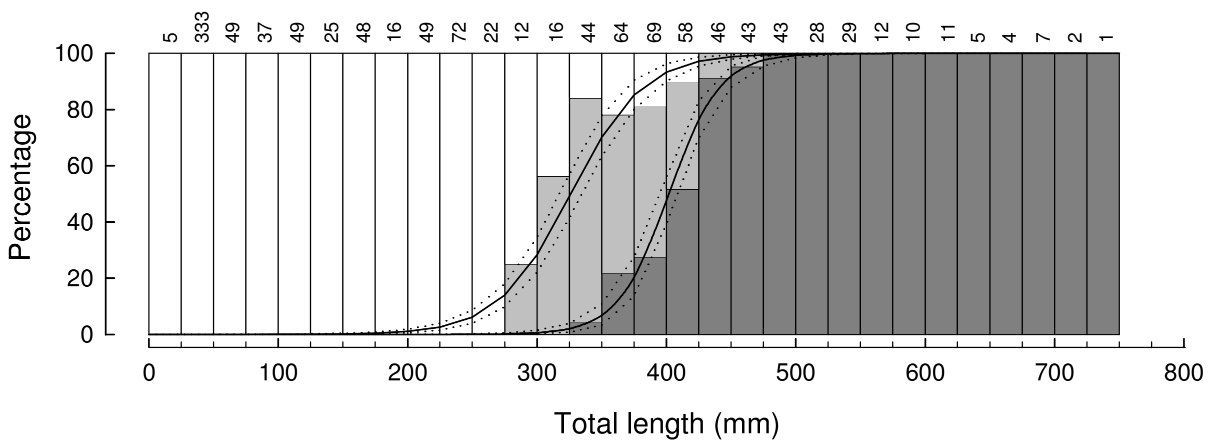

Figure 3.7. Frequencies of male (white), transitional (light grey) and female (dark grey) *Eleutheronema tetradactylum* in each 25 mm length class. The logistic curves (solid line) and their associated 95% confidence limits (dotted lines) were derived from logistic regression analyses that described the relationships between total length and the probability that an individual was, in the case of the first curve, either transitional or female, and in the case of the second curve, just female. The resultant L_{50}s correspond to the L_{50} for the initiation and completion of sex change, respectively. Numbers above bars are sample sizes for each length class.

all of those in their fourth and subsequent years of life were females (**Figure 3.8**). Fish in their second and third years of life contained males and females and also transitional individuals, with the percentage of males declining from 48.3 to 3.9% and that of females increasing from 16.7 to 75.7% between the second and third years of life (**Figure 3.8**).

The lengths of *P. macrochir* collected using all methods ranged from 19 to 1393 mm, with the lengths of males ranging from 19 to 1159 mm, ($\bar{x}$ = 558 mm) and those of females ranging from 440 to 1393 mm ($\bar{x}$ = 878 mm). In contrast to the situation with *E. tetradactylum,* where transitional fish were concentrated in a relatively narrow length range, the lengths of transitional *P. macrochir* ranged widely from a minimum of 313 mm to a maximum of 1139 mm ($\bar{x}$ = 723 mm) and typically contributed < 10% to any 50 mm length class.

In the samples collected by our seine netting and gill netting and by recreational fishers, all but three of the 539 fish < 400 mm were males and all of the fish > 1150 mm were females **(Figure 3.9**). The logistic curve relating the total length to proportions of female *P. macrochir* at each length, derived from logistic regression analysis, yielded a L_{50} of 814.3 mm (**Table 3.4, Figure 3.9**). This corresponds to the length at which 50% of *P. macrochir* complete their change to females.

All 0+ fish and virtually all 1+ *P. macrochir* were males (**Figure 3.10**). The percentage contributions of females rose progressively from 4.4% in the 1+ age class to 34.3% in the 4+ age class and 60.0% in age class 7+. Small numbers of transitional fish were found in each age class between 1+ and 7+ (**Figure 3.10**). All of the seven individuals of the 8+ and 9+ age classes collectively, which were obtained from commercial fish samples and not included in Figure 3.10, were females.

Some of the *E. tetradactylum* found in each month of the year contained transitional gonads. However, the mean monthly gonadosomatic index (GSIs) for the testicular component of transitional gonads of *E. tetradactylum* underwent pronounced seasonal changes, rising from < 0.4 in June to August to > 1.5 in September to November and then declining to 0.8 in December and < 0.3 in January and subsequent months (**Figure 3.11**). In contrast, the mean monthly GSIs for the ovarian component of

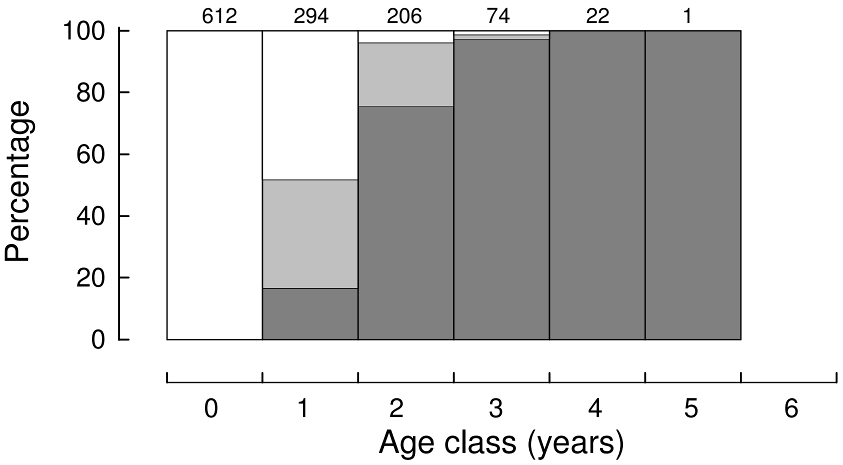

Figure 3.8. Frequencies of male (white), transitional (light grey) and female (dark grey) *Eleutheronema tetradactylum* in each age class. Numbers above bars are sample sizes for each age class.

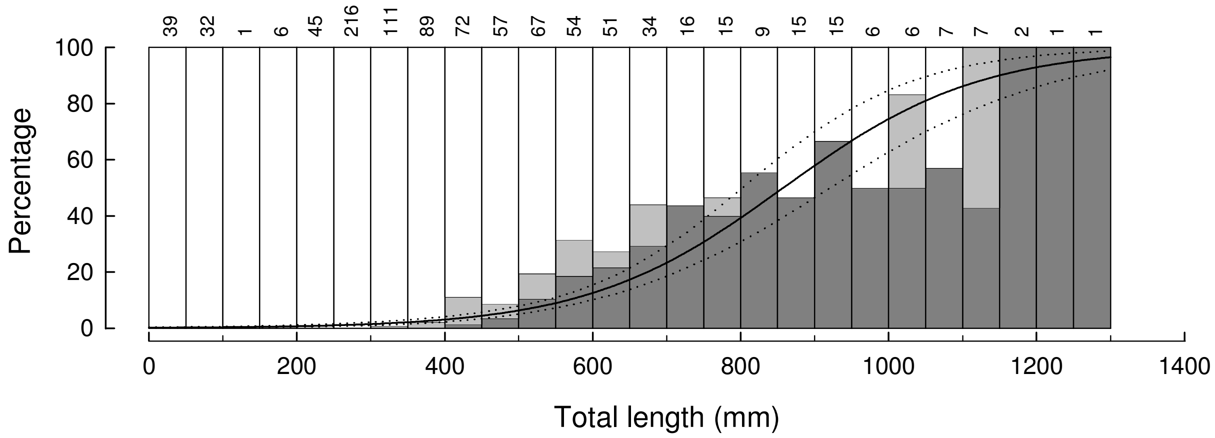

Figure 3.9 Frequencies of male (white), transitional (light grey) and female (dark grey) *Polydactylus macrochir* in each 100 mm length class collected from nearshore waters in north-western Australia. The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and probability that an individual had completed sex change to become a female. The resultant L_{50} corresponds to the completion of sex change. Numbers above bars are sample sizes for each length class.

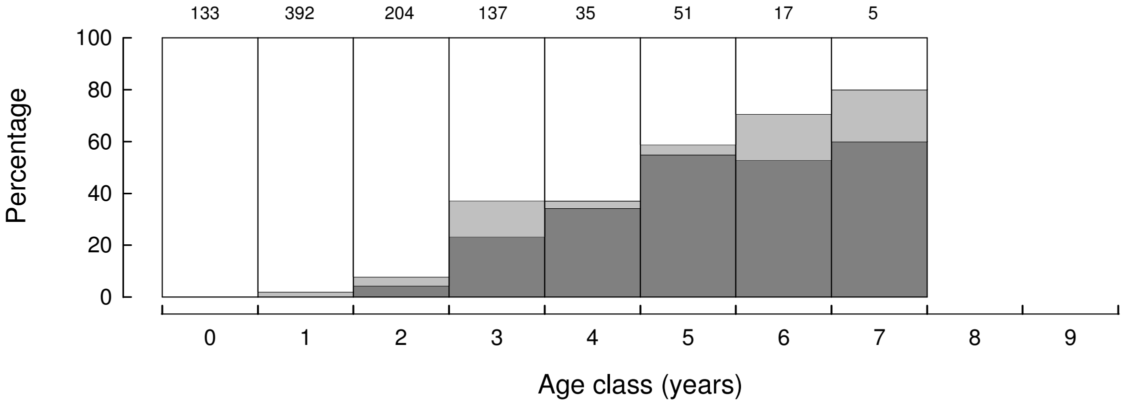

Figure 3.10 Frequencies of male (white), transitional (light grey) and female (dark grey) *Polydactylus macrochir* in each age class collected from nearshore waters in north-western Australia. Numbers above bars are sample sizes for each age category.

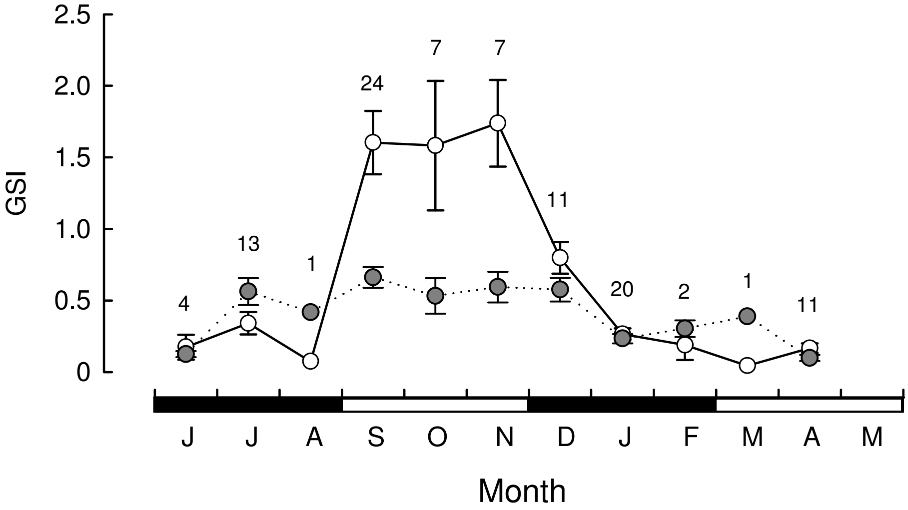

Figure 3.11 Mean monthly GSIs (±1SE) for the male (open circles) and female (closed circles) portions of the gonads of transitional individuals of *Eleutheronema tetradactylum*. Numbers above bars and points are sample sizes for each month.

transitional gonads did not undergo a pronounced seasonal change and always remained < 0.5 (**Figure 3.11**).

3.3.5 Timing and duration of spawning.

The mean monthly GSIs for male *E. tetradactylum* rose sharply from 0.3 in June to 1.4 in August and remained high during the following months, reaching a maximum of 2.2 in November and then declining to 0.2 by January (**Figure 3.12a**). The mean monthly GSIs for transitional *E. tetradactylum* followed the same seasonal trend as males, attaining a maximum of 2.7 in October (**Figure 3.12b**). Although there was a small decline in the mean monthly GSIs for female *E. tetradactylum* in October, they otherwise showed a very consistent seasonal trend, rising progressively through winter and reaching a maximum in spring, with values > 3 in September and November, and then declining sequentially during summer and early autumn (**Figure 3.12c**).

Female *E. tetradactylum* with resting ovaries (stage II) were caught in all months between January and August and this ovarian stage was the only one found in females sampled between March and June (**Figure 3.13**). Fish were first observed with developing gonads (stages III and IV) during July and by the following month constituted *ca* 80% of all females. A small percentage of females possessed mature ovaries (stages V and VI) in the latter month. Females of *E. tetradactylum* with mature ovaries were caught during the next five months, with their percentage contributions peaking at *ca* 85% in September and December. Fish with spent and recovering ovaries (stages VII and VIII) were found between October and February. No mature individuals were recorded between February and July (**Figure 3.13**).

The ovaries of the two spawning (stage VI) females of *E. tetradactylum* examined both contained oocytes at each developmental stage between the chromatin nucleolar and yolk granule stage (**Figure 3.14**). The distributions of the oocyte diameters were essentially continuous in the first ovary, but formed two groups in the second ovary. The difference is due to the fact that the yolk granule oocytes in the second ovary were larger, producing a modal class at 375-399 mm. The distributions of

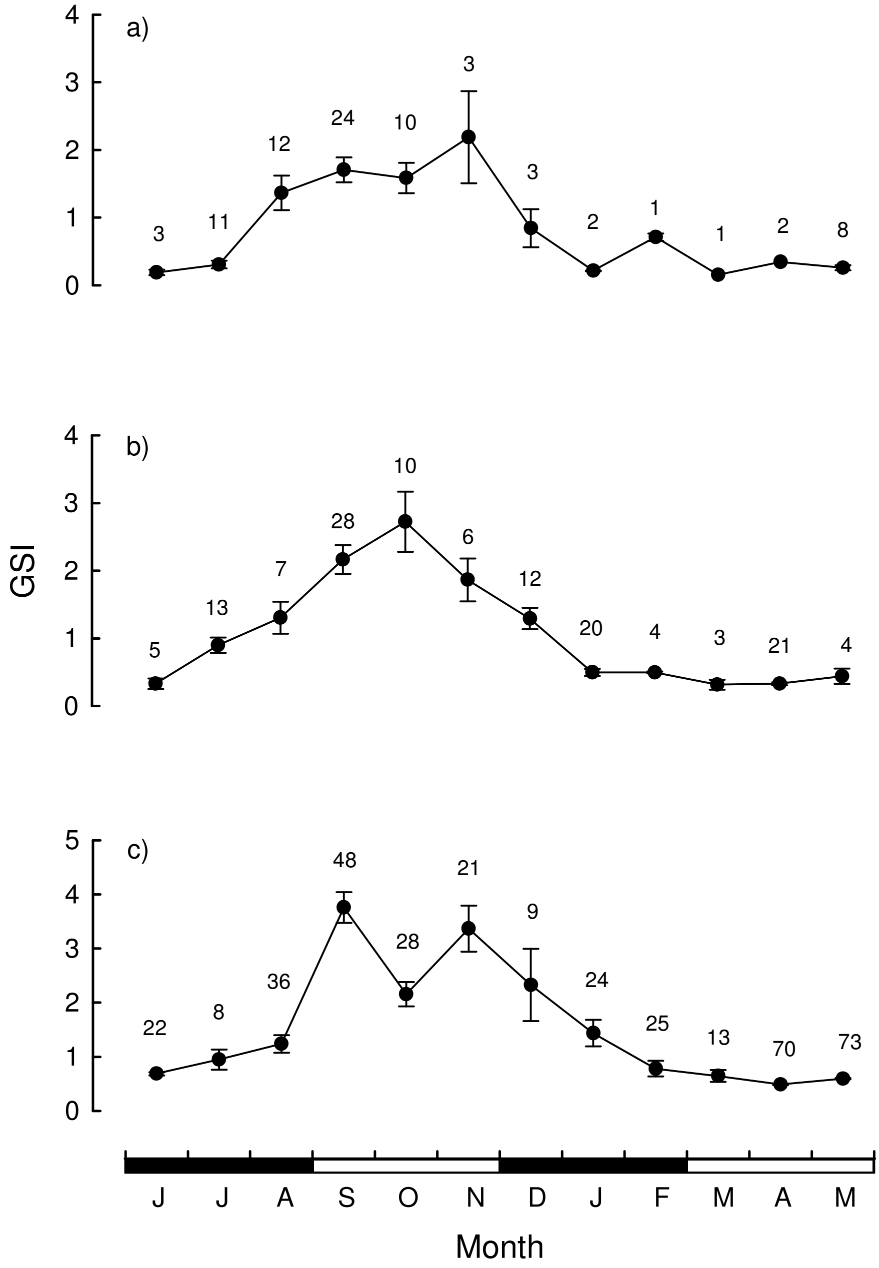

Figure 3.12. Mean monthly GSIs (±1SE) for a) male, b) transitional and c) female *Eleutheronema tetradactylum*. Data for males are derived from fish with lengths greater or equal to the length at 50% maturity.

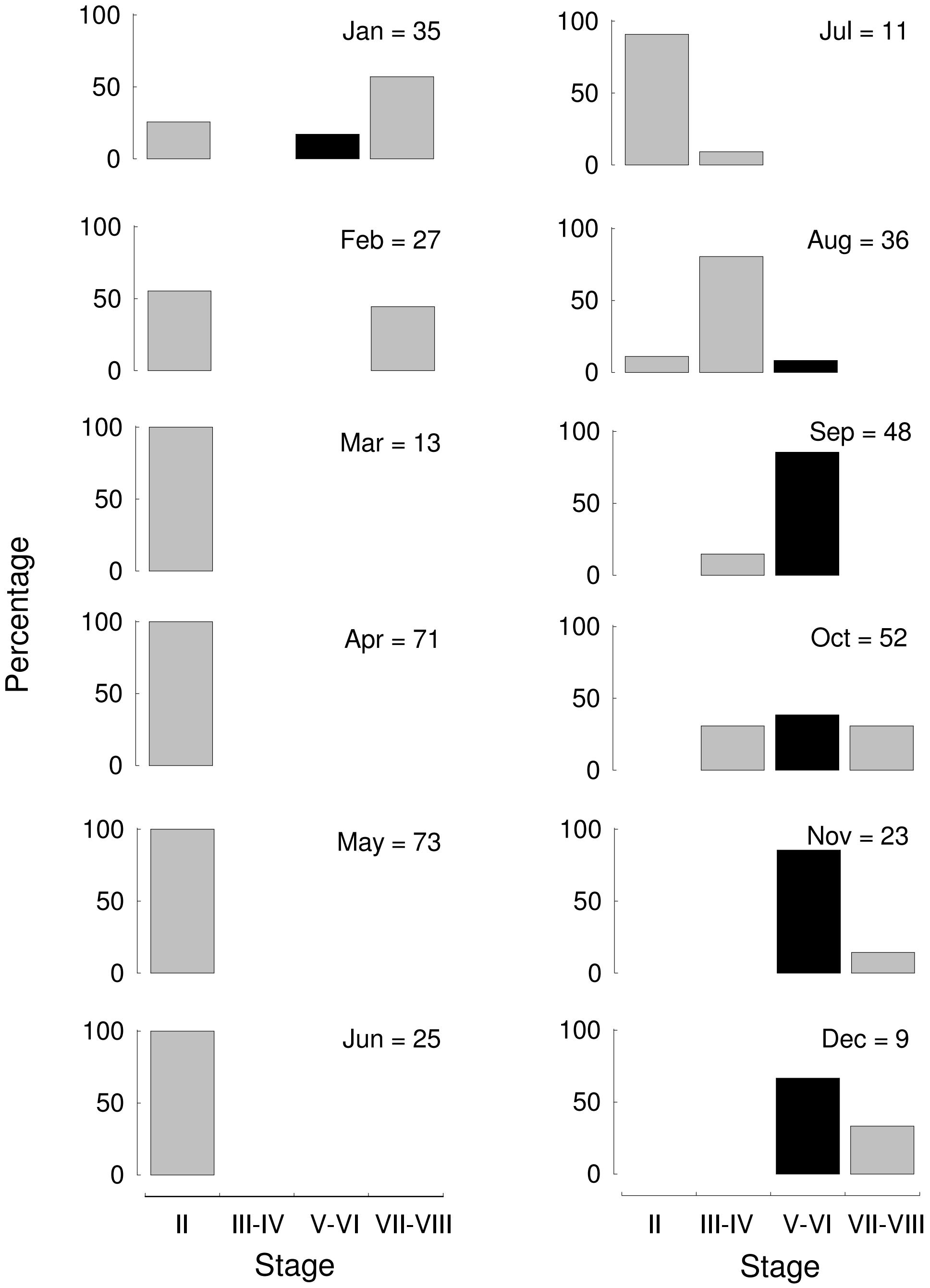

Figure 3.13. Monthly percentage frequencies of occurrence of sequential gonadal maturity stages in females of *Eleutheronema tetradactylum*.

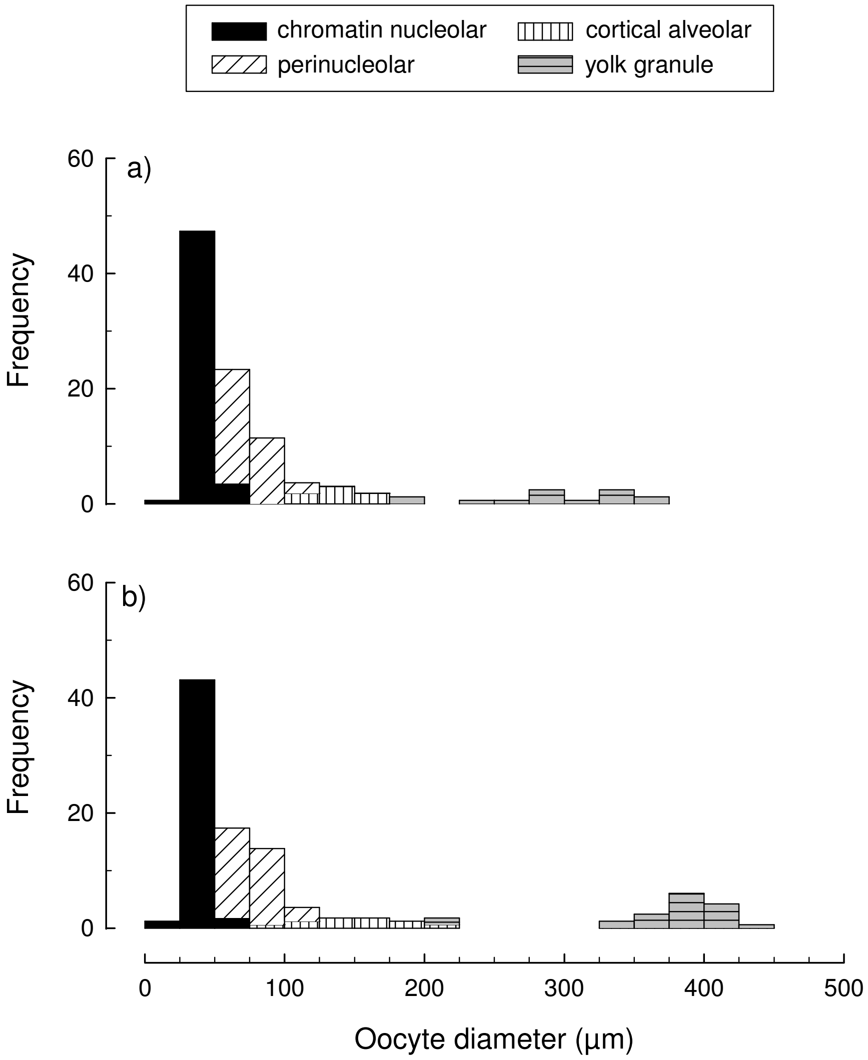

Figure 3.14 Frequency distributions for oocyte diameters in the different stages of oocyte development in histological sections of the ovaries of two spawning (stage VI) *Eleutheronema tetradactylum*. Ovaries are from a) a 598 mm fish caught in early December and b) a 400 mm fish caught in late October. Note migratory nucleus and hydrated stage oocytes have not been included.

the oocyte diameters for the chromatin nucleolar, perinucleolar and cortical alveolar oocytes in the two ovaries were very similar (**Figure 3.14a, b**).

The mean monthly GSIs for male *P. macrochir* rose gradually from *ca* 0.1 in June and July to reach a maximum of *ca* 0.8 in October and then declined in the ensuing four months (**Figure 3.15a**). The mean monthly GSIs for transitional *P. macrochir* fluctuated little during the year, with their highest value of *ca* 0.5 being recorded in September (**Figure 3.15b**). The mean monthly GSIs for female *P. macrochir* rose sharply from a low of 0.3 in August to high levels in October, December and January and then declined (**Figure 3.15c**).

Female *P. macrochir* with resting ovaries (stage II) were present in most months, whereas those with developing ovaries (stages III and IV) were almost entirely restricted to July to October (**Figure 3.16**). Mature and spawning female *P. macrochir* (stages V and VI) were caught during September and October and females with spent ovaries were found in October to February (**Figure 3.16**).

The oocyte diameter distributions for the chromatin nucleolar, perinucleolar and cortical alveolar oocytes in the ovaries of two spawning (stage VI) *P. macrochir* were each similar to those of the ovaries of the two spawning females of *E. tetradactylum* (*cf* **Figures 3.14** and **3.17**). The oocyte diameters approached more closely a continuous distribution in the first of the two ovaries (**Figure 3.17a, b**).

3.3.6 Habitats of threadfins

ANOVA showed that the gill net catch rates of *E. tetradactylum* and *P. macrochir* over bare sand differed significantly among regions, *i.e.* at Port Smith, Eighty Mile Beach and Cape Keraudren, but not among seasons (**Table 3.5**). Mean catch rates of *E. tetradactylum* were significantly greater at Cape Keraudren ($p<0.001$) and Eighty Mile Beach ($p<0.01$) than at Port Smith (**Figure 3.18a**) and those of *P. macrochir* were greater at Eighty Mile Beach than at Cape Keraudren ($p<0.001$), which, in turn, were greater than at Port Smith ($p<0.01$) (**Figure 3.18b**). When the catch rates of *E. tetradactylum* in gill nets in mangroves and over bare sand at Port Smith and Cape Keraudren were subjected to ANOVA, the effects of region, habitat and season were

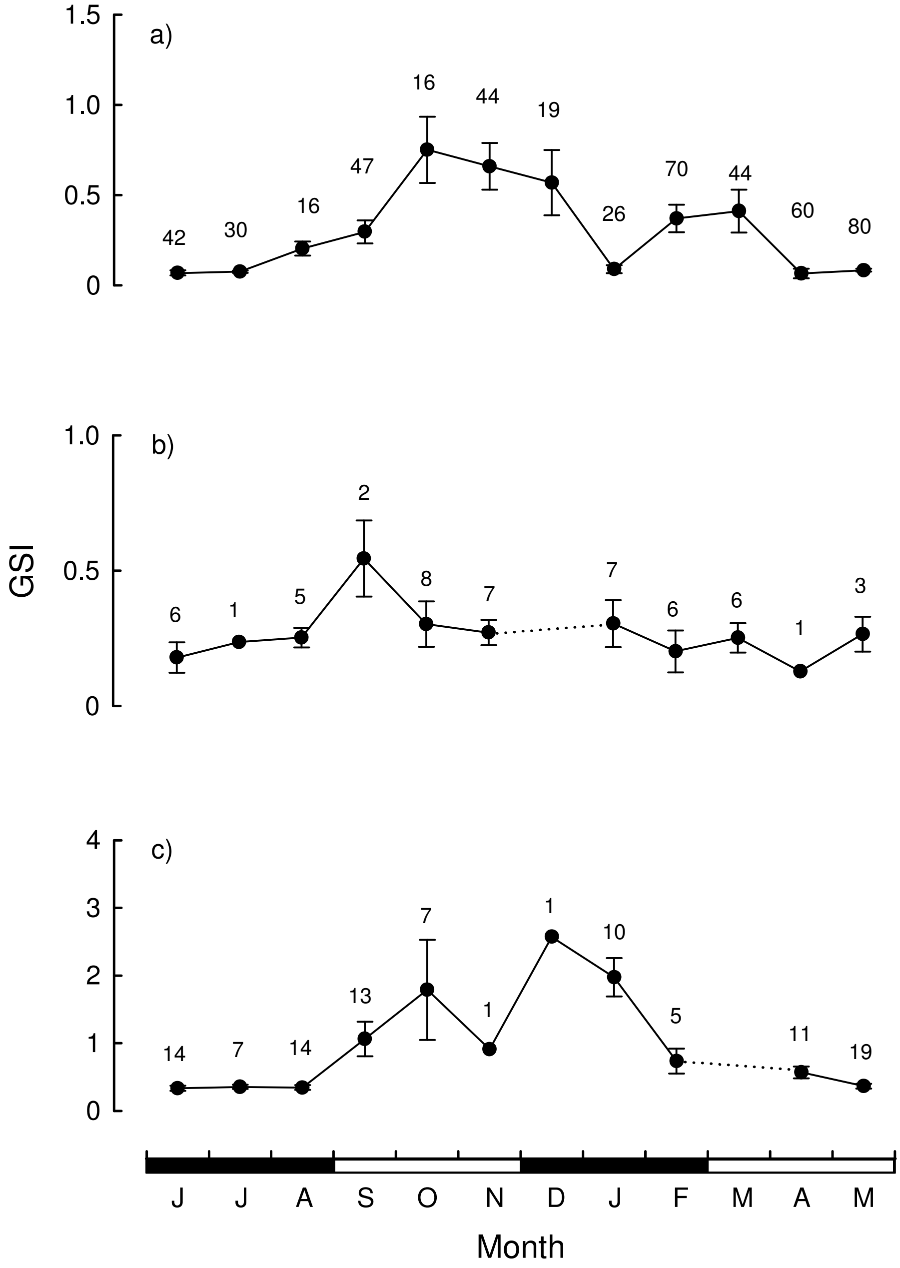

Figure 3.15 Mean monthly GSIs (±1SE) for a) male, b) transitional and c) female *Polydactylus macrochir* collected from nearshore waters. Data for males are derived from fish with lengths greater or equal to the length at 50% maturity.

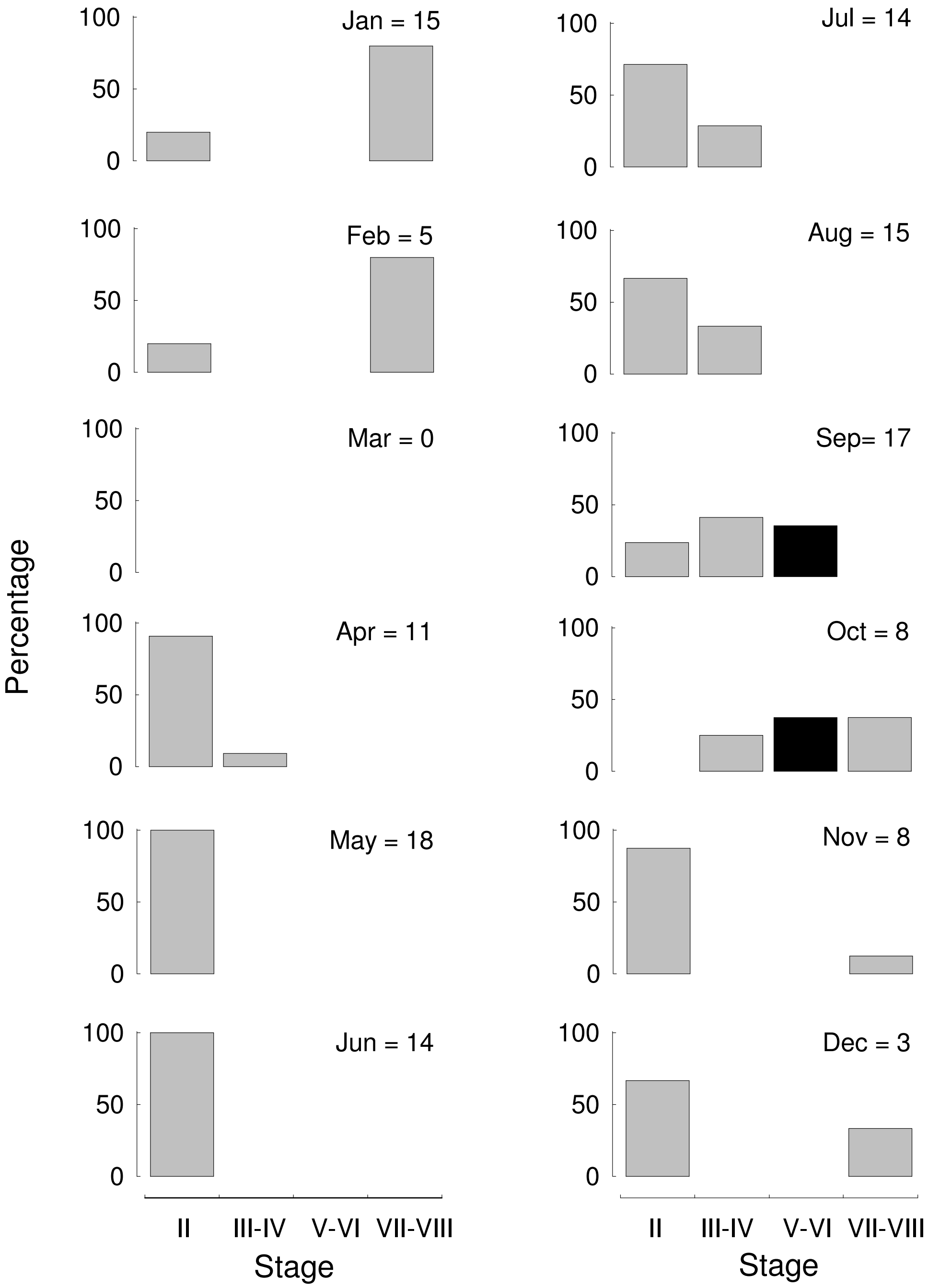

Figure 3.16. Percentage frequencies of occurrence of sequential gonadal maturity stages in females of *Polydactylus macrochir*.

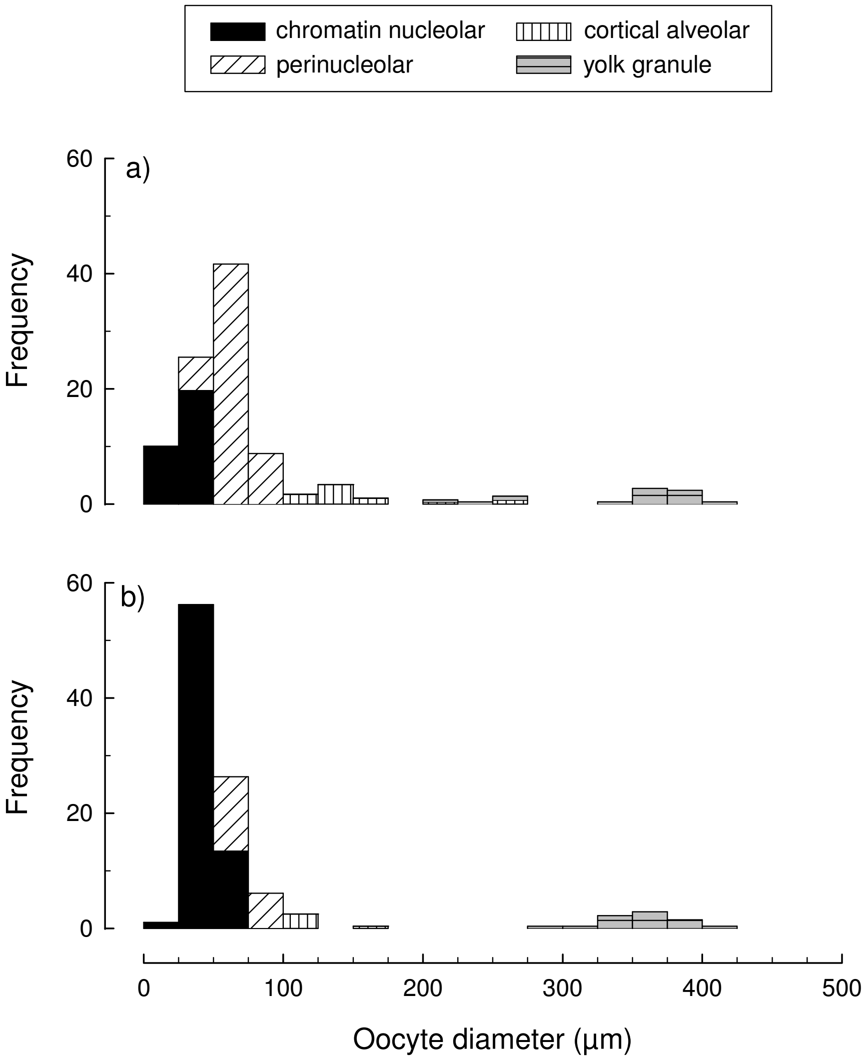

Figure 3.17 Frequency distributions of the oocyte diameters in the different stages in oocyte development in histological sections of the ovaries of two spawning (stage VI) *Polydactylus macrochir*. Ovaries are from a) a 1339 mm fish and b) a 1155 mm fish caught in late October. Note migratory nucleus and hydrated stage oocytes have not been included.

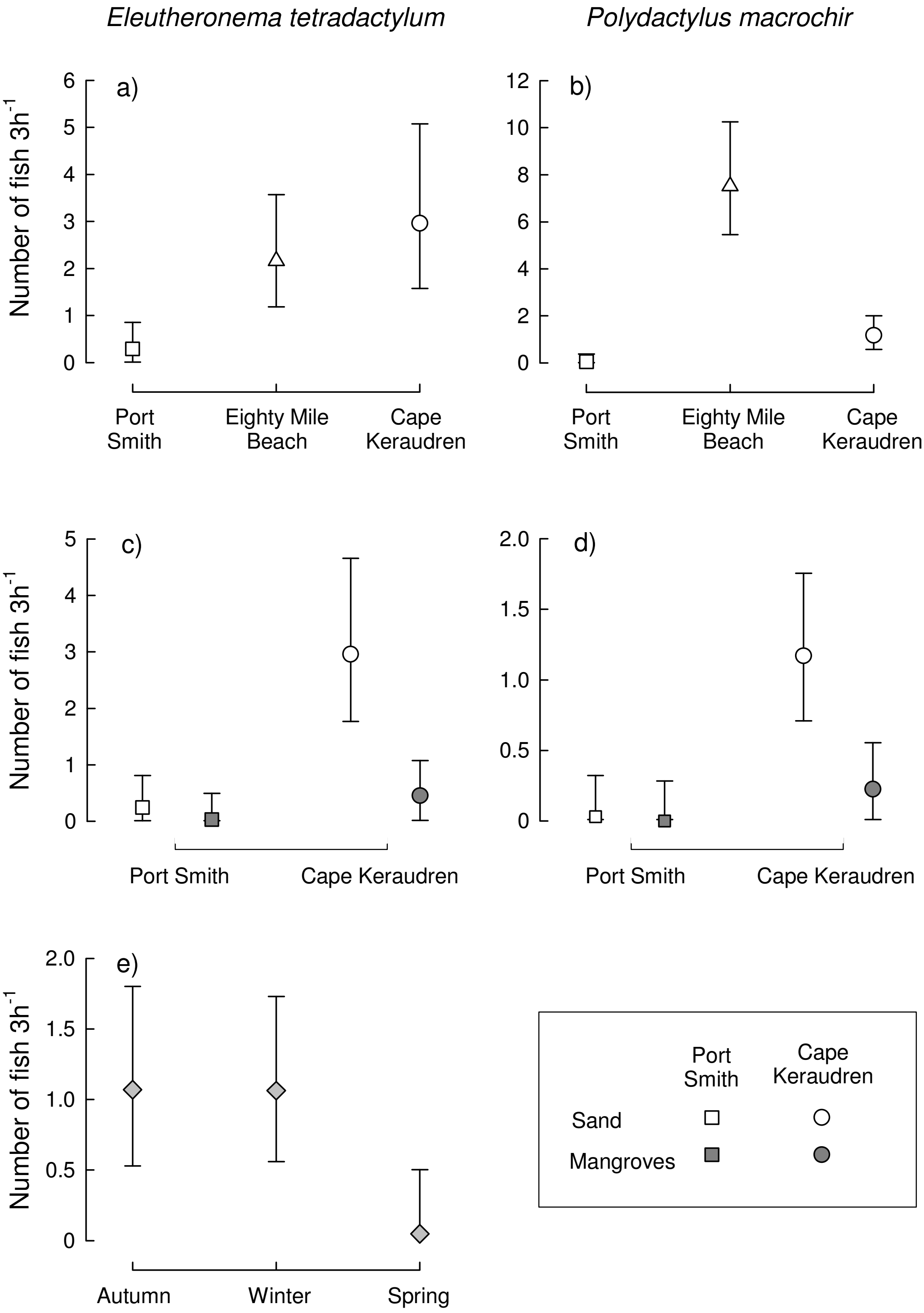

Figure 3.18. Mean catch rate (number of fish $3h^{-1}$) for a) *Eleutheronema tetradactylum* and b) *Polydactylus macrochir* in gill nets set over sand at Port Smith, Eighty Mile Beach and Cape Keraudren, c) *E. tetradactylum* and d) *P. macrochir* in gill nets set over sand and in mangroves at Port Smith and Cape Keraudren and for e) *E. tetradactylum* over both habitat types at Port Smith and Cape Keraudren, collectively, in each season. Legend applies to graphs c) & d) only.

