

Comparative biology of the west coast and south coast populations of the Breaksea Cod *Epinephelides armatus* in Western Australia



This Photo by Ben Jones is licensed under CC BY Attribution

By Jacob Kyle Buckland

This thesis is presented for the degree of Bachelor of Marine Science Honours,
Murdoch University, 2022

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 tertiary education institution.

.....

Jacob Buckland

Abstract

The Breaksea Cod *Epinephelides armatus* (Serranidae) is endemic to ~ 1,600 km of Western Australian coast, ranging from Shark Bay on the west coast (~26°S) to Esperance on the south coast (~122 E) and is an important recreational fishery resource. The aims of this study were to 1) determine the length and age distributions for *E. armatus* on the west and south coast; 2) estimate the parameters for growth, reproduction (spawning periods and sexual maturity) and natural mortality (*M*) of west and south coast populations; 3) compare these parameters between a) the west and south coast, and b) for west coast fish, compare estimates of those biological characteristics from this study with those from ~10 years previously; and 4) determine whether the patterns of growth and reproduction on the west and south coast follow the predictions of the three ecological theories (Metabolic theory of ecology, Temperature size rule, Gill oxygen limitation theory).

Samples of *E. armatus* total length >300 mm were obtained mainly from fish frames submitted by recreational fishers to the Department of Primary Industries and Regional Development, while smaller fish were collected during this study by spear fishing on both the west and south coasts. The results of this study demonstrated von Bertalanffy growth curves differed significantly between the west and south coasts, with fish on the south coast reaching a

larger size than those on the west coast but had a lower instantaneous growth rate (k). The mean length at age of west coast males were always greater than those reported by previous studies. *Epinephelides armatus* had a protracted spawning period (November to April), with a peak in February which would influence the wide ranges of length at age. The length at maturity estimates for females did not differ significantly between the west (285 mm) and south coast (280 mm) populations and these estimates were smaller than the minimum legal length of 300 mm.

Acknowledgements

I would like to express the utmost gratitude to my supervisor Emeritus professor Neil Loneragan in allowing me to participate in this project and providing me with the support, advice, knowledge, and motivation that has driven me throughout the past two years. This gratitude is also passed along to my co-supervisors Dr Peter Coulson who provided tremendous support and guidance in the ageing and analyses of the project, and Dr David Fairclough who provided invaluable knowledge and feedback with the analyses for the project. I would also like to thank to Dr Jeffrey Norriss, Dr Emily Fisher, Brett Crisafulli, and Elaine Lek who offered their time, advice, and assistance with the analyses and lab work (in particular R coding) for the project.

Thank you to AJ Langford's and Geordie Buscombe for allowing me to collect measurements on commercially caught fish. I would like to thank my incredible volunteers who gave up their precious time and assisted in the fieldwork for this project, especially Warrick Goets and James Anstey who assisted with multiple trips and with lab work, thank you to the other

volunteers who also assisted; Alex Brunswick, Caitlan Davis, Kiera Gordon, Rachel Newsome, and Charlie Maus.

To my loving and supportive family, I would not be where I am today, you have been my rock during some of the most stressful times in my life and will always be eternally grateful for support and belief that you have instilled in me throughout my entire life. Thank you so much.

Lastly, to my good friend and mentor Ken Spykers who also assisted in scouting and collection of juveniles, gone too soon mate.

Table of Contents

Abstract	3
Acknowledgements	5
1. Introduction	9
1.1 Breaksea cod <i>Epinephelides armatus</i>	10
1.2 Fisheries	12
1.2.1 Environment and fisheries in Western Australia	12
1.2.2 Management methods.....	16
1.3 Previous research on <i>Epinephelides armatus</i>	19
1.4 Aims of the Thesis	20
2. Materials and Methods	22
2.1 Southern oscillation index and sea surface temperatures	22
2.2 Sources of fish for biological measurements.....	22
2.2.1 Fish Frames collected by DPIRD.....	23
2.2.2 Samples from fish market	24
2.2.3 Collection of small fish (< 300 mm TL)	25
2.3 Gonad staging.....	29
2.4 Preparation of otoliths for aging.....	32
2.5 Ageing & age validation	33
2.6 Data Analyses	38
2.6.1 Otolith weight and distributions	38
2.6.2 Age and growth	39
2.6.3 Natural Mortality and M/k	41
2.6.4 Reproduction.....	42
3. Results.....	44
3.1 Sea surface temperature	44
3.2 Source of <i>Epinephelides armatus</i> samples	48
3.3 Ageing & Validation	49
3.4 Length distribution	54
3.5 Age distributions	59
3.6 Otolith weight by total length relationship.....	60
3.7 Growth.....	63
3.8 Natural mortality and M/k	69

3.9	Reproduction.....	70
3.9.1	Gonad weight	70
3.9.2	Gonad stages	73
3.9.3	Length and age at maturity	75
4.	Discussion	82
4.1	Age, Length & Growth.....	84
4.1.1	Length distribution	84
4.1.2	Otolith weight – total length relationship.....	85
4.1.3	Age validation	87
4.1.4	Age distribution.....	88
4.1.5	Estimates of Growth	89
4.1.6	Natural mortality and M/k	93
4.2	Reproduction.....	94
4.2.1	Spawning period.....	94
4.2.2	Estimated length and age at maturity	95
4.3	Implications for stock assessment	98
4.4	Data limitations	99
4.5	Further research and implications for management.....	100
4.6	Conclusion	102
5.	References	104
6.	Appendix.....	112
6.1	Summary	113
6.2	Introduction	116
6.2.1	Biology and life history strategies.....	118
6.2.2	Aims of the review	120
6.3	Reproductive strategies in the Serranidae	122
6.3.1	Protogyny.....	124
6.3.2	Gonochorism.....	125
6.4	The biology and ecology of gonochoristic serranids of south-western Australia.....	128
6.5	The biology and ecology of gonochoristic Serranids of the <i>Paralabrax</i> genus.....	137
6.6	Comparisons of reproductive biology	146
6.7	Fisheries management and conservation	149
6.7.1	Management of Southwest gonochoristic serranids	149
6.7.2	Management and conservation of <i>Paralabrax</i> species.....	151
6.8	Conclusion	159

6.9	References.....	163
6.10	Appendix	170

1. Introduction

The Serranidae is a wide ranging (temperate to tropical environments), diverse family of teleosts that includes an estimated 597 species from 71 genera and several important fishery species (Fairclough, 2016; Love et al., 1996; Mackie, 2000; Mason & Lowe, 2010). The family includes three main subfamilies: the Serraninae (Perchlets), Anthiadae¹ (Basslets) and Epinephlinae (Groupers) and three lesser-known subfamilies: the Diploprioninae (and Grammistinae (Soapfish) and Liopropomatinae (Basslets) (Craig & Hastings, 2007; Shepherd et al., 2018; Williams & Carpenter, 2015; WoRMS, 2021).

Many serranids have a hermaphroditic reproductive strategy. However, there is a small group of serranids that are gonochorists i.e., have separate sexes throughout their life cycle (Sadovy & Domeier, 2005). These include five species from the *Paralabrax* genus; White-Spotted Sand Bass *Paralabrax albomaculatus* (Salinas-de-León et al., 2017), Gold-Spotted Rock Bass *Paralabrax auroguttatus* (Pondella et al., 2001), Kelp Bass *Paralabrax clathratus* (Love et al., 1996), Spotted Sand Bass *Paralabrax maculatofasciatus* (Allen et al., 1995; Andrews et al., 2005; Hovey & Allen, 2000) and Barred Sand Bass *Paralabrax nebulifer*

¹ The subfamily Anthiinae has been used for this group of fish but this name conflicts with a sub-family of beetles. Therefore, the name Anthiadae is used for this subfamily in this review.

(Hovey et al., 2002). Two serranid species from southwestern Australia are also gonochorists, including Breaksea cod *Epinephelides armatus* (Moore et al., 2007) and Harlequin fish *Othos dentex* (French et al., 2014).

Although these gonochorists share the same reproductive strategy, males in the *Paralabrax* genus contain a central membrane-lined ‘ovarian’ lumen within their testes (Sadovy & Domeier, 2005), indicating they begin life as females, while *E. armatus* (Moore et al., 2007) and *O. dentex* (French et al., 2014) juvenile gonads consist solely of ovarian or testicular tissue. It is believed that the ancestors of *E. armatus* and *O. dentex* were gonochoristic with no evidence of hermaphroditism whereas the ancestors for the *Paralabrax* genus was thought to be a protogynous hermaphrodite (female to male sex transition) (French et al., 2014; Sadovy & Domeier, 2005).

1.1 Breaksea cod *Epinephelides armatus*

The Breaksea Cod *Epinephelides armatus* is a benthic serranid belonging to the Anthiadinae subfamily and is a monospecific genus (Fairclough, 2016; Moore et al., 2007; Platell et al., 2010; WoRMS, 2021). This species is endemic to the continental shelf of south-western Australia, with a distribution that extends from Shark Bay in the north (25.8° S, 113.30° E), south to Cape Naturaliste (33.5° S, 115.0° E), then east to Esperance (33.7° S, 121.9° E) on the south coast (Figure 1.1).



Figure 1.1: A map of Australia displaying the distribution range of *Epinephelides armatus* from fishes of Australia.

Source: <https://fishesofaustralia.net.au/home/species/4375#:~:text=Endemic%20to%20Western%20Australia%2C%20from,commonly%20to%20about%2035%20m.>

Epinephelides armatus inhabits rocky reefs, which are comprised limestone on the west coast and granite on the south coast (Fairclough, 2016; Moore et al., 2007). These habitats are important nurseries and provide refuge from predators with juvenile fish <100 mm in total length (TL) showing cryptic behaviour by swimming upside down under roofs and ledges, alongside the Foxfish *Bodianus frenchii* (Fairclough, 2016). The diet of *E. armatus* consists mainly of small teleosts and crustaceans (Platell et al., 2010). *Epinephelides armatus* has a maximum recorded total length and weight of 510 mm and 3 kg, respectively, and a maximum recorded age of 20 years (Moore et al. 2007).

1.2 Fisheries

Coastal fisheries around the world are vitally important to food security, particularly in developing countries (Lauria et al., 2018; Virtanen et al., 2001; FAO, 2022). Fisheries species may be harvested by commercial operations where fish resources are caught for profit and fisheries may be large or small-scale (Cross, 2015; Halim et al., 2020; Kanyerere et al., 2018). This contrasts with recreational fishing, which is an activity where fish are caught for pleasure or food but can also be small to large in scale (Arlinghaus & Cooke, 2008; Cooke et al., 2019; Crowe et al., 2013). With continued technological advancements and increase in the human population across the globe, the impacts that fisheries have on our oceans has become an environmental issue that cannot be ignored (Crowe et al., 2013; Lassen, 1998). If fisheries are mismanaged, it can lead to the stock collapse of fishery significant species resulting in devastating environmental, economic and social impacts (Crowe et al., 2013; Lassen, 1998; Virtanen et al., 2001).

1.2.1 Environment and fisheries in Western Australia

The Western Australian coastline is >2000 km long, extending from tropical regions at low latitudes to temperate regions at high latitudes (Caputi et al., 2018; Fairclough et al., 2021). One of the key oceanic features of this coastline is the unique southward flowing, warm water, Leeuwin Current (Feng et al., 2013; Pearce et al., 2011). This current is an extension of the Indonesian

Throughflow, starting at Exmouth, flowing down the west Australian coastline, around Cape Naturaliste and into the Great Australian Bight. The Leeuwin Current transports warmer waters further southwards than usually found at southern latitudes on this coast, resulting in the mixing of tropical with temperate marine species at higher latitudes (Pearce et al., 2011). The Leeuwin Current's strength is heavily influenced by changes in the Southern Oscillation Index (SOI), a circulation system whereby east to west trade winds in the Pacific Ocean push warmer waters to the west across northern Australia and down the west coast. There are two main SOI events known as a La Niña (strong east to west trade wind, which produce a positive SOI value) and El Niño (weakened or not east to west trade winds, which produce a negative SOI value) (Feng et al., 2013; Zinke et al., 2014). During El Niño events the Leeuwin Current is weaker resulting in cooler waters at higher latitudes, while during La Niña events, the Leeuwin Current is stronger and warmer waters reach higher latitudes (Feng et al., 2013; Zinke et al., 2014).

In Western Australia, the management of fish resources is divided into four regions by the Department of Primary Industries and Regional Development (DPIRD): the North Coast Bioregion (NCB), the Gascoyne Coast Bioregion (GCB), the West Coast Bioregion (WCB), and the South Coast Bioregion (SCB), based primarily on ecological characteristics. The WCB extends from the Zuytdorp cliffs north of Kalbarri (27° S) to Blackpoint, east of

Augusta (115° 30 E), while the SCB extends from 115° 30 E to the West Australian/South Australian border at longitude 129°E (Fletcher et al., 2011; Newman et al., 2021). The WCB is dominated by limestone reefs and caves with a mean annual sea surface temperature (SST) of 20.3°C, while the SCB is dominated by granite rocky outcrops with cooler waters (mean annual SST = 17.6°C) than the WCB (Fletcher et al., 2011; Moore et al., 2007; Newman et al., 2021).

One of the major commercial and recreational fisheries in Western Australia is the West Coast Demersal Scalefish Fishery (WCDSF), which operates in the WCB and fishes benthic dwelling species that inhabit areas of the water column close to, or near, the sea floor. Commercial and recreational fishers for demersal species focus their fishing effort on three main species; the Western Australian Dhufish *Glaucosoma hebraicum*, the Snapper *Chrysophrys auratus* (Fairclough et al., 2021) and the Baldchin Groper *Choerodon rubescens* (Norriss & Walters, 2017). These three species are used as indicator species for the WCDSF in the WCB. In other words, the status of their stocks is used to represent the status of all species in the demersal resource (Newman et al., 2018). The biology of these species in different regions of Western Australia has been well documented (Hesp et al., 2002; Lenanton et al., 2009; Nardi et al., 2006). Lenanton et al. (2009) found that the growth of these species differed between regions, with a greater

instantaneous growth rate (k) and a smaller asymptotic length (L_{∞}) at lower than higher latitudes (Wakefield, 2006).

The results of two of those species (*C. auratus* and *G. herbraicum*) are consistent with the predictions from three theories of ecology: the Metabolic Theory of Ecology (MTE) (Meer, 2006); the Temperature Size Rule (TSR) (Walters & Hassall, 2012); and the Gill Oxygen Limitation Theory (GOLT) (Pauly, 2019). The MTE hypothesizes that ectotherms will expend more energy to find food at higher temperatures and therefore have an elevated metabolic rate, leading to faster growth (Lek et al., 2012; Meer, 2006). The TSR predicts that ectotherms in low temperature environments will grow slower but reach larger sizes and a larger size at sexual maturity than those in warmer environments, as a result of an increased metabolic rate in regard to unequal response to growth and development rates to temperature (Forster & Hirst, 2012; Walters & Hassall, 2012). The GOLT predicts that warmer water contains less oxygen than cooler waters, this limits metabolism resulting in smaller fish in warm water. The GOLT could thus cause shifts in the distributions of fish species to meet oxygen demands with increasing sea surface temperature due to climate change (Pauly, 2019; Pörtner & Knust, 2012; Pratchett et al., 2017), making management and its associated methods important in tracking such potential shift.

1.2.2 Management methods

Commercial fishers in Western Australia target the key indicator demersal species in the WCDSF, such as *G. hebraicum* and *C. auratus*, with other demersal species, such as *E. armatus* and *O. dentex*, being caught as by-product (Newman et al., 2021). On the west coast, the commercial catch limit for the WCDSF is 450 tonnes per year (Gaughan & Santoro, 2021). However, in 2020/21, only 271 tonnes (60.2%) out of the allocated catch limit were caught and this was deemed acceptable (Gaughan & Santoro, 2021). On the south coast, demersal scalefish are caught commercially mainly as by-product in the Southern Demersal Gillnet and Longline Fishery (SDGLF) that target elasmobranchs, such as the Gummy Shark *Mustelus antarcticus*. The SDGLF has an allocated a catch limit of 725 to 1095 tonnes per year, with 774 tonnes caught in 2020/21, which was deemed acceptable (Newman et al., 2021). The management of the commercial fisheries that target demersal species in the WCB and SCB sector is based on limiting effort to maintain catches below an identified limit.

In Western Australia, recreational fishers catch demersal scalefish from mainly private vessels, with some catch also coming from charter boats (Ryan et al., 2015, 2019). Recreational fishing from a private vessel in Western Australia requires that a Recreational Boat Fishing Licence holder is on board the vessel

(Ryan et al., 2015). The daily bag limit per fisher on the west coast is two mixed demersal species per licence holder, with a maximum of two *G. hebraicum* per vessel (DPIRD, 2022; Smallwood et al., 2013). The daily bag limit for demersal scalefish on the south coast of is five mixed demersal species per licence holder. Minimum legal length for retention (MLL) are set for a number of key demersal species including: 300 mm for *E. armatus* (Smallwood et al., 2013). In the WCB, under current restrictions, demersal recreational fishing is not permitted from the 15th of October to the 15th of December to limit fishing effort and thus, total catch by this sector. In 2020/21, recreational fishers caught an estimated 210 to 253 tonnes (95% confidence interval (CI)) off private vessels, with charter boats catching a further 36 tonnes. The total recreational catch was greater than the total annual recreational catch allocation of 275 tonnes, and this catch level was deemed not acceptable (See Overview Table 1 in Newman et al. (2021)).

Another aspect of the demersal scalefish fishery is the depth at which these species are caught and the effect of barotrauma on fish caught in deep waters and raised to the surface (Fairclough et al., 2021; Newman et al., 2021). When demersal species are captured and pulled up from depth, these species are often susceptible to barotrauma where physical damage to the swim bladder is caused by the sudden decrease in ambient pressure resulting in significant mortality (Schreer et al., 2009). Other aspects that influence mortality on capture is capture/release handling time, hook damage and shark depredation

(Fairclough et al., 2021; Newman et al., 2021; Schreer et al., 2009). When management strategies are being developed and implemented, it is important to take potential mortality into account, with the best strategy to select measures that minimise the need to release fish (Fairclough et al., 2021; Newman et al., 2021; Schreer et al., 2009).

Epinephelides armatus is a demersal scalefish species targeted by recreational fishers and is also caught as by-product by commercial fishers (Newman et al., 2021; Smallwood et al., 2013). As noted above, in Western Australia, *E. armatus* has a 300 mm MLL for both commercial and recreational fishers. Catches of *E. armatus* are considered in the bag limit of two mixed demersal species on the WCB and five mixed demersal species on the south coast but with no individual bag limits specified (Smallwood et al., 2013). It also falls under the seasonal closure on recreational fishing for west coast demersal species from the 15th of October to the 15th of December. According to the status of the fishery report 2021, commercial fishers caught 5 tonnes of *E. armatus*, while recreational fishers caught 20 tonnes (Newman et al., 2021). In 2013/14, recreational boat ramp surveys estimated that 30,667 *E. armatus* were caught by Recreational Boat Fishing Licence holders, with 62% of fish being retained and the remaining 38% released. This survey also showed that in 2013/14 that fishing pressure was seven times higher on the west coast (293,112 boat-based days) than the south coast (40,073 boat-based days) (Ryan et al., 2015, 2019).

In 2020/21, an assessment of the status of the WCDSF found that the catch recovery benchmark for the commercial sector was acceptable while the catch effort for the recreational sector was unacceptable (Fairclough et al., 2021). This assessment concluded that the implemented management strategies had halted the decline in spawning biomass of key indicator species, but that these species were showing only limited recovery and that the benchmarks set for the stock recoveries 2030 would not be achieved.

1.3 Previous research on *Epinephelides armatus*

Moore et al. (2007) collected *E. armatus* from the west coast region by recreational fishing and from research using rotenone for small fish <100 mm on the reef tops and in caves, mainly around Rottnest Island (32°0'S, 115°5 E). The von Bertalanffy growth curve estimates from Moore et al. (2007) showed that *E. armatus* females grew to a larger length than males, while males had a greater instantaneous growth rate (k). They also studied the reproductive biology of *E. armatus* by estimating the seasonal pattern of change of the gonadosomatic index (gonad weight/total fish weight x 100) and histological studies of gonads from a wide size range of female ($n = 128$) and male fish ($n = 106$). The result demonstrated *E. armatus* had a protracted spawning period between October and April. The length at 50% maturity was also found to be greater for females (306 mm) than males (256 mm). Female and male fish also had distinct ovarian tissue and no remnant ovarian tissues were present in

males (Moore et al., 2007). Although males had a greater TL (Total length) and modal TL (400-449mm) than females (250-299mm), the fact that no transitional individuals were found was used to classify *E. armatus* as a gonochore, one of few gonochoristic serranids (Moore et al., 2007).

1.4 Aims of the Thesis

Although Moore et al. (2007) conducted a thorough biological study on *E. armatus*, they focused on fish collected in waters 10 – 30 m in depth around Rottnest Island, a relatively small area within its broad geographic range (Figure 1.1). As *E. armatus* is distributed from warmer waters in Shark Bay to cooler waters in Esperance, it is important to understand the biology of *E. armatus* throughout its distribution to determine whether the patterns of growth and reproduction vary across this range and to be able to account for any such variation in stock assessments of this species.

As such, the aims of this study were to:

- 1) Determine the length and age distributions for *E. armatus* on the west and south coast.
- 2) Estimate, for female and male *E. armatus*, on the west and south coast
(a) von Bertalanffy growth parameters, (b) reproductive characteristics, including the spawning period and length and age at maturity, and (c) natural mortality (M) and the life history ratio M/k .

- 3) Evaluate whether the patterns of growth and reproduction differ between sexes and coasts.
- 4) Compare the biological parameters for *E. armatus* on the west coast with those determined ~10 years previously and
- 5) Determine whether the patterns of growth and reproduction on the west and south coast follow the predictions of three common ecological theories (i.e., the MTE, TSR and GOLT).

It is hypothesised that:

- 1) Fish grow faster and to a smaller size in the warmer waters of the west coast than in the cooler water of the south coast; and
- 2) The length and age distribution of fish on the more heavily fished west coast will have fewer older and larger fish than on the south coast.

With increasing fishing pressure and lower bag limits for other sought after demersal scalefish, such as *G. herbraicum* and *C. auratus* on the west coast, fishing pressure is likely to increase on less sought-after species, such as *E. armatus*. This research on the age, growth and reproduction of *E. armatus* provides the information to allow stock assessments to be completed for this species to inform management of the status of these populations on the west and south coast of Western Australia.

2. Materials and Methods

2.1 Southern oscillation index and sea surface temperatures

Data on the southern oscillation index (SOI) were extracted from NOAA (2022) using the R (citation) package RSOI by Albers (2022) for the years 2000 to 2022. These years were selected as recruitment occurred for fish in this project over that period. Data on the mean monthly sea surface temperature (mean SST) were extracted for the west coast (31.9485°S, 115.4481°E) and south coast (35.0748°S 118.00144°E) of Western Australia from the ERDAPP data set of NOAA (Huang, 2022) using the R package rerddapXtracto (Mendelssohn, 2021).

2.2 Sources of fish for biological measurements

Samples of *E. armatus* came from three different sources: 1) Fish frames donated by recreational fishers to the Department of Primary Industries and Regional Development (DPIRD) as part of the “Send Us Your Skeletons” program (SUYS) (Fairclough et al., 2014), 2) Whole fish caught by commercial fishers on the south coast, that were accessed at a wholesale market (A.J. Langford Perth Fish Market), for which only lengths and weights were recorded and otoliths removed, and 3) Smaller fish (< 300 mm) collected by spearfishing to obtain information on individuals below the minimum legal length (MLL). This study utilised only those fish collected between 2012 and 2014, as these years

corresponded to when samples of *E. armatus* were collected from south coast waters (Norris et al., 2016). In addition, samples of small *E. armatus* (<300 mm TL) were collected from west coast waters between 2021 and 2022 to gain a greater understanding of the age and growth of this species throughout its size distribution.

2.2.1 Fish Frames collected by DPIRD

Length, gonad stage and gonad weight were recorded by DPIRD after submission of the fish frames as part of their SUYS program. The SUYS program was established in December 2010 and designed to data recreational fishers to donate the filleted fish frame via drop-off points at fishing tackle stores and regional DPIRD offices. Fishers donated the fish frames with information on the method, date, and location of capture (Fairclough et al., 2014). The program was developed to collect information mainly on three indicator species for the West Coast Inshore Demersal suite, i.e., Snapper (*Chrysophrys auratus*, formerly *Pagrus auratus*), West Australian Dhufish (*Glaucosoma hebraicum*) and Baldchin Groper (*Choerodon rubescens*). However, the frames of other species were also submitted through this program, including a total of 1214 *E. armatus* between 2012 and 2014 and in 2022. Nearly all *E. armatus* frames lodged through the SUYS program (96.8%%) were >300 mm, i.e., the MLL for retaining *E. armatus*.

Where possible, the total length (TL, mm), fork length (FL, mm), sex, macroscopic gonad stage and gonad weight for each fish donated were recorded and their sagittal otoliths removed, dried, and stored in seed envelopes (see later for description of methods). In some cases, total weight was also recorded. Sex, gonad stage and gonad weight could not always be recorded as the gonad had been removed or damaged when the fish was filleted. The date of capture, bioregion, management zone, approximate location of capture, method of capture, fishing sector (i.e., commercial, and recreational) and depth were also provided by the fisher.

The data provided by DPIRD also included information on some *E. armatus* <300 mm TL that were confiscated by fishery officers in 2013-2014, measured, and lodged in the dataset.

2.2.2 Samples from fish market

Data were also recorded, and otoliths collected, for *E. armatus* caught by commercial fishers on the south coast at a wholesale market in Perth through 2021. The TL, FL, and total weight (to the nearest 0.1 g) of 47 fish were recorded as well as the approximate location and date of capture. Otoliths were extracted from these fish using a rapid extraction method that causes very little damage to the appearance of the fish. A surgical grade chisel (20 – 25 mm in width) was used to access the otic capsule from under the operculum. The pointed end of

the chisel was used to shave off part of the basioccipital bone of the otic capsule and reveal the otolith (Wakefield et al., 2016).

2.2.3 Collection of small fish (< 300 mm TL)

Small *E. armatus* were collected by freediving with spearguns and multi-speared (pranger) heads around shallow inshore reefs at three main locations in 2021 and 2022 (Figure 2.1). A total of 22 small fish were collected at Lancelin on the west coast, ~150 km north of Perth (31.0215° S, 115.3319° E) and 30 fish were collected at Albany and Bremer Bay on the south coast, 450-500 km south-east of Perth (Figure 2.1).



Figure 2.1: Map of Western Australia showing sampling sites where small (< 300 mm total length) Breaksea Cod *Epinephelides armatus* were collected in 2021 and 2022, Image obtained from Google maps.

The Lancelin area has a number of limestone reefs close to shore that could be accessed under different weather conditions (Figure 2.2a). Small *E. armatus* were observed near limestone ledges or under overhangs, but mostly within limestone caves, often swimming upside down on the ceilings of limestone caves (Fairclough, 2016). The cryptic nature of small *E. armatus* and

the complexity of the limestone reefs made collecting these individuals difficult.

Two locations were sampled for small *E. armatus* on the south coast: Albany (35.0268° S, 117.8837° E) and Bremer Bay (34.3979° S, 119.3763° E) (Figure 2.1). These two locations had either granite reef ledges/cliffs or granite outcrops close to shore (Figure 2.2b). Juveniles were often observed swimming around small ledges or along drop-offs, and sometimes resting under small ledges.

For these fish, the TL, FL, and total weight (to the nearest 0.01 g) of each individual were recorded and their gonads removed, macroscopically staged, and weighed to the nearest 0.01 g. Otoliths were dissected cleaned, dried, placed in a gel capsule, and then stored in a paper seed envelope. Before otoliths were prepared for sectioning, otoliths were also weighed to the nearest 0.001 g on a Sartorius analytic balance. Juvenile *E. armatus* collected under Murdoch University animal ethics permit RW3331/21 and DPIRD exemption 3720.

(a) Edwards Island



(b) Mistaken Island



Figure 2.2 Photos of a) Edwards Island, near Lancelin on the west coast and b) Mistaken Island, near Albany on the south coast of Western Australia, where small (< 300 mm total length) Breaksea Cod *Epinephelides armatus* were collected by free diving with small spearguns.

2.3 Gonad staging

For fish whose gonads had not been removed during filleting, gonads were removed and weighed to the nearest 0.01 g. The gonads were assigned macroscopic stages following the WCD gonad staging system as outlined for juvenile fish above (Table 2.3).

The macroscopic stages of gonads of 53 juvenile fish collected in 2022 and 660 fish from the west coast SUYS program were determined using the West Coast Demersal (WCD) gonad staging system developed by DPIRD scientists for staging the gonads of *C. auratus* (Jackson, 2007; Wakefield, 2006) (Table 2.3). The WCD macroscopic staging system is a condensed version of the Laevastu (1965) eight-stage gonad staging system. The reasoning behind condensing the stages before statistical analyses is due to not having histology to validate differences in stages where macroscopic staging cannot distinguish the stages.

The West Coast Demersal (WCD) gonad staging system recognises six stages of development for females and five for males, spanning immature fish (Stage 1) to those that are spent (Stage 6 for females and Stage 5 for males) (Table 2.3). This categorisation has two less stages for females and three less stages for males than Laevastu (1965) (Table 2.3). The Laevastu categories of Gravid and Spawning for females were condensed into Spawning in the WCD,

while Spent and Resting were condensed into Spent. Similar pooling of the latter male Laevastu stages was done for males, i.e., Developed, Gravid and Spawning were condensed into the WCD M4-Spawning; and Laevastu's (1965) Spent and Resting into WCD M5 – Spent (Table 2.3).

Table 2.2: A table showing how the WCD macroscopic staging system compares with the eight-stage macroscopic staging system from Laevastu, 1965.

Laevastu staging system (Females and males)	WCD staging system (Females)	WCD staging system (Males)
I – virgin	1 – Immature	M1 - Virgin
II – Maturing	2 – Resting/regressed	M2 – Mature resting
Virgin/recovering spent		
III – Developing	3 – Developing	M3 - Developing
IV – Developed	4 – Developed	
V – Gravid	5 – Spawning	M4 - Spawning
VI – Spawning		
VII – Spent	6 – Spent	M5 - Spent
VIII – Resting		

Table 2.3: Macroscopic stages and characteristics of development for ovaries and testes for Breaksea Cod <i>Epinephelides armatus</i> (Mackie et al., 2009; Moore et al., 2007)			
Ovary Stage	Ovaries	Testes stage	Testis
1 – Immature	Small strands, grey/white in color.	M1	Small strands, ivory in color, No milt present.
2– Resting/regressed	Ovary more rounded, pale pink or red. Slightly larger than previous stage, Oocytes not visible.		
3 – Developing	Ovary enlarged, pink or pale orange with oocytes visible and blood vessels noticeable.	M2	Larger than M1, opaque and strap like with little to no milt extruded when squeezed. Grey – white in color.
4 – Developed	Ovary enlarged occupying half the body cavity. Reddish/orange with oocytes large and clearly visible through ovarian wall.	M3	Larger than M2 with larger exterior blood vessels, milt extruded when pressure applied to testicular lobes. White in color.
5 – Spawning	Ovary much more enlarged, occupying 2/3 of body cavity. Hydrated clear oocytes with blood vessels prominent. Eggs may extrude with pressure.	M4	Large testes that is opaque and ivory or bone in color. Exterior blood vessel is larger with small blood vessels present. Milt extruded with little to no pressure from central sperm sinus.
6 – Spent	Small dark red and flaccid	M5	Flaccid testes, when pressure applies to testicular lobes milt maybe released. Sometimes reddish in color

2.4 Preparation of otoliths for aging

Sagittal otoliths were prepared for sectioning by marking the sulcus and the primordium of the otolith before embedding them in clear epoxy resin (Figure 2.4a). The resin block was cut into ~300 μm sections using a Buehler Isomet low speed saw with a diamond-tipped wafering blade. The sections were cut at right angles to the sulcus of the otolith (Figure 2.4c). After the section was cut, they were dipped into a 2% HCl solution for 15 to 20 seconds before being dipped into water to clear the embedded calcium carbonate dust on the sections. They were then dried, cleaned, and mounted on slides using clear casting resin (From Fibreglass & Resin Sales Pty Ltd). Sections were then examined against a black background using a dissecting microscope (Leica MZ 7.5) using reflected light. An image of each otolith was captured using a Leica DC 300 digital microscope mounted on the dissecting microscope. The image was examined in detail using Leica Application Suite software (version 3.6), which allowed growth (opaque) zones to be marked and measurements for marginal increments to be obtained (see below, 2.5).

