



The diet, reproductive biology, age and growth of  
yellowtail, *Seriola lalandi*, in South Africa

Kieron Dunn

DNNKIE001

Dissertation presented for the degree of Masters of Science

Department of Biological Sciences

University of Cape Town

February 2014



Supervisors

Associate Professor Colin Attwood (UCT)

Associate Professor Astrid Jarre (UCT)

Dr Sven Kerwath (DAFF)

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

## GENERAL ABSTRACT

Yellowtail, *Seriola lalandi*, is an important line-caught fish in South African waters, yet little information is available on their life-history. This study aims to add information on the diet and feeding habits, reproductive biology and the age and growth of yellowtail in South Africa.

The diet of 62 yellowtail caught in the Western Cape of South Africa between 2011 and 2012 was investigated. Fish sampled by line and speargun ranged from 488 to 916 mm fork length (FL). Prey items were removed from stomachs, sorted, counted and weighed in order to calculate the percentage number (% N), percentage weight (% W), frequency of occurrence (% F) and index of relative importance (% IRI). Of the 62 stomachs examined 11 (17.7 %) were empty, 16 (26.0 %) contained only unidentifiable remains and 47 (82.5 %) contained identifiable remains. Prey items covered 18 species belonging to five classes: bony fishes, crustaceans, cephalopods, polychaetes and bivalves. Small pelagic fish were the dominant prey type, followed by crustaceans. The remaining taxa were of negligible importance. Some dietary differences were observed between sample areas. Most notable was the increased importance of crustaceans at Dassen Island on the West Coast compared to the sites at Robben Island, False Bay and Struisbaai.

The reproductive characteristics of yellowtail were documented from fish collected from 1974 to 2012. Samples were collected from Cape Infanta on the South Coast to Lamberts Bay on the West Coast of South Africa. Histological validation of macroscopic staging criteria revealed that active and developing ovaries are commonly staged incorrectly. A protracted spawning season from November to February with peak spawning in December and January was deduced from GSI values. No hydrated eggs were observed. Females matured at 550 mm FL (95 % CI = 532 - 570 mm) and males matured at 585 mm FL (95 % CI = 555 - 619 mm).

The age and growth characteristics of yellowtail in South African waters were determined from readings of whole sagittal otoliths collected from 1974 to 2012. Whole otoliths were considerably easier to read than sectioned otoliths. A total of 524 whole otoliths were taken from fish ranging from 430 to 1080 mm FL, of which 141 (27 %) were discarded and 384 (73

%) were readable. Agreement between all three readers was 13 % (n = 50) and between any two was 71 % (n = 274). Maximum ages for male and female yellowtail were 7 and 8 years respectively. Age at 50 % maturity ( $A_{50}$ ) for males it was 2.3 years while females matured ( $A_{50}$ ) at 3.6 years. von Bertalanffy growth parameters did not differ between males and females ( $P > 0.05$ ). A statistical *penalty* was used to keep the estimated growth parameters within biological limits and produced a von Bertalanffy growth equation with an  $L_{\infty}$  and K of 1064 mm and  $0.17 \text{ y}^{-1}$  respectively. The growth performance index ( $\Phi'$ ) of yellowtail in South African waters was found to be 3.51. This is high for the family Carangidae but on par with other species in the genus *Seriola*.

The life history characteristics for yellowtail in South African waters closely resemble those of other yellowtail populations. The diet of yellowtail in South African waters represents that of a robust generalist feeder that is not reliant on specific prey for its survival. The age, growth and reproductive characteristics of yellowtail in South African waters indicate that they are a fast growing and relatively early maturing species. These life-history characteristics indicate that the stock is resilient in relation to other line-fish species, but the large proportion (41 %) of fish caught below the 50 % size at maturity suggests that a revision of the minimum size limit should be considered.

## PLAGIARISM DECLARATION

1. I know that plagiarism is wrong. Plagiarism is using another's work and to pretend that it is ones own.
2. Each significant contribution to, and quotation in, this project from the work, or works of other people has been attributed and has cited and referenced.
3. This project is my own work.
4. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.
5. I acknowledge that copying someone else's assignment or essay, or part of it, is wrong, and declare that this is my own work

Kieron Dunn: \_\_\_\_\_

DATE: \_\_\_\_\_

University of Cape Town

# ACKNOWLEDGEMENTS

To my three supervisors, Associate Professor Colin Attwood (UCT), Associate Professor Astrid Jarre (UCT) and Dr Sven Kerwath, I thank you greatly for all the time and effort you put in to get me through and to the end of this project. Especially for all the guidance needed to study the biology of this tricky fish species.

Thanks to Dr Henning Winker (UCT) for the many hours of brainstorming and statistical counselling.

Thanks again to Sven and Colin for making it through the tedious task of reading yellowtail otoliths!

Thanks to Megan van Zyl for all the moral support in the lab and through many dissections and Struisbaai fishing trips!

Financial support for this project was provided by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation, through the UCT merit fund and WWF South Africa.

And finally thanks to all the yellowtail for being such good sport and showing me a side of fishing I'll most likely follow for the rest of my life. (At least while my legs and back can carry me down to the ledges).

# Table of Contents

CHAPTER 1 .....	8
<b>GENERAL INTRODUCTION</b> .....	8
GENERAL DESCRIPTION .....	8
HABITAT .....	8
MOVEMENT .....	10
FISHERY .....	11
AQUACULTURE.....	13
DIET AND FEEDING.....	14
REPRODUCTION.....	15
AGE AND GROWTH .....	16
THESIS OUTLINE.....	18
CHAPTER 2 .....	19
<b>THE DIET OF <i>SERIOLA LALANDI</i> IN SOUTH AFRICAN WATERS</b> .....	19
ABSTRACT.....	19
INTRODUCTION .....	19
METHODS .....	22
SAMPLE COLLECTION.....	22
SAMPLE REGIONS .....	22
LABORATORY EXAMINATION OF STOMACH CONTENTS .....	23
RESULTS .....	24
DISCUSSION.....	28
CHAPTER 3: .....	32
<b>THE REPRODUCTIVE BIOLOGY OF <i>SERIOLA LALANDI</i> IN SOUTH AFRICA</b> ...	32
ABSTRACT.....	32
INTRODUCTION .....	33
METHODS .....	36
SAMPLE COLLECTION.....	36
PREPARATION AND ANALYSIS OF GONADS.....	36
MATURITY .....	37
ANALYSIS OF HISTORICAL RECORDS .....	38
RESULTS .....	39
HISTOLOGICAL OBSERVATIONS.....	40
OOCYTE LENGTH-FREQUENCY DISTRIBUTION .....	41
SEX RATIO.....	44
ANNUAL REPRODUCTIVE CYCLE .....	45
MATURITY .....	47

DISCUSSION .....	49
CHAPTER 4 .....	55
<b>THE AGE AND GROWTH OF <i>SERIOLA LALANDI</i> IN SOUTH AFRICA.....</b>	<b>55</b>
ABSTRACT.....	55
INTRODUCTION .....	56
METHODS .....	58
SAMPLE COLLECTION.....	58
OTOLITH AND SCALE REMOVAL AND PROCCESING .....	58
LENGTH WEIGHT RELATIONSHIP .....	59
GROWTH.....	61
GROWTH PARAMETER COMPARISON.....	62
AGE AT MATURITY .....	63
RESULTS .....	64
INTERPRETATION OF GROWTH ZONES .....	64
SAMPLE DISTRIBUTION.....	67
MORPHOMETRIC RELATIONSHIP.....	69
PRECISION.....	69
AGE VALIDATION .....	70
GROWTH.....	70
LIFE HISTORY COMPARISON.....	72
AGE AT MATURITY .....	73
DISCUSSION.....	75
CHAPTER 5 .....	82
<b>CONCLUSIONS .....</b>	<b>82</b>
BIOLOGY.....	82
FISHERY AND MANAGEMENT .....	84
FUTURE RESEARCH.....	86
REFERENCES .....	88
APPENDIX.....	104

## CHAPTER 1

# GENERAL INTRODUCTION

### *GENERAL DESCRIPTION*

Yellowtail (*Seriola lalandi*) is a member of the large and diverse Carangidae family, comprising of 151 species in 32 genera (Smith and Heemstra 2003, Heemstra and Heemstra 2004). Most Carangid species are fast swimming predators. They occupy a variety of habitats including open water, reef pinnacles, surf zones and estuaries. Many species in the family are of economic importance in both commercial and recreational sectors. Of the nine *Seriola* species three are commonly found in South African waters, namely yellowtail, amberjack (*Seriola dumerili*) and highfin amberjack (*Seriola rivoliana*). Amberjack and highfin amberjack are found east of Port Elizabeth up into Mozambique in tropical and warmer temperate waters.

Yellowtail are a large predatory species and can attain 60 kg (Gillanders et al. 1999a), however, specimens found in South African waters seldom exceed 20 kg. Yellowtail are a circum-global species occurring in temperate and subtropical waters, with large populations off the coasts of Japan, southern Australia and the California (Baxter 1960, Gillanders et al. 1999a, Shiraishi et al. 2010). Yellowtail are distributed along the majority of the South African and Namibian coastline from Aliwal Shoal on the east coast and as far north as Walvis Bay in Namibia (Branch et al. 2008). The vast distribution of this species demonstrates its adaptability and wide range of tolerances to environmental conditions.

### *HABITAT*

Yellowtail are a pelagic species often forming shoals that cover “football field” sized areas in shallow embayments and above temperate reefs in inshore and offshore regions (Nepgen 1982). Inshore reefs and seamounts are the primary habitat of the species. High productivity is a common feature of areas inhabited by yellowtail. The distribution of the Japanese population of yellowtail ranges from the Pacific Ocean to the Japan and East China seas around the islands of Japan (Shiraishi et al. 2010). This region is characterized by high levels

of primary production and dynamic hydrological conditions (Uye et al. 1987, Gong et al. 2000, Gong et al. 2003). High concentrations of nutrients from river influxes and upwelling systems support a high biomass ecosystem ideal for top predators. The Australian population ranges from the coastal waters off southern Queensland to central Western Australia as well as off the eastern coastal waters of Tasmania and the offshore seamounts of Lord Howe and Norfolk Islands (Scandol et al. 2008). The Australian yellowtail population also occurs in productive and dynamic regions associated with upwelling systems and nutrient rich ocean currents (Young et al. 1997, Oschiles and Garçon 1998, Roughan and Middleton 2002, Worm et al. 2003, Kämpf et al. 2004). An eastern Pacific population ranges from British Columbia, Canada to Mazatlan, Mexico and throughout the Gulf of California and Californian coast line (Crooke 2001, Vergani 2005). The west coast of North America has a number of highly productive upwelling regions with a dynamic coastline scattered with offshore islands creating ideal habitat for yellowtail (Zeitzschel 1969, Bakun and Parrish 1982, Santamaria-del-Angel et al. 1994, Ware and Thomson 2005). An eastern Atlantic population ranges from Massachusetts to Argentina. Yellowtail have also been documented occurring around offshore seamounts in the Atlantic Ocean such as the Vema seamount and the islands of Gough and Tristan da Cunha.

Although yellowtail are distributed along the majority of the South African coastline, the species is concentrated in the Southern and Western Cape over the Agulhas Bank and along the West Coast. Large-scale upwelling along these coasts drives an influx of nutrient rich water into the region, boosting productivity (Schumann et al. 1982, Probyn et al. 1994, Hutchings et al. 2002, Moloney et al. 2005). This region supports a high biomass of small pelagic fish species and squid including sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*), horse mackerel (*Trachurus trachurus*) and chokka squid (*Loligo vulgaris*) (Crawford 1987, Augustyn 1990, Roberts and Sauer 1994, van der Lingen et al. 2006), all of which are potential prey species of yellowtail (Nepgen 1982). These productive waters are also characterized by a highly dynamic and seasonal hydrology. The mixing of the warm western boundary current and cool eastern boundary current over the western Agulhas shelf produces unique and complex water masses (Probyn et al. 1994). The outer regions of the Agulhas Bank are mostly influenced by the Agulhas Current. The inner bank is mostly influenced by coastal upwelling dictated by the climatic conditions typical of these latitudes (30 – 40 °S) with some influx of warmer water from outer currents (Probyn et al. 1994,

Schumann et al. 1995). These highly variable hydrological conditions create patches of favorable conditions utilized by prey and predator. Highly mobile species such as yellowtail are ideally suited to follow and move between these patches to find high concentrations of suitable prey.

## *MOVEMENT*

Yellowtail are a highly mobile, migratory species, which may be described as a pelagic nomad (Griffiths 2000). They are known to remain over a reef area for extended periods of time while conditions remain favorable before moving off. Throughout their global distribution their movements are often seasonal and strongly influenced by hydrological conditions and the movement of their pelagic prey (Baxter 1960, Penny 1982, Wilke and Griffiths 1999). Yellowtail have been documented following the 'sardine run' up the South African East Coast during the winter months, after which they are hypothesized to return to the eastern Agulhas Bank in the spring (Penney 1982, Payne and Bandenhorst 1989).

Baxter (1960) noted that during an exceptionally warm winter season yellowtail remained in the waters off the Californian coast, when in previous colder winters they were absent. This further links the movements of the species to hydrological conditions.

The species is capable of undergoing multiple rapid and extensive movements over a short time scale, as evidenced by tagging studies. Penney (1982) documented yellowtail moving at speeds of up to 20 nautical miles per day between Cape Point and the Struisbaai banks, a distance of 100 nautical miles. Rapid movements between aggregation sites have been shown to occur throughout a season according to localized changes in conditions. Gillanders et al. (2001) recorded distances of 1,619 nautical miles off the coast of Australia, Holdsworth and Saul (2003) recorded distances of up to 1,400 nautical miles off the east coast of New Zealand, while Baxter (1960) recorded a distance of 414 nautical miles off the Californian coast. Tagging studies have also indicated some site fidelity in larger specimens of the species at certain sites, providing further support for a nomadic existence (Baxter 1960, Holdsworth and Saul et al. 2003).

## *FISHERY*

Yellowtail began to form part of the commercial fishery in the late 1890s in South African waters. It was however considered a second grade species at the time with catches and market value being less than half that of geelbek, the preferred species at the time (Payne and Badenhorst 1989). However by the 1960's yellowtail was the dominant line-fish species taken around the Agulhas area as catches of geelbek had dropped drastically. Large catches of yellowtail were also made in the late 1920 and early 1930's. Yellowtail were primarily targeted by line and beach-seine fishermen up until the 1970's. An exceptionally large catch of 1,093 tons was recorded for these fisheries in 1970 which prompted the start of a purse-seine fishery (Penney 1982). The fishery started when purse-seine operators possessing licenses for small pelagic species started targeting yellowtail. Their success encouraged a larger scale operation (Penney 1982). Initial catches of the purse-seine fishery were below those of the line-fishery, but by 1973 the purse-seine landings were on par with those of the line-fishery (Penney 1982, Payne and Badenhorst 1989). In 1973 tuna purse-seiners also began targeting yellowtail on the Agulhas Bank, and this species soon comprised between 49 - 100 % of their catch (Penney 1982). This led to a record catch of 1265 tons for the combined line-fish, beach-seine and purse-seine fisheries in 1975. As competition for resources developed between the line, beach seine and purse-seine fisheries, concern over the state of the yellowtail stock was raised. A total allowable catch (TAC) of 450f tons was placed on the purse-seine fishery in 1976 (Penney 1982, Payne and Badenhorst 1989). However this quota was never attained again and both line and purse-seine landings decreased to a combined low of 317 tons in 1980. The following season of 1981/82 saw a ban on the purse-seine fishing for yellowtail, which has persisted until today. The ban on this industry caused an increase in landings by the line-fish industry into the late 1980's (Payne 1989).

The beach-seine fishery is one of the oldest and most controversial fisheries in South Africa. Since the start of the fishery there has been conflict between beach seine and line fishermen (Penney 1991). The main conflict arises when beach seine fisheries target angling species, which is the case for yellowtail. In areas such as False Bay there are high levels of competition as beach seine catches of yellowtail can account for up to 77 % of the total catch in the bay (Lamberth et al. 1994). However, beach seine landings of yellowtail only

account for 3.2 % of the total catch in South Africa, and have a low overall impact on the species (Lamberth et al. 1994).

Yellowtail catches have shown high levels of variability since an apparent population decline in the late 1970's. These high levels of variability for a documented 25 year period between 1985 and 2010 can be seen in Figure 1.1. Annual catches of the species have fluctuated by up to 540 tons between years (unpublished data, DAFF). The annual catch averaged 523 tons with a standard deviation of 228 tons around this value. In South African waters yellowtail have shown a pattern of decreasing catches followed by a steep increase in catches, followed by a steady decline. Similar catch trends and high variability have been experienced in other large commercial fisheries for the species in California and Australia (Baxter 1960, Crooke 2001, Scandol et al. 2008). Although the species has displayed decreasing catches in South African waters over the last few years (Figure 1.1), recent stock assessment models have shown a positive recovery and depict the yellowtail stock as optimally exploited (Winker et al. 2012). The decrease in catches is related to a forced reduction in effort in the line-fishery.



Figure 1.1: Total landings of *S. lalandi* in the South African line-fishery from 1985 to 2010.

Yellowtail is highly regarded by recreational anglers for its fighting capabilities and desirable flesh. The recreational fishery for this species is large throughout its distribution and landings can often equal that of the commercial fishery in some parts of the world. Scandol et al. (2008) reported landings of up to 340 tons by the recreational fishery in New South Wales, a similar value to that of the commercial fishery in the area. The recreational fishery for yellowtail is large in South Africa, especially in the waters surrounding Cape Town and on the Struisbaai banks off Cape Agulhas. With up to 4,000 registered recreational vessels (DAFF 2010) operating in South African waters and an allowance of 10 fish per angler for yellowtail there is the potential for a substantial harvest to be made by this sector. The yellowtail fishery has a strong seasonality which is predominately in the summer months when the fish are plentiful. Although it is possible to catch this species during winter months, most recreational fishers will target other species. Monitoring the recreational fishery of such a species is vital as large amounts may be harvested. As the recreational harvest is not recorded in the total annual catch of the species, the total landings can be greatly under reported and underestimated.

## **AQUACULTURE**

Four *Seriola* species are farmed globally, namely the Japanese yellowtail, yellowtail, amberjack and highfin amberjack. Japanese yellowtail makes up 80% of global *Seriola* species production, of which the majority comes from Japan (Miranda and Peet 2008). Japan produces up to 150 000 tons of *Seriola* species annually, yellowtail only makes up a small proportion of this (Miranda and Peet 2008). However yellowtail is considered a higher grade fish than Japanese yellowtail and is consumed primarily as sushi in Japan, this has shifted the market demand somewhat towards yellowtail (Nakada 2002, Miranda and Peet 2008).

The commercial culture of yellowtail occurs in most countries where prominent stocks occur in offshore waters, but not in South Africa. In these countries, farmed production generally outweighs that of wild commercial harvesting by up to 75 % (Miranda and Peet 2008). This has become common for a number of species farmed in sea cages (Poole 2000). Australia's average annual commercial harvest of wild stocks is below 200 tons, however at 5000 tons their annual production of the species is 24 times higher (Miranda and Peet 2008, Scandol et al. 2008). These figures reflect the high potential of yellowtail as an aquaculture species.

Their robustness, resistance to disease and high growth rates give them a high production value (Primary Industries and Resources SA 2003). Sea cages are the commonly used method in yellowtail aquaculture and are either stocked with wild caught or hatch reared fingerlings (Nakada 2002, Primary Industries and Resources SA 2003, Kolkovski and Sakakuru 2004, Miranda and Peet 2008). The Japanese method relies almost entirely on wild caught fingerlings which potentially affects the state of wild stocks, while the Australian method relies on hatchery reared fingerlings, thus not diminishing wild stocks.

Aquaculture of the species in South Africa has not yet taken hold, although some recent pilot projects have shown positive results (Porter et al. 2012). The South African coastline has been found to be problematic for sea cage style aquaculture as it has few protected bays with stable oceanic conditions to set up an industry.

### **DIET AND FEEDING**

Baxter (1960) and Nepgen (1982) described the diet of yellowtail in California and South Africa and a number of other authors have mentioned its main prey types (Schmitt and Strand 1982, Crooke 2001, Vergani 2005, Scandol et al. 2008). As with most pelagic species digestion rates are high making diet analysis difficult as recently consumed prey can be digested beyond identification.

The majority of literature on the diet of *Seriola* species is based on nutritional needs and advancements for aquaculture purposes. Few of these studies describe natural diets of the species (Jover et al. 1999, Talbot et al. 2000, Nakada 2002, Webster and Lim 2002, Primary Industries and Resources SA. 2003, Kolkovski and Sakakura 2004, Miranda and Peet 2008, Moran et al. 2009).

Baxter (1960) found yellowtail to be an opportunistic feeder in California. Yellowtail commonly preyed on similar species throughout its global distribution, with sardine, anchovy and squid being most common. However up to 14 teleost species and a number of crustaceans and molluscs were documented by Baxter (1960) and Nepgen (1982). It was also noted that the stomachs of yellowtail are usually dominated by one species, indicating that with enough sampling it would be possible that any one species making up the diet of individual yellowtail could become the most important. A high number of empty stomachs

were also noted by Nepgen (1982) and he postulated that yellowtail may be present over a certain reef for a number of days before feeding, displaying intermittent feeding behavior.

Similar diets and prey species have been noted for other *Seriola* species. The diet of amberjack is similar to that of yellowtail, with sardine, anchovy, squid and various crustaceans being most important (Matallanas et al. 1995). The diet of the highfin amberjack was dominated by teleost species, with blue jack mackerel (*Trachurus picturatus*), club mackerel (*Scomber japonicus*) and sardine being most important (Barreiros et al. 2003).

## **REPRODUCTION**

A number of studies have documented various aspects of the reproduction of yellowtail in captivity (Kolkavdki and Sakakura 2004, Katsunori et al. 1997, Moran et al. 2007) and other *Seriola* species (Garcia and Diaz 1995, Micale et al. 1999, Mylonas et al. 2004, Jerez et al. 2006). In the wild the reproductive biology of yellowtail has been documented by a number of studies throughout its natural distribution (Baxter 1960, Penney 1982, Gillanders et al. 1999b, Poortenaar et al. 2001, Shiraishi et al. 2010). A summer spawning period was documented in all studies for the species, both in the Northern and Southern hemispheres (Baxter 1960, Penney 1982, Gillanders et al. 1999b, Poortenaar et al. 2001, Shiraishi et al. 2010).

Only Baxter (1960) noted an actual spawning event of the coast of California where large shoals of yellowtail were observed “swimming small circles and spewing eggs and milt” 112 km offshore in 95 m of water on a shallow bank. The presence of yellowtail larva and eggs found on the Agulhas Bank suggests that their spawning grounds are 6 - 20 km offshore of the South African coastline (Penney 1982). Mature oocytes have been found in the ovaries of yellowtail throughout the spawning season, indicating that the species is capable of multiple spawning events within one season (Baxter 1960, Poortenaar et al. 2001). A similar spawning strategy was observed for amberjack (Marino et al. 1995).

Lengths at maturity for yellowtail were found to be variable between studied populations (Baxter 1960, Gillanders et al. 1999b, Poortenaar et al. 2001, Shiraishi et al. 2010). Variation in growth and maturity between populations are not uncommon and can often be linked to differences in environmental variables (Hewett and Kraft 1993). It is common practice to set

a minimum size limit on a fish species in a fishery based on lengths at maturity, this is done to protect immature individuals from being removed from the population before contributing to it. Length at first maturity for female yellowtail ranged between 506 - 775 mm fork length (FL) in Californian, Australian and Japanese populations (Baxter 1960, Gillanders et al. 1999b, Poortenaar et al. 2001, Shiraishi et al. 2010). Length at 50% maturity for female yellowtail ranged between 843 - 944 mm (FL) in studies done by Gillanders et al. (1999b) and Poortenaar et al. (2001) respectively. Both studies found that most fish harvested in the Australian and New Zealand fisheries were under the size at which 50% of the population was mature ( $L_{50}$ ).

### *AGE AND GROWTH*

The susceptibility of fish populations to over-exploitation often depends on the characteristic of their life-history strategy. Knowing the age parameters of a fish species can give insights into the population dynamics, such as age at maturity, mortality, growth rates, and fecundity (Shirripa and Burns 1997). Age and growth studies are vital as a basis for managing fish populations and identifying species suited to aquaculture.

The commercial importance of the *Seriola* species has resulted in a large amount of interest in their age and growth for both improving management and aquaculture production. Dorsal spines, vertebrae, otoliths and scales were used by Gillanders et al. (1999a) for ageing yellowtail, whereas Penney (1982) focused on whole otoliths, Stewart et al. (2004) focused on sectioned otoliths and Shiraishi et al. (2010) focused on vertebrae and Baxter (1960) focused on scales. Leonard (2009) and Manooch and Potts (1997) used sectioned otoliths and Kožul et al. (2001) used scales to age amberjack. Marayama (1992) and Mitani (1958) used vertebrae, Mitani (1955) used scales and Mitani and Sato (1959) used opercular bones to age Japanese yellowtail. Age and growth studies on other *Seriola* species are few, mostly due to their limited commercial importance and difficulty to age.

Four hard structures have been used to age yellowtail, namely dorsal spines, vertebral columns, scales and both sectioned and whole otoliths, each with varying success. The first study on the age and growth of yellowtail by Baxter (1960) utilized scales after attempts to use other structures had failed. Otoliths are the most commonly used structure for ageing fish as they provide the clearest indication of growth zones. However for most pelagic fish

species they are less useful in that they accumulate large numbers of false annuli which could lead to an over-estimate of age (Chilton and Beamish 1982). Gillanders et al. (1999a) compared the usefulness of whole otoliths versus sectioned otoliths for ageing yellowtail. Their study found that growth zones in whole otoliths are more readily defined than in sectioned otoliths. Whole otoliths do however thicken with age in larger fish and recently formed increments may only be visible in sectioned otoliths (Beamish 1979, Eltink and Kuitert 1989, Stewart et al. 2004). Sectioned otoliths have been found to give more precise estimates of age for older fish as recent growth increments are more readily visible (Gillanders et al. 1999a, Stewart et al. 2004). Vertebrae have been found useful for ageing yellowtail and produce similar age results as sectioned otoliths, but do however have a tendency to overestimate age (Gillanders et al. 1999a, Shiraishi et al. 2010). Dorsal spines were examined by Gillanders et al. (1999a) for ageing, but were found to be unusable for ageing yellowtail as early growth increments are re-absorbed.

Maximum age estimates for yellowtail have ranged between 9 - 21 years in various studies. Otoliths gave the highest observed age of all hard structures (Stewart et al. 2004). Age estimates from scales ranged between 9 - 12 years (Gillanders et al. 1999a, Baxter 1960) and vertebrae between 9 - 11 years (Gillanders et al. 1999a, Shiraishi et al. 2010). Japanese yellowtail recorded lower maximum ages, Mitani and Sato (1959) found a maximum age of 6 using operculae, Murayama (1992) found a maximum age of five using vertebrae and Mitani (1955) found a maximum age of five using scales.

The growth performance of yellowtail and *Seriola* species in general has been shown to be far above average with  $\Phi' = 3.6$  for the genus, while the average across most fish species being only  $\Phi' = 2$  (Pauly 1979, Froese and Pauly 2000).

Understanding the growth rate and age structure of a population can be useful on a broader scale when studying population structure. Fish in close proximity to each other should display similar characteristics if they belong to the same population and if environmental conditions are similar. If they differ there is the potential that two different populations exist (Bernard 1981). Combining age, growth and length information can prove invaluable for stock assessments and defining management strategies for the species.

## THESIS OUTLINE

*Chapter two* covers the diet of 62 yellowtail in three areas in the Western Cape, namely Dassen Island on the West Coast, False Bay and the Cape Point area and Struisbaai. The most important prey species in the diet of yellowtail in these areas are identified and the differences analyzed.

*Chapter three* covers the reproductive characteristics of yellowtail in South African waters. Up to 6142 samples were used to determine the spawning season, length at 50% maturity ( $L_{50}$ ), spawning strategy and ovarian structure.

*Chapter four* covers the age and growth of yellowtail in South African waters. Up to 6142 samples were available to determine the length-weight relationship for yellowtail. Otoliths were used to estimate the age of yellowtail, 524 whole otoliths were used in this process. The age at 50 % maturity ( $A_{50}$ ), age at length, minimum and maximum ages and growth rates were determined.

*Chapter five* presents the most important and relevant findings of the study and discuss their potential applications.