Table 3.5. Mean squares and significance levels for ANOVAs of the number of *Eleutheronema tetradactylum* and *Polydactylus macrochir* caught $3h^{-1}$ in gill nets set over bare sand in nearshore, shallow waters seasonally at Port Smith, Eighty Mile Beach and Cape Keraudren. *** $p<0.001$

	Main effects		Interaction	
Source	Region (R)	Season (S)	R x S	Residual
Degrees of freedom	2	3	5	68
E. tetradactylum $3h^{-1}$	1.48 ***	0.33	0.37	0.17
P. macrochir $3h^{-1}$	5.67 ***	0.15	0.18	0.10

significant, with the mean squares being appreciably greater for region and habitat than for season (**Table 3.6**). When the catch rates of *P. macrochir* were subjected to ANOVA, the effects of region and habitat, but not season, were significant, with the mean square for region being greatest (**Table 3.6**). There was a significant interaction ($p<0.05$) between region and habitat for both *E. tetradactylum* and *P. macrochir*. This was attributable to the fact that, for both species, the catch rates over sand were far greater than those in mangroves at Cape Keraudren, whereas they were similarly low for both habitat types at Port Smith (**Figure 3.18c, d**). In the case of *E. tetradactylum*, for which the effect of season was significant, the catch rates of gill nets during autumn and winter were higher than those recorded during spring (**Figure 3.18e**).

Table 3.6. Mean squares and significance levels for ANOVAs of the number of *Eleutheronema tetradactylum* and *Polydactylus macrochir* caught $3h^{-1}$ in gill nets set in mangroves and over bare sand in nearshore, shallow waters in each season at Port Smith and Cape Keraudren. *** $p<0.001$, ** $p<0.01$, * $p<0.05$

	Main effects			Interactions				
Source	Region (R)	Season (S)	Habitat (H)	R x S	R x H	H x S	R x S x H	Residual
Degrees of freedom	1	3	1	3	1	3	3	15
E. tetradactylum $3h^{-1}$	1.99 ***	0.63 **	1.26 **	0.34	0.58 *	0.22	0.08	0.12
P. macrochir $3h^{-1}$	0.80 ***	0.03	0.32 *	0.01	0.26 *	0.01	0.04	0.05

The densities of *E. tetradactylum,* determined from catches obtained using a 60 m long seine net, differed significantly among regions (Port Smith, Eighty Mile Beach and Cape Keraudren) and seasons and there was a significant interaction between region and season (**Table 3.7**). Although the density in each season was greater at Eighty Mile Beach than Port Smith and Cape Keraudren, that difference was particularly marked only in spring, when large numbers of the new 0+ age class were recruited into that region (**Figure 3.19a**). The densities of *P. macrochir*, likewise derived from catches taken with the 60 m long net, differed significantly among regions, but not seasons, and there was no interaction between these two main effects. The densities were significantly greater ($p<0.001$) at Eighty Mile Beach than at both Port Smith and Cape Keraudren (**Table 3.7, Figure 3.19b**).

During spring, when the 0+ age classes of both species are recruited into the shallows, the densities of *P. macrochir* but not of *E. tetradactylum*, derived from catches obtained using the 21.5 m long seine net over a fine substrate at Anna Plains and over sand at Eighty Mile Beach, were significantly greater at the former than latter locations ($p<0.05$) (**Figure 3.19c, d**).

Table 3.7. Mean squares and significance levels for ANOVAs of the density of *Eleutheronema tetradactylum* and *Polydactylus macrochir* caught 500 m^{-2} in gill nets set over bare sand in nearshore, shallow waters in each season at Port Smith, Eighty Mile Beach and Cape Keraudren *** $p<0.001$

	Main effects		Interaction	
Source	Region (R)	Season (S)	R x S	Residual
Degrees of freedom	2	3	6	88
E. tetradactylum 500 m^{-2}	3.45 ***	0.48 ***	0.56 ***	0.04
P. macrochir 500 m^{-2}	1.08 ***	0.08	0.06	0.04

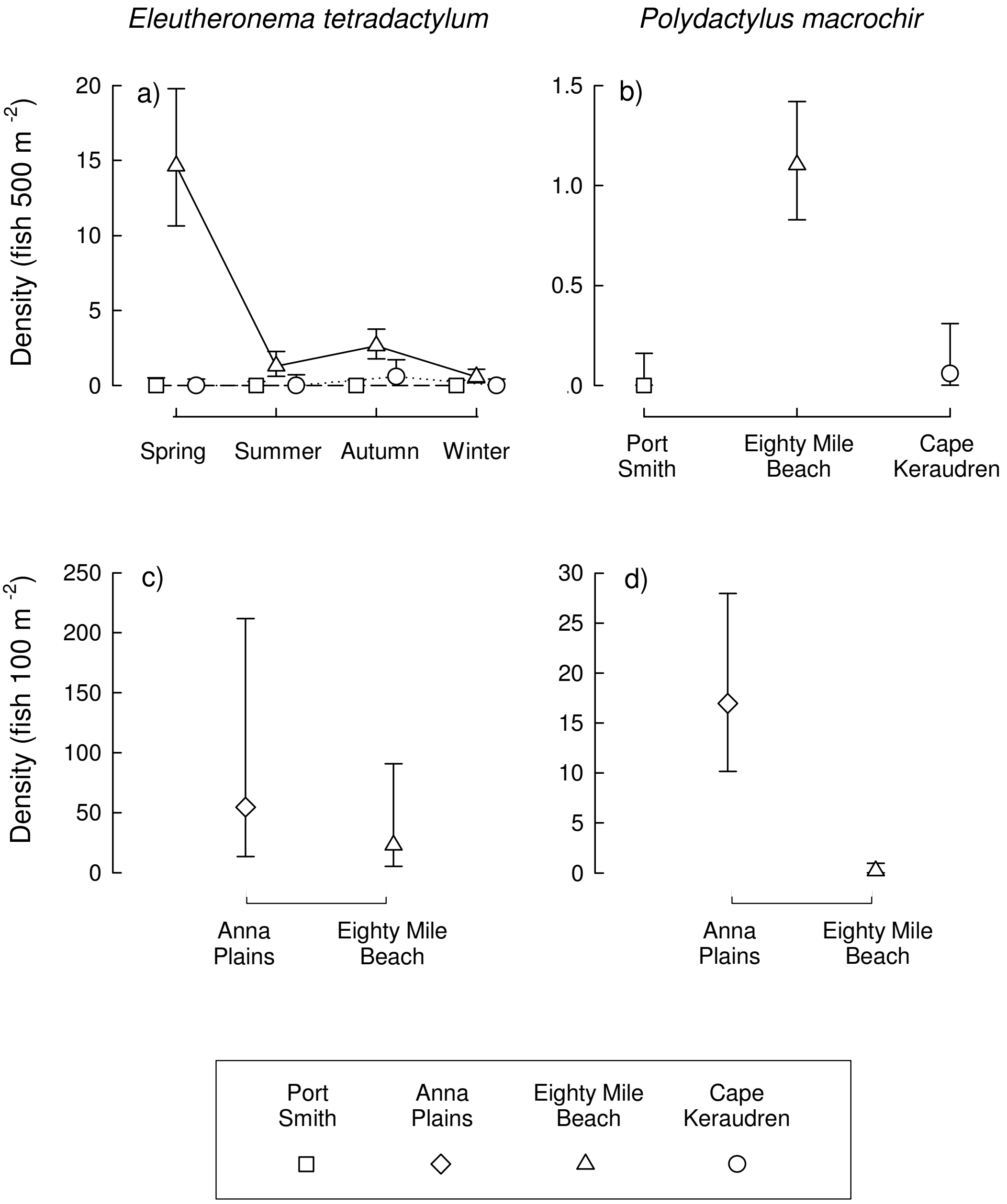

Figure 3.19. Mean densities of a) *Eleutheronema tetradactylum* over sand at Port Smith, Eighty Mile Beach and Cape Keraudren in each season and b) *Polydactylus macrochir* over sand at Port Smith, Eighty Mile Beach and Cape Keraudren and of c) *E. tetradactylum* and d) *P. macrochir* over silt at Anna Plains and sand at Eighty Mile Beach during spring. Densities in (a) and (b) were derived from catches taken with a 60 m long seine net, while those in (c) and (d) were derived from catches obtained with a 21.5 m seine net.

3.3.7 Length - weight relationships

The relationships between wet weight (*W*) and total length (*TL*) of *Eleutheronema tetradactylum* and *Polydactylus macrochir* were:

E. tetradactylum $W = 1.736\text{x}10^{-6} \text{ x } TL^{3.262}$ ($R^2 = 0.989$, $n = 682$)
P. macrochir $W = 8.848\text{x}10^{-6} \text{ x } TL^{2.963}$ ($R^2 = 0.974$, $n = 872$)

The relationships between total length (*TL*) and the caudal fork length (*FL*) of *Eleutheronema tetradactylum* and *Polydactylus macrochir* were:

E. tetradactylum $TL = (0.8381 \text{ x } FL) - 1.6604$ ($R^2 = 0.999$, $n = 895$)
P. macrochir $TL = (0.8413 \text{ x } FL) - 6.4416$ ($R^2 = 0.999$, $n = 1089$)

3.3.8 Validation that opaque zones on otoliths are formed annually

In an initial comparison, there was 100% agreement between the number of opaque zones (annuli) observed in 100 otoliths of *E. tetradactylum* prior to and after the sectioning of those otoliths and the same was true for the 100 otoliths of *P. macrochir* that were examined. Although it was unnecessary to section the otoliths of *E. tetradactylum* to obtain counts of their opaque zones, it was decided to section the larger otoliths of *P. macrochir* as this lead to better definition of their opaque zones, which were greater in number than those on the otoliths of *E. tetradactylum.*

The mean monthly marginal increments on *E. tetradactylum* otoliths with 1, 2 and 3 or more opaque zones rose from low values in January to high values in July to October and then declined precipitously to their minima in November or December (**Figure 3.20**). The trends exhibited by the mean monthly marginal increments on the otoliths of *P. macrochir,* irrespective of the number of opaque zones*,* were similar to those of *E. tetradactylum,* with values being least in late spring and early summer and greatest during winter and early spring (**Figure 3.21**).

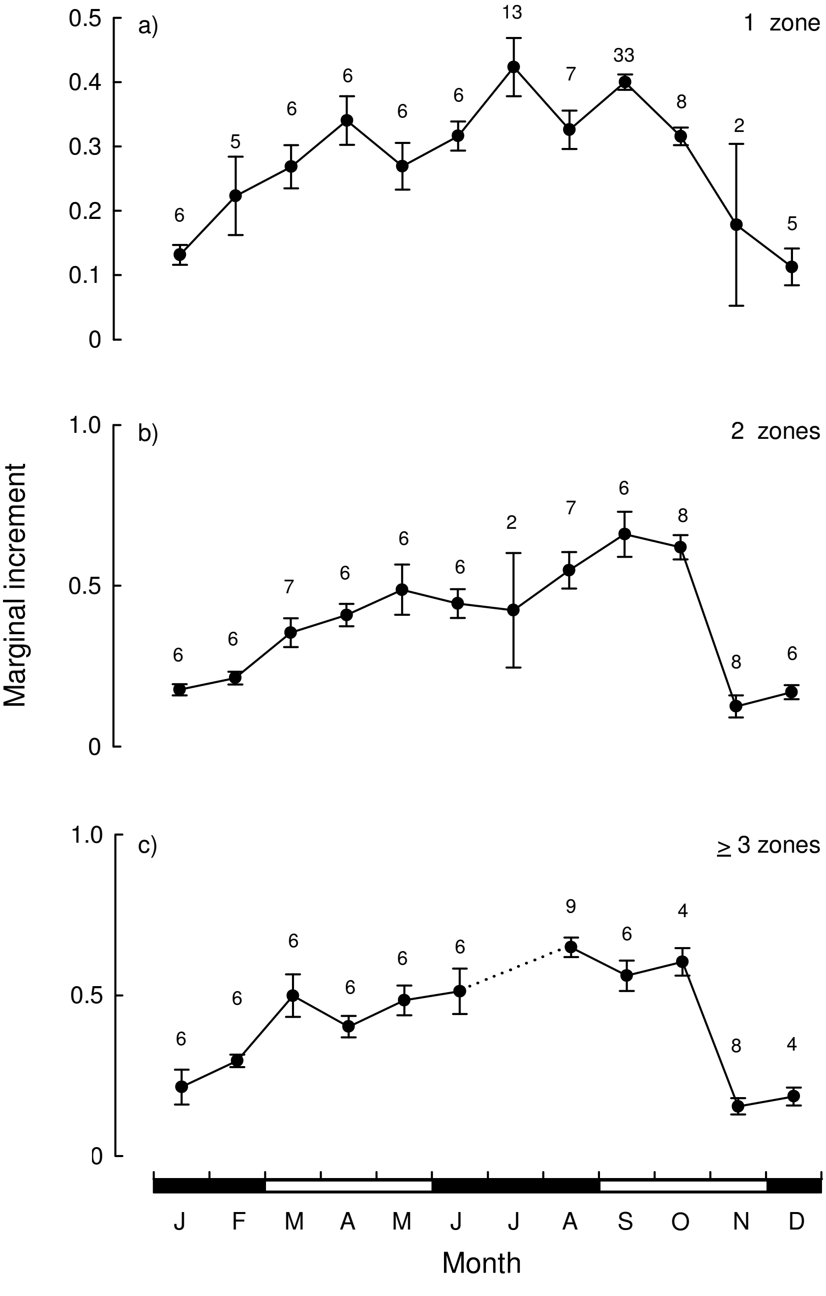

Figure 3.20. Mean monthly marginal increments (±1SE) for the otoliths of *Eleutheronema tetradactylum* with different numbers of opaque zones.

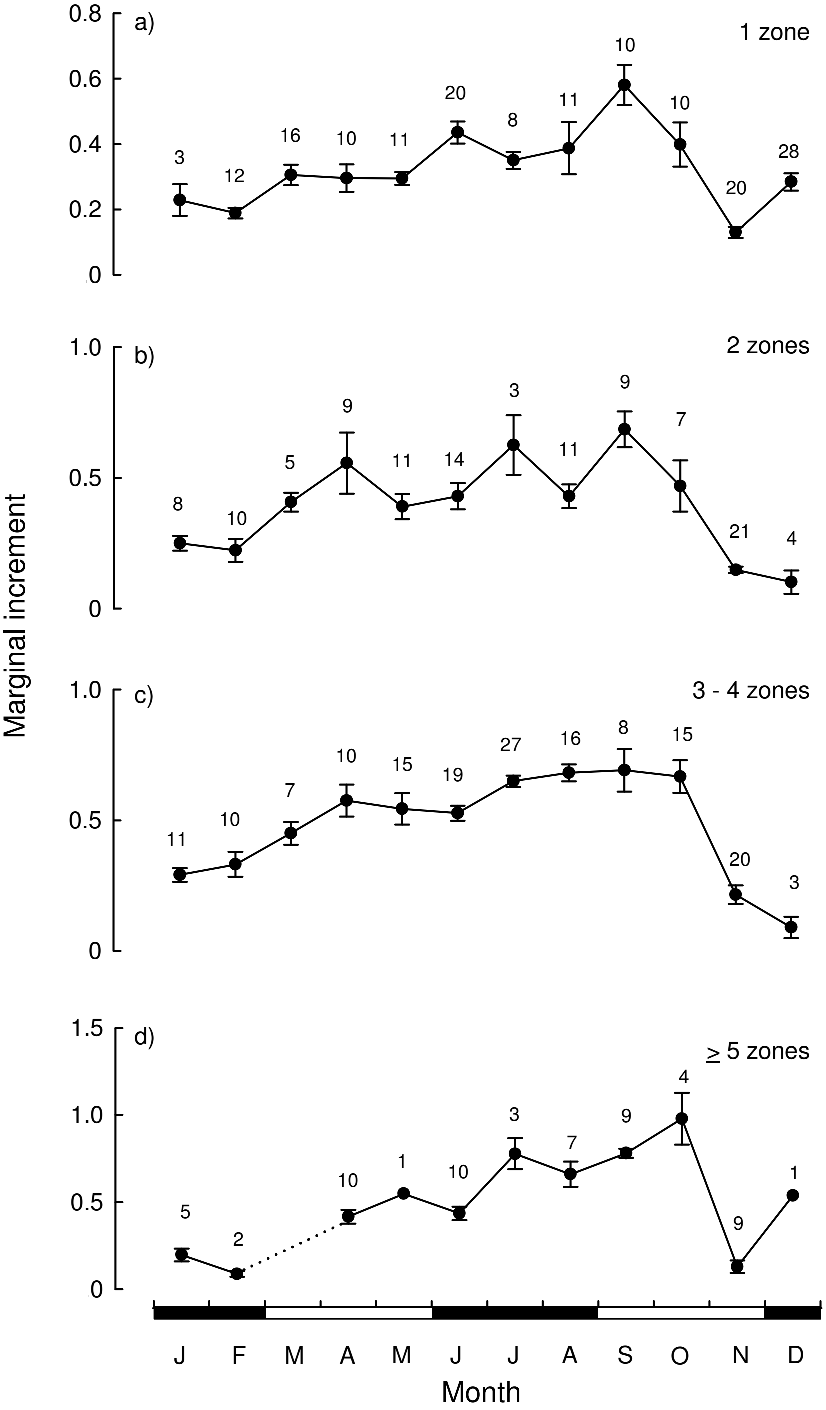

Figure 3.21. Mean monthly marginal increments (±1SE) for the otoliths of *Polydactylus macrochir* with different numbers of opaque zones.

3.3.9 von Bertalanffy growth curves

The von Bertalanffy growth curve provided a very good fit to the lengths at age of the individuals of *E. tetradactylum* (**Figure 3.22**), which is reflected in a high coefficient of determination (**Table 3.8**). The von Bertalanffy growth curve also provided a good fit to the lengths at age of individuals of *P. macrochir* (**Table 3.8, Figure 3.23**). *Polydactylus macrochir* attained a greater maximum length and age than *E. tetradactylum* and the L_∞ was greater for *P. macrochir* than *E. tetradactylum, i.e.* 1587 *vs* 762 mm, whereas the reverse was true for the growth coefficient (*k*), *i.e.* 0.170 *vs* 0.351 years^{-1} (**Table 3.8, Figure 3.24**).

Table 3.8. Maximum length (L_{max}) and the parameters and their 95% confidence intervals for the von Bertalanffy growth equation fitted to the lengths at age of individuals of *Eleutheronema tetradactylum* and *Polydactylus macrochir*. L_∞ = asymptotic length, k = growth coefficient, t_0 = the hypothetical age at which fish would have zero length, R^2 = coefficient of determination, n = number of fish.

Species	**L_{max} (mm)**	**L_∞ (mm)**	**k (years^{-1})**	**t_0 (years)**	**R^2**	**n**
Eleutheronema tetradactylum	793	762	0.351	-0.103	0.967	1466
Upper 95% CI		786	0.370	-0.088		
Lower 95% CI		739	0.333	-0.118		
Polydactylus macrochir	1393	1587	0.170	-0.338	0.871	1377
Upper 95% CI		1709	0.192	-0.262		
Lower 95% CI		1466	0.148	-0.415		

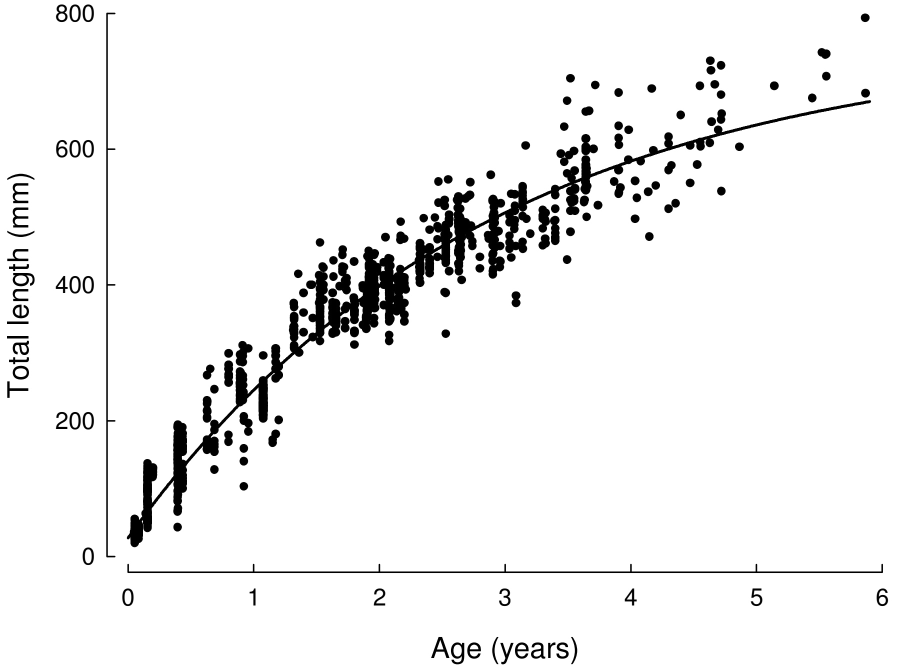

Figure 3.22. von Bertalanffy growth curve fitted to lengths at age of individuals of *Eleutheronema tetradactylum* collected from nearshore waters at Roebuck Bay, Anna Plains, Eighty Mile Beach and Cape Keraudren.

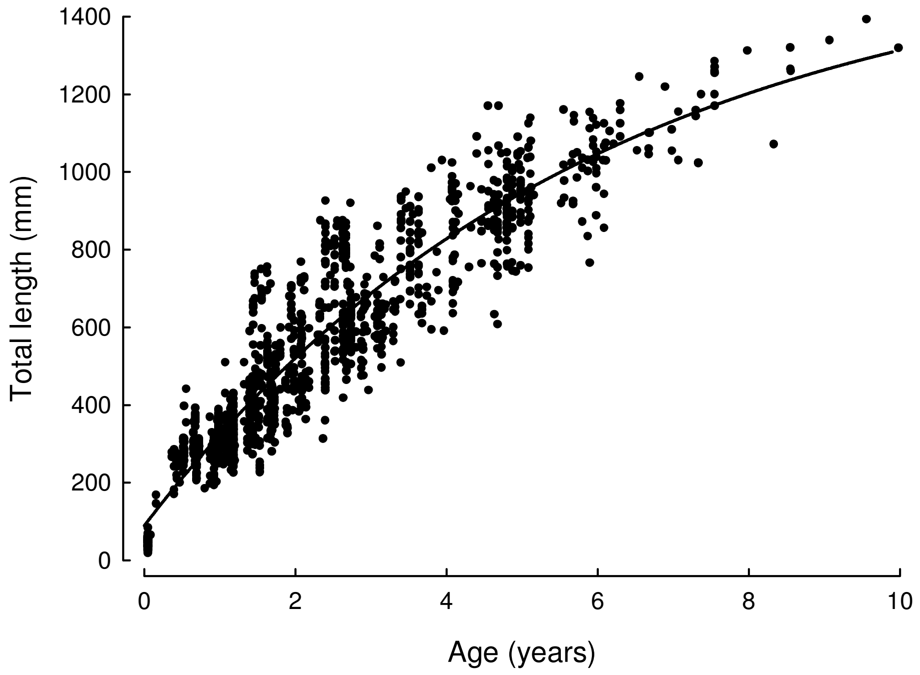

Figure 3.23. von Bertalanffy growth curve fitted to lengths at age of individuals of *Polydactylus macrochir* collected from nearshore waters at Derby, Roebuck Bay, Anna Plains and Eighty Mile Beach.

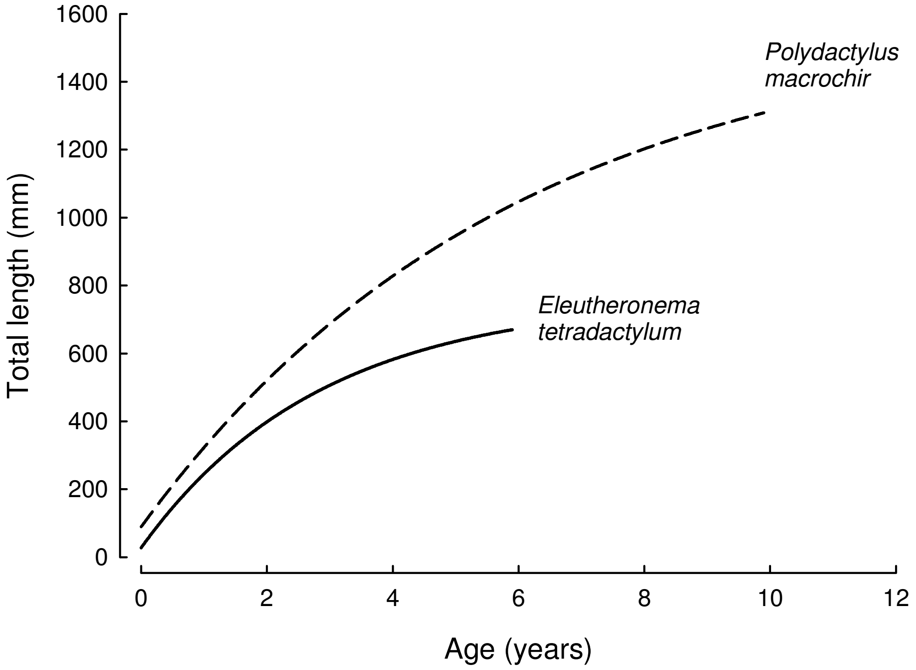

Figure 3.24. von Bertalanffy growth curves fitted to lengths at ages of individuals of *Polydactylus macrochir* and *Eleutheronema tetradactylum*.

3.3.10 Length and age compositions of threadfin caught by various methods.

The lengths of *E. tetradactylum* caught in our research seine nets at Eighty Mile Beach ranged largely from 26 to 250 mm, whereas those caught by the research gill nets at the same location ranged from 210 to 550 mm (**Figure 3.25a, b**). The latter range is similar to that of fish caught by recreational angling at Eighty Mile Beach (**Figure 3.25c**). The vast majority of the fish caught by commercial fishing at Anna Plains and Roebuck Bay exceeded 375 mm and included some fish with length in excess of 675 mm (**Figure 3.25e, f**).

The fish caught by our research seine nets were almost exclusively in their first year of life, whereas those of research gill nets contained fish of all age classes between 0+ and 5+ (**Figure 3.26a, b**). The fish caught by recreational anglers were predominately in their first and second years of life (**Figure 3.26c**), while those taken by commercial gill nets, included all age classes from 1+ to 5+ (**Figure 3.26e, f**)

In contrast to the situation with *E. tetradactylum*, the length distributions of the *P. macrochir* caught using our research seine and gill nets did not differ markedly with most fish lying between 200 and 550 mm (**Figure 3.27a, b**). The fish caught by recreational anglers covered a broad range from 450 to 1300 mm (**Figure 3.27c**), while those taken by recreational haul nets lay between 450 and 850 mm (**Figure 3.27d**). The catches obtained by commercial gill netting at Anna Plains (mesh size = 165 mm) and Roebuck Bay (mesh size = 140 mm) produced well defined modes at 850 to 899 mm and 800 to 849 mm and contained few fish < 550 mm (**Figure 3.27e, f**).

The fish caught by our seine netting and gill netting were predominantly fish in their first three years of life, whereas those of recreational anglers were mainly in their third to fifth years of life and included fish in their ninth and tenth years of life (**Figure 3.28a-c**). Recreational hauling tended overall to catch younger fish than recreational angling (*cf* **Figure 3.28c, d**). The ages of the fish caught by commercial gill netting differed markedly between Anna Plains and Roebuck Bay with the modal age class being 4+ at the former locality and 2+ at the latter locality, where the mesh size is smaller (**Figure 3.28e, f**).

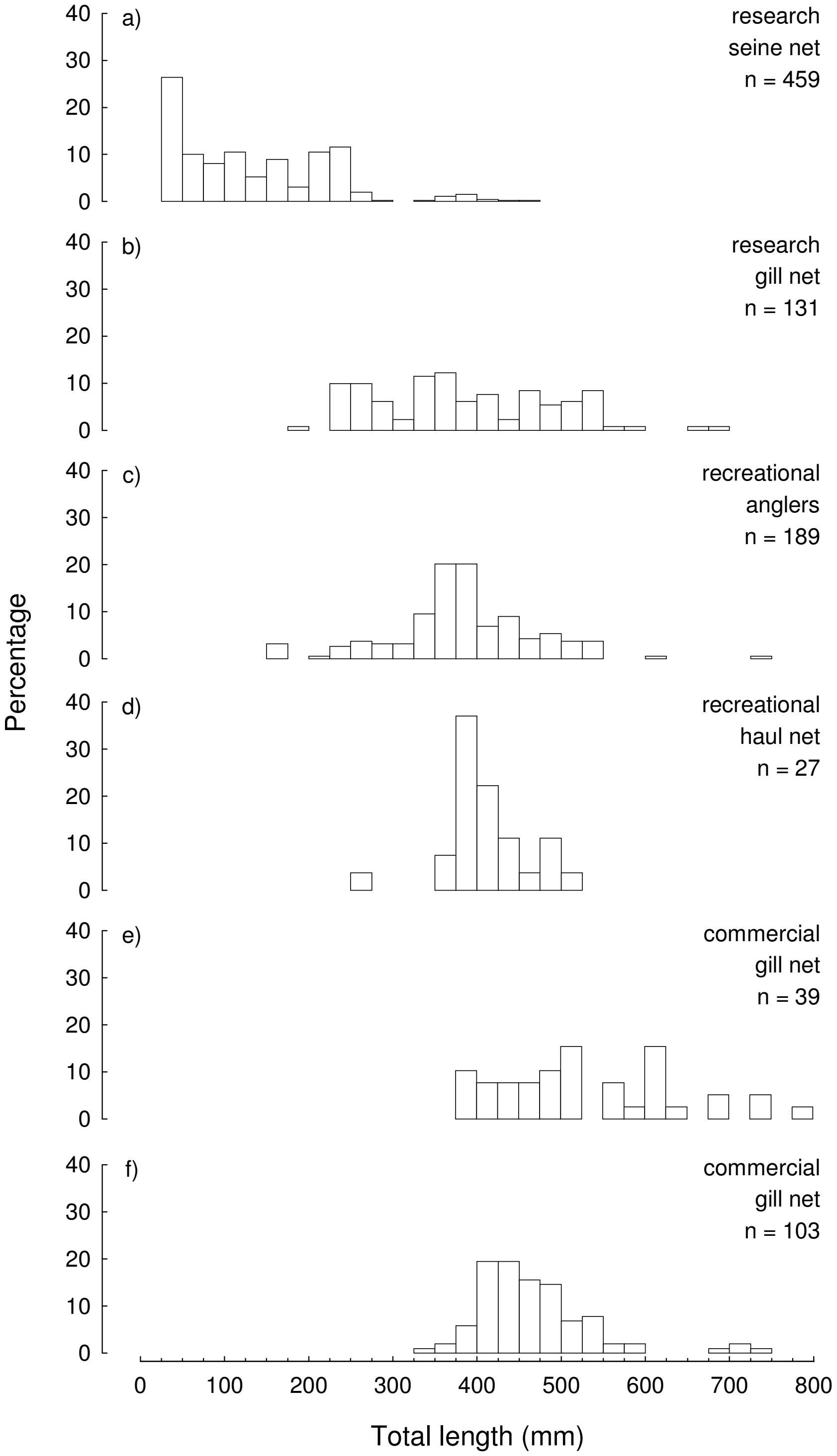

Figure 3.25. Length-frequency distributions for *Eleutheronema tetradactylum* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

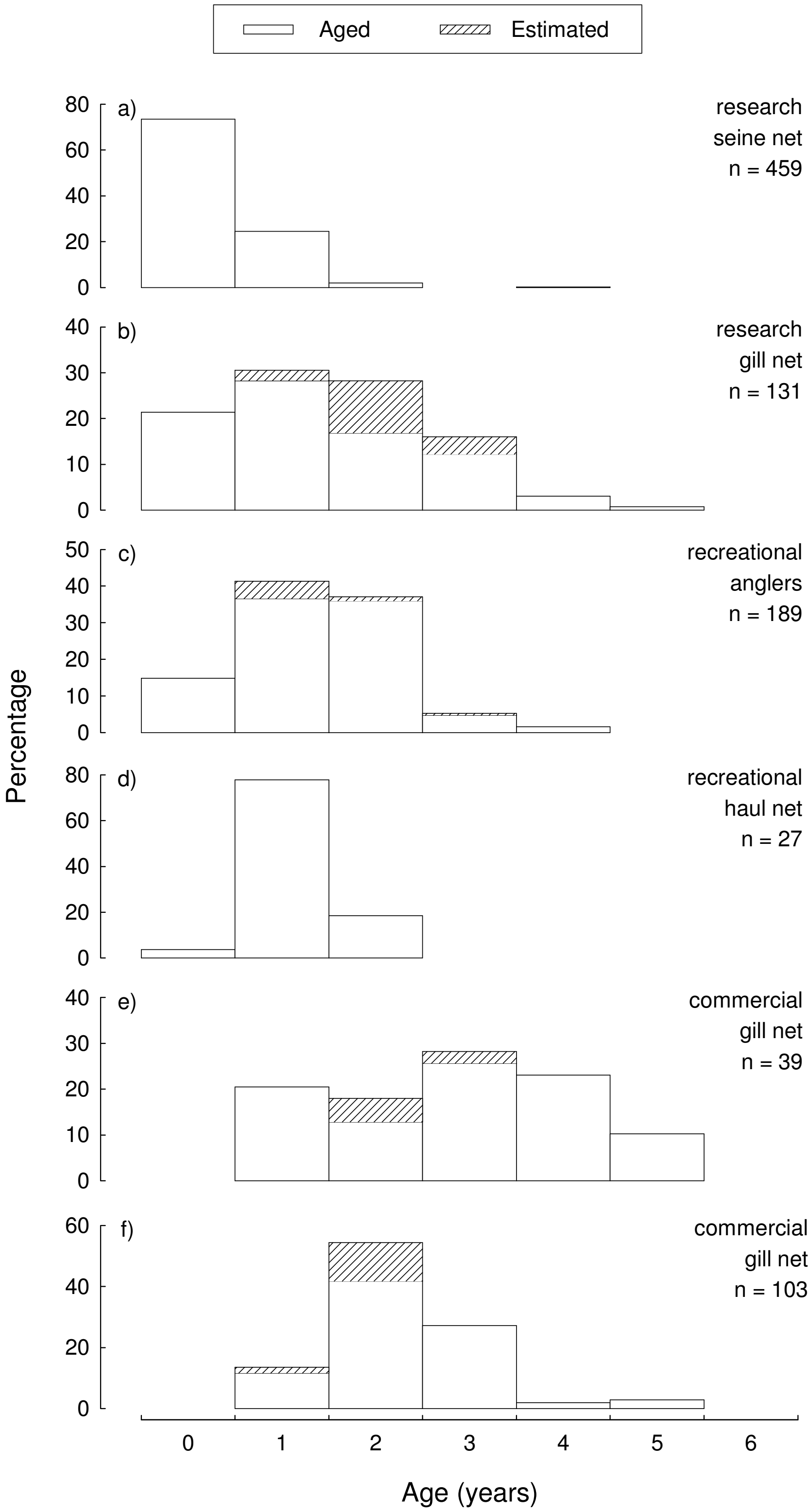

Figure 3.26. Age-frequency distributions for *Eleutheronema tetradactylum* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

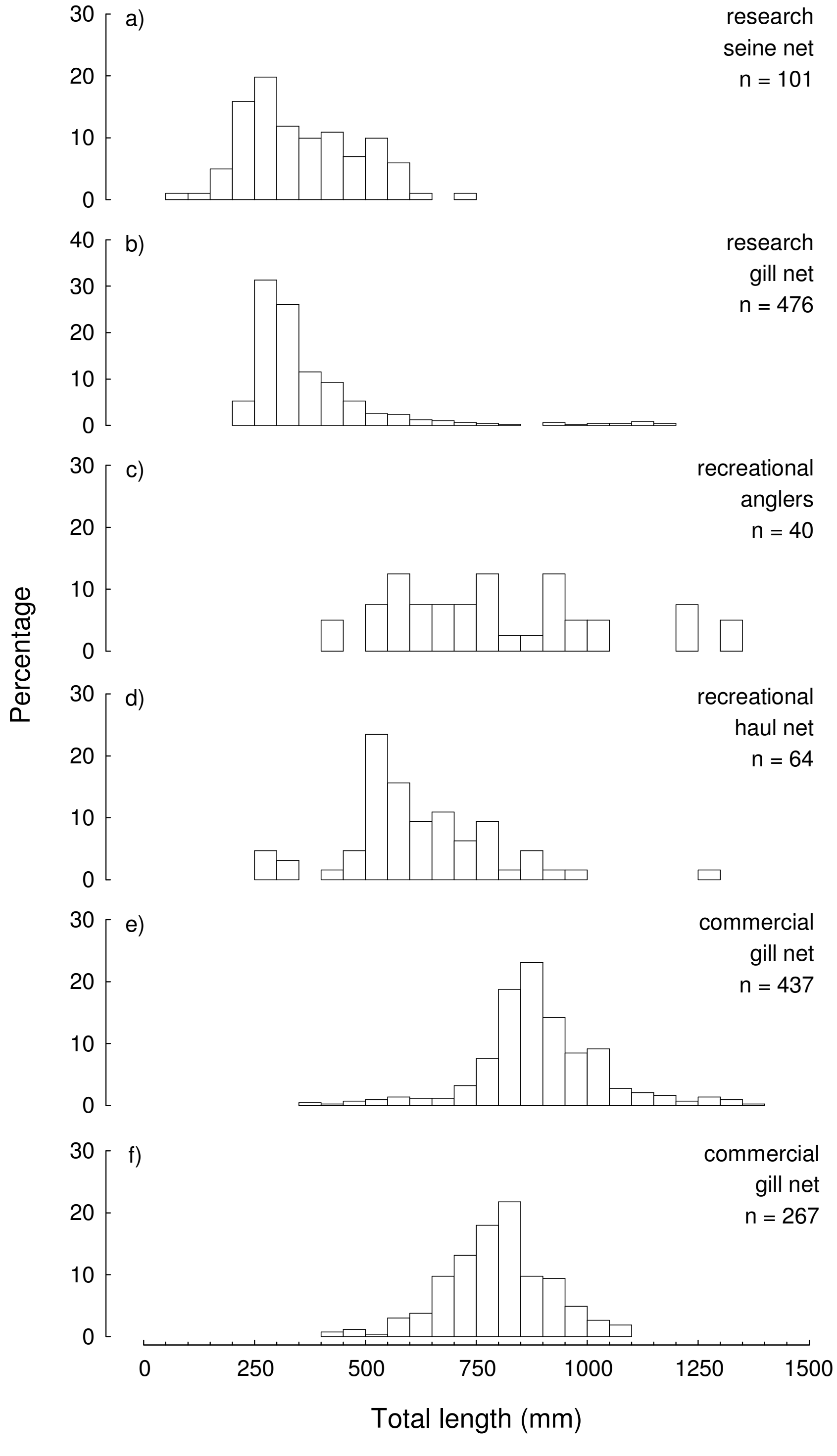

Figure 3.27. Length-frequency distributions for *Polydactylus macrochir* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

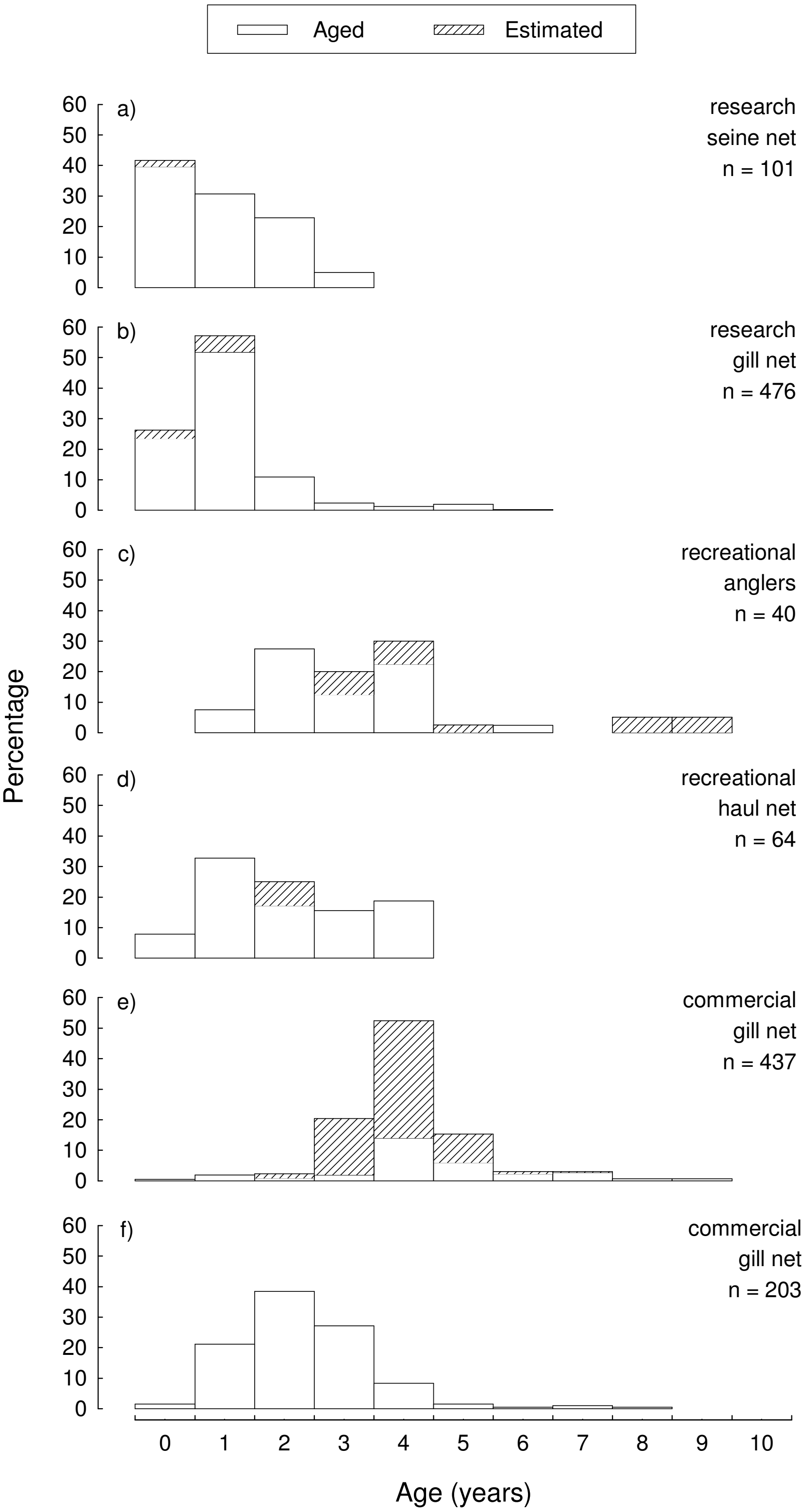

Figure 3.28. Age-frequency distributions for *Polydactylus macrochir* caught at Eighty Mile Beach (a-d), Anna Plains (e) and Roebuck Bay (f) using different methods.