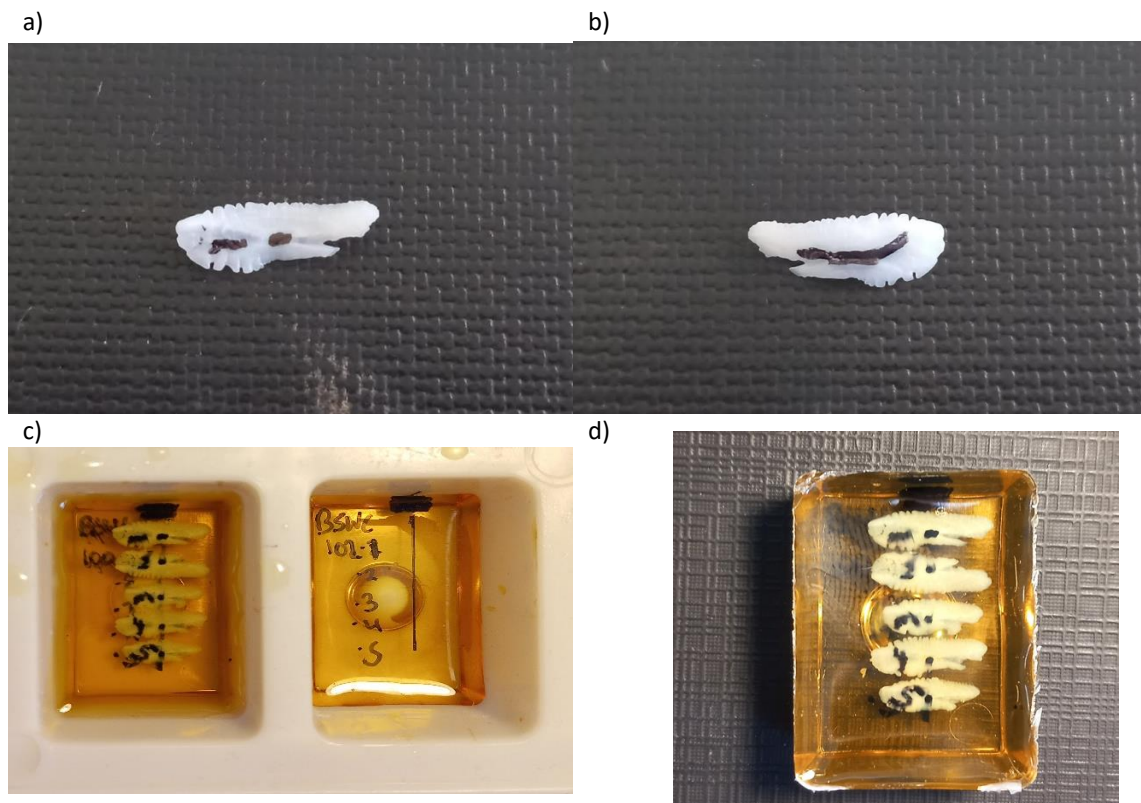


Figure 2.4: Preparation of *Epinephelides armatus* otoliths before being sectioned, a) marking of primordium, b) marking of sulcus, c) otoliths placed with sulcus 90° to marked line and d) prepared otolith block.

2.5 Ageing & age validation

The readability of the otolith and the type of marginal edge were assessed qualitatively (Table 2.4). The readability of the otolith was classified on a scale of 1 (great – clear, continuous opaque zones), to 4 (poor - opaque zones difficult to distinguish, multiple split zones, unsure on first opaque zone, almost unreadable) (Table 2.4). Otoliths that had a readability of 4 were not included in the analyses. Following the criteria of Wakefield et al. (2010), the marginal edge was classed as either narrow translucent (NT– Translucent zone <50% width of the last completed zone), wide translucent (WT - Translucent zone >50% width

of the last completed zone) or opaque (O - New opaque zone forming on the edge) (Table 2.4).

The otoliths were read twice by the same reader – one read was conducted on two separate occasions without knowledge of the fish length or date of capture. All otoliths were also read by a second, experienced otolith reader, Dr Peter Coulson (University of Tasmania. In cases where the count of the number of opaque zones recorded by the two readers differed by >2, discussions were held between the two readers to determine what caused the discrepancy. It was determined that the differences were mainly due to the presence of ‘split’ opaque zones and/or difficulty in identifying the first opaque zone, which is in part, caused by the extended spawning period and thus the wide variation in hatching dates.

Table 2.4: Values and descriptions used to assess the readability and marginal edge of Breaksea Cod *Epinephelides armatus* otoliths.

Readability value	Readability description	Marginal Edge	Marginal edge description
1	Great – Clear continuous zones.	O	Opaque edge – New zone forming on edge
2	Fair – Opaque zones are able to be distinguished, splits present.	NT	Narrow Translucent – Translucent zone <50% width of the last completed zone.
3	Ordinary – Opaque zones have splits and with some difficulty in determining the first opaque zone, counts were still able to be determined.	WT	Wide Translucent - Translucent zone >50% width of the last completed zone.
4	Poor - Opaque zones difficult to distinguish, multiple splits, unsure on first opaque zone, almost unreadable.	—	—

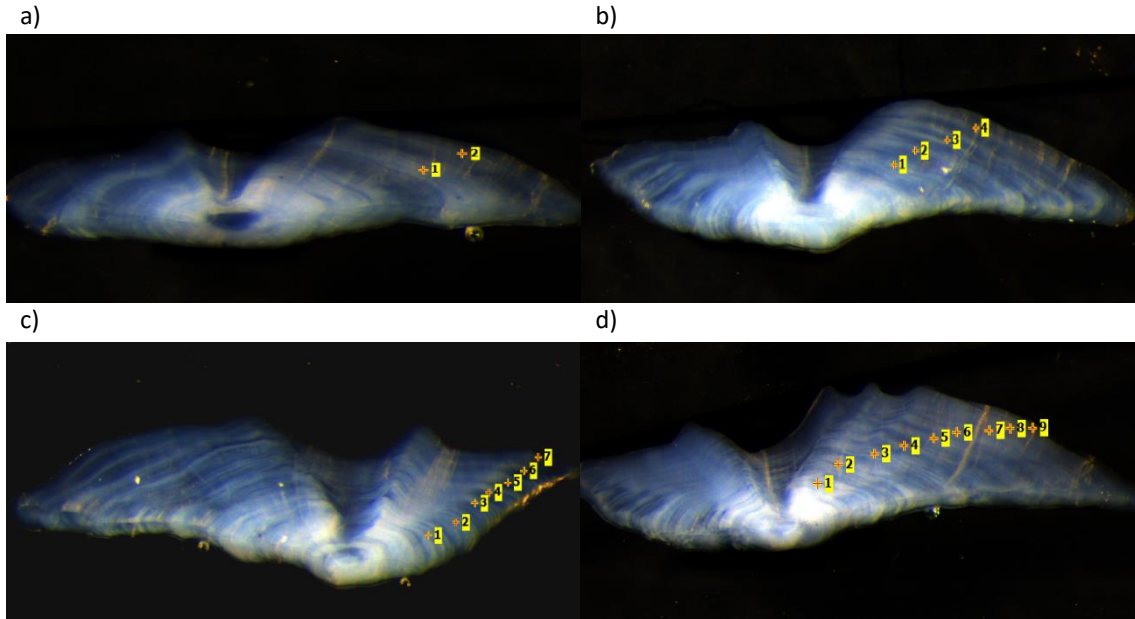


Figure 2.5: Four sectioned otolith of *Epinephelides armatus* showing sections with a) two opaque zones, b) four opaque zones, c) seven opaque zones and d) nine opaque zones.

The precision of ageing is defined as the reproducibility of repeated measurements on a given otolith. The accuracy and precision of reading otoliths by the two readers was assessed by calculating the index of average percent error (IAPE). An IAPE value of <5.5 is required for counts to be considered acceptable for determining age, while an IAPE >10 indicates an unacceptable level of precision (Beamish & Fournier, 1981). The equation of IAPE is described by Beamish and Fournier (1981) is.

$$IAPE = 100 * \frac{\sum_{j=1}^n \sum_{i=1}^R \frac{|x_{ij} - \bar{x}_j|}{\bar{x}_j}}{nR}$$

Where, x_{ij} is the i th age determination for the j th fish, \bar{x}_j is the mean age estimate of the j th fish, n is the number of aged fish in the sample size and R is the number of times that each fish was aged.

Moore et al. (2007) demonstrated that the opaque zones in the otoliths of *E. armatus* from the lower west coast are formed annually. However, this validation has not been undertaken for fish from the south coast where environmental conditions are different (see Figure 1 in Coulson et al. 2010). To validate that opaque zones were laid down annually, the trends in the mean monthly marginal increment (MI), i.e., the distance between the outer edge of the single or outermost opaque zone and the otolith periphery, were investigated for fish from the west and south coasts separately. The MI was expressed as a proportion of either the distance between the primordium and the outer edge of the single opaque zone, when one such zone was present, or of the distance between the outer edges of the two outermost opaque zones when two or more such zones were present. All distances were measured to the nearest 0.01 mm and along the same perpendicular axis to the opaque zones. The MI for fish with all numbers of zone counts were pooled before determining the mean monthly MI.

In addition to the visual trends displayed by the mean monthly MIs, the approach described by Okamura and Semba (2009) was used to statistically

determine the periodicity of occurrence of otoliths with marginal increments that fell within the 30th percentile of values for each category of zones. In order to perform these analyses, binomial models coupled with von Mises circular distributions, were fitted assuming (I) no annual cycle, (II) an annual cycle and (III) a biannual cycle. The Akaike Information Criterion (AIC) was then used to compare these models and the model with the lowest AIC value was selected as the “best” model representing the data. For a model to be identified as better than other models, the AIC for the selected model needed to be >2 units less than the other models in regard to the Kullback–Leibler distance (Burnham et al., 2011; Okamura & Semba, 2009).

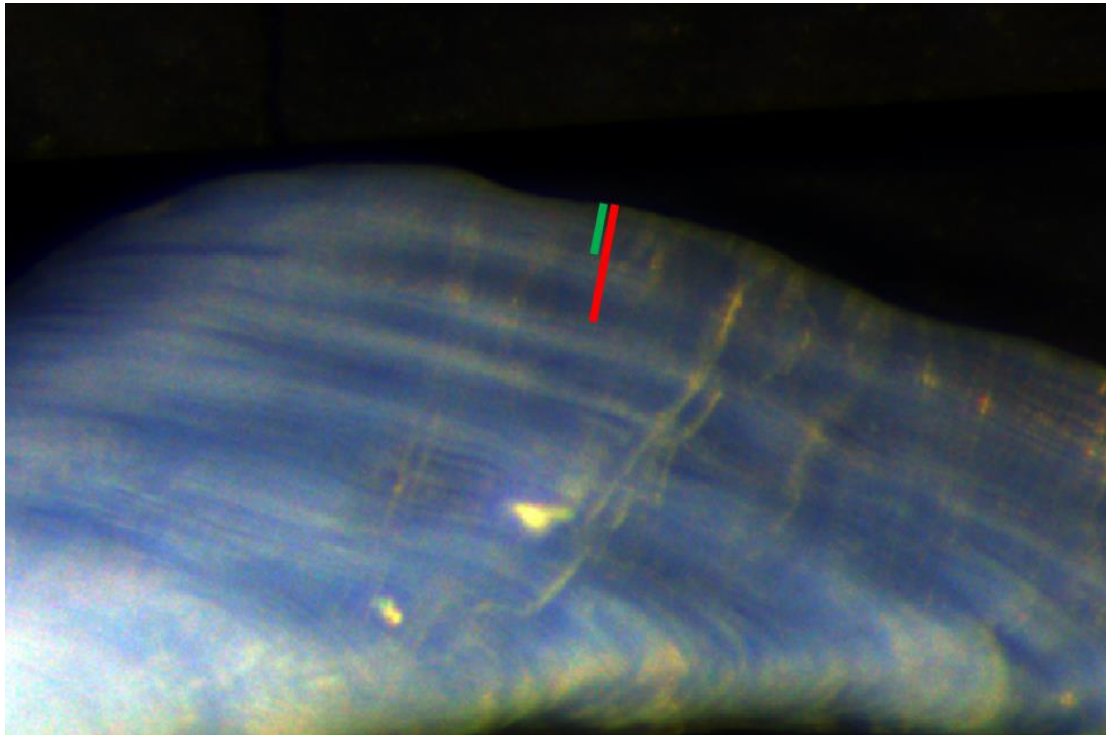


Figure 2.6: Sectioned otolith of Breaksea Cod, *Epinephelides armatus*, showing the measurements recorded for the marginal increment analysis. Green line shows the marginal increment and orange line shows the distance between the two outermost, complete opaque zones.

2.6 Data Analyses

2.6.1 Otolith weight and distributions

The relationship between otolith weight and fish total length (TL) was examined for 718 fish on the west coast and 472 fish on the south coast using linear regressions. The left otolith was chosen for consistency in case of differences in weights between left and right otoliths. Using R (R Core Team, 2021), an analysis of covariance (ANCOVA) was undertaken to determine

whether the relationship between otolith weight and fish length differed between the sexes on each coast. The relationship is expressed as:

$$y = m \log(x) + b$$

where y is the TL, x is the otolith weight, m is the slope and b is the y-intercept of TL when the log of the otolith weight is 0.

Differences in the length and age distribution *E. armatus*, collected by recreational fishers, between sexes and regions were tested using the Kolmogorov–Smirnov goodness-of-fit test (Ks test) (O'Neill & Stern, 2012).

2.6.2 Age and growth

Each fish was assigned an age, based on the number of opaque zones in its otolith, but considering the date of capture of the fish, the “average” birth date (approximate mid-point of the spawning period) of 1 February (see, 4.2.1 below and Moore et al., (2007)) and the time of year when the single or outermost of those zones become delineated. For fish captured between February and December, their age was calculated as follows.

$$A = ZC + ((M - 2)/12) + (D/365)$$

where A is the calculated age, ZC is the opaque zone count, M is the month of capture and D is the day of capture. When fish were captured in January, the following equation was used to calculate age:

$$A = ZC + ((M + 10)/12) + (D/365)$$

von Bertalanffy growth curves were fitted to the lengths at age of female and male *E. armatus* from the west coast and the south coast using nonlinear regression in R (R Core Team, 2021). Data were pooled for years and sampling method. The equation for the von Bertalanffy growth curve is.

$$L_t = L_{\infty}(1 - \exp^{-k(t-t_0)}),$$

where L_t is the total length (mm) at age t (years), L_{∞} is the mean asymptotic length (mm), k is the instantaneous growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which the fish has zero length.

A log-likelihood ratio test (Cerrato, 1990) was used to I) compare the growth curves between sexes on each coast and II) compare the growth curves of the each sex between the west and south coast. The test statistic was determined as twice the difference between the log-likelihoods obtained by fitting a common growth curve to the data for the individuals of both sexes, or both coasts, and by fitting separate growth curves for the individuals of each sex, or each coast. 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, λ , 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. Data for female and male *E. armatus* collected on the west coast comprised older fish than those of Moore et al. (2007) from the same region, while the latter data comprised younger and smaller fish than the contemporary west coast data set. Therefore, a log-likelihood ratio test could not be used to test for significant differences between the von Bertalanffy growth curves fitted to these data sets. Instead, a paired t-test was used to test the differences of the predicted mean lengths at age for ages 5, 8 and 10 of females and males in these two data sets.

2.6.3 Natural Mortality and M/k

Hoenig (1983) completed a meta-analysis of 113 species to calculate point estimates of total mortality (Z) based on the maximum age of a fish (t_{max}):

$\ln(Z) = a + b \ln(t_{max})$, where t_{max} is the observed maximum age, a and b are coefficients of the linear equation and \ln is the natural logarithm. When fishing mortality (F) is low, Z approximates natural mortality (M). The original equation developed by Hoenig (1983), however, does not provide an evaluation of prediction error. Thus, Then et al. (2015) developed a method of estimating M using the refitted version of Hoenig (1983), i.e., $M = at_{max}^b$, where t_{max} is the observed maximum age, a and b are coefficients of the linear equation, with $a = 4.899$ and $b = -0.916$. Compared to other methods for determining point

estimates of M , such as Pauly (1980) and Hoenig (1983), the Then et al. (2015) method performs better, with less prediction error.

Using the estimates of M and the growth coefficient (k), the Beverton-Holt life history ratio of M/k was calculated. This life history ratio can be used to predict the size distribution of the unfished population, assuming equilibrium conditions. This allows the SPR to be calculated from a representative sample of the current size distribution. (Hordyk et al., 2015b; Prince et al., 2015).

2.6.4 Reproduction

It was not possible to determine the gonadosomatic index for many fish from the SUYS program as total fish weights were rarely available. Therefore, gonad weight for females and males was used to determine the mean monthly gonad weight for each sex that was in turn used to help determine the time and duration of spawning of *E. armatus* in waters off the west and south coasts. Note, means were calculated only when gonad weights for five or more fish were available. Data were pooled for years and sampling method (see Coulson et al., 2010, 2016).

The total length (TL_{50}) and age (A_{50}) at maturity of female and male *E. armatus* from the west and south coasts were determined using data from the spawning season (see 4.2.1 below) for each coast. Females with ovaries at stages 3 to 6 and males with testes at stages 3 to 5, caught during the spawning period,

were considered to be mature or likely to become mature during the spawning period, while fish that were stage 1 and 2 were considered immature or would not mature during the spawning period (Moore et al., 2007). The TL_{50} and A_{50} at maturity were determined using logistic regression analysis to fit logistic curves to the probabilities that female and male fish at a given length during the spawning period would possess mature gonads (stages 3 – 6 for females and 3 – 5 for males). The data were randomly resampled and analysed to generate 1000 sets of bootstrap estimates, which were used to determine the 95% confidence limits of the parameters of the logistic regression analyses. The logistic equation used to estimate length at maturity was;

$$P_{TL} = 1 / \{1 + \exp [- \ln(19) (TL - TL_{50}) / (TL_{95} - TL_{50})]\}$$

Where P_{TL} is the probability of *E. armatus* having mature gonads at length (TL , mm); TL_{50} and TL_{95} = the total lengths at which 50% and 95% were mature, respectively. The logistic equation used for age at maturity was;

$$P_A = 1 / \{1 + \exp [- \ln(19) (A - A_{50}) / (A_{95} - A_{50})]\}$$

Where P_A = proportion mature at a particular age (A , years); A_{50} and A_{95} = the age at which 50% and 95% of *E. armatus* were mature.

A log-likelihood ratio test, performed in R (R core team, 2021), was used to test whether the length and age at maturity curves differed between females

and males, with the same test used to determine whether the length and age at maturity curves differed between corresponding sexes on the two coasts.

3. Results

3.1 Sea surface temperature

The monthly Southern Oscillation Index (SOI) index for Western Australia was >0 from 2007 to early 2010, late 2010 to 2012 and in recent years from 2020-2022 (Figure 3.1), with La Niña events occurring in 2001, 2008, 2009, 2011, 2018 and 2021-2022 (Huang, 2022; Zinke et al., 2014). The monthly SOI values were mainly negative in 2003, 2004, 2007, 2010, 2015 – 2016 and 2018 -2019 (Figure 3.1), indicating El Niño events in these years. The maximum SOI value was 2.9 (La Niña) in 2010, while the minimum SOI value was -3.1 (El Niño) in 2005.

The maximum mean monthly sea surface temperatures (SST) at Rottnest Island on the west coast were always $>21^{\circ}\text{C}$ with the highest value of 23.6°C recorded in April 2011 during a La Niña event (Figure 3.2a). At Albany on the south coast, the maximum mean monthly SSTs never rose above 21°C , with the highest value of 20.4°C also occurring in March 2011 (Figure 3.2b). The minimum mean monthly SSTs on the west coast were rarely below 17°C , with the lowest mean monthly SST of 16.9°C recorded in October 2016 (El Niño). In comparison, the minimum mean monthly SSTs on the south coast were always

<16°C with the lowest SST of 14.4°C recorded in November 2016. Seasonally the west and south coast follow a similar trend with cooler mean monthly SSTs from August to December and warmer mean monthly SSTs from January to June (Figure 3.3).

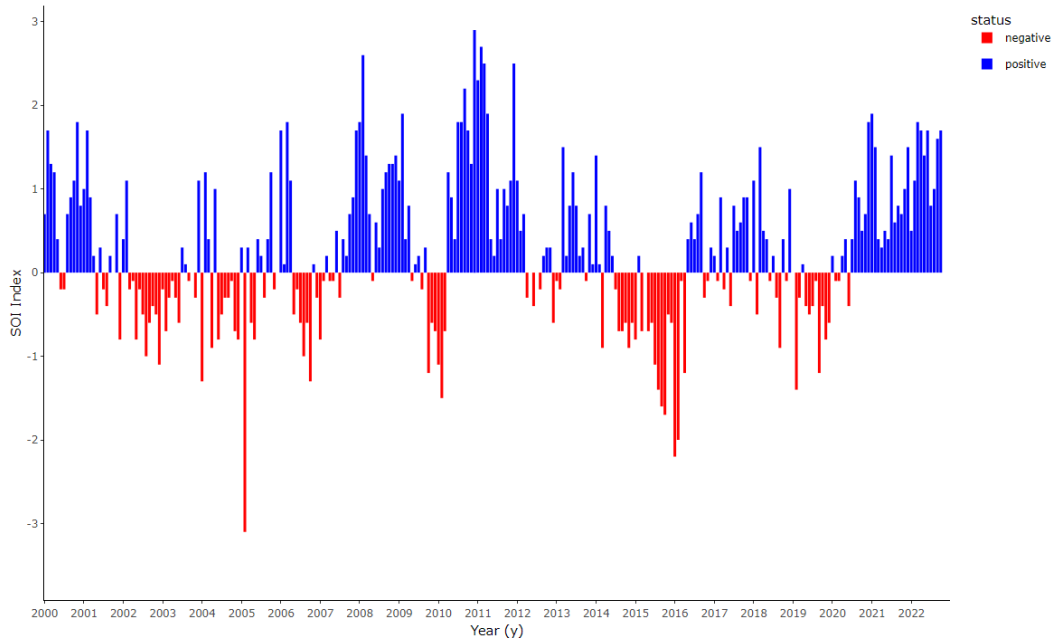


Figure 3.1: Southern Oscillation Index (SOI) from January 2000 to 2022.

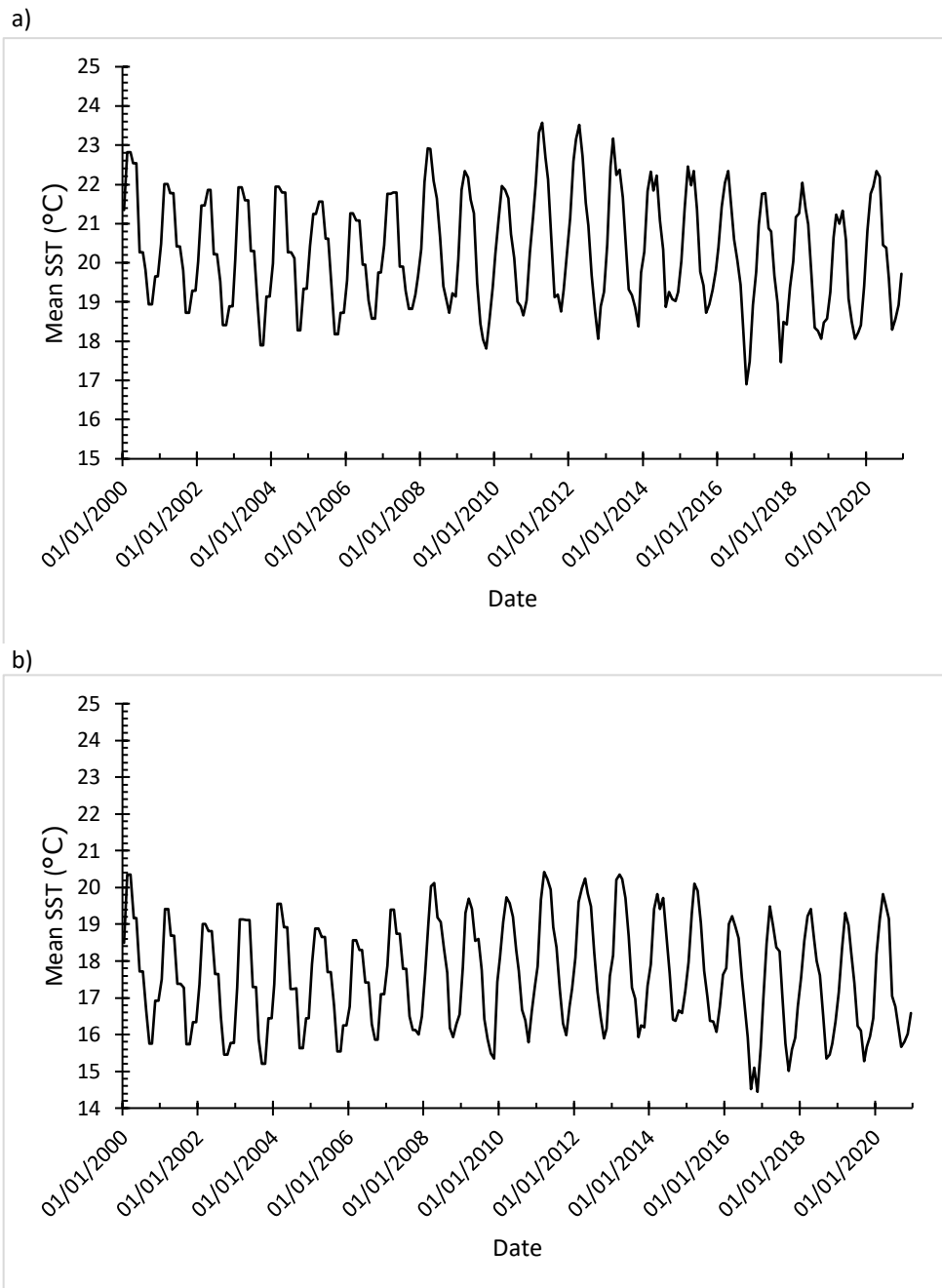
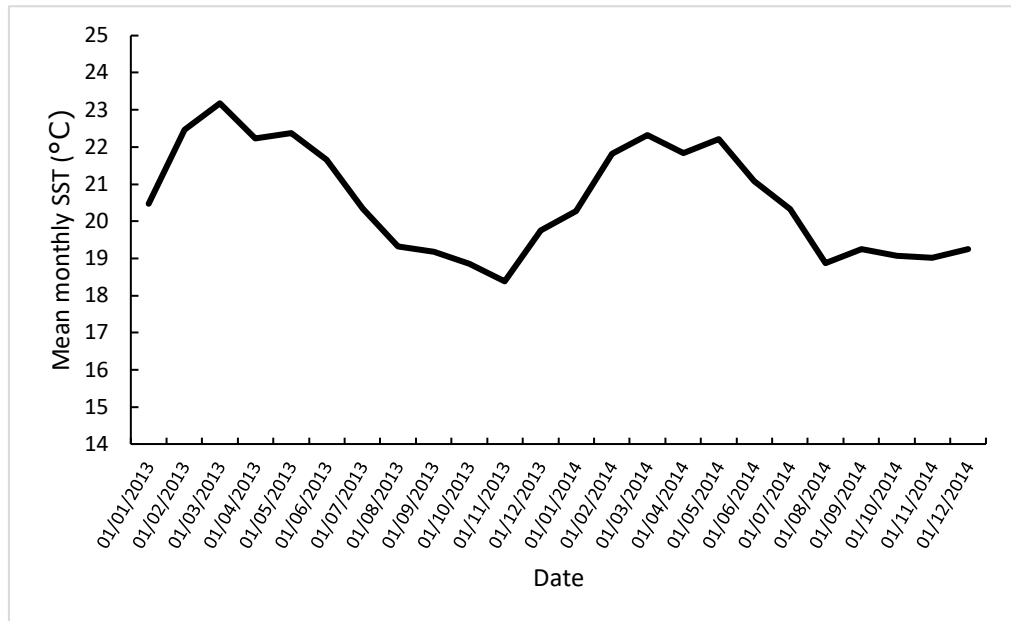


Figure 3.2: Mean Sea surface temperature (SST) between 1/1/2000 to 1/12/2020 from a) the west coast and b) the south coast of Western Australia.

a)



b)

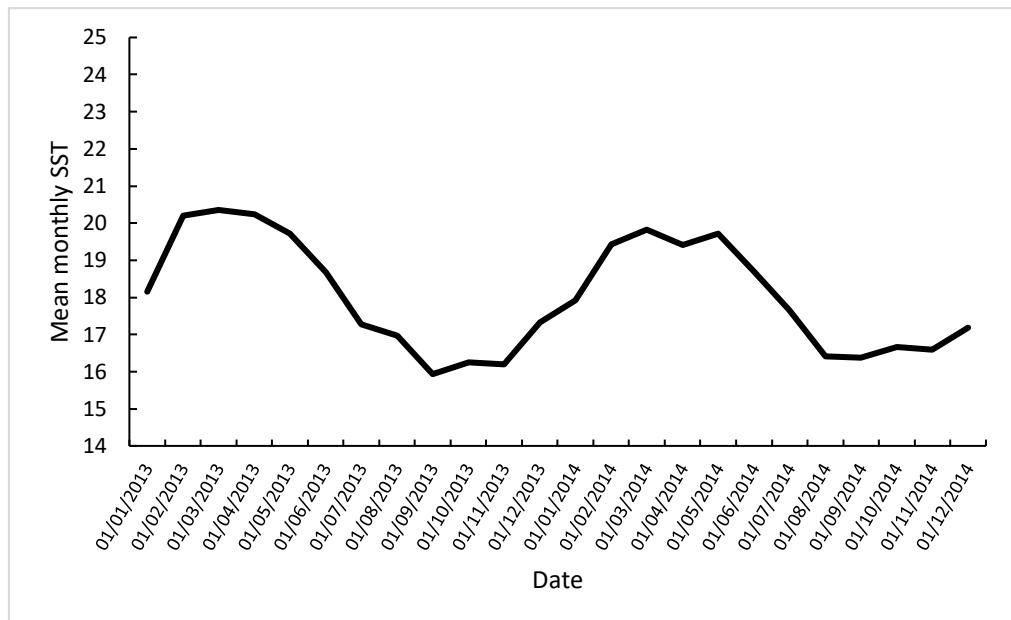


Figure 3.3: Mean Sea surface temperature (SST) between 1/1/2013 to 1/12/2014 from a) the west coast and b) the south coast of Western Australia.

3.2 Source of *Epinephelides armatus* samples

Over 84% of the *E. armatus* frames used in this study were \geq MLL and came from the years 2012, 2013 and 2014. Fish $<$ MLL comprised 4.7% of the total number of fish included in the analyses and all came from the 2022 juvenile sampling and fish larger than the MLL were sampled in the years of 2012 (6.6%), 2013 (52.4%), 2014 (26.7%), 2020 (6.3%) and 2021 (3.3%) while fish below the MLL were sampled in 2022 (4%), fish collected in 2020 from the fish markets (6.3%) has associated fish total weights (Table 3.1).

Table 3.1 The number (and %) of Breaksea cod, *Epinephelides armatus* collected from commercial line and gill net fishers, recreational fishers (including fishers on board charter fishing vessels), and by researchers in waters off the west and south coasts of Western Australia.

Data/Sector	Method of capture	West coast	South coast	Total
a) Commercial	Line	6 (0.9%)	90 (15.6%)	96 (8.0%)
	Gill net	-	3 (0.5%)	3(0.2%)
	Total	(6, 0.9%)	(93, 16.1%)	(99, 8.3%)
Recreational	Individuals	660 (95.5%)	420 (72.9%)	1080 (90.8%)
	Charter		7 (1.2%)	7 (0.6%)
	Total	(660, 95.5%)	(427, 74.1%)	(1168, 98.1%)
Research	Line	3 (0.4%)	—	3 (0.2%)
	Spearfishing	22 (3.2%)	30 (5.2%)	52 (4.4%)
	Total	(25, 3.6%)	(30, 5.2%)	(55, 4.6%)
Total		691	576	1267

3.3 Ageing & Validation

The level of agreement between the two readers in determining the number of opaque zones on the 990 otoliths of *E. armatus* was 78%. Counts by the two readers differed by one in 20 % of cases and by two in 2% of cases. No counts of opaque zones differed by >2. The index of average percent error (IAPE,) which takes into account the reproducibility of repeated measurements on a given otolith, was 2.3%, and thus well below the reference level of 5.5% used to determine precision and accuracy (Beamish & Fournier, 1981).

The age-bias plot demonstrated little difference in the number of opaque zones counted by the two readers for otoliths with 1 to 3 zones while there was variation in the counts for those otoliths with 4 to 8 zones (Figure 3.4a,b). The agreement between readers did not decrease with increasing zones >8 (Figure 3.4 c, d). While there is some variation in the counts of opaque zones recorded by the two readers, neither reader appears to be biased by either under or over counting the opaque zones.