## CHAPTER 2

# THE DIET OF *SERIOLA LALANDI* IN SOUTH AFRICAN WATERS

### ABSTRACT

The diet of 62 yellowtail was investigated in the Western Cape, South Africa from Dassen Island, Robben Island, False Bay, Cape Point and Struisbaai between 2011 and 2012. Fish were sampled by line and spearfishing, ranging in size from 488 to 916 mm FL. Prey items were removed from stomachs and identified, sorted, counted and weighed to calculate the percentage number (% N), percentage weight (% W), frequency of occurrence (% F) and the index of relative importance (% IRI). Eleven (17.7 %) stomachs were empty, 16 (26 %) contained only unidentifiable remains and 47 (82.5 %) contained food. Prey items consisted of 18 species belonging to classes: bony fish, crustaceans, cephalopods, polychaetes and bivalves. Small pelagic fish were the dominant prey type, followed by crustaceans with the remaining taxa being of negligible importance. Some dietary differences were observed between sample areas, most notable was the increased importance of crustaceans around Dassen Island on the West Coast. The diet of yellowtail in South African waters represents that of a robust generalist feeder preying on an array of different species.

### INTRODUCTION

Understanding the feeding ecology of a species provides essential information on the niche it occupies in the ecosystem and the analysis of its diet provides an understanding of the role it plays in the ecosystem and how it will behave in it (Hyslop 1980, Ben-Tuvia 1995). Top predators are known to influence and sometimes structure the communities of their prey through the hunting tactics and intensity of predation (Sih et al. 1985). Investigating the diet of top predators is therefore crucial to understand an ecosystem.

Competition among predators and between predators and fisheries can be reflected in diet. A decline in the abundance of a top predator can be linked to the abundance of its prey which could be reduced through direct competition with other predator species or through competition with fisheries. The overexploitation of prey species has been directly linked to a decrease in top predators (Furness and Tasker 2000). This link has been made in the Benguela ecosystem for the small pelagic prey species European anchovy and South African Sardine, as large scale fisheries for these species have seen their stocks fluctuate (Cury et al. 2000, Pichegru et al. 2009). These species occupy the mid-trophic level and form a link between lower trophic levels and top predators (Cury et al. 2000). The breeding success of African penguins *Spheniscus demersus* has been correlated to the abundance of these small pelagic fish species (Crawford et al. 2006). Concerns over the status of predatory fish in False Bay were raised when a decline in predatory line-fish was noticed in the 1970's and was suspected to be linked to purse-seine fishing for small pelagics in the bay. Nepgen (1982) explored the diet of predatory fish in False Bay and found that small pelagic species were most important to the majority of the species examined. These predators included geelbek (*Atracoscion aequidens*), silver cob (*Argyrosomus inodorus*), snoek (*Thyrsites atun*), yellowtail and elf (*Pomatomus saltarix*). The diet of these predators puts them in direct competition with purse-seine fisheries and the effects they can have on populations of small pelagics. The robustness of predator species will depend on their ability to adapt their diet in periods of low prey abundance.

Recruitment failure or years of poor recruitment can also be linked to the abundance of prey available to a predator (Rothschild 2000). The availability of sufficient resources plays a vital role in the reproductive success. During and leading up to the spawning season fish must improve their body condition to fuel the production of gametes (Rothschild 2000). If prey abundance is limited then the energy requirements needed for survival and successful reproduction will not be met, leading to a low recruitment year.

Description of the dietary importance of prey has been done using a number of numerical indices. These indices can describe how many individuals of a species are collectively found in stomachs (% N), what weight the prey item contributes to the overall diet (% W) and in how many stomachs the item was found (% F). Each index describes a different aspect of how the prey item contributes to the overall diet. However, describing dietary importance

based on individual indices can lead to a bias towards certain prey types (Liao et al. 2001). Small numerous prey items may dominate importance by number (% N) and may be considered more important than high weight (% W) items found in low numbers (% N). Heavy prey items may be considered more important by % W than small light items found in high numbers (% N). The use of a compound index such as the index of relative importance (IRI) can eliminate bias by using a combination of individual indices to determine importance (Pinkas et al. 1971, Hyslop 1980, Liao et al. 2001). The use of a compounded index gives an overall importance, useful for describing the general dietary make up of a species.

Describing the importance of a prey species based solely on an IRI importance rating lacks the depth given by using individual indices (Liao et al. 2001). A small prey item may still be rated as important if found in high numbers at a high frequency, but will contribute little in the form of nutrition due to a low weight. The use of % W gives a better indication of the nutritional contribution of a prey item to the overall diet, while % N gives an idea of the feeding behaviour of the predator (Triasin and Jørgensen 1999). Percentage frequency provides a broader description of how the predator population selects prey and how widely available and abundant a prey item is (Triasin and Jørgensen 1999). It is therefore useful to describe dietary importance by using both individual indices and compounded indices such as the IRI.

Baxter (1960) and Nepgen (1982) described the diet of yellowtail in South Africa and California, while others have mentioned its main prey types (Schmitt and Strand 1982, Croke 2001, Vergani 2005, Scandol et al. 2008). However, recent comprehensive studies on the diet of yellowtail are lacking.

The aim of this chapter is to provide a description of the general diet of yellowtail in the Western Cape of South Africa. Differences in diet between three sampling regions are examined. The index of relative importance (IRI) is used to analyse the importance of prey species and taxa in the diet of yellowtail.

## *METHODS*

### *SAMPLE COLLECTION*

Sixty-two yellowtail were sampled by rod and reel and spearfishing from ski-boats on the West Coast at Dassen Island, Robben Island in False Bay and the Cape Point area and at Struisbaai on the South-Western Cape coast between January 2011 and November 2012 (Figure 2.1, chapter 2). Various tactics were employed while fishing for yellowtail. Bird activity was used as an indicator of the presence of yellowtail. Artificial lures were used to catch the fish. Yellowtail were also targeted on rod and reel from shore on the ledges of Cape Point as yellowtail moved in and out of False Bay.

### *SAMPLE REGIONS*

Sampling was conducted at three regions in the Western Cape, namely the West Coast Islands of Dassen and Robben, Cape Point area (including False Bay) and the Struisbaai banks (Figure 2.1). With the exception of some Cape Point samples, all fish were caught in water ranging from 5 to 30 m above rocky bottom structure. Some samples captured 20 to 40 miles off Cape Point were in water depths exceeding 100 m.

The West Coast Islands of Dassen and Robben both serve as offshore aggregation areas where yellowtail can be found during winter months. Both islands are situated ~10 km offshore. Dassen Island is located 55 km north of Cape Town offshore of Ysterfontein, while Robben Island is found in Cape Town's Table Bay.

Cape Point forms the south-western corner of False Bay, a dynamic region scattered with offshore reefs and highly variable water conditions. Yellowtail frequent the reefs off Cape Point in the summer months and move in and out of False Bay along the eastern margin of the peninsula.

Rockybank is a large raised rocky bank in the mouth to False Bay approximately 11 km off of Cape Point. The bank ranges in depth from 22 - 30 m and yellowtail occur over it for the majority of summer months and on occasion in winter if water conditions are favourable.

Struisbaai is a region accommodating a number of offshore banks around and off the tip of Cape Agulhas. Banks sampled ranged from 6 to 19 km offshore of the Struisbaai harbour.

Yellowtail will frequent these banks in the summer months from October onwards when warmer water moves in.

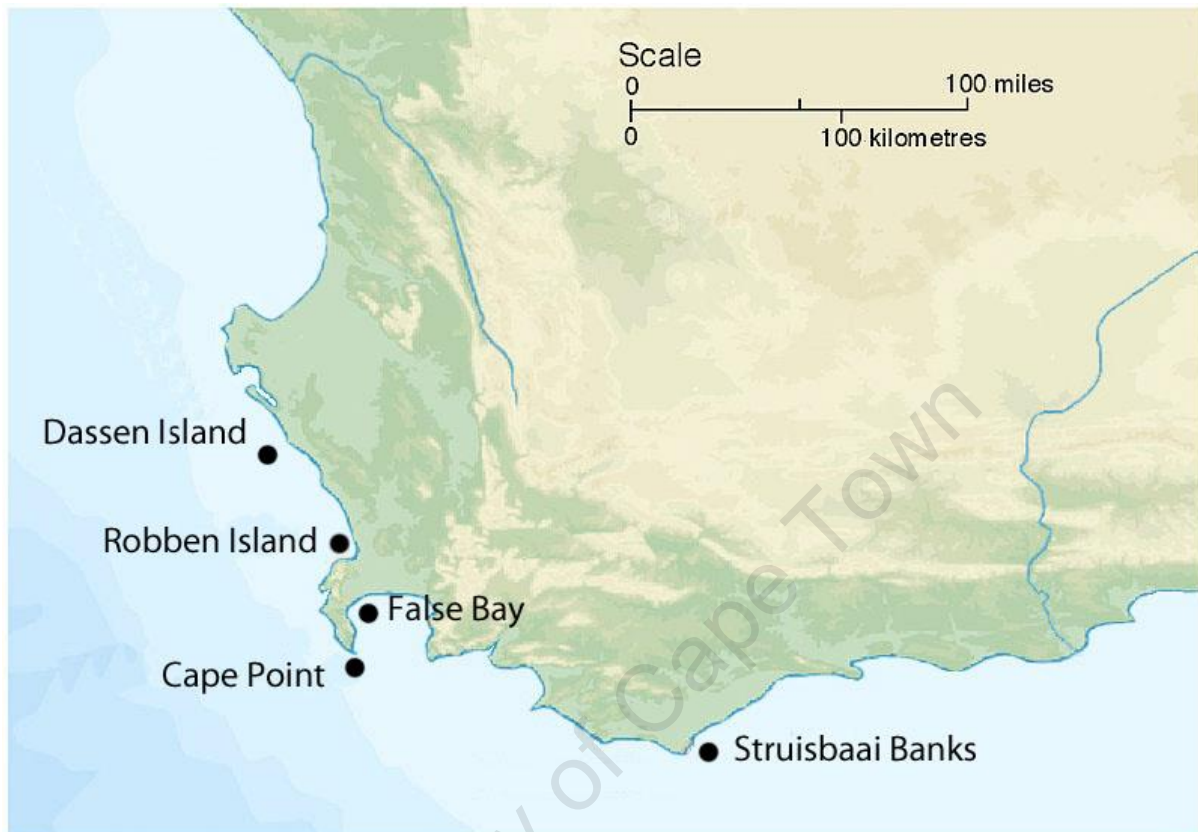


Figure 2.1: *S. lalandi* sample sites along the Western Cape coastline, Dassen Island, Robben Island, Cape Point, False Bay and Struisbaai.

#### LABORATORY EXAMINATION OF STOMACH CONTENTS

Yellowtail were dissected fresh, stomachs were severed at the oesophagus and behind the pyloric sphincter and stored in 10% buffered formalin solution until further processing. Stomachs were later removed from their jars and excess formalin allowed to drain off before weighing to the nearest 0.1 g. Stomachs were then opened and all contents placed onto a large sorting tray. The contents were then sorted into groups of similar items macroscopically and further identified down to the lowest possible taxon using a dissecting microscope. Excess liquid was then removed from prey items before being counted and weighed to the nearest 0.001 g in groups. Certain prey items such as sardine and horse mackerel were measured (TL) for purposes outside of this study. Some prey were unidentifiable using general macroscopic methods, these were further preserved in 10 %

buffered formalin for later processing. Unidentifiable bony fish, with heads still intact were measured (TL). Crustaceans were identified by exoskeleton remains. Certain crustaceans were possible to count by pairing eyes when bodies were digested beyond recognition.

The importance of prey species was calculated using the index of relative importance (IRI);

$$\text{IRI} = (\%N + \%W) * \%F \quad \text{Equation 2.1}$$

where % N is the numerical percent of a prey item in the pooled stomachs, % W is the percent of the weight (g) occupied by the prey item in the pooled stomachs and % F is the number of stomachs containing the prey item out of all stomachs. The % IRI was then used to describe the overall importance of a prey species, while the individual indices used to calculate IRI were used to describe how it gained its importance.

Differences in prey composition among regions were tested using Primer 6.0 using a one-way analysis of similarity (ANOSIM) (Clarke and Warick 2001). In preparation for this test, the data were standardized and transformed to the fourth root. The Bray-Curtis similarity index was calculated for each pair of samples and represented in a resemblance matrix. Multi-dimensional scaling (MDS) plots were used to visually display similarity among regions.

## **RESULTS**

A total of 62 stomachs were examined from fish ranging between 488 to 916 mm FL. Of the 62 stomachs examined 11 (17.7 %) were empty, 16 (26 %) contained only unidentifiable food remains and 47 (82.5 %) contained food. Prey items covered 18 species in five classes. Seventy-four percent of stomachs had bony fish present, 20.96 % had crustaceans present, 9.68 % had cephalopods present and 1.61 % contained polychaetes and bivalves (Table 2.1). Bony fish dominated with 92.50 % IRI, with crustaceans being second dominant at 7.19 % IRI (Table 2.1). Cephalopods, polychaetes and bivalves all scored below 0.5 % IRI making up very little of the diet of yellowtail (Table 1.1). Unidentifiable fish remains (UFR) was found to be the most important prey group with an IRI of 39.82 % and was found in 50 % of stomachs (% F) (Figure 2.2 and Table 2.1). The second most important prey item was sardine with an IRI of 29.91 % making up 60.63 % of the weight (% W) (Figure 2.2 and Table 2.1). The

only invertebrate group making a significant contribution to the diet of yellowtail were the crab megalopa larva with an IRI of 20.09 % and which also accounted for 34.74 % of the prey by number (Figure 2.2 and Table 2.1).

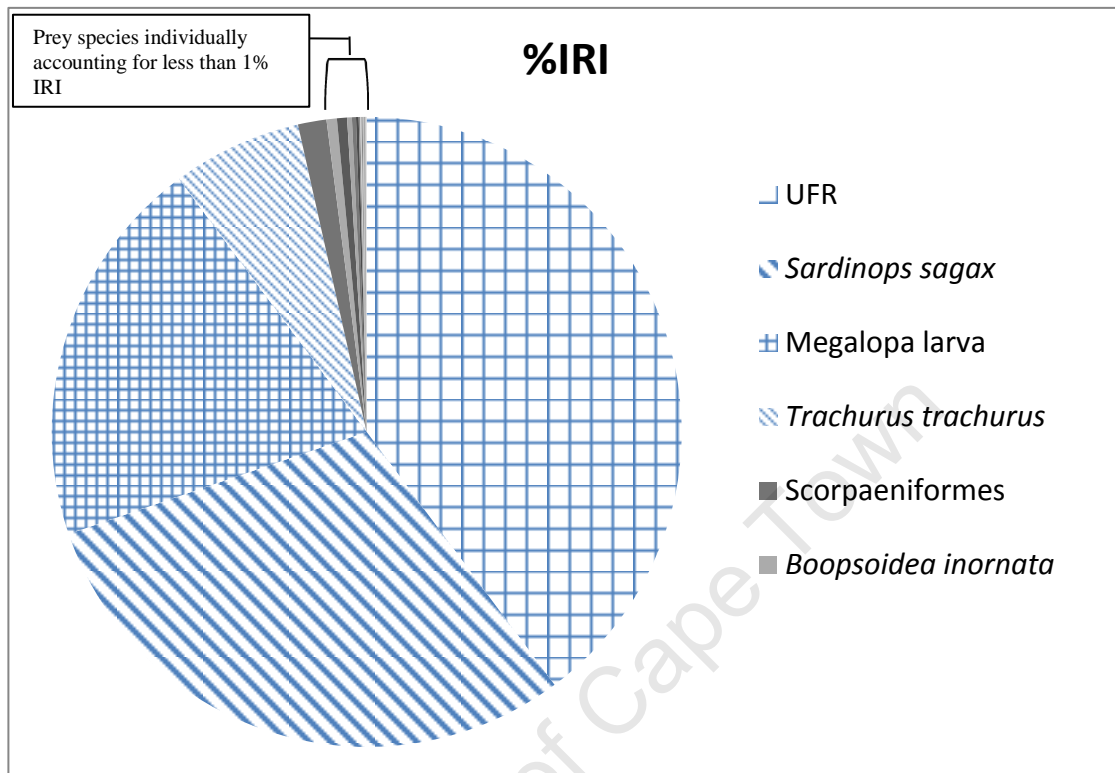


Figure 2.2: Pie chart displaying the percentage IRI of main prey species in the overall diet of *S. lalandi* in the Western Cape, South Africa. UFR-Unidentified fish remains.

Table 2.1: Prey items from stomachs of *S. lalandi* in the Western Cape with percentage number (% N), percentage weight (% W), frequency of occurrence (% F) and index of relative importance (% IRI). UCR-Unidentified crustacean remains, UFR-Unidentified fish remains, USR-Unidentified squid remains.

Species	% N	% W	% F	% IRI
<b>Crustaceans</b>				
<b>Class total</b>	<b>37.17</b>	<b>2.94</b>	<b>20.97</b>	<b>7.19</b>
Amphipoda spp.	0.40	0.05	3.23	0.04
<i>Euphausia lucens</i>	0.20	0.03	1.61	0.01
Euphausia spp.	0.81	0.04	3.23	0.08
<i>Gastrosaccus psammodytes</i>	0.20	0.05	1.61	0.01
Crab megalopa	34.75	2.48	19.35	20.09
<i>Themisto gaudichaudi</i>	0.61	0.11	3.23	0.06
UCR	0.20	0.20	1.61	0.02
<b>Teleosts</b>				
<b>Class total</b>	<b>51.92</b>	<b>93.90</b>	<b>74.19</b>	<b>92.50</b>
<i>Boopsoidea inornata</i>	0.20	11.61	1.61	0.53
<i>Decapterus macrosoma</i>	0.61	0.16	1.61	0.03
Hemiramphidea	0.81	1.92	3.23	0.25
<i>Sardinops sagax</i>	5.86	60.64	16.13	29.91
<i>Scomberesox saurus</i>	0.61	3.21	4.84	0.52
Scorpaeniformes	6.46	1.65	6.45	1.46
Sparidae	0.20	0.08	1.61	0.01
<i>Trachurus trachurus</i>	15.35	5.80	11.29	6.66
UFR	21.82	8.82	50.00	39.83
<b>Cephalopods</b>				
<b>Class total</b>	<b>2.17</b>	<b>1.17</b>	<b>9.68</b>	<b>0.28</b>
<i>Loligo vulgaris</i>	0.61	0.94	4.84	0.21
<i>Argonauta argo</i>	0.20	0.05	1.61	0.01
USR	1.37	0.18	5.36	0.14
<b>Polychaeta</b>				
<b>Class Total</b>	<b>0.69</b>	<b>0.07</b>	<b>1.61</b>	<b>0.01</b>
Polycheata	0.69	0.07	1.61	0.01
<b>Bivalvia</b>				
<b>Class total</b>	<b>1.38</b>	<b>0.08</b>	<b>1.61</b>	<b>0.02</b>
<i>Perna perna</i>	1.38	0.08	1.61	0.02

There was a significant difference in prey composition between sample locations ( $R = 0.181$ ,  $P < 0.005$ ). Dassen Island clustered separately to False Bay and Struisbaai, showing it to be the least similar of the three sites (Figure 2.3). Bony fish were the dominant prey group at all three sampling locations, accounting for 73.36 %, 99.53 % and 99.97 % of the prey importance (IRI) for Dassen Island, Struisbaai and False Bay respectively (Table 2.2). Bony

fish were however less important at Dassen Island where crustaceans accounted for 26.01 % IRI (Table 2.2). Megalopa crab larvae were the most important taxon at Dassen Island with an IRI of 45.87 % and accounted for 54.40 % by number. Sardine was the second most important species with an IRI of 16.95 % and accounted for 82.54 % by weight (%M).

False Bay showed less dominance by individual species, UFR accounted for 54.53 % IRI and sardine ranked second at 23.23 % IRI. Both scorpaeniformes species and horse mackerel contributed large portions by number at 30.43 % and 16.13 % respectively. Horse mackerel was found to be the most important species at Struisbaai with an IRI of 40.99 %, also making up 63.73 % by number and was found in 21.42 % of stomachs. UFR was found to be the second most important prey type with an IRI of 40.13 % and was found in 50 % of stomachs (% F).

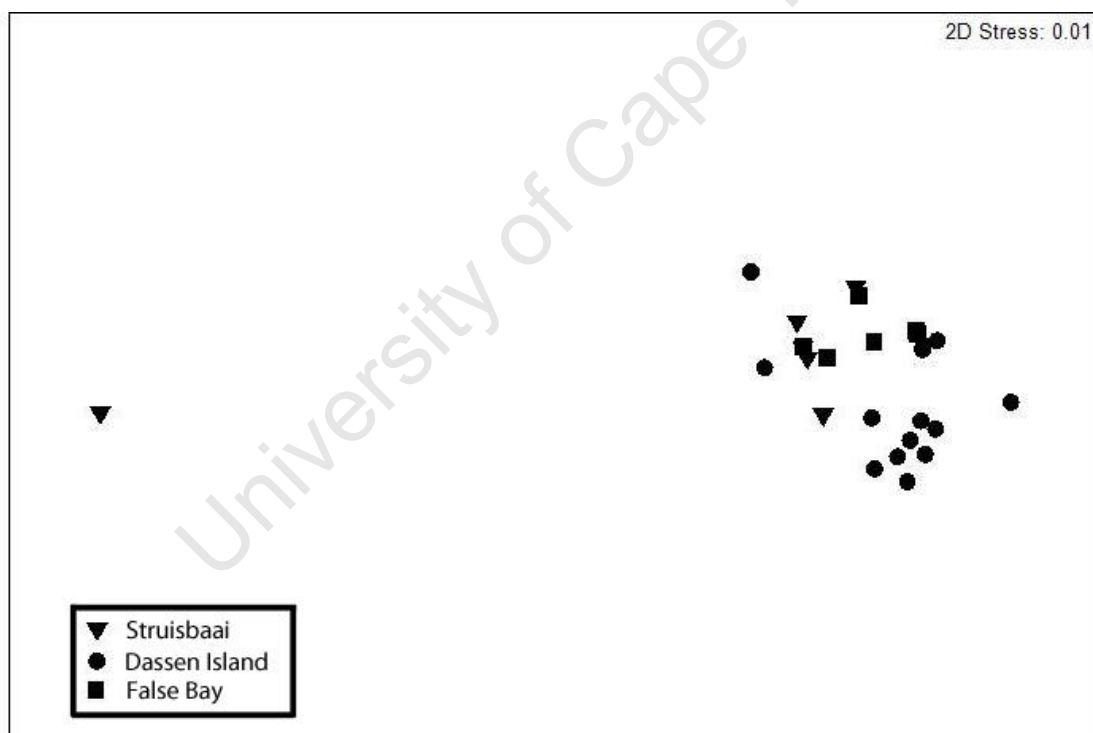


Figure 2.3: MDS plot showing similarity of prey composition among three sample locations for *S. lalandi* (n=24).

Table 2.2: Percentage IRI of the top three most important taxa at the three main sampling regions for *S.lalandi*.

	TELEOSTS	CRUSTACEANS	CEPHALOPODS
Dassen Island	73.36	26.01	0.49
False Bay	99.87	0.08	0.05
Struisbaai	99.53	0	0.47

## DISCUSSION

*Seriola* species are known to be opportunistic generalist feeders preying on small pelagic fish, crustaceans and squid (Baxter 1960, Nepgen 1982, Schmitt and Strand 1982, Crooke 2001, Vergani 2005, Scandol et al. 2008). The diet of yellowtail in South African waters represents that of a generalist feeder with small pelagic fish being the primary prey group.

The prey species making up the diet of yellowtail are highly cosmopolitan with species such as the anchovy, sardine and squid being most important in their diet globally. Baxter (1960) and Nepgen (1982) conducted dietary studies on yellowtail previously and found similar results. The exception being the negligible importance of cephalopods in this study, where cephalopods accounted for up to 23 % by frequency of occurrence (% F) in Nepgen's (1982) study. In the current study, cephalopods were found in relatively few stomachs, contributing little to the overall diet of yellowtail. The highly variable biomass of squid may also play a role as samples were only collected for a short period which could correspond to a low biomass period for squid (Roberts 2005).

All dominant species found in the diet of yellowtail are species known to aggregate in high densities or form large shoals, such as sardine, horse mackerel and crab megalopa in this study. The shoaling behaviour of yellowtail allows them to target other active shoaling species with great success through cooperative foraging. Schmitt (1982) observed yellowtail actively hunting horse mackerel through group cooperation with several individuals herding and taking turns attacking shoaling prey. Yellowtail are a high energy species and may have to expend large amounts of energy locating shoaling prey (Pirozzi and Booth 2009), however, targeting high density shoaling species allows for potentially high energy gain by acquiring prey in high numbers.

Nepgen (1982) recorded yellowtail having stomach contents comprising of 58 % pelagic fish species and of the top six recorded species in his study only one (*Octopus granulatus*) is not found in high densities/shoals. A similar trend was also found by Baxter (1960) where the top four most important species are all known to occur in high densities. Nepgen (1982) recorded anchovy, sardine and horse mackerel as the three highest teleost species by % F. In the current study anchovy was entirely absent in the diet of yellowtail, however sardine and horse mackerel are recorded in the top three teleost species in this study (Figure 2.2). The lack of anchovy may be due to misidentification as their overall body shape is similar to that of sardines. The rapid digestion rates of yellowtail were also responsible for breaking down distinguishing features before identification could be made. Fluctuation in anchovy biomass can reach an order of magnitude and may explain their dominance in the diet of yellowtail in Nepgen's (1982) study (Hampton 1987) and absence in the current study. These fluctuations seen in small pelagic species in the Benguela may explain the shift in importance of species between the diet in the current study and that of Nepgen (1982).

Opportunistic pelagic feeders can be efficient biological samplers of locally available prey species through analysis of stomach contents (Potier et al. 2007). The effectiveness of yellowtail as a sampler of its habitat would depend on them not preferring one prey species. They however appear to be true generalists and feed on the most abundant accessible prey available. Cape gannets have been identified as good species specific indicators of sardine abundance in the Benguela because of the amount of sardine in their diet (Berruti 1987). The current diet of yellowtail may be reflecting a period where sardines are more accessible than anchovy locally. Due to the relatively small sample size used in this study it is unlikely that a full array of available prey species has been sampled.

UFR accounted for the highest % IRI in this study (Figure 2.2). This prey group is likely to be made up of a number of the most important fish species identified. The size range of UFR samples emphasizes that yellowtail is feeding on small fish. The average size of UFR samples was only 40 mm (5.8 % of yellowtails FL) with UFR seldom exceeding 60 mm. Identified horse mackerel were most commonly found in this size range, suggesting that a high proportion of the UFR could belong to this species. However the rapid rate of digestion made identification difficult. Further processing and identification of UFR may have decreased its importance as a prey group and added to the importance of individual species.

Differences between sampling regions were expected due to the differing environmental conditions of each region. Crab megalopa were the dominant prey species at Dassen Island occurring in the highest numbers (% N) and at the highest frequency (% F). Crab megalopa were absent at all other sample sites. The high importance observed in the Dassen Island samples concurs with the higher inshore concentration of zooplankton during winter months when upwelling on the west coast reduces in strength (Shannon and Pillar 1986). Ram suspension feeding has been observed in amberjack while feeding on small prey species (Sanderson et al. 1996). It is likely this method was also utilized by yellowtail while feeding on crab megalopa due to their similar morphology to amberjack.

Sardine was found in stomachs at all three sites and was highly important at False Bay and Dassen Island but was of little importance at Struisbaai. Sardine was commonly the largest (~21 % of yellowtail FL) prey item taken by yellowtail and accounted for the largest weight (% W) at Dassen Island and False Bay. They were however found in low numbers (% N) and in few stomachs (% F). The largest individual prey item recorded was an individual fransdam (*Boopsoidea inornata*) with a weight of 175.1 g, but this species was only recorded on this single occasion at Struisbaai.

Horse mackerel were the third most important species overall. They were present in stomachs at all three sample sites, but were of little importance at Dassen Island. The small size (~5.8 % of yellowtail FL) of horse mackerel found in stomachs means they only became important when found in high numbers, as seen at False Bay and Struisbaai. Some seasonality may be affecting the variation in diets between sites as summer samples came exclusively from False Bay and Struisbaai, while samples from Dassen Island came from late winter.

The use of compounded indices such as the IRI in dietary analysis is a useful tool and can greatly improve our understanding of the biology and habits of a species. They should however be used in conjunction with the individual indices they are comprised of in order to gain an understanding of which species are truly important. The differences seen in the diet between regions in the Western Cape and the array of species found in the diet of yellowtail suggests that they will feed on the most abundant accessible prey. The differences seen between the diet described by Nepgen (1982) and this study are likely due to the change in abundance in prey available to yellowtail. Further study on the diet of yellowtail will

undoubtedly add to the list of prey species, but is unlikely to change the overall trends found in this study.