3.3.11 Estimates of total and natural mortality

The values derived for total mortality, *Z*, for *E. tetradactylum,* using the regression equation refitted to Hoenig's (1983) fish data, relative abundance (catch curve) analysis (**Figure 3.29a**) and simulation (based on the nine oldest (≥ 4) of the 121 fish comprising the descending limb of the catch curve for the recreational sample) ranged from 0.73 to 1.37 year^{-1} (**Table 3.9, Figure 3.30a**). These values were thus all greater than the 0.68 year^{-1} derived for natural mortality, *M*, using the refitted equation of Pauly (1980). The use of the Bayesian method of Hall *et al*. (2004), which combines the separate likelihood estimates of *Z* and takes into account the fact that *M* must be < *Z*, yielded values of 1.31 and 0.61 for *Z* and *M*, respectively (**Table 3.9, Figure 3.30c, 3.31**). The value for fishing mortality, *F*, was 0.70, but had very wide confidence limits (**Table 3.9**).

As with *E. tetradactylum*, the values derived for *Z*, for *P. macrochir,* using the equation of Hoenig (1983), relative abundance analysis (**Figure 3.29b**) and simulation (based on the seven oldest (≥ 7) of the 267 fish comprising the descending limb of the catch curve for the recreational sample), *i.e.* 0.44 to 0.80 year^{-1}, exceeded the value of 0.35 year^{-1} derived for *M* using the refitted equation of Pauly (1980) (**Table 3.9, Figure 3.30b**). The Bayesian method of Hall *et al*. (2004) yielded values of 0.76 and 0.31 year^{-1} for *Z* and *M*, respectively (**Table 3.9, Figure 3.30d, 3.31**). The value for fishing mortality, *F*, was 0.45, but, as with *E. tetradactylum*, had very wide confidence limits (**Table 3.9**).

3.3.12 Yield per recruit, spawning potential ratio and spawning biomass per recruit

The yield per recruit analysis (YPR) for *E. tetradactylum*, calculated assuming knife edge recruitment to the fishery of 2 years, indicated that, as *F* increased from 0 to 1.5 year^{-1}, the YPR also continued to increase (**Figure 3.32a**). The predicted YPR and associated 95% confidence intervals for *E. tetradactylum* at the estimated current level of *F* of 0.7 year^{-1} and age of recruitment to the fishery of 2 years, is 0.12 kg recruit^{-1} (0.00 – 0.42 kg recruit^{-1}) (**Table 3.10**). As YPR continued to increase, it was not

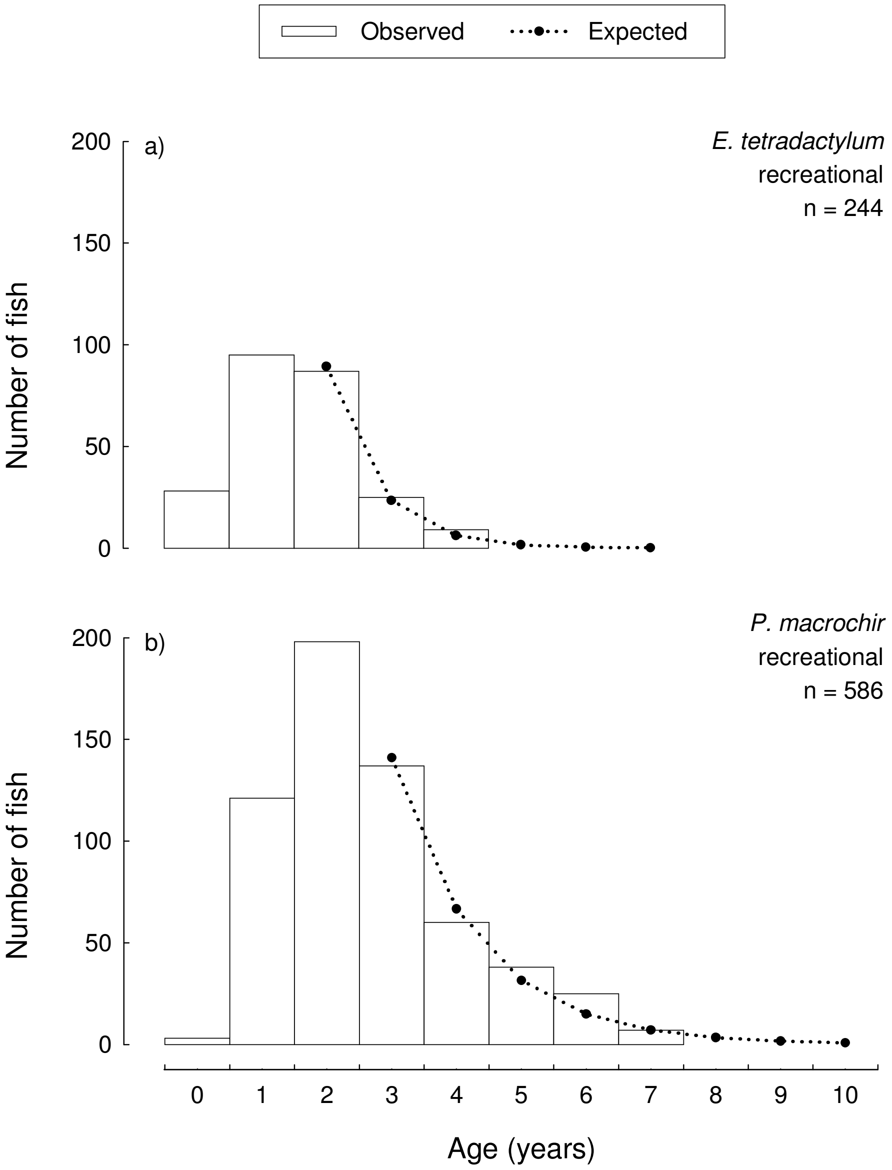

Figure 3.29 Relative abundance (catch curve) analyses were used to fit lines to the observed frequency of abundance of fish in each year class of a) *Eleutheronema tetradactylum* and b) *Polydactylus macrochir* and assuming that recruitment is constant. Abundance data for *E. tetradactylum* is from recreational catches aged from random samples collected between Karratha and Broome during the study and for *P. macrochir* relates to ages back transformed from the lengths of fish released during a recreational tagging study.

Table 3.9. Mortality (year^{-1}) of *Eleutheronema tetradactylum* and *Polydactylus macrochir* in north-western Australia calculated using different life history models, simulation based on the number of fish in the sample with ages in excess of a specified age or relative abundance analyses. M = natural mortality, Z = total mortality.

Method of analysis	***M* or *Z* or *F* (year^{-1})**	**Estimate**	**Lower 95%**	**Upper 95%**
Eleutheronema tetradactylum				
Refitted Hoenig (1983)	*Z*	0.73	0.26	2.05
Relative abundance - recreational anglers	*Z*	1.37	1.14	1.62
Simulation based on maximum age	*Z*	1.08	0.75	1.49
Combined Bayesian estimate of *Z*	***Z***	**1.31**	**1.11**	**1.51**
Refitted Pauly (1980)	*M*	0.68	0.22	2.11
Combined Bayesian estimate of *M*	***M***	**0.61**	**0.21**	**1.31**
Monte Carlo estimate of *F*	***F***	**0.70**	**0.00**	**1.11**
Polydactylus macrochir				
Refitted Hoenig (1983)	*Z*	0.44	0.16	1.21
Relative abundance - tagging release data	*Z*	0.78	0.67	0.85
Simulation based on maximum age	*Z*	0.80	0.62	1.02
Combined Bayesian estimate of *Z*	***Z***	**0.76**	**0.71**	**0.86**
Refitted Pauly (1980)	*M*	0.35	0.11	1.07
Combined Bayesian estimate of *M*	***M***	**0.31**	**0.11**	**0.71**
Monte Carlo estimate of *F*	***F***	**0.45**	**0.05**	**0.65**

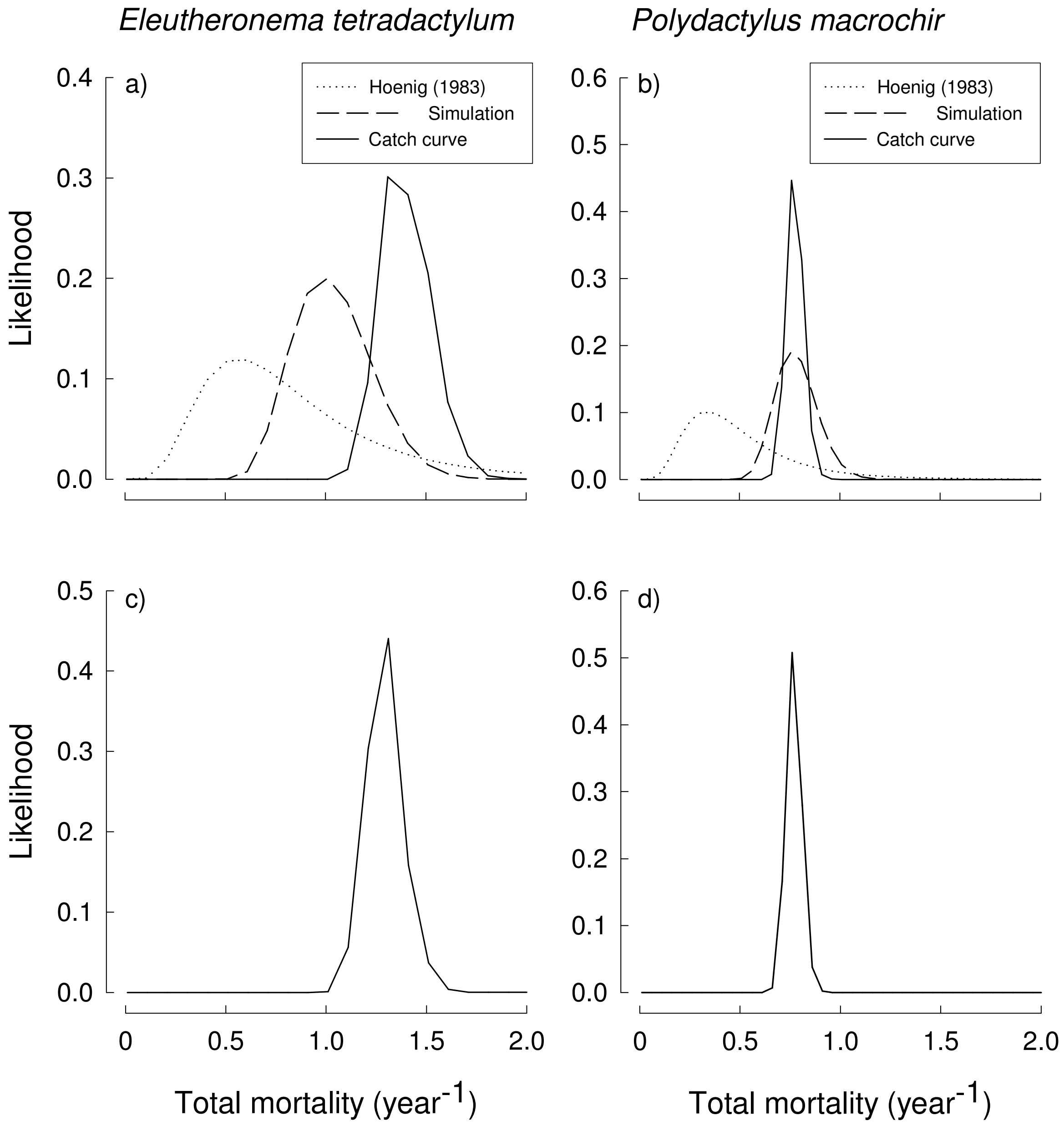

Figure 3.30. Estimated likelihood functions for total mortality *Z* of (a) *Eleutheronema tetradactylum* and (b) *Polydactylus macrochir* derived using Hoenig's (1983) regression equation for fish, relative abundance (catch curve) analysis, and a simulation method based on the number of fish in the samples that exceeded specified ages and the sizes of the samples. (c,d) Combined posterior probability distributions for *Z* for (c) *E. tetradactylum* and (d) *P. macrochir* derived from the separate likelihood functions shown in (a) and (b).

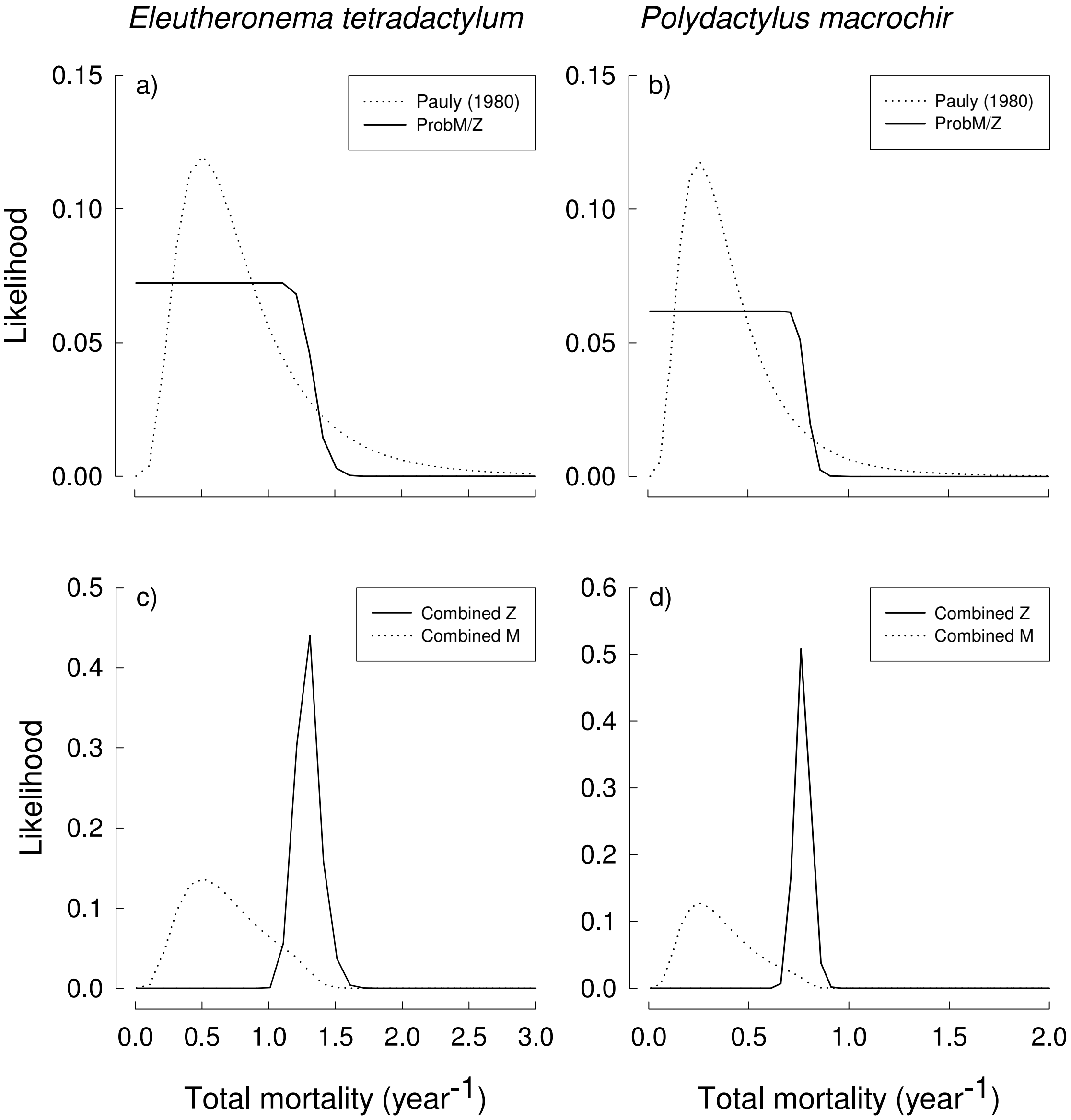

Figure 3.31. Likelihood functions for natural mortality *M* for (a) *Eleutheronema tetradactylum* and (b) *Polydactylus macrochir* from Pauly's (1980) equation and the likelihood function for *M* assuming that it is less than the combined estimate for *Z* and the combined posterior probability distributions for *Z* and *M* for (c) *E. tetradactylum* and (d) *P. macrochir*.

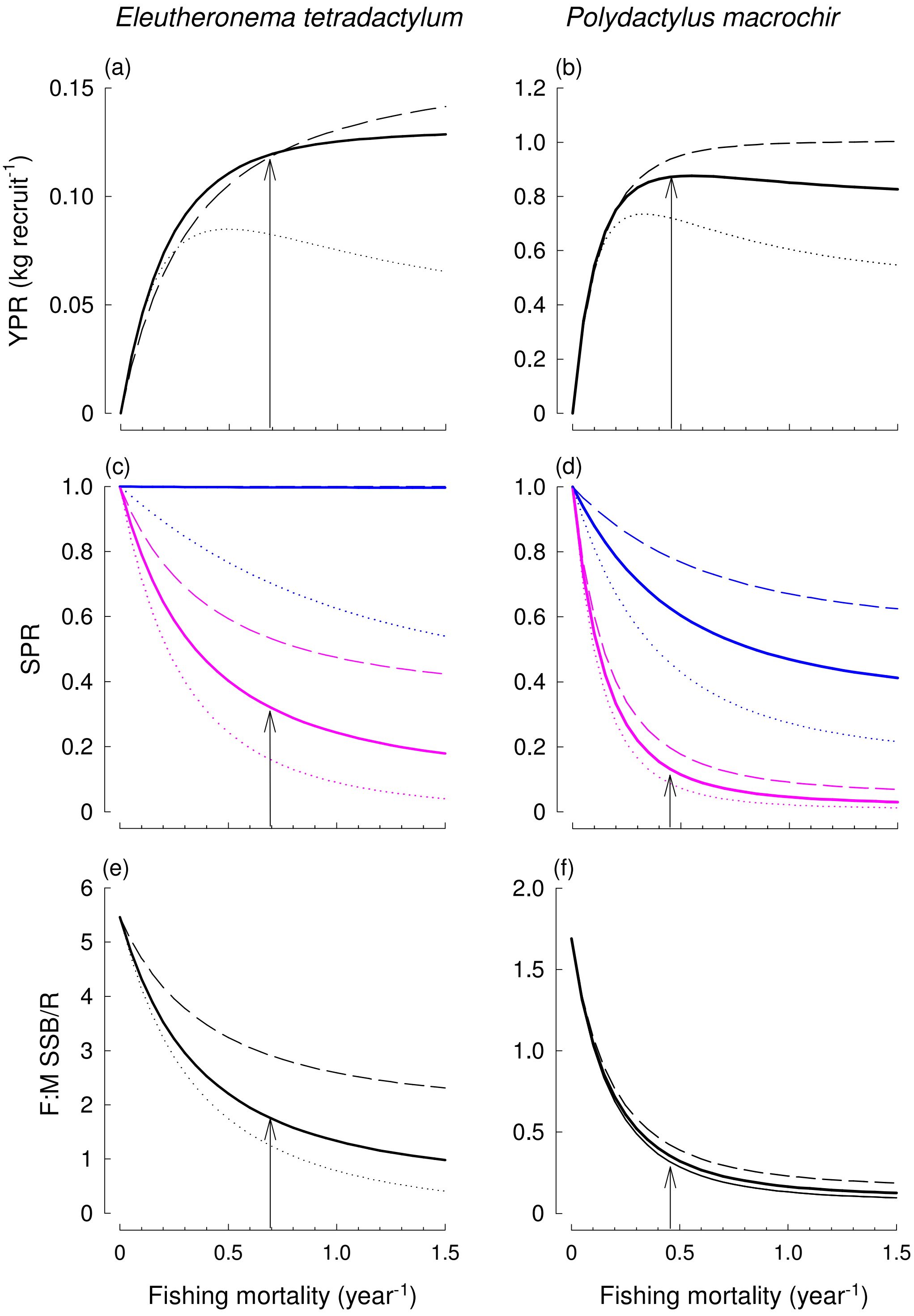

Figure 3.32. Effect, for *Eleutheronema tetradactylum* and *Polydactylus macrochir*, of different levels of fishing mortality (year^{-1}) and at different ages of recruitment to the exploited stock on the yield per recruit (a, b), spawning potential ratio, for male (blue) and female (pink) spawning stock biomass (c, d) and on the ratio of female to male spawning stock biomass (e, f). The dotted, solid and dashed lines correspond to ages at full recruitment of 1, 2 & 3 and 2, 3 & 4 for *E. tetradactylum* and *P. macrochir*, respectively. The arrows indicate the current level of fishing mortality estimated for *E. tetradactylum* and *P. macrochir* of 0.7 and 0.45 year^{-1}, respectively.

Table 3.10. Estimates of the current level of yield per recruit (YPR), $F_{\max}$, $F_{0.1}$ and the current levels of total spawning stock biomass per recruit (SSB/R) and spawning potential ratio (SPR) for females, males and females and males combined, for *Eleutheronema tetradactylum* and *Polydactylus macrochir*, calculated using 2 and 3 years as the ages at full recruitment to the fishery for *E. tetradactylum* and *P. macrochir*, respectively. N.B. It was not possible to determine $F_{\max}$ for *E. tetradactylum.*

Method of analysis	Estimate	Lower 95%	Upper 95%
Eleutheronema tetradactylum			
Monte Carlo estimate of YPR (kg recruit^{-1})	0.12	0.00	0.42
$F_{0.1}$ (year^{-1})	0.57		
Monte Carlo estimate of SSB/R	0.37	0.13	0.79
SPR (males)	1.00	0.99	1.00
SPR (females)	0.36	0.06	1.00
SPR (males & females)	0.46	0.09	1.00
Polydactylus macrochir			
Monte Carlo estimate of YPR (kg recruit^{-1})	0.86	0.02	2.29
$F_{\max}$ (year^{-1})	0.55		
$F_{0.1}$ (year^{-1})	0.24		
Monte Carlo estimate of SSB/R	3.25	1.04	6.03
SPR (males)	0.65	0.45	0.97
SPR (females)	0.15	0.02	0.87
SPR (males & females)	0.34	0.07	0.95

possible to determine a value for $F_{\max}$ for *E. tetradactylum*. The $F_{0.1}$ value of 0.57 year^{-1} calculated for *E. tetradactylum* is lower than the current level of *F* estimated for this species (**Table 3.10**). Although YPR also increases with *F* if the age of recruitment to the fishery was 3 years, if it was 1 year, the YPR begins to decline at levels of *F* exceeding *ca* 0.4 year^{-1} (**Figure 3.32a**).

At the current age of recruitment to the exploited stock of 3 years, the YPR for *P. macrochir* began to decline at levels of *F* greater than *ca* 0.55 year^{-1} (**Table 3.10, Figure 3.32b**). The estimated YPR and associated 95% confidence intervals for *P. macrochir* at the estimated current level of *F* of 0.45 year^{-1} and recruitment age of 3 years, is 0.86 kg recruit^{-1} (0.02 – 2.29 kg recruit^{-1}) (**Table 3.10**). The value of $F_{\max}$ (0.55 year^{-1}) calculated for *P. macrochir,* with an age of recruitment to the fishery of 3 years, exceeded the estimated current level of *F* of 0.45 year^{-1}, and that for $F_{0.1}$ (0.24 year^{-1}) was even less (**Tables 3.9, 3.10**). Although YPR continued to increase with *F* if the age of recruitment to the fishery was 4 years, it began to decline at levels of *F* exceeding *ca* 0.3 year^{-1} if the age of recruitment was 2 years (**Figure 3.32b**).

The spawning potential ratio (SPR) of male *E. tetradactylum* decreased with increasing levels of *F* only when the age at full recruitment to the exploited stock was 1 year. At the recruitment ages of 2 and 3 years, there was no reduction in the SPR (**Figure 3.32c**). In contrast, irrespective of recruitment age, the YPR of female *E. tetradactylum* decreased with increasing levels of *F* and was less than that of males (**Figure 3.32c**). The rate at which female SPR declined varied with recruitment age and was greatest for age 1 and least for age 3. The current estimated SPRs for male and female *E. tetradactylum* are 1.00 and 0.36, respectively (**Table 3.10, Figure 3.32c**).

Regardless of the age at recruitment, an increase in *F* for *P. macrochir* resulted in the spawning potential ratio (SPR) decreasing far more rapidly for its females than its males (**Figure 3.32c**). In the case of both female and males, the rate at which SPR is predicted to decline decreases substantially as the age at recruitment increases from 2 to 4 years **(Figures 3.32d)**. The current estimated SPRs for male and female *P. macrochir* are 0.65 and 0.15, respectively (**Table 3.10**).

For both *E. tetradactylum* and *P. macrochir,* as *F* increases from 0 year^{-1} , the ratio of female to male spawning stock biomass per recruit (SSB/R) declines exponentially from initial values of *ca* 5.46 and 1.69, respectively (**Figure 3.32e, f**). The current estimated ratios of female to male SSB/R for *E. tetradactylum* and *P. macrochir* are 1.5 and 0.46, respectively (**Figure 3.32**).

3.4 DISCUSSION

3.4.1 Habitats

Analysis of the numerous samples collected by ourselves and commercial and recreational fishers using seine, gill and haul nets and rod and line fishing provide information on the types of habitat occupied by *E. tetradactylum* and *P. macrochir* during their life cycles. Thus, these data, together with the absence of these species in catches obtained in offshore waters (Newman *et al*., 2003), demonstrate that the Blue and King Threadfins live predominantly over unvegetated substrates in nearshore, shallow waters. However, in comparison with *E. tetradactylum*, *P. macrochir* tends to live, to a greater extent, in areas where the substrate contains larger amounts of organic material and fine particles. The fact that newly-recruited juveniles of *P. macrochir* were found almost exclusively in such habitats, *i.e.* at Roebuck Bay and Anna Plains, demonstrates that this type of habitat constitutes an important nursery area for this species. This importance presumably reflects, in part, the presence of substantial amounts of food, which is consistent with the fact that both Roebuck Bay and Anna Plains are known to have an extremely high intertidal invertebrate fauna (Piersma *et al*., 1999, 2002).

3.4.2 Evidence that threadfin species are protandrous hermaphrodites in Western Australia

This study provides comprehensive details of the macroscopic and histological characteristics of the gonads of both the Blue Threadfin *Eleutheronema tetradactylum* and the King Threadfin *Polydactylus macrochir* in north-western Australia*,* with the results being derived from material obtained from fish covering a wide range of lengths and ages and different locations.

The following evidence, which applies to both *E. tetradactylum* and *P. macrochir*, overwhelmingly supports the hypothesis that both of these threadfin species are protandrous hermaphrodites in north-western Australia. 1. All small and young fish were males and the prevalence of females increased progressively with increasing length and age. 2. The length range of those fish with gonads containing both testicular and ovarian tissue spanned the length range between the upper end of that for males and the lower end of that for females and this was particularly the case with *E. tetradactylum*. 3. Some of the transitional gonads clearly contained proliferating ovarian tissue and degenerating testicular tissue.

The above findings satisfy the criteria of Sadovy & Shapiro, (1987) for demonstrating that a species is a sequential protandrous hermaphrodite. The conclusion that *E. tetradactylum* and *P. macrochir* are protandrous hermaphrodites is consistent with the conclusions drawn for these two polynemids in the Northern Territory and Queensland (Stanger, 1974; R. Griffin unpubl. data, cited in Kailola, 1993; McPherson, 1997) and a number of other polynemid species, (Longhurst, 1965; Hida, 1967; Kagwade, 1970; Dorairaj, 1973; Santerre & May, 1977; Szyper *et al.*, 1991). However, the finding that *E. tetradactylum* is a protandrous hermaphrodite in Australian waters contrasts with the situation found in Indian waters, in which this species is typically gonochoristic (Patnaik, 1967, 1970; Gopalakrishnan, 1972).

The structures of the transitional gonads of *E. tetradactylum* and *P. macrochir* were very similar, with the testicular tissue being located along the dorsal and inner lateral regions of the paired gonads and separated by connective tissue from the ovarian tissue on the ventral and outer regions of those lobes. These locations of the testicular and ovarian components and their separation by connective tissue parallel the situation described for other protandrous polynemids (Nyak, 1959; Kagwade, 1970; Dorairaj, 1973). The transition from testis to ovary in *E. tetradactylum* and *P. macrochir* involves a complete restructuring of the whole gonad, with the result that no evidence of its testicular ancestry can be detected even histologically.

The trends exhibited by the mean monthly GSIs for the testicular and ovarian components of the gonads of transitional fish demonstrate that, during the spawning period, the GSIs for the male component rise to levels far in excess of the female component and indeed were comparable with those of definitive males. The implications that, during the spawning period, transitional fish function as males are substantiated by the fact that substantial amounts of spermatozoa are present in the testicular component of the gonads of such fish.

3.4.3 Timing of maturation and sex change

Although *E. tetradactylum* and *P. macrochir* differ markedly in their maximum sizes, the vast majority of the individuals of both species reach maturity at the end of their first year of life when their lengths typically range from 200 to 300 mm. However, very few males of *E. tetradactylum* were older than two years, whereas males were found in all year classes of *P. macrochir* between one and seven. This implies that the males of *E. tetradactylum* spawn in only one or two years, whereas some males of *P. macrochir* spawn in several years.

The extent of the ranges in lengths and ages over which the males change to females differs markedly between *E. tetradactylum* and *P. macrochir*. In the case of *E. tetradactylum*, most transitional fish ranged from 275 to 425 in length and belonged to the 1+ or 2+ age classes and females and males were both present only in the length classes between 325 and 425 mm. However, males of *P. macrochir* changed to females over the length range of 400 to 1200 mm and in all but the 0+ age class. These interspecific differences can be attributed in part to the fact that the males of *E. tetradactylum* spawn in only one or two years, whereas some of those of *P. macrochir* spawn during several years.

Eleutheronema tetradactylum typically changes sex at a far smaller size and younger age than *P. macrochir,* as is demonstrated by the values of 401 and 814 mm for the L_{50} at the completion of sex change and the corresponding ages of 2 and 5 years, respectively. Since all females were mature during the spawning period, the L_{50} of 401 mm for the completion of sex change in *E. tetradactylum* will correspond closely to the L_{50} of females at maturity. The above L_{50} of 401 mm was less than the 543 mm recorded by McPherson (1997) for the females of *E. tetradactylum* at maturity in the Gulf of Carpentaria. The L_{50} of 840 mm for sex change in *P. macrochir* in north-western Australia waters is also less than the value of *ca* 1150 mm for this species in the Gulf of Carpentaria (McPherson, 1997).

3.4.4 Spawning period and mode

The presence of females of *E. tetradactylum* with mature ovaries (stage V/VI) in each month between August and January implies that this species spawns between late winter and mid summer. This conclusion is broadly consistent with the fact that the mean monthly GSIs of females were greatest between September and December.

The above spawning period of *E. tetradactylum* in north-western Australia is similar to that recorded for this species on the east coast of Queensland, where spawning peaks in October to December (Stanger, 1974; Russell, 1988). In contrast, the spawning of *E. tetradactylum* in the Gulf of Carpentaria in northern Australia peaks slightly earlier, *i.e.* during late winter and early spring (McPherson, 1997).

Although we were only able to attain one large female in each of November and December, due to a combination of poor weather in the first of these months and the cessation of fishing by commercial fishers who were responsible for providing the largest fish during this study, the trends exhibited by the mean monthly GSIs for females strongly indicated that spawning occurred between September and January. This conclusion is broadly consistent with the progressive rise that took place in the mean monthly GSIs of males between September and October and the continuation of high values in the subsequent two months. The above estimate for the spawning period, *i.e.* early spring to mid summer, is slightly earlier than that of this species in the Gulf of Carpentaria, where spawning is estimated as peaking in late winter to early spring (McPherson, 1997). Although very few mature females of *P. macrochir* were caught in the study of Russell (1988), this author concluded from data for males that this threadfin species spawns in October to March in eastern Queensland.

The frequency distributions for the diameters of each of the sequential stages in the development of oocytes in stage VI ovaries provided no evidence that there was a marked discontinuity between the sizes of those successive stages in either *E. tetradactylum* or *P. macrochir*. It is thus concluded that these two threadfin species have indeterminate fecundity, *i.e.* there is continuous development and maturation of oocytes throughout the spawning period. Although this conclusion differs from that reached for *E. tetradactylum* by Stanger (1974), it does agree with those of other workers for other threadfin species (Karekar & Bal, 1960).

The presence of both post-ovulatory follicles and migratory nucleus stage oocytes in individual mature ovaries of both threadfin species strongly suggests that these species spawn on several occasions and within relatively short time intervals. This type of repetitive spawning has been observed directly in *E. tetradactylum* and in other threadfin species under aquaculture conditions (May *et al*., 1979; Chao *et al*., 1994).

3.4.5 Age and growth

Although *E. tetradactylum* and *P. macrochir* both grow relatively rapidly early in life, attaining lengths of *ca* 400 mm by the end of their second years of life, the latter species subsequently grows more rapidly than the former species, with asymptotic lengths of 1590 *vs* 760 mm and attaining maximum lengths of *ca* 1400 *vs* 800 mm. The King Threadfin also lives far longer than the Blue Threadfin, with several of its individuals in our samples being six to ten years in age, whereas none of the latter species exceeded six years in age.

The size and age compositions and patterns of growth of *E. tetradactylum* and *P. macrochir* in north-western Australia are similar to those recorded for these species elsewhere in Australia (Stanger, 1974; Russell, 1988; Garrett, 1992; Bibby & McPherson, 1997). However, *E. tetradactylum* attains a far greater length in Indian waters than along the coast of north-western Australia, *i.e.* 1800-2000 *vs ca* 800 mm (Gopalakrishnan, 1972; Krishhnamurthy & Jeyaseelan, 1981; Feltes, 1999).

3.4.6 Mortality and yield and spawning biomass per recruit

The far greater growth coefficient, *k*, and smaller asymptotic length recorded for *E. tetradactylum* than *P. macrochir* would be expected to be accompanied by a higher rate of natural mortality, *M* (*e.g.* Beverton and Holt, 1957; Pauly, 1980). This prediction is borne out by the greater values derived for *M* for *E. tetradactylum* using both the refitted equation of Pauly (1980) and the Bayesian approach of Hall *et al.* (2004), *i.e.* 0.68 and 0.61 year^{-1}, respectively, than those derived for *P. macrochir* using the same methods, *i.e.* 0.35 and 0.31 year^{-1}, respectively. These comparisons imply that the stock of Blue Threadfin is more productive and more likely to sustain exploitation than that of the King Threadfin. Although the estimate of fishing mortality, *F*, was similar to that for *M* for *E. tetradactylum*, the estimate of *F* for *P. macrochir* greatly exceeded that of *M*. This suggests that *E. tetradactylum* is fully exploited and that *P. macrochir* is subject to overfishing. In the context of *P. macrochir*, it may thus be relevant that commercial fishing for threadfin species in north-western Australia is now focused mainly on this larger species. The extremely high values for *F* for another species of threadfin in India provide strong indications that such species are highly vulnerable to fishing. From a management point of view, it is important to recognise that the two threadfin species in north-western Australia are restricted to nearshore waters and are therefore easily targeted by fishers.

The view that the King Threadfin is subject to overfishing and that Blue Threadfin is also relatively heavily fished is supported by the fact that the current estimates for *F* for both species exceed those for the $F_{0.1}$ reference points for those species. The yield per recruit analysis also indicates that the age at recruitment of both threadfin species to the fishery has an important influence on the potential yield. Thus, if the ages at recruitment to the fisheries for *E. tetradactylum* or *P. macrochir* were to be reduced by only one year, the yield of particularly the former species would be substantially reduced.

A marked reduction in spawning stock biomass could lead to recruitment overfishing. In this context, the more dramatic declines in the spawning potential ratios of the females than males of *E. tetradactylum* and *P. macrochir* as fishing mortality increases from 0 to 1.5 year^{-1} demonstrate that, for these hermaphroditic species, it is critically important to take into account the lengths over which individuals change sex. At the current estimated level of fishing mortality of 0.45 year^{-1} for *P. macrochir*, the SPR of the females of this species is predicted to have declined to 0.15, which is well below the limit reference point of 0.3, *i.e.* 30% of mature female virgin stock biomass. This strongly indicates that this species is overfished and is therefore at high risk of recruitment failure. In the case of the females of *E. tetradactylum*, the point estimate of 0.36 for the current level of SPR is approaching the 0.3 reference point. Thus, the SPR of this latter species requires monitoring to ensure that it does not decline beyond the limit reference point of 0.3.

The age at recruitment of *E. tetradactylum* to the exploited stock has important consequences for its management. For example, if this age was to be reduced by one year to age 1, the SPR of the stock at the current estimated level of F would lie well below the 0.3 reference point. In this respect, it is important to recognise that a considerable number of *E. tetradactylum* are currently caught at 1 year of age. Thus, further increases in the capture and retention of this age class should be avoided.

3.4.7 Implications for management of the sizes at maturity and sex change

As our data demonstrate that recreational fishers currently retain appreciable numbers of the Blue Threadfin that have lengths below that at which this species changes from male to female (L_{50} at sex change = 401 mm), managers and stakeholders need to consider introducing a legal length for retention that takes into account this length at sex change. Such a management measure would be appropriate as *E. tetradactylum* is caught mainly by recreational fishers and would be likely to survive release following their capture by rod and line.

The current minimum legal length (MLL) for retention of 450 mm for King Threadfin is well below the length at which this species typically changes sex (L_{50} at sex change = 814 mm). However, as most of the catch of *P. macrochir* are taken by commercial gill net fishers, and few of these threadfin survive capture by gill nets, an increase in the MLL on its own would not be an effective way to facilitate the conservation of the stocks of this species. Thus, managers and stakeholders will need to consider introducing other regulations that will result in the capture of this species at a far larger size than at present to ensure that sufficient females survive to maintain spawning potential, *e.g*. through a balance of controls on fishing effort and appropriate regulations on fishing gear to adjust the length range of fish that are selected by that gear.

