The biology of three teleost species with divergent life cycle characteristics and their implications for fisheries management

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

Submitted by
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I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any university

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ABSTRACT

The overall aim of this thesis was to determine the size and age compositions, growth and reproductive biology of Western Blue Groper (*Achoerodus gouldii*), Blue Morwong (*Nemadactylus valenciennesi*) and Yellowtail Flathead (*Platycephalus endrachtensis*) in south-western Australian waters, in which these three species have divergent life cycle characteristics. As *A. gouldii* and *N. valenciennesi* are commercially and recreationally important in coastal waters and *P. endrachtensis* is one of the most recreationally important species in the Swan River Estuary, these biological data were then used to produce estimates of mortality and spawning stock biomass per recruit for each of these species. The biological data and stock assessment parameters were finally employed comparatively to ascertain whether any of the three species possessed characteristics that would make them particularly susceptible to the effects of fishing and whether there was evidence that any of the species is fully or even overexploited.

*Achoerodus gouldii* typically uses reefs in protected inshore waters along the coast and around neighbouring islands as a nursery habitat and then, as it increases in size, moves to deeper, offshore reefs, where it spawns between early winter and mid-spring. The maximum total length and age of *A. gouldii* were 1162 mm and 70 years, the latter being the greatest age by far yet recorded for any species of labrid. However, most growth occurs in the first 20 years of life. Histological and demographic analyses demonstrated that all individuals begin life as females and, after attaining maturity, many become males, *i.e.* *A. gouldii* is a monandric protogynous hermaphrodite. The *L*₅₀ at maturity and sex change were 653 and 821 mm, respectively, which correspond to ages of c. 17 and 37 years, respectively. As sex change took place over a narrower range in lengths (650 to 900 mm) than in ages (15 to 49 years), that change is apparently related more to size than age. Since sex change is typically accompanied by a change from green to blue, body colour can be
used as a proxy for determining the length ($L_{50}$) at which females change to males. von Bertalanffy growth curves fitted to the lengths at age of individuals of each sex of this hermaphroditic species using a novel technique demonstrated that, with increasing age, the lengths of males became increasingly greater than those of females. Thus, at ages 15, 30 and 60 years, the estimated lengths at age of females were $c.$ 600, 670 and 680 mm, respectively, whereas those of males were $c.$ 695, 895 and 975 mm, respectively.

As $A. gouldii$ is very long-lived and sexual maturity, and even more particularly sex change, occur late, this labrid is potentially very susceptible to overfishing. Thus, because the mortality estimates and per recruit analyses indicated that, at present, this species is close to or fully exploited, fisheries managers will need to take a precautionary and watchful approach to managing and thus conserving the stocks of this species.

As with $A. gouldii$, $N. valenciennesi$ moves to deeper, offshore waters as it increases in size and then matures and spawns in those waters. Although $N. valenciennesi$ has a maximum length of nearly 1 m and thus, like $A. gouldii$, is moderately large, it has a far shorter life span, i.e. 19 vs 70 years. While female $N. valenciennesi$ does not grow to as large a size as its males (max. lengths = 846 and 984 mm, respectively), the maximum age of both sexes was 19 years. From the growth curves, the females by ages 3, 6 and 10 years had attained, on average, lengths of 435, 587 and 662 mm, respectively, compared with 446, 633 and 752 mm, respectively, for males. Both sexes grew little after 10 years of age.

Juvenile $N. valenciennesi <$ 400 mm in total length were found exclusively in shallow, coastal waters on the south coast, whereas their adults were abundant in offshore waters of both the south and lower west coasts. The females and males typically mature in offshore waters of the south coast at lengths of $c.$ 600-800 mm and ages of $c.$ 7-9 years. In contrast, the vast majority of females caught in offshore waters of the lower west coast (where they were of a similar length and age range to those in offshore waters on the south
coast) became mature at lengths of 400-600 mm and 3-4 years of age. The attainment of maturity by *N. valenciennesi* at far lesser lengths and ages on the lower west coast than south coast suggests that the former coast provides better environmental conditions for the gonadal maturation and spawning of this species. Furthermore, the contrast between the almost total absence of the juveniles of *N. valenciennesi* in nearshore waters on the lower west coast and their substantial numbers in comparable waters on the south coast indicates that the larvae of this species produced on the lower west coast are transported southwards to the south coast, where they become juveniles. As spawning occurs between mid-summer and late autumn, the larvae, which spend a protracted period in the plankton, would be exposed, on the lower west coast, to the influence of the southwards-flowing Leeuwin Current at the time when that current is at its strongest.

Although *N. valenciennesi* is caught by recreational line fishing and commercial gillnet fishing when they are as young as 3-4 years old, they do not become fully vulnerable to these fisheries until they are about 9 years old. Consequently, the individuals of this species can potentially breed over a number of years before they become particularly prone to capture by fishers. Mortality estimates and per recruit analyses suggested that *N. valenciennesi* in south-western Australia is not currently overfished. A greater resilience to fishing by *N. valenciennesi* than *A. gouldii* presumably reflects, in part, its far shorter lifespan, earlier maturity and possession of gonochorism rather than hermaphroditism.

*Platycephalus endrachtensis* spawns in the Swan River Estuary between late spring and early autumn and completes the whole of its life cycle in this system. Although females attain a far larger length (615 mm) than males (374 mm), females and males were present in each age class. These data, together with a detailed examination of histological sections of a wide size and age range of individuals, demonstrated that this species, unlike
some of its relatives, is not a protandrous hermaphrodite, \textit{i.e.} it does not change from male to female with increasing body size. The combination of the presence of females and males in all age classes and the observation that all of the large number of individuals between 374 and 615 mm were females shows that the far greater length attained by that sex is largely related to its faster growth rate. The fact that females outnumbered males in each age class of \textit{P. endrachtensis} in which the sample size was substantial, \textit{i.e.} > 25, with the overall sex ratio being 2.7 females: 1 male, indicate that there has been strong selection for egg production in this species. As the minimum legal length for retention of \textit{P. endrachtensis} is 300 mm, and relatively few males exceeded this length, the recreational fishery which targets this species is based largely on its females.

The estimates of mortality and results of per recruit analyses provided no evidence that \textit{P. endrachtensis} is currently overfished. From a management point of view, it is advantageous that the current size limit for this species exceeds the average length at which its females (259 mm) attain maturity. Furthermore, this species appears to be resilient to capture and release.

The data presented in this thesis demonstrate that \textit{A. gouldii} possesses biological characteristics which make it potentially more prone to the effects of fishing than is the case with either \textit{N. valenciennesi} or \textit{P. endrachtensis}. This presumably accounts, at least in part, for the indications that \textit{A. gouldii} is the only one of these three species that is likely to be close to or at full exploitation.
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THREE GREAT YEARS
(Photographs: Peter Coulson, Steve Cossington, Nick Thake)
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CHAPTER 1 - GENERAL INTRODUCTION

1.1 OVERALL AIMS

The overall aim of the research conducted for this thesis was to derive sound quantitative data for the biology of three species, the Western Blue Groper (*Achoerodus gouldii*), Blue Morwong (*Nemadactylus valenciennesi*) and Yellowtail Flathead (*Platycephalus endrachtensis*), which have divergent life cycle characteristics in south-western Australian waters. Although *A. gouldii* and *N. valenciennesi* are relatively large reef-dwelling marine species, the first is a putative protogynous hermaphrodite, while the second is a gonochorist. In contrast to those two marine species, *P. endrachtensis* is essentially confined to the Swan River Estuary in south-western Australia.

Particular attention has been focused on determining the size and age compositions, growth and reproductive biology of the above three species and on ascertaining whether any of these species is fully or over exploited. Comparisons are made between the three species to elucidate some of the key similarities and differences in their biology and whether any interspecific differences in the biology would tend to make a particular species more likely to be susceptible to the effects of fishing and thus influence the approaches that would be most appropriate for their management. The specific aims associated with each of the three species and, where appropriate, hypotheses concerning those species, are given in the respective chapters for those species.

1.2 TEMPERATE REEF ENVIRONMENTS OF WESTERN AUSTRALIA

Following Neira *et al.* (1998), Australian temperate marine waters are regarded as those which lie to the south of Geraldton at 29°S, 114°E on the west coast of Australia and to the south of Coffs Harbour at 30°S, 153°E on the east coast of Australia. This coastline houses five of Australia’s seven largest cities and consequently 90% of Australia’s
population (Kingsford, 1998; Andrew, 1999). As a result, the resources in the coastal waters of Australia’s temperate zone are under pressure from the effects of various forms of coastal developments, pollution, and commercial and recreational fishing (Underwood and Chapman, 1995; Kingsford et al., 1998).

The lower west coast of Western Australia is a region of biogeographical overlap, containing a mixture of Indo-West Pacific tropical and southern Australian temperate species, which reflects, in part, the effects of the warm, southward-flowing Leeuwin Current (Wilson and Allen, 1987; Morgan and Wells, 1991; Pearce, 1991; Wells and Walker, 1993). This coastline is protected from the prevailing winds and swell by the presence of a long stretch of islands and high aspect limestone reefs, which are located in relatively shallow waters and close to the shore (Sanderson et al., 2000). These reefs and those further offshore constitute the main habitat for a number of teleost species, some of which are of recreational and/or commercial importance. These species include the Dhufish *Glaucosoma herbracium*, one of the most important recreational angling and commercial gillnet and long-lining reef species in south-western Australian waters (Fletcher and Head, 2006). Studies by Hesp et al. (2002) demonstrated that this iconic species moves from low-lying reefs to more prominent reefs as it increases in size and approaches maturity. The latter reefs also house the Breaksea Cod *Epinephelides armatus*, which is becoming increasingly heavily fished by recreational fishers (Moore et al., 2007) and also the adults of the King George Whiting *Sillaginodes punctata*, which is targeted by recreational anglers fishing on those reefs (Hyndes et al., 1998).

In contrast to the situation with the lower west coast, the south coast of Western Australia is more strictly a temperate zone and is influenced less by the Leeuwin Current (Semeniuk and Johnson, 1985; Morgan and Wells, 1991). This coast is characterised by the intermittent presence of large granite outcrops and headlands and nearshore low profile
granite reefs. Unlike the lower west coast, its relatively shallow waters do not contain a prominent high aspect reef system which would break the influence of the strong south-west swells found along this coast (Semeniuk and Johnson, 1985; Morgan and Wells, 1991). The reefs in the more offshore waters of this coast are typically located in deep water, reflecting the steeper inshore to offshore gradient in water depth. An exception to the generalisation that the south coast does not contain an extensive shallow reef system is provided by the Esperance region, where the presence of approximately 105 granite islands and 1500 islets, collectively known as the Recherche Archipelago, provides some protection to the coastline (Kendrick et al., 2005). Nearshore and offshore reefs on the south coast represent a crucial habitat for a number of important recreational and/or commercial species, such as *A. gouldii* and *N. valenciennesi*. The work of Shepherd and Brook (2007), which was based mainly on studies conducted in South Australian waters but did extend westwards into those in the Esperance Region, demonstrated that the Western Blue Groper moves from protected inshore to more exposed offshore reef areas as it increases in size.

1.3 THE LABRIDAE

The Labridae is the second largest family of marine fishes and the third most speciose of all perciform families, containing approximately 680 species and 82 genera (Allen et al., 2006a). This family comprises three sub-families, *i.e.* the Labrinae (wrasses), Odacinae (weed whittings) and Scarinae (parrot fishes), the first of which contains 67% of the species recorded for this family (Allen et al., 2006a, b). Although the Labridae occurs in tropical, subtropical and temperate waters worldwide, 82% of its species are found in the Indo-Pacific region, with the largest concentration occurring in Australian waters, where 33% of its species and 70% of its genera are found (Parenti and Randall, 2000). Ninety species of wrasse occur in temperate Australian waters and, unlike their tropical relatives,
many of these, such as the Senator Wrasse *Pitcilabrus laticlavius* and the Maori Wrasse *Ophthalmolepis lineolatus*, are endemic (Jones, 1999). Most labrids live in shallow waters and in the vicinity of reefs or other hard substrates, but a few occupy seagrass and very occasionally sand (Parenti and Randall, 2000; Westneat and Alfaro, 2005; Allen *et al.*, 2006b).

The Labridae is a morphologically and ecologically diverse family of mostly reef-associated marine fishes that are characterised by a particular form of movement, known as labriform locomotion, which involves the use of the pectoral fins as the main source of propulsion when swimming (Webb, 1994). Although labrids range in maximum total length from the 40 mm recorded for *Minilabrus striatus* to the 2300 mm recorded for *Chelinus undulatus* (Nelson, 2006), the majority of species are small, with maximum lengths < 200 mm (Parenti and Randall, 2000; Westneat and Alfaro, 2005; Allen *et al.*, 2006b). The diversity of morphology shown by the members of the Labridae helps account for their ability to live in a range of environments, including coral reefs, rocky reefs, sand and seagrass (Parenti and Randall, 2000; Westneat and Alfaro, 2005; Allen *et al.*, 2006). For example, labrids possess two types of pectoral fin, the first of which is rounded (low aspect-ratio) and characteristic of slow-swimming species that are closely associated with reef structures in deeper, less turbulent waters, while those of the second are tapered (high aspect-ratio) and used for sustained faster swimming by species inhabiting shallow, turbulent waters (Walker and Westneat, 1997, 2002; Bellwood and Wainwright, 2001; Fulton *et al.*, 2001; Wainwright *et al.*, 2002). The success of labrids in many environments is further reflected in their occupation of every feeding guild in reef environments (Westneat and Alfaro, 2005). Some species, such as many tuskfishes, possess robust jaws that are used to crush hard-bodied prey such as urchins and molluscs, whilst, at the other end of the spectrum, lie species with long, slender jaws and protrusable
mouths that are adapted for extracting plankton from the water column or capturing fast-moving prey, such as amphipods or other fish (Wainwright, 1988; Westneat, 2004).

The biology of several wrasse species has been studied in tropical and subtropical waters, where these species are in greatest abundance (e.g. Warner, 1975; Robertson and Warner, 1978; Warner and Robertson, 1978; Ross, 1984; Platten et al., 2002; Choat et al., 2006). Research on wrasses in temperate Australian and New Zealand waters has tended to focus on commercially and recreationally important species, such as Notolabrus fucicola, Notolabrus tetricus, Pseudolabrus celidotus, Achoerodus viridis and Choerodon rubescens (Jones, 1980; Gillanders, 1995a, b, 1997a, b; Denny and Schiel, 2002; Ewing et al., 2003; Welsford, 2003; Welsford and Lyle, 2005; Nardi et al., 2006). Elsewhere, research has been conducted on Semicossyphus pulcher and Tautog onitis on the west and east coasts of temperate Northern America (Cowen, 1985, 1986, 1990; Sogard et al., 1992; Hostetter and Munroe, 1993; Dorf and Powell, 1997), as well as on many small species in the Mediterranean and in northern Europe (Dipper et al., 1977; Dipper and Pullin, 1979; Treasurer, 1996; Sayer et al., 1995, 1996; Cardinale et al., 1998; Pallaoro and Jardas, 2003; Candi et al., 2004).

Most of the labrids that have been studied are protogynous hermaphrodites, i.e. change from females to males (e.g. Robertson and Warner, 1978; Jones, 1980; Andrew et al., 1996). Such species are either monandric (all males are derived from mature females), e.g. Xyrichthys novacula, Choerodon rubescens and Lachnolaimus maximus (Candi et al., 2004; Nardi et al., 2006; McBride and Johnson; 2007) or diandric (males are derived directly from juveniles or from mature females), e.g. Thalassoma lunare, Thalassoma bifasciatum and Thalassoma duperrey (Robertson and Choat, 1974; Ross, 1984; Shapiro and Rasotto, 1993). However, a few species, such as Symphodus ocellatus,
Symphodus melops and Centrolabrus exoletus, are gonochoristic, i.e. do not undergo sex change (Dipper and Pullin, 1979; Bentivegna and Benedetto, 1989).

In temperate waters, labrids range in maximum total length from 138 mm for Ctenolabrus exoletus to 1600 mm for A. gouldii (Hutchins and Swainston, 1986; Sayer et al., 1996), while their maximum ages range from 4 years for C. exoletus to 35 years for A. viridis (Gillanders, 1995a; Sayer et al., 1996), recognising that, until the present study A. gouldii had not been aged.

1.4 BLUE GROPERS (GENUS ACHOERODUS)

The “blue gropers” found in temperate Australian waters are not true gropers, i.e. members of the Serranidae, but are a wrasse (Labrini), i.e. a member of the Labridae. The genus to which they belong, Achoerodus, contains two species, i.e. the Eastern Blue Groper Achoerodus viridis and the Western Blue Groper Achoerodus gouldii. The Eastern Blue Groper is restricted to south-eastern Australian waters between Caloundra in Queensland at 26° 48’ S and Wilson’s Promontory in Victoria at 146° 25’ E, whilst the Western Blue Groper is found throughout southern Australia, southwards from the Houtman Abrolhos at 28° 35’ S on the west coast and eastwards along the south coast to Portland in Victoria at 141° 36’ E (Hutchins and Swainston, 1986; Gommon et al., 1994), but is most abundant on the south coasts of Western Australia and South Australia. Achoerodus gouldii is one of the three species that are the subject of the biological studies reported in this thesis.

The Achoerodus species are distinguished by their possession of prominent fleshy lips (the upper one of which is broad and cowl-like), peg-like teeth and a large body size (Hutchins and Swainston, 1986; Gillanders, 1999). Although A. viridis and A. gouldii are morphologically similar, they can be readily distinguished visually from each other by a number of different features. In the case of the Eastern Blue Groper, the juveniles are green.
when small, but later change to brown to reddish brown as they become adult females, which frequently have a series of pale spots along their sides. The males are grey to blue (Hutchins and Swainston, 1986; Gommon et al., 1994). All life cycle stages *A. viridis* possess blue and orange lines radiating from the eyes (Gillanders, 1999). In contrast, the Western Blue Groper does not possess the latter radiating lines and the adult females and males are green and blue, respectively (Gommon et al., 1994; Gillanders, 1999; Fig. 1.1). Furthermore, the Western Blue Groper reaches a far greater length and weight than the Eastern Blue Groper, *i.e.* 175 cm and 40 kg *vs* 100 cm and 18 kg (Gommon et al., 1994; Gillanders, 1999).

1.5 THE CHEILODACTYLIDAE

The 22 species of the Cheilodactylidae (morwongs), which are found mainly in temperate regions of the southern hemisphere, are characterised by their possession of thick fleshy lips and enlarged pectoral fins in which the lower fin rays are extended (Lowry and Cappo, 1999; Allen et al., 2006c). Cheilodactylids make an important contribution to reef fish populations in New Zealand (Tong and Vooren, 1973; Leum and Choat, 1980; McCormick, 1989a, b), Australia (Branden et al., 1986; Cappo, 1995; Lowry and Suthers, 1998a, b), South Africa, Japan and South America (Nielsen, 1963; Lowry and Cappo, 1999). They attain maximum lengths of between 300 and 1200 mm and have been aged to 97 years (Hutchins and Swainston, 1986; Gommon et al., 1994; Ewing et al., 2007). All three genera in the Cheilodactylidae, namely *Nemadactylus*, *Cheilodactylus* and *Dactylophora*, are represented in waters along the southern coastline of Australia, where nine of the twelve species found in Australian waters occupy habitats from inshore reefs to the continental slope (Allen et al., 2006c).

The fact that few morwong species are highly prized as food accounts for the biology and ecology of only a few of their species having been studied in detail. However,
Figure 1.1. Western Blue Groper *Achoerodus gouldii* at different stages in its life cycle. a) Juvenile (60 mm), b) immature female (300 mm), c) mature female (729 mm) and d) mature male (1008 mm).
there have been several studies of those few species, such as *Nemadactylus macropterus*, *Cheilodactylus fuscus*, *Cheilodactylus spectabilis*, that are commercially and recreationally important in southern Australia and New Zealand (Tong and Vooren, 1973; Smith, 1982; McCormick, 1989a, b; Lowry and Suthers, 1998a, b; Murphy and Lyle, 1999; Jordan, 2001a, b; Lowry, 2003; Ewing et al., 2007; Ziegler et al., 2007).

The Blue Morwong *Nemadactylus valenciennesi*, which is large and brightly coloured, inhabits rocky reefs in southern Western Australian and South Australian waters (Hutchins and Swainston, 1986), is the second species whose biology is the subject of this thesis. This species, identified by its bright blue colour and yellow lines around the eyes, can reach a length of c. 900 mm and a weight of c. 11 kg (Fig. 1.2) (Lowry and Cappo, 1999). Despite the commercial importance of *N. valenciennesi* in southern Western Australia, very little is known about its biology.

![Figure 1.2. Blue Morwong Nemadactylus valenciennesi, showing the central blue and surrounding yellow of the eye that are characteristic of this species, and the thick fleshy lips and enlarged pectoral fins, in which the lower fin rays are extended, which are characteristic of the Cheilodactylidae.](image_url)
1.6. FISHERIES FOR *ACHOERODUS GOULDI* AND *NEMADACTYLS VALENCIENNESI*

*Achoerodus gouldii* and *Nemadactylus valenciennesi* both make an important contribution to the combined commercial scale fish catches of the West Coast Demersal Gillnet and Demersal Longline Managed Fishery (WCDGDLF) and Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery (JASDGDLF) in south-western Australia (McAuley and Simpfendorfer, 2003). These fisheries are divided into six regions, ranging in location from the easternmost one on the south coast, *i.e.* region 1, to the northernmost on the west coast, *i.e.* region 6 (Fig. 1.3). Between 1994 and 1999, *N. valenciennesi* and *A. gouldii* made, on average, the first and third largest contributions, *i.e.* 25% (49t) and 15% (30t), respectively, to the total combined annual landings of the two fisheries (McAuley and Simpfendorfer, 2003). *Nemadactylus valenciennesi* was the most important component of the scale fish catch in regions one, two and three and the second most important in regions four and five. *Achoerodus gouldii* was the second most important scale fish in regions one, two and three and the third and fifth most important scale fish in regions four and five (McAuley and Simpfendorfer, 2003). However, in region six, the most northern region, *N. valenciennesi* and *A. gouldii* account for only 1.1 and 1.4% of the catch, respectively (McAuley and Simpfendorfer, 2003), reflecting the fact that these two species have an essentially southern Australian distribution (Hutchins and Swainston 1986; Gommon, 1994). Current (2007) market fillet prices for Western Blue Groper and Blue Morwong are both c. AUS $25 per kg.

Although *A. gouldii* is taken by recreational line and spear fishers, this iconic species is not allowed to be included in weigh-ins at the majority of large fishing competitions in Western Australia because it is considered particularly vulnerable to overexploitation by fishers (pers. obs.). In Western Australia, the current size limit for
Figure 1.3. Boundaries of the six fishing regions of the West Coast Demersal Gillnet and Demersal Longline Fishery (WCDGDLF) and the Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery (JASDGDLF) on the lower west and south coasts of Western Australia. Black circles denote regions where *Achoerodus gouldii* and *Nemadactylus valenciennesi* were sampled. Figure adapted from McAuley and Simpfendorfer (2003).
A. gouldii is 500 mm and the daily bag limit is 1 fish per angler (Anon., 2005a). In South Australia, where the Western Blue Groper is protected from all forms of fishing in Spencer Gulf, Gulf St. Vincent, Backstairs Passage and Investigator Strait, a minimum and maximum size limit of 600 and 1000 mm, respectively, and a daily bag limit of 2 fish per angler apply in all other areas where fishing is allowed (Anon., 2006). In New South Wales, the Eastern Blue Groper A. viridis was protected from all methods of fishing between 1969 and 1974, after which this species could be taken only by recreational line anglers (Gillanders, 1999). Currently there is a minimum legal length for retention (MLL) of 300 mm for A. viridis and a daily bag limit of two fish per angler per day in New South Wales, with only one of these allowed to exceed 600 mm (Anon., 2005b).

Nemadactylus valenciennesi was the second, third and fourth most retained species (by weight) by anglers on recreational charter fishing vessels operating on the south coast of Western Australia in 2002/2003, 2003/2004 and 2004/2005, respectively (Johnson and Lai, 2006a), while, on the west coast of this state, it was the fifth most retained species in 2002/2003 and 2003/2004 and sixth most retained species in 2004/2005 (Johnson and Lai, 2006b). Nemadactylus valenciennesi is currently managed using a minimum size limit for retention of 410 mm and a daily bag limit of 4 fish per angler in Western Australian waters and a minimum size limit for retention of 380 mm and a daily bag limit of 5 fish per angler in South Australian waters (Anon. 2005a, 2006).

1.7 ESTUARY DEFINITIONS

There have been numerous definitions of estuaries since Odum (1959) described estuaries as a “river mouth where tidal action brings about a mixing of salt and freshwater”. Pritchard (1967) described estuaries as “semi-enclosed bodies of water which have a free connection with the open sea and within which sea water is measurably diluted by fresh water from land drainage” and Fairbridge (1980) based his definition on tidal
action. These definitions were derived, however, from studies of those estuaries in temperate regions of the northern hemisphere that are permanently open to the ocean and experience strong tidal currents (Elliott and McLusky, 2002). They thus do not take into account the particular characteristics of southern hemisphere estuaries, especially those of South Africa and southern Australia. The definition of an estuary was thus subsequently modified by Day (1980) to take into account the fact that, when there is little freshwater discharge during dry periods, sand bars often form at the mouth of these estuaries and salinities, through evaporation, sometimes exceed that of sea water (Whitfield, 1998). Day (1980) thus defined estuaries as “a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from the land”. Most of the estuaries of south-western Australia, and particularly those along its south coast, become seasonally or permanently closed and are thus land-locked at such times (Ranasinghe and Pattiaratchi, 2003).

1.8 SWAN RIVER ESTUARY

The Swan River Estuary, which is located on the lower west coast of Australia at c. 32°S, is the second largest estuary in south-western Australia, covering an area of approximately 55 km². The Swan River Estuary is one of only seven of the 80 estuaries on the coast of south-western Australia that remain permanently open to the ocean (Hodgkin and Lenanton, 1981; Lenanton and Hodgkin, 1985; Hodgkin and Hesp, 1998). This estuary extends for 60 km from Fremantle at its mouth to Ellen Brook in the upper Swan Avon River and to Kent Street Weir 6 km upstream in the Canning River and it draws water from a catchment of approximately 120,000 km² (Hodgkin and Hesp, 1998; Pen, 1999; Brearley, 2005). A port was constructed in the mouth of the Swan River Estuary in 1892 to 1897. This involved blasting away the rock bar at the entrance of the estuary and dredging to
make that entrance wider and deeper and thus able to accommodate international shipping (Brearly, 2005).