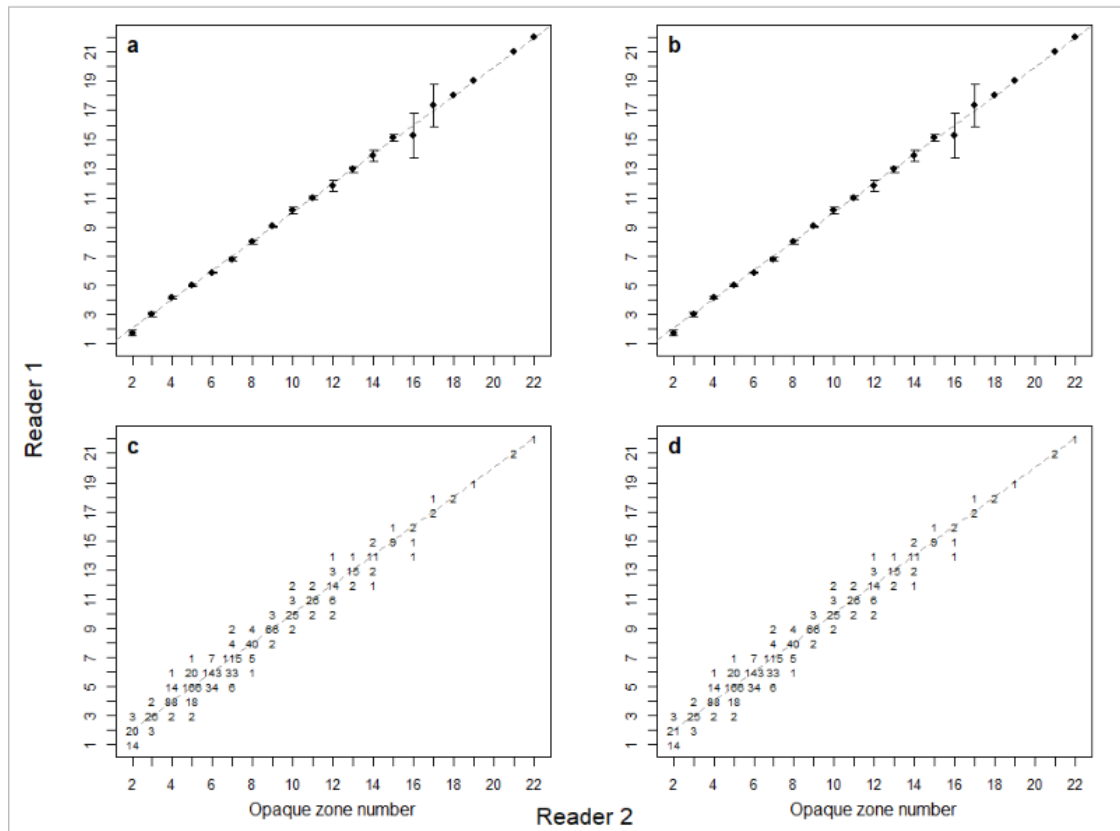


Figure 3.4: Age-bias plot to visualize differences in paired estimates of opaque zone counts (a and c) and age class estimates (b and d) of *Epinephelides armatus* ($n = 990$). Reader 1 counts are on the y-axis, reader 2 counts are on the x-axis.

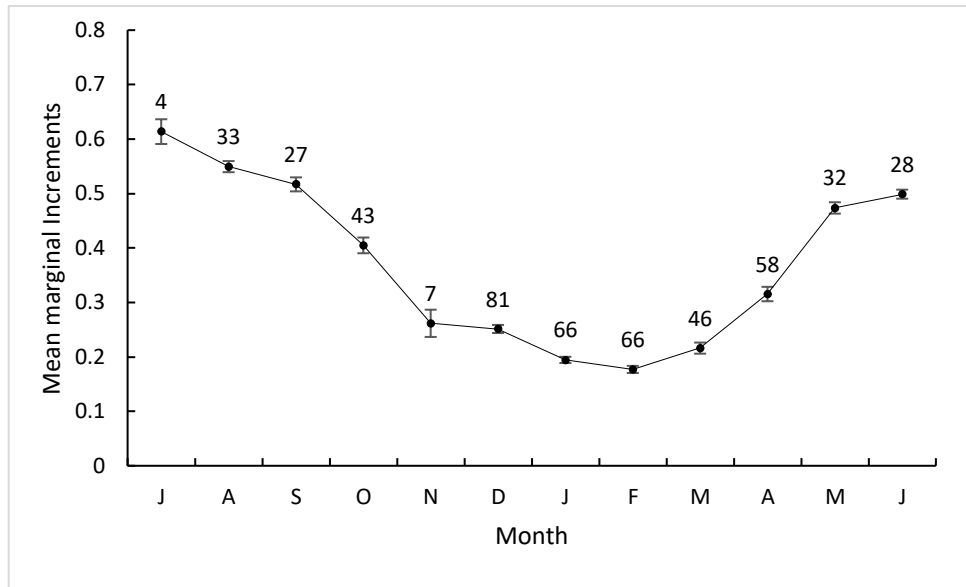
The mean monthly marginal increment for otoliths from west coast fish were >0.40 from May to October before declining to 0.26 in November (Figure 3.5a). The mean monthly marginal increment continued to decline to a minimum value of 0.18 in February before increasing to 0.30 in April. The mean monthly marginal increments for otoliths from south coast fish were >0.37 from May to October (Figure 3.5b). There was a small decline in October and November before a steep decline in to a minimum value in December. The marginal increments remained <0.26 until April, before a steep increase in May to 0.46 (Figure 3.5b).

The circular distribution model with the lowest AIC value for the marginal increments for otoliths from west (18.5) and south (27.59) coast *E. armatus* were both obtained for the annual cycle model (i.e. AIC 2). Furthermore, the difference between these values and the values for the no annual trend model (AIC 1) and biannual cycle model (AIC 3) were >2 (Table 3.2), the number required to identify definitively the best model in terms of the Kullback–Leibler distance (Burnham & Anderson, 2002).

The progressive increase and then single pronounced decline in the mean monthly marginal increments during the year imply that, irrespective of

the number of opaque zones, a single opaque zone is typically formed annually in the otoliths of *E. armatus*. This conclusion is supported by the results of circular distribution models and the concomitant AIC values. Thus, the number of opaque zones in sectioned otoliths can be used to age the individuals of *E. armatus* for fish collected on both the west and south coasts.

a) West coast



b) South coast

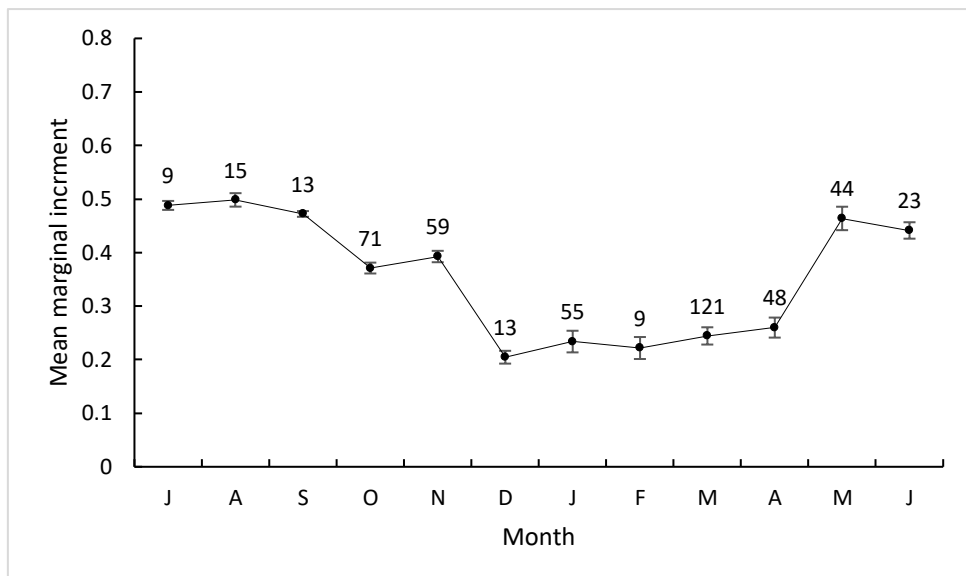


Figure 3.5: Mean monthly marginal increments ± 1 SE in sectioned sagittal otoliths of *Epinephelides armatus* from the a) west and b) south coasts of Western Australia with a different number of opaque zones. The sample sizes for each month are given above each mean.

Table 3.2: The Akaike Information Criterion values for testing whether the marginal increments on otoliths of *Epinephelides armatus* fell within the lower 30 percentile of values for each category of zones with AIC 1 representing a no cycle trend, AIC 2 representing an annual trend and AIC 3 representing a biannual trend. Bold text shows the lowest of the three AIC values by >2 units.

Bioregion	AIC 1	AIC 2	AIC 3
West coast	22.25	18.49	21.99
South coast	32.98	27.58	29.98

3.4 Length distribution

Female *E. armatus* sampled from the west coast ranged from 100 mm (research sampling) to 550 mm (recreational sampling), with a modal size of 375 mm and most fish present in the 325 mm to 450 mm size range (83.8%; Figure xx). The percentage of females ≥ 400 mm was 46.5%, which dramatically decrease to 1.0% for fish ≥ 500 mm (Figure 3.6a, Table 3.3). The female length distribution was dominated by fish donated by recreational fishers (95.3% of samples). Female *E. armatus* caught by recreational fishers on the west coast ranged in lengths between 275 mm and 550 mm with the 375 mm length class possessing the highest proportion of fish (20.3%). Very few female *E. armatus* > 500 mm ($n = 3$) were caught by recreational fishers (Figure 3.6a). The small sample of commercially caught female *E. armatus* ranged from 375 mm to 400 mm ($n = 5$).

West coast males had a similar size range to that for the females but a larger modal size class (425 mm), and most fish were in the 325 to 475 mm size range (87.2%), with a good portion of male fish (5.1%) in the 500 mm size class.

Males below the MLL comprised 3.3% of all males on the west coast and all came from research sampling by spearfishing (3.3%). The proportion of males that were ≥ 400 mm was 63.7% while the proportion of fish dramatically decrease for fish that were ≥ 500 mm at 5.9% (Figure 3.6b, Table 3.3). The male length class was dominated by recreational samples (95.6%) with recreationally caught fish ranging from 275 mm to 525 mm with the 425 mm possessing the highest proportion of recreationally caught fish (18.2%). There was only one commercially caught *E. armatus* present in the 400 mm length class (Figure 3.6b). The Ks test for goodness of fit showed that the length distributions west coast females and males that were caught by recreational fishers were significantly different ($P < 0.05$).

Female *E. armatus* on the south coast had a similar range of sizes to those on the west coast (125 to 500 mm) but showed evidence of two modes in the distribution; the first at 350mm, and the second at 425mm. The proportion of females that were ≥ 400 mm was 43.7% while the proportion of fish dramatically decrease for fish that were ≥ 500 mm at 2.8% (Figure 3.6c). The female length was dominated by recreational samples (77.5%), with recreationally caught fish ranging from 250 mm to 500 mm with the 425 mm length class having the highest proportion of fish (15.4%). There was a low number of fish in the highest length class at 500 mm ($n = 6$). Compared to the west coast there were more commercial samples (17.9%) present in the south

coast. Commercially caught fish ranged from 300 mm to 500 mm with the highest proportion of fish in the 350 mm length class (21.6%). There was a low number of commercially caught fish > 450 mm ($n = 12$). There was a low number of fish caught through charters with two fish in the 400 mm length class and two fish in the 450 mm length class (Figure 3.6c). The Ks test for goodness of fit showed that the length distributions of west coast females and south coast females that were caught by recreational fishers were significantly different ($P < 0.05$), this was the same for west coast and south coast males ($P < 0.05$)

South coast males had a larger size range than females, ranging from 125 mm to 550 mm, the modal size classes between were 350-375 mm and again at 450-475 mm (Fig. 3.6d). The proportion of males that ranged from 400 to 499 mm was 40.6% while the proportion of fish decreased for fish that were ≥ 500 mm to 11.0% (Figure 3.6d). Male *E. armatus* caught through research sampling ranged from 125 mm to 250 mm with the highest proportion of fish in the 150 mm length class (28.6%). Male *E. armatus* caught by recreational fishers ranged from 300 mm to 550 mm with the 375 mm length class possessing the highest proportion of fish (14.8%). Very few male *E. armatus* > 500 mm ($n = 3$) were caught by recreational fishers on the south coast. Commercially caught male *E. armatus* ranged from 325 to 525 mm with the 475 mm length class possessing the highest proportion of fish (17.1%). Very few male *E. armatus* > 500 mm ($n =$

3) were caught by commercial fishers on the south coast (Figure 3.6d). The Ks test for goodness of fit showed that the south coast females and males that were caught by recreational fishers were not significantly different ($P = 0.59$)

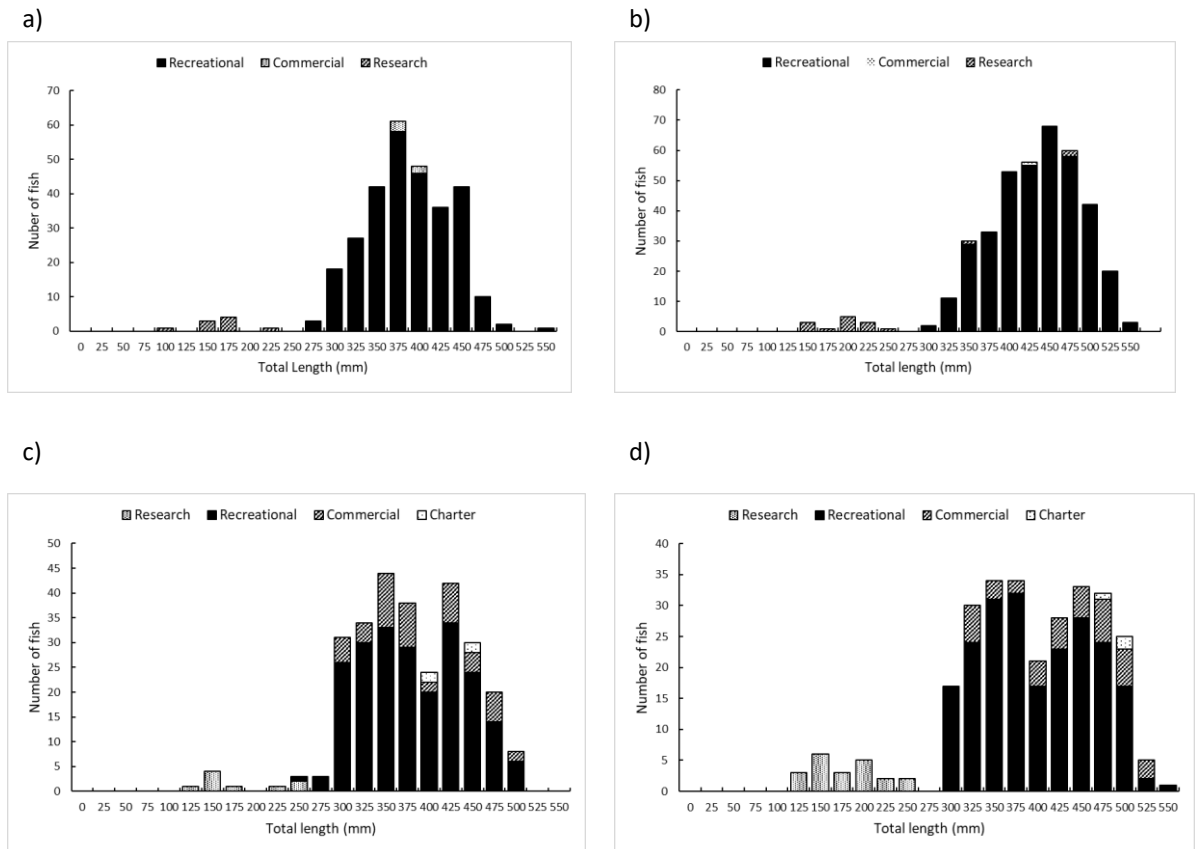


Figure 3.6: Length-frequency distributions for a ($n = 299$), c ($n = 284$) female and b ($n = 391$), d ($n = 281$) male *Epinephelides armatus* caught by researchers and collected from the recreational, commercial, charter fishers on the a, b) west and c, d) south coasts of Western Australia.

Table 3.3: Summary table of Minimum, maximum, mean and median values of total length (<i>TL</i> , mm) and age (years) of female and male <i>Epinephelides armatus</i> from the south coast and west coast bioregions of Western Australia. <i>n</i> = 1263.											
Region	Sex	Sector	Minimum <i>TL</i> (mm)	Maximum <i>TL</i> (mm)	Mean <i>TL</i> (mm)	Median <i>TL</i> (mm)	Minimum Age	Maximum Age	Mean Age	Median Age	<i>n</i>
West coast											
	Females	Combined	123	550	392	395	1.33	21.93	7.5	6.73	298
		Recreational	286	550	399	397	3.6	21.93	7.7	6.89	284
	Males	Combined	128	544	413	422	1.33	22.55	6.81	6.21	391
		Recreational	293	544	421	426	3.01	22.55	7.05	6.32	374
South coast											
	Females	Combined	148	523	389	387	1.27	21.75	7.77	6.69	285
		Recreational	272	522	392	386	3.09	21.75	7.95	6.75	221
	Males	Combined	145	565	400	403	1.09	16.11	6.71	6.11	288
		Recreational	300	565	411	404	3.09	16.11	7.03	6.16	221

3.5 Age distributions

The smaller female and male *E. armatus* caught by researchers on the west coast ranged from 1-3 and 1-6 years of age, respectively (Figure 3.7a, b). Female *E. armatus* caught by recreational fishers on the west coast ranged from 3 to 20 years in age with a modal age class of 6 years (Figure 3.7a). More than half (54.3%) of the females occurred in the 5 – 7-year age classes while only 6.4% were ≥ 11 years of age (Figure 3.7a). The age range of male *E. armatus* caught by recreational fishers on the west coast ranged from 2 to 22 years of age with a modal age class of 5 years (Figure 3.7b). Like females, a large percentage (58.9%) of the males caught by recreational fishers were between 5 and 7 years of age. Very few males (16, 6.4%) were ≥ 11 years of age (Figure 3.7b).

The age of female and male *E. armatus* targeted by researchers on south coast ranged in age from 1 – 3 years for both sexes (Figure 3.7c). Female and male *E. armatus* caught by recreational fishers on the south coast ranged in age from 2-21 years and 3-16 years, respectively, with the majority for both sexes (i.e., 44.7% and 49.3%, respectively) being 4-6 years of age. The few females (n=4) and males (n=3) caught by charter fishers on the south coast ranged in age from 5-13 and 10-

12 years, respectively. The age of females and males caught by commercial fishers ranged from 4-19 and 4-14 years, respectively (Figure 3.7c).

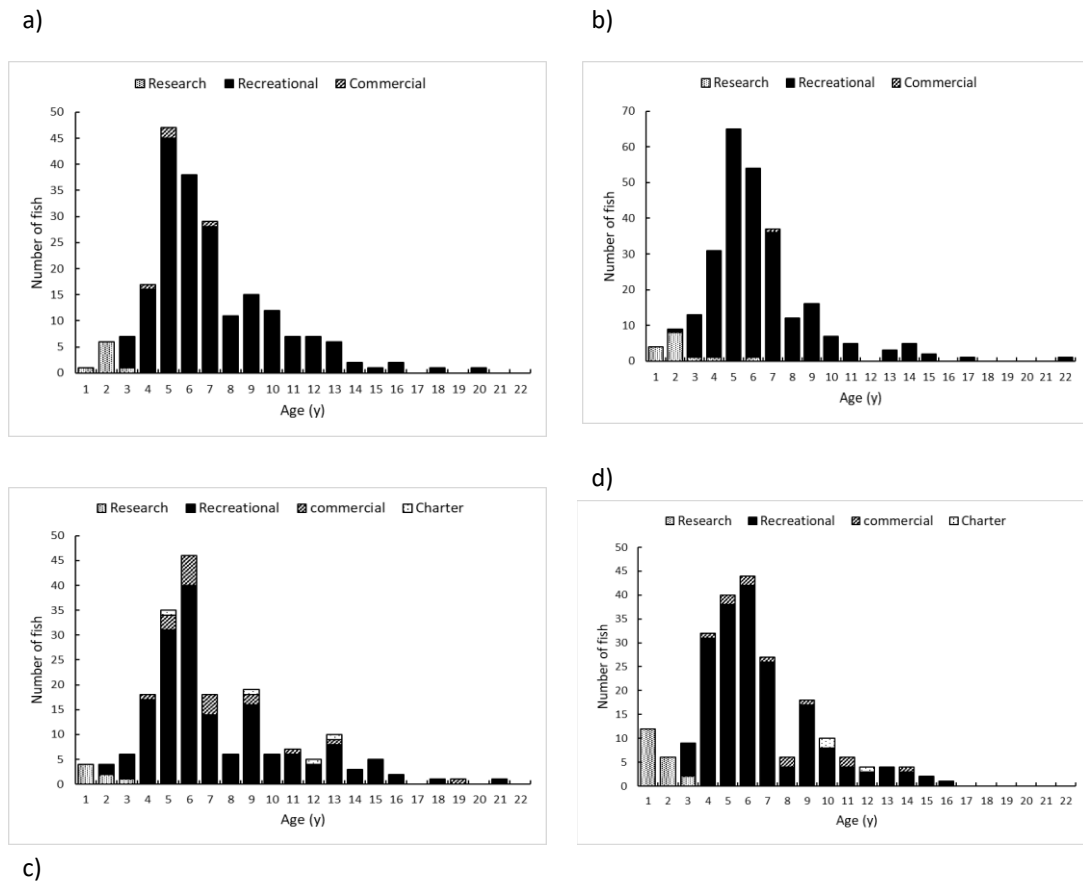


Figure 3.7: Age frequency distributions for Breaksea cod *Epinephelides armatus* from a) west coast females (n = 210), b) west coast males (n = 265), c) south coast females (n = 197) and d) south coast males (n = 225) age-frequency distributions for *Epinephelides armatus* caught by the recreational, commercial, charter and research sectors in Western Australia.

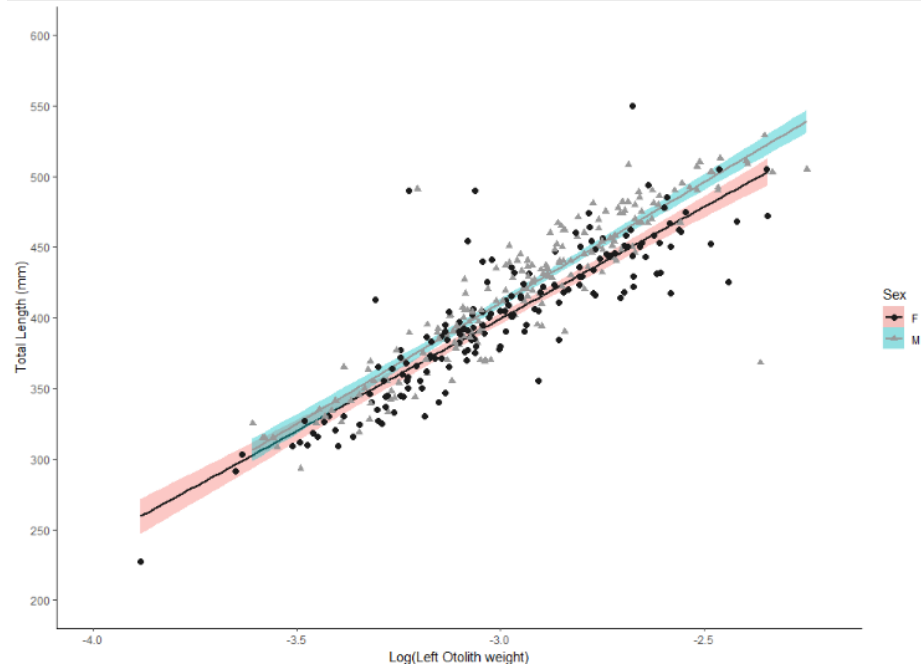
3.6 Otolith weight by total length relationship

There was a significant difference ($p < 0.001$) in the linear relationships between otolith weight (OW) and total fish length (TL) for west coast female and male *E. armatus*. The linear relationships for females ($TL = 853.1 + 151.2 \log(OW)$)

and males ($TL = 913.2 + 167.5 \log(OW)$) provided a good fit to the data for each sex as demonstrated by the high R^2 values of 0.86 and 0.91, respectively (Figure 3.8a).

The linear relationships between OW and TL for south coast female and male *E. armatus* were also significantly different ($p < 0.001$). The linear relationships for females ($TL = 869.0 + 156.7 \log(OW)$) and males ($TL = 914.9 + 166.9 \log(OW)$) had high R^2 values of 0.87 and 0.89, respectively (Figure 3.8b).

a)



b)

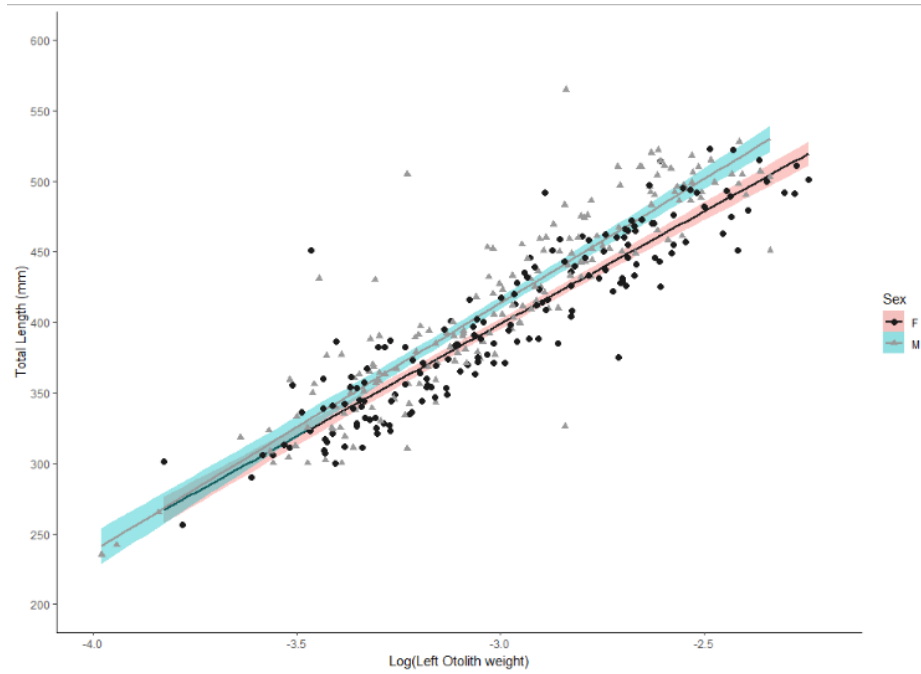


Figure 3.8 Linear relationship between total length (mm) and the log of otolith weight (g) for a) female ($n = 173$) and male ($n = 203$) *Epinephelides armatus* from the west coast and b) female ($n = 171$) and male ($n = 188$) *Epinephelides armatus* from the south coast. Shaded areas around lines indicate the 95% confidence intervals.

3.7 Growth

Visually, the individual von Bertalanffy growth curves for female and male *E. armatus* on the west and south coasts fitted well to the length at age data (Figure 3.9). The log-likelihood ratio test showed that the growth curves of female and male *E. armatus* on the west coast and females and males on the south coast differed significantly (both $p < 0.001$). The lower R^2 values associated with the fit of the curves to the length at age data for females (0.64) and males (0.59) on the west coast (cf. 0.82 for each sex on the south coast) is, in part, a result of the high variability in the length at age, i.e., eight-year-old females range in TL from 324-453 mm, and the concentration of fish between the ages of 5 and 8 years (Figure 3.9a, b; Table 3.4).

On both coasts, and based on the von Bertalanffy growth curves, males attained a larger size at age than females (Fig 3.9). The log-likelihood ratio test demonstrated that the growth curves differed significantly between the sexes on both the west and south coast (both $p < 0.001$). The estimated L_{∞} for each sex on the south coast was greater than the L_{∞} for the corresponding sex on the west coast and the estimated length at age was also greater for males. For example, at 4 and 8 years of age west coast females would attain a larger mean length (314.9 and 418.1

mm) than south coast females (311.8 and 408.5 mm) and at 12 years of age south coast females attained a larger mean (457.5 mm) length than west coast females (445.6 mm). Likewise, males followed the same trend as females, on the south coast males reached TLs of 326.9, 446.16 and 495.6 mm in comparison to TLs of 351, 459.8 and 474.1 mm attained by their males on the west coast. The L_{∞} s of females and males of 500 and 531 mm on the south coast are both ~10 % larger than those for females (456 mm) and males (477 mm) on the west coast (Table 3.4).

A paired t-test of the observed mean lengths at age of west coast females in 2004 to 2006 and west coast females from the current study showed that at age 5, the mean length for the 2004 to 2006 females was significantly greater ($p < 0.05$, , 371.6 mm \pm 6.3) than those from the current study (302.1 \pm 4.8 mm). However, the mean length at ages 8 and 10 did not differ significantly between the two eras ($p = 0.38$, 393.4 mm \pm 7.9 and 406.1 mm \pm 12.2; $p = 0.18$, 412 mm \pm 8.4 and 431.6 mm \pm 8.9). The von Bertalanffy growth curves in Moore et al. (2007) showed that females reached 400 mm at 8.7 years of age, compared with the current study that found west coast females reached 400 mm at 6.8 years of age. Historically, *E. armatus* females approached an estimated asymptotic length of 561 mm, 105 mm greater than the estimate in the current study. The instantaneous growth rate for

historic data was 0.14 year^{-1} with a t_0 of -0.24 years, this was much lower than the current west coast females (0.31 year^{-1} , Figure 3.10a, Table 3.4).

The historical observed mean lengths at age for male *E. armatus* at ages 5, 8 and 10 were significantly less (by >45 mm, $P < 0.05$ for each age comparison) ($340.6 \text{ mm} \pm 5.7$, $403.2 \text{ mm} \pm 11.2$ and $434 \text{ mm} \pm 6.6$) than the mean male lengths from the current study ($403.3 \text{ mm} \pm 5.6$, $451 \text{ mm} \pm 9.8$ and $494.1 \text{ mm} \pm 5.6$). The historic data for males found that males grew to 400 mm at 7.4 years of age, approaching an asymptotic length at 558 mm, 81 mm longer than current estimates for males on the west coast. Historic males also had a lower instantaneous growth of 0.17 year^{-1} (cf. 0.36 year^{-1}) while the t_0 of -0.04 years was lower (cf. 0.39, Figure 3.10b, Table 3.4).

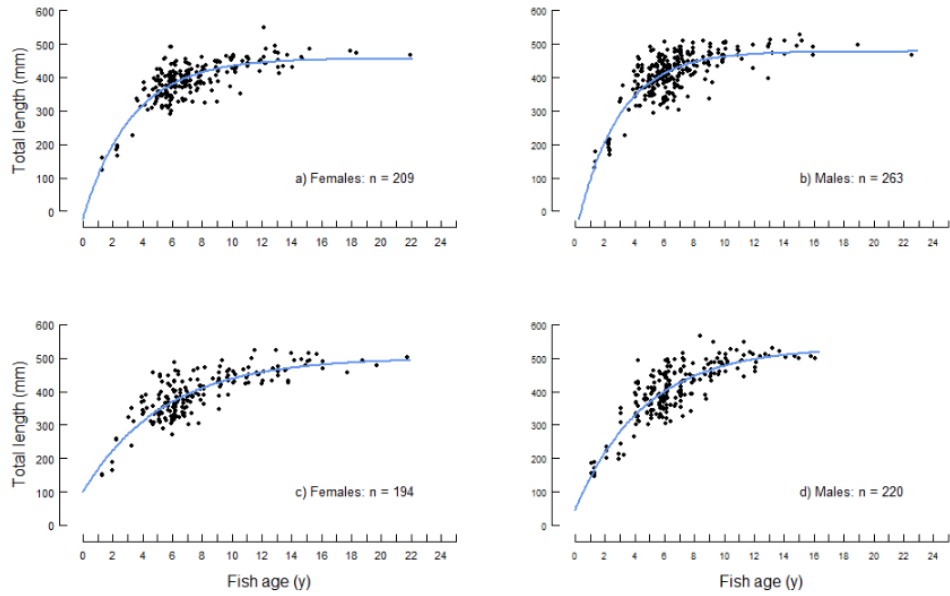
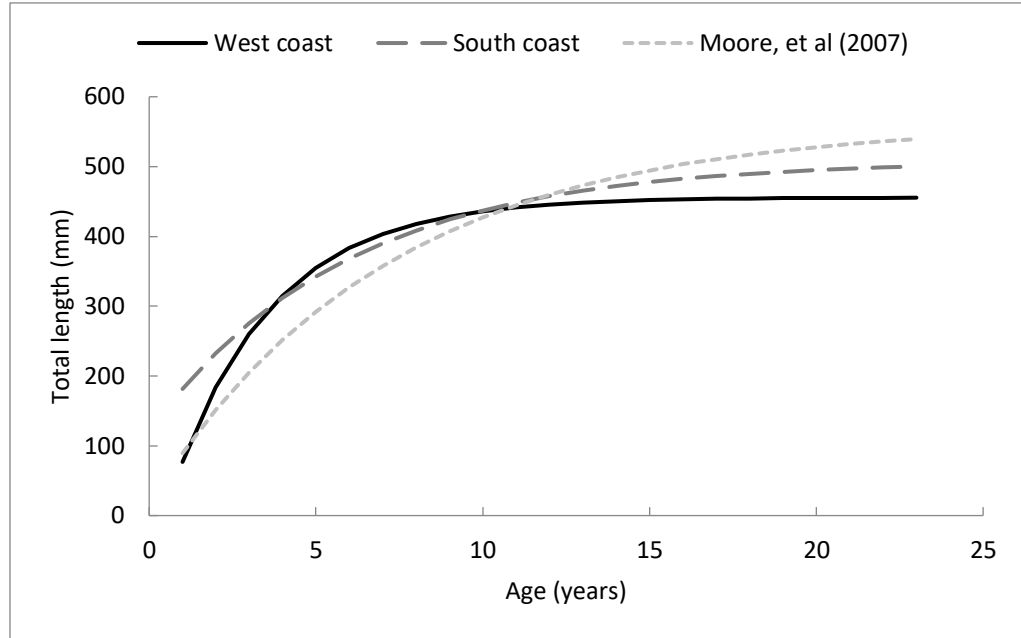


Figure 3.9: von Bertalanffy growth curves fitted to the total lengths (mm) at age of a, c) female and b, d) male *Epinephelides armatus* from a, b) west coast and c, d) south coast bioregions of Western Australia.

a)



b)

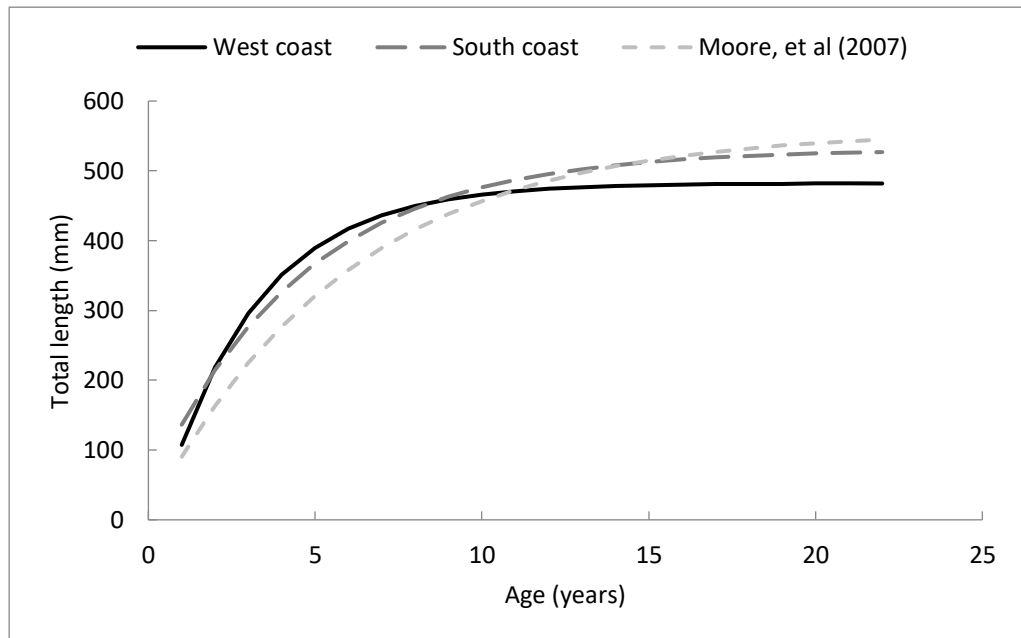


Figure 3.10: Comparison of the von Bertalanffy growth curves for a) female and b) male *Epinephelides armatus* collected during the present study from the west and south coasts of Western Australia and those derived from the west coast by Moore et al. (2007).

