

OCEANOGRAPHIC RESEARCH INSTITUTE, DURBAN, SOUTH AFRICA,
AFFILIATED TO THE UNIVERSITY OF KWAZULU-NATAL

The biology of and fishery for king mackerel,
Scomberomorus commerson (Scombridae), along the
southern Mozambique and KwaZulu-Natal coast

By

Brendon Lee

A dissertation submitted in fulfilment of the academic requirements for the degree of
Master of Science in the School of Life Sciences, University of KwaZulu-Natal,
Durban

Oceanographic Research Institute

June 2013

Abstract

The king mackerel, *Scomberomorus commerson*, is an epipelagic, schooling predator supporting significant commercial, artisanal and recreational fisheries throughout the coastal waters of its Indo-Pacific distribution. Despite the importance of the species within the South West Indian Ocean, little research has been undertaken on its biology and fisheries on a regional basis over the past 20 years. The aim of this study was to evaluate the fishery and biology of *S. commerson* in the South West Indian Ocean and identify gaps in information required to ensure its effective management. Catch and effort data for the KwaZulu-Natal recreational *S. commerson* linefishery were extracted from the National Marine Linefish System in order to assess spatial and temporal trends in abundance. Generalized linear models utilizing the delta method were used to quantify the effect of year, month, region, rainfall and sea surface temperature on CPUE. Biological samples of *S. commerson* were collected monthly from within KwaZulu-Natal and southern Mozambique. Samples were analysed using standard biological techniques. A per-recruit analysis was conducted using the biological parameters from KwaZulu-Natal and southern Mozambique in order to assess the status of the *S. commerson* stock and provide management recommendations based on the findings. Long-term trends in CPUE were cyclic in nature with peaks and troughs appearing to be independent of fishing pressure. Seasonal abundance reflects the south-north migration into KwaZulu-Natal waters with short term environmental factors such as sea surface temperature significantly affecting spatial and temporal extent of the migration among regions. *S. commerson* spawn in southern Mozambique waters from September to January (spring-summer) with males maturing at a smaller size (65.2cm FL) compared to females (82.3cm FL). The overall sex ratio (M: F) was 1:1.36 possibly as a result of linefishing selecting for faster growing, larger females. *S. commerson* in KwaZulu-Natal and southern Mozambique display rapid growth over the first two years before slowing down considerably after maturity is reached. Females grow faster and live longer compared to males dominating the older and larger size classes, and attaining a maximum observed age of 14 years, although fish probably live up to 20 years. Natural mortality rate was estimated at 0.27 year⁻¹. Fishing mortality for the combined region was 0.21 year⁻¹. The per-recruit analyses for the KwaZulu-Natal and southern Mozambique indicated that the fishery is being optimally exploited with a current spawner biomass per recruit at 49% of its theoretical pristine level. Uncertainty with regards to the fishing pressure in southern Mozambique as a result of illegal fishing

and fishing sectors targeting smaller *S. commerson* is a cause for concern. The current recreational daily bag limit of 10 fish.person.day⁻¹ is considered excessive by many stakeholders. Given the similarity of the recreational ski-boat fishery in southern Mozambique, a reduction in the DBL of *S. commerson* to five fish pppd in both KwaZulu-Natal and southern Mozambique waters would benefit recreational fishers by more equitable sharing of the catch and potentially by reducing fishing mortality at times when the fish are aggregated and vulnerable to high catch rates. A reduced DBL limit would also reduce the incentive of individual anglers to make large catches and to sell their fish illegally.

Preface

The work described in this dissertation was carried out at the Oceanographic Research Institute (ORI), which is an institute affiliated with the School of Life Sciences, University of KwaZulu-Natal, Durban. Field work was conducted from March 2012 to February 2013 within KwaZulu-Natal and southern Mozambique, under the supervision of Mr Bruce Mann and Prof. Rudy van der Elst. This dissertation represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institute. Where use has been made of the work of others, it is duly acknowledged in the text.

Declaration - Plagiarism

I, Brendon Lee, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. The thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other person's data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other person's writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a) Their words have been re-written but the general information attributed to them has been referenced.
 - b) Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.
5. This thesis does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the thesis and in the references sections.

Signed:

Brendon Lee; June 2013

Table of Contents

Abstract	i
Preface	iii
Declaration - Plagiarism	iv
Acknowledgements	viii
Chapter 1	
General Introduction	
1.1 Background	1
1.2 Rationale	9
1.3 Overall aims and objectives	9
1.4 Study Area	11
1.5 General Sampling Methods.....	14
Chapter 2	
Retrospective analysis of <i>S. commerson</i> catches in the KwaZulu-Natal recreational ski-boat fishery	
2.1. Introduction.....	16
2.2. Materials and Methods.....	18
2.2.1 Study area.....	18
2.2.2 Data collection	20
2.2.3 Data selection.....	21
2.2.4 Nominal catch and effort data.....	22
2.2.5 Statistical modelling.....	22
2.3 Results.....	25
2.3.1 Nominal effort.....	25
2.3.2 Standardized catch and effort data for KwaZulu-Natal	26
2.3.3 Catch data for sub-regions within KwaZulu-Natal	33
2.4 Discussion	37
2.4.1 Fishing effort.....	37
2.4.2 Spatial distribution of <i>S. commerson</i> catches	38
2.4.3 Long-term trends in <i>S. commerson</i> catches	38
2.4.4 Seasonality of <i>S. commerson</i> catches	40

2.4.5 Conclusions.....	42
------------------------	----

Chapter 3

Reproductive Biology

3.1. Introduction.....	43
3.2. Materials and Methods.....	45
3.2.1 Sampling	45
3.2.2 Histological macroscopic stage validation.....	46
3.2.3 Spawning area and season	49
3.2.4 Length and age at sexual maturity	49
3.2.5 Population structure	50
3.3. Results.....	51
3.3.1 Sample breakdown.....	51
3.3.2 Stages and reproductive season	51
3.3.3 GSI and reproductive cycle.....	54
3.3.4 Histological validation of macroscopic stages.....	56
3.3.5 Size and age at first maturity	58
3.3.6 Length composition and sex ratio	61
3.4. Discussion.....	64
3.4.1 Spawning.....	64
3.4.2 Length at maturity	67
3.4.3 Sex ratios.....	68
3.4.4 Length composition	69
3.4.5 Conclusions.....	71

Chapter 4

Age and Growth

4.1 Introduction.....	73
4.2 Materials and Methods.....	76
4.2.1 Sampling	76
4.2.2 Data analysis	77
4.3 Results.....	88
4.3.1 Somatic Relationships.....	88
4.3.2 Otolith interpretation.....	91
4.3.3 Validation – marginal zone analysis	95
4.3.4 Growth models.....	96
4.3.5 Tag-recapture data	100

4.4 Discussion	105
4.4.1 Assignment and reliability of ages.....	105
4.4.2 Validation and formation of annuli.....	106
4.4.3 Growth	109
4.4.4 Conclusions.....	112

Chapter 5

Mortality and biological reference points

5.1 Introduction.....	114
5.2 Materials and Methods.....	118
5.2.1 Mortality	118
5.2.2 Per-recruit analysis.....	120
5.2.3 Management scenarios.....	122
5.2.4 Biological reference points	122
5.2.5 Stock status	122
5.3 Results.....	123
5.3.1 Mortality	123
5.3.2 Per-recruit analysis.....	125
5.4 Discussion	130
5.4.1 Mortality	130
5.4.2 Per-recruit analyses	132
5.4.3 Conclusions.....	135

Chapter 6

Conclusion and Management Considerations

6.1 Introduction.....	136
6.2 Management options.....	137
6.2.1 Closures.....	137
6.2.2 Daily bag limit (DBL).....	137
6.2.3 Minimum size limit (MSL).....	139
6.3 Future monitoring and research priorities.....	141

References	143
-------------------------	------------

Acknowledgements

I would like to thank my supervisors, Mr Bruce Mann and Prof. Rudy van der Elst for their mentorship and support over the past two years in both the office and field. To Jorge Santos and James Robey for assisting me with some of my data analyses and to Jorge for accompanying me on my field work to Mozambique, without you I would have struggled to achieve success in collecting the required samples.

To Club 15, Willie Rothman and Steve Stewart in particular, for generously allowing me to join their group on their vacation to Mozambique in order for me to sample their catch and for letting me feel most welcome.

To KZN angling clubs for permitting me to set up my table and obtain biological samples at your competitions. Additionally, to all those fishers for unselfishly allowing me to sample their catch and for showing such an interest in my work; for someone to reject my request was rare.

To the South West Indian Ocean Fisheries Projects (SWIOFP) for providing me with the necessary funding in order to complete this work. To the Oceanographic Research Institute, part of the South African Association of Marine Biological Research (SAAMBR) and its entire staff for guidance, assistance and facilities, all of which provided an open and friendly environment to work in.

To all my friends and work colleagues that have assisted me on my sampling trips, without you I would not have managed to obtain such reliable samples and have had time for fun on these trips.

To my friends and the guys in the office, many thanks for the pleasant times.

I would like to express my appreciation to my parents whom have given unconditional support and financial aid throughout my university career.

'I believe then that the cod fishery, the herring fishery, pilchard fishery, the mackerel fishery, and probably all the great sea fisheries are inexhaustible: that is to say that nothing we do seriously affect the numbers of fish. And any attempt to regulate these fisheries seems consequently from the nature of the case to be useless.'

- T. H. Huxley in an address to the International Fisheries Exhibition, London, 1883.

Chapter 1

General Introduction



1.1 Background

Taxonomy

The king mackerel, *Scomberomorus commerson* is a large, pelagic predator belonging to the family Scombridae (Mackerels, tunas, bonitos), subfamily: Scombrinae (Collette and Nauen, 1983). It is the largest of the mackerel family growing up to 240cm TL and 70kg (McPherson, 1992).

Distribution and habitat

S. commerson inhabit waters throughout the Indo-Pacific regions from South Africa to the Red Sea and south-east Asia, north to China and Japan and south along the east and west coasts of Australia (Heemstra and Heemstra, 2004; Branch *et al.*, 2007). Catches have additionally been reported in the eastern Mediterranean Sea where it is an immigrant by way of the Suez Canal (Ben-Tuvia, 1978; Corsni-Foka and Kalogiru, 2008). Within the South West Indian Ocean (SWIO) region *S. commerson* are commonly found through Mozambique, Tanzania and Kenya, and around the islands of Madagascar and Comoros (Sideek, 1996), south to the southern border of KwaZulu-Natal, although they may on occasions be found as far south as Mossel Bay in the Western Cape (Heemstra and Heemstra, 2004).

S. commerson are epipelagic, occurring from the edge of the continental shelf to shallow coastal waters along drop-offs, gently sloping reefs, current lines and lagoon waters from 10 – 100 m (Grandcourt *et al.* 2005; Tobin and Mapleston, 2004). *S. commerson* are found in tropical and temperate coastal waters, generally above thermal fronts of about 20°C. It has been suggested that the distribution and movement of the species is related to these fronts of warmer water (Begg *et al.*, 2006). Furthermore, warm coastal waters and high rainfall have been suggested to lead to increased primary production with associated positive effects on larval survival and recruitment (Shoji and Tanaka, 2006; Lamberth *et al.*, 2009). Large adult *S. commerson* may be solitary, whereas juveniles and younger adults occur in small schools made up of similar-sized individuals (Grandcourt *et al.*, 2005).

Stock Structure

There is considerable uncertainty regarding the stock structure of *S. commerson* throughout its range, particularly regarding the actual stock boundaries and relationships of fish between regions of close proximity (Begg *et al.*, 2005). The wide geographic distribution of *S. commerson* contrasts with that of all other species in the genus *Scomberomorus* (Fauvelot and Borsa, 2011). Within the south-west Pacific three main stocks, centred on northern Australia, Papua New Guinea, and Fiji, with a fourth stock off the east coast of Australia have been delineated (Fauvelot and Borsa, 2011). Studies on the stock structure along the Australian coastline alone indicate a meta-population stock structure with a high degree of site attachment of the adult population (Lester *et al.*, 2001; Moore *et al.*, 2003; Williams and Lester, 2006; Newman *et al.*, 2009). However, the level of mixing within populations of *S. commerson* off Australia is variable among regions (Newman *et al.*, 2009). In the cooler southern waters of Western and eastern Australia, units of *S. commerson* range over large distances, while in the northern regions populations range over much smaller units (Newman *et al.*, 2009). Conversely, Hoolihan *et al.* (2006) and van Herwarden (2006) found that *S. commerson* within the Arabian Sea, Arabian Gulf and the Gulf of Oman constituted a single stock suggesting shared regional management for sustainable long-term use of the resource. However, van Herwarden (2006) concluded that resident non-migratory populations also appear to exist. The geographic extent of the *S. commerson* stock along the east coast of Africa, however, is unknown. In this assessment it was assumed to display similar characteristics to the stocks on the west and east coasts of Australia with *S.*

commerson in KwaZulu-Natal and southern Mozambique comprising a single stock undertaking seasonal north-south migration (as suggested by Govender, 1994).

Biology and ecology

Research indicates that *S. commerson* have a protracted spawning season with peak spawning commonly occurring in the spring to early summer (Devaraj, 1983; Dudley *et al.*, 1992; McPherson, 1993; Mackie *et al.*, 2005). Spawning peaks appear to be synchronised with the monsoon/rainfall season in the South West Indian Ocean possibly to exploit the post-monsoon/rainfall plankton and small pelagic fish production in coastal waters (Siddeek, 1996; Lamberth *et al.*, 2009; Mualeque and Santos, 2011). Spawning has been associated with an aggregation of all size groups and equivalent sex ratios (Begg *et al.*, 2005). Along the east coast of Australia, large spawning aggregations within specific areas appear to occur. Devaraj (1983) reported the landing of spawning *S. commerson* by shore seines on the south Indian coast. The species are asynchronous spawners, with individual fish spawning several times over the spawning season, usually late afternoon and early evening and during the new and full moon phases (Jenkins *et al.*, 1985; McPherson, 1993).

In Queensland Australia, larval and small juvenile *S. commerson* occur in estuaries, sheltered mudflats and inshore coastal lagoon regions during the wet season (Jenkins *et al.*, 1984a; McPherson, 1992; Grandcourt *et al.* 2005). The occurrence of larvae during spring and summer also coincides with maximum planktonic food production, where in combination with higher water temperatures, these conditions optimize rapid growth through the early life stages that are vulnerable to predation (Jenkins *et al.*, 1985). Little is known about the early life history stages of *S. commerson* and their habitats and dispersal patterns along the east coast of southern Africa.

Growth is extremely rapid during the first two years of life before slowing down considerably with the onset of maturity (Claereboudt *et al.*, 2005). Sex-specific growth has been observed with females tending to live longer and growing to larger sizes (McPherson, 1992; Tobin and Mapleston, 2004; McIlwain *et al.*, 2005; Mackie *et al.*, 2005; Newman *et al.*, 2012).

Juvenile and adult *S. commerson* are carnivorous and predominantly piscivorous, with the diet consisting mainly of small pelagic fish such as clupeids (e.g. anchovies

and sardines) and small carangids, although squids and shrimps are also occasionally consumed (Rao, 1962; Kumaran, 1964; McPherson, 1987; Sideek, 1996; Devaraj, 1998; Bakhoun, 2007). The species is an active predator with observations of it shadowing shoals of mackerel and sardine to feed upon them (Dhawan et al., 1972). *S. commerson* larvae feed almost exclusively on larval fish and larvaceans (Jenkins et al., 1984b).

Migrations

S. commerson are known to undertake lengthy long-shore as well as onshore-offshore migrations (Sideek, 1996). Tagging experiments off Australia have shown that *S. commerson* are coastal migrants, undertaking annual north-south migrations along the east and west coasts as well as onshore-offshore spawning migrations (McPherson, 1981). These have been linked to the warmer currents that push down the west and east coasts during the summer months (Tobin and Mapleston, 2004). *S. commerson* in northern Australian waters appear to be more site-attached than those off the east and west coast which undertake these lengthy seasonal migrations (Newman et al., 2009). Such migrations have also been reported for the coastal areas of the Middle East with fish moving into the Arabian Gulf for spawning before returning to the Arabian Sea and Indian Ocean towards the end of summer (Sideek, 1996, Grandcourt et al., 2005). The return migration coincides with reduced water temperatures and an increase in the abundance of small pelagic species upon which they feed. An onshore-offshore migration has been postulated, with very large fish moving from offshore to nearshore waters shortly before the spawning migration period (Sideek, 1996). It has also been suggested that large-scale feeding migrations occur annually along the east coast of southern Africa (van der Elst, 2003). While *S. commerson* is prominent within Mozambique waters throughout the year, southward migrations linked to the warmer currents that penetrate further down the east coast into KZN during the summer and autumn months (November to June) have been reported (Govender, 1992).

Fisheries

This species is a prized market fish and is taken throughout its range by commercial, artisanal and recreational fisheries (Collette and Russo, 1984). They are often targeted due to their preference for shallow coastal and continental shelf waters, known annual migration routes and areas of aggregation, as well as voracious

feeding behaviour (Tobin and Mapleston, 2004). *S. commerson* is caught with a variety of gears including gill- and seine-nets, bamboo stake traps, mid-water trawls and trolling lines in coastal waters throughout its range (Collette, 2001; Grandcourt *et al.*, 2005).

In Mozambique, it is targeted by the recreational, artisanal and commercial fisheries, while in KZN it is almost exclusively targeted by the recreational sector and to a far lesser extent by the commercial line-fishery. The three recreational sectors that target *S. commerson* are the ski-boat, jet-ski and kayak fisheries with anglers' almost exclusively utilizing rod and reel (Mann *et al.* 2012, Dunlop and Mann 2013). Methods can vary considerably with a wide range of live and dead fish-baits as well as various artificial lures and flies employed at times. The majority of recreational anglers, however, target *S. commerson* by trolling artificial lures or by using specially made wire traces to which a live or dead bait is attached. Drifting with live or dead baits such as pilchard (*Sardinops sagax*) or mackerel (*Scomber japonicus*) is also a productive method of targeting *S. commerson*. In KZN and Mozambique *S. commerson* is also actively pursued by boat-based and shore-based spearfishers (Mann *et al.* 1997). *S. commerson* are also occasionally targeted by shore anglers fishing off deep-water points but catches are rare compared to boat-based anglers (Dunlop and Mann 2012). All the above-mentioned recreational sectors host angling tournaments or competitions from time to time and *S. commerson* is one of the main target species of these tournaments. Fishing tournaments generally occur over the season of peak *S. commerson* abundance (March to June) in KZN and move to Mozambique waters during the late winter to summer months where the fish are caught all year round over the KZN off-season. During these tournaments, prizes are normally awarded for the largest *S. commerson* captured.

In Mozambique, *S. commerson* is frequently targeted by artisanal fishermen. The main type of fishing that takes place is through opportunistic targeting in which *S. commerson* is taken by fishers as an additional catch to their primary fishing activity. Artisanal fishermen generally paddle wooden outrigger canoes or sail dhows to offshore reefs where they target demersal reef fishes. During such fishing activity they will often set a number of baited drift lines in the hope of catching passing pelagic game fish such as *S. commerson*. Juvenile and sub-adult *S. commerson* are also occasionally caught in artisanal beach seines and gill nets set within sheltered inshore bays throughout Mozambique (WIOFISH 2011). Historically, *S. commerson* was a prime target of the KZN commercial line fishery with it making up 12% of the

catch by weight in 1989 (Govender, 1992). However, high catch rates are required to make this method of fishing (i.e. trolling) economically viable, especially nowadays with increased fuel prices. As a consequence *S. commerson* is now mainly captured within the KZN commercial line-fishery as an opportunistic catch, whereby fishers set baited drift lines while targeting demersal reef fish species (Dunlop and Mann 2013). This situation is similar in the commercial line-fishery in Mozambique, although there are times when aggregations of *S. commerson* allow fishers to target them directly. This occasionally happens at night and fishers can make substantial catches by casting out metal lures (called spoons or spinners) and retrieving them quickly, so inducing the fish to strike (R. van der Elst, ORI, pers. comm.). Mozambique also has a record of illegal fisheries predominantly driven by foreigners (R. van der Elst, pers. comm.). Due to the shoaling behaviour of the species, the use of lights at night can enable these illegal, unreported and unregulated (IUU) fisheries to capture several tons of fish in a relatively short time span. Catch records from commercial linefishers off the coast of Mozambique during the 1980s and early 1990s indicated that boats frequently captured up to 200 *S. commerson* over a single day.

Catch

The annual world catch of *S. commerson* has steadily increased from less than 70 000 tons in the 1970s to over 220 000 tons in 2008 (FAO Statistics Service, 2013). The total reported catch of *S. commerson* in the West Indian Ocean (FAO Statistical Area 51) increased substantially between 1981 and 1985, and has remained at around 70 000 tonnes since 1995 (Ye, 2011). The annual recorded catch for *S. commerson* was greater than any other medium-sized pelagic species in the SWIO, recorded as 6977 tons (Cochrane and Japp, 2012). Catch data for two countries (South Africa and Mozambique) within the SWIO region indicate a total catch of 883 tonnes, with 77%, 21% and 13% of this being attributed to artisanal, commercial and the recreational fisheries sectors respectively (Table 1.1; WIOFISH, 2011). It has been assessed that SWIO catches, particularly from small-scale and artisanal fisheries operating within areas of national sovereignty, are poorly estimated (Ye, 2011).

Table 1.1: Summary of linefishery catch data (2007-2010) for *Scomberomorus commerson* in KwaZulu-Natal (KZN), South Africa and Mozambique (MOZ) (data from WIOFish, 2011)

Country	Fishery	Overall catch rate	Catch composition (%) of <i>S. commerson</i>	Area
MOZ	Sport, ski-boat, line	12.8kg/boat/day	36	Maputo and Inhaca
	Recreational, ski-boat, line	9.375 kg/boat/day	14	Ponta do Ouro
	Recreational, Shore, line	0.9kg/man/day	<1%	Ponta do Ouro
	Commercial, Line	270kg/boat/day	19	Sofala Bank, Southern Region
	Artisanal, Line	12.6 kg/boat/day	4	Entire Coastline
KZN	Recreational, ski-boat, line	15 kg/boat/day	12.4	KZN coastline
	Recreational, fishing kayak, line	2.98 kg/man/trip	34	KZN coastline
	Recreational, jet-ski, line	2.8 kg/man/trip	18	KZN coastline
	Commercial, line	235kg/boat/day ¹	3.44	KZN coastline

¹From Dunlop and Mann (2013)

Management

Many fish populations in KZN and Mozambique have been heavily exploited and fishing effort may be above the optimum sustainable yield for some species (Mann, 2000). Based on per recruit modelling, Govender (1995) estimated that the spawner biomass per recruit (SBR) of *S. commerson* in KZN had been reduced to 33% of the pristine level. Furthermore, high fishing mortality as a result of the intensive harvest of juvenile *S. commerson* caught in artisanal fisheries off Mozambique may lead to recruitment failure and is of a particular concern in the region (Govender, 1992). Govender and Radebe (2000) therefore highlighted the urgent need for joint management of the *S. commerson* stock between Mozambique and South Africa. Currently, the only management controls for the recreational fishery in KZN and Mozambique is a catch limit of 10 fish per angler per day, while no restrictions are

applied to Mozambique artisanal fishers. Commercial fishers are also not restricted by any bag limit, but by total allowable effort in both countries.

Research history

Apart from the work done by Govender (1992, 1995) in KZN, relatively little is known about the biology and population dynamics of *S. commerson* along the east coast of southern Africa, with the majority of studies being undertaken in areas within the Arabian Sea (Al-Hosni and Siddeek, 1999; Claereboudt *et al.*, 2005; McIlwain *et al.*, 2005; Shojaei *et al.*, 2007) the Persian Gulf (Kaymaram *et al.*, 2010; Claereboudt *et al.*, 2007; Grandcourt *et al.*, 2005), India (Devaraj, 1981, 1983, 1998) and the north, east and west coasts of Australia (McPherson, 1992; McPherson, 1993; Buckworth, 1998; Mackie *et al.*, 2002; Ballagh *et al.*, 2006; Ballagh *et al.*, 2011; Newman *et al.*, 2012).

Monitoring

The recreational ski-boat fishery in KZN is monitored through the National Marine Linefish System (NMLS) and the Boat Launch Site Monitoring System (BLSMS).

The BLSMS was implemented in KZN in 2004. It is based on the completion of a boat launch register placed at all licensed boat launch sites along the KZN coast. It is compulsory for skippers to complete part of the register before launching for safety reasons. On return, skippers must sign in and complete the register that includes a catch return of all fish caught for recreational anglers. A drawback of the data is that it has only been recorded from 2004 onwards. There is also a relatively high level of non-compliance by skippers or provision of false data on the catch return section of the register. Additionally, vandalism of the catch register at certain launch sites has required authorities to remove the register when inspection officers finish work. This results in boats launching or returning outside of inspection officers work hours and skippers thus not being able to complete the boat launch register.

The NMLS is a data capture and analysis system designed to store and summarise linefish catch and effort data. It incorporates both the commercial linefish catch and effort records required by the South African Department of Agriculture, Forestry and Fisheries (DAFF) and the recreational data collected by the Oceanographic Research Institute (ORI) and Ezemvelo KwaZulu-Natal Wildlife (EKZNW) (Winker *et*

al., 2013). Recreational data are collected by EKZNW through ski-boat inspections at launch sites throughout KZN. Since the inception of the NMLS in 1984, it was accepted that the data captured by the system was never going to be completely accurate. It was also generally accepted that a proportion of the data submitted by fishers would be incomplete, exaggerated, under-reported or falsified (Penny *et al.*, 1999; Donovan, 2010). However, the NMLS was primarily designed to provide indices of catch rates in order to monitor major trends in various sectors of South African linefishery (Penny *et al.*, 1999). On the assumption that biases and inaccuracies of the data are consistent on a temporal scale, the NMLS could correctly reflect major trends in the line-fishery (Penny *et al.*, 1999; Donovan, 2010).

In MOZ, the recreational and artisanal line-fishery is only monitored by random dockside inspections, while the commercial line-fishery is additionally monitored by on-board observers as well as routine inspections at landing sites.

1.2 Rationale

The South West Indian Ocean Fisheries Projects (SWIOFP) has been developed over five years, by government scientists from nine SWIO countries. The main objective of SWIOFP was to link studies on fisheries, human impacts on the environment, and marine ecosystems and to integrate these into frameworks needed to link science to management structures and governance (van der Elst *et al.*, 2009). SWIOFP focuses primarily on transboundary fishery resources, including migratory fish and straddling stocks, with the intention of ultimately building towards, scientifically-based regional strategies to manage shared stocks while at the same time conserving biodiversity. This research project was funded by SWIOFP and aimed to provide guidance for the management of the *S. commerson* resource in the SWIO on both a national and regional level for this shared stock.

1.3 Overall aims and objectives

Geographically, the study area covered falls within the South West Indian Ocean (SWIO) which includes the exclusive economic zones of nine continental and island nations: Kenya, Tanzania, Mozambique, South Africa, Madagascar, Comoros, Mauritius, Seychelles and France, the latter because of its islands in the region including La Reunion and Mayotte (Figure 1.1). Comparisons of population trends and the biology of *S. commerson* at various sites within the SWIO can therefore be

used to determine the extent of feeding and/or reproductive migrations off eastern Africa, and thus the extent to which this species is shared by SWIO countries. This information is crucial for the development of local, sub-regional and regional management strategies.

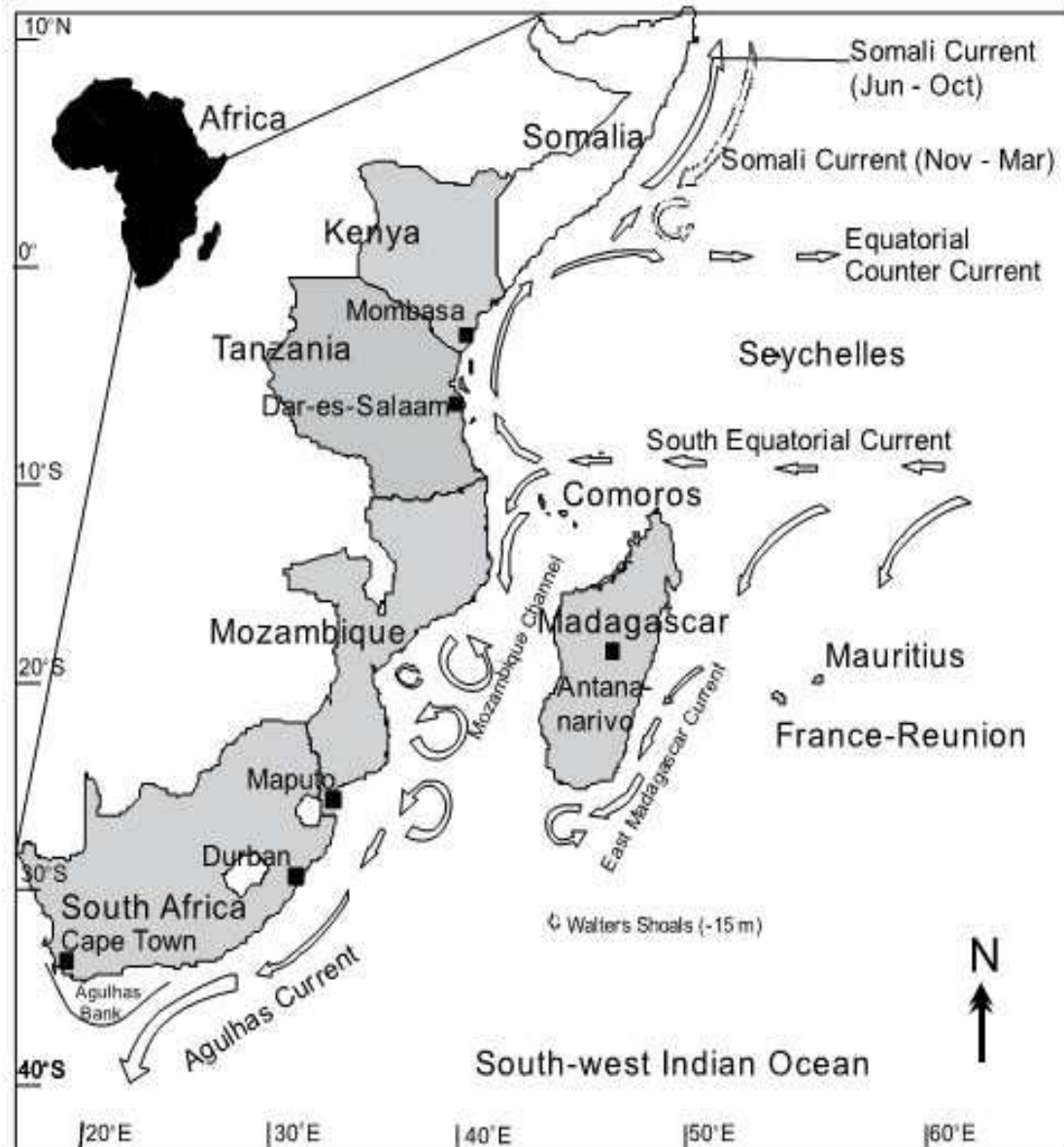


Figure 1.1: Countries and major ocean currents of the South West Indian Ocean (van der Elst *et al.*, 2009).

However, because of the size of the SWIO and the logistical difficulties associated with acquiring suitable data within the entire region, field-based biological data collection was focused on a sub-region of the study area including the coast of KwaZulu-Natal, South Africa and southern Mozambique. Additionally, difficulties in acquiring reliable historical catch and effort data for southern Mozambique meant

that this aspect of the project focused on the data obtained in KwaZulu-Natal. The primary aim of this study was therefore to evaluate the fishery and biology of *S. commerson* along the southern Mozambique and KwaZulu-Natal coastline and to identify the data gaps required for its effective management.

The specific objectives of the study were:

1. To evaluate historical catch and effort data of *S. commerson* from KwaZulu-Natal and to determine trends in abundance over time.
2. To improve the understanding of the biology of *S. commerson* in terms of its age and growth and reproductive biology within the sampled area.
3. To determine the exploitation levels and stock status of *S. commerson* within the sampled area.
4. To provide national and sub/regional management recommendations given the outcomes and uncertainties of the current research.
5. To identify uncertainties with regards to the research findings and provide future monitoring and research opportunities to provide an improved holistic understanding of the resource within the SWIOF region on the whole.

1.4 Study Area

The study area includes the Exclusive Economic Zones (EEZs) of two of the nine nations that fall within the South West Indian Ocean Fisheries Project (SWIOFP) area: namely KwaZulu-Natal (KZN), South Africa and southern Mozambique (MOZ). A retrospective analysis of historical catch and effort data was undertaken with data obtained from KZN databases. Biological sampling was conducted along the coasts of KZN and MOZ between the towns of Port Edward in the south and Beira, Mozambique in the north (Figure 1.2).



Figure 1.2: Map displaying the area of the coastline where biological sampling of *S. commerson* was undertaken, including key sampling sites.

The study area falls within the Agulhas Current Large Marine Ecosystem (ACLME) which stretches from the northern Mozambique Channel to Cape Agulhas and is considered to be composed of three components: the Agulhas source currents, Agulhas Current proper and the Agulhas retroflection and return current (Lutjeharms, 2006). The study area falls within two of these components namely the source region and the northern Agulhas Current proper.

The source region of the Agulhas Current consists of the subtropical gyre of the south Indian Ocean, the East Madagascar Current, and the Mozambique Channel (Lutjeharms, 2006). The flow through the Mozambique Channel consists of anti-cyclonic eddies that are formed in the narrows of the channel and that move in a southerly direction. The East Madagascar Current carries water along the edge of the narrow continental shelf of east Madagascar in a southward direction. Once reaching the southern tip of Madagascar, this current turns towards the African mainland where it meets up with the southward flow from the Mozambique Channel forming the northern part of the Agulhas Current. Upwelling cells with enhanced nutrient contents have been observed both along the shelf of Mozambique and the shelf of eastern Madagascar.

The Agulhas Current is a powerful western boundary current forming part of the anticyclonic Indian Ocean gyre (Lutjeharms, 2006). The current follows the continental shelf edge from Maputo in Southern Mozambique to the tip of the Agulhas Bank where, after it retroflects back into the Indian Ocean gyre. The current increases in depth and volume as it moves southward. The current follows the narrow shelf edge quite closely, only diverging from the coastline where the continental shelf is wide, such as off the Natal Bight between Richards Bay and Durban (Lutjeharms, 2006). The water movement on the shelf itself is generally parallel and in the same direction as the Agulhas Current apart from two exceptions: immediately south of Durban and within the Natal Bight. South of Durban there is a persistent eddy, while within the Natal Bight the inshore water movement is often in a northerly direction but is largely dependent on the prevailing wind. At the northern tip of the Natal Bight off Richards Bay there is a concentrated and persistent upwelling cell enhancing the local nutrient supply (Lutjeharms, 2006).

1.5 General Sampling Methods

Historical data

A retrospective analysis was undertaken to analyse historical catch and effort data for the *S. commerson* fisheries within KZN to evaluate trends in catch composition, catch per unit effort (CPUE) and mean size. These data were obtained from a number of different databases including:

- The National Marine Linefish System (NMLS) – KZN recreational data
- The KZN Boat Launch Site Monitoring System (BLSMS)

The ORI Cooperative Fish Tagging Project (ORI-CFTP) database provided biological information for age validation, length-frequency analysis and movements of *S. commerson* within the study area. The ORI-CFTP project was initiated in 1984, and currently over 251 900 fish from 368 different species have been tagged and released, of which 13 192 (5.2%) have been recaptured (Dunlop *et al.*, 2013).

Field sampling

Biological sampling was undertaken on a monthly basis between April 2011 and March 2012. Data were collected from recreational and artisanal fisherman through sampling at boat launch sites and fish markets across the study area. Additionally, samples were collected at angling and spearfishing tournaments to enable the collection of data over a short time period.

Information recorded during sampling included the date of capture, the landing site and region of capture, and the gear and method of capture. Biological data were collected from a target sample of at least 30 fish per month from a representative size range. However, due to the seasonal nature of *S. commerson* in KZN, achieving the target sample size was not always possible. Total length (TL) and fork length (FL) were recorded to the nearest millimetre using a measuring board. Whole wet weight was measured with an electronic balance and recorded to the nearest gram.

Fish were sexed and the stage of reproductive maturity determined using a macroscopic staging system (Chapter 3). Gonads were dissected out and subsequently weighed to the nearest gram using an electronic balance. A sub-set of

36 gonads (three per macroscopic stage for males and females) were dissected out and preserved for later histological validation of macroscopic staging. Stomachs were removed, cut open and the contents preserved in 10% formalin for future analysis. A visual estimation of percentage stomach fullness was recorded. The sagittal otoliths were extracted, cleaned in freshwater, dried with paper towel and stored in labelled envelopes in preparation for ageing.

Voluntary support from fishers was gathered by widely advertising the project through a range of media including articles in fishing magazines, oral presentations at club meetings and competitions, interviews, phone conversations, emails and face to face meetings.

Chapter 2

Retrospective analysis of *S. commerson* catches in the KwaZulu-Natal recreational ski-boat fishery

2.1. Introduction

One of the primary functions of fisheries scientists is to advise managers on sustainable harvesting levels based on the results of some form of stock assessment (Hillborn and Walters, 1992; Maunder and Punt, 2004). The majority of modern stock assessment methods involve fitting a population dynamic model to an index of abundance (Maunder, 2001). Stock assessments that utilize multiple sources of data such as catch, life history and abundance trends are the most robust analyses to determine the status of an exploited species (Carlson *et al.*, 2012; Shono, 2008). Reliable abundance indices based on the analysis of catch and effort data for the underlying fish stock to be modelled are therefore an essential input for many stock assessment methods (Hillborn and Walters, 1992; Quinn and Deriso, 1999; Maunder and Langley, 2004; Maunder and Punt, 2004).

In the absence of biological information on an exploited species, trends in abundance can provide a general picture of the species' status, provided the data sources utilized are appropriate (Carlson *et al.* 2009). Information about changes in abundance of fish stocks is therefore an important part of information required for fisheries management (Lo *et al.*, 1992).

An index of abundance should preferably be based on fishery-independent data, especially if they are collected with a standardized procedure that is kept constant as much as possible from year to year (Maunder, 2001). However collection methods, such as fishery surveys, are often not available, extremely costly or difficult to collect (Maunder and Punt, 2004). This is particularly the case for relatively low value pelagic fish stocks, such as the *S. commerson* fishery off KZN and MOZ, in which the large spatial extent of the fisheries usually precludes any attempt to conduct fishery-independent surveys of stock status (Campbell, 2004). Therefore, assessments of many stocks are based on fishery-dependent data. The most common and easily collected source of fishery-dependent data is catch and effort information from

commercial and recreational fishers, usually summarized in the form of catch-per-unit-of-effort (CPUE) or catch rate.

One of the common assumptions in fisheries research is that relative stock abundance can be estimated from knowledge of catch and fishing effort for that stock (Richards and Schnute, 1986). Fisheries-dependent CPUE is therefore commonly used as an index of abundance as it is assumed to be linearly proportional to the product of catchability and abundance of the fish stock, where catchability is defined as the fraction of abundance that is captured by one unit of effort (Hillborn and Walters, 1992; Maunder and Langley, 2004; Maunder and Punt, 2004). Hence, provided catchability is constant over time and space, catch rate can be used as a valid index of abundance (Haddon, 2001; Campbell, 2004). Based on these assumptions trends in catch rate over time may reflect changes in the proportion of the population caught (Quinn and Deriso, 1999).

However, the use of CPUE as an index of abundance is notoriously problematic (Hillborn and Walters, 1992; Harley *et al.*, 2001; Maunder *et al.*, 2006; Bentley *et al.*, 2012). Despite this, these methods have been widely adopted and routinely used in fisheries assessments (Harley *et al.*, 2001; Campbell, 2004). The persisting reliance on the use of annual abundance indices based on the use of nominal CPUE data has thus been highly criticized given the continued concern regarding the failure of the underlying assumptions (Campbell, 2004). Changes in fishing pattern over time can cause distortions in the relationship between CPUE and abundance (Bentley *et al.*, 2012). This may be due to changes in the composition of the fishing fleet; improvements in the technology used by the fleet, where fishing occurs, when fishing occurs and weather conditions causing changes to CPUE that are independent of stock abundance (Hillborn and Walters, 1992; Bishop *et al.*, 2008; Bentley *et al.*, 2012). Additionally, CPUE based on fisheries-dependent data may be “hyperstable” or insensitive to changes in abundance (Harley *et al.*, 2001). This is particularly problematical for species displaying schooling or aggregating behaviour whereby catch rates remain high even if the fish stock is being seriously depleted (Hillborn and Walters, 1992). “Hyperstability” can lead to overestimation of biomass and underestimation of fishing mortality (Harley *et al.*, 2001).

Therefore, in order to make any inferences about abundance trends, raw CPUE data require adjustment to remove factors which influence the index of abundance, other than abundance itself (Hillborn and Walters, 1992; Maunder, 2001; Maunder and

Punt, 2004). These may include the effects of spatial and temporal variation with changes in fishing methods, fishing equipment, fisher experience and behaviour, areas fished and environmental factors (e.g. temperature) (Campbell, 2004; Maunder and Langley, 2004; Maunder and Punt, 2004). This process is referred to as catch-effort standardization (Beverton and Holt, 1957; Campbell, 2004; Maunder and Punt, 2004; Begg *et al.*, 2006). The use of generalized linear models (GLMs) is the most common approach for standardizing catch rate (Kimura, 1981; Maunder, 2001; Punt *et al.*, 2001; Maunder and Langley, 2004; Maunder and Punt, 2004; Venables and Dichmont, 2004; Begg *et al.*, 2005).

GLMs are defined by the statistical distribution for the response variable and how some linear combinations of a set of explanatory variables relate to the expected value of the response variable (Campbell, 2004; Maunder and Punt, 2004). The standardization of CPUE using GLMs is not an attempt to build a predictive model for forecasting or to explain variance in a dataset. It is more an attempt to remove the confounding effects of extraneous variables, resulting in an index that is as representative as possible of the actual stock biomass (Bentley *et al.*, 2012). It is therefore necessary to explore the results of the CPUE indices arising from a GLM, and to understand the standardization effects achieved by including each of the explanatory variables in the model (Bishop *et al.*, 2008; Bentley *et al.*, 2012).

In this study, GLMs were used to standardize the annual catch rate of *S. commerson* in KwaZulu-Natal (KZN). The analysis considered a number of different climate variables thought to affect the catchability of *S. commerson* including rainfall and sea temperature. Weather and sea conditions are commonly associated with variable catch rates, since fishers report that unfavourable conditions often result in lower catches. Standardized annual and monthly catch rates were used in this assessment as a relative index of population abundance.