The Swan River Estuary comprises the following three main regions: 1) The lower estuary, which comprises a 7.5 km long narrow entrance channel that extends from the estuary mouth to the first of two large shallow basins. Its maximum depth of 11 m is found in the harbour at the mouth. 2) The middle estuary, which consists of two large basins (Melville Water and Perth Water) that are 4 and 1.5 km in width, respectively. Although the depth of Melville Water reaches 21 m, it is typically < 6 m. Perth Water is on average 1-2 m deep. 3) The upper estuary, which has maximum and average depths of 5 and 2-3 m, respectively, comprises the saline lower reaches of the Swan-Avon River and Canning Rivers that flow into Perth Water and Melville Water, respectively (Spencer, 1956; Potter and Hyndes, 1994; Stephens and Imberger, 1996; Hodgkin and Hesp, 1998).

The Mediterranean climate of south-western Australia, with warm, dry summers and cool, wet winters results in rainfall, and thus also fresh water input, being highly seasonal, with maximum discharge occurring in winter, i.e. May to September (Spencer, 1956; Hodgkin and Hesp, 1998). Since the dredging of what is now Fremantle Harbour, the tidal range in the mouth of the estuary has increased from < 20% to 80% of that of the ocean (Hodgkin and Hesp, 1998). However, although the Swan River Estuary has a free connection with the ocean, the mean and maximum daily tidal range is only 0.4 and 1.1 m, respectively, and thus tidal action within the estuary is limited (Spencer, 1956; Hodgkin, 1974; Stephens and Imberger, 1996).

The many modifications, such as dredging, land clearing, bridge construction and land reclamation that have occurred in the Swan River Estuary and its catchment since European settlement have led to increased runoff, higher maximum flows, sedimentation, eutrophication and salinisation of the upper regions of the estuary (Harris, 1996; Pen,
More recently, increased eutrophication of the estuary has been reflected in a greater frequency of algal blooms and, on occasions, these have had devastating effects on fish populations, particularly in the upper regions of the estuary (Hosja and Deeley, 1994; Smith, 2006). For example, 7.1 t of dead fish, including 200,000 Black Bream, *Acanthopagrus butcheri*, were collected from this region during the “clean up” after an algal bloom in 2003 (Smith, 2006).

The commercial fish catch in the Swan River Estuary has declined dramatically since 1973, when catches peaked at 322 tonnes (Smith, 2006). This largely reflects the decline in the number of licensed commercial fishers operating in the Swan River Estuary, with the number of vessels registered for fishing falling from 30 in the 1960s and 1970s to just two vessels in 2007 (Smith, 2006; K. Smith, pers. comm.). The most common commercial fish species include the Sea Mullet (*Mugil cephalus*), Yelloweye Mullet (*Aldrichetta forsteri*), Perth Herring (*Nematolosa vlaminghi*), Cobbler (*Cnidoglanis macrocephalus*), Black Bream (*Acanthopagrus butcheri*), Tailor (*Pomatomus saltatrix*), Yellowfin Whiting (*Sillago schomburgkii*) and the Blue Swimmer Crab (*Portunus pelagicus*) (Smith, 2006).

1.9 ESTUARINE FISH FAUNAS

Estuaries are unique transitional environments that connect rivers with the ocean and in which marine, estuarine and freshwater species may all be found. They provide highly productive environments, which are utilised as nursery areas by the juveniles of many fish species and particularly those of certain marine species (Blaber and Blaber, 1980; Kennish, 1990; Potter and Hyndes, 1999; Elliott *et al.*, 2007). Although the adults of some fish species are found in estuaries, very few species complete their entire life cycle within these systems, at least in temperate regions of the Northern Hemisphere (Claridge *et al.*, 1986; Elliott *et al.*, 2007). Despite the benefits that estuaries provide to their
permanent and transitory residents, these species must be able to cope with the highly variable salinities, temperatures, currents, turbidity, oxygen levels and, in some cases, extreme tidal movements that are found in these systems (Day, 1981; Elliott and McLusky, 2002).

Many authors have allocated these fish species that are present in estuaries at some point during their life to categories or guilds that best represent the ways in which they “use” estuaries (e.g. Cronin and Mansueti, 1971; Claridge et al., 1986; Kennish, 1990; Potter and Hyndes, 1999; Elliott et al., 2007). Potter and Hyndes (1999) thus categorised the species found in temperate estuaries, and in particular those of south-western Australia, in the following manner. The marine species were divided into two categories, i.e. those that are present regularly and usually in large numbers in estuaries and typically as juveniles (marine estuarine-opportunists), and those that occur irregularly and generally in low numbers, and typically in the lower reaches of estuaries (marine stragglers). The estuarine species, i.e. those that complete their life cycle in estuaries, comprise two categories, i.e. those that are found only in estuaries (estuarine) and those that are also represented by discrete populations in coastal waters outside the estuary (estuarine & marine). There are also three migratory groups, i.e. anadromous, semi-anadromous and catadromous. The semi-anadromous and anadromous species spend the majority of their lives in the marine environment and, at the approach of maturity, enter rivers and migrate to upstream areas where they spawn in the brackish regions of the estuary and in the freshwaters beyond the limits of the estuary, respectively. In contrast, catadromous species typically live in the freshwater regions of rivers and, as they approach maturity, migrate through the estuary to the ocean where they then spawn. Freshwater species are typically found only in the upper reaches of estuaries, where the salinity is relatively low.
The contributions that the members of each life cycle category or guild make to estuarine fish faunas vary among estuaries, and especially between those of temperate south-western Australian and temperate regions of the Northern Hemisphere. However, although a number of marine species utilise estuaries of both regions, and particularly during their juvenile phase (e.g. Chubb et al., 1981; Claridge et al., 1986; Elliot and Dewaily, 1995), the number of species that complete their life cycles in the macrotidal estuaries that are typical of temperate regions of the Northern Hemisphere (e.g. Haedrich, 1983; Claridge et al., 1986; Kennish, 1990; Elliott et al., 2007) is less than in the microtidal estuaries that are found in south-western Australia (Loneragan et al., 1986; Potter et al., 1990; Valesini et al., 1997; Young et al., 1997). The greater abundance in south-western Australian estuaries of a number of estuarine species, such as the Black Bream *Acanthopagrus butcheri* and the Western Hardyhead *Leptatheria wallacei* (Prince et al., 1982; Potter et al., 1986; Laurenson et al., 1993; Sarre and Potter, 1999), has been considered to reflect adaptations that were evolved in response to the tendency of these estuaries to become closed off from the ocean by the sand bar that forms at the estuary mouth during periods of low flow (Day, 1980).

It has been estimated that 75% of commercially important fish species of North America are dependent on estuaries in one way or another (McHugh, 1976; Chambers, 1992). Species with some degree of estuarine dependency make similar contributions to commercial fisheries operating in eastern Australia (Newell and Barber, 1975; Pollard, 1976, 1981). An analysis of commercial catch data by Lenanton and Potter (1987) for the years between 1976 and 1984 demonstrated that the collective weight of fish, crustaceans and molluscs that typically use estuaries during at least one point in their life cycle contributed 12.1% to the total weight from all of these three sources in Western Australia.
1.10 THE PLATYCEPHALIDAE

The Platycephalidae, which comprises c. 65 species that represent 18 genera, is found in estuarine and coastal waters throughout mainly the Indo-Pacific region (Nelson, 2006). Forty four of these flathead species, belonging to 15 genera, occur in Australian waters, 17 of which are endemic (Knapp, 1984; Keenean, 1991; Paxton et al., 2006). The genus Platycephalus contains 14 of the species found in Australian waters (Paxton et al., 2006). In Western Australia, all but one of the nine Platycephalus species found in this state live in protected inshore regions and/or estuaries (Hutchins and Swainston, 1986; Hyndes et al., 1992b).

The species of the Platycephalidae are small to medium-sized benthic fish, which possess a greatly depressed head (Keenan, 1991). These carnivorous species have a dorso-ventrally flattened body and are well camouflaged which allows them to burrow and remain concealed in the sediment and to ambush prey (Gommon et al., 1994).

Although a number of studies have shown that species within the genera Ingocia, Onigocia and Kumococius are protandrous hermaphrodites, i.e. undergo male to female sex change (Aoyama et al., 1963; Okada, 1966, 1968; Fujii, 1970, 1971, 1974; Shinomiya et al., 2003), there is no evidence that members of the genus Platycephalus are hermaphroditic (Lewis, 1971; Hyndes et al., 1992b; Jordan, 2001b). The only biological study of platycephalids in West Australian waters is that conducted by Hyndes et al. (1992a, b) on the Southern Blue-Spotted Flathead Platycephalus speculator (for details see Introduction to Chapter 5).

Many of the platycephalids inhabiting coastal lagoons and estuaries, such as Platycephalus fuscus, P. speculator, P. endrachtensis (Lenanton and Potter, 1987; Gray et al. 2002; Smith, 2006), and those found in coastal and offshore marine waters, such as Neoplatycephalus conatus, Platycephalus richardsoni and Platycephalus bassensis
(Burnell and Newton, 1989; Kailola et al., 1993; Lyle and Jordan, 1998), are targeted by recreational and commercial fishers. A recent Australia-wide creel survey highlighted the importance of platycephalids and estuaries to recreational fishing, with the species in this family accounting for 12% (by number) of the entire recreational finfish catch and with 57% of those flathead being caught in estuaries (Henry and Lyle, 2003).

The Yellowtail Flathead *Platycephalus endrachtensis*, which is readily distinguished by the yellow blotch and three black bars present on its caudal fin, reaches a maximum length of 1000 mm (Hutchins and Swainston, 1986; Fig. 1.4). Although *P. endrachtensis*, which is distributed across northern Australia and in New Guinea (Allen, 1997), is essentially a tropical species, it is found as far south as the Swan River Estuary, within which it is abundant and apparently completes its life cycle (Potter et al., 1990; Potter and Hyndes, 1999). This species is absent or rarely found in marine waters between the Swan River Estuary (c. 32ºS) and Shark Bay (c. 26ºS) (Ayvazian and Hyndes, 1995; Valesini et al., 2004) where, in the absence of estuaries, it is found in the waters of this large subtropical embayment (Lenanton, 1977).

![Figure 1.4](image.png)

**Figure 1.4.** Yellowtail Flathead, *Platycephalus endrachtensis*. The yellow blotch and three black bars on the caudal fin is a characteristic of this species and the dorso-ventral flattened body is a characteristic of the Platycephalidae. Photo by P. McKeown.
Although commercial landings of *P. endrachtensis* in the Swan River Estuary rose to as much as 5 tonnes in 1945 (Smith, 2006), the commercial catches of this species are now mainly restricted to those taken as by-catch when gill netting for Black Bream *A. butcheri*, Sea Mullet *M. cephalus* and Blue Swimmer Crab *P. pelagicus* (pers. obs.). *Platycephalus endrachtensis* is, however, one of the fish species most commonly retained by recreational anglers in the Swan River Estuary, in which the minimum length for its retention is 300 mm and the bag limit is 8 fish per angler (Henry and Lyle, 2003; Smith, 2006). Despite its recreational importance, very little is known about the biology of *P. endrachtensis* and how this species uses estuaries.
CHAPTER 2 - GENERAL MATERIALS AND METHODS

2.1 SAMPLING

_Achoerodus gouldii_ and _Nemadactylus valenciennesi_ were collected from coastal waters off the south coast, including Albany, Bremer Bay Hopetoun and Esperance, and lower west coast, including Perth, of Western Australia, while _Playcephalus endrachtensis_ was obtained from the Swan River Estuary on the lower west coast of Australia. Details of the sampling regime and specific aspects of the details of the biological studies of each species are given in the subsequent chapters that deal individually with these species.

Offshore sea surface temperatures (SST) were derived from NOAA-AVHRR satellite imagery, complemented by surface temperatures recorded by shipping and drifting buoys since 1982 (Reynolds and Smith, 1994). SSTs for each 1° latitude/longitude grid square for offshore waters from Perth, Albany and Esperance were taken from the grid squares 31°S to 32°S and 115°E to 116°E, 34°S to 35°S and 118°E to 119°E and 34°S to 35°S and 122°E to 123°E, respectively. The corresponding monthly SSTs for 2004, 2005 and 2006 were averaged. Water temperatures for some months in inshore waters at Albany and Esperance during the current study were limited. Thus, the water temperatures recorded at irregular intervals, by the Department of Fisheries, Western Australia, over a longer period, _i.e._ 1994 to 2006, were pooled and the average for each calendar month calculated. The water temperature and salinity at each site in the Swan River Estuary on each sampling occasion were recorded to the nearest 0.1°C and 0.1‰, respectively, using a Yellow Springs Instruments YSI-30 salinity and conductivity meter.

2.2 LENGTH AND WEIGHT MEASUREMENTS

Each fish was sexed when its gonad could be identified macroscopically as an ovary or testis. The total length (TL) and wet weight (W), and also the wet weight of the gonad when the sex could be determined, were recorded to the nearest 1 mm, 0.1 and
0.01 g, respectively, for each individual of each species. The $TL$ vs $W$ relationships for the females and males of each species were compared using analysis of covariance (ANCOVA) and employing the natural logarithm of weight as the dependent variable, sex as the fixed factor and the natural logarithm of length as the covariate. The relationship between $TL$ and $W$ was used, in the case of each species, to estimate the weights of filleted fish that had been collected from fish processors and recreational fishers and which had not been weighed.

2.3 AGE DETERMINATION AND GROWTH

The increasing thickness of the otoliths of $A. gouldii$, $N. valenciennesi$ and $P. endrachtensis$ as these species increased in size and age meant that the otoliths of all individuals of the three species required sectioning in order to reveal all of their opaque zones (Figs 2.1, 2.2, 2.3). One of the sagittal otoliths of each individual of each species was embedded in clear epoxy resin and cut transversely through its primordium into c. 0.3 mm sections using an Isomet Buehler low-speed diamond saw. The sections were polished on wet and dry carborundum paper (grade 1200) and mounted on microscope slides using DePX mounting adhesive and a cover slip. Images of each sectioned otolith were photographed under transmitted light using an Olympus DP70 camera mounted on an Olympus BX51 compound microscope.

Validation that a single opaque zone is formed annually in the otoliths of each species was carried out using marginal increment analysis. The marginal increment, $i.e.$ the distance between the outer edge of the single or outermost opaque zone and the outer edge of the otolith, was expressed as a proportion of the distance between the primordium and the outer edge of the single opaque zone, when only one such zone was present, or as the distance between the outer edges of the two outermost opaque zones when two or more opaque zones were present. All measurements, which were taken along the same axis and
Figure 2.1. The whole and corresponding sectioned otoliths of a 456 mm *Achoerodus gouldii* with six opaque zones (a, b) and an 851 mm *A. gouldii* with 32 opaque zones (c, d). Yellow circles in (a) and (b) indicate position of each single opaque zone and in (d) indicate the position of every tenth opaque zone. Dashed lines indicate the transverse plane in which otoliths were sectioned. **D, dorsal surface; p, primordium; v, ventral surface. Scale bars = 0.5 mm.**
Figure 2.2. The whole and corresponding sectioned otoliths of a 494 mm *Nemadactylus valenciennesi* with three opaque zones (a, b) and an 860 mm *N. valenciennesi* with 12 opaque zones. (c, d) Yellow circles in (a), (b) and (d) indicate position of each single opaque zone. Dashed lines indicate the transverse plane in which otoliths were sectioned. d, dorsal surface; p, primordium; v, ventral surface. Scale bars = 0.5 mm.
Figure 2.3. The whole and corresponding sectioned otoliths of a (a, b) 281 mm *Platycephalus endrachtensis* with 1 opaque zones and an (c, d) 550 mm *P. endrachtensis* with 6 opaque zones. Yellow circles in (b) and (d) indicate position of each single opaque zone. Dashed lines indicate the transverse plane in which otoliths were sectioned. d, dorsal surface; p, primordium; v, ventral surface. Scale bars = 0.5 mm.
perpendicular to the opaque zones, were recorded to the nearest 0.01 mm employing the imaging package Leica Image Manager 1000 (Leica Microsystems Ltd, 2001). The marginal increments for the corresponding months of the different years were pooled for various groups of otoliths, categorised on the basis of their numbers of opaque zones. The mean monthly marginal increments and their standard errors for each of those groups were then calculated.

Leica Image Manager 1000 was used to help count the number of opaque zones in an image of each sectioned otolith on two occasions, and also on a third occasion if the first two counts were not the same. In the latter situation, two of the three counts were the same in 100% of *N. valenciennesi* and *P. endrachtensis* and in *A. gouldii* with otoliths containing < 30 opaque zones and c. 95% for otoliths of the latter species with ≥ 30 opaque zones. In those few instances when all three counts for the third species differed, the final count was considered likely to be the most reliable, noting that this count never differed by more than two from either of the other two counts.

Each fish was assigned an age, based on the number of opaque zones in its otoliths, but taking into account the timing of delineation of those zones, the date of capture of the fish and the estimated average birth date for the members of the population. The birth dates assigned to *A. gouldii*, *N. valenciennesi* and *P. endrachtensis*, which were taken as the approximate mid-point of the spawning period for each species, were 1 August, 1 March and 1 January, respectively (see Results in relevant chapters).

von Bertalanffy growth curves were fitted to the lengths at age of the females and males of *N. valenciennesi* and *P. endrachtensis* using SPSS Inc. (2001). The von Bertalanffy growth equation is

\[ L_t = L_\infty (1 - \exp(-kt \cdot t)) \]

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

Although the sex of *P. endrachtensis* > 100 mm (TL) during the spawning period could be determined macroscopically, this could not be achieved with fish caught outside the spawning period until they had reached a length of c. 150 mm. The lengths at age of those individuals whose sex could not be determined were allocated alternately to the female and male *P. endrachtensis* data sets used for calculating the von Bertalanffy growth curves.

von Bertalanffy growth curves were fitted to the lengths at age of *A. gouldii* in the cases of (a) all fish irrespective of their sex, (b) females and males that had been sexed on the basis of gonadal type and (c) those that were green and blue among individuals used for von Bertalanffy growth curves for each sex in (b). Growth curves were next fitted to the lengths at age of sexed females and males, but including the lengths at age of all unsexed fish that were assigned to a sex after assessing the probability that, on the basis of their length and colour (see later), a fish would be either female and male. See section 3.2 for further details for the treatment of ageing data for *A. gouldii*.

A likelihood-ratio test was used to compare the growth curves of the two sexes of *N. valenciennesi* and *P. endrachtensis* and of *A. gouldii* and *N. valenciennesi* in different regions. Details of the particular comparisons of growth made for each species are given in the materials and methods of the separate chapters for those species.

When comparing growth curves between either sexes or individuals in different regions, the difference between the log-likelihoods obtained by fitting a common growth curve to the data for the two groups and by fitting separate growth curves for each group was calculated, and the resultant value multiplied by two. The hypothesis that the growth of the two groups could appropriately be represented by a single growth curve was rejected.
at the $\alpha = 0.05$ level of significance if the above test statistic exceeded $\chi^2_{\alpha}(q)$, where $q$ is the difference between the numbers of parameters in the two approaches, i.e. 3 (Cerrato, 1990). The log-likelihood, $\lambda$, for each curve, ignoring constants, was calculated as $\lambda = (n/2)\ln(ss/n)$, where $n$ refers to the sample size and $ss$ refers to the sum of the squared residuals between the observed and expected lengths at age.

2.4 REPRODUCTIVE VARIABLES

On the basis of their macroscopic characteristics, the gonads of each fish that could be sexed were allocated to one of eight maturity stages: I/II = virgin and immature/resting; III = developing; IV = maturing; V = prespawning; VI = spawning; VII = spent and VIII = recovering, which were adapted from the criteria described by Laevastu (1965). Note that however no individuals of $A. gouldii$ and $N. valenciennesi$ were found containing stage VIII gonads. The characteristics of each macroscopic stage in the development of the ovaries of $A. gouldii$ and the ovaries and testes of $N. valenciennesi$ and $P. endrachtensis$ and the corresponding histological stage in the development of the ovaries of the three species are presented in their respective chapters. Mean monthly gonadosomatic indices (GSIs) for the females of $A. gouldii$ and of both sexes of $N. valenciennesi$ and $P. endrachtensis$ were calculated using the equation $GSI = W_1/W_2 \times 100$, where $W_1 =$ wet gonad weight and $W_2 =$ wet body weight and employing fish with lengths $\geq$ their respective $L_{50}$s at maturity (see Results in relevant chapters). In each month of sampling, gonads from a subsample of the females and males of each species and which encompassed all gonad stages recorded in that month were placed in Bouin’s fixative for 24 to 48h. The gonads were dehydrated in a series of increasing concentrations of ethanol and their mid-regions embedded in paraffin wax and then cut into 6 µm transverse sections and stained with Mallory’s trichrome. The sections were examined using a compound microscope to (1)
ensure that individuals of each species had been sexed correctly and, in the case of *A. gouldii*, to determine whether a gonad contained both ovarian and testicular material, (2) ensure that the macroscopic assignments to maturity stages were appropriate, (3) determine whether each of these species had determinate or indeterminate fecundity and (4) help elucidate whether *A. gouldii* and *P. endrachtensis* are hermaphroditic.

The lengths at which 50% of the females of *A. gouldii* and 50% of both the females and males of *N. valenciennesi* and *P. endrachtensis* attained maturity (*L*<sub>50</sub>) were determined by fitting logistic curves to the probability that, during the spawning period, a female fish at a specific length would possess gonads at one of stages III to VIII. As such, fish were potentially destined to become mature or had reached maturity during that period, they are, for convenience, subsequently referred to as mature (see Results). The form of the logistic equation used for this analysis is \( P = \frac{1}{1+\exp\left[-\log_e(19)\left(\frac{L-L_{50}}{L_{95}-L_{50}}\right)\right]} \), where \( P \) = proportion mature, \( L \) = total length in mm, and \( L_{50} \) and \( L_{95} \) = the length in mm at which 50 and 95% of fish were mature, respectively. On the basis of its length, the likelihood of the \( j \)th fish possessing or not possessing gonads at a stage \( \geq \) III was calculated as \( P_j \) or \( 1-P_j \), respectively. Setting \( X_j = 0 \), if the \( j \)th fish did not possess gonads at stage \( \geq \) III, and \( X_j = 1 \), if it did possess such gonads, the overall log-likelihood was calculated as \( \sum_j \left[ X_j \log_e P_j + \left(1-X_j\right)\ln\left(1-P_j\right)\right] \). The logistic equation was fitted using Markov Chain Monte Carlo simulation in WinBUGS (from 500,000 iterations, discarding the first 1,000 iterations as the initial burn in set and using a thinning interval of 100). After assessment in WinBUGS that convergence was likely to have been achieved, the point estimates and associated 95% confidence intervals of the parameters of the logistic equation, and of the probabilities of fish being mature at a range of specified lengths, were determined as the medians and the 2.5 and 97.5 percentiles of the estimates produced by WinBUGS.
2.5 FECUNDITY

To ascertain whether *A. gouldii*, *N. valenciennesi* and *P. endrachtensis* have determinate or indeterminate fecundity *sensu* Hunter and Macewicz (1985) and Hunter *et al.* (1985), the distribution of the diameters of 100 randomly-selected oocytes in histological sections of stage V ovaries of each of two females of each species were plotted. A fish species with determinate fecundity is one in which the total fecundity is determined prior to the onset of the spawning period, whereas a fish species with indeterminate fecundity is one in which this is not the case. The diameter of each oocyte was derived from measurements made of the circumference of that oocyte to the nearest 0.01 µm using the computer imaging package Leica IM 1000 (Leica Microsystems Ltd. 2001). Note that measurements were restricted to oocytes in which the nucleus was clearly visible to ensure that the oocyte had been sectioned through its centre. The stage in the development of each measured oocyte was recorded, *i.e.* early previtellogenic, cortical alveolar or yolk granule oocyte.

For determining the batch fecundity of *A. gouldii*, *N. valenciennesi* and *P. endrachtensis*, each of the two ovarian lobes of females with stage VI ovaries, which contained hydrated oocytes scattered throughout the ovary, was weighed to the nearest 0.1g. One of these ovarian lobes was preserved in 10% neutrally buffered formalin and used for calculating batch fecundity. The other lobe was preserved in Bouin’s fixative and prepared, sectioned and stained in the same way as described earlier (section 2.4). The resultant histological sections were then used to confirm that 1) no newly-formed post-ovulatory follicles were present (*i.e.* spawning had commenced or recently occurred), 2) hydrated oocytes were not concentrated in the ovarian duct (*i.e.* ovulation and thus possibly spawning had commenced) and 3) that, as fish can produce a small number of hydrated oocytes in ovaries undergoing atresia, which are most likely to be unviable,
atresia of yolked oocytes was limited to only a small percentage (< 10%) of these oocytes (Hunter et al., 1992; Nichol and Acuna, 2001; Hesp et al., 2003). In other words, the number of hydrated oocytes in the ovaries of a female represented the true batch fecundity for that individual at the time of its capture. Note that most of the stage VI ovaries of the three species could not be used for fecundity estimates as the majority of fish with such ovaries had been caught by commercial fishermen and then frozen and were thus not suitable for the counting of their eggs.

The ovarian lobes that had been preserved in 10% neutrally buffered formalin were blotted dry with paper towel and weighed to the nearest 1 mg. Approximately 75-100 mg of tissue was then removed from the anterior, middle and posterior regions of each ovary and weighed to the nearest 0.001 mg. The ovarian tissue was placed in Petri dishes and covered in 100% glycerol. The tissue was teased apart under a dissecting microscope using probes and the number of its hydrated oocytes recorded. The number of hydrated oocytes in each of the three regions of the ovarian lobe that was processed from a fish was then used, in conjunction with their weights and that of the other ovarian lobe, to estimate the total number of hydrated oocytes (batch fecundity) in the ovaries of that fish (Hunter and Macewicz, 1985; Hunter et al., 1985).

2.6 ESTIMATES OF MORTALITY

The total mortality, $Z$, for $A. gouldii$, $N. valenciennesi$ and $P. endrachtensis$ was estimated by fitting catch curves simultaneously to the age composition data for each of those species in the different years, assuming that this mortality and annual recruitment were constant. As $A. gouldii$ exhibited variable recruitment (see Results) it also employed relative abundance analysis, which is an extension of catch curve analysis (Deriso et al., 1985) and allows for the possibility that annual recruitment is variable. The analyses for the first two species used data obtained from the commercial gillnet fishery on the lower
west and south coasts, while those for *P. endrachtensis* employed data obtained from recreational rod and line, commercial gillnet and research seine net fishing in the Swan River Estuary. The analyses for each species (except *N. valenciennesi*, see later) assumed knife edge recruitment into the fishery, and were therefore restricted to data for the descending limbs of the catch curves (Ricker, 1975). Total mortality was estimated for both sexes combined in the case of the protogynous *A. gouldii* and the gonochoristic *N. valenciennesi*, for which the lengths attained by the two sexes were not markedly different. In contrast, as the females of *P. endrachtensis* grew to a far greater size than their males, Z was estimated separately for each sex of this species.