Table 3.4: von Bertalanffy growth model parameters (L_{∞} , k and t_0) for the Breaksea Cod *Epinephelides armatus* from a) the west coast, b) the south coast of Western Australia and c) fish from Moore et al. (2007), including upper and lower 95% confidence intervals and coefficient of determination (R^2). n is number of fish in sample.

West coast			L_{∞}	k	t_0	R^2	n
	Female	Estimate	456.4	0.31	0.15	0.64	210
		Upper	474.5	0.38	0.71	—	
		Lower	439.1	0.25	-0.41	—	
	Male	Estimate	477.1	0.36	0.39	0.59	264
		Upper	493.7	0.42	0.76	—	
		Lower	462.3	0.30	0.02	—	
South coast							
	Female	Estimate	500	0.19	-1.19	0.82	196
		Upper	530.3	0.24	-0.16	—	
		Lower	471.5	0.14	-2.21	—	
	Male	Estimate	531.3	0.22	-0.42	0.82	220
		Upper	559.6	0.26	0.04	—	
		Lower	504.5	0.18	-0.87	—	
West coast Moore et al. (2007)							
	Female	Estimate	561	0.14	-0.24	0.794	
		Upper	628	0.16	-0.14	—	
		Lower	505	0.11	-0.62	—	
	Male	Estimate	558	0.17	-0.04	0.789	
		Upper	619	0.21	-0.38	—	
		Lower	498	0.13	-0.29	—	

Table 3.5: The L_{∞} , average, minimum and maximum percentage (%) differences of growth curve estimates between region and Moore, et al. (2007).

Relationship	% Difference in L_{∞}	Average % Difference	Minimum % Difference	Maximum % difference
West coast Females vs south coast Females	-8.72	7.32	0.19	61
West coast Males vs south coast Males	-10.2	8.17	0.38	51.55
West coast Females vs Moore, et al (2007) Females	-18.64	12.6	0.93	24.18
West coast Males vs Moore, et al. (2007) Males	-14.5	10.55	1.16	22.52

3.8 Natural mortality and M/k

The Then et al. (2015) point estimates of M for *E. armatus* were always greater than estimates from the Hoenig (1983) equation, but this difference only ranged from 0.04 to 0.05 year⁻¹ (Table 3.6). The estimated M values showed that all the point estimates for Then et al. (2015) ranged from 0.28 year⁻¹ for males on the west coast, to 0.39 year⁻¹ for males on the south coast and were always greater than Hoenig (1983) M estimates for males on the west and south coasts. While the M estimates from Then et al. (2015) for females and males on the west coast were very similar (0.30 and 0.28 y⁻¹, respectively), on the south coast the estimated female M was much lower than that for males (i.e., 0.29 and 0.39 year⁻¹). Although M for

females on both coasts were similar, a lower M estimate was recorded for males on the west coast than on the south coast.

The M/k ratios calculated from using the point estimates derived from the Then et al. (2015) equation for M and the k estimated from the von Bertalanffy growth curves were greater than the M/k values that used the Hoenig point estimates of M point (Table 3.6). The Then M/k value for west coast females (0.97) was greater than that for west coast males (0.73). The M/k values for the south coast were much greater than those males and in contrast to the west coast were lesser females (1.52) than males (1.75) (Table 3.6).

Table 3.6: Natural mortality point estimates and M/k values of west coast and south female and male <i>Epinephelides armatus</i> from Western Australia.					
Region	Sex	M (Hoenig, 1983)	M (Then, et al. 2015)	M/k (Hoenig, 1983)	M/k (Then, et al. 2015)
West coast					
	Female	0.26	0.3	0.83	0.97
	Male	0.23	0.28	0.62	0.73
South coast					
	Female	0.25	0.29	1.29	1.52
	Male	0.34	0.39	1.54	1.75

3.9 Reproduction

3.9.1 Gonad weight

The mean monthly gonad weights of female *E. armatus* on the west coast \geq (L_{50}) of 285 mm TL (see 3.3.4 below) was elevated (>25.0 g) from December to May, with a maximum of 76.1 g in February (Figure 3.10a). The mean gonad weight

remained very low (<17.0 g) in June and from August to October (Figure 3.10a).

Note that no data, or fewer than five female fish with gonad weights were available for July and November. The mean monthly gonad weights of male *E. armatus* on the west coast were greater than the estimated L_{50} of 419 mm (see 3.9.3 below) followed the same trend as their females, being elevated (i.e., > 1.0 g) between October and April, noting that there were no male gonad weight data for July, September, and December. However, the mean monthly values for males were much lower than those for females, with a maximum mean of only 1.5 g in October (Fig 3.10b).

The mean monthly gonad weights of female *E. armatus* on the south coast $\geq L_{50}$ of 280 mm (see 3.3.4 below) followed a similar pattern to females on the west coast with elevated means (> 15 g) from October to April and similarly high values of ~35 g in January and April (Figure 3.10c). The mean gonad weights for female $\geq L_{50}$ on the south coast remained low (i.e., < 10 g) between April and August. While the trend in the mean monthly gonad weights of male *E. armatus* on the south coast $\geq L_{50}$ of 379 mm (see 3.3.4 below) was not as marked as that for females and there were no data in four months. The mean gonad weights for males were highest between December and April and lowest in May, June, October, and November. As on the west coast, the maximum mean monthly gonad weights of male *E. armatus*

were far lower than those for their females with a maximum value attained in December of only 1.6 g (Figure 3.10d).

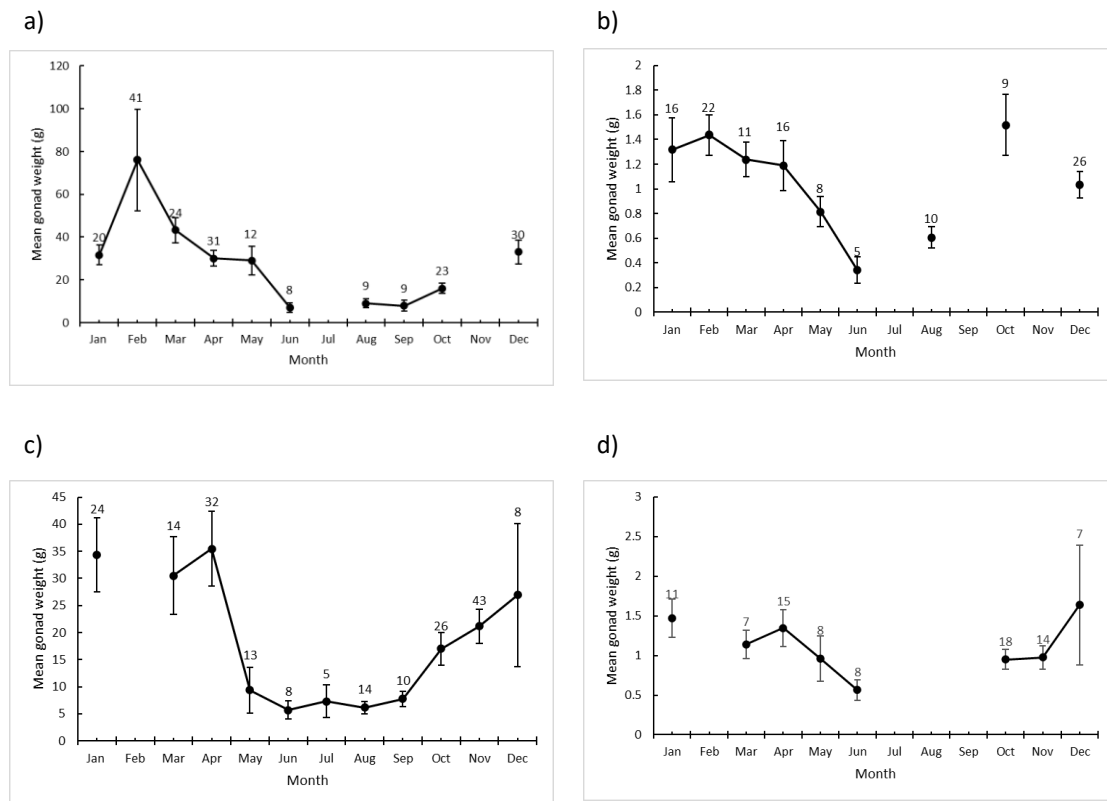


Figure 3.11: Mean monthly gonad weights (± 1 SE) for a) female and b) male *Epinephelides armatus* on west coast and c) females and d) males on the south coast of Western Australia \geq their respective L_{50} s at maturity. Sample sizes are shown above each mean. Only mean values based on more than five fish are shown.

3.9.2 Gonad stages

The monthly percentage frequencies of occurrence of female *E. armatus* $\geq L_{50}$ on the west coast with ovaries at stage 2 (resting) were > 50% between June and August and < 15% from December to May (Figure 3.11a). The proportion of west coast females with ovaries at stages 3 (developing) or 4 (developed) were first observed in August and were present in each month until May. Females on the west coast possessing stage 5 (spawning) ovaries were first present in October and then observed from December to June, being most prevalent from February to April (Figure 3.11a). Females on the west coast possessing stage VI (spent) ovaries were only present from April to June.

The monthly percentage frequencies of occurrence of male *E. armatus* $\geq L_{50}$ on the west coast showed that individuals with testes at M3 (developing) and IV (mature) were present in nearly all months of the year but were most abundant from October to March and in May, noting that no samples were collected in November (Figure 3.11b). Male *E. armatus* on the west coast with testes at stage V (spent) were present between January and April.

The monthly percentage frequencies of occurrence of south coast female *E. armatus* $\geq L_{50}$ with ovaries at different stages of development showed that stage II

were present in January and from April to December with the percentage being > 50% in June, August, and September and < 15% from January to April and December (Figure 3.11c). The proportion of south coast females with ovaries at stages II or IV were observed in every month of the year with stage III females were not present in June and August. Females with stage V ovaries were present from January to May and October to December, Stage V ovaries were most prevalent in February March and May. Females with stage VI ovaries were present from March to December (Figure 3.11c).

The monthly percentage frequencies of occurrence of south coast male *E. armatus* $\geq L_{50}$ on the south coast showed that individuals with stage III and IV testes were present from January to June and September to December, these stages were most abundant in January, February, and March. South coast males with stage V testes were present in April, May, and December (Figure 3.11d).

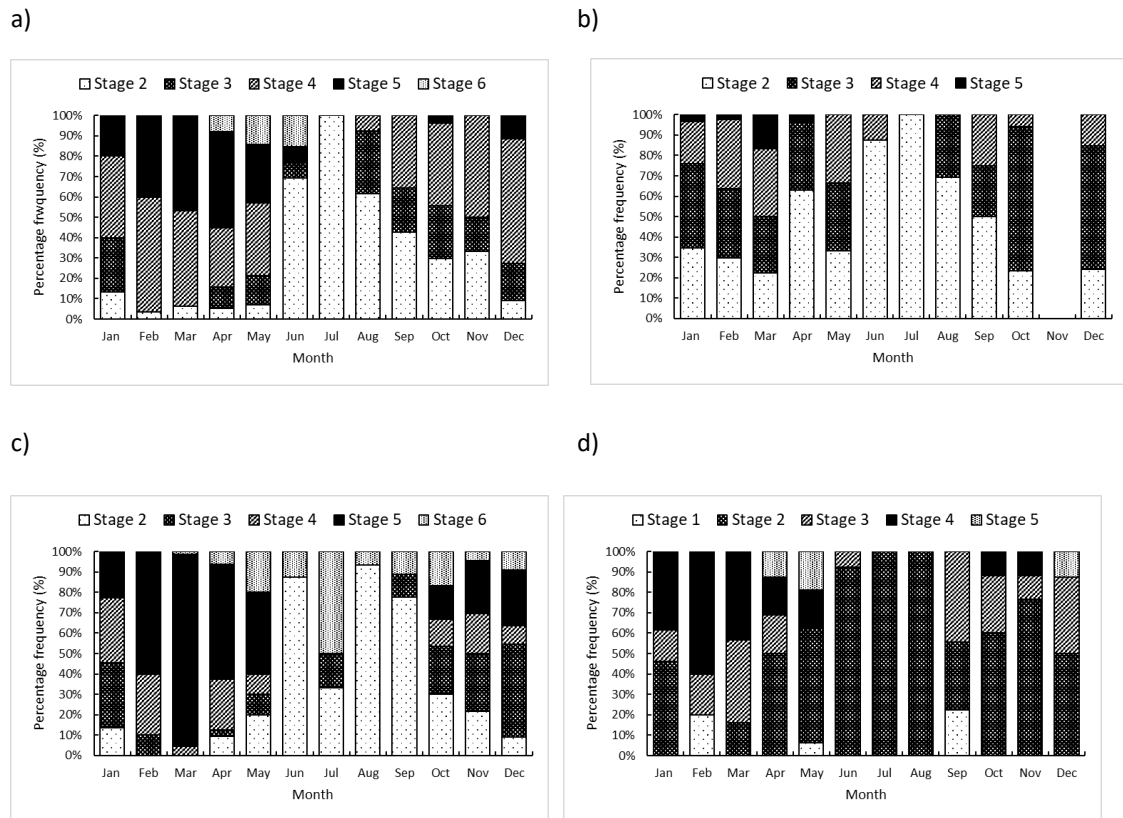


Figure 3.12: Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of a) female ($n = 288$) and b) male ($n = 209$) *Epinephelides armatus* on west coast and c) female ($n = 267$) and d) male ($n = 171$) *Epinephelides armatus* on the south coast of Western Australia \geq their respective L_{50} s at maturity.

3.9.3 Length and age at maturity

The smallest female *E. armatus* (180 mm) caught on the west coast during the spawning period (November to April) possessed immature (M2) ovaries (Fig.?). The proportion of females caught during the spawning period in those successive length classes for which there were fish, shows that $> 50\%$ of females between 330 and 359 mm possessed mature (stages III-VI) ovaries and virtually all females ≥ 420 mm possessed mature ovaries (Figure 3.12a). The smallest (270 mm) male *E.*

armatus caught on the west coast during the spawning period was immature (stage II). There was also a large proportion ($> 25\%$) of stage II males present in the 300 – 449 mm length classes. The proportion of males possessing mature testes (stages III-V) increased from 11.1% in the 300-329 mm length class to almost 50% in the 420-449 mm length class and to 70% in the 480-509 mm length class. The four largest males, all > 500 mm were mature (Figure 3.12b). The L_{50} at maturity for females and males on the west coast was estimated to be 285 and 419 mm, respectively (Table 3.7). The log-likelihood ratio test showed that the length at maturity curves of female and male *E. armatus* on west coast were significantly different ($p < 0.05$).

The youngest (2 y) west coast female *E. armatus* caught during the spawning period possessed immature (stage II) ovaries. The proportion of females caught during the spawning period in those successive age classes for which there were fish, shows that $> 50\%$ of females between 4 and 12 years of age possessed mature (stages III-VI) ovaries and virtually all females ≥ 13 years possessed mature ovaries (Figure 3.12c). Half of the youngest age class (3 years) of west coast male *E. armatus* caught on the west coast during the spawning period was immature (stage II). The proportion of males possessing mature testes (stages III-V) increased from $< 40\%$ in the 4 -6 year age class to 50% in the 8 year age class, it remained above 50% to

age class 13 and in age classes ≥ 14 all fish were mature. The A_{50} at first maturity for females and males on the west coast was estimated to be at 2.17 and 5.7 years, respectively (Table 3.7). Log-likelihood ratio test showed that the age at maturity curves of female and male *E. armatus* on the west coast were significantly different ($p < 0.05$).

The smallest (150 mm) south coast female *E. armatus* caught during the spawning period possessed immature (stage II) ovaries. The proportion of females caught during the spawning period in those successive length classes for which there were fish, shows that $> 50\%$ of females between 270 and 359 mm possessed mature (stages III-VI) ovaries and virtually all females ≥ 360 mm possessed mature ovaries (Figure 3.13a). The smallest (180 mm) south coast male *E. armatus* caught on the west coast during the spawning period was immature (stage II). There were also a large proportion ($> 25\%$) of stage II males present in the length classes 330 – 419 mm. The proportion of males possessing mature testes (stages III-V) increased from 40% in the 300-329 mm length class to almost 50% in the 490-450 mm length classes and to 70% in the 480-509 mm length class. 90% of the largest males in the 510-539 length classes were mature (Figure 3.13b). The L_{50} at first maturity for females and males on the south coast was 280 and 379 mm, respectively (Table 3.7). The likelihood ratio test showed that the length at

maturity curves of female and male *E. armatus* on south coast were significantly different ($p < 0.05$).

The youngest south coast female *E. armatus* caught during the spawning period possessed immature (stage II) ovaries. The proportion of females caught during the spawning period in those successive age classes for which there were fish, shows that $> 50\%$ of females between 4 and 6 years of age possessed mature (stages III-VI) ovaries and all females ≥ 8 years possessed mature ovaries (Figure 3.12c). The youngest age class (4 years) of south coast male *E. armatus* caught on the west coast during the spawning period was immature (stage II). The proportion of males possessing mature testes (stages III-V) increased from $< 30\%$ at the 3 year age class to $\geq 40\%$ in each year class between 4-10, age classes ≥ 11 years were all mature. The A_{50} at first maturity for females and males on the south coast was estimated to be at 2.81 and 6.02 years, respectively (Table 3.7). The Log-likelihood ratio test showed that the age at maturity curves of female and male *E. armatus* on south coast were significantly different ($p < 0.05$). There were no significant difference between west coast female and south coast female length and age at maturity ($p = 0.35$, $p = 0.62$, respectively).

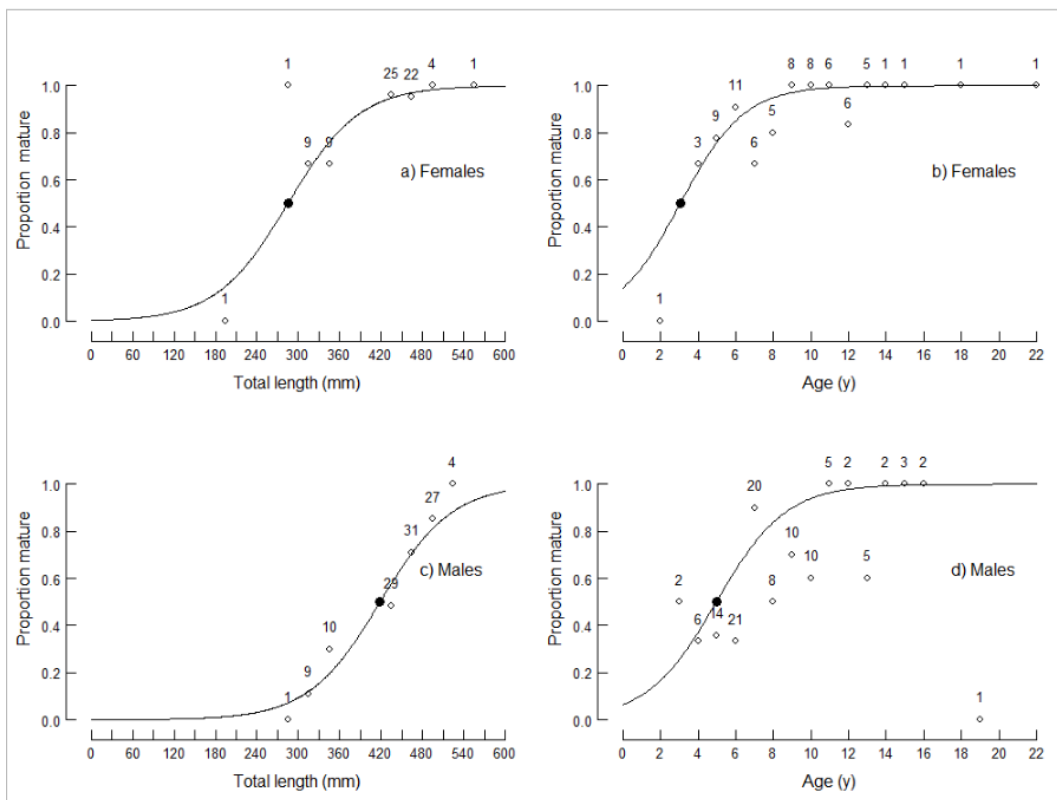


Figure 3.13: The proportion of fish with ovaries at stages III–VI or testes at stages II–V in sequential (a, c) 30 mm length classes and (b, d) 1-year age classes of *Epinephelides armatus* during the spawning season on the west coast of Western Australia between x and y. The logistic curves (solid lines) were derived from a logistic regression analysis that described the relationship between LT and the probability that an individual female or male possessed gonads at stages II–VI or II–V, respectively. Black plot point represents L_{50} for figures a and c, the black point represents A_{50} on figures b and d, clear dots represent the observed proportion of mature fish. Sample sizes of fish in each length and age class are shown.

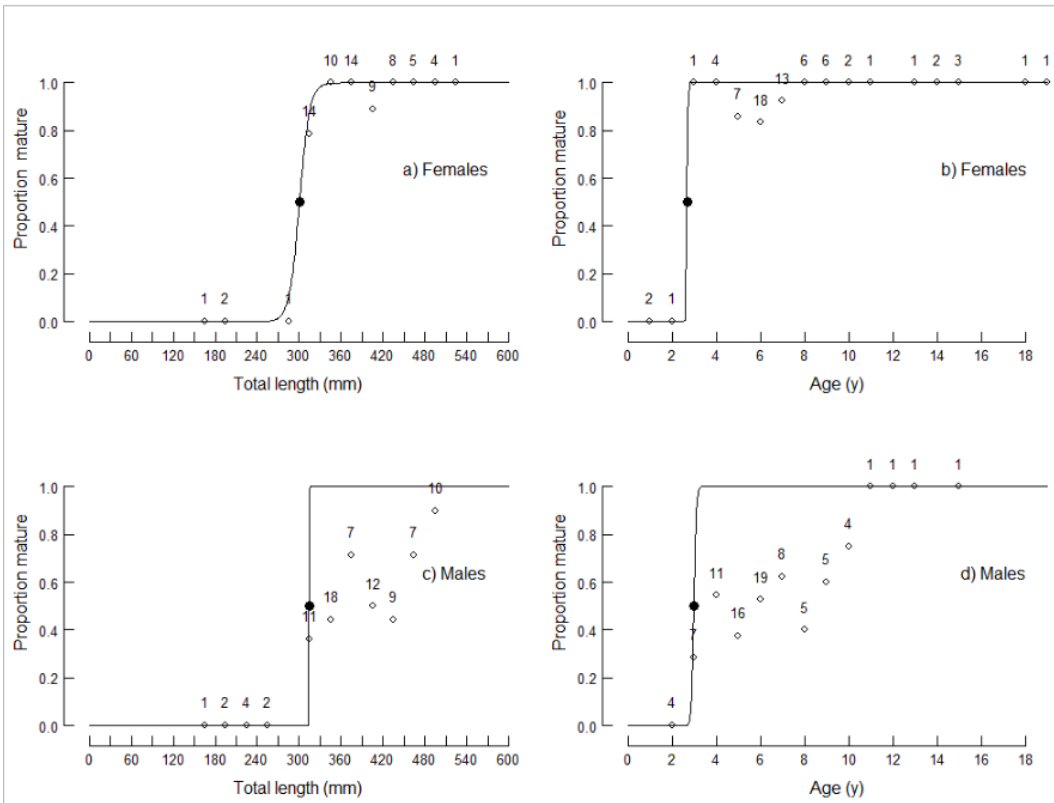


Figure 3.14: The proportion of fish with ovaries at stages III–VI or testes at stages II–V in sequential (a) 30 mm length classes and (b) 1-year age classes of *Epinephelides armatus* during the spawning season on the south coast. The logistic curves (solid lines) were derived from a logistic regression analysis that described the relationship between LT and the probability that an individual female or male possessed gonads at stages II–VI or II–V, respectively. Black plot point represents L_{50} for figures a and b, the black point represents A_{50} on figures c and d, clear dots represent observed proportion of mature fish. Sample sizes of fish in each length and age class are shown. Black plot point represents L_{50} for figures a and b, the black point represents A_{50} on figures c and d.

Table 3.7: Average length and age at maturity and 95% confidence limits for *Epinephelides armatus* of a) the west coast, b) the south coast and c) Moore et al. (2007) from Western Australia.

Region/data	Sex	<i>L50</i>	<i>L95</i>	<i>A50</i>	<i>A95</i>
a) West coast	Female	285 (221-349)	437 (374-501)	2.17 (2.10-2.23)	10.21 (10.14-10.28)
	Male	419 (393-444)	572 (510-635)	5.70 (5.67-5.73)	19.91 (19.87-19.94)
b) South coast	Female	280 (240-321)	359 (321-396)	2.81 (1.94-3.68)	7.14 (6.33-7.95)
	Male	379 (342-415)	605 (476-735)	6.02 (5.99-6.06)	16.06 (16.03-16.10)
c) Moore, et al. (2007)	Female	293.5 (278.5-310.8)	339.3 (285.9-382.5)	—	—
	Male	250.6 (216.1-271.3)	341.2 (285.9-382.5)	—	—

4. Discussion

In this study, 1250 samples of the Breaksea Cod *Epinephelides armatus*, one of the few gonochoristic serranids globally, were used to determine its biological characteristics on the west and south coasts of Western Australia. The greatest proportion of fish (>95% of the west coast and >75% on the south coast) came from the citizens science program, Send Us Your Skeletons (SUYS), coordinated by DPIRD to collect fish frames from recreational fishers and thus were mostly fish larger than 300 mm caught during 2013 and 2014. These data sets were supplemented with small fish collected in 2021 and 2022 by spearfishing to estimate the age, growth, and reproduction of *E. armatus*.

The von Bertalanffy growth equation was used to estimate fish growth on both coasts and the results from these analyses found that fish on the west coast had a greater instantaneous growth rate (k) than fish on the south coast, while fish on the south coast approached a larger asymptotic length (L_{∞}). This supports the hypotheses that fish in warmer waters grow faster but reach smaller sizes than fish in cooler waters and is consistent with the predictions from the Metabolic Theory of Ecology (MTE, Meer, 2006), Temperature Size Rule (TSR, John et al., 2012) and Gill Oxygenation Limitation Theory (GOLT, Pauly, 2019).

The less extensive data on gonad stages and weight from the SUYS program allowed estimates of spawning season and size at maturity to be made for female fish but with less certainty for males. Mean gonad weight data suggest a spawning season from November to April with a peak in February, similar to the timing of spawning for west coast fish derived previously (Moore et al., 2007). The estimated size-at-maturity (L_{50}) from this study for female west coast fish (285 mm) was very similar and not significantly different from that for females on the south coast (280 mm), which does not support the predictions of the TSR. The much lower weight of male gonads makes discerning the macroscopic gonad stage difficult and meant that the male L_{50} was not accurately estimated in this study. However, the findings from this study provide information for managing *E. armatus*, a demersal species that has been increasingly fished and retained on the west coast (Moore et al., 2007). The current restrictions on fishing in the WCDSF have been proposed in 2022 for the primary indicator species (especially Snapper and Dhufish) on the west coast of Western Australia are likely to increase fishing pressure on 'secondary' species such as *E. armatus*.

4.1 Age, Length & Growth

4.1.1 Length distribution

The maximum length of *E. armatus* recorded in this study was 565 mm for male fish on the south coast, and 550 mm for females, also on the south coast, with the majority of fish collected \geq MLL (300 mm). Most samples were provided by recreational fishers. The maximum length recorded was about 50 mm greater than maximum lengths recorded ~8 years previously (2004 to 2006) for *E. armatus* on the west coast (510 mm for females and 498 mm for males; Moore et al. (2007)), and was similar to the maximum length of 560 mm listed by Whisson and Hoschke (2021) of 560 mm. The sampling regime differed between the current study and the previous study by Moore et al. (2007), with fish in the current study being collected over a wide area on the west and south coast through SUYS allowing for larger fish at higher number to be collected. Previously, Moore et al. (2007) collected *E. armatus* from a smaller area around Rottnest Island which would result in less larger fish being collected. They also collected small fish through the use rotenone. This also allowed for the capture of a larger number of smaller fish (100 mm) than in the current study using spearfishing.

The sex related differences in maximum size have been recorded for other gonochoristic serranids such as *Othos dentex*, in south-western Australia, and for

some species in the *Paralabrax* genus in the western Pacific Ocean. *Paralabrax auroguttatus* (470 and 430 mm (Pondella et al., 2001)) and *P. clathratus* (437 and 397 mm (Erisman & Allen, 2006)) followed a similar trend in sex differences with females recording a longer TL than males. Like *E. armatus*, the males are also longer than females for two other large, relatively long-lived species in southern western Australia; Blue Morwong *Nemadactylus valenciennesi* (females = 868 and males = 958 mm) (Coulson et al., 2010) and *Glaucosoma hebraicum* (females = 1047 and males = 1178 mm) (Lenanton et al., 2009).

However, the maximum size of female *O. dentex* was 605 mm, 35 mm longer than the maximum size of males (570 mm) (French et al., 2014; Saunders et al., 2010). Similar to *O. dentex*, females of two gonochoristic serranids from the *Paralabrax* genus also reach a longer maximum length than males; *P. albomaculatus* (640 and 550 mm for females and males, respectively) and *P. nebulifer* (375 and 460 mm) (Hovey et al., 2002; Salinas-de-León et al., 2017).

4.1.2 Otolith weight – total length relationship

As the SUYS relies on recreational fishers donating their filleted fish frames, it is not possible to record data on total weights, an important parameter for estimating the length-weight relationship, condition, age-based stock assessments and spawning potential ratio (Fairclough et al., 2014; Pilling et al., 2007; Smith et

al., 2012). In this study, otolith measurements, which can be collected from dissecting otoliths from the frames submitted to the SUYS program, were investigated to see if they can provide a way of estimating fish total length.