2.2. Materials and Methods

2.2.1 Study area

Although it is currently assumed that there is a single *S. commerson* stock along the entire east coast of southern Africa, catch and effort data were not available from Mozambique. As a consequence, this study was limited to the ~560km KZN coastline where catches of the recreational ski-boats have been monitored by Ezemvelo KZN

Wildlife (EKZNW) since 1984 as part of the National Marine Linefish System (NMLS). EKZNW are entrusted with the long-term conservation of the KZN region's biodiversity. For purposes of analysis KZN was divided up into four sub-regions (Maputaland, Zululand, Greater Durban and the South Coast) consisting of 15 zones (Table 2.1; Figure 2.1). The Maputaland sub-region is based on the separation of KZN at Cape Vidal into two separate biogeographic areas (Sink et al., 2005). The separation of central and southern KZN into the three remaining sub-regions was in order to include sub-regionally specific climate data (Section 2.2.2) for areas of similar length in coastline. The monitoring of catches of *S. commerson* in the databases described below has enabled an analysis and comparison of long-term trends in CPUE in KZN.

Table 2.1: Description of Ezemvelo KwaZulu-Natal Wildlife ski-boat inspection zones.

Region	Zone	Code	Location	Length (km)	
Maputaland	Bhanga Nek	BN	Maputo/R.S.A. Border - Hulley Point	55	157
	Sodwana	SD	Dewitts Bay - Red Cliffs (N.Natal)	41	
	Cape Vidal	CV	Ochre Hill - Mission Rocks	61	
Zululand	St Lucia	SL	3732 Km - St Lucia estuary mouth	9	162
	Mapelane	MP	St.Lucia South Bank - Cape St Lucia	13	
	Richards Bay	RB	Barge Reef - Mainhulyami Hill	61	
	Mtunzini	MT	Umlalazi River - Amatikulu River Mouth	28	
	Tugela	TG	Matigulu Bluff - Umhlali River	51	
Greater Durban	Ballito	BT	Xmas Bay - Umhloti River	24	93
	Durban	DB	Umhloti Water Tower - Isipingo	43	
	Kingsburgh	KB	Tiger Rocks - Ilfracombe	26	
South Coast	Scottburgh	SB	Umkomaas Pipeline - 4041 Km	35	116
	Umtentweni	UT	Mtwalume River - Umzimkulu River	35	
	Uvongo	UV	Port Shepstone - Ramsgate	20	
	Trafalgar	TF	Mbizana - Transkei Border	26	

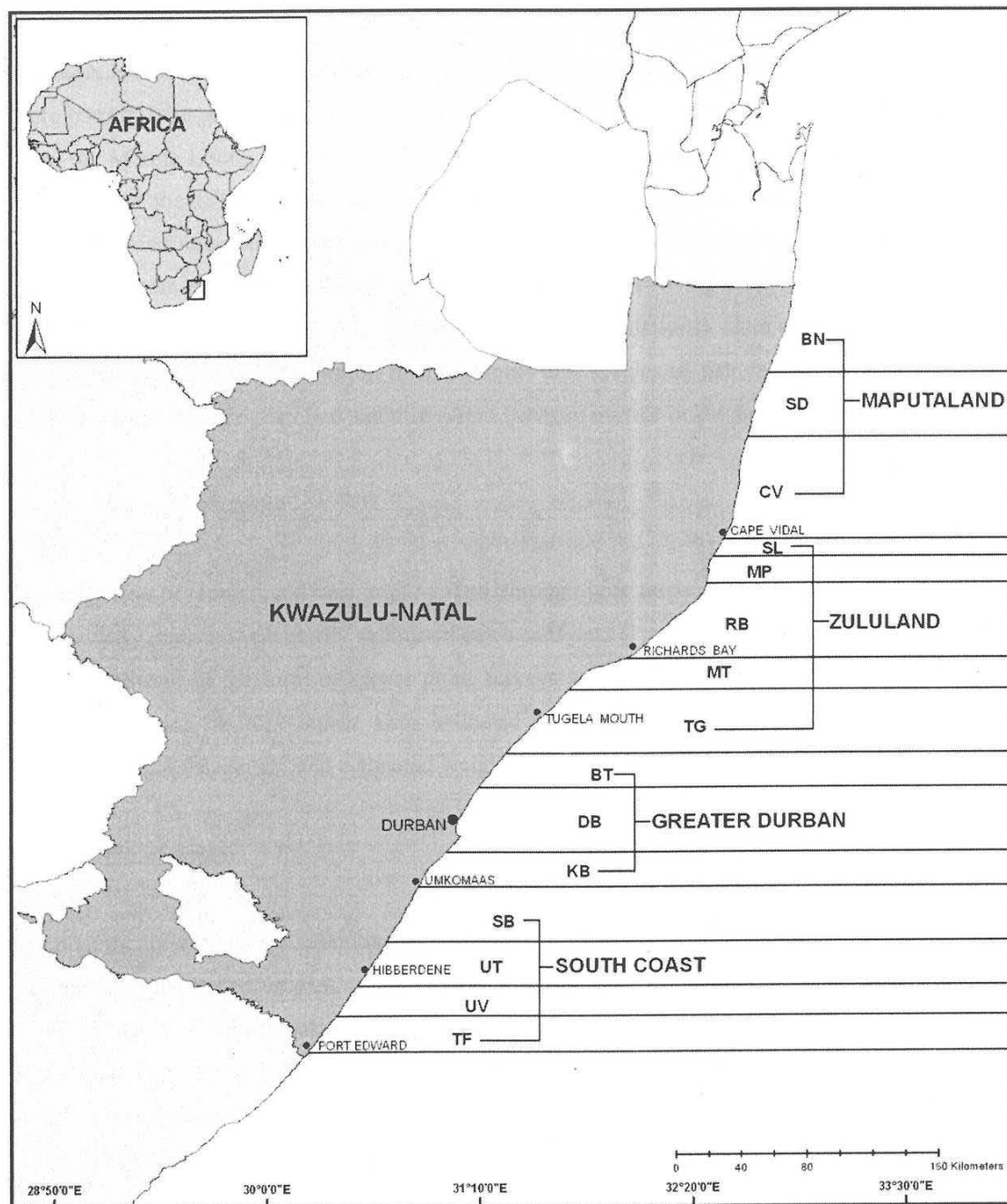


Figure 2.1: 15 Ezemvelo KwaZulu-Natal Wildlife ski-boat inspection and shore patrol zones along the KwaZulu-Natal coast grouped into four sub-regions.

2.2.2 Data collection

National Marine Linefish System (NMLS)

Ski-boat based catch and effort data for the *S. commerson* recreational linefishery were extracted from the NMLS in KZN from 1986 to 2011. As *S. commerson* are

seldom found in estuaries or nearshore, no estuarine or shore-based angling data was included. Ski-boat-based linefishing data were collected during routine access point boat inspections conducted by EKZNW staff at boat launch sites along the KZN coast. Data extracted for recreational ski-boat fishing included year, month, sub-regions, area, specific locality, effort (number of hours fished per boat) and catch (number of fish caught).

Inspections are undertaken by trained EKZNW personnel and are generally reliable. However, the primary objective of inspections is law enforcement and as such, the distribution of sampling effort in these data sources is not always random and may be biased towards high-effort areas and periods of fishing (Mann-Lang 1996).

Climate data

Climate data were obtained for two sites within each of the four KZN zones. Average monthly rainfall data were obtained from the South African Weather Service for the period 1986 to 2011. The monthly average sea surface temperature were obtained for two sites within three of the four KZN zones from the KZN Sharks Board whose staff record this information on a daily basis (depending on swell conditions). For the Maputaland region sea surface temperature data was obtained from underwater temperature recorders situated at Sodwana Bay and Leven Point (data provided by ORI and EKZNW).

2.2.3 Data selection

Certain catch data were eliminated from the analyses for several reasons. Records were rejected because information on number of crew members or hours at sea was missing. Additionally, records containing highly unrealistic catches over extremely short time-periods were also removed (e.g. 10 *S. commerson* captured over a 0.05hr fishing trip).

While additional catch and effort data were available on the BLSMS, these were only available from the year 2005 to 2011. Additionally, due to the bias associated with the BLSMS database (Chapter 1), the NMLS derived catch and effort data were considered more reliable. Finally, shore and boat-based spearfishers have been monitored by EKZNW since 2002 as part of the NMLS. However, due to the relatively

short time frame and irregular collection of this data compared to the ski-boat based NMLS data, spearfisher data were excluded from the analyses.

2.2.4 Nominal catch and effort data

Recreational catch and effort data were extracted from the NMLS database as mentioned in section 2.2.2. The raw data comprising annual monthly catch (number of fish) and effort (number of hours fished) for each zone were used to determine the nominal CPUE. The nominal data provides a coarse indication of CPUE (and thus assumed abundance) on an annual, monthly and regional basis. The data contained a large number of zero *S. commerson* catches. This was considered to reflect the temporally and spatially unpredictable nature of the species. In favourable conditions, or when a school of fish is encountered, catch rates can be very high. However, if *S. commerson* is not available or only present in low numbers, anglers will often switch targeting to other more readily available species. For the nominal data, it was therefore assumed that all fisher outings targeted *S. commerson*, at least for a short period of time during each outing.

2.2.5 Statistical modelling

The relative standardized catch rate of the recreational KZN *S. commerson* fishery was estimated using generalized linear models. The effects of year, month, region, sea surface temperature and rainfall were first quantified using a GLM, and thereafter a standardized index of abundance was calculated to correct for the influences of the variables shown above. The statistical software package R version 2.14.0 (R Development Core Team, 2011) was used to fit the GLMs.

A major challenge in modelling catch rates in fisheries is dealing with data containing large quantities of zero catches, even though effort is recorded as non-zero. The presence of many zeros can invalidate the assumptions of the analysis and jeopardize the integrity of the inferences if not properly modelled (Maunder and Punt, 2004; Li *et al.*, 2011). Additionally, zero catches may lead to computational problems (Li *et al.*, 2011). The traditional CPUE model uses a log-normal error structure and as such cannot be applied in this case (Shono, 2008). It is advantageous to attempt to account for the process that caused the zeros when standardizing catch and effort data. Simple ways of dealing with zero catches is to ignore them, aggregate data, or to add a small constant to each catch (Maunder and Punt. 2004). However, ignoring

a considerable proportion of zeros may result in a loss of information that reflects the spatial or temporal distribution characteristics of the stock (Li *et al.*, 2011). Currently the most popular way to deal with zero catches is through the delta method, which was utilized in the current study (Lo *et al.* 1992; Ortiz *et al.*, 2000; Punt *et al.*, 2000; Ye *et al.*, 2001; Rodriguez-Marin *et al.*, 2003; Maunder and Langley, 2004; Li *et al.*, 2011).

In the delta method the zero and non-zero records are analysed separately which involves fitting two sub-models to the data. The first models the probability of obtaining a zero catch, while the second models the catch rate, given that the catch is non-zero. The first sub-model assigns a value of 0 or 1 based on the respective absence or presence of a species. The probability of obtaining a zero observation (the response variable) was therefore modelled using a binomial distribution (Haddon, 2001):

$$P\{m|n, p\} = \left[\frac{n!}{m!(n-m)!} \right] p^m (1-p)^{(n-m)} \quad 2.1$$

where, p is the probability of m events proving to be true out of n trials. The logit link function was used as it is the natural link function for the binomial distribution:

$$\ln\left(\frac{\mu_i}{1-\mu_i}\right) = x_i^T \beta \quad 2.2$$

where, $\mu_i = E(Y_i)$, x_i the vector of size m that specifies the explanatory variable for the i th value of the response variable, β is a vector of the parameters, Y_i the i th random variable and E is effort. An analysis of variance (ANOVA) hypothesis test was used to determine if the selected variables were still significant in the final model.

In the second model, the catch-rate (response variable) given that it is non-zero was modelled assuming a gamma error distribution with a log-link function (Haddon, 2001):

$$L\{x|c, b\} = \frac{x^{c-1} e^{-x/b}}{b^c \Gamma(c)}$$

were, x is the value of the variate, b is the scale parameter, c is the shape parameter and $\Gamma(c)$ is the gamma function for the c parameter. An ANOVA hypothesis test was used to determine if the selected variables were still significant in the final model.

The standardized CPUEs were computed as a product of the binomial and Gamma model outputs. For both sub-models the year 1994, month March, the greater Durban region and the average sea surface temp and rainfall for these particular variables were used as reference points. In the separate regional analyses, the year 2000 was used as the reference year, as no catch data was available for 1994 for the Maputaland sub-region. Categorical variables are over-parameterized in GLMs if an intercept is estimated (Maunder and Punt, 2004). The value of the first parameter was therefore fixed to zero and the values for the remaining parameters were estimated given the fixed value. The standardized and nominal CPUE were plotted for each explanatory variable. Explanatory variables considered included categorical (year, month and sub-region) and continuous variables (sea surface temperature and rainfall). An Akaike information criterion (AIC; 1973) was used to establish the optimum combination of covariates that contributed to the best fit of the GLMs:

$$AIC = -2\ln[L(\theta_{p,y})] + 2p$$

where, $L(\theta_{p,y})$ is the likelihood of model parameters given the data y , and p is the number of free parameters.

Explanatory variables included in the final analyses included regions (or area) to account for spatial variation in *S. commerson* abundance at a given time (Table 2.2). Fishing years and months were additionally included in the analyses to account for temporal variation. Final standardized CPUE using the delta method GLMs were plotted for each of the explanatory variables for the combined region and separately for the sub-regions within KZN. Due to the absence of catch and effort data for certain years within some of the sub-regions, KZN was divided into northerly (Maputaland and Zululand) and Southerly (Greater Durban and South Coast) sub-regions for the annual analyses.

2.3 Results

2.3.1 Nominal effort

The NMLS recorded a total of 2718008.86 total hours of recreational ski-boat fishing effort (irrespective of whether *S. commerson* was caught) with a catch of 50980 *S. commerson*, between 1986 and 2011. There was an increase in recorded effort and catch from 2341 hours (56 fish) in 1986 to 309 315 hours (6174 fish) in 2011. This was primarily due to an increase in law enforcement and the number of ski-boat inspections conducted by EKZNW over this time period. Note that the nominal effort excludes non-motorized fishing vessels such as fishing-ski's, which generally are not required to launch through registered launch sites and are thus seldom checked during ski-boat inspections (Mann *et al.*, 2012).

Seasonally, three peaks were evident in fishing effort occurring over the school holiday periods (i.e. December, April and July; Figure 2.2). Effort is at its lowest in late winter and spring (August to October) coinciding with the windy months along the KZN coast. Monthly effort steadily increased from its lowest point in September to its peak in December. Effort dropped slightly in January before increasing to its second peak in April. Apart from a third peak in July, effort gradually decreased from April through to September.

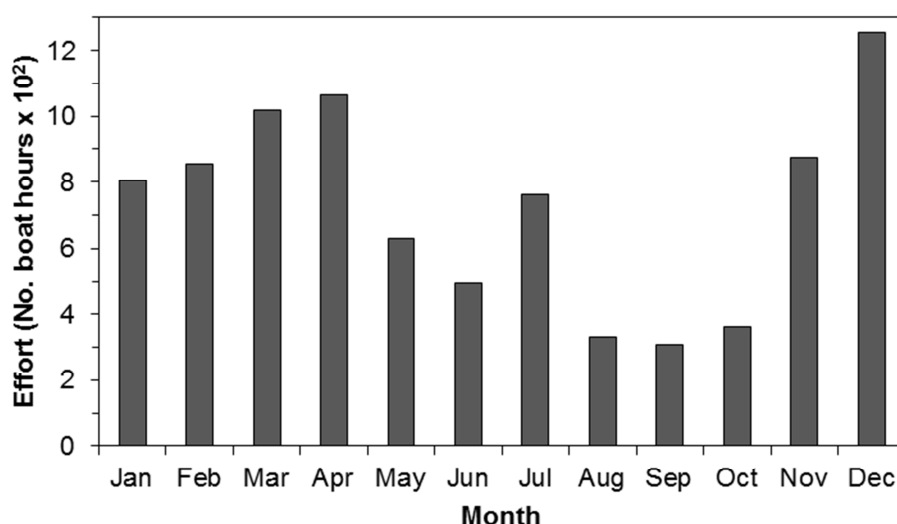


Figure 2.2: Average monthly distribution of recreational ski-boat angling effort in KwaZulu-Natal as recorded by Ezemvelo KZN Wildlife ski-boat inspections conducted between 1986 and 2011.

Spatially, the fishing effort for *S. commerson* differed along the KZN coast between sub-regions. The majority of effort was expended within Maputaland (Figure 2.3). Zululand and the South Coast displayed almost the exact same amount of effort on the resource. Surprisingly, the Greater Durban sub-region had the least amount of recorded effort by fishers but this is likely as a result of sampling bias due to the data reflecting sampling activity rather than true fishing effort.

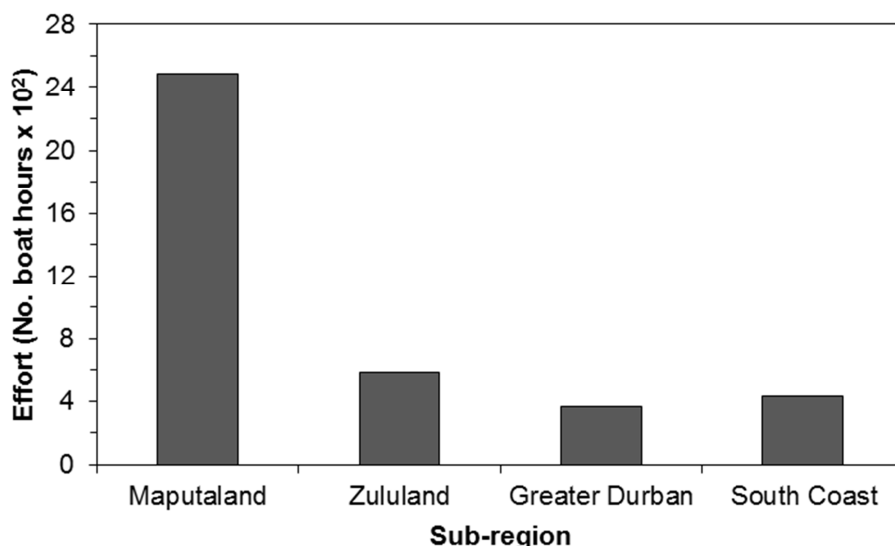


Figure 2.3: Average regional distribution of recreational ski-boat angling effort in KwaZulu-Natal as recorded by Ezemvelo KZN Wildlife ski-boat inspections conducted between 1986 and 2011.

2.3.2 Standardized catch and effort data for KwaZulu-Natal

Analysis of variance (ANOVA) indicated that region, year and month were all significant variables influencing catch rates of *S. commerson* in KZN for both the first (Presence/absence, binomial model) and second (gamma model for positive catches) sub-models (Table 2.2). Climate data were not found to be significant explanatory variables (Rainfall: ANOVA, $p > 0.05$; SS temperature, $p > 0.05$). This was likely due to interactions between explanatory variables, and as such temporal changes in climatic data are already reflected in the monthly variable. To test this, when SS temperature was included and month removed as explanatory variables, SS temperature was found to be highly significant (ANOVA; $p < 0.0001$). Additionally, when year was removed as an explanatory variable, SS temperature was found to provide a significant explanation for catch rates (ANOVA; $p < 0.05$). However, when rainfall was included and month/year removed as explanatory variables, rainfall was not found to be significant ($p > 0.05$). A method to deal with these interactions is to

retain the climatic data in the analyses while using the averages for the specified reference year, month and region (area) (AIC; 3746.4). This technique however over-parameterizes the GLM, thereby unnecessarily complicating the analyses, and as such climatic data were excluded as explanatory variables from further GLMs unless otherwise specified (AIC; 3743.9).

Table 2.2: Analysis of variance test showing significant factors in the final generalized linear model used for catch rate (CPUE) standardization for *S. commerson* in the recreational ski-boat linefishery in KwaZulu-Natal. $P < 0.0001$ indicated by ***, $p < 0.001$ **, $p < 0.01$ * and $p < 0.05$ ·

Error	Binomial			Gamma			
Explanatory variable	Chisq	df	P	SS	df	F	P
Year	141.66	26	***	878.5	26	9.44	***
Month	673.37	11	***	204.8	11	5.20	***
Region	554.75	3	***	38.5	3	3.59	*
Residuals				5618	1569		

The probability of capturing *S. commerson* fluctuated to a large degree between 1986 and 2011 (Table 2.3). Peaks in the probability of capture occurred in 1990, 2001 and from 2006 to 2008. Peaks in the probability of capture were generally interspersed with troughs. The lowest probability of capture occurred between 1986 and 1988, with a particularly prolonged period from 1991 to 1997. By month, the probability of capture of *S. commerson* followed a clear pattern increasing steadily from September to its greatest in April, before slowly declining again (Table 2.4). Regionally, the probability of capturing *S. commerson* was the greatest in Maputaland, significantly decreasing in the regions to the south (Table 2.5).

Table 2.3: Coefficients (\pm SE) of year parameters tested in the final generalized linear models describing catch rate (CPUE) for *S. commerson* in the recreational ski-boat linefishery in KwaZulu-Natal. $P < 0.0001$ indicated by ***, $p < 0.001$ **, $p < 0.01$ * and $p < 0.05$.

Error Explanatory variables	Binomial			Gamma		
	Estimate	P	SE	Estimate	P	SE
1986	-0.19		0.56	-3.182	***	0.73
1987	-1.18	*	0.52	-3.39	***	0.65
1988	-0.29		0.47	-2.51	***	0.54
1989	0.41		0.30	-2.71	***	0.39
1990	0.47		0.36	-2.76	***	0.45
1991	-0.46		0.36	-3.13	***	0.55
1992	-0.39		0.27	-3.54	***	0.39
1993	0.30		0.23	-2.82	***	0.29
1994	-0.49	.	0.25	-3.45	***	0.36
1995	-0.20		0.31	-4.22	***	0.41
1996	-0.73	*	0.31	-3.40	***	0.43
1997	0.05		0.29	-4.08	***	0.39
1998	0.26		0.26	-3.30	***	0.33
1999	0.32		0.28	-3.18	***	0.344
2000	0.26		0.28	-3.49	***	0.32
2001	0.96	***	0.24	-2.64	***	0.25
2002	0.17		0.24	-2.86	***	0.27
2003	0.37		0.26	-3.07	***	0.28
2004	0.06		0.22	-3.49	***	0.26
2005	-0.27		0.22	-2.99	***	0.26
2006	1.15	***	0.21	-2.62	***	0.22
2007	0.82	***	0.21	-2.91	***	0.23
2008	0.66	***	0.20	-2.78	***	0.22
2009	0.06		0.19	-3.70	***	0.23
2010	-0.10		0.20	-3.57	***	0.24
2011	0.42	*	0.28	-3.05	***	0.23

Table 2.4: Coefficients (\pm SE) of month parameters tested in the final generalized linear models describing catch rate (CPUE) for *S. commerson* in the recreational ski-boat linefishery in KwaZulu-Natal. $P < 0.0001$ indicated by ***, $p < 0.001$ **, $p < 0.01$ * and $p < 0.05$.

Error	Binomial			Gamma		
Explanatory variables	Estimate	P	SE	Estimate	P	SE
January	0		0	0		0
February	0.33	.	0.18	0.41	*	0.20
March	0.61	***	0.17	0.28		0.19
April	0.68	***	0.17	0.23		0.19
May	0.51	**	0.17	-0.05		0.20
June	-0.18		0.17	0.27		0.21
July	-1.16	***	0.19	-0.53	*	0.24
August	-2.20	***	0.23	-0.03		0.32
September	-2.55	***	0.25	-0.86	*	0.35
October	-2.20	***	0.24	-0.47		0.33
November	-1.80	***	0.22	-0.87	**	0.29
December	-0.35	*	0.17	-0.71	***	0.21

Table 2.5: Coefficients (\pm SE) of regional parameters tested in the final generalized linear models describing catch rate (CPUE) for *S. commerson* in the recreational ski-boat linefishery in KwaZulu-Natal. $P < 0.0001$ indicated by ***, $p < 0.001$ **, $p < 0.01$ * and $p < 0.05$.

Error	Binomial			Gamma		
Explanatory variables	Estimate	P	SE	Estimate	P	SE
Maputaland	2.55	***	0.17	-0.15		0.14
Zululand	0		0	0		0
Greater Durban	-0.36	***	0.11	0.32	*	0.14
South Coast	-0.68	***	0.11	0.10		0.14

The standardized catch rates correlated well with the nominal catch rates for year, month and region (Figures 2.4, 2.5 and 2.6). Although following similar trends, the annual standardized catch rates were greater than the nominal CPUE. By year, the standardized catch rates for *S. commerson* appeared to be cyclic in nature, with peaks and troughs occurring every two to four years (Figure 2.4). Four major and two minor peaks in catch rate have occurred between the years 1986 and 2011. Two peaks in catch rate occurred in 1989 and 1993. This was followed by seven years of relatively low, but still fluctuating catch rates. Another large peak occurred in 2001,

followed by a trough in 2004. High catch rates were again experienced in 2006 and 2008. The 2009 and 2010 seasons displayed relatively poor catch rates before increasing somewhat during 2011. These peaks and troughs in catch rate appear to follow a similar pattern to the peaks in the annual average SS temperature and rainfall patterns (Figure 2.4).

The monthly trend in standardized CPUE showed a marked increase from November to February (Figure 2.5). The CPUE was lowest between July and November and peaked at its highest from February to April. The CPUE declined sharply between April and July. As was the case with the annual standardized CPUE, there appeared to be a relationship with the mean monthly SS temperature and rainfall data. While there was a close correlation between CPUE and the SS temperature, this relationship appeared to be offset with a time lag for the rainfall data.

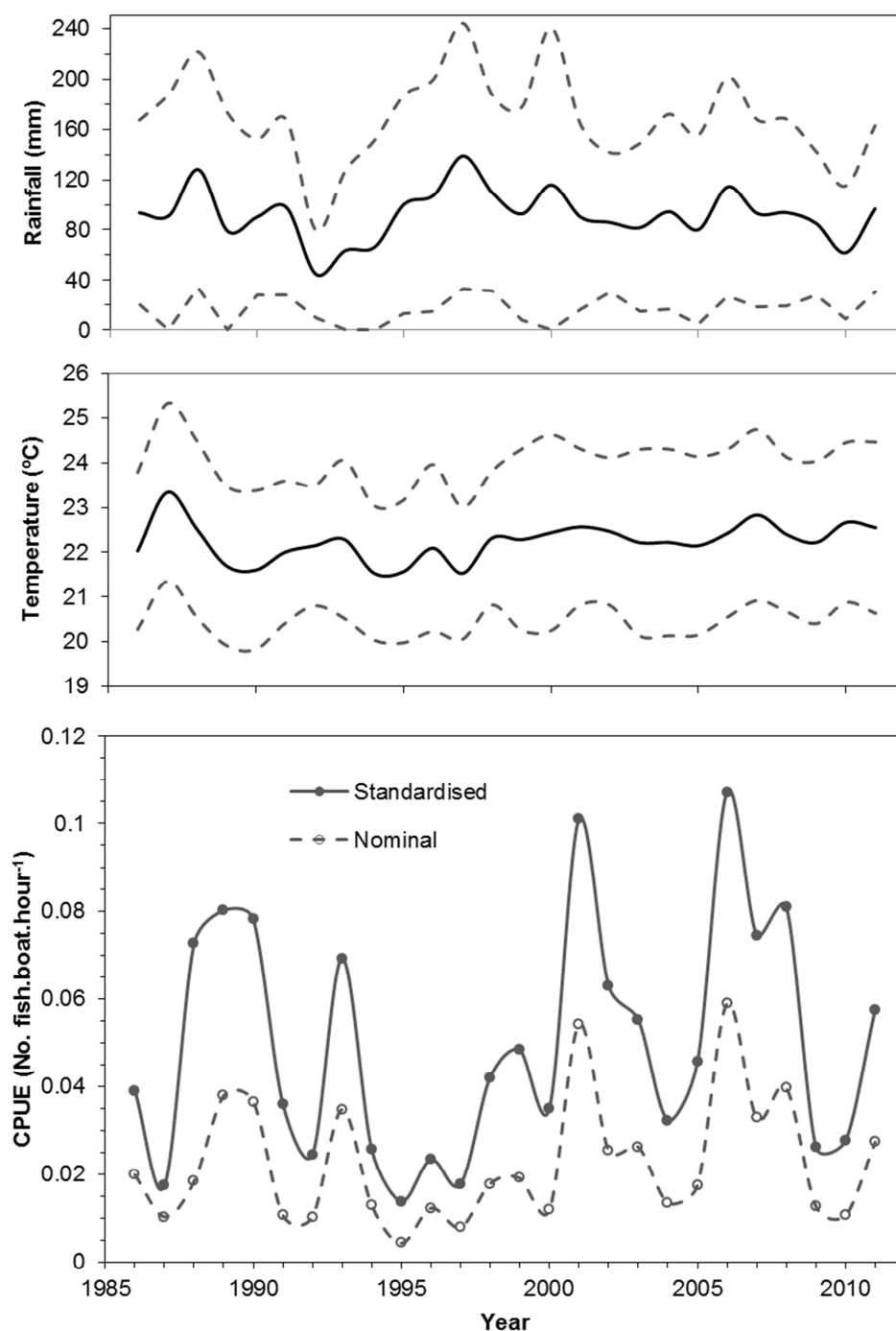


Figure 2.4: Annual mean rainfall (mm; \pm SD), temperature ($^{\circ}$ C; \pm SD) and relative mean observed (Nominal) and standardized catch rates (CPUE) pooled across all four sub-regions (Maputaland, Zululand, Greater Durban and South Coast) for *S. commerson* in the recreational ski-boat linefishery in KwaZulu-Natal. Standardized CPUE is used as an index of abundance in the assessment. Climate data were obtained from eight sites within KwaZulu-Natal.

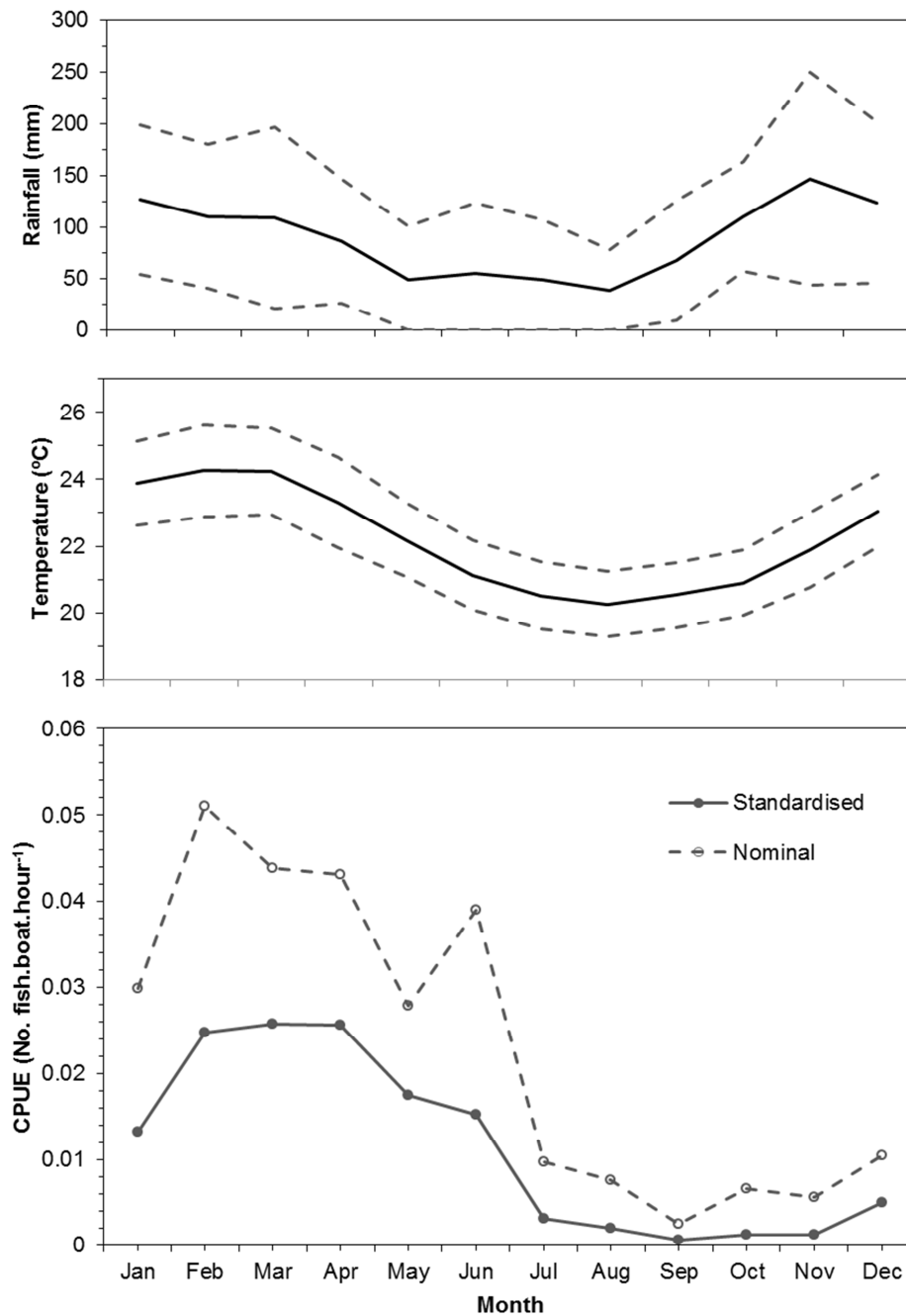


Figure 2.5: Monthly mean rainfall (mm; \pm SD), temperature ($^{\circ}$ C; \pm SD) and relative mean observed (Nominal) and standardized catch rates (CPUE) pooled across all four sub-regions (Maputaland, Zululand, Greater Durban and South Coast) for the *S. commerson* recreational ski-boat linefishery in KwaZulu-Natal between 1986 and 2011.

Catch rates were greatest in the Maputaland region and lowest along the South Coast (Figure 2.6). Although similar, CPUE was slightly higher in the Greater Durban region compared to Zululand.

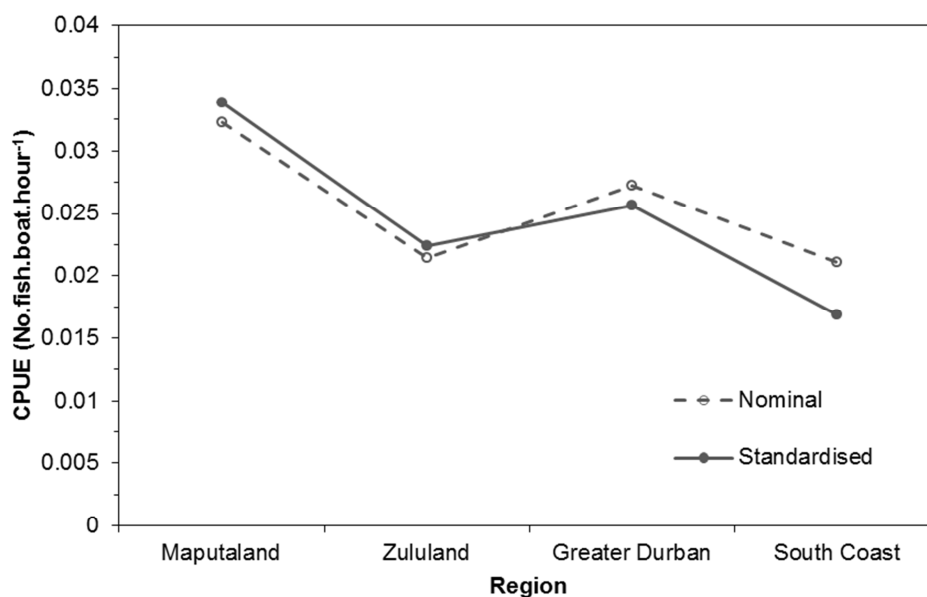


Figure 2.6: Regional relative mean observed (Nominal) and standardized catch rates (CPUE) for *S. commerson* in the recreational ski-boat linefishery in KwaZulu-Natal between 1986 and 2011.

2.3.3 Catch data for sub-regions within KwaZulu-Natal

Climate data were excluded from the KZN sub-regional GLM analyses as described in section 2.3.2 above. Year, month and region were all significant variables influencing the catch rates of *S. commerson* in the binomial and gamma error distribution sub-models within both the northerly and southerly sub-regions of KZN (Table 2.5 and 2.6; ANOVA, $p < 0.001$).

Table 2.5: Analysis of variance test showing significant factors in the final generalized linear model used for catch rate (CPUE) standardization for *S. commerson* in the recreational ski-boat linefishery in the Maputaland and Zululand sub-regions of KwaZulu-Natal. $P < 0.0001$ indicated by ***, $p < 0.001$ **, $p < 0.01$ * and $p < 0.05$.

Error	Binomial			Gamma			
Explanatory variable	Chisq	df	P	SS	df	F	P
Year	94.82	26	***	179.15	26	4.93	***
Month	235.79	11	***	149.95	11	9.75	***
Region	399.25	7	***	616.47	7	63.00	***
Residuals				1130.92	809		

Table 2.6: Analysis of variance test showing significant factors in the final generalized linear model used for catch rate (CPUE) standardization for *S. commerson* in the recreational ski-boat linefishery in the Greater Durban and South Coast sub-regions of KwaZulu-Natal. P<0.0001 indicated by ***, p<0.001 **, p<0.01 * and p<0.05 ·

Error	Binomial			Gamma			
Explanatory variable	Chisq	df	P	SS	df	F	P
Year	132.17	26	***	355.09	26	5.41	***
Month	529.34	11	***	76.96	11	2.77	**
Region	97.53	6	***	279.71	6	18.48	***
Residuals				1798.31	713		

The comparison of trends in standardized CPUE between the southern and northern regions of KZN displays a similar cyclical trend (Figure 2.7). Generally, the northern region possesses a higher catch rate compared to the southerly region. Interestingly, high catch rates during certain years in the northern region did not necessarily correspond with high catch rates further south and vice versa.

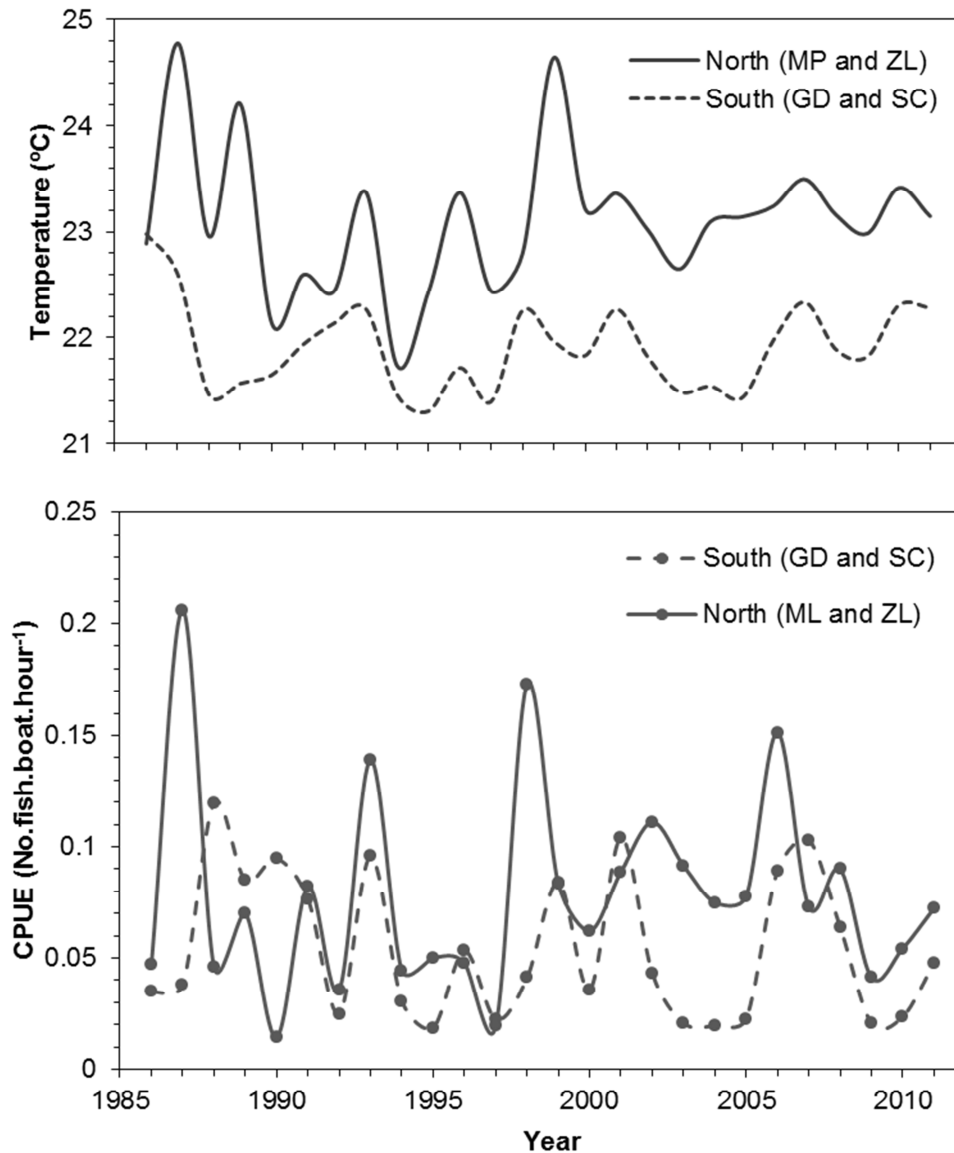


Figure 2.7: Comparison of the standardized catch rates (CPUE) for *S. commerson* in the recreational ski-boat linefishery between the northerly (Maputaland: ML and Zululand: ZL) and southerly (Greater Durban: GD and South Coast: SC) sub-regions of KwaZulu-Natal.

Within the monthly analyses, year, month and area all significantly affected the catch rates of *S. commerson* within each sub-region (Table 2.7). A clear trend was evident for the monthly catch rates for each sub-region (Figure 2.8). The catch rates within the northerly regions (Maputaland and Zululand) were significantly greater than those in the southerly regions (Greater Durban and South Coast) of KZN. The trend in CPUE for the South Coast follows the same trend as that of the Greater Durban region, except for the peak occurring slightly later in April.