Total mortality was estimated in the following manner. For a fish stock that experiences a constant level of Z from the age of full recruitment, \( a = t_c \) years, the estimated proportion \( \hat{P}_{a,t} \) at age \( a \) in year \( t \) is

\[
\hat{P}_{a,t} = \frac{R_{t,a} \exp[-(a-t_c)Z]}{\sum_{j=t_c}^{A} R_{t,j} \exp[-(j-t_c)Z]},
\]

where \( A \) is the maximum observed age. It is assumed that the age composition of fish with ages \( t_c \leq a \leq A \) observed in year \( t \) represents a random sample from a multinomial distribution with uniform selectivity from the age of full recruitment and thereby overcomes the problem of applying a log transformation to the frequencies for older age classes with zero fish. Thus, ignoring constants, the log-likelihood \( \lambda \) of the age compositions observed in the various years may be calculated as,

\[
\lambda = \sum_{t} \sum_{a=t_c}^{A} n_{a,t} \log[\hat{P}_{a,t}],
\]

where \( n_{a,t} \) is the observed number of fish of age \( a \) in year \( t \). Microsoft Excel was used to estimate Z for each of the three species by maximizing the log-likelihood, with the assumption that recruitment was constant.

For estimating Z for *A. gouldii*, when assuming variable recruitment, the average level of recruitment for each of the different year classes was initially set to a value of 1.
The relative levels of recruitment of the different year classes were then, one by one, successively introduced as additional parameters to be estimated by the model, which involved estimating $Z$ and a relative level of recruitment, $R_y$, for each candidate year class, $y$, in Microsoft Excel. The resulting log-likelihoods associated with these year classes were compared and the year class that produced the greatest increase in the log-likelihood was determined. A likelihood-ratio test was used to determine whether the difference between the log-likelihood after introducing the parameter $R_y$ for this year class and that obtained prior to introducing this parameter was statistically significant (e.g. Cerrato, 1990). If so, the parameter $R_y$ for this year class was included as a parameter to be estimated in the model. This forward selection algorithm was then repeated, estimating $Z$ and values of $R_y$ for year classes already included in the model, to determine whether further year classes should be included (e.g. Sokal and Rohlf, 1995). The process was terminated when introduction of $R_y$ as a parameter to be estimated for any further year class failed to produce a statistically significant improvement in the fit of the model to the data, as determined using the likelihood-ratio test. At this stage, the relative levels of recruitment for year classes not included as parameters to be estimated in the model continued to be constrained to the average level.

In the case of *N. valenciennesi* and *P. endrachtensis*, the 95% confidence intervals for $Z$ (determined assuming constant recruitment) were estimated through resampling, with replacement, *i.e.* bootstrapping. The age composition data for each species were randomly resampled to produce 1000 sets of bootstrap estimates for $Z$. The 95% confidence intervals were determined as the 2.5 and 97.5 percentiles of the corresponding estimated values. As it was not practical to use bootstrapping to estimate the 95% confidence intervals for $Z$ for *A. gouldii*, when assuming variable recruitment, these intervals were obtained from the profile likelihood for $Z$, which was calculated using Microsoft Excel. For consistency, the
profile likelihood method (Hilborn and Mangel, 1997) was also used to estimate the 95% confidence intervals for $Z$ for *A. gouldii* when assuming constant recruitment and fitting catch curves simultaneously to the age composition data for the different years.

The 95% confidence intervals for the natural mortality, $M$, of *A. gouldii, N. valenciennesi* and *P. endrachtensis*, as well as the point estimates, were obtained by including, for each species, the maximum recorded age for that species in the data set of Hoenig (1982) for the mortalities and maximum ages for 82 unexploited or lightly-exploited fish stocks. The data were then described using the form of the equation given by Hoenig (1983).

The approach of Hall *et al.* (2004) was used to determine, for *A. gouldii, N. valenciennesi* and *P. endrachtensis*, the likelihood for $M$, calculated using the likelihood for $Z$, as derived from the catch curve analysis. This estimation 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 $M$ that had been derived using the method of Hoenig (1983).

A Monte Carlo resampling approach was used to derive estimates of $F$ for fully-recruited age classes of each species. Estimates of $Z$ and $M$ were randomly resampled, with replacement, from their respective probability distributions. This involved combining, for each species, the estimate for $Z$ from the catch curve or relative abundance analysis (derived assuming variable recruitment with *A. gouldii* and constant recruitment with *N. valenciennesi* and *P. endrachtensis*) and the value of $M$ extracted using the Hall *et al.* (2004) approach. However, these estimates were rejected when the values for $M$ were greater than those for $Z$. 10,000 sets of estimates of $Z$ and $M$ were produced, from which 10,000 estimates of $F$ were determined using the equation $F = Z - M$. The point estimate of
and associated 95% confidence limits were taken as the median value and the 2.5 and 97.5 percentiles of the 10,000 estimates derived from the resampling analysis.

The age compositions derived for *N. valenciennesi* from catches obtained by the recreational and commercial fishers in each of the various years of sampling were pooled to produce a combined age composition that was assumed to represent the catches taken by each sector as a whole. The age compositions of the recreational and commercial fishing sectors were compared by expressing the observed frequency for each age class as a fraction of the total frequency of the fully-recruited fish in the pooled age-frequency data for that fishing sector and plotting the resulting values against age. Subsequently, an estimate of the relative number of fully-recruited fish, $N_a$, at each age in the population was calculated by multiplying the expected proportion at age by the total number of fully-recruited fish in the commercial sample, *i.e.* those fish with ages $t_c \leq a \leq A$. The fishing mortalities for age classes below the age at full recruitment to the fishery were then calculated by estimating the values $F_a$, such that

$$n_a = \left[ F_a / (M + F_a) \right] \left( 1 - \exp \left[ - (M + F_a) \right] \right) N_{a+1} \exp [M + F_a],$$

where $n_a$ is the observed number of fish of age $a$ in the pooled age composition of fish caught by the commercial fishers. After calculating each value of $F_a$, an estimate of $N_a$ was calculated as $N_a = N_{a+1} \exp [M + F_a]$. An estimate of the relative vulnerability at age, $V_a$, was then obtained for *N. valenciennesi* by calculating the ratio of each $F_a$ to the estimate of the fishing mortality of the fully-recruited age classes, $F$.

### 2.7 YIELD AND SPAWNING BIOMASS PER RECRUIT

The yield (YPR) and spawning stock biomass (SSB/R) per age 0 recruit were calculated for each species assuming constant recruitment at age 0, full recruitment to the exploited stock at age $t_c$, constant total mortality for fully-recruited fish and a maximum
age of 100 years for *A. gouldii*, 50 years for *N. valenciennesi* and 25 years for *P. endrachtensis*. Recruitment was assumed to be knife-edged for *A. gouldii* and *P. endrachtensis*. Yield per recruit, $YPR$, for these two species was calculated as

$$YPR = \sum_{a=t_i}^{A} \frac{F}{Z} (1 - \exp(-Z)) W_a \exp(-Za) ,$$

where $F$ and $Z$ refer to the estimated current levels of fishing and total mortality, respectively, and $W_a$ is the weight of the fish at age $a$. Because *N. valenciennesi* is recruited into the fishery gradually over several years, the age-dependent fishing mortalities for partially-recruited age classes of this species, $F_a$, were calculated by multiplying the fishing mortality for fully-recruited fish, $F$, by the age-dependent vulnerability, $V_a$. $YPR$ for this species was calculated as

$$YPR = \sum_{a=1}^{A} \frac{F_a}{M + F_a} (1 - \exp[-(M + F_a)]) W_a \exp \left[ \sum_{j=0}^{a-1} (M + F_j) \right] .$$

$W_a$, the total body weight at age $a$, was determined from the predicted length at age determined using the von Bertalanffy growth curve for the species and employing the relationship between its total body weight (g) and length (mm). Note that combined values of $Z$, $F$ and $W_a$ for both sexes were used in the $YPR$ (and subsequently $SSB/R$) analyses for *A. gouldii* and *N. valenciennesi*, whereas, because of marked differences in the sizes attained by the two sexes of *P. endrachtensis*, separate values for the above three variables were used in the $YPR$ and $SSB/R$ analyses for that species. The values for $F$ 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 Microsoft Excel. This value was used as the biological reference point for the fishing mortality for each species against which the estimate of the current level of $F$ was compared (Hilborn and Walters, 1992; Haddon, 2001).

The spawning stock biomasses per recruit, $SSB/R$, for the females and males of *A. gouldii* and *P. endrachtensis* were calculated as
SSB/R = \sum_{a=1}^{A} W_a P_{sex,a} P_{mat,a} \exp(-Za) \) and those for \( N. valenciennesi \) as

\[
SSB/R = \sum_{a=1}^{A} W_a P_{sex,a} P_{mat,a} \exp \left[ \sum_{j=0}^{a-1} \left( M + F_a \right) \right].
\]

\( W_a \), 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) relationships for the females and males of both of those species. In the case of the hermaphroditic \( A. gouldii \), the proportion of fish of age \( a \) that were of each sex, \( P_{sex,a} \), was determined from the logistic function relating the proportion at each length of that sex and the von Bertalanffy growth equation for that 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 \( N. valenciennesi \), \( P_{sex,a} \) was always assumed to equal 0.5. For the gonochoristic \( P. endrachtensis \), for which the sex ratio was not close to parity, \( P_{sex,a} \) was determined directly from the age composition data for each sex, \( i.e. \) as the proportion of females and males recorded for each age. The proportions of mature females of \( A. gouldii \) and of mature females and males of \( N. valenciennesi \) and \( P. endrachtensis \) at age \( a \), \( P_{mat,a} \), were determined using the logistic function relating the proportions of mature fish to length, and the lengths at age predicted using the von Bertalanffy growth function. All males of the protogynous \( A. gouldii \) were assumed to be mature.

Estimates for the current levels of \( YPR \) and \( SSB/R \) were determined for each of the 10,000 values generated for \( F \) by the Monte Carlo resampling 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 0.025 and 0.975 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).
CHAPTER 3 - BIOLOGY OF THE WESTERN BLUE GROPER
ACHOERODUS GOULDII

3.1 INTRODUCTION

Most species of labrid live in shallow waters and in the vicinity of reefs or other hard substrates (Parenti and Randall, 2000; Westneat and Alfaro, 2005; Allen et al., 2006b). The small size of most labrids is reflected in their relatively short life spans of less than ten years (e.g. Sayer et al., 1996; Treasurer, 1996; Cardinale et al., 1998). Although a few of the larger species of labrids live for a substantially longer period, the oldest age yet published for a member of this family is still only 35 years (Gillanders, 1995a). On the basis of demographic analyses of large labrid species, Choat et al. (2006) concluded that such species were characterised by indeterminate growth rates and relatively short life spans.

The Western Blue Groper Achoerodus gouldii is most abundant on the south coasts of Western Australia and South Australia, where it attains a maximum length of 1.75 m (Gommon et al., 1994), which, among labrids, is apparently exceeded only by Cheilinus undulatus (Sadovy et al., 2003). The females of A. gouldii tend to be green and their males tend to be blue (Gommon et al., 1994; Gillanders, 1999). Although A. gouldii is the second most important of the teleost species caught commercially on the south coast of Western Australia (McAuley and Simpendorfer, 2003), and is also a highly-prized recreational species (Shepherd and Brook, 2007), detailed studies of its biology have been restricted to investigations of its foraging behaviour, diet and ontogenetic changes in habitat (Shepherd, 2005; Shepherd and Brook, 2005, 2007). The fact that some aspects of the biology of A. gouldii are only now being studied is surprising in view of the severe decline undergone by its numbers in the 1960s as a result of a vulnerability to spear and line fishing and which, as a consequence, led to it being protected from fishing on the central coasts of
South Australia (Shepherd and Brook, 2003). Shepherd and Brook (2007) later estimated that, in the most heavily-fished, shallow waters in South Australia, the instantaneous rate of fishing mortality was as high as 0.8 year⁻¹.

In contrast to the situation with *A. gouldii*, several aspects of the biology of the Eastern Blue Groper *Achoerodus viridis*, which is distributed along the eastern and south-eastern coasts of Australia (Hutchins and Swainston, 1986), have been studied (Gillanders, 1995a, b, 1997a, b; Gillanders and Kingsford, 1993, 1998; Leis and Hay, 2004). This congeneric species has thus been shown, for example, to be a monandric protogynous hermaphrodite that reaches lengths of 1 m, lives for up to 35 years and attains maturity at lengths of 200-280 mm (*FL*) and by 1-2 years of age. The apparently detrimental effects of fishing on *A. viridis* in New South Wales led to this iconic species being protected from both recreational and commercial fishing in 1969, although these regulations were subsequently eased to some extent in 1974 (Gillanders, 1999).

The aim of the present study was to test the following hypotheses. 1) As with *A. viridis*, *A. gouldii* is a monandric protogynous hermaphrodite. 2) The far greater size of *A. gouldii* than *A. viridis* is accompanied by a far greater maximum age and a greater size and age at both the attainment of maturity by females and at sex change. If *A. gouldii* does live for a substantially longer period than *A. viridis*, it will have the greatest longevity of any labrid species. 3) Because protogynous labrids that exhibit dichromatism tend to change colour at about the same size and age as that at which sex change occurs, the *L₅₀* at colour change is very similar to that at sex change, *i.e.* as determined from gonadal data. The extent to which the length at colour change can be used as a proxy for length at sex change is explored. 4) If, as hypothesized, *A. gouldii* is particularly long-lived, late-maturing and undergoes late sex change, this important commercial species would possess characteristics that would make it potentially very vulnerable to fishing pressure and may
thus already be experiencing an undesirable level of fishing mortality. Finally, the implications of the biological data for management plans aimed at conserving the stocks of *A. gouldii* are discussed.

3.2 MATERIALS AND METHODS

3.2.1 Sampling regime

*Achoerodus gouldii* was collected at monthly or bimonthly intervals between April 2004 and October 2007 from numerous sites in coastal waters between Albany at 35° 01’S, 117° 58’E and Esperance at 33° 45’S, 121° 55’E off the south coast of Western Australia (Fig. 3.1). These fish were either caught by spear fishing while free-diving or SCUBA diving in shallow (< 20 m) inshore coastal waters or were obtained from fish processors, who had been supplied by commercial gillnet fishers (mesh range = 165-178 mm) operating in deeper (c. 20-100 m) and more offshore waters. A small number of *A. gouldii* (c. 3% of all fish) were collected directly from commercial gillnet fishers operating in deeper, offshore waters at a latitude of about c. 32° S on the lower west coast of Australia. Although most of the individuals obtained from commercial gillnet fishers on both coasts were supplied as gutted, filleted frames and could thus neither be sexed nor used to provide information on their gonadal status, some of those from the south coast were intact, *i.e.* still contained their gonads.

The method of capture (*i.e.* spear fishing or commercial gill netting) and length range of *A. gouldii* caught in each month during the study are provided in Table 3.1.
Figure 3.1. Map showing the five main sampling locations on the south (Albany, Bremer Bay Hopetoun and Espeance) and lower west (Perth) coasts of Western Australia from which *Achoerodus gouldii* and *Nemadactylus valenciennesi* were collected. Insets show regions of sampling in south-western Australia and the locations of inshore sampling sites at each of the four main sampling locations on the south coast. Note that offshore samples were obtained mainly from waters off Esperance and Albany.
Table 3.1. Sample sizes and length ranges of *Achoerodus gouldii* collected by spear fishing and in catches obtained from the commercial gillnet fishers on the south and lower west coasts of Western Australia.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Spear fishing</th>
<th>Commercial gill netting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>n</em></td>
<td>Length range (mm)</td>
</tr>
<tr>
<td>2004</td>
<td>April</td>
<td>1</td>
<td>810</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>24</td>
<td>606-1091</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>30</td>
<td>556-1058</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>64</td>
<td>521-1033</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>16</td>
<td>124-483</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>93</td>
<td>479-1104</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>52</td>
<td>129-608</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>35</td>
<td>474-954</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>48</td>
<td>475-844</td>
</tr>
<tr>
<td>2005</td>
<td>January</td>
<td>11</td>
<td>184-301</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>5</td>
<td>266-343</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>100</td>
<td>108-921</td>
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<td></td>
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<td>100</td>
<td>108-921</td>
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<td></td>
<td>May</td>
<td>56</td>
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<td>88</td>
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<td>12</td>
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<tr>
<td></td>
<td>December</td>
<td>82</td>
<td>106-758</td>
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<td>2006</td>
<td>January</td>
<td>5</td>
<td>211-1050</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>74</td>
<td>60-954</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>44</td>
<td>90-823</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>48</td>
<td>104-849</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>1</td>
<td>550</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>2</td>
<td>670-775</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>54</td>
<td>222-850</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>32</td>
<td>530-891</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>6</td>
<td>541-1008</td>
</tr>
<tr>
<td></td>
<td>October</td>
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<td>November</td>
<td>45</td>
<td>40-1041</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>9</td>
<td>291-647</td>
</tr>
<tr>
<td>2007</td>
<td>January</td>
<td>21</td>
<td>154-659</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>1</td>
<td>704</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>4</td>
<td>526-690</td>
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<tr>
<td></td>
<td>August</td>
<td>17</td>
<td>123-943</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>33</td>
<td>521-1063</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>8</td>
<td>567-1134</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>822</td>
<td>40-1050</td>
</tr>
</tbody>
</table>
3.2.2 Laboratory procedures and analyses

The following provides details of the extension for *A. gouldii* of the procedures and analyses described in the General Materials and Methods and which were applicable to all three species. The colour of each *A. gouldii*, *i.e.*, green or blue, was recorded. To facilitate comparisons between the total lengths of *A. gouldii* and those of the congener *A. viridis*, which were recorded as standard lengths (SL) by Gillanders (1995a), those latter standard lengths were converted to total lengths (TL) using the equation $TL = 1.19(SL) + 7.93$ ($n = 455$, $p < 0.001$, $r^2 = 0.99$), which was derived from data kindly provided by B. Gillanders. Note that as the tail of *A. gouldii* is not forked, the fork length of this species is the same as its total length. Thus, the total lengths for *A. gouldii* can be compared directly with the lengths of those other labrid species which are recorded as fork lengths by workers such as Choat *et al.* (2006).

3.2.3 Sex change

Logistic regression analysis was employed to relate the probability, $p_M$, that a fish was a male rather than a female to length and/or colour, where

$$p_M = \frac{1}{1 + \exp[-\alpha - \beta_1 TL - \beta_2 x]}$$

and $\alpha$, $\beta_1$ and $\beta_2$ are constants and $x$ is the value of the factor representing the colour of the fish (green = 0, blue = 1). The proportion of fish of length $TL$ that possess female gonads, $p_F$, was determined as $1 - p_M$. The Akaike Information Criterion (AIC) (Burnham and Anderson, 2003) was used to determine which of the models based solely on length or colour or both length and colour provided the better prediction of the probability that a fish was male. The AIC is determined as $AIC = -2\lambda + 2K$, where $\lambda$ is the log-likelihood and $K = \text{number of parameters}$. The model with the lowest AIC value was selected as the best of the alternative models. The likelihood ratio test was then used to determine whether the nested model that contained the combination
of the two variables, i.e. length and colour, improved the prediction of the proportion of fish that were male.

3.2.4 Growth

A single von Bertalanffy growth curve was fitted to the lengths at age of all _A. gouldii_ aged during the present study. The von Bertalanffy growth equation, which was fitted using SPSS Inc. (2001), is 

\[ L_t = L_\infty \left(1 - \exp\left(-k(t - t_0)\right)\right) \]

where \( L_t \) is the length (mm TL) at age \( t \) (years), \( L_\infty \) is the mean asymptotic length (mm) predicted by the equation, \( k \) is the growth coefficient (year\(^{-1}\)) and \( t_0 \) is the hypothetical age (years) at which fish would have zero length. Separate curves were then fitted to the lengths at age of females and males that had been sexed using gonad type and then again for the same fish but using colour, i.e. green or blue.

von Bertalanffy growth curves for each sex \( s \) (where \( s = f \) for a female and \( m \) for a male) were next fitted to the combination of the lengths at age of sexed and unsexed individuals, where the latter group comprised those fish for which the colour had been recorded.

The expected length for each sex, \( s \), was first calculated as

\[
\hat{L}_j^s = \begin{cases} 
L_f^f \left(1 - \exp\left[-k_f^f(t_j - t_0^f)\right]\right) & \text{if } s = f \text{ or } t_j \leq t_{\text{diverge}}^m \\
L_m^m \left(1 - \exp\left[-k_m^m(t_j - t_0^m)\right]\right) & \text{if } s = m \text{ and } t_j > t_{\text{diverge}}^m 
\end{cases}
\]

where \( t_j \) is the age of fish \( j \) and \( t_{\text{diverge}} \) is the age at which the growth curve of the males was assumed to begin diverging from that of females. Note that, if \( L_{\text{diverge}}^m \) is the expected length of the females at age \( t_{\text{diverge}}^m \), then

\[
t_0^m = t_0^f - \frac{1}{k_f^f} \log_e \left(1 - \frac{L_{\text{diverge}}^m}{L_f^f}\right) + \frac{1}{k_m^m} \log_e \left(1 - \frac{L_{\text{diverge}}^m}{L_m^m}\right)
\]

The observed lengths of fish of that age were assumed to be normally-distributed about the predicted length for each sex, with
a common standard deviation, i.e. \( L_j = \hat{L}_j + \varepsilon'_j \), where \( L_j \) is the observed length for fish \( j \) and where \( \varepsilon'_j \sim N(0, sd^2) \). The value of the normal probability density function for the deviation \( \varepsilon'_j \) was calculated for each sex \( s \) as 
\[
\phi'_j = \frac{1}{\sqrt{2\pi sd^2}} \exp\left[-\frac{(L_j - \hat{L}_j)^2}{2 sd^2}\right].
\]

The probability that fish \( j \) was of sex \( s \) was denoted by \( p'_j \), where \( p'_j = 1 - p''_j \) and where

\[
p''_j = \begin{cases} 1 & \text{if the fish possessed male gonads} \\ 0 & \text{if the fish possessed female gonads} \\ \left(1 + \exp(-\alpha - \beta_1 L_j - \beta_2 C_j)\right)^{-1} & \text{if the fish had not been sexed} \end{cases}
\]

The parameters \( \alpha \), \( \beta_1 \) and \( \beta_2 \) for estimating the probability that a fish of length \( L_j \) and colour \( C_j \) (0=green, 1=blue) is male were calculated using logistic regression analysis.

The value of the log-likelihood, 
\[
\lambda = \sum_j \log\left( \sum_s p'_j \phi'_j \right)
\]
was maximised to estimate the parameters \( L'_0 \), \( k'^f \), \( t'_0 \), \( L'_m \), \( k'^m \), \( t'_\text{diverge} \) and \( sd \). Bootstrap confidence limits were calculated by resampling with replacement and fitting the model to the resampled data. The 2.5 and 97.5 percentiles of the resulting estimates from 1000 resampled data sets were taken as the approximate 95% confidence limits for the parameters.

Comparisons between the growth curves of \( A. gouldii \) were restricted to those derived for individuals from inshore waters of the only two areas (Albany and Esperance) where the samples contained both a substantial number of fish and encompassed a wide length and age range of fish.

3.2.5 Length, age and colour at sex change

For determining the length and age at which \( A. gouldii \) changes sex, the six fish with gonads containing both testicular and ovarian tissue, and which were thus considered to be changing from female to male (see Results), were combined with those fish with
gonads comprising only testicular material. The lengths at which 50 and 95% of individuals of *A. gouldii* change sex and colour (*L*<sub>50</sub>, *L*<sub>95</sub>) were then estimated by fitting logistic curves to the probability that a fish, at a specified length, were male and blue, respectively. This was undertaken using Markov Chain Monte Carlo simulation in WinBUGS, as described above for length at maturity. Logistic curves were also fitted to the probability that individuals of *A. gouldii* at a specified length were blue, the colour of the majority of males and which thus contrasted with the green colour that characterized most females.

The number of fish in each year class in three successive twelve month periods were calculated. As this study commenced in August and 1 August coincides with the birth date selected for *A. gouldii* (see Results), these counts were made for each of the three 12 month periods between August and the following July.

3.3 RESULTS

### 3.3.1 Validation of ageing method

Sectioning of the otoliths of *A. gouldii* resulted in their opaque zones becoming clearly defined and demonstrated that those zones were numerous in otoliths of the largest fish (Fig. 3.2).

Although the monthly sample sizes of fish with otoliths with 1 opaque zone were often small, the mean monthly marginal increments on such otoliths could still be seen to undergo a clear seasonal pattern of change, with values declining markedly between late winter and mid-spring and rising between early autumn and winter (Fig. 3.3). The mean monthly marginal increments on sectioned otoliths of *A. gouldii* with 2-10 zones, for which the monthly sample sizes were far greater, remained relatively high (≥ 0.39) between July and October, before declining sequentially to 0.36 in November and to a minimum of 0.26 in January and February, and then rising progressively in the ensuing months (Fig. 3.3).
Figure 3.2. Sectioned otoliths of *Achoerodus gouldii* with a) 10, b) 30 and c) 69 opaque zones. ⚫ denotes every fifth opaque zone in (a) and every tenth opaque zone in (b) and (c). Scale bars = 0.5 mm.
Figure 3.3. Mean monthly marginal increments ± 1 SE on sectioned sagittal otoliths of *Achoerodus gouldii* with different numbers of opaque zones. Sample sizes are shown above each mean. In this Fig. and Fig 3.6, closed rectangles on the x-axis refer to winter and summer months and the open rectangles to spring and autumn months.
Although the mean monthly marginal increments on otoliths with 11-20, 21-30 and > 30 zones followed very similar trends to those just described for otoliths with 2-10 zones, the minima of the last two groups were reached later. Thus, as the number of zones in otoliths increases, the opaque zone in otoliths becomes visually detectable later, i.e. in autumn rather than mid-summer. The similar and single pronounced decline and subsequent progressive rise in the mean monthly marginal increments in sectioned otoliths, irrespective of the number of opaque zones they contained, demonstrate that a single opaque zone is formed annually in the otoliths of *A. gouldii*. The number of opaque zones in the otoliths of *A. gouldii* can thus be used to facilitate the ageing of the individuals of this species.

### 3.3.2 Length and age compositions and growth

From the trends exhibited by the mean monthly GSIs and prevalence in each month of females with stages V/VI ovaries (see later), the approximate mid-point of the spawning period was estimated to be August, i.e. end of the Austral winter. The small fish caught in November were c. 40 mm in length, while those captured in February and March were c. 60 and 90 mm, respectively. The otoliths of these fish contained no opaque zones, which is consistent with these fish, on average, having been spawned in late winter and thus not having had the opportunity to lay down the opaque zone that is deposited annually during that season in older fish. The first of these zones becomes delineated in the spring of the second year of life, i.e. when fish are c. 140 mm in length and c. 18 months old.