4. BIOLOGY OF EPINEPHELUS COIOIDES AND EPINEPHELUS MALABARICUS

4.1 INTRODUCTION

The cods and groupers, which belong to the sub-family Epinephelinae of the Serranidae, are found throughout the Indo-West Pacific, where they are fished commercially and recreationally (Randall & Heemstra, 1991; Randall *et al.*, 1997; Carpenter & Niem, 1999; Mackie, 2000; Yeh *et al.*, 2003). They are typically slow-growing, long-lived and monandric protogynous hermaphrodites, *i.e.* all males are derived from females (Shapiro, 1987; Shpigel & Fishelson, 1991; Sadovy *et al.*, 1992, 1994; Chan & Sadovy, 2002; Rhodes & Sadovy, 2002). They can be caught using a wide variety of fishing methods and, in the case of the larger species, often form spawning aggregations that are temporally and spatially predictable. The combination of the above characteristics make epinepheline serranids highly susceptible to fishing pressure (Bannerot *et al.*, 1987; Sadovy *et al.*, 1992; Huntsman *et al.*, 1999. Mackie, 2000; Rhodes & Sadovy, 2002).

Their economic value has led to the biology of several serranid species being studied in the Caribbean and Western Atlantic (*e.g.* Sadovy *et al.*, 1994; Sadovy & Colin, 1995; Mackie, 2000). However, although a number of serranids are commercially and/or recreationally important in Western Australia, sound biological data are available in this state only for the Halfmoon Grouper *Epinephelus rivulatus* (Mackie, 2000). Two of the most important commercial and recreational species of serranid in north-western Australia are the Estuary Rockcod *Epinephelus coioides* and the Malabar Grouper *Epinephelus malabaricus*.

In north-eastern Queensland, *E. coioides* and *E. malabaricus* are abundant in the mangroves of estuaries within which they undergo little movement and are represented entirely by juvenile females (Sheaves, 1992, 1993, 1995). Sheaves (1995) thus concluded that these two species are monandric protogynous hermaphrodites, as is the case with other species of *Epinephelus* (Yeh *et al.*, 2003). Tank experiments involving hormonal and social induction of sex change also indicated that *E. coioides* is a protogynous hermaphrodite (Quinitio *et al.*, 2001; Yeh *et al.*, 2003).

In the Arabian Gulf, *E. coioides* exceeds 1000 mm in total length, attains a maximum age of 22 years (Mathews & Samuel, 1991) and is reported to spawn during a very restricted period, *i.e.* May (Grandcourt *et al.*, 2005). On the basis of the ages they determined for three large individuals of *E. malabaricus*, Mathews & Samuel (1991) concluded that this species grows “exceptionally quickly”.

When managing a fish stock, it is desirable to estimate the potential yield of the stock at different levels of exploitation (Buxton, 1992). Due to the fact that the empirical data for most reef fisheries are limited, per-recruit analyses have frequently been used for this purpose (Bannerot *et al.*, 1987; Buxton, 1992; Punt *et al.*, 1993). However, development of per-recruit models is more complex when dealing with hermaphroditic species than gonochorists as it requires a thorough understanding of the details of the relationship between sex change and the size and age of the fish (*e.g.* Buxton, 1992; Punt *et al.*, 1993; Hesp *et al.*, 2004a).

The first aim of this study of *E. coioides* and *E. malabaricus* was to confirm that, in northern Western Australian waters, these species are monandric protogynous hermaphrodites and, if so, then to determine the sizes and ages at which they change sex. The second aim was to determine the sizes and ages at which both species reach maturity, the duration of their spawning periods, and whether they spawn on several occasions during the spawning period and have determinate or indeterminate fecundity. The third aim was to determine their size and age compositions and growth characteristics and to estimate their total, natural and fishing mortality. The final aim was to undertake per-recruit analyses for both species that would incorporate information on the lengths and ages at which sex change occurs.

4.2 MATERIALS AND METHODS

Details of the materials and methods are given in Chapter 2. Note that two individuals of *E. coioides* possessed gonads comprising both ovarian and testicular tissue. Since the oocytes in the ovarian component of the gonads of these two *E. coioides* were all at an early previtellogenic stage, whereas the testicular component contained spermatids, these two fish were considered more likely to be functioning as males rather than females. For this reason, the data for these two individuals were grouped together with male *E. coioides* and regarded as males when determining the size and age at which this species changes sex.

4.3 RESULTS

4.3.1 Gonad histology

Histological sections showed that the gonads of *E. coioides* < 600 mm and *E. malabaricus* < 900 mm consist exclusively of ovarian tissue. The gonads of two individuals of *E. coioides*, with lengths of 855 and 872 mm, contained both ovarian and testicular tissue. None of the oocytes in either of those two gonads had developed beyond the previtellogenic stage, while the testicular tissue consisted predominantly of spermatogonia, spermatocytes and spermatids (**Figure 4.1a**). The gonads of both of these individuals belonged to what was described by Sadovy and Shapiro (1987) as the undelimited type 2 category, *i.e.* male and female tissues are intermixed and not separated by connective tissue. None of the gonads of *E. malabaricus* contained both ovarian and testicular tissue.

The testes of mature *E. coioides* and *E. malabaricus* possessed a conspicuous membrane-lined lumen (**Figure 4.1b**) and numerous sperm sinuses in their outer wall (**Figure 4.1c**), which contained spermatids and spermatozoa (**Figure 4.1d**). The spermatogenic tissue within the main body of mature testes consisted predominantly of spermatids.

4.3.2 Length- and age-related sex ratios

All *E. coioides* < 600 mm and all *E. malabaricus* < 900 mm TL were females. For *E. coioides*, the contributions made to each 100 mm length class by the males increased from 1% in the 600-699 mm length class to 55% in the 900-999 mm length class and

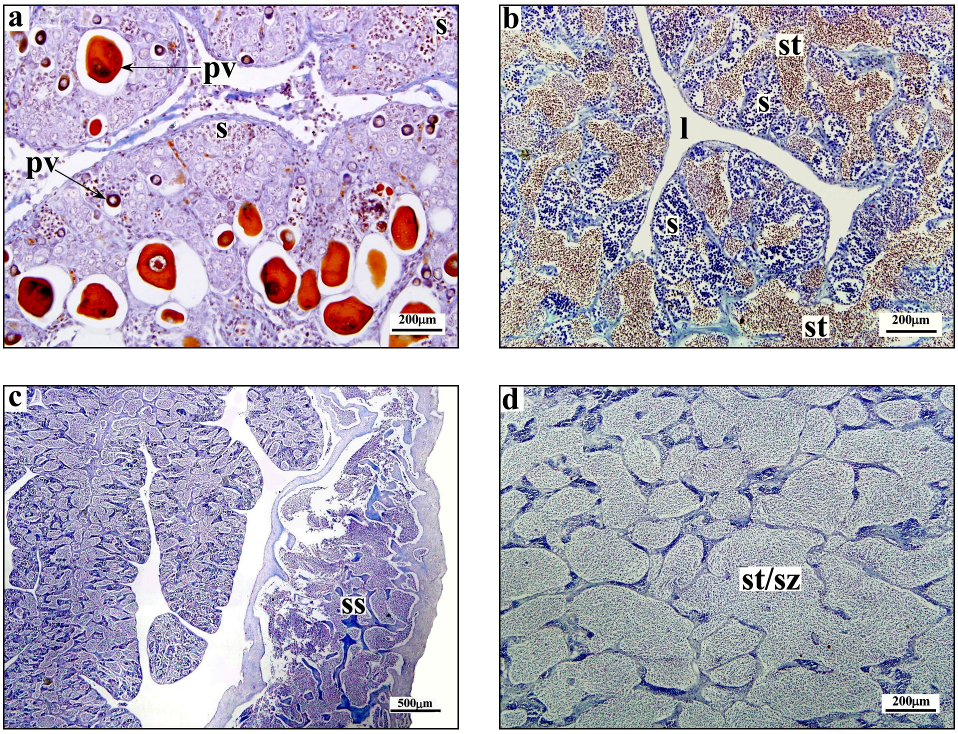

Figure 4.1. Histological sections of gonads of *Epinephelus coioides*. (a) Gonad containing both ovarian and testicular tissue, (b) an immature testis and (c,d) mature testes. The testes of *E. coioides* contain a lumen and, in the case of mature testes, sperm sinuses in their outer membrane. l, lumen; pv, previtellogenic oocyte; s, spermatocytes; ss, sperm sinus; st, spermatids; sz, spermatozoa.

100% in all individuals ≥ 1100 mm (**Figure 4.2**). For *E. malabaricus*, the contributions made to each length class by males increased from 5% in the 900-999 mm length class to 24% in the 1000-1100 mm length class and 100% in all fish ≥ 1200 mm (**Figure 4.2**). The L_{50} at sex change from female to male of 925 mm for *E. coioides* was significantly less than that of 1103 mm for *E. malabaricus* ($p < 0.001$) (**Table 4.1**).

Table 4.1. Estimates of the L_{50} and L_{95} and the associated lower and upper 95% confidence limits for *Epinephelus coioides* and *Epinephelus malabaricus* at sex change.

Parameter	**L_{50} (mm)**	**L_{95} (mm)**
Epinephelus coioides		
Estimate	925	1060
Lower	901	1018
Upper	953	1112
Epinephelus malabaricus		
Estimate	1103	1224
Lower	1055	1147
Upper	1147	1300

All *E. coioides* < 7 years and all *E. malabaricus* < 12 years were females (**Figure 4.3**). The percentage of *E. coioides* that were males increased progressively with increasing age, *i.e.* from 14 and 30% at 7 and 9 years of age, respectively, to 48% in all fish > 11 years of age collectively. In the case of *E. malabaricus*, the percentage of male fish increased from 13% between 12 and 14 years, to 29% between 15 and 21 years and 91% in fish > 21 years of age (**Figure 4.3**).

4.3.3 Reproductive biology

The mean monthly GSIs of female *E. coioides* ≥ L_{50} at maturity remained low, *i.e.* < 1.1, between July and September, before increasing to > 2.5 between November and January, and then declining precipitously to *ca* 1 in February and < 0.5 between April and June (**Figure 4.4**). The mean monthly GSIs of female *E. malabaricus* ≥ L_{50} at maturity followed a similar trend to that of *E. coioides* (**Figure 4.4**). The macroscopic

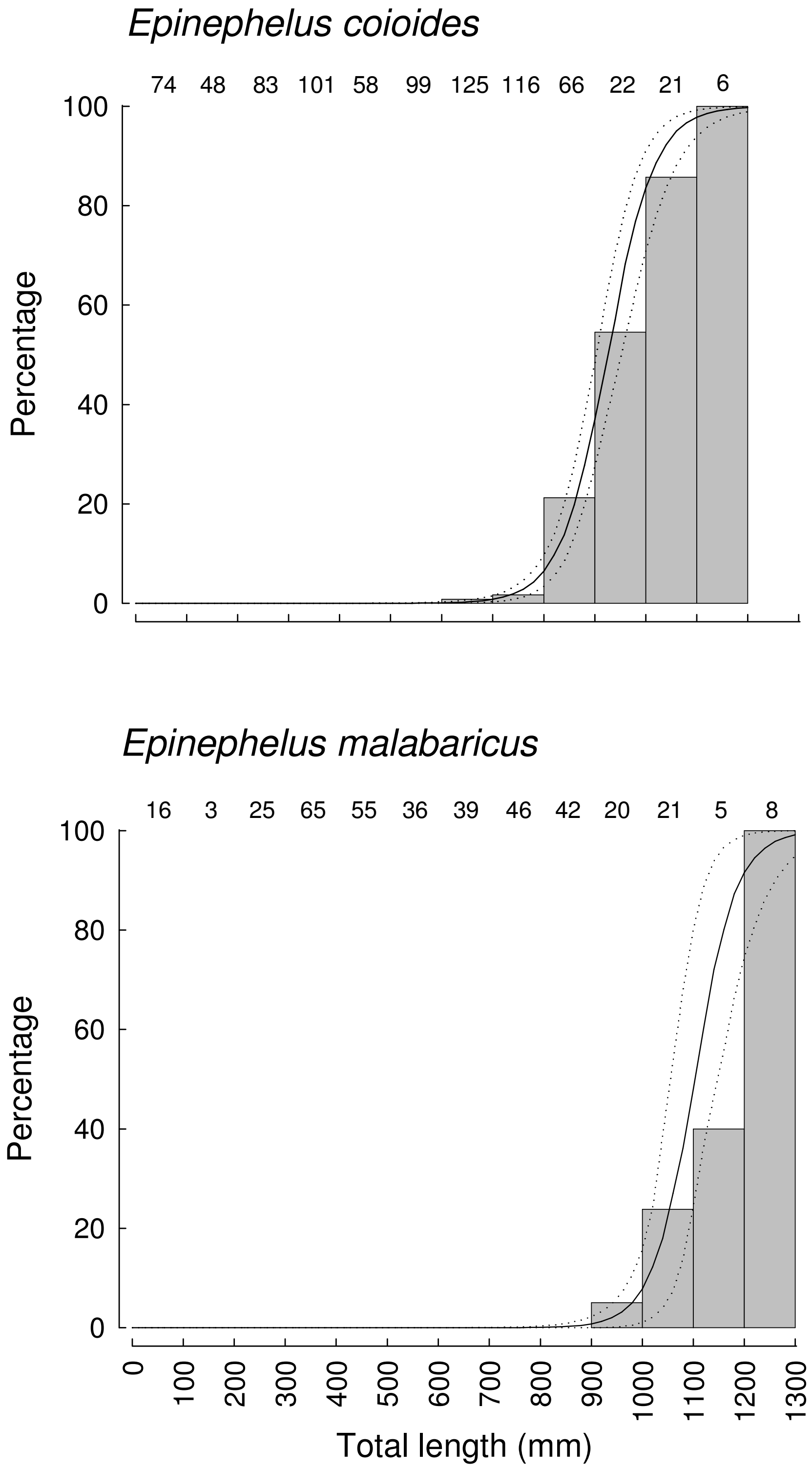

Figure 4.2. Percentage frequencies of occurrence of male fish (grey bars) in sequential 100 mm length classes of *Epinephelus coioides* and *Epinephelus malabaricus*. The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and the probability that an individual had changed sex to become a male. Sample sizes of fish for each 100 mm length class are shown.

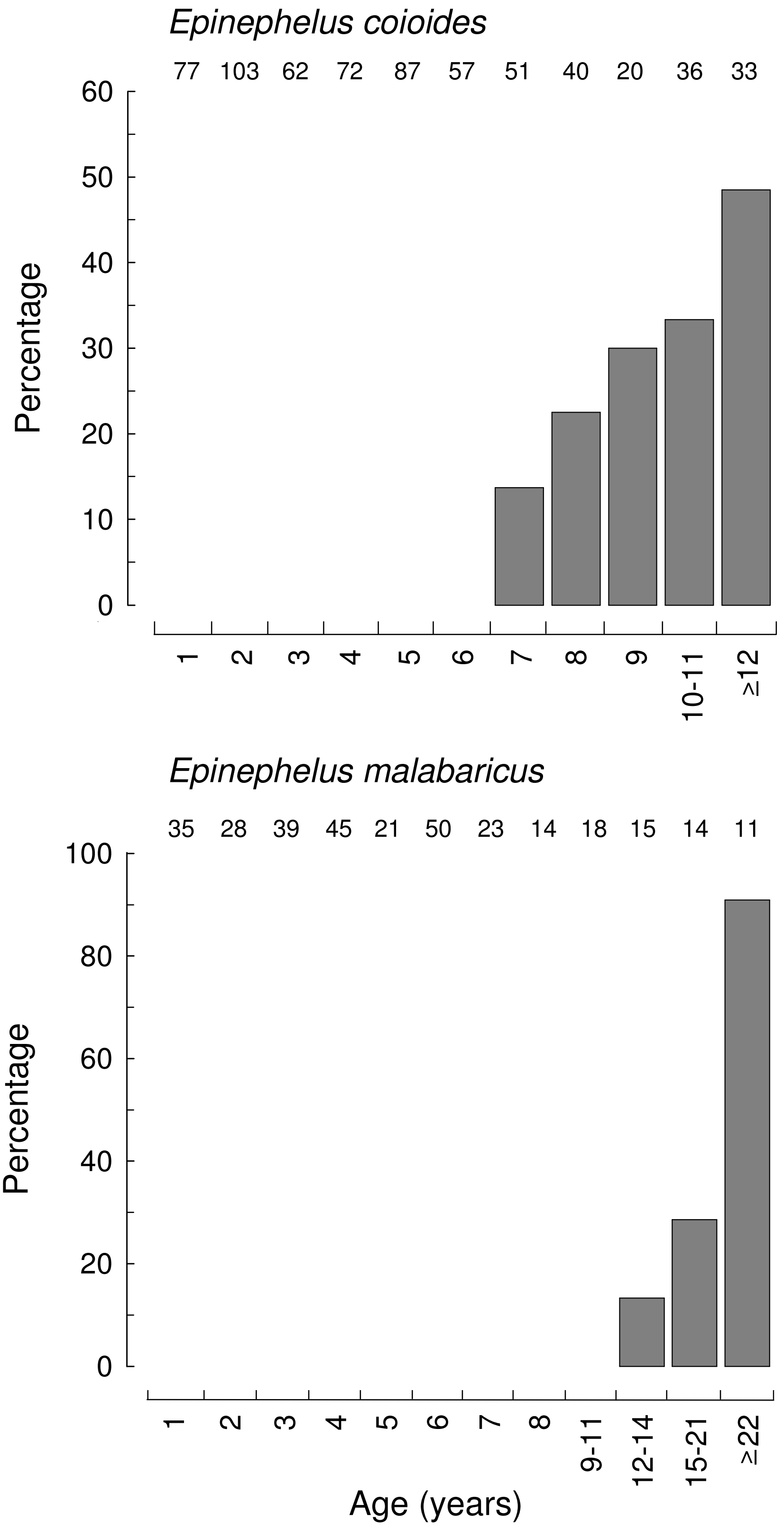

Figure 4.3. Percentage frequencies of occurrence of male *Epinephelus coioides* and *Epinephelus malabaricus* at sequential ages. Sample sizes for each age class are shown.

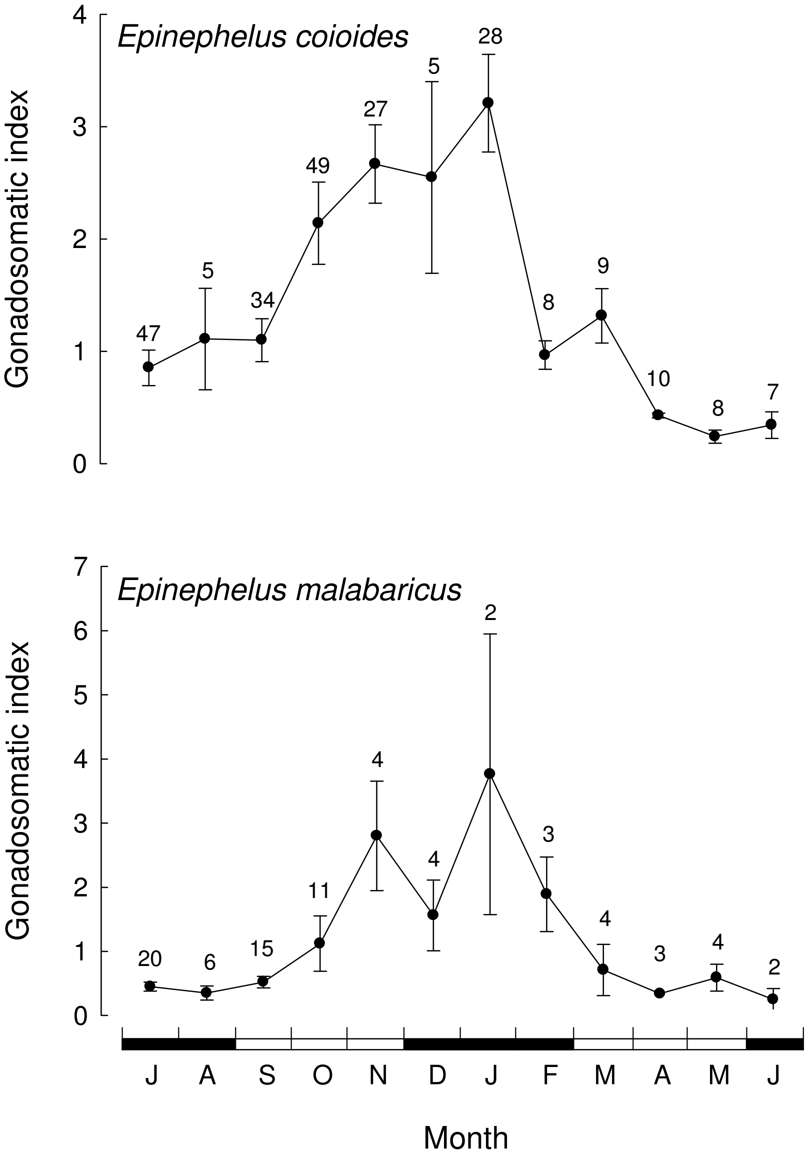

Figure 4.4. Mean monthly gonadosomatic indices ±1SE of female *Epinephelus coioides* and *Epinephelus malabaricus* with lengths > their L_{50}s at first maturity. Closed rectangles on horizontal axis refer to winter and summer months and the open rectangles to spring and autumn months. Number of fish used to derive each mean is shown.

characteristics of the different stages in the development of the ovaries of *E. coioides* and *E. malabaricus*, together with the cytological characteristics of each of those stages, are presented in **Table 4.2** and **Figure 4.5.** The ovaries of all *E. coioides* $\geq L_{50}$ at maturity in April were at stage II (immature/resting) and this was the dominant stage in the next two months. Fish with ovaries at stage III (developing) were first found in May and those at stage IV (maturing) in July (**Figure 4.6**). Ovaries at stages V/VI (mature or spawning) were recorded in nine months, *i.e.* July to March, and collectively were the predominant ovarian stage between November and January. *Epinephelus coioides* with stage VII (spent) ovaries were recorded between January and March, and in one individual that was caught in July. One individual in October and another in January possessed ovaries at stage VIII (spent/recovering) (**Figure 4.6**). The trends exhibited by the prevalences of the different stages in the gonadal development of the females of *E. malabaricus* were similar to those just described for the females of *E. coioides*. Thus, females possessing stage V/VI ovaries were caught in ten months and constituted the dominant category between November and February.

During the main part of the spawning period of *E. coioides*, *i.e.* November to January, the ovaries of all females < 500 mm were at stages I-II (**Figure 4.7**). Ovaries of *E. coioides* at stages III-VIII were first recorded in the 500-599 mm length class, to which they contributed 73% of all ovaries, and they constituted ≥ 75% of ovaries in each subsequent length class. The L_{50} for female *E. coioides* at first maturity, derived from the logistic curve fitted to the percentage contributions made at each length by females with gonads at stages III-VIII during the spawning period, was 575 mm (**Table 4.3**).

No females of *E. malabaricus* that were caught during the spawning period (October to February) possessed ovaries at stages III-VIII until the 700-799 mm length classes, to which they contributed 22% of all ovaries (**Figure 4.7**). The percentage of female *E. malabaricus* with such ovaries increased to 71% in the 800-899 mm length class and 100% in all subsequent length classes. The L_{50} for *E. malabaricus* at first maturity, *i.e.* 803 mm, was significantly greater than that of *E. coioides*, *i.e.* 575 mm ($p < 0.001$) (**Table 4.3**). The upper and lower 95% confidence limits for the logistic

Table 4.2. Macroscopic and histological characteristics of stages in the development of the ovaries of *Epinephelus coioides* and *Epinephelus malabaricus*. Adapted from Laevastu (1965). Terminology for oocyte stages follows Wallace & Selman (1989).

Stage	Macroscopic characteristics	Histological characteristics
I or II – Virgin or Immature resting	Small and transparent. Yellowish-orange in colour. Oocytes not visible through ovarian wall.	Ovigerous lamellae highly organised. Chromatin nucleolar and perinucleolar oocytes dominate the complement of oocytes. Oogonia sometimes present. Chromatin nucleolar oocytes present in all subsequent ovarian stages.
III – Developing	Slightly larger than stage II. Reddish colour. Oocytes visible through ovarian wall.	Chromatin nucleolar, perinucleolar and cortical alveolar oocytes present.
IV – Maturing	Larger than stage III. Reddish-orange in colour. Yolk granule oocytes visible through ovarian wall.	Cortical alveolar and yolk granule oocytes abundant.
V – Mature	Larger than stage IV, occupying half to two thirds of body cavity. Extensive capillaries visible in ovarian wall.	Yolk granule oocytes predominant.
VI – Spawning	Hydrated oocytes visible through ovarian wall. Note that fish with ovaries in "spawning condition" can only be detected macroscopically when caught during the oocyte hydration period.	Migratory nucleus oocytes, hydrated oocytes or post-ovulatory follicles present.
VII – Spent	Smaller than V/VI and flaccid. Some yolk granule oocytes visible through ovarian wall.	Some remnant yolk granule oocytes present, all or almost all of which are undergoing atresia.
VIII-Spent/Recovering	Small and dark red.	Extensive connective tissue present. Ovarian lamellae becoming reorganised. No yolk granule oocytes present.

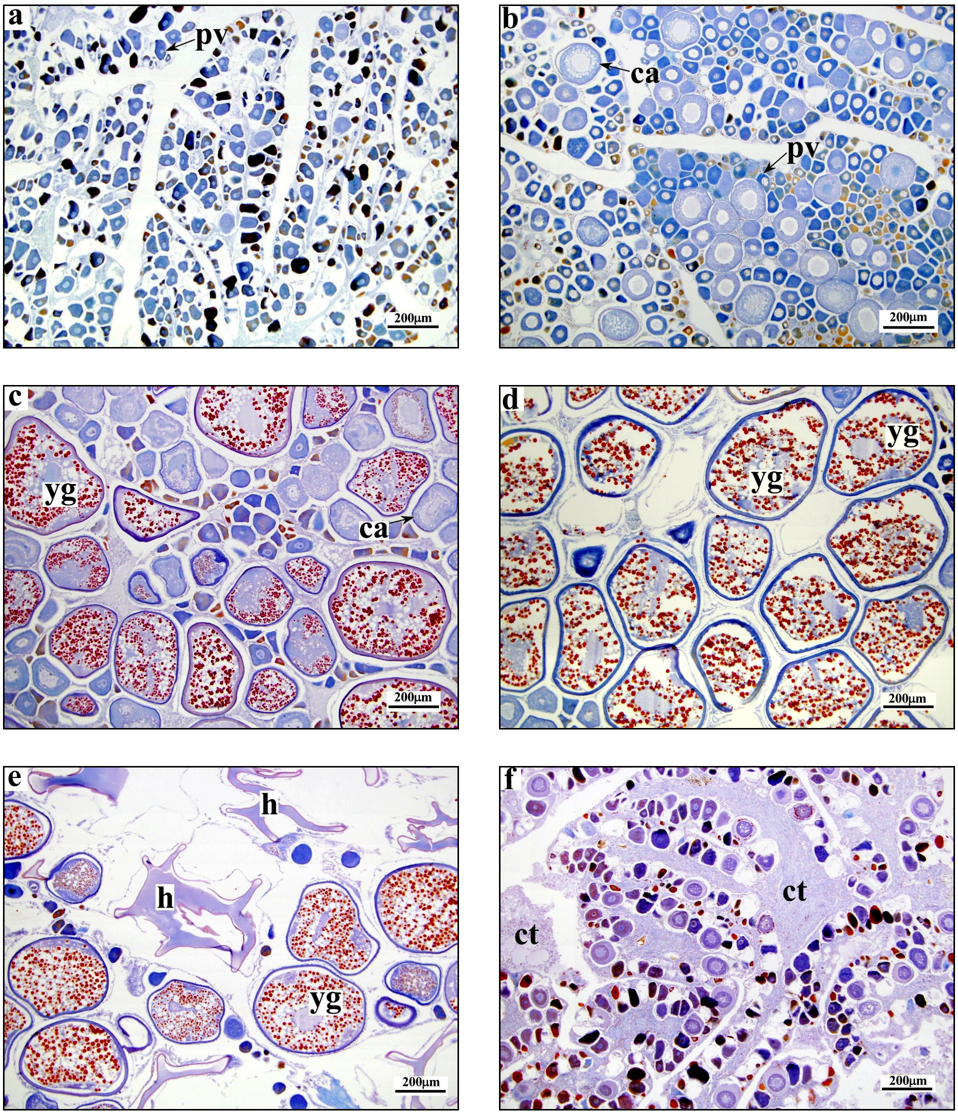

Figure 4.5. Histological sections of ovarian stages of *Epinephelus coioides*. (a) I-II, (b) III, (c) IV, (d) V, (e) VI and (f) VIII. ca, cortical alveolar oocyte; ct, connective tissue; h, hydrated oocyte; pv, previtellogenic oocyte; yg, yolk granule oocyte.

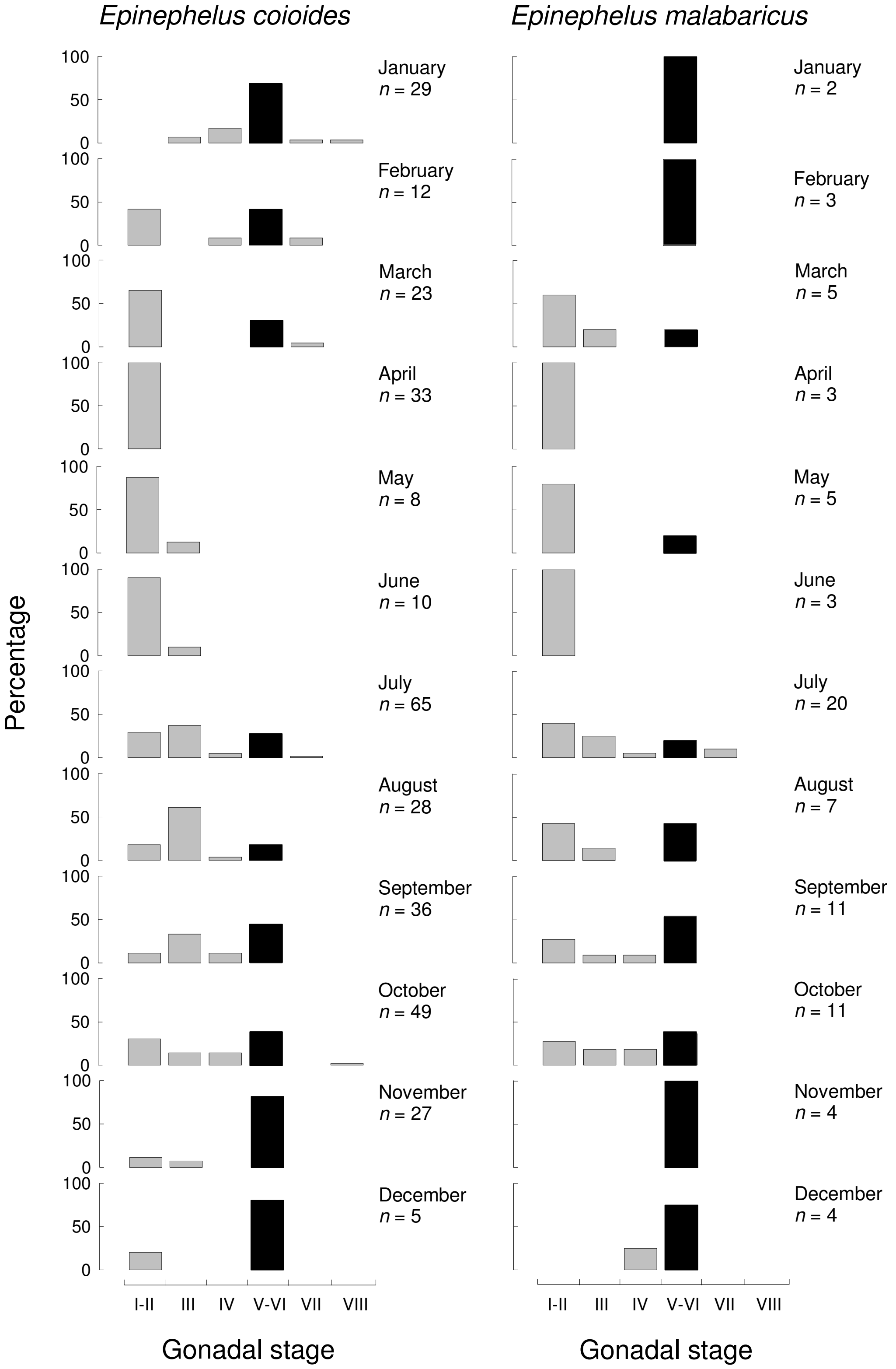

Figure 4.6. Monthly percentage frequencies of the sequential stages in gonadal maturation of female *Epinephelus coioides* and *Epinephelus malabaricus*. *n* = sample size.

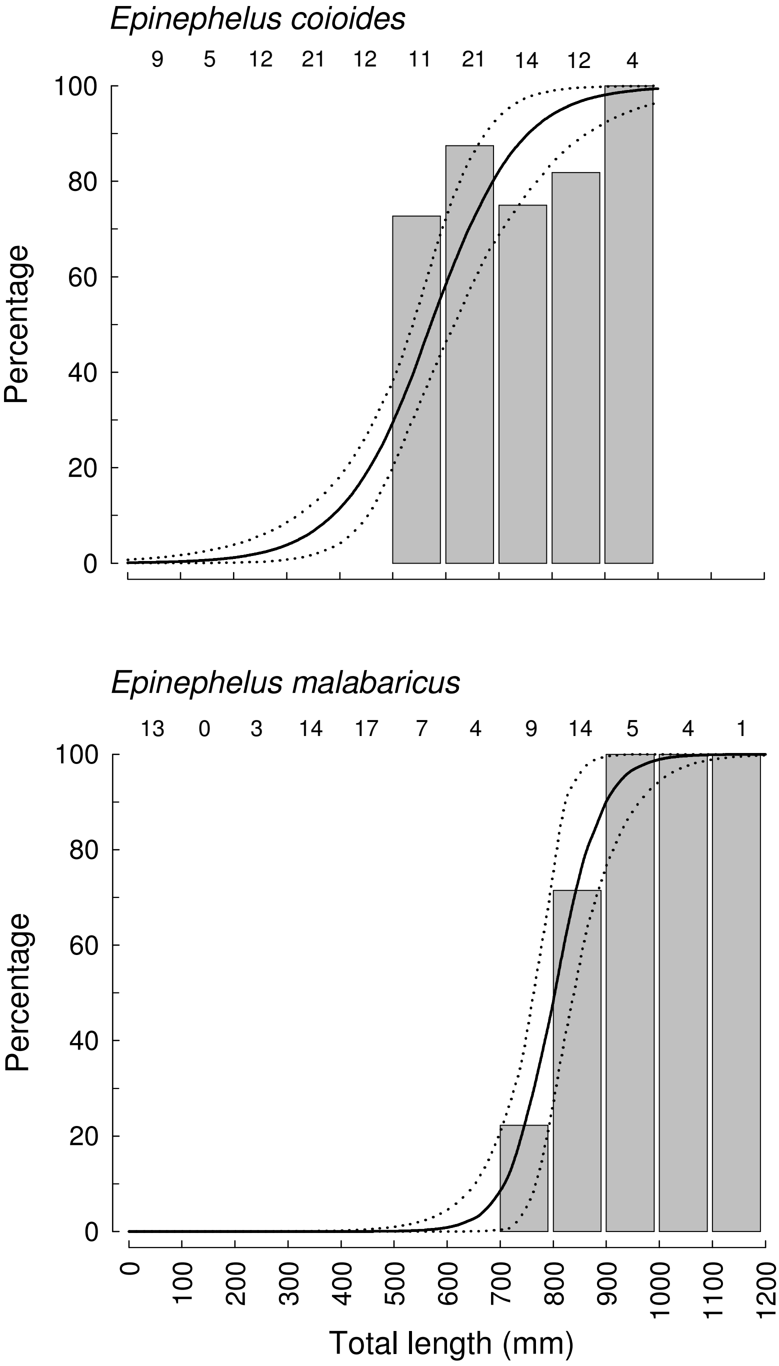

Figure 4.7. Percentage frequencies of occurrence of *Epinephelus coioides* and *Epinephelus malabaricus* with ovaries at stages III-VIII (grey bars) in sequential 100 mm length classes during the spawning period. The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and the probability that an individual was mature. Sample sizes of fish in each 100 mm length class are shown.

Table 4.3. Estimates of the L_{50} and L_{95} and their lower and upper 95% confidence limits for female *Epinephelus coioides* and *Epinephelus malabaricus* at first maturity.

Parameter	L_{50} (mm)	L_{95} (mm)
Epinephelus coioides		
Estimate	575	817
Lower	537	714
Upper	616	955
Epinephelus malabaricus		
Estimate	803	931
Upper	762	842
Lower	839	1008

parameters, *i.e.* L_{50} and L_{95}, for *E. coioides* and *E. malabaricus*, are presented in **Table 4.3**.

With *E. coioides*, maturity was attained by 25% of females at the end of their fourth year of life and by 80% of females by the end of their fifth year of life (**Figure 4.8**). All females of nine years of age or older were mature during the spawning season. In the case of *E. malabaricus*, no females reached maturity until the end of their seventh year of life. The proportion of mature *E. malabaricus* increased from 7% at the end of their seventh year of life to 100% by the end of their ninth and subsequent years of life (**Figure 4.8**).

4.3.4 Oocyte diameters of mature ovaries

The stage VI ovaries of two spawning females of each of *E. coioides* and *E. malabaricus*, that were representative of other such ovaries of these species during the spawning season, contained oocytes at each developmental stage from the chromatin nucleolar to yolk granule stage (**Figure 4.9**). Note that oocytes beyond the yolk granule stage, *i.e.* migratory nucleus and hydrated stage oocytes, were not measured (see materials and methods for reason). The distribution of oocyte diameters was continuous in the first of the ovaries of *E. coioides*, and almost continuos in the second of the ovaries of this species. The chromatin nucleolar, perinucleolar and cortical alveolar

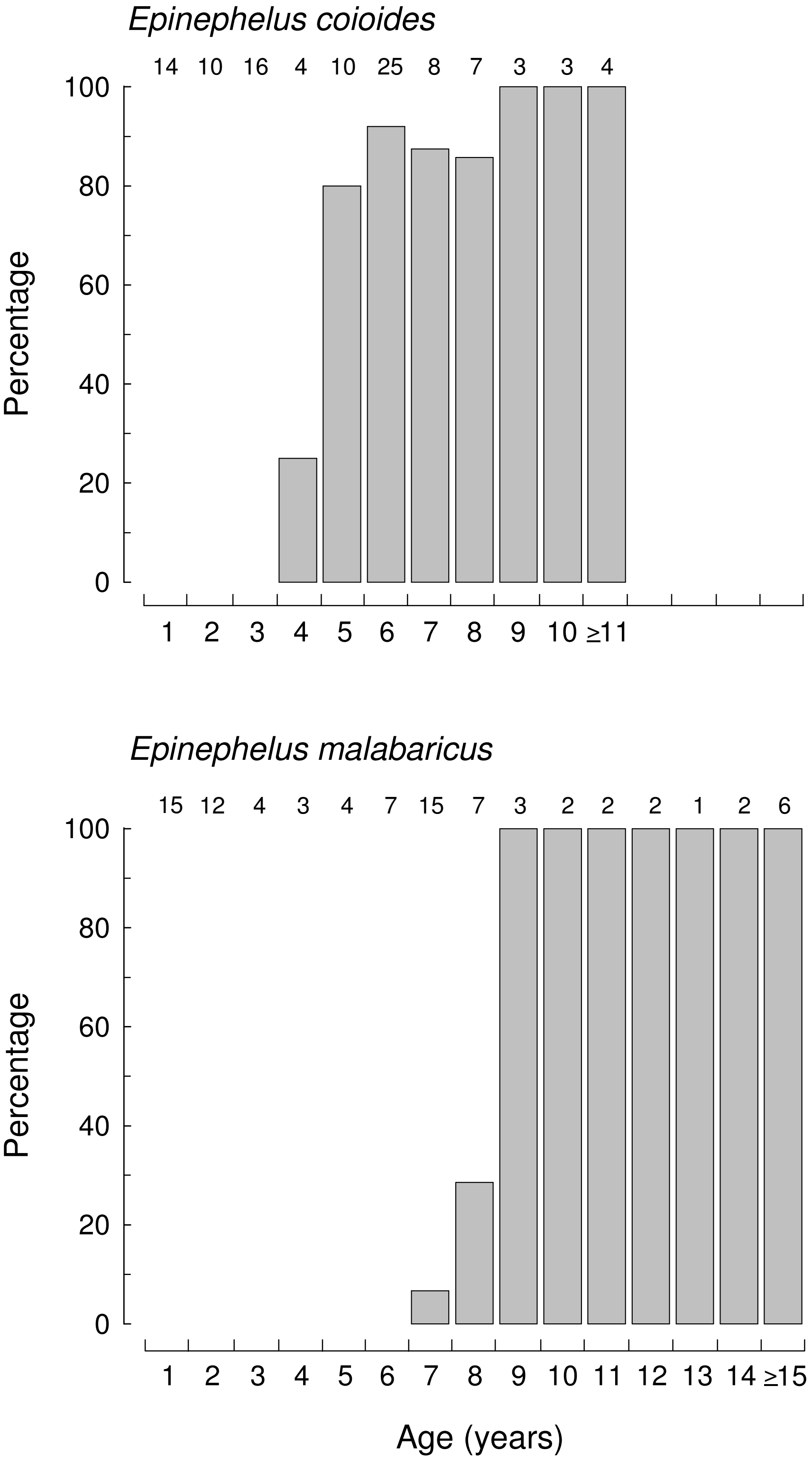

Figure 4.8. Percentage frequency of occurrence of female *Epinephelus coioides* and *Epinephelus malabaricus* with ovaries at stages III-VIII in sequential age classes during the spawning period. Sample sizes for each age class are shown.