Table 2.7: Analysis of variance test showing significant factors in the final generalized linear model used for monthly catch rate (CPUE) standardization for *S. commerson* in the recreational ski-boat linefishery in the four sub-regions of KwaZulu-Natal. P<0.0001 indicated by ***, p<0.001 **, p<0.01 * and p<0.05 `

	Error	Binomial			Gamma			
	Explanatory variable	Chisq	df	P	SS	df	F	P
Maputaland	Year	45.44	23	**	127.46	21	7.48	***
	Month	27.91	11	**	107.30	11	12.03	***
	Area	66.07	4	***	170.04	4	52.42	***
	Residuals				339.80	419		
Zululand	Year	100.08	26	***	351.96	25	9.14	***
	Month	247.95	11	***	55.28	11	3.26	***
	Area	96.23	2	***	331.33	2	107.53	***
	Residuals	100.08	26		554.61	360		
Greater Durban	Year	84.84	26	***	231.61	25	4.79	***
	Month	251.82	11	***	54.51	11	2.56	**
	Area	45.48	2	***	21.12	2	5.46	**
	Residuals	84.84	26		650.01	336		
South Coast	Year	108.79	26	***	288.27	26	6.18	***
	Month	305.15	11	***	88.90	11	4.50	***
	Area	42.70	3	***	218.91	3	40.66	***
	Residuals	108.79	26		613.77	342		

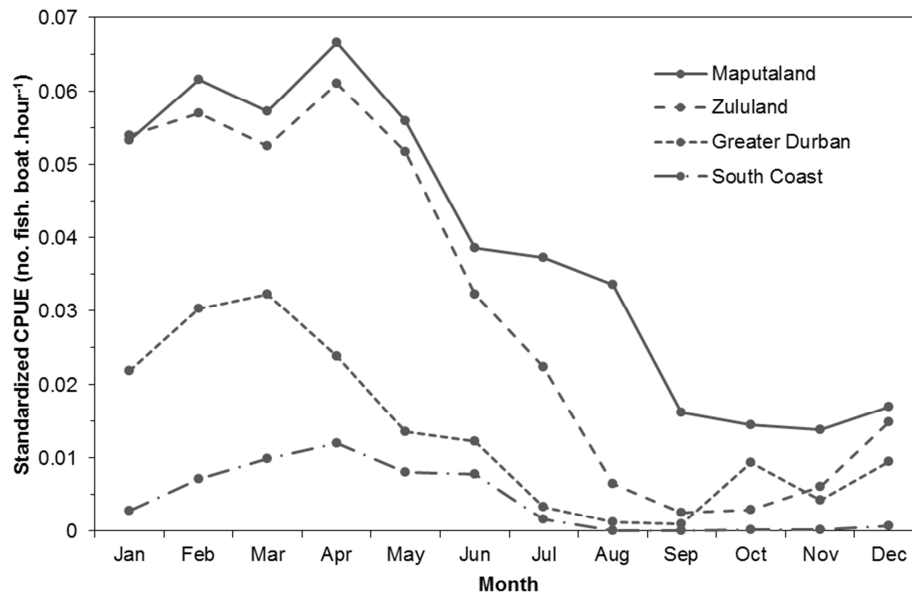


Figure 2.8: Comparison of the standardized catch rates (CPUE) for *S. commerson* in the recreational ski-boat linefishery between the four sub-regions of KwaZulu-Natal.

2.4 Discussion

2.4.1 Fishing effort

High levels of fishing effort appear to correspond with three main factors; the presence of popular holiday periods, the seasonal abundance of gamefish such as *S. commerson*, and favourable weather conditions. In several countries sportfishing only occurs when catch rates are high (Sosa, 1998). However, the availability of a great diversity of species enables this activity to occur throughout the year in certain regions (Zuniga Flores *et al.*, 2008). This may explain the high levels of effort observed in Maputaland compared to the more southerly regions. Maputaland falls within the same biogeographic zone as southern MOZ (Sink *et al.*, 2005) resulting in a prolonged gamefish season compared to the more southerly regions where the gamefish season falls over a much shorter time period. Furthermore, high effort in this region can be attributed to the area being a popular holiday destination that attracts a broad spectrum of recreational fishers from all over KZN and inland areas during the holiday periods (Dunlop, 2011). The three highest peaks in effort coincided with the school holiday periods. This is consistent with analyses of effort in the southern Gulf of Mexico where effort was at its peak during the peak tourist season (Zuniga Flores *et al.*, 2008). The minimum values of effort were recorded between August and October, similar to the findings of Dunlop (2011) which was attributed to

the occurrence of strong prevailing winds and high seas generally occurring in KZN over this time period thus reducing the launching of ski-boats. Similarly, Zuniga Flores *et al.*, (2008) attributed diminished effort within the southern Gulf of Mexico to the influence of hurricanes whose maximum frequency occurred over September.

2.4.2 Spatial distribution of *S. commerson* catches

S. commerson are far more prevalent in Maputaland compared to the more southerly sub-regions. This is likely due to this section of the KZN coastline falling into the same biogeographic region as southern MOZ (Sink *et al.*, 2005). This means that the abundance of *S. commerson* in this region is far more temporally consistent compared to the more southerly regions which possibly are more reliant on favourable environmental conditions for high catch rates. Whilst the abundance of *S. commerson* follows a consistent annual cycle within Maputaland, it is not uncommon for poor catch rates to occur in the southerly regions, possible due to erratic migration patterns (see Section 2.4.4). Additionally, the season for catching *S. commerson* in Maputaland is far longer allowing for far greater consistency in total catches to occur on an annual basis.

2.4.3 Long-term trends in *S. commerson* catches

Assuming that the standardized CPUE series are proportional to abundance, despite being cyclic in nature, there is no evidence to suggest a general increase or decline in the abundance of *S. commerson* off the coast of KZN between 1986 and 2011. The lowest annual catch rates of *S. commerson* were recorded in 1987, 1995 and 1997 although relatively low catches were also recorded in 1992, 2000, 2004 and the 2009 to 2010 season. These were interspersed with periods of high catches during 1989, 2001 and the 2006 to 2008 seasons. Large fluctuations in the annual catch rates of *Coryphaena hippurus* (Dorado) in the southern Gulf of California were attributed to the species' migratory nature and consequent ability to quickly respond to environmental changes and prey availability (Zuniga Flores *et al.*, 2008).

The El Nino event of 1997 had a direct effect on the abundance and availability of *C. hippurus* along the west coast of Central America with a large displacement of the species towards higher latitudes. This was attributed to the increase in the SS temperature in the California current (Zuniga Flores *et al.*, 2008; Norton, 1999). Similarly, fluctuations in the catch rates of striped marlin (*Tetrapturus audax*) off

Mexico have been attributed to the species' preference for specific temperature regimes, migrating further offshore during unfavourable coastal conditions (Ortega-Garcia *et al.*, 2003). SS temperature has also been found to show a positive correlation with sport fishing effort off eastern Australia (Zischke *et al.*, 2012) as well as other sport fisheries in the eastern Pacific Ocean (Ortega-Garcia *et al.*, 2008). Additionally, a positive correlation has been found to exist between SST and annual catch rates of pelagic species in commercial fisheries worldwide (Su *et al.*, 2011; Teo and Block, 2010). The influence of SS temperature had a significant impact on the catch rates of *S. commerson* off the KZN coastline with increases in SS temperature significantly leading to improved catch rates on an annual basis. Similarly, Norton (1999) found that two important climatic mechanisms affect the abundance and movements of *C. hippurus* in the California current. During some periods, decreased local and topical wind-forced upwelling and onshore transport appeared more important, whilst in other periods SS temperature appeared more important. In addition, interannual and multi-year events interacted to affect abundance of *C. hippurus* within the study region (Norton, 1999).

It is likely that the adaptability of *S. commerson* allows for variation in the migratory pattern of the species depending on prevailing environmental conditions. This would affect the availability of *S. commerson* in KZN, potentially increasing or prolonging its occurrence in other areas within its range such as southern MOZ. Differences in SST may explain why high catch rates in the northern regions of KZN, which fall into the same biogeographic region as southern MOZ, do not appear to automatically indicate that abundance will be high in the southern KZN. It is important to note that while warmer SS temperatures have a positive effect on catch rates of *S. commerson* in KZN, this factor appears to control the limits of migratory movement of the species in the region, and not the basis for the movement into KZN waters.

In this study, rainfall was not found to be a significant factor affecting catch rates in KZN. This is consistent with the results of Zischke *et al.* (2012), who found that rainfall did not have a significant effect on the catch rates of pelagic gamefish off the coast of eastern Australia. Govender (1992) and later Lamberth *et al.* (2009) linked catches of *S. commerson* in KZN to freshwater inflows in MOZ. He deduced that high rainfall and the increased input of freshwater into the marine environment off MOZ where *S. commerson* breeds (Chapter 3) provide good conditions for spawning and larval survival there. This is likely given the high abundance of important dietary species to *S. commerson*, such as *Thryssa vitirostris* and other engraulid species,

along the central coast of MOZ during the rainy season (Mualeque and Santos, 2011). This is likely to result in good catches in KZN when fish recruit into the fishery one to two years later (Chapter 3 and 5). This is comparable to the findings of Kraul (1999) whose results indicated that the annual abundance of *C. hippurus* in Hawaii was linked to cohort survival under favourable environmental conditions. Shoji and Tanaka (2006) postulated that scombrid fishes have adopted a survival strategy characterised by fast growth and the ability to consume large prey at an early age. They further documented that variability in feeding conditions can significantly affect larval growth as well as controlling growth-related survival during the early larval stage. An interannual comparison showed that variability in ichthyoplankton prey concentration and availability is one of the most important determinants that affects the larval survival window and recruitment dynamics (Shoji and Tanaka, 2003; Shoji and Tanaka, 2006). These findings link well with those of Lamberth *et al.* (2009), as increased freshwater inflow results in increased primary production (King, 1995) leading to optimum feeding conditions for larval and juvenile *S. commerson*.

Overall, the findings of this study were consistent with those of Lamberth *et al.* (2009) in that freshwater inflow and rainfall within KZN are unlikely to have a large impact on the catches of *S. commerson*, as the major driving factors driving recruitment to the fishery are environmental conditions (especially mean annual runoff) in MOZ.

2.4.4 Seasonality of *S. commerson* catches

The highest catch rates made by recreational ski-boat fishers in KZN between 1986 and 2011 were in summer through to early autumn (January to April), although catch rates remained relatively high through to mid-June. High catch rates on a seasonal basis coincided with warm average SS temperatures. Similar findings were reported by Zuniga Flores *et al.* (2008) explaining the seasonal catch rates of *C. hippurus* as a function of SS temperature in the southern Gulf of California, Mexico. Seasonal peaks in abundance of *C. hippurus* off the coast of Hawaii were attributed to the species' north and south migrations to stay associated with the 23 °C isotherm (Kraul, 1999). Additionally, seasonal variation in catch rate values of *T. audax* off the west coast of Central America were related to increases in SS temperature, showing a preference of the species for temperate waters between 22 and 24°C. These results are in contrast to those found by Trent *et al.* (1987) who found that a temperature-dependent north-south seasonal migration pattern displayed by *Scomberomorus cavalla* off the south Atlantic coast of USA were not indicated by

CPUE data. Surprisingly *S. commerson* has been recorded as far south as Mossel Bay off the Western Cape Coast (Smith and Heemstra 1991) where the SST is much cooler. Although such occurrences are rare, it is likely that at such times fish are associated with an eddy of warm water moving south onto the Agulhas Banks during the summer (Lutjeharms, 2006).

Lamberth *et al.* (2009) suggested that on a seasonal basis, increased productivity as a result of greater freshwater inflows may lead to increased prey availability within certain regions potentially influencing the migratory pattern of *S. commerson* in KZN. Although not significant, increases in rainfall in KZN indicated an immediate decrease in the catch rates of *S. commerson*. This is likely to be a result of poor weather conditions associated with increased rainfall leading to greater turbidity and less than ideal fishing conditions on a short-term basis (Lamberth *et al.*, 2009).

Seasonal patterns of CPUE for *S. cavalla* off the south Atlantic coast were distinctly different among the areas compared (Trent *et al.*, 1987). However, the seasonal trends in catch rate between the four sub-regions of KZN generally mapped the temporal and spatial abundance of the species during its annual migratory route from MOZ waters southwards into northern and then southern KZN (Chapter 1). The migratory route of *S. commerson* is evident through the trend in peak abundance within the regions over time. The initial peak in abundance in Maputaland and Zululand occurs in February followed by peaks over March in Greater Durban and April along the South Coast reflecting the southward movement of *S. commerson* during these months. These southward migrations are confirmed by a number of recaptured *S. commerson* that were tagged in MOZ. A number of *S. commerson* tagged off Bazaruto Island between July and November have been recaptured in Maputaland (February), Zululand (May), Greater Durban (March through to May) and the South Coast (April and May), sometimes within as little time as five months. The 'step' in catch rates, occurring in May to June along the South Coast and Greater Durban region progressing through June to August in Maputaland may reflect the return migration of *S. commerson* back into southern MOZ. The lower catch rates on the return migration may reflect the direct impact of fishing pressure on the resource or the possibility of reduced feeding during the return migration. Size and sex specific migration patterns have been observed to occur in the Arabian Sea and Gulf of Oman (Siddeek, 1996; McIlwain *et al.*, 2005) as well as off the west coast of Australia (Lester *et al.*, 2001). Following the spawning season, an initial migration occurs consisting of shoals of newly recruited cohorts of smaller fish; this is followed by a

second migration consisting mostly of larger female *S. commerson*. It is likely that a similar migratory pattern occurs off the southern MOZ and KZN coastline, although size frequency data over time would need to be acquired to complement the catch rate data. The higher catch rates occurring in the northern regions compared to the southern regions reflects the variation in the extent of the migration of *S. commerson* between different years. This is likely to be due to variations SST within KZN influencing the extent of the migration of *S. commerson* into the more southerly regions. Whilst fish generally move into Maputaland most years, the arrival of *S. commerson* into South Coast waters is much more fickle.

2.4.5 Conclusions

The levels of fishing effort by recreational ski-boat fishers targeting *S. commerson* displayed peaks corresponding to holiday periods, the seasonal abundance of gamefish, and favourable weather conditions. Spatially, catch rates of *S. commerson* were far higher in Maputaland compared to the more southerly regions probably reflecting a more consistent migration into the former region on an annual basis. Seasonal catch rates reflect a consistent fixed pattern with the bulk of fish entering the northern waters of KZN in February, migrating south by April and returning north into MOZ by the end of August. The southerly extent of these migrations is likely to be controlled by short term environmental factors with SS temperature being found to significantly affect catch rates among regions.

The abundance of *S. commerson* on an annual basis is cyclic in nature and is most likely a result of environmental influences in MOZ. It is likely that years of high rainfall and consequent increased freshwater inflow in MOZ may result in high abundance of *S. commerson* in KZN with a one to two year time lag (age at recruitment into the fishery; see Chapter 3, 4 and 5). The trends in long-term CPUE in KZN are therefore more a reflection of favourable environmental conditions resulting in increased larval survival and recruitment pulses and not a reflection of fishing pressure on the resource.

Chapter 3

Reproductive Biology

3.1. Introduction

Reproduction is one of the major events in the life history of a species (King, 1995). In fisheries science a description of the reproductive biology of an exploited species is required for many age-based stock assessment models and to provide management options for the protection of spawning stocks (Jakobsen *et al.*, 2009). Management options such as closed seasons, closed areas and minimum size limits are usually based on knowledge of the reproductive seasons, spawning areas and lengths-at-maturity of a species (Jakobsen *et al.*, 2009). Reproductive parameters do not provide direct evidence of stock structure, but do offer information to assist in understanding biological processes that may be responsible for maintaining the underlying stock structure of a species and the mechanisms by which sympatric species coexist (Begg, 1998).

The gonads of fish generally have a relatively long period of inactivity, followed by a period whereby they develop to a ripe or spawning state. This spawning period in the reproductive cycle, when fully developed gametes are released, is of particular interest in fisheries studies (King, 1995). The spawning event may take place within certain specific areas, extending over short or long time periods, and be at either regular or irregular intervals. The stimuli inducing resting gonads to develop into a spawning state may include endogenous factors and exogenous events in the surrounding environment (King, 1995). Exogenous stimuli could include photoperiod and periodicity, salinity, freshwater inflow, food availability, moon phase or tidal cycle, and temperature (Miller and Kendall, 2009). In temperate water species it is common for larvae to be produced in early winter spring so that they can feed on the blooms of phytoplankton, zooplankton and, ultimately, the other larval, juvenile and adult fish that depend on these planktonic food sources (King, 1995; Miller and Kendall, 2009). In tropical species, which are not subjected to great temperature differences over the year, it is common for protracted spawning seasons to occur (Miller and Kendall, 2009). While the stimuli inducing gonads to develop occurs over a relatively long

period of time and are triggered by sustained influence, those triggering spawning usually occur through brief environmental events (Miller and Kendall, 2009).

A closed season or area reduces effort in the fishery while protecting the resource during a vulnerable portion of its life history. This is especially important for species that aggregate during the breeding season making them easier to target and capture (Forsgren *et al.*, 2002). There are two main methods most commonly used in fisheries science to study reproductive cycles and the timing of spawning. The first is by studying the appearance of gonads, macro- and/or microscopically according to predefined stages of maturation over time. The second method is by using the gonadosomatic index (GSI) by analysing the relative size or weight of gonads over time (King, 1995).

Although gonad development and subsequent spawning may depend on various environmental stimuli, individuals must reach a certain age or size before they are capable of reproduction (King, 1995). The mean length at sexual maturity is commonly defined as the length at which 50% of all individuals are sexually mature (King, 1995). A minimum size of capture is based on the theory that a fish should be allowed to spawn at least once prior to being exploited and thereby contribute to future stocks.

Information on the reproductive biology of *Scomberomorus commerson* within its global distributional range throughout the Indo-Pacific is fragmentary. Reproduction of the species is relatively well understood in the northern Indian Ocean (Devaraj, 1983; Claereboudt *et al.*, 2005; Grandcourt *et al.*, 2005) and along the Australian coastline (McPherson, 1993; Mackie and Lewis, 2001; Mackie *et al.*, 2002). Large data gaps are however clearly evident throughout much of the remainder of its distributional range.

S. commerson has a gonochoristic life history in which the gonad differentiates into an ovary or testis at between 30 and 40 cm FL (Mackie *et al.* 2005). Spawning of *Scomberomorus* species has been inferred from hatching experiments (Munro, 1942), egg and larval surveys (Jenkins *et al.*, 1985; Beckley and Leis, 2000), gonad condition (Beaumarriage, 1973; Devaraj, 1983; McPherson, 1993; Mackie and Lewis, 2001; Mackie *et al.* 2002; Claereboudt *et al.*, 2005; Grandcourt *et al.*, 2005; Kaymaran *et al.*, 2010) and hormonal changes (Macgregor *et al.*, 1981). At least three distinct stocks of *S. commerson* have been identified along the north, west and

east coast of Australia. Although they exhibit temporal and spatial variability in their reproductive biology, spawning appears to generally occur in spring-summer season (McPherson, 1993; Mackie *et al.*, 2002). The equatorial northern Australian stock displays a protracted spawning season from early spring to mid-summer (August to December) (McPherson, 1993). No spawning was found to occur in the most southerly regions of the west and east coasts of Australia (McPherson, 1993; Mackie *et al.*, 2002). Off the coast of India the spawning season occurred from January through to September, peaking during April and May (Devaraj, 1983). In the Gulf of Oman and Arabian Sea single spawning period occurred from May to June, just prior to the onset of summer (Claereboudt *et al.*, 2005). In the Arabian Gulf, spawning occurred between April and August. Females generally reach 50% maturity at a larger length (79 to 86.3 cm FL) compared to males (62.8 to 72.8 cm FL) (McPherson, 1993; Mackie *et al.*, 2002).

Govender (1992) described the reproductive biology of *S. commerson* off the coast of KZN. He concluded that the principal spawning area for *S. commerson* is likely to be along the MOZ coast, protracted, and over the spring-summer season (November to March). It was estimated that males matured at a smaller size (70.6cm FL) as compared to females (109.6cm FL). However, a small sample size, particularly for large males, during the spawning season may have resulted in maturity data being poorly represented in the results.

The aim of this study was to describe the reproductive biology and spawning patterns of *S. commerson* along the combined KZN and southern MOZ coastline. Specific objectives were to examine the sex ratios and sex-specific size distributions, to determine the length and age at maturity (taken as the length and age at 50% maturity), to describe the maturity stages of *S. commerson* over an annual cycle and to identify peaks in spawning using maturity stages and gonadosomatic indices (GSI).

3.2. Materials and Methods

3.2.1 Sampling

Data for the reproductive analysis of *S. commerson* were collected between April 2011 and March 2012 from recreational and artisanal catches along the KZN and

MOZ coastline as discussed in Chapter 1. Additional length data were obtained from the MOZ recreational/sport line-fishery (2005–2011) from the ORI tagging database.

Each fish was weighed to the nearest gram (g, Wt), measured in centimetres (cm FL and TL), sexed and macroscopically staged. The macroscopic stages of reproductive maturity were determined using a six-element scheme based on gonad size and appearance (Tables 3.1 and 3.2). Difficulties were encountered differentiating between immature and resting gonads, particularly in smaller fish. Therefore, these two stages (i.e. I and II) were combined to avoid subjective stage interpretation based on the size of the fish. The maturity stages are based on keys described by Mackie and Lewis (2001), Grandcourt *et al.* (2005) and Claereboudt *et al.* (2005) and modified for this study.

The gonads were removed and weighed to the nearest gram (0.1g). If the gonads were indistinguishable as male or female, the individual was classed as juvenile. At least five gonad samples for each macroscopic stage of reproductive development were stored in 10% formalin for histological analysis.

3.2.2 Histological macroscopic stage validation

Transverse sections of preserved gonad samples (normally taken approximately midway along the length of the gonad) were dehydrated in an ethanol series, embedded in paraffin wax and sectioned at 8 microns for fish in all stages of reproductive development (Austin and Austin, 1989). Samples were stained with haematoxylin and eosin yellow. Stained sections were examined microscopically and a photograph taken to validate macroscopic gonad maturity stages assigned during field sampling (see tables 3.1 and 3.2).

Table 3.1: Macroscopic and microscopic staging criteria used for assessing the gonads of female *S. commerson* sampled from southern Mozambique and KwaZulu-Natal between April 2011 and March 2012.

Development Stage		Macroscopic description	Microscopic description
I	Juvenile	Gonads too small to distinguish between testes or ovaries.	Gonad can be distinguished as either male or female Stage II (Immature).
II	Inactive/ Immature	Ovaries appear glassy, translucent pink, small and compact. Ovaries may be opaque purple/pink, flattened and flaccid in larger fish. Oocytes not visible to the human eye resulting in smooth, uniform appearance.	Small oocytes imbedded in ovigerous tissue. Tunica thin, tightly encases ovarian lamellae. Cytoplasm strongly basophilic with no vacuoles
III	Developing	Ovaries becoming progressively rounder and firmer as the gonad wall contracts and thickens and the ovarian tissue develops. Colour typically semi-translucent rose, pink or ivory, although often red. Small eggs visible.	Small, but expanding oocytes imbedded in ovigerous tissue. Tunica thick, atretic bodies common. Cytoplasm more lightly coloured.
IV	Developed	Ovaries appear semi-translucent and speckled. As more oocytes develop, ovaries become large, round and opaque with prominent blood vessels. Opaque oocytes are visible through the gonad wall and the colour is typically pale yellow or apricot.	Oocytes at maximum development. Cortical alveoli abundant, coalescing towards the centre. Yolk globules abundant and progressively replacing cytoplasm. Zona radiata thick.
V	Ripe/ripe-running	Ovaries are very large and swollen. Colour is apricot to peach with a prominent network of external blood vessels. The presence of translucent, hydrated oocytes gives the ovaries a distinctive speckled or granular appearance through the thin gonad wall.	Widespread hydration and increase in size of oocytes. Zona radiata thin. Oocytes free in the ovarian lumen.
VI	Spent	Gonad flaccid and dark in colour. Few residual eggs may be present	Residual oocytes in various stages of atresia. Tunica stretched and follicles mostly empty.

Table 3.2: Macroscopic and microscopic staging criteria used for assessing the gonads of male *S. commerson* sampled from southern Mozambique and KwaZulu-Natal between April 2011 and March 2012.

Development Stage		Description	
I	Juvenile	Gonads too small to distinguish between testes or ovaries.	Gonad can be distinguished as either male or female Stage II (Immature).
II	Inactive/ Immature	Testes are small and straplike with a smooth appearance and opaque, ivory or bone colour. No sperm is present.	Peripheral sperm sinuses may contain spermatozoa, testis is dominated by connective tissue and little sperm tissue is present. The central sperm sinus is small and empty.
III	Developing	Testes are small, opaque and straplike. Sperm is extruded when squeezed. Central tissue often browner than bone- or ivory-coloured peripheral tissue. Testes may occasionally be tinged in red.	Peripheral sperm sinus is present but contains little sperm. Spermatocytes are the dominant sperm tissue.
IV	Developed	Testes are large, opaque, and ivory in colour. Exterior dorsal blood vessels are large and small blood vessels are usually present. Internally, sperm can be squeezed from the central sperm sinus.	Abundance of spermatozoa and/or spermatids in the outer portion of the gonad. Central sperm sinus may be small with a thick muscular wall and may contain little or no sperm. Peripheral sperm sinuses are conspicuous and filled with spermatozoa. Crypts of spermatozoa and spermatids are confined to the outer portion of the testis. In some fish, early stage spermatid tissue is abundant, although peripheral sperm sinuses are well developed, and spermatozoa and spermatids dominate the inner regions of the testes. The central sperm sinus may contain sperm.
V	Ripe/ripe-running	Testes opaque, swollen and with large exterior blood vessels. Sperm is released with little or no pressure on the abdomen, or when the testes are cut.	Testis is large in size and dominated by large peripheral and central sperm sinuses that are filled with spermatozoa. Crypts of spermatocytes are uncommon and confined to the outer most region of each lobe.
VI	Spent	Testes are short, dark-reddish brown and have a bruised appearance. A small amount of residual sperm may be present, but usually no sperm is released. Wall flaccid and rich in blood vessels.	Peripheral sperm sinuses contain little sperm. Yellow-brown bodies, connective and muscle tissue are prominent.

3.2.3 Spawning area and season

To determine the spawning area, the frequency of mature and ripe gonads (stage IV and V) in relation to the number of sexually mature fish sampled in each region was examined in three areas based on the NMLS areas discussed in Chapter 2: MOZ, Maputaland (ML) and the combined Zululand, Greater Durban and South Coast regions (Central to Southern KZN; CSKZN). The separation of the two KZN areas from MOZ was based on the assumption that the species will/may be treated separately for management purposes based on political boundaries. The separation of the KZN region into Maputaland and CSKZN is based on the separation of KZN at Cape Vidal into two separate biogeographic areas (Sink *et al.*, 2005). The spawning season was identified by comparing the proportion of ripe-running individuals (stage V) in each monthly sample and this was corroborated by examining peaks in the mean monthly gonadosomatic index (GSI). The GSI was calculated for males, females and combined sexes by expressing the gonad weight as a proportion of the total body weight:

$$GSI = \frac{\text{Gonad mass (g)}}{\text{Body mass (g)}} \times 100 \quad 3.1$$

where gonad mass is the mass of the fresh gonad, and body mass is the wet body weight of the fish prior to gutting. Differences in mean GSI values between males and females were tested using a student's *t*-test. Tests were conducted for the entire sample, the months during the spawning season, and the months outside of the spawning season. Differences were considered significant if $p < 0.05$.

3.2.4 Length and age at sexual maturity

The mean length at sexual maturity was defined as the length at which 50% of all individuals are sexually mature. Length at 50% maturity for combined and separate sexes was determined by fitting a logistic ogive to the observed proportion of mature fish per 5cm length class. Only data obtained during the months of peak reproductive activity (September to January), as determined from macroscopic gonad staging and GSI, were used. The two parameter logistic ogive is described by the equation:

$$P_l = \frac{1}{1 + \exp(-(l - l_{50})/\delta)} \quad 3.2$$

where P_l is the proportion of fish mature in length class l , l_{50} the length at which 50% of the animals are mature, and δ is a parameter that determines the width of the maturity ogive. Model parameters were estimated by minimizing the negative log-likelihood using standard non-linear optimization methods (Solver, Microsoft Excel, 2010). Variability of the parameter estimates were calculated using a parametric bootstrapping procedure (Efron, 1987) with 1000 iterations and 95% confidence intervals constructed from the bootstrap data using the percentile method. A likelihood ratio test (LRT) was used to test for differences in length at 50% maturity between the sexes.

Length at 50% maturity was transformed into age at 50% maturity using the empirical growth equations as described in Chapter 4.

3.2.5 Population structure

The length and age structure of the population was investigated using length frequency and age frequency distributions (see Chapter 4). Length and age distributions between regions and sexes were compared using χ^2 tests (Zar, 1999; Townend, 2002). Independent tests were conducted to determine whether length and age distributions differed significantly for the whole sample and for individual length frequencies within the sample.

The sexual structure of the population was examined using χ^2 goodness of fit tests. Independent tests were conducted to determine whether sex ratios differed significantly from unity. The probability level was set at 0.05 and Yates correction factor was used on account of there being only 1 degree of freedom for each comparison (Zar, 1999; Townend, 2002). A generalized linear model (GLM) for binary regression (Venables and Ripley, 2002) was used to predict the probability (P) of *S. commerson* being female. The probability was modelled using a logistic-link function and binomial error distribution with month and fork length as the explanatory variables. Length was treated as a continuous variable and month as categorical. The statistical software package R version 2.14.0 (R Development Core Team, 2011) was used to fit the GLM.

3.3. Results

3.3.1 Sample breakdown

A total of 439 *S. commerson* gonads were macroscopically staged and weighed during the sampling period. Of these, 312 (114 males, 195 females and 3 juveniles) were sampled in KZN and 127 (69 males, 56 females and 2 juveniles) within MOZ (Section 3.3.2 and 3.3.3). Only fish sampled during the peak reproductive period (September to January) were used to estimate the length at 50% maturity (71 males; 122 females) (Section 3.3.5). In addition to the biological sample, length data for 373 fish captured in MOZ between January 2005 and October 2011, were obtained from the ORI tagging database for use in the length frequency analyses (Section 3.3.6).

3.3.2 Stages and reproductive season

A high incidence of near-spawning individuals (stages IV and V) (79.2%), accompanied by a lower frequency of spent individuals (stage VI) (10.9%) was sampled in MOZ over September and October (Table 3.3; Figure 3.1 and 3.2). Relatively high frequencies of mature individuals were sampled in a spawning state off Maputaland (30.5%) between December and February. These gonads were mostly in an advanced stage V (i.e. ripe-running) and some were beginning to regress to stage VI. This coincided with a high incidence of spent individuals (56.8%) occurring off the Maputaland coastline. Almost all the mature fish sampled in CSKZN were either in a resting or developing stage (stages II and III) occurring between April and July (Table 3.3; Figure 3.1 and 3.2).

Table 3.3: Frequency of reproductive maturity stages in *S. commerson* in three adjoining regions along the east coast of southern Africa. The (%) refers to the percentage of all mature fish (ie. Stage III to stage VI).

Region	Immature/Resting (Stages I and II)	Developing (Stage III)	Developed and Ripe (Stages IV and V)	Spent (Stage VI)
	n	n (%)	n (%)	n (%)
MOZ	26	10 (9.9)	80 (79.2)	11 (10.9)
Maputaland	45	95 (12.7)	29 (30.5)	54 (56.8)
Southern and central KZN	109	63 (95.2)	3 (4.8)	0 (0)

Gonad development, based on macroscopically determined stages of both males and females, followed a clear seasonal trend (Figure 3.1). Abundance of immature/resting fish was at its greatest during the late summer months (February – April), accounting for up to 90% of the sampled catch during this period. The gametogenetic cycle began in April with fish entering the developing stages (Stage III) of the reproductive cycle. Developed and spawning stages (Stage IV, V) were observed predominantly from July to December with no mature stages occurring between April and June. By December, most of the fish were in post-spawning/spent stages (Stage VI) indicating the end of the spawning season. Fish in their spent stage were observed as early as October, through to January.

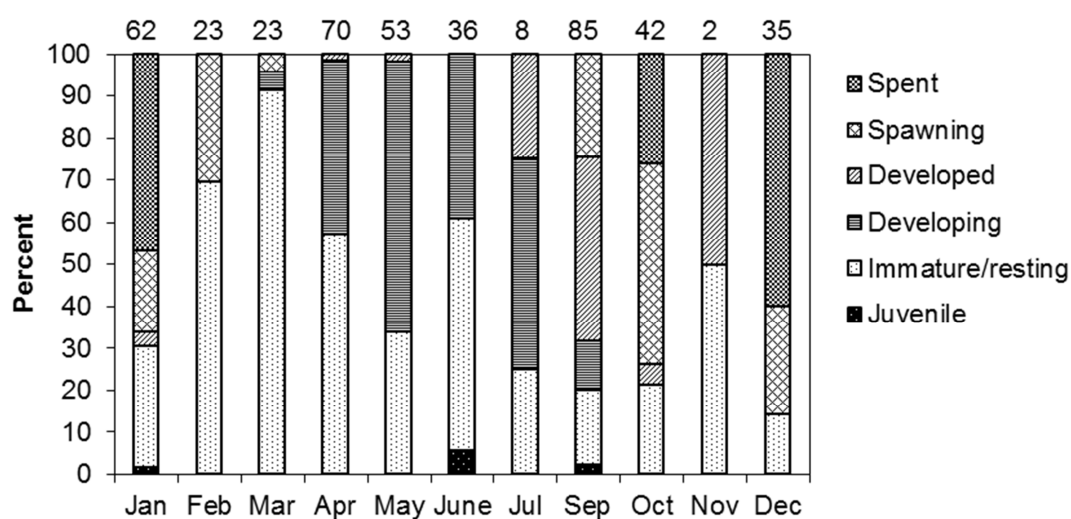


Figure 3.1: Monthly percentage of each macroscopic stage for gonads of *Scomberomorus commerson* from southern Mozambique and KwaZulu-Natal. (Monthly sample sizes are presented above the graph, no samples taken in August).

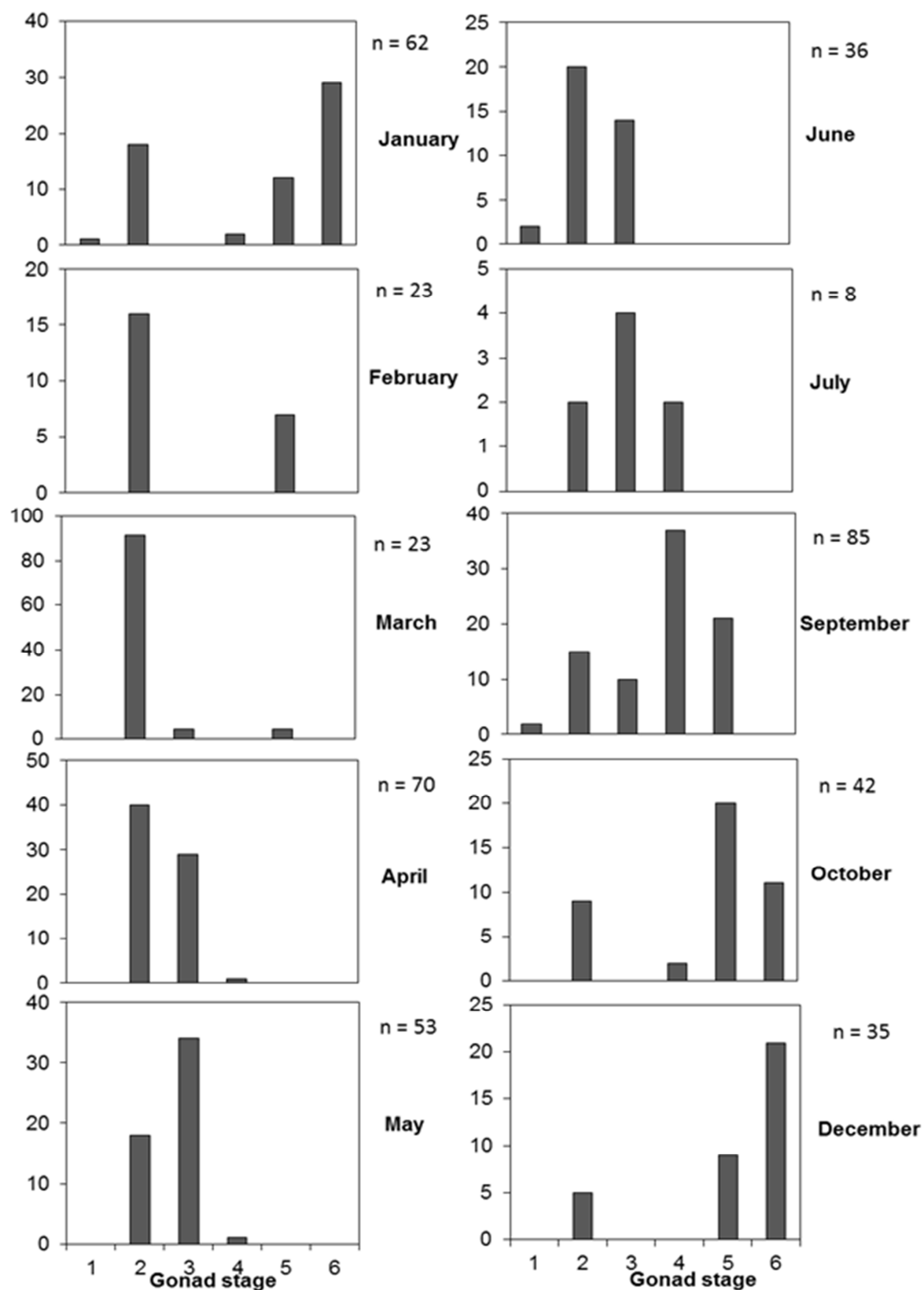


Figure 3.2: Distribution of reproductive stages of *Scomberomorus commerson* (males and females combined) in southern Mozambique and KwaZulu-Natal (no samples collected in August)

3.3.3 GSI and reproductive cycle

The monthly variation in GSI followed that of the macroscopic gonad staging substantiating a spring/early summer spawning season (Figure 3.3). Maximum gonad development occurred simultaneously in both sexes during September and October. The peak in GSI was preceded by a three month growth period of the gonads from June to August. Following the peak in gonad development, there was a decline in GSI from November through to February. The decline in GSI coincides with onset of the summer oceanographic regime. Along the east coast of southern Africa, the onset of spring (October to March) bring changes to the temperature regime and most notably rainfall, increasing freshwater inflow and nutrient richness. For the entire study period, the average GSI for males (13.69) was significantly higher than that of females (10.08) (t -test, $p < 0.05$) (Table 3.3). Although the male GSI values were still higher, a statistically significant difference was not observed during the spawning season. For the months outside of the spawning season, the average GSI for females (5.94) was significantly higher than for that of males (3.94) (t -test, $p < 0.05$).

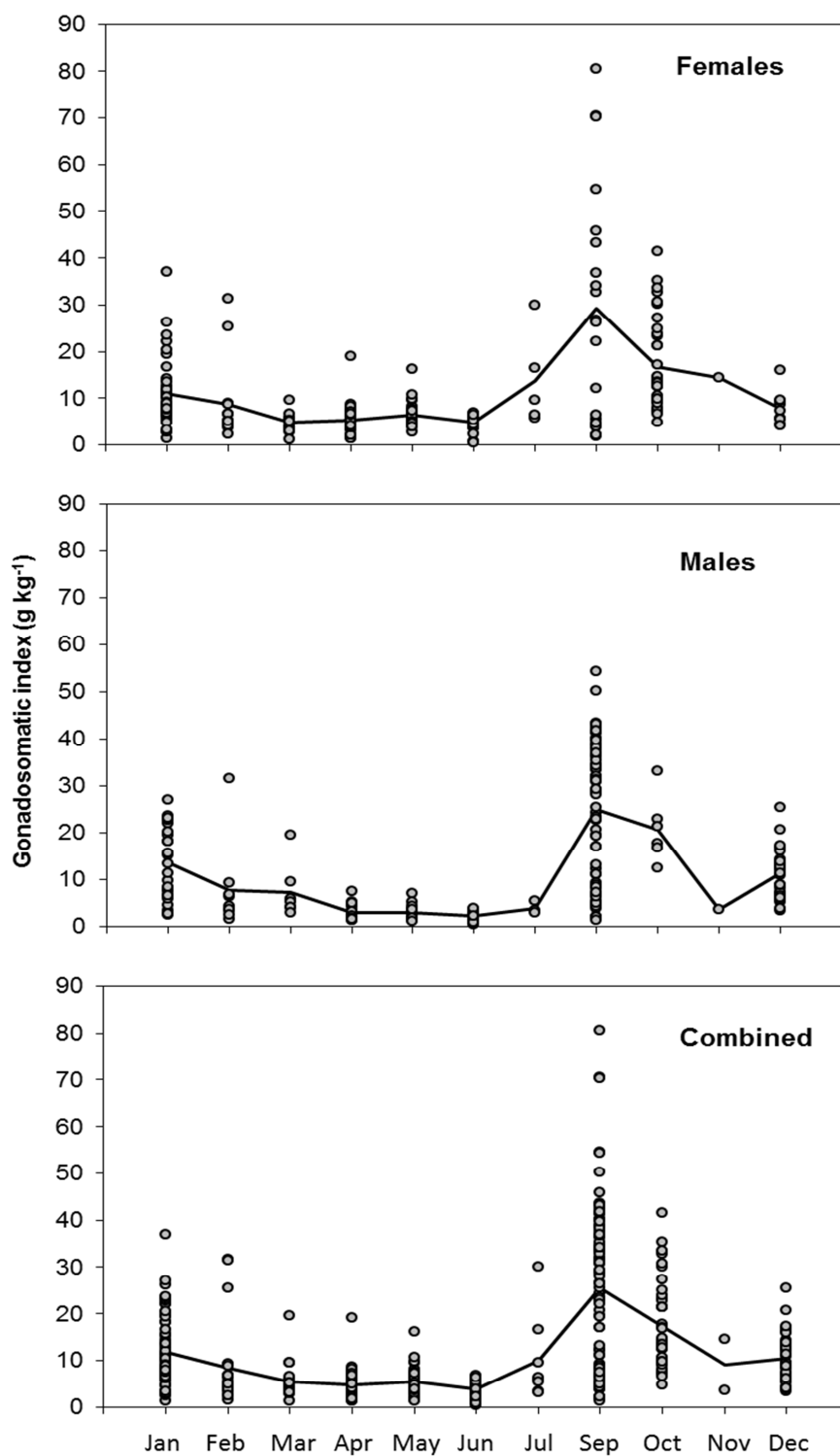


Figure 3.3: Individual gonadosomatic indices (GSI) of *Scomberomorus commerson* for female, male and combined sexes from southern Mozambique and KwaZulu-Natal (no samples collected during August).

Table 3.3: Average gonadosomatic indices calculated for female and male *Scomberomorus commerson* sampled from southern Mozambique and KwaZulu-Natal and *p*-values from *t*-tests conducted for the average GSI between males and females during different periods.

	Average GSI \pm S.D.		<i>p</i> - value
	Females	Males	
All months	10.08 \pm 11.13	13.69 \pm 12.96	0.0018
During spawning season	15.85 \pm 14.71	18.96 \pm 13.01	0.091
Outside spawning season	5.94 \pm 4.15	3.94 \pm 4.42	0.0016

3.3.4 Histological validation of macroscopic stages

Unfortunately, a number of issues were encountered, particularly with female tissues during the processing of histological samples. Due to the lengthy storage of samples, tissues were extremely brittle. This resulted in the tissues not readily absorbing the paraffin wax during preparation. This caused the tissues to crumble during the sectioning and/or staining process, ultimately resulting in either, sections not setting or collapsed cells on the slides. Selected microscopic stages are displayed in Figure 3.4 and 3.5 and described in Table 3.1 and 3.2.