The samples of *A. gouldii* contained individuals that ranged in length from 40 to 1162 mm and in age from a few months to 70 years (Fig. 3.4). The largest and oldest *A. gouldii*, from which the gonads had not been removed during gutting and filleting and could thus be sexed, were 880 mm and 49 years for females and 1134 mm and 57 years for males.
**Figure 3.4.** Length and age-frequency distributions for *Achoerodus gouldii* caught by spear fishing (open histograms) and commercial gillnetting (grey histograms). $n_s$ and $n_g$, number of fish caught by spear fishing and gill netting, respectively.
Although the 822 A. gouldii collected by spear fishing ranged from 40 to 1050 mm in total length, the majority of those individuals were between 100 and 600 mm, which correspond to ages of 1 to 11 years (Fig. 3.4). The 1107 A. gouldii obtained from the commercial gillnet fishery ranged from 428 to 1162 mm in length and from 6 to 70 years in age, but most were between 500 and 800 mm 10 and 34 years (Fig. 3.4).

The growth curves of A. gouldii in inshore waters off Albany and Esperance, locations separated by 500 km and representing the extreme locations at which samples were obtained on the south coast, were not significantly different ($p < 0.05$). Thus, the lengths at age of fish from the different regions were pooled, and a common growth curve constructed for all aged fish (Fig. 3.5a). A von Bertalanffy growth curve provided a good fit to the lengths at age of all fish, as is demonstrated by the relatively high value of 0.84 for the coefficient of determination (Table 3.2). On the basis of the von Bertalanffy growth equation, A. gouldii at ages 5, 10, 20, 30, 40 and 50 years attain, on average, lengths of 335, 509, 678, 741, 764 and 773 mm, respectively. The marked similarity in the estimated lengths at 30, 40 and 50 years of age reflects the markedly asymptotic pattern of growth of A. gouldii, with relatively little overall growth occurring after 30 years.

The von Bertalanffy growth curves fitted separately to the lengths at age of known females and males, i.e. those able to be sexed using gonadal criteria, demonstrated that, at the same age, the mean length of males was always greater than that of females (Fig. 3.5b). Furthermore, with increasing age, the estimated lengths at age of males increasingly diverged from those of females. Thus, for example, at 20, 35 and 50 years, the estimated lengths at age for males were 805, 923 and 965 mm, respectively, and those for females were 679, 737 and 746 mm, respectively (Fig. 3.5b). The above differences in growth are reflected in the estimate for $k$ for males (0.08 year$^{-1}$) being less than that for females.
Figure 3.5. von Bertalanffy growth curves fitted to the lengths at age of a) all sexed and unsexed individuals, b) females (white circles) and males (grey circles) sexed on the basis of gonadal type, c) the same individuals as in b) but now sexed according to whether they are green or blue and d) for females and males using gonadal criteria, but including the lengths at age of all unsexed fish that were assigned to a sex after assessing the probability that, on the basis of their length and colour, a fish would be either female and male.
Table 3.2. The von Bertalanffy growth curve parameters $L_\infty$, $k$ and $t_0$ ($\pm$ 95% confidence limits) for *Achoerodus gouldii* caught in waters off the lower west and south coasts of Western Australia. a) For all fish, b) for females and males sexed using gonad type, c) for the same fish as in b) but sexed according to whether they were green or blue, and d) for females and males using gonadal criteria, but including the lengths at age of all unsexed fish that were assigned to a sex after assessing the probability that, on the basis of their length and colour, a fish would be either female and male. Parameters were derived from the lengths at age of individuals. $L_\infty$ is the asymptotic length (mm), $k$ is the growth coefficient (year$^{-1}$), $t_0$ is the hypothetical age (years) at which fish would have zero length, $r^2$ is the coefficient of determination and $n$ is the number of fish.

<table>
<thead>
<tr>
<th></th>
<th>$L_\infty$ (mm)</th>
<th>$k$ (year$^{-1}$)</th>
<th>$t_0$ (years)</th>
<th>$r^2$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) All fish</td>
<td>Estimate</td>
<td>777</td>
<td>0.10</td>
<td>-0.65</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>766,789</td>
<td>0.09,0.11</td>
<td>-0.90,-0.39</td>
<td></td>
</tr>
<tr>
<td>b) Females</td>
<td>Estimate</td>
<td>748</td>
<td>0.12</td>
<td>-0.15</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>732,764</td>
<td>0.11,0.12</td>
<td>-0.30,0.00</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>Estimate</td>
<td>975</td>
<td>0.08</td>
<td>-0.91</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>879,1072</td>
<td>-0.02,0.19</td>
<td>-22.84,21.03</td>
<td></td>
</tr>
<tr>
<td>c) Green</td>
<td>Estimate</td>
<td>748</td>
<td>0.12</td>
<td>-0.17</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>731,765</td>
<td>0.11,0.12</td>
<td>-0.32,-0.02</td>
<td></td>
</tr>
<tr>
<td>Blue</td>
<td>Estimate</td>
<td>966</td>
<td>0.08</td>
<td>-0.10</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>867,1055</td>
<td>0.03,0.13</td>
<td>-8.38,8.18</td>
<td></td>
</tr>
<tr>
<td>d) Females</td>
<td>Estimate</td>
<td>682</td>
<td>0.14</td>
<td>0.06</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>675,692</td>
<td>0.14,0.15</td>
<td>0.00,0.10</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>Estimate</td>
<td>982</td>
<td>0.08</td>
<td>-0.48</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>Lower, upper</td>
<td>952,1013</td>
<td>0.07,0.09</td>
<td>-1.09,-0.14</td>
<td></td>
</tr>
</tbody>
</table>

(0.12 year$^{-1}$), whereas the reverse trend occurred with the $L_\infty$, for which the respective values were 975 and 748 mm (Table 3.2). Unlike the situation with females, the 95% confidence limits for $t_0$ for males were very wide (Table 3.2), reflecting the fact that none of the smaller fish was a male, as females do not change to male until a certain size and age has been reached, and thus there were no length-at-age data to tie down and refine the bottom end of the growth curve for males.

When von Bertalanffy growth curves were fitted separately to the lengths at age of those individuals that were either green or blue, but constituted the same subset of fish as those just used to describe the growth of males and females, the values for $L_\infty$ and $k$ for blue and for green fish were either identical or very similar to those for female and male
fish, respectively (Fig. 3.5c; Table 3.2).

The von Bertalanffy growth curves were next fitted to the lengths at age of all sexed and unsexed individuals, but incorporating the probability that, in the latter group, the green fish will be females and the blue fish males (see Material and Methods). The resultant curves for the “females” and “males” fitted the length at age data very well (Fig. 3.5d), as is demonstrated by the high and identical $r^2$ values of 0.93 for both groups (Table 3.2). The inclusion of lengths at age for unsexed individuals, the majority of which were larger and older fish and taken by the commercial gillnet fishery, have resulted in slightly lower and higher values for the $L_\infty$ for “females” and “males”, respectively, than those for the subset of sexed fish (Table 3.2).

The relationship between the total length ($TL$) in mm and total weight ($W$) in g for $A. gouldii$ is described by the following regression equation: $\ln W = 3.041(\ln TL) – 11.017$ ($r^2 = 0.997, p < 0.001, n = 756$). The relationship between standard length ($SL$) in mm and total length ($TL$) in mm for $A. gouldii$ is described by the following regression equation: $TL = 1.201 (SL) – 11.883$ ($r^2 = 0.995, p < 0.001, n = 101$).

3.3.3 Water temperatures

Mean monthly temperatures in offshore waters at Albany on the south coast declined from a maximum of 20.1°C in early autumn to a minimum of 16.4°C in mid-spring (Fig. 3.6b). Although water temperature at Esperance on the south coast followed essentially the same seasonal trends as those at Albany, they were 1 to 1.5°C lower in each month. Temperatures in inshore waters at both Albany and Esperance underwent more pronounced seasonal changes than in offshore waters and peaked earlier, i.e. mid- to late-summer, and declined to their minima earlier, i.e. mid- to late-winter (Fig. 3.6a). Furthermore, the differences between water temperatures in inshore waters at the two locations in corresponding months were not as great as in offshore waters and, in many
Figure 3.6. a) Mean monthly water temperatures ± 1 SE for a) inshore and b) offshore waters at Albany (grey circles) and Esperance (black circles) on the south coast of Western Australia and c) mean monthly gonadosomatic indices ± 1 SE for female *Achoerodus gouldii* on the south coast and the corresponding mean monthly percentage frequencies of occurrence of fish with ovaries at stages III/VI (dark grey) and V/VI (light grey). Sample sizes for mean monthly gonadosomatic indices and mean monthly percentage frequencies of occurrence of ovaries are given above each mean.
months, were greater at Esperance than at Albany.

3.3.4 Description of gonadal stages

The characteristics of selected macroscopic stages and of the corresponding histological stages in the development of the ovaries of *A. gouldii* are presented in Tables 3.3 and 3.4, respectively.

3.3.5 Gonadal development and time and duration of spawning

The mean monthly GSIs for female *A. gouldii* ≥ the *L*\textsubscript{50} at maturity, *i.e.* 653 mm (see later), remained low, *i.e.* < 0.50, between December and May, after which they rose sharply to reach a peak of 2.3 in July, before declining to 1.6 in October and 0.1 in November (Fig. 3.6c). The gonads of all females collected between November and May with lengths ≥ the *L*\textsubscript{50} at maturity possessed immature/resting ovaries (stage II). Female fish with ovaries at stages III/IV were caught in June and July and those with ovarian stages V/VI between June and October (Fig. 3.6c). The above monthly trends strongly indicate that females with ovaries that develop beyond stage II will become mature during the spawning period.

The above trends in the mean monthly values for the female GSIs and prevalences in each month of females with stage V/VI ovaries demonstrate that spawning occurs predominantly between June and October.

3.3.6 Length and age at maturity of females

The smallest female that was mature (*i.e.* at one of stages III-VII) during the spawning period measured 391 mm (Fig. 3.7a). The prevalence of mature females increased from 2% in the 350–399 length class to > 50% in the 700–749 mm and 750–799 mm length classes and to 100% in fish > 800 mm (Fig. 3.7a). The *L*\textsubscript{50} for female *A. gouldii* at first maturity was 653 mm (Table 3.5).
Table 3.3. Macroscopic characteristics of selected stages in the development of the ovaries of *Achoerodus gouldii*. Scheme adapted from Laevastu (1965). Scale bars = 10 mm.

<table>
<thead>
<tr>
<th>Macroscopic stage</th>
<th>Macroscopic view</th>
<th>Macroscopic characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage II</td>
<td><img src="image" alt="Stage II" /></td>
<td>Pink, thin and narrow and extending 1/2 the length of the body cavity. Capillaries visible on dorsal surface of ovarian lobes.</td>
</tr>
<tr>
<td>Immature</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage III</td>
<td><img src="image" alt="Stage III" /></td>
<td>Deep pink and similar in length as stage II, but wider. Capillaries more prominent than in stage II. Under a dissecting microscope small white oocytes can bee seen through the ovarian wall.</td>
</tr>
<tr>
<td>Developing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage V</td>
<td><img src="image" alt="Stage V" /></td>
<td>Yellow, orange or pink and large, occupying 2/3 of body cavity and containing yellow (yolk granule) oocytes. Blood capillaries very prominent on dorsal wall of ovaries.</td>
</tr>
<tr>
<td>Mature</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage VI</td>
<td><img src="image" alt="Stage VI" /></td>
<td>Colour and size similar to previous stage, but with numerous translucent oocytes visible through ovarian wall. This stage is only identifiable during oocyte hydration period.</td>
</tr>
<tr>
<td>Spawning</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage VII</td>
<td><img src="image" alt="Stage VII" /></td>
<td>No image available</td>
</tr>
<tr>
<td>Spent</td>
<td></td>
<td>Pinkish red, flaccid and occupying 1/3 of body cavity. Remnant yolk granule oocytes visible through ovarian wall Capillaries still visible on dorsal surface of ovarian lobes.</td>
</tr>
</tbody>
</table>
Table 3.4. Histological characteristics of selected macroscopic stages in the development of the ovaries of female *Achoerodus gouldii*. Terminology for oocyte stages follows Wallace and Selman (1981). Scale bars = 200µm

<table>
<thead>
<tr>
<th>Macrosopic stage</th>
<th>Histological section</th>
<th>Histological characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage II Immature</td>
<td><img src="image1" alt="Histological section" /></td>
<td>Numerous chromatin nucleolar (cn) and perinucleolar oocytes (p) present. These oocyte stages are present in all subsequent ovarian stages.</td>
</tr>
<tr>
<td>Stage III Developing</td>
<td><img src="image2" alt="Histological section" /></td>
<td>Cortical alveolar (ca) oocytes are abundant. No yolk granule oocytes present.</td>
</tr>
<tr>
<td>Stage V Mature</td>
<td><img src="image3" alt="Histological section" /></td>
<td>Cortical alveolar oocytes (ca) and yolk granule oocytes (y) are abundant and tightly packed.</td>
</tr>
<tr>
<td>Stage VI Spawning</td>
<td><img src="image4" alt="Histological section" /></td>
<td>Cortical alveolar (ca) and yolk granule (y) oocytes present. The presence of migratory nucleus (m) and hydrated (h) oocytes and/or post-ovulatory follicles typify this stage.</td>
</tr>
<tr>
<td>Stage VII Spent</td>
<td><img src="image5" alt="Histological section" /></td>
<td>Most or all of the remnant yolk granule oocytes (y) are undergoing atresia.</td>
</tr>
</tbody>
</table>
Figure 3.7. Percentage frequency of occurrence of female *Achoerodus gouldii* with mature gonads (grey histograms) in sequential a) 50 mm length classes and b) five year age categories in samples obtained during the spawning period, *i.e.* June to October. Logistic curve (solid line) and its 95% confidence limits (dotted lines) in (a) were derived from the probability that a fish at a given length is mature. Sample sizes in each 50 mm length class are shown above each histogram.
The youngest female that was mature during the spawning period was 5 years old. The prevalence of mature females in sequential five year age categories increased from 7% in those fish aged 5-9 years to 63% in those fish aged 20-24 years (Fig. 3.7b). Despite the prevalence of mature females caught during the spawning period reaching 81% in those fish aged between 25 and 29 years, it did not reach 100% in either of the following two age class categories (Fig. 3.7b).

Table 3.5. Estimates of the lengths, and their lower and upper confidence limits, at which 50% of the females of *Achoerodus gouldii* attained maturity (*L*<sub>50</sub>) in waters of the lower west and south coasts of Western Australia.

<table>
<thead>
<tr>
<th></th>
<th><em>L</em>&lt;sub&gt;50&lt;/sub&gt; (mm)</th>
<th><em>L</em>&lt;sub&gt;95&lt;/sub&gt; (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimate</td>
<td>653</td>
<td>926</td>
</tr>
<tr>
<td>Lower</td>
<td>623</td>
<td>853</td>
</tr>
<tr>
<td>Upper</td>
<td>693</td>
<td>1029</td>
</tr>
</tbody>
</table>

### 3.3.7 Batch Fecundity

The frequencies of the various oocyte diameters in the ovaries of two typical mature (ovaries at stage V) female *A. gouldii*, and which contained early previtellogenic oocytes, *i.e.* chromatin nucleolar and perinucleolar oocytes, as well as cortical alveolar and yolk granule oocytes, formed essentially a continuous distribution (Fig. 3.8). This continuity provides very strong evidence that *A. gouldii* possesses indeterminate fecundity (*sensu* Hunter *et al.*, 1985), *i.e.* the annual fecundity is not fixed prior to the onset of the spawning season.

Batch fecundity estimates for 12 females of *A. gouldii*, with lengths ranging from 530 to 850 mm and weights from 3 to 14 kg, respectively, ranged from 150,420 to 402,912 and produced a mean ± 95% CL of 256,484 ± 54,983.
Figure 3.8. Oocyte diameter frequency distributions for two mature (stage V) female *Achoerodus gouldii*. Early previtellogenic oocytes (white), cortical alveolar oocytes (grey), yolk granule oocytes (black).
3.3.8 Histological characteristics of gonads

Among the 200 *A. gouldii* that ranged in length from 100 to 1041 mm and whose gonads were examined histologically, the gonads of all 150 individuals < 655 mm contained exclusively ovarian tissue (*e.g.* Fig. 3.9a) and were thus females. All but six of the 50 individuals with lengths ≥ 655 mm contained exclusively either ovarian tissue, as in Figure 3.10b, or testicular tissue (Fig. 3.9d). The gonadal tissue of those six exceptions, whose lengths ranged from 655 to 850 mm, comprised testicular tissue within which were distributed previtellogenic oocytes (Fig. 3.9c).

All immature ovaries, *i.e.* those containing only previtellogenic oocytes, possessed a prominent central lumen (Fig. 3.9a). This lumen was largely or fully occluded in mature and spawning ovaries (stage V/VI) (Fig. 3.9b). A conspicuous central lumen and peripherally-located sperm sinuses (Fig. 3.9d) were present in all testes examined histologically.

3.3.9 Length and age at sex change

On the basis of a macroscopic examination of all gonads dissected from fish and histological examination of a large subsample of those gonads, all *A. gouldii* < 655 mm in length were females (Fig. 3.10a). The prevalence of male fish increased progressively from 3% in the 650–699 mm length class to 80% in the 850-899 mm length class and 100% among fish ≥ 900 mm (Fig. 3.10a). The *L*$_{50}$ at sex change was 821 mm (Table 3.6). 866 of the 891 females (97%) were green and 39 of the 44 males (89%) were blue. All fish < 550 mm were green (Fig. 3.10b). The prevalence of fish with blue coloration increased rapidly from 8% in the 550-599 mm length class to 86% in the 800-849 mm length class and reached 100% in all fish ≥ 900 mm (Fig. 3.10b). The confidence intervals for the *L*$_{50}$ of 779 mm at colour change overlapped those for the *L*$_{50}$ of 821 mm at sex change (Table 3.6).
Figure 3.9. Histological sections of gonads of *Achoerodus gouldii*. a) Ovary of immature female containing numerous previtellogenic oocytes and a prominent lumen (l); b) ovary of mature female containing early previtellogenic oocytes (p), cortical alveolar oocytes (ca), yolk granule oocytes (y), migratory nucleolar oocyte (m) and hydrated oocytes (h); c) gonad comprising mainly testicular tissue (t) and numerous previtellogenic oocytes (o) and d) mature testes with prominent lumen (l) and sperm sinuses (ss). Scale bars = 1000 µm in (a) and 200 µm in (b), (c) and (d).
Figure 3.10. Percentage frequency of occurrence of *Achoerodus gouldii* with testes (grey histograms) in a) sequential 50 mm length classes and 5 year age categories and the percentage frequency of occurrence of *Achoerodus gouldii* with blue coloration (grey histograms) in b) sequential 50 mm length classes and 5 year age categories. Logistic curves (solid line) and their 95% confidence limits (dotted lines) in (a) and (b) were derived from the probability that a fish at a given length would have testes and blue coloration, respectively. Sample sizes shown above each histogram.
Table 3.6. Estimates of the lengths, and their lower and upper confidence limits, at which 50% of *Achoerodus gouldii* change sex to male ($L_{50}$) and the lengths at which 50% of *Achoerodus gouldii* change from green to blue ($L_{50}$) in south-western Australia.

<table>
<thead>
<tr>
<th></th>
<th>$L_{50}$ (mm)</th>
<th>$L_{95}$ (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex change</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estimate</td>
<td>821</td>
<td>930</td>
</tr>
<tr>
<td>Lower</td>
<td>800</td>
<td>890</td>
</tr>
<tr>
<td>Upper</td>
<td>845</td>
<td>1102</td>
</tr>
<tr>
<td>Colour change</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estimate</td>
<td>779</td>
<td>961</td>
</tr>
<tr>
<td>Lower</td>
<td>753</td>
<td>910</td>
</tr>
<tr>
<td>Upper</td>
<td>809</td>
<td>1028</td>
</tr>
</tbody>
</table>

All fish < 15 years old were females (Fig. 3.10a). The prevalence of males subsequently increased with age to 67% in fish aged between 35 and 39 years and to 100% in those fish ≥ 50 years (Fig. 3.10a).

The values for the AIC showed that the dichotomous factor, colour, does not provide as good a predictor as the continuous variable, length, that an individual is male (Table 3.7). However, the likelihood ratio test demonstrated that the combination of colour and length provided a significantly better fit than length on its own ($p < 0.05$).

Table 3.7. Results of logistic regression analysis for determining whether colour or total length ($TL$), or colour and total length combined, were the best predictors as to whether an individual of *Achoerodus gouldii* was male. LL, log-likelihood; $\alpha$, $\beta_1$, $\beta_2$, constants; AIC = Akaike’s Information Criterion.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Colour</th>
<th>$TL$</th>
<th>Colour and $TL$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL</td>
<td>-84.424</td>
<td>-48.644</td>
<td>-45.457</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>-4.631</td>
<td>-17.275</td>
<td>-15.505</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>0.021</td>
<td>0.018</td>
<td></td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>4.979</td>
<td>1.477</td>
<td></td>
</tr>
<tr>
<td>AIC</td>
<td>172.847</td>
<td>101.289</td>
<td>96.913</td>
</tr>
</tbody>
</table>

3.3.10 Variations in year class strength and estimates of mortality

The frequencies of the different year classes of *A. gouldii* in the commercial gillnet catches taken between August and July in three successive 12 month periods, demonstrate
that, in each of those periods, the 1972, 1980, 1983 and 1990 year classes were relatively strong (Fig. 3.11). From the data shown in Figure 3.4, it is assumed that *A. gouldii* has become fully recruited to the commercial gillnet fishery by 15 years of age, *i.e.* the year following the year in which there is the peak in recruitment into the commercial fishery. The fact that a substantial number of fish in excess of 35 years of age were caught and the distribution of the lengths of the males does not appear to be truncated suggests that mesh selectivity was not having a major influence on the upper end of the length distribution.

From the catch curve analysis assuming constant recruitment (Fig. 3.12), Z was estimated to be 0.086 year\(^{-1}\) (Table 3.6). However, because the strengths of the different year classes varied markedly, a relative abundance analysis was undertaken to take into account this variable recruitment (see Section 2.6 in Materials and Methods). This analysis demonstrated that 11 of the year classes between 1936 and 1992 differed significantly from the average level of recruitment, set at 1. In terms of their influence on the resultant log-likelihood for the estimate for Z determined using the relative abundance analysis, the four most important of these year classes were those of 1972, 1980, 1983 and 1990, which were 3.6, 2.6, 2.1 and 1.5 times greater than the average level of recruitment, respectively, and which had been shown to be relatively strong in the initial plots of the age composition data (Fig. 3.12). Among the other year classes which differed significantly from the average level of annual recruitment, the 1981, 1958, 1971 and 1944 year classes were strong, whereas the reverse was true for the 1991, 1992 and 1985 year classes (Fig. 3.12).

The point estimate for Z increased slightly from 0.086 year\(^{-1}\), when constant recruitment was assumed, to 0.093 year\(^{-1}\) when variable recruitment was taken into account (Table 3.8; Fig. 3.13). The point estimate for M derived from Hoenig’s (1983) equation for fish (0.072 year\(^{-1}\)) was greater than the 0.054 year\(^{-1}\) derived when, by taking into account the probability distribution of Z, the approach of Hall *et al.* (2004) was used to modify that
Figure 3.11. Numbers of individuals of each age class of *Achoerodus gouldii* in commercial gillnet samples obtained from the south coast of Western Australia between August and July in 2004/5, 2005/6 and 2006/7.
Figure 3.12. Numbers of individuals of the 1933 - 1992 year classes of *Achoerodus gouldii* in samples collected by commercial gillnetting on the south coast of Western Australia in a) 2004/5, b) 2005/6 and c) 2006/7. Catch curve and relative abundance analyses were used to fit lines to the observed frequency of abundance of fish in each year class (black circles), assuming that recruitment is either constant (black triangles) or variable (grey circles), respectively.
estimate of Hoenig (1983) (Table 3.8; Fig. 3.13). Furthermore, the use of the latter
approach was accompanied by greatly reduced confidence intervals for the estimates of $M$.

The estimate of fishing mortality, $F$, estimated by Monte Carlo resampling and by
employing the probability distribution derived for $Z$ assuming variable recruitment and for
$M$ from the method of Hall et al. (2004), was 0.039 year$^{-1}$ (Table 3.8).

3.3.11 Current yield and spawning biomass per recruit and spawning potential ratio

The von Bertalanffy growth parameters derived for the females and males of
$A. gouldii$ using the lengths at age for all individuals (Fig. 3.5d, Table 3.2) were used for
the per recruit analyses. Yield per recruit (YPR) analyses for $A. gouldii$, which assumed
that full recruitment into the fishery occurred by 15 years of age, indicate that YPR
increases with increasing fishing mortality until it reaches $c.$ 0.07 year$^{-1}$ and then begins to
decline precipitously (Fig. 3.14). At the current estimated level of $F$ of 0.039 year$^{-1}$, the
YPR is estimated to be 1.88 kg. The estimated level of $F$ corresponding to the reference
point $F_{0.1}$ is 0.051 year$^{-1}$ (Table 3.7).

The current level of spawning stock biomass per recruit (SSB/R) was estimated to
be 44.2 kg for both sexes collectively, and 8.9 and 35.2 kg for females and males,
respectively (Table 3.9). The current level of spawning potential ratio (SPR), in terms of
SSB/R, is estimated to be 0.56 for both sexes combined, and 0.88 for females and 0.52 for
males (Fig. 3.14, Table 3.9).
Table 3.8. Estimates of mortality for *Achoerodus gouldii*. Total mortality (\(Z\)) was derived using catch curve analysis (CCA) assuming constant recruitment and relative abundance analysis (RAA) assuming variable recruitment, while natural mortality (\(M\)) was determined by refitting the empirical equation for fish of Hoenig (1983) and using the approach of Hall *et al.* (2004). Fishing mortality (\(F\)) was estimated employing a Monte Carlo resampling analysis and using the estimates of \(Z\) from the RAA assuming variable recruitment and of \(M\) from the method of Hall *et al.* (2004).