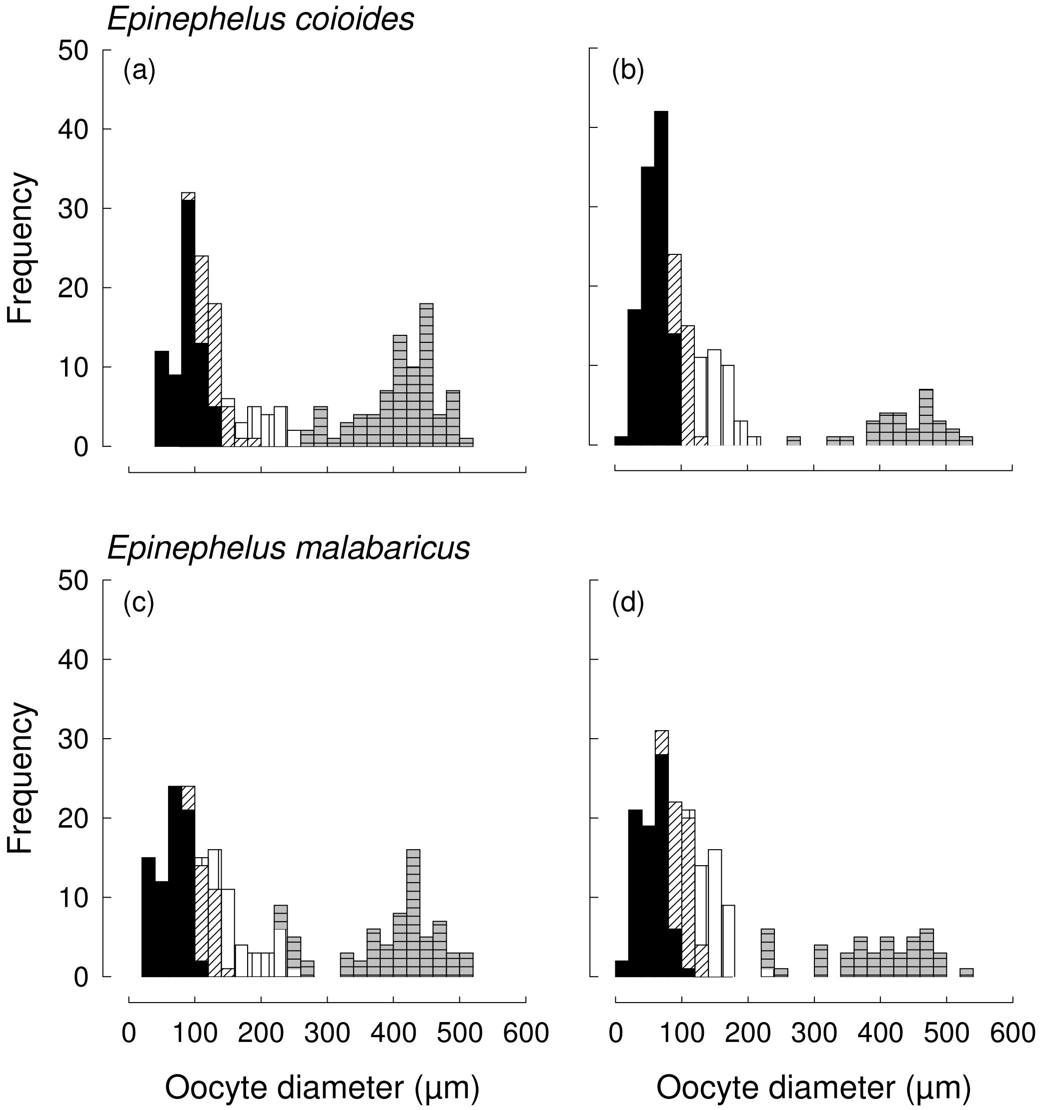

Figure 4.9. Oocyte diameter frequency distributions for stage VI (spawning) ovaries of (a,b) two *Epinephelus coioides* and (c,d) two *Epinephelus malabaricus*. Black bars refer to chromatin nucleolar oocytes, bars with diagonal lines to perinucleolar oocytes, bars with vertical lines to cortical alveolar oocytes and grey bars with horizontal lines to yolk granule oocytes.

oocytes ranged between the 0-19 and 240-259 µm diameter classes, with an overall modal diameter class of 60-99 µm, while the yolk granule oocytes ranged between the 260-279 and 540-559 µm diameter classes and exhibited a modal diameter class of 440-479 µm (**Figure 4.9b**). The distributions of the oocyte diameters in the ovaries of the two mature *E. malabaricus* were similar to those of *E. coioides* (*cf* **Figs 4.9c-d**).

4.3.5 Length composition of the samples

The length compositions of both species varied markedly according to the method of capture (**Figure 4.10**). The use of rotenone in nearshore waters yielded the smallest individuals of both *E. coioides* and *E. malabaricus*, with lengths ranging from 10 to 340 and 23 to 393 mm, respectively, and producing means of 114 and 108 mm, respectively. Line fishing caught larger *E. coioides* and *E. malabaricus* than those obtained by rotenone, with the lengths ranging from 104 to 872 and 212 to 1270 mm, respectively, and producing a modal length class at 300-399 mm for both species. Research traps caught a relatively wide length range of *E. coioides* (160 to 936 mm) and *E. malabaricus* (356 to 1056 mm), whereas virtually all of those individuals of both species caught by commercial trapping and trawling exceeded 500 mm. The average lengths of *E. coioides* and *E. malabaricus* taken by commercial trawling (811 and 906 mm, respectively) were greater than those obtained by all other methods. Furthermore, the largest individuals of both species, *i.e.* 1156 and 1216 mm, respectively, were caught by commercial trawling. The trends exhibited by differences in the length distributions of *E. malabaricus* were essentially the same as those of *E. coioides* (**Figure 4.10**).

All of the individuals of *E. coioides* and *E. malabaricus* < 200 and 300 mm, respectively, were obtained from nearshore, shallow waters (*i.e.* < 5 m deep) (**Figure 4.11**). With increasing length, the percentage *E. coioides* and *E. malabaricus* in

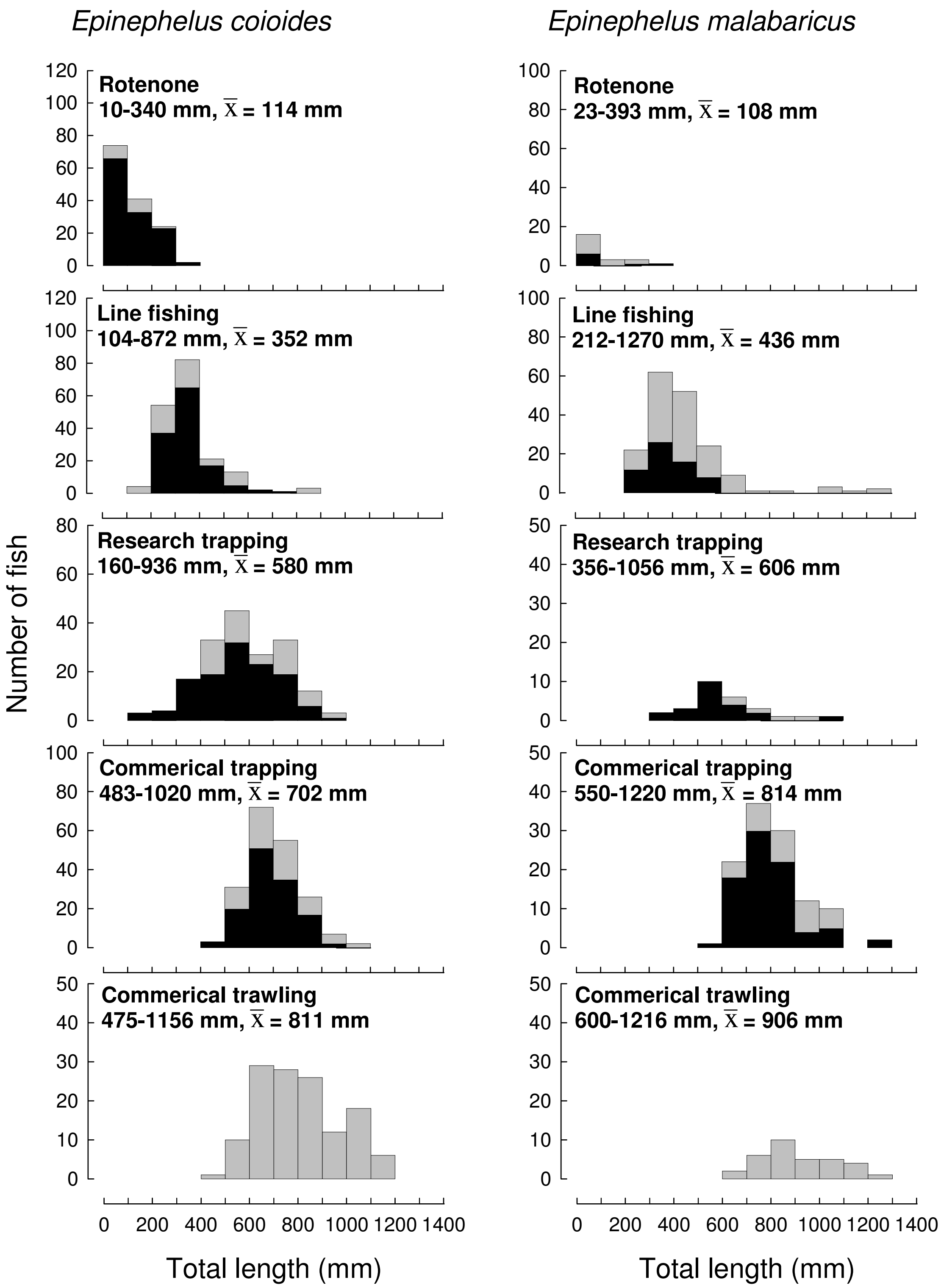

Figure 4.10. Length-frequency distributions of *Epinephelus coioides* and *Epinephelus malabaricus* caught by different methods along the Kimberley (black bars) and Pilbara (grey bars) coasts.

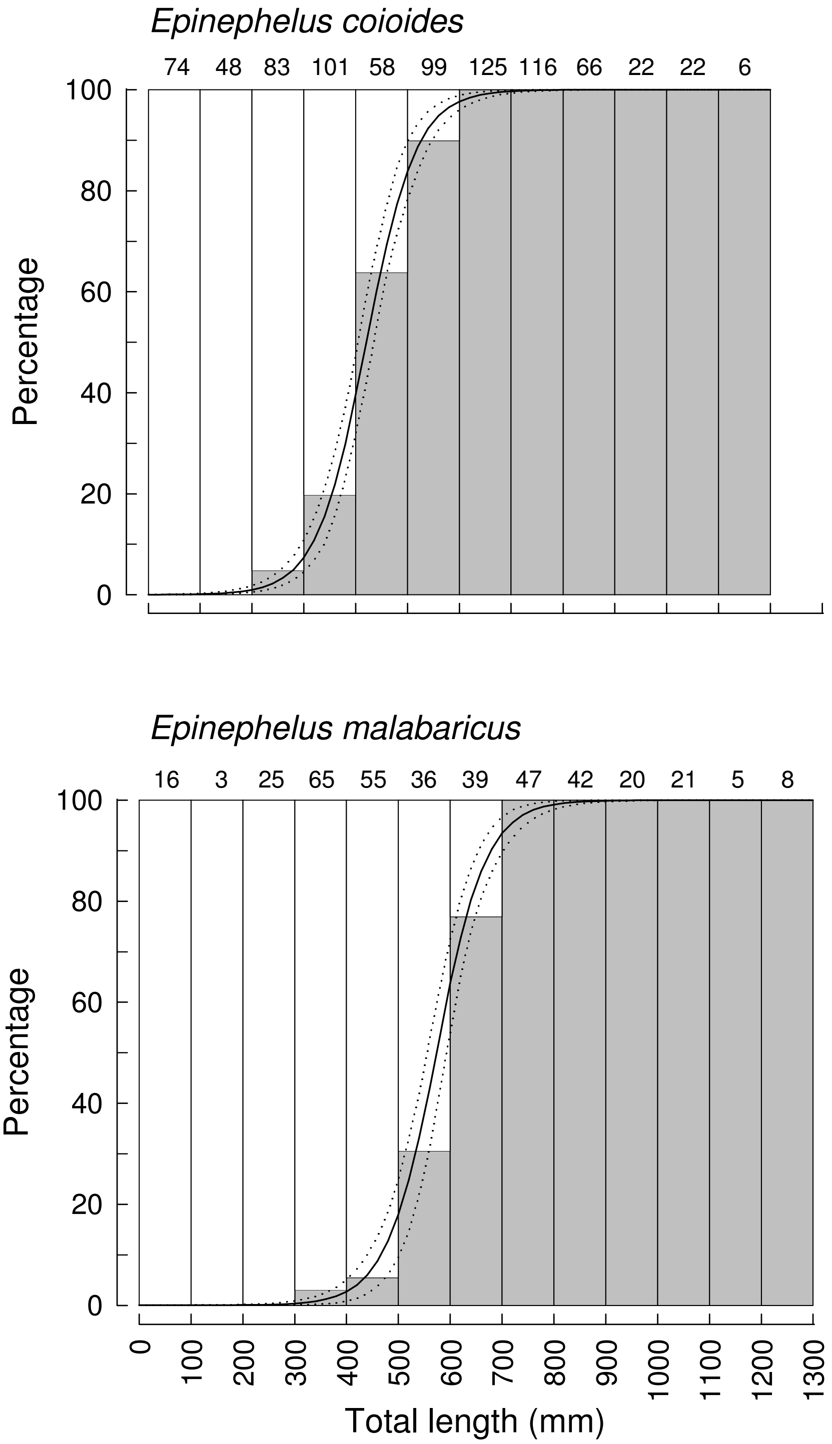

Figure 4.11. Percentage frequency of occurrence of length classes of *Epinephelus coioides* and *Epinephelus malabaricus* caught in nearshore waters with depths < *ca* 5 m (open bars) and offshore waters with depths > *ca* 5 m (grey bars). The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and the probability that an individual had been caught in offshore waters.

the samples that had been caught in offshore, deeper waters (*i.e.* > 20 m deep) increased. Thus, for *E. coioides*, the percentage of fish in deeper offshore waters increased from 5% in the 200-299 mm length class to 20 and 64% in the 300-399 and 400-499 mm length classes, respectively, and to 100% for fish > 600 mm in length. In the case of *E. malabaricus*, the percentage increased from 3% in the 300-399 mm length class to 31 and 77% in the 500-599 and 600-699 mm length classes, respectively, and to 100% for all fish > 700 mm in length (**Figure 4.11**). The L_{50} at which *E. coioides* in samples were caught in offshore waters was 420 mm (95% CIs = 404-435 mm) whereas that for *E. malabaricus* was 562 mm (95% CIs = 533-587 mm).

The relationships between total length, *TL*, and body weight, *W*, for *E. coioides* and *E. malabaricus* are as follows:

Epinephelus coioides $\ln W = 3.023 \times \ln TL - 11.246$ ($R^2 = 0.997$, $n = 745$)

Epinephelus malabaricus $\ln W = 3.132 \times \ln TL - 11.904$ ($R^2 = 0.996$, $n = 346$).

The relationships between standard length, *SL*, and total length, *TL*, for the two species are as follows:

Epinephelus coioides $SL = (0.852 \times TL) - 9.033$ ($R^2 = 0.999$, $n = 813$)

Epinephelus malabaricus $SL = (0.855 \times TL) - 15.251$ ($R^2 = 0.998$, $n = 365$).

4.3.6 Validation that the opaque zones are formed annually

The mean monthly marginal increments on otoliths of *E. coioides* with one opaque zone declined precipitously from 0.4 to 0.5 in July to September to a minimum of 0.1 in January and then rose progressively to reach 0.4 in June (**Figure 4.12**). Similar trends were exhibited by the mean monthly marginal increments for *E. coioides* with otoliths containing greater numbers of opaque zones, and for those of otoliths of *Epinephelus malabaricus*, regardless of the number of opaque zones (**Figure 4.12**). Since, irrespective of the number of opaque zones in the otoliths of *E. coioides* and

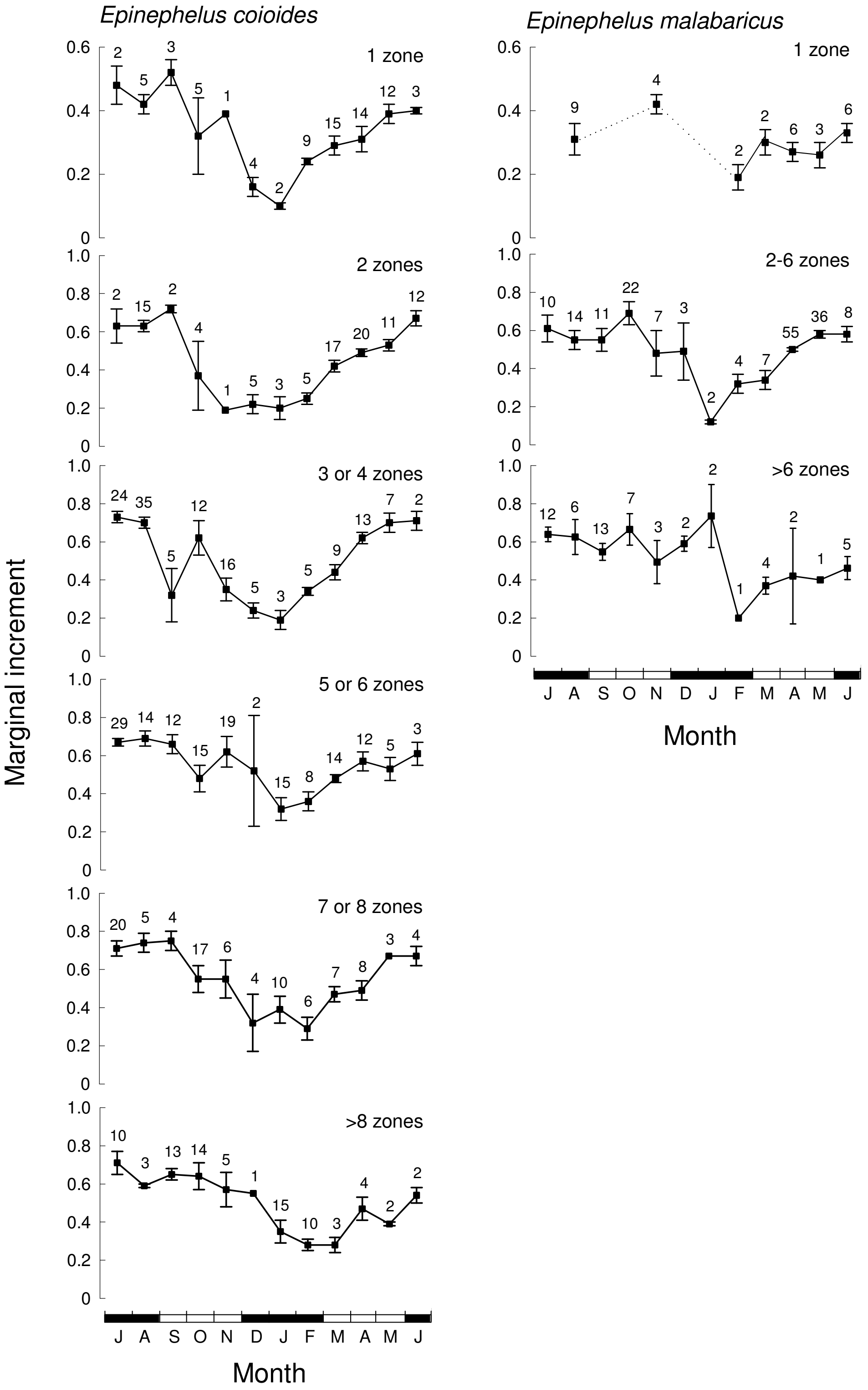

Figure 4.12. Mean monthly marginal increments ±1SE on sagittal otoliths of *Epinephelus coioides* and *Epinephelus malabaricus*. Closed rectangles on horizontal axis refer to winter and summer months and open rectangles to spring and autumn months.

E. malabaricus, the mean monthly marginal increment declined and rose only once during the year, a single opaque zone is laid down annually in the otoliths of these species. As the mean monthly marginal increments for *E. coioides* and *E. malabaricus* declined between early spring and late summer and spawning of both species peaked in early to mid summer, the first opaque zone is laid down in the otoliths of these species when their individuals are about one year of age.

4.3.7 Age composition and growth

The maximum age of *E. malabaricus*, *i.e.* 31 years, was far greater than that of *E. coioides*, *i.e.* 22 years, and, whereas 26 *E. malabaricus* were > 16 years old, only three *E. coioides* exceeded this age. von Bertalanffy growth curves provided good fits to the lengths at age of individuals of *E. malabaricus* and *E. coioides*, as is demonstrated by the relatively high values for the coefficients of determination of 0.886 and 0.908, respectively. Furthermore, the estimated values of -0.56 and -0.01 years, respectively, for the ages at zero length were both close to zero (**Table 4.4, Figure 4.13**). The estimate of the asymptotic length was far greater for *E. malabaricus* (1278 mm) than for *E. coioides* (1082 mm), whereas the reverse was true for the growth coefficient, *i.e.* 0.10 *vs* 0.15 year^{-1}. A likelihood ratio test demonstrated that the growth curves for the two species were significantly different ($P < 0.05$).

The estimated lengths at ages 2, 5, 10, 15 and 20 years were 282, 572, 841, 968 and 1028 mm, respectively, for *E. coioides*, compared with 287, 545, 833, 1008 and 1114 mm, respectively for *E. malabaricus* (**Figure 4.14**). Thus, both species grow at a similar rate until they reach *ca* 10 years of age, after which *E. malabaricus* grows faster (**Figure 4.14**). The distributions of the lengths at age of the females and males of *E. coioides* demonstrate that, amongst the older age classes, *i.e.* > 8 years, the males were typically longer than the females of the same age (**Figure 4.13**). In comparison, the older age classes of *E. malabaricus*, *i.e.* > 24 years, comprised only male fish and, in age classes represented by both sexes, the lengths of females and males were not conspicuously different (**Figure 4.13**).

Table 4.4. von Bertalanffy growth parameters derived from lengths at age for *Epinephelus coioides* and *Epinephelus malabaricus*, including lower and upper 95% confidence limits, the coefficient of determination (R^2) and number of fish aged (n).

	L_∞ (mm)	k (year^{-1})	t_0 (years)	R^2	n
Epinephelus coioides					
Estimate	1082	0.15	-0.01	0.908	745
Lower	1030	0.14	-0.10		
Upper	1136	0.17	0.08		
Epinephelus malabaricus					
Estimate	1278	0.10	-0.56	0.886	334
Lower	1234	0.09	-0.86		
Upper	1337	0.11	-0.27		

4.3.8 Mortality estimates

The point estimates for the instantaneous coefficient of total mortality, Z, for *E. coioides*, derived by refitting Hoenig's (1983) equation for fish, relative abundance (catch curve) analysis and simulation based on the number of fish (= 5 fish) ≥ 14 years of age, ranged between 0.20 and 0.32 year^{-1} (**Table 4.5**). The posterior probability distribution for Z, determined by combining the separate likelihood distributions for the various estimates of Z (**Figure 4.15 a,b**), yielded a combined point estimate for Z of 0.29 year^{-1} (**Table 4.5**). Although the point estimate for the instantaneous coefficient of natural mortality, M, for *E. coioides*, derived by refitting Pauly's (1980) equation (0.36 year^{-1}), was higher than the combined point estimate for Z, the 95% confidence intervals for these estimates of M and Z overlapped (**Table 4.5**). The resultant posterior probability distribution for the point estimate for M, determined from the combined likelihood distribution for Z and the requirement that $M \leq Z$, yielded a point estimate for M of 0.21 year^{-1} (**Table 4.5, Figure 4.16 a,b**).

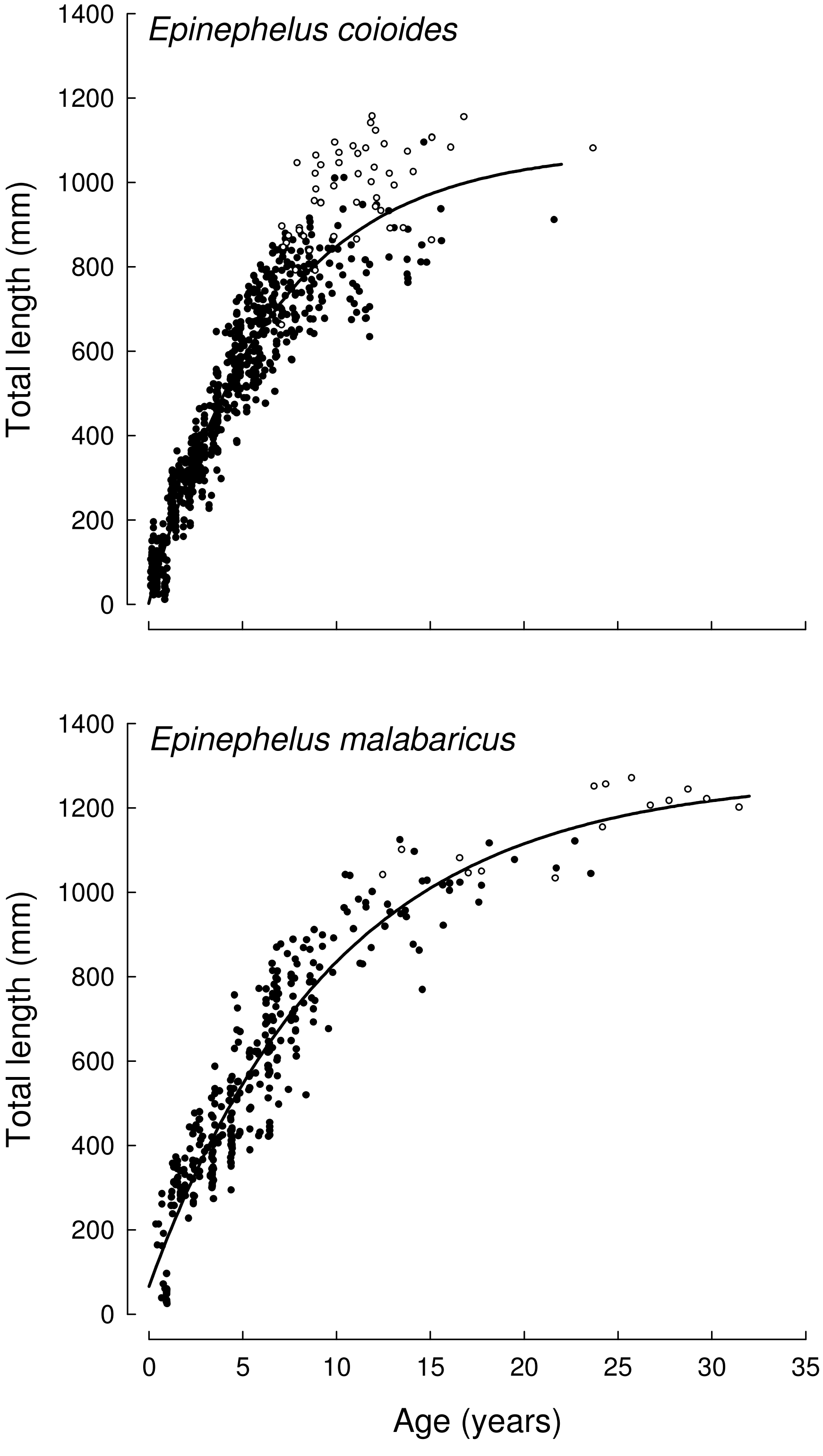

Figure 4.13. von Bertalanffy growth curves fitted to the lengths at age of 805 *Epinephelus coioides* and 355 *Epinephelus malabaricus*. Closed circles refer to females and open circles to males.

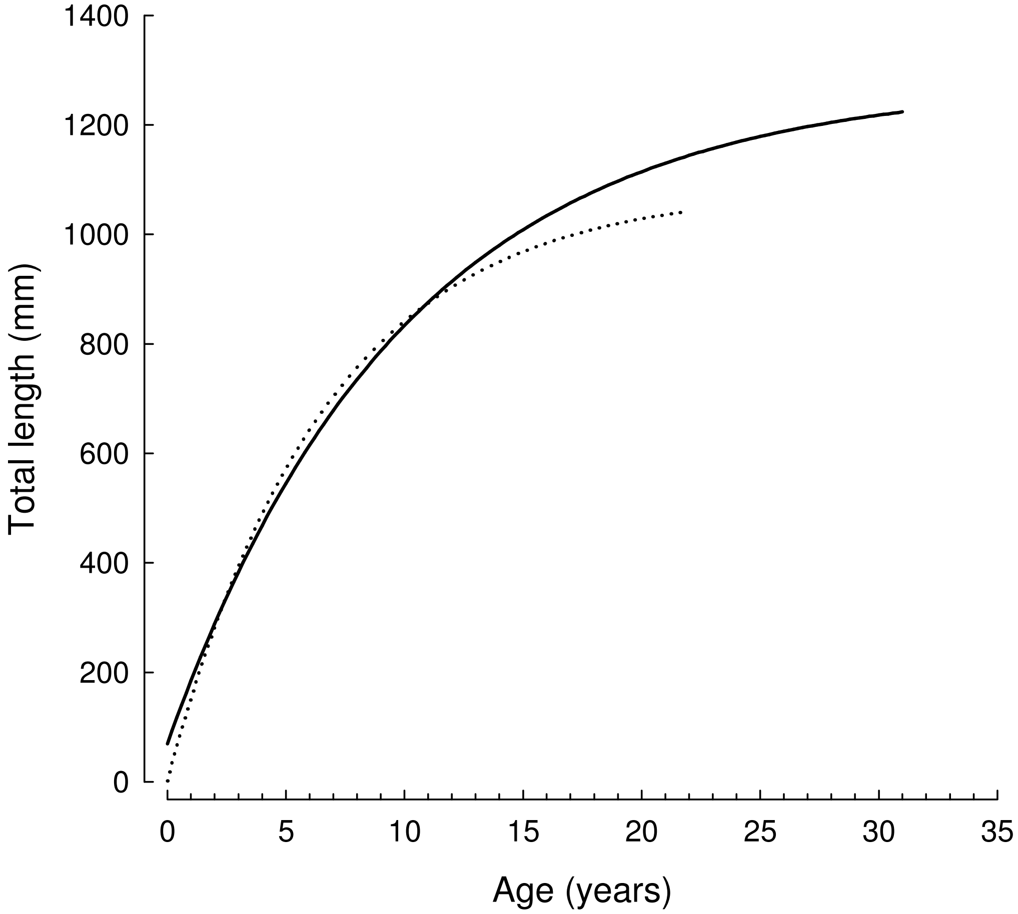

Figure 4.14. von Bertalanffy growth curves for *Epinephelus coioides* (dotted line) and *Epinephelus malabaricus* (solid line).

Table 4.5. Mortality estimates for *Epinephelus coioides* and *Epinephelus malabaricus* calculated using life history models, estimation of longevity based on simulation and relative abundance (catch curve) analysis. Methods used for main interpretations of mortality are in bold.

Method of analysis	***Z, M or F*** **(year^{-1})**	**Estimate**	**Lower 95%**	**Upper 95%**
Epinephelus coioides				
Refitted Hoenig (1983) fish equation	Z	0.20	0.07	0.55
Relative abundance analysis	Z	0.29	0.24	0.34
Simulation (number of fish ≥ 14 years)	Z	0.32	0.22	0.45
Combined *Z* (Bayesian method)	***Z***	**0.29**	**0.25**	**0.34**
Refitted Pauly (1980)	M	0.36	0.12	1.11
Combined *M* (Bayesian method)	***M***	**0.21**	**0.10**	**0.31**
Monte Carlo	***F***	**0.07**	**0.00**	**0.20**
Epinephelus malabaricus				
Refitted Hoenig (1983) fish equation	Z	0.14	0.05	0.39
Relative abundance analysis	Z	0.17	0.11	0.24
Simulation (number of fish ≥ 16 years)	Z	0.15	0.07	0.24
Combined *Z* (Bayesian method)	***Z***	**0.15**	**0.12**	**0.21**
Refitted Pauly (1980)	M	0.26	0.08	0.81
Combined *M* (Bayesian method)	***M***	**0.12**	**0.06**	**0.19**
Monte Carlo	***F***	**0.03**	**0.00**	**0.10**

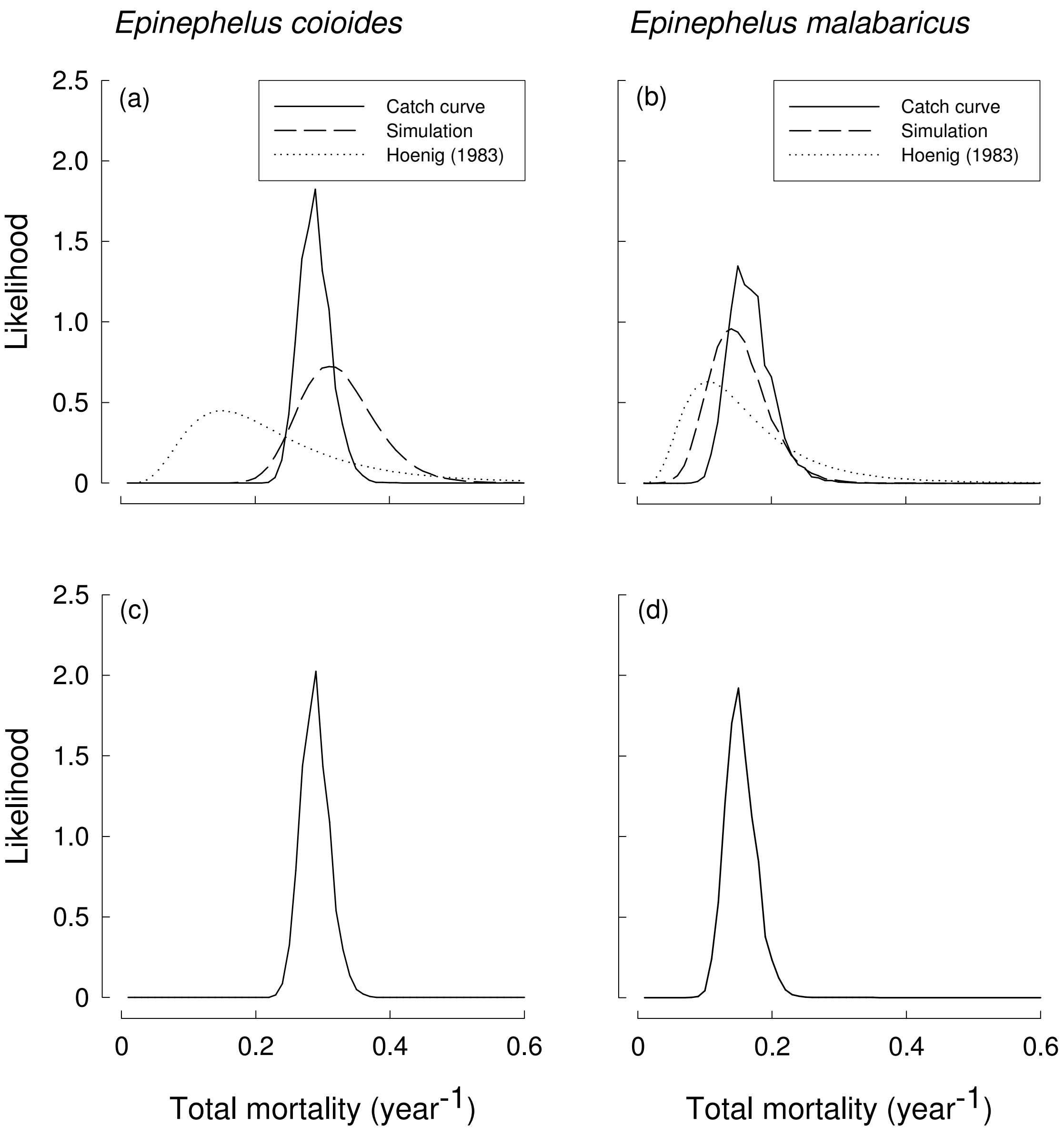

Figure 4.15. Estimated likelihood functions for total mortality Z of (a) *Epinephelus coioides* and (b) *Epinephelus malabaricus* derived using Hoenig's (1983) regression equation for fish, relative abundance (catch curve) analysis, and a simulation method based on the number of individuals above a certain age and sample size. (c,d) Combined posterior probability distributions for Z for (c) *E. coioides* and (d) *E. malabaricus* derived from the separate likelihood functions shown in a and b.

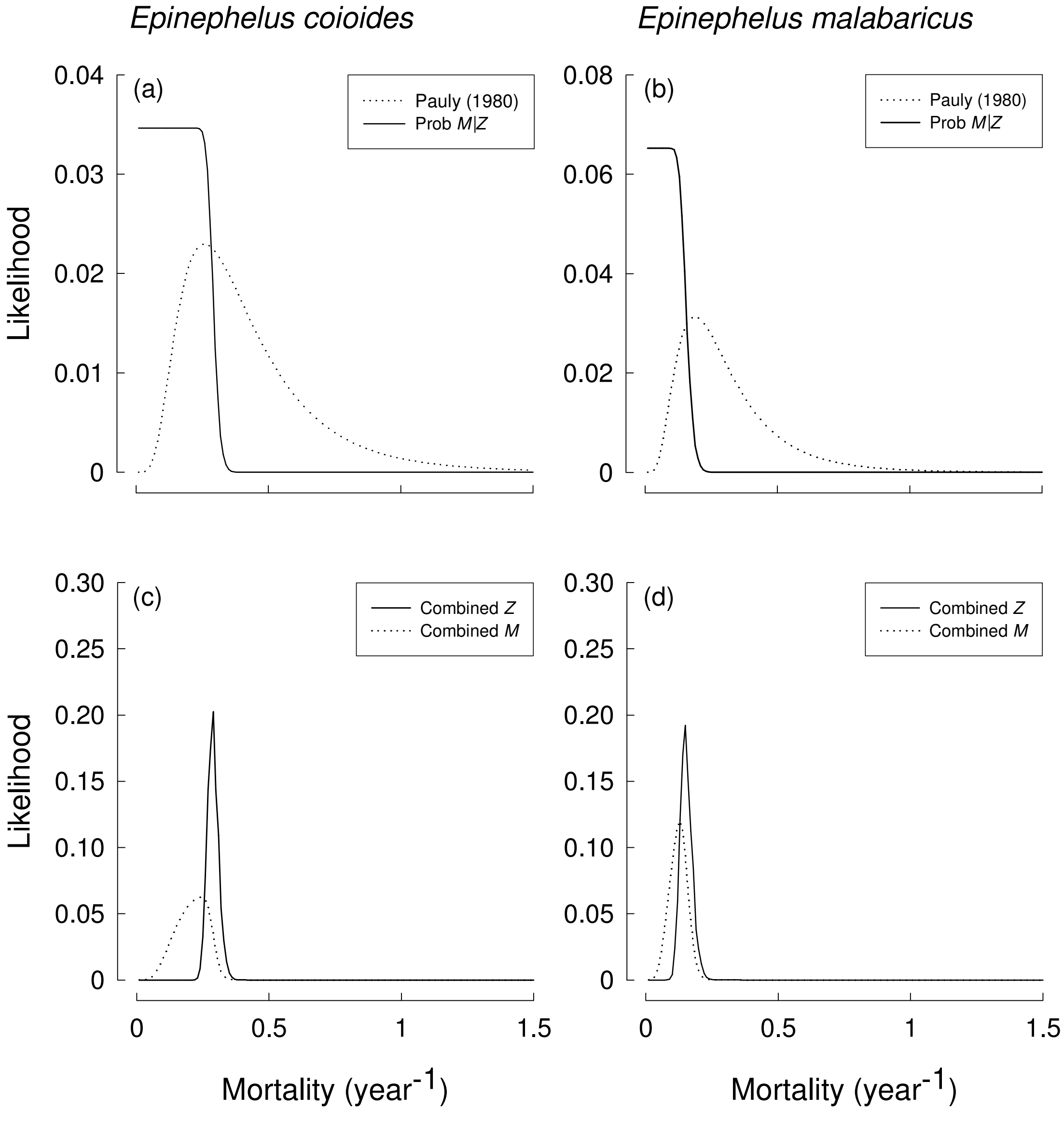

Figure 4.16. Likelihood functions for natural mortality *M* for (a) *Epinephelus coioides* and (b) *Epinephelus malabaricus* from Pauly's (1980) equation and the likelihood function for *M* assuming that it is less than the combined estimate for *Z* and the combined posterior probability distributions for *Z* and *M* for (c) *E. coioides* and (d) *E. malabaricus*.