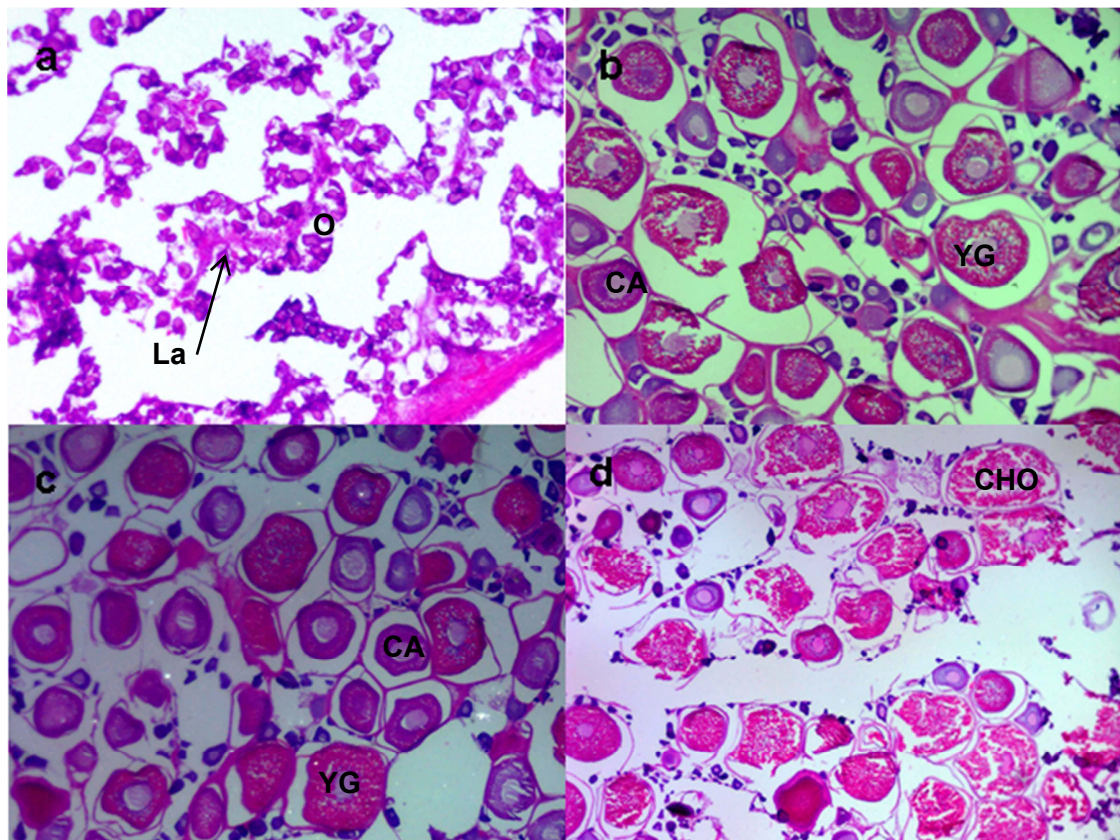


Figure 3.4: Transverse sections through ovaries of *Scomberomorus commerson* illustrating the microscopic appearance of macroscopic stages II, IV, and VI. (a) Inactive/immature (stage II) with small oocytes (O) containing basophilic cytoplasm with no vacuoles (La: lamellae); (b and c) developed (stage IV) ovary containing many cortical alveoli (CA), yolk globules (YG) abundant replacing cytoplasm; (d) Spent (stage VI) ovary dominated by collapsed hydrated oocytes (CHO).

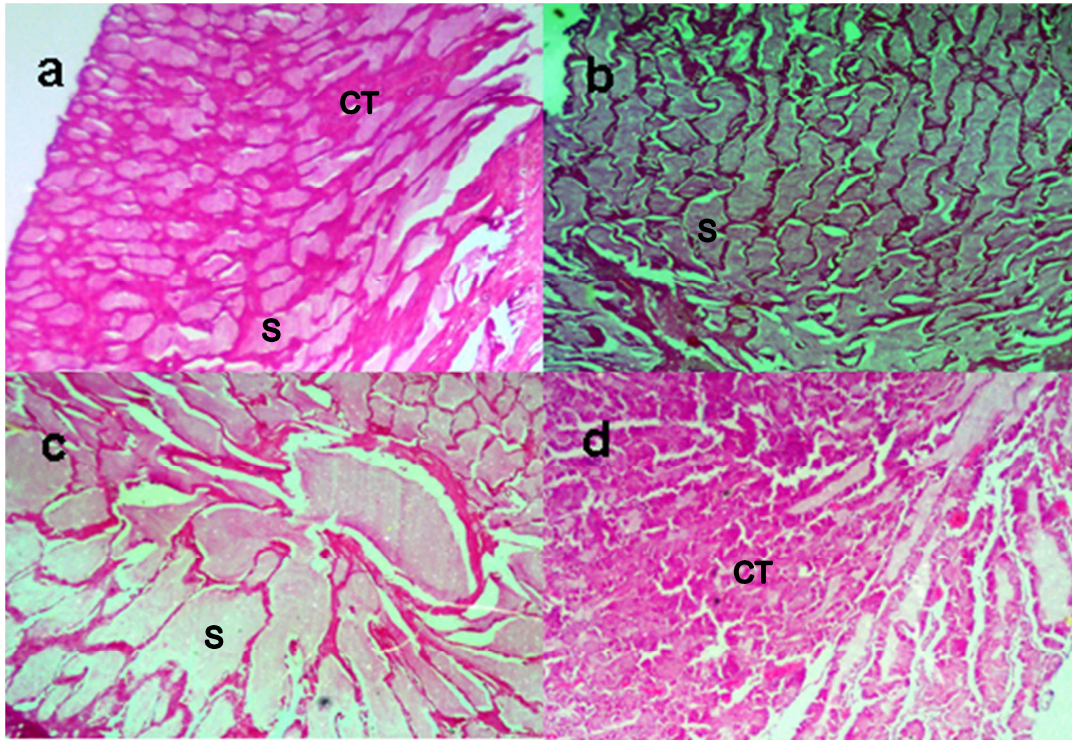


Figure 3.5: Transverse sections through the testes of *Scomberomorus commerson* illustrating the microscopic appearance of macroscopic stages II, III, IV and VI. Late immature/inactive (stage II-stage III) testis with large portions of connective tissue (CT) and pockets of sperm (S); Developing (stage III) testes with increased sperm present; Developed (stage IV) testes with an abundance of sperm in central and outer portion of testes; and Spent (stage VI) testes containing little sperm and prominent connective tissue.

3.3.5 Size and age at first maturity

The logistic ogive fitted to the observed proportion of mature fish versus fork length indicated differences in the length at 50% maturity between male and female *S. commerson* (Table 3.4; Figure 3.6). Male *S. commerson* matured at a significantly smaller length (65.1cm) compared to females (82.3cm) (LRT, $p < 0.05$). When the sexes were combined, the length at 50% maturity was calculated as 67.7cm. A transformation of length at maturity into age at 50% maturity using the empirical growth equations (Chapter 4) indicated that female fish (1.5 years) matured later than males (0.6 years).

Table 3.4: Parameters of the logistic ogive indicating size at 50% maturity of *Scomberomorus commerson* calculated for females, males and combined sexes in KwaZulu-Natal and southern Mozambique.

	Females		Males		Combined sexes	
	L50	δ	L50	δ	L50	δ
Best fit parameter	82.33	7.09	65.12	4.83	67.73	9.01
Mean	82.41	6.96	65.09	4.70	67.62	9.06
Std dev	2.38	1.63	1.52	1.30	1.91	1.68
CV%	2.88	23.40	2.34	27.61	2.83	18.53
UCI	78.27	4.17	61.93	1.10	63.79	6.10
LCI	86.59	10.03	68.04	6.80	71.18	12.58

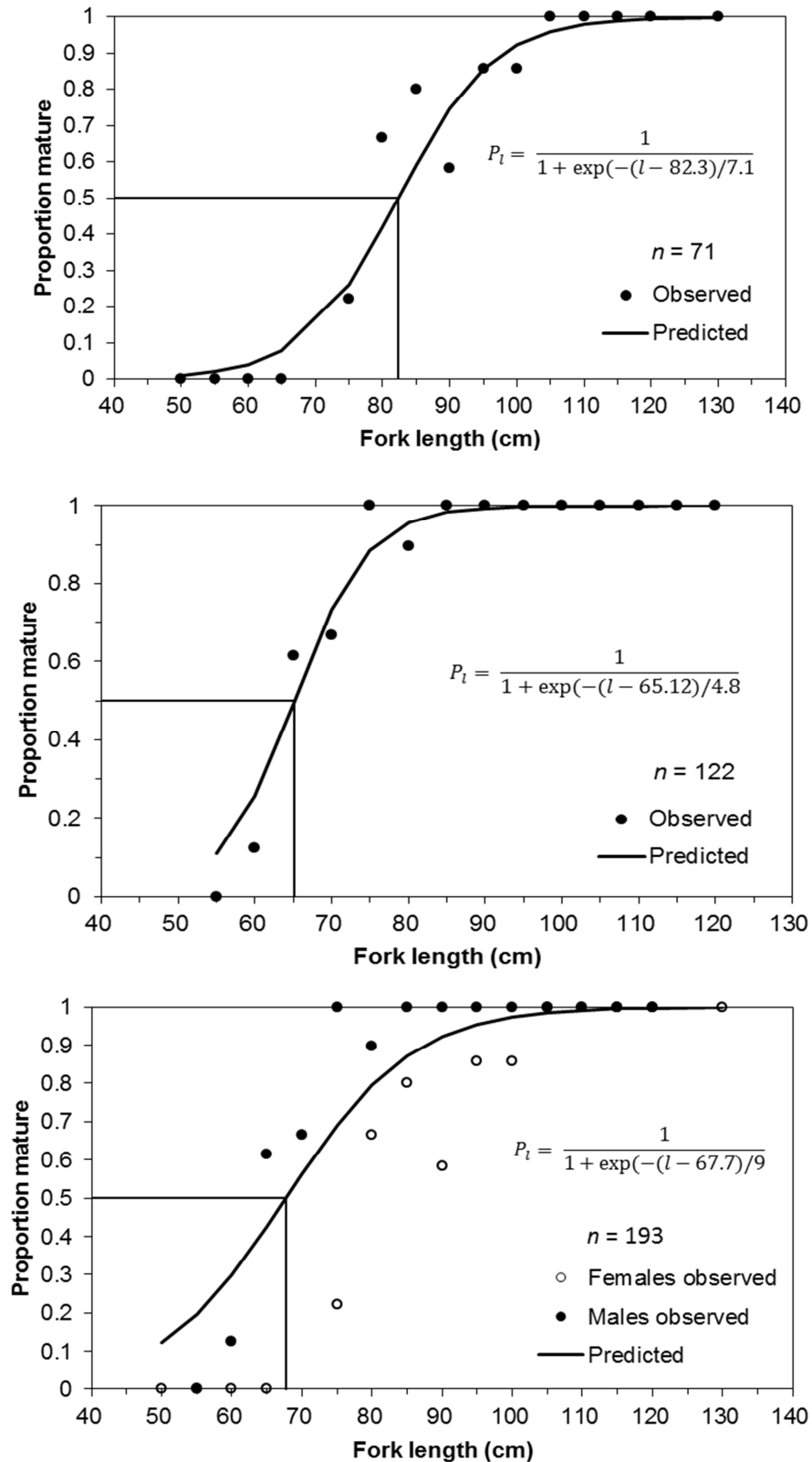


Figure 3.6: Logistic ogives fitted to the observed proportion of mature individuals in 5cm length classes for *Scomberomorus commerson* females (top), males (middle) and combined sexes (bottom) in southern Mozambique and KwaZulu-Natal.

3.3.6 Length composition and sex ratio

The length frequency distribution for *S. commerson* sampled off KZN and MOZ (combined sexes including all fish measured in the ORI Tagging Project) displays multiple modal peaks throughout the distribution (Figure 3.7). The main peak occurred at 90cm FL.

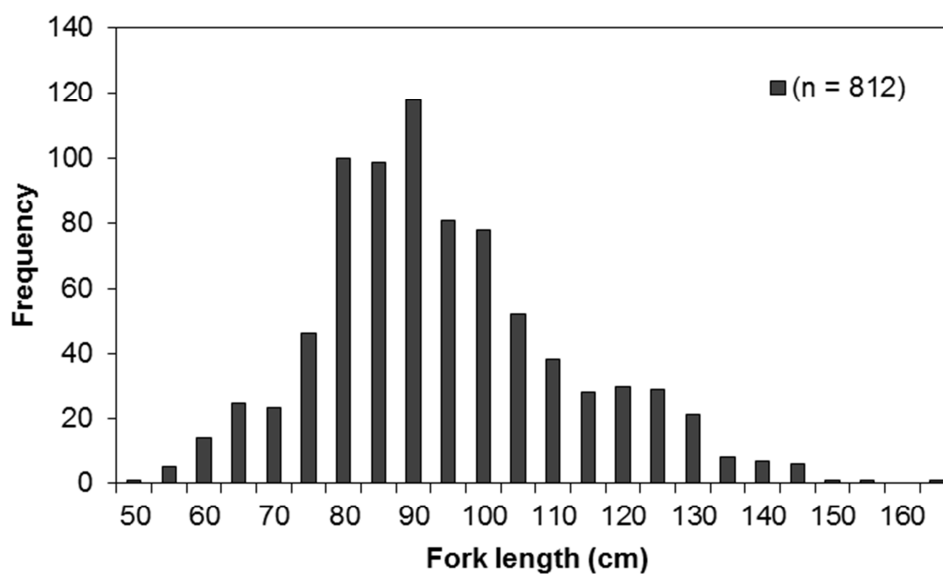


Figure 3.7: Length frequency distribution of *Scomberomorus commerson* for combined sexes sampled within KwaZulu-Natal and southern Mozambique between January 2005 and March 2011.

Length frequencies of *S. commerson* samples from KZN and MOZ were significantly different (χ^2 test, d.f. =17, $\chi^2=73.81$, $p<0.05$). There were a higher proportion of smaller (50 to 90cm) and larger (120 to 170cm) fish along the KZN coast, while a greater proportion of intermediate sized fish (90 to 115cm) were captured along the MOZ coast (Figure 3.8).

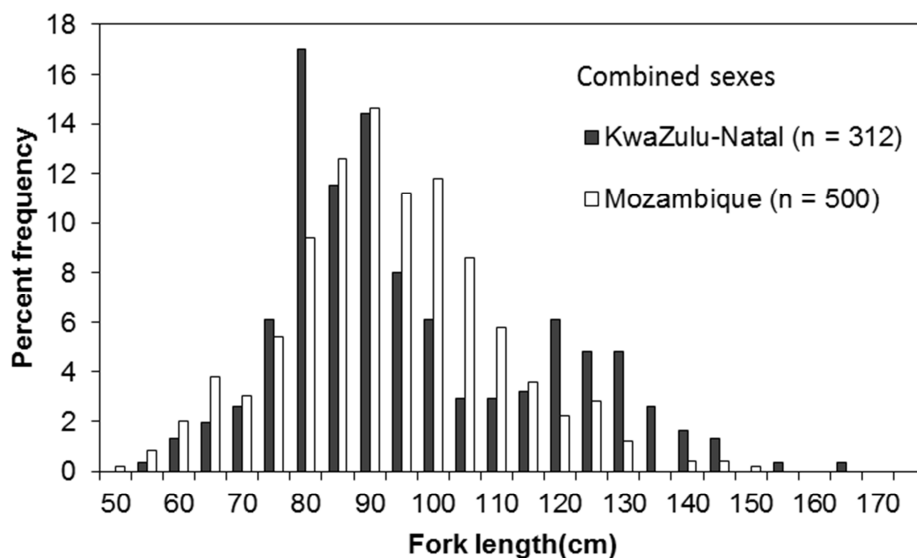


Figure 3.8: Comparative length frequency distributions for *Scomberomorus commerson* captured in KwaZulu-Natal (April 2011 to March 2012) and southern Mozambique (January 2005 to October 2011).

The length frequency distribution within KZN and MOZ according to sex displayed a bimodal distribution for both males and females with modal lengths of 90cm (120-130cm) for females and 80cm (120cm) for males (Figure 3.9). The distribution of sizes among males and females were significantly different (χ^2 test, d.f. =14, $\chi^2=29.11$, $p<0.05$). This was particularly evident in the larger length classes where females were dominant.

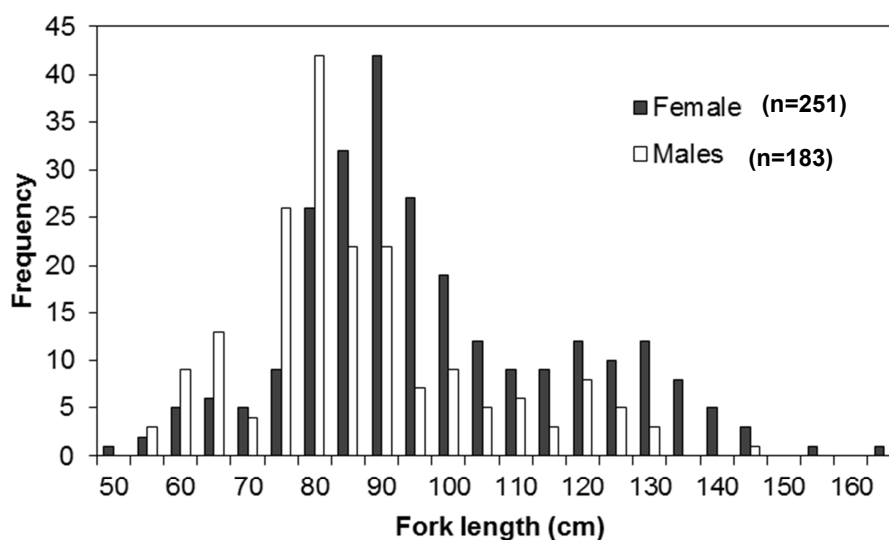


Figure 3.9: Length frequency distributions for *Scomberomorus commerson* captured along the KwaZulu-Natal and southern Mozambique coast between April 2011 and March 2012.

In total, 183 males and 251 females were included in the analysis providing a sex ratio (M: F=1:1.37) which was significantly different from 1 (χ^2 test with Yates correction, d.f. =1, $\chi^2=13.53$, $p<0.05$). The M:F sex ratio was calculated as 1:1.69 (117 males and 198 females) in KZN respectively, differing significantly from a 1:1 ratio ($\chi^2=5.26$, $p<0.05$ and d.f.=1, $\chi^2=10.07$, $p<0.05$). However, there were a greater number of males relative to females in the smaller length classes (< 85cm FL). The number of females relative to males increased with increasing fish size (Figure 3.10).

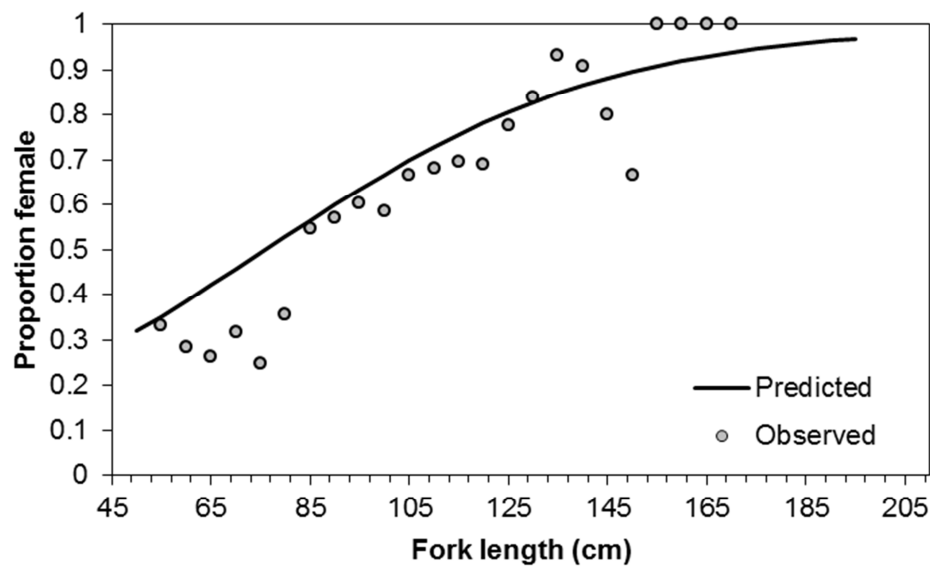


Figure 3.10: Binary regression model used to predict the probability of *S. commerson* being female based on fork length (cm) in KwaZulu-Natal and southern Mozambique.

The majority of fish sampled in KZN and MOZ were less than four years old (Figure 3.11). The age frequencies of male and female *S. commerson* followed a similar distribution up to nine years of age. Peaks for both males and females occurred at two years. Female *S. commerson* continued to occur in samples up to 14 years of age, while only a solitary male was captured above nine years of age.

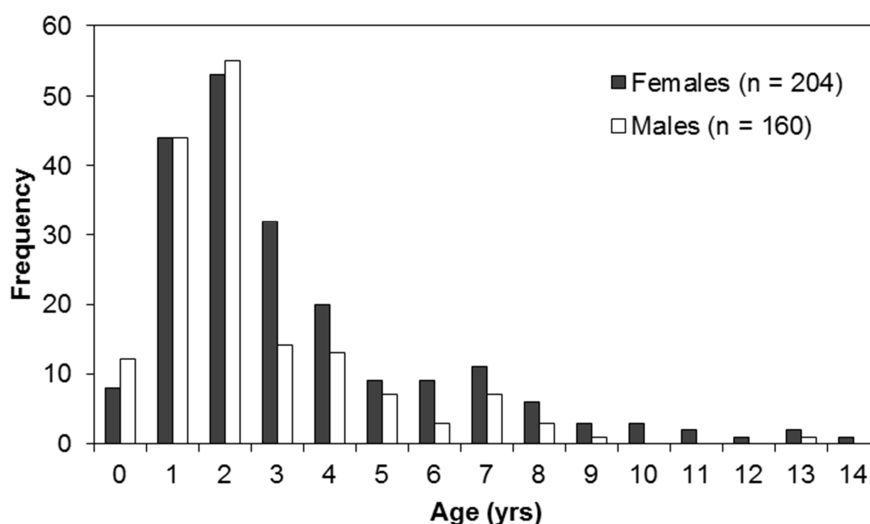


Figure 3.11: Age frequency distributions for *Scomberomorus commerson* captured in KwaZulu-Natal and southern Mozambique between April 2011 and March 2012.

3.4. Discussion

3.4.1 Spawning

Spawning patterns are useful population characteristics that can assist in defining the stock structure of a species. Genetic isolation of stocks must involve the spawning stage in order to restrict gene flow to a degree that effectively isolates population units (Begg, 1998). Estimates of reproductive biological characteristics, including knowledge of the area and timing of spawning can provide information on intraspecific variation in life-history traits that can be used indirectly to discriminate separate fish stocks (Schaefer, 1987; Begg, 1998).

The results of this study indicated that the principal spawning area for *S. commerson* is within MOZ waters. Spawning occurs over a protracted time period from September to January (spring-summer), with marginal spawning occurring in the very north of KZN in late summer. These results agree with those of Govender (1992), who postulated that *S. commerson* are likely to spawn north of KZN, most probably in Mozambique. This is supported by Beckley and Leis (2000), who reported only a single *S. commerson* larva captured south of the Tugela River during surveys off the east coast of South Africa. Additionally, Harris *et al.* (1999) recorded only 12 *Scomberomorus* sp. larvae during monthly sampling while investigating the larval fish assemblage in the nearshore waters off the St Lucia estuary in northern KZN. Finally,

no mention is made of any *S. commerson* eggs and larvae being identified in larval surveys undertaken off Park Rynie on the south coast of KZN between 1987 and 2012 (Connell, 2012). The spring-summer spawning seasonality observed in this study is similar to that of *S. commerson* along the east (McPherson, 1992) and west coast (Mackie *et al.*, 2005) of Australia.

Jenkins *et al.* (1985) indicates that the presence of small *S. commerson* larvae in the middle and inner lagoon waters of the shelf waters of the Great Barrier Reef indicates the occurrence of spawning in this region. He further postulates that juvenile *S. commerson* occupy coastal-estuarine habitats through directed movement by the juvenile stage rather than through passive transport of eggs and larvae.

Govender (1992) estimated a protracted although slightly shorter spawning season in KZN and MOZ, occurring later in the season from November to March. His results may have been influenced by a low sample size of fish in MOZ. Therefore his conclusions were based on the timing of post-spawning fish returning to KZN, and less on the capture of spawning fish in MOZ. This is consistent with the results of the current study in which marginal spawning and post-spawning fish were sampled returning to Maputaland between November and February. A similar pattern was observed along the east (McPherson, 1993) and west coast of Australia (Mackie *et al.*, 2005), where spawning of *S. commerson* occurred earlier in the northern regions compared to those sampled further south.

Water temperature may influence spawning in fish by affecting gametogenesis, gonad atresia, and spawning behaviour (Lam, 1983). Mackie *et al.* (2005) attributed *S. commerson* spawning to be triggered as a result of increasing water temperatures. Latitudinal differences in temperatures may account for earlier spawning in northern waters. As in the case of the current study, hardly any spawning fish were sampled in the most southerly regions along the east and west coasts of Australia (McPherson, 1993; Mackie *et al.*, 2005). This is despite the range in water temperatures overlapping with those in which spawning occurs further north. Marginal spawning of *S. commerson* on the east coast of Australia occurs at similar latitudes to the northern parts of the West Coast region of Australia (Mackie *et al.*, 2005). Anecdotal evidence suggests that spawning along these more southerly regions may be restricted in some years (Mackie *et al.*, 2005). This indicates that temperature along with other potential factors may play a role in the extent of the spawning area of *S. commerson* on an annual basis.

As previously discussed, high rainfall and the input of freshwater and associated nutrients into the marine environment off the coast of MOZ may provide good conditions for spawning and larval survival (Lamberth *et al.*, 2009). Species of dietary importance to *S. commerson* such as *Thryssa vitirostris* move towards the coast and estuaries at the onset of the rainy season or summer, from October to December, with juveniles remaining there for some time (Mualeque and Santos, 2011). As Maputaland falls into the same biogeographic region (Sink *et al.*, 2005) as southern MOZ (i.e. the Delagoa Bioregion), it is possible that high rainfall and increased freshwater inflow events may play a role in fish spawning further south during certain years. These factors may explain the presence of some spawning fish in northern KZN in the present study, compared to only post-spawning fish being sampled in the region by Govender (1992).

A final factor that must be considered is the potential for error in the macroscopic stages assigned to fish as well as differences in the actual macroscopic staging keys used between different studies. Error or inconsistencies in the assignment of macroscopic stages to fish may lead to fundamentally different observations of patterns in reproductive behaviour between different studies.

The strong seasonality in the fishery of KZN (most fish are caught between January and July) combined with the presence of spawning fish in MOZ and Maputaland during September to January supports the idea of a return migration out of KZN waters during the reproductive season. This is consistent with Govender (1992) who postulated that *S. commerson* migrate north to MOZ to spawn before returning back into KZN waters to feed. This migration pattern is partly supported by tag and release data discussed in Chapter 4 but few recaptures were made of KZN fish heading north back into MOZ waters. Similar migrations have been postulated for a congener, namely *S. plurilineatus* in South Africa (Chale-matsau *et al.*, 1999). Longshore migrations are known to occur along the east and west coasts of Australia, with adults accumulating in large numbers around several reefs just prior to spawning in the spring (Welsh *et al.*, 2002).

A single spawning area for *S. commerson* (ie. MOZ) may be indicative of a stock that is maintained by a discrete spawning population (Begg *et al.* 1997) and supports the theory of a single MOZ and KZN population. A more intensive sampling regime at key sites within MOZ is needed to strengthen the results of this study in terms of the

exact timing and area of spawning of *S. commerson*. Spawning of *S. commerson* may be further validated by conducting egg and larval surveys along specific areas of the MOZ coastline. Potential survey areas would be identifiable through the results of the current study combined with previous larval work that has been undertaken along the east coast of Australia and KZN (Jenkins *et al.*, 1985; Beckley and Leis, 2000).

3.4.2 Length at maturity

The combined sexes of *S. commerson* were estimated to mature just below 70cm FL off the coast of MOZ and KZN. This was slightly smaller but still comparable to that of McPherson (1993) who estimated a length at maturity of along the north and east coast of Australia between 79 and 82cm FL. *S. commerson* has been found to mature between 70 and 80cm FL off Madagascar, Papua New Guinea and Fiji (Colette and Russo, 1984). Female *S. commerson* were sexually mature at 82.3cm FL, 30% larger than that of males that matured at 65.1cm FL. These lengths at 50% maturity corresponded to fish within their first to second year of life. This is again consistent with the results of Mackie *et al.* (2005) who estimated that males differentiate and reach sexual maturity younger and at a smaller body size (62.8cm FL) compared to females (80.9cm FL). Grandcourt *et al.* (2005) estimated the mean size at first sexual maturity as 72.8cm FL for males and 86.3cm FL for females in the southern Arabian Gulf. However, these results differ to Claereboudt *et al.* (2005) who estimated a larger size at first maturity for males (84.7cm FL) compared to females (80.4cm FL) in Oman.

Govender (1992) estimated a larger size at spawning of 70.5cm FL for males and 109.6cm FL for females off the coast of KZN. Govender (1992) conceded that a lack of reproductively active fish resulted in a poor model fit to the observed data, particularly for the males. He attempted to distinguish between immature and resting fish within his macroscopic staging key. It is relatively straight forward to differentiate between these two stages in larger fish that have spawned over a number of years. However, it is almost impossible to distinguish the difference between mature resting and immature *S. commerson* within the first two years of their life (Mackie and Lewis, 2001; pers. obs.). The resultant characterization of mature resting fish as immature will incorrectly lead to a larger length at maturity. It is for this reason that only reproductively active fish sampled during the spawning season were used to calculate the length at 50% maturity, thereby justifying the methods used. Contrary to this explanation, the smaller size at maturity estimated in the current study compared

to Govender (1992) may be due to progressive changes in reproductive biology induced by intense fishing pressure (Claereboudt, 2005). In the Arabian Sea where *S. commerson* is largely targeted through the use of gillnets, 40% of the fishery is supported by immature fish caught before their first spawning whereas along the Gulf of Oman, 25% of the fish caught were immature (Claereboudt, 2005). Fortunately this is not the case for the line-fishery within KZN and MOZ, which selects for larger, faster-growing fish. However, data for the MOZ gillnet fishery remained largely unavailable and the scope of this project prevented the large-scale collection of such data for spatial and temporal quantification of the fishery. Baloi *et al.* (2000) reported that Scombridae made up 16% of the beach seine fishery, 10.3% of the surface gill-net fishery and 22% of the bottom gill-net fishery compared to 10% for the linefishery by weight in Nampula Province, Mozambique during 1999. It is therefore likely that the gillnet fishery in MOZ places intense fishing pressure on small (<60cm FL) individuals. Gillnet fisheries off the coast of Sri Lanka, India and Iran capture significant quantities of juvenile *S. commerson* (9 to 45cm FL) in the late summer (Siddeek, 1996). This kind of fishing pressure could progressively push the population towards maturation at smaller lengths and increase the risk of recruitment failures (Claereboudt, 2005). Whilst the values estimated in this study compare favourably with those of other regions, more comprehensive monthly sampling in MOZ and histological diagnosis of the maturity development stage would have improved the estimates.

3.4.3 Sex ratios

The proportion of female *S. commerson* tended to increase with length over 75cm FL (see Figures 3.7 and 3.8). The dominance of females in the catch may either be a result of differences in the actual sex ratio in the fish stock, or from a bias introduced in the samples by the fishing methods used. Unequal sex ratios in the larger size classes are likely to be caused by differential rates of growth and mortality (Schaefer, 1987). Similar results have been observed by Mackie *et al.* (2005) and McPherson (1993) along the east and west coasts of Australia. Ageing data indicates that female *S. commerson* grow to a larger maximum size than males (see Chapter 5). The dominance of females in the size classes above the length at maturity may therefore be due to their faster growth and attaining a larger body size. Claereboudt *et al.* (2005) found that significantly more female *S. commerson* were caught in two regions along the coast of Oman and suggested this to be a result of the methods used by traditional fishermen. Along the Gulf of Oman, a combination of hook and line and

drift gill nets are used, with line-fishing favouring larger females. Along the Arabian Sea, the majority of landings are through drift gill nets which are not sex selective if selecting for smaller fish. Additionally, Lester *et al.* (2001) indicated that there is some evidence to suggest that males and females migrate separately off the west coast of Australia. Grandcourt *et al.* (2005) concluded that if sex-specific migrations occur off the southern Arabian Gulf, this sex bias may be explained by the differential targeting of females by the fishery. This indicates the possibility that the strong female bias off KZN and southern MOZ is a reflection of line-fishing methods selecting for larger, faster-growing females.

Although length-based sex ratios indicated the possible occurrence of sex change, no evidence of hermaphroditism was observed in any histological gonad section, supporting the findings of gonochorism in all *Scomberomorus* species (Devaraj, 1983; McPherson, 1993; Begg, 1998; Claereboudt, 2005; Grandcourt *et al.*, 2005; Mackie *et al.*, 2005).

3.4.4 Length composition

S. commerson frequently occur in large shoals consisting of similar-sized fish (Begg *et al.*, 2006). The selectivity of fishing methods and gears, and the targeting of aggregations has been known to create bias in *S. commerson* length frequency data (Tobin and Mapleston, 2004; Ballagh *et al.*, 2006). The multiple modal peaks observed in the length frequency distribution for the combined region and sexes may be indicative of the rapid early growth rates displayed by *S. commerson* combined with a short peak in reproductive output and consequent low variation in the length at recruitment into the fishery (Claereboudt *et al.*, 2005; Devaraj, 1981; Dudley *et al.*, 1992; McPherson, 1992). Length frequency distribution of *S. commerson* displayed at least four cohorts off the east coast of Australia (McPherson, 1992), while those off Oman showed a minimum of three distinct cohorts (Dudley *et al.*, 1992). Govender (1992) however only observed a single modal peak for *S. commerson* sampled off the KZN and MOZ peaking at 90cm FL. Govender (1992) attributed this to potential sources of variation in recruitment as a result of the protracted spawning season and variation in individual growth rates.

The difference in length frequency distribution between fish caught along the KZN and MOZ coast may be explained by a combination of fishery-dependent sampling biases and biological characteristics such as recruitment, growth and mortality. The

length frequency distribution of *S. commerson* captured off KZN indicates that on average recreational fishers harvest small, young fish of 75-100cm FL (≤ 3 years). This is consistent with those sampled by Govender (1992) in the same area from 1972 to 1991 from both commercial and recreational catches. Contrary to this, the fish captured off MOZ represent a much broader length frequency distribution with a much greater proportion caught in the larger length classes (90-110cm FL). Although the recreational harvest in KZN was dominated by smaller younger fish, a small percentage of fishers selectively target very large fish, greater than 120cm FL (≥ 7 years). This generally takes place on the lower KZN south coast towards the end of the “cuda season” from March to June.

Tobin and Mapleston (2005) noted differences in the length frequencies obtained for catches of *S. commerson* between recreational and commercial fishers off the east coast of Australia. Recreational fishers, on average, harvested smaller and younger *S. commerson* compared to their commercial fisher counterparts. Likewise, a small percentage of recreational fishers selectively targeted very large fish. This was attributed to the selective nature of the commercial fishery with their fishing gears tending to select against very large fish. Additionally, the commercial fishers actively move away from schools of small fish due to poor marketability and economic returns (Tobin and Mapleston, 2005). The differences in length distribution between KZN and MOZ can possibly be explained by differences in fishing gear and behaviour of fishers in these two regions. The peak in large fish captured off KZN is likely due to fishery dependent bias associated with samples attained at fishing competitions in CSKZN. Within these competitions, fishers often go to great lengths to modify their gears and behaviours in order to maximize their chances of landing large fish. Contrary to this, the majority of fish sampled off MOZ were obtained from recreational charter fishermen and through the ORI tagging database. These local resort-based MOZ fishers are reliant on the continued presence of game fish within the region for their tourism (Guy Ferguson, pers. comm. Mozambique fishing guide, Nyathi Beach Lodge). As a result, the sustainable utilization of the game-fish resource on a whole is encouraged. As in the case with the commercial fishers off the east coast of Australia, these fishers tend to largely either target larger *S. commerson* specimens for tag and release, or they target other larger more prestigious game and billfish species such as sailfish (*Istiophorus platypterus*) and the black marlin (*Makaira indica*).

A second more plausible factor that may have influenced the observed differences in length distribution between the two regions is that length samples were obtained from MOZ over a seven year time period, whereas sampling was only undertaken within KZN over a single year. High rainfall and the consequent input of freshwater into the marine environment off MOZ, where *S. commerson* breeds, will provide good conditions for spawning and larval survival (Lamberth *et al.*, 2009). This may result in the survival of strong cohorts during years of improved environmental conditions and consequent good catches when these fish recruit into the fishery off KZN. Likewise, drought and associated poor conditions for recruitment in *S. commerson* off MOZ a few years ago may have resulted in poor catches of *S. commerson* off KZN during the year of sampling (see Chapter 2 on trends in catches)

3.4.5 Conclusions

The results of this study indicate that the principal spawning area for *S. commerson* sampled in this study is within southern MOZ waters occurring over a protracted time period from September to January (spring-summer). However, it is possible that certain conditions such as increased water temperature, high rainfall and increased freshwater inflow may play a role in fish spawning further south during certain years. The common occurrence of post-spawning fish off Maputaland towards the end of the spawning season indicates the occurrence of a post-spawning feeding migration into KZN waters supporting the theory of a single southern MOZ and KZN population. Male *S. commerson* spawn at a smaller size compared to females. Intense fishing pressure on small individuals by the gill net fishery in MOZ could possibly be pushing the population towards maturation at smaller lengths increasing the risk of recruitment failures. The overall length frequency distribution of *S. commerson* displays multiple modes characterizing the species' rapid growth rate and the existence of strong cohorts within the population. The peak mode in the overall length frequency distribution occurs at 90cm FL and an age of two years. There is a significant difference in the sizes of the sexes with females attaining a larger size compared to males. A strong female bias is observed in the catch off KZN and MOZ which may be a reflection of line-fishing methods selecting for larger faster growing females. There is a significant difference in the length frequency distribution of *S. commerson* captured off KZN compared to MOZ. The length frequency of *S. commerson* captured off KZN is bimodal with smaller and larger fish captured compared to the intermediate-sized unimodal length distribution observed off MOZ. This may be explained by a number of factors including sampling bias between the

two regions; different targeting strategies and gear used; or variations in year class strength due to fluctuations in recruitment from previous years.

Chapter 4

Age and Growth

4.1 Introduction

The growth of a species is one of the most studied of all parameters used to describe the life-history of exploited fish (Ballagh *et al.*, 2011). In South Africa, the assessment of the status of many line-fishery species has been based on single species per-recruit models (Govender, 1994, Griffiths *et al.* 1999). Such age-structured techniques used for assessing the state of exploited fish stocks rely on the availability of reliable age composition data. These data allow for the determination of parameters such as growth rate, mortality and longevity, parameters that are beneficial to population modelling, stock assessments, and management of the harvesting of exploited species.

Generally two types of data are used in studies of growth in fishes. The most common of these consist of estimates and measurements of age, size and weight (Haddon, 2001). This is largely because of the relative cheapness and ease of collection. The other is tag-recapture data, which includes the initial length at tagging, the length at recapture and the dates of tagging and recapture. While different methods are required for fitting growth models to these two distinct types of data, neither are without difficulties (Attwood and Swart, 2000; Haddon, 2001). The collection of tag-recapture information is expensive and time-consuming and the growth increment of recovered fish may be biased due to the effect of the tagging procedure or by the tag itself on subsequent growth (McFarlane and Beamish, 1990; Attwood and Swart, 2000). Additionally, measurement error is problematic for tag-recapture data as it depends on the difference of two measurements, both of which are often not executed by trained personnel. However tag-recapture data provide an accurate measure of individual fish growth over the time span between tagging and recapture, which does not require knowledge of a fish's actual age (Baker *et al.*, 1991). Estimates based on otolith ring counts may also be inaccurate because of the difficulty of interpreting rings (Campana, 2001). This is particularly the case for tropical fish species where growth is more uniform throughout the year (Haddon, 2001). In temperate species, there tends to be a slowing of growth in the less

productive months. Many body parts can be affected by this differential growth and these effects can be used to age the fish (Haddon, 2001). Growth rings can be found in calcified tissues such as scales, vertebrae, fin-ray spines, but particularly in the various ear bones known as otoliths. Most commonly, age estimates and consequent growth parameters for fish have been obtained from counting these seasonally deposited opaque and hyaline bands or growth rings that are laid down in these tissues (Campana and Therrold, 2001).

The selection of models or curves for description of the growth of fish, has posed many problems to biologists over the years (Baker *et al.*, 1991). There are several historical growth models that describe differing rates of growth including the von Bertalanffy, Gompertz, Richards, Schnute, logistic, linear, exponential (see Ricker (1979) for a review). However, the most appropriate model and the best method for estimating model parameters are often selected subjectively (Baker *et al.*, 1991).

When obtaining age estimates using otoliths, it is imperative that the rate or periodicity of band deposition is known or can be validated (Campana, 2001). Indirect techniques for the validation of hard structure banding include marginal zone analysis (MZA), while tag-recapture data have been used less frequently such as in the study by Govender (1999) on the growth of *Pomatomus saltatrix*. The examination of the marginal zone of otoliths as a validation method has frequently been used in South African studies, but has not always proven conclusive (eg. Govender, 1994 and Chale-Matsau *et al.*, 1999). Similarly, validation using tag recapture data is based on the assumption that a growth curve derived from size-at-age data (assuming an arbitrary periodicity) can reasonably describe the observed growth increment of tagged individuals between the times of tagging and recapture. This would indicate that the growth parameter and periodicity assumed for the seasonal bands must be valid (Govender, 1999).

Growth rates for fish populations can provide an indication of, and influence the sustainable catch weight that can be taken from a fish stock (King, 1995). Faster-growing fish are able to mature, reproduce and die earlier (Miller and Kendall, 2009; Fennessy, 2000). Furthermore, those reaching a larger size earlier are often able to produce and carry more and/or larger eggs, increasing the chances of larval survival (King, 1995). Faster growing fish can therefore withstand greater harvesting pressures than slow growing fish.

Published estimates of growth parameters for *Scomberomorus commerson* have been undertaken using length-frequency analysis and otolith ageing. Several studies have been carried out on the age and growth of *S. commerson* in the Arabian Gulf (Grandcourt *et al.*, 2005, Shojaei *et al.*, 2007), Oman (Al-hosni and Sideek, 1999; McIlwain *et al.*, 2005) and Australia (McPherson, 1992; Lewis and Mackie, 2002; Ballagh *et al.*, 2006; Ballagh *et al.*, 2011; Newman *et al.*, 2012). Mean length-at-age and demographic parameter estimates differed to varying degrees between geographic locations. The different estimates of demographic parameters among studies may be largely due to the method of age estimation (e.g. length frequency - Al-hosni and Sideek, 1999; Shojaei *et al.*, 2007; whole otoliths – Devaraj, 1981; McPherson, 1992; sectioned otoliths – Govender, 1994; Grandcourt *et al.*, 2005; McIlwain *et al.*, 2005; Newman *et al.*, 2012; otolith back-calculations - Ballagh *et al.*, 2006), or errors in interpreting otolith ages as a result of the occurrence of false annuli, or simply that different growth rates occur in different areas.