<table>
<thead>
<tr>
<th>Method of analysis</th>
<th>(Z, M \text{ or } F) (\text{(year}^{-1}))</th>
<th>Estimate</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCA (constant recruitment)</td>
<td>(Z)</td>
<td>0.086</td>
<td>0.080</td>
<td>0.092</td>
</tr>
<tr>
<td>RAA (variable recruitment)</td>
<td>(Z)</td>
<td>0.093</td>
<td>0.086</td>
<td>0.100</td>
</tr>
<tr>
<td>Refitted Hoenig (1983) fish equation</td>
<td>(M)</td>
<td>0.072</td>
<td>0.022</td>
<td>0.180</td>
</tr>
<tr>
<td>Combined (M) (Hall <em>et al.</em>, 2004)</td>
<td>(M)</td>
<td>0.054</td>
<td>0.021</td>
<td>0.090</td>
</tr>
<tr>
<td>Monte Carlo resampling</td>
<td>(F)</td>
<td>0.039</td>
<td>0.003</td>
<td>0.073</td>
</tr>
</tbody>
</table>

Table 3.9. Estimates for *Achoerodus gouldii* of the current level of yield per recruit (YPR), \(F_{0.1}\) and the current levels of spawning stock biomass per recruit (SSB/R) and spawning potential ratio (SPR) for females, males and both sexes combined. Calculations assumed that full recruitment to the fishery had occurred by the age of 15 years.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Estimate</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>YPR (kg)</td>
<td>1.88</td>
<td>0.08</td>
<td>5.7</td>
</tr>
<tr>
<td>(F_{0.1}) (year(^{-1}))</td>
<td>0.051</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SSB/R (females &amp; males)</td>
<td>44.2</td>
<td>25.3</td>
<td>72.7</td>
</tr>
<tr>
<td>SPR (females)</td>
<td>0.88</td>
<td>0.75</td>
<td>0.99</td>
</tr>
<tr>
<td>SPR (males)</td>
<td>0.52</td>
<td>0.27</td>
<td>0.96</td>
</tr>
<tr>
<td>SPR (females &amp; males)</td>
<td>0.56</td>
<td>0.31</td>
<td>0.96</td>
</tr>
</tbody>
</table>
Figure 3.13. Probability distributions, for *Achoerodus gouldii*, of natural mortality, $M$ (dotted line) (derived using the method of Hall *et al.* (2004) and an estimate of $M$ obtained by refitting the Hoenig (1983) regression equation for fish) and total mortality, $Z$ (solid line), determined using relative abundance analysis and assuming variable recruitment.
Figure 3.14. The effect of fishing mortality ($F$) at the current age at recruitment into the commercial gillnet fishery of *Achoerodus gouldii* on the a) yield per recruit (YPR) and b) spawning potential ratio (SPR).
3.4 DISCUSSION

3.4.1 Demonstration of protogynous hermaphroditism

The fact that all of the numerous *A. gouldii* caught with lengths < 655 mm were females and males subsequently rose in prevalence with increasing body size to the point where this sex constituted 100% of the larger fish, suggest that, as hypothesised, this labrid is a protogynous hermaphrodite. Such a conclusion is consistent with all but one of the 164 individuals < 15 years being females and the proportion of males subsequently increasing progressively to about 50% in individuals > 20 years old. It is also consistent with the results of our histological investigation of the gonads of a substantial number of individuals, covering the full size range of *A. gouldii* and all months of the year. These demonstrated that the mature testes of males contained conspicuous sperm sinuses in their outer walls and possessed a prominent and central lumen very similar to that found in the ovaries of females. Furthermore, this prominent structure was present in the gonads of each of the six “intermediate-sized” individuals that contained both ovarian and testicular tissues and were thus assumed to be changing from female to male. Thus, as with other protogynous labrids, the prominent central lumen in the testis is considered to represent a retention of the ovarian lumen and, as in other protogynous hermaphroditic labrids, accounts for the peripheral location of the sperm ducts in those testes (*e.g.* Reinboth, 1970; Sadovy and Shapiro, 1987; Gillanders, 1995a; Denny and Schiel, 2002). From the above, it follows that *A. gouldii* possesses the characteristics that fulfill the criteria of Sadovy and Shapiro (1987) for demonstrating that it is a protogynous hermaphrodite and the universal presence of a central “ovarian” lumen in testes and prominent peripherally-located sperm sinuses in mature testes demonstrate that it is monandric, *i.e.* all males are derived from mature females.
3.4.2 Growth

Although the von Bertalanffy growth curve provided a good fit to the lengths at age of all aged individuals of *A. gouldii* irrespective of their sex, the variation in the lengths at age became very marked after c. 30 years of age (Fig. 3.5a). This variation clearly reflects a marked divergence in the growth of females and males among the larger and older fish (Fig. 3.5b). The fact that the von Bertalanffy growth parameters for green and blue fish in the same subset of individuals were very similar to those derived for females and males demonstrate that growth curves based on colour provide a good proxy for those derived from known sex. Although a substantial number of the larger and older fish caught had been gutted prior to their receipt and could thus not be sexed and used for constructing growth curves for the two sexes, the colour of these unsexed fish was recorded. This was used to develop a novel technique for constructing growth curves for females and males, which incorporated the lengths at age of all sexed and unsexed individuals, but took into account the probability that, on the basis of its length and colour, each unsexed fish would be either female or male. The von Bertalanffy growth curves thus derived for females and males are considered to provide very effective representations of the growth of the two sexes of *A. gouldii* and thus the associated growth parameters for those sexes were used for the per recruit models.

From the lengths at age of the two sexes shown in Fig. 3.5b, it is evident that the fastest growing *A. gouldii* have the greatest tendency to change from female to male. The greater length of the males than females at corresponding ages parallels the situation recorded for a number of other protogynous fishes, *e.g.* *Parapercis cylindrical*, *Chlorurus gibbus*, *Chlorurus sordidus*, *Scarus niger* and *Scarus frenatus* (Munday et al., 2004; Walker and McCormick, 2004; Choat et al., 2006), as well as its congener *Achoerodus viridis* (Gillanders, 1995a). However, although all individuals had apparently become
males by a length of c. 900 mm (Fig. 3.11a), approximately half of the oldest females had not become males (Fig. 5b). These data strongly indicate that some females of *A. gouldii* are not destined to become males, as is also the case with *Cheilinus undulatus*, another large labrid (Choat *et al.*, 2006). Moreover, the conclusion that it is only the fastest growing *A. gouldii* that become males parallels that drawn by Munday *et al.* (2004) for the labrid *S. frenatus*. It is thus concluded that sex change is related more to size than age.

### 3.4.3 Habitats and ontogenetic offshore movements

The vast majority of the *A. gouldii* caught by spear fishing in nearshore waters were obtained from over the granite reefs that dominate the hard-structured substrate found in those waters along the south coast of Western Australia, including its islands (Kendrick, 1999; Sanderson *et al.*, 2000). The size composition of these catches is considered representative of those observed in the assemblages in the main productive sampling sites. The fact that these fish were predominantly < 600 mm and < 12 years old and few were mature during the spawning season strongly suggests that smaller, younger and immature fish occupy nearshore waters, which parallels the conclusions of Shepherd and Brook (2007). Although commercial gillnets would have selected for larger fish, the presence in deeper waters of large numbers of *A. gouldii* > 500 mm and many mature fish during the spawning season is consistent with the offshore movement recorded for this species by Shepherd and Brook (2007).

### 3.4.4 Maximum length and age

As hypothesized in the introduction, the greater total length attained by *A. gouldii* than *A. viridis*, as reflected in the 1162 mm *TL* recorded in the present study vs the 773 mm *TL* (after conversion from *SL*) recorded in the detailed study of Gillanders (1995a) was accompanied by a marked difference in the maximum age determined for these two species.
in the two studies, *i.e.* 70 vs 35 years. The maximum age of *A. gouldii* is thus twice as great as that estimated by Gillanders (1995a) for *A. viridis*, which is apparently the greatest yet recorded for any other species of labrid, including the largest member of this family, *C. undulatus*, which reaches total lengths of 2300 mm and a maximum age of 32 years (Choat *et al*., 2006; Nelson, 2006). From the above, it follows that *A. gouldii* does not have the relatively short life span that is typically a characteristic of large labrids (Choat *et al*., 2006). It is thus relevant that the two *Achoerodus* species, which are the longest living labrids, are essentially temperate species, whereas *C. undulatus* and other large labrids are mainly tropical.

### 3.4.5 Year class strength

The fact that the 1972, 1980, 1983 and 1990 year-classes of *A. gouldii* were particularly strong (Fig. 3.11) raises the question as to what factors led to the production of these strong year classes. Unfortunately, there is a paucity of high quality environmental data for the south coast in the 1970s and 1980s. It could be hypothesised that spawning and recruitment success is greatest in years when the Leeuwin Current is weakest and thus does not exert such a marked tendency to disperse the larvae offshore, as occurs with the western rock lobster *Panulirus cygnus*, but is of advantage to that species (Pearce and Phillips, 1988). In other words, as the juveniles of *A. gouldii* are found inshore, recruitment into those waters would be most likely to occur when the Leeuwin Current was at its weakest. The importance of the role played by Leeuwin Current in dispersing larvae was recently emphasised by Gaughan (2007), who suggested that this current most likely has a negative effect on the larvae of teleosts in that it leads to their loss to offshore waters. In the absence of direct measurements of the Leeuwin Current in earlier years, it is necessary to use sea water levels as a proxy for the strength of the Leeuwin Current (Pearce and Phillips, 1988). Comparisons between the four years of strong recruitment and sea water
levels showed three of those four years coincided with years of weak Leeuwin Current strength (Rochford, 1986; Caputi et al., 1996). However, there was no clear evidence that weak recruitment of *A. gouldii* corresponded to years of strong Leeuwin Current and thus no definitive conclusion can be drawn on the role played by the Leeuwin Current on the recruitment of this labrid.

### 3.4.6 Length and age at maturity and sex change

The hypothesis that the far greater length and age attained by *A. gouldii* than *A. viridis* is accompanied by a far greater length and age at maturity of females has been confirmed. In the case of *A. gouldii*, no mature female was found at a length < 391 mm *TL* and the *L*\(_{50}\) of females at maturity was as high as 653 mm *TL*. Furthermore, only one of the 164 females < 5 years old was mature and maturity was only reached by c. 50% of females after they had reached 15-19 years in age. Although Gillanders (1995a) did not estimate the *L*\(_{50}\) at maturity for females, she recorded that females first matured at 200-220 mm *SL* (= 246-270 mm *TL*) and that the majority matured at 240-280 mm *SL* (= 294-341 mm *TL*). She also found that, while a few female *A. viridis* became mature at the end of their second year of life, the majority matured between their third and fifth years of life.

The trends for maturity to be attained at a greater length and age by *A. gouldii* than by the smaller *A. viridis* is paralleled by the situation with the length and, even more particularly the age at sex change. Thus, whereas *A. gouldii* did not start changing sex until it was 655 mm *TL*, and its *L*\(_{50}\) at sex change was as high as 821 mm (*TL*), males of *A. viridis* were found at lengths as low as 500 mm *SL* (= 603 mm *TL*) (Gillanders 1995a). Only four of 728 *A. gouldii* < 20 years old were males and their prevalence did not reach 50% until they had reached 35-39 years in age. In contrast, sex change was observed in *A. viridis* as young as 10 years old (Gillanders 1995a).
3.4.7 Colour change

*Achoerdus gouldii* undergoes the type of colour change that is found during the life cycle of most protogynous labrids and which is broadly associated with sex change (*e.g.* Roede, 1972; Gillanders 1995a; McBride and Johnson, 2007). This involved a change from green to blue in *A. gouldii*, compared with red/brown to blue in *A. viridis* (Gillanders, 1999). However, as with the latter congeneric species, some females (3%) were not of the initial colour and some of the males (11%) did not have the terminal colour. Furthermore, the continuous variable, length, was found to be a better predictor of sex than the dichotomous variable, colour, although a combination of both of these variables did improve further the predictive ability. This raised the question as to whether colour of *A. gouldii* can be used as a proxy for gonadal type, *i.e.* ovary or testis, and thus of sex to derive a reasonable estimate of the length at sex change. The fitting of logistic curves to the length data for fish with testes and with blue coloration yielded $L_{50}$s of 821 and 779 mm, respectively. Although these two $L_{50}$s differed by 42 mm, their 95% confidence limits overlapped. While caution must be exercised in using colour change to derive an $L_{50}$ for sex change, it does enable a “ball park” value for this $L_{50}$ to be estimated when it is not possible to record the sex of individuals because, for example, they could not be dissected or were carcasses, *i.e.* their viscera had been removed.

3.4.8 Management implications

A combination of extreme longevity (maximum age = 70 years), late maturity ($L_{50}$ = 653 mm and c. 17 years) and late sex change ($L_{50}$ = 821 mm and c. 35 years), make *A. gouldii* potentially very susceptible to even moderate levels of fishing. The data also demonstrated that the strength of recruitment of the different year classes varied greatly and thus certain year classes made large contributions to the overall catch. Consequently,
truncation in the age composition through fishing mortality would be likely to increase the
susceptibility of the stock to overfishing.

The yield per recruit analyses indicate that, at the current estimated level of
exploitation (i.e. $F/Z$) of 45%, the yield per recruit (1.88 kg) is close to the maximum of
2.2 kg, and that, if fishing mortality were to increase beyond 0.07 year$^{-1}$, growth
overfishing would commence. The yield per recruit analyses also suggest that the current
level of fishing mortality is close to the yield per recruit-based reference point of $F_{0.1}$
(year$^{-1}$), often considered more appropriate than the fishing mortality reference point
associated with the maximum yield per recruit, $F_{\text{max}}$.

In the context of the potential for recruitment overfishing of $A. gouldii$, it is relevant
that its much smaller and earlier maturing congener, $A. viridis$, suffered such heavy
mortality in eastern Australia that those waters were closed to commercial and recreational
fishing for this species and still remain closed to spear fishing and commercial fishing
(Gillanders, 1999, NSW State of Fisheries Management Regulations 2002). Recently, the
instantaneous rate of fishing mortality for heavily-fished local populations of $A. gouldii$ in
South Australia was estimated to be as high as 0.8 year$^{-1}$ (Shepherd and Brook, 2007). As
the current level of fishing mortality for $A. gouldii$ in south-western Australian waters is
estimated to be 74% of natural mortality, when using the recently-developed approach of
Hall et al. (2004), this species is apparently close to or at full exploitation in these waters.
Even if the unadjusted Hoenig (1983) point estimate of $M$ is used, the corresponding value
is still nearly 55%.

The conclusion that $A. gouldii$ is close to or at full exploitation is consistent with
the estimate of spawning potential ratio (SPR) for the males of this protogynous
hermaphroditic labrid having declined to 0.52 and, given the steepness of the curve relating
SPR to fishing mortality, is rapidly approaching the value of 0.30 often regarded as the one
at which a stock is considered to be overfished (Mace and Sissenwine, 1993; Goodyear, 1993). Indeed the lower 95% CL of 0.27 for SPR lies below this reference point. From a fisheries management point of view, it is also relevant that 52% of the A. gouldii taken by the commercial fishery are below the $L_{50}$ of 653 mm at which females attain maturity, and 88% are below the $L_{50}$ of 821 mm at which females change sex to males. The potential for overfishing of A. gouldii is compounded by the fact that its current minimum legal length (MLL) in Western Australia is 500 mm and thus well below the $L_{50}$ at both maturity and sex change. This is particularly pertinent in the case of recreational line and spear fishing, which occurs mainly in the more accessible, shallow waters (< 20 m) and where the individuals of A. gouldii are smaller than in deeper waters.

From the above, it follows that, as with other hermaphroditic species, management plans for A. gouldii must take into account the ways in which the lengths and ages at which sex change occur are likely to influence that species susceptibility to fishing (see also Bannerot et al., 1987; Buxton, 1992; Hesp et al., 2004; Pember et al., 2005). Furthermore, our data for A. gouldii emphasize that per recruit analyses for hermaphroditic species, in which the growth of the two sexes differ markedly, should ideally incorporate the separate estimates of growth for the females and males. This point is emphasized by the fact that the estimates of SPR for males decline more rapidly with increasing fishing mortality when the different growth of the sexes are taken into account, than when they are not included as separate components in the analysis.

The implications of the life cycle characteristics possessed by A. gouldii and the results of the per recruit analyses demonstrate that managers will need to take a precautionary approach to managing A. gouldii to ensure its sustainability. They will also need to recognize that the individuals of A. gouldii often suffer barotrauma-related injuries when brought to the surface from deep waters (P. Couslon, pers. observ.), thereby
paralleling the situation with many other demersal species (e.g. True et al., 1997; St John and Syers, 2005; Parker et al., 2006), including other species of labrid (e.g. Nardi et al., 2006). Plans for conserving A. gouldii will thus probably have to be directed towards controlling fishing effort, rather than, for example, regulating the size for legal retention.
4.1 INTRODUCTION

The species of the Cheilodactylidae are frequently associated with reefs (Allen et al., 2006c). They vary greatly in the length they attain and recent studies have shown that, in the case of the Banded Morwong Cheilodactylus spectabilis, individuals can exceed 90 years in age (Ewing et al., 2007). Unlike the situation recorded by Choat et al. (2006) for large labrids in tropical waters, the growth of the C. spectabilis is markedly asymptotic (Ewing et al., 2007).

The Blue Morwong Nemadactylus valenciennesi, which is readily identifiable by its bright blue colour and yellow lines around the eyes, is common around inshore and offshore reefs in south-western Western Australian and South Australian waters, where it can reach lengths of c. 100 cm and weights of c. 11 kg (Hutchins and Swainston, 1986; Lowry and Cappo, 1999). Although N. valenciennesi is the most abundant species of scalefish caught by the commercial gillnet fishery operating off the south coast Western Australia (McAuley and Simpfendorfer, 2003), there have been no studies of its biology.

The aim of the present study was to determine the length and age compositions, growth and key aspects of the reproductive biology, i.e. spawning time and period and length and age at maturity, of N. valenciennesi. Comparisons have been made between the characteristics of the individuals caught in inshore and offshore waters and on the lower west and south coasts of Western Australia, in which, for example, water temperatures differ. The length and age compositions of N. valenciennesi caught by different methods (spear fishing, recreational line fishing and commercial gill netting) are compared. Finally, estimates were made of mortality, yield per recruit and spawning stock biomass per recruit to ascertain whether there is evidence that this species is being heavily or over exploited.
4.2 MATERIALS AND METHODS

4.2.1 Sampling regime

*Nemadactylus valenciennesi* was collected mainly using the same methods and localities, except Hopetoun, as described for *A. gouldii* (Chapter 3). Additional fish were obtained from weigh-ins held after annual recreational fishing competitions in Esperance, Bremer Bay and Albany and at monthly recreational fishing competitions in Perth (Fig. 3.1). The sources (*i.e.* spear fishing, recreational line fishing or commercial gill netting), locations and length ranges of *N. valenciennesi* in each of the total sample for each month of each year of sampling are provided in Table 4.1.

4.2.2 Laboratory procedures and analyses

*Nemadactylus valenciennesi* was subjected to the same procedures and analyses as described in the General Materials and Methods (Chapter 2). In addition, the fork length (*FL*) and total length (*TL*) in a subsample covering a wide size range of *N. valenciennesi* were recorded in order to derive the relationship between these two length variables and thus facilitate comparisons between the lengths recorded in the present study and those in other studies of *Nemadactylus macropoterus*, *Cheilodactylus spectabilis* and *Cheilodactylus fuscus* where *FL* rather than *TL* was recorded (Smith, 1982; Murphy and Lyle, 1999; Jordan, 2001a; Lowry, 2003; Ewing et al., 2007).

The growth curves of the females and males of *N. valenciennesi* caught in waters on the lower west coast were compared with those of the corresponding sexes on the south coast in the same manner as described in Chapter 2.
Table 4.1. Sample sizes and length ranges of *Nemadactylus valenciennesi* collected by spear fishing, recreational line fishing and commercial gill netting on the south and lower west coasts of Western Australia.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Spear fishing (south coast)</th>
<th>Line fishing (south coast)</th>
<th>Line fishing (lower west coast)</th>
<th>Gill netting (south coast)</th>
<th>Gill netting (lower west coast)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>n</td>
<td>Length range (TL mm)</td>
<td>n</td>
<td>Length range (TL mm)</td>
<td>n</td>
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<tr>
<td>2004</td>
<td>March</td>
<td>4</td>
<td>431-747</td>
<td>23</td>
<td>480-919</td>
<td>27</td>
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<tr>
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<td>April</td>
<td>2</td>
<td>561-704</td>
<td>3</td>
<td>703-784</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>1</td>
<td>563</td>
<td>1</td>
<td>564</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>3</td>
<td>703-784</td>
<td>2</td>
<td>703-784</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>5</td>
<td>556-808</td>
<td>23</td>
<td>511-800</td>
<td>19</td>
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<tr>
<td></td>
<td>September</td>
<td>9</td>
<td>270-720</td>
<td>23</td>
<td>511-800</td>
<td>19</td>
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<tr>
<td></td>
<td>October</td>
<td>6</td>
<td>550-789</td>
<td>23</td>
<td>511-800</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>December</td>
<td>79</td>
<td>568-897</td>
<td>23</td>
<td>511-800</td>
<td>19</td>
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<td>2005</td>
<td>January</td>
<td>8</td>
<td>549-870</td>
<td>4</td>
<td>651-723</td>
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<td>32</td>
<td>535-850</td>
<td>33</td>
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<tr>
<td></td>
<td>April</td>
<td>5</td>
<td>646-765</td>
<td>2</td>
<td>709-755</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>30</td>
<td>185-689</td>
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<td>880</td>
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<tr>
<td></td>
<td>June</td>
<td>20</td>
<td>197-712</td>
<td>1</td>
<td>825</td>
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<td>3</td>
<td>584-653</td>
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<td>649-805</td>
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<td></td>
<td>August</td>
<td>29</td>
<td>255-592</td>
<td>3</td>
<td>706-812</td>
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<tr>
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<td>September</td>
<td>16</td>
<td>280-648</td>
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<td></td>
<td>October</td>
<td>3</td>
<td>616-774</td>
<td>65</td>
<td>530-891</td>
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<tr>
<td></td>
<td>November</td>
<td>89</td>
<td>404-902</td>
<td>2</td>
<td>709-755</td>
<td>79</td>
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<tr>
<td></td>
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<td>25</td>
<td>330-758</td>
<td>2</td>
<td>709-755</td>
<td>12</td>
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<tr>
<td>2006</td>
<td>January</td>
<td>44</td>
<td>312-772</td>
<td>9</td>
<td>549-724</td>
<td>6</td>
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<tr>
<td></td>
<td>February</td>
<td>25</td>
<td>330-758</td>
<td>89</td>
<td>404-902</td>
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<td>342-689</td>
<td>11</td>
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<td></td>
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<td>4</td>
<td>495</td>
<td>6</td>
<td>512-872</td>
<td>48</td>
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<td>May</td>
<td>30</td>
<td>495-984</td>
<td>3</td>
<td>614-716</td>
<td>108</td>
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<tr>
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<td>June</td>
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<td>495-984</td>
<td>3</td>
<td>614-716</td>
<td>108</td>
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<td>Avg-Max</td>
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<td></td>
</tr>
<tr>
<td>July</td>
<td>22</td>
<td>366-835</td>
<td>103</td>
<td>491-958</td>
<td></td>
<td></td>
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<tr>
<td>August</td>
<td>144</td>
<td>491-859</td>
<td></td>
<td></td>
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<td></td>
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<td>September</td>
<td>11</td>
<td>402-686</td>
<td>144</td>
<td>491-859</td>
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<td>October</td>
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<td>448-721</td>
<td>95</td>
<td>528-950</td>
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<td>November</td>
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<td>373-779</td>
<td>528</td>
<td>950-1900</td>
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</tr>
<tr>
<td>December</td>
<td>13</td>
<td>598-786</td>
<td></td>
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<tr>
<td>2007</td>
<td>13</td>
<td>598-786</td>
<td></td>
<td></td>
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<tr>
<td>January</td>
<td>15</td>
<td>336-641</td>
<td>43</td>
<td>497-951</td>
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<td></td>
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<td>24</td>
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<tr>
<td>April</td>
<td>12</td>
<td>493-765</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>June</td>
<td>11</td>
<td>457-817</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>July</td>
<td>2</td>
<td>593-636</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>October</td>
<td>8</td>
<td>587-820</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
<td>322</td>
<td>185-835</td>
<td>113</td>
<td>431-919</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
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<td>404-984</td>
<td>1013</td>
<td>442-958</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>102</td>
<td>517-850</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
4.3 RESULTS

4.3.1 Environmental measurements

Mean monthly water temperatures in inshore waters at Albany and Esperance, which, in most months, differed by < 1.5°C, rose from their minima of c. 14.5 to 15.5°C in July and August to c. 21.2 to 21.7°C in January and then declined to c. 15.5 to 16.5°C in June (Fig. 4.1). The mean monthly water temperatures were less at Albany than Esperance in July to October and from March to July, whereas the reverse was true for November to February.

Although the mean monthly water temperatures followed very similar trends throughout the year in the deeper waters at the three locations at which *N. valenciennesi* were caught, they were, in any one month, always greater at Rottnest than at Albany, which, in turn, were always greater than at Esperance (Fig. 4.1). The minimum mean monthly temperatures at those three localities, which were recorded in either September or October were 18, 16.5 and 15°C, respectively, whereas the maximum mean temperatures, which were recorded in March, were 22, 20 and 19°C, respectively.

4.3.2 Validation of ageing using otoliths

The alternating opaque and translucent zones were clearly defined in sectioned otoliths of *N. valenciennesi* when these otoliths were viewed using transmitted light (Fig. 4.2). The central primordium region of the otolith is wide and opaque and surrounded by a translucent zone. The first opaque zone is relatively wide and, like the previous translucent zone on its inner edge, becomes increasingly less defined in older fish and particularly in those with > 9 opaque zones (Fig. 4.2). Each opaque zone, which was most clearly defined on the lower ventral region of the sectioned otolith, tends to become successively narrower towards the otolith periphery.
Figure 4.1. Mean monthly water temperatures ± 1 SE for a) inshore waters at Albany (grey circles) and Esperance (black circles) and b) offshore waters at Albany (grey circles), Esperance (black circles) and Rottnest (black triangles) on the south and lower west coasts of Western Australia. In this Fig. and Figs. 4.3 and 4.6, closed rectangles on the x-axis refer to winter and summer months and the open rectangles to spring and autumn months.
Figure 4.2. Sectioned otoliths of *Nemadactylus valenciennesi* with a) 1, b) 3, c) 8, d) 14 and e) 17 opaque zones (○). Scale bars = 0.5 mm.
The mean monthly marginal increments for otoliths with two to four zones remained > 0.37 between September and November and then declined precipitously to 0.30 in December and 0.25 in January, after which they increased progressively to 0.34 in July (Fig. 4.3). The mean monthly marginal increments for otoliths with five to seven, eight to ten and > 10 zones followed essentially the same trend as that described above for otoliths with two to four zones, with values declining markedly to their minima in mid-summer (Fig. 4.3). Although the number of fish with otoliths containing one opaque zone in many months was low, the trends exhibited by the mean monthly marginal increments could still be seen to follow the same seasonal pattern as those just described for otoliths with a greater number of opaque zones (Fig. 4.3). The single pronounced decline and then progressive increase undergone by the mean monthly marginal increments during the year demonstrate that a single opaque zone is formed annually in the otoliths of *N. valenciennesi* and that the number of opaque zones in those otoliths could thus be used to estimate the age of the individuals of this species.