The three point estimates for *Z* for *E. malabaricus*, derived by refitting Hoenig's (1983) equation for fish, relative abundance analysis and simulation based on the number of fish (= 5 fish) ≥ 16 years of age, were similar, *i.e.* ranged from 0.14-0.17 year^{-1}, and were each lower than the corresponding *Z* estimates for *E. coioides* (**Table 4.5, Figure 4.15 c,d**). The posterior probability distribution for *Z* for *E. malabaricus*, yielded a combined point estimate for *Z* of 0.15 year^{-1}. As was the case with *E. coioides*, the point estimate for *M* for *E. malabaricus*, derived by refitting Pauly's (1980) equation of 0.26 year^{-1} was higher than the estimates for *Z* and the 95% confidence intervals were very broad (**Table 4.5**). The combined estimate for *M*, as determined from the Bayesian analysis, was 0.12 year^{-1}. In the case of both *E. coioides* and *E. malabaricus*, the 95% confidence intervals for the combined estimate for *M* were far narrower than for the estimate of *M* derived by refitting Pauly's (1980) equation. The point estimates of the current level of fishing mortality, *F*, derived from the Monte Carlo analysis for *E. coioides* (0.07 year^{-1}) and *E. malabaricus* (0.03 year^{-1}) were relatively low, *i.e.* < half the level of *M* (**Table 4.5**).

4.3.9 Yield per recruit, spawning potential ratio and spawning biomass per recruit

The yield per recruit analysis (YPR) for recruits to the stock of *E. coioides*, calculated using knife-edge recruitment to the exploited stock at 6 years, as determined for this species in the trawl fishery, indicated that with increasing fishing mortality (*F*) from 0 to 0.4 year^{-1}, the YPR will continue to increase (**Figure 4.17a**). Although the same situation would pertain if the age at recruitment to the fishery was 9 years, if it was 3 years, the YPR begins to decline when *F* exceeds 0.25 year^{-1} (**Figure 4.17a**). The estimated YPR and associated 95% confidence intervals for *E. coioides* at the estimated current level of *F* of 0.07 year^{-1} and assuming knife edge recruitment to the fishery at 6 years, is 0.53 kg year^{-1} (0.00 – 2.94 kg recruit^{-1}) (**Table 4.6**). For *E. malabaricus*, assuming knife edge recruitment to the exploited stock at 6 years, the estimated YPR increases rapidly at relatively low levels of *F* (*i.e.* <0.05 year^{-1}), and declines when *F* exceeds 0.16 year^{-1} (**Figure 4.17b**). If the age at recruitment of *E. malabaricus* to the fishery was 3 years, YPR is estimated to begin declining at a lower level of *F* (0.10

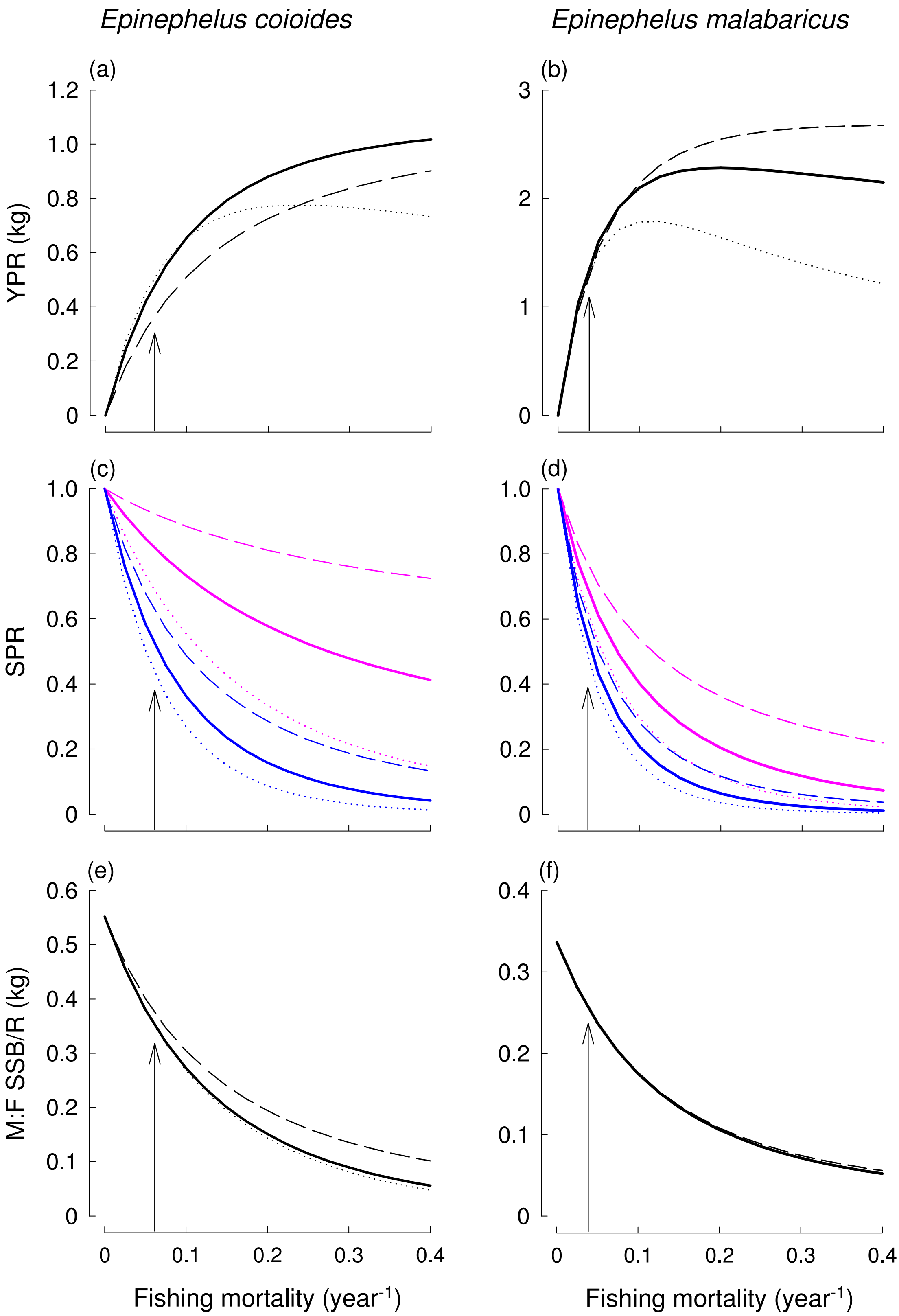

Figure 4.17. Effect, for *Epinephelus coioides* and *Epinephelus malabaricus*, of different levels of fishing mortality and at different ages at recruitment on the yield per recruit (a, b), spawning potential ratio, for female (pink) and male (blue) spawning stock biomass (c, d) and on the ratio of male to female spawning stock biomass (c, d). The curves corresponding to ages 3, 6 and 9 years at full recruitment are represented by dotted, solid and dashed lines, respectively. The arrows indicate the current level of fishing mortality.

Table 4.6. Estimates of the current level of yield per recruit (YPR), $F_{0.1}$, and the current levels of total spawning stock biomass per recruit (SSB/R) and spawning potential ratio SPR) for females, males and females and males combined, for *Epinephelus coioides* and *Epinephelus malabaricus*, calculated using 6 years, as the age at full recruitment to the exploited stock for both species.

Analysis	**Estimate**	**Lower 95%**	**Upper 95%**
Epinephelus coioides			
YPR (kg recruit^{-1})	0.53	0	2.94
$F_{0.1}$ (year^{-1})	0.14	--	--
SSB/R (kg recruit^{-1})	7.82	3.93	16.36
SPR (females)	0.78	0.45	1.00
SPR (males)	0.44	0.08	1.00
SPR (females & males)	0.67	0.22	1.00
Epinephelus malabaricus			
YPR (kg recruit^{-1})	1.18	0	5.07
$F_{0.1}$ (year^{-1})	0.09	--	--
SSB/R (kg recruit^{-1})	26.49	11.56	49.91
SPR (females)	0.74	0.31	1.00
SPR (males)	0.59	0.14	1.00
SPR (females & males)	0.70	0.24	1.00

year^{-1}). However, if it were 9 years, YPR is estimated to continue to increase with increasing levels of *F*. The estimated YPR and associated 95% confidence intervals for *E. malabaricus* at the estimated current level of *F* of 0.03 year^{-1} and assuming knife-edge recruitment to the fishery at 6 years is 1.18 kg year^{-1} (0.00 – 5.07 kg recruit^{-1}) (**Table 4.6**). The estimated values for $F_{0.1}$ for *E. coioides* and *E. malabaricus* are 0.14 and 0.09 year^{-1}, respectively.

Regardless of the age at recruitment, with increasing *F*, the spawning potential ratio (SPR) for male *E. coioides* decreased far more rapidly than for females (**Figure 4.17c**). In the case of both female and male *E. coioides*, the rate at which SPR is predicted to decline decreases substantially as the age at recruitment increases. In comparison to *E. coioides*, the rate at which the SPR for *E. malabaricus* declines with increasing levels of *F* is greater, and altering the age at recruitment has less of an effect on the rate at which SPR declines (**Figure 4.17d**). The current estimated SPRs for female and male *E. coioides* and *E. malabaricus* are 0.78 and 0.44, and 0.74 and 0.59, respectively (**Figures 4.17c,d**; **Table 4.6**). In the case of both species, the confidence intervals associated with the SPR estimates are broad.

As *F* increases, the ratio of male to female spawning stock biomass per recruit (SSB/R) for *E. coioides* and *E. malabaricus* is predicted to decline exponentially (**Figures 4.17 e,f**). The male to female ratio of SSB/R for *E. coioides* and *E. malabaricus* is estimated to have declined from 0.55 and 0.33 respectively (*i.e.* at $F = 0$ year^{-1}) to 0.34 and 0.27, respectively (*i.e.* at the current levels of *F* for these two species) (**Figures 4.17 e,f**).

4.4 DISCUSSION

4.4.1 Protogynous hermaphroditism

This study represents the first detailed histological examination of the gonads of wild *E. coioides* and *E. malabaricus* and which covered essentially the full size and age range of these species from individuals caught throughout the year. The results were thus able to be used to determine the type of hermaphroditism exhibited by each species and the lengths and ages at which the individuals of these species change sex. The results provide the following evidence that *Epinephelus coioides* and *Epinephelus malabaricus* are protogynous hermaphrodites. In the case of both species, all small and young fish were females, the prevalence of males increased with increasing size and age and the gonads possessed characteristics which, as outlined by Sadovy and Shapiro (1987) in their extensive review of hermaphroditism in fishes, are strongly indicative of protogynous hermaphroditism. The latter characteristics are as follows. (i) The gonads of all small individuals contained solely ovarian tissue. (ii) The testes of all mature males contained a distinct membrane-lined cavity similar in form to the ovarian lumen of females, and there was no evidence that this cavity is used for sperm transport by males. (iii) All mature testes were of an ovarian lamellar form and contained sperm sinuses in their outer wall. The latter two characteristics of the testes of *E. coioides* and *E. malabaricus* are typical of monandric protogynous hermaphrodites (Sadovy and Shaprio, 1987), *i.e.* all males are derived exclusively by sex change from adult females. Most other species of grouper have been shown to be monandric protogynous hermaphrodites (*e.g.* Shapiro, 1987; Shpigel & Fishelson, 1991; Shapiro *et al.*, 1993; Sadovy *et al.*, 1994; Chan & Sadovy, 2002; Rhodes & Sadovy, 2002).

In addition to the above histological findings, the gonads of two *E. coioides* possessed ovarian tissue containing previtellogenic oocytes and testicular tissue, comprising predominantly spermatocytes and spermatids. Because a variety of conditions other than hermaphroditism can lead to the development of previtellogenic occytes in testes, Sadovy and Shapiro (1987) have emphasized that such a condition does not, on its own, provide strong evidence for protogynous hermaphroditism. However, in view of the other strong evidence that these two cod species are protogynous hermaphrodites, it is likely that, at their time of capture, these two individuals were changing sex. This view is consistent with their lengths (872 and 855 mm) and ages (~ 7.5 years) being similar to those at which the males of this species first became prevalent in the samples. That only two such "transitional" individuals of *E. coioides* were found is consistent with the work of Quinitio *et al.* (1997), which showed that, under culture conditions, sex change in this species is rapid, *i.e.* can occur within two months.

The finding that *E. coioides* and *E. malabaricus* in north-western Australian waters are monandric protogynous hermaphrodites is consistent with conclusions drawn by several workers in other parts of the world (Sheaves, 1995; Quinitio *et al.*, 2001; Yeh *et al.*, 2003; Grandcourt *et al.*, 2005). Previous evidence that either *E. coioides* or *E. malabaricus* is a protogynous hermaphrodite includes the following. (1) All of the small individuals of *E. coioides* and *E. malabaricus* Sheaves (1995) collected in mangroves areas in tropical north-east Queensland were females. (2) Sex inversion can be induced in *E. coioides* by social control (Quinitio *et al.*, 1997). (3) Tank experiments with *E. coioides* showed that sex change was able to be induced by oral administration of mibolerone or an androgen mixture (Quinitio *et al.*, 2001; Yeh *et al.*, 2003).

The results of our study demonstrate that sex change typically occurs at a smaller size and younger age in *E. coioides* than *E. malabaricus*, *i.e.* L_{50} = 925 mm (= 13.2 years) *vs* 1103 mm (= 19.9 years). The length and age at sex change recorded for *E. coioides* during this study differs markedly from that recorded by Grandcourt *et al.* (2005) for this species in the Arabian Gulf, *i.e.* fish recorded as males in that study ranged between 274 and 784 mm and 1.1 and 6.1 years. However, Grandcourt *et al.* (2005) did not derive their data from an histological study.

4.4.2 Spawning period, location and mode

The elevated GSIs and high prevalence of ovaries at stages V-VI (mature and spawning) exhibited by *E. coioides* in October to January and by *E. malabaricus* in October to February, demonstrate that these two species spawn predominantly during these respective monthly periods. For the purpose of constructing growth curves, both species were thus accorded a birth date of 1 January. The occurrence of ovaries of *E. coioides* and *E. malabaricus* at stages V-VI in nine and ten months of the year, respectively, also demonstrate that both species spawn over a highly protracted period. This finding differs markedly from that of Grandcourt *et al.* (2005) for *E. coioides* in the Arabian Gulf, who reported that spawning occurs only during May. The latter far more restricted spawning period may be due, at least in part, to data for juvenile fish being included in the calculations of the mean monthly GSIs and to the small number of large fish that were caught during their study.

The capture of mainly small *E. coioides* (< 400 mm) and *E. malabaricus* (< 500 mm) in shallow (<5 m), nearshore mangrove creeks, and of larger, older fish in deeper, offshore waters, strongly indicates that these species use the former environment as a nursery area and then migrate offshore as they increase in size and age. The view that shallow, nearshore mangrove areas act as nursery areas is consistent with the fact that all of the *E. coioides* and *E. malabaricus* collected from this type of environment possessed immature gonads. It is also consistent with the finding of

Sheaves (1995) that all of the *E. coioides* and *E. malabaricus* he collected in mangroves in tropical north-east Queensland were juveniles. As mature (stage V gonads) *E. coioides* and *E. malabaricus* were taken from over reefs in offshore waters, these two species presumably spawn in those waters.

As each of the various stages in oocyte development, *i.e.* chromatin nucleolar, perinucleolar, cortical alveolar and yolk granule oocytes, were typically represented in ovaries of individual mature and spawning (stages V-VI) females (and migratory nucleus and hydrated oocytes in some stage VI females) of *E. coioides* and *E. malabaricus*, these species have indeterminate fecundity. In such species, the number of oocytes released during the spawning season is not determined prior to the commencement of that season (Hunter *et al.*, 1985). As estimates of annual fecundity for such species require data on both batch fecundity and spawning frequency, it is far more difficult to derive estimates for species with indeterminate than determinate fecundity. Unfortunately, the very remote locations in which this study was conducted made it essentially impossible to be able to sample as intensively as would be necessary to obtain such data.

4.4.3 Age and growth

Since, regardless of the number of zones in their otoliths, the trends exhibited throughout the year by the mean monthly marginal increments for otoliths of *E. coioides* and *E. malabaricus* exhibited a single conspicuous decline and then single progressive rise, one opaque zone is formed in those otoliths each year. Thus, as with the two threadfin salmon species and mangrove jack, the number of zones in their otoliths can be used to age these two cod species.

As demonstrated by the von Bertalanffy growth curves, *E. coioides* and *E. malabaricus* grow at essentially the same rate for the first 10 years of life, but the latter species subsequently grows faster and attains a greater maximum size (*i.e.* 1156 *vs* 1216 mm) and lives longer (*i.e.* 31 vs 22 years). The maximum age of 22 years recorded for *E. coioides* in this study is the same as that recorded by Mathews and Samuel (1991) for this species (referred to as *Epinephelus suilus* in that paper) in waters of the Arabian

Gulf. This maximum age is slightly greater than the 16 years recorded by Sheaves (1995) for one of five relatively large *E. coioides* collected in offshore waters in north-east Queensland waters. The maximum age of 31 years determined for *E. malabaricus* in our study is the greatest yet recorded for this species, and far greater than the 18 years derived by Mathews & Samuel (1991), from a sample size of only three individuals. The far greater longevity of *E. malabaricus* than *E. coioides* is consistent with the former species taking far longer to attain first maturity (9.4 *vs* 5.0 years, respectively) and to undergo protogynous sex change (19.9 *vs* 13.2 years, respectively).

The greater length of the males than females of *E. coioides* at corresponding ages parallels the situation for a number of other protogynous fishes, *e.g.* the Sandperch *Parapercis cylindrical* (Walker & McCormick, 2004) and *Chlorurus gibbus*, *Chlorurus sordidus*, *Scarus niger* and *Scarus frenatus* and (Choat *et al.*, 1996; Munday *et al.*, 2004). As outlined by Walker and McCormick (2004), three alternative hypotheses have been proposed to explain sex-related size at age differences in protogynous species. These are (1) somatic growth accelerates after sex change (= "transitional growth-spurt hypothesis"), (2) different growth trajectories are established early in life (= "juvenile growth hypothesis") and (3) enhanced larval growth may bias post-settlement growth, thereby influencing the timing of maturation and, in turn, determine which individuals change sex (= "larval growth hypothesis" (Walker and McCormick, 2004). Future work employing back-calculation methods will by used to investigate these alternative hypotheses.

The finding that, in contrast to the situation with *E. coioides*, the males of *E. malabaricus* were not conspicuously greater in length than their females at corresponding ages suggests that these two *Epinephelus* species exhibit different reproductive strategies, *i.e.* possibly different haremic social structures. The fact that males and females are both present in almost all older age classes (*i.e.* > 8 years) of *E. coioides* but that, at corresponding ages, the males are larger, indicates that sex change in this species is size-related rather than age-related. This view is supported by the work of Quinitio *et al.* (1997), who showed that, when female *E. coioides* of different sizes were stocked in net cages or tanks, many larger individuals (initial body weight 5.0-6.1 kg) changed sex to become males, while all smaller individuals (initial weight (4.5-5.2 kg) remained female. In the case of *E. malabaricus*, and in contrast to *E. coioides*, the absence of females in the older age classes (*i.e.* > 24 years) and absence of a conspicuous difference between the lengths of males and females at corresponding ages, implies that sex change in this species is age, and not size-related.

4.4.4 Mortality and yield and spawning biomass per recruit

As has been demonstrated for several other species (see Hall *et al.*, 2004), the point estimate of *M* derived for *E. coioides* using Pauly's (1980) equation was higher than the point estimates derived for *Z* using Hoenig's (1983) equation for fish, relative abundance (catch curve) analysis and the simulation method of (Hall *et al.*, 2004). Furthermore, as is typically the case with the Pauly equation, the confidence intervals for *M* for both *E. coioides* and *E. malabaricus* were very broad. The use of Hall *et al.*'s method (developed in our FRDC project 2000/137) reconciled the inconsistencies between *M* and *Z* for *E. coioides* and, particularly for *M*, provided far more precise estimates for both species. However, those estimates of *M*, derived using the Bayesian method of Hall *et al.* (2004) are still likely to represent an underestimate of this parameter and consequently also of *F*, because the estimate of *M* derived using the empirical approach of Pauly (1980) was so erroneously high. Thus, although the resultant low estimates of *F* for *E. coioides* and *E. malabaricus* suggest that these species are not being subjected to heavy fishing pressure in north-western Australia, this result should be treated with caution.

Since the size composition data for *E. coioides* and *E. malabaricus* indicated that the gear used by the commercial trap fishery does not catch the largest *E. coioides* and *E. malabaricus*, the samples collected from this fishery were considered biased and therefore not used in the catch curve analysis. As a consequence of the restriction of the data to those derived from the commercial trawl fishery, which only operates in the Pilbara region, the mortality estimates are representative only of the fish in that region. It should also be noted that the estimates are based on the assumption that the trawl and trap fisheries in the Pilbara region operate in the same areas. Although the catch and effort statistics data (Catch and Effort Statistics, Department of Fisheries, Western Australia) indicate that this is the case, there is presumably some degree of spatial segregation, since trawling would be restricted to areas of either bare substrate or low-lying reefs.

The per recruit analyses undertaken during this study demonstrate that, for hermaphroditic species, it is critical to take into account the relationship describing the lengths over which individuals sex change. The finding that the spawning potential ratio of males declines dramatically at relatively low levels of fishing mortality implies that the stocks of *E. coioides* and *E. malabaricus* could be susceptible to recruitment overfishing at even low levels of mortality. As pointed out by Buxton (1992), the fundamental assumption of the yield per recruit model that recruitment is constant is more likely to fail when dealing with hermaphroditic species. This point is highlighted by the fact that, at fishing mortalities equivalent to $F_{0.1}$ for *E. coioides* (0.14 year^{-1}) and *E. malabaricus* (0.10 year^{-1}), the corresponding spawning stock biomass per recruit for males of these two species is predicted to fall to 26 and 20% of their original levels, respectively. Since the point estimates of current spawning potential ratios of 0.44 and 0.78 for the males and females of *E. coioides*, respectively, and of 0.59 and 0.74 for *E. malabaricus*, respectively, are above 30% of their original level, this suggests that the current level of fishing pressure on these two species in the Pilbara region is sustainable (see Mace and Sissenwine, 1993; Goodyear, 1993). However, because of the very large uncertainty in the estimates obtained for F for both *E. coioides* and *E. malabaricus*, there is also very large uncertainty in the above estimates of the current SPRs. It is thus recommended that fisheries managers adopt a cautious approach to managing these species.

The finding that the relationship between fishing mortality and spawning potential ratio of males and females of these two cod species, and particularly for *E. coioides*, changes markedly depending on the age at full recruitment to the exploited stock, is likely to be important for managing these species in the future. Although most of the current fishing pressure on these two species is likely to come from the commercial trap and trawl fisheries, at least some individuals are taken by recreational anglers and from nearshore waters, *i.e.* when they are still juveniles. Thus, as recreational fishing pressure on these two species inevitably increases, the impact of the recreational fishery will also need to be taken into account when managing these species.

5. BIOLOGY OF THE MANGROVE JACK *LUTJANUS ARGENTIMACULATUS*

5.1 INTRODUCTION

The mangrove jack *Lutjanus argentimaculatus* (Forsskål, 1775), also known as the mangrove red snapper, is widely distributed throughout the tropical Indo-West Pacific (Allen, 1985). In Western Australia, *L. argentimaculatus* is found from Mindarie (31°41'S) northwards to the Northern Territory border. Although this species is classified as oceanodromous (migrates within oceans), its juveniles and subadults inhabit structurally-complex habitats in freshwater, brackish and estuarine waters and only later move offshore to deeper waters where there are reefs and small to large epibenthic organisms (Brouard & Grandperrin, 1984; Allen, 1985; Sheaves, 1995; Newman & Williams, 1996; Russell *et al.*, 2003; Riede, 2004).

Although the Mangrove Jack is commercially and recreationally important in Western Australia, there are no detailed biological data of the type that can be used by fisheries managers for developing plans for conserving the stocks of this species in this state. However, there is sound information on certain aspects of the biology of this species in eastern Australia. Thus, for example, in that region, it has been shown that it spawns over summer, with a peak in December and that, on the basis of the number of annually-formed growth zones in their otoliths, it can live for up to 37 years (Russell *et al.*, 2003).

The aims of this study were to determine the following for Mangrove Jack in the Pilbara and Kimberley regions of north-western Australia. 1. The lengths and ages of females and males at maturity. 2. The duration of the spawning season, batch fecundity and whether spawning occurs on several occasions during the spawning period and whether fecundity is determinate or indeterminate. 3. Length and age compositions and growth characteristics. 4. Total, natural and fishing mortality. 5. Yield, spawning stock biomass per-recruit and spawning potential ratio.

5.2 MATERIALS AND METHODS

Materials and methods are given in the General Materials and Methods section (Chapter 2). Note that, in this study, lengths are given as fork lengths unless otherwise stated.

5.3 RESULTS

5.3.1 Commerical catch statistics

The total annual commercial catch of *L. argentimaculatus* in Western Australia increased progressively from 0.04 to 19 tonnes between 1988 and 1993, and has subsequently fluctuated between 8.6 and 25.4 tonnes (**Figure 5.1**). The values and trends exhibited by the commercial catch in the Pilbara region are very similar to that just described for the overall catch in Western Australia, reflecting the fact that most of the catches come from the Pilbara. The total annual catch of Mangrove Jack in the Kimberley region increased from < 1 tonne between 1988 and 1994 to a peak of 2.0 tonnes in 1996 before declining to 0.4 tonnes in 2000 and then increasing again to their maxima of 2.6 tonnes in 2004 (CAES, Department of Fisheries WA). Most of the catch in the Pilbara was taken by trawling, whereas most of that taken in the Kimberley was obtained by trapping (**Figure 5.1**).

5.3.2 Lengths and ages at maturity

All of the females and males of *L. argentimaculatus* caught in both the Pilbara and Kimberley regions with fork lengths < 400 mm were immature, *i.e.* possessed gonads at stages I-II (**Figure 5.2**). Mature females and males of *L. argentimaculatus* first appeared in the 400-449 mm or 450-499 mm length classes in both regions and all or the majority of individuals were mature, *i.e.* possessed gonads at stages III-VIII, by the time they had reached 550 mm FL. The L_{50}s at first maturity in the Pilbara region for females (461 mm) and males (452 mm) were not significantly different ($p > 0.05$), whereas that for females in the Kimberley region (498 mm) was significantly greater ($p < 0.001$) than that of the males (472 mm) (**Table 5.1**). In addition, the L_{50}s for females and males in

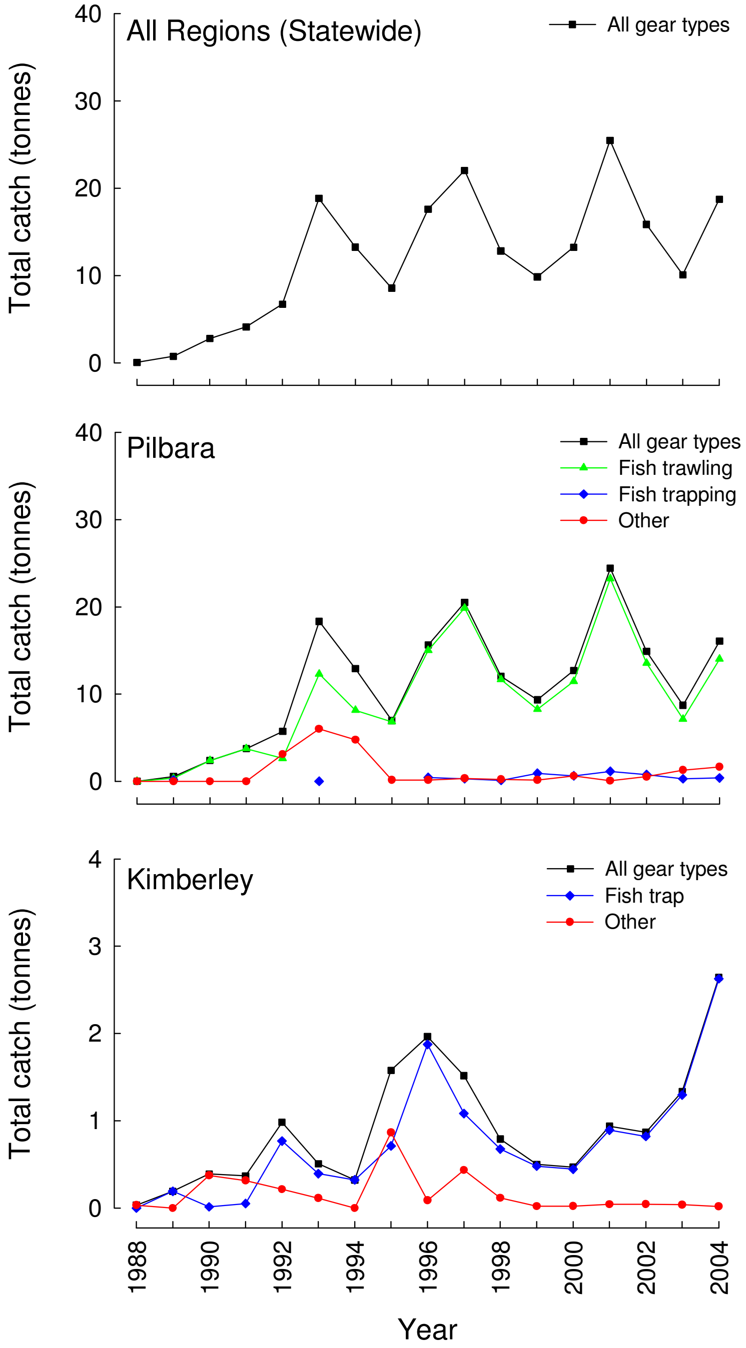

Figure 5.1. Commercial catch (tonnes) of *Lutjanus argentimaculatus* in north-western Australia in each year between 1988 and 2004.

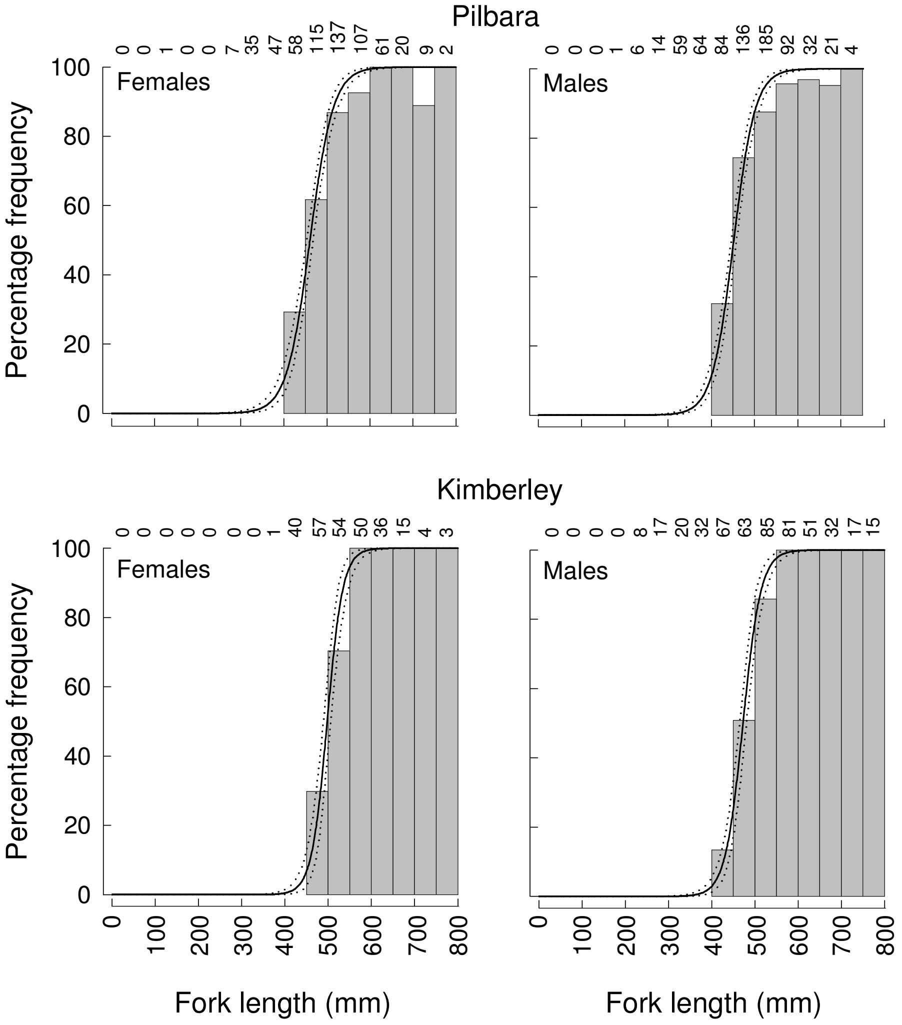

Figure 5.2. Percentage frequencies of occurrence of fish with ovaries or testes at stages III-VIII in sequential 50 mm length classes of *Lutjanus argenticmaculatus* in the Pilbara and Kimberley regions. In each case, the logistic curves (solid line) and their 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and the probability that an individual possessed gonads at stages III-VIII. Sample sizes of fish in each 50 mm length class are shown.

the Kimberley region were significantly greater than those of the corresponding sexes in the Pilbara ($p < 0.001$ and $p < 0.01$, respectively, for the two sexes) (**Table 5.1**).

Table 5.1. Estimates of the L_{50} and L_{95} at first maturity and their lower and upper 95% confidence limits for female and male *Lutjanus argentimaculatus* from the Pilbara and Kimberley coasts.

Parameter	**L_{50} (mm)**	**L_{95} (mm)**
Pilbara		
Females		
Estimate	461	540
Lower 95%	453	527
Upper 95%	468	554
Males		
Estimate	452	525
Lower 95%	446	512
Upper 95%	458	537
Kimberley		
Females		
Estimate	498	551
Upper 95%	489	537
Lower 95%	506	566
Males		
Estimate	472	533
Upper 95%	464	519
Lower 95%	480	547

All *L. argentimaculatus* < 4 years of age were immature (**Figure 5.3**). Maturity had been attained by a few females and males in the Pilbara region and males in the Kimberley region by 4 years of age, and by a small number of females from that latter region by 5 years of age. *Lutjanus argentimaculatus* typically attained maturity slightly earlier in the Pilbara than Kimberley region, with > 50% of fish being mature by 6 years in the former region, but not until 7 years in the latter region. Furthermore, although

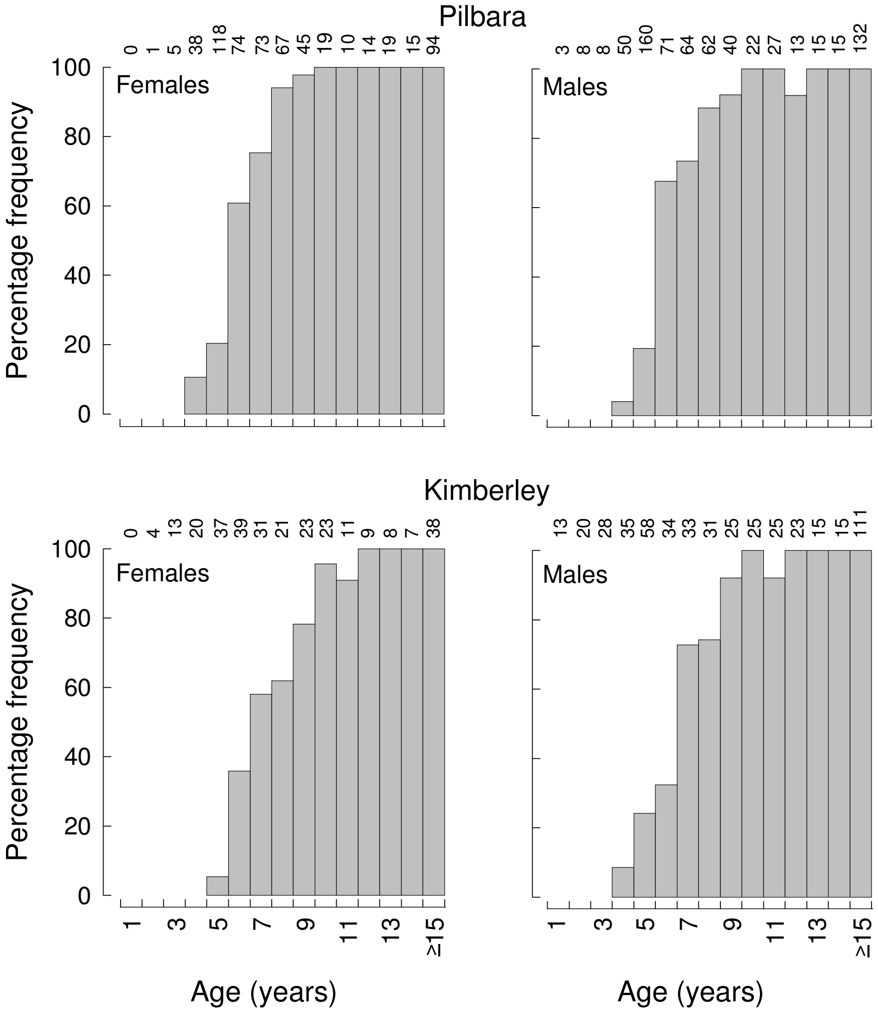

Figure 5.3. Percentage frequencies of occurrence of fish caught during the spawning period with ovaries at stages III-VIII in sequential age classes of *Lutjanus argenticmaculatus* from the Pilbara and Kimberley regions. Sample sizes of fish in each age class are shown.

almost all *L. argentimaculatus* (*i.e.* > 90%) in the Pilbara region were mature by 8 years, this was not the case in the Kimberley until fish were 9 years old (**Figure 5.3**).

5.3.3 Gonadal development and spawning season

On the basis of pooled data for corresponding months during the whole sampling period, the monthly mean GSIs of female *L. argentimaculatus* in the Pilbara region rose from their minima of about 1 in July and August to their maxima of > 4 in November to February and then declined sequentially in the ensuing months (**Figure 5.4**). The trends exhibited by the mean monthly GSIs of male *L. argentimaculatus* followed the same seasonal trend, but with the minimum and maximum values being lower, *i.e. ca* 0.25 *vs* 1 and *ca* 1.8 *vs* 6, respectively (**Figure 5.4**). Although, in pooled data, the mean monthly GSIs started to rise as temperatures increased, this relationship is shown more clearly when the data for the different years were plotted separately (**Figure 5.5**). The trends exhibited by the mean monthly GSIs for *L. argentimaculatus* from the Kimberley region were similar to those just described for the Pilbara region (**Figure 5.6**). However, the greatest mean monthly values were found between October and December rather than from November to January (**Figure 5.6**).

In the samples from the Pilbara, females with ovaries at stages I-II (immature) were abundant in each month between April and September and absent or rare in all other months (**Figure 5.7**). Females with stage V (mature) ovaries were caught in all months between August and March and those with stage VI (spawning) ovaries were found in some of those months. Spent or recovering spent females (stages VII-VIII) were found in all but three months. The trends exhibited by the prevalence of the sequential stages in ovarian development by females from the Kimberley region were similar to those just described for the Pilbara region. Although females with stage V ovaries were first recorded in the Kimberley region in June and July rather than in August, as in the Pilbara region, this may have partly reflected the acquisition of larger samples from that former region during the winter months (**Figure 5.7**).