University of Cape Town

## CHAPTER 3:

# **THE REPRODUCTIVE BIOLOGY OF *SERIOLA LALANDI* IN SOUTH AFRICA**

### **ABSTRACT**

The reproductive characteristics of *Seriola lalandi* were documented from samples collected from 1971 to 2010. Samples were collected from the South Coast, False Bay and the West Coast of South Africa. Oocyte development and distribution showed weak multiple group synchronous gamete development. No females were recorded having hydrated oocytes. Histological validation of macroscopic staging criteria revealed that active and developing ovaries are more commonly staged incorrectly. A protracted spawning season from November to February peaking in December and January was observed. Females matured at 550 mm FL ( $L_{50}$ ) (95 % CI = 532 - 570 mm), while males matured at a larger size of 585 mm FL ( $L_{50}$ ) (95 % CI = 555- 619 mm). The smallest mature male observed in this study was 520 mm FL and 100 % of males were mature above 820 mm FL. The smallest mature female observed in this study was 520 mm FL and 100 % of females were mature above 780 mm FL. The ability to spawn at a relatively small size and on multiple occasions within a spawning season gives yellowtail a high probability of having successful annual recruitments.

## *INTRODUCTION*

Reproductive strategies are governed to a large extent by the environment and natural selection favours those making the greatest contribution to future generations. This process will lead to variations in reproductive strategies between and within species, promoting the fitness of future generations. Commonly, size at maturity, fecundity, spawning period and frequency of spawning show the greatest variation.

The periodicity of spawning is variable among species and distinct to certain reproductive strategies. Synchronous spawners will spawn only once in a season or lifetime, releasing all eggs during one event (Helfman et al. 2009). More commonly eggs will be released on multiple occasions during a spawning season as in batch spawning species (Helfman et al. 2009). The period in which spawning occurs will often be linked to a season when egg and larval survival will be highest. The timing of the spawning season can be linked to biotic variables such as food availability as the match-mismatch theory suggests (Cushing 1975) and physical variables such as inshore larval retention as the member-vagrant hypothesis suggests (Sinclair 1988). The length of the spawning season will be influenced by the type of spawning strategy displayed by a fish species and the environmental conditions under which it spawns. The success of spawning may vary between seasons due to annual fluctuations of environmental variables (King and McFarlane 2003). The spawning season can be identified by monitoring trends in the gonadosomatic index (GSI) which will increase and peak during the spawning season. The presence of ripe gonads and post-ovulatory follicles (POF's) can give a more detailed indication as to when the spawning season will begin and end (Hunter and Goldberg 1980).

The sizes of eggs spawned by fish are a tradeoff between quantity and quality. Producing small eggs in large quantities increases the chances of eggs hatching in a 'patch' where conditions are favorable, but individual survivorship is lower per egg (Durate and Alcaraz 1989). Producing fewer large eggs increases individual survivorship, but at the risk of the few spawned eggs hatching in unfavorable conditions (Durate and Alcaraz 1989).

Most marine fishes have high fecundity, producing thousands to millions of eggs annually (Reynolds et al. 2001). Estimating the annual fecundity of fish species is vital in fisheries management for assessing the reproductive potential of the species and potential stock size

(Maack and George 1999). Annual fecundity of a fish species is defined as the number of yolked oocytes matured by a female (Murua et al. 2003). Techniques used to estimate annual fecundity are based on a number of assumptions which vary between and within species according to their specific reproductive strategy (Murua et al. 2003) and spawning location (Witthames et al. 1995). A species may have a fixed fecundity where all yolked oocytes present before the onset of the spawning season is equivalent to the annual fecundity, as with species displaying determinate fecundity (Murua et al. 2003). Species with indeterminate fecundity are able to mature new oocytes during the spawning season and therefore fecundity is not fixed (Murua et al. 2003). Spawning on multiple occasions during the spawning season such as in multiple group synchronous species makes determining annual fecundity more difficult. In these species fecundity estimates are based on a single batch of eggs and scaled up according to the number of batches released in a spawning season. Batch fecundity can be used to estimate annual fecundity if the frequency of spawning is known and specimens with fully mature hydrated eggs are attainable (Murua et al. 2003).

Size at maturity in fish is a trade-off between reproducing successfully at a larger size and the risk of mortality before reproducing (Helfman et al. 2009). Within a specific life-history strategy a number of variables will affect when and at what size a species will mature. Mortality rates, temperature and growth rates are all potential factors affecting the size at which a species will attain maturity (Stearns and Koella 1986). Commonly, length at maturity is estimated to be the length at which 50 % of the population is mature ( $L_{50}$ ), which may vary between populations of the same species (Yoneda and Wright 2004). Estimating  $L_{50}$  for a population is particularly useful to guide fishery management plans that set a minimum size limit on a fish species based on length at maturity. This is used to protect immature individuals from being removed from the population before contributing to it.

A number of studies have documented various aspects of the reproduction of yellowtail in captivity (Kolkovski and Sakakura 2004, Katsunori et al. 1997, Moran et al. 2007) and other *Seriola* species. (Garcia and Diaz 1995, Micale et al. 1999, Mylonas et al. 2004, Jerez et al. 2006). The reproductive biology of yellowtail has been documented by a number of studies throughout its natural distribution. Baxter (1960) was the first to document the spawning of female yellowtail in the waters off the Californian coastline. Penney (1982) made

observation on the spawning season of yellowtail in South African waters. Gillanders (1999b) produced the first full account of the reproductive characteristics of the species followed by Poortenaar et al. (2001) and Shiraishi et al. (2010). Gilchrist (1903) and Bronwell (1979) documented the eggs of yellowtail sampled from False Bay, South Africa. A summer spawning period was documented in all studies for yellowtail. In the northern hemisphere Shiraishi et al. (2010) documented an early summer spawning period which peaked in May, while Baxter (1960) documented a late summer period which peaked in June. All three studies done on yellowtail in the southern hemisphere documented elevated spawning periods between November and January with peaks in December (Penney 1982, Gillanders et al. 1999b, Poortenaar et al. 2001).

Only Baxter (1960) noted an actual spawning event; large shoals of yellowtail were observed swimming in small circles and spawning eggs and milt 112 km offshore in 95 m of water on the Uncle Sam Bank in California. The presence of yellowtail larva and eggs found on the Agulhas Bank suggests that their spawning grounds are 6 - 20 km offshore of the South African coastline (Penney 1982). Mature oocytes have been found in the ovaries of yellowtail throughout the spawning season indicating that the species is capable of multiple spawning events within one season (Baxter 1960, Poortenaar et al. 2001). A similar spawning strategy was documented for amberjack (Marino *et al.* 1995) and it is likely that all *Seriola* species follow a similar strategy.

Lengths at maturity for yellowtail were found to be variable between populations (Baxter 1960, Gillanders et al. 1999b, Poortenaar et al. 2001, Shiraishi et al. 2010). Variation in growth and maturity between populations are not uncommon and can often be linked to differences in environment (Hewett and Kraft 1993). Length at first maturity for female yellowtail ranged between 506 - 775 mm fork length (FL) (Baxter 1960, Gillanders et al. 1999b, Poortenaar et al. 2001, Shiraishi et al. 2010). Length at 50 % maturity for female yellowtail ranged between 843 - 944 mm (FL) in studies done by Gillanders et al. (1999b) and Poortenaar et al. (2001) respectively. Both these studies found that most fish harvested in the Australian and New Zealand fisheries were under the size at which 50 percent ( $L_{50}$ ) of the population was mature.

The aim of this study is to document the reproductive characteristics of yellowtail in South African waters. Aspects of the reproductive biology investigated include a description of the

various stages of ovarian development, the length-frequency distribution of oocytes in females, length at 50 % maturity ( $L_{50}$ ) and extent of the spawning season

## *METHODS*

### *SAMPLE COLLECTION*

Seventy-one yellowtail were sampled by rod and reel and spearfishing from ski-boats from January 2011 to November 2012. Yellowtail data from 6149 fish collected during DAFF (Department of Forestry and Fisheries) surveys between 1974 and 2010 were also used for reproductive analysis.

### *PREPARATION AND ANALYSIS OF GONADS*

Gonads were removed from each fish ( $n = 71$ ), staged macroscopically (Table 3.1), weighed to the nearest 0.01 g and preserved in 10 % buffered formalin. Samples of roughly 5 mm thickness were taken from the anterior, distal and proximal regions of both gonad lobes, these were dehydrated and set in paraffin wax. Sections were then cut (5 - 10  $\mu\text{m}$ ) and stained using Mayers haematoxylin and eosin stain. Ovaries were then staged microscopically based on the most mature stage oocyte present. A number of previous studies documenting the ovarian development of yellowtail were used as a guideline (Gillanders et al. 1999b, Poortenaar et al. 2001, Shirashi et al. 2010). Histological sections were taken from anterior, middle and posterior ovarian sections to check for consistency of oocyte distribution. Macroscopic staging criteria were validated through microscopic observations made on females in each stage of development.

An additional three representative samples (0.1 g) were taken from the anterior, middle and posterior section of mature ovaries. The sample was agitated to separate oocytes from remaining tissue and placed in a petri dish. Digital images were taken of all oocytes in each representative sample using a dissecting microscope. The first 1000 oocytes in each sample were measured using Image J software (<http://rsbweb.nih.gov/ij/>). Samples were taken from either ovary lobe as oocytes are known to be equally distributed between the left and right lobes (Poortenaar et al. 2001).

## MATURITY

Only fish collected between 1985 and 2012 along the South African coast line were used to estimate length at maturity, as data collected prior to this period was considered unreliable (C. Wilke pers. comm, Department of Agriculture, Forestry and Fisheries). Only fish sampled in December and January were used to calculate  $L_{50}$  for male ( $n = 138$ ) and female ( $n = 150$ ) yellowtail as this was deemed the peak spawning season. The gonad stage was determined macroscopically (Table 3.1) and individuals with active (stage 2) and above gonads were considered mature for both sexes.  $L_{50}$  was calculated by fitting a logistic ogive (Equation 3.1) to the observed proportion of mature male and female yellowtail per 25 mm length class.

Table 3.1: Criteria for macroscopic staging for male and female *S. lalandi*, with corresponding histological observations for females. Adapted from Gillanders et al. (1999b) and Poortenaar et al. (2001). CN- Chromatin nuclear, PN- Perinuclear, GV- Germinal vesicle, CA- Cortical aveolar, V- Vitellogenic, GVM- Germinal vesicle.

Maturity stage	Macroscopic condition	Histological condition
<b>Females</b>		
(1) Immature	Ovary lobes are oval in shape and thread-like at less than 60 mm in length.	Only CN and PN stage oocytes visible.
(2) Active	Ovary lobes rounded in shape and much larger in size than in immature fish.	Most mature oocytes present are in the CA stage.
(3) Developing	Ovary lobes rounded and greater than 60 mm in length.	Most mature oocytes present are in the V stage, CA dominate by number.
(4) Late Developing	Ovary large and yellow in colour with oocytes becoming visible.	Most mature oocytes present are in V and GVM stage and dominate numerically.
(5) Ripe	Ovary firm and large mature and hydrated oocytes are visible.	Most mature oocytes are in GVM and hydrated stages, POF's may be present.
(6) Spent	Ovary flaccid, decreased in size and bloody, no oocytes are visible.	Mature oocytes may be present, but undergoing atresia.
<b>Males</b>		
(1) Immature	Thread-like lobes.	.
(2) Active	Elongated, oval to triangular in cross-section.	.
(3) Mature	Elongated, larger in size and triangular in cross-section, pink tinge.	.
(4) Ripe	Large and soft, creamy white in colour, milt present in main duct.	.

The logistic ogive is described as:

$$P_l = \frac{1}{\left(1 + e^{\left(\frac{l-l_{50}}{\delta}\right)}\right)} \quad \text{Equation 3.1}$$

where  $l$  is the midpoint of each size class,  $P_l$  is the proportion of mature fish in size class  $l$ ,  $l_{50}$  is the length at which 50 % of the sex is mature and  $\delta$  is the width of the ogive. The model was fitted to the data by minimising the negative log likelihood function of the form:

$$-\ln(L) = \sum_l (m_l \ln(\hat{P}_l) + (n_l - m_l) \ln(1 - \hat{P}_l)) \quad \text{Equation 3.2}$$

where  $m_l$  is the number of mature fish in size class  $l$ ,  $n_l$  is the total number of fish in size class  $l$ , and  $\hat{P}_l$  is the predicted proportion of mature fish.

A conditioned parametric bootstrap procedure was used to estimate the 95 % confidence intervals for  $l_{50}$  and  $\delta$  as well as the expected proportion of mature fish in each size class,  $\hat{P}_l$  (Efron and Tibshirani, 1986). For this purpose, 1000 'new' datasets were generated by drawing  $n_l$  random Bernoulli variables (0 = immature; 1 = mature) as a function of  $\hat{P}_l$  to obtain new random observations of proportions of mature fish for each size class  $l$ ,  $\tilde{P}_l$ . The logistic ogive model was fitted to each random dataset and the percentile method (Buckland 1984) was applied to estimate the 95 % confidence intervals from the resulting bootstrap vectors, where the 2.5 % and 97.5 % percentiles were chosen to obtain the lower and upper 95 % confidence intervals respectively.

#### *ANALYSIS OF HISTORICAL RECORDS*

The records of 6149 yellowtail captured between 1974 and 2010 by a number of methods, namely rod and reel, hand line, spearfishing, beach seine and purse seine netting were examined. A chi-square test was used to determine whether the sex ratio differed significantly from a ratio of 1:1. Samples were collected and processed by different government agency personnel conducting fisheries surveys. During these surveys total length (TL), fork length (FL), total weight, gonad weight, sex, date and location of capture were recorded. Unfortunately various macroscopic gonad staging protocols were used over the years and these details were not consistently recorded in the database, which made the

use of assigned gonad stages un-reliable. Because gonad weights and fish weight were deemed to be reliable, GSI was used to infer the maturity stage. GSI was calculated as follows;

$$GSI = \frac{\text{gonad weight}}{\text{total weight}} \quad \text{Equation 3.3}$$

A gonadosomatic index (GSI) backstaging procedure was used to standardize the maturity of fish recorded in the historical database. The mean GSI per gonad stage of fish captured between 2010 and 2012 was used to estimate the stage of fish in the historical records based on their GSI values. The geometric mean of mean GSI values of successive stages was used to set limits of the GSI of each gonad stage for male and female yellowtail in the database. The geometric mean was calculated as follows;

$$L_{n,n+1}^S = \sqrt{\overline{GSI}_n^S + \overline{GSI}_{n+1}^S} \quad \text{Equation 3.4}$$

where  $L_{n,n+1}^S$  is the limit between stage  $n$  and  $n + 1$ ,  $S$  is the sex,  $n$  is gonad stage,  $\overline{GSI}_n^S$  is the mean of the GSI for gonad stage  $n$ .

The set of limits calculated with Equation 3.4 was used to classify the gonad stage of fish for which macroscopic evaluations were unavailable (Appendix 2).

Histological observations were used to refine the macroscopic staging criteria (Table 3.1) used to stage the gonads. Maturity corresponded to active (stage 2) gonads or higher stages in male and female yellowtail. The cut-off limit for mature fish was then set at a GSI of 0.3 and 0.7 for males and females respectively.

## RESULTS

Of the 71 yellowtail collected 35 were male ranging from 500 to 911 mm FL and 36 were female ranging from 488 to 916 mm FL. Samples came from the Dassen Island, Table Bay, False Bay and Struisbaai (Chapter 2, Figure 2.1). A total of 4087 fish with recorded sexes were used from the historic records. In the length-weight regression of which 1902 were males ranging in size from 340 mm FL to 1110 mm FL and 2185 were female ranging in size from 380 mm FL to 1290 mm FL. A total of 1945 samples were available from the period

1985 to 2010 in the historic records, of which 925 were males ranging from 340 to 1110 mm FL and 1020 were female ranging from 420 to 1290 mm FL.

### *HISTOLOGICAL OBSERVATIONS*

Immature ovaries were characterised by only previtellogenic oocytes. Chromatin nuclear (CN) stage oocytes were present along with more mature perinucleolar stage (PN) oocytes where the germinal vesicle (GV) had increased in size and numerous nucleoli appeared around the periphery of the GV (Figure 3.1 A).

Active ovaries were characterized by primary yolk vesicle oocytes, these are cortical alveolar (CA) oocytes. PN oocytes were still numerous while the number of CN oocytes had decreased (Figure 3.1 B).

Developing ovaries, in the vitellogenic stage were characterised by the presence of secondary yolk vesicle oocytes or vitellogenic oocytes (V) where oocyte size increased substantially and yolk proteins become visible from the eosin stain. PN and CA oocytes were still dominant at this stage (Figure 3.1 C).

Late developing ovaries were characterised by presence of tertiary yolk vesicle oocytes which then began germinal vesicle migration (GVM). This is when the germinal vesicle begins to move towards the periphery of the oocyte and yolk globules merge and increased in size. V and GVM stage oocytes dominate by volume (Figure 3.1 C). Post-ovulatory follicles (POF's) were present in some instances at this stage (Figure 3.1 E).

GVM stage oocytes were extremely rare and only a few were observed in mature ovaries. They were always found in conjunction with POF's indicating that spawning had recently occurred and may explain the low numbers. Atretic cells were also apparent in some mature fish, but were difficult to identify (Figure 3.1 F). These cells are indicative of oocyte degeneration and reabsorption (Geten et al. 2009). This may occur if oocytes are not ovulated or the body condition of the fish deteriorates.

All subordinate ovary stages were present in mature ovaries with mature oocyte (V and GVM) stages dominating but CN, PN and CA oocytes were present in high numbers.

GVM stage oocytes were the most mature oocytes observed during histological examinations, but were rare and only seen in one fish. No hydrated oocytes were present

in mature ovaries in this study. POF's were however found along with atretic oocytes indicating that spawning had occurred recently. Atretic oocytes were found in extremely low numbers in individuals during the peak spawning season indicating that they would likely spawn again and were not yet spent.

#### *OOCYTE LENGTH-FREQUENCY DISTRIBUTION*

Oocyte distribution was found to be homogenous throughout the lobes of mature yellowtail ovaries. All oocyte stages present were found in similar numbers at anterior, distal and proximal regions of the ovary lobes (Figure 3.3). Oocytes smaller than 0.1 mm in diameter dominated by number, accounting for 54 % of oocytes counted. Two cohorts of oocytes can be seen, a large group of smaller immature oocytes and a second group of larger oocytes growing towards maturation above 0.6 mm (Figure 3.2). The small size of the second cohort is due to the absence of maturing and fully hydrated eggs larger than 1 mm diameter. These oocytes would give better definition to the second cohort. Oocytes in the second cohort are likely to undergo the final stages of maturation and form part of the clutch of oocytes released during the next spawning event of the season.

Batch fecundity could not be estimated due to the extremely low abundance of GVM and hydrated eggs.

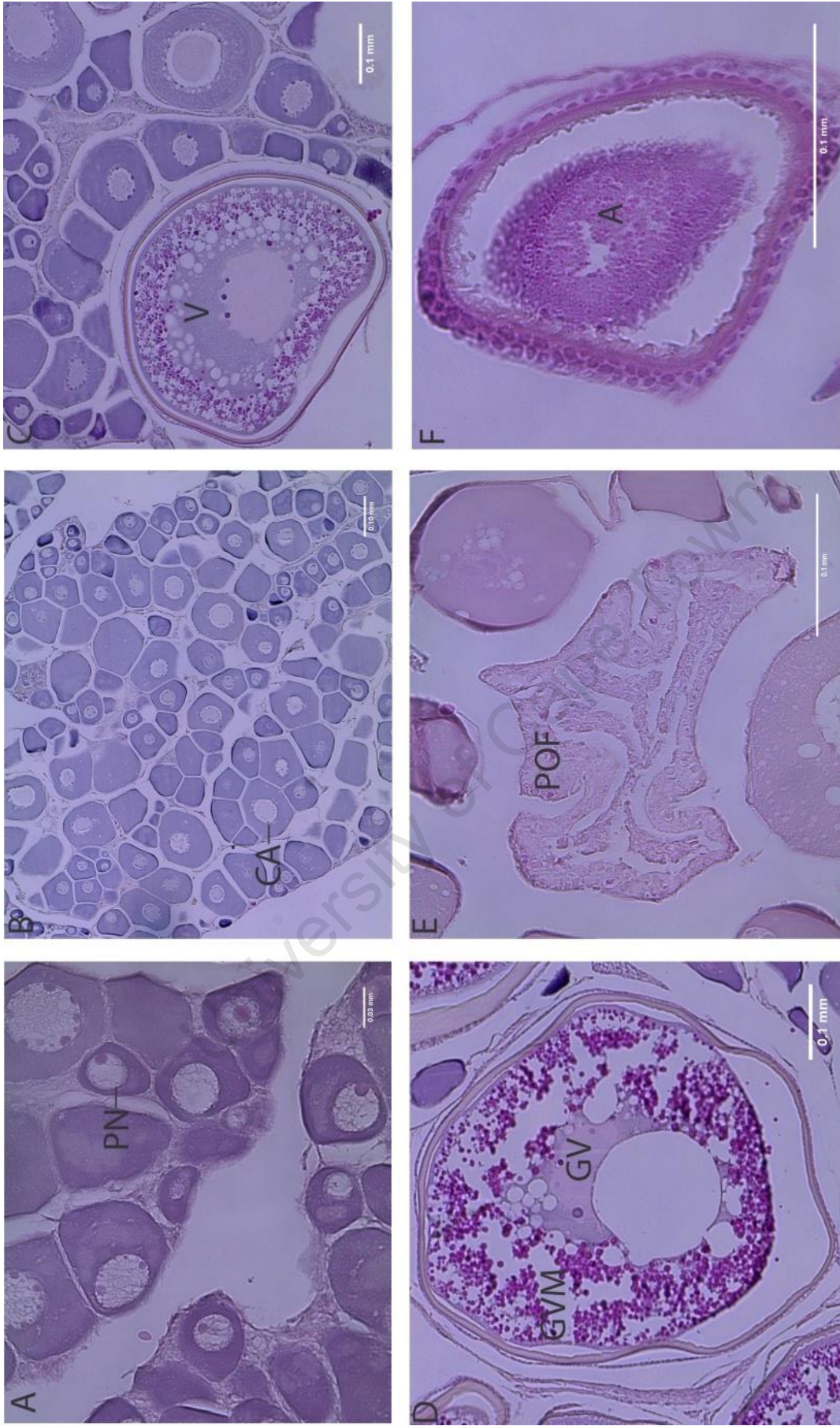


Figure 3.1: Histological sections through ovaries of *S. lalandi* individuals in various stages of maturation; A) stage two ovary (active), C) stage three ovary (developing), D) stage four ovary (maturing), E) stage five ovary (mature), F) stage six ovary (post-ovulatory follicle just after spawning) atretic oocyte. PN; perinucleolar stage; CA, cortical alveolar; V; vitellogenic; GVM; germinal vesicle migration; GV; germinal vesicle, POF; post-ovulatory follicle, A; atretic oocyte .

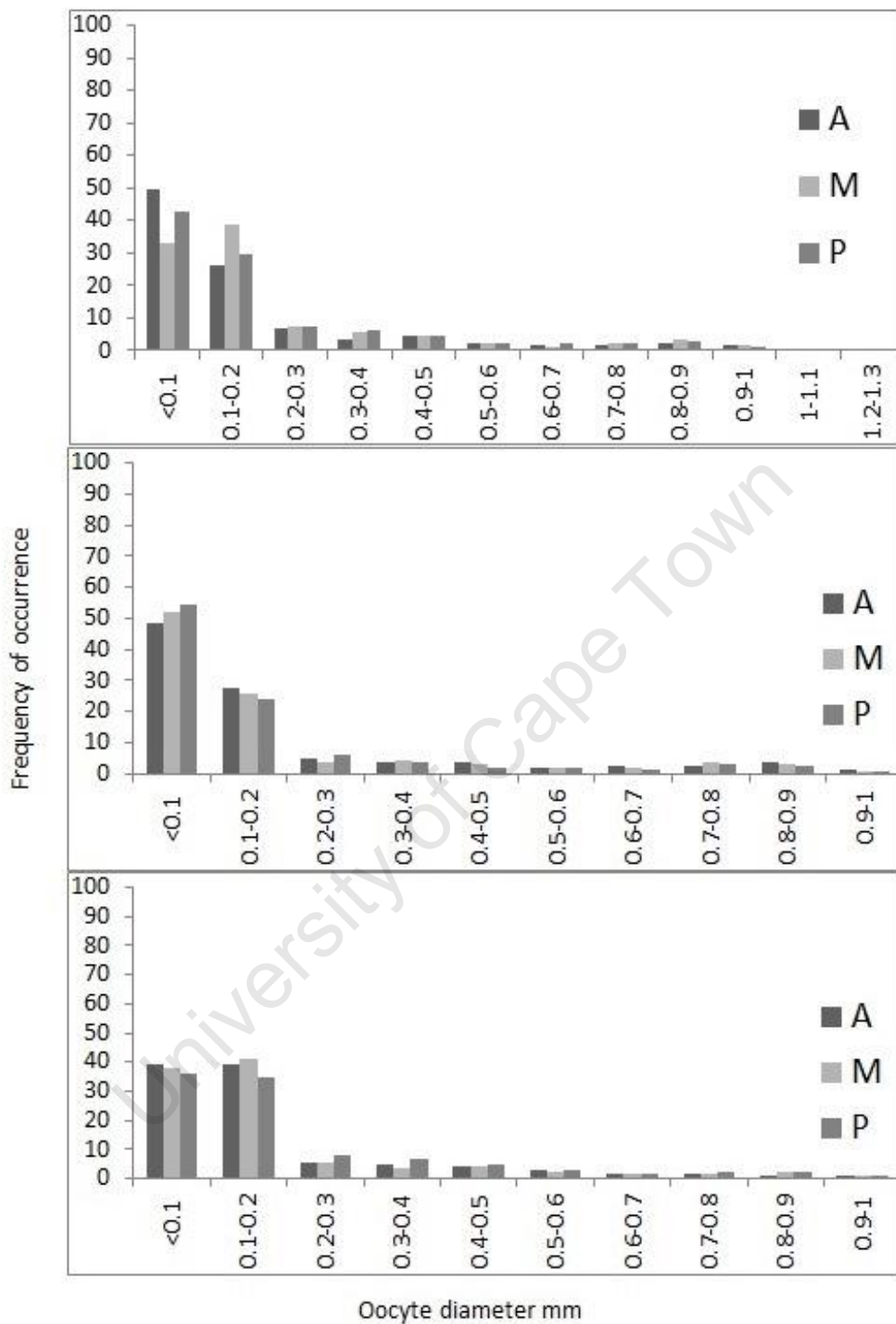


Figure 3.2: Similarity of oocyte diameters between three regions (A; Anterior, M; Middle and P; Proximal) in the ovaries of three mature *S. lalandi* in the spawning season, indicating that oocyte distribution is consistent throughout the ovary.