For ageing purposes, 1 March was considered to represent the birth date of *N. valenciennesi* as the trends exhibited by reproductive variables demonstrated that the approximate mid-point of the spawning period of this species was March (see later).

The two smallest *N. valenciennesi*, whose otoliths were not damaged during capture, as occurred with the smallest fish of 157 mm, were caught in May and June and measured 185 and 197 mm, respectively. On the basis of studies of other cheilodactylids (*e.g.* *N. macropeterus*), the lengths of these individuals is far greater than would be expected if they were derived from spawning in the immediately preceding summer/autumn spawning period. Their otoliths contained a central opaque primordium and a surrounding translucent area and no clearly defined outer opaque zone. A single, recently-formed opaque zone was seen in the otoliths of fish that were caught in December and
Figure 4.3. Mean monthly marginal increments ± 1 SE on sectioned sagittal otoliths of *Nemadactylus valenciennesi* with different numbers of opaque zones. Sample sizes shown above each mean.
measured 294, 297 and 299 mm.

From the sizes and times of capture of the above fish and the characteristics of their otoliths, it is assumed that an opaque zone is not laid down until the second winter of life when the fish are just over a year old. In other words, the above fish caught in May and June were c. 15 and 16 months old, while those from December were c. 22 months old.

4.3.3 Length and age compositions of catches

The individuals of *N. valenciennesi* that could be sexed during this study ranged in length and age from 157 to 846 mm and 1 to 19 years for females and from 192 to 984 mm and 1 to 19 years for males. The largest and oldest *N. valenciennesi*, from which the gonads had been removed during filleting and could thus not be sexed was 958 mm and 21 years.

The *N. valenciennesi* collected by spear fishing (inshore), recreational line fishing (offshore) and commercial gill netting (offshore) ranged in length from 157 to 868 mm ($\bar{x} = 494$ mm), 404 to 984 mm ($\bar{x} = 653$ mm) and 442 to 958 mm ($\bar{x} = 682$ mm), respectively (Fig. 4.4a). These lengths correspond to fish ranging in age from 1 to 16 years, 2 to 19 years and 3 to 21 years of age, respectively (Fig. 4.4b). The length and age compositions show that *N. valenciennesi* becomes fully recruited into the recreational and commercial fisheries at lengths of 600 to 649 mm and 650 to 699 mm, respectively, and at 6 and 9 years of age, respectively.

The likelihood ratio test demonstrated that, on both the south and lower west coasts, the growth curves of females and males of *N. valenciennesi* were significantly different ($p < 0.05$). Although the growth curves of the corresponding sexes on the two coasts were significantly different ($p < 0.05$), the differences in the lengths estimated from those curves for females and males at each age between five and 12 years, for which there were substantial samples, was always less than 4%. Thus, these differences between
Figure 4.4. Length and age-frequency distributions for *Nemadactylus valenciennesi* caught in inshore waters by spear fishing (grey histograms) and recreational line fishing (black histograms) and commercial gillnetting (white histograms) in offshore waters. $n_s$, $n_r$ and $n_g$, number of fish caught by spear fishing, recreational line fishing and commercial gill netting, respectively.
regions are considered to be of little biological significance and consequently the lengths at age of females and of males in the two regions have been pooled to produce a growth curve for each sex based on pooled data for the two regions (Fig. 4.5).

The von Bertalanffy growth curves fitted well the lengths at age of the individuals of those sexes (Fig. 4.5) as demonstrated by the relatively high values of 0.86 and 0.80 for the coefficients of determination for the curves for females and males, respectively (Table 4.2). The growth curves of females and males were significantly different ($p < 0.001$). On average, at ages 5, 7 10, 13 and 15 years, females attain lengths of 550, 615, 662, 682 and 688 mm, compared with 583, 673, 752, 793 and 809 mm by males.

The relationship between total length ($TL$) in mm and total weight ($W$) in g for *N. valenciennesi* is described by the following regression equation: $\ln W = 2.969(\ln TL) - 11.154$ ($r^2 = 0.991$, $n = 330$, $p = < 0.001$). The relationship between fork length ($FL$) and total length ($TL$) in mm for *N. valenciennesi* is described by the following regression equation: $TL = 1.118(FL) + 25.105$ ($r^2 = 0.993$, $n = 1374$, $p = < 0.001$).

| Table 4.2. The von Bertalanffy growth parameters $L_\infty$, $k$ and $t_0$, and their lower and upper 95% confidence limits, for the females and males of *Nemadactylus valenciennesi* in southwestern Australia. $L_\infty$ is the asymptotic length (TL mm), $k$ is the growth coefficient (year$^{-1}$), $t_0$ is the hypothetical age (years) at which fish would have zero length, $r^2$ is the coefficient of determination and $n$ is the number of fish. |
|---|---|---|---|---|---|
| Female | $L_\infty$ (TL mm) | $k$ (year$^{-1}$) | $t_0$ (years) | $r^2$ | $n$ |
| Estimate | 696 | 0.29 | -0.36 | 0.86 | 356 |
| Lower | 678 | 0.25 | -0.65 |  |  |
| Upper | 713 | 0.33 | -0.07 |  |  |
| Male | Estimate | 839 | 0.22 | -0.52 | 0.80 | 460 |
| Lower | 808 | 0.18 | -0.87 |  |  |
| Upper | 870 | 0.25 | -0.17 |  |  |
Figure 4.5. von Bertalanffy growth curves fitted to the lengths at age of females and males of *Nemadactylus valenciennesi*. $n = \text{sample size}$. 
4.3.4 Reproductive biology

The characteristics of each macroscopic stage in the development of ovaries and testes and the corresponding histological stages in the development of the ovaries of *N. valenciennesi* are presented in Tables 4.2 and 4.3, respectively.

As the vast majority of fish caught in inshore waters on the south coast were immature (see Fig. 4.8a), the mean monthly GSIs were not calculated for either the females or males in these waters. The mean monthly GSIs for female *N. valenciennesi* in south coast offshore waters rose progressively from 0.8 in December to reach a maximum of 2.2 in March, before declining precipitously to 0.5 in June (Fig. 4.6a).

Since all or the vast majority of each length class of both the females and males of *N. valenciennesi* in offshore waters of the lower west coast were mature during the spawning period (see Fig. 4.8), the mean monthly GSIs for fish in these waters were constructed using the data for all fish caught in those waters. Although the mean monthly GSIs for female *N. valenciennesi* in lower west coast offshore waters displayed a similar seasonal trend to those of females in offshore waters of the south coast, the maximum mean monthly GSIs were far greater, *i.e.* 3.8 vs 2.2 (Fig. 4.6b). The mean monthly GSIs for male *N. valenciennesi* in offshore waters of the south and lower west coasts displayed similar trends to those described for their females and likewise reached higher maxima on the latter coast (Fig. 4.6a, b).

The ovaries of all females caught in offshore waters on the south coast from January to November were at stages I/II (Fig. 4.7). The prevalence of females with stages V/VI ovaries was low, *i.e.* ≤ 25%, in all months in which they were present except for March, when it was 83%, but in which the sample size was small. Males with testes at stages V/VI were present in samples from offshore waters of the south coast only in February and March (Fig. 4.7).
Table 4.2. Description of macroscopic stages in the development of the ovaries and testes of the females and males of *Nemadactylus valenciennesi*. Details of stages are adapted from Laevastu (1965).

<table>
<thead>
<tr>
<th>Macroscopic stage</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I virgin</td>
<td>Ovaries pink, short and wide. No visible capillaries. As in all maturation stages, the two ovarian lobes are tightly joined by a thin membrane.</td>
<td>Very fine strand-like testes connected tightly to roof of the body cavity. Transparent to white.</td>
</tr>
<tr>
<td>Stage II immature</td>
<td>Ovaries, round and pink and twice as long as previous stage and often surrounded by fat. Capillaries just visible.</td>
<td>Thicker and longer and still tightly connected to roof of body cavity. Partially covered by fat.</td>
</tr>
<tr>
<td>Stage III developing</td>
<td>Ovary orange with small white oocytes just visible through ovarian wall. Capillaries more prominent.</td>
<td>White, thin, long testes. May still be surrounded by fat.</td>
</tr>
<tr>
<td>Stage IV maturing</td>
<td>Ovary occupies $\frac{1}{4}$ of body cavity. Numerous orange to yellow oocytes clearly visible through ovarian wall.</td>
<td>Testes white and occupying $\frac{1}{4}$ of body cavity. Milt extruded under strong pressure.</td>
</tr>
<tr>
<td>Stage V mature</td>
<td>Ovary occupies $\frac{1}{2}$ to $\frac{2}{3}$ of body cavity. Yellow oocytes visible through ovarian wall give ovary a yellow appearance. Prominent red capillaries.</td>
<td>White testes occupying $\frac{1}{3}$ of body cavity. Milt extruded under light pressure.</td>
</tr>
<tr>
<td>Stage VI spawning</td>
<td>Large ovary, occupying $\frac{2}{3}$ of body cavity. Orange to red. Yolk granule and translucent hydrated oocytes visible through ovarian wall. During ovulation and spawning, the presence of hydrated oocytes in the ovarian duct produces a translucent region that runs down the ventral surface of both ovarian lobes.</td>
<td>White testes very soft and easily perforated. Occupying $\frac{1}{2}$ of body cavity. Milt extruded at slightest pressure.</td>
</tr>
<tr>
<td>Stage VII spent</td>
<td>Very similar in size to stage IV. Ovary flaccid and orange, with a very thick, opaque wall. Capillaries thin containing little blood.</td>
<td>Testes grey and similar in size to stage III and some residual milt.</td>
</tr>
</tbody>
</table>
Table 4.3. Histological characteristics of the macroscopic stages in the development of the ovaries of female *Nemadactylus valenciennesi*. Terminology for oocyte stages follows Wallace and Selman (1981). Scale bar in Stage I = 50 µm, scale bars in all other stages = 200 µm.

<table>
<thead>
<tr>
<th>Macroscopic stage</th>
<th>Histological section</th>
<th>Histological characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I <em>Virgin</em></td>
<td><img src="image1.png" alt="Image" /></td>
<td>Small oogonia (o) and chromatin nucleolar oocytes (c) present.</td>
</tr>
<tr>
<td>Stage II <em>Immature</em></td>
<td><img src="image2.png" alt="Image" /></td>
<td>Chromatin nucleolar (c) and perinucleolar oocytes (p) arranged along ovarian lamellae. Previtellogenic oocytes are present in all subsequent ovarian stages.</td>
</tr>
<tr>
<td>Stage III <em>Developing</em></td>
<td><img src="image3.png" alt="Image" /></td>
<td>Cortical alveolar oocytes (ca) are abundant. Yolk granule oocytes not present.</td>
</tr>
<tr>
<td>Stage IV <em>Maturing</em></td>
<td><img src="image4.png" alt="Image" /></td>
<td>Cortical alveolar oocytes (ca) and yolk granule oocytes (y) are abundant.</td>
</tr>
<tr>
<td>Stage V <em>Mature</em></td>
<td><img src="image5.png" alt="Image" /></td>
<td>Cortical alveolar oocytes (ca) and yolk granule oocytes (y) are present. The latter are more abundant than in previous stage.</td>
</tr>
<tr>
<td>Stage VI <em>Spawning</em></td>
<td><img src="image6.png" alt="Image" /></td>
<td>Cortical alveolar oocytes (ca) and yolk granule oocytes (y) present, together with hydrated oocytes (h) and and/or post-ovulatory follicles (pof).</td>
</tr>
<tr>
<td>Stage VII <em>Spent</em></td>
<td><img src="image7.png" alt="Image" /></td>
<td>Ovary contains residual yolk granule oocytes (y) undergoing atresia and connective tissue (t).</td>
</tr>
</tbody>
</table>
Figure 4.6. Mean monthly gonadosomatic indices ± 1 SE for (a) females and males \( \geq L_{50} \) at maturity, *i.e.* 637 mm and 725 mm, respectively, from south coast offshore waters and (b) female and male *Nemadactylus valenciennessi* \( \geq 400 \) and 500 mm, respectively, from lower west coast offshore waters. Sample sizes are shown above each mean.
Females and males with ovaries and testes at stages V/VI, respectively, were far more prevalent in offshore waters of the lower west coast than south coast and were present for a more protracted period in those former waters (Fig. 4.7).

The above trends exhibited by the mean monthly values for female and male GSIs and prevalence of females and males with stages V/VI ovaries and testes, respectively, demonstrate that spawning occurs predominantly between January and May. For this reason, 1 March was chosen as the birth date for *N. valenciennesi*.

### 4.3.5 Length and age at maturity

Few mature females or males were caught in inshore waters of the south coast (Fig. 4.8a). The percentage of mature females in offshore waters of the south coast increased progressively from 12% in fish of 500 to 549 mm to c. 50% in those of 600 to 699 mm and 100% in females > 750 mm (Fig. 4.8b). A similar trend occurred with males. Although the prevalence of mature females and males in offshore waters of the south coast increased with total length, the pattern of change did not follow a logistic trend (Fig. 4.8b) and thus the approximate length at which maturity was reached by 50% of females (650 mm) and males (725 mm) were derived from an examination of the data shown in Figure 4.8b.

The proportion of mature fish among females and males in offshore waters of the south coast were 48 and 43%, respectively. Although the length ranges of females and males in offshore waters of the lower west coast were similar to those on the south coast, the vast majority of the females (89%) and males (82%) on the lower west coast were mature (Fig. 4.8c).

None of the females caught below the age of five years in nearshore waters of the south coast was mature and the same was true of males under the age of ten years (Fig. 4.9a). In south coast offshore waters, the percentage frequency of occurrence of mature females was as low as 16% in fish of six years, but subsequently increased in an essentially
Figure 4.7. Monthly percentage frequencies of occurrence of sequential stages in gonadal development of female and male *Nemadactylus valenciennesi* $\geq L_{50}$ at maturity, *i.e.* 637 mm and 725 mm, respectively, from south coast offshore waters and females and males $\geq$ 400 and 500 mm, respectively, from lower west coast offshore waters. Histograms for stages V and VI collectively are highlighted in black. $n =$ sample size.
Figure 4.8. Percentage frequency of occurrence of female and male *Nemadactylus valenciennesi* with mature gonads (grey histograms) in sequential 50 mm length classes in samples obtained during spawning period, *i.e.* January to May, from a) south coast inshore waters, b) south coast offshore waters and c) lower west coast offshore waters. Sample sizes shown above each histogram.
progressive manner to 100% in fish of ≥ 13 years (Fig. 4.9b). The prevalence of mature male fish in those waters also rose with increasing age (Fig. 4.9b). In contrast, all female *N. valenciennesi* caught in offshore waters of the lower west coast were ≥ three years old and, of those, all but four 5 year olds and two 9 year olds were mature (Fig. 4.9c). Similarly, all males caught in these waters were ≥ three years old and the vast majority of these fish were mature (Fig. 4.9c).

### 4.3.6 Batch fecundity

The diameter frequencies of oocytes in the ovaries of two mature (stage V) female *N. valenciennesi*, and which contained early previtellogenic, cortical alveolar and yolk granule oocytes, formed essentially continuous distributions (Fig. 4.10). This continuity in the distribution of the sizes of oocytes demonstrates that *N. valenciennesi* possesses indeterminate fecundity and indicates that females release batches of eggs at intervals throughout its spawning period.

Batch fecundity estimates for seven females of *N. valenciennesi*, with lengths and weights ranging from 534 and 710 mm and from 1.8 to 4.2 kg, respectively, ranged from 67,977 and 388,995 eggs and produced mean ± 95% CL of 231,006 ± 77,528.

### 4.3.7 Estimates of mortality

The data in Figure 4.4 demonstrate that *N. valenciennesi* has become fully recruited into the commercial gillnet fishery by an age of 9 years. Catch curve analysis of the commercial gillnet data (i.e. for the fishery for which the data were most substantial and reliable) yielded an estimate of 0.40 year^{-1} for Z (Table 4.3). The point estimate of 0.24 year^{-1} for *M* derived using the equation of Hoenig (1983) was greater than the 0.19 year^{-1} derived for this variable using the approach of Hall *et al.* (2004) (Fig. 4.11). As with *A. gouldii*, the use of this latter method produced far narrower confidence intervals for the
Figure 4.9. Percentage frequency of occurrence of female and male *Nemadactylus valenciennesi* with mature gonads (grey histograms) in one year age groups sampled during the spawning period, *i.e.* January to May, from a) south coast inshore waters, b) south coast offshore waters and c) lower west coast offshore waters. Sample sizes are shown above each histogram.
Figure 4.10. Oocyte diameter frequency distributions of two mature (stage V) female *Nemadactylus valenciennesi*. Early previtellogenic oocytes (white), cortical alveolar oocytes (grey), yolk granule oocytes (black).
Table 4.3. Estimates of mortality for *Nemadactylus valenciennesi*. Total mortality (Z) was derived using catch curve analysis (CCA) assuming constant recruitment, while natural mortality (M) was determined by refitting the empirical equation for fish of Hoenig (1983) and using the approach of Hall *et al.* (2004). Fishing mortality (F) was estimated employing a Monte Carlo resampling analysis and using the estimates of Z from the CCA and of M from the method of Hall *et al.* (2004).

<table>
<thead>
<tr>
<th>Method of analysis</th>
<th>Z, M or F (year(^{-1}))</th>
<th>Estimate</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCA (constant recruitment)</td>
<td>Z</td>
<td>0.40</td>
<td>0.36</td>
<td>0.44</td>
</tr>
<tr>
<td>Refitted Hoenig (1983) fish equation</td>
<td>M</td>
<td>0.24</td>
<td>0.08</td>
<td>0.58</td>
</tr>
<tr>
<td>Combined M (Hall <em>et al.</em>, 2004)</td>
<td>M</td>
<td>0.19</td>
<td>0.07</td>
<td>0.38</td>
</tr>
<tr>
<td>Monte Carlo re-sampling</td>
<td>F</td>
<td>0.20</td>
<td>0.02</td>
<td>0.33</td>
</tr>
</tbody>
</table>

An estimate of M (Table 4.3). Fishing mortality, F, estimated using Monte Carlo resampling and employing the probability distributions derived for Z assuming constant recruitment and for M from the Hall *et al.* (2004) analysis, was 0.20 year\(^{-1}\) (Table 4.3).

After adjusting for sample size, the age compositions of fish collected from recreational and commercial catches of *N. valenciennesi* were found to be very similar, suggesting that the selectivity curves of the fishing methods employed by the two fishing sectors, *i.e.* hand lining and gill netting, are also similar. This implies that estimates of age-dependent selectivity, derived using the age composition of fish collected from the commercial fishery, are likely to be representative of the selectivity curves for both fishing sectors.

### 4.3.8 Current yield and spawning biomass per recruit and spawning potential ratio

Analysis of commercial gillnet data for *N. valenciennesi* indicates that yield per recruit (YPR) increases with increasing fishing mortality over the range from 0 to 0.80 year\(^{-1}\) (Fig. 4.12). At the current estimated level of 0.20 year\(^{-1}\) for F, the YPR is estimated to be 0.54 kg. The estimated level of F corresponding to the reference point \(F_{0.1}\) is 0.31 year\(^{-1}\) (Table 4.4).
Figure 4.11. Probability distributions, for *Nemadactylus valenciennesi*, of natural mortality, $M$ (dotted line) (derived using the method of Hall *et al.* (2004) and an estimate of $M$ obtained by refitting the Hoenig (1983) regression equation for fish) and total mortality, $Z$ (solid line), determined using catch curve analysis and assuming constant recruitment.
The current level of spawning stock biomass per recruit (SSB/R) was estimated to be 2.40 kg for both sexes collectively and 1.48 and 0.91 kg for females and males, respectively (Table 4.5). The current level of spawning potential ratio (SPR), in terms of SSB/R, is estimated to be 0.57 for both sexes combined, and 0.59 for females and 0.56 for males (Fig. 4.12, Table 4.4).

Table 4.4. Estimates for *Nemadactylus valenciennesi* of the current level of yield per recruit (YPR), $F_{0.1}$ and the current levels of spawning stock biomass per recruit (SSB/R) and spawning potential ratio (SPR) for females, males and both sexes combined.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Estimate</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>YPR (kg)</td>
<td>0.54</td>
<td>0.02</td>
<td>1.92</td>
</tr>
<tr>
<td>$F_{0.1}$ (year$^{-1}$)</td>
<td>0.31</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SSB/R (females &amp; males)</td>
<td>2.40</td>
<td>0.83</td>
<td>4.69</td>
</tr>
<tr>
<td>SPR (females)</td>
<td>0.59</td>
<td>0.24</td>
<td>0.93</td>
</tr>
<tr>
<td>SPR (males)</td>
<td>0.56</td>
<td>0.22</td>
<td>0.97</td>
</tr>
<tr>
<td>SPR (females &amp; males)</td>
<td>0.57</td>
<td>0.23</td>
<td>0.97</td>
</tr>
</tbody>
</table>
Figure 4.12. The effect of fishing mortality ($F$) at the relative vulnerability at age for the commercial gillnet fishery of *Nemadactylus valenciennesi* on the a) yield per recruit (YPR) and b) spawning potential ratio (SPR).
4.4 DISCUSSION

4.4.1 Ageing

A preliminary comparison of the counts for opaque zones on the same otoliths of *Nemadactylus valenciennesi*, prior to and after sectioning, demonstrated that particularly the larger otoliths of this species required sectioning for all of their opaque zones to be revealed (see Fig. 2.2). This parallels the situation with the jackass morwong *Nemadactylus macropterus* in Tasmania, where the maximum ages derived using the number of opaque zones in sectioned otoliths were far greater than those estimated previously on the basis of the number of such zones in whole otoliths of this species in New South Wales (cf. Smith, 1982; Jordan, 2001a; Table 4.5). Our use of marginal increment analysis for sectioned otoliths of *N. valenciennesi* demonstrated that, irrespective of the number of opaque zones on an otolith of this species, a new opaque zone is formed on that otolith annually. Thus, the number of opaque zones visible in sectioned otoliths of *N. valenciennesi* can be used to help age this cheilodatylid. Since the individuals of *N. macropterus* in Tasmania were aged using the number of opaque zones in sectioned otoliths (Jordan, 2001a), and the same was true for *Cheilodactylus fuscus* in New South Wales (Lowry, 2003) and *Cheilodactylus spectabilis* in Tasmania (Murphy and Lyle, 1999), the ageing of those three species are likewise assumed to be reliable. In the case of the latter species, the validation process included the use of oxytetracycline and bomb radiocarbon methods (Ewing *et al*., 2007).

Because the individuals of *N. macropterus* in New South Wales were aged using counts of growth zones in whole otoliths (Smith, 1982), the age estimates derived for older fish in that study may have been underestimated. Yet, it could be argued that, in the
Table 4.5. Comparisons between growth and maturity characteristics of *Nemadactylus valenciennesi* and other species of the Cheilodactyliidae for which there are substantial data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Max. Length</th>
<th>Max. Age</th>
<th>L&lt;sub&gt;∞&lt;/sub&gt;</th>
<th>k</th>
<th>t&lt;sub&gt;0&lt;/sub&gt;</th>
<th>L&lt;sub&gt;50&lt;/sub&gt;</th>
<th>A&lt;sub&gt;50&lt;/sub&gt;</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nemadactylus valenciennesi</em></td>
<td>Female</td>
<td>731</td>
<td>19</td>
<td>599</td>
<td>0.29</td>
<td>-0.36</td>
<td>503</td>
<td>7 Western Australia (This study)</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>853</td>
<td>19</td>
<td>725</td>
<td>0.22</td>
<td>-0.52</td>
<td>600</td>
<td>7</td>
</tr>
<tr>
<td><em>Nemadactylus macropterus</em></td>
<td>Female</td>
<td>455</td>
<td>30</td>
<td>384</td>
<td>0.33</td>
<td>0.40</td>
<td>250</td>
<td>3 Tasmania (Jordan, 1998, 2001a)</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>423</td>
<td>41</td>
<td>362</td>
<td>0.42</td>
<td>0.15</td>
<td>270</td>
<td>3</td>
</tr>
<tr>
<td><em>Cheilodactylus fuscus</em></td>
<td>Female</td>
<td>460</td>
<td>34</td>
<td>376</td>
<td>0.22</td>
<td>-3.60</td>
<td>324</td>
<td>5 Tasmania (Lowry, 2003)</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>450</td>
<td>40</td>
<td>454</td>
<td>0.13</td>
<td>-5.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cheilodactylus spectabilis</em></td>
<td>Female</td>
<td>428</td>
<td>94</td>
<td>432</td>
<td>0.45</td>
<td>0.15</td>
<td>324</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>513</td>
<td>97</td>
<td>550</td>
<td>0.30</td>
<td>-0.10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
case of *N. macropterus*, the seasonal trends exhibited by the mean monthly marginal increments on otoliths and the percentage of otoliths with a hyaline edge validate the use of the number of opaque zones for ageing this species. However, the above two otolith variables were recorded for a single presumed age cohort (V) and thus did not include otoliths with larger numbers of growth zones, which, as in the case of *P. speculator* (Hyndes et al., 1992a), might not show the same seasonal trends in their marginal increments as those recorded for the otoliths of fish with a small number of opaque zones. In other words, all of the opaque zones of *N. macropterus* and, in particular, those near the periphery of the otolith, may not have been clearly visible when viewing whole otoliths.

To facilitate comparisons between the biological variables for *N. valenciennesi* that involved length, the total length (*TL*) measurements for *N. valenciennesi* have been converted to fork lengths (*FL*), the form of length measurement used in other studies of the biology of cheilodactylids (Table 4.5). The females and males of *N. valenciennesi* have by far the greatest maximum lengths (853 mm for females and 731 mm for females) of any of the five species, but live for a maximum of only 19 years, whereas the females and males of the congeneric *N. macropterus*, which are much smaller (maximum lengths = 455 and 423 mm, respectively), live for up to 30 and 41 years, respectively (Table 4.5). Although the maximum lengths and ages of *Cheilodactylus fuscus* are similar to those of *N. macropterus*, the maximum ages for the females and males of another similar sized cheilodactylid species, *C. spectabilis*, were 97 and 94 years, respectively, and thus over twice that of any other member of this family (Table 4.5). There is thus no consistent pattern of relationship between maximum length and maximum age among the cheilodactylids listed in Table 4.5, even at the generic level.

The relationship between age at maturity and maximum age also varies markedly among cheilodactylids. Thus, although *C. spectabilis* can live for nearly 100 years, it
reaches maturity as early as 5 years of age (Table 4.5). Likewise, *N. macropterus*, which can live for up to 30-40 years, attains maturity as early as 3 years of age (Table 4.5). In contrast, *N. valenciennesi* has a maximum age of 19 years and yet, on the south coast of Australia, does not attain maturity until 7 years of age.