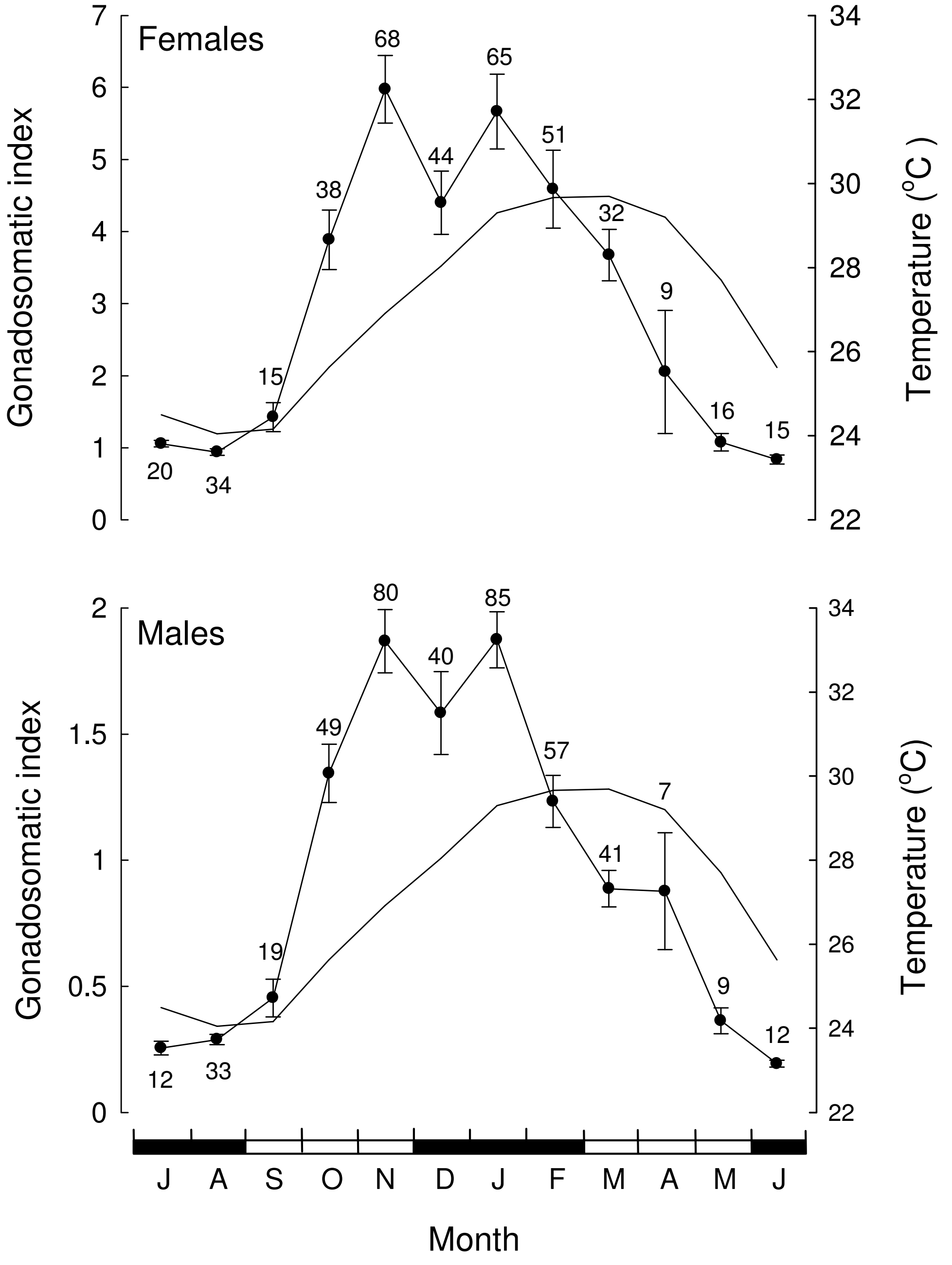

Figure 5.4. Mean monthly gonadosomatic indices ±1SE of those female and male *Lutjanus argentimaculatus* from the Pilbara region that had lengths greater than their L_{50}s at first maturity. The mean monthly water temperatures have also been plotted. Data for the corresponding months between October 2002 and February 2005 have been pooled. Closed rectangles on horizontal axis refer to winter and summer months and the open rectangles to spring and autumn months. Number of fish used to derive each mean is shown.

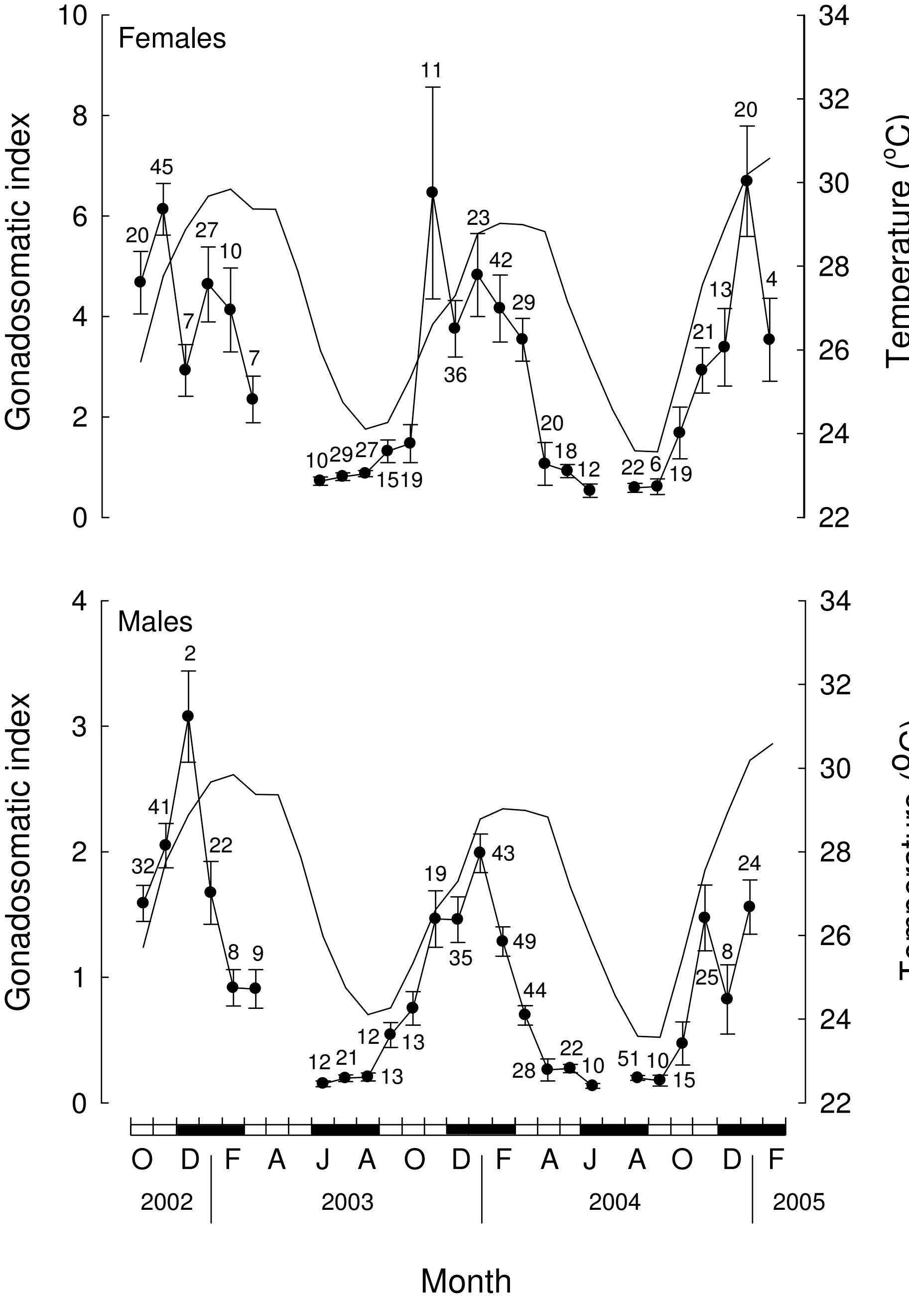

Figure 5.5. Mean monthly gonadosomatic indices ±1SE of female and male *Lutjanus argentimaculatus* from the Pilbara region that had lengths greater than their L_{50}s at first maturity. The mean monthly water temperatures have also been plotted. In contrast to Figure 5.4, the months between October 2002 and February 2005 have been kept separate. Closed rectangles on horizontal axis refer to winter and summer months and the open rectangles to spring and autumn months. Number of fish used to derive each mean is shown.

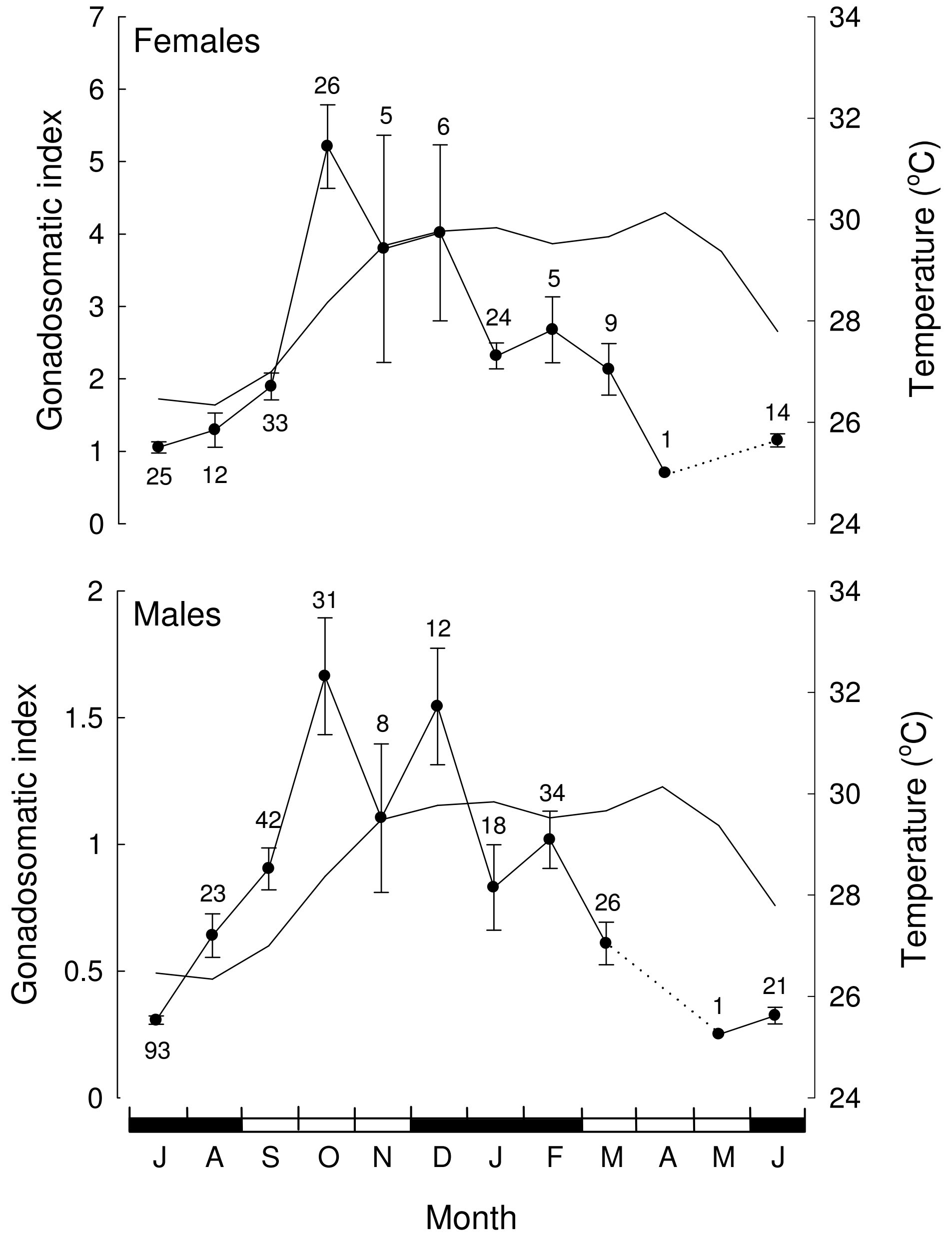

Figure 5.6. Mean monthly gonadosomatic indices ±1SE of those female and male *Lutjanus argentimaculatus* from the Kimberley region that had lengths greater than their L_{50}s at first maturity. The mean monthly water temperatures have also been plotted. Data for the corresponding months between October 2002 and February 2005 have been pooled. Closed rectangles on horizontal axis refer to winter and summer months and the open rectangles to spring and autumn months. Number of fish used to derive each mean is shown.

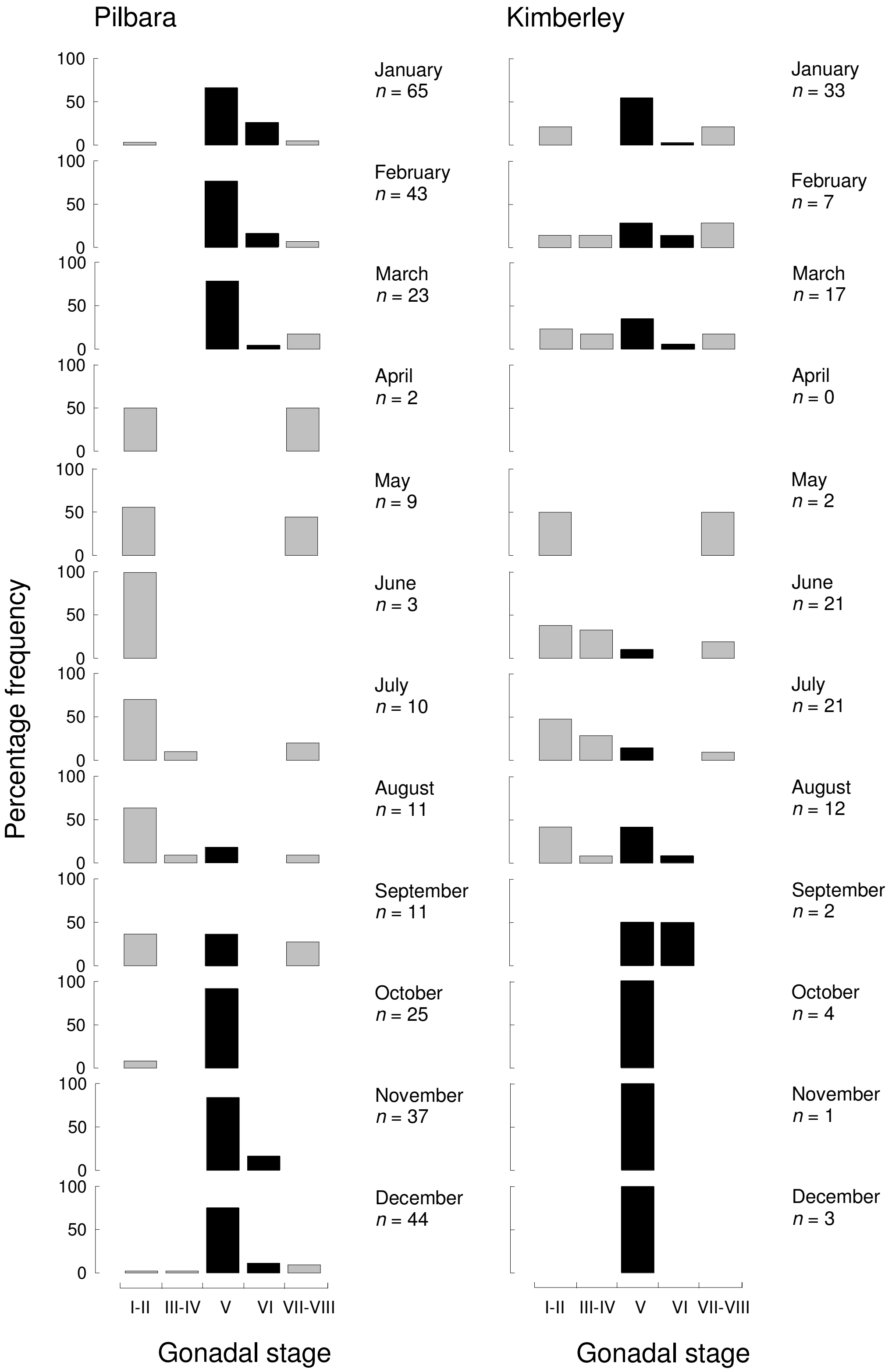

Figure 5.7. Monthly percentage frequency histograms for gonadal maturity stages of female *Lutjanus argentimaculatus* from the Kimberley and Pilbara regions. *n* = sample size.

5.3.4 Aspects related to fecundity

The stage VI ovaries of two female *L. argentimaculatus*, that were representative of stage VI ovaries during the spawning season, contained oocytes at each developmental stage from the chromatin nucleolar to yolk granule stage (**Figure 5.8**). Note that oocytes beyond the yolk granule stage were not measured (see Chapter 2 for reason). In both ovaries, the oocyte diameters formed an essentially continuous distribution. The diameters of the smallest oocytes, *i.e.* chromatin nucleolar oocytes, produced a sharp modal class at 40-59 µm, while those of the largest oocytes, *i.e.* yolk granule oocytes, ranged between 220-559 µm (**Figure 5.8**).

The fecundities of 13 female *L. argentimaculatus* from the Pilbara region, derived from estimates of the number of hydrated oocytes in stage VI ovaries of fish with lengths of 460 to 679 mm and weights of 1.6 to 5.6 kg, ranged from *ca* 0.4 to 2.4 million. The relationship between batch fecundity, F, and both fork length in mm, FL, and total body weight in g, W, are shown in **Figure 5.9** and described by the following equations:

$$F = 9.425\text{x}10^{-6} \text{ x } FL^{4.021} \qquad R^2 = 0.826, n = 13.$$

$$F = 449.350\ W - 261584 \qquad R^2 = 0.886, n = 13.$$

5.3.5 Sex ratio

Although the ratio of females to males of *L. argentimaculatus* caught by the commercial trawl fishery in offshore waters in the Pilbara region was close to parity, *i.e.* 47.4 : 52.6, far fewer females than males were caught by the commercial trap fishery in offshore waters of the Kimberley region, *i.e.* 38.3 : 61.7.

5.3.6 Spawning location

All of the fish sampled in rivers and the mangrove regions of estuaries were immature. In contrast, in offshore waters, 78 and 77% of the females and males in the Pilbara

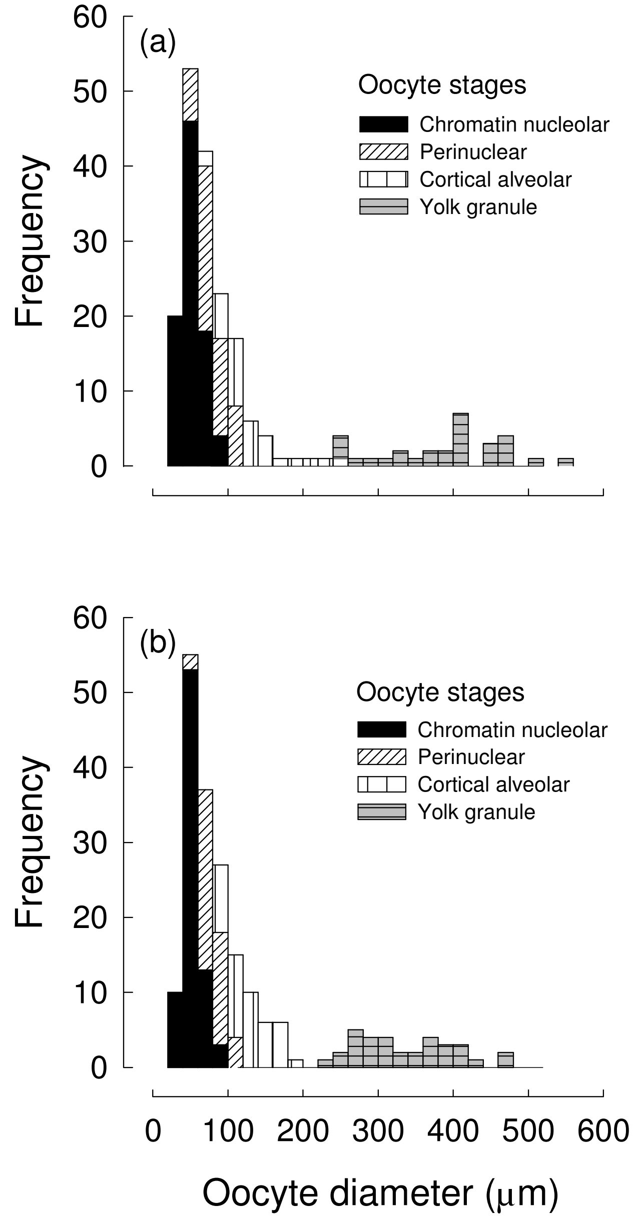

Figure 5.8. Oocyte diameter frequency distributions for stage (VI) spawning ovaries of (a,b) two *Lutjanus agentimaculatus*.

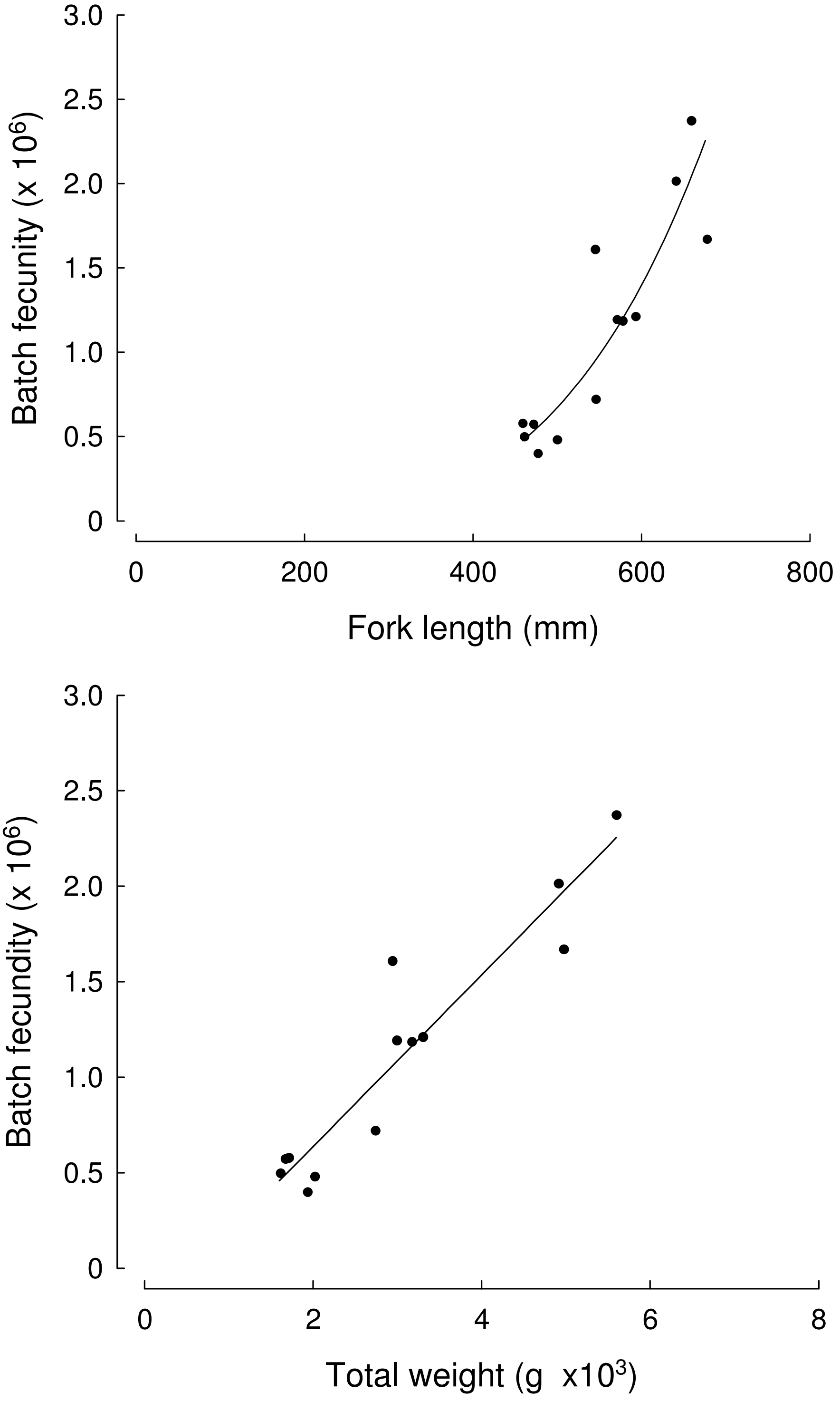

Figure 5.9. Relationship between batch fecundity (=number of hydrated oocytes) and fork length (mm) and total weight (g) for *Lutjanus argentimaculatus*.

region and 61 and 74% of the corresponding sexes in the Kimberley region were mature.

5.3.7 Validation that opaque zones in otoliths are formed annually

The mean monthly marginal increments on otoliths of *L. argentimaculatus* with 4-6 opaque zones rose progressively from 0.45 to reach *ca* 0.65 in July to September and then declined precipitously to about 0.4 in October (**Figure 5.10**). Similar trends were exhibited by the mean monthly marginal increments with 7-9 opaque zones.

5.3.8 Age composition and growth

The maximum observed age of females and males of *L. argentimaculatus* were 52 and 49 years, respectively, in the Pilbara region and 41 and 43 years, respectively, in the Kimberley region. The von Bertalanffy growth curve provided a good fit to the lengths at age of females and males of *L. argentimaculatus* in both the Pilbara and Kimberley regions, as is demonstrated by the high values for the coefficient of determination (**Figure 5.11**, **Table 5.2**). The growth curves of females and males were significantly different ($p < 0.001$) in both the Pilbara and Kimberley regions. The asymptotic lengths of females and males were greater in the Kimberley than in the Pilbara. In both regions, the females and males grew rapidly during the first 10 years of life, attaining, during that period, lengths that were between 83 and 93% of their asymptotic lengths. The estimated lengths at ages 2, 5, 10, 20 and 30 years were 220, 397, 526, 585, and 592 mm, respectively, for females, and 218, 407, 549, 619 and 628 mm for males, respectively in the Pilbara. The estimated lengths for fish of the same age in the Kimberley were 265, 414, 553, 649 and 671 mm for females, respectively, and 248, 429, 565, 632 and 641 mm, respectively, for males (**Figure 5.11**).

ANCOVA demonstrated that the relationships between fork length, FL, and body weight, W, for *L. argentimaculatus* from the Pilbara and Kimberley regions were significantly different ($p < 0.001$). The above relationships for the two regions are:

Pilbara $\ln W = 2.957 \times \ln FL - 10.801$ ($R^2 = 0.986$, $n = 1088$)

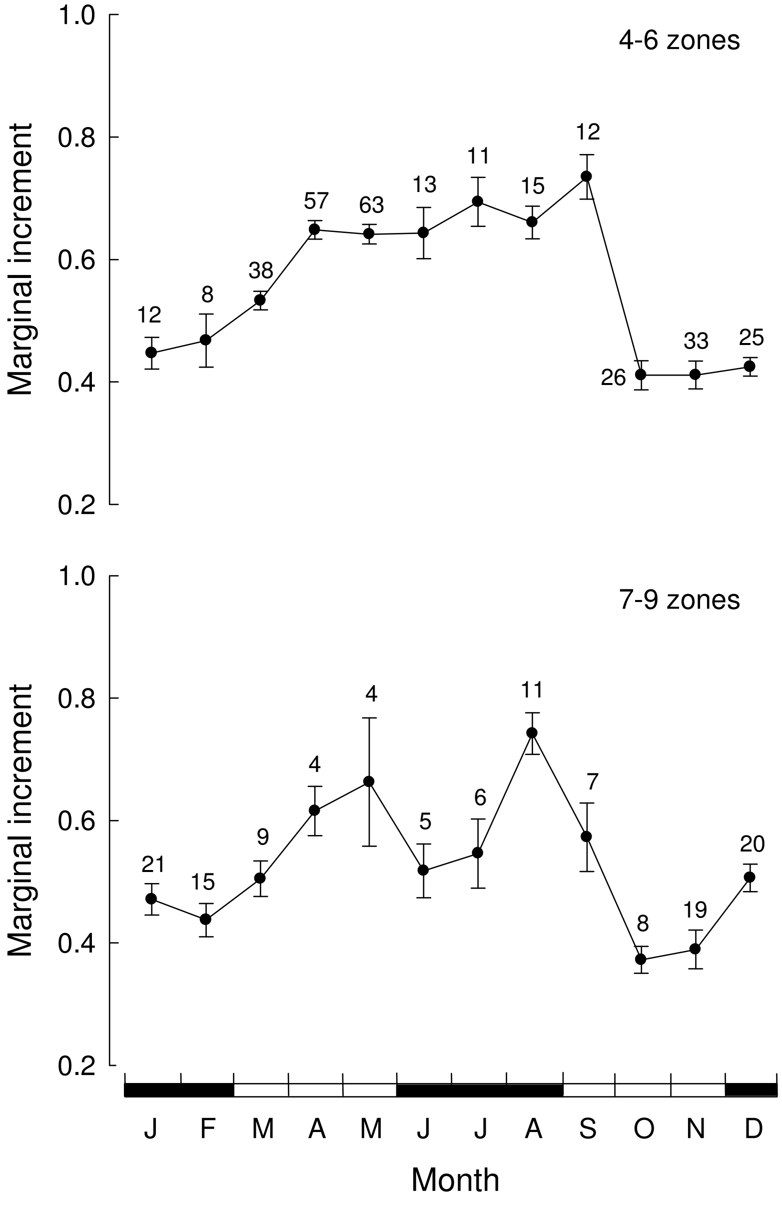

Figure 5.10. Mean monthly marginal increments ±1SE on sectioned sagittal otoliths of *Lutjanus argentimaculatus* from the Pilbara region. Closed rectangles on the horizontal axis refer to winter months and summer months and open rectangles to spring and autumn months.

Table 5.2. von Bertalanffy growth parameters derived from lengths at age for *Lutjanus argentimaculatus* from the Pilbara and Kimberley regions, including lower and upper 95% confidence limits, the coefficient of determination (R^2) and number of fish aged (n).

	L_∞ (mm)	k (year^{-1})	t_0 (years)	R^2	n
Pilbara					
Females					
Estimate	630	0.205	-0.076	0.751	607
Lower 95%	617	0.192	-0.263		
Upper 95%	642	0.220	0.096		
Males					
Estimate	593	0.215	-0.152	0.745	705
Lower 95%	583	0.201	-0.351		
Upper 95%	604	0.228	0.032		
Kimberley					
Females					
Estimate	642	0.204	-0.393	0.841	296
Lower 95%	622	0.172	-0.997		
Upper 95%	666	0.230	-0.171		
Males					
Estimate	677	0.150	-1.313	0.851	502
Lower 95%	657	0.128	-1.922		
Upper 95%	702	0.169	-0.874		

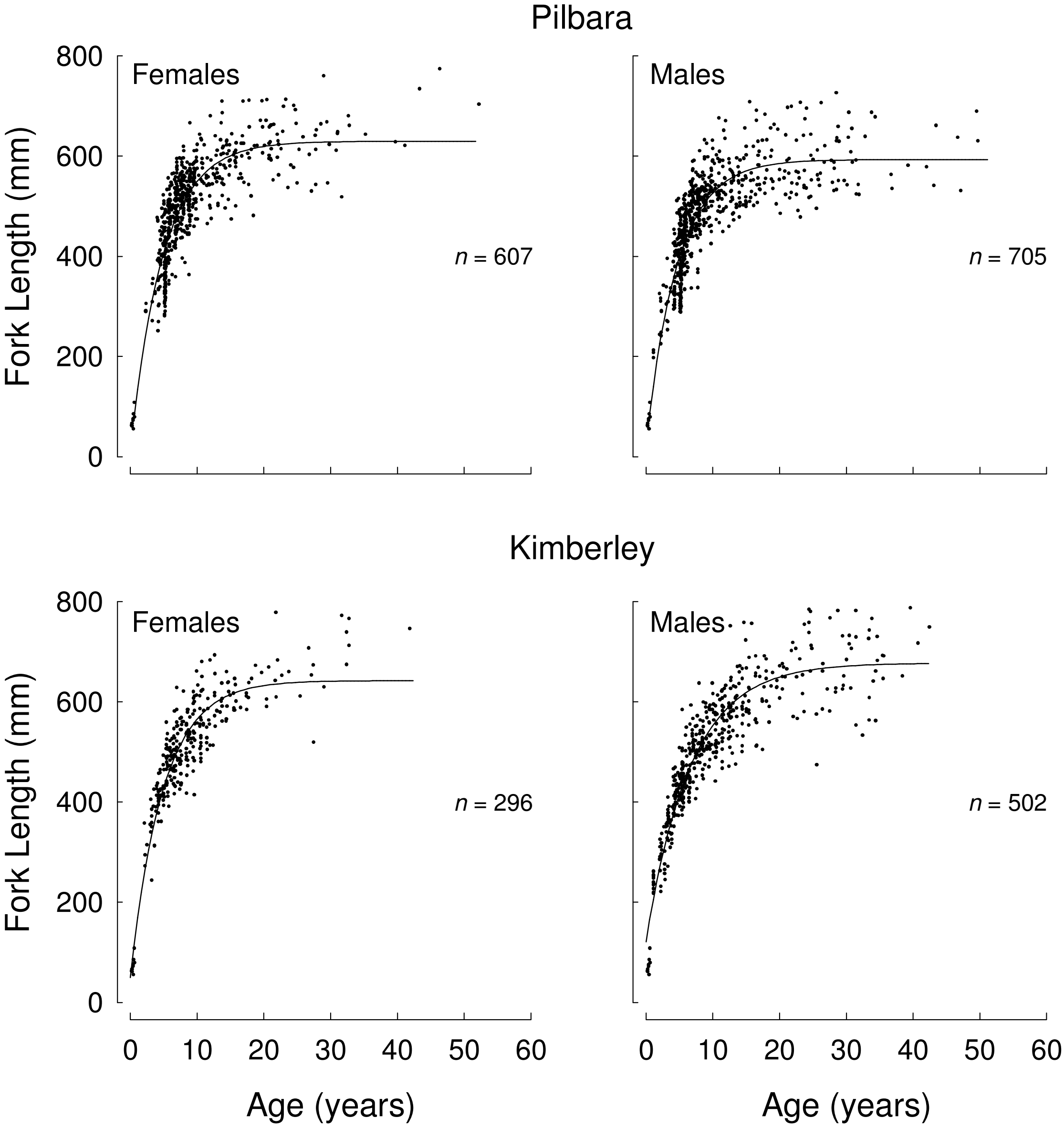

Figure 5.11. von Bertalanffy growth curves fitted to the lengths at age of females and males of *Lutjanus argentimaculatus* from the Pilbara and Kimberley regions. *n* refers to the number of fish used for constructing each growth curve.

Kimberley $\ln W = 3.045 \times \ln FL - 11.328$ ($R^2 = 0.979$, $n = 635$).

The relationships between fork length, *FL*, and both total length, *TL*, and standard length, *SL*, for *L. argentimaculatus* are as follows:

$$TL = (1.052 \times FL) - 5.126 \quad (R^2 = 0.995, n = 1976)$$

$$SL = (0.851 \times FL) - 10.952 \quad (R^2 = 0.996, n = 1974).$$

5.3.9 Length and age compositions

The length and age compositions of *L. argentimaculatus* varied markedly according to the method of capture (**Figure 5.12**). The use of rotenone in nearshore waters yielded the smallest individuals, with lengths ranging from 54 to 107 mm and producing a modal length class of 50 to 99 mm. All of these fish were in their first year of life. The lengths of fish caught by line fishing by recreational fishers in nearshore waters ranged from 125 to 494 mm, with the majority lying between 300-399 mm, whereas line fishing by commercial fishers in offshore waters caught fish with lengths ranging from 495 to 916 mm. The fish caught by recreational anglers were all < 8 years of age, whereas those obtained by commercial line fishers were all > 9 years of age and the three oldest of these fish ranged from 46 to 52 years in age (**Figure 5.12**).

The length and age distributions of *L. argentimaculatus* caught by commercial trapping in the Kimberley region and by commercial trawling in the Pilbara region were similar, with lengths ranging from 372 to 865 mm and from 338 to 759 mm, respectively, and with ages ranging from 3 to 43 years and 4 to 43 years, respectively. The majority of fish were between 400 and 650 mm in length and < 15 years in age (**Figure 5.12**).

All *L. argentimaculatus* that were caught at lengths < 300 mm were obtained from mangroves in nearshore waters (**Figure 5.13**). The percentage of sampled fish in the Pilbara region caught in offshore waters, with respect to length, increased from 4% in the 300-449 mm length class to 24 and 91% in the 350-399 and 400-449 mm length classes, respectively and to 100% for fish > 450 mm. With respect to age, the percentage of *L. argentimaculatus* caught in offshore waters increased from 0% in fish < 4 years, to 51% in fish at 4 years and to all or virtually all fish ≥ 6 years. The trends

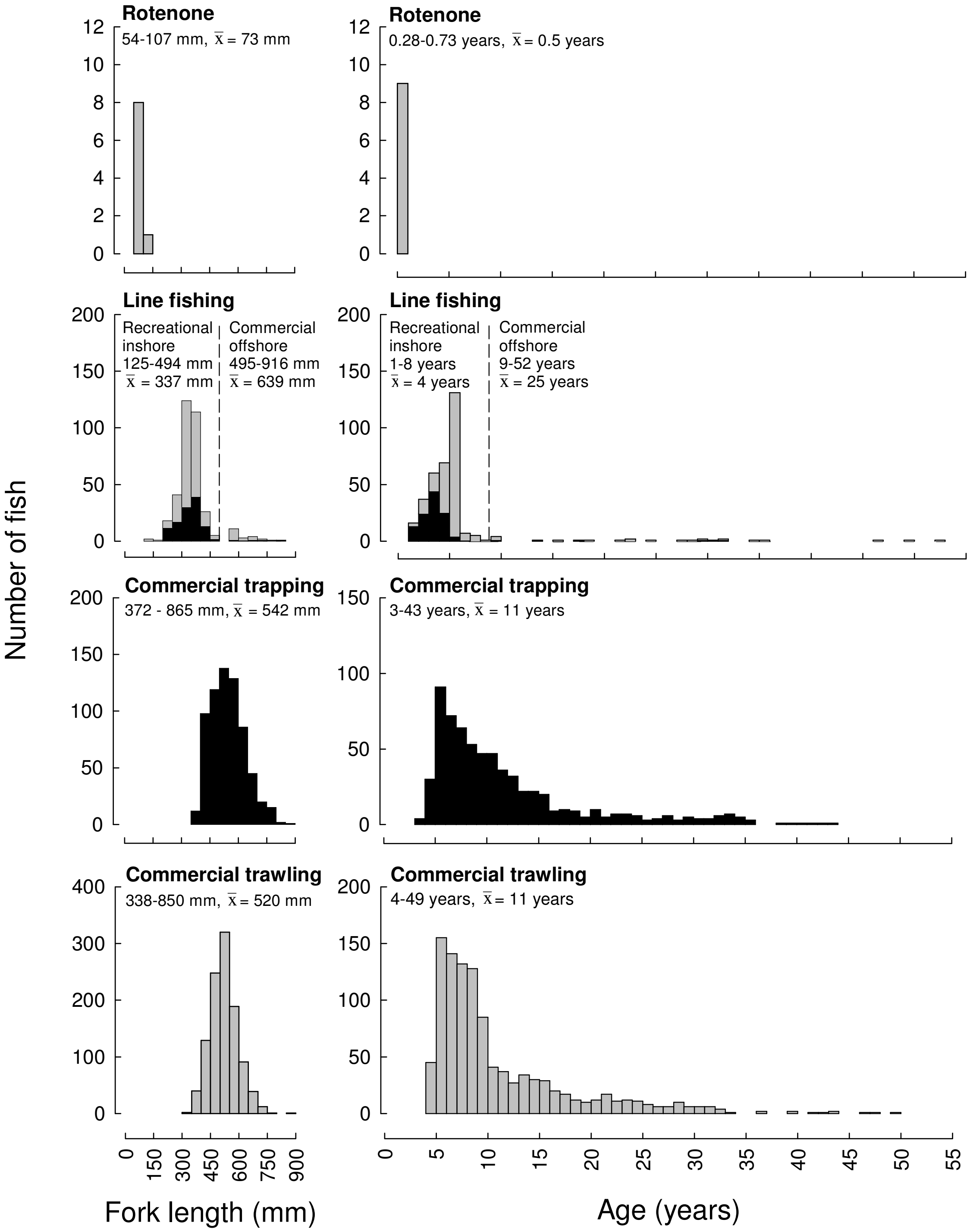

Figure 5.12. Numbers of *Lutjanus argentimaculatus* caught by different methods in each 50 mm length class along the Pilbara (grey bars) and Kimberley (black bars) coasts. The bars for line fishing are stacked rather than overlaid.