The otolith weight and fish total length of *E. armatus* were strongly correlated for both sexes on both the west and south coast regions ($R^2 > 0.85$ for all combinations of sexes and coasts). Otolith weight and fish length are also strongly correlated for other fish species such as the Tailor *Pomatomus saltatrix* ($R^2 = 0.71$) in the southeastern coast of Brazil (de Souza et al., 2019), Common Sole *Solea solea* ($R^2 > 0.6$) in İskenderun Bay, Hatay, Turkey (Başusta et al., 2020) and Red Grouper *Hyporthodus acanthistius* ($R^2 = 0.87$) in the National Natural Park, Gorgona, Columbia (Puentes-Granada et al., 2019).

These latter studies were also able to estimate the relationship between otolith weight and total weight and found that otolith weight was strongly correlated with fish total weight (de Souza et al., 2019; Pilling et al., 2007; Smith et al., 2012). The strong correlations between otolith weight and fish length for *E. armatus* and these findings on otolith weight/total fish weight relationship for three other species studies suggest that otolith weight will also be a good predictor of total weight for *E. armatus*.

4.1.3 Age validation

The pattern of change in the mean monthly marginal increments of the otoliths of *E. armatus* for both the west and south coast displayed a single sharp decline in the summer months (October to November) and a single increase in the mean marginal increment in May. The opaque zones were shown to be deposited after the cooler winter months, with delineation of the zones from the edge of the otolith occurring in October to December. This pattern of change in the mean marginal increment follows a similar trend to that previously observed by Moore et al. (2007) and shows that the opaque zones are laid down once per year. This conclusion is supported by the results of the AIC models for three patterns of temporal change: no pattern; zones laid down annually; and zones laid down biannually, with the model for annual zones having the lowest AIC values for both coasts and both sexes.

The timing and formation of *E. armatus* opaque and translucent zones coincide with that of other southwestern coastal demersal species such as *O. dentex* (French et al., 2014; Platell et al., 2010), *G. hebraicum* (Hesp et al., 2002), Western Blue Groper *Achoerodus gouldii* (Coulson et al., 2009) and Blue morwong *Nemadactylus valenciennesi* (Coulson et al., 2010).

The accuracy and precision of reading the opaque zones was tested by comparing the findings from two independent readers using the index of average percent error estimation (IAPE) (Beamish & Fournier, 1981). The IAPE value of 2.33% from this study was less half the IAPE acceptable level of 5.5%, specified by Beamish and Fournier (1981), and shows a high level of agreement between readers with only minor deviations in counts of opaque zones throughout the age range (<2 opaque zones). This shows an acceptable level of precision between readers and that the opaque zones of *E. armatus* can be counted with a good level of accuracy. This is the first instance of using a test to quantify the accuracy and precision of counting opaque zones for *E. armatus*.

4.1.4 Age distribution

The maximum age for female *E. armatus* was 21 years on the west and south coasts, 2 years older than that for females determined previously (Moore et al., 2007). The maximum age of males on the west coast was 22 years compared with 16 years on the south coast. This is much greater than 13 years which was previously recorded on the west coast (Moore et al., 2007).

Both the west and south coast populations of *E. armatus* had high proportions of fish in the 4 - 7-year age classes, similar to of the age distribution recorded by Moore et al. (2007). The proportion of fish in the older age classes

decreased sharply after age 7 on the west coast, while there was a more gradual decrease in the proportion of older fish on the south coast. The sharp decline in the proportion of fish >7 on the west coast was similar to that recorded previously (Moore et al., 2007).

The pattern of age distribution recorded for *E. armatus* on both the west and south coast differs from that for *O. dentex* on the south coast, which lives much longer (37 years for females and 31 for males) and has a high proportion of fish from ages 5 to 15 (French et al., 2014). The maximum ages of the gonochoristic serranids in the *Paralabrax* genus, found in the eastern Pacific Ocean, were lower than those for *E. armatus* for *P. maculatofasciatus* - ~14 years (Andrews et al., 2005); similar for *P. nebulifer* and *P. auroguttatus* ~24 years (Love et al., 1996; Pondella et al., 2001), while those for *P. clathratus* (33 years, (Erisman & Allen, 2006; Love et al., 1996) were older than *E. armatus* in this study.

4.1.5 Estimates of Growth

On both the west and south coast males reached a larger asymptotic length (477.1 and 531.3 mm, respectively) and had a faster instantaneous growth rate (0.31 year^{-1} ; 0.22 year^{-1}) than those for females ($L_{\infty} = 456.4 \text{ mm}$ and 500 mm ; $k = 0.31 \text{ year}^{-1}$ and 0.19 year^{-1}). This explains why males were predicted to reach the minimum legal length (MLL) for retention (300 mm TL) at younger ages (3.44 and

3.07 years on the west and south coast, respectively) than females (3.70 and 3.66 years). Also note that the protracted spawning period for the west and south coast fish would contribute to the relatively wide range of observed lengths at age.

The growth parameters and growth curves for the west coast fish from the current study differed from those in the previous study of *E. armatus* growth on the west coast (Moore et al., 2007). In contrast to this study, Moore et al. (2007) found that females reached a larger asymptotic length than males on the west coast, but consistent with the current study, males had a faster instantaneous growth coefficient than females. The current estimated L_{∞} for female *E. armatus* on the west coast (456.4 mm) was ~ 100 mm less than the estimate from the previous study Moore et al. (2007) of 561 mm, while the instantaneous growth rate was greater for *E. armatus* on the west coast in the current study (0.31 year^{-1}) than the previous study by Moore et al. (2007) (0.14 year^{-1}). This could be due to the low sample numbers of small (< 300 mm) *E. armatus* in the present study which may not be anchoring the lower end of the growth curve. Previous studies have highlighted the importance of having estimates of small individuals to anchor the growth curve (Gwinn et al., 2010; Neves et al., 2022; Siegfried & Sansó, 2006). In the study by Moore et al. (2007). Larger numbers of older and larger fish in the current study means that the L_{∞} is likely to be better estimated than Moore et al.

(2007). Conversely, the greater numbers of small *E. armatus* in the previous study means that age at 0 size (t_0) is likely to be better estimated by Moore et al. (2007).

In contrast to *E. armatus*, *O. dentex* males have a faster instantaneous growth rate than females while females reach a much larger asymptotic length (654 mm) than males (562 mm) (French et al., 2014). The difference in asymptotic length between males and females of *E. armatus* followed similar trends to other southwestern demersal species *G. hebraicum* and *N. valenciennesi* (Coulson et al., 2010).

On the west coast, both sexes of *E. armatus* had greater instantaneous growth rates than *E. armatus* on the south coast. On the south coast, *E. armatus* females and males reached a greater estimated asymptotic length than west coast female and male *E. armatus*. This trend of faster growth reaching smaller asymptotic lengths in higher latitudes mirrored similar relationships in the species *C. Auratus* and *G. hebraicum* whereby northern populations of both species expressed more rapid growth but reach a lower asymptotic length than fish on the lower west coast (Lenanton et al., 2009; Wakefield, 2006).

As hypothesised the growth of *E. armatus* in the warmer waters of the west coast was more rapid than that in the colder waters on the south coast population, with an average temperature difference of ~3 °C. Furthermore, temperatures on

the south coast did not increase to the same extent as those on the west coast during the marine heat wave in the summer of 2011/12 (20.4°C vs 23.6°C) (Caputi et al., 2019). These results on differences in growth follow the predictions on the metabolic theory of ecology, the metabolic rate of *E. armatus* is higher on the west coast than the south coast due to warmer waters, which results in a greater consumption of food and energy expenditure to obtain resources, i.e., capture food (Lek et al., 2012; Meer, 2006). Lek et al. (2012) demonstrated that the length of three labrid species (*Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolata*) were greater off Perth than at the Jurien Bay Marine Park (JBMP) (30.3030° S, 115.0379° E) ~ 200 km north of Perth, the instantaneous growth rate (k) was greater at JBMP than off Perth (Lek et al., 2012).

The temperature size rule (TSR) for ectotherms predicts that fish in cooler waters grow slower but attain a larger size than fish in warmer waters as a result of an unequal response to growth and development rates to temperature in ectotherms (Aguilar-alberola & Mesquita-joanes, 2014; Forster & Hirst, 2012; Walters & Hassall, 2012). The predictions of the TSR for responses of growth rate to changes in temperature follow those of the MTE, i.e., that *E. armatus* will grow more rapidly on the west coast than the south coast but with fish on the south coast

attaining a larger size (Aguilar-alberola & Mesquita-joanes, 2014; Forster & Hirst, 2012).

The third theory of relevance to examining differences in growth in waters with differing temperature regimens is the gill oxygen limitation theory (GOLT) (Pauly, 2019; Pörtner & Knust, 2012). This theory predicts that warmer waters contain less oxygen than cooler waters as this limits metabolism and results in slower growth and smaller fish in warmer waters. As the metabolism of ectotherms is faster in warmer than cold waters, the oxygen demands of fish also increase in warmer waters (Pauly, 2019; Pörtner & Knust, 2012). The GOLT predicts that smaller *E. armatus* will be found in the warmer waters of the west coast than the south coast. With increasing sea surface temperatures, the ability of sea water to hold oxygen decreases for temperate species such as *E. armatus*, which is likely to stimulate a shift in distribution to higher latitude waters (cooler waters) to meet their oxygen demands (Caputi et al., 2019; Pratchett et al., 2017).

4.1.6 Natural mortality and M/k

The estimated natural mortality (M) point estimates for female west coast *E. armatus* (0.30 year⁻¹) (following Then et al. (2015)) was almost identical to that for the south coast (0.29 year⁻¹), while west coast males M point estimates (0.28 year⁻¹) were much lower than south coast male M point estimates (0.39 year⁻¹). Females on

both coasts had similar maximum ages while the oldest male fish on the west coast (22 years) was 16 years older than that for males on the south coast, which would account for differences in the estimates of M for male fish on the west and south coast.

The Beverton Holt M/k ratio values for the west coast female and male *E. armatus* were <1.0 , suggesting that the size distribution of unfished populations grow slowly and survive long enough to accumulate around the asymptotic length (Hordyk et al., 2015b; Prince et al., 2015). The M/k ratio value for the south coast female and male *E. armatus* was >1.0 , suggesting that the size distribution of unfished populations on this coast do not exhibit an adult modal size due to fish from these populations growing and dying too rapidly, resulting in fish from the population being unable to accumulate around the asymptotic length (Prince et al., 2015).

4.2 Reproduction

4.2.1 Spawning period

The mean gonad weights for west coast females and males were elevated from November to April, with a peak in February. High gonad weights for males were also present in October. Macroscopic staging of *E. armatus* gonads showed that mature female (Stages III-VI) and male fish (Stages III-V) were found mainly

during those months when gonad weights were elevated. These findings on the duration and peak reproduction for the west coast match closely with those determined by Moore et al. (2007) derived ~10 years previously.

The south coast females had a longer period of elevated mean gonad weight than the west coast females, while west coast males and south coast males had the same period of elevated mean gonad weight. Mature south coast female and male fish were most prevalent in the months where mean gonad weight was elevated (November to April). This protracted spawning period observed in the west and south coast populations were similar to the study by Moore et al. (2007).

Based on the trends in gonadosomatic index and macroscopic gonad staging for *E. armatus* on the west coast, Moore et al. (2007) assigned a birthdate of February 1, which is consistent with the trends in gonad development in this study. As a consequence, this was also the birthdate chosen for the analysis of *E. armatus* age and growth on both coasts.

4.2.2 Estimated length and age at maturity

The estimated length- and age-at-maturity (L_{50} and A_{50}) for *E. armatus* males (437 mm, 5.7 years) was much greater than females (285 mm, 2.2 years) on the west coast. This was also found on the south coast where the estimated L_{50} and A_{50} for south coast males (379 mm, 6 years) were ~100 mm longer and three years

older than those for females (280 mm, 2.8 years). This differed to the study by Moore et al. (2007) where females had a greater L_{50} (306 mm) than males (256 mm). This also differs to other southwestern species such as *O. dentex* (345 (female) and 356 mm (male)), *G. hebraicum* (301 (females) and 320 mm (males)) and *C. auratus* (375 (female) and 407 mm (male)) where females had greater estimates of L_{50} than males (French et al., 2014; Hesp et al., 2002; Wakefield, 2006). However, it must be noted that the 95% confidence intervals for the mean length-at-maturity for both west coast and south coast from the current study are quite large, i.e., 64 mm for west coast females and 41 mm for the south coast. This is likely because of the small number of fish <300 mm and ~3 years old that were available for estimating the maturity logistic curves. The 95% confidence intervals for the mean sizes-at maturity for Moore et al. (2007), based on histological staging of gonads were only 8 mm for females and 15 mm for males. These confidence intervals are much lower and more reliable than the current study.

In the current study, it was noted that stage 2 males were present in the large male size classes during the spawning period, e.g., a male that was recorded as stage 2 was 548 mm. *Epinephelides armatus* males had much smaller gonads than females, which makes the macroscopic staging of males difficult. Moore et al. (2007) conducted histological studies on both female and male *E. armatus*, and the

gonads from these samples were also in good condition as they were collected through research and not reliant on fish frames from the SUYS program. This would make Moore et al. (2007) L_{50} estimates more accurate and precise than those from the current study. Although macroscopic gonad staging is a quick and inexpensive method for determining gonad development, it relies on the visual interpretation of the processor, which can lead to error, particularly for small male gonads (Saber et al., 2019).

The length- and age-at-maturity estimates for female *E. armatus* on the west coast did not differ significantly from those on the south coast. The TSR predicts that the west coast females would mature at a smaller length than those in the cooler waters of the south coast as has been found for *Oryzias latipes* (native to marshes, ponds and rice paddies of East Asia) and *Artemia franciscana* (Great Salt Lake (Utah, USA)) (Forster & Hirst, 2012; Loisel et al., 2019). The most likely explanation for these results would be the low number of fish present in smaller length classes during the spawning period, especially on the west coast where there was only one immature female below 300 mm caught, whereas the south coast had four immature fish below 300 mm. With more immature fish at lower length classes the length at maturity was able to be anchored to the lower length classes in the south coast, which could explain the lower L_{50} in south coast females. The

importance of smaller fish below the size at maturity in anchoring the maturity curve providing accurate estimates of L_{50} and A_{50} has been highlighted for other species including Knifejaw *Oplegnathus woodwardi* (Coulson & Wakefield, 2022) where a logistic regression could not be employed due to low number of small fish.

4.3 Implications for stock assessment

The length distribution data and growth, mortality and female reproduction parameters estimated in the current study provide important life history parameters for length-based and age-based stock assessment methods such as yield-per-recruit analyses to estimate the spawning potential ratio.

Not only can these parameters be used in the calculation of stock assessments, but they can also be used in the calculation in the life history ratios of this species. Life history ratios (particularly M/k and L_m/L_∞) utilize the life history parameters to predict the size distributions of an unfished population, assuming that conditions are at equilibrium (Beverton & Holt, 1959; Hordyk et al., 2015; Prince et al., 2015). These ratios and the growth parameters, including instantaneous growth rate and asymptotic length, and length at maturity, are used to calculate spawning potential ratio (SPR) using a simple length based spawning potential ratio (LBSPR) stock assessment method (Hordyk et al., 2015a, 2016). This method of stock assessment has been used to evaluate data-limited fisheries and is

readily available on GitHub². By comparing the LBSPR method with an aged-based spawning potential ratio method, it would help to determine whether LBSPR methods can be used with certainty for assessing *E. armatus*.

4.4 Data limitations

As noted previously, the data collected from the SUYS program have provided extensive information on the length, age and otolith weight of fish >300 mm but much less data on total weight and gonad weight (see also Fairclough et al. (2014)). Thus, the gonadosomatic index could not be calculated. for SUYS fish as it depends on both gonad weights, fish total weight and the gonads from the SUYS were sometimes in poor condition, which makes staging male gonads macroscopically particularly difficult.

The collection of juveniles also proved to be difficult, with no fish below 100 mm being collected. This combined with low numbers of small fish <300 mm, especially during the spawning period, creates uncertainty in the estimation L_{50} for both male and female fish. These smaller fish would also assist in anchoring the von Bertalanffy growth curve towards t_0 (Campbell & Phillips, 1972; Neves et al., 2022) and providing more realistic estimates of k and L_{∞} . In addition, the juvenile fish were collected about 8-9 years after the larger individuals from the SUYS

² LBSPR GitHub URL: <https://adrianhordyk.github.io/LBSPR/articles/LBSPR.html>

program which may also introduce variability into the estimation of the growth parameters.

4.5 Further research and implications for management

The gaps in the data from the current study highlight the value of further research to determine the size and age-at-maturity for *E. armatus* to evaluate the appropriateness of the current MLL based on the size at maturity. More accurate estimates of length- and age-at-maturity will allow more comprehensive comparisons between the west coast and south coast regions and between data sets from different time periods for the west coast, allows the size at maturity on both coast to be compared with the minimum legal limit with more confidence. To achieve this, in addition to the fish > 300 mm in length, greater numbers of fish below this size should be collected. This collection of a larger number of fish below 300 mm and in particular < 100 mm is highly recommended.

Epinephelides armatus has a protracted spawning period ranging from November to April. Although the demersal seasonal closure from the 25th of October to the 15th of December does protect the initial part of the spawning period of *E. armatus*, it does not coincide with the peak spawning of January to March. Understanding the peak spawning period of *E. armatus* may thus help to refine the

seasonal closure period to allow fish time to successfully reproduce, with efforts to refine the closure recommended.

The recent 2021 assessment of the status of the west coast demersal scalefish resource of key indicator species, i.e., *C. auratus* and *G. herbraicum*, found that the current management strategies on the west coast had stopped the decline in spawning biomass of these species. However, it concluded that their level of recovery was not sufficient, with recovery being limited by high fishing pressure (Fairclough et al., 2021). Based on the status of these indicator species in the demersal scalefish, a stock assessment of *E. armatus* would be valuable for determining whether this less targeted species has also been impacted by fishing (Fairclough et al., 2021). Following an estimation of the age-based and length-based spawning potential ratio, using the parameters and length distributions from the current study, it would be possible to determine how the SPR from 2013-14 compares with the generally accepted target and limit SPRs for teleosts of 40% and 20% (Mace & Sissenwine, 1993; Prince et al., 2015). Repeating this process for *E. armatus* on the west coast using the data collected by Moore et al. (2007) in 2004 to 2006 would determine whether there had been major changes in SPR between then and 2012-2014. Frames from the more recent SUYS collections could be dissected to estimate the current age and size distributions and growth rates to

provide a third time period for comparison, this is if LBSPR is proven to be a good indicator for SPR. This would also allow the estimates from length-based and age-based methods of SPR to be compared between the three time periods. If the LBSPR was found to be a good estimator for the SPR, it saves a lot of time and resources required to estimate SPR using the age-based method.

4.6 Conclusion

The data collected from diverse sources (i.e., research and SUYS program) showed differences in size- and age- distribution, and growth parameters between the west and south coast of Western Australia. West coast fish had a greater instantaneous growth coefficient and lower asymptotic length than those on the south coast. These findings support the predictions by the MTE, TSR and the GOLT (Aguilar-alberola & Mesquita-joanes, 2014; Meer, 2006; Pörtner & Knust, 2012). However, the female size-at-maturity estimated for the west and south coast do not confirm to the predictions of the theories, and further studies focussing on collecting reproductive data from the entire size distribution, are needed to confirm the L_{50} for *E. armatus* on the west and south coast, particularly for males.

Differences were also found in the *E. armatus* growth parameters on the west coast compared with those determined ~10 years previously (Moore et al., 2007). In 2013-2014, *E. armatus* had a greater instantaneous growth coefficient on the

west coast in 2013 – 2014 than in 2004 - 2006, and fish from this more recent study a longer asymptotic length than previously, noting that the historical data had a larger number of smaller fish and fewer larger fish than in the current study.

Further studies of the *E. armatus* populations to investigate the current growth and reproduction parameters and estimate the spawning potential ratio would help inform management of this species (King, 2013) and determine whether length-based methods of assessment are appropriate.

Overall, the findings of this thesis highlight the importance of assessing fish biology across a broad range of their spatial distribution as key traits affecting their populations and stocks can vary. Understanding and utilising this fine-scale variation can ensure more reliable management and sustainability of *E. armatus* populations into the future.

5. References

- Aguilar-alberola, J. A., & Mesquita-joanes, F. (2014). Breaking the temperature-size rule : Thermal effects on growth, development and fecundity of a crustacean from temporary waters. *Journal of Thermal Biology*, 42, 15–24. <https://doi.org/10.1016/j.jtherbio.2014.02.016>
- Albers, S. (2022). rsoi: Import Various Northern and Southern Hemisphere Climate Indices. R Package Version 0.5.5. <https://cran.r-project.org/package=rsoi>
- Allen, L. G., Hovey, T. E., Love, M. S., & Smith, J. T. W. (1995). The life history of the Spotted Sand Bass (*Paralabrax maculatofasciatus*) within the Southern California Bight. *Reports of California Cooperative Oceanic Fisheries Investigations*, 36, 193–203.
- Andrews, A. H., Laman, E. A., Bennett, T., Jones, E., & Cailliet, G. M. (2005). Age and growth of Spotted Sand Bass, *Paralabrax maculatofasciatus*, in Bahia de Los Angeles, Baja California, Mexico, with age validation using otolith edge analysis. *Bulletin, Southern California Academy of Sciences*, 104(1), 14–25. [https://doi.org/10.3160/0038-3872\(2005\)104\[14:aagoss\]2.0.co;2](https://doi.org/10.3160/0038-3872(2005)104[14:aagoss]2.0.co;2)
- Arlinghaus, R., & Cooke, S. J. (2008). Recreational fisheries: socioeconomic importance, conservation issues and management challenges. *Recreational Hunting, Conservation and Rural Livelihoods: Science and Practice*, 39–58. <https://doi.org/10.1002/9781444303179.ch3>
- Başusta, A., Çetinkaya, B., & Başusta, N. (2020). The relationships between fish size and otolith dimensions in the Common Sole (*Solea solea* (Linnaeus, 1758)) captured in the Northeastern Mediterranean. *Journal of Applied Ichthyology*, 36(6), 888–892. <https://doi.org/10.1111/jai.14137>
- Beamish, R. J., & Fournier, D. D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, 38(8), 982–983. <https://doi.org/10.1139/f81-132>
- Beverton, R. J. H., & Holt, S. J. (1959). A review of the life-spans and mortality rates of fish in nature, and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquia on Ageing*, 142–180.
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65(1), 23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Campbell, N. A., & Phillips, B. F. (1972). The von Bertalanffy growth curve and its application to capture - recapture data in fisheries biology. *ICES Journal of Marine Science*, 34(2), 295–299. <https://doi.org/10.1093/icesjms/34.2.295>
- Caputi, N., Feng, M., Denham, A., de Lestang, S., Penn, J., Slawinski, D., Pearce, A., & How, J. (2018). Optimizing an oceanographic-larval model for assessment of the puerulus settlement of the Western Rock Lobster, *Panulirus cygnus*, in Westernaustralia. *Bulletin of Marine Science*, 94(3), 775–800. <https://doi.org/10.5343/bms.2017.1146>
- Caputi, N., Kangas, M. I., Chandrapavan, A., Hart, A., Feng, M., Marin, M., & de Lestang, S. (2019). Factors affecting the recovery of invertebrate stocks from the 2011 Western Australian extreme marine heatwave. *Frontiers in Marine Science*, 6(JUL), 1–18.

<https://doi.org/10.3389/fmars.2019.00484>

- Cerrato, R. M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(7), 1416–1426. <https://doi.org/10.1139/f90-160>
- Cooke, S. J., Twardek, W. M., Reid, A. J., Lennox, R. J., Danylchuk, S. C., Brownscombe, J. W., Bower, S. D., Arlinghaus, R., Hyder, K., & Danylchuk, A. J. (2019). Searching for responsible and sustainable recreational fisheries in the Anthropocene. *Journal of Fish Biology*, 94(6), 845–856. <https://doi.org/10.1111/jfb.13935>
- Coulson, P. G., Hall, N. G., & Potter, I. C. (2016). Biological characteristics of three co-occurring species of armorhead from different genera vary markedly from previous results for the Pentacerotidae. *Journal of Fish Biology*, 89(2), 1393–1418. <https://doi.org/10.1111/jfb.13049>
- Coulson, P. G., Hesp, A., Norman, G., & Potter, I. C. (2009). The Western Blue Groper (*Achoerodus gouldii*), a protogynous hermaphroditic labrid with exceptional longevity, late maturity, slow growth, and both late maturation and sex change. *Fishery Bulletin*, 107(1), 57–76.
- Coulson, P. G., Hesp, S. A., Potter, I. C., & Hall, N. G. (2010). Life cycle characteristics of the Blue Morwong *Nemadactylus valenciennesi*, compared with those of other species of Cheilodactylidae. *Marine and Freshwater Research*, 61(1), 104–118. <https://doi.org/10.1071/MF08341>
- Coulson, Peter G., & Wakefield, C. B. (2022). Reproduction, sexually dimorphic growth, exceptional longevity and low natural mortality of the Knifejaw, *Oplegnathus woodwardi*, from temperate waters in the south-eastern Indian Ocean. *Fisheries Research*, 256(December 2021), 106466. <https://doi.org/10.1016/j.fishres.2022.106466>
- Craig, M. T., & Hastings, P. A. (2007). A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. *Ichthyological Research*, 54(1), 1–17. <https://doi.org/10.1007/s10228-006-0367-x>
- Cross, H. (2015). Elasmobranch capture by commercial small-scale fisheries in the Bijagós Archipelago, Guinea Bissau. *Fisheries Research*, 168, 105–108. <https://doi.org/10.1016/j.fishres.2015.03.018>
- Crowe, F. M., Longson, I. G., & Joll, L. M. (2013). Development and implementation of allocation arrangements for recreational and commercial fishing sectors in Western Australia. *Fisheries Management and Ecology*, 20(2–3), 201–210. <https://doi.org/10.1111/j.1365-2400.2012.00858.x>
- de Souza, G. M., Tubino, R. de A., Monteiro-Neto, C., & da Costa, M. R. (2019). Relationships between fish and otolith dimensions of *Pomatomus saltatrix* (Linnaeus, 1766) (Perciformes: Pomatomidae) in southeastern Brazil. *Neotropical Ichthyology*, 17(1), 1–8. <https://doi.org/10.1590/1982-0224-20180032>
- DPIRD. (2022). Recreational fishing rules. <https://www.fish.wa.gov.au/Fishing-and-Aquaculture/Recreational-Fishing/Recreational-Fishing-Rules/Pages/default.aspx>
- Erisman, B. E., & Allen, L. G. (2006). Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, U.S.A. *Journal of Fish Biology*, 68(1), 157–184. <https://doi.org/10.1111/j.0022-1112.2006.00886.x>
- Fairclough, D. V. (2016). Similar cryptic behaviour during the early juvenile phase of two unrelated

- reef fishes: *Epinephelides armatus* and *Bodianus frenchii*. *Marine and Freshwater Behaviour and Physiology*, 49(2), 109–117. <https://doi.org/10.1080/10236244.2015.1125122>
- Fairclough, D. V., Brown, J. I., Carlish, B. J., Crisafulli, B. M., & Keay, I. S. (2014). Breathing life into fisheries stock assessments with citizen science. *Scientific Reports*, 4. <https://doi.org/10.1038/srep07249>
- Fairclough, D. V., Hesp, A. S., Denham, A., Fisher, E., Marks, R., Ryan, K. L., Lek, E., Allen, R., & Crisafulli, B. M. (2021). 2021 assessment of the status of the West Coast Demersal Scalefish Resource. *Fisheries Research Report No. 316* (Issue 316).
- Feng, M., McPhaden, M. J., Xie, S. P., & Hafner, J. (2013). La Niña forces unprecedented Leeuwin Current warming in 2011. *Scientific Reports*, 3, 1–10. <https://doi.org/10.1038/srep01277>
- Fletcher, W. J., Shaw, J., Gaughan, D. J., & Metcalf, S. J. (2011). Ecosystem based fisheries management case study report - West Coast Bioregion. In *Fisheries Research Report No. 225* (Issue 225). <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.231.4278&rep=rep1&type=pdf>
- Forster, J., & Hirst, A. G. (2012). The temperature-size rule emerges from ontogenetic differences between growth and development rates. 483–492. <https://doi.org/10.1111/j.1365-2435.2011.01958.x>
- French, B., Potter, I. C., Hesp, S. A., Coulson, P. G., & Hall, N. G. (2014). Biology of the harlequin fish *Othos dentex* (Serranidae), with particular emphasis on sexual pattern and other reproductive characteristics. *Journal of Fish Biology*, 84(1), 106–132. <https://doi.org/10.1111/jfb.12258>
- Gwinn, D. C., Allen, M. S., & Rogers, M. W. (2010). Evaluation of procedures to reduce bias in fish growth parameter estimates resulting from size-selective sampling. *Fisheries Research*, 105(2), 75–79. <https://doi.org/10.1016/j.fishres.2010.03.005>
- Halim, A., Loneragan, N. R., Wiryawan, B., Hordyk, A. R., Sondita, M. F. A., & Yulianto, I. (2020). Evaluating data-limited fisheries for grouper (Serranidae) and snapper (Lutjanidae) in the Coral Triangle, eastern Indonesia. *Regional Studies in Marine Science*, 38, 101388. <https://doi.org/10.1016/j.rsma.2020.101388>
- Hesp, A., Potter, I. C., & Norman, G. (2002). Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species. *Fishery Bulletin*, 100(2), 214–227.
- Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. In *Fishery Bulletin*, 82. 898–902.
- Hordyk, A., Ono, K., Prince, J., & Walters, C. J. (2016). A simple length-structured model based on life history ratios and incorporating size-dependent selectivity: application to spawning potential ratios for data-poor stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(12), 13. <https://doi.org/10.1139/cjfas-2015-0422>
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., & Prince, J. (2015a). A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES Journal of Marine Science*, 72(1), 204–216. <https://doi.org/10.1093/icesjms/fst235> Original

- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., & Prince, J. (2015b). Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES Journal of Marine Science*, 72(1), 204–216. <https://doi.org/10.1093/icesjms/fst235> Original
- Hovey, C. B., Allen, L. G., & Hovey, T. E. (2002). The reproductive pattern of Barred Sand Bass (*Paralabrax nebulifer*) from southern California. *California Cooperative Oceanic Fisheries Investigations Reports*, 43(May), 174–181.
- Hovey, T. E., & Allen, L. G. (2000). Reproductive patterns of six populations of the Spotted Sand Bass, *Paralabrax maculatofasciatus*, from southern and Baja California. *Copeia*, 2000(2), 459–468. [https://doi.org/10.1643/0045-8511\(2000\)000\[0459:RPOSPO\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2000)000[0459:RPOSPO]2.0.CO;2)
- Huang, B. (2022). Extended reconstructed sea surface temperatures Version 4 (ERSST.v4), Part I. Upgrades and Intercomparisons. *Journal of Climate*. <https://doi.org/10.1175/JCLI-D-14-00006.1>
- Kanyerere, G. Z., Kaonga, D., Mponda, O., Nkhoma, B., & Ngulande, E. (2018). Status of the large-scale commercial trawl fisheries in southern Lake Malawi. *Aquatic Ecosystem Health and Management*, 21(2), 121–131. <https://doi.org/10.1080/14634988.2018.1457388>
- King, M. (2013). Fisheries biology, assessment and management: Second edition. *Fisheries Biology, Assessment and Management: Second Edition* (2nd ed.). Blackwell. <https://doi.org/10.1002/9781118688038>
- Laevastu, T. (1965). Manual of methods in fisheries biology. FAO, Rome.
- Lassen, H. (1998). The future fisheries: Constraints and possibilities sustainability - ecological impact from fisheries, the political environment and how this may affect the future of capture fisheries. *Journal of Northwest Atlantic Fishery Science*, 23, 27–39. <https://doi.org/10.2960/J.v23.a3>
- Lauria, V., Das, I., Hazra, S., Cazcarro, I., Arto, I., Kay, S., Ofori-Danson, P., Ahmed, M., Hossain, M. A. R., Barange, M., & Fernandes, J. A. (2018). Importance of fisheries for food security across three climate change vulnerable deltas. *Science of the Total Environment*, 640–641(June), 1566–1577. <https://doi.org/10.1016/j.scitotenv.2018.06.011>
- Lek, E., Fairclough, D. V., Hall, N. G., Hesp, S. A., & Potter, I. C. (2012). Do the maximum sizes, ages and patterns of growth of three reef-dwelling labrid species at two latitudes differ in a manner conforming to the metabolic theory of ecology? *Journal of Fish Biology*, 81(6), 1936–1962. <https://doi.org/10.1111/j.1095-8649.2012.03446.x>
- Lenanton, R. C., StJohn, J., Keay, I., Wakefield, C. B., Jackson, G., Wise, B., & Gaughan, D. (2009). Spatial scales of exploitation among populations of demersal scalefish: implications for management. Part 2: Stock structure and biology of two indicator species, Western Australian dhufish (*Glaucosoma hebraicum*) and pink snapper (*Pagrus auratus*), in the West Coast Bioregion. *Western Australian Fisheries*, 174, 1–188.
- Loisel, A., Isla, A., & Daufresne, M. (2019). Variation of thermal plasticity in growth and reproduction patterns: Importance of ancestral and developmental temperatures. *Journal of Thermal Biology*, 84(February), 460–468. <https://doi.org/10.1016/j.jtherbio.2019.07.029>
- Love, M. S., Brooks, A., Busatto, D., Stephens, J., & Gregory, P. A. (1996). Aspects of the life