Despite the variations in estimates of growth between these locations, the results of these growth studies all suggest rapid growth in juveniles. In eastern Australia the peak months for the formation of primary opaque margins occurred between June and August (winter) (McPherson, 1992). The formation of opaque bands over such a short time period validated their use for age determination purposes (i.e. one opaque band deposited annually). In Oman, marginal increment analysis also revealed strong seasonality in the deposition of the opaque zone at the otolith margin from September to February (autumn – winter) (McIlwain *et al.*, 2005).

Despite the importance of *S. commerson* along the east coast of southern Africa as a recreational, artisanal and commercial species, little fisheries research on the species has been undertaken in the region apart from work undertaken by Govender (1994) in KwaZulu-Natal (KZN). Length composition analysis and age estimates based on otolith readings yielded von Bertalanffy growth parameters describing the growth of the species up to a maximum of six years. These growth parameters were based on the assumption that two opaque bands were deposited annually. The growth curves from both length composition analysis and otoliths described rapid growth of young individuals and reasonably predicted the time at liberty for two tagged and recaptured individuals.

Given the migratory nature of *S. commerson* along the eastern coast of southern Africa, a major limitation of the previous study in the region was that the majority of

data were collected from the KZN coast. Additionally, the tag-recapture data used to validate the deposition of growth rings was based on only two individuals from a tag-recapture program with fish that displayed relatively short time at liberty (1 and 2.8 years at liberty).

The primary aim of this chapter is therefore to analyse the patterns of growth for *S. commerson*, both through the assessment and validation of growth rings in whole otoliths and through the analysis of tag-recapture data, from several landing sites off the coast of southern Mozambique (MOZ) and KZN, South Africa. A study examining the age and growth of *S. commerson* over this spatial scale has not previously been attempted in the South West Indian Ocean region. The specific objectives of the chapter are (1) to describe and compare length-length and length-weight relationships for each sex and region; (2) to compare the age structure between male and female *S. commerson* within the study area; (3) to describe the sex-specific growth curves and to construct age-length keys for the region as a whole; and (4) to compare growth rates estimated from tag-recapture data with those predicted from otolith derived data. The growth parameter estimates determined in this chapter will be used in the following chapter dealing with the estimation of mortality and to undertake a per-recruit stock assessment of *S. commerson* within the study area.

4.2 Materials and Methods

4.2.1 Sampling

Scomberomorus commerson samples were collected in KZN and MOZ between April 2011 and March 2012. Fish were captured on rod and line by recreational anglers and research staff throughout the study area. Additional fish were purchased from artisanal line fishers in MOZ. Each fish sampled was weighed, measured and sexed (juvenile, male, female) and the sagittal otoliths removed and stored as described in Chapter 1.

Mark-recapture data for *S. commerson* were obtained from the ORI Tagging Project. Length data from 29 recaptured fish could be verified and were used in the analysis. Unfortunately, being a voluntary tagging program, many anglers forget to measure the fish they tag whilst others simply guess the size. Those that do measure the length of the fish often fail to indicate the type of length measurement recorded (i.e. FL or TL). In some cases, although length measurements appeared accurate,

negative growth was recorded and consequently these individuals were excluded from the analysis.

4.2.2 Data analysis

Somatic Relationships

The total length-fork length (cm) relationship for *S. commerson* was expressed using a linear regression of the form:

$$FL = mTL + c \quad 4.1$$

Where m and c are the slope and intercept coefficients, respectively. Differences in the fork length-total length relationship between regions as well as between separate sexes for the pooled sample were calculated using a multiple regression at a 95% confidence level. The length/weight relationship between fork length (FL, cm) and weight (Wt, g) was estimated using the power relationship:

$$Wt = aFL^\beta \quad 4.2$$

where a is the intercept (scaling constant) and β is the regression coefficient (slope) of the linear regression which ranges from 2.5 to 3.5 in fishes and when equal to three indicates isometric growth (Pauly, 1984). The parameters a and β were estimated by transforming equation 4.2 into a linear regression by taking logarithms on both sides of the equation, such that:

$$\ln(Wt) = \ln(a) + \beta \ln(FL) \quad 4.3$$

The fit of the model to the data was determined by the coefficient of determination (R^2). Multiple regression tests at a 95% confidence level were used to compare the relationship between transformed fork length and weight among regions and sexes with weight as the dependent variable, length as the independent variable and region or sex as the categorical variable.

Otolith preparation and reading

A pilot study was conducted in order to evaluate the most suitable method for preparing otoliths for ageing. The otolith pairs from a sub-sample of 30 fish were investigated using two methods of preparation; whole otoliths and transverse sectioned otoliths. At least one otolith pair was used in the pilot study for each 5 cm size class of the total sample. This process served multiple purposes. It allowed the readers to become familiar with the variation in appearance and readability of individual otoliths. Secondly, it enabled the determination of seasonal trends in band formation, assisting in otolith interpretation. Finally, it allowed for the statistical comparison of the repeatability of the four methods and to determine if any systematic error could be produced by either method (Lewis and Mackie, 2002).

In order to enhance readability whole otoliths were immersed in water and methyl salicylate separately. While both liquids improved readability there was no noticeable difference between the two and otoliths were subsequently read in distilled water. A further attempt was made to enhance readability of whole otoliths by baking a sub-sample of 30 otoliths in a convection oven at 250°C for 7.5 minutes until they changed to a golden brown colour (Robillard *et al.*, 2009). Both un-baked and baked otoliths from each pair were then examined in distilled water using a dissection microscope under low power (10x magnification) and reflected light on a black background.

For sectioning of otoliths the left otolith from each pair was embedded in clear casting resin and a 0.4mm transverse section was taken through the nucleus using a twin-blade, diamond-edged saw. The sections were mounted on glass slides using DPX mountant and the sample identification number of the fish was written on the slide. The number of opaque zones on the sectioned and whole otoliths was counted on three separate occasions by one reader using a low-powered dissecting microscope under reflected light over a black background for whole otoliths and under transmitted light for sectioned otoliths. An attempt was made to count annuli along the same transect from the nucleus to the outer edge of the otolith. A minimum of two weeks was maintained between each of the three reading sessions. Each otolith was assigned a readability index of one to five with one being unreadable and five being perfectly readable (Table 4.1) (Lewis and Mackie, 2002). The ease of growth zone interpretation was assessed by averaging the readability index across all readings for each method.

Table 4.1: Readability index (RI) categories for *S. commerson*

RI Category	Annuli Readability
1	Unreadable
2	Poor
3	Fair
4	Good
5	Perfectly readable

The precision of each method was established using the index of average percent error (APE) (Beamish and Fournier, 1981) as:

$$100 \left[100 \frac{1}{N} \sum_{j=1}^N \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right] \right] \quad 4.5$$

where N is the number of fish aged, R is the number of times each fish j is aged, X_{ij} is the i th age determination of the j th fish and X_j is the average age calculated for the j th fish.

The method with the lowest APE value, which corresponded to the highest precision or reproducibility of the age readings, was selected for final reading. Two independent readers counted the annual increments separately and without knowledge of the other reading or length data. A third reading was undertaken simultaneously by reader 1 and 2 together. The third reading occurred two weeks after the first and second reading with no reference to the previous readings and without knowledge of the length or weight of the fish. If age estimates did not coincide with the first two readings, the age from the third reading was taken as the final age as this was considered the most accurate. When conducting the third reading if no consensus was reached between the two readers on the number of growth rings, the otolith was rejected. In order to avoid inconsistency when determining the position of the first opaque band, measurements were taken from the otolith nucleus to where the first band was clearly visible through the use of a microscope micrometrer and this was used as a guideline when viewing otoliths that had less well-defined growth zones or juvenile rings (Lewis and Mackie, 2002). An age-bias plot was constructed to provide an age by age measure of deviation between readers. The average percent error (APE) and co-efficient of variance (CV) were calculated to evaluate the precision of the three sets of age readings as above.

Validation – Marginal zone analysis

Marginal zone analysis (MZA) was used to validate the annual deposition of the opaque zone on the otoliths of *S. commerson*. The margin of each otolith was categorized as having one of three appearances ranging from opaque to completely translucent as described in Lewis & Mackie, (2002) and Ballagh *et al* (2011), and modified in Tobin and Mapleston (2004) and Begg *et al.* (2006) (Table 4.2). The percent frequency of each margin zone was plotted against the month of the year to determine the period when the opaque zone was deposited.

Table 4.2: Otolith marginal zone category index for *S. commerson*

MZ Category	Otolith margin appearance
1	Complete and continuous opaque band is formed along the edge of the margin of the otolith with no translucent material beyond the last opaque band
2	Translucent band has started to be laid onto the outer edge comprising 1-50% of previous translucent zone
3	Translucent band has started to be laid onto the outer edge comprising 51-100% of previous translucent zone

Growth model

The von Bertalanffy (1938) growth function (VBGF) is widely regarded as the most suitable for expressing growth of fishes (Hillborn and Walters, 1992; King, 1995; Haddon, 2001). Furthermore, the majority of studies have assumed von Bertalanffy growth in *S. commerson* (McPherson, 1992; Grandcourt *et al.*, 2005; McIlwain *et al.*, 2005; Ballagh *et al.*, 2006; Shojaei *et al.*, 2007; Ballagh *et al.*, 2011). Schnute (1981) presented a generalized growth model that mathematically casts the historical growth models as sub-models. Investigations into the age and growth of *S. commerson* utilizing the Schnute (1981) growth model have been undertaken by Govender (1994) and Newman *et al.* (2012). Candidate models explored in this study for describing the growth of *S. commerson* were the von Bertalanffy growth model (VBGF) and the more versatile growth models of Schnute (1981).

Subsequently, the specialized VBGF curves were fitted to length at age data for individual sexes and the pooled data set. The VBGF curve is described by the following equation:

$$Lt = L_{\infty}(1 - e^{-K[t-t_0]}) \quad 4.6$$

where Lt is the mean length at age t (cm, FL), L_{∞} is the asymptotic or theoretical maximum mean length (cm, FL), K is the growth co-efficient that determines how quickly the maximum is attained, and t_0 is the theoretical age where length is equal to zero (years). The t_0 parameter fixes the position of the curve along the x-axis and can affect the steepness of the curve (Haddon, 2001; Begg *et al.*, 2006). This is an observation error model such that:

$$L_i = \hat{L}_i + \varepsilon_i$$

Where L_i and \hat{L}_i are the observed and predicted lengths of the i th fish in the population, and ε_i is an independent normally distributed error with zero mean and a common variance (Francis, 1995). Model parameters were estimated by minimizing the negative log-likelihood (Kimura, 1980) using standard non-linear optimization methods (Solver, Microsoft Excel, 2010).

The four parameter growth model of Schnute (1981) was also fitted to length at age data:

$$Y_t = \left[Y_1^b + (Y_2^b - Y_1^b) \frac{1 - \exp[-a(t-T_1)]}{1 - \exp[-a(T_2 - T_1)]} \right]^{\frac{1}{b}} \quad 4.7$$

where a and b are estimable parameters relating to growth curvature, T_1 and T_2 are values representing the youngest and oldest sampled ages respectively, and Y_1 and Y_2 are estimable parameters representing the lengths of fish at ages T_1 and T_2 respectively. The traditional von Bertalanffy parameters can be obtained from the parameters of equation 4.7 (Schnute, 1981):

$$L_{\infty} = \frac{\exp(aT_2)Y_2 - \exp(aT_1)Y_1}{\exp(aT_2) - \exp(aT_1)}$$

$$K = a$$

$$t_0 = T_1 + T_2 - \frac{1}{a} \ln \left[\frac{\exp(aT_2)Y_2 - \exp(aT_1)Y_1}{Y_2 - Y_1} \right]$$

The Akaike's Information Criterion (AIC) was calculated for determining which candidate model was the best approximating type of model for describing growth trends:

$$AIC = 2LL + 2p \quad 4.8$$

where LL is the negative log-likelihood and p is the number of parameters. The lowest AIC value identified the best approximating model.

The length-at-age models for the combined and separate sexes were tested for random distribution of the residuals by a simple visual assessment of the residual plot to detect any systematic trends (Butterworth *et al.*, 1989).

Variability of the parameter estimates was determined using a parametric bootstrapping procedure (Efron, 1982) with 1000 iterations and 95% confidence intervals constructed from the bootstrap data using the percentile method. An analysis of residual sum of squares was used to determine whether there were significant differences between the von Bertalanffy growth curves of males and females. The likelihood ratio test (LRT, Kimura, 1980) was used to test for differences in individual VGBF parameters of *S. commerson* between separate sexes. Four juvenile fish that could not be identified as male or female were excluded from the sex specific curves. An age-length key was constructed for the combined sexes in order to convert the length frequency into an age frequency (Haddon, 2001).

Growth parameter estimates from tag-recapture data

The Gulland and Holt (1959) and Fabens (1965) models were used to generate von Bertalanffy growth functions from the tag-recapture data.

Gulland and Holt's (1959) model allows preliminary estimates of the von Bertalanffy parameters L^∞ and K from growth increments (tag-recapture data) and is based on

growth rate declining linearly with length, reaching zero at L^∞ under the von Bertalanffy growth function. Growth rate in cm per year was determined as follows:

$$\frac{dFL}{dt} = a + \beta \overline{FL} \quad 4.9$$

Where: $dFL = FL_{rec} - FL_{rel}$

$$dt = t_{rec} - t_{rel}$$

$$\overline{FL} = \frac{FL_{rec} + FL_{rel}}{2}$$

where, $\frac{dFL}{dt}$ is the growth per year (cm), FL_{rel} is the length at release (cm), FL_{rec} the length at recapture (cm), with t_{rel} and t_{rec} the corresponding dates, and \overline{FL} , the mean of the release and recapture lengths. The growth per year of individual tag-recaptured fish was plotted against the \overline{FL} , and von Bertalanffy growth parameters were estimated from the linear regression as $L^\infty = \frac{-a}{\beta}$ (the value at the x-intercept where $y = 0$) and $K = -\beta$ (slope).

Fabens (1965), formalized the translation of the von Bertalanffy curve into a form that could be used with data obtained from tag-recapture programs (Haddon, 2001). By manipulating the normal von Bertalanffy growth function, Fabens produced:

$$dL = (L^\infty - Lt)(1 - e^{-K(dt)}) \quad 4.10$$

where Lt is the initial length of the fish and dL is the change in length through the period dt . The parameters L^∞ and K are determined by minimizing the square differences between the observed and expected dL for each tag-recapture. A difficulty with this method is that both equations 4.6 and 4.10 relate to the growth of individuals and thus do not predict the average length at age t or the average growth increment for a given initial length and time passed, dt (Haddon, 2001). A major assumption is that these curves can be applied to collections of individuals, ignoring the fact that there will be variation in the growth of individuals. On a residual plot, it is evident that the variability around the residuals declines as dL declines with Lt . When fitting Fabens (1965) model, a weighted least squares approach or a maximum likelihood method that directly estimates the variance is required (Haddon, 2001). Francis (1988a) described a maximum likelihood approach that fitted the model to the data assuming the residuals were normally distributed. He suggested a number

of functional forms used to describe the relationship between residual variance and expected dL . In order to obtain the best possible fit of Fabens' (1965) model, three different formulations for describing this variance were simulated:

- i) an inverse linear relationship between standard deviation and the expected dL :

$$\sigma = v(d\hat{L}) \quad 4.11$$

- ii) a lognormal residual standard deviation:

$$\sigma = \tau(1 - e^{-v(d\hat{L})}) \quad 4.12$$

- iii) residual standard deviation which followed a power law:

$$\sigma = v(d\hat{L})^\tau \quad 4.13$$

Where v and τ are constant parameters which are estimated and σ is the residual standard deviation. For each error structure, the Fabens (1965) model was fitted and parameters estimated by minimizing the negative log-likelihood using standard non-linear optimization methods (Solver, Microsoft Excel, 2010):

$$L(dL|Data) = \sum_i \left(\frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(dL-d\hat{L})^2}{2\sigma^2}} \right) \quad 4.14$$

The various fits of the functional forms were compared using Akaike's information criterion as described above.

In Fabens (1965) method, t_0 is redundant and was therefore calculated by solving for t_0 using $Lt = 5.5$ mm SL, the different values of L_∞ and K were determined through each method (Gulland and Holt, 1959; Fabens, 1965) and $t = 0$. The value for Lt was determined by Jenkins *et al.* (1985) as the mean length of *S. commerson* larvae ($n = 62$) collected over a three year period from the shelf waters of the Great Barrier Reef, Australia.

It has been shown that von Bertalanffy growth parameters estimated from age-at-length data and tagging data are not directly comparable (Francis, 1988b; Francis, 1995). In particular, the parameter L_{∞} means asymptotic mean length at age for age-at-length data, and maximum length for tagging data. These differences result in Eq. 5.6 and Eq. 5.10 being different models and not different formulations of the same model (Francis, 1988b).

Comparison of growth rates

In this study, the methods described by Attwood and Swart (2000) were applied to compare growth rates determined from tag-recapture data to predictions from length-at-age data. The growth rate of individual fish was estimated from tag-recapture data using the following equation:

$$G_i = 365.25 \frac{FL_{i\text{rec}} - FL_{i\text{rel}}}{dt} \quad 4.15$$

where, G_i is the growth rate of an individual fish ($\text{cm} \cdot \text{year}^{-1}$), $FL_{i\text{rel}}$ is the fork length at tagging (cm), $FL_{i\text{rec}}$ is the fork length at recapture (cm), and dt is the days at liberty. The G_i values were plotted against the fork length (cm) of the fish midway during its time at liberty. The length midway between release and recapture was estimated as follows:

$$\overline{FL}_i = L_{\infty} - \exp \frac{\ln(L_{\infty} - FL_{i\text{rel}}) + \ln(L_{\infty} - FL_{i\text{rec}})}{2} \quad 4.16$$

where L_{∞} was estimated from tag-recapture data (Gulland and Holt, 1959; Fabens, 1965; Francis 1988a). To compare the growth rates determined by tag-recapture with those derived from length-at-age data, the von Bertalanffy growth model was transformed to:

$$\frac{dFL}{dt} = L_{\infty} \times K \left(1 - \frac{FL}{L_{\infty}}\right) \quad 4.17$$

where L_{∞} and K were taken from length-at-age data. For each tag-recapture the measured growth (G_i) was compared to the expected growth rate ($\frac{dFL}{dt}$) from the observed length-at-age data using a linear regression and further von Bertalanffy growth parameters were estimated as $L_{\infty} = -a/\beta$ and $K = -\beta$. A one-factor

ANOVA was used to test the null hypothesis that the growth rate determined from tag-recapture data is not different from the growth rate predicted by the models fitted to otolith data and Fabens' (1965) data. Critical values were selected at the 99% confidence level. Where significant differences were evident, a Tukey's post-hoc analysis was used to determine where these differences existed.

Age estimate validation

Baker *et al.*, (1991), and Govender (1999) described a growth model that incorporates tag-recapture data to validate age estimates derived from otoliths. The model consists of two components. The first estimates the growth parameters from length-at-age data based on different deposition periods of hard structure bands. The second predicts the growth increment during the time at liberty of tagged and recaptured individuals by using the growth parameters derived from the first model component (Govender, 1999).

The original parameterization of the von Bertalanffy function was discarded for that of Schnute (1981). This parameterization results in statistically more stable parameter estimates (Schnute, 1981; Baker *et al.*, 1991; Govender, 1999; Newman *et al.*, 2012). Schnute's parameterization of the von Bertalanffy growth function is given as:

$$Y_t = Y_1 + (Y_2 - Y_1) \frac{1 - \exp[-a(t - T_1)]}{1 - \exp[-a(T_2 - T_1)]} \quad 4.18$$

where Y_t is the size of a t -aged fish, Y_1 and Y_2 are the sizes corresponding to two selected ages T_1 and T_2 , such as the youngest and oldest observed ages, and a is a constant, where $a \neq 0$, $Y_2 > Y_1$ and $T_2 > T_1$. The variable t is redefined as:

$$t_i = \frac{B_i}{P}$$

where t_i is the age of fish i , B_i is the number of opaque bands counted for fish i , and P is the assumed periodicity of the otolith band. If $P = 1$ then it is assumed a single opaque band is deposited annually, whereas if $P = 2$, then a biannual periodicity of opaque band deposition is assumed. Given the size at age data based on an assumed value for P , parameter estimates were obtained by specifying the ages T_1 and T_2 prior to minimizing the residual sum-of squares using a non-linear

minimization routine (Solver: Microsoft Excel 2010). An absolute error model was assumed:

$$\hat{Y}_i = Y_i + \varepsilon_i$$

where, \hat{Y}_i and Y_i is the predicted and observed length of the i th fish and ε_i is an independent normally distributed error with zero mean and a common variance.

The traditional von Bertalanffy parameters can be obtained from the parameters of Equation 4.18 (Schnute, 1981) as described above.

Schnute's growth model (Equation 4.18) can be modified to predict the growth increments, given the times at liberty and size at marking of tagged individuals; and the parameter estimates obtained from the length-at-age data. The general model can first be recast so that age t is made the subject of Equation 4.18:

$$t = T_1 - \frac{1}{a} \ln \left(1 - \frac{Y_t - Y_1}{Y_2 - Y_1} (1 - \exp[-a(T_2 - T_1)]) \right) \quad 4.19$$

If fish grow from size Y_m , when tagged at age t_m , to size Y_r , when recaptured at age t_r , then from equation 4.19:

$$t_m = T_1 - \frac{1}{a} \ln \left(1 - \frac{Y_m - Y_1}{Y_2 - Y_1} (1 - \exp[-a(T_2 - T_1)]) \right) \quad 4.20$$

and

$$t_r = T_1 - \frac{1}{a} \ln \left(1 - \frac{Y_r - Y_1}{Y_2 - Y_1} (1 - \exp[-a(T_2 - T_1)]) \right) \quad 4.21$$

Subtracting Equation 4.21 from 4.20 and rearranging to solve for Y_r yields:

$$Y_r = \left(Y_m \exp[-a(t_r - t_m)] + (Y_2 - Y_1 \exp[-a(T_2 - T_1)]) \frac{1 - \exp[-a(t_r - t_m)]}{1 - \exp[-a(T_2 - T_1)]} \right) \quad 4.22$$

Equation 4.23 can be rewritten as:

$$Y_r = Y_m[\exp(-a\Delta t)] + v[1 - \exp(-a\Delta t)] \quad 4.23$$

where v can be found by comparing Equations 4.23 and 4.22, and $\Delta t = t_r - t_m$. Noting that $Y_r = Y_m + \Delta l$ where Δl , is the growth increment during the time at liberty, substitution into Equation 4.23 results in:

$$\Delta l = Y_m[\exp(-a\Delta t) - 1] + v[1 - \exp(-a\Delta t)] \quad 4.24$$

Using the parameter estimates from Equation 4.18 and a range of assumed P values, the best estimates of P , Y_1 , Y_2 and a are those that minimize the criteria:

$$SS_{tag} = \sum_{i=1}^M (\Delta l - \Delta g)^2 \quad 4.25$$

where Δg is the observed growth increment during the time at liberty for fish l , and M is the number of fish tagged and recaptured. The choice between the different models of P was achieved by a simple plot of the residuals (Butterworth *et al.*, 1989). The residual plot that showed no systematic trend was then the chosen model.

4.3 Results

4.3.1 Somatic Relationships

TL-FL relationship

A total of 432 (248 females; 179 males and 4 unsexed juveniles) *S. commerson* were used to determine the total length-fork length relationship for the species. This included 127 and 305 fish sampled within MOZ and KZN respectively.

The FL-TL relationship for the pooled sample (for the range 49 – 161.5 cm FL), females (49 – 161.5 cm FL), males (52.5 to 141 cm FL) and for the two regions (52.1 – 161.5 cm FL) for KZN and (49 – 119 cm FL) for MOZ are summarized in Table 4.3 and displayed for the pooled sample in Figure 4.1. All FL-TL linear regressions were highly significant ($p < 0.001$), with R^2 ranging from 0.987 – 0.995. There was no significant difference in the TL-FL relationship between MOZ and KZN or between separate sexes (Multiple regression test, $p > 0.05$) (Table 4.3).

Table 4.3: The relationships between total and fork lengths of male and female *S. commerson* caught in KwaZulu-Natal and southern Mozambique.

Sex/Region	Equation	R^2	std error of slope	std error of constant
Female ($n = 248$)	$TL (cm) = 1.082 (FL cm) + 4.713$ $FL (cm) = 0.912 (TL cm) - 3.036$	0.987	0.0080 0.0067	0.78 0.74
Male ($n = 179$)	$TL (cm) = 1.095 (FL cm) + 3.359$ $FL (cm) = 0.909 (TL cm) - 2.647$	0.995	0.0057 0.0047	0.49 0.46
KZN ($n = 305$)	$TL (cm) = 1.089 (FL cm) + 3.862$ $FL (cm) = 0.910 (TL cm) - 2.622$	0.991	0.0061 0.0051	0.59 0.56
Moz. ($n = 127$)	$TL (cm) = 1.109 (FL cm) + 2.740$ $FL (cm) = 0.891 (TL cm) - 1.472$	0.988	0.0109 0.0087	0.90 0.83
Pooled sample ($n = 432$)	$TL (cm) = 1.089 (FL cm) + 3.998$ $FL (cm) = 0.910 (TL cm) - 2.795$	0.991	0.0051 0.0042	0.473 0.447

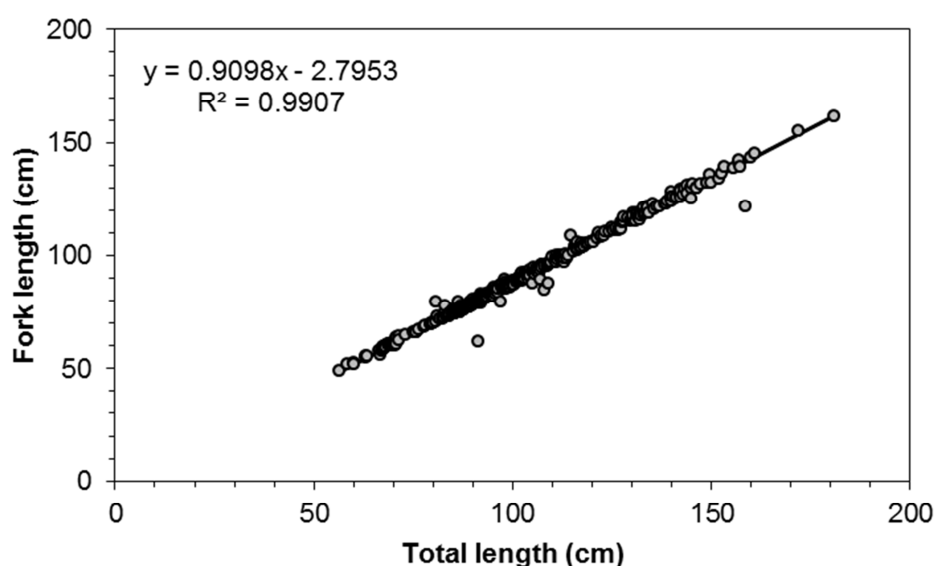


Figure 4.1: Total length-fork length relationship for the pooled sample of *S. commerson* caught in southern Mozambique and KwaZulu-Natal ($n=432$).

FL-Wt relationship

A total of 398 (230 females, 163 males and 4 juveniles) *S. commerson* were used to determine the FL-Wt relationship. This included 117 and 281 fish sampled within MOZ and KZN respectively. The length-weight results were found to be highly significant ($p < 0.001$), with the coefficient of determination (R^2) ranging from 0.971 – 0.977. There was no significant difference in the FL-Wt relationships between male and female *S. commerson* (Multiple regression test, $p > 0.05$). The data, therefore,

were pooled across sexes to determine a common total length-weight relationship. However, the FL-Wt regressions differed significantly between KZN and MOZ (Multiple regression test, $p < 0.05$).

The exponential relationship for the pooled sample was described by the equation $Wt (g) = 0.00345 (FL \text{ cm})^{3.18}$ (Figure 4.2). A smaller average length and weight was recorded in MOZ (83.6 cm, 4.84 kg) compared to KZN (95.7 cm, 8.42 kg) (Table 4.4). For all the individuals measured, the minimum and maximum fork lengths and weights recorded were 49 cm (0.95 kg) and 161.5 cm (33.16 kg). Overall, female fish (97.1 cm, 8.56 kg) were on average longer and heavier than males (85.9 cm, 5.81 kg) (Table 4.4). The longest female fish recorded was 161.5 cm FL compared to the longest male at 141 cm FL. The heaviest female fish was 33.16 kg compared to the heaviest male at 23.2 kg.

Table 4.4: Parameters of the length-weight relationship for male and female *S. commerson* sampled in KwaZulu-Natal and southern Mozambique.

Sex/ Region	<i>n</i>	Length			R^2	Parameters		α CL _{95%}		β CL _{95%}	
		Min	Max	\overline{FL} (SE)		α	β	Lower	Upper	Lower	Upper
Female	230	49	161.5	97.06 (1.36)	0.97	0.0035	3.18	0.0026	0.0048	3.11	3.25
Male	163	52.5	141	85.89 (1.38)	0.98	0.0030	3.22	0.0021	0.0041	3.15	3.30
KZN	281	52.1	161.5	95.70 (1.26)	0.98	0.0031	3.21	0.0024	0.0041	3.15	3.27
MOZ	117	49	119	83.65 (1.36)	0.97	0.0068	3.02	0.0045	0.011	2.93	3.12
Pooled sample	398	49	161.5	92.07 (1.02)	0.98	0.0035	3.18	0.0028	0.0043	3.13	3.23

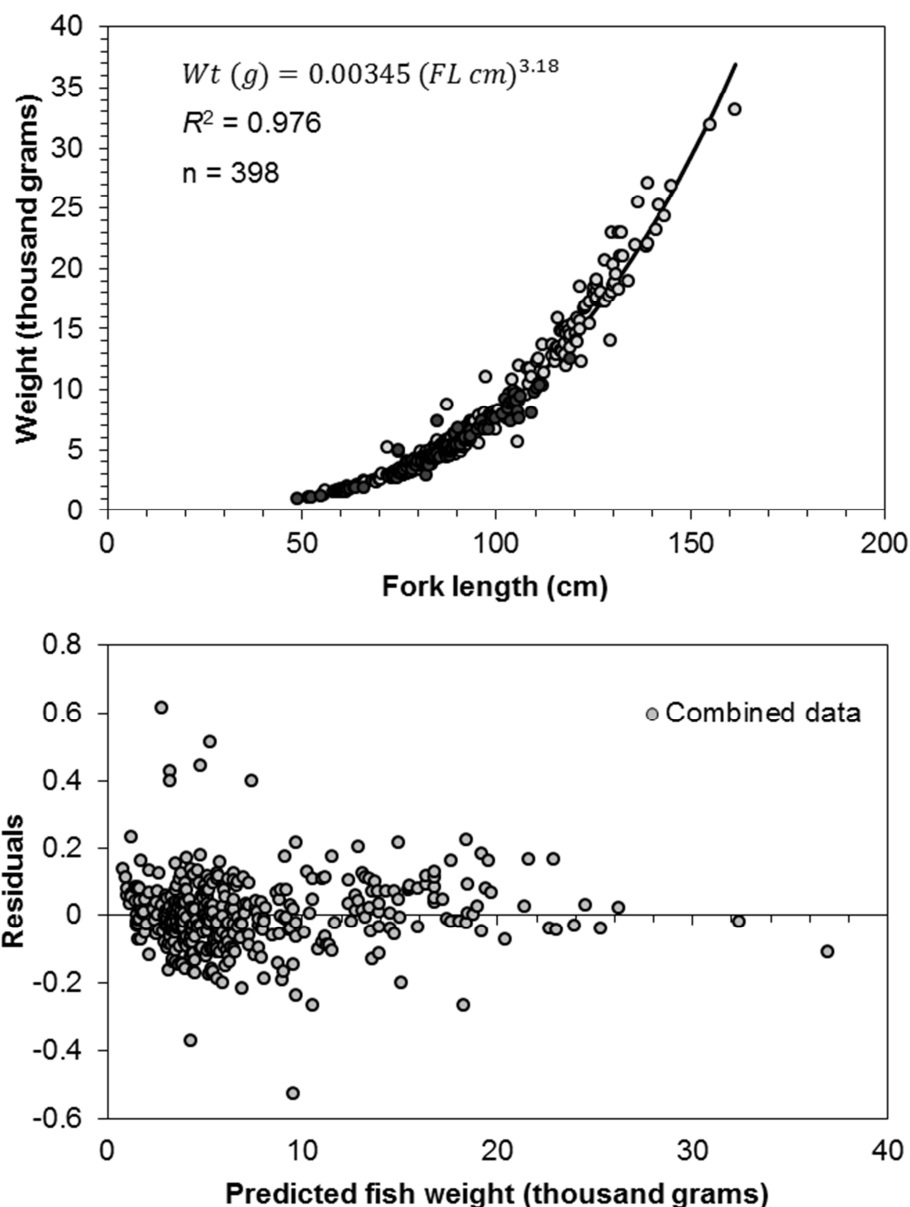


Figure 4.2: Length-weight relationship and its associated residual plot for *S. commerson* sampled in southern Mozambique and KwaZulu-Natal ($n=398$).

4.3.2 Otolith interpretation

Alternating translucent and opaque bands were observed in transverse sections and whole otoliths in both baked and un-baked states. Of the four methods evaluated using the sub-sample of otoliths, whole un-baked otoliths had the highest average readability index (3.8) and the lowest average percent error (APE) of 9.2% (Table 4.5). All subsequent otoliths were therefore aged using whole, un-baked otoliths.

Table 4.5: Average readability (AR) indices and index of average percent error (APE) for the two methods of sagittal otolith preparation of *S. commerson* in southern Mozambique and KwaZulu-Natal

Method of preparation	AR	APE
Transverse sections	2.9 ± 1.17	12.98%
Whole un-baked otoliths	3.8 ± 0.96	9.21%
Whole baked otoliths	3.05 ± 0.83	10.99%

Of the 375 pairs of otoliths that were processed, 13 (3.5%) were rejected and excluded from the age-associated analyses due to being unclear and with a consequent lack of agreement between the two readers of age-estimations. Age estimates were accepted for 362 (96.5%) of the sample (200 females, 156 males and 6 juveniles), of which 269 were from KZN and 91 from MOZ.

Opaque zones of whole otoliths were most easily viewed under reflected light with a black background (Figure 4.3a). Clear annuli were identifiable as opaque zones that appeared whiter than the adjacent hyaline (translucent) zones. In the case of the otoliths from larger, older fish, it was often necessary to switch between transmitted and reflected light in order to clearly see the annuli, especially towards the otolith margin. Under transmitted light the opaque zones appear darker (Figure 4.3b). The first opaque zone or annulus was usually much wider, with subsequent annuli becoming narrower and increasingly stacked the older the fish.

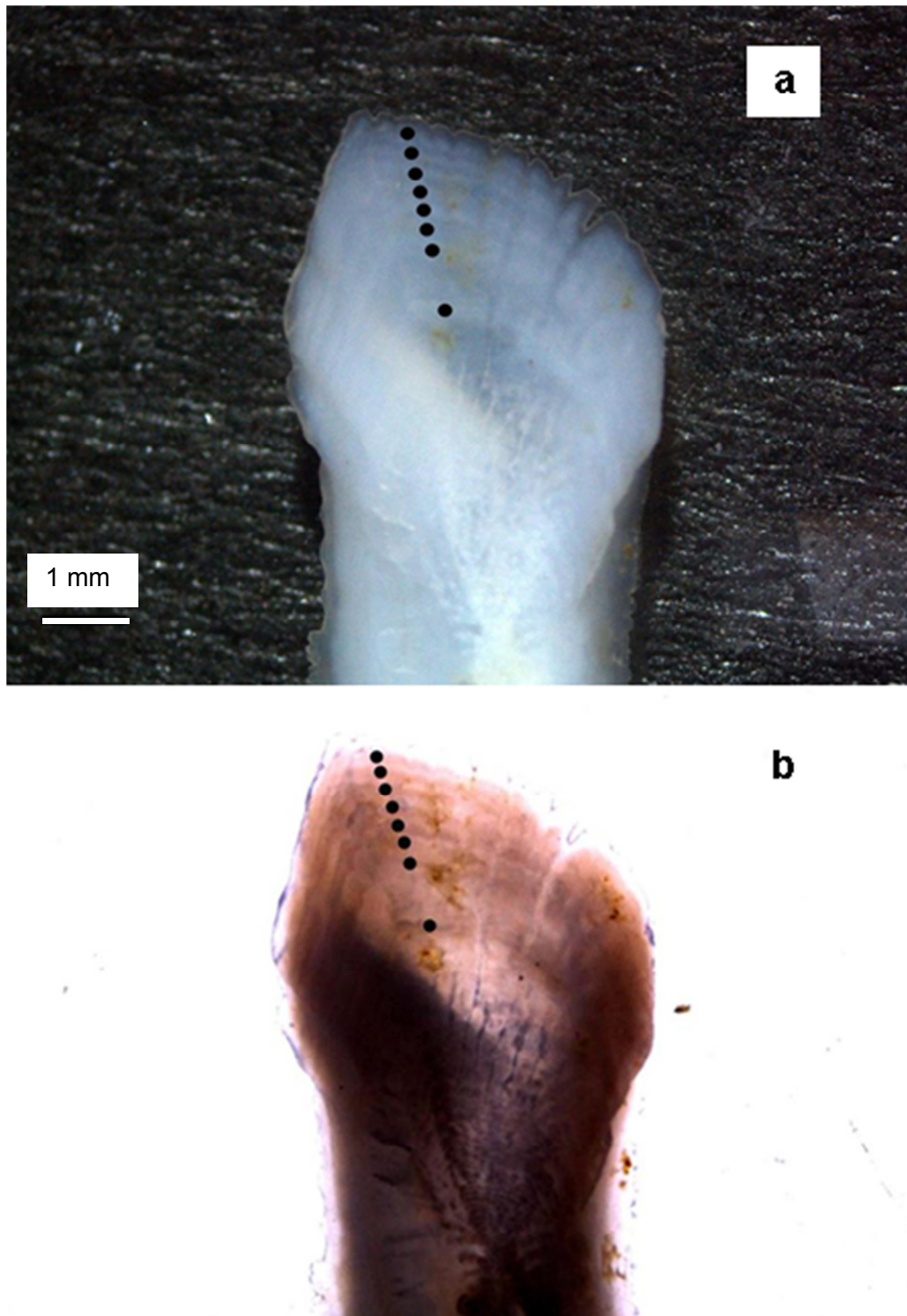


Figure 4.3: Whole otoliths of 125.9cm FL *S. commerson* viewed at 10x magnification under (a) reflected light over a black background and (b) transmitted light indicating an eight year old individual.

The APE and CV values were 9.56% and 12.8% respectively, representing relatively good reproducibility between readings. The comparison of the mean of the first reader (R_1) with the second readers (R_2) age estimates indicates little bias (Figure 4.4). A high correlation existed between the mean of the estimates ($R^2 = 0.99$).

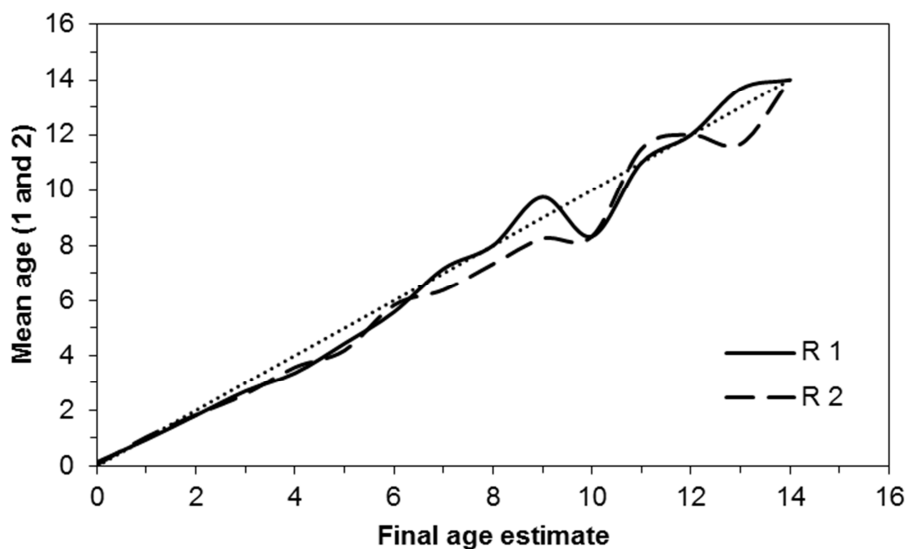


Figure 4.4: Age bias plot for inter-reader comparison between the mean of the first (R_1) and second (R_2) age readings. The dotted line represents a 1:1 ratio

Age estimates for the total sample ranged from 0+ (<50 – 75 cm FL) to 14 (>145 cm FL) years. The eight youngest age classes (0 – 7 years) dominated the sample, with 94% of all fish being between the 0+ and 7+ year classes. This is confirmed by the age at length key as shown in Table 4.6.

Table 4.6: The observed age-length key for *S. commerson* sampled along the southern Mozambique and KwaZulu-Natal coast (2011-2012).

FL (cm)	Age (years)															Total
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
<50	1															1
55	1	2														3
60	5	8														13
65	5	13														18
70	4	4														8
75	2	7	12	1												22
80		28	30	3	1											61
85		16	20	9	1	1										46
90		7	26	9	6	1										49
95		2	10	6	5											23
100			9	5	6	1										21
105				5	4	3		1								13
110				5	3	2	1									11
115			1	2	1	3	1		1	1						10
120			1	1	4	2	4	5	1							18
125					1	3	2	3	2							11
130					1		1	5	1	1	2	1	1			13
135							2	3	2	1		1				9
140							1		2	1	1					5
145								1						3		4
>145															1	1
Total	18	87	109	46	33	16	12	18	9	4	3	2	1	3	1	362
Mean	61.6	73.7	84.0	93.1	99.8	107.6	121.6	123.3	126.2	128.5	132.3	130.6	142.7	161.5		
S.D.	6.4	10.1	8.2	10.8	12.8	11.2	9.0	8.7	9.1	10.5	5.9	2.3	-	2.1	-	

The lengths are the lower limits of each 5 cm length class

4.3.3 Validation – marginal zone analysis

There was strong seasonality to the deposition of the opaque zone at the otolith margin which occurred primarily from September through to December (Figure 4.5). The percentage of opaque margins decreased markedly after December. This formation of opaque zones over a restricted time of year provides strong circumstantial evidence for the assumption that one opaque and one hyaline band are deposited each year.