4.4.2 Growth

The following comparisons of the patterns of growth in cheilodactylids will concentrate on those described in this report for *N. valenciennesi* and by Jordan (2001a) for *N. macropterus* and by Ewing et al. (2007) for *C. spectabilis*. Focus will be placed neither on the growth curves of Smith (1982) for *N. macropterus* as the ageing of individuals in that study are questionable (see above) nor on those produced by Lowry (2003) for *C. fuscus* as those growth curves provided a very poor fit to the length at age data and the number of older males was very restricted and the estimates for \( k \) appear erroneous in view of the shape of the von Bertalanffy growth curve.

The growth curves of the females and males of *N. valenciennesi*, *C. spectabilis* and *N. macropterus* were remarkably similar for the first four years of life, during which each species underwent a substantial amount of growth (Fig. 4.13). However, while the growth of each species, and particularly of *N. macropterus* and *C. spectabilis*, subsequently asymptoted markedly, this occurred at very different lengths at age, *i.e.* in the case of females at c. 350 mm and 4 years for *N. macropterus*, 400 mm and 7 years for *C. spectabilis* and 570 and 10 years for *N. valenciennesi* (Fig. 4.13). These differences account for the respective values for \( k \) of 0.29, 0.33 and 0.45 year\(^{-1}\) (Table 4.5). The extent to which growth asymptoted was remarkable in the case of *N. macropterus* and *C. spectabilis* in that essentially no growth occurred during approximately the last 25 and 75 years of those species, respectively (Fig. 4.13).
Figure 4.13. von Bertalanffy growth curves fitted to the fork lengths at age of females and males of *Nemadactylus valenciennesi*, *Cheilodactylus spectabilis* and *Nemadactylus macropterus*. Data for *Nemadactylus macropterus* were taken from Jordan (2001a) and those for *Cheilodactylus spectabilis* were kindly provided by G. Ewing.
4.4.3 Movements, sexual maturation and spawning

All of the individuals of *N. valenciennesi* that were caught at lengths < 400 mm *TL* were obtained by spear fishing over granite reefs and their immediately surrounding sandy areas. Furthermore, these small fish were all obtained from the south coast and nearshore shallow waters (< 20 m depth) along that coast or its islands. As few of even the larger fish in these waters were mature, these waters act as a nursery area and larger fish apparently move out of those waters when they approach maturity. The failure to catch or even observe the juveniles of *N. valenciennesi* in comparable waters depths along the lower west coast is consistent with the absence of this species in catches obtained during extensive sampling of those waters in other studies (*e.g.* Lenanton, 1982; Ayvazian and Hyndes, 1995; Hyndes *et al.*, 1999). Although the length ranges of both the females and males of *N. valenciennesi* caught in offshore waters of the south coast were similar to those of the corresponding sexes in offshore waters of the lower west coast, the prevalence of mature fish in the two regions differ markedly. Thus, whereas the prevalence of such fish increased progressively from low levels in the smaller fish to 100% in the larger fish in offshore waters of the south coast, the majority or all fish in each length class in offshore waters of the lower west coast were mature.

From the above comparisons, it is proposed that the juveniles of *N. valenciennesi* are largely confined to the south coast and that substantial numbers of the fish on this coast subsequently move to the lower west coast where they become fully mature and presumably spawn. In contrast, it is hypothesised that the other larger individuals move out from their nearshore habitats into offshore waters on that coast, but don’t typically become mature until they have become substantially longer and older. The suggestion that many *N. valenciennesi* move from the south to the lower west coast for spawning parallels, to a large extent, that proposed by Smith *et al.* (2004) for the champagne crab *Hypothalassia*
acerba and, if true, indicates that the conditions for spawning of certain species are better on the lower west coast than on the south coast.

Despite the presence of substantial numbers of fully mature *N. valenciennesi* on the lower west coast, trawling for fish larvae in waters near where those mature fish were caught, yielded only five cheilodactylid larvae (Muhling, 2006). In contrast, *Nemadactylus* larvae was abundant in trawl samples collected by Fletcher *et al.* (1996) from offshore waters of the south coast in the winter, *i.e.* following the spawning period of *N. valenciennesi*. These results suggest that, after *N. valenciennesi* spawns on the lower west coast, their larvae are transported southwards and then become distributed eastwards along the south coast. Such a proposed movement by larvae would coincide with the time when the Leeuwin Current, which flows southwards and eastwards, is at its strongest (Smith *et al.*, 1991). Transport over such a substantial distance would be facilitated not only by that current but also by the fact that the pelagic larval phase of cheilodactylids, such as its congener *N. macropterus*, is protracted (Vooren, 1972, 1973). The larvae of *N. macropterus* on the east coast of Australia are transported southwards by the Eastern Australian Current (Bruce *et al.*, 2001).

4.4.4 Management implications

The fact that the estimate for the current level of fishing mortality, $F$ (0.20 year$^{-1}$) for *N. valenciennesi* of age 9 and older is very similar to that for natural mortality, $M$ (0.19 year$^{-1}$), suggests that the stocks of fully-recruited age classes of this species in south-western Australia are experiencing substantial fishing pressure. In this context, it is noted that *N. valenciennesi* is the most abundant scalefish species in the catches taken by the commercial gillnet fishery operating in marine waters off the south coast of Australia (McAuley and Simpendorfer, 2003). However, this fishing mortality for fully-recruited age classes lies well below the $F_{0.1}$ reference point (0.31 year$^{-1}$). Furthermore, the point
estimate of the current level of SPR (for SSB/R) for females and males combined (0.57) is well above the value of 0.3 at which a stock is often considered to be overfished (Goodyear, 1993; Mace and Sissenwine, 1993) and the trend exhibited by the curve relating SPR to fishing mortality is very shallow. Although fully-recruited age classes are subjected to a high level of fishing mortality, younger age classes, i.e. those less than 9 years old, are not fully-recruited and thus, with current fishing practices, are subjected to considerably less fishing mortality. Thus, in contrast to the situation with _A. gouldii_ (Chapter 3), _N. valenciennesi_ appears to be relatively resilient to fishing pressure. In this context, it is thus relevant that, in comparison with _A. gouldii_ (Chapter 3), _N. valenciennesi_ possesses life cycle characteristics that would make it less susceptible to fishing pressure, _i.e_. it is gonochoristic _vs_ hermaphroditic, has a far shorter life span (max. age = 19 years _vs_ 70 years) and typically matures at a younger age (3-7 years _vs_ 20-24 years). Furthermore, full recruitment into the same commercial gillnet fishery occurs at 9 years for _N. valenciennesi_, and thus above the age at which maturity is typically attained, whereas the reverse is true for _A. gouldii_.

Although there is strong evidence that _N. valenciennesi_ is more resilient to the effects of fishing than _A. gouldii_, the apparent implications of the results of the per recruit analyses should be treated with caution as there is considerable uncertainty in the estimates of both mortality and SPR, and the lower confidence intervals for current estimates of SPR for both females and males (0.24 and 0.22, respectively) are below the 0.3 reference point for a stock being overfished.
CHAPTER 5 - BIOLOGY OF YELLOWTAIL FLATHEAD

PLATYCEPHALUS ENDRACHTENSIS

5.1 INTRODUCTION

The estuaries on the lower west coast of Australia are almost invariably open to the sea, whereas many of those along the south coast of this region of Australia are either seasonally or normally closed through the presence of sand bars across their mouths (Lenanton and Hodgkin, 1985). The permanently-open Swan River Estuary at c. 32°S is the second largest estuary on the lower west coast of Australia, occupying an area of 55 km², while the seasonally-open Wilson Inlet at c. 35°S is the largest estuary on the south coast, covering an area of 48 km² (Brearley, 2005). The latter estuary is opened artificially during winter or spring, when the water in the basin rises and threatens to flood roads, developments and farms in low-lying areas along its shoreline (Brearley, 2005).

The fish faunas of estuaries are typically dominated by marine species that use these systems as nursery areas (e.g. Blaber and Blaber, 1980; Kennish, 1990; Whitfield, 1999; Elliott and Dewially, 1995). However, in south-western Australia, a number of fish species complete their life cycles in estuaries (Potter and Hyndes, 1999). Some of these are confined to estuaries, e.g. the Black Bream Acanthopagrus butcheri and the Western Hardyhead Leptatheria wallacei (Prince et al., 1982; Potter et al., 1986; Laurenson et al., 1993; Sarre and Potter, 1999), whereas others, such as the Estuary Cobbler Cnidoglanis macrocephalus and the Southern Bluespot Flathead Platycephalus speculator, are also represented by discrete marine populations (Hyndes et al., 1992a, b; Ayvazian et al., 1994).

Although the Yellowtail Flathead Platycephalus endrachtensis, which occurs across northern Australia and in New Guinea (Allen, 1997), is essentially a tropical species, it is found as far south as the Swan River Estuary, within which it is abundant and apparently completes its life cycle (Potter et al., 1990; Potter and Hyndes, 1999). In
contrast, *Platycephalus speculator* is a temperate species, which is most abundant in estuaries and coastal embayments along the south coast of Western Australia, but is also found in protected coastal marine waters northwards along the west coast to c. 27°S (Hutchins and Swainston, 1986; Potter et al., 1990, 1993). Work on *P. speculator* demonstrated that, in Wilson Inlet, this platycephalid can reach lengths of 700 mm and live for 11 years and spawns predominantly between early summer and early autumn (Hyndes et al., 1992a, b). *Platycephalus endrachtensis* and *P. speculator* are fished recreationally and commercially (Smith, 2006; Smallwood and Sumner, 2007), as also are several other *Platycephalus* species, such as *P. fuscus* in eastern Australian estuaries (Gray et al., 2002), *P. bassensis* in south-eastern Australian and Tasmanian waters (Jordan, 2001b) and *P. indicus* in Japanese waters (Masuda et al., 2000). Furthermore, *Platycephalus endrachtensis*, which is targeted by recreational anglers in the Swan River Estuary, has been identified as an “indicator” species for management purposes (Fisheries Management Paper 153; Report of 2003 RFAC/RecFishWest research planning meeting) and a priority for research (Harrison, 2001).

The present study provides quantitative data on the length and age compositions, growth, spawning period and length and age at maturity of *P. endrachtensis* in the Swan River Estuary. These data are used to confirm that this species completes its life cycle in this estuary and is gonochoristic and to ascertain, from mortality estimates and per recruit analyses, whether it is close to or being overfished. Finally, the data are compared with those derived previously for the comparably-sized and morphologically and behaviourally similar congeneric *Platycephalus speculator* in Wilson Inlet (Hyndes et al., 1992a, b).
5.2 MATERIALS AND METHODS

5.2.1 Sampling regime

*Platycephalus endrachtensis* was collected monthly between August 2004 and December 2006 by using 21.5 and 40.5 m seine nets and rod and line angling at several sites located throughout the lower, middle and upper regions of the Swan River Estuary on the lower west coast of Western Australia (31° 57’S, 115° 52’E) (Fig. 5.1). The 21.5 m seine net comprised two 10 m long wings, each consisting of 6 m of 9 mm mesh and 4 m of 3 mm mesh, and a 1.5 m long pocket made of 3 mm mesh. This net, which was laid parallel to the shore and then hauled on to the beach, fished to a maximum depth of 1.5 m. The 40.5 m seine net contained two 20 m long wings, consisting of 25 mm mesh, and a 1.5 m wide central bunt made of 9 mm mesh. This net, which was laid from a boat in a semi-circle outwards from the bank and then hauled on to the beach, fished to a maximum depth of 2 m. Water temperature was recorded at each site when it was sampled.

In addition, whole or filleted *P. endrachtensis* were obtained monthly from commercial fishers operating in the Swan River Estuary in 2005 and whole fish were purchased from a local wholesale fish market during the winter and spring of 2005 and 2006. A number of fish were also kindly provided by recreational fishers. The sources, *i.e.* seine netting or recreational line fishing, and the length ranges of *P. endrachtensis* collected by each method are provided in Table 5.1.

Table 5.1. Sample sizes and length ranges of *Platycephalus endrachtensis* collected from the Swan River Estuary by each sampling method.

<table>
<thead>
<tr>
<th>Method</th>
<th>n</th>
<th>Length range (TL mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>21.5 m seine</td>
<td>121</td>
<td>24-541</td>
</tr>
<tr>
<td>40.5 m seine</td>
<td>72</td>
<td>69-506</td>
</tr>
<tr>
<td>Rod and line</td>
<td>144</td>
<td>231-531</td>
</tr>
<tr>
<td>Gill net (commercial)</td>
<td>197</td>
<td>253-615</td>
</tr>
<tr>
<td>Total</td>
<td>534</td>
<td>24-615</td>
</tr>
</tbody>
</table>
Figure 5.1. Map of south-western Australia, with insets of a) the Swan River Estuary and b) Wilson Inlet. Box in inset of Australia shows region of south-western Australia illustrated in main map.
5.2.2 Laboratory procedures and analyses

The procedures and analyses used for *P. endrachtensis* are the same as those described in the General Materials and Methods (Chapter 2) and which were applicable to all three species. Note that *P. endrachtensis* could be sexed on the basis of the macroscopic appearance of its gonads when individuals had reached lengths of c. 100 mm during the spawning period and < 150 mm at other times.

5.3 RESULTS

5.3.1 Validation of ageing method

The opaque zones in the otoliths of *Platycephalus endrachtensis* became clearly visible once the otoliths of this species had been sectioned (Fig. 5.2).

The mean monthly marginal increments on sectioned otoliths of *P. endrachtensis* with two or three opaque zones remained at just below 0.40 between July and September and then decreased to a minimum of 0.15 in December, after which it rose progressively to 0.37 in June (Fig. 5.3). The mean monthly marginal increments for sectioned otoliths with ≥ 4 opaque zones followed essentially the same trend as that just described for otoliths with two or three opaque zones, with values declining precipitously to a minimum in December. Although none of the fish caught in January and June contained otoliths with one opaque zone, the mean monthly marginal increments for otoliths of such fish in other months of the year followed a similar trend to that just described for fish with greater numbers of opaque zones (Fig. 5.3). The single pronounced decline and then progressive increase undergone by the mean monthly marginal increments during the year demonstrate that a single opaque zone is formed annually in the otoliths of *P. endrachtensis* and that the number of opaque zones in those otoliths can thus be used for estimating the ages of the individuals of this species.
Figure 5.2. Sectioned otoliths of Platycephalus endrachtensis with a) 1, b) 3, c) 5 and d) 7 opaque zones (●). Scale bars = 0.5 mm.
Figure 5.3. Mean monthly marginal increments ± 1 SE on sectioned sagittal otoliths of *Platycephalus endrachtensis* with different numbers of opaque zones. Sample sizes are shown above each mean. In this Fig. and Fig. 5.6, closed rectangles on the x-axis refer to winter and summer months and the open rectangles to spring and autumn months.
As the trends in the mean monthly gonadosomatic indices and percentage frequencies of gonads at different maturity stages indicated that *P. endrachtensis* spawns predominantly from late spring to early autumn (see later), the individuals of this species were assigned, for the purpose of ageing, a birth date in the middle of this period, *i.e.* 1 January.

### 5.3.2 Length and age composition and growth

The structure of the length-frequency distributions for the females and males of *P. endrachtensis* differed markedly (Fig. 5.4a). Thus, all but four of the males were < 350 mm, whereas 57% of the females exceeded this length. The strongest length classes were the 300-349 and 350-399 mm for females and the 250-299 and 300-349 mm for males. The largest male was only 374 mm and thus far smaller than the largest female, which measured 615 mm.

In contrast to the situation with length classes, females and males were both represented in each of the nine age classes recorded in the samples (Fig. 5.4b). However, the number of females was greater than that of males in each of the 1+ to 6+ age classes, and thus for all of those for which the sample size was substantial, *i.e.* at least 25. The ratio of females to males in those age classes ranged from 2.2:1 to 4.9:1 and was significantly different from parity in all cases except the 6+ age class, with all *p* values < 0.001 and *χ*² values ranging from 12.8 to 56.9. The overall sex ratio of 2.7 females to 1 male was significantly different (*p* < 0.001) from zero (*χ*² = 109.1).

The length-weight relationships for the females and males of *P. endrachtensis* were not significantly different (*p* > 0.05) and thus the length-weight data for the two sexes were pooled and were then described by the equation \(\ln W = 3.144(\ln TL) - 12.776\) (*r*² = 0.994, *n* = 388).
**Figure 5.4.** a) Length-frequency and b) age-frequency distributions for females (black bars) and males (grey bars) of *Platycephalus endrachtensis.*
von Bertalanffy growth curves provided a good fit to the lengths at age of both the females and males of *P. endrachtensis* (Fig. 5.5), as is demonstrated by the relatively high values for the coefficient of determination for the two sexes (Table 5.2). The growth curves for the two sexes were significantly different (*p* < 0.05). These growth curves and the associated von Bertalanffy growth parameters demonstrate that the patterns of growth of females and males differ markedly (Fig. 5.5; Table 5.2). Thus, the *L*∞ was far greater for females (530 mm) than males (319 mm), whereas *k* was far less for females (0.41 year⁻¹) than males (0.82 year⁻¹) (Table 5.2). The above differences between the values for *L*∞ and *k* are reflected in an increasing divergence in the lengths of the two sexes as age increased. Thus, for example, from the von Bertalanffy growth equation, the lengths at ages 1, 2, 3, 5 and 7 years were 184, 300, 377, 462 and 500 mm, respectively, for females, compared with 173, 255, 291, 313 and 317 mm, respectively, for males.

5.3.3 Water temperatures and reproductive biology

The mean monthly water temperatures at the main sites at which *P. endrachtensis* was caught in the Swan River Estuary rose progressively from a minimum of c. 16°C in mid-winter to c. 21°C in mid-spring to a maximum of c. 25°C in late summer and early autumn, after which they fell to c. 17°C in early winter (Fig. 5.6a). Although the mean monthly temperatures followed the same overall trend in Wilson Inlet, the corresponding monthly values in that estuary were generally at least 3°C less than those in the Swan River Estuary (Fig. 5.6a).

The characteristics of each macroscopic stage in the development of ovaries and testes and the corresponding histological stages in the development of the ovaries of *P. endrachtensis* are presented in Tables 5.3 and 5.4, respectively.
Figure 5.5. von Bertalanffy growth curves fitted to the lengths at age of females and males of *Platycephalus endrachtensis*. The lengths of the small individuals that could not be sexed were assigned alternately to the female and male data sets. *n* = sample size
Table 5.2. The von Bertalanffy growth curve parameters $L_\infty$, $k$ and $t_0$, and their lower and upper 95% confidence limits, for the females and males of *Platycephalus endrachtensis* in the Swan River Estuary and of *Platycephalus speculator* in Wilson Inlet. Parameters were derived from the lengths at age of individuals. Data for Wilson Inlet were taken from Hyndes *et al.* (1992a). $L_\infty$ is the asymptotic length (mm), $k$ is the growth coefficient (year$^{-1}$), $t_0$ is the hypothetical age (years) at which fish would have zero length, $r^2$ is the coefficient of determination and $n$ is the number of fish.

<table>
<thead>
<tr>
<th></th>
<th>$L_\infty$ (mm)</th>
<th>$k$ (year$^{-1}$)</th>
<th>$t_0$ (years)</th>
<th>$r^2$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Platycephalus endrachtensis</em> (Swan River Estuary)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female Estimate</td>
<td>530</td>
<td>0.41</td>
<td>-0.04</td>
<td>0.76</td>
<td>384</td>
</tr>
<tr>
<td>Lower</td>
<td>502</td>
<td>0.34</td>
<td>-0.22</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>557</td>
<td>0.48</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male Estimate</td>
<td>319</td>
<td>0.82</td>
<td>0.05</td>
<td>0.88</td>
<td>150</td>
</tr>
<tr>
<td>Lower</td>
<td>310</td>
<td>0.71</td>
<td>-0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>327</td>
<td>0.95</td>
<td>0.15</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Platycephalus speculator</em> (Wilson Inlet)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female Estimate</td>
<td>482</td>
<td>0.59</td>
<td>-0.06</td>
<td>0.89</td>
<td>711</td>
</tr>
<tr>
<td>Lower</td>
<td>469</td>
<td>0.55</td>
<td>-0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>494</td>
<td>0.64</td>
<td>-0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male Estimate</td>
<td>429</td>
<td>0.57</td>
<td>-0.13</td>
<td>0.93</td>
<td>630</td>
</tr>
<tr>
<td>Lower</td>
<td>420</td>
<td>0.53</td>
<td>-0.20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>438</td>
<td>0.62</td>
<td>-0.07</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

An examination of histological sections of the gonads of 150 fish covering essentially the full length range of individuals in the samples failed to find any gonadal sections with both ovarian and testicular tissue.

The mean monthly GSIs for female *P. endrachtensis* ≥ the $L_{50}$ of females at maturity, *i.e.* 259 mm (see later), rose sharply from 1.9 in October to 3.3 in November and then to a well defined maximum of 5.4 in December, after which it declined precipitously to 3.6 in February and 1.6 in April and finally to a minimum of 0.8 in June (Fig. 5.6b). Although the mean monthly GSIs for male *P. endrachtensis* ≥ the $L_{50}$ of males at maturity, *i.e.* 187 mm (see later), followed the same trend as that for females, and thus likewise
Table 5.3. Description of the macroscopic stages in the development of the ovaries and testes of female and male *Platycephalus endrachtensis*, respectively. Macroscopic stages are adapted from Laevastu (1965). Scale bars = 10 mm.

<table>
<thead>
<tr>
<th>Macroscopic stage</th>
<th>Females</th>
<th>Males</th>
<th>Macroscopic characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I Virgin</td>
<td><img src="image1" alt="Image" /></td>
<td><img src="image2" alt="Image" /></td>
<td>Gonads slightly transparent and strand-like. Very difficult to differentiate between ovaries and testes.</td>
</tr>
<tr>
<td>Stage II Immature</td>
<td><img src="image3" alt="Image" /></td>
<td><img src="image4" alt="Image" /></td>
<td>Ovaries pink, cylindrical with fine capillaries. Testes white, smaller and strand-like.</td>
</tr>
<tr>
<td>Stage III Developing</td>
<td><img src="image5" alt="Image" /></td>
<td><img src="image6" alt="Image" /></td>
<td>Ovaries occupies 1/4 of body cavity. Small white eggs visible through ovarian wall. Testes firm and white.</td>
</tr>
<tr>
<td>Stage IV Maturing</td>
<td><img src="image7" alt="Image" /></td>
<td><img src="image8" alt="Image" /></td>
<td>Ovaries orange and occupying 1/3 of body cavity. Yolked eggs visible through ovarian wall. Testes white, large and firm. Milt extruded when pressure is applied to testes.</td>
</tr>
<tr>
<td>Stage V Mature</td>
<td><img src="image9" alt="Image" /></td>
<td><img src="image10" alt="Image" /></td>
<td>Yolked eggs visible through ovarian wall. Capillaries more conspicuous than previous stage. Ovaries and testes occupy 1/2 of body cavity. Milt extruded from testes under light pressure.</td>
</tr>
<tr>
<td>Stage VI Spawning</td>
<td><img src="image11" alt="Image" /></td>
<td><img src="image12" alt="Image" /></td>
<td>Hydrated eggs visible through ovarian wall. Thick capillaries. Ovaries and testes occupy 2/3 of body cavity. Testes creamy white. Milt extruded with little or no pressure.</td>
</tr>
<tr>
<td>Stage VII Spent</td>
<td><img src="image13" alt="Image" /></td>
<td>No image available</td>
<td>Ovaries flat, flaccid and dark red, with small remnant eggs visible through ovarian wall. Capillaries thin. Testes grey and of similar size to stage III.</td>
</tr>
<tr>
<td>Stage VIII Resting</td>
<td><img src="image14" alt="Image" /></td>
<td>No image available</td>
<td>Ovaries dark red/purple, occupying 1/4 of body cavity. Round in cross-section. Testes are greyish and reduced further in size.</td>
</tr>
</tbody>
</table>
Table 5.4. Histological characteristics of the macroscopic stages in the development of the ovaries of female *Platycephalus endrachtensis*. Terminology for oocyte stages follows Wallace and Selman (1981). Scale bars = 250 µm.

<table>
<thead>
<tr>
<th>Macroscopic stage</th>
<th>Histological section</th>
<th>Histological characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage II Immature</td>
<td></td>
<td>Chromatin nucleolar oocytes (c) and perinucleolar oocytes (p) present. Oocytes arranged along ovarian lamellae. Previtellogenic oocytes are present in all subsequent stages.</td>
</tr>
<tr>
<td>Stage III Developing</td>
<td></td>
<td>Cortical alveolar oocytes (ca) but not subsequent oocyte stages are present.</td>
</tr>
<tr>
<td>Stage IV Maturing</td>
<td></td>
<td>Cortical alveolar oocytes (ca) and yolk granule oocytes (y) present.</td>
</tr>
<tr>
<td>Stage V Mature</td>
<td></td>
<td>Cortical alveolar oocytes (ca) present. Yolk granule oocytes (y) are abundant.</td>
</tr>
<tr>
<td>Stage VI Spawning</td>
<td></td>
<td>Cortical alveolar oocytes and yolk granule oocytes (y) present, together with Migratory nucleus oocytes, hydrated oocytes (h) and/or post-ovulatory follicles.</td>
</tr>
<tr>
<td>Stage VII Spent</td>
<td></td>
<td>Ovaries contain remnant yolk granule oocytes (y), most or all of which are atretic and connective tissue (t).</td>
</tr>
<tr>
<td>Stage VIII Recovering</td>
<td></td>
<td>Ovaries contain predominantly chromatin nucleolar oocytes (c), perinucleolar oocytes (p) and extensive connective tissue (t).</td>
</tr>
</tbody>
</table>
Figure 5.6. a) Mean monthly water temperatures ± 1 SE at sites sampled in the Swan River Estuary (black circles) and Wilson Inlet (grey circles) and mean monthly gonadosomatic indices ± 1 SE for b) females and c) males of *Platycephalus endrachtensis* ≥ L₅₀ at maturity (black circles) from the Swan River Estuary and of *Platycephalus speculator* ≥ 2+ (grey circles) from Wilson Inlet. Sample sizes for gonadosomatic indices for females and males of *Platycephalus endrachtensis* are shown above or below each mean. Water temperatures and gonadosomatic indices for *Platycephalus speculator* in Wilson Inlet represent pooled data for the years shown in Hyndes *et al.* (1992a, b).
reached a maximum in December, the maximum mean monthly GSI for males was substantially less than that for females (Fig. 5.6c).