- histories of the Kelp Bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight. *Fishery Bulletin*, 94(3), 472–481.
- Mace, P., & Sissenwine, M. (1993). How much spawning per recruit is enough? Risk Evaluation and Biological Reference Points for Fisheries Management. 101–118.
- Mackie, M, Jackson, G., Tapp, N., Norriss, J., & Thomson, A. (2009). Macroscopic and microscopic description of snapper (*Pagrus auratus*) gonads from Shark Bay, Western Australia. *Fisheries Research*, 184, 35.
- Mackie, M. (2000). Reproductive biology of the Halfmoon Grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. *Environmental Biology of Fishes*, 57(4), 363–376.
<https://doi.org/10.1023/A:1007658027359>
- Mason, T. J., & Lowe, C. G. (2010). Home range, habitat use, and site fidelity of Barred Sand Bass within a southern California marine protected area. *Fisheries Research*, 106(1), 93–101.
<https://doi.org/10.1016/j.fishres.2010.07.008>
- McGurk, M.D., (1986) Natural mortality of marine pelagic fish eggs and larvae: The role of spatial patchiness. *Marine Ecology Progress Series*, 34, 227–242.
- Meer, J. Van Der. (2006). *Metabolic theories in ecology*. *Trends in Ecology & Evolution*, 21(3), 136–140. <https://doi.org/10.1016/j.tree.2005.11.004>
- Moore, S., Hesp, A., Hall, N., & Potter, I. (2007). Age and size compositions, growth and reproductive biology of the Breaksea Cod *Epinephelides armatus*, a gonochoristic serranid. *Journal of Fish Biology*, 71(5), 1407–1429. <https://doi.org/10.1111/j.1095-8649.2007.01614.x>
- Nardi, K., Newman, S. J., Moran, M. J., & Jones, G. P. (2006). Vital demographic statistics and management of the Baldchin Groper (*Choerodon rubescens*) from the Houtman Abrolhos Islands. *Marine and Freshwater Research*, 57(5), 485–496. <https://doi.org/10.1071/MF05187>
- Neves, A., Vieira, A. R., Sequeira, V., Silva, E., Silva, F., Duarte, A. M., Mendes, S., Ganhão, R., Assis, C., Rebelo, R., Magalhães, M. F., Gil, M. M., & Gordo, L. S. (2022). Modelling fish growth with imperfect data: The case of *Trachurus picturatus*. *Fishes*, 7(1), 52.
<https://doi.org/10.3390/fishes7010052>
- Newman, S.J., Wise, B.S., Santoro, K.G. and Gaughan, D.J. (eds). 2021. Status reports of the fisheries and aquatic resources of Western Australia 2020/21: The State of the Fisheries. Department of Primary Industries and Regional Development, Western Australia.
- Newman, S. J., Brown, J. I., Fairclough, D. V., Wise, B. S., Bellchambers, L. M., Molony, B. W., Lenanton, R. C. J., Jackson, G., Smith, K. A., Gaughan, D. J., Fletcher, W. J., McAuley, R. B., & Wakefield, C. B. (2018). A risk assessment and prioritisation approach to the selection of indicator species for the assessment of multi-species, multi-gear, multi-sector fishery resources. *Marine Policy*, 88 (August 2017), 11–22.
<https://doi.org/10.1016/j.marpol.2017.10.028>
- NOAA. (2022). *El Niño / Southern Oscillation (ENSO)*.
<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/MJO/enso.shtml>
- Norriss, J. V., & Crisafulli, B. (2010). Longevity in Australian snapper *Pagrus auratus* (Sparidae). *Journal of the Royal Society of Western Australia*, 93(3), 129–132.
- Norriss, J. V., Fisher, E. A., Hesp, S. A., Jackson, G., Coulson, P. G., Leary, T., & Thomson, A. W. (2016). Status of inshore demersal scalefish stocks on the south coast of Western Australia

- NRM Project 12034 Final Report. Fisheries Research Report No. 276. (Vol. 276, Issue 276).
http://www.fish.wa.gov.au/Documents/research_reports/fr276.pdf
- Norriss, J., & Walters, S. (2017). South coast demersal scalefish resource status report 2017. *Status Reports of the Fisheries and Aquatic Resources of Western Australia 2016/17: South Coast Bioregion*, 181–184.
http://www.fish.wa.gov.au/Documents/sofar/status_reports_of_the_fisheries_and_aquatic_resources_2016-17_south_coast_bioregion.pdf
- O'Neill, T. J., & Stern, S. E. (2012). Finite population corrections for the Kolmogorov-Smirnov tests. *Journal of Nonparametric Statistics*, 24(2), 497–504.
<https://doi.org/10.1080/10485252.2011.650169>
- Okamura, H., & Semba, Y. (2009). A novel statistical method for validating the periodicity of vertebral growth band formation in elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(5), 771–780. <https://doi.org/10.1139/F09-039>
- Pauly, D. (2019). A précis of Gill-Oxygen Limitation Theory (GOLT), with some emphasis on the eastern Mediterranean. 20(4), 660–668. <https://doi.org/10.12681/mms.19285>
- Pauly, D. (1980) On the Interrelations between Natural Mortality, Growth Parameters and Mean Environmental Temperature in 175 Fish Stocks. *ICES Journal of Marine Science*, 39, 175-192.
<https://doi.org/10.1093/icesjms/39.2.175>
- Pearce, A., Slawinski, D., Feng, M., Hutchins, B., & Fearn, P. (2011). Modelling the potential transport of tropical fish larvae in the Leeuwin Current. *Continental Shelf Research*, 31(19–20), 2018–2040. <https://doi.org/10.1016/j.csr.2011.10.006>
- Pilling, G. M., Wakeford, R. C., & Mees, C. C. (2007). Comparisons of length- and age-based stock assessment methods (D. Hoggarth (ed.); 487th ed.). FAO Fisheries Technical Paper.
- Platell, M. E., Hesp, S. A., Cossington, S. M., Lek, E., Moore, S. E., & Potter, I. C. (2010). Influence of selected factors on the dietary compositions of three targeted and co-occurring temperate species of reef fishes: Implications for food partitioning. *Journal of Fish Biology*, 76(6), 1255–1276. <https://doi.org/10.1111/j.1095-8649.2010.02537.x>
- Pondella, D. J., Allen, L. G., Rosales Casian, J. A., & Hovey, T. E. (2001). Demographic parameters of Golden Spotted Rock Bass *Paralabrax auroguttatus* from the northern Gulf of California . *Transactions of the American Fisheries Society*, 130(4), 686–691.
[https://doi.org/10.1577/1548-8659\(2001\)130<0686:dpogsr>2.0.co;2](https://doi.org/10.1577/1548-8659(2001)130<0686:dpogsr>2.0.co;2)
- Pörtner, H. O., & Knust, R. (2012). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, 95(2007). <https://doi.org/10.1126/science.1135471>
- Pratchett, M. S., Cameron, D. S., Donelson, J., Evans, L., Frisch, A. J., Hobday, A. J., Hoey, A. S., Marshall, N. A., Messmer, V., Munday, P. L., Pears, R., Pecl, G., Reynolds, A., Scott, M., Tobin, A., Tobin, R., Welch, D. J., & Williamson, D. H. (2017). Effects of climate change on Coral Grouper (*Plectropomus spp.*) and possible adaptation options. *Reviews in Fish Biology and Fisheries*, 27(2), 297–316. <https://doi.org/10.1007/s11160-016-9455-9>
- Prince, J., Hordyk, A., Valencia R, S. R., Loneragan, N., & Sainsbury, K. (2015). Revisiting the concept of Beverton–Holt life-history invariants with the aim of informing data-poor fisheries assessment. *Encyclopedia of Environment and Society*, 1959.
<https://doi.org/10.4135/9781412953924.n678>

- Puentes-Granada, V., Rojas, P., Pavolini, G., Gutiérrez, C. F., & Villa, Á. A. (2019). Morphology and morphometric relationships for sagitta otoliths in *Lutjanus argentiventris* (Pisces: Lutjanidae) and *Hyphorhodus acanthistius* (Pisces: Serranidae) from the Colombian Pacific Ocean. *Universitas Scientiarum*, 24(2), 337–361. <https://doi.org/10.11144/Javeriana.SC24-2.mamr>
- R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Ryan KL, Hall NG, Lai EK, Smallwood CB, Tate A, Taylor SM, Wise BS 2019. State-wide survey of boat-based recreational fishing in Western Australia 2017/18. Fisheries Research Report No. 297, Department of Primary Industries and Regional Development, Western Australia. 195pp.
- Ryan, Karina L., Hall, N. G., Lai, E. K. M., Smallwood, C. B., Taylor, S. M., & Wise, B. S. (2015). State-wide survey of boat-based recreational fishing in Western Australia 2013/14. *Fisheries Research Report No. 268. Department of Fisheries, Western Australia* (Issue 268). http://www.fish.wa.gov.au/Documents/research_reports/frr268.pdf
- Saber, S., Lino, P.G., Ciércoles, C., Gómez-Vives, M. J., Muñoz-Lechuga, R., Godoy-Garrido, M. D., Ortiz-de-Urbina-Gutiérrez, J. M., Coelho, R., Macías-López, & Ángel D. (2019). Macroscopic and microscopic maturity stages. living working document for small Tuna Species. 76(7), 111–148.
- Sadovy, Y., & Domeier, M. . (2005). Perplexing problems of sexual patterns in the fish genus *Paralabrax* (Serranidae, Serraninae). *Journal of Zoology*, 267(2), 121–133. <https://doi.org/10.1017/S0952836905007466>
- Salinas-de-León, P., Bertolotti, A., Chong-Montenegro, C., Gomes-Do-Régo, M., & Preziosi, R. F. (2017). Reproductive biology of the endangered White-Spotted Sand Bass *Paralabrax albomaculatus* endemic to the Galapagos Islands. *Endangered Species Research*, 34, 301–309. <https://doi.org/10.3354/esr00858>
- Saunders, R., Bryars, S., & Fowler, A., (2010). Preliminary consideration of the biology of several of South Australia's marine fish species that have conservation or management interest. *Report to the Department for Environment and Heritage. SARDI Aquatic Sciences*, SARDI Aquatic Sciences, West Beach, S. Aust.
- Schreer, J. F., Gokey, J., & DeGhett, V. J. (2009). The incidence and consequences of barotrauma in fish in the St. Lawrence River. *North American Journal of Fisheries Management*, 29(6), 1707–1713. <https://doi.org/10.1577/m09-013.1>
- Shepherd, B., Phelps, T., Pinheiro, H. T., Pérez-Matus, A., & Rocha, L. A. (2018). *Plectranthias ahiahiata*, a new species of perchlet from a mesophotic ecosystem at Rapa Nui (Easter Island) (Teleostei, Serranidae, Anthiadinae). *ZooKeys*, 762(2), 105–116. <https://doi.org/10.3897/zookeys.762.24618>
- Siegfried, K. I., & Sansó, B. (2006). Two Bayesian methods for estimating parameters of the von Bertalanffy growth equation. *Environmental Biology of Fishes*, 77(3–4), 301–308. <https://doi.org/10.1007/s10641-006-9112-6>
- Smallwood, C. B., Hesp, S. A., & Beckley, L. E. (2013). Biology, stock status and management summaries for selected fish species in south-western Australia. In *Fisheries Research Report No. 242* (Issue 242).
- Smith, M. W., Then, A. Y., Wor, C., Ralph, G., Pollock, K. H., & Hoenig, J. M. (2012). Recommendations for catch-curve analysis. *North American Journal of Fisheries*

- Management*, 32(5), 956–967. <https://doi.org/10.1080/02755947.2012.711270>
- Virtanen, J., Ahvonen, A., & Honkanen, A. (2001). Regional socio-economic importance of fisheries in Finland. *Fisheries Management and Ecology*, 8(4–5), 393–403.
<https://doi.org/10.1046/j.1365-2400.2001.00265.x>
- Wakefield, C. (2006). Latitudinal and temporal comparisons of the reproductive biology and growth of snapper, *Pagrus auratus* (Sparidae), in Western Australia. PhD thesis, Murdoch University, 162.
- Wakefield, C. B., Boddington, D. K., & Newman, S. J. (2016). Rapid lateral extraction of otoliths that maintains the integrity of fish product to improve access to catches and reduce potential sampling biases. *The Open Fish Science Journal*, 9(1), 26–28.
<https://doi.org/10.2174/1874401x01609010026>
- Wakefield, C. B., Newman, S. J., & Molony, B. W. (2010). Age-based demography and reproduction of Hapuku, *Polyprion oxygeneios*, from the south coast of Western Australia: Implications for management. *ICES Journal of Marine Science*, 67(6), 1164–1174.
<https://doi.org/10.1093/icesjms/fsq021>
- Walters, R. J., Hassall, M., (2006). The temperature-size rule in ectotherms: may a general explanation exist after all? *The American Naturalist*, 167(4), 510–523.
<https://doi.org/10.1086/501029>
- Whisson, G., & Hoschke, A. (2021). The Perth coast fish book - Identification guide Mandurah to Two Rocks (1st ed.). *Aqua Research and Monitoring Services*, Western Australia.
www.aquamonitoring.com.au
- Williams, J. T., & Carpenter, K. E. (2015). A new fish species of the subfamily Serraninae (Perciformes, Serranidae) from the Philippines. *Zootaxa*, 3911(2), 287–293.
<https://doi.org/10.11646/zootaxa.3911.2.10>
- Wootton, H.F., Morrongiello, J.R., Schmitt, T. & Audzijonyte, A. (2022). Smaller adult fish size in warmer water is not explained by elevated metabolism. *Ecology Letters*, 25, 1177– 1188.
Available from: <https://doi.org/10.1111/ele.13989>
- WoRMS. (2021). World Register of Marine Species. <https://doi.org/10.14284/170>
- Zinke, J., Rountrey, A., Feng, M., Xie, S. P., Dissard, D., Rankenburg, K., Lough, J. M., & McCulloch, M. T. (2014). Corals record long-term Leeuwin Current variability including Ningaloo Niño/Niña since 1795. *Nature Communications*, 5, 1–9.
<https://doi.org/10.1038/ncomms4607>

6. Appendix

The biology and ecology of gonochoristic serranids

Literature review submitted as requirement of Bachelor of Science (Honours).

Student name: Jacob Buckland

Student number: 33420848

3



Four species of gonochoristic serranids: top two from south-western Australia and bottom two from the north-western Pacific.

³ From top Left to Right south-western Australian gonochoristic serranids: *Epinephelides armatus* (Image from: <https://www.inaturalist.org/observations/67391327> Source: shanediver, some rights reserved (CC-BY-NC)); *Othos dentex* (Image from: <https://fishesofaustralia.net.au/home/species/4383> Source: Graham Edgar / Reef Life Survey. License: CC BY Attribution). Bottom left to right Eastern Pacific gonochorists: *Paralabrax maculatofasciatus* (Image from: <https://reeflifesurvey.com/species/paralabrax-maculatofasciatus/> Source: Rick Stuart-Smith, Reef Life Survey); *Paralabrax albomaculatus* (Image from: <https://reeflifesurvey.com/species/paralabrax-albomaculatus/> Source Graham Edgar, Reef Life Survey).

6.1 Summary

The Family Serranidae is a large, diverse family of teleost fishes that express all forms of sexual reproduction (except protandry) with gonochorism being the rarest strategy in this family. The aims of this review are to summarise and compare the age, growth, reproductive biology, fisheries and management of gonochoristic serranids. This review also considers the taxonomy of the Serranidae, for which there is some confusion and debate surrounding the sub-families, especially the Epinephelinae, which recently was that was elevated to family i.e., the Epinephelidae. Gonochoristic species were identified and distinguished from hermaphrodites based on five criteria established by Sadovy and Shapiro (1987), in particular the presence of transitional individuals (i.e., individuals in the process of changing sex). Species selected for this literature review include *Epinephelides armatus*, which is endemic to the south-west coast of Australia and *Othos dentex*, which is distributed through the south-west coast and southern coasts of Australia, and five of the nine *Paralabrax* species, with some biological data, from the eastern Pacific. These five species include *Paralabrax maculatofasciatus* (distributed from Monterey Bay, California to Mazatlán, Mexico), *P. clathratus* (distributed from the Colombia River, Washington, in the north to Baja California), *P. nebulifer* (distributed from Santa Cruz, California to Magdalena Bay,

Baja California Sur), *P. auroguttatus* (from Isla Cedros in the north to Cabo San Lucas, including the Gulf of California) and *P. albomaculatus* (endemic to the Galapagos Islands).

The seven species considered in this review are medium sized demersal species (450 to 720 mm in length) that have a moderate longevity (14 to 33 years old).

The male reproductive tissues of the two south-western Australian gonochorists differed from those of the five *Paralabrax* species from the Eastern Pacific. *E. armatus* and *O. dentex* males contain only a sperm duct in male gonads; while males of the five *Paralabrax* species contain a central membrane lined 'ovarian' lumen. The *Paralabrax* genus were found to be aggregation spawners making them prone to over-exploitation while the south-western gonochorists appear to be pair spawners.

The south-western Australian species have a number of management strategies in place for both recreational and commercial fishers that include a minimum legal length (MLL) for retention for *E. armatus* (300 mm total length) and in association with other demersal species, bag limits for recreational fishers and set total allowable catch limits for commercial fishers. The *Paralabrax* species have mixed management strategies with bag limits and a MLL of 355.6 mm for three

species (*P. clathratus*, *P. maculatofasciatus* and *P. nebulifer*). However, the management of these species does not include a seasonal closure that protect spawning aggregations. The tropical *Paralabrax albomaculatus* has very limited management strategies put in place and this species is most likely vulnerable to overfishing by the artisanal fishing fleet in the Galapagos Islands. This review has highlighted the lack for information of growth and reproduction for the *Paralabrax* species, particularly *P. albomaculatus*, and the need for this information to inform the management of these species.

6.2 Introduction

The Groupers, Basses and Sea Perch/Perchlets belong to the family Serranidae, which is one of the most diverse families of teleost fishes, with species ranging from small tropical perchlets with maximum lengths of 40 mm to large groupers that can attain length of up to 3000 mm. The Serranidae includes an estimated 597 species from 71 genera that are distributed from temperate to tropical environments (Bertoncini, 2018; Fairclough, 2016; Love et al., 1996; Mackie, 2000; Mason & Lowe, 2010; Pondella et al., 2003; Robbins, 2014; WoRMS Editorial Board, 2021).

Before 2011, the Serranidae included three main sub-Families: The Serraninae (Perchlets), Anthiadae⁴ (Basslets) and Epinephelinae (Groupers); and three lesser-known subfamilies: the Diploprioninae (Soapfish), Grammistinae and Liopropomatinae (Craig & Hastings, 2007; Shepherd et al., 2018; Williams & Carpenter, 2015; WoRMS Editorial Board, 2021). The Serraninae consist of basses and rock basses; the Anthiadae is mainly comprised of basslets and small ornamental coral reef species making this subfamily quite diverse; and the Epinephelinae are mainly comprised of larger grouper species with tropical and

⁴ The subfamily Anthiinae has been used for this group of fish but this name conflicts with a sub-family of beetles. Therefore, the name Anthiadae is used for this subfamily in this review.

temperate representatives (Craig & Hastings, 2007; Shepherd et al., 2018; Williams & Carpenter, 2015). However, the taxonomic relationships within the Serranidae have been debated and alternative relationships and sub-families have been proposed (Craig & Hastings, 2007). For example, more recent publications suggest that the Epinephelinae should be elevated to the family Epinephelidae (Craig & Hastings, 2007). In this review, I follow the more recent classification of the group and discuss the taxonomy of the Serranidae and Epinephelidae in further detail in Section 2: *Taxonomy of the Serranidae* below.

Species belonging to the Serranidae and the closely related Epinephelidae have been fished by commercial or recreational fishers for many years with a number of species being over-exploited (Frisch et al., 2016; Pet et al., 2005; Sadovy & Domeier, 2005). This is demonstrated by the International Union for the Conservation of Nature (IUCN) listing of some species of serranids and epinephelids as endangered which is discussed in more detail in Section 8: *Fisheries management and conservation* (see also Table 5) (Craig & Hastings, 2007; French et al., 2014; Moore, 2005)

Most serranids are hermaphrodites and all forms of hermaphroditism are found in the family except protandry i.e., individuals developing initially as male

and changing sex to female (Allen et al., 1995; Love et al., 1996; Pondella et al., 2001). However, a small number of serranids are gonochoristic i.e., they have separate sexes that are maintained throughout the life cycle, including five confirmed species from the *Paralabrax* genus (Rock and Sand Basses) and two species endemic to Australian waters – *Epinephelides armatus* (Breaksea Cod) and *Othos dentex* (Harlequin Fish) (French et al., 2014; Moore et al., 2007; Pondella et al., 2003).

6.2.1 Biology and life history strategies

Life history strategies are defined by the growth, mortality and reproductive biology of a species and some of the important characteristics include maximum age, natural mortality, growth rates and size at reproduction (Khan & Afzal, 2014). Growth models, combined with length-weight relationships, are essential for determining the rate of increase in biomass by the population (Campbell & Phillips, 1972; Khan & Afzal Khan, 2014; Vincenzi et al., 2020). The von Bertalanffy growth curve, with its three parameters of L_{∞} – the asymptotic length, k – the instantaneous growth rate, and t_0 – the theoretical age at length zero, is widely used for estimating age and length relationships in fish populations (Campbell & Phillips, 1972; Khan & Afzal Khan, 2014; Vincenzi et al., 2020).

Traditional fisheries stock assessments rely on detailed historical data on catch effort and biomass of the population and the biology of the harvested species to provide information for the effective management of fish populations (Haddon, 2011, Hordyk et al., 2015; Prince et al., 2015). These data are not available for all fisheries, particularly small-scale fisheries, due to the cost and logistic challenges of obtaining them from many small operators. In the last ~10 years, a suite of techniques has been developed to enable data-limited fisheries to be assessed, including the length-based spawning potential ratio (LB-SPR) (Hordyk et al., 2015; Prince et al., 2015). This methodology uses the relationships between life history parameters such as natural mortality, growth rate (k), asymptotic length (L_{∞}) and length at maturity (L_m) to predict the size distribution of the unfished population, assuming equilibrium conditions. Combined with a representative length distribution from the current population, the spawning potential ratio (SPR) can be estimated (Beverton & Holt, 1959; Hoenig, 1983; Hordyk et al., 2015; Prince et al., 2015).

The life history ratios include M/k , L_m/L_{∞} and $M \cdot T_M$, where T_M is the age of maturity (Hordyk et al., 2015b; Prince et al., 2015). Beverton and Holt (1959) first identified that there was a correlation between the instantaneous natural mortality rate and the von Bertalanffy growth parameters, this relationship was later coined

the Beverton-Holt life history invariants (Charnov, 1993, Jensen, 1996), e.g., Jensen (1996) gave the definition of these ratios as; $M/k = 1.5$, $L_m/L_\infty = 0.66$, $M \cdot T_M = 1.65$, based largely on studies of clupeids in the Northern Hemisphere. However, a meta-analysis of more than 120 species from a diverse range of families found that these ratios are not invariant and vary widely between species (Hordyk et al., 2015b; Prince et al., 2015). I have calculated estimates of the life-history ratios for the species of interest in this review from published information. However, some species, especially those in the genus *Paralabrax* had unreliable estimates due to an unrealistically large estimates of t_0 (>1 year) and this will influence the estimates of L_∞ and k . For these species, L_m and L_∞ were calculated using equations in Froese and Binohlan (2003).

6.2.2 Aims of the review

The aims of this review are to summarise and compare the life history strategies of a small group of gonochoristic serranids found in latitudes 35 to 27 ° in both the Northern and Southern hemispheres, summarise and compare the reproductive biology of these species and to review and compare the fisheries and management of these species among species and regions. Note that one of the *Paralabrax* species (*P. albomaculatus*), occurs outside the above range of latitudes and is found in the tropical waters of the Galapagos Islands. The gonochoristic Serranid species investigated in this literature review include two species from the

south-western Australia (*Epinephelides armatus* and *Othos dentex*); and five out of the nine species from the *Paralabrax* genus for which some biological data was available (*P. maculatofasciatus*, *P. nebulifer*, *P. clathratus*, *P. auroguttatus* and *P. albomaculatus*) (French et al., 2014; Love et al., 1996; Moore et al., 2007; Sadovy & Domeier, 2005). The remaining four *Paralabrax* species located in the eastern Pacific Ocean had very limited biological data available and are not considered in this review (Froese & Pauly, 2022a, 2022b, 2022c, 2022d).

The review starts with a summary of the taxonomy of the Serranidae because, as noted above, this is a major topic of debate. It then investigates reproductive strategies in the Serranidae, followed by an overview of the biology of gonochoristic serranids in south-western Australia and the Eastern Pacific. The fisheries and conservation status of these species are discussed followed by the overall conclusions.

Taxonomic relationships in the Serranidae

Some recent studies using molecular techniques have suggested that the sub-families of Serranidae should be elevated to individual families. Craig et al. (2007) revised the classification of the sub-family Epinephelinae using genetic data from two nuclear (Tmo-4C4 and histone H3) and two mitochondrial genes (16S

and 12S) from 155 species of serranids. They concluded that the Epinephelinae should be classed as a separate family, known as Epinephelidae (Craig & Hastings, 2007; Ma et al., 2016; Tucker et al., 2016). Based on their results, they also recommended that more data were needed to decide on the taxonomic standing of the Anthiadae and Serraninae sub-families. Some data bases, such as FishBase and WoRMS still consider the Epinephelidae as part of the Serranidae, while the IUCN considers the Epinephelidae as a separate family (Craig & Hastings, 2007; How, 2013; IUCN, 2021). In this literature review, I use the IUCN designation of the Epinephelidae as a separate family, consisting of 12 genera and 102 species (Craig & Hastings, 2007; How, 2013; IUCN, 2021). This leaves 59 genera and 495 species in the Serranidae and its remaining five sub-families (Anthiadae, Serraninae, Diploprioninae, Grammistinae and Liopropomatinae).

6.3 Reproductive strategies in the Serranidae

Fish exhibit a diverse range of reproductive strategies, from gonochorism to simultaneous hermaphroditism (Godwin, 2011; Prevedelli et al., 2006). Hermaphroditism is a mode of reproduction where an individual is able to transition from one sex to another.

Within the Serranidae, three main reproductive strategies have been documented: (1) protogynous hermaphroditism, where juveniles develop as females

and then change sex to males: (2) simultaneous hermaphroditism, where individuals can function as a male and female at the same time; and (3) gonochorism, where individuals develop and remain as one sex throughout their lifetime. Protandric hermaphroditism, where individuals develop as males and change sex to females, is not present within the Serranidae (French et al., 2014; Gemmell et al., 2019; Moore et al., 2007; Sadovy, 1987).

In the Serranidae, the protogynous hermaphroditism reproductive strategy is thought to be the primitive strategy for the Anthiadinae, with simultaneous hermaphroditism and gonochorism evolving from this strategy (Erisman & Hastings, 2011). However, the two species of Anthiadinae from south-western Australia are exceptions to this rule and are thought to have evolved from an ancestor that was an offshoot(s) where protogyny had not evolved (French et al., 2014; Moore et al., 2007). Identifying the reproductive strategy of a species is important for understanding their ecology and behavior. A number of criteria are used to identify whether a species is protogynous monandric, protogynous diandric or a simultaneous hermaphrodite, with all forms having unique characteristics (Gemmell et al., 2019; Sadovy & Shapiro, 1987).

6.3.1 Protogyny

Protogyny is a form of sex change where an individual begins their lifecycle as a female and transitions into a male, in two possible ways (Gemmell et al., 2019; Godwin, 2011; Sadovy & Shapiro, 1987): i) monandric protogynous hermaphrodites – where all fish start as juveniles and first mature as a female before transitioning into a male; and ii) diandric protogynous hermaphrodites – where individuals may have started life and mature as a female before transitioning to male, or may mature directly as a male (Gemmell et al., 2019; Sadovy & Shapiro, 1987).

Sadovy & Shapiro (1987) specified criteria for assessing whether a species is a protogynous hermaphrodite based on population demographics including the size distribution of males and females and histology of the gonads (Table 1). Monandric hermaphrodites lack males in the smaller age/length classes and males dominate older age/ larger length classes, whereas diandric species have males also present in the smaller age and length classes, albeit very few, depending on the proportion of males in the population (Gemmell et al., 2019; Godwin, 2011; Sadovy & Shapiro, 1987). The histological characteristics of the gonads of the males of monandric species retention of a central ovarian lumen. This contrasts with those individuals of diandric species that start life as males and have not undergone sex

change and consequently do not have ovarian lumen located in the testes (Sadovy & Shapiro, 1987) (Table 1).

6.3.2 Gonochorism

Gonochorism is where individuals within a population express separate sexes, maturing as either a male or female and remaining as that gender throughout life (Moore et al., 2007; Prevedelli et al., 2006; Sadovy & Shapiro, 1987). In the Serranidae, gonochorism is an extremely rare reproductive strategy with only a few species using this strategy (Allen et al., 1995; French et al., 2014; Love et al., 1996; Moore et al., 2007; Salinas-de-León et al., 2017). The only known gonochorists in the ~495 species of Serranidae (excluding the Epinephelidae) include species from the genera *Paralabrax*, *Epinephelides armatus* (Breaksea cod – a single species genus) and *Othos dentex* (Harlequin fish- also a single species genus). Most of these species, including *E. armatus* and the *Paralabrax* species, were initially thought to be protogynous hermaphrodites (French et al., 2014; Moore et al., 2007; Sadovy & Domeier, 2005). However, subsequent detailed biological studies showed that these species were in fact gonochorists (Allen et al., 1995; French et al., 2014; Love et al., 1996; Moore et al., 2007; Salinas-de-León et al., 2017). A species is assessed as gonochoristic when there is insufficient evidence of sex change upon a robust histological analysis of the gonads from a wide size range

of individuals (French et al., 2014; Moore et al., 2007; Sadovy & Shapiro, 1987; Sadovy & Domeier, 2005). However, a gonochoristic species can show demographic traits that are inherent to hermaphroditic species, which makes gonochorism difficult to determine (French et al., 2014; Moore et al., 2007; Sadovy & Domeier, 2005). These traits include, for example, a bimodal size (Females and males exhibit different size structures) and age distribution with larger, older male *E. armatus* than females and the presence of membrane-lined ovarian lumen in the testes of some males in the *Paralabrax* genus where species have been confirmed to be gonochoristic from that genus (Moore et al., 2007; Sadovy & Domeier, 2005). Clear histological evidence of former female functions, such as degenerating vitellogenic oocytes, is needed for a species to be confirmed as a hermaphrodite (French et al., 2014; Moore et al., 2007; Sadovy & Domeier, 2005; Sadovy & Shapiro, 1987).

Table 1: Description and characteristics of five criteria for the three forms for hermaphroditism found in the Serranidae (from Sadovy and Shapiro, 1987).

Criteria	Protogyny monandric (All males begin development as females)	Protogyny diandric (Some males begin development as males, while other males begin development as females)	Simultaneous Hermaphroditism (Functional male and female structures present)
Population structure	Bimodal size/age structure, female modal size smaller than males.	Depends on proportion of males present. Low proportion of male's results in bimodal size structure in the population similar to monandry; large proportion of male's results in bimodality in the size frequency distribution being obscured as primary males occupy all size ranges.	All individuals function as both male and female simultaneously, sex ratio is generally 1:1.
Gonadal structure	Gonads of initial sex in most protogynous species are purely ovarian with no testicular tissue or some tissue undelimited in type. Following sex reversal, testis retain the ovarian lumen which is a strong indicator of former female functions.	Secondary males undergo gonadal transformation similar to that of monandry. Testis in primary males do not contain ovarian lumen but possess peripheral sperm ducts.	Sperm ducts and oviducts are located in close proximity but are separate structures.
Germ cell remnants: Atretic follicles	Atretic follicle is the most commonly used oocytic remnant to diagnose protogynous hermaphrodites. These remnants persist in testes after females transition to males.		No germ cell remnants present due to the separation of sperm and oviducts.
Germ cell remnants: Oocytes	The presence of oocytes in the testis has been used to diagnose protogynous hermaphroditism. Note however, that similar structures may be present in some gonochoristic species.		Oocytes present in the testis are mature and have the ability to leave the gonads.
Transitional individuals	Discovery of individuals that are transitioning, i.e., have the simultaneous presence of ovarian and testicular tissues.		