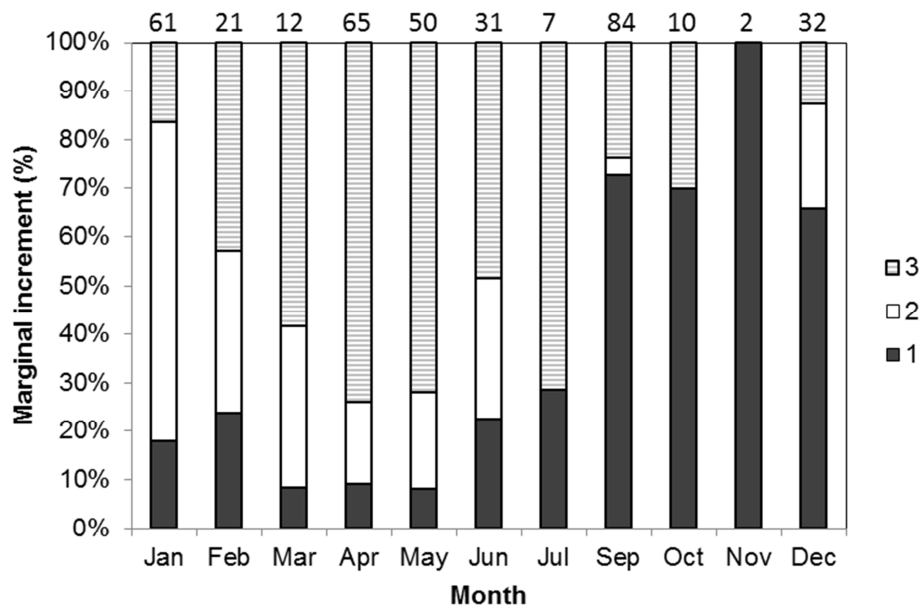


Figure 4.5: The percentage frequency of *S. commerson* displaying the three marginal increment zones (1: opaque; 2: 1-50% hyaline; 3: 51-100% hyaline) along the otolith margin. Sample size for each month is indicated on the top axis.

4.3.4 Growth models

Goodness of fit statistics for the growth models fitted to individual and combined sexes are presented in Table 4.7. The VBGF model consistently provided the equivalent best fit to length at age data.

Table 4.7: Model fits to fork length (cm) at age (year) data grouped by sex, evaluated using Akaike's information criterion indicating the best approximating fit (lower values indicate better fit).

Sex	VBGF	Schnute
Females	1116.4	1118.4
Males	813.8	814.9
Combined	1971.7	3655.9

The length at age relationship was asymptotic in form with the majority of growth occurring during the first six years of life (Figure 4.6). There was no systematic visual trend in the residuals, therefore the VBGF is considered to adequately describe the observed length-at-age data. *S. commerson* displayed extremely fast initial growth averaging about 75cm FL in their first year and reaching nearly half the asymptotic size (84.1cm FL \pm 8.9cm S.D.) by the second year. There was a high degree of

individual variability in length at age with the largest one year old fish observed to be 96.2cm FL compared to the smallest at 59.1cm FL.

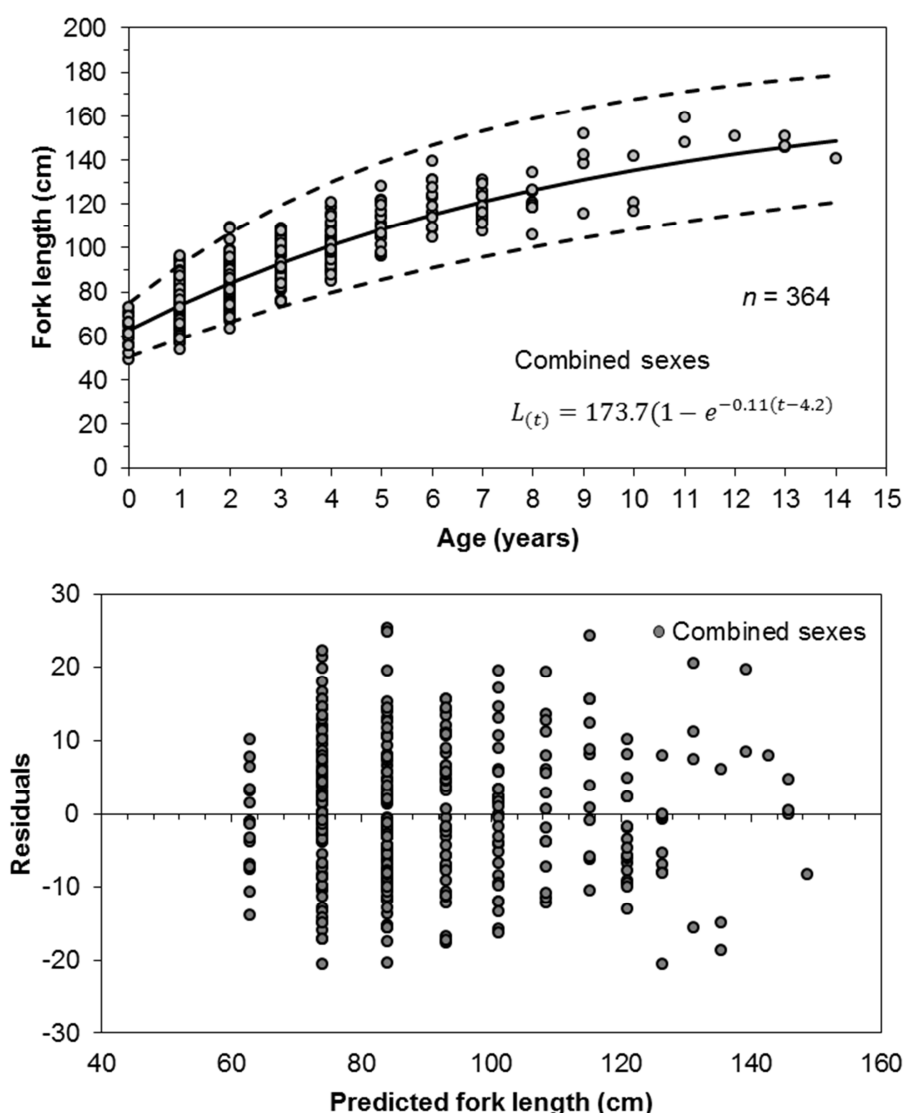


Figure 4.6: von Bertalanffy growth curve for combined sexes and their associated residual plots fitted to observed length-at-age data for *S. commerson* from southern Mozambique and KwaZulu-Natal, South Africa. Dashed lines represents 95% confidence intervals. Age 0 refers to 0+ fish.

The fitted curves were influenced by the selectivity of the fishing gear; inherent characteristics of fisheries-dependent data (Begg *et al.*, 2006). The selectivity of the gear resulted in low numbers of animals taken in the younger age classes (Haddon, 2001). Although the models for females and the combined sexes demonstrated reasonable reflections of the growth coefficient (K) and average maximum size (L_{∞}) of *S. commerson*, estimates of t_0 appeared to be low. Estimations of the parameters

for the male growth curve in particular resulted in an almost linear curve with excessively high L^∞ values corresponding to low t_0 values. Biological realism could be maintained if one of these two parameters (L^∞ and t_0) was fixed to a reasonable value. In these circumstances, Pauly (1980) recommended the largest male recorded in the sample to be set to 95% of the asymptotic length. This is unfortunate as this parameter is one of the two important parameters (L^∞ and K) estimated by the VBGF. The third alternative used for the estimation of VBGF parameters was to make t_0 of males equal to the t_0 of females. The methods whereby t_0 and L^∞ were fixed produced very similar von Bertalanffy growth parameters with estimates of K and L^∞ appearing more biologically realistic (as discussed from Pauly, 1980). The method which fixed male t_0 to equal that of female t_0 provided the most biologically realistic parameter estimates for the male VBGM and was used subsequently (Figure 4.7). The analysis of residual sums of squares (ARSS) indicated that male and female *S. commerson* had significantly different growth rates (ARSS; $p < 0.05$). Males attained a smaller asymptotic length than females with slightly slower growth towards L^∞ . With the more detailed analyses (LLR), there was evidence that the male L^∞ parameter might be different to that of the female curve; however, this difference was not significant (LRT, $p > 0.05$). Point estimates and summary statistics for the VBGF parameters derived from a parametric bootstrap procedure with 1000 iterations are presented in Table 4.7.

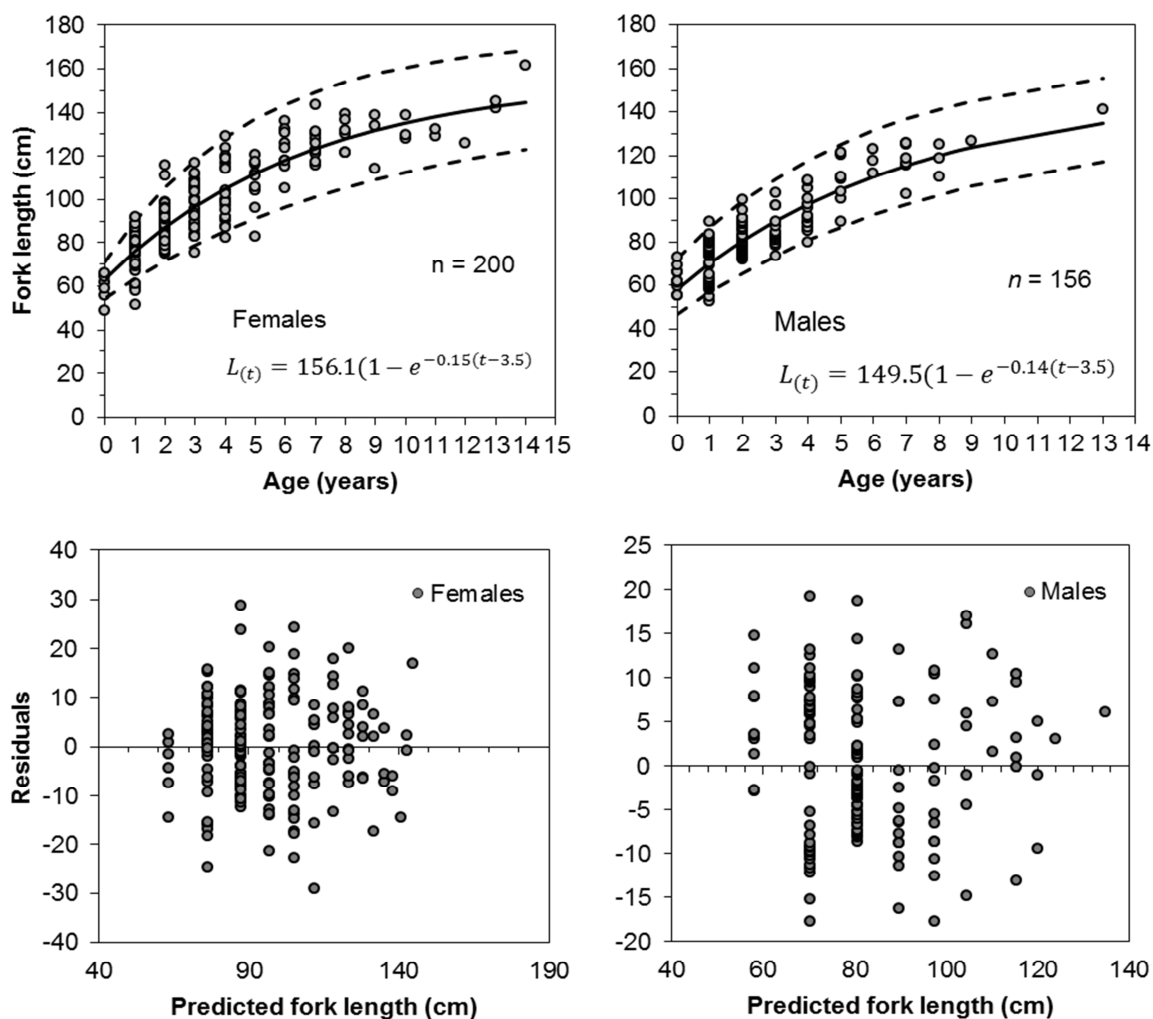


Figure 4.7: Sex-specific von Bertalanffy growth curves and their associated residual plots fitted to observed length-at-age data for *S. commerson* from southern Mozambique and KwaZulu-Natal, South Africa. Dashed line represents 95% confidence intervals. Age 0 refers to 0+ fish.

Table 4.8: Point estimates and summary statistics for the von Bertalanffy growth function parameters for male, female and combined sexes of *S. commerson* sampled from southern Mozambique and KwaZulu-Natal.

	Parameter	Point estimate	Summary statistics				
			Mean	Coefficient of variation	Standard error	Confidence intervals	
Females	L_{∞} (cm FL)	156.02	158.14	5.22	8.35	142.25	174.07
	K (year ⁻¹)	0.15	0.14	17.86	0.025	0.11	0.21
	t_0 (years)	-3.50	-3.56	13.76	0.49	-4.45	-2.60
Males ($t_{0m} = t_{0f}$)	L_{∞} (cm FL)	149.52	153.10	5.01	7.67	136.25	166.88
	K (year ⁻¹)	0.14	0.14	7.86	0.011	0.12	0.16
	t_0 (years)	-3.50	-3.56	-	-	-	-
Combined	L_{∞} (cm FL)	173.69	165.55	6.20	10.26	150.69	191.66
	K (year ⁻¹)	0.11	0.12	15.0	0.018	0.087	0.16
	t_0 (years)	-4.22	-3.99	10.03	0.40	0.16	-3.12

4.3.5 Tag-recapture data

Between 1984 and 2011, 1303 *S. commerson* were tagged in the ORI Tagging Project, of which only 52 (4%) were recaptured. After filtering the data, only 29 recaptures provided suitable data to enable construction of a growth curve. The average length at tagging was 94.4 cm FL compared to 109.7 cm FL for the recaptured fish (Table 5.8). The time at liberty of recaptured fish ranged from 17 to 2604 days.

Table 4.9: Summary statistics for lengths at tagging and recapture, and the times spent at liberty for 29 *S. commerson* caught in southern Mozambique and KwaZulu-Natal between 1984 and 2011.

Parameter	Mean	S.D.	Maximum	Minimum
Length at tagging (cm FL)	94.4	155.9	122.0	68.6
Length at recapture (cm FL)	109.7	169.3	140.0	69.5
Time at liberty Days	725.6	692.9	2604	17

Using Gulland and Holt's (1959) method, the von Bertalanffy growth parameter estimates based on tag-recapture data were $L_{\infty} = 183.2$ cm FL, $K = 0.12$ year⁻¹ and $t_0 = -0.03$ (Figure 4.7).

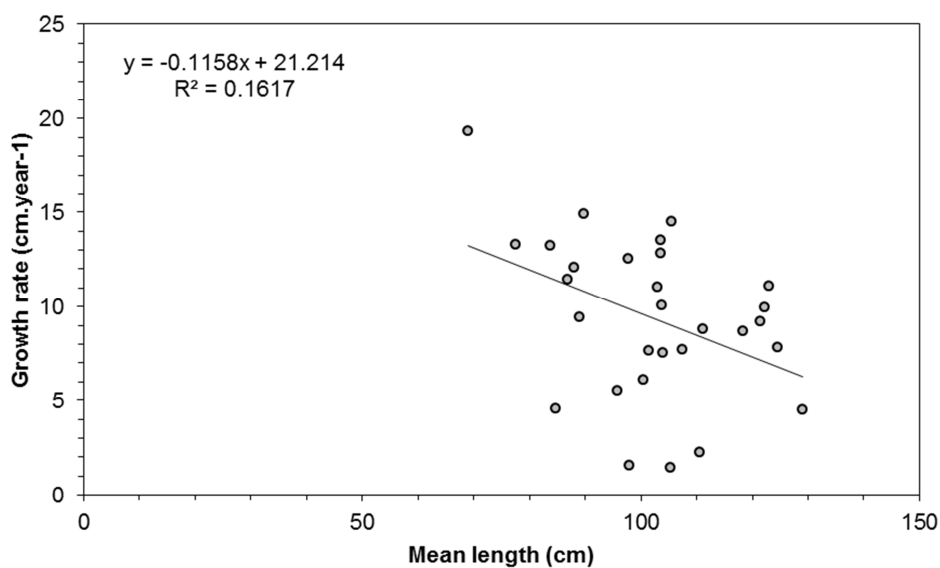


Figure 4.8: Annual growth rates of recaptured *Scomberomorus commerson* using Gulland and Holt's (1959) method.

The von Bertalanffy growth parameters estimated using Faben's (1965) method for the three different functional forms from Francis (1988a) are shown in Table 4.9. The parameter estimates are all very similar, particularly the inverse linear and power law functional forms. The best fit to the model as determined using Akaike's information criterion, was obtained using the inverse linear functional form.

Table 4.10: Different parameter estimates and AIC values using Faben's (1965) method for different functional forms as suggested by Francis (1988a) with calculated t_0 values.

Functional form	Parameters				$-LnI$	No. of parameters	AIC value	t_0
	L^∞	K	ν	τ				
Inverse linear	177.1	0.13	0.37	-	147.54	3	301.08	-0.024
Lognormal	160.0	0.13	0.0039	176.42	151.09	4	310.18	-0.027
Power law	177.1	0.13	0.36	1.01	147.54	4	303.08	-0.024

By solving for t_0 for the inverse linear functional form, von Bertalanffy growth curves could be plotted for the parameter estimates obtained using the tag-recapture and length-at-age data (Figure 4.8). The tag-recapture curve displayed a similar L^∞ to that of the length-at-age data. The tag-recapture data however resulted in a higher K value indicating a steeper curve to the asymptotic length (L^∞)

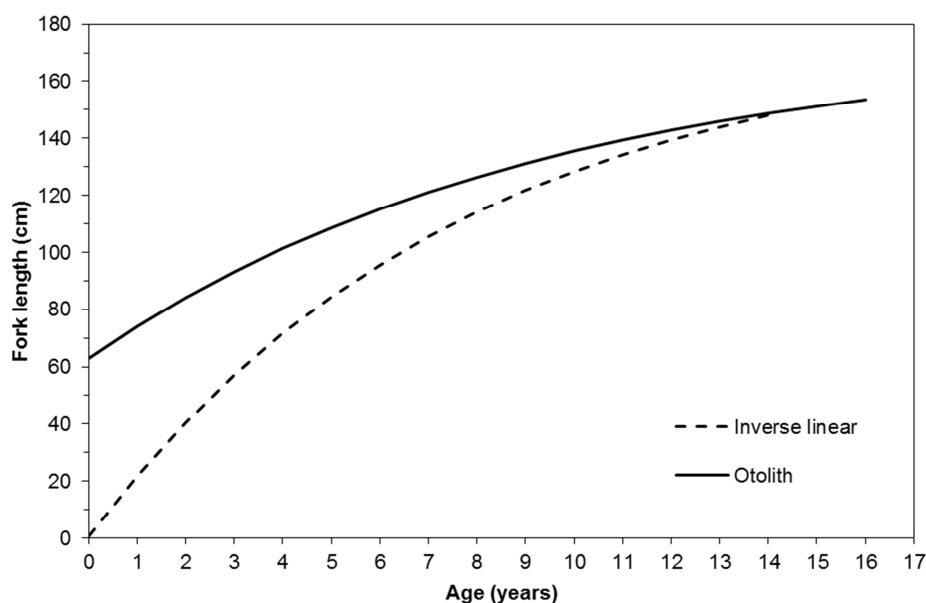


Figure 4.9: Von Bertalanffy growth curves fitted to tag-recapture (Inverse linear) ($n=29$) and otoliths derived length-at-age data ($n = 362$) for combined sexes of *S. commerson* sampled off southern Mozambique and KwaZulu-Natal.

The von Bertalanffy growth parameters estimated using the method described by Attwood and Swart (2000) resulted in the estimated growth rates from tag-recaptures lying above the corresponding values predicted by the growth model based on otolith ring counts (Figure 4.10). The growth rates predicted from Fabens' (1965) model were initially greater than those derived from otolith data. However these decreased at a faster rate with increasing fork length and the growth rates derived from the length-at-age model became greater than from Fabens' (1965) model above 110cm fork length. A one-factor ANOVA followed by a Tukeys post-hoc analysis indicated a significant difference between the estimated growth rates using the tag-recapture data and the predicted growth rates from the otolith data ($t = 4.28$, $p = 4.8 \times 10^{-5}$), as well as with the growth rates derived from Fabens' (1965) model ($t = 3.83$, $p = 0.0002$).

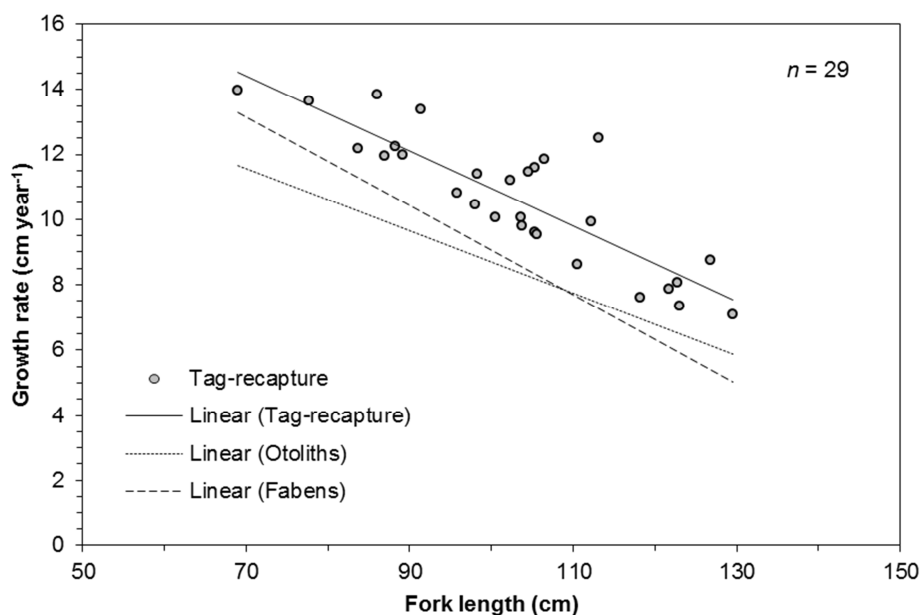


Figure 4.10: The predicted growth rate of *Scomberomorus commerson* from tag-recaptures (solid line), length-at-age (dotted line) and Fabens' (1965) model (dashed line).

The assumption that otolith bands are deposited annually resulted in a smaller residual sum of squares between the observed and predicted growth increments for the tagged *S. commerson* ($SS_{\text{tag}} = 54007.88$), than that obtained under an assumption of biannual deposition ($SS_{\text{tag}} = 203991$). The residual plot of the model for annual deposition of growth increments displays less of a trend compared to that of the biannual model (Figure 4.11). Additionally, the biannual model under-estimates the growth increments of the tagged fish more than the annual model. The underestimation of the biannual model residuals increases as predicted fork length increases, resulting in a clear systematic trend in the residuals (Figure 4.11b). It is evident that fish with long times at liberty grew faster than what was expected on the basis of otolith readings (Figure 4.11 and 4.12). Due to the above evidence, the model for annual deposition of opaque bands was preferred, supporting the marginal zone analysis results in Section 4.3.3 above. The observed and predicted growth increments for both periodicity models are displayed in Figure 4.12.

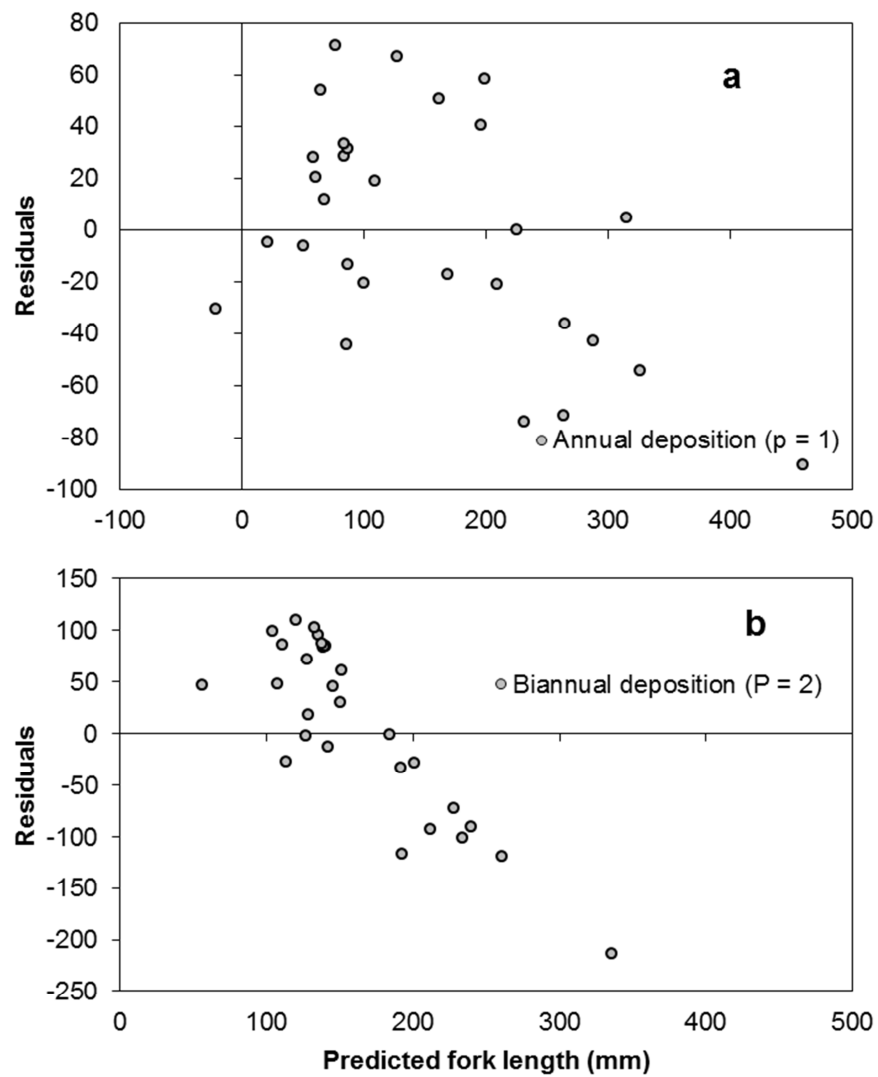


Figure 4.11: Residual plot of the growth increment model fitted to observed growth increments of tagged *S. commerson*, based on the assumption of (a) annual deposition ($P=1$) and (b) biannual deposition ($P=2$) of the otolith bands.

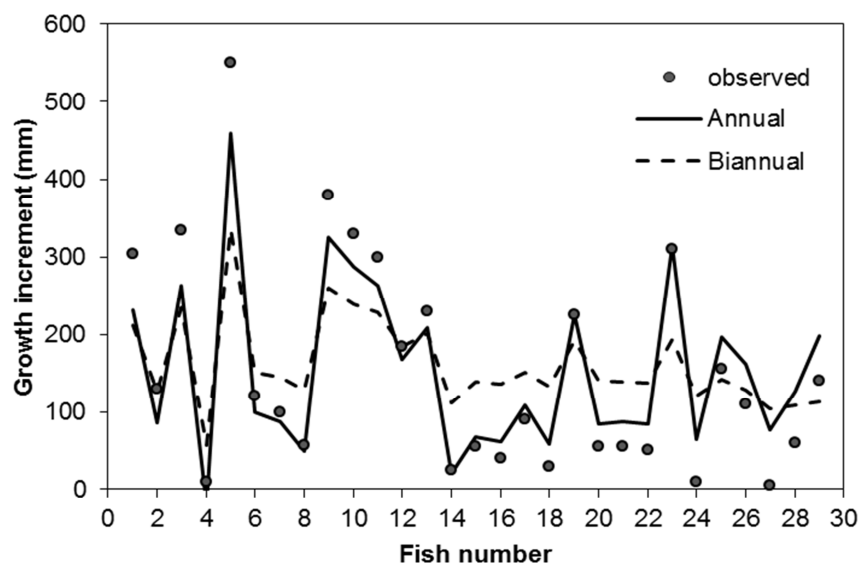


Figure 4.12: Observed and predicted growth increments for *S. commerson* based on the annual and biannual models.

4.4 Discussion

4.4.1 Assignment and reliability of ages

Unburned, unbaked, whole otoliths were easiest to read and produced the most consistent age estimations for *S. commerson* in KZN and MOZ. The precision of otolith readings from this study (APE = 9.21%) was comparable with the results attained by a number of other authors ageing whole otoliths for *S. commerson*. An APE of 14.4% and 6.63% was obtained in the Arabian Gulf (Grandcourt *et al.*, 2005) and the Northern territories of Australia (Buckworth, 1998) respectively. These are all much higher indexes than those obtained in Queensland, Australia by Tobin and Mapleston (2004; IAPE = 3.14%) and McPherson (1992; IAPE = 0.9%). These comparisons reveal a high degree of variability in the precision of otolith reading between different regions. It has been suggested that this may be a result of latitudinal differences and corresponding differences in water temperatures between the regions (Newman *et al.*, 2012). This is due to the otoliths of warm water tropical fish often varying in clarity and readability compared to more temperately distributed species (Fowler, 1995). The otoliths of larger fish in this study were more difficult to read and had less consistent readings than those of smaller fish. This was due to a very narrow translucent zone separating the annuli in older, larger fish often making it difficult to distinguish between annuli (Lewis and Mackie, 2002). Govender (1994)

obtained a much higher IAPE of 20.25% in South Africa with age readings differing by as much as three to five bands in larger fish.

4.4.2 Validation and formation of annuli

Validating the periodicity of growth increment formation is of critical importance to age and growth studies (Campana, 2001). To date, marginal zone analysis (MZA) is the only form of age validation that has been successfully used for *S. commerson*. Campana and Thorrold (2001) considered validation using this method to be appropriate when validation attempts using other methods were not feasible. Govender (1994) made use of MZA to validate the periodicity of opaque zone formation for *S. commerson* in South Africa. He also made use of tagging data for two recaptured individuals to corroborate his findings. However, his results provided inconclusive evidence due to poor weather conditions resulting in a lack of adequate samples for August to October, combined with difficulties in interpreting the banding at the margin of older fish (Govender, 1994). Problems with adequate monthly samples have also been encountered among other *Scomberomorus* studies when validating periodicity using marginal zone analysis (Beaumarrige, 1973; Johnson *et al.*, 1983; Sturn and Salter, 1990, Chale-Matsau *et al.*, 1999). In this study, this problem was overcome by continuing to sample *S. commerson* in MOZ during the months of its seasonal absence in KZN.

Despite inconclusive evidence, Govender (1994) concluded that it is possible that two opaque bands are laid down annually, a minor opaque band in May and a major one during August to January. This was consistent with the results of Devaraj (1981), who estimated that two opaque zones were formed each year in *S. commerson* otoliths from Indian waters. McPherson (1992) and Newman *et al.* (2012), noted the formation of a narrow secondary opaque zone forming between January and May in Eastern and Western Australia, although it is important to note that these were not counted as annuli in these studies. Lewis and Mackie (2002) demonstrate how secondary annuli appear as a fine line between opaque bands. These can combine with true annuli in later increments for some individuals creating a broad opaque band and a thin translucent zone. It is likely that these secondary bands are what may have led Devaraj (1981) and Govender (1994) to conclude that two growth zones are formed annually.

Using MZA the current study clearly indicated that opaque bands form on an annual basis between September and December in KZN and MOZ waters. This finding was corroborated by the tag-recapture data whereby the assumption that opaque bands are laid down on *S. commerson* otoliths annually, and not biannually, resulted in estimates of growth increments that reasonably predict those observed in tagged individuals. This study concludes that opaque bands are deposited annually, but are sometimes difficult to detect or distinguish from false rings.

The deposition of the opaque zone in sub-tropical species generally occurs in the spring and summer months during periods of reduced metabolic growth, whereas the translucent zone forms during periods of accelerated growth (Beckman and Wilson, 1995). Climate, food resources, spawning season, and hydrologic conditions are all factors likely to affect the timing and control of opaque and translucent zone formation in otoliths (Beckman and Wilson, 1995). The formation of the opaque zone in this study followed this generalized pattern (September to December). Although restricted by his lack of samples between September and October, this is consistent with the results obtained by Govender (1994) in South Africa. In eastern Australia, the opaque zone is apparent between July and October (Late winter/early spring) (McPherson, 1992), earlier than in Western Australia, where the greatest incidence of opaque margins occurred from November to March (Late spring/summer). The results from these three regions of similar latitude support the hypothesis of a concurrent seasonal formation of opaque and translucent zones in otoliths of *S. commerson*.

Panella (1980) suggested that structural differences in otolith zones are a reflection of physiological effects of seasonal environmental variation with temperature, followed by food supply being the most important. The results are consistent with those found by Grandcourt *et al.* (2005) in the Arabian Gulf, with peaks in the formation of the opaque margins occurring between June and September (summer/autumn). This pattern was linked to seasonal variability in oceanographic characteristics in the region (Grandcourt *et al.*, 2005). Seasonal fluctuations in sea water temperatures along with variables such as productivity and subsequent food availability are associated with seasonal growth rate changes and the deposition of translucent and opaque bands observed in the otoliths of *S. commerson* (Grandcourt *et al.*, 2005; King, 1995).

Observed differences in the timing and duration of zone formation may arise as a result of the influence of a number of factors. A possible source of variation among studies may relate to differences in assessment criteria among studies (Beckman and Wilson, 1995). Classification of an otolith zone could also be affected by methods of otolith observation, such as light conditions, magnification, or human variability in interpretation (Beckman and Wilson, 1995). Otolith preparation techniques could be another source of variability (McIlwain *et al.*, 2005). Additionally, studies have reported that timing of zone formation determined from whole otoliths may differ from those determined using sectioned otoliths (Beckman and Wilson, 1995). Collins *et al.* (1989) reported that the opaque zone in *Scomberomorus cavalla* was detected two months earlier in whole otoliths compared to sectioned otoliths.

Many studies have reported, based on correlative evidence that otolith annuli correspond to the spawning period (Beckman and Wilson, 1995). These observations are likely to be more relevant in tropical regions where spawning periodicity may have a more significant physiological effect than environmental seasonality and be reflected in otolith zone formation (Beckman and Wilson, 1995). In the current study, the peak in the proportion of otoliths with opaque margins coincided with the peak in spawning activity (Chapter 3). Opaque zone formation was associated with spawning in populations of *S. commerson* in the Arabian Gulf (Grandcourt *et al.*, 2005), the east coast of Australia (Tobin and Mapleston, 2004) and Western Australia (Newman *et al.*, 2012). The variability in the timing of opaque zone formation in the otoliths of *S. commerson* is further evidence that controlling factors are a complex of environmental and endogenous factors (Beckman and Wilson, 1995).

In order to validate age estimates of a species, it is suggested that age of the fish at the formation of the first opaque zone should be identified (Campana, 2001). This can be undertaken through ageing from daily growth increments on otoliths. McPherson (1992) confirmed the age of the first year group by counting daily increments, assuming a constant relationship between increments and days. Although the temporal periodicity of micro-increments in *S. commerson* otoliths has not been validated, back-calculations of birth dates from the dates of capture estimate that juvenile *S. commerson* in Western Australia hatched during the spawning season (Newman *et al.*, 2012). In the current study, it was therefore assumed that the first opaque zone formed one year after the birth date.

4.4.3 Growth

The growth of *S. commerson* in KZN and MOZ was characterized by a very rapid initial increase in size with fish achieving a mean size of 84.1cm FL during the first two years of life. This rapid growth of young *S. commerson* concurs with data from related studies (Dudley *et al.*, 1992; McPherson, 1992; Govender, 1994; Grandcourt *et al.*, 2005; McIlwain *et al.*, 2005; Newman *et al.*, 2012). McPherson (1992) noted that gear selectivity was acting in the line fishery for *S. commerson*, and as such his average size of one year old fish was most likely over-estimated. Trent *et al.* (1983) acknowledged similar selectivity against small *S. cavalla* along the south-eastern coast of the United States. This has been overcome through the use of back-calculation methods allowing the estimation of lengths at ages of younger fish that are rarely observed in fishery-dependent samples (Campana, 2001), and enable biases associated with gear selectivity to be estimated (Campana, 1990; Ballagh *et al.*, 2006). Back-calculation of length at age has been a commonly used technique for describing the growth of large, fast-growing mackerels such as *S. cavalla* (Beaumariage, 1973; Johnson *et al.*, 1983; Collins *et al.*, 1989) and *S. commerson* (McPherson, 1992; Tobin and Mapleston, 2004; Ballagh *et al.*, 2006; Ballagh *et al.*, 2011) for which fishing gear typically selects for faster growing, younger fish. It is evident that the rate of growth in older fish is slower when compared to young fish (Figure 5.6). This observation is consistent with the fact that once fish reach maturity (Chapter 3), the available energy prior to and during the spawning season is mostly used for reproduction rather than continued somatic growth (Weatherly, 1972). A more accurate estimate of length at age may be achieved for younger *S. commerson* in KZN and MOZ by back-calculating from the first annulus for all fish (Ballagh *et al.*, 2006). This is because back-calculated lengths for younger fish may be assumed to better represent the entire population, as both fast and slower growing fish will be included in the sample (Ballagh *et al.*, 2006).

Differences in growth rates were evident between male and female fish. The observed growth curves, particularly for male *S. commerson* in KZN and MOZ displayed excessively high L_{∞} values corresponding to low K and t_0 parameter estimates. This was most likely due to the absence of smaller and younger fish in the samples and the strong correlation among VBGF parameters. Ferreira and Russ (1994) demonstrated that excluding smaller fish in an age and growth study can result in an overestimate of L_{∞} and an underestimate of K and t_0 . The lack of smaller fish in the current study is most likely due to biases associated with gear selectivity

and size selective mortality acting on *S. commerson* observed and adjusted length at age data (Campana, 1990). The lack of smaller fish in the current study is most likely due to biases associated with gear selectivity and size selective mortality acting on *S. commerson* observed length at age data as discussed above (Campana, 1990).

Female *S. commerson* approached their mean asymptotic length at a faster rate than males, as well as growing to a greater mean length at age. In previous research within the region, no attempts were made to fit growth curves to separate sexes of *S. commerson* or the closely related *S. plurilineatus*, as only a few of the specimens from which otoliths were sampled were sexed (Govender, 1994; Chale-Matsau *et al.*, 1999). Devaraj (1981) found that there were no differential growth characteristics between sexes for *S. commerson* in India. However, female *S. commerson* exhibited a larger asymptotic size compared to males throughout the waters of Northern (Buckworth, 1998), Western (Newman *et al.*, 2012) and Eastern (McPherson, 1992) Australia as well as within the waters of Oman (McIlwain *et al.*, 2005) and the Arabian Gulf (Grandcourt *et al.*, 2005) (Table 4.11). The value of K was slightly lower for female *S. commerson* compared to males in KZN and MOZ. This is consistent with the majority of research on *S. commerson* indicating a higher K value in males (McPherson, 1992; Grandcourt *et al.*, 2005; McIlwain *et al.*, 2005; Newman *et al.*, 2012). The growth parameters from the VBGF model for *S. commerson* in KZN and MOZ indicated lower K values compared to other studies in which these values were generally >0.2 (Table 5.11). Larger sample sizes, particularly for specimens closer to the maximum reported size and for juvenile fish less than 60cm FL would have improved the integrity of the results derived from the comparison of growth characteristics between sexes (Grandcourt *et al.*, 2005).

Table 5.11: Parameters of the von Bertalanffy growth function for *S. commerson* derived from length at age data.

VBGF parameter			Sex	Country/Region	Source
L^{∞}	K	t_0			
156.0	0.15	-3.50	Females	KZN and MOZ	This study
149.5	0.14	-3.50	Males	KZN and MOZ	This study
173.7	0.11	-4.22	Combined	KZN and MOZ	This study
134.3	0.29	-2.99	Combined	South Africa	Govender (1994)
136.1	0.24	-1.70	Females	Arabian Gulf	Grandcourt <i>et al.</i> (2005)
125.6	0.22	-2.30	Males	Arabian Gulf	Grandcourt <i>et al.</i> (2005)
138.6	0.21	-1.90	Combined	Arabian Gulf	Grandcourt <i>et al.</i> (2005)
140.4	0.31	-1.50	Females	Sultanate of Oman	McIlwain <i>et al.</i> (2005)
118.8	0.59	-0.73	Males	Sultanate of Oman	McIlwain <i>et al.</i> (2005)
146.4	0.22	-2.62	Combined	Sultanate of Oman	McIlwain <i>et al.</i> (2005)
155.0	0.17	-2.22	Females	Eastern Australia	McPherson (1992)
127.5	0.25	-1.72	Males	Eastern Australia	McPherson (1992)
183.3	0.10	-4.85	Females	Western Australia	Newman <i>et al.</i> (2012)
122.9	0.33	-1.83	Males	Western Australia	Newman <i>et al.</i> (2012)
116.9	0.70	-0.26	Combined	Western Australia	Newman <i>et al.</i> (2012)

The maximum age estimate for *S. commerson* in KZN and MOZ (14 year old female) was greater than the maximum age of six years estimated by Govender (1994) and that of Dudley *et al.* (1992) who estimated the oldest fish to be 12.7 years in Oman. It corresponds to that of McPherson (1992) who estimated the oldest fish to be a 14 year old female from samples taken off the eastern coast of Australia. Maximum age estimates of 17 years (Tobin and Mapleston, 2004) and 18 years (Newman *et al.*, 2012) were estimated for the east and west coasts of Australia. McIlwain *et al.* (2005) indicated that this species reached a maximum age of 20 years in Oman and Grandcourt *et al.* (2005) reported a maximum age of 16.2 years in the Southern Arabian Gulf. However, the largest *S. commerson* recorded in SA waters was 48kg (van der Elst 1993), significantly larger than the largest fish sampled in this study (33kg). It is thus likely that *S. commerson* may also reach greater ages in SA waters

The VBGF parameters estimated from length at age data are not directly comparable to those derived from tagging data (Francis, 1988b; Francis, 1995). Although realistic values for L^{∞} and K were estimated using the tag-recapture data, the VBGF model parameters predicted significantly slower early growth compared to observed (aged) samples. The size range of fish tagged within a cooperative tagging program can be difficult to control (Gillanders *et al.*, 2001). The majority of the fish used in the analyses were larger than the length at 50% maturity when the fish were first tagged.

By this stage of their life-history it is likely that growth had already slowed down significantly when compared to the initial spurt characterizing the first two years of growth in the species. This would result in the model reflecting the slower growth rates that occur in *S. commerson* that are evident once maturity has been reached (Gillanders *et al.*, 2001).

Estimating growth using tag-recapture data can lead to a number of biased results. It has been suggested that discrepancies between tag-recapture growth rates and predictions from other data sources are a result of either the capture event or the subsequent effect of external tags slowing growth (Attwood and Swart, 2000). Elasmobranch growth is particularly affected negatively by external tags (Ketchen, 1975; Davenport and Stevens, 1988; Gruber, 1982). Surprisingly, the growth rates estimated for tagged *S. commerson* using the methods of Attwood and Swart (2000) portrayed significantly faster growth compared to the growth rates estimated using length-at-age data. This suggests that external tags do not have the same depressing effect on *S. commerson* growth as has been found for a number of other line-fish species (Attwood and Swart, 2000; Brouwer and Griffiths, 2004). Research undertaken on a fast growing carangid, *Lichia amia*, along the South African coastline produced similar results while estimating growth rates from tag-recapture and otolith data (Smith, 2008). Despite the majority of tagged *L. amia* being small and therefore more likely to be susceptible to the effects of tagging, significantly faster growth rates were observed in the tagged individuals (Attwood and Swart, 2000; Smith 2008). This was attributed to *L. amia* being a robust species. Comparisons of growth rates derived from length-frequency, age at length and tagging data on another fast growing pelagic carangid, *Seriola lalandi*, in New South Wales, Australia showed agreement for fish aged two to four years but varied largely for fish with one growth zone (Gillanders *et al.*, 1999). The large differences in growth for younger fish compared to older fish may have been caused by inaccuracies in aging, influence of tagging on growth, within or between year differences, and variations in year-class strength (Gillanders *et al.*, 1999).