All female *P. endrachtensis* that were sampled in July and August and were ≥ the $L_{50}$ at maturity possessed either immature/resting (II) or recovering spent (VIII) ovaries (Fig. 5.7). The percentage of females possessing stage II ovaries declined progressively after September and remained low or absent until April. Female *P. endrachtensis* with ovaries at stage III (developing) and stage IV (maturing) first appeared in September and were both present in October and November, but not in the ensuing months. Females with stage V/VI (prespawning/spawning) ovaries were first caught in October and dominated the samples from November through to March. Fish with stage V/VI ovaries were still present in April and May, when females with stage VII (spent) ovaries were also found (Fig. 5.7). The presence of several females with stage III and IV ovaries in September to November, together with the contrast between their virtual absence and an abundance of females with stage V/VI ovaries during the following four months, implies that any female with gonads that develop to stage III would potentially progress through to later stages and thus become mature. Indeed, the ovaries of some female fish had already reached the prespawning stage by October and more particularly November. The trends exhibited by the monthly percentage frequencies for the sequential stages in the gonadal maturation of male *P. endrachtensis* followed closely those of females (Fig. 5.7). Thus, for the purpose of estimating the $L_{50}$ at maturity, fish with either ovaries or testes at stages III to VIII were considered mature.

### 5.3.4 Length and age at maturity

The lengths of the smallest mature female and male caught during the spawning period of *P. endrachtensis* were 231 and 156 mm, respectively. In this period, few females
Figure 5.7. Monthly percentage frequencies of occurrence of sequential stages in gonadal development of female and male *Platycephalus endrachtensis* $\geq L_{50}$ at maturity. Histograms for stages V and VI collectively are highlighted in black. $n =$ sample size.
with lengths of 200 - 249 mm were mature. However, the vast majority of those between 250 and 399 mm and all of those > 400 mm possessed ovaries at stages III to VIII and were thus mature (Fig. 5.8). All males caught during the spawning period with lengths > 200 mm contained testes at stages between III and VIII and were thus mature (Fig. 5.8). The $L_{50}$ at maturity was far greater for females than males, i.e. 259 vs. 187 mm, respectively (Table 5.5). Although few females and relatively few males of *P. endrachtensis* had attained maturity by the end of their first year of life, the majority of females and all males had reached maturity by the end of their second year of life (Fig. 5.8).

### Table 5.5. Estimates of the lengths at which 50% of the females and males of *Platycephalus endrachtensis* attained maturity ($L_{50}$) in the Swan River Estuary and their lower and upper confidence limits.

<table>
<thead>
<tr>
<th></th>
<th>$L_{50}$ (mm)</th>
<th>$L_{95}$ (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Estimate</td>
<td>259</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>233</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>280</td>
</tr>
<tr>
<td>Male</td>
<td>Estimate</td>
<td>187</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>163</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>211</td>
</tr>
</tbody>
</table>

### 5.3.5 Batch Fecundity

The abundance and continuous distribution of previtellogenic, cortical alveolar and yolk granule oocytes in the oocyte diameter frequencies in the ovaries of two mature (stage V) female *P. endrachtensis* collected during the spawning period demonstrate that this species has indeterminate fecundity (Fig. 5.9).

Batch fecundity estimates for seven females of *P. endrachtensis*, with lengths and weights ranging from 354 to 541 mm and from 300 to 1115 g, respectively, ranged from c. 14,200 and 197,650 eggs and produced a mean ± 95% CL of 56,825 ± 48,317.
Figure 5.8. Percentage frequency of occurrence of fish with gonads at stages III-VIII (grey histograms) in sequential 50 mm length classes and sequential age classes of female and male *Platycephalus endrachtensis* caught between November and March. Logistic curves (solid lines) and their 95% confidence limits (dotted lines) describing the probability of fish at each length being mature are plotted. Sample sizes are shown above each histogram.
Figure 5.9. a, b) Oocyte diameter frequency distributions of two mature (stage V) female *Platycephalus endrachtensis*. Early previtellogenic oocytes (white), cortical alveolar oocytes (grey), yolk granule oocytes (black).
5.3.6 Mortality and per recruit analyses

The estimate derived from the catch curve analysis for total mortality, $Z$, for female *P. endrachtensis*, the sex on which the fishery for this species in the Swan Estuary is largely based, is 0.89 year$^{-1}$ (Fig. 5.10, Table 5.6). The value derived for natural mortality, $M$, for females, by refitting Hoenig’s (1983) equation for fish, is 0.63 year$^{-1}$. After adjustment of this estimate using the method of Hall *et al.* (2004), the value for $M$ declined to 0.49 year$^{-1}$ (Fig. 5.10, Table 5.6). The estimate of fishing mortality, $F$, for females is 0.39 year$^{-1}$, which is 80% of the estimate for $M$ (0.49 year$^{-1}$) (Table 5.6). The yield per recruit (YPR) analysis for female *P. endrachtensis*, which assumed full recruitment into the fishery occurred at 4 years, indicated that the YPR for female *P. endrachtensis* continues to increase towards an asymptote with increasing fishing mortality (Fig. 5.11). At the current estimated level of $F$, the estimated YPR for females is 0.04 kg. The level of $F$ associated with the $F_{0.1}$ reference point is as high 0.82 year$^{-1}$ (Table 5.7). The estimate for current female spawning stock biomass per recruit (0.78 kg) represents 82% of the level estimated for females for an unfished stock (Fig. 5.11, Table 5.7).

Table 5.6. Mortality estimates for females of *Platyccephalus endrachtensis*. Total mortality ($Z$) was calculated using catch curve analysis (CCA) assuming constant recruitment, while natural mortality ($M$) was determined using the empirical equation of Hoenig (1983) and the method of Hall *et al.* (2004). Fishing mortality ($F$) was calculated using a Monte Carlo re-sampling analysis.

<table>
<thead>
<tr>
<th>Method of analysis</th>
<th>$Z$, $M$ or $F$ (year$^{-1}$)</th>
<th>Estimate</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCA</td>
<td>$Z$</td>
<td>0.89</td>
<td>0.77</td>
<td>1.02</td>
</tr>
<tr>
<td>Refitted Hoenig (1983) fish</td>
<td>$M$</td>
<td>0.63</td>
<td>0.20</td>
<td>1.53</td>
</tr>
<tr>
<td>Combined $M$ (Hall <em>et al.</em>, 2004)</td>
<td>$M$</td>
<td>0.49</td>
<td>0.19</td>
<td>0.87</td>
</tr>
<tr>
<td>Monte Carlo re-sampling</td>
<td>$F$</td>
<td>0.39</td>
<td>0.03</td>
<td>0.83</td>
</tr>
</tbody>
</table>
Table 5.7. Estimates for female *Platycephalus endrachtensis* of the current level of yield per recruit (YPR), $F_{0.1}$ and the current levels of spawning stock biomass per recruit (SSB/R). Calculations assumed that full recruitment of female *P. endrachtensis* to the fishery had occurred by the age of 4 years.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Estimate</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>YPR (kg)</td>
<td>0.04</td>
<td>0.00</td>
<td>0.26</td>
</tr>
<tr>
<td>$F_{0.1}$ (year$^{-1}$)</td>
<td>0.82</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SSB/R</td>
<td>0.78</td>
<td>0.42</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 5.10. Probability distributions, for females of *Platycephalus endrachtensis*, of natural mortality, $M$ (dotted line) (derived using the method of Hall *et al.* (2004) and an estimate of $M$ obtained by refitting the Hoenig (1983) regression equation for fish) and total mortality, $Z$ (solid line), determined using catch curve analysis and assuming constant recruitment.
Figure 5.11. The effect of fishing mortality ($F$) at the current age at recruitment into the commercial gillnet fishery of *Platycephalus endrachtensis* on the a) yield per recruit (YPR) and b) spawning potential ratio (SPR).
5.4 DISCUSSION

The samples of *Platycephalus endrachtensis* from the Swan River Estuary contained individuals that ranged widely in length from 24 to 615 mm and, during the spawning period, comprised substantial numbers of females and males with prespawning, spawning and spent gonads. Several larvae of this platycephalid were also caught at sites throughout this estuary during a previous study (Neira *et al*., 1992). However, no individuals at any stage in the life cycle of Yellowtail Flathead were caught during extensive sampling of estuaries either further south (e.g. Potter *et al*., 1990, 1993, 2000; Potter and Hyndes, 1994, Valesini *et al*., 1997) or in the only estuary immediately to the north (Young *et al*., 1997). Furthermore, during thorough and frequent sampling of the coastal waters and marine embayments of this region, this species was either not caught (Ayvazian and Hyndes, 1995) or rarely caught (Valesini *et al*., 2004). Thus, in southwestern Australia, well to the south of its typical subtropical and tropical distribution, *P. endrachtensis* is essentially restricted to the Swan River Estuary. It is therefore hypothesised that the colonisation of the Swan River Estuary by *P. endrachtensis* occurred following the southwards transport of its larvae and/or juveniles by the warm Leeuwin Current, which is known to transport such life cycle stages of other fish species in this direction (Hutchins, 1991). They would then have entered the Swan River Estuary, where the environment proved to be conducive to their recruitment and subsequent development through to maturation and successful spawning.

*Platycephalus speculator* is found in the coastal waters and estuaries of southwestern Australia (Ayvazian and Hyndes, 1995; Potter and Hyndes, 1999; Valesini *et al*., 2004) and has been shown to complete its life cycle in some estuaries on the south coast of Western Australia, such as Wilson Inlet, in which it is abundant (Hyndes *et al*., 1992a, b). *Platycephalus endrachtensis* and *P. speculator* are thus among a suite of species which
contains populations whose individuals are permanent residents of estuaries in south-western Australia (Potter and Hyndes, 1999). The unusually high prevalence of estuarine species in south-western Australian estuaries has been attributed to the selection for adaptations that would facilitate this life style among marine species that enter estuaries in a region in which those systems are often cut off from the sea for variable periods by the formation of sand bars at their mouths (Potter and Hyndes, 1999). While the Swan River Estuary now has a relatively deep entrance, access from the sea in the past, prior to the removal of the rock bar at its entrance, was far more restricted (Brearley, 2005). Although several estuaries in southern Africa also become closed for periods, the prevalence of such species is, for some reason, not as high in this region (Whitfield, 1999). While *P. endrachtensis* is at least largely restricted to estuaries in the southern part of its distribution on the lower west coast of Australia, it lives in marine embayments, such as Shark Bay, in those areas further to the north where there are no estuaries (Travers and Potter, 2002), thus paralleling the situation with the terapontid *Amniataba caudavittata* (Lenanton, 1977; Potter *et al*., 1994; Wise *et al*., 1994).

The presence of substantial numbers of *P. endrachtensis* in the Swan Estuary contrasts with the absence of *P. speculator* from this system, particularly as the latter species is found in estuaries immediately to the south (Loneragan *et al*., 1986; Valesini *et al*., 1997; Potter *et al*., 2000) and occurs in coastal waters much further north (Hutchins and Swainston, 1986; Ayvazian and Hyndes, 1995). This suggests that, in the Swan Estuary, *P. speculator* may have been displaced by the morphologically and behaviourally very similar *P. endrachtensis*. 
5.4.1 Growth and length and age distributions of females and males

The representation of females and males throughout the full age range of *P. endrachtensis* in the Swan River Estuary and the fact that the number of females exceeded that of males in all but the 0+, 7+ and 8+ age classes, which were each represented by limited numbers of fish, strongly indicate that this species is gonochoristic. This conclusion is substantiated by the fact that, in histological sections of the gonads of individuals covering a wide size and age range and time of year, testicular and ovarian tissues were never found together in the same gonad.

Although both sexes of *P. endrachtensis* were represented in all age classes and thus each had the same maximum age (8+ years), the females grew to a far larger size than their males. This accounts for the fact that, in our samples, 57% of the 368 females were > 350 mm, whereas only four of the 134 males were greater than this length and none exceeded 375 mm. Females also greatly outnumbered males (3.7 females: 1 male) in the total catch of *P. endrachtensis* collected by Jones (1971) from an embayment on the tropical east coast of Australia and within which all fish were greater than 300 mm in length. An extreme dominance of females among the larger length classes has also been recorded for other platycephalid species and led, in some cases, to the erroneous conclusion that those species were protandrous hermaphrodites, such as occurred, for example, with *Platycephalus indicus* in Japanese waters (see Masuda et al., 2000).

During the early years of life, the females and males of *P. endrachtensis* in the Swan River Estuary did not grow as fast as *P. speculator* in Wilson Inlet (Fig. 5.12). This parallels the differences in growth that would typically be expected if these species represented conspecific populations, *i.e.* growth was slower at the lower latitude. However, although the growth curves for the females and males of both *P. endrachtensis* and *P. speculator* were significantly different, the differences in the pattern of growth of the
Figure 5.12. von Bertalanffy growth curves fitted to the lengths at age of females and males of *Platycephalus endrachtensis* (solid line) from the Swan River Estuary and of *Platycephalus speculator* (dashed line) from Wilson Inlet. Data for *Platycephalus speculator* were taken from Hyndes et al. (1992a).
two sexes were far more pronounced in the former species (Fig. 5.12). Thus, in the von Bertalanffy growth equations, the $L_\infty$ was 66% greater for females than males with $P. endrachtensis$, compared with only 12% for $P. speculator$, and the value for $k$ was 50% less for females than males with the former species, but differed little between the sexes of the latter species (Table 5.2). Although the maximum ages of 8+ years recorded for both the females and males of $P. endrachtensis$ were less than those recorded for the corresponding sexes of $P. speculator$, i.e. 10+ and 12+, respectively, the vast majority of the individuals of both species were < 7+ years.

The attainment of far greater lengths by females than males with $P. endrachtensis$ than with $P. speculator$ was accompanied by a far greater domination by its females (2.7 females: 1 male) than was the case with the latter species (1.1 females: 1 male). In addition, although female $P. endrachtensis$ does not grow as fast as female $P. speculator$ early in life, their growth also does not asymptote so rapidly and thus length at maximum age (8+ years) is greater than that of $P. speculator$ at the same age. The above trends indicate that there has been particularly strong selection for a large size of females and thus for egg production in $P. endrachtensis$ and suggest that the above characteristics could represent the type of intermediate step that was taken by gonochoristic platycephalids in their development of the protrandrous hermaphroditic condition found in some species of this family (Aoyama et al., 1963; Okada, 1966, 1968; Fujii, 1970, 1971, 1974; Shinomiya et al., 2003). As the sex ratio remained biased towards females throughout the length and age range over which the gonads had become sufficiently well developed for the sex of the fish to be determined macroscopically, that bias developed early in life, i.e. through those genetic and/or environmental factors which influence sex determination or through differential mortality of the sexes during the larval or early juvenile stage.
5.4.2 Gonadal maturation and spawning period

In the case of *P. endrachtensis*, the presence of elevated mean monthly female GSIs (> 3) and a predominance of females with ovaries at stages V/VI between November and March, together with the occurrence of low mean monthly female GSIs (< 2) in all other months, imply that this species spawns predominantly between late spring and early autumn in the Swan River Estuary. This period is similar to that estimated for *P. speculator* in Wilson Inlet (Hyndes *et al.*, 1992b). However, as females of *P. endrachtensis* with ovaries at stages V/VI were caught in October, April and May, and males with testes at those stages were found in the last two of those months, its spawning season in the Swan River Estuary apparently extends from mid-spring to late autumn.

Water temperature plays an important role in initiating gonadal recrudescence and the timing of spawning in teleosts (Lam, 1983). In the case of *P. endrachtensis*, the prevalence of fish with gonads at stages ≥ III increases between September and November and thus just after water temperatures have started rising from their winter minima (Fig. 5.6a). Although the mean water temperature in each month was almost invariably 3-6 °C less in Wilson Inlet than in the Swan River Estuary, the overall trends exhibited by the mean monthly GSIs of particularly the females of *P. endrachtensis* in that system and those recorded for *P. speculator* in Wilson Inlet are very similar (Fig. 5.5). Thus, although the gonads of both species are apparently responding in the same way to the very similar patterns of change in water temperature, gonadal recrudescence and spawning activity are triggered by higher temperatures in the case of *P. endrachtensis* in the Swan River Estuary than with *P. speculator* in Wilson Inlet. However, the mean monthly GSIs of *P. endrachtensis* rose less rapidly early and declined more rapidly later, which implies that spawning peaks more sharply in the former species. Yet, the spawning period of *P. endrachtensis* in the Swan River Estuary is still relatively protracted, a point emphasised
by the fact that the sparid *Acanthopagrus butcheri*, another important recreational fish species in the Swan River Estuary, spawns over only four months in that estuary (Sarre and Potter, 1999). Thus, the population of *P. endrachtensis* in this temperate estuary has apparently become adapted to breeding at lower temperatures than it normally does in its typical subtropical/tropical environment. Such a view is consistent with the fact that the mean water temperatures in the Swan River Estuary at the beginning and end of the spawning period are less than even the lowest mean monthly water temperatures at, for example, a latitude of 20-22°S on the north-west tropical coast of Australia (Lough, 1998).

The data demonstrate that, while maturity is attained by relatively few *P. endrachtensis* at the end of their first year of life, it is achieved by the vast majority of this species by the end of their second year of life. In the case of females, this parallels the situation with *P. speculator* (Hyndes et al., 1992b). Thus, as female *P. endrachtensis* do not grow as rapidly as female *P. speculator* in the first two years of life, its $L_{50}$ at maturity is less. In contrast to the situation with female *P. speculator*, the males of this species typically reach maturity at the end of their first of life and therefore one year earlier than those of *P. endrachtensis* and thus at a smaller size. Thus, although the females of *P. endrachtensis* matured at a smaller size than of those of *P. speculator*, this was not case with their males.

5.4.3 Management implications

The following points strongly indicate that female *P. endrachtensis*, the sex on which the fishery for this species is based and the one which, for gonochoristic species, is typically assumed to be the key for ensuring sustainability, is not currently overfished. 1. The estimate of fishing mortality (0.39 year$^{-1}$) is less than that for natural mortality (0.49 year$^{-1}$). 2. The current fishing mortality lies well below the yield per recruit-based reference point $F_{0.1}$. 3. The estimate of current SPR (0.82) lies well above the 0.3 reference
point for SPR at which stocks are often considered overfished (Mace & Sissenwine, 1993; Goodyear, 1993).

As the spawning potential ratio (SPR) does not decline markedly, even at high levels of fishing mortality, *P. endrachtensis* is apparently resilient to fishing pressure under existing management regulations for this species. In this context, it is relevant that the current MLL for *P. endrachtensis* exceeds the $L_{50}$ at maturity for both its females (259 mm) and even more particularly its males (187 mm). Thus, as there is no indication that the individuals of this species suffer high mortality after release, it is likely that the individuals caught prior to reaching the MLL and then released will potentially have the opportunity subsequently to mature and spawn. Furthermore, the short life-span (8 years) and early maturity (essentially all fish by 2 years) are likely to make this species resilient to overfishing. This resilience is particularly important as the individuals in the population of *P. endrachtensis* in the Swan River Estuary complete their life cycle within this system. From the above, it follows that the current management policies for *P. endrachtensis* are working effectively for ensuring the sustainability of the stocks of this species in the Swan Estuary.
CHAPTER 6 – GENERAL DISCUSSION

6.1 SPAWNING PERIOD AND SPAWNING MODE

Optimisation of the conditions for the survival of the early life cycle stages of a fish species and their dispersal into or retention within appropriate nursery habitats depend on the larvae of those species being produced during a certain critical period (Norcross and Shaw, 1984; Levin, 2006). Since larval production is directly related to the time of spawning, the markedly different times of the year at which *A. gouldii*, *N. valenciennesi* and *P. endrachtensis* spawn implies that there have been very different selection pressures among these species for the timing of spawning. This is hardly surprising in view of the very different environments in which these species spawn and, in the case of *P. endrachtensis*, spends its juvenile life.

The spawning of *A. gouldii* from June to October in offshore waters of the south coast would have the benefit of larvae being produced when the prevailing south-westerly winds, swell and water movements are particularly strong (Van Hazel *et al.*, 2001) as those would facilitate larval transport into nearshore waters, where this species subsequently spends its juvenile life (Chapter 3). In contrast to *A. gouldii*, *N. valenciennesi* spawns between January and May, which corresponds to the period immediately prior to that when the southwards-flowing Leeuwin Current is at its strongest (Cresswell, 1991). This current thus provides a potential mechanism for transporting this species from offshore waters of the west coast (in which much spawning apparently occurs) to the south coast, where this species spends its juvenile life (Chapter 4). In this context, it is relevant that, on the basis of studies of its congener *N. macropterus* (Vooren, 1972, 1973), this cheilodactylid is also considered likely also to have a very extended larval phase which would enhance the likelihood that larvae can potentially be transported considerable distances.
The spawning of *P. endrachtensis* in the Swan River Estuary between November and March results in the larvae of this species being produced mainly during the summer, when rainfall is limited and freshwater discharge is thus greatly reduced (Spencer, 1956; Hodgkin and Hesp, 1998). Consequently, the larvae are provided with a very stable and productive environment, which would greatly enhance their chances of retention within the estuary and enable them to grow rapidly. This spawning period is similar to that of other medium to large estuarine-spawning species within this estuary, such as the Black Bream *Acanthopagrus butcheri*, the Perth Herring *Nematalosa vlaminghi* and the Yellowtail Grunter *Amniataba caudavitta* (Chubb and Potter, 1984; Sarre and Potter, 1999; Wise et al., 1994).

In the case of *N. valenciennesi*, the sex ratio in each length and age class is close to parity, the growth rates of the two sexes did not differ markedly and the females and males have similar longevity (and mortality). Thus, this nemadactylid possesses characteristics which are typical of many gonochorists. In contrast, as *A. gouldii* starts life as a female and many of its individuals subsequently change sex to males as they increase in size and age, with the sex ratio thus changing with increasing length and age, it is a protogynous hermaphrodite. Moreover, since all males are derived from mature females, this species is specifically a monandric protogynous hermaphrodite. The domination of the larger size classes of *P. endrachtensis* by females suggested that this platycephalid is a protandrous hermaphrodite, *i.e.* individuals change from male to female. However, the presence of a similar sex ratio in each age class, although almost always skewed towards females, together with detailed histological studies of the gonads through the full size and age range, demonstrated that this platycephalid is a gonochorist. This species thus provides an excellent example of the dangers of attempting to use length composition data alone for determining whether a species is hermaphroditic (Sadovy and Shapiro, 1987). Yet, as there
are protandrous hermaphrodites among the species of the Platycephalidae (e.g. Fujii, 1970, 1971, 1974; Shinomiya et al., 2003), the far greater size attained by females than males may represent an intermediate step in the evolution of protandrous hermaphroditism in this family.

6.2 LIFE CYCLE CHARACTERISTICS, MORTALITY ESTIMATES AND PER RECRUIT ANALYSES AND THEIR MANAGEMENT IMPLICATIONS

The mortality estimates and results of per recruit analyses described and discussed in Chapters 3, 4 and 5 imply that the stocks of *A. gouldii*, *N. valenciennesi* and, to a lesser extent, *P. endrachtensis* are each experiencing substantial fishing pressure. Unfortunately, there are no published quality catch, effort and catch per unit effort data for any of the above three species. This is mainly attributable to the fact that the commercial fisheries for *A. gouldii* and *N. valenciennesi* are multi-species, while the fishery for *P. endrachtensis* in south-western Australia is essentially recreational. There is thus insufficient data to be able to elucidate, with any degree of certainty, the extent to which each of these species is targeted and has undergone changes in relative abundance over recent years due to increases in fishing activity and/or the efficiency of fishing methods.

The results of mortality and per recruit analyses strongly indicated that *A. gouldii* is far more vulnerable to fishing pressure than *N. valenciennesi* or *P. endrachtensis*. Thus, in the case of *A. gouldii*, per recruit analysis indicate that it would take only a small increase in fishing mortality to produce a rapid decline in the spawning potential ratio (SPR) of particularly the males of this hermaphroditic labrid, *i.e.* to below the critical value of 0.3 at which stocks are often considered overfished (Goodyear, 1993). In other words, at its current estimated level of fishing mortality, *A. gouldii* is close to or at full exploitation. In contrast, the trends exhibited by the SPRs for *N. valenciennesi* and *P. endrachtensis*
with increasing fishing mortality suggest that the SPRs of these two species are likely to remain well above 0.3, even if there were substantial increases in fishing mortality.

*Achoerodus gouldii* is likely to be far more vulnerable to fishing than *N. valenciennesi* or *P. endrachtensis* for the following reasons: 1) It has far greater longevity, *i.e.* 71 years vs 21 and 8 years, respectively and thus has far lower natural mortality and therefore, in turn, low long-term productivity. 2) On average, females mature relatively later in life, *i.e.* 17 vs 4-7 and 3 years, respectively, and thus, unlike the other two species, after the individuals of this species have typically become fully vulnerable to fishing (15 years). This means that many of its individuals can potentially be removed from the population before they have had the chance to contribute to egg production. 3) As sex change to male occurs, on average, when *A. gouldii* is as old as 35 years and individuals become fully recruited to the fishery at the much earlier age of 15 years, the individuals destined to become males can potentially be taken by the fishery over many years before they have become males. This, in turn, could lead either to a marked reduction in the number of males in the population, and/or, if the size at sex change is a plastic life history trait, to a lowering of the size at sex change. Either of the above two responses to selective fishing of males would have deleterious effects on the population of *A. gouldii*, *i.e.* a disruption of the “normal” mating system in the first case, or a reduction in average female size and thus overall population egg production and also yield per recruit, in the second case.

Although the mortality estimates and particularly the per recruit analyses indicate that *A. gouldii* is the only one of the three species that is close to or at full exploitation, it must be recognised that the above conclusions are drawn from analysis of current data. Thus, any marked changes to the fisheries and/or management practices for any of those species can potentially make them more or less prone to the effects of fishing pressure. It
should also be recognised that the very long time lag between spawning and full recruitment to the exploited stock, *i.e.* 15 years, has important implications for managing the stocks of *A. gouldii*, as any effects of the exploitation of the mature fish on recruitment to the stock will take 15 years to become apparent in fishery data. Such lags in detection of adverse trends in recruitment and in response of the stock to management actions pose a difficult problem to fisheries managers.

It should also be pointed out that per recruit analyses implicitly assume that the population is in equilibrium, *i.e.* natural mortality, growth, size at maturity and other variables all remain constant. However, numerous studies have demonstrated that these parameters can change markedly over time (*e.g.* Ziegler *et al.*, 2007), and particularly when fish stocks have experienced substantial fishing pressure (*e.g.* Hutchings and Baum, 2005). This point will need to be borne in mind when undertaking stock assessments, such as per recruit analyses, for these species in the future.

One of the most striking comparisons between the three species is that the estimated current level of fishing mortality for *A. gouldii* (0.039 year$^{-1}$) is only a fraction of that recorded for either *N. valenciennesi* (0.20 year$^{-1}$) or *P. endrachtensis* (0.39 year$^{-1}$), and yet the per recruit analyses suggest the former species is likely to be close to or at full exploitation. The above comparison demonstrates that, in species such as *A. gouldii*, even relatively low levels of fishing can have an important impact on stock abundance. As a relatively small shift in the dynamics of the fishery for *A. gouldii* could have a marked impact on its abundance, it is imperative that the status of its stocks, and those of species with similar life cycle characteristics, *i.e.* longevity and late maturity and sex change, be monitored carefully.
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