6.4 The biology and ecology of gonochoristic serranids of south-western Australia

The west coast of Australia extends over a distance of >10,000 km covering both tropical and temperate latitudes (Akhir et al., 2020; Caputi et al., 2018; Coulson et al., 2019). The Leeuwin Current brings warmer waters southwards and transports tropical species further south to temperate waters (Coulson et al., 2019). Nine species of serranids are found in south-western Australia, including two sub-families: with eight species in the Anthiadae (*Acanthistius pardalotus*, *Acanthistius serratus*, *Caesioperca* sp., *Caprodon longimanus*, *Epinephelides armatus*, *Hypoplectrodes cardinalis*, *Hypoplectrodes nigroruber*, *Hypoplectrodes wilsoni* and *Othos dentex*) and one species in the Diploprioninae (*Diploprion bifasciatum*). Except for detailed studies on the growth and reproduction of two of the Anthiadae species, *Epinephelides armatus* (Moore et al., 2007) and *Othos dentex* (French et al., 2014; Moore et al., 2007). There is little to no biological data on the other eight species including whether they are gonochoristic or hermaphrodites. *Acanthistius pardalotus*, *A. serratus*, *Caesioperca* sp., *H. cardinalis* and *H. wilsoni* are endemic to southwestern Australia while *D. bifasciatum* is a tropical species that extends down

the west coast (WoRMS, 2021). *C. longimanus* is also distributed in New South Wales and *H. nigroruber* from Western Australia to Tasmania (WoRMS, 2021).



Figure 1: The distribution (blue) of *Epinephelides armatus* from fishes of Australia. Source: <https://fishesofaustralia.net.au/home/species/4375#:~:text=Endemic%20to%20Western%20Australia%2C%20from,commonly%20to%20about%2035%20m.>

The Breaksea Cod, *Epinephelides armatus*, is in a monospecific genus (Eastman, 2021; Fairclough, 2016; Moore et al., 2007) and is endemic to the continental shelf waters of south-western Australia. Its range extends from Shark Bay in the north (25.783° S, 113.299° E), south to Cape Naturaliste (33.533° S, 115.017° E) and then east to Esperance (33.861° S, 121.891° E) on the south coast (Fairclough, 2016; Moore et al., 2007; Smallwood et al., 2013) (Figure 1).

Epinephelides armatus is found in benthic habitats, mainly rocky reefs including limestone reefs on the west coast and granite reefs on the south coast of south-western Australia (Fairclough, 2016; Moore et al., 2007). These habitats are also important nurseries and provide refuge from predators (Moore et al., 2007). The diet of *E. armatus* consists mainly of small teleosts and crustaceans (Fairclough, 2016; Platell et al., 2010). *Epinephelides armatus* has a maximum total length and weight of 510 mm and 3 kg, respectively, and a maximum age of 20 years old (Moore et al., 2007).

Initial studies on the biology of *E. armatus* assessed this species as a protogynous hermaphrodite (Eastman, 2001) using one of the five criteria from Sadovy and Shapiro (1987). However, this assessment on the increasing ratio of males to females with increasing size of fish and did not consider the other four

criteria as no information was from histological studies of the gonads (Eastman, 2001). In addition to studies of size, age and gonad stage, Moore et al. (2007) also carried out a detailed histological study of *E. armatus* gonads, including those from 128 females and 106 males. The gonads of juvenile female and male fish consisted solely of either ovarian or testicular tissue, respectively, and no remnant ovarian tissue was present in the testes of any of the male fish examined (Moore et al., 2007). Although males had a greater modal length (400-449mm) than females (250-299mm), females had a greater maximum size (510mm) than males (498 mm). No transitional individuals were identified from the histological examination of male gonads, and this was used to classify *E. armatus* as a gonochore (Moore et al., 2007).

Epinephelides armatus has an extended spawning period of nine months (October to April) with a peak in spawning from January to April (Moore et al., 2007). This extended spawning and the timing of peak spawning is unusual for fish in the temperate waters of south-western Australia, which tend to spawn for shorter durations in the spring-summer months (Moore, 2005; Moore et al., 2007). The gonadosomatic indices (GSIs) of females were greater than those of males, which is considered a trait of pair spawners and hence, *E. armatus* were hypothesized to be pair spawners (Moore et al., 2007). The size at 50% sexual

maturity (L_{50}) for females (306 mm) was about 50 mm greater than that of males (256 mm) (Moore et al., 2007).

The growth rates of *E. armatus* (Table 2) differed significantly between males and females with the instantaneous growth coefficient (k) for males being 0.17 year⁻¹, slightly faster than that of females (0.14 year⁻¹). The asymptotic length (L_{∞}) of females (561 mm) was slightly greater than that for males (558 mm), while males had a greater t_0 value (-0.04 years) than females (-0.24 years) (Moore et al., 2007). The natural mortality (M) rates calculated using the Hoenig (1983) method were 0.2201 year⁻¹ for both females and males, based on maximum ages of 19 years for both sexes (Table 2).

The data from Moore et al. (2007) were used to estimate the Beverton-Holt life history ratios for female and male *E. armatus*. The M/k values were 1.57 for females and 1.29 for males which suggests that the size distribution of the unfished population has relatively more immature than mature fish in the population (see Figure 2 in Prince et al. (2015)). The size at maturity relative to the asymptotic length (L_{50}/L_{∞}) was 0.545 for females and 0.459 for males indicating that they are reaching maturity at about 50% of their asymptotic length.

Empirical estimates of L_{∞} and L_{50} were also calculated following Froese and Binohlan (2003) using the formulae:

1) $\bar{L}_{\infty}: \log_{10} L_{\infty} = 0.44 + 0.9841 \log_{10}(L_{max}), L_{max} = \text{Maximum recorded length}$

2) $\bar{L}_m: \log_{10} L_m = 0.8979 * \log_{10} (L_{\infty}) - 0.0782, L_m = \text{Length at 50\% maturity.}$

These empirical estimates were compared with those derived from the biological data only for *E. armatus* because this was the only species with realistic estimates of t_0 , and hence reliable estimates of k and L_{∞} . The estimates of \bar{L}_{∞} for female *E. armatus* was 530.2 mm and 517.9 mm for males, while the estimates of \bar{L}_m for females and males were 295.2 and 289.1 mm, respectively. The life history ratio of $\bar{L}_m / \bar{L}_{\infty}$ derived using the empirical estimates were 0.557 for females (cf 0.545) and 0.558 for males (cf 0.45). which are close to the biological estimates for females (0.558) but not males (~25.5% greater) (Table 4).

The genus *Othos* is monospecific, containing only the Harlequin Fish *Othos dentex*, a benthic Serranid in the Anthiadinae sub-family (French et al., 2014, 2017). It is found from Porth Phillip Bay in Victoria (38.1732° S, 144.8731° E) to the Houtman Abrolhos islands in Western Australia (28.3001° S, 113.5952° E) (Figure 2). However, in recent times *O. dentex* has not been observed in Victoria (French et al., 2014; Saunders et al.2010).

Othos dentex occurs in shallow rocky reefs and around caves in nearshore waters to ~30 m in depth (French et al., 2014; Saunders et al., 2010). The maximum recorded total length (TL) for *O. dentex* is 760 mm and the maximum recorded age is 42 years in Victorian waters (Saunders et al., 2010). This compares with the maximum recorded TL and age in Western Australian waters of 605 mm and 37 years, respectively (French et al., 2014). *Othos dentex* feeds exclusively on teleost's, with 10 families being recorded in its diet, which is dominated by species in the Labridae (French et al., 2017).

French et al. (2014) concluded that *O. dentex* was a gonochorist based on the following demographic and histological information: (1) no marked overall bimodality was present in the male and female length-frequency distributions; (2) no evidence of sex-based modality in the age-frequency distributions was found; and (3) histological examination of 10 -20 gonads from individuals of each sex in each month including a range of length and age classes which contained solely ovarian or testicular tissue (French et al., 2014). The testes of male *O. dentex* were quite small suggesting that there is little sperm competition and combined with field observations of one male and one female found together during the spawning season, suggests that this species is a pair spawner (French et al., 2014).



Figure 2: The distribution (blue) of the Harlequin Fish *Othos dentex* from Fishes of Australia. <https://fishesofaustralia.net.au/home/species/4383>

Female *O. dentex* have a lower instantaneous growth rate ($k = 0.05 \text{ year}^{-1}$) and much greater asymptotic length (654 mm) than males ($k = 0.10 \text{ year}^{-1}$, 562 mm) (Table 2). The von Bertalanffy growth equations for both female and male *O. dentex* had high negative t_0 values (-7.92, -3.73 years, respectively) as a result of a lack of small/ young (< 250 mm and 5 years) fish in the growth model (French et al., 2014). The length at which 50% of females reached maturity (L_{50}) was 345 mm and about 10 mm smaller than the L_{50} for males of 356 mm (French et al., 2014). The value of natural mortality (M) estimated for *O. dentex* combined sexes was 0.3 year^{-1} and is 0.11 year^{-1} from the Hoenig equation, using a maximum age of 37 years (French et al., 2014).

The t_0 estimated for *O. dentex* using the von Bertalanffy equations for females and males were large and negative (French et al., 2014; Table 2) and thus the estimated values of L_∞ and particularly k may not truly reflect those parameters for the growth of this species. The life history ratios in Table 4 would be an unreliable estimate of the population, the empirical estimates for L_∞ were calculated (Table 3). The L_m/L_∞ life history ratio calculated from the empirical estimates was 0.55 for females and 0.602 for males (Table).

6.5 The biology and ecology of gonochoristic Serranids of the *Paralabrax* genus

The *Paralabrax* genus (Rock basses) contains nine species with a distribution ranging along the eastern Pacific, western Atlantic and the Galapagos Island chain with temperate and tropical representatives. This genus consists of near-shore species ranging from the intertidal zone to 155 m in depth. Initially, like *E. armatus* and *O. dentex*, species of *Paralabrax* were believed to be protogynous hermaphrodites (Sadovy & Domeier, 2005). More detailed reproductive studies have shown, however, that at least five members of this species are functional gonochores (Len & Hovey, 1995; Love et al., 1996; Mason & Lowe, 2010; Pondella et al., 2001; Salinas-de-León et al., 2017). These five species are:

P. maculatofasciatus, *P. nebulifer*, *P. clathratus*, *P. auroguttatus* and *P. albomaculatus*.

Paralabrax maculatofasciatus (spotted sand bass) is a higher order carnivore that feeds on crustaceans and molluscs, mainly crabs and clams (Andrews et al., 2005). This species is found around shallow reefs during the spring, summer, and autumn months, while it migrates to deeper water in winter. The distribution of *P. maculatofasciatus* ranges from Mazatlán, Mexico in the south (23.2494° N, 106.4111° W) to the Gulf of California (26.7313° N, 110.7122° W) and Monterey Bay, California (36.8007° N, 121.9473° W) in the north (Allen et al., 1995).

Paralabrax maculatofasciatus reaches a maximum length and weight of 450 mm and 2.6 kg, respectively, and a maximum age of 14 years (ref). It feeds mainly on crustaceans and bivalves, particularly the jackknife clam, *Ensis* spp. (Allen et al., 1995; Andrews et al., 2005; T. E. Hovey & Allen, 2000; Sadovy & Domeier, 2005).

This species is the most well studied species within the *Paralabrax* genus, as there has been confusion surrounding its reproductive mode i.e., whether it is a diandric protogynous hermaphrodite or gonochoristic (Allen et al., 1995; Hovey & Allen, 2000; Sadovy & Domeier, 2005). Hovey and Allen (2000) described the presence of transitional individuals in some populations. However, in these studies, no degenerating vitellogenic oocytes were found within the testicular tissue of male gonads, a necessary criterion for categorizing a species as a diandric protogynous hermaphrodite (Sadovy and Domeier 2005, Table 1). Hovey and Allen (2000) concluded that *P. maculatofasciatus* had no published evidence of sex change and was therefore a gonochorist.

The pooled growth curve for male and female *P. maculatofasciatus* had an asymptotic length of 351.3 mm, a growth coefficient of 0.108 year^{-1} and t_0 of -6.99 years. The highly negative t_0 value suggests that that fish from smaller size classes were not present in the data set. The estimated size at 50% maturity for females was 155 mm and 180 mm for males.

The estimates of k and L_{∞} are likely to be inaccurate due to the value of t_0 being quite large and therefore the empirical estimates for L_{∞} and L_m (Table 3) were used to estimate the L_m/L_{∞} ratio value of 0.331.

The Kelp Bass *Paralabrax clathratus* is a nearshore species ranging from the intertidal zone to 60 m in depth and is distributed from the mouth of the Colombia River (46.247° N, 124.093° W) in Washington in the north to Baja California (30.841° N, 115.284° W) in the south (Erisman & Allen, 2006; Erisman & Allen, 2005; Love et al., 1996). This species is generally associated with benthic rocky habitats (Erisman & Allen, 2006). It reaches a maximum length and age of 720 mm and 33 years, respectively (Love et al., 1996; Mason & Lowe, 2010). Smith and Young (1966), did not find any transitional male *P. clathratus* from their histological studies and concluded that this species was a gonochorist. It has been observed to be an aggregation spawner with aggregations of 200 fish being common throughout the year. The estimated sizes at sexual maturity (L_{50}) are similar for female (226 mm) and male (220 mm) fish (Erisman & Allen, 2006; Love et al., 1996).

The von Bertalanffy growth curve combined for both sexes had an asymptotic length of 569.9, an instantaneous growth coefficient of low 0.06 and highly negative t_0 of -3.50, which suggests that fish from smaller size classes were

not present in the data set, which together with the mean L_m for females and males (223 mm) gives a L_m/L_∞ ratio of 0.231 (Love et al., 1996).

The Barred Sandbass *Paralabrax nebulifer* is a benthic species found in subtidal waters out to depth of 183 m but are generally found living in close proximity (<3 m) to the substrate in habitats such as sand flats and kelp beds (Hovey et al., 2002; Mason & Lowe, 2010). This species distribution ranges from Santa Cruz, California (36.9741° N, 122.0308° W) to Magdalena Bay, Baja California Sur (24.5833° N, 112.0000° W) (Hovey et al., 2002; Love et al., 1996). The diet of *P. nebulifer* consists mainly of small benthic teleosts (Hovey et al., 2002; Love et al., 1996; Mason & Lowe, 2010; Sadovy & Domeier, 2005).

Paralabrax nebulifer can reach a max size of 650 mm and a maximum age of 24 years (Mason & Lowe, 2010). While the males also show many similar traits to those of protogynous hermaphrodites, i.e., the testes contain a central membrane lined ovarian lumen (Sadovy & Domeier, 2005), the histological study of this species showed little to no evidence of transitional individuals and led to the conclusion that *P. nebulifer* was a functional gonochore (Hovey et al., 2002; Love et al., 1996; Sadovy & Domeier, 2005).

The von Bertalanffy growth curve, pooled for both sexes, estimated the L_∞ for *P. nebulifer* as 536.9 mm, k as 0.08 years⁻¹ and t_0 as 2.63 years. Females of *P.*

nebulifer reach L_{50} at 239 mm while males reach L_{50} at 219 mm. Empirical estimates for L_{∞} and L_m (Table 3) and the L_{∞}/L_m was 0.269, therefore the length at maturity was 26.9% of the estimated asymptotic length.

The Gold-spotted Sandbass *Paralabrax auroguttatus* is a high-level carnivore that inhabit rocky reefs between the depths of 25 and 155 m from Isla Cedros (28.1902° N, 115.2126° W) in the north to Cabo San Lucas (22.8905° N, 109.9167° W) in the south and is very abundant throughout the Gulf of California (Pondella et al., 2001). It has a maximum length of 479 mm, maximum weight of 2.7 kg and a maximum age of 24 years (Pondella et al., 2001). The sex ratio (female: male) for *P. auroguttatus* is close to parity (0.84:1) (Pondella et al., 2001). A paucity of data on the reproductive biology of *P. auroguttatus* and the findings of identical length-weight relationships for females and males and uniform distribution of sexes across all age classes has led to the assumption that this species is gonochoristic (Pondella et al., 2001). Note, however, that the gonads of males have not been examined histologically to assess whether or not they contain any ovarian tissue (Pondella et al., 2001; Sadovy & Domeier, 2005; Sadovy & Shapiro, 1987).

The estimated growth rates of females and males were reported to be significantly different, however these estimates are unreliable due to the lack of samples at larger size-classes and the pooled growth rates were calculated

(Pondella et al., 2001). The estimated asymptotic length for both sexes was 474.4 mm, the growth rate (k) was 0.115 year^{-1} and t_0 was 2.094 years (Pondella et al., 2001). Again, the estimates of k and L_∞ for *P. auroguttatus* are likely to be inaccurate due to the value of t_0 being quite large (2.094), the empirical estimates produced for L_∞ (mm) and L_m (mm) (Table 3) and the L_∞/L_m ratio value was 0.353.

Paralabrax albomaculatus (Camotillo) is a Serranid endemic to the Galapagos Islands (0.9538° S , 90.9656° W) which is associated with rocky reefs from the nearshore to 200 m but is most commonly found at a depth of 50 m (Salinas-de-León et al., 2017). It grows to a maximum recorded size of 640 mm, but no information is available on its maximum total weight and age. Although both sexes are represented throughout the size range, males were proportionally more abundant in the larger size classes (Salinas-de-León et al., 2017).

A histological examination of the gonads of 31 male *P. albomaculatus* (Salinas-de-León et al., 2017) found that, although there were no transitional individuals, the testes of most males contained ovarian lumen, a common feature in the *Paralabrax* genus. The lack of transitional males indicates that this species is a functioning gonochore (Y Sadovy & Domeier, 2005; Sadovy & Shapiro, 1987; Salinas-de-León et al., 2017). The mean monthly GSI peaked in the months from November to January with further study needed to determine whether this species

is an aggregation spawner like other members in the *Paralabrax* genus such as *P. clathratus* (Erisman & Allen, 2006; Salinas-de-León et al., 2017).

The lack of juveniles in the biological studies has prevented the estimation of the size at maturity L_{50} . However, the size at 100% maturity (L_{100}) was reported to be 370 mm (Salinas-de-León et al., 2017). Due to the lack of age data on this species, growth rates and the Beverton-Holt life history ratios could not be estimated.

The estimates of k and L_{∞} are likely to be inaccurate due to the value of t_0 being quite large and therefore the estimates for L_{∞} (662.92) and L_m (360.82) and the L_{∞}/L_m ratio value was 0.544.

Table 2: The Von Bertalanffy growth curve parameters, maximum age, and maximum length for gonochoristic species of Serranidae from the sub-families of Anthiadinae and Serraninae. Sources of data are listed in Table 4. Where sex is not shown, no data were available for separate sexes. — = no data available.

Taxonomy		Growth						
Family and Sub-family	Species	Sex	Max size (mm)	Max age	Natural Mortality (M)	L_{∞}	k	t ₀
Serranidae								
Anthiadinae								
	<i>Epinephelides armatus</i>	F	510	19	0.22	561	0.14	0.24
		M	498	13	0.22	558	0.17	0.04
	<i>Othos dentex</i>	F	605	37	0.11	654	0.05	-7.92
		M	570	31	0.11	562	0.10	-3.73
Serraninae								
	<i>Paralabrax maculatofasciatus</i>		450	14	0.23	351.3	0.11	-6.99
	<i>Paralabrax clathratus</i>		720	33	0.13	569.9	0.06	-3.50
	<i>Paralabrax nebulifer</i>		650	24	0.17	536.9	0.08	2.63
	<i>Paralabrax auroguttatus</i>		479	24	0.17	474.9	0.12	2.09
	<i>Paralabrax albomaculatus</i>		640	—	—	—	—	—

Table 3: Summary of empirical estimates of asymptotic length and size at 50% maturity for the seven gonochoristic serranids studies in this literature review. Empirical estimates calculated using equations of; 1) $L_{\infty} \log_{10} L_{\infty} = 0.44 + 0.9841 \log_{10}(L_{max})$; 2)

$$\bar{L}_m \log_{10} L_m = 0.8979 * \log_{10} (L_{\infty}) - 0.0782$$

Taxonomy Family and Sub-family	Species	Sex	Max size (mm)	L_{∞}	\bar{L}_{∞}	\bar{L}_m	L_m / \bar{L}_{∞}
Serranidae							
Anthiadinae	<i>Epinephelides armatus</i>	F	510	561	530.18	295.23	0.577
		M	498	558	517.9	289.08	0.494
	<i>Othos dentex</i>	F	605	654	627.23	343.33	0.55
		M	570	562	591.5	325.71	0.602
Serraninae							
	<i>Paralabrax maculatofasciatus</i>		450	351.3	468.73	264.32	0.331
	<i>Paralabrax clathratus</i>		720	569.9	744.39	400.4	0.231
	<i>Paralabrax nebulifer</i>		650	536.9	673.11	365.8	0.269
	<i>Paralabrax auroguttatus</i>		479	474.9	498.45	279.31	0.353
	<i>Paralabrax albomaculatus</i>		640	—	662.92	360.82	0.544

Table 4: Summary of the size at maturity and estimated natural mortality of females and males and Beverton Holt life-history ratios for gonochoristic species of Serranidae from the sub-families of Anthiadinae and Serraninae.

Taxonomy Family	Species	Sex	Reproduction				Source
			L_{50}	L_{95}	L_{50}/L_{∞}	M/k	
Serranidae							
Anthiadinae	<i>Epinephelides armatus</i>	F	306	357	0.545	1.57	Moore et al (2007)
		M	256	317	0.459	1.29	
	<i>Othos dentex</i>	F	345	412	0.528	2.25	French et al (2014)
		M	356	408	0.633	1.122	
Serraninae							
	<i>Paralabrax maculatofasciatus</i>		155	180	0.49	2.126	Allen et al (1995)
	<i>Paralabrax clathratus</i>		172	142	0.302	2.1	Milton et al (1996)
	<i>Paralabrax nebulifer</i>		181	177	0.289	1.511	
	<i>Paralabrax auroguttatus</i>		176	178	0.375	1.511	Pondella et al (2001)
	<i>Paralabrax albomaculatus</i>		370 (L_{100})	350	—	—	Salinas-de-León et al (2017)

6.6 Comparisons of reproductive biology

Although the *Paralabrax* genus, and two gonochorists from the southern hemisphere (*E. armatus* and *O. dentex*), share the same reproductive strategy of gonochorism, the evolution of gonochorism probably differs between these two groups (Allen et al., 1995; ; French et al., 2014; Moore et al., 2007). In the *Paralabrax*, adult males contain a central membrane lined ovarian lumen within their testes (Allen et al., 1995; Sadovy & Domeier, 2005; Salinas-de-León et al., 2017), which is thought to be remnant from a juvenile bisexual stage in the *Paralabrax* (Sadovy & Domeier, 2005). In contrast, *E. armatus* and *O. dentex* do not contain this central membrane lined ‘ovarian’ lumen, and instead possess a central sperm duct (French et al., 2014; Moore et al., 2007).

These differences in internal structure of the testes of males are derived from the ancestors of the associated species (Erisman & Hastings, 2011b; French et al., 2014). The *Paralabrax* genus along with the majority of Serranid species are thought to have evolved from an ancestor that utilized protogynous hermaphroditism (Erisman & Hastings, 2011a; French et al., 2014). However, *E. armatus* and *O. dentex* do not exhibit these ancestral reproductive traits and it is hypothesized that the ancestor of these species was likely to be an offshoot(s) of a serranid that had not evolved protogyny as a reproductive strategy (Erisman & Hastings, 2011b; French et al., 2014).

Fish spawning behaviour is an important component of reproduction and some species form spawning aggregations where large numbers of fish gather for a short period of time for mating and reproduction (Allen et al., 1995; Sadovy, 2016; Erisman et al., 2017; Erisman & Allen, 2006). Aggregation spawning is a method of spawning that maximizes the fertilization rate by increasing the rate of encounters between males and females in the aggregation (Sadovy, 2016; Erisman et al., 2017). Species that utilize aggregation spawning are more prone to over-exploitation as these aggregations may be predictable in location and time and are readily targeted by fishers. Management strategies, such as closed seasons and spatial closures, may be required to manage exploited populations of aggregation spawners successfully (Sadovy, 2016; Erisman & Allen, 2006; Erisman et al., 2017).

Paralabrax maculatofasciatus, *P. clathratus*, *P. nebulifer*, *P. auroguttatus*, and *P. albomaculatus* are all aggregation spawners (it is not known whether the four data deficient species utilize this strategy) for reproduction with great success (Pondella et al., 2001; Salinas-de-León et al., 2017). However, with the technological advances in the fishing methods and the vessels used in commercial and industrial fishing there has been steep declines in the populations in these species with significant impact on *P. clathratus* and *P. albomaculatus* populations (Erisman & Allen, 2006; Love et al., 1996; Sadovy & Domeier, 2005). Very marked declines followed the end of World War II when

species such as *P. clathratus* experienced steep declines in populations due in part to the fishing of aggregations that were not fished beforehand (Erisman & Allen, 2006; Love et al., 1996). These commercial and industrial fishing practices in California were banned in 1953, with only recreational fishing being permitted for a number of species (Erisman & Allen, 2006; Love et al., 1996). *Paralabrax albomaculatus* is an exception, as it is fished by artisanal fishers in the Galapagos, with 1200 fishers being permitted to operate in a year (Salinas-de-León et al., 2017).

Monogamous pair spawning is where a male and a female individual restrict most spawnings to the same partner, a strategy that has been observed for *O. dentex* and is hypothesized as the strategy utilized by *E. armatus* (French et al., 2014; Moore et al., 2007). Monogamy involves strategies including aggregating and then breaking off into pairs, such as occurs in aggregations of the Bigeye Trevally *Caranx sexfasciatus* (Sadovy & Colin, 2012) or existing in lone pairs such as found in the Oval Butterflyfish *Chaetodon lunulatus* (Nowicki et al., 2018). It is not known whether *O. dentex* aggregates before spawning although it is unlikely due to individuals of this species being widely dispersed along the south coast of Western Australia and it is not very abundant in this coast or along the west coast (French et al., 2014). Paired spawning has the advantages of increasing chances of fertilizations, bi-parental care, mate

guarding and cooperative defenses for valuable resources such as food and shelter (Nowicki et al., 2018; Sadovy & Colin, 2012).

6.7 Fisheries management and conservation

6.7.1 Management of Southwest gonochoristic serranids

Both *E. armatus* and *O. dentex* are targeted by recreational fishers and are caught as bycatch by commercial line fishers (DoF, 2016; Smallwood et al., 2013). In late 2007 and early 2010 a recovery program was implemented by Department of Fisheries due to an assessment by that showed that key demersal indicator species Dhufish *Glaucosoma herbraicum* and Pink Snapper *Chrysophrys auratus* were being overfished (Wise et al, 2007). A very recent stock assessment on the West Coast Demersal Scalefish Resource (WCDSR) for these two indicator species demonstrated that in 2020, commercial catches for *G. herbraicum* and *C. auratus* were below the original catch recovery benchmark and were deemed to be acceptable (Fairclough et al., 2021). However, in 2017/18. the estimated recreational catch range (\pm 95% Confidence Intervals [CI]) was close to or above the catch recovery rate for *G. herbraicum* and was deemed unacceptable. Since 2011/12 the catch range (\pm 95%CI) for *Chrysophrys auratus* was also close to or above the catch recovery rate and also deemed unacceptable (Fairclough et al., 2021). Due to these unacceptable catch levels, it has been suggested that the catch rate for these indicator species be lowered by 50% through reduced bag

limits for demersal species, which would then flow on to *E. armatus* on the west coast (Fairclough et al., 2021).

The coastline along Western Australia is divided into four bioregions for fisheries management; the Gascoyne Coast (GCB), the North Coast (NCB), the South Coast (SCB) and the West Coast (WCB) (Gaughan & Santoro, 2021; Smallwood et al., 2013), with *Epinephelides armatus* and *O. dentex* found in the latter two, temperate, bioregions (French et al., 2014; Moore et al., 2007; Smallwood et al., 2013). Both species are classed as demersal species under fisheries management in Western Australia (DoF, 2012; Fairclough et al., 2021; Smallwood et al., 2013).

Recreational fishing and spearfishing for these two species is generally conducted offshore from boats, although they can be caught from shore (DPIRD, 2021; Smallwood et al., 2013). To fish for these species from a vessel a recreational boat fishing license is required (DPIRD, 2021). The minimum legal limit (MLL) for retention by recreational and commercial fishers of *E. armatus* is 300 mm while *O. dentex* does not have a MLL for retention (Table 4) (Smallwood et al., 2013). Individual bag limits are not specified for this species, they are instead apart of a mixed demersal daily bag limit which is two for the West coast and five for the South coast (DPIRD, 2021). In the WCB there is a closed season to the demersal fishery from the 15th of October to 15th (Recreational fishers

only) of December to protect the spawning stock of the main indicator species – Dhufish *Glaucosoma herbraicum* and Pink Snapper *Chrysophrys auratus* (Neville, 2009; Smallwood et al., 2013; Wise et al., 2007) (Table 4). Both *E. armatus* and *O. dentex* are retained as bycatch by commercial fishers in Western Australia (Smallwood et al., 2013). A status of the fisheries report was released in 2021 that showed *E. armatus*. The target for the total catch of demersal species on the south coast from the southern demersal gillnet and longline fishery is 725 – 1095 tonnes. This catch is dominated by four species of elasmobranch – Gummy Shark *Mustelus antarcticus*, Dusky Shark *Carcharhinus obscurus*, Whiskery Shark *Furgaleus macki* and Sandbar Shark *Carcharhinus plumbeus* (DoF, 2016). Although these are the key species, by-catch is often caught and retained for sale by commercial fisheries on the south coast (DoF, 2016).

The *E. armatus* catches for 2019/20 for commercial fishes was 5 tonnes, 3 tonnes for charter operators and estimated 20 tonnes for recreational fishers (71% of the total *E. armatus* catch) (Newman et al., 2021). No commercial or charter catches were reported for *O. dentex* in 2018/19 and the estimated catch of recreational fishers was 6 tonnes (Newman et al., 2021).

6.7.2 Management and conservation of *Paralabrax* species

Paralabrax clathratus, *P. maculatofasciatus* and *P. nebulifer* are important local fishery resources in California and the Channel Islands in the eastern

Pacific (Allen et al., 1995; Love et al., 1996). Following a massive increase in fishing pressure after World War II the major populations of *P. clathratus* and *P. nebulifer* declined steeply, which forced the closure of commercial fishing for *P. clathratus*, *P. maculatofasciatus* and *P. nebulifer* in 1953 and still no longer operates (Allen et al., 1995; Jarvis et al., 2010; Love et al., 1996).

The IUCN red list of threatened species shows that *P. clathratus*, *P. maculatofasciatus* and *P. nebulifer* are all of Least Concern while their trend is unknown (Iwamoto et al., 2010; Smith-vaniz et al., 2010a; Smith-Vaniz et al., 2010) (Table 5). However, *P. clathratus* spawning aggregations are more predictable than *P. maculatofasciatus* and *P. nebulifer*, which means that it is even more susceptible than the other two species (Allen et al., 1995; Erisman et al., 2017; Erisman & Allen, 2006; Love et al., 1996).

Currently, the Californian fishery for these three *Paralabrax* species is open to recreational fishers who have purchased a sport fishing license from the California Department of Fish and Wildlife (California Department of Fish and Wildlife, 2022). These three species are collectively classed as rock bass by the California Department of Fish and Wildlife and the same rules and regulations are applied to each species (California Department of Fish and Wildlife, 2022). Recreational fishers have a combined mixed Rock bass species bag limit of 5

fish, a MLL of 355.6 mm, no seasonal closures and they must record all captures in a logbook (California Department of Fish and Wildlife, 2022) (Table 4).

While a combined MLL for the three species could be a concern as it may not encompass all species equally, the size at 50% maturity for *P. maculatofasciatus*, *P. clathratus*, *P. nebulifer* and *P. auroguttatus* are well below the MLL which indicates the MLL should be effective for conserving the spawning stock for these species (Table 3 & 4) (Allen et al., 1995; California Department of Fish and Wildlife, 2022; Erisman & Allen, 2006; Love et al., 1996; Semmens & Parnell, 2014).

Although *P. auroguttatus* is not specifically listed by the California Department of Fish and Wildlife, it can also be caught in this jurisdiction and would fall under the same rules and regulations as the other species. Very few biological data are available for *P. auroguttatus*, so it is difficult to determine the effectiveness of the MLL in this region (California Department of Fish and Wildlife, 2022; Pondella et al., 2001).

Paralabrax albomaculatus within the Galapagos marine reserve is managed by the Galapagos National Park Directorate (Castrejon et al., 2014; Ramirez-Gonzalez et al., 2019; Reynolds, 2018; Salinas-de-León et al., 2017). Within this reserve only an artisanal fishery is allowed to operate (Salinas-de-León et al., 2017). A total of 1,200 artisanal fishers were registered with

Galapagos National Park Directorate in 2016 (Salinas-de-León et al., 2017). Few rules and regulations seem to apply to this species in the Galapagos – there is no MLL, no catch limit and no seasonal closure for this species, even though it is listed as Endangered with a decreasing population on the IUCN red list (Table 5) (Castrejon et al., 2014; Ramirez-Gonzalez et al., 2019; Reynolds, 2018; Salinas-de-León et al., 2017).

Paralabrax albomaculatus is also an aggregation spawner making this species susceptible to overfishing by fishers targeting the breeding stock (Erisman et al., 2017; Salinas-de-León et al., 2017). A number of rules and regulations have been suggested to arrest this decreasing trend, including a MLL of 370 mm, a maximum legal limit of 520 mm and a seasonal closure of November to January to protect the spawning aggregations (Castrejon et al., 2014; Ramirez-Gonzalez et al., 2019; Reynolds, 2018; Salinas-de-León et al., 2017), but these recommendations have not been implemented. *Paralabrax albomaculatus* had not information on the length at 50% maturity, therefore, the empirical estimate for length at maturity (360.82) was calculated, which although is below the suggested MLL, this gap in the data needs further investigation (Froese & Binohlan, 2003; Salinas-de-León et al., 2017). Further research and management of *P. albomaculatus* is needed to ensure that the fishery for this species is sustainable for future years (Castrejon et al., 2014; Ramirez-Gonzalez et al., 2019; Reynolds, 2018; Salinas-de-León et al., 2017).