4.4.4 Conclusions

Aging *S. commerson* utilizing whole, unbaked, unburnt otoliths produced relatively consistent age estimations in KZN and MOZ. Opaque bands were formed on an annual basis between September and December, although false rings appear to occasionally occur during the first two years of growth. The annual deposition of

opaque bands was validated using tag-recapture data. Seasonal formation of opaque bands is likely to be linked to complex environmental and endogenous controlling factors. Growth during the first two years is extremely rapid in *S. commerson* prior to the onset of maturity. Following maturity, growth rates slow down rapidly with fish likely investing increased energy into reproduction. However, due to the selectivity of linefishing methods, it is likely that observed samples comprise the faster growing individuals in the population elevating the modelled growth rates early in the life-history of the species. Female *S. commerson* grow faster and live longer compared to males, with fish living between 14 and 20 years. Tagging data provided reasonable estimates of growth parameters in *S. commerson*. However, the majority of tagged and recaptured fish in the study were larger than the length at 50% maturity and had passed the initial growth spurt that is characteristic in the species. This resulted in slower growth being reflected in the tagging model over the first two years of their life-history.

Chapter 5

Mortality and biological reference points

5.1 Introduction

It is widely accepted that the fundamental purpose of fisheries management is to ensure sustainable production over time from a particular fish stock (Hillborn and Walters, 1992). The key to successful fishery management lies in limiting the long-term impacts of the fishery on the resource, but simultaneously trying to harvest as much of the resource as possible each year (King, 1995). A fisheries manager is therefore less interested in the life history parameters discussed in the preceding chapters, than in how they may be used to estimate the maximum yield or weight which may be taken from a stock without adversely affecting future reproduction and recruitment.

If the intensity of fishing effort on a fish stock is increased beyond a certain level, the biological system is thrown out of balance in two ways. First, young recruits entering the fishery may be caught before they grow to a commercially acceptable size known as growth overfishing. Secondly, the adult stock may be reduced to the extent that insufficient offspring are produced to maintain the population, known as recruitment overfishing. However, even in the absence of exploitation, the abundance of a fish stock can vary greatly as a result of environmental effects. Furthermore, the models used to predict the potential yield often rely on assumptions that are often not easily fulfilled. An important principle to consider is that it is extremely difficult to determine the potential yield from a fish stock without overexploiting it (Hillborn and Walters, 1992).

Surplus production models (biomass dynamic models) are the simplest of the commonly used stock assessment models (King, 1995). They have been widely used in managing fisheries due to their minimal data requirements, being based only on catch and effort data, which are relatively easy to obtain (Haddon, 2001). A major disadvantage of these models is that they are based on an extremely simple view of population dynamics as they ignore biological processes such as growth, recruitment and mortality that affect stock biomass (Hillborn and Walter, 1992). The proportion of

a stock that can be taken without recruitment overfishing is related to fecundity and life span, factors which are not specifically accounted for in surplus production models (King, 1995). Furthermore the concept of maximum sustainable yield is least appropriate for short lived, highly fecund species, where yield is more directly related to recruitment which varies greatly under the influence of environmental factors. Finally, the assumption of an equilibrium state fails to allow for the fact that the age structure of the stock, and therefore the biological parameters, alter with changing levels of exploitation.

Yield per recruit models examine the trade-off between capturing a large number of smaller fish early in their life span and capturing a smaller number of large fish later in their life span. The model considers the dependence of yield upon growth, age at first capture and fishing mortality (Beverton and Holt, 1957). The estimation of a spawner stock-recruitment relationship is difficult, and it is for this reason that the YPR model was developed. The model assumes equilibrium conditions with natural mortality, age at first capture and recruitment being constant over the fishable life of a cohort. A steady-state stock structure is therefore assumed in that the total yield in any one year from all age classes is the same as that from a single cohort over its whole life span.

The yield per recruit model is commonly used to suggest the changes in yield which would result from changing fishing effort and therefore fishing mortality, and by delaying the age at first capture (King, 1995). The main disadvantages of the model are its assumptions of a steady state, whereas in a stock where exploitation is increasing or natural mortality fluctuates, the proportion of number of fish in the various age groups, and even the stock parameters, are likely to be changing (Haddon, 2001). The exclusion of recruitment also means that the model provides no guide to the fishing levels at which recruitment overfishing occurs. This assumption is unreasonable as it suggests that no matter how high the fishing mortality rate, it would be impossible to overfish a stock that had constant recruitment, since in this case YPR is never reduced to zero (Shepherd and Pope, 2002). It is for this reason that the target reference points that form the basis of the management recommendations of a YPR analysis only provide an indication of the level of growth overfishing, but fail to address the threat of recruitment overfishing, which is thought to be the leading cause of stock collapse and depletion of many species (Myers *et al.*, 1997). It is therefore important to incorporate the results of spawner biomass per recruit (SBR) models in biological reference point recommendations as this will

maintain the reproductive capacity of stocks within safe biological levels (Butterworth, 1989).

Attwood (2002) suggested that the SBR should only be used as a relative measure of the spawning potential of the average recruit at a given fishing mortality rate (F). Obtaining reliable estimates of mortality presents one of the greatest challenges in fisheries stock assessment (Hillborn and Walters, 1992). Most studies that use SBR analysis have relied on Pauly's (1980) empirical equation to calculate natural mortality (M). The reliance on this method to calculate M is largely due to most fisheries assessments being carried out on already exploited populations. The majority of SBR assessments compare the current SBR to that of a theoretical pristine level. The pristine level is usually simply back-calculated from the exploited stock information by simulating an unfished scenario. It has been shown that fisheries-induced selection can alter certain variables such as growth, size/age at maturity and longevity (Haddon, 2001). As a result, estimates of pristine levels are likely to be inaccurate, highlighting the importance of a sensitivity analysis of a range of natural mortality rates to the outcomes of the SBR model.

Yield per recruit (YPR) and spawner biomass per recruit (SBR) models have frequently been used to assess the status of many southern African line-fisheries (*inter alia*: Bennett, 1988; Pulfrich and Griffiths, 1988; Smale and Punt, 1991; Buxton, 1992; Punt *et al.*, 1993; Govender, 1995; Chale-Matsau *et al.*, 2001; Mann *et al.*, 2002; Olbers and Fennessy, 2007). Although the assumptions upon which these models are based are not valid for many exploited stocks, the technique does allow a quantitative assessment of exploited fish stocks when few historical data are available (Haddon, 2001).

A number of biological reference points are utilized in the YPR and SBR analyses when assessing the current status of an exploited fishery or when recommending minimum size limits or target fishing mortalities. Reference points are divided into those that are considered a limit and those that are targets. Limit reference points are those fishing mortality (F) rates that should not be exceeded because of the risk of recruitment failure or of exceeding maximum yield levels (e.g. F_{max} ; F_{SB25}). Target reference points are used to guide managers to move towards a particular fishing mortality rate (e.g. $F_{0.1}$; F_{SB40}). F_{max} is the fishing mortality rate that maximizes YPR. The YPR model works best when applied to species with low natural mortality rates (King, 1995). If mortality rates are high, as is often the case in tropical species, the

yield per recruit curve may not be asymptotically shaped i.e. the curve may increase monotonically, thereby not reaching a maximum (F_{max}) within a reasonable range of fishing mortality values. In short lived species with high mortality rates, the results of YPR analyses may be misleading, often suggesting that an extremely high or sometimes infinite fishing mortality is required to secure the maximum yield (King, 1995). In short-lived species, assumptions of constant recruitment may be violated, and at higher levels of fishing mortality, recruitment may decline in spite of marginal predicted increases in yield (King, 1995). If the mean age at first capture is less than the mean age at sexual maturity, the spawning biomass per recruit (SBR) approaches zero at high levels of fishing mortality in spite of predictions of high values of YPR. Even if the age at first capture is greater than the age at 50% maturity, SBR may still be reduced to levels below that required to maintain recruitment at high levels of fishing mortality (Haddon, 2001). When a YPR curve continues to increase, or approaches a broad, flat-topped maximum, the optimum fishing mortality is sometimes taken to be the value at which an increase in one unit of F increases the catch by one tenth (0.1) of the amount caught by the first unit of F . In other words, the optimum level of F occurs at the point where the slope of the yield curve is 0.1 of the value of the slope at low levels of fishing mortality ($F_{0.1}$). Many fisheries managers are basing the total allowable fishing effort on $F_{0.1}$ as this is believed to be a more robust and conservative replacement for F_{max} . Similarly $F_{0.1}$ has been proposed since it produces nearly as much yield as F_{max} without reducing the spawning biomass as severely (Sissenwine and Shepherd, 1987).

The critical limit SBR reference point is imprecisely known in most species, but may be between 20 and 50% of the unexploited levels. Clark (1991) recommends for groundfish that maintaining a SBR at 35% of its unfished level will provide high yields at low risk even if there is no knowledge of the yield curve or spawner-recruit relationship. The management protocol developed for the South African linefishery (Griffiths *et al.*, 1999) classifies a stock's status into one of four management categories ranging from under-exploited to collapsed. These are defined by the biological reference points as described in Sections 6.2.4 and 6.2.5. Based on such biological reference points, optimum fishing mortality rates and minimum size limits can be evaluated in relation to some objective, such as maximizing YPR (Govender, 1995). Usually there is a trade-off between maximizing YPR and maintaining the SBR at a reasonable level.

Currently the *S. commerson* fishery in MOZ and KZN is regulated only by a catch limit of 10 fish per person per day for recreational fishers (commercials are unlimited in terms of a daily bag limit but are limited in terms of total allowable effort). However there are no restrictions on the MOZ artisanal fishers. Additionally in the Sofala Bank area, the inshore three nautical miles are reserved exclusively for artisanal fisheries.

Recently a Direct Principal Component method has been developed to standardize CPUE within a Generalized Additive Model (GAM) framework, potentially unlocking the key to utilizing catch records to be applied for routine stock assessment applications (Winker *et al.*, 2013). However, in the absence of a reliable catch and effort time series, the utilization of a per-recruit analysis is still likely to be the best method for stock assessment of *S. commerson* at present (C. Attwood, UCT, pers. comm.). Biological reference points were estimated for *S. commerson* captured in the linefishery off KZN and MOZ utilizing a per-recruit model. Based on the assumption of a single stock within KZN and MOZ, a per-recruit assessment was undertaken for the region as a whole. As a result of the differences in growth between male and female *S. commerson*, Govender (2006) undertook sex-specific per-recruit assessments within Omani waters. However, management of the *S. commerson* fishery is impossible on a sex-specific basis and as such mortality and per-recruit assessments were only undertaken within the region described above using growth and mortality rates determined for combined sexes. A range of mortality estimates for *S. commerson* was also investigated. Total mortality was estimated from length-converted age data while natural mortality was estimated from various methods that relate life history parameters to the rate of natural mortality. Sensitivity of the biological reference points to a range of natural mortality rates was examined. The imposition of minimum size limits was evaluated by analysing the potential biological benefits to the fish population.

5.2 Materials and Methods

5.2.1 Mortality

The data and parameters used in determining the mortality rate estimates of *S. commerson* are reported on in Chapter 3 and 4. The instantaneous rates of total (Z), natural (M) and fishing (F) mortality were estimated for KZN and MOZ as a combined region.

Total mortality rate (Z)

The total instantaneous rate of total mortality (Z) was estimated by two different techniques. Firstly an age length key for combined sexes was developed with length-at-age data following the method of Ricker (1975) (Chapter 3). This was used to convert aggregated length frequency data (Chapter 3) into an age frequency distribution. The annual instantaneous rate of total mortality (Z) was subsequently determined using the age-based catch curve method (Beverton and Holt, 1975). The natural logarithm of the number of fish in each age class was plotted against the corresponding age and Z was estimated from the descending slope of the best fit line using a least-squares linear regression. Initial ascending points representing fish that were not fully recruited into the fishery were excluded from the analysis (i.e. slope calculated from the top of the catch curve). In the second method Z was estimated using the following equation (Butterworth *et al.*, 1989):

$$Z = \ln \left[1 + \frac{1}{a_m - a_r} \right] \quad 5.1$$

where a_r is the age at full recruitment into the fishery and a_m is the mean age of all fully recruited fish sampled, with approximate 95% confidence limits:

$$Z \pm 2 \frac{Z}{\sqrt{N}}$$

where N is the number of fully recruited fish sampled.

Natural mortality rate (M)

Two empirical equations were used to estimate the instantaneous natural mortality rate (M) for the the combined region. Firstly M was estimated using the empirical equation derived by Hoenig (1983) expressed as:

$$\ln(M) = 1.46 - 1.011 \ln(t_{max}) \quad 5.2$$

Where t_{max} (years) is the maximum observed age, set at 14 years.

Secondly, M was estimated using the Pauly's (1980) empirical equation:

$$\ln(M) = -0.0066 - 0.279\ln(L_{\infty}) + 0.6543 \ln(K) + 0.463 \ln(T) \quad 5.3$$

where L_{∞} (cm TL) and K (y^{-1}) are parameters estimated from the von Bertalanffy growth function as estimated in Chapter 4 and T ($^{\circ}\text{C}$) is the mean annual surface water temperature. The mean environmental temperature was taken to be 25°C for the combined region of KZN and MOZ. A range of values from 20 to 29°C was used to determine the sensitivity of M to changes in temperature. The parameter L_{∞} was converted from FL to TL using the FL/TL relationship estimated in Chapter 4.

Fishing mortality rate (F)

The annual instantaneous rate of fishing mortality (F) was calculated by subtracting the natural mortality rate from the total mortality rate derived from the age-based catch curve ($F = Z - M$). The calculation was also made for the upper and lower 95% confidence intervals for Z in order to derive a range of fishing mortality rate estimates.

Exploitation rate

The exploitation rate (E) was calculated as the proportion of fishing mortality relative to total mortality ($E = \frac{F}{Z}$).

5.2.2 Per-recruit analysis

The status of the *S. commerson* stock in KZN and MOZ was assessed using a per-recruit analysis. Growth and biological parameters used in the per-recruit analyses were obtained from Chapters 3 and 4. Two variables, the yield-per-recruit (YPR) and spawning biomass-per-recruit (SBR), were calculated for various fishing mortalities ranging from zero to very large values. A maximum age of 14 years was assumed for *S. commerson* corresponding to the oldest individuals observed in the sample. The SBR (expressed in mass g) for the combined regions was calculated using the following equation:

$$SBR(F, S_t) = \sum_{t=0}^{t_{max}} W_t \widetilde{N}_t G_t \quad 5.4$$

where W_t is the weight of fish at age t , G_t is the maturity at age t , t_{max} is the age of the oldest aged fish in the population, and \tilde{N}_t is the number of number of fish at age t calculated as:

$$\tilde{N}_t = 1 \quad \text{if } t = 0$$

$$\tilde{N}_t = \tilde{N}_{t-1} \exp^{-M-S_{t-1}F} \quad \text{if } t > 0$$

where M and F are the natural and fishing mortality rates and S_t is the selectivity of the fishing gear on fish of age t years. In this analysis selectivity has been assumed to be knife-edged so that:

$$S_t = 0 \quad \text{if } t < t_c$$

$$S_t = 1 \quad \text{if } t \geq t_c$$

where t_c is the age at first capture and was assumed to be represented by the age corresponding to the top of the catch curve. Maturity, G_t , was also assumed to be a knife-edge process:

$$G_t = 0 \quad \text{if } t < t_m$$

$$G_t = 1 \quad \text{if } t \geq t_m$$

where t_m is the age-at-50% maturity.

YPR for each region was calculated as:

$$YPR(F, S_t) = \sum_{t=0}^{t_{max}} W_{t+\frac{1}{2}} S_t \frac{F}{M+S_t F} \tilde{N}_t (1 - \exp^{-M-S_t F}) \quad 5.5$$

where YPR is the yield per recruit in mass (g) for age class t and the other parameters are defined as in equation 5.4. The impact of the estimated current F can be quantitatively assessed against the assumed pristine (unexploited) steady state of the population which is usually simply estimated by setting $F = 0$.

5.2.3 Management scenarios

A number of different management strategies that were different from the current base case were evaluated. The different strategies were compared to the base case to evaluate the sensitivity of the per-recruit approach to variation in life-history and mortality estimates; and to evaluate the best compromise between the conservation of SBR and maximizing of YPR:

Scenario 1: A baseline assessment was undertaken whereby the current status of the *S. commerson* fishery was assessed for MOZ and KZN.

Scenario 2: The sensitivity of the per-recruit model for the combined region to various estimates of M and the resultant biological reference points were tested to investigate the potential bias when using an empirical equation to estimate M .

Scenario 3: Various ages/lengths at first capture were examined in the per-recruit analysis to determine the impact that different minimum size limits would have on the fishery.

5.2.4 Biological reference points

A number of biological reference points were estimated in order to determine the current status of the *S. commerson* resource off the coast of KZN and MOZ, as well as to evaluate the effectiveness of possible new regulations. Target reference points estimated were $F_{0.1}$ and F_{SB40} . Limit reference points estimated were F_{MAX} and F_{SB25} .

5.2.5 Stock status

The status of the stock was classified into one of four management categories, defined by the biological reference points as described by Griffiths *et al.*, (1999) (Table: 5.1):

Table 5.1: Description of the stock status categories and their associated biological reference points for the *Scomberomorus commerson* linefishery in KwaZulu-Natal and southern Mozambique. $SBR_{F=0}$ refers to the spawner biomass per recruit at the theoretical pristine state.

Status	Description	Reference Point
Under-exploited	The fishery has not impacted substantially on the stock.	$SBR > 50\% SBR_{F=0}$
Optimally-exploited	The SBR ratio of the stock corresponds to the target reference point range.	$40-50\% SBR_{F=0}$
Over-exploited	The SBR ratio of the stock lies between the target and limit reference points. The stock is over-exploited; producing less than optimum yield, but the immediate risk of collapse is low.	$25-40\% SBR_{F=0}$
Collapsed	The SBR ratio of the stock lies below the threshold limit reference point. It is over-exploited, and there is a high risk of recruitment failure and stock collapse.	$<25\% SBR_{F=0}$

5.3 Results

5.3.1 Mortality

Mortality estimates

The linear-based catch curve (Ricker, 1975) estimates of Z differed markedly from those estimated using equation 5.1 (Table 5.2, Figure 5.1). The catch curve provided estimates of Z higher than those using equation 5.1. A precautionary approach was utilised whereby the average of these two estimates was considered to be the best estimate of Z (Govender, 1995). The estimate of F was therefore 0.21 for the combined region.

Table 5.2: Estimates of natural mortality (M), total mortality (Z) and the exploitation rate obtained for *Scomberomorus commerson* combined sexes in southern Mozambique and KwaZulu-Natal.

Combined region	
M (Pauly, 1980)	0.24
M (Hoenig 1983)	0.30
Average M	0.27
Z (Ricker, 1975)	0.52 ± 0.06
Z (Butterworth, 1989)	0.43 ± 0.05
Average Z	0.48
F	0.21
E	0.44

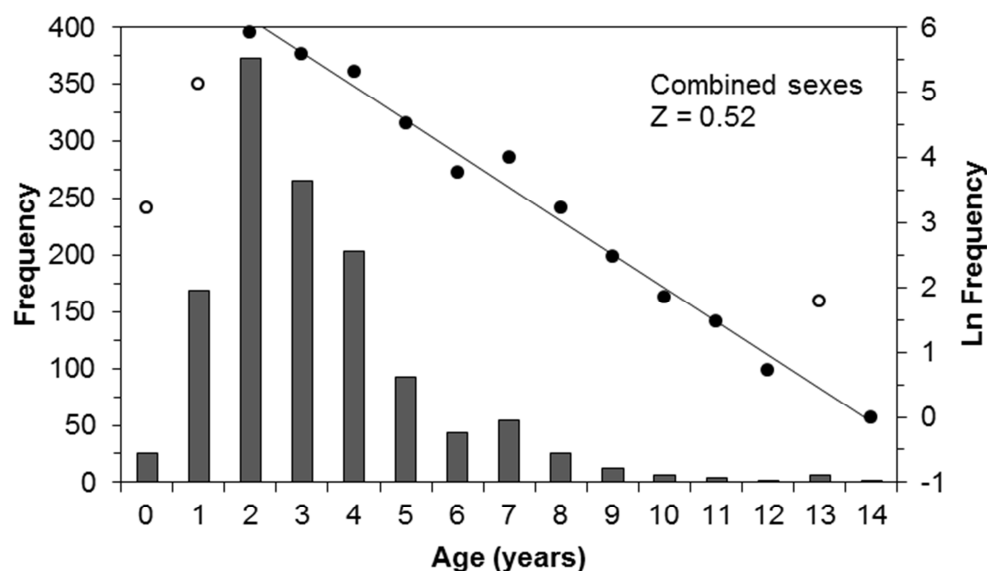


Figure 5.1: Total mortality rate (Z) estimate derived from the regression based catch curve analysis for *Scomberomorus commerson* in southern Mozambique and KwaZulu-Natal. Filled circles indicate points that were used in the analysis and open circles indicate points that were excluded from the analysis.

The effect of temperature on the estimates of natural mortality (M) using equation 5.3 is shown in Table 5.3. Temperature had little effect with estimates of M ranging from 0.22 to 0.26 over 10°C .

Table 5.3: Estimates of natural mortality (M) using Pauly's (1980) empirical equation for *Scomberomorus commerson* sampled in KwaZulu-Natal and southern Mozambique over a range of temperatures.

Temperature (°C)	Natural mortality (M)
20	0.22
22	0.23
24	0.24
26	0.24
28	0.25
30	0.26

5.3.2 Per-recruit analysis

The values of the parameters utilised in the per-recruit analysis are given in Table 5.4. The catch curve indicated that *S. commerson* were fully recruited (S_{50}) into the fishery by two years of age. Age at 50% maturity (t_m) was estimated at 0.7 years for males and 1.6 years for females (see Chapter 3). A conservative approach was undertaken and as female *S. commerson* mature at a greater size and age compared to males, this value (t_m) was utilized for the analysis of combined sexes.

Table 5.4: Input growth parameter values, mortality and biological estimates utilized in the per-recruit analyses for *Scomberomorus commerson*.

Parameter	Combined
L_{∞} (cm)	173.69
K (year ⁻¹)	0.11
t_0 (year ⁻¹)	-4.22
M (year ⁻¹)	0.27
F (year ⁻¹)	0.21
S_{50} (years)	2
t_M (years)	2
a	0.0035
b	3.18

At the current fishing mortality rates the SBR for MOZ and KZN was estimated at 49% compared to a state of no exploitation (Figure 5.2). This indicates that the stock

status of the *S. commerson* fishery is optimally exploited in the combined region of KZN and MOZ.

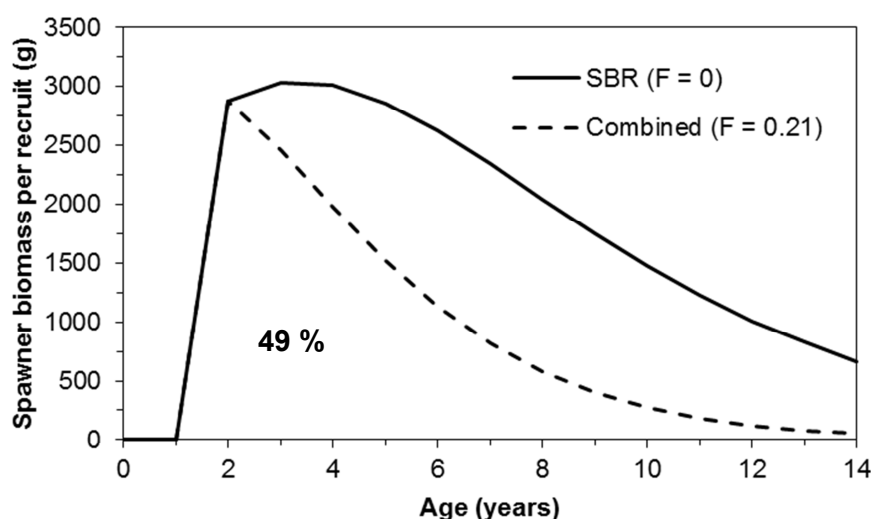


Figure 5.2: Spawner biomass per recruit at the current fishing mortality rates ($F_{current}$) compared to a state of no exploitation ($F=0$) for combined sexes of *Scomberomorus commerson* in southern Mozambique and KwaZulu-Natal combined.

The SBR and YPR curves for KZN and MOZ are shown in Figure 5.3. For Scenario 1 (Baseline), the YPR curve does not attain an asymptote, indicating that the maximum yield is only obtained at unrealistically high rates of fishing mortality ($>1.2 \text{ year}^{-1}$). The $F_{0.1}$ reference point however provided more reasonable values, indicating that maximum yield will be obtained at a fishing mortality rate of 0.28 year^{-1} for the region (Table 5.5). Regionally, the SBR would be reduced to 40% at fishing mortality rates at 0.29 year^{-1} . The SBR for the combined sexes would be further reduced to 25% of its pristine state at a considerably higher fishing mortality rate of 0.59 year^{-1} . The proportion of YPR increased largely with an increase in F from 0 to 0.3 year^{-1} , after which YPR rose extremely slowly, remaining almost constant from an F of 0.5 year^{-1} .

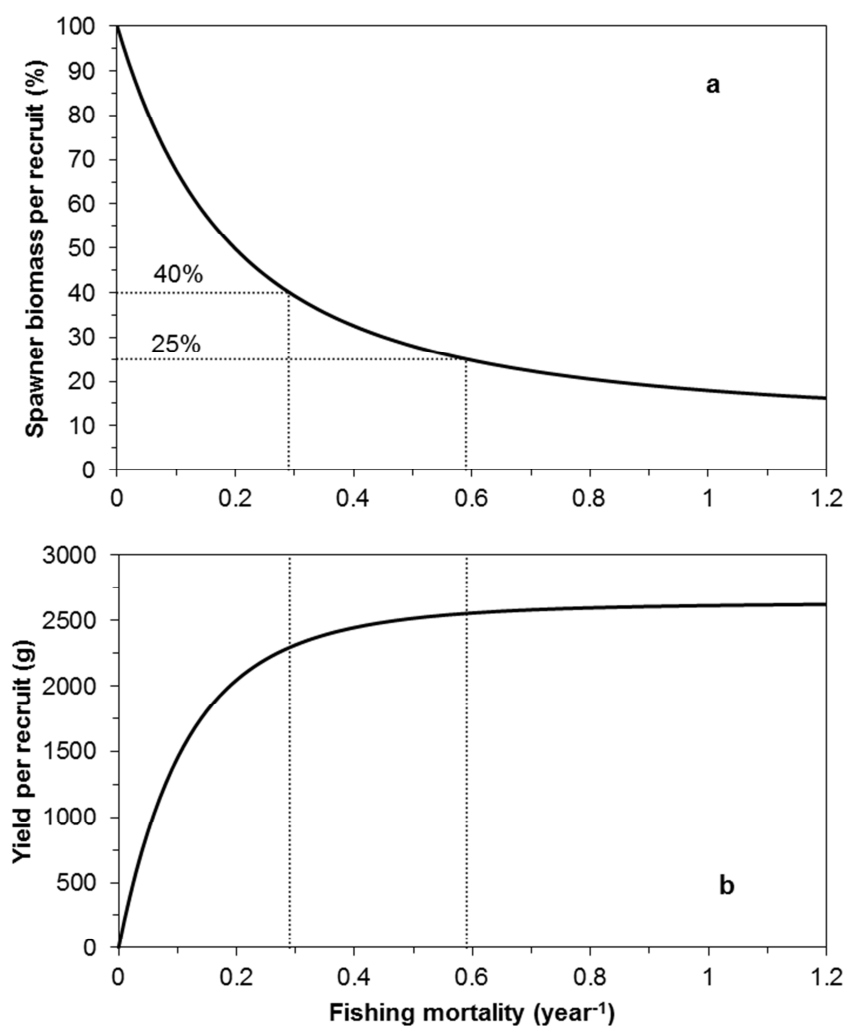


Figure 5.3: Projected trajectories of (a) spawner biomass per recruit and (b) yield per recruit based on the input parameters (Table 5.4) for *Scomberomorus commerson* in southern Mozambique and KwaZulu-Natal combined (with target and threshold reference points indicated by a dotted line).

Table 5.5: Target and threshold reference points estimated for the *Scomberomorus commerson* fishery in southern Mozambique and KwaZulu-Natal.

Reference point	
F_{max}	/
$F_{0.1}$	0.28
F_{SB40}	0.29
F_{SB25}	0.59

The sensitivity analysis of the per-recruit curves and their associated biological reference points displayed a high degree of variation between different M values for the combined regions (Table 5.6). At low rates of natural mortality ($M = 0.1$),

biological reference points were at substantially lower rates of fishing mortality and the opposite was true for high rates of natural mortality ($M=0.4$). At greater natural mortality rates ($M=0.5$) the threshold reference point of F_{SB25} became too large to be realistic.

Table 5.6: Biological reference points for *Scomberomorus commerson* based on a range of natural mortality rates (M). Other input parameters are shown in Table 5.4.

Reference point	$M = 0.1$	$M = 0.2$	Base case ($M = 0.27$)	$M = 0.4$	$M = 0.5$
Combined					
F_{max}	0.24	0.49	/	/	/
$F_{0.1}$	0.15	0.22	0.28	0.45	0.62
F_{SB40}	0.17	0.23	0.29	0.48	0.72
F_{SB25}	0.29	0.43	0.59	1.20	/

Table 5.7 indicates the potential benefits that can be realized for three different minimum size limits based on 1 (± 75 cm FL), 2 (± 85 cm FL) and 3 (± 90 cm FL) year old fish. Figure 5.4 illustrates the per-recruit analyses based on these minimum sizes for *S. commerson* from KZN and MOZ combined. With all three trajectories it can be shown that by increasing the size/age at first capture there is a corresponding increase in SBR. Strangely, the YPR curves for the three minimum size/age limits are almost the same. As the minimum size/age at first capture increases fishing effort could theoretically be increased to achieve the predicted biological reference points displayed in Table 5.7.

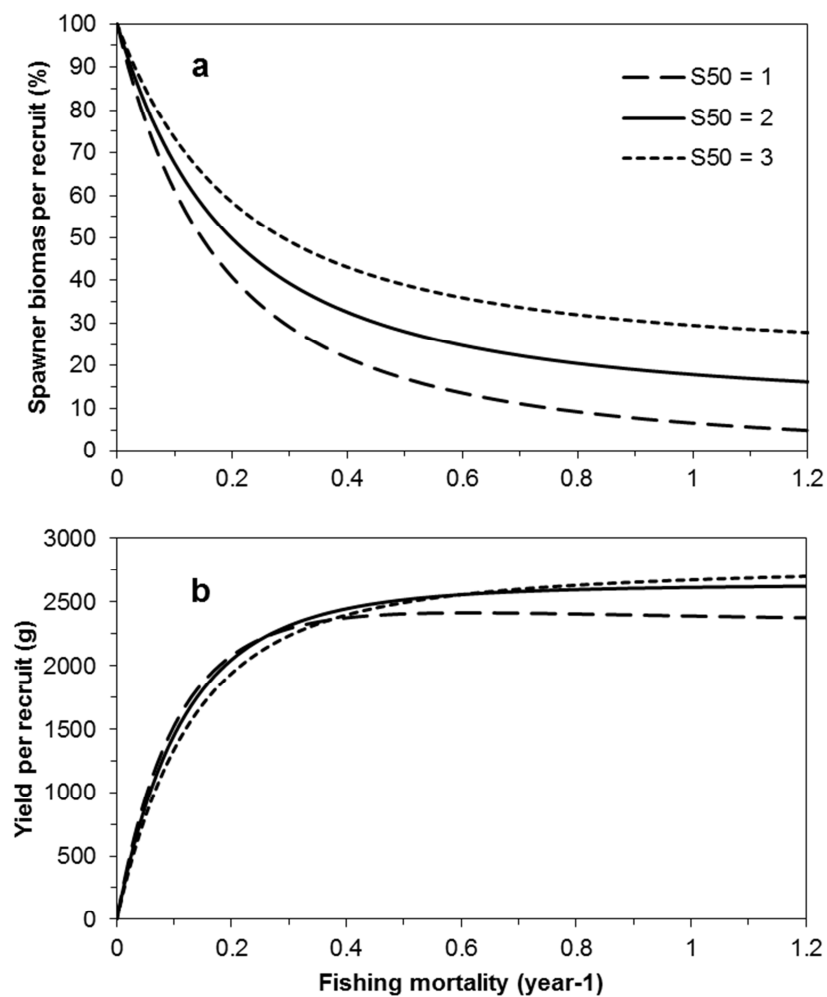


Figure 5.4: Spawning biomass-per-recruit (a) and yield-per-recruit (b) based on *Scomberomorus commerson* from southern Mozambique and KwaZulu-Natal combined for three different minimum size limits.

Table 5.7: Biological reference points for combined sex *S. commerson* for three minimum size limits in KwaZulu-Natal and southern Mozambique.

Reference point	S ₅₀ = 1	S ₅₀ = 2	S ₅₀ = 3
F_{max}	0.62	/	/
$F_{0.1}$	0.24	0.28	0.32
F_{SB40}	0.20	0.29	0.47
F_{SB25}	0.35	0.59	>1.20

5.4 Discussion

5.4.1 Mortality

The instantaneous rate of total mortality (Z) estimated was 0.48 year^{-1} for *S. commerson* in the combined region. Tobin and Mapleston (2004) estimated similar total mortality rates to those of KZN and MOZ at 0.40 and 0.35 year^{-1} for the commercial and recreational fisheries, respectively, in eastern Australia. The previous estimates of Z for *S. commerson* in South African waters (0.75 year^{-1}) were much higher than that found in the present study (Govender, 1995) but are likely as a result of the different age estimates used (see Chapter 4). High rates of total and fishing mortality for *S. commerson* have been reported in Oman (Al-Hosni and Siddeek, 1999; McIlwain *et al.*, 2005; Govender *et al.*, 2006 Meriem *et al.*, 2006) and the southern Arabian Gulf (Grandcourt *et al.*, 2005; Shojaei, *et al.*, 2007). Govender *et al.* (2006) estimated Z values for male and female *S. commerson* of 0.89 and 0.90 year^{-1} in Omani waters. Newman *et al.* (2012) estimated sex and regionally-specific Z values using catch curves along the west coast of Australia. For all the regions, females possessed a higher rate of total mortality compared to males. *S. commerson* in the most northerly Kimberly region possessed the highest rate of total mortality (0.60 year^{-1} for females, 0.44 year^{-1} for males) compared to the more southerly Pilbara (0.29 year^{-1} for females, 0.17 year^{-1} for males) and West Coast (0.38 year^{-1} for females, 0.22 year^{-1} for males) regions.

The use of a catch curve can result in an overestimate of Z if there is a lack of fish numbers sampled in the larger length classes or an inflated number of smaller/younger fish, as this will result in a steeper regression curve (Govender, 1995). Similarly, equation 5.1 may also overestimate the Z value if the mean age of fully recruited fish (a_r) is underestimated, which was probably the case for *S. commerson* in the study conducted by Govender (1995). The upwards bias can potentially be due to the differential targeting of younger schooling fish (Grandcourt *et al.*, 2005). Furthermore, McPherson and Williams (2002) considered that certain gear types resulted in larger older fish being proportionately higher on fishing grounds than their representation in catches would suggest. As it was uncertain as to which method provided the more reliable estimate of Z , the method used by Govender (1995) was utilized whereby the average Z value obtained from both methods was selected. The impact of fishing, however, cannot be discounted, especially given the

intensity and limited quantified data from the fisheries targeting *S. commerson* in KZN and more specifically in MOZ.

The M estimates in this study varied over the temperature range and between estimation methods. Whilst estimates derived from the Hoenig (1983) relationship have been shown to provide a reasonable approximation of M in tropical species (Hart and Russ, 1996; Newman *et al.*, 1996; Grandcourt *et al.*, 2005), the generalized nature of the derivation of this parameter is a potential source of error. Estimates of natural mortality derived from the empirical equation of Pauly (1980) have been shown to commonly overestimate M (Russ *et al.*, 1998; Newman *et al.*, 2000). Furthermore, Pauly (1980) found that the standard deviation of $\log M$ to be 0.245, equivalent to an M range of one-third to three times the estimate of M . Fisheries assessments are sensitive to estimates of M (Vetter, 1988). For this reason, the per-recruit analysis should be repeated using different values of M in order to assess the sensitivity of the results to this potential inaccuracy (Butterworth *et al.*, 1989). In light of this uncertainty, a precautionary approach has been adopted and the average M value taken from the two methods was adopted (Govender, 1995; Dankel *et al.*, 2012). It is however still important to note that the estimates of M derived in this study are likely to be overestimates, as they may include an unknown component of fishing mortality (F). This is likely to occur due to the maximum age parameter in the Hoenig (1983) equation, which is why this method is more commonly used for lightly exploited stocks.

The best estimate of the natural mortality rate was 0.27 year^{-1} for the combined region. This estimate was much lower than those estimated by other authors using only Pauly's empirical equation. Govender (1995) estimated a natural mortality rate ranging from 0.45 to 0.55 year^{-1} in South Africa. Dudley *et al.* (1992) estimated the natural mortality rate of *S. commerson* as 0.44 year^{-1} while Govender (2007) estimated similar rates of 0.49 and 0.38 year^{-1} , both in the Gulf of Oman. A similar value of M to the current study was reported by Grandcourt *et al.* (2005) ($M = 0.26 \text{ year}^{-1}$) using the Hoenig (1983) relationship. Welsh *et al.* (2002) and Hoyle (2003) used a natural mortality rate of 0.34 year^{-1} in their assessment models for *S. commerson* in eastern Australia though this value was also considered to be an overestimate. Along the west coast of Australia a lower M was estimated to be in the range 0.16 to 0.20 year^{-1} (Newman *et al.*, 2012).

5.4.2 Per-recruit analyses

Based on the results of this study the regionally combined *S. commerson* SBR is at 49% of the unfished levels meaning the species is being optimally-exploited off the coast of MOZ and KZN.

The mean size at which fish were fully recruited to the fishery was considerably larger than the size at 50% maturity. Male *S. commerson* reach a length at 50% maturity at 65cm (± 0.7 years) compared to 82cm (± 1.5 years) for females. The length at which fish were fully recruited to the fishery by linefishing were larger (80cm for males; 90cm for females) and older (2 years for both males and females) than the lengths at 50% maturity. However, the length at first capture was a great deal smaller than the lengths/ages at 50% maturity (49.6cm FL). As such, a large proportion of the catch by number ($\pm 30\%$) was being targeted and captured between the length at first capture and the length at full recruitment. Age and growth research comparing back-calculations with age at length data for *S. commerson* along the east coast of Australia has shown that the majority of the younger fish (<2 years) being selected for in the linefishery are the faster growing more aggressively feeding individuals (Ballagh *et al.*, 2006; Ballagh *et al.*, 2011). However, the majority of *S. commerson* of these younger ages have not yet reached the length at full recruitment to the fishery. Line-fishing, the only method used to capture *S. commerson* in KZN, selects for fish predominantly larger than the length at 50% maturity and as such, fishing mortality is currently at a lower rate than all the limit and target biological reference points. In MOZ, however, there is much uncertainty regarding the current fishing mortality rates in due to an excessively high fishing pressure being place upon the *S. commerson* resource in MOZ as well as an unquantified number of smaller/younger *S. commerson* being captured using other fishing methods that do not select for larger fish. Exceedingly high fishing pressure can simply be accounted for by the illegal, unreported and unregulated fisheries in MOZ driven predominantly by foreigners as described in Chapter 1.

Although not identified to the species level, Scombridae made up 16% of the beach seine fishery, 10.3% of the surface gill-net fishery and 22% of the bottom gill-net fishery compared to 10% for the linefishery by weight in Nampula Province, Mozambique during 1999 (Baloi *et al.*, 2000). However, although Scombridae contribute substantially to the artisanal fisheries by weight, this may be skewed due to their large size compared to other species being caught (ie. Clupeidae,

Chirocentridae, Mugilidae etc.). This stresses the need for additional quantitative research on these fisheries. Nonetheless, this indicates that the status of the *S. commerson* stock is likely to be impacted by the artisanal beach seine and gill-net fisheries in MOZ and not just linefishing on its own. The migration of *S. commerson* into KZN may therefore provide a limited form of refuge for young (<2 years) individuals from exploitation. While these younger individuals are in KZN they would be less likely to be captured compared to the fishing gears selecting for smaller individuals used in MOZ. This may provide young, slower growing *S. commerson* with a much greater chance of reaching the size/age at maturity prior to their capture.

Clearly the seasonal abundance of *S. commerson* combined with the biological findings in the current study indicates a single stock within KZN and MOZ. It is likely that the stock is of a metapopulation-type stock structure with a permanent resident population in MOZ and random offshoots undertaking a south-north migration each year. This is similar to what has been established to exist along the east (Williams and Lester, 2006) and west (Lester *et al.*, 2001) coasts of Australia. Williams and Lester (2006) concluded that the permanent north-east and seasonal south-east Australian *S. commerson* comprised a single stock with extensive mixing. The seasonal fishery along the south-east coast was based on a random group of fish with the same origin as the fish on the north east coast and not a subpopulation that moves south each year. This is opposed to the northern Australian stock structure characterised by a lack of any substantial movement of fish among spatially discrete assemblages (Moore *et al.*, 2003; Newman *et al.*, 2009). A metapopulation-type stock structure suggests the importance of effective management of *S. commerson* in MOZ, whilst providing an important aspect to consider for future research.

The basic per-recruit analyses simulated the way that most present-day stock assessments are conducted by only using information collected from exploited fish stocks. An analysis was conducted to investigate the extent to which the traditional empirical estimates of M influence the model outputs. It is evident that even slight variations in the value of M introduce a degree of uncertainty into the fishery assessment model outputs. For example a deviation of M by 0.1 for the combined region with a fishing mortality rate of 0.21 year^{-1} alters the $F_{SBcurrent}$ by 8-10%. Govender (1995), however found that although estimates of biological reference points varied for the range of M values examined, $M = 0.2-0.3$ and $M = 0.5-0.7 \text{ year}^{-1}$ produced very comparable results with little variation in estimates of the biological reference points. Despite the inherent difficulty in obtaining reliable estimates of

natural mortality for many fish stocks, almost all mathematical models of fish stock dynamics require M as an input parameter (Vetter, 1988; Hillborn and Walters, 1992). Therefore, the use of empirical equations to obtain estimates of M has become common practice in fisheries science, despite these models not necessarily producing reliable estimates as a result of variation among these stocks.