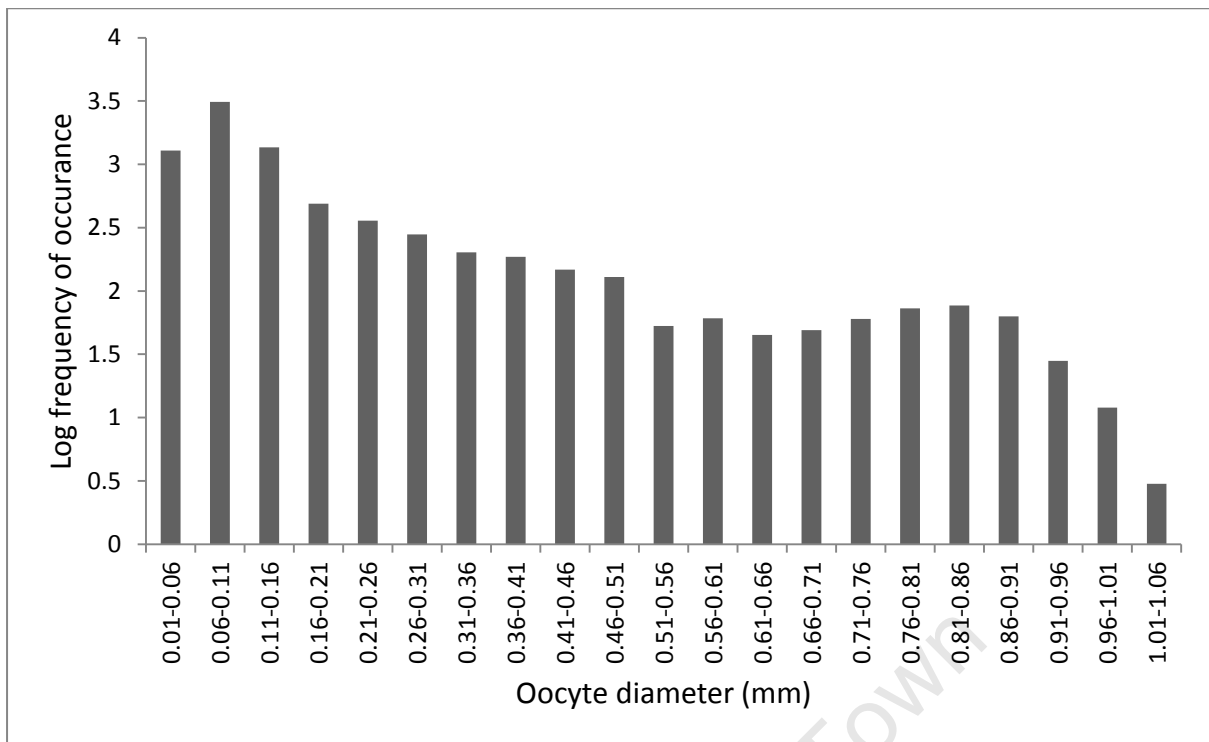


Figure 3.3: Log scale of oocyte diameter distributions in 0.5 mm classes from three ripe female *S. lalandi*. (n = 8084)

#### SEX RATIO

A total of 6220 specimens were sampled from 1974 to 2012, ranging in size from 340 mm FL to 1290 mm FL, including fish sampled during this study (2011 - 2012) (Figure 3.4). Of these (with recorded sexes) 1914 were male and 2199 female. A sex ratio of 1:1.15 males to females was found not to be significantly different from 1:1 ( $\chi^2 = 19.74$ ,  $df = 1$ ,  $p > 0.05$ ).

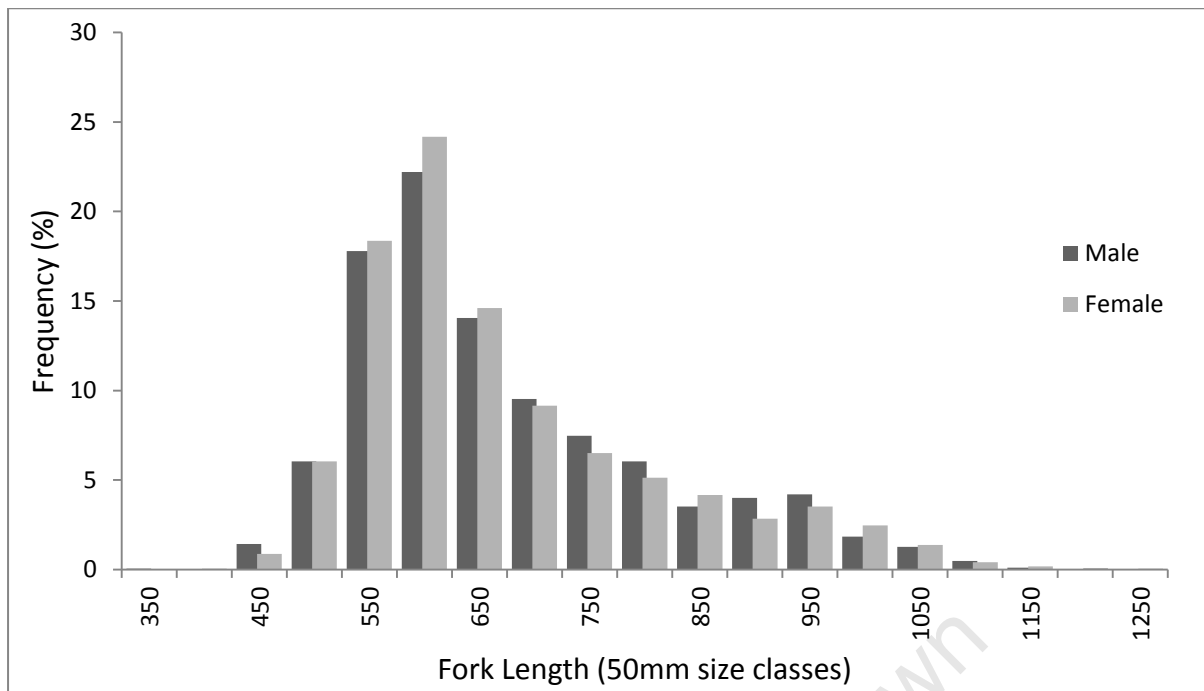


Figure 3.4: Size frequency histogram for male and female *S. lalandi* in 50 mm size classes. n = 4113.

#### ANNUAL REPRODUCTIVE CYCLE

The gonadosomatic index (GSI) was elevated between November and February for both males and females (Figure 3.5). Mean GSI for males and females peaked in January at 1.79 % and 1.42 % respectively (Figure 3.5). Mean GSI values decreased rapidly from the beginning of March reaching low's of 0.2 % and 0.68 % in August for males and females respectively (Figure 3.5). A brief winter peak in GSI was observed in both males and females (Figure 3.5). Grouping mean GSI values for combined male and female yellowtail into 5-year increments revealed similar trends over all the year groupings, with peaks and lows being found at the same times of year among time periods (Figure 3.6). Fish with mature gonads were present throughout the year for both males and females. Ripe gonads were present in males from November to March and from September to March for females with the highest proportion of ripe gonads for both sexes in January (Figure 3.7 A and B).

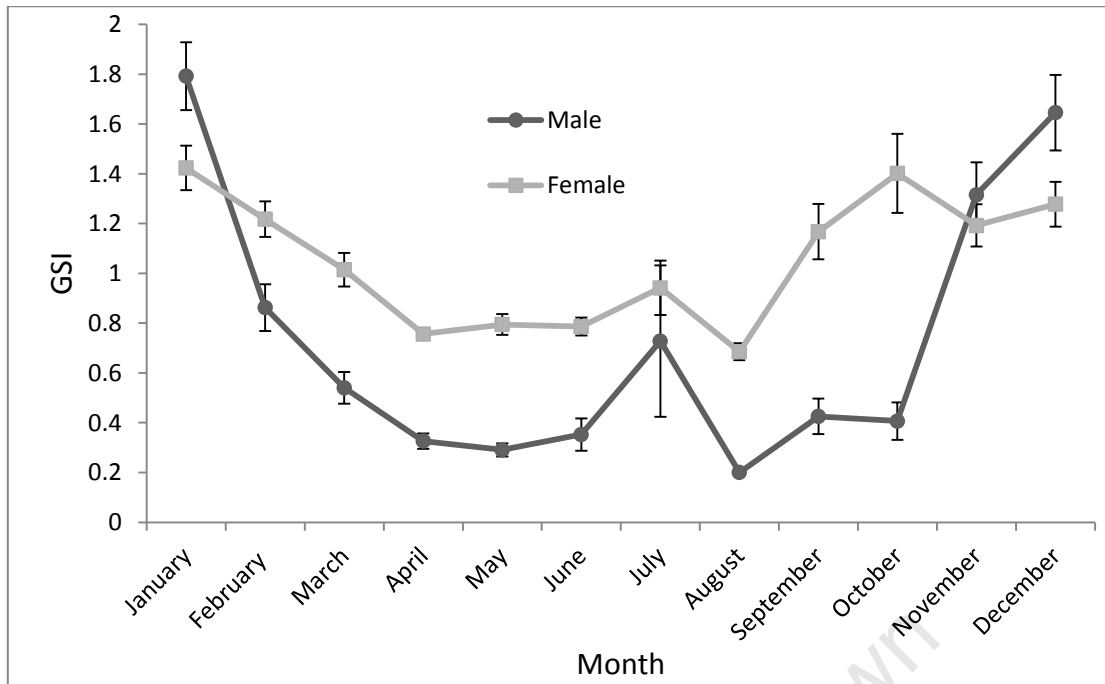


Figure 3.5: Mean monthly GSI values with standard error for male (n = 1018) and female (n = 1717) *S. lalandi*.

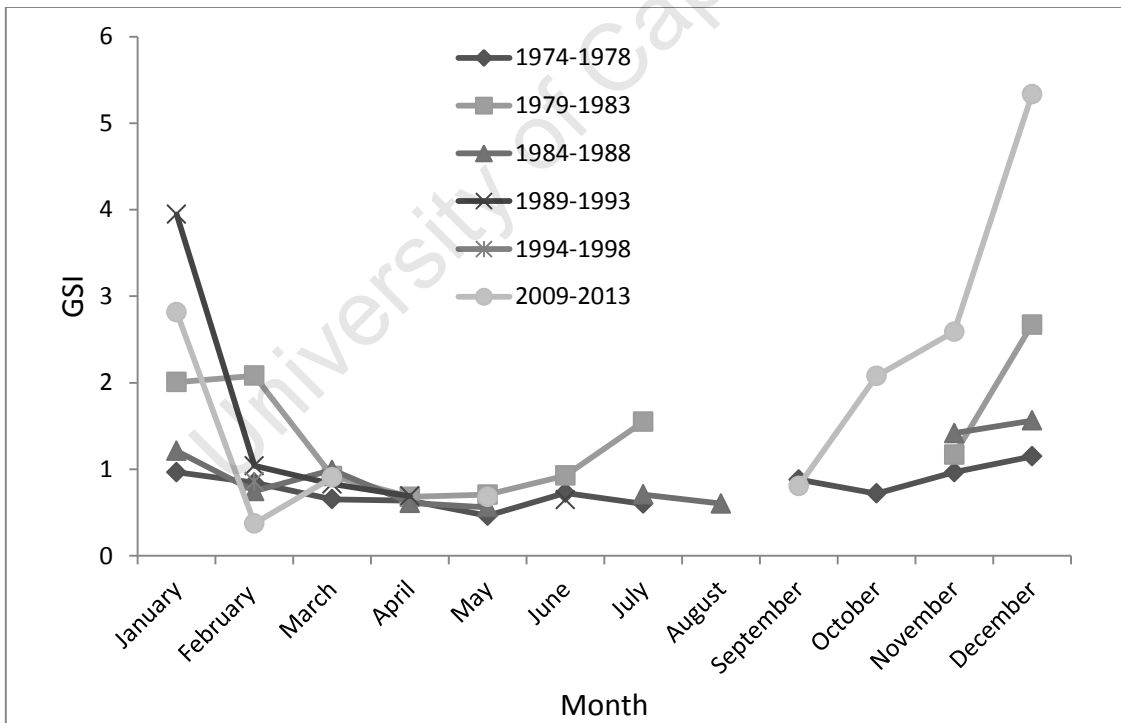


Figure 3.6: Temporal monthly trends in mean GSI values for *S. lalandi* in five year groupings (n = 2735).

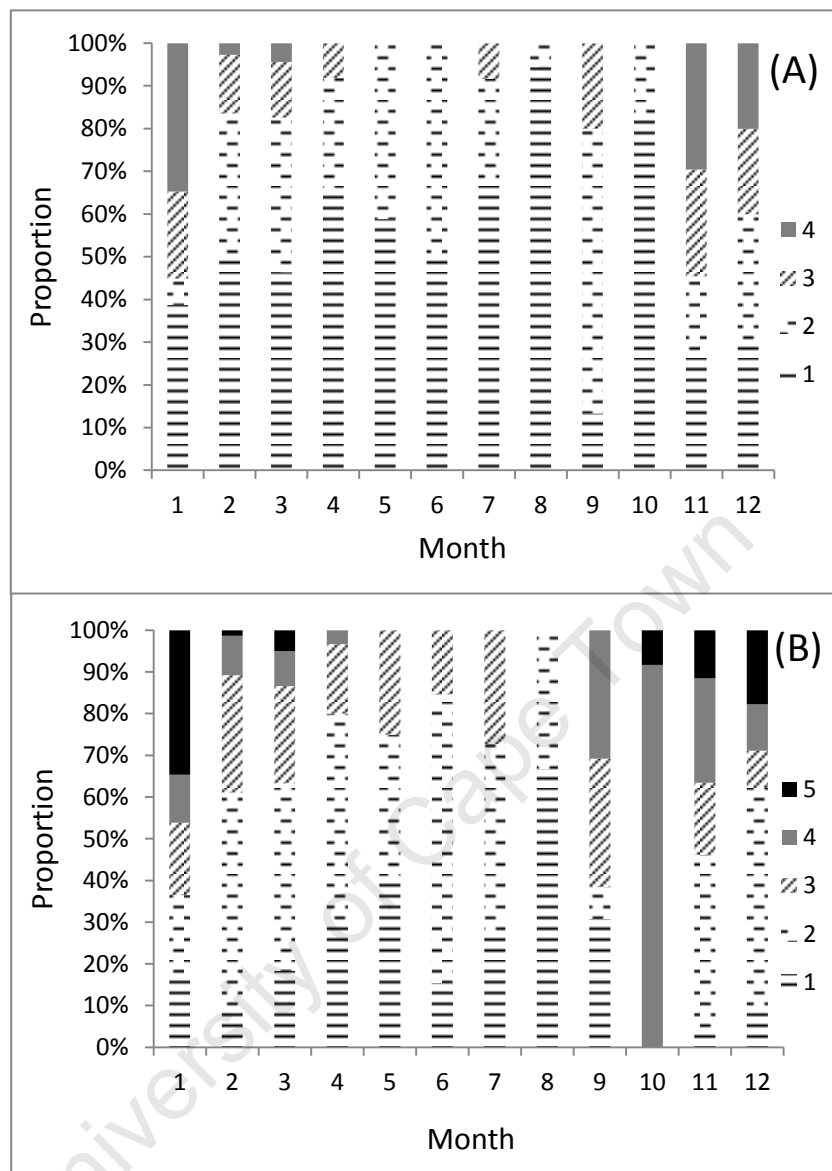


Figure 3.7: Observed monthly proportion of gonad stages for male (A) and female (B) *S. lalandi* from 1985 to 2012.

### MATURITY

The estimated size at which 50 % of males were mature ( $L_{50}$ ) was 585 mm FL (95 % CI = 555 - 619 mm) with a delta ( $\delta$ ) of 58.42 mm<sup>-1</sup> (95 % CI = 11.68 - 80.68 mm) (Figure 3.8) and 550 mm FL (95 % CI = 532 - 570 mm) with a  $\delta$  of 39.31 mm<sup>-1</sup> (95 % CI = 25.18 - 57.50 mm) for females (Figure 3.9) The 95 % confidence interval was narrower for females (38 mm) than males (63 mm). The smallest mature male observed in this study was 520 mm FL and 100 %

of males were mature above 820 mm FL. The smallest mature female observed in this study was 520 mm FL and 100 % of females were mature above 780 mm FL.

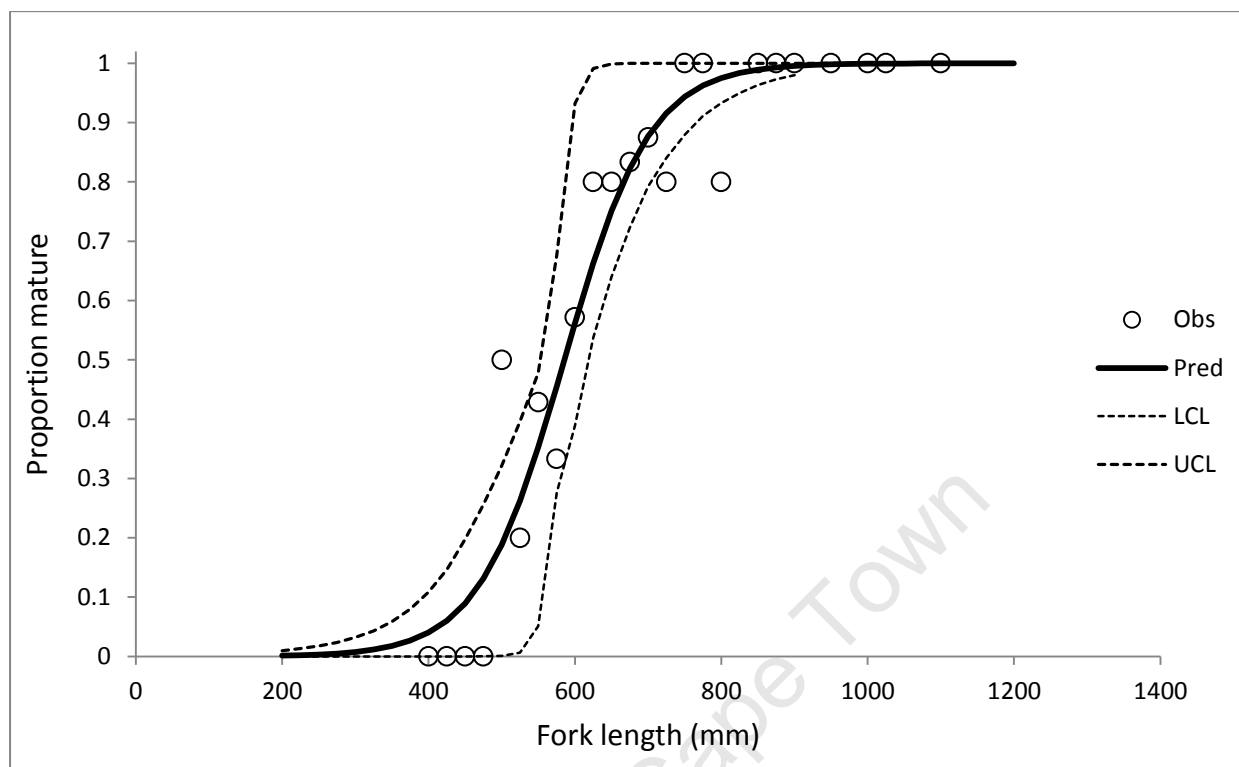


Figure 3.8: Distribution of mature male *S. lalandi* with upper (UCL) and lower (LCL) 95 % confidence intervals around the predicted (Pred) proportion mature based on observed values (Obs).  $L_{50} = 585$  mm FL,  $\Delta = 58.4$  mm<sup>-1</sup>.

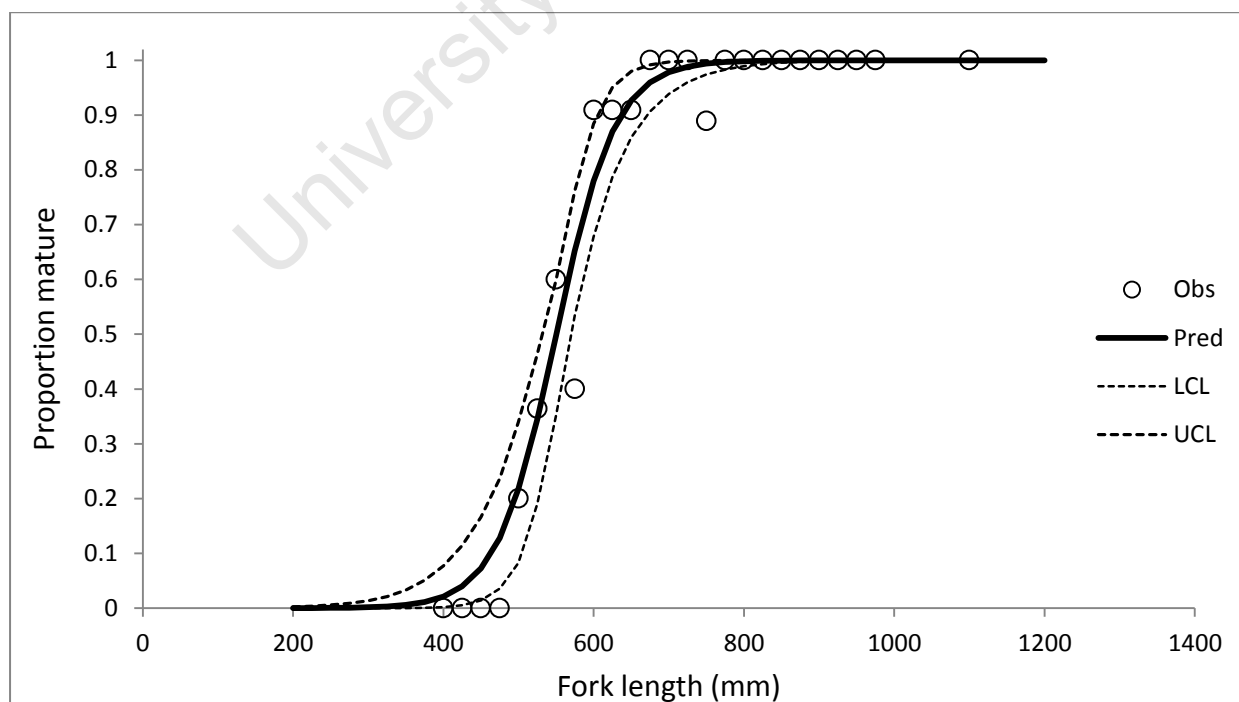


Figure 3.9: Distribution of mature female *S. lalandi* with upper (UCL) and lower (LCL) 95 % confidence intervals around the predicted (Pred) proportion mature based on observed values (Obs).  $L_{50} = 550$  mm FL,  $\Delta = 39.3$  mm<sup>-1</sup>.

## DISCUSSION

Appendix 1 shows the full distribution of samples in the historic records. The records cover fish sampled over 36 years between 1974 and 2010 in which 6149 fish were sampled. The historic records have a distinct bias towards summer period samples, specifically the months of January and February. This is a common problem for studies on yellowtail as the species is mostly caught during this period and is scarcely caught in winter months. Even with the 36 years of sample collections the number of winter samples in the historic records is still low. There are however a sufficient number of samples from May to August for use in this study. The bulk of the samples in the records originate from the early years of the survey from 1975 to 1979. The sample size over this period was boosted by additional purse-seining for yellowtail in conjunction with other methods.

Histological examination of ovaries revealed some discrepancies between macroscopic staging and histological observations. Discrepancies were most common between active and developing ovaries and thus not likely to affect the overall length at maturity. The use of histological validation of macroscopic staging is commonly done to improve the accuracy of assigned maturity. It is however labour, time and cost intensive and thus not always practical. Baxter (1960) found the macroscopic staging of females to be inadequate and used oocyte diameter as a more precise means of staging. Other studies on yellowtail have coupled histological observations with macroscopic staging for both sexes (Gillanders et al. 1999b, Poortenaar et al. 2001), while Shiraishi et al. (2010) used only histological methods.

Table 3.2: Revised gonad stage criteria for *S. lalandi*.

<b>Old stage</b>	<b>Revised stage</b>	<b>Macroscopic appearance</b>	<b>Histological evidence</b>
1 Immature	Immature	Translucent and less than 60 mm in length.	CN and PN oocytes
2 Active	n.a.		n.a.
3 Developing	Developing/ resting	Grainy in appearance, rounded shape and greater than 60 mm in length.	CA and V oocytes
4 Late developing	Mature	Yellow in appearance, oocytes becoming visible.	V and GVM oocytes
5 Ripe	Mature and spawning	Yellow in appearance, large and firm to the touch with hydrated oocytes clearly visible.	GVM and hydrated oocytes with the possibility of POF's.
6 Spent	Spent	Bloodshot in appearance and flaccid to the touch	Atretic oocytes

During the course of this study the staging criteria for ovaries in Table 3.1 were used. However it was found that a five stage criteria would be adequate for future studies on the species. Table 3.2 provides revised ovary stages for yellowtail where the active stage (stage 2) has been removed. The macroscopic and histological criteria have remained much the same and give guidelines defining each stage.

The presence of oocytes at a wide range of developmental stages in mature yellowtail suggests the capacity to spawn on multiple occasions during the spawning season which corresponds with the findings of previous studies (Baxter 1960, Poortenaar et al. 2001). Poortenaar et al. (2001) stated that size distribution and proportions of oocytes in yellowtail ovaries indicate multiple group synchronous oocyte development. Multiple group synchronous ovarian development shows two oocyte cohorts, a synchronous group of larger oocytes and a more heterogeneous group of smaller oocytes (Murua et al. 2003). This is only easily observed when all developmental stages of oocytes are present in ripe fish. Oocyte diameters ranged from  $< 0.01$  to 1.2 mm in this study, however eggs above 1 mm were extremely rare ( $n = 4$ , 0.04 %). This explains the extremely low observations of GVM stage and total absence of hydrated oocytes in this study. GVM stage oocytes have been observed between 1 and 1.2 mm and hydrated oocytes between 1.2 and 1.4 mm (Poortenaar et al. 2001). Gilchrist (1916) also noted that ripe ovaries of yellowtail sampled from South African waters contained oocytes of 1.27 mm in diameter, although the exact sample location is unknown. Two oocyte cohorts were observed in this study. However while the first cohort of smaller oocytes was distinct, the second cohort of larger eggs was small by comparison. It is possible that as oocytes develop towards final maturity the second cohort may strengthen as the frequency of larger oocytes will increase.

No females with fully mature oocytes were found in this study, as was the case in studies done by Baxter (1960) and Gillanders et al. (1999b). This is likely due to them spawning outside of feeding grounds as their prey is likely to feed on their eggs. A small number of yellowtail eggs were collected in False Bay by Gilchrist (1903), but if spawning did occur in False Bay larger numbers of eggs should be present. However, fully ripe females with mature and hydrated oocytes were found in more recent studies conducted in New Zealand and Japan (Poortenaar et al. 2001, Shiraishi et al. 2010). The absence of mature oocytes in three out of five studies documenting the ovarian development of yellowtail indicates that it

is rare to find ripe females. It is likely that hydration of oocytes occurs rapidly in yellowtail. Although not recorded in *Seriola* species the final maturation of oocytes from the GVM stage to final hydration has been recorded occurring in less than 12 hours (Scott et al. 1993, McMillan 2007). Oocyte hydration is also likely to be rapid in amberjack as no females with hydrated oocytes were found over a two year sampling period in a study done by Harris et al. (2007). Thus acquiring ripe females is only likely through intensive sampling throughout the peak spawning season or by chance.

The absence of hydrated eggs and extreme scarcity of mature GVM stage oocytes has made estimation of batch fecundity impossible in this study. Baxter (1960) was able to determine batch fecundity for females ranging from 568 - 1053 mm FL with batches ranging from 458,000 to 3,914,000 eggs. Baxter's (1960) study did not give any indication of the frequency of spawning of yellowtail, however Harris et al. (2007) was able to determine that amberjack is capable of spawning up to 14 times a season. Given the similarity in reproductive and life history characteristics of these two species it is likely yellowtail is capable of spawning at a similar frequency and batch size. Based on a batch size estimated for yellowtail by Baxter (1960) and frequency of spawning estimated for amberjack by Harris et al. (2007) potential annual fecundity could be estimated. Batches of 6,412,000 to 54,796,000 eggs for individual yellowtail ranging from 568 to 1053 mm FL were estimated. Although these estimates are based on assumptions of consistency within the genus they can give a prior estimate of the potential annual fecundity of yellowtail.

Post-ovulatory follicles (POFs') were observed in three mature yellowtail between December and January indicating that spawning had recently occurred. POFs' can be observed in ovaries for up to two days after spawning has occurred (Fitzhugh and Hettler 1995, Ganas 2012). This however varies between species and at different water temperatures making ageing POFs' specific to each species under specific environmental variables (Fitzhugh 1995). Using POFs' to determine spawning frequency requires accurate ageing of POFs' and a much larger sample size and higher sampling frequency than in this study (Ganas 2012). They do however in the absence of hydrated eggs indicate that the mature individuals sampled had spawned that season and were likely in the process of developing towards the next spawning event.

As observed in other studies (Baxter 1960, Gillanders et al. 1999b, Poortenaar et al. 2001, Moran et al. 2007, Shiraishi et al. 2010) yellowtail appears to be a summer spawner. Based on the presence of ripe gonads and elevated GSI values, the spawning season of yellowtail in South African waters appears to be from November to February. The eggs of yellowtail have been collected in False Bay between November and January indicating that spawning has occurred over this period (Gilchrist 1903, Brownwell 1979). The presence of POF's in mid-December further substantiates a peak spawning season between December and January. Penney (1982) found a more protracted spawning season for yellowtail in South African waters from November to April. He did however find the peak spawning season to be in December and January which corresponds to the two consecutive months with the highest average GSI's in this study. A winter peak in GSI was also observed for both sexes in the month of July, indicating that some gonad activity occurs even during the winter months. The sample size for July is low in comparison to summer months and further sampling in July is likely to substantiate this peak. However, all fish making up the July peak were sampled from Struisbaai and high July peaks were found in samples from 1980 and 1989. It is likely that this peak may have corresponded to a unique set of environmental variables inducing gonad activity and not a difference in the timing of spawning between sample regions. Baxter (1960) found that spawning was uniform throughout the range of the species off the Californian coast.