Table 4: Fisheries and their management for gonochoristic Serranids (*Epinephelides armatus*, *Othos dentex* and the *Paralabrax* genus

Species	Management Agency/Fishing sectors	Total catch/ bag limit	Aggregation spawner	Seasonal closures	Minimum Legal Limit (length mm)
Species on the west coast of Australia	DPIRD	Recreational/ Commercial (By-catch)			
<i>E. armatus</i>	Commercial	West coast demersal scalefish TAC < 465 ton (Commercial) – south coast	No	No commercial closure	300 mm
	Recreational	Bag limit west coast: 2 per fisher South coast: 3 per fisher	No	15 th of October – 15 th of December	300 mm
<i>O. dentex</i>	Recreational/ Commercial (By-catch)				
	Commercial	West coast demersal scalefish TAC < 465 ton (Commercial)	No	No commercial closure	No size limit applies to this species
	Recreational	South Coast Bag limit west coast: 2 per fisher 5 per fisher in all other regions	No	15 th of October – 15 th of December	No size limit
<i>Paralabrax</i> species in the eastern Pacific California					
<i>P. auroguttatus</i> +	Recreational				
<i>P. clathratus</i>	Recreational	Bag limit: 5 combined species of <i>Paralabrax</i>	Yes	No seasonal closure	355.6
<i>P. maculatofasciatus</i>	Recreational	Bag limit: 5 combined species of <i>Paralabrax</i>	Yes	No seasonal closure	355.6
<i>P. nebulifer</i>	Recreational	Bag limit: 5 combined species of <i>Paralabrax</i>	Yes	No seasonal closure	355.6

Galapagos Islands					
<i>P. albomaculatus</i>	Artisanal fishery	No catch limit	Yes	No seasonal closure	None

Table 5: Conservation status of Serranidae species on the IUCN list. DD = Data Deficient; LC = Least common; VU = vulnerable; NT = near threatened; EN = endangered (IUCN, 2021).

Family	Sub-family	Species	IUCN Category	Trend	Source
Serranidae	Anthiinae	<i>Anthias regalis</i>	VU	Unspecified	Roberts, 1996
		<i>Epinephelides armatus</i>	NT	Unknown	Cornish, 2004
		<i>Plectranthias chungchowensis</i>	VU	Unspecified	
	Grammistinae	<i>Rypticus courtenayi</i>	VU	Unknown	Smith-vaniz et al., 2010b
	Serraninae	<i>Cratinus agassizii</i>	NT	Unknown	
		<i>Hypoplectrus maya</i>	EN	Decreasing	Moran & Puebla, 2020
		<i>Paralabrax albomaculatus</i>	EN	Decreasing	Robertson et al., 2010
		<i>Paralabrax auroguttatus</i>	DD	Unknown	Findley et al., 2010
		<i>Paralabrax clathratus</i>	LC	Unknown	Iwamoto et al., 2010
		<i>Paralabrax maculatofasciatus</i>	LC	Unknown	Smith-vaniz et al., 2010a
		<i>Paralabrax nebulifer</i>	LC	Unknown	Smith-Vaniz et al., 2010
		<i>Serranus dewegeri</i>	NT	Unspecified	Acero, 1996
		<i>Serranus socorroensis</i>	VU	Unknown	Smith-vaniz et al., 2010c
	Total	13 species	DD LC VU = 4; NT = 3. EN = 2	Unknown = 8; Unspecified = 3; Decreasing = 2	
Epinephelidae		<i>Epinephelus aeneus</i>	NT	Decreasing	Pollard, Francour, et al., 2018
		<i>Epinephelus akaara</i>	EN	Decreasing	Sadovy et al., 2018
		<i>Epinephelus albomarginatus</i>	VU	Decreasing	Fennessy, 2018
		<i>Epinephelus andersoni</i>	NT	Decreasing	
		<i>Epinephelus daemeli</i>	NT	Unknown	
		<i>Epinephelus goreensis</i>	NT	Decreasing	Pollard & Rocha, 2018
		<i>Epinephelus itajara</i>	VU	Decreasing	Bertoncini, et al., 2018

	<i>Epinephelus morio</i>	VU	Decreasing	Thierry Brule et al., 2018
	<i>Epinephelus polyphemadion</i>	VU	Decreasing	Rhodes, Choat, et al., 2018
	<i>Epinephelus striatus</i>	CR	Decreasing	Sadovy et al., 2018
	<i>Epinephelus bruneus</i>	VU	Decreasing	To et al., 2018
	<i>Epinephelus fuscoguttatus</i>	VU	Decreasing	Rhodes, et al., 2018
	<i>Epinephelus goreensis</i>	NT	Decreasing	Pollard & Rocha, 2018
	<i>Hyphorhodus acanthistius</i>	VU	Decreasing	Erisman & Craig, 2018
	<i>Hyphorhodus ergastularius</i>	NT	Decreasing	Pollard, 2018
	<i>Hyphorhodus flavolimbatus</i>	VU	Decreasing	Padovani-ferreira et al., 2018
	<i>Hyphorhodus nigrinus</i>	NT	Unknown	Aguilar-perera et al., 2018
	<i>Hyphorhodus niveatus</i>	VU	Decreasing	Bertoncini, Ferreira, et al., 2018
	<i>Mycteroperca bonaci</i>	NT	Decreasing	Padovani-Ferreira, , et al., 2018
	<i>Mycteroperca fusca</i>	VU	Decreasing	Pollard, et al., 2018
	<i>Mycteroperca interstitialis</i>	VU	Decreasing	Padovani-Ferreira, et al, 2018
	<i>Mycteroperca jordani</i>	EN	Decreasing	Erisman & Craig, 2018
	<i>Mycteroperca microlepis</i>	VU	Decreasing	Koenig et al., 2018
	<i>Mycteroperca venenosa</i>	NT	Decreasing	Brule & Ferreira, 2018
	<i>Plectropomus areolatus</i>	VU	Decreasing	Rhodes, 2018
	<i>Plectropomus marisrubri</i>	VU	Decreasing	Choat et al., 2018
Total	26 species. VU = 14 CR = 1 EN = 2 NT = 9		Unknown = 2; Decreasing = 24	

6.8 Conclusion

Serranids utilize a wide range of reproductive strategies except protandrous hermaphroditism (i.e., changing sex from male to female). In order

to establish the reproductive strategy of a species and determine conclusively whether a species is a hermaphrodite or gonochorist, histological evidence for individuals from a wide range of different sizes is required. This provides the basis for investigating whether ovarian tissue is present within the testes of male fish and assessing the four other criteria defined by Sadovy and Shapiro (1987), including the sex ratio across the full-size distribution of the species. Of these five criteria, the observation of transitional individuals from histological sections of gonads is the most conclusive evidence for determining that a species is hermaphroditic.

Gonochorism is a rare reproductive strategy in the Serranidae, with only seven species (*E. armatus*, *O. dentex*, *P. maculatofasciatus*, *P. clathratus*, *P. nebulifer*, *P. auroguttatus* and *P. albomaculatus*) out of 495 species utilizing this strategy, although there are a number of serranid species yet to be studied. However, in the two south-western Australian gonochorists (*E. armatus* and *O. dentex*), this strategy appears to have evolved from a gonochoristic ancestor, while from the Eastern Pacific the 5 *Paralabrax* species considered in this review, gonochorism appears to have evolved from a protogynous hermaphrodite ancestor. This conclusion is based on the presence of a central membrane lined 'ovarian' lumen in the male testes of the *Paralabrax* species, due to juveniles having a bisexual gonad structure. Another key difference between the two species groups is that *E. armatus* and *O. dentex* in south-western Australia are

hypothesized to be pair spawners, whereas the *Paralabrax* species are aggregation spawners, making them more susceptible to overexploitation.

The von Bertalanffy growth estimates for all species, except for *E. armatus*, had large t_0 values making the published estimates for L_∞ and k unreliable. Therefore, further research is required for *O. dentex* and the *Paralabrax* species in order to attain length at age data from particularly smaller fish so that the t_0 values are biologically more realistic. *Epinephelides armatus* had reliable estimates of t_0 and hence the life history ratios for this species were calculated which showed that the unfished population had a higher proportion of immature than mature individuals in the population. The empirical estimates of L_∞ and L_m and the life history ratios for this species were also calculated from Binohlan and Froese (2003).

Management of the south-western Australian gonochores includes a range of measures for the commercial and recreational fishing sectors. These include a minimum legal length (MLL) for retention, a total allowable catch for commercial fishing and bag limits for recreational fishing and a three-month temporal closure (September to November) to commercial and recreational fishing for all demersal species on the west coast during the peak spawning season for the two main indicator species (Dhufish and Pink Snapper).

Paralabrax maculatofasciatus, *P. clathratus*, *P. nebulifer* and *P. auroguttatus* are

only fished recreationally in the waters off the western United States, with a license required to fish, a generic MLL and a bag limit in place, but no temporal closures for these aggregation spawners. *Paralabrax albomaculatus* in the Galapagos has an associated artisanal fishery but with little or no management. Further management of this endangered species is required with suggested MLL of 370 mm and a temporal closure during the peak breeding season to protect its spawning aggregations.

In conclusion, although there have been a number of studies conducted on gonochoristic serranids, this review has highlighted the gaps that are present in the available biological information that limit the assessment of their stocks. Further detailed studies of growth and reproduction are needed that include very small individuals are needed to determine more accurate estimates of the growth parameters and the size at 50% maturity. This would better inform management on some of the current regulations, particularly the minimum legal size for retention and allow yield-per-recruit models to be developed and the spawning potential ration to be estimated.

6.9 References

- Acero, A. (1996). *Serranus dewegeri*, Meo Viejo. The IUCN red list of threatened species, 8235. <http://dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T39304A10187156.en%0D>
- Aguilar-perera, A., Padovani-Ferreira, B., & Bertoncini, A. (2018). *Hyporthodus nigritus*, Warsaw Grouper. *The IUCN Red List of Threatened Species*. <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T7860A46909320.en>.
- Akhir, M. F., Pattiaratchi, C., & Meuleners, M. (2020). Dynamics and seasonality of the Leeuwin Current and the surrounding counter-current system in the region south of Western Australia. *Journal of Marine Science and Engineering*, 8(8), 1–20.
- Allen, L. G. ., Hovey, T. E., Love, M. S., & Smith, J. T. W. (1995). The life history of the Spotted Sand Bass (*Paralabrax maculatofasciatus*) within the Southern California Bight. 36.
- Andrews, A. H., Laman, E. A., Bennett, T., Jones, E., & Cailliet, G. M. (2005). Age and growth of Spotted Sand Bass, *Paralabrax maculatofasciatus*, in Bahia de Los Angeles, Baja California, Mexico, with age validation using otolith edge analysis. *Bulletin, Southern California Academy of Sciences*, 104(1), 14–25.
- Bertoncini, A. A., Aguilar-Perera, A., Barreiros, J., Craig, M. T., Ferreira, B. T., & Koenig, C. (2018). *Epinephelus itajara*, Atlantic Goliath Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T44683A46915269.en>
- Bertoncini, A. A., Ferreira, B. T., & Aguilar-perera, A. (2018). *Hyporthodus niveatus*, Snowy Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T7861A46909546.en>
- Beverton, R. J. H., & Holt, S. J. (1959). A review of the life-spans and mortality rates of fish in nature, and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquia on Ageing*, 142–180.
- Brule, T., & Ferreira, B. (2018). *Mycteroperca venenosa*, Yellowfin Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T44683A46915269.en>
- Brule, Thierry, Bertoncini, A. A., Ferreira, B., Aguilar-Perera, A., & Sosa-Cordero, E. (2018). *Epinephelus morio*. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T44681A46914636.en%0D>
- California Department of Fish and Wildlife. (2022). 2021-2022 California Ocean sport fishing regulations. <https://wildlife.ca.gov/Fishing/Ocean>
- Campbell, N. A., & Phillips, B. F. (1972). The von bertalanffy growth curve and its application to capture - recapture data in fisheries biology. *ICES Journal of Marine Science*, 34(2), 295–299.
- Caputi, N., Feng, M., Denham, A., Simon de, L., Penn, J., Slawinski, D., Pearce, A., & How, J. (2018). Optimizing an oceanographic-larval model for assessment of the puerulus settlement of the Western Rock Lobster, *Panulirus cygnus*, in Western Australia. *Bulletin of Marine Science*, 94(3), 775–800.
- Castrejon, M., Defeo, O., Reck, G., & Charles, A. (2014). Fishery science in Galapagos: from a resource-focused to a social–ecological systems approach. *The Galapagos Marine Reserve: A Dynamic Social-Ecological System, January 2015*, 23–60. <https://doi.org/10.1007/978-3-319-02769-2>

- Choat, J. H., Gaspar, A. L., Samoilys, M., & Myers, R. (2018). *Plectropomus marisrubri*. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T118360372A118360410.en>
- Coulson, P. G., Norriss, J. V., Jackson, G., & Fairclough, D. V. (2019). Reproductive characteristics of the fishery important temperate demersal berycid *Centroberyx gerrardi* indicate greater reproductive output in regions of upwelling. *Fisheries Management and Ecology*, 26(3), 236–248.
- Craig, M. T., & Hastings, P. A. (2007). A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. *Ichthyological Research*, 54(1), 1–17.
- Department of Fisheries. (2012). A resourced-based management approach for recreational fishing in Western Australia 2012–2017. *Fisheries Management Paper No. 252*, 252, 50.
- Department of Fisheries. (2016). Major commercial fisheries. <https://www.fish.wa.gov.au/Fishing-and-Aquaculture/Commercial-Fishing/Commercial-Fishing-Management/Pages/Major-Commercial-Fisheries.aspx>
- Department of Primary Industries and Regional Development. (2021). Recreational fishing guide 2021. 2–64. <https://www.fish.wa.gov.au/About-Us/Publications/Recreational-Fishing/Pages/Recreational-Fishing-Guides.aspx>
- Eastman, A. (2001). Age, growth and reproductive biology of the Breaksea Cod -*Epinephelides armatus*. Honours Thesis, Curtin University of Technology.
- Erisman, B. E., & Allen, L. G. (2005). Color patterns and associated behaviors in the Kelp Bass, *Paralabrax clathratus* (Teleostei: Serranidae). *Bulletin, Southern California Academy of Sciences*, 104(2), 45–62.
- Erisman, B. E., & Allen, L. G. (2006). Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, U.S.A. *Journal of Fish Biology*, 68(1), 157–184.
- Erisman, B. E., & Craig, M. T. (2018). *Hyporthodus acanthistius*, Rooster Hind. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T132730A100569342.en>
- Erisman, B. E., & Hastings, P. A. (2011). Evolutionary transitions in the sexual patterns of fishes: Insights from a phylogenetic analysis of the seabasses (Teleostei: Serranidae). *Copeia*, 3, 357–364.
- Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., & Nemeth, R. S. (2017). Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries*, 18(1), 128–144.
- Erisman, Brad E., & Craig, M. T. (2018). *Mycteroperca jordani*, Gulf Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T14049A100466315.en>
- Fairclough, D. V. (2016). Similar cryptic behaviour during the early juvenile phase of two unrelated reef fishes: *Epinephelides armatus* and *Bodianus frenchii*. *Marine and Freshwater Behaviour and Physiology*, 49(2), 109–117.
- Fairclough, D. V., Hesp, A. S., Denham, A., Fisher, E., Marks, R., Ryan, K. L., Lek, E., Allen, R., & Crisafulli, B. M. (2021). 2021 assessment of the status of the West Coast Demersal Scalefish Resource. *Fisheries Research Report No. 316* (Issue 316).

- Fennessy, S. (2018). *Epinephelus albomarginatus*, White-edged Rockcod. *The IUCN Red List of Threatened Species*, 8235. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T44677A100460097.en%0ACopyright:>
- Findley, L., Lea, B., Allen, G., & Edgar, G. (2010). *Paralabrax auroguttatus*. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183712A8162678.en>
- French, B., Platell, M. E., Clarke, K. R., & Potter, I. C. (2017). Optimization of foraging and diet by the piscivorous *Othos dentex* (Serranidae). *Journal of Fish Biology*, 90(5), 1823–1841.
- French, B., Potter, I. C., Hesp, S. A., Coulson, P. G., & Hall, N. G. (2014). Biology of the harlequin fish *Othos dentex* (Serranidae), with particular emphasis on sexual pattern and other reproductive characteristics. *Journal of Fish Biology*, 84(1), 106–132. <https://doi.org/10.1111/jfb.12258>
- Frisch, A. J., Cameron, D. S., Pratchett, M. S., Williamson, D. H., Williams, A. J., Reynolds, A. D., Hoey, A. S., Rizzari, J. R., Evans, L., Kerrigan, B., Muldoon, G., Welch, D. J., & Hobbs, J. P. A. (2016). Key aspects of the biology, fisheries and management of Coral grouper. *Reviews in Fish Biology and Fisheries*, 26(3), 303–325.
- Froese, R., & Pauly, D. (2022a). Fish Base: *Paralabrax callaensis* (Starks, 1906). <https://www.marinespecies.org/aphia.php?p=taxdetails&id=282053>
- Froese, R., & Pauly, D. (2022b). Fish Base: *Paralabrax Dewegeri* (Metzelaar, 1919). <https://www.marinespecies.org/aphia.php?p=taxdetails&id=282055>
- Froese, R., & Pauly, D. (2022c). FishBase: *Paralabrax humeralis* (Valenciennes, 1828). <https://www.marinespecies.org/aphia.php?p=taxdetails&id=282056>
- Froese, R., & Pauly, D. (2022d). FishBase: *Paralabrax loro* (Walford, 1936). <https://www.marinespecies.org/aphia.php?p=taxdetails&id=282057>
- Froese, Rainer, & Binohlan, C. (2003). Simple methods to obtain preliminary growth estimates for fishes. *Journal of Applied Ichthyology*, 19(6), 376–379.
- Gaughan, D. J., & Santoro, K. (2021). Status reports of the fisheries and aquatic resources of Western Australia 2019/20: State of the fisheries. *Department of Primary Industries and Regional Development, Western Australia*.
- Gemmell, N. J., Todd, E. V., Goikoetxea, A., Ortega-Recalde, O., & Hore, T. A. (2019). Natural sex change in fish. In *Current Topics in Developmental Biology* (1st ed., Vol. 134). Elsevier Inc.
- Godwin, J. (2011). Social and reproductive behaviors: Socially Controlled Sex Change in Fishes. In *Encyclopedia of Fish Physiology* (Vol. 1). Elsevier Inc.
- Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. In *Fishery Bulletin* (Vol. 82, pp. 898–902).
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., & Prince, J. (2015a). A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES Journal of Marine Science*, 72(1), 204–216.
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., & Prince, J. (2015b). Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES Journal of Marine Science*, 72(1), 204–216. I

- Hovey, C. B., Allen, L. G., & Hovey, T. E. (2002). The reproductive pattern of Barred Sand Bass (*Paralabrax nebulifer*) from southern California. *California Cooperative Oceanic Fisheries Investigations Reports*, 43(May), 174–181.
- Hovey, T. E., & Allen, L. G. (2000). Reproductive patterns of six populations of the Spotted Sand Bass, *Paralabrax maculatofasciatus*, from southern and Baja California. *Copeia*, 2000(2), 459–468.
- How, J. (2013). The Biology and Ecology of Epinephelidae Species and Their Implications to Fisheries Management. Honours Thesis, Edith Cowan University.
- IUCN. (2021). *The IUCN Red List of Threatened Species*. <https://www.iucnredlist.org>
- Iwamoto, T., Smith-Vaniz, B., & Robertson, R. (2010). *Paralabrax clathratus*. *The IUCN Red List of Threatened Species*. <https://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183858A8189690.en>.
- Jarvis, E. T., Linardich, C., & Valle, C. F. (2010). Spawning-related movements of Barred Sand Bass, *Paralabrax nebulifer*, in southern California: interpretations from two decades of historical tag and recapture data. *Bulletin, Southern California Academy of Sciences*, 109(3), 123–143.
- Khan, S., & Afzal Khan, M. (2014). Importance of age and growth studies in fisheries management. *Proceedings of the National Seminar "Next Generation Sciences: Vision 2020 and Beyond"*, "October, 194–201.
- Koenig, C., Bertoncini, A. A., & Ferreira, B. T. (2018). *Mycteroperca microlepis*, Gag. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T14050A46910927.en>
- Love, M. S., Brooks, A., Busatto, D., Stephens, J., & Gregory, P. A. (1996). Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight. *Fishery Bulletin*, 94(3), 472–481.
- Ma, K. Y., Craig, M. T., Choat, J. H., & van Herwerden, L. (2016). The historical biogeography of groupers: Clade diversification patterns and processes. *Molecular Phylogenetics and Evolution*, 100(February), 21–30.
- Mason, T. J., & Lowe, C. G. (2010). Home range, habitat use, and site fidelity of barred sand bass within a southern California marine protected area. *Fisheries Research*, 106(1), 93–101.
- Moore, S. (2005). *The biology of the Breaksea Cod Epinephelides armatus* in coastal marine waters of south-west Australia Submitted for the Honours Degree of Murdoch University June 2005. June.
- Moore, S., Hesp, A., Hall, N., & Potter, I. (2007). Age and size compositions, growth and reproductive biology of the breaksea cod *Epinephelides armatus*, a gonochoristic serranid. *Journal of Fish Biology*, 71(5), 1407–1429.
- Moran, B., & Puebla, O. (2020). *Hypoplectrus maya*, Maya Hamlet. *The IUCN Red List of Threatened Species*. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T16759101A86415416.en>
- Neville, P. J. (2009). A review of management arrangements for the recreational fishery for demersal scalefish in the west coast bioregion. *Department of Fisheries, Western Australia*. http://www.fish.wa.gov.au/Documents/occasional_publications/fop065.pdf

- Newman, S.J., Wise, B.S., Santoro, K.G. and Gaughan, D.J. (eds). 2021. Status reports of the fisheries and aquatic resources of Western Australia 2020/21: the state of the fisheries. Department of Primary Industries and Regional Development, Western Australia.
- Nowicki, J. P., Walker, S. P. W., Coker, D. J., Hoey, A. S., Nicolet, K. J., & Pratchett, M. S. (2018). Pair bond endurance promotes cooperative food defense and inhibits conflict in coral reef butterflyfish. *Scientific Reports*, 8(1), 1–11.
- Padovani-ferreira, B., Bertoncini, A. A., & Aguilar-perera, A. (2018). *Hyporthodus flavolimbatus*, Yellowedge Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T64400A46915591.en>
- Padovani-Ferreira, B., Bertoncini, A. A., & Craig, M. T. (2018). *Mycteroperca interstitialis*, Yellowmouth Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T64410A46915949.en>
- Padovani-Ferreira, B., Bertoncini, A. A., Pollard, D. ., Erisman, B. E., Sosa-Cordero, E., Rocha, L. A., Aguilar-perera, A., & Brule, T. (2018). *Mycteroperca bonaci*, Black Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T64409A42691809.en>
- Pet, J. S., Mous, P. J., Muljadi, A. H., Sadovy, Y. J., & Squire, L. (2005). Aggregations of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* (groupers, Serranidae) in the Komodo National Park, Indonesia: Monitoring and implications for management. *Environmental Biology of Fishes*, 74(2), 209–218.
- Platell, M. E., Hesp, S. A., Cossington, S. M., Lek, E., Moore, S. E., & Potter, I. C. (2010). Influence of selected factors on the dietary compositions of three targeted and co-occurring temperate species of reef fishes: Implications for food partitioning. *Journal of Fish Biology*, 76(6), 1255–1276.
- Pollard, D. . (2018). *Hyporthodus ergastularius*, Banded Rockcod. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T132795A100569671.en>
- Pollard, D. ., Afonso, P., & Barreiros, J. (2018). *Mycteroperca fusca*, Island Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T64409A42691809.en>
- Pollard, D. ., Francour, P., & Fennessy, S. (2018). *Epinephelus aeneus*, White Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T132722A100459597.en>en%0ACopyright:
- Pollard, D. ., & Rocha, L. A. (2018). *Epinephelus goreensis*, Dungat Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T132765A100545387.en>en%0ACopyright:
- Pondella, D. J., Allen, L. G., Rosales Casian, J. A., & Hovey, T. E. (2001). Demographic parameters of Golden Spotted Rock Bass *Paralabrax auroguttatus* from the northern Gulf of California . *Transactions of the American Fisheries Society*, 130(4), 686–691.
- Pondella, D. J., Craig, M. T., & Franck, J. P. C. (2003). The phylogeny of *Paralabrax* (Perciformes: Serranidae) and allied taxa inferred from partial 16S and 12S mitochondrial ribosomal DNA sequences. *Molecular Phylogenetics and Evolution*, 29(1), 176–184.
- Prevedelli, D., N’Siala, G. M., & Simonini, R. (2006). Gonochorism vs. hermaphroditism: relationship between life history and fitness in three species of Ophryotrocha (Polychaeta: Dorvilleidae) with different forms of sexuality. *Journal of Animal Ecology*, 75(1), 203–212.

- Prince, J., Hordyk, A., Valencia R, S. R., Loneragan, N., & Sainsbury, K. (2014). Revisiting the concept of Beverton–Holt life-history invariants with the aim of informing data-poor fisheries assessment. *Encyclopedia of Environment and Society*, 1959.
- Ramirez-Gonzalez, J., Jarrin, J., Andrade-Vera, S., Tanner, M., Salinas-de-León, P., & Barragan, M. (2019). How to achieve sustainable finfish fisheries in Galapagos. Fairfax, VA. <https://www.galapagosreport.org/english/2019/6/29/a-holistic-community-based-approach-to-improve-the-galapagos-tuna-fishery>
- Reynolds, D. (2018). Analysis of agreements reached in the participatory Management Board 2010–2015. *IHS Jane’s Defence Weekly*, 55(13).
- Rhodes, K., Choat, J., Myers, R., To, A., Ma, K., Samoilys, M., Suharti, S., Law, C., & Amorim, P. (2018). *Epinephelus polyphekadion*, Camouflage Grouper. *The IUCN Red List of Threatened Species*, 1–2.
- Rhodes, K. L. (2018). *Plectropomus areolatus*, Squaretail Coralgrouper. *The IUCN Red List of Threatened Species*. <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T64411A192479585.en>
- Rhodes, K., Sadovy, Y., & Samoilys, M. (2018). *Epinephelus fuscoguttatus*, Brown-marbled Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T44673A100468078.en>
- Robertson, R., Allen, G., Dominici-Arosemena, A., Edgar, G., Rivera, F., & Merlen, G. (2010). *Paralabrax albomaculatus*, Camotillo. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183769A8173211.en>
- Sadovy, Y., Aguilar-perera, A., & Sosa-Cordero, E. (2018). *Epinephelus striatus*, Nassau Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T7862A46909843.en>
- Sadovy, Y., & Colin, P. (2012). Reef fish spawning: biology, research and management. Springer, Dordrecht.
- Sadovy, Y, & Domeier, M. . (2005). Perplexing problems of sexual patterns in the fish genus *Paralabrax* (Serranidae, Serraninae). *Journal of Zoology*, 267(2), 121–133.
- Sadovy, Y, & Shapiro, D. (1987). Criteria for the diagnosis of Hermaphroditism in Fishes. *Copeia*, 1(1), 136–156.
- Sadovy, Yvonne. (2016). Mainstreaming Fish Spawning Aggregations into Fishery Management Calls for a Precautionary Approach. *BioScience*, 66(4), 295–306.
- Sadovy, Yvonne, Liu, M., Amorim, P., Choat, J. H., Law, C., Ma, K., Myers, R., Rhodes, K., Samoilys, M., Suharti, S., & To, A. (2018). *Epinephelus akaara*, Hong Kong Grouper. *The IUCN Red List of Threatened Species*, 8235.
- Salinas-de-León, P., Bertolotti, A., Chong-Montenegro, C., Gomes-Do-Régo, M., & Preziosi, R. F. (2017). Reproductive biology of the Endangered white-spotted sand bass *Paralabrax albomaculatus* endemic to the Galapagos Islands. *Endangered Species Research*, 34, 301–309.
- Saunders, R., Bryars, S., Fowler, A., & Centre, S. A. A. S. (2010). Preliminary consideration of the biology of several of South Australia’s marine fish species that have conservation or management interest. *Report to the Department for Environment and Heritage. SARDI Aquatic Sciences*, SARDI Aquatic Sciences, West Beach, S. Aust.

- Semmens, B., & Parnell, E. (2014). Final Report: Mortality and Population Abundance of Three Species of *Paralabrax* off San Diego, California.
https://caseagrant.ucsd.edu/sites/default/files/3A_Semmens_Paralabrax.pdf
- Shepherd, B., Phelps, T., Pinheiro, H. T., Pérez-Matus, A., & Rocha, L. A. (2018). *Plectranthias ahiahiata*, a new species of perchlet from a mesophotic ecosystem at Rapa Nui (Easter Island) (teleostei, serranidae, anthiadae). *ZooKeys*, 2018(762), 105–116.
- Smallwood, C. B., Hesp, S. A., & Beckley, L. E. (2013). Biology, stock status and management summaries for selected fish species in south-western Australia. In *Fisheries Research Report No. 242* (Issue 242).
- Smith-vaniz, B., Robertson, R., Dominici-Arosemena, A., Molina, H., Salas, E., & Guzman-Mora, A. G. (2010a). *Paralabrax maculatofasciatus*. *The IUCN Red List of Threatened Species*.
<http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183576A8137928.en>
- Smith-vaniz, B., Robertson, R., Dominici-Arosemena, A., Molina, H., Salas, E., & Guzman-Mora, A. G. (2010b). *Rypticus courtenayi*, Socorran soapfish. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183621A8146180.en>
- Smith-vaniz, B., Robertson, R., Dominici-Arosemena, A., Molina, H., Salas, E., & Guzman-Mora, A. G. (2010c). *Serranus socorroensis*, Socorro Serrano. *The IUCN Red List of Threatened Species*, 8235. <http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183852A8188656.en>
- Smith-Vaniz, B., Robertson, R., Dominici-Arosemena, A., Molina, H., Salas, E., & Guzman-Mora, A. G. (2010). *Paralabrax nebulifer*. *The IUCN Red List of Threatened Species*.
<http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183861A8190471.en>
- To, A., Amorim, P., Choat, J. H., Law, C., Ma, K., Myers, R., Rhodes, K., Sadovy, Y., Samoilys, M., & Suharti, S. (2018). *Epinephelus bruneus*, Longtooth Grouper. *The IUCN Red List of Threatened Species*. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T135381188A100573599.en>
- Tucker, S. J., Kurniasih, E. M., & Craig, M. T. (2016). A new species of grouper (*Epinephelus*; *Epinephelidae*) from the indo-pacific. *Copeia*, 104(3), 658–662.
- Vincenzi, S., Jesensek, D., & Crivelli, A. J. (2020). Biological and statistical interpretation of size-at-age, mixed-effects models of growth. *Royal Society Open Science*, 7(4).
- Williams, J. T., & Carpenter, K. E. (2015). A new fish species of the subfamily Serraninae (Perciformes, Serranidae) from the Philippines. *Zootaxa*, 3911(2), 287–293.
- Wise, B. S., St John, J., & Lenanton, R. C. (2007). Spatial scales of exploitation among populations of demersal scalefish: implications for management. Part 1: Stock status of the key indicator species for the demersal scalefish fishery in the West Coast Bioregion. *Final FRDC Report – Project 2003/052. Fisheries Research Report no. 163. Department of Fisheries, Western Australia*, 130.
- WoRMS. (2021). *World Register of Marine Species*. <https://doi.org/10.14284/170>

6.10 Appendix

Epinephelides armatus (Breaksea cod)



Image from: <https://fishesofaustralia.net.au/home/species/4375>,
source: Rick Stuart-Smith / Reef Life Survey. License: CC by Attribution

Othos dentex (Harlequin fish)



Image from: <https://fishesofaustralia.net.au/home/species/4383>, source:
Sascha Schultz / iNaturalist.org. License: CC by Attribution-Noncommercial

Paralabrax albomaculatus (Camotillo)



Image from: <https://reeflifesurvey.com/species/paralabrax-albomaculatus/> Source: Graham Edgar

Paralabrax auroguttatus (Gold-spotted sand bass)



Image from: <https://biogeodb.stri.si.edu/sfstep/en/pages/random/1561>
Source: Daniel Pondella

Paralabrax clathratus (Kelp bass)



Image from: <https://inaturalist.ala.org.au/observations/32133081>

Paralabrax maculatofasciatus (Spotted sand bass)



Image from: <http://www.oceanlight.com/spotlight.php?img=07935>

Source: Phillip Colla, all rights reserved worldwide.

Paralabrax nebulifer (Barred sand bass)



Image from: <https://www.reeflifesurvey.com/species/paralabrax-nebulifer/> source: Rick Stuart-Smith