Gulland (1970) suggested that in an optimally exploited stock, fishing mortality should be about equal to natural mortality resulting in an exploitation rate of 0.5 year^{-1} . However, exploitation rates should be very conservative considering that potential yields may be over-estimated by a factor of 3 to 4 where $F = M$ (Beddington and Cooke, 1983). Govender (1995) predicted, using per-recruit analyses, a virtual collapse of the *S. commerson* fishery off South Africa when the fishing mortality rate was equal to the natural mortality rate. Noting the uncertainty in the estimates of F and M , this study estimated F was less than M in the combined region. This implies that fishing pressure in the combined region on a whole is not at a biologically critical level, however pressure on the resource arising from the fishing effort from within MOZ is unknown.

These estimates are supported by the numbers of older fish sampled from each sex and region. In the combined region the oldest male was 13 compared to the oldest female at 14. Regionally, the oldest fish sampled in MOZ was only seven years. The small number of older fish sampled in MOZ is likely to be a result of sampling bias on a limited temporal and spatial scale. The length frequency data used in the catch curve estimates of Z (Chapter 3) indicate that although larger/older individuals are infrequent, it is not on the scale estimated by the sampling data thus confirming the bias. The level of fishing pressure in MOZ is likely to be higher than in KZN, although to what extent this is due to other fishing methods selecting for smaller fish compared to linefishing is not known. The level of fishing pressure in both KZN and MOZ is likely to be driven by increases in demand and human population growth. If increases in fishing effort are realized, the status of *S. commerson* populations in the region will need to be re-assessed.

For the combined sexes, a modelled increase in the size at first capture resulted in the *S. commerson* resource being increasingly resistant to exploitation. By selecting for increasingly larger fish, biological reference points indicate that *S. commerson* would be tolerant of a higher fishing effort, would have a greater SBR and relatively stable yields. This is consistent with the results of Govender (1995), who suggested

that the three minimum size limits (based on length at 50% maturity and the associated 95% confidence limits) would roughly maximize the YPR at the same fishing effort. However conservation of the SBR increases with an increase in size at capture. In principle, setting a minimum size above the length at 50% maturity will offer a refuge for immature and first spawning individuals. Although males (1 year) and females (2 years) have already reached the length at 50% maturity by the age at first capture, a substantial number of individuals are captured prior to two years of age. Setting a minimum size limit at 80cm FL (1.5 years) will ensure that both males and females would have had the opportunity to spawn at least once prior to capture. Although the fishery off KZN is in a healthy state, this strategy will not only benefit local fishermen in KZN, but also relieve pressure on the species in MOZ owing to the coastal migratory nature of *S. commerson*. However, implementation of a minimum size limit in the beach seine and gill-net fisheries in MOZ could prove problematical.

5.4.3 Conclusions

In this study the natural mortality rate was estimated to be 0.27 year^{-1} for the KZN and MOZ region. This was lower than the majority of previous research estimates that utilized Pauly's (1980) empirical equation. The estimate obtained in this study was, however comparable to a number of studies utilizing Hoening's (1983) empirical equation or an average of the estimates obtained using the two methods. The F estimate for the combined regions was 0.21, relatively smaller than the estimated natural mortality rate (0.27). This suggests that the fishing effort is not at a critically high level in the combined region. Additional research is required in MOZ to better understand the different mortality rates for non-size selective fishing gears such as beach seines and gill-nets.

The YPR and SBR analyses indicate that the per-recruit estimates are highly sensitive to M . The per-recruit analyses for the combined region of MOZ and KZN indicate that the fishery is being optimally-exploited with a current SBR at 49% of its unfished level. Exploitation of *S. commerson* is unlikely that this is due to linefishing alone, as the size at full recruitment into the fishery is larger than the length at 50% maturity. This may therefore be either due to IUU fisheries heavily exploiting the *S. commerson* resource, or due to the artisanal beach seine and gill-net fisheries that are non-size selective and catch large quantities of juvenile *S. commerson* during certain times of the year.

Chapter 6

Conclusion and Management Considerations

6.1 Introduction

Information on the biological characteristics of a species is crucial for the successful management of its fisheries (King, 1995). The biology and life-history of *S. commerson*, as investigated in Chapters 1 – 4 provide ample evidence to support the assumption of a single stock existing off the coast of southern MOZ and KZN. It is therefore important that national strategies be implemented with a regional objective to ensure effective management of this shared stock.

This project encapsulates our current understanding of the biological characteristics of the *S. commerson* fishery in the region, thereby facilitating its analysis and assessment. Some of the life-history traits displayed by *S. commerson* render the species susceptible to overexploitation. The potential metapopulation stock structure, highly aggregated schooling, voracious feeding behaviour, and predictable seasonal occurrence facilitate targeting of *S. commerson* (Tobin and Mapleston, 2004). These factors combined with the species' reproductive biology, larval survival and consequent abundance being positively dependent on favourable climatic conditions renders the stock potentially susceptible to over-fishing, localized depletion and stock collapse. In contrast, the extremely fast growth of *S. commerson* prior to the onset of maturity combined with the relatively small size at 50% maturity (i.e. maturity is reached before the size at full recruitment into the linefishery) provide support for the species' resilience to heavy fishing pressure.

It is the susceptibility of the species to other fishing methods that selects for fish prior to the onset of maturity that creates cause for concern. The results of the mortality and per-recruit analyses in Chapter 5 support this postulation by concluding that while the SBR in the region is at 49%, a lack of quantifiable data in MOZ where a variety of fishing gears target the species creates cause for concern. This indicates a clear requirement for the improved management of the *S. commerson* fishery in MOZ.

6.2 Management options

The *S. commerson* fishery in KZN and MOZ is essentially an open access fishery. Currently the only restrictions on *S. commerson* are a bag limit on recreational catches while commercial and artisanal fishermen have no restrictions on catch. Questions regarding the suitability and sustainability of this strategy have been raised in recent years. Common management options utilized to reduce fishing effort may include minimum size or bag limits or closed seasons or areas, although usually a combination of these restrictions is implemented.

6.2.1 Closures

Temporal or spatial closures of a fishery during certain time periods, or in particular areas, or a combination of both, are commonly utilized to protect the spawning stock and/or small juveniles. Closed seasons during a well-defined spawning period can allow adults to breed without interference. If the period of recruitment into a fishery is short and well defined, a closed season at the time of recruitment can allow small individuals to reach an optimum size. Due to the spawning area of *S. commerson* lying principally within MOZ waters; the length at 50% maturity being less than the size at full recruitment into the linefishery; and the strong seasonal abundance within KZN waters; the utilization of a closed season would not be a realistic management option within KZN waters. Prior to any recommendations regarding possible temporal or spatial closures in MOZ, a thorough assessment of the artisanal seine-net and gill-net fisheries catching *S. commerson* would need to be undertaken.

6.2.2 Daily bag limit (DBL)

DBLs are a common management tool applied to recreational fishers and are generally used to ensure a fair distribution of catches of a limited resource to be distributed among a large number of anglers (King, 1995; Griffiths *et al.*, 1999). Some recreational fishers make large catches, which are then sold illegally on the black market resulting in resentment among recreational and commercial fishers (King, 1995). The current recreational DBL of 10 fish per person per day (pppd) enforced in South Africa and MOZ is considered by many stakeholders to be excessively generous. Furthermore, this regulation is particularly poorly enforced within MOZ.

Examining the characteristics of the recreational ski-boat fishery in KZN, there is an average of three anglers per ski-boat on any given trip (Dunlop 2011). This equates to a potential total catch of 30 fish if each angler catches their bag limit. The average mass of *S. commerson* captured by recreational fishers over the sample period was 7kg, after gutting and filleting this could provide an estimated 25 standard meals of 200g per fish. Furthermore, based on a conservative estimate of R40/kg, this would mean that the average fish could be worth close to R280 on the black market.

In order to predict the effect that reductions in the DBL of *S. commerson* would have on recreational fishers' data were extracted from the NMLS database. The data extracted included individual angler catch records for *S. commerson* between 1986 and 2011. The vast majority of anglers captured two or less fish during each fishing trip (Table 6.1). The current DBL therefore offers very little control over the harvest of *S. commerson* in KZN with extremely low frequencies of anglers catching more than five *S. commerson* on a fishing trip. By excluding zero catches, the data demonstrates that 99% of angler's catches consist of five fish or less.

Table 6.1: Number of *S. commerson* caught by recreational ski-boat anglers per fishing trip in KwaZulu-Natal between 1986 and 2011.

Number of fish	% Frequency
0	82.66
1	13.57
2	2.26
3	0.80
4	0.37
5	0.18
6	0.063
7	0.037
8	0.024
9	0.013
10	0.015
more	0.0068

Given the similarity of the recreational ski-boat fishery in MOZ (pers. obs) a reduction in the DBL of *S. commerson* to five fish pppd in both KZN and MOZ waters would benefit recreational fishers by more equitable sharing of the catch and potentially by reducing fishing mortality at times when the fish are aggregated and vulnerable to

high catch rates. A reduced DBL limit would also reduce the incentive of individual anglers to make large catches and to sell fish illegally.

With regard to the commercial linefisheries in both countries, DBLs are not considered to be a practical management option for *S. commerson*. It is therefore recommended that these fisheries continue to be managed in terms of an area-based total allowable effort (i.e. restrict the number of commercial vessels and crew per area to a level that can ensure sustainability).

6.2.3 Minimum size limit (MSL)

Traditionally the reasons for the application of a MSL have been to allow most individuals to reach maturity and spawn at least once prior to capture in order to prevent recruitment overfishing (King, 1995). Currently there is no MSL for *S. commerson* in KZN or MOZ. As discussed in Chapter 3 and 5, a MSL of 80cm FL (90cm TL) would ensure that these reasons are satisfied. Using length frequency data from this study, the effect of raising the minimum legal size to 80cm FL on the harvested catch was estimated.

Creating a minimum size limit of 80cm FL would mean that only 9% of the current catch in the linefishery would need to be released.

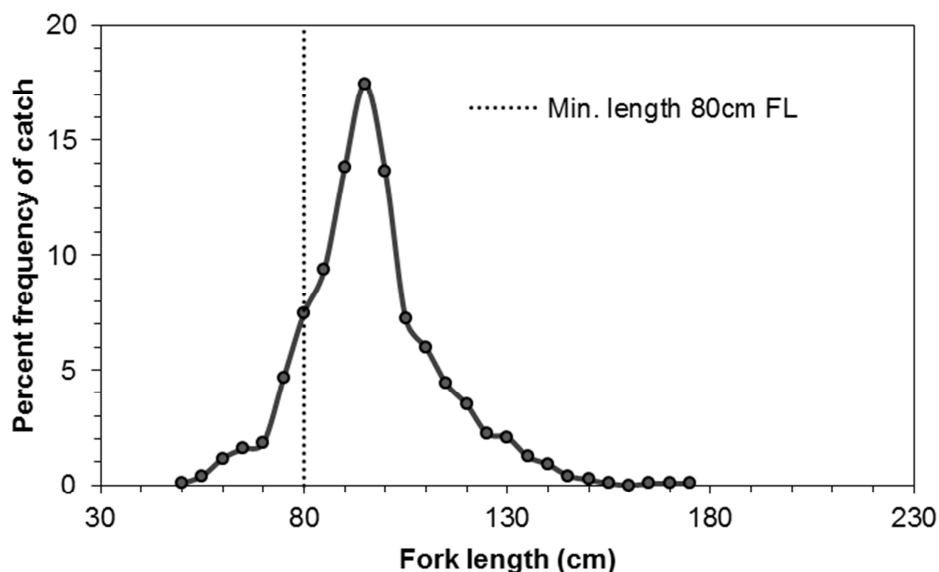


Figure 6.1: The effect of implementing a minimum size limit of 80cm FL on the length frequency distributions of the recreational *S. commerson* catch within KwaZulu-Natal and southern Mozambique.

This management strategy may be acceptable to recreational anglers as the species is predominantly pursued by sport anglers for its trophy value as well as its fighting potential, both of which would be enhanced. However, this management measure is unlikely to be accepted within MOZ, particularly within the artisanal seine-net and gill-net fisheries, due to the inevitable socio-economic effects such a strategy would have as it is believed that a large percentage of *S. commerson* caught in these fisheries are juvenile fish less than 80cm FL. This is supported by data derived from these fisheries along the Arabian Peninsula, in India and in Sri Lanka (Pillai *et al.*, 1996; Siddeek, 1996; Claereboudt, 2007).

Management measures such as MSLs need to take into consideration the fate of captured and released fish. Although no research has specifically addressed this issue, *S. commerson* are considered notoriously difficult to catch and release in good condition. *S. commerson* struggle and fight hard during the period of capture often completely exhausting themselves and their skin and small scales are sensitive to any form of handling (S. Chater, uShaka Sea World, pers. comm.). Additionally, the multiple hook rigs (including treble hooks) used by most fishers to catch *S. commerson* often lodge in areas of the oesophagus, head, eyes, cheek area and gills resulting in significant tissue damage during capture. Any contemplation given to the possible implementation of a MSL for *S. commerson* should realize that the survival

rate of captured and released fish is likely to be low. For this reason this method is not recommended for *S. commerson* as a management option within KZN and MOZ.

6.3 Future monitoring and research priorities

This research project has highlighted various sources of uncertainty that exist in the data and model assumptions which may confound interpretation of the status of the fishery. However, this should not be used as a basis for management inaction. A precautionary approach dictates that management should be more prudent given greater uncertainty (Dankel *et al.*, 2012). The following research and monitoring priorities would further strengthen the outcomes of the current research providing a more holistic understanding of the biology, fishery and stock status of *S. commerson* in KZN and MOZ:

- There is a need to genetically confirm the single stock assumption for the MOZ and KZN *S. commerson* resource. The current assumption is based on the reproductive biology, seasonal catch rates and movements of tagged individuals between the two countries. Furthermore, such a genetic study should consider the entire SWIO and identify if there are separate stocks within the region.
- There is a need to assess the historical and current impact of the artisanal beach seine and gillnet fisheries within MOZ and the impact that these fisheries have on *S. commerson*. Such a study would need to achieve a better understanding of the seasonal length frequencies and catch rates of *S. commerson* on an annual basis. These data would provide valuable information on the biology and stock status of *S. commerson*, particularly due to the inclusion of smaller younger fish into the analyses, which would strengthen the current research.
- There is a need for a comprehensive investigation into the biology and fishery of *S. commerson* in MOZ including growth, maturity, fecundity and spawning. A more intensive sampling regime is required throughout the year from a range of areas to validate and enhance biological patterns derived by the present study which are based on a limited sampling period. Such a study would be greatly complemented by a spatially and temporally stratified egg and larval survey to validate assumed life-history patterns determined in the current assessment. Such a study could also identify key spawning sites of

S. commerson which could then be further protected by temporal and/or spatial closures.

- There is a need to develop a long-term monitoring programme in MOZ that provides a structured approach to capturing catch and effort data at key points along the coastline.

Due to the shared nature of the *S. commerson* stock between KZN and MOZ, a much greater degree of cooperation is required between these two countries with regard to fisheries management. The sustainable utilization of *S. commerson* and other shared fish resources between KZN and MOZ is likely to be mutually beneficial. As such the sharing of information and knowledge about these resources for improved research and management should be encouraged.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B. N. and Csaki, F. (eds.) *Proceedings of the 2nd international symposium on information theory*. Budapest: Publishing house of the Hungarian academy of sciences pp. 268-281.
- Al-Hosni, A. H. S. and Sideek, S. M. 1999. Growth and mortality of the narrowbarred Spanish mackerel, *Scomberomorus commerson* (Lacepede), in Omani waters. *Fisheries Management and Ecology* 6: 145-160.
- Attwood, C. G. 2002. Spatial and temporal dynamics of an exploited reef-fish population. PhD thesis, University of Cape Town, South Africa.
- Attwood, C. G. and Swart, L. 2000. Discrepancy between otolith and tag-recovery estimates of growth for two South African surf-zone teleost species. *South African Journal of Marine Science* 22: 9-15.
- Austin, B. and Austin, D. A. 1989. *Methods for the microbiological examination of fish and shellfish*. Chichester: Ellis Horwood.
- Baloi, A. P., Premegi, N., Masquine, Z., van der Elst, R. and Govender, A. 2000. Towards sustainable development: the artisanal fisheries of the southern part of Nampula province. Instituto de Investigacao Pesqueira, *unpublished report*. 50pp.
- Backhoum, S. A. 2007. Diet overlap of immigrant narrow-barred Spanish mackerel *Scomberomorus commerson* (Lac., 1802) and the largehead hairtail ribbonfish *Trichiurus lepturus* (L., 1758) in the Egyptian Mediterranean coast. *Animal Biodiversity and Conservation* 30.2.
- Baker, T. T., Lafferty, R. and Quinn II, T. J. 1991. A general growth model for mark-recapture data. *Fisheries Research* 11: 257-281.
- Ballagh, A. C., Begg, G. A., Mapleston, A. and Tobin, A. 2006. Growth trends of Queensland east coast Spanish mackerel (*Scomberomorus commerson*) from otolith back-calculations. *Marine and Freshwater Research* 57: 383-393.
- Ballagh, A. C., Welch, D., Williams, A. J., Mapleston, M., Tobin, A. and Marton, N. 2011. Integrating methods for determining length-at-age to improve growth estimates for two large scombrids. *Fisheries Bulletin* 109: 90-100.
- Beamish, R. J. and Fournier, D. A. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Science* 38: 982-983.
- Beaumarrige, D. S. 1973. Age, growth, and reproduction of king mackerel, *Scomberomorus cavalla*, in Florida. *Florida marine research publication* 1: 1-45.

- Beckley, L. E. and Leis, J. M. 2000. Occurrence of tuna and mackerel larvae (Family: Scombridae) off the east coast of South Africa. *Marine and Freshwater Research* 51: 777-782.
- Beckman, D. W. and Wilson, C. A. 1995. Seasonal timing of opaque zone formation in fish otoliths. In: Secor, D. H., Dean, J. M. and Campan, S. E. (Eds.) *Recent developments in fish otolith research*. University of South Carolina Press, Columbia, SC, pp. 27-43.
- Beddington, J. R. and Cooke, J. G. 1983. The potential yield of fish stocks. Food and Agricultural Organisation, Fisheries Technical Paper No. 242. Food and Agricultural Organisation, Rome, 47 pp.
- Begg, G. A. 1998. Reproductive biology of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) in Queensland east-coast waters. *Marine and Freshwater Research* 49: 261-270.
- Begg, G. A., Cameron, D. S. and Sawynok, W. 1997. Movement and stock structure of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) in Australian east-coast waters. *Marine and Freshwater Research* 48: 295-301.
- Begg, G. A., O'Neill, M. F., Cadrin, S. X. and Bergenius, M. A. J. 2005. Stock assessment of the Australian east coast spotted mackerel fishery. CRC Reef Research Centre Technical Report No. 58. CRC Reef Research Centre. Townsville.
- Begg, G. A., Chen, C. C. M., O'Neill, M. F. O., and Rose, D. B. 2006. Stock assessment of the Torres Strait Spanish mackerel fishery. CRC Reef Research Centre Technical Report No. 66. CRC Reef Research Centre. Townsville.
- Bennett, B. A. 1988. Some considerations for the management in South Africa of galjoen *Coracinus capensis* (cuvier), an important shore-angling species. *South African Journal of Marine Science* 6: 133-142.
- Ben-Tuvia, A. D. A. M. 1978. Immigration of fishes through the Suez Canal. *Fishery Bulletin* 76: 249-255.
- Bentley, N., Kendrick, T. H., Starr, P. J. and Breen, P. J. 2012. Influence plots and metrics: tools for better understanding fisheries catch-per-unit-effort standardizations. *ICES Journal of Marine Science* 69: 84-88.
- Beverton, R. J. H. and Holt, S. J. 1957. On the dynamics of exploited fish populations. *Fisheries investigational series II* (London) 19: 1-533.
- Bishop, J., Venables, W. N., Dichmont, C. M. and Sterling, D. J. 2008. Standardizing catch rates: is logbook information by itself enough? *ICES Journal of Marine Science* 65: 255-266.
- Branch, G.M., Griffiths, C. L., Branch, M. L. and Beckley, L. E. 2007. *Two Oceans: a guide to the marine life of Southern Africa*. Struik Publishers: Cape Town.

- Brower, S. L. and Griffiths, M. H. 2004. Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a marine protected area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark-recapture. *Fisheries Research* 67: 1-12.
- Buckworth, R. C. 1998. Age structure of the commercial catch of northern territory narrow-barred Spanish mackerel. Final report to the Fisheries Research and Development Corporation, Fishery report No. 42. 28 pp.
- Butterworth, D. S., Punt, A. E., Borchers, D. L., Pugh, J. B. and Hughes, G. S. 1989. A manual of mathematical techniques for linefish assessment. South African National Scientific Programmes Report No. 160.
- Buxton, C. D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. *Fisheries Research* 15: 1-16.
- Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2219-2227.
- Campana, S. E. 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.
- Campana, S. E. and Thorrold, S. R. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* 58: 30-38.
- Campbell, R. A. 2004. CPUE standardisation and the construction of indices of stock abundance in a spatially varying fishery using general linear models. *Fisheries Research* 70: 209-227.
- Carlson, J. K., McCandless, C., Cortes, E., Grubbs, R. D., Andrews, K. I., MacNeil, M. A. and Musick, J. A. 2009. An update on the status of the sand tiger shark, *Carcharias Taurus*, in the northwest Atlantic Ocean. NOAA Technical Memorandum NMFS-SEFSC-585.
- Carlson, J. K., Hale, L. F., Morgan, A. and Burgess, G. 2012. Relative abundance and size of coastal sharks derived from commercial shark longline catch and effort data. *Journal of Fish Biology* 80: 1749-1764.
- Chale-Matsqu, J. R., Govender, A. and Beckley, L. E. 1999. Age and growth of the queen mackerel, *Scomberomorus plurilineatus*, in KwaZulu-Natal, South Africa. *Fisheries Research* 44: 121-147.
- Claereboudt, M. R. G., al-Oufi, H. S., McIlwain, J. and Goddard, J. S. 2007. Relationships between fishing gear, size frequency and reproductive patterns for the kingfish (*Scomberomorus commerson* Lacepede) fishery in the Gulf of Oman. In: *Management of shared fish stocks*. Eds. Payne, A. I. L., O'Brien, C. M. and Rogers, S. I. Blackwell Publishing Ltd. Oxford: United Kingdom.
- Claereboudt, M. R., McIlwain, J. L., Al-Oufi, H. S. and Ambu-Ali, A. A. 2005. Patterns of reproduction and spawning of the kingfish (*Scomberomorus commerson*, Lacepede) in the coastal water of the Sultanate of Oman. *Fisheries Research* 73: 273-282.

- Clark, W. G. 1991. Groundfish exploitation rates based on on life history parameters. *Canadian journal of Fisheries and Aquatic Sciences* 48: 734-750.
- Cochrane, K. L. and Japp, D. W. 2012. Retrospective analysis on perlagic fishes in the South West Indian Ocean. Capricorn Fisheries Monitoring cc. Cape Town.
- Collette, B. B. 2001. Scombridae. Tunas (also, albacore, bonitos, cackerles, seerfishes, and wahoo). In: Carpenter, K. E., Niem, V. (eds.). *FAO Species Identification Guide for Fishery Purposes. The living marine resources of the Western Central Pacific, Vol 6. Bony fishes, part 4 (Labridae to Latimeriidae)*. FAO, Rome. Pp. 3721-3756.
- Collette, B. B. and Nauen, C. E. 1983. FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of Tunas, Mackerels, Bonitos and related species known to date. *FAO Fish. Synop.*, 125: 1-137.
- Collette, B. B. and Russo, J. L. 1984. Morphology, systematics and biology of the Spanish mackerels (*Scomberomorus*, Scombridae). *Fishery Bulletin* 82: 545-689.
- Collins, M. R., Schmidt, D. J., Walz, C. W. and Pickney, J. L. 1989. Age and growth of king mackerel, *Scomberomorus cavalla*, from the Atlantic coast of the United States. *U.S. Fishery Bulletin* 87: 49-62.
- Connell, A. 2012. *Marine fish eggs and larvae from the east coast of South Africa*. Available Online: <http://www.fisheggsandlarvae.com>.
- Corsini-Foka, M. and Kalogirou, S. 2008. On the finding of the Indo-Pacific fish *Scomberomorus commerson* in Rhodes (Greece). *Mediterranean Marine Science* 9: 167-171.
- Dankel, D. J., Aps, R., Padda, G., Rockmann, C., van der Sluijs, J. P., Wilson, D. C. and Degnobol, P. 2012. Advice under uncertainty in the marine system. *ICES Journal of Marine Science* 69: 3-7.
- Davenport, S. and Stevens, J. D. 1988. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 417-433.
- Devaraj, M. 1981. Age and growth of three species of seerfishes, *Scomberomorus commerson*, *S. guttatus*, and *S. lineolatus*. *Indian Journal of Fisheries* 28: 104-127.
- Devaraj, M. 1983. Maturity, spawning and fecundity of the king seer, *Scomberomorus commerson* (Lacepede), in the seas around the Indian peninsula. *Indian Journal of Fisheries* 30: 203-230.
- Devaraj, M. 1998. Food and feeding habits of the kingseer, *Scomberomorus commerson* (Lacepede), in the seas around the Indian Peninsula. *Journal of Marine Biological Association of India* 40: 69-90.
- Dhawan, R. M., Namboothiri, P. V. S. and Gopinathan, V. G. 1972. Results of trolling line operations in Goa waters during 1965-68. *Ibid* 16: 181-187.

- Donovan, B. 2010. A retrospective assessment of the Port Alfred linefishery with respect to the changes in the South African fisheries management environment. M.Sc thesis. Rhodes University, Grahamstown.
- Dudley, R. G., Arundhati, P. A. and Brothers, E. B. 1992. Management of the Indo-Pacific Spanish mackerel (*Scomberomorus commerson*) in Oman. *Fisheries Research* 15: 17-43.
- Dunlop, S. 2011. An assessment of the shore-based and offshore boat-based linefisheries of KwaZulu-Natal, South Africa. MSc thesis. Oceanographic Research Institute. University of KwaZulu-Natal.
- Dunlop, S. and Mann, B. Q. 2012. An assessment of participation, catch and effort in the KwaZulu-Natal shore-based marine line-fishery, with comments on management effectiveness. *African Journal of Marine Science* 34: 479-496.
- Dunlop SW, Mann BQ. 2013. An assessment of the offshore boat-based linefishery in KwaZulu-Natal, South Africa. *African Journal of Marine Science* 35(1): 79-97.
- Dunlop, S., Mann, B. Q. and van der Elst, R. P. 2013. A review of the Oceanographic Research Institute's Cooperative Fish Tagging Project: 27 years down the line. *African Journal of Marine Science*.
- Efron, B. 1987. Better bootstrap confidence intervals. *Journal of the American Statistical Association* 82: 171-185.
- Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29: 265-289.
- Fauvelot, C. and Borsa, P. 2011. Patterns of genetic isolation in a widely distributed pelagic fish, the narrow-barred Spanish mackerel (*Scomberomorus commerson*). *Biological Journal of the Linnean Society* 104: 886-902.
- Fennessy, S. T. 2000. Comparative life histories and stock assessments of rockcods (Family *Serranidae*) from the East coast of South Africa. PhD thesis, University of KwaZulu-Natal, South Africa.
- Ferreira, B. P., Russ, G. R. 1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacepede, 1802) from Lizard Island, Northern Great Barrier Reef. *Fishery Bulletin*. 92, 46-57.
- Fowler, A. J. 1995. Annulus formation in otoliths of coral reef fish – a review. In: Secor, D. H., Dean, J. M. and Campana, S. E. (Eds.). *Recent developments in fish otolith research*. University of South Carolina, Columbia. SC. pp 45-63.
- Francis, R. I. C. C. 1988a. Maximum likelihood estimation of growth and growth variability from tagging data. *New Zealand Journal of Marine and Freshwater Research* 22: 42-51.
- Francis, R. I. C. C. 1988b. Are growth parameters estimated from tagging and age-length data comparable? *Canadian Journal of Fisheries and Aquatic Science* 45: 936-942.

- Francis, R. I. C. C. 1995. The analysis of otolith data – a mathematicians's perspective (what, precisely, is your model?). In: Secor, D. H., Dean, J. M. and Campan, S. E. (Eds.) *Recent developments in fish otolith research*. University of South Carolina Press, Columbia, SC, pp. 81-95.
- Gillander, B. M., Ferrell, D. J. and Andrew, N. L. 1999. Aging methods for yellowtail kingfish, *Seriola lalandi*, and results from age- and size-based growth models. *Fishery Bulletin* 97: 812-827.
- Gillander, B. M., Ferrell, D. J. and Andrew, N. L. 2001. Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): how useful are data from a cooperative tagging programme? *Marine and Freshwater Research* 52: 179-192.
- Griffiths, M. H., Attwood, C. G. and Thompson, R. 1999. A new management protocol for the South African linefishery. In: Proceeding of the third southern African marine linefish symposium, Arniston, 28 April – 1 May 1999. Mann, B. Q. (ed). SANCOR Occasional Report 5: 145-156.
- Gruber, S. H. 1982. Lemon sharks: supply-side economists of the sea. *Oceanus* 24: 56-64.
- Govender, A. 1992. Biology and population dynamics of the king mackerel (*Scomberomorus commerson*, (Lacepede, 1800) off the coast of Natal. MSc. Thesis. Oceanographic Research Institute. University of Natal.
- Govender, A. 1994. Growth of the king mackerel (*Scomberomorus commerson*) off the coast of Natal, South Africa-from length and age data. *Fisheries Research* 20: 63-79.
- Govender, A. 1995. Mortality and biological reference points for the king mackerel (*Scomberomorus commerson*) fishery off Natal, South Africa (based on a per-recruit assessment). *Fisheries Research* 23: 195-208.
- Govender, A. 1999. A statistical procedure for validating age estimates from otolith bands using mark-recapture data, with an illustration for *Pomaomus saltatrix*. *South African Journal of Marine Science* 21: 1-8.
- Govender, A., and Radebe, P. V. 2000. Pomatomidae. In 'Southern African Marine Linefish Status Reports'. *Special Publication of the Oceanographic Research Institute*. 7: 74-6.
- Govender, A., Al-Oufi, H. S., McIlwain, J. L. and Claereboudt, M. R. 2006. A per-recruit assessment of the kingfish (*Scomberomorus commerson*) resource of Oman with an evaluation of the effectiveness of some management regulations. *Fisheries Research* 77: 239-247
- Grandcourt, E. M., Al Abdessalaam, T. Z., Francis, F. and Al Shamsi, A. T. 2005. Preliminary assessment of the biology and fishery for the narrow-barred Spanish mackerel, *Scomberomorus commerson* (Lacepede), in the southern Arabian Gulf. *Fisheries Research* 76: 277-290.
- Gulland, J. A. and Holt, S. J. 1959. Estimation of growth parameters for data at unequal time intervals. *ICES Journal of Marine Science* 25: 47-49.

- Gulland, J. A. 1970. The fish resources of the ocean. FAO Fisheries Technical Paper No, 97. *Food and Agricultural Organisation*, Rome.
- Haddon, M. 2001. *Modelling and quantitative methods in fisheries*. Chapman and Hall/CRC: Boca Raton.
- Harley, S. J., Myers, R. A. and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1760-1772.
- Harris, S. A., Cyrus, D. P. and Beckley, L. E. 1999. The larval fish assemblage in nearshore coastal waters off the St Lucia estuary, South Africa. *Estuarine, Coastal and Shelf Science* 49: 789-811.
- Forsgren, E., Reynolds, J. D. and Berglund, A. 2002. Behavioural ecology of reproduction in fish. In: Hart, P. J. B. and Reynolds, J. D. 2002. Handbook of fish biology and fisheries: Volume 1 Fish biology. Blackwell Science Ltd. Oxford.
- Hart, A. M. and Russ. 1996. Response of herbivorous fish to crown of thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofusus*. *Marine Ecology Progress Series* 136: 25-35.
- Heemstra, P. and Heemstra, E. 2004. *Coastal fishes of southern Africa*. South Africa: National Inquiry Service Centre (NISC) and South African Institute for Aquatic Biodiversity (SAIAB).
- Hillborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 635-643.
- Hillborn, R. and Walters, C. J. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, Inc: London.
- Hoening, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* 82: 898-903.
- Hoolihan, J. P., Anandh, P. and van Herwerden, L. 2006. Mitochondrial DNA analyses of narrow-barred Spanish mackerel (*Scomberomorus commerson*) suggest a single genetic stock in the ROPME sea area (Arabian Gulf, Gulf of Oman, and Arabian Sea). *ICES Journal of Marine Science* 63: 1066-1074.
- Hoyle, S. 2003. Management strategy evaluation for the Queensland east coast Spanish mackerel fishery. Brisbane, Department of Primary Industries: 56pp.
- Jakobsen, T., Fogarty, M., Megrey, B. A. and Moksness, E. 2009. Fish reproductive biology: implications for assessment and management. Blackwell Publishing Ltd. West Sussex. 440pp.
- Jenkins, G. P., Milward, N. E. and Hartwick, R. F. 1984a. Identification and description of larvae Spanish mackerels, Genus *Scomberomorus* (Teleostei: Scombridae), in shelf waters of the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 35: 341-353.

- Jenkins, G. P., Milward, N. E. and Hartwick, R. F. 1984b. Food of larvae of Spanish mackerels, Genus *Scomberomorus* (Teleostei: Scombridae), in shelf waters of the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 35: 477-482.
- Jenkins, G. P., Milward, N. E. and Hartwick, R. F. 1985. Occurrence of larvae of Spanish mackerels, genus *Scomberomorus* (Teleostei: Scombridae), in shelf waters of the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 36: 635-640.
- Johnson, A. G., Fable jr. W. A., Williams, M. L. and Barger, L. E. 1983. Age and growth and mortality of king mackerel, *Scomberomorus cavalla* from the southern United States. *Fisheries Bulletin of the United States* 81: 97-106.
- Kaymaram, F., Hossainy, S. A., Darvishi, M., Talebzadeh, S. A. and Sadeghi, M. S. 2010. Reproduction and spawning patterns of the *Scomberomorus commerson* in the Iranian coastal waters of the Persian Gulf and Oman Sea. *Iranian Journal of Fisheries Science* 9: 233-244.
- Ketchen, K. S. 1975. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 32: 43-59.
- Kimura, D. K. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77: 765-776.
- Kimura, D. K. 1981. Standardized measures of relative abundance based on modelling log(c.p.u.e.), and the application to Pacific ocean perch (*Sebastes alutus*). *International Council for the Exploration of the Sea Journal du Conseil* 39: 211-218.
- King, M. 1995. *Fisheries Biology Assessment and Management*. Blackwell Science Ltd. London.
- Kraul, S. Seasonal abundance of the dolphinfish, *Coryphaena hippurus*, in Hawaii and the tropical Pacific Ocean. *Scientia Marina* 63: 261-266.
- Kumaran, M. 1964. Observations on the food of juveniles of *Scomberomorus commerson* (Lacepede) and *S. guttatus* (Bloch and Schneider) from Vizhinham, west coast of India. Marine biological association of India, Proceedings: *Symposium of Scombrid fishes. Part II*: 586-590.
- Lam, T. J. 1983. Environmental influences on gonadal activity in fish. In. Hoar, W. S., Rnadall, D. J. and Donaldson, E. M. (Eds.). *Reproduction, part B, Behaviour and fertility control*. Academic Press, New York and London. pp. 65-115.
- Lamberth, S. J., Drapeau, L. and Branch, G. M. 2009. The effects of altered freshwater inflows on catch rates of non-estuarine-dependent fish in a multispecies nearshore linefishery. *Estuarine, Coastal and Shelf Science* 84: 527-538.
- Lester, R. J. G., Thompson, C., Moss, H. and Barker, S. C. 2001. Movement and stock structure of narrow-barred Spanish mackerel as indicated by parasites. *Journal of Fish Biology* 59: 833-842.

- Lewis, P. D. and Mackie, M. 2002. Methods used in the collection, preparation and interpretation of narrow-barred Spanish mackerel (*Scomberomorus commerson*) otoliths for a study of age and growth in Western Australia. *Fisheries Research Report No. 143*, Department of Fisheries, Western Australia, 23pp.
- Li, Y., Jiao, Y. and He, Q. 2011. Decreasing uncertainty in catch rate analyses using Delta-AdaBoost: an alternative approach in catch and bycatch analyses with high percentage of zeros. *Fisheries Research* 107: 261-271.
- Lo, N. C. H., Jacobson, L. D. and Squire, J. L. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2515-2526.
- Lutjeharms, J. R. E. 2006. *The Agulhas Current*. Springer. Germany, Berlin.
- MacGregor, R. III., Dindo, J. J. and Finucane, J. H. 1981. Changes in serum androgens and estrogens during spawning in bluefish, *Pomatomus saltator*, and king mackerel, *Scomberomorus cavalla*. *Canadian Journal of Zoology* 59: 1749-1754.
- Mackie, M. and Lewis, P. D. 2001. Assessment of gonad staging systems and other methods used in the study of the reproductive biology of narrow-barred Spanish mackerel, *Scomberomorus commerson*, in Western Australia. *Fisheries Research Report No. 136*, Department of Fisheries, Western Australia, 32pp
- Mackie, M. C., Lewis, P. D., Graughan, D. J. and Newman, S. J. 2005. Variability in spawning frequency and reproductive development of the narrow-barred Spanish mackerel (*Scomberomorus commerson*) along the west coast of Australia. *Fishery Bulletin* 103: 344-354.
- Mann, B. Q. 2000. Southern African marine linefish status reports. *South African Association of Marine Biological Research: Oceanographic Research Institute*. Special Publication.
- Mann, B. Q., Fennessy, S. T., Govender, A. and van der Walt, B. A. 2002. Age and growth and a preliminary stock assessment of stonebream *Neoscorpis lithophilus* (Pisces: Scorpididae) along the KwaZulu-Natal coast, South Africa. *Marine and Freshwater Research* 53: 131-138.
- Mann, B. Q., Pradervand, P., Maggs, J. Q. and Wintner, S. 2012. A characterization of the paddle-ski fishery in KwaZulu-Natal, South Africa. *African Journal of Marine Science* 34: 119-130.
- Mann, B. Q., Scott, G. M., Mann-Lang, J. B., Brower, S. L., Lamberth, S. J., Sauer, W. H. H. and Erasmus, C. 1997. An evaluation of participation in and management of the South African spearfishery. *African Journal of Marine Science* 18: 179-193.
- Mann-Lang, J. B. 1996. National Marine Linefish System recreational data – a critical review. *Unpublished report*. Oceanographic Research Institute. 136: 1-11.

- Maunder, M. N. 2001. A general framework for integrating the standardization of catch per unit of effort into stock assessment models. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 795-803.
- Maunder, M. N. and Langley, A. D. 2004. Integrating the standardization of catch-per-unit-of-effort into stock assessment models: testing a population dynamics model and using multiple data types. *Fisheries Research*: 389-395.
- Maunder, M. N. and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* 70: 141-159.
- Maunder, M. N., Sibert, J. R., Fonteneau, A., Hampton, J., Kleiber, P. and Harley, S. J. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science* 63: 1373-1385.
- McFarlane, G. A. and Beamish, R. J. 1990. Effect of an external tag on growth of sablefish and consequences to mortality and age at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1551-1557.
- McIlwain, J. L., Claereboudt, M. R., Al-Oufi, H. S., Zaki, S. and Goddard, J. S. 2005. Spatial variation and growth of the kingfish (*Scomberomorus commerson*) in the coastal water of the Sultanate of Oman. *Fisheries research* 73: 283-298.
- McPherson, G. R. 1981. Research helps track Spanish mackerel. *Australian Fisheries* 40: 9-11.
- McPherson, G. R. 1987. Food of narrow barred Spanish mackerel in north Queensland waters, and their relevance to the commercial troll fishery. *Queensland Journal of Agricultural and Animal Sciences* 44: 69-73.
- McPherson, G. R. 1992. Age and growth of the narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepede, 1800) in North-eastern Queensland waters. *Australian Journal of Marine and Freshwater Research* 43: 1269-1282.
- McPherson, G. R. 1993. Reproductive biology of the narrow barred Spanish mackerel (*Scomberomorus commerson* Lacepede, 1800) in Queensland waters. *Asian Fisheries Science* 6: 169-182.
- McPherson, G. R. and Williams, L. E. 2002. Narrow-barred Spanish mackerel, pp. 88-93 in Williams, L. E. (ed.). 2002. *Queenslands fisheries resources: current condition and recent trends 1988-2000*. QI02012. Department of Primary Industries. Brisbane.
- Meriem, S. B., Al-Marzouqi, A. and Al-Mamry, J. 2006. Fisheries exploitation pattern of narrow-barred Spanish mackerel, *Scomberomorus commerson*, in Oman and potential management options. *Journal of Applied Ichthyology* 22: 218-224.
- Miller, B. S. Kendall JR, A. W. 2009. Early life history of marine fishes. University of California Press, Los Angeles.

- Moore, B. R., Buckworth, R. C., Moss, H. and Lester, R. J. G. 2003. Stock discrimination and movements of narrow-barred Spanish mackerel across northern Australia as indicated by parasites. *Journal of Fish Biology* 63: 765-779.
- Mualeque, D. and Santos, J. 2011. Biology, fisheries and distribution of *Thryssa vitirostris* (Gilchrist & Thompson 1908) and other Engraulidae along the coast of the Sofala Bank, western Indian Ocean. *African Journal of Marine Science* 33: 127-137.
- Munro, I. S. R. 1942. The eggs and early larvae of the Australian barred Spanish mackerel, *Scomberomorus commersoni* (Lacepede) with preliminary notes on the spawning of that species. *Proceedings of the Royal Society of Queensland* 54: 33-48.
- Myers, R. A., Hutchings, J. A. and Barrowman, N. J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* 7: 91-106.
- Newman, S. J., Williams, D. and Russ, G. R. 1996. Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. *Australian Journal of Marine and Freshwater Research* 47: 575-584.
- Newman, S. J., Buckworth, R. C., Mackie, M. C., Lewis, P. D., Wright, I. W., Williamson, P. C., Bastow, T. P. and Ovenden, J. R. 2009. Spatial subdivision among assemblages of Spanish mackerel, *Scomberomorus commerson* (Pisces: Scombridae) across northern Australia: implications for fisheries management. *Global Ecology and Biogeography* 18: 711-723.
- Newman, S. J., Mackie, M. C. and Lewis, P. D. 2012. Age-based demography and relative fisheries productivity of Spanish mackerel, *Scomberomorus commerson* (Lacepede) in Western Australia. *Fisheries Research* 129-130: 46-60.
- Newman, S. J., Cappel, M. Williams, D. and McB. 2000. Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, *L. vitta* (Quoy and Gaimard) from the central Great Barrier Reef, Australia. *Fisheries Research* 48: 263-275.
- Norton, J. G. 1999. Apparent habitat extensions of dolphinfish (*Coryphaena hippurus*) in response to climate transients in the California Current. *Scientia Marina* 63: 239-260.
- Olbers, J. M. and Fennessey, S. T. 2007. A retrospective analysis of the stock status of *Otolithes ruber* (Pisces: Sciaenidae) as bycatch on prawn trawlers from KwaZulu-Natal, South Africa. *African Journal of