Male gonadal activity was elevated between November and January with a single peak in January. Female gonadal activity began to rise earlier in September and reached two summer peaks in October and January. This early peak in female GSI was also observed by Poortenaar et al. (2001), but no explanation was given. Male GSI remained lower than that of females over the winter months, but increased to greater values during the spawning season.

Size at first maturity, size at 50 % maturity ( $L_{50}$ ) and size at 100 % mature varied greatly between various populations of yellowtail throughout its distribution. In studies documenting these populations females always matured at larger sizes than males. Gillanders et al. (1999b) obtained an  $L_{50}$  of 470 mm FL for males and 834 mm FL for females in New South Wales (NSW) Australia, Poortenaar et al. (2001) obtained an  $L_{50}$  of 812 mm FL for males and 944 mm FL for females in Northern New Zealand. Baxter (1960) documented

female yellowtail first maturing at 606 mm FL and 100 % were mature at 634 mm in Californian waters and McGregor (1995) documented yellowtail maturing between 580 and 670 mm FL in New Zealand. However in this study males matured at larger sizes than females at 585 mm FL and 550 mm FL respectively. The difference of 35 mm in  $L_{50}$  between males and females was however small in comparison to the differences recorded in previous studies. Poortenaar et al. (2001) and Gillanders et al. (1999b) found females maturing at 132 mm and 364 mm larger than males. Similar trends were found for amberjack in the Mediterranean to those of this study where males matured at larger sizes than females at 1139 mm SL and 1090 mm SL respectively (Marino et al. 1995). Amberjack and yellowtail seem to exhibit similar reproductive strategies and also high variability between studied populations. Amberjack exhibits a spring/summer spawning season with a two month peak and is a batch spawner with indeterminate fecundity (Marino et al. 1995, Harris et al. 2007).

The high variation in length at maturity between populations of yellowtail can also be seen between populations of amberjack in the Mediterranean and Atlantic US (Marino et al. 1995, Harris et al. 2007). It is not uncommon for life history characteristics of fish to be influenced by different environmental variables between populations. These may include water temperature, available resources, fishing pressure and the potential for genetic diversion. Consideration must also be made as to the criteria used in staging the maturity of fish between studies. The use of histology to validate gonad staging on all samples guarantees a higher level of accuracy, while macroscopic staging may be more objective based on the observers judgment of defining macroscopic characteristics. Histological validation of gonads was only done for a small proportion of samples in this study. This may have possibly led to some form of inaccuracy in maturity staging. Staging of ovaries using histology and microscopic staging criteria revealed that in general the stage of ovaries can be overestimated using macroscopic staging. This was most common in active, developing and ripe ovaries. The difference between stage active and developing ovaries can be difficult to distinguish microscopically to the untrained eye. Ripe ovaries were seen as late developing ovaries under microscopic staging criteria as no hydrated eggs were present, however POF's were present in these ovaries indicating that spawning had occurred and hydrated eggs have already been present during that spawning season. The large lobe and egg size of these ovaries led to them being staged as a ripe macroscopically. Although ovary stages may have been overestimated in this study they do not affect the final results. The

difference between immature and active ovaries is distinct both macroscopically and microscopically. Wrongly staging an immature ovary is highly un-likely and therefore the over-estimation of stages in this study did not affect the maturity state and age and length at maturity.

The absence of ripe females with mature and hydrated eggs in samples collected between 2011 and 2012 has left certain questions unanswered in this study. This has been the case in other studies and in studies on similar species and further indicates the likelihood of rapid maturation of oocytes in yellowtail and spawning outside of feeding grounds. Further sampling should be done in order to find ripe and running females so that estimates of batch fecundity and a full description of ovarian development can be done. The presence of POF's and elevated GSI indicated that the peak spawning season for yellowtail in South African waters was between December and January with a protracted spawning season extending from November to February. These findings are on par with other studies done on yellowtail globally.

Length at 50 % maturity ( $L_{50}$ ) was found to be similar for both sexes in the study, with males maturing at slightly larger sizes than females. This was not observed in other studies done on yellowtail where females always mature at larger sizes than males. In general the length at 50 % maturity ( $L_{50}$ ) for yellowtail in this study was smaller than that recorded by others. This may be an indicator of some factors acting on the reproductive strategy of the yellowtail population in South African waters. These may be environmental variables such as water temperature or fishing pressure forcing earlier maturation in the species. The protracted spawning season and ability to spawn on multiple occasions from a relatively small size gives yellowtail a large window to produce recruits successfully when conditions are favourable.

## THE AGE AND GROWTH OF *SERIOLA* *LALANDI* IN SOUTH AFRICA

### ABSTRACT

The age and growth characteristics of *Seriola lalandi* in South Africa were determined by reading sagittal otoliths. Both whole and sectioned otoliths displayed growth zones which could be interpreted as annuli. Sectioned otoliths proved difficult to age due to high levels of striations obscuring true growth zones. Whole otoliths displayed clearer growth zones and were thus chosen as the primary ageing structure. A total of 524 whole otoliths were used from fish ranging from 430 to 1080 mm FL, of which 141 (27 %) were discarded initially and 384 (73 %) were readable. Sectioned otoliths were used only for edge analysis. Agreement among three readers of whole otoliths was 13 % (50) and between any two was 71 % (274). Maximum ages for male and female yellowtail were 7 and 8 years, respectively. Age at 50 % maturity for males ( $A_{50}$ ) was 2.3 years while females matured ( $A_{50}$ ) at 3.6 years. von Bertalanffy growth parameters did not differ between males and females ( $P > 0.05$ ). A statistical penalty was placed on  $L_{\infty}$  to keep the growth parameters of the von Bertalanffy equation within plausible biological limits. The best-fit von Bertalanffy growth equation had  $L_{\infty}$  and K values of 1064 mm FL and 0.173 ( $\text{year}^{-1}$ ) respectively. The growth performance index of yellowtail in South African waters was found to be high ( $\Phi' = 3.51$ ). A total of 6149 fish ranging from 340 to 1250 mm FL were used to calculate the combined-sex length-weight relationship for yellowtail. The age and growth characteristics were found to be similar to those found in previous studies on Japanese, Australian, North American and New Zealand populations. The use of calcareous structures for ageing the species is difficult and similar problems were encountered to those mentioned in previous studies. The age and growth estimates of this study will prove useful in future stock assessments and management plans.

## *INTRODUCTION*

Knowing the elapsed time or time scale over which processes occur is paramount to understanding rates and potential. The estimation of vital parameters such as growth rates, mortality rates and production depend on being able to accurately estimate the age of a fish species. Age determination forms the basis of understanding the life history and population dynamics of a fish population (Campana 2001). The maximum age of a fish defines a temporal scale over which a fish can grow, spawn and ultimately contribute to the population. Accuracy is important when applying age information to the population dynamics of a species. Underestimating the age of a species can result in the overestimation of growth and mortality rates, and in an overestimation in production (Campana 2001).

Each fish species poses difficulties of its own when estimating age. These difficulties are often related to the life history of the species and the environmental conditions in which it lives. Environmental conditions are the driving forces behind variations in fish growth and ultimately affect the markings found on various calcified hard structures used to estimate age in fish. These markings are concentric density bands known as growth increments and are formed by alternating periods of rapid and slow growth. An increment is made up of two zones, rapid growth lays down a wide zone, while slow growth lays down a narrow zone (XY Etherton Unpublished data). These two zones are generally known as translucent and opaque zones depending on whether the otolith is viewed with reflected or transmitted light under a microscope. For example in this study the otoliths were viewed with reflected light, making the opaque zone summer growth zone dark and the translucent zone winter growth zone light. Generally otoliths, scales and vertebrae are used to count increments, each with varying success depending on the fish species being aged (Campana 2001). The clarity and periodicity of increment formation on these hard structures depend on a number of controlling variables, both endogenous and exogenous. Endogenous controls are based on the regulation of endolymph fluid chemistry by changes in the concentration of hypo and a hyper calcemic hormone in the blood which affect mineral deposition in otoliths (Wright et al. 1992). Exogenous controls affecting increment formation include light, temperature, oxygen concentration and food density (Campana 1983, Campana 1984). Metabolism is most commonly affected by these variables and has been directly linked to increment formation (Neilson and Geen 1983).

Fish species that reside in a small area for the majority of their lives are affected by their surroundings as the seasons change. These changes will be predictable and repeated. Resident species will show seasonal trends to a greater extent than more mobile migratory species. Nomadic species such as yellowtail have the ability to cover vast distances and move through a variety of conditions in a short period of time hereby making them difficult to age (Gillanders et al. 2001). The nomadic lifestyle of pelagic species allows them to avoid unfavourable conditions associated with winter such as cooler water and decreased food densities. This aspect of their life history means that growth increments may be less defined and consistent compared to more resident species subjected to unfavourable winter conditions.

The process of ageing fish requires some form of quality control to improve the accuracy of age estimates. Incorporating age validation, precision and error into an ageing protocol gives an indication of how difficult the species is to age and how reliable the age estimates will be. Age validation may be done on ageing structures in order to determine the periodicity of increment formation. However, age validation requires a number of procedures that are commonly not possible or viable. Knowing the true age of a fish is often unachievable, however there are a number of techniques that provide some validation of age. Marginal increment analysis (MIA) and edge analysis relies on tracking the formation of an increment over the period of a year to determine when and how often an increment is formed (Campana 2001). Tag-recapture methods give a known time interval over which the fish have aged (Campana 2001). These validation techniques are difficult to conduct and can take a long time until they provide results. MIA can be problematic due to difficulties viewing partial increments on the edge of otoliths and tag-recapture studies take many years to gather enough returns (Campana 2001). The precision of age estimates refers to the repeatability of the results obtained from the same structure. Most commonly the percentage of agreement between readers is used as a measure of precision, giving an indication of the subjective error between readers (Campana 2001). Two types of error can occur in an age estimate, that of process error and error occurring due to the observational subjectivity of readers. Process error is the result of inconsistencies in hard structures, these may include incomplete increment sequences, compression of increments in old fish and general increment "noise" in hard structures (Campana 2001). Noise refers to the obstruction of true growth increments by finer striations or other visual distractions.

Observational error arises when different reader's age fish based on personal criteria that may be slightly different to each other.

The difficulty of ageing *Seriola* species is reflected in the wide range of structures previously used for age estimation. Otoliths, scales, vertebrae, dorsal spines and opercular bones have all been used across the genus. A series of early studies focused on Japanese yellowtail due to its importance as an aquaculture species. Scales, vertebrae and opercular bones were used by Mitani (1955), Mitani (1958) and Mitani and Sato (1959) respectively. Vertebrae have been used to age the species in recent times by Murayama (1992). Studies on amberjack have used scales (Burch 1979) and sectioned sagittal otoliths (Manooch and Pots 1997a). Four hard structures have been used to age yellowtail namely dorsal spines, vertebral columns, scales and both sectioned and whole otoliths, each with varying success (Baxter 1960, Gillanders et al. 1999a, Stewart et al. 2004, Shiraishi et al. 2010).

The aim of this chapter is to determine the age and growth characteristics of yellowtail in South African waters. The age at 50 % maturity ( $A_{50}$ ), maximum age, average age at length, growth characteristics and length-weight relationship will be explored.

## **METHODS**

### **SAMPLE COLLECTION**

Seventy-one yellowtail were sampled by rod and reel and spearfishing from ski-boats on the West Coast at Dassen Island, Robben Island in False Bay and the Cape Point area and at Struisbaai on the South-Western Cape coast between January 2011 and November 2012 (Figure 2.1, chapter 2). The historic records also provided otoliths from surveys conducted between 1974 and 2010.

### **OTOLITH AND SCALE REMOVAL AND PROCCESING**

Specimens were dissected fresh on the day of capture in most cases, or frozen whole until an appropriate time. Frozen specimens were thawed over night before dissection. Sagittal otoliths were removed, cleaned and placed dry in Eppendorf vials. Only paired otoliths were used for sectioning as one otolith was always to be kept whole. Scales were removed from

behind the pectoral fin as previous studies have found this position to have the least scale regrowth (Gillanders et al. 1999a)

Sectioned otoliths totaled 183 and 524 were used whole. Otoliths were selected to cover a size range and each month of the year. Sagittal otoliths were sectioned while set in two mediums. The otoliths from fish sampled between 2011 and 2012 were set in polyester resin in 12x297 mm blocks for sectioning. Sections were cut with a twin blade slow rotation saw at a thickness of ~0.25 mm. Sections were mounted on glass slides with DPX mounting medium. DPX was placed between the section and glass slide, as well as on top of the section to increase clarity when viewing under a microscope. Sagittal otoliths from historical collections were set whole in plastic trays covered in resin and a glass cover slip for viewing otoliths whole with reflected light. Some of these otoliths were sectioned as few loose otoliths were available for sectioning. The trays held otoliths in four rows of four. These were cut into single rows of four otoliths before being sectioned following the same methods as described earlier. These otoliths were set in this manner for viewing whole and subsequently sectioned in order to compare ageing results obtained from those kept whole and those that were sectioned.

Scales were set in DPX mounting medium between two standard glass slides to improve readability and prevent the scales from curling up.

Whole otoliths set in black plastic trays were viewed and imaged under a Nikon dissecting microscope at 8 - 16x magnification with reflected light. Images of sectioned otoliths were taken at 100x magnification with a Nikon compound microscope with transmitted light. Each otolith was read independently by three different readers, an age was accepted when any two or all three of the readers agreed and discarded if none agreed.

#### *LENGTH WEIGHT RELATIONSHIP*

Specimens used to calculate the length weight relationship came from the historic records and from samples collected during this study. A power curve was fitted to the weight (W) vs. fork length (FL, mm) relationship between all fish and males and females separately in the form;

$$W = aFL^b \quad \text{Equation 4.1}$$

The data were log-transformed and a linear regression was carried out to estimate the values of  $a$  and  $b$ , as well as the 95 % confidence intervals around each parameter.

#### *SECTIONED VS WHOLE*

To test whether it is better to section otoliths or to leave them whole, each otolith was scored as either readable or unreadable, a condition which was judged by a single reader. A Chi<sup>2</sup> test was used to determine if there was a significant difference between the frequency of readability between sectioned and whole otoliths.

#### *PRECISION and ERROR*

The average percent error (APE) was used to determine the precision of the age readings.

$$APE_j = 100\% \times \frac{1}{R} \sum_{i=1}^R \frac{|x_{ij} - x_j|}{X_j} \quad \text{Equation 4.2}$$

Where  $X_{ij}$  is the  $i$ th age determination of the  $j$ th fish,  $X_j$  is the mean age estimate of the  $j$ th fish and  $R$  is the number of times each fish is aged.

The coefficient of variation ( $CV_j$ ) of the  $j$ th was calculated as follows;

$$CV_j = 100\% \times \frac{\sqrt{\frac{\sum_{i=1}^R (x_{ij} - X_j)^2}{R-1}}}{X_j} \quad \text{Equation 4.3}$$

#### *VALIDATION*

Edge analysis was done on sectioned otoliths to determine the frequency of increment formation. Sectioned otoliths were photographed with a compound microscope using transmitted light. The images were viewed with no knowledge of the date of fish capture. The edge of each otolith was either noted as having a translucent or opaque growth increment. The number of translucent and opaque increments was plotted for each month to determine when and how often each growth zone was formed.

## GROWTH

To determine the growth of male and female yellowtail, a von Bertalanffy growth model was fitted to the observed length-at-age data. The growth equation is of the form:

$$FL_t = L_\infty(1 - e^{(-K(t-t_0))}) \quad \text{Equation 4.4}$$

where  $FL_t$  is the fork length (mm) at age  $t$ ,  $L_\infty$  is the asymptotic FL (mm),  $K$  ( $\text{year}^{-1}$ ) is the growth coefficient and  $t_0$  is the theoretical age in years at which the FL of the fish is equal to zero. Maximum likelihood estimates for  $L_\infty$ ,  $K$  and  $t_0$  were obtained by minimising the negative normal log-likelihood function of the form:

$$-LL = n \log(\hat{\sigma}) + \frac{n}{2} \quad \text{Equation 4.5}$$

where  $n$  is the sample size and  $\hat{\sigma}$  denotes the estimated residual standard deviation of the model. A likelihood ratio test was used to determine whether growth estimates differed significantly between sexes (Haddon 2001).

Initial growth model fits resulted in a large  $L_\infty$  (> 3000 mm FL) estimates associated with small values for  $K$  (< 0.003) and  $t_0$  (< -6 years). In order to keep the growth parameter estimates within biologically plausible limits, a penalty was placed on  $L_\infty$ . The penalty was derived from the strong empirical relationship between the asymptotic and maximum length laid out by Froese and Binohlan (2000) based on 511 studies ( $R^2 = 0.959$ ), which is given by:

$$\log \tilde{L}_\infty = 0.044 + 0.9841 \log L_{\max} \quad \text{Equation 4.6}$$

where  $\tilde{L}_\infty$  denotes the empirical estimate of  $L_\infty$  and  $L_{\max}$  was taken as the maximum observed length (mm FL) in the sample. The penalty was assumed to be normal distributed and associated with a CV of 10 %. The extended negative log-likelihood function to be minimized is then given by:

$$-LL = n \log(\hat{\sigma}) + \frac{n}{2} + \frac{(\tilde{L}_{\infty} - L_{\infty})}{\tau^2} \quad \text{Equation 4.7}$$

where  $\tilde{L}_{\infty}$  was estimated at 1064 mm FL, based on an observed  $L_{max}$  of 1030 mm FL and the variance was calculated as a function of  $\tau^2 = (\tilde{L}_{\infty} CV)$ .

A conditioned parametric bootstrap method was used to estimate the 95 % confidence intervals for the expected length-at-age values and von Bertalanffy growth parameters (Efron and Tibshirani 1986). For this purpose, 1000 'new' datasets were generated with vectors of random FL observations, by drawing  $n$  normally distributed residuals,  $N \sim (0, \hat{\sigma}^2)$ , and adding them to the predicted length-at-age  $\hat{L}_{t,i}$  for each observations  $i$ . The von Bertalanffy model was fitted to each random dataset and the percentile method (Buckland 1984) was applied to estimate the 95 % confidence intervals from the resulting bootstrap vectors, where the 2.5 % and 97.5 % percentiles were chosen to obtain the lower and upper 95 % confidence intervals respectively.

A likelihood ratio test was used to test for differences in the growth curves of male and female yellowtail.

$$\chi_k^2 = 2(LL_{full} - LL_{reduced}) \quad \text{Equation 4.8}$$

Where  $LL_{reduced}$  is the log-likelihood for the reduced model, including only three parameters for both sexes combined.  $LL_{full}$  is the log-likelihood for the full model with six parameters for both sexes and  $k$  denotes the difference between the number of parameters estimated for the full model and the reduced model.

#### GROWTH PARAMETER COMPARISON

To directly compare the growth of yellowtail in this study to that of studies conducted on different populations the growth performance index ( $\Phi'$ ) was calculated:

$$\Phi' = \log K + 2 \log L_{\infty} \quad \text{Equation 4.9}$$

where  $\Phi'$  is measured in cm (Pauly and Munro 1984).

The life history parameters for documented carangid species were collated from published results (Froese and Pauly 2000).  $\log_{10}K$  was plotted against  $\log_{10}L_{\infty}$  for all species as well as for yellowtail in this study. As all length estimates were given in total length TL and fork length FL is used in this study, FL (mm) was first converted to TL (mm) as follows:

$$FL = \frac{TL-239.3}{0.846} \quad \text{Equation 4.10}$$

#### AGE AT MATURITY

Only fish sampled in December and January were used to calculate the age at which 50 % of the fish were mature ( $A_{50}$ ) as this was deemed the peak spawning season.  $A_{50}$  was calculated by fitting a logistic ogive to the observed proportion of mature male and female yellowtail in each age group. The logistic ogive is described as:

$$P_a = \frac{1}{\left(1 + e^{\left(\frac{a-A_{50}}{\delta}\right)}\right)} \quad \text{Equation 4.11}$$

Where  $a$  is the midpoint of each size class,  $P_a$  is the probability of mature fish in age  $a$ ,  $A_{50}$  is the age at which 50 % of the sex is mature and  $\delta$  is the width of the ogive. The model was fitted to the data by minimizing the negative Binomial log-likelihood function:

$$-\ln(A) = \sum_a (x_a \ln(\hat{P}_a) + (n_a - x_a) \ln(1 - \hat{P}_a)) \quad \text{Equation 4.12}$$

A conditioned parametric bootstrap procedure was used to estimate the 95 % confidence intervals for  $A_{50}$  and  $\delta$  as well as the expected proportion of mature fish in each age class,  $\hat{P}_a$  (Efron and Tibshirani 1986). For this purpose, 1000 'new' datasets were generated by drawing  $n_a$  random Bernoulli variables (0 = immature; 1 = mature) as a function of  $\hat{P}_a$  to obtain new random observations of proportions of mature fish for each size class  $A, \hat{P}_a$ . The logistic ogive model was fitted to each random dataset and the percentile method (Buckland 1984) was applied to estimate the 95 % confidence intervals from the resulting bootstrap vectors, where the 2.5 and 97.5 percentiles were chosen to obtain the lower and upper 95 % confidence intervals respectively.

## RESULTS

### INTERPRETATION OF GROWTH ZONES

All structures examined showed growth zones that could be interpreted as annuli (Figure 4.1). Scale readings were inconsistent and zones were rarely interpretable and thus not used in age estimation. Sectioned and whole sagittal otoliths showed more defined growth zones, these were however not interpretable in all fish. Sectioned otoliths displayed high levels of “noise” with multiple narrow increments distorting annual growth zones. Sectioned otoliths did however display clear annual growth zones in a number of fish and produced higher ages than other whole otoliths. Growth zones in whole otoliths were more consistently interpretable than in sectioned otoliths with less overall noise distracting readers from true annual growth increments. Two distinct axes were most readily interpretable on whole otoliths, namely the rostrum and region between the anti-rostrum and the sulcus acusticus (Figure 4.2). The post rostrum displayed multiple narrow increments, thus readings were not taken from this region. It was found that there was a significant difference between the readability of sectioned and whole otoliths at 49 % and 73 % respectively ( $\chi^2 = 32.03$ ,  $df = 1$ ,  $p < 0.001$ )

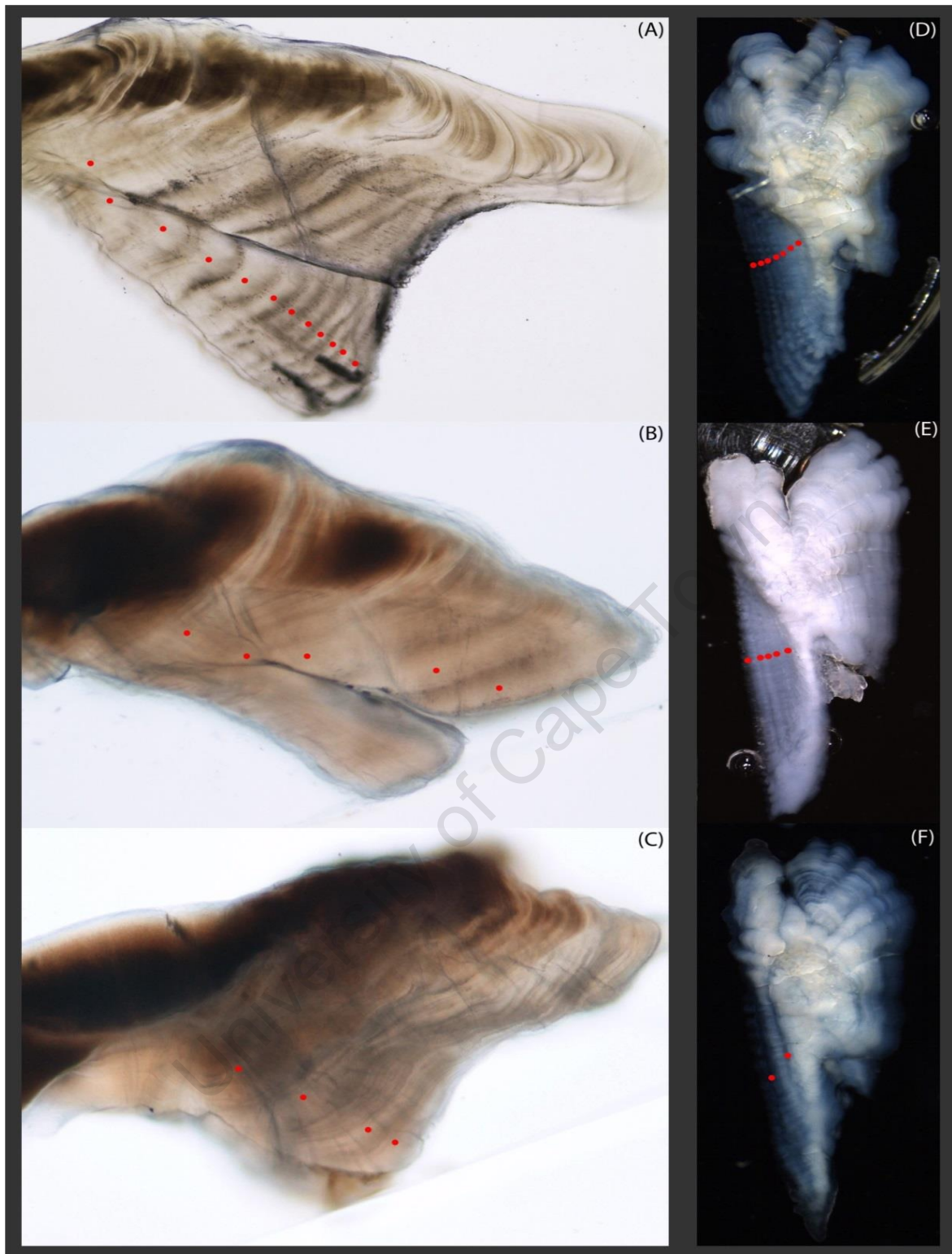


Figure 4.1: Image showing sectioned (A-C) and whole (D-F) sagittal otoliths from *S. lalandi* of various ages. A) 12 years, B) 5 years, C) 4 years, D) 7 years, E) 5 years and F) 2 years.

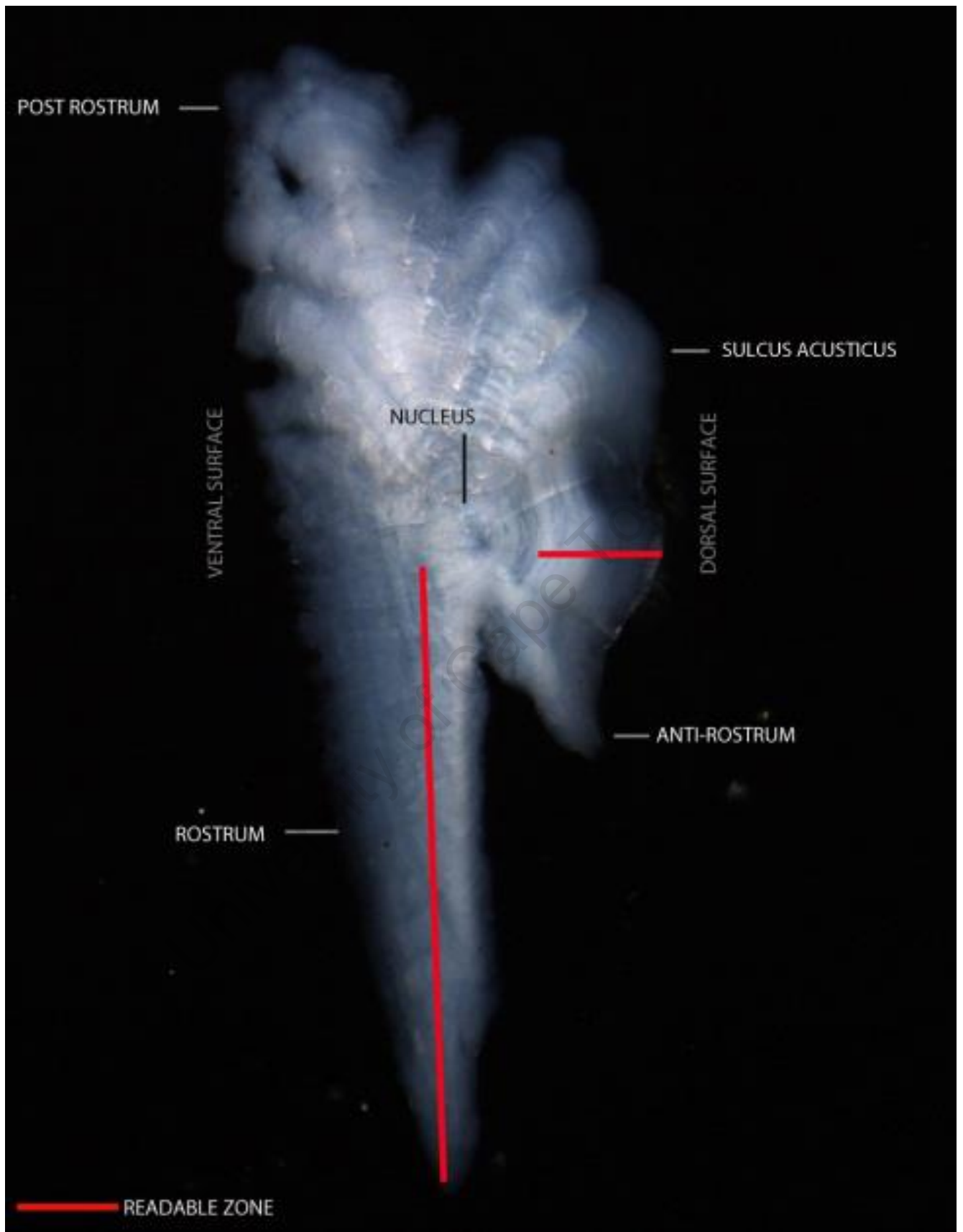


Figure 4.2: Description of whole sagittal otolith of *S. lalandi* (40x).