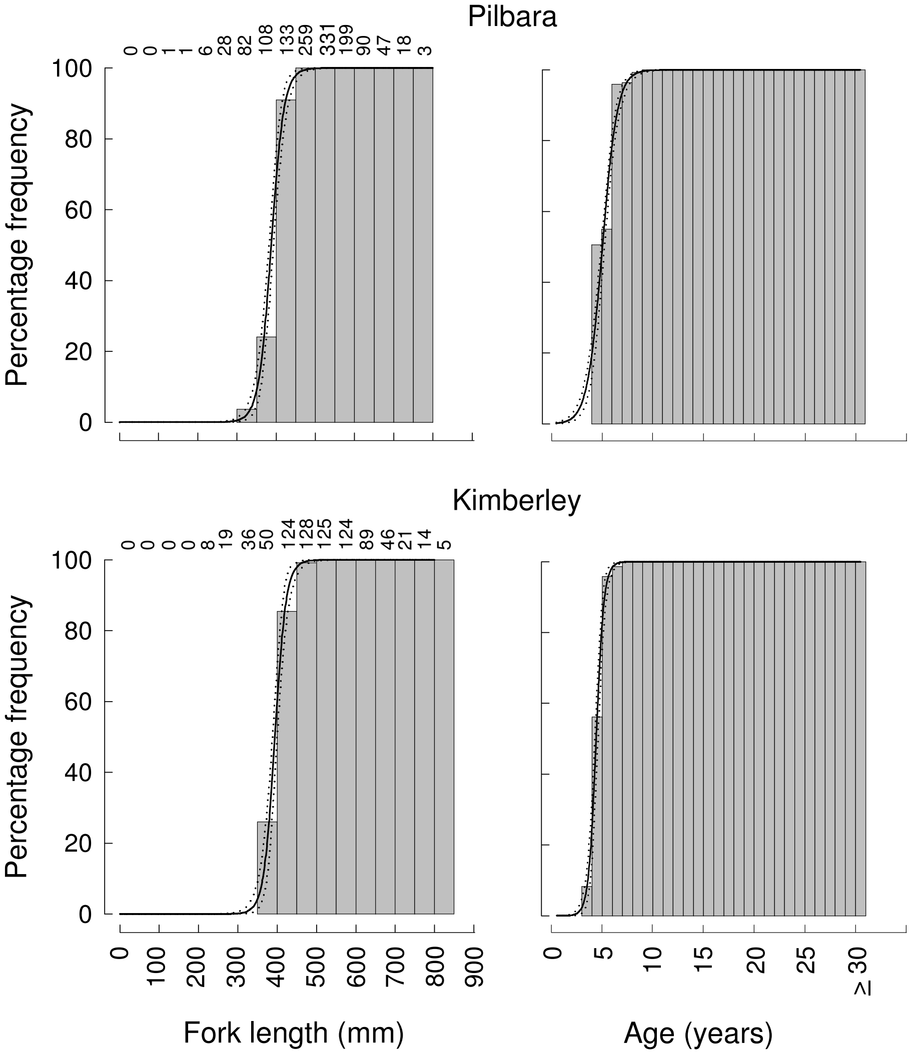

Figure 5.13. Percentage frequencies of occurrence of fish in offshore waters in the Pilbara and Kimberley regions in sequential 100 mm length classes and age classes of *Lutjanus argenticmaculatus* (data shown in grey). The logistic curve (solid line) and its 95% confidence limits (dotted lines) were derived from a logistic regression analysis that described the relationship between total length and the probability that an individual had been caught in offshore waters. Sample sizes of fish in each 100 mm length class are shown.

exhibited by sampled fish in the Kimberley region were similar to those just described for *L. argentimaculatus* in the Pilbara reigon. The lengths and ages at which 50% of *L. argentimaculatus* in the Pilbara and Kimberley regions move to offshore waters (*i.e.* L_{50}s and A_{50}s) were 387 and 394 mm and 4.6 and 3.9 years, respectively (**Table 5.3**). A likelihood-ratio test demonstrated that A_{50}s were significantly different ($p < 0.001$) but that this was not the case with the L_{50}s (**Figure 5.13**).

Table 5.3. Estimates for *Lutjanus argentimaculatus* from the Pilbara and Kimberley coasts of the lengths and ages at which 50 and 95% of fish in the samples had been caught in offshore waters (*i.e.* L_{50}, L_{95}, A_{50} and A_{95}, respectively) and associated lower and upper 95% confidence limits.

Parameter	L_{50}	L_{95}	A_{50}	A_{95}
Pilbara				
Estimate	387	435	4.57	6.71
Lower 95%	382	424	4.43	6.43
Upper 95%	393	445	4.77	7.05
Kimberley				
Estimate	394	436	3.91	5.02
Lower 95%	388	424	3.78	4.77
Upper 95%	399	448	4.07	5.26

5.3.10 Mortality estimates

The point estimates for the instantaneous coefficient of total mortality, *Z*, for *L. argentimaculatus*, from both the Pilbara and Kimberley regions, derived by refitting Hoenig's (1983) equation for fish, relative abundance (catch curve) analysis (*sensu* Deriso *et al.*, 1985) and simulation based on the number of fish greater than or equal to a specified age, *i.e.* 5 fish ≥ 46 years for the Pilbara region and 5 fish ≥ 40 years for the Kimberley region, ranged between 0.08 and 0.15 year^{-1} (**Table 5.4**, **Figure 5.14**). The posterior probability distribution for *Z*, determined by combining the separate likelihood distributions for the various estimates of *Z*, yielded a combined point estimate for *Z* of

Table 5.4. Mortality estimates for *Lutjanus argentimaculatus* from the Pilbara and Kimberley regions calculated using life history models, estimation of longevity based on simulation and relative abundance analysis.

Method of analysis	***Z, M or F*** **(year^{-1})**	**Estimate**	**Lower 95%**	**Upper 95%**
Pilbara				
Refitted Hoenig (1983) fish equation	*Z*	0.08	0.03	0.23
Relative abundance analysis	*Z*	0.15	0.14	0.16
Simulation (number of fish ≥ 46 years)	*Z*	0.13	0.10	0.15
Combined *Z* (Bayesian method)	***Z***	**0.15**	**0.14**	**0.17**
Refitted Pauly (1980)	*M*	0.53	0.17	1.62
Combined *M* (Bayesian method)	***M***	**0.13**	**0.08**	**0.16**
Monte Carlo	***F***	**0.02**	**0.00**	**0.08**
Kimberley				
Refitted Hoenig (1983) fish equation	*Z*	0.08	0.03	0.23
Relative abundance analysis	*Z*	0.13	0.12	0.14
Simulation (number of fish ≥ 40 years)	*Z*	0.15	0.11	0.18
Combined *Z* (Bayesian method)	***Z***	**0.14**	**0.13**	**0.16**
Refitted Pauly (1980)	*M*	0.42	0.14	1.30
Combined *M* (Bayesian method)	***M***	**0.12**	**0.07**	**0.15**
Monte Carlo	***F***	**0.02**	**0.00**	**0.08**

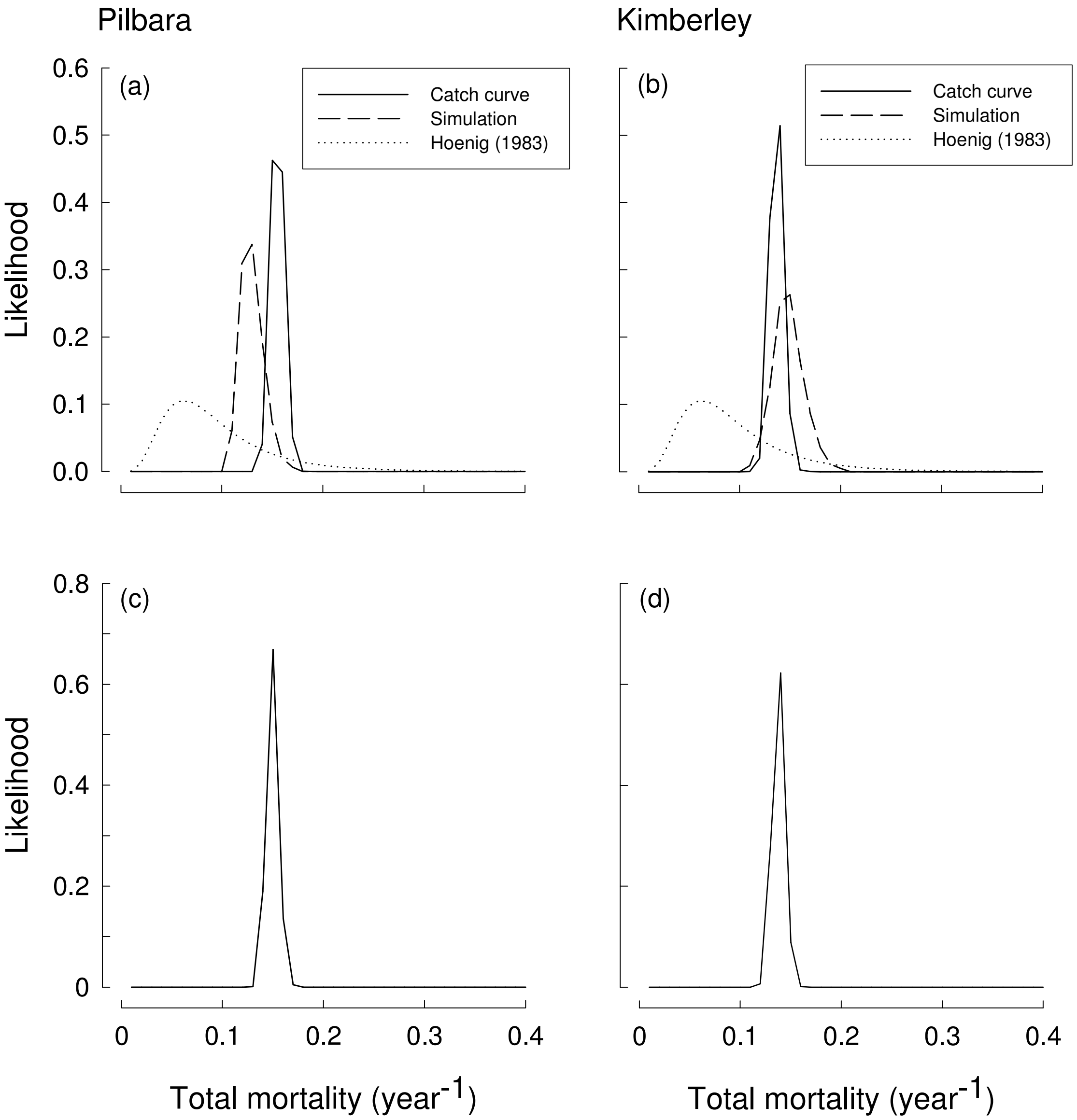

Figure 5.14. Estimated likelihood functions for total mortality, *Z*, of *Lutjanus argentimaculatus* from the Pilbara and Kimberley regions derived using Hoenig's (1983) regression equation for fish, relative abundance (catch curve) analysis, and a simulation method based on the number of individuals above a certain age and sample size. (a,b) Combined posterior probability distributions for *Z* for *L. argentimaculatus* derived from the separate likelihood functions are shown in a and b.

0.15 year^{-1} for the Pilbara region and 0.14 year^{-1} for the Kimberley region (**Table 5.4, Figure 5.14**).

The point estimates for the instantaneous coefficient of natural mortality, *M*, for *L. argentimaculatus*, derived by refitting the equation of Pauly (1980) of 0.53 year^{-1} for the Pilbara region and 0.42 year^{-1} for the Kimberley region, were substantially higher than the combined point estimates of *Z* for the two regions (**Table 5.4**). The resultant posterior probability distribution for the point estimate for *M*, determined from the Bayesian analysis of the combined likelihood distribution for *Z* and the requirement that $M \leq Z$, yielded a point estimate for *M* of 0.13 year^{-1} in the Pilbara and 0.12 year^{-1} in the Kimberley (**Table 5.4, Figure 5.15**). The 95% confidence intervals for the combined estimate for *M* were far narrower than for the estimate of *M* derived by refitting Pauly's (1980) equation. The point estimates of the current level of fishing mortality, *F*, derived from the Monte Carlo analysis for *L. argentimaculatus* from the Pilbara and Kimberley regions were both low, *i.e.* 0.02 year^{-1} for both regions (**Table 5.4**).

5.3.11 Yield per recruit, spawning potential ratio and spawning biomass per recruit

The yield per recruit analysis (YPR) for *L. argentimaculatus*, calculated using knife-edge recruitment to the vulnerable stock at 6 years, as determined for this species from the data for the samples caught by both the trawl fishery in the Pilbara region and the trap fishery in the Kimberley region, indicated that with increasing fishing mortality, *F*, from 0 to 0.50 year^{-1}, the YPR will continue to increase, after which it begins to decline (**Figure 5.16**). If the age at recruitment to the fishery was 9 years, with an increase in *F* from 0 to 0.8 year^{-1}, the YPR in both regions will continue to increase. In contrast, if the age at recruitment to the exploited stock was 3 years, the YPR of *L. argentimaculatus* in the Pilbara and Kimberley regions is expected to begin to decline when *F* exceeds 0.19 and 0.21 year^{-1}, respectively, in those two regions (**Figure 5.16**). The estimated YPR and associated 95% confidence intervals for *L. argentimaculatus* at the estimated current level of *F* of 0.02 year^{-1} and assuming knife edge recruitment to the fishery at 6 years, is $0.17 \text{ kg recruit}^{-1}$ ($0.00 - 0.88 \text{ kg recruit}^{-1}$) in the Pilbara region and 0.21 kg

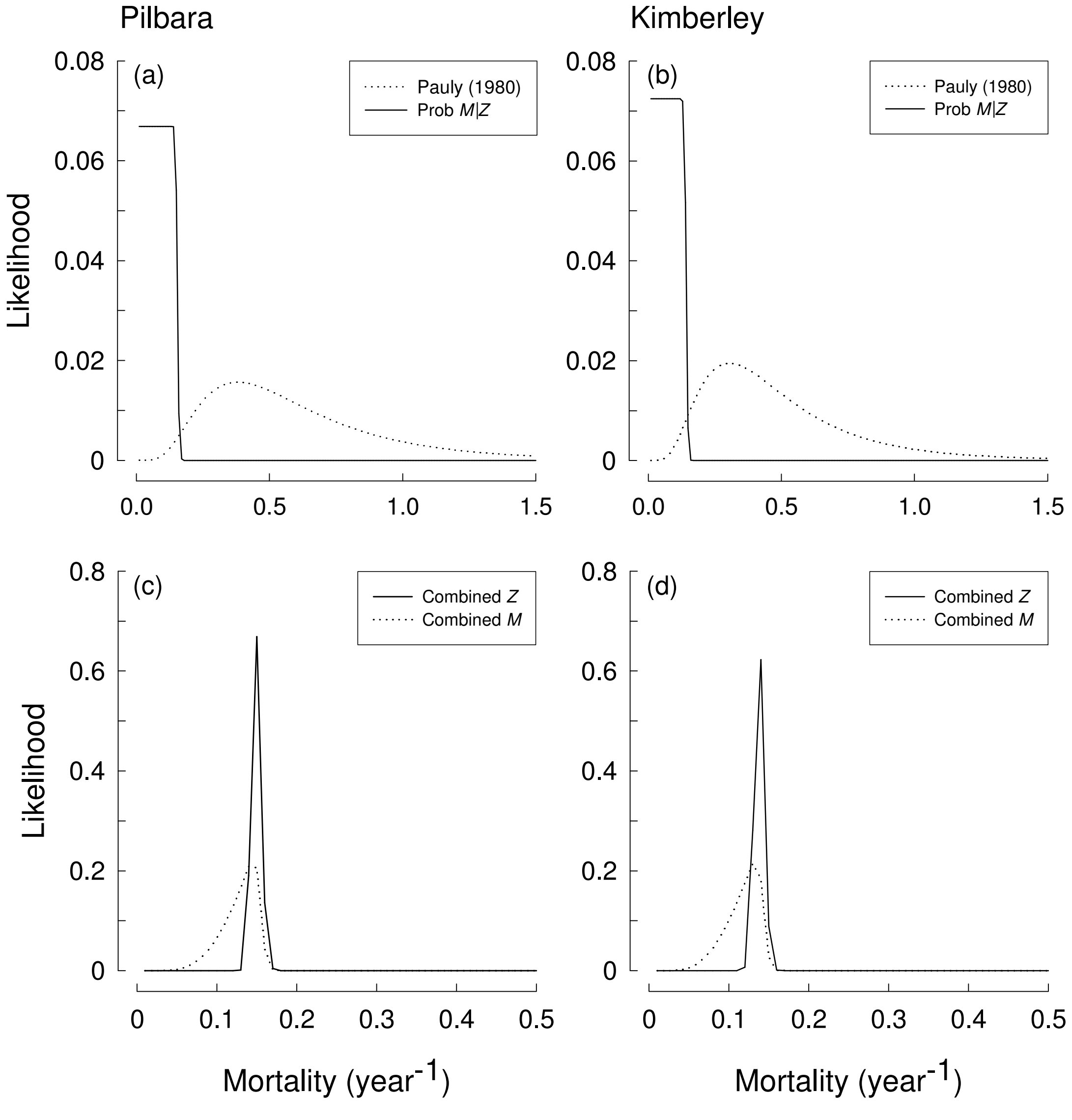

Figure 5.15. Likelihood functions for natural mortality M for *Lutjanus argentimaculatus* from the Pilbara and Kimberley regions (a,b) from Pauly's (1980) equation and the likelihood function for M assuming that it is less than the combined estimate for Z and the combined posterior probability distributions for Z and M for *L. argentimaculatus* from those regions (c,d).

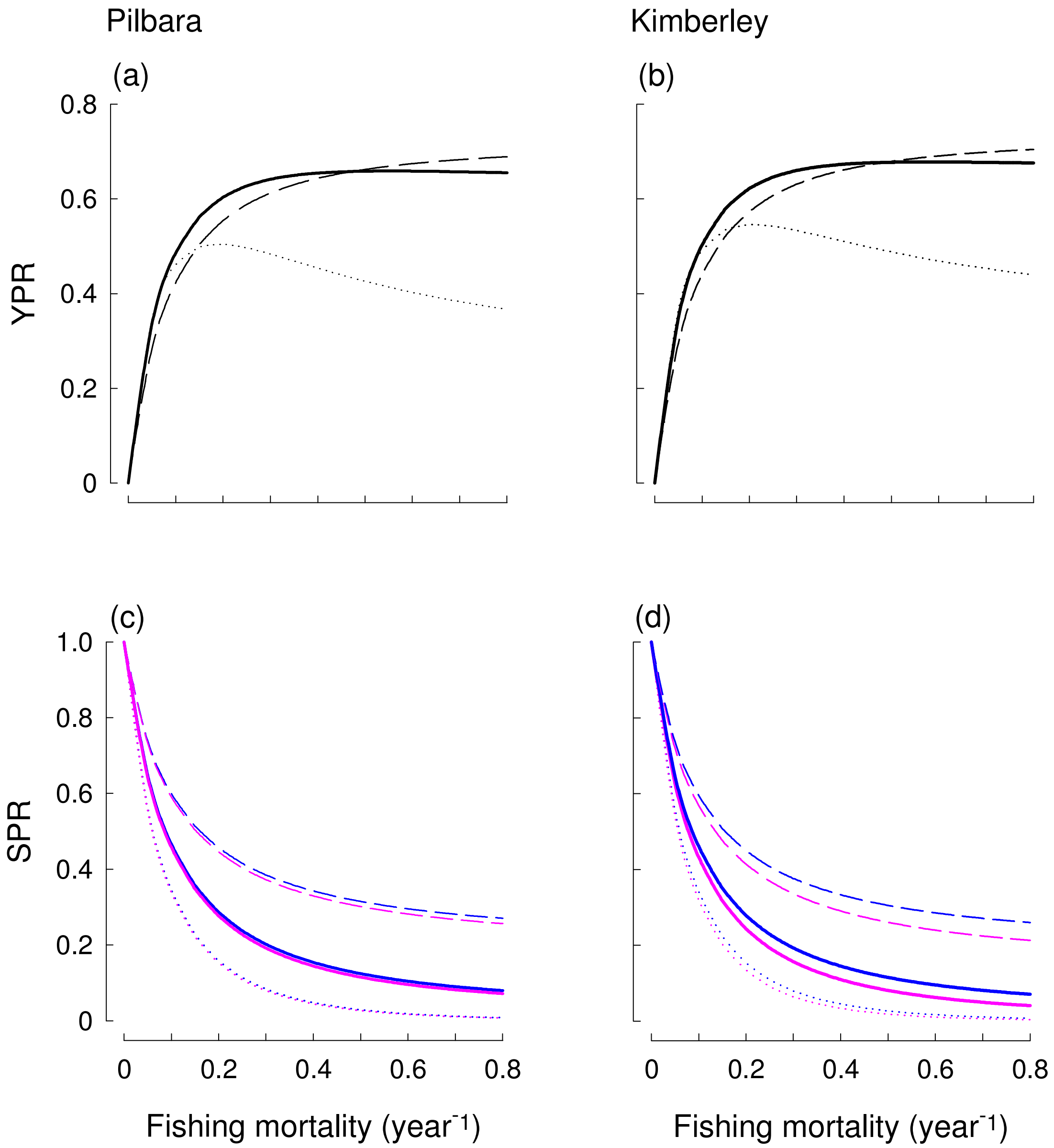

Figure 5.16. Effect, for *Lutjanus argentimaculatus* from the Pilbara and Kimberley regions, of different levels of fishing mortality and at different ages at recruitment to the exploited stock on the yield per recruit (a, b) and spawning potential ratio for females (pink) and males (blue). The curves corresponding to ages 3, 6 and 9 years at full recruitment to the exploited stock are represented by dotted, solid and dashed lines, respectively.

recruit^{-1} (0.00 - 1.14 kg recruit^{-1}) in the Kimberley region. The estimated value of $F_{0.1}$ for *L. argentimaculatus* is 0.15 year^{-1} for both regions (**Table 5.5**).

Table 5.5. Estimates of the current level of yield per recruit (YPR), $F_{0.1}$, and the current levels of total spawning stock biomass per recruit (SSB/R) and spawning potential ratio (SPR) for females, males and females and males combined, for *Lutjanus argentimaculatus* from the Kimberley and Pilbara regions, calculated using 6 years as the age at full recruitment to the fishery for both regions.

Analysis	**Estimate**	**Lower 95%**	**Upper 95%**
Pilbara			
YPR (kg recruit^{-1})	0.17	0	0.88
$F_{0.1}$ (year^{-1})	0.15	--	--
SSB/R (kg recruit^{-1})	8.59	5.53	24.88
SPR (females)	0.82	0.38	1.00
SPR (males)	0.83	0.39	1.00
SPR (females & males)	0.83	0.39	1.00
Kimberley			
YPR (kg recruit^{-1})	0.21	0	1.14
$F_{0.1}$ (year^{-1})	0.15	--	--
SSB/R (kg recruit^{-1})	12.11	8.73	39.08
SPR (females)	0.81	0.38	1.00
SPR (males)	0.82	0.39	1.00
SPR (females & males)	0.81	0.38	1.00

Regardless of the age at recruitment to the exploited stock, with increasing *F*, the spawning potential ratio (SPR) for females and males of *L. argentimaculatus* declines at a similar rate in the two regions (**Figure 5.16**). In the case of both sexes, the rate at which SPR is predicted to decline decreases substantially as the age at recruitment to the fishery increases. The current estimated SPRs for females and males combined, for *L. argentimaculatus* from the Pilbara and Kimberley regions, are 0.83 and 0.81, respectively (**Table 5.5**).

5.4 DISCUSSION

5.4.1 Reproductive biology

As with other species of the Lutjanidae in the tropics (Grimes, 1987), *L. argentimaculatus* in Western Australia is gonochoristic, *i.e.* the sexes are separate. The lengths at which the females and males of this species typically attain maturity (L_{50}) in the Pilbara (461 and 452 mm, respectively) and Kimberley regions (498 and 472 mm, respectively) far exceed the minimum legal length for retention (MLL) of 300 mm TL (= *ca* 290 mm FL) for *L. argentimaculatus* in Western Australia. From a management point of view, it is also relevant that, because this species migrates from nearshore to offshore waters as they increase in size and age and approach maturity, the recreational fisheries for *L. argentimaculatus* in the nearshore waters of north-western Australia is based on immature fish. Furthermore, the lengths of an appreciable number of the individuals retained by the commercial trap fishery in the Kimberley region and commercial trawl fishery in the Pilbara region are below the size at which this species attains maturity.

The greater size of the females than males of *L. argentimaculatus* at maturity parallels the situation found for this species in eastern Australia (Russell *et al.*, 2003). The females and males of *L. argentimaculatus* reach maturity at a relatively smaller size, with respect to their asymptotic length, *i.e.* 67 and 72%, respectively, in the Pilbara region than in the Kimberley region, *i.e.* 79 and 80%, respectively. It may thus be relevant that the commercial catches in the Pilbara region are an order of magnitude greater than those in the Kimberley region.

The far greater ratio of males to females recorded for the Kimberley region (61.7 : 38.3) than in the Pilbara region (52.6: 47.4), which are close to parity, possibly reflects the different fishing methods employed by commercial fishers in the two regions, *i.e.* trawling *vs* fish trapping. For example, the males may be more aggressive and thus exhibit a greater tendency than females to be caught by traps.

The spring/summer spawning period of *L. argentimaculatus* in Western Australia is similar to that recorded for this species in eastern Australia (Russell *et al.*, 2003) and in the waters off Thailand (Doi & Singhagraiwan, 1993). The period of spawning of Mangrove Jack in the spring/summer also parallels that of other lutjanid species which occupy areas of the continental shelf (Grimes, 1987). The mean monthly GSIs of *L. argentimaculatus* in the Pilbara region during the separate years of this study strongly indicated that gonadal recrudescence commences as water temperatures begin to rise and that spawning peaks when water temperatures are at their maxima. This finding is consistent with the fact that, in fish, water temperature plays a crucial role in providing a cue for the onset of gonadal development after a quiescent phase and in stimulating spawning activity (Lam 1983). Surprisingly, in contrast with the situation in Western Australia, the spawning of Mangrove Jack in the waters off Thailand is associated with falling water temperatures and high rainfall (Doi & Singhagraiwan, 1993).

Since virtually all of the mature Mangrove Jack caught during the spawning period in the Pilbara and Kimberley regions were obtained from over reefs in offshore waters, this species presumably spawns in this type of habitat. Furthermore, as hydrated oocytes were found only in the ovaries of females of *L. argentimaculatus* caught during the day, and the period between the onset of oocyte hydration and ovulation in marine fish species is typically *ca* 7-10 h (Lisovenko & Andrianov, 1991, McBride *et al.*, 2003, Hesp *et al.*, 2004b), *L. argentimaculatus* apparently spawns during the afternoon or at dusk. Such a conclusion is consistent with the finding that the congeneric species *Lutjanus vitta* in north-western Australia spawns during the afternoon (Davis & West, 1993). The latter workers hypothesized that the timing of the large tidal cycles and strong currents in north-western Australia would thus facilitate the dispersal of the eggs and larvae of this lutjanid (Davis & West, 1993).

The presence, within individual stage VI (spawning) ovaries, of oocytes at all stages of development, *i.e.* chromatin nucleolar, perinucleolar, cortical alveolar and yolk granule oocytes, together with either migratory nucleus oocytes, hydrated oocytes and/or post ovulatory follicles, demonstrates that this species has indeterminate fecundity. Thus, the number of oocytes released by individual females during a spawning season is not determined prior to the commencement of that season (Hunter *et al.*, 1985). The 13 females of *L. argentimaculatus* for which we could obtain estimates of batch fecundity had a maximum weight of 5.6 kg, which is substantially less than the maximum weight attained by this species. The fact that the largest of our batch fecundity estimates, *i.e. ca* 2.4 million oocytes, is far less than the *ca* 4 million eggs recorded for this species in eastern Australia is thus almost certainly attributable to the far smaller size of our fish (Russell *et al*., 2003).

5.4.2 Age and growth

Since the mean monthly marginal increments for sectioned otoliths of *L. argentimaculatus* exhibited a single progressive rise and then decline during the year, a single opaque zone is formed annually in the otoliths of this species in north-western Australia. Thus, as with the two threadfin species, the Estuary Rockcod and Malabar Grouper, the number of opaque zones in the otoliths can be used to age this species.

The Mangrove Jack lives for a far longer period than the two threadfin species, the Estuary Rockcod and the Malabar grouper, that were the other species studied during this FRDC project. The maximum age of 52 years we recorded for *L. argentimaculatus* is substantially greater than the 37 and 32 years recorded for this species in eastern Australia by Russell *et al.* (2003) and Sheaves (1995), respectively, and the 18 years recorded for *L. argentimaculatus* in New Caledonia by Loubens (1980). However, all of the above estimates of maximum age are markedly greater than the 7 years recorded for this species on the east coast of Malaysia. This difference is almost certainly due to the fact that this latter study was based on analysis of length-frequency data, which would have made it impossible to distinguish between the length distributions of the older fish (Ambak *et al*., 1985). The far greater maximum age recorded for Mangrove Jack in north-western Australia than in all other regions suggests that fishing pressure on this species in this region is still relatively light, which is consistent with the results of our mortality analyses (see later).

5.4.3 Mortality and yield and spawning biomass per recruit analyses

The point estimates derived for *M* for *L. argentimaculatus* in the Pilbara and Kimberley regions using the equation of Pauly (1980) were greater than the point estimates derived for Z using Hoenig's (1983) equation for fish, relative abundance (catch curve) analysis and the simulation method of Hall *et al.* (2004). This clearly erroneous situation parallels that found for the Estuary Rockcod and Malabar Grouper (Chapter 4). Furthermore, as is typically the case with the Pauly equation, the estimates for M for Mangrove Jack are very imprecise, *i.e.* have very broad confidence intervals.

The Bayesian approach of Hall *et al*. (2004), developed during FRDC project 2000/137, combines the various mortality estimates and takes into account the fact that M cannot exceed Z. The resulting low estimates of M of *ca* 0.12-0.13 year^{-1} and large maximum age (> 50 years) recorded for *L. argentimaculatus* suggests that this species is likely to be prone to over-exploitation. However, even with this Bayesian approach, which incorporates the distribution of the values for M derived from the Pauly (1980) equation, an erroneously high estimate for this variable will bias the ultimate estimate for M derived from the Bayesian approach. Thus, in turn, the estimate for F will be biased and, consequently, should be treated with caution. Nevertheless, the point estimates for F for *L. argentimaculatus* from both regions were particularly low, which suggests that this species is not currently subjected to heavy fishing pressure in north-western Australia.

The above indication that fishing mortality of Mangrove Jack in north-western Australia is light is consistent with the presence in our samples of one very old fish of 52 years and several in excess of 35 years. This conclusion is further enhanced by the fact that these older individuals were far greater in age than those caught in eastern Australia (Russell *et al.*, 2003).

The estimates of 0.83 and 0.81 for the SPRs of *L. argentimaculatus* in the Pilbara and Kimberley regions, respectively, far exceed 0.3, *i.e.* greatly exceed 30% of the spawning stock biomass of the virgin stock. This suggests that the current level of fishing pressure on this species in these regions is likely to be sustainable (Mace & Sissenwine, 1993; Goodyear, 1993). Nevertheless, because the estimates of mortality are imprecise, caution must be exercised in placing too much weight solely on the results of these SPR analyses. At the same time, it must be recognised that, as Mangrove Jack become fully recruited to the fishery at a length below that at which this species typically attains maturity, the SPR will decline markedly as fishing mortality increases. Furthermore, these per recruit analyses do not take into account the fact that the recreational fishery for *L. argentimaculatus*, which is largely concentrated in nearshore waters, is based on fish that have not reached the size at maturity. Thus, should the recreational fishery continue to increase, managers and stakeholders will need to consider increasing the MLL for *L. argentimaculatus* to a length equivalent or greater than that at which this species typically attains maturity. However, at the same time, managers will need to take into account the fact that the introduction of such a policy would prohibit many recreational anglers from catching Mangrove Jack, as these anglers fish in nearshore waters where only the juveniles of this species occur. Alternatively, managers might need to consider policies which reduce fishing effort.

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BENEFITS

This study has achieved the following.

1. Provides the first sound quantitative data for two protandrous species (Blue and King Threadfin), two protogynous species (Estuary Rockcod and Malabar Grouper) and one gonochoristic species (Mangrove Jack) in the Kimberley and Pilbara regions of north-western Australia. These species are important components of the commercial and recreational fisheries in the remote coastline of north-western Australia.
2. Enables fisheries managers, in conjunction with stakeholders, to develop strategies for conserving the stocks of the above important commercial and recreational species.
3. The provision of baseline data on the current biological characteristics and levels of total mortality of these five species will enable fisheries managers to detect and therefore, if necessary, respond to any changes in these crucial parameters for the overall stocks of these finfish in the future.
4. Facilitate the sustainability of the stocks of the above five species and thus ensure that recreational and commercial fishers will be able to take appropriate numbers of each of those species.
5. The training of research students in contemporary techniques for analyzing quantitatively key aspects of the biology and stock status of finfish species and refining aspects of certain of those techniques.

FURTHER DEVELOPMENT

Once accepted by the FRDC, the final report will be provided to managers at the Department of Fisheries, Western Australia. This will enable managers and stakeholders to take into account the highly relevant biological data on Blue and King Threadfin, Estuary Rockcod, Malabar Grouper and Mangrove Jack, when developing management plans for these species in the Pilbara and Kimberley regions.

The accepted final report will also be provided to the Western Australia Fishing Industry Council (WAFIC), RecFishwest, Recreational Fishing Advisory Committee (RFAC), CALM, the Regional Manager and Northern Policy Officer of the Department of Fisheries, Western Australia. This will ensure that stakeholders are made aware of the biology of these five species and the implications of the results for sustainable management.

Poster(s) and/or reports summarising the main biological results of this study will be sent to appropriate bodies and individuals. The results of this study will be submitted for publication in international journals so that their implications are subject to critical peer group review. The responses of the referees will facilitate the refinement of our approaches to studying crucial aspects of the biology of hermaphroditic and gonochoristic species.

PLANNED OUTCOMES

The following planned outcomes, as outlined in B6 of the original project application, have been achieved.

1. The results of this study provide managers with the types of data that they require to maintain effectively and appropriately the stocks of the Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack in north-western Australia.
2. The results of the study will facilitate the development of more informed and thus more robust management strategies to ensure the sustainability of the above species for the benefit of commercial, recreational, charter boat and aboriginal fishers.

3. As a result of a thorough understanding of the biology of the above five species and their implications, stakeholders will understand the basis for management plans, which will thus reduce the likelihood of conflict between different user groups that fish these species.
4. A resource that is crucial to the economy and lifestyle of the isolated communities of north-western Australia will be conserved.
5. Training of research students and staff in important methods for analyzing data that are a crucial component of fisheries science and essential for the development of appropriate fisheries management plans.

GENERAL CONCLUSIONS

Despite the difficulties in sampling species over very large distances in different habitats in a very remote environment, we managed to achieve the vast majority of the objectives of this FRDC study on the Blue Threadfin *Eleutheronema tetradactylum*, the King Threadfin *Polydactylus macrochir*, the Estuary Rockcod *Epinephelus coioides*, the Malabar Grouper *Epinephelus malabaricus* and the Mangrove Jack *Lutjanus argentimaculatus*. Thus, we have obtained sound and reliable quantitative data for key aspects of the biology and the status of the stocks of these five commercially and recreationally important fish species in the Pilbara and Kimberley regions of north-western Australia.

The major findings are as follows:

- Blue and King Threadfins complete their life cycles in unvegetated, nearshore waters. In contrast, Estuary Rockcod, Malabar Grouper and Mangrove Jack live in mangrove and nearshore rocky areas as juveniles and move offshore into deeper waters over reefs as they increase in size and age.

- All five species have protracted spawning periods, *i.e.* between 6 and 10 months, with the spawning of each species peaking at some stage between early spring and early autumn. All five species have indeterminate fecundity.
- In north-western Australia, the Blue and King Threadfins are protandrous hermaphrodites, *i.e.* individuals change sex from male to female, and both typically reach sexual maturity as males at the end of their first year of life when they are *ca* 200 and 230 mm in length, respectively. They typically become females at *ca* 400 mm (= *ca* 2 years) and *ca* 810 mm (= *ca* 4 years), respectively.
- Estuary Rockcod and Malabar Grouper are monandric protogynous hermaphrodites, *i.e.* all individuals mature first as females. All of the former species, but only a proportion of the latter, subsequently change to males as they increase in size. Female Estuary Rockcod and Malabar Grouper typically mature at *ca* 570 and 800 mm, respectively, and change sex at *ca* 920 and 1100 mm, respectively. The youngest Estuary Rockcod and Malabar Grouper to have become males were 7 and 13 years of age, respectively.
- Mangrove Jack is a gonochoristic species (does not change sex). Females typically attain maturity at lengths of *ca* 460 mm in the Pilbara region and *ca* 500 mm in the Kimberley region and at 6-7 years of age in both regions.
- In comparison with the Blue Threadfin, the King Threadfin lives longer (10 *vs* 6 years), grows more rapidly and attains a greater length (1393 *vs* 793 mm).
- Estuary Rockcod and Malabar Grouper grow initially at a similar rate, but the latter subsequently attains a greater maximum length (1216 *vs* 1156 mm) and lives longer (31 *vs* 22 years).
- Mangrove Jack are very long lived (> 50 years), and grow to *ca* 400 and 550 mm in 5 and 10 years, respectively, after which they do not increase markedly in length.

- Estimates for current fishing mortality and spawning potential ratios strongly indicate that Blue Threadfin is fully-exploited and King Threadfin is over-exploited. Although Estuary Rockcod, Malabar Grouper and Mangrove Jack appear to be only lightly to moderately exploited, the estimates for fishing mortality are likely to be conservative because of unrealistic estimates of natural mortality.
- As the Blue Threadfin is exploited at lengths below that at which this species changes from male to female, managers and stakeholders need to consider introducing a minimum legal length for retention (MLL) that takes into account the length at sex change.
- The current MLL of 450 mm for King Threadfin is well below the length at which this species typically changes sex (L_{50} at sex change = *ca* 810 mm). Thus, managers need to consider introducing regulations that will ensure that sufficient numbers of both sexes are conserved, *e.g.* through gear regulations or size limits.
- In principle, the recent reduction from 1200 to 1000 mm of the upper legal length for retention of cods (Serranidae) will help protect the males of large serranid species. However, the effectiveness of this upper limit will depend on the ability of these large fish to survive being caught and released. Furthermore, if exploitation increases markedly, the concomitant introduction of 400 mm as a minimum legal length for retention for the Estuary Rockcod may not allow a sufficient number of individuals to survive capture to mature as females and thus contribute to egg production, let alone ensure that sufficient females survive to become males and contribute to sperm production.
- The stock of Mangrove Jack, because of the high value of this species, will inevitably attract increasing attention from the recreational, commercial and charter boat sectors. Consequently, as the current minimum legal length for

Mangrove Jack is far lower than the size at which this species typically attains maturity and the species has low natural mortality and thus low productivity, managers should consider increasing the MLL to ensure that the fishery can be sustained as fishing pressure increases. However, at the same time, managers will need to take into account the fact that the introduction of such a policy would prohibit many recreational anglers from catching Mangrove Jack, as these anglers fish in nearshore waters where only the juveniles of this species occur. Alternatively, managers might need to consider policies which reduce fishing effort.

- Finally, our study has raised the following very important points regarding the use of the empirical approaches that are currently available for estimating natural mortality for a fish stock. Estimates of natural mortality, M, for fish, which are typically derived from life history information for stocks of other species, are almost invariably imprecise, *i.e.* have very broad confidence limits (Vetter, 1988). This applies to the two threadfin species, the Estuary Rockcod and Malabar Grouper and the Mangrove Jack (see Chapters 4 and 5). Furthermore, the values for natural mortality derived for Estuary Rockcod, Malabar Grouper and Mangrove Jack using traditional models based on the life history characteristics of fish species, exceeded those for total mortality. This is clearly an erroneous result. A major reason for the above imprecision and anomalous results is due to the empirical models, such as that of Pauly (1980), being derived using life history data collected for species at a time when life cycle studies were less rigorous than today. For example, it used to be common to employ the number of growth zones in the hard structures of fish to age those fish without having first validated that these zones were formed annually (Beamish and McFarlane, 1987). Another problem with the data used by Pauly

(1980), for example, is that the species used to provide data often had very divergent life cycle characteristics and came from very different regions, *i.e.* temperate *vs* tropical waters. Yet, in the context of the model of Pauly (1980), the only environmental variable, used as an explanatory factor, was water temperature. It is also relevant that the Pauly (1980) model, for example, assumes a direct relationship between natural mortality and growth and is thus empirical rather than mechanistic.

- From the issues raised above, there is clearly an urgent need to use more contemporary and higher quality data for use as a basis for producing empirical models that will facilitate more precise and reliable estimates of natural mortality for individual fish stocks.

INTELLECTUAL PROPERTY

The value of FRDC's intellectual property will be 48.5%, based on the financial contributions of FRDC and Murdoch University, as described in the project application.