### SAMPLE DISTRIBUTION

The distribution of samples used for ageing yellowtail covered size classes from 400 mm FL to 1100 mm FL, a range of 700 mm. The highest concentration of samples was from 600 to 1000 mm FL with few fish outside of this range (Figure 4.3). More distinct is the lack of fish below 400 mm FL (smallest aged fish was 460 mm FL) and few fish in the 400 mm size class. Figure 4.4 shows the size distribution of samples in the historic records from 1974 to 2010. The 1970's and 1980's show similar trends in size composition, illustrating that catch sizes had not changed drastically over the time period. Few samples were collected from 1990 to 2010 during the survey, all that were collected were in the mid-range size classes.

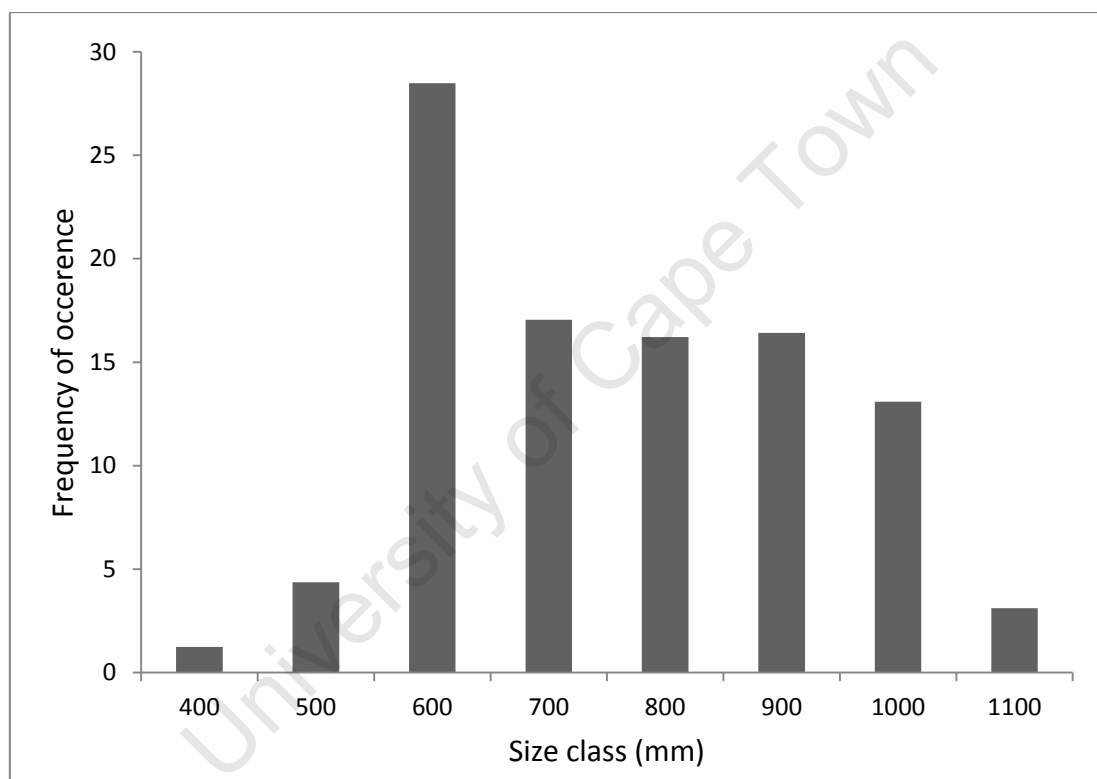


Figure 4.3: Size distribution of aged *S. lalandi* in 100 mm (FL) classes (n=524).

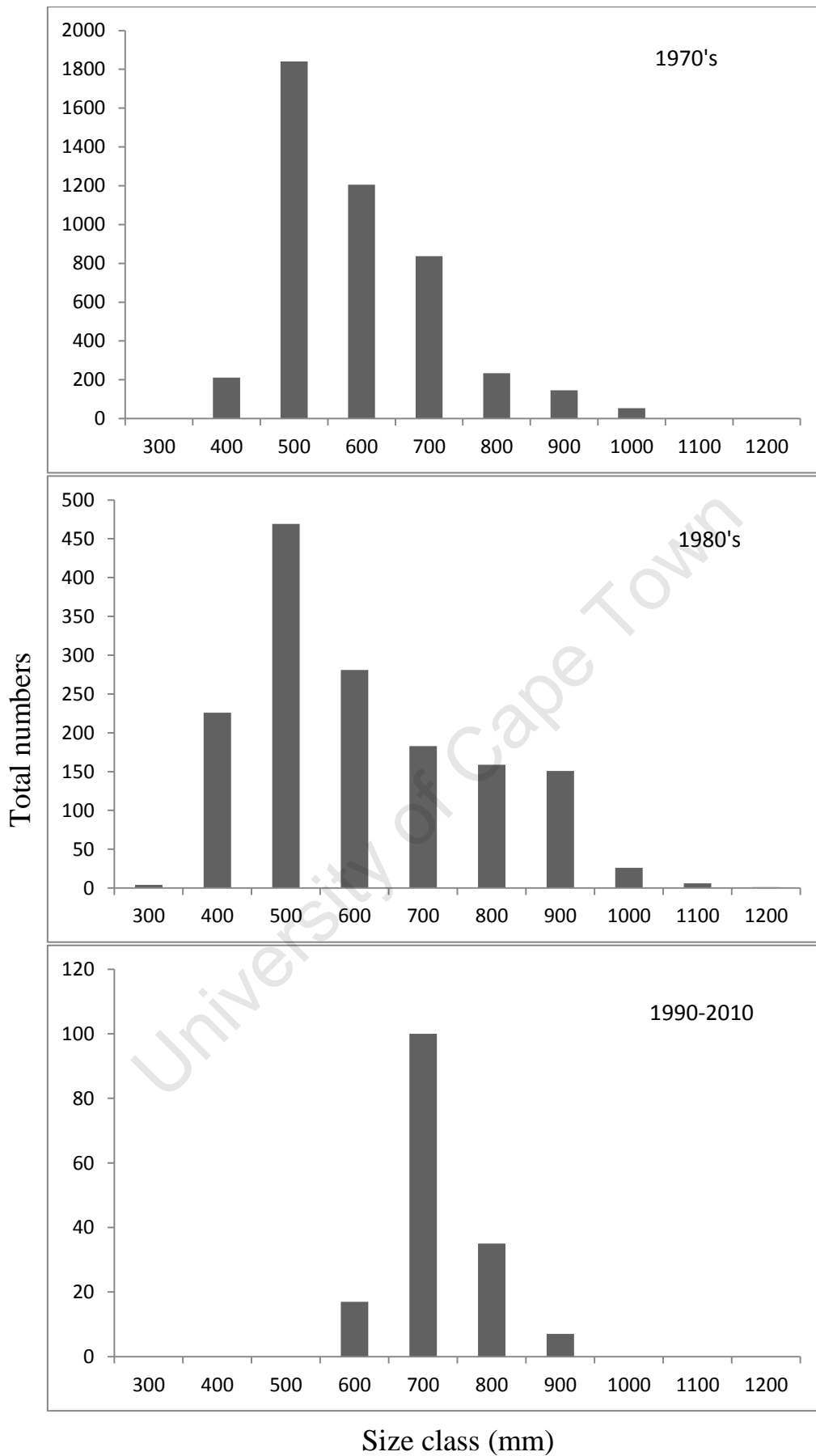


Figure 4.4: The size distribution of samples in the historic records from 1974 to 2010. Data were grouped into three time periods: Top 1970 to 1979 (n=4530), middle 1980 to 1989 (n=1506) and bottom 1990 to 2010 (n=159).

## MORPHOMETRIC RELATIONSHIP

The length weight relationship for yellowtail was:

$$W = 6.0 \times 10^{-5} FL^{2.7514}$$

Equation 4.13

The total number of fish in the equation was 6149, FL ranged between 340 and 1250 mm and  $R^2 = 0.966$ . The 95 % confidence limits of the coefficient were  $5.535 \times 10^{-5}$  and  $6.524 \times 10^{-5}$  and around the exponent they were 2.738 and 2.764 (Figure 4.5).

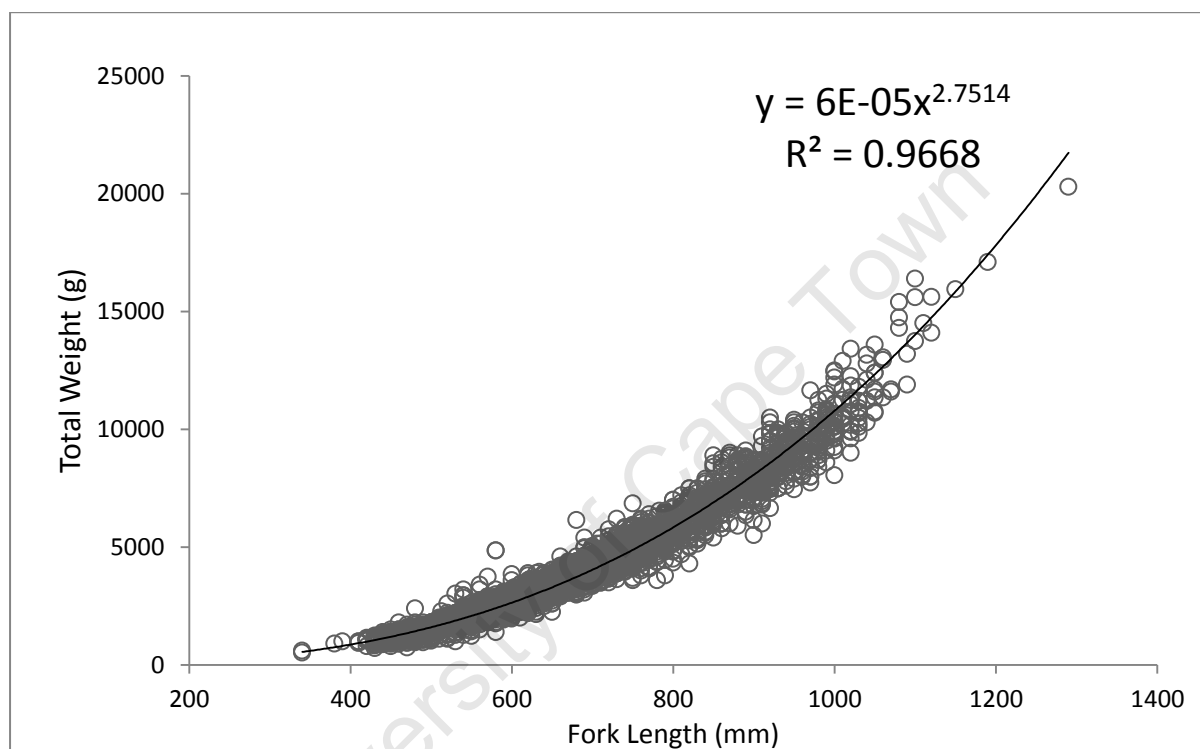


Figure 4.5: Length-weight relationship of male and female *S. lalandi* in South African waters.  $n = 6149$

## PRECISION

Of the 524 whole otoliths 141 (27 %) were discarded initially and 383 (73 %) otoliths were read. Any two of three readers agreed on 274 fish (71 %) and all three readers only agreed on 50 fish (13 %). Agreement between combinations of the three readers (1&2, 1&3 and 2&3) ranged from 27 % to 49 % with a maximum disagreement of five growth zones. Error between readers was considered high with the APE and CV values at 16.24 % and 21.72 %.

## AGE VALIDATION

Edge analysis was conducted on 120 sectioned otoliths with readable edges to reveal when growth zones were formed. Results showed no trends in increment formation (Figure 4.6).

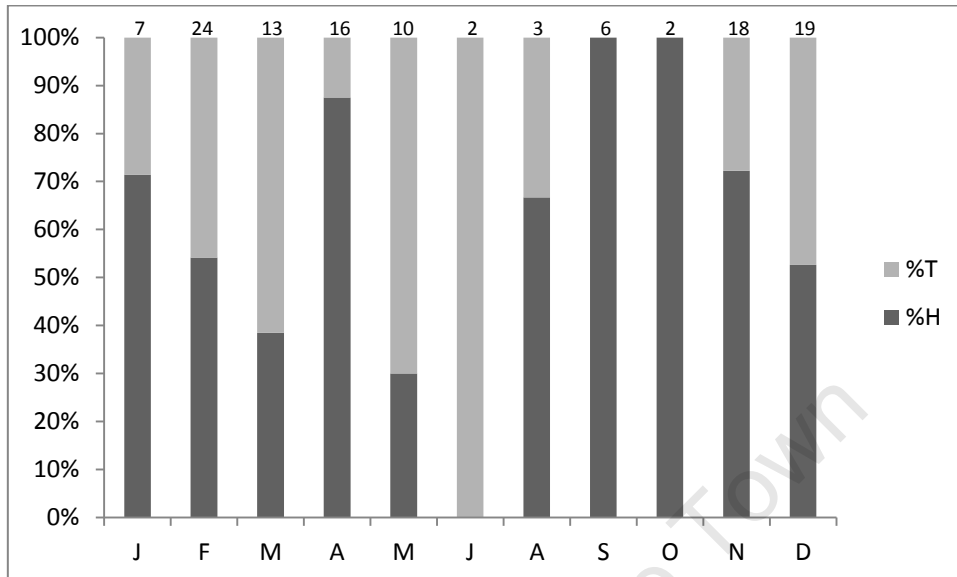


Figure 4.6: Monthly sample sizes and proportions of transparent (T) and opaque (H) bands from edge analysis on sectioned otoliths from *S. lalandi* in South African waters. Numbers above bars indicate monthly sample size of sectioned otoliths with readable edges n=120 for all months.

## GROWTH

A total of 524 specimens were examined for ageing using whole otoliths from specimens ranging in size from 430 to 1080 mm FL. Of the 524 otoliths examined 141 were discarded and considered un-readable. The remaining 383 otoliths were readable, however only 274 of these were used in the final age estimates (agreement of two or more readers). 115 Males and 135 females were aged ranging from 510 to 1030 mm FL and 490 to 1020 mm FL respectively and 24 individuals had no recorded sex. Maximum ages for males and females were 7 and 8 years respectively. Females were aged as being in their first year of growth, however no 1 year old males were found. The likelihood ratio test revealed that there was no significant difference ( $\chi^2 = 0.066$ ,  $df = 3$ ,  $p > 0.05$ ) between the growth curves of male and female yellowtail and thus both sexes were pooled.

Figure 4.7 represents the best fit von Bertalanffy growth model with no penalty restricting the growth parameters. The growth model was estimated as:

$$FL_t = 3476(1 - e^{(-0.023(t+6.12)})$$

Equation 4.14

Where  $FL_t$  is the fork length (FL) at age  $t$ .

Figure 4.8 represents the best fit von Bertalanffy growth model with a penalty restricting  $L_\infty$  based on its empirical relationship to  $L_{max}$ . The growth model using this method was estimated as:

$$FL_t = 1064(1 - e^{(-0.173(t+2.75)})$$

Equation 4.15

The corresponding 95 % confidence intervals derived from the parametric bootstrap procedure were estimated as: 898.1 to 1174.5 mm FL for  $L_\infty$ , 0.128 to 0.324  $y^{-1}$  for  $K$  and -4.05 to -1.17 years for  $t_0$ .

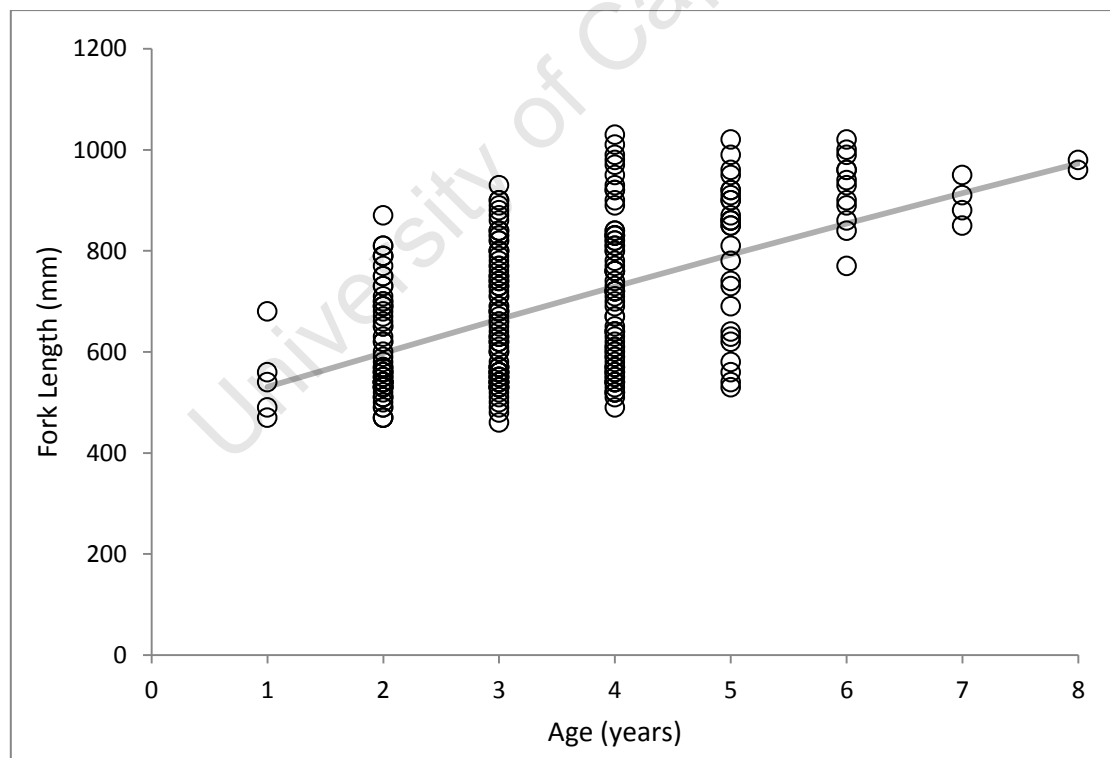


Figure 4.7: Relationship between age and fork length for male and female *S. lalandi* in South African waters. The line represents the best fit von Bertalanffy growth model without any added penalty restriction.

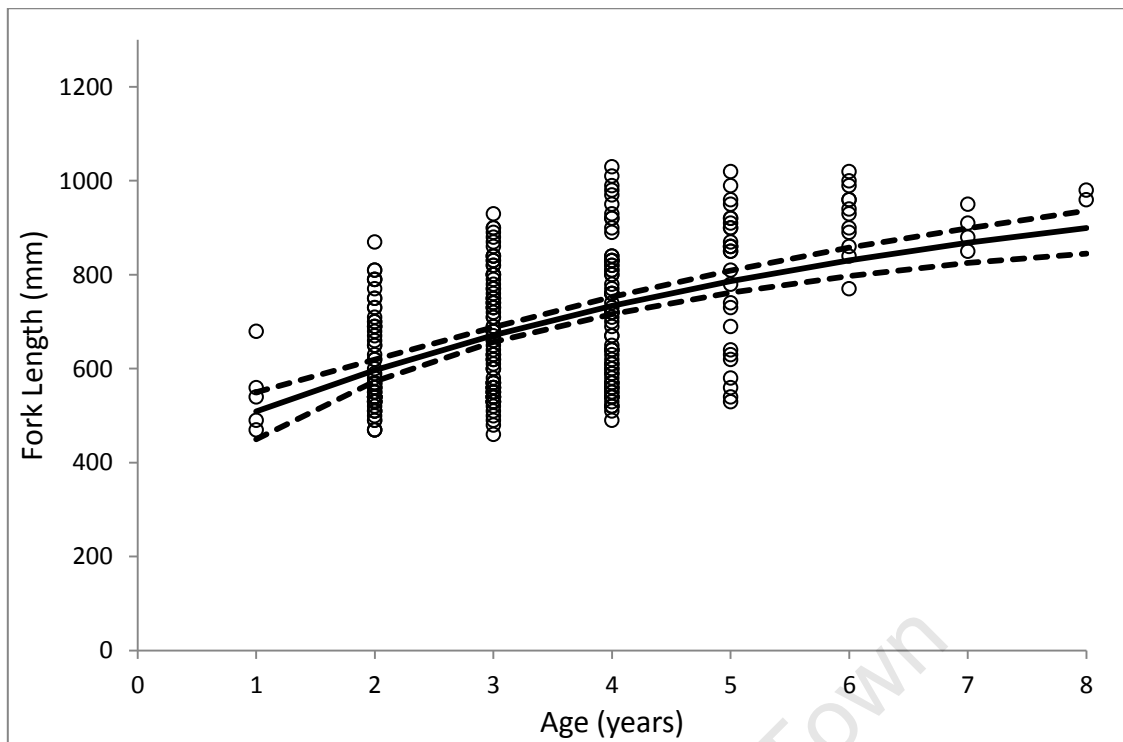


Figure 4.8: Relationship between age and fork length for male and female *S. lalandi* in South African waters. The line represents the best fit von Bertalanffy growth model with penalty restriction on  $L_{\infty}$ . The estimated 95% confidence intervals around the growth curve are represented by the broken lines.

#### LIFE HISTORY COMPARISON

The South African population of yellowtail displayed slightly slower growth performance compared to other *Seriola* species, but was similar to other documented populations of yellowtail (Table 4.1). The Japanese population displayed the highest growth performance and had a substantially larger K value than the other populations. The growth performance seen in this study still falls into reasonable biological limits for the species and genus (Figure 4.9). Of all the Carangid species documented, the *Seriola* genus displays some of the highest growth performance.

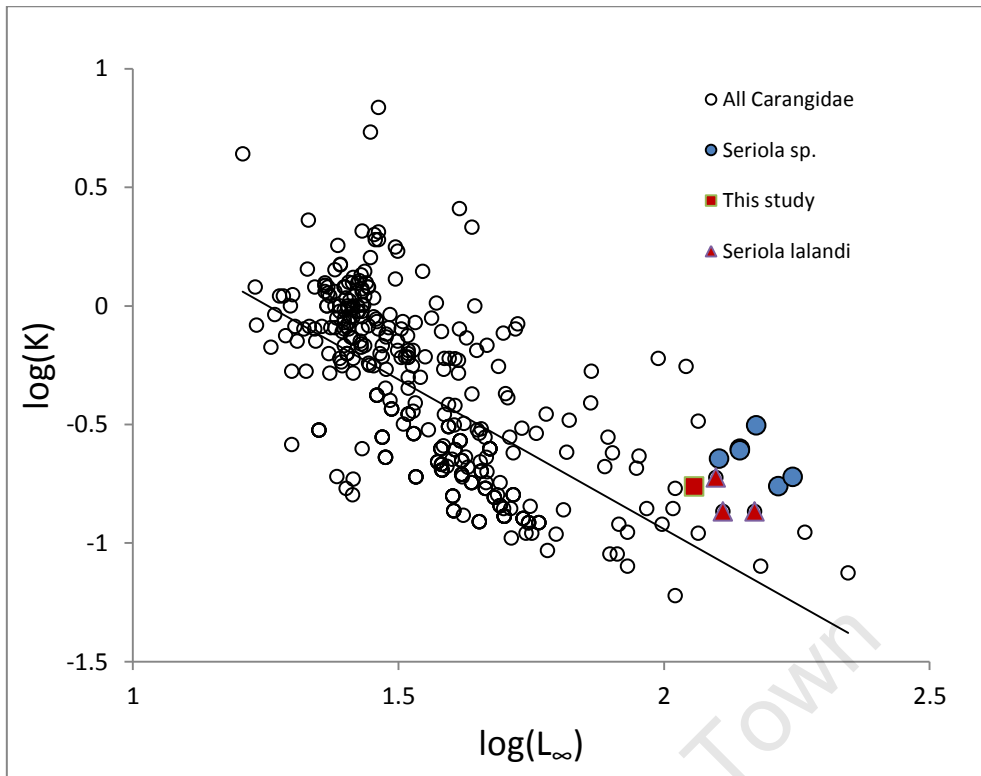


Figure 4.9: Comparison of growth performance between 386 studies on Carangid species (Froese and Pauly 2000) and within the *Seriola* genus including this study. The fast growth performance of the *Seriola* genus and *S. lalandi* can be seen.

#### AGE AT MATURITY

The estimated age at which 50 % of males were mature ( $A_{50}$ ) was 2.3 years (95 % CI = 0.57 – 3.18 years) with a  $\delta$  of  $1.22 \text{ y}^{-1}$  (Figure 4.10) and 3.7 years (95 % CI = 1.29 – 5.79 years) with a  $\delta$  of  $2.45 \text{ y}^{-1}$  for females (Figure 4.11).

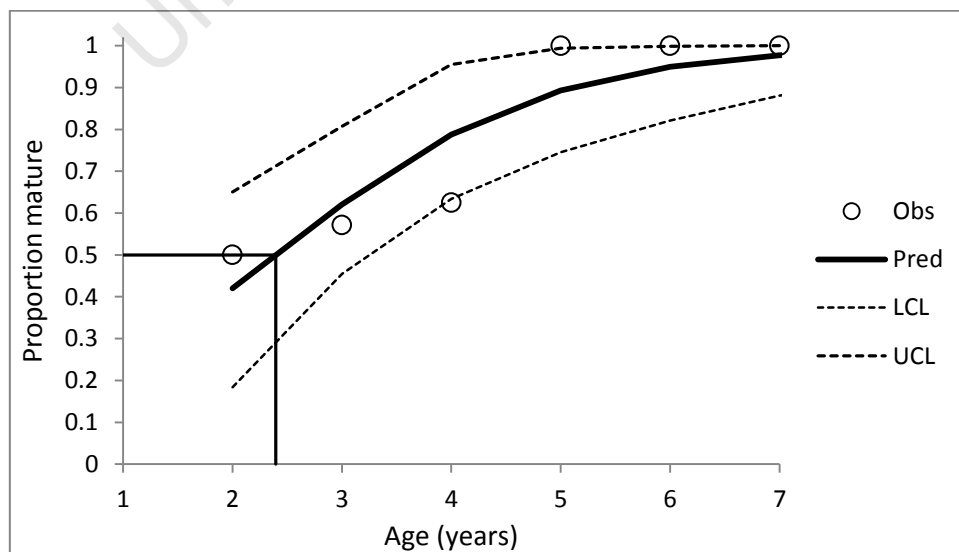


Figure 4.10:  $A_{50}$  for male *S. lalandi* in South African waters *lalandi* with upper (UCL) and lower (LCL) 95 % confidence intervals around the predicted proportion mature.  $A_{50} = 2.3$  years,  $\Delta = 1.22 \text{ y}^{-1}$ .

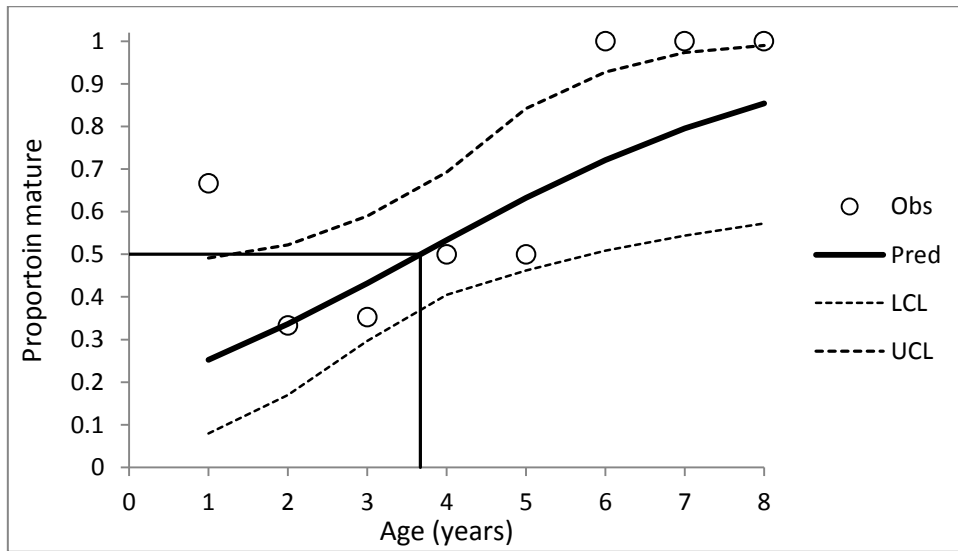


Figure 4.11:  $A_{50}$  for female *S. lalandi* in South African waters with upper (UCL) and lower (LCL) 95 % confidence intervals around the predicted proportion mature.  $A_{50} = 3.6$  years,  $\Delta = 2.45 \text{ y}^{-1}$ .

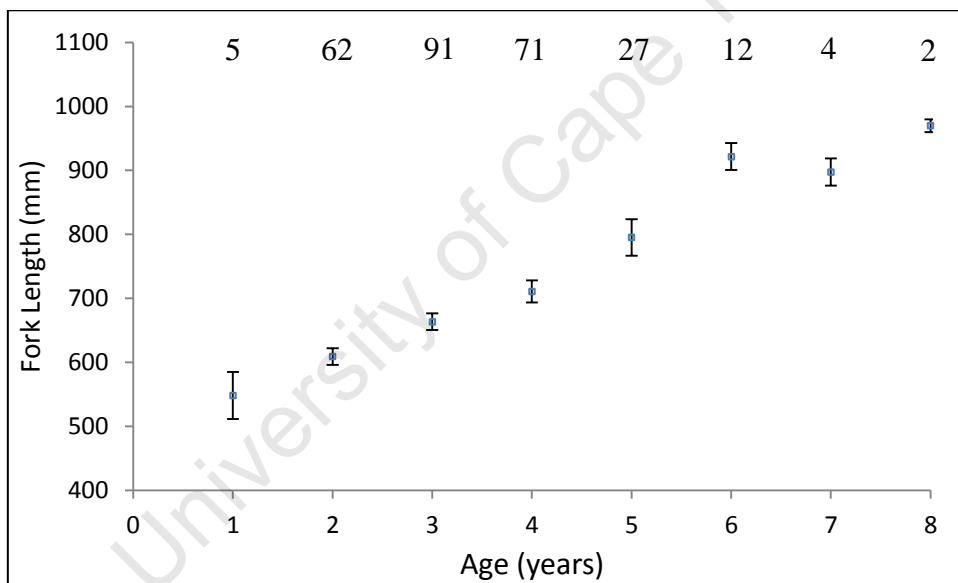


Figure 4.12: Average fork length at age with standard error and sample size per age class for *S. lalandi* in South African waters.

Fish aged in their first year of growth showed the highest error for fork length ( $\pm 36.79 \text{ mm}$ ) (Figure 4.12).

## *DISCUSSION*

As observed in previous studies ageing yellowtail is difficult and problematic with regard to all techniques and structures available for ageing the species. The wide range of hard structures used to age the species further confirms this. Baxter (1960) conducted the first study on the age and growth of yellowtail and found that scales were the most appropriate structure for ageing the species. In this study however, scales were difficult to read as no distinct bands are present, but denser concentric bands can be visible. Yellowtail are also known to have high scale regeneration rates, thus acquiring scales with the full age range can be difficult (Baxter 1960). Gillanders et al. (1999a) found that all hard structures (vertebrae, scales and both whole and sectioned sagittal otoliths) except dorsal spines showed legible annual growth increments and could be used for ageing. Most recently Shiraishi et al. (2010) used the vertebrae of yellowtail for ageing. All these studies had difficulties in ageing the species regardless of the structure used. The use of all possible structures in these studies has given a good indication of which structures give the most accurate estimation of age. In this study the possibilities of using scales, sectioned and whole otoliths were explored. Scales were discarded due to the difficulty of distinguishing annuli and a lack of samples. Both sectioned and whole sagittal otoliths were explored as potential structures for ageing yellowtail in this study. Both showed distinct bands that could be interpreted as annuli. However sectioned otoliths showed high levels of noise in the form of numerous fine striations which confused readers. This has been noted as a difficulty of using sectioned otoliths in previous studies (Gillanders et al. 1999a). It was also noted that reading sectioned otoliths results in higher ages than other structures as they display the dense annuli of older fish to a better effect. This was observed by Stewart et al. (2004) where a maximum age of 21 was observed for yellowtail in Australia. This was also the case in this study where trial readings done on sectioned otoliths suggested a maximum observed age of 13 years and a number of fish were aged older than the maximum age of 8 observed for whole otoliths. Although reading sectioned otoliths suggested higher maximum ages it also resulted in fewer young individuals with extremely low numbers of 1 and 2 year old fish. For this study whole otoliths were used because identifying the first growth zone was easier and whole otoliths were more consistently readable. Only 49 % of the sectioned otoliths were readable compared to 73 % for whole otoliths. Whole otoliths

had distinctly less noise along the rostrum than sectioned otoliths making the identification of annuli easier for readers.

The length-weight relationship was not found to be different for males and females and thus the sexes were grouped together. Baxter (1960) similarly found no difference between the sexes and produced a similar relationship to that described in this study.

Precision gives an indication of the repeatability of age readings and therefore also a measure of how difficult the species is to age (Campana 2001). Precision does however not give any indication of how accurate the determined age is in comparison to the true age of the fish (Campana 2001). Various measures of precision exist, the simplest of them being percent agreement between readers. Percent agreement has been criticized as it does not take into account the age range of the species and is therefore only truly useful for age specific comparisons within and between species with similar age ranges (Beamish and Fournier 1981, Campana 2001). This method does however prove useful when trying to understand the variation between readers and how many samples they agree on. Percent agreement between any two of the three readers was good in this study, however agreement between all three readers was extremely low. This further displays the difficulty in ageing yellowtail as the probability of all three readers assigning the same age to a fish is low. Percentages ranged from 27 % to 49 % for the lowest and highest agreement of the three combinations of readers.

APE and CV are two measures of precision considered to be more statistically sound than percent agreement (Beamish and Fournier 1981). These methods take into account multiple age groups and express precision based on all age groups, whereas percent agreement can have high levels of variation between age groups (Hoenig et al. 1995, Campana 2001). It is therefore more appropriate to use APE and CV when comparing precision between studies. CV values were high when compared to Gillanders et al. (1999a) who recorded a CV of 12 % for otoliths compared to the 21 % recorded in this study. This suggests that yellowtail were more difficult to age in this study, although sectioned otoliths were used by Gillanders et al. (1999a) as opposed to whole otoliths in this study. Gillanders et al. (1999a) also recorded various levels of precision between vertebrae, scales and otoliths, this may explain the high CV recorded in this study as different otolith formats were read.

Validation of ageing methods is vital in age and growth studies and a number of methods exist to accomplish this. They are however not all feasible or possible as is the case in this study. Marginal increment and edge analysis are two common techniques of age validation when using calcareous structures (Campana 2001). Increment validation techniques have been used in previous studies with success for yellowtail and other *Seriola* species (Gillanders et al. 1999a, Shiraishi et al. 2010, Manooch and Potts 1997b). Edge analysis conducted during this study revealed no pattern in increment formation and was not useful as a validation technique. Studies conducted in both hemispheres determined that yellowtail lays down one growth increment annually (Gillanders et al. 1999a, Shiraishi et al. 2010). Similar results were found for amberjack (Manooch and Potts 1997b) where one growth increment was laid down annually during northern spring months. Although all studies presenting increment validation results for *Seriola* species have noted that only one increment is laid down per year the method is only a partial confirmation. Mitani and Sato (1959) noted that a wide range marginal of increment growth conditions may be found over the same time period, suggesting that it is possible for the method to provide false results. Ideally a mark recapture study where chemical markers are used to confirm increment formation should be used in any future age studies on the species.

The growth of a fish can be defined in its simplest form as the change in body mass over time through the results of the two antagonistic processes of anabolism and catabolism (Pauly 1984a). Growth in fish varies greatly between species depending on life history strategies and various environmental factors such as temperature, resource abundance, oxygen, nutrient levels, predator density and genetics (Helfman et al. 2009). An empirical relationship exists between the age of fish and various aspects of their growth which can be used to define important life history characteristics. The relationship between age and growth produces an asymptotic curve which should flatten out as fish become older, the shape of this curve depends greatly on the growth characteristics of the species (Helfman et al. 2009). However, to gain an accurate representation of the growth curve for a species, all age/size classes must be present. Badly represented or absent age/size classes will result in the curve being weighted towards age/size classes with sufficient data. Small/young fish were scarce and absent to a certain degree in this study resulting in a growth curve that does not curve towards zero. The smallest aged fish was 460 mm FL at one year of age, this was only one of five one year old fish in this study. Yellowtail of below 400 mm FL would

greatly improve the representation of growth for yellowtail put out by the von Bertalanffy growth curve of in this study. The lack of small fish also explains the small  $t_0$  observed in this study and therefor the resulting growth curve will not describe the growth of smaller fish accurately. This was also the case in the study done by Stewart et al. (2004) where a  $T_0$  of -4.4 was found for yellowtail in Australia. The parameters of the von Bertalanffy growth equation describe various aspects of the growth of fish based on age and length data for the species. These parameters should ideally fall within realistic biological constraints. Two versions of the von Bertalanffy growth equation are presented in this study (Equations 4.14 and 4.15). Equation 4.14 represents the growth equation for yellowtail without any constraints on the parameters. This resulted in an unrealistically large  $L_\infty$  and a slow growth rate  $K$  which are uncharacteristic of the species and large fast growing pelagic fish in general. The relationship between these two parameters is antagonistic, as  $L_\infty$  gets larger, so does  $K$  decrease (Alvarez-Lajonchere and Ibarra-Castro 2012). By using a penalty restricting  $L_\infty$  based on its empirical relationship to  $L_{max}$  a more realistic growth equation can be produced where  $K$  is greater and  $L_\infty$  is smaller (Equation 15). Froese and Binohlan (2000) produced a large database of various fish species was used to find the mean relationships between various aspects of age and growth parameters. The study found that  $L_\infty$  should generally fall within 10 % of  $L_{max}$  based on 511 publications.

The growth parameters found for yellowtail in this study are comparable to those found in previous studies (Baxter 1960, Penney 1982, Gillanders et al. 1999a and Shiriashi et al. 2010). The growth performance index  $\Phi'$  is based on the relationship between two parameters of the von Bertalanffy growth equation,  $K$  and  $L_\infty$  and gives a better and more comparable index of growth (Munro and Pauly 1983). As  $K$  and  $L_\infty$  are directly related, comparing just one of these parameters between populations is likely to give a false impression of any differences in growth.  $K$  and  $L_\infty$  can show large levels of variation between populations while  $\Phi'$  has been shown to vary less between populations and can serve as a more meaningful tool in growth comparisons (Munro and Pauly 1983). Table 1 displays the variation that can be seen in  $K$  and  $L_\infty$  between populations of the same species and within the *Seriola* genus. The growth performance across the family relatively consistent with all species and populations showing fast growth. Pauly (1979) sowed that the average growth performance across all documented species was 2 ( $\Phi'$ ) and any value above to is considered fast growth.

Table 4.1: Global variation in the growth parameters and growth performance for various populations of *Seriola* species sourced from Fishbase and found this study\* (Froese and Pauly 2000).

Species	$L_{\infty}$ (cm)	Length Type	K	$t_0$	$\Phi'$	Country	Locality
<i>S. quinqueradiata</i>	110	TL	0.56	0.11	3.83	Japan	Rensen
	116	TL	0.33	0.05	3.64	Japan	Wakasa Bay
<i>S. dumerili</i>	127	TL	0.23	0.72	3.56	USA	Naples, Florida, Texas
	139	FL	0.25	0.79	3.68	USA	off Louisiana
	139	FL	0.25	0.79	3.68	USA	Gulf of Mexico, Louisiana
	149	FL	0.31		3.84	USA	Hawaii
	164	FL	0.17	0.65	3.67	USA	South Florida
	174.6	TL	0.19	0.31	3.76	Croatia	Adriatic Sea
<i>S. lalandi</i>	125.2	FL	0.19	0.74	3.47	Australia	New South Wales
	129.1		0.14	-1.9	3.36	USA	California
	148	TL	0.14	-1.9	3.47	USA	Southern California
	110.8	FL	0.3	0.58	3.57	Japan	Western Kyushu
	106.4	FL	0.17	-2.75	3.51	South Africa*	Eastern and Western Cape
	184	FL	0.054	-4.4	3.26	Australia	New South Wales

Although the  $\Phi'$  value of 3.51 for yellowtail in this study is low for the genus it is still considered a fast growing species as its  $\Phi'$  value is well above the average of 2  $\Phi'$  for all species and still falls within reasonable range of the genus and species from other studies. A lower growth performance ( $\Phi' = 3.26$ ) was observed for yellowtail in Australia, this was due to a low K and high  $L_{\infty}$  (Sterwart et al. 2004).

The fast growth performance of yellowtail is evident through a high  $\Phi'$  which makes the species well suited to the highly productive temperate waters it inhabits. The region from the Agulhas Bank and up to the west coast of South Africa is highly dynamic with large scale upwelling on the west coast and an influx of nutrient rich eddies over the Agulhas Bank (Schumann et al. 1982, Probyn et al. 1994, Hutchings et al. 2001, Moloney et al. 2005). This in turn creates an abundant food supply for yellowtail in the form of a number of pelagic prey species which can sustain a high growth rate (Crawford 1987, Augustyn 1990, Roberts and Sauer 1994, van der Lingen et al. 2006). This region also supports another extremely fast growing pelagic predator *snoek* which has a documented K of  $0.42 \text{ y}^{-1}$  and a  $\Phi'$  of 3.54 (Griffiths 2002, Froesy and Pauly 2000).

The largest of the *Seriola* species the amberjack displayed a similar growth rate (K) to yellowtail were K was  $-0.115 \text{ y}^{-1}$  Its  $L_{\infty}$  was however larger due to the larger maximum size of this species (Manooch and Potts 1997b). A difference in growth parameters was observed for amberjack where a second population showed faster growth rates (K) and a smaller  $L_{\infty}$  (Manooch and Potts 1997a and Moonach and Potts 1997b). The difference was attributed to the larger fish included in the first study, which shows that ideally all size classes of a species need to be included in growth studies (Manooch and Potts 1997b). This further demonstrates the variation that can occur between populations and how the size distribution of the samples in a study can affect the growth parameters.

Average length at age was found to be similar at one and 8 years of age (maximum) to other studies at 548 mm FL (Baxter 1960, Gillanders et al. 1999a, Shiraishi et al. 2010). At five years old yellowtail in this study had a similar mean length to Gillanders et al. (1999a) at 795 and 788 mm FL, but was smaller than that found by Baxter (1960) at 831 mm FL and Shiraishi et al. (2010) at 911 mm FL. Maximum observed ages of 7 and 8 years for males and females were the same for yellowtail in Japanese waters (Shiraishi et al. 2010) and less than the 9

years observed in Australian waters respectively (Gillanders et al. 1999a). Females matured in their third year (663 mm FL) whereas males matured earlier in their second year (609 mm FL) in this study. Both Baxter (1960) and Gillanders et al. (1999a) found yellowtail maturing in their second year in Californian and Australian waters. Murayama (1992) found that Japanese yellowtail also matured in their second year and only attained a maximum age of five years in Japanese waters. Amberjack was found to mature at 5 years of age (Micale et al. 1999) and between 3 and 4 years (Marino et al. 1992). Amberjack is the largest species in the *Seriola* genus as well as one of the oldest, attaining a maximum age of 17 years (Moonach and Potts 1997).

As mentioned in previous studies yellowtail are an inherently difficult species to age using calcareous structures. This is not specific to yellowtail but common across all *Seriola* species and typical of fast growing pelagic species. The low levels of precision and agreement in this study are testament to this. Although ageing was difficult the growth parameters, maximum ages and age at maturity found for yellowtail in South African waters were on par with previous studies done on populations globally of the species. The results of this study show that the South African population of yellowtail is an early maturing and fast growing species with a relatively short life span. Further studies should focus on the age validation of the species. A tag-recapture program releasing chemically tagged fish is suggested to give further confirmation on the frequency of growth increment formation.

## CHAPTER 5

# CONCLUSIONS

Various aspects of the life-history of *Seriola lalandi* have been described for the first time in South African waters. Previously its diet had only been investigated as part of a multi-species project and some unpublished data on its movements, age and spawning season has been compiled and analysed. As an important line-fish species which has undergone strong changes in abundances, understanding of its life-history is necessary to improve management of its fishery.

Three main aspects of the life-history of South African yellowtail were explored in this study, namely the diet and feeding habits, reproductive characteristics and the age and growth. All three of these aspects were either not well understood or completely unknown.

### *BIOLOGY*

Few studies have documented the diet of *Seriola* species. Those that have describe the genus as generalist feeders (Matallanas et al. 1995, Barreiros et al. 2003). The results of this study show similar habits to those observed in other dietary studies on the family. A shift in the importance of targeted prey species was observed in the diet of *S. rivoliana* in the Azores between sampling periods (Barreiros et al. 2003). This shift in prey species was predicted to be due to a change in the abundance of small pelagic teleost species in the area. *S. rivoliana* can also be classified as a generalist feeder, preying on a wide variety of species and targeting those that are most abundant (Barreiros et al. 2003). It is likely that the diet of yellowtail will shift in a similar manner as that of *S. rivoliana* in response to prey abundance. The differences in diet between regions observed in this study reflect a similar situation where differences in regional prey species abundance are reflected in the diet of yellowtail, confirming its classification as an opportunistic feeder.

The opportunistic manner in which yellowtail feed on a variety of prey species allows it to exploit diverse habitats. It also makes the species robust in that it is not dependent on a few

prey species for survival and is not directly linked to their wellbeing. Declines in certain prey species will simply drive yellowtail to targeting the next abundant and accessible species. In the dynamic waters surrounding the Western Cape shifts in small pelagic prey are common (Cury et al. 2000, Roberts 2005). This is likely to be represented in the diet of yellowtail in any future studies correlating its diet to current regional prey abundance.

As has been the case for all *Seriola* species ageing yellowtail using calcareous structures has been difficult. Scales, sectioned and whole sagittal otoliths were explored as possible ageing structures in this study and all but scales proved useful to some extent. The growth characteristics of yellowtail in South African waters were found to be similar to those of other populations in Australia, Japan and North America (Baxter 1960, Gillanders et al. 1999a and Shiraishi et al. 2010). *Seriola lalandi* in South African waters showed an estimated slow annual growth rate (K) of  $0.17 \text{ y}^{-1}$  compared to other documented *Seriola* species, but was consistent with that of other yellowtail populations. Integrating the independence of K and  $L_{\infty}$  estimates into the growth performance parameter yielded the fast growth performance  $\Phi' = 3.51$  for yellowtail in this study. This fast growth performance may be explained by the highly productive waters yellowtail occupies along the South African coastline.

Yellowtail in South African waters have shown similar spawning patterns to those of other populations globally. Elevated GSI revealed the spawning season to be over the summer months, peaking in December, similar to other documented populations in the Southern Hemisphere (Gillanders et al. 1999a). Females matured at 550 mm FL ( $L_{50}$ ) whereas males matured larger at 585 mm FL ( $L_{50}$ ) which is smaller than that observed in other populations for both sexes. The lack of hydrated eggs in the ovaries of mature fish indicated that the final hydration of oocytes is likely to be a rapid process. Post-ovulatory follicles (POF's) were found in a number of ovaries indicating spawning had occurred recently and it is likely that spawning took place outside of the feeding grounds of yellowtail limiting the chance of capturing fish with hydrated oocytes.

### *CHALLENGES OF THE STUDY*

Estimating the age of the species using sagittal otoliths proved problematic. Initially sectioned otoliths were examined as they had displayed the greatest age range in other studies. They were however extremely difficult to read due to the numerous narrow striations obscuring true annual growth increments. Whole otoliths were thus chosen as annual growth zones were more readily interpretable. They were not without their challenges either as the final results showed high levels of error in the ageing.

Sample distribution has proved to be a problem in all studies done on the age and growth of yellowtail as small fish are extremely elusive. No fish under the 460 mm FL size class were aged in this study. An individual fish was found in the 300 mm FL size class in the historic records, but was not available for ageing as no otoliths were kept for this specimen. The lack of small fish reduces the effectiveness of the growth estimation of the species as there are no data for the steepest part of the growth curve. The historical records provided a strong dataset covering a substantial time period as well as a large sample size. The vast majority of the dataset was reliable, however the macroscopic gonad stage assigned for each fish was not consistently recorded and the staging criteria was unknown and potentially variable. All attempts to standardise the gonad staging failed and thus GSI backstaging was used to assign stages to the fish in the historic records so they could still be used.

The small sample sized used to determine the diet of yellowtail may not have been adequate to fully describe its diet. A larger monthly sample size may be helpful in giving a more in depth description of its diet. Also the number of unidentified remains could be reduced by using hard parts such as otoliths and squid beaks to further identify the remains found in diet samples.

### *FISHERY AND MANAGEMENT*

Although a recent stock assessment done on yellowtail in South African waters has shown that the species stock is in a good state, this has not always been the case (Winker et al. 2012). Natural ecosystems can be viewed at an evolutionally scale where individuals die and populations disappear or they can be viewed on a smaller time scale where population

numbers and consistency become more important (Holling 1973). Fish populations are dynamic and are influenced by a vast variety of variables, both natural and anthropogenic. Changes in stock size and characteristics experience change over temporal and spatial scales and are thus not constant and must be assessed as such, in order to provide the best advice for fisheries

Management of the recreational fishery of yellowtail is currently only regulated by a bag limit of 10 fish per angler per day. There are however no constraints on commercial line and beach seine fisheries for the species, no total allowable catch (TAC) and no closed season. Previously a TAC and no take areas were placed on the purse-seine fishery during its brief period of operation in the 1970/1980's. This was mostly due to large catches made by purse-seine fisheries and the competition between this fishery and the line-fishery. The closed areas were set for False Bay and between Quin point and Struisbaai to 15 miles offshore which protected the majority of major banks fished by the line-fishery for yellowtail (Penney 1982). However, even with these measures in place catches reached an all-time low in the early 1980's indicating a potential crash in the population (Penney 1982). This could be linked to the large nominal catches (>1000 tonnes) made by the combined effort of the line and purse-seine fisheries for yellowtail. These catches may also be underestimated by up to a factor of 3 based on discrepancies between nominal and actual catches (Sauer et al. 1997). Catches of those magnitudes (>1000 tonnes) are not sustainable for the species. As there is currently no regulation of catches of the species in the commercial sector, catches of those magnitudes are possible in principle. Managing a fishery like yellowtail which displayed highly variable inter-annual catches with a set TAC is difficult, however if annual catches remain elevated at a level equivalent to that seen in the 1970's it would be wise to limit catches. This may be done most effectively by setting a minimum size limit at the  $L_{50}$  or slightly above (600 mm FL) for the species as 41 % of fish caught in the historic records fall below the  $L_{50}$  of males in this study (Figure 5.1). This has been done for the species in both North America and New South Wales Australia where the minimum size limit has been set at 600 mm TL (520 mm FL) and 650 mm TL (570 mm FL) respectively (Scandol et al. 2008, CDFG 2013). This method of limiting catches will protect fish that have not yet contributed to the population, but leaves larger fish unprotected. It has been documented that larger females have much greater fecundity than smaller

individuals (Baxter 1960). However large fish are seldom caught in the South African fishery and protecting them may not prove efficient or practical. *Seriola lalandi's* greatest form of protection may simply be their behaviour or lack of predictable behaviour, making targeting them difficult and lowering potential catches.

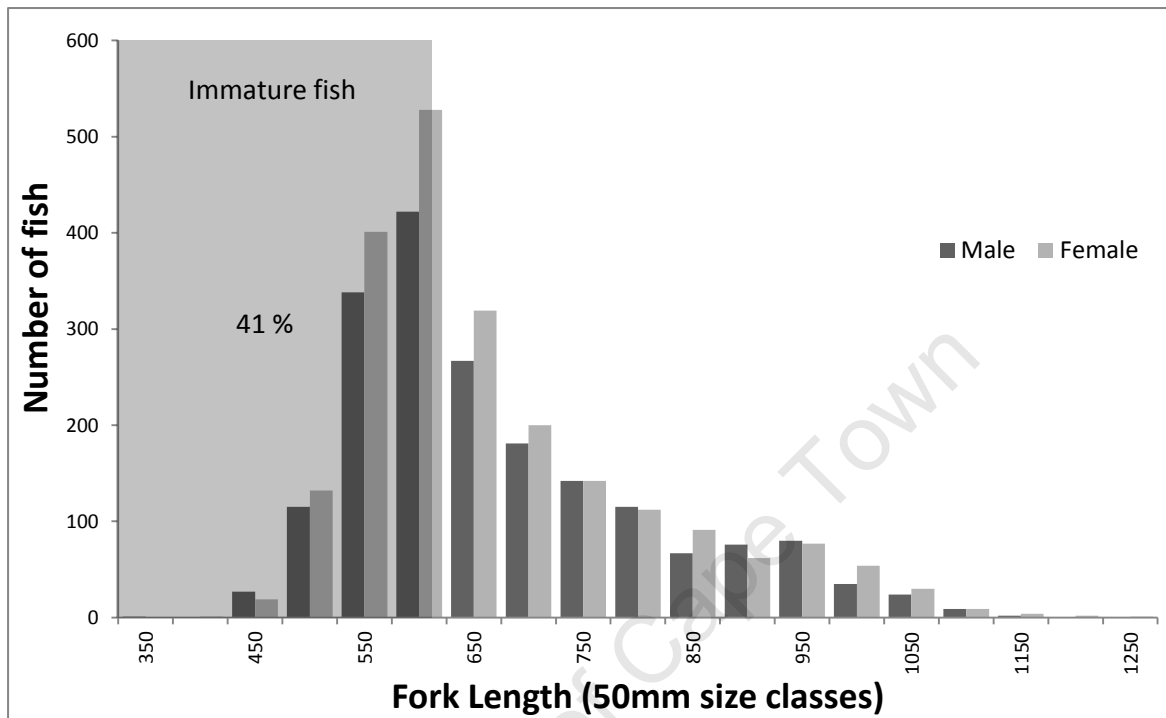


Figure 5.1: Size histogram for male and female *S. lalandi* in 50 mm size classes (n=6142). Shaded area represents immature fish below 585 mm FL which represents the  $L_{50}$  of male *S. lalandi* who mature at a larger size than females.

#### FUTURE RESEARCH

The movement of yellowtail in South African waters has been documented to some extent through tagging programs conducted by ORI (oceanographic Research Institute) and DAFF (Penney 1982, Dunlop and Mann 2012) and internationally (Baxter 1960, Gillanders et al. 2001, Holdsworth and Saul 2003, Hutson et al. 2007). These studies provide broad scale movement patterns and some seasonal trends, but fail to document finer scale movements. From observations made through the fishery of species we know yellowtail moves rapidly between aggregation areas as water conditions change. This is highly evident in the movements of the species in False Bay and off the Cape Point region. These movements would best be documented through the deployment of pop-up satellite tags on a number of fit individuals. Pop-up satellite can provide fine-scale movement patterns coupled with

simultaneous collection of temperature data (Block et al. 2001, Block et al. 2005). One of the major anomalies in the South African population is why the fish in the Eastern Cape are generally larger than those in the Western Cape and where do all the big fish go? Understanding the stock structure may explain some of these questions and tracking large (>18 kg's) fish may give insight into their movements.

This information will be highly valuable in relating the movement of yellowtail to changing water conditions and temperature. The movement and "mixing" of tagged fish from various locations along the coastline will also give insight into the stock structure of the South African population.

University of Cape Town

## REFERENCES

- Alvarez-Lajonchere L, Ibarra-Castro L. 2012. Relationships of maximum length, length and first sexual maturity and growth performance index in nature with absolute growth rates of intensive cultivation of some tropical marine fish. *Journal of the World Aquaculture Society* 43: 607-620.
- Augustyn CJ. 1990. Biological studies on the chokker squid *Loligo vulgaris renaudii* (cephalopoda; myopsida) on the spawning grounds off the south-east coast of South Africa. *South African Journal of Marine Science* 9: 11-26.
- Bakun A, Parrish RH. 1982. Turbulance, transport and pelagic fish in the Californian and Peru Current systems. *California Cooperative Oceanic Fisheries Investigations* 23: 99-112.
- Barreiros JP, Morato T, Santos RS, De Borba AE. 2003. Interannual changes in the diet of the almoco jack, *Seriola rivolina* (Perciformies: Carangidea) from the Azores. *Cybium* 27: 37-40.
- Baxter JL. 1960. A study of the yellowtail *Seriola dorsalis* (GILL). *State of California Department of Fish and Game; Fish Bulletin* : 110.
- Beamish RJ, Fournier DA. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Science* 38: 982-983.
- Beamish RJ. 1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. *Journal of the Fisheries Research Board of Canada* 36: 141-151.
- Ben-Tuvia A. 1995. Biological characteristics of middle-sized pelagic fishes. *Scientia Marina* 59: 205-209.
- Bernard DR. 1981. Multivariate analysis as a means of comparing growth in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 233-236.

- Berruti A, Colclough J. 1987. Comparison of the abundance of pilchard in Cape gannet diet and commercial catches off the Western Cape, South Africa. *South African Journal of Marine Science*. 5: 863-869.
- Block AB, Dewar H, Blackwell SB, Williams TD, Prince ED, Farwell CJ, Boustany A, Teo SLH, Seitz A, Walli A, Fudge D. 2001. Migratory movements, depth preferences and thermal biology of Atlantic Bluefin tuna. *Science* 293: 1310-1314.
- Block BA, Teo SLH, Walli A, Boustany A, Stokesbury MJW, Farwell CJ, Weng KC, Dewar H, Williams TD. 2005. Electronic tagging and population structure of Atlantic Bluefin tuna. *Nature* 434: 1121-1126.
- Brownell CL. 1979. Water quality requirements for first feeding in marine fish larvae: ammonia, nitrite, nitrate, pH, oxygen and carbon dioxide. PhD thesis, Department of Zoology, University of Cape Town.
- Branch G, Griffiths CL, Branch ML, Beckley LE. 2008. Two Oceans: A guide to the marine life of southern Africa. Struik Publishers, Cape Town.
- Burch RK. 1979. The greater amberjack, *Seriola dumerili*: Its biology and fishery off southeastern Florida. MSc thesis, University of Miami, Coral Gables.
- Buckland ST. 1984. Monte-Carlo confidence intervals. *Biometrics* 40: 811-817.
- Campana SE. 1983. Calcium deposition and otolith check formation during periods of stress in coho salmon, *Oncorhynchus kisutch*. *Comparative Biochemistry and Physiology* 75A: 215-220.
- Campana SE. 1984. Interactive effects of age and environmental modifiers on the production of daily growth increments in otoliths of plaifin midshipman, *Porichthys notatus*. *Fishery Bulletin* 82: 165-177.
- Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59: 197-242.
- CDFG 2013. California sport fishing regulations 2012-2013. <http://www.dfg.ca.gov/marine/>.

- Crawford RJM. 1987. Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. *South African Journal of Marine Science* 5: 735-757.
- Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro M, Upfold L. 2006. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation* 132: 119-125.
- Clark KR, Warwick RM. 2001. Change in marine communities: An approach to statistical analysis and interpretation. 2<sup>nd</sup> Edition, PRIMER-E: Plymouth.
- Chilton DE, Beamish RJ. 1982. Age determination methods for fishes studied by the ground fish program of the Pacific Biological Station. *Canadian Special Publication of Fisheries and Aquatic Sciences* 60: pp 102.
- Crooke SJ. 2001. California's marine living resources: A status report: yellowtail. *California Department of Fish and Game*. December 212-214.
- Cushing DH. 1975. Marine ecology and fisheries. Cambridge University Press. pp 278.
- Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Verheye HM. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science* 57: 603-618.
- DAFF 2010. Status of the South African marine fishery resources: Line-fish. Department of Agriculture, Forestry and Fisheries.
- Dunlop SW, Mann BQ. 2012. ORI Tagging Project: summary of tag and recapture data for Cape yellowtail (*Seriola lalandi*) caught along the South African coastline: Jan 1984-Oct 2012. Oceanographic Research Institute, Durban: 4pp. (ORI Data Report 2012/09).
- Durate SM, Alcaraz M. 1989. To produce many small or few large eggs: A size-independent reproductive tactic of fish. *Oecologia* 80: 401-404.

- Efron B, Tibshirani R. (1986). Bootstrap methods for standard errors, confidence intervals and other measures of statistical accuracy. *Statistical Science* 1: 54-75.
- Eltink A, Kuitert CJ. 1989. Validation of ageing techniques on otoliths of horse mackerel (*Trachurus trachurus* L.). *International Council for the Exploration of the Sea*, CM 43: pp 15.
- Etherton M. (Unpublished). A guide to the Cefas age determination program for finfish species of the UK coastal waters. Center for Environment Fisheries and Aquaculture Science, Lowestoft, United Kingdom.
- Fitzhugh GR, Hettler WF. 1995. Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tyrannus*. *Fishery Bulletin-national Ocean and Atmospheric Administration* 93: 568-572.
- Froese R, Binohlan C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology* 56: 758-773.
- Froese R, Pauly D. Editors. 2000. FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines. pp 344.
- Furness RW, Tasker ML. 2000. Seabird-fishery interactions: Quantifying the sensitivity of seabirds to reductions in sandeel abundance and identification of key species for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* 202: 253-264.
- Ganias K. 2012. Thirty years of using the postovulatory follicles method: Overview, problems and alternatives. *Fisheries Research* 118: 63-74.
- García A, Díaz MV. 1995. Culture of *Seriola dumerili*. *Cahiers Options Méditerranéennes, Marine Aquaculture Finfish Species Diversification*. 16: 103-114. CIHEAM, Zaragoza, Spain.
- Geten F, Terwinghe E, Danguy A. 2009. Atlas of fish histology. BIOS Scientific Publishers Limited, Oxfordshire.

- Gillanders BM, Ferrell DJ, Andrew NL. 1999b. Size and maturity and seasonal changes in gonad activity of the yellowtail kingfish (*Seriola lalandi*; Carangidae) in New South Wales, Australia. *New Zealand Journal of Marine and Freshwater Research* 33: 457-468.
- Gillanders BM, Ferrell DJ, Andrew NL. 1999a. Ageing methods for yellowtail kingfish, *Seriola lalandi*, and results from age and size based growth models. *Fisheries Bulletin* 97: 812-827.
- Gillanders BM, Ferrell DJ, Andrew NL. 2001. Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): how useful are data from a cooperative tagging program? *Marine and Freshwater Research* 52: 179-192.
- Gilchrist JDF. 1903. The development of the South African fishes. Part-1. *Marine Investigations in South Africa* 2: 181-201.
- Gilchrist JDF. 1916. Eggs and larvae of Cape fishes. Province of the Cape of Good Hope. *Marine Biology Report* 3: 1-26.
- Gong G, Shiah F, Liu K, Wen Y, Liang M. 2000. Spatial and temporal variation of chlorophyll *a*, primary productivity and chemical hydrography in the southern East China Sea. *Continental Shelf Research* 20: 411-436.
- Gong G, Wen Y, Wang B, Lui G. 2003. Season variation of chlorophyll *a* concentration, primary production and environmental conditions in the subtropical East China Sea. *Deep-Sea Research II* 50: 1219-1236.
- Griffiths MH. 2000. Long-term trends in catch and effort of commercial line-fish of South African Cape province: snapshots of the 20<sup>TH</sup> century. *South African Journal of Marine Science* 22: 81-110.
- Griffiths MH. 2002. Life history of South African snoek, *Thysites atun* (Pisces: Gempylidae): a pelagic predator of the Benguela ecosystem. *Fishery Bulletin-National Oceanic and Atmospheric Administration* 100: 690-710.

- Haddon M. 2001. Modelling and quantitative methods in fisheries. Chapman and Hall, New York.
- Hampton I. 1987. Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. *South African Journal of Marine Science* 5: 901-917.
- Harris PJ, Wyanski DM, White BD, Mikell PP, Eyo BP. 2007. Age, growth, and reproduction of greater amberjack off the Southeastern U.S. Atlantic Coast. *Transactions of the American Fisheries Society* 136:6, 1534-1545.
- Helfman SG, Collette BB, Facey DE, Bowen BW. (2009). Early life history. In: *The diversity of fishes, biology, evolution and ecology*. Wiley-Blackwell, Oxford. pp 129-148.
- Heemstra P, Heemstra E. 2004. Coastal fishes of Southern Africa. Grahamstown, South Africa: NISC and SAIAB.
- Hewett SW, Kraft CE. 1993. The relationship between growth and consumption: comparisons across fish populations. *Transactions of the American Fisheries Society* 122: 814-822.
- Hoenig JM, Morgan MJ, Brown CA. 1995. Analyzing differences between two age determination methods by tests of symmetry. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 364– 368.
- Holdsworth J, Saul P. 2003. New Zealand billfish and gamefish tagging 2001 - 02. *Report of the Meeting of the Standing Committee on Tuna and Billfish*, Whangarei 16: 39 pp.
- Holling CS. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1-23.
- Hunter JR, Goldberg SR. 1980. Spawning incidence and batch fecundity in Northern anchovy, *Engraulis mordax*. *Fishery Bulletin* 77: 641-652.
- Hutchings L, Beckley LE, Griffiths MH, Roberts MJ, Sundby S, van der Lingen C. 2001. Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. *Marine and Freshwater Research* 53: 307-318.

- Hutson KS, Smith BP, Godfrey RT, Whittington ID, Chambers CB, Ernest I, Gillanders BM. 2007. A tagging study on yellowtail kingfish (*Seriola lalandi*) and Samson fish (*S. hippos*) in South Australian waters. *Transactions of the Royal Society of Southern Australia* 131: 128-134.
- Hyslop EJ. 1980. Stomach content analysis- a review of methods and their application. *Journal of Fish Biology* 17: 411-429.
- Image J software. <http://rsbweb.nih.gov/ij/>.
- Jerez S, Samper M, Santamaría FJ, Villamandos JE, Cejas JR, Felipe BC. 2006. Natural spawning of the greater amberjack (*Seriola dumerili*) kept in captivity in the Canary Islands. *Aquaculture* 252: 199-207.
- Jover M, Gracia-Gómez A, Tomás A, De la Gándra F, Pérez L. 1999. Growth of Mediterranean yellowtail (*Seriola dumerili*) fed extruded diets containing different levels of protein and lipid. *Aquaculture* 179: 25-33.
- Kämpf J, Doubell M, Griffin D, Matthews RL, Ward T. 2004. Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia. *Geophysical Research Letters* 31: 1-4.
- Katsunori T, El-Zibdeh MK, Ishimatsu A, Tagwa M. 1997. Improved seep production of goldstriped amberjack *Seriola lalandi* under hatchery conditions by injection of tridothyronine ( $t_3$ ) to broodstock fish. *Journal of the World Aquaculture Society* 28: 34-44.
- King JR, McFarlane GA. (2003). Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology* 10: 249-264.
- Kožul B, Skaramuca B and Kraljevič M, Dulčić, Glamuzina B. 2001. Age, growth and mortality of the Mediterranean amberjack *Seriola dumerili* (Risso 1810) from the south-eastern Adriatic Sea. *Journal of Applied Ichthyology* 17: 134-141.

- Kolkovski S, Sakakura Y. 2004. Yellowtail kingfish, from larvae to mature fish – problems and opportunities. In: Cruz Suárez LE, Ricque Marie D, Nieto López MG, Villarreal D, Scholz U, González M. 2004. Avances en Nutrición Acuícola VII. Memorias del VII Simposium Internacional de Nutrición Acuícola. 16-19 Noviembre, 2004. Hermosillo, Sonora, México.
- Lamberth SJ, Bennett BA, Clark BM. (1994). Catch composition of the commercial beach-seine fishery in False Bay, South Africa. *South African Journal of Marine Science* 14: 69-78.
- Leonard EE. 2009. Comparative age and growth of greater amberjack (*Seriola dumerili*) from charterboat and headboat fisheries of west Florida and Alabama, Gulf of Mexico. PhD thesis, University of Florida, Gainesville 2009.
- Liao H, Pierce CL, Larscheid JG. 2001. Empirical assessment of indices of prey importance in the diets of predacious fish. *Transactions of the American Fisheries Society* 130: 583-591.
- Maack G, George MR. 1999. Contributions to the reproductive biology of *Encraicholm puntifer* Fowler, 1938 (engraulidae) from West Sumatra, Indonesia. *Fisheries Research* 44: 113-120.
- Manooch CS, Potts JC. 1997a. Age, growth and mortality of greater amberjack *Seriola dumerili*, from the U.S. Gulf of Mexico headboat fishery. *Bulletin of Marine Science* 61: 671-683.
- Manooch CS, Potts JC. 1997b. Age, growth and mortality of greater amberjack from the southeastern United States. *Fisheries Research* 30: 229-240.
- Matsunari H, Hamada K, Mushiake K, Takeuchi T. 2006. Effects of taurine levels in broodstock diet on reproductive performance of yellowtail *Seriola quinqueradiata*. *Fisheries Science* 72: 955-960.
- Matallanas J, Casadevall M, Carrasson M, Bolx J, Fernandez V. 1995. The food of *Seriola dumerili* (Pisces: Carangidae) in the Catalan Sea (Western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* 75: 257-260.

- Marino G, Mandich A, Massari A, Andaloro F, Porrello S, Finoia G, Cevalco F. 1995. Aspects of reproductive biology of the Mediterranean amberjack (*Seriola dumerili* Risso) during the spawning period. *Journal of Applied Ichthyology* 11: 9-24.
- McGregor G. 1995. Is the northern region the kingfish capital of the Pacific? Part 1: the fish. *Seafood New Zealand June 1995*, pp 28-30.
- McMillan DB. 2007. Fish Histology. Female Reproductive System. Springer, Dordrecht.
- Micale V, Maricchiolo G, Genovese L. 1999. The reproductive biology of the amberjack, *Seriola dumerili* (Risso 1810). I. Oocyte development in captivity. *Aquaculture Research* 30: 349-355.
- Michel P, Marsac F, Cherel Y, Lucas V, Sabatié R, Maury O, Ménard F. 2007. Forage fauna in the diet of three large pelagic fishes (lanvetfish, swordfish and yellowfin tuna) in the eastern equatorial Indian Ocean. *Fisheries Research* 83: 60-72.
- Miranda IT, Peet C. 2008. Farmed yellowtail; *Seriola* spp Seafood Watch, Seafood Report, Monterey Bay Aquarium, Final Report, October 22.
- Mitani F. 1955. Relation between the scale of the yellow-tail, *Seriola quinqueradiata* and fork length and age. *Bulletin of Japanese Society of Scientific Fisheries* 21: 463-466.
- Mitani F. 1958. Studies on the growth and age of the yellowtail, *Seriola quinqueradiata* T. & S., found in Japan and the adjacent region-I. A fundamental consideration on the age estimation by vertebrae. *Bulletin of the Japanese Society of Scientific Fisheries* 24: 626-631.
- Mitani F, Sato T. 1959. Studies on the growth and age of the yellowtail, *Seriola quinqueradiata* T. & S., found in Japan and the adjacent region-II. Estimation of age and growth from the opercular bone. *Bulletin of the Japanese Society of Scientific Fisheries* 24: 803-808.
- Moloney CL, Jarre A, Arancibia H, Bozec Y, Neira S, Roux JP, Shannon LJ. 2005. Comparing the Benguela and Humbolt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES Journal of Marine Science* 62: 483-502.

- Moran D, Gara B, Wells, RMG. 2007. Energetics and metabolism of yellowtail kingfish (*Seriola lalandi* Valenciennes 1933) during embryogenesis. *Aquaculture* 265: 359-369.
- Moran D, Pether SJ, Lee PS. 2009. Growth, feed conversion and faecal discharge of yellowtail kingfish (*Seriola lalandi*) fed three commercial diets. *New Zealand Journal of Marine and Freshwater Research* 43: 917-927.
- Munro JL, Pauly D. 1983. A simple method for comparing the growth of fishes and invertebrates. *ICLARM Fishbyte*, 1: 5-6.
- Murayama T. 1992. Growth of the yellowtail *Seriola quinqueradiata* in the Japan Sea in recent years. *Nippin Suisan Gakkaishi* 58: 601-609.
- Murua H, Kraus G, Sadorido-Rey F, Witthames PR, Thorsen A, Junquera S. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwestern Atlantic Fisheries Science* 33: 33-54.
- Mylonas CC, Papandroulakis N, Smboukis A, Papadaki M and Divanach P. 2004. Inductions of spawning of cultures of greater amberjack (*Seriola dumerili*) using GnRH $\alpha$  implants. *Aquaculture* 141: 141-154.
- Nakada N. (2002). Yellowtail culture development and solutions for the future. *Reviews in Fisheries Science* 10: 559-575.
- Neilson JD, Geen GH. 1983. Effects of feeding regimes and diel temperature cycles on otolith increment formation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Fishery Bulletin* 83: 91-101.
- Nepgen CS. 1982. Diet of predatory and reef fish in False Bay and possible effects of pelagic purse-seining on their food supply. *Fisheries Bulletin* 16: 75-93.
- Oschiles A, Garçon V. 1998. Eddy-induced enhancement of primary production in model of the North Atlantic Ocean. *Nature* 394: 266-269.

- Pauly D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Berichte des Instituts für Meereskunde an der Universität Kiel* 63.
- Pauly D, Munro JL. 1984. Once more on the comparison of growth in fish and invertebrates. *Fishbyte* :2.
- Pauly D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. *ICLARM Studies & Reviews* 8: 1–325.
- Payne AIL, Badenhorst A. 1989. Oceans of Life off Southern Africa. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg.
- Penney AJ. 1982. The southern Cape yellowtail fishery – a research perspective and preliminary results. *Internal Report, Sea Fisheries Research Institute*. 108: 1-19.
- Penney, AJ 1991. The interaction and impact of net and line-fisheries in False Bay, South Africa. *Transactions of the Royal Society of South Africa* 47: 663-681.
- Pichegru L, Ryan PG, Le Bohec C, Van der Lingen C. D, Navarro R, Petersen S, Lewis S, van der Westhuizen J, Grémillet D. 2009. Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecological Progress Series* 391: 199–208.
- Pinkas L, Oliphant MS, Iverson ILK. 1971. Food habits of albacore, blue fin tuna and bonito in California waters. *Department of Fish and Game Fish Bulletin California* 152: 1-105.
- Pirozzi I, Booth MA. 2009. The routine metabolic rate of mulloway (*Argyrosomus japonicus*: Sciaenidae) and yellowtail kingfish (*Seriola lalandi*: Carangidae) acclimated to six different temperatures. *Comparative biochemistry and Physiology, part A* 152: 586-592.
- Poole WR. 2000. Occurrence of canthaxanthin in Atlantic salmon, *Salmo salar* L., fry in Irish rivers as an indicator of escaped farmed salmon. *Fisheries Management and Ecology* 7: 377-385.

- Poortenaar CW, Hooker SH, Sharp N. 2001. Assessment of yellowtail kingfish (*Seriola lalandi*) reproductive physiology, as a basis for aquaculture development. *Aquaculture* 201: 271-286.
- Porter S, Hutchings K, Clark BM. 2012. Marine aquaculture development zones for finfish cage aquaculture in the Eastern Cape. Baseline Marine Report, DAFF.
- Potier M, Marsac F, Cherel Y, Lucas V, Sabatié R, Maury O, Ménard F. 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fisheries Research* 83: 60-72.
- Primary Industries and Resources SA. 2003. Yellowtail kingfish aquaculture in SA. Fact Sheet, FS No: 26/03. [www.pir.sa.gov/au/factsheets](http://www.pir.sa.gov/au/factsheets).
- Probyn TA, Mitchell-Innes BA, Brown PC, Hutchings L, Carter RA. 1994. A review of the primary production and related processes on the Agulhas Bank. *South African Journal of Science* 90: 166-173.
- Reynolds JD, Jennings S, Dulvy NK. 2001. Life histories of fishes and population responses to exploitation. Conservation Biology Series, Cambridge. pp 147-168.
- Roberts MJ. 2005. Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and early life cycle. *ICES Journal of Marine Science* 62: 33-55.
- Roberts MJ, Sauer WHH. 1994. Environment the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? *Antarctic Science* 6: 249-258.
- Roughan M, Middleton, JH. 2002. A comparison of observed upwelling mechanisms off the east coast of Australia. *Continental Shelf research* 22: 2551-2572.
- Rothschild BJ. 2000. "Fish stocks and recruitment": the past thirty years. *ICES Journal of Marine Science* 57: 191-201.

- Santamaña-del-Angel E, Alvarez-Borrego S, Müller-Karger F. 1994. Gulf of California biogeographic regions based on coastal zone colour scanner imagery. *Journal of Geophysical Research* 99: 7411-7421.
- Sanderson SL, Chesnutt, CR, Lobel PS. 1996. Evidence for ram suspension feeding by the piscivore, *Seriola dumerili* (Carangidae). *Environmental Biology of Fish* 46: 365-373.
- Sauer WHH, Penney AJ, Erasmus C, Mann BQ, Brouwer SL, Lamberth SJ, Stewart TJ. 1997. An evaluation of attitudes and responses to monitoring and management measures for the South African boat-based line-fishery. *South African Journal of Marine Science* 18: 147-163.
- Scandol J, Rowling K, Graham K. 2008. Status of the fisheries resources in NSW 2006/07. *NSW Department of primary Industries, Cronulla*, 334 pp.
- Schmitt RL and Strand SW. 1982. Cooperative foraging by yellowtail, *Seriola lalandei* (carangidae), on two species of fish prey. *Copeia* 3: 717-719.
- Schirripa MJ, Burns KM. 1997. Growth estimates of three species of reef fish in the eastern Gulf of Mexico. *Bulletin of Marine Science* 61: 581-591.
- Schumann EH, Perrins LA, Hunter IT. 1982. Upwelling along the South Coast of the Cape Province, South Africa. *South African Journal of Science* 78: 232-242.
- Schumann EH, Cohen AL, Jury MR. 1995. Coastal sea surface temperature variability along the south coast of South Africa and the relationship to regional and global climate. *Journal of Marine Research* 53: 231-248.
- Scott SG, Zeldis JR, Pankhurst NW. 1993. Evidence of daily spawning in natural populations of New Zealand snapper *Pargus auratus* (Sparidae). *Environmental Biology of Fisheries* 36: 149-156.
- Shannon LV, Pillar SC. 1986. The Benguela ecosystem part III: plankton. *Oceanography and Marine Biology Annual Review* 24: 65-170.

- Shiraishi T, Ohshimo S and Yukami R. 2010. Age, growth and reproductive characteristics of gold striped amberjack *Seriola lalandi* in the waters off western Kyushu, Japan. *New Zealand Journal of Marine and Freshwater Research* 44: 117-127.
- Sih A, Crowley P, McPeck M, Petranka J and Strohmeier K. 1985. Predation, competition and prey communities: A review of field experiments. *Annual Review of Ecology and Systematics* 16: 269-311.
- Sinclair M. 1988. Marine populations. An essay on population regulation and speciation. Washington Sea Grant, Seattle.
- Smith M, Heemstra P. 2003. Smiths sea fishes. Cape Town, South Africa: Struik Publishers.
- Stearns SC, Koella JC 1986. The evolution of plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution* 40: 893-913.
- Stewart J, Ferrell DJ and van der Walt B. 2004. Sizes and ages in commercial landings with estimates of growth, mortality and yield per recruit of yellowtail kingfish (*Seriola lalandi*) from New South Wales, Australia. *Marine and Freshwater Research* : 55 489-497.
- Tachihara K. 1997. Improved seed production of goldstriped amberjack *Seriola lalandi* under hatchery conditions by injection of triiodothyronine (T<sub>3</sub>) to broodstock fish. *Journal of the World Aquaculture Society* 28: 34-44.
- Talbot C, Gracia-Gómez A, De la Gándara F, Muraccioli P. 2000. Food intake, growth and body composition in Mediterranean yellowtail (*Seriola dumerili*) fed isonitrogenous diets containing different lipid levels. *Cahiers Options Méditerranéennes* 47: 259-266.
- Triasin EM, Jørgensen T. 1999. An evaluation of precision of diet description. *Marine Ecology Progress Series* 182: 243-252.
- Uye S, Kuwata H, Endo T. 1987. Standing stocks and production rates of phytoplankton and planktonic copepods in the inland Sea of Japan. *Journal of the Oceanographic Society of Japan* 42: 421-434.

- Vergani M. 2005. Feeding of the yellowtail kingfish, *Seriola lalandi* (Valenciennes, 1833 in Cuvier y Valenciennes, 1833) in waters from Buenos Aires province. Thesis for degree in biological sciences. University of Mar del Plata. Mar del Plata.
- van der Lingen CD, Hutchings L, Field JG. 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* 28: 465-477.
- Ware GW, Thomson RE. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* 308: 1280-1284.
- Webster CD, Lim CE. 2002. Nutrient requirements and feeding of finfish for aquaculture. CABI Publishing, Wallingford, UK.
- Wilke CG, Griffiths MH. 1999. Movement patterns of offshore line-fish based on tagging results. *SANCOR Occasional Report* 5: 98-107.
- Winker H, Kerwath SE, Attwood CG. 2012. Report on stock assessments of important South African line-fish resources. Report of the Line-fish Scientific Working Group, LSWG No. 3, 2012. Department of Agriculture, Forestry and Fisheries, Cape Town, p. 65.
- Witthames PR, Walker G, Dinis MT, Whiting CL. 1995. The geographical variation in the potential annual fecundity of dover sole *Solea solea* (L.) from European shelf waters during 1991. *Netherlands Journal of Sea Research* 34: 45-58.
- Worm B, Lotze HK, Myers RA. 2003. Predator diversity hotspots in the blue ocean. *Proceeding of the National Academy of Science* 100: 9884-9888.
- Wright PJ, Talbot C, Thorpe JE. 1992. Otolith calcification in Atlantic salmon parr, *Salmo salar* L. and its relation to photoperiod and calcium metabolism. *Journal of Fish Biology* 40: 779-790.
- Yoneda M, Wright PJ. 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. *Marine Ecology Progress Series* 276: 237-249.

Young JW, Lamb TD, Le D, Bradford RW, Whitelaw AW. 1997. Feeding ecology and interannual variations in diet of southern Bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. *Environmental Biology of Fishes* 50: 275-291.

Zeitzschel B. 1969. Primary productivity in the Gulf of California. *Marine Biology* 3: 201-207.

University of Cape Town

## APPENDIX

Appendix 1: Age-Length key for *S. lalandi* in South African waters.

Length mm (Fork Length)	Age							
	1	2	3	4	5	6	7	8
450-499	2	5	3	1				
500-549	1	19	15	9	2			
550-599	1	12	17	11	2			
600-649		4	11	9	3			
650-699	1	8	10	4	1			
700-749		5	9	8	2			
750-799		6	8	6	1	1		
800-849		2	11	12	1	1		
850-899		1	4	1	6	2	2	
900-949			3	4	5	3	1	
950-999				4	3	3	1	2
1000-1050				2	1	2		

Appendix 2: Gonadosomatic index cut off points for assigned gonad stages for male and female *S. lalandi* in the historic records.

sex	Gonad stage				
	1	2	3	4	5
Female	0-0.53	0.53-0.94	0.94-1.28	1.28-2.66	>2.66
Male	0-0.26	0.26-0.44	0.44-1.88	>1.88	na

Appendix 3: Distribution of samples in the historic records.

Year	Month												Total
	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sept	Oct	Nov	Dec	
1974												67	67
1975	632	537	275	49	16						43	23	1575
1976	49	112	67	15	1	37	1			1	24	192	499
1977	148	147	74	253					21	50	32	214	939
1978	249	50	97	61		44	20					27	548
1979	364	220	149	25	6		10				65	63	902
1980	111	31	45	13	3	5					35	19	262
1981	63	25	25	10									123
1982	156	41	34		12								243
1983				1	21							15	37
1984	62	32	16								34		144
1985	13	22	18	38			11	9			48		159
1986		77	20					24				40	161
1987	25	9	40		18		12						104
1988											44	33	77
1989	60	56	33	30		19							198
1996		132											132
2010					1				7	15	4		27
Total	1932	1491	893	495	78	105	54	33	28	66	329	693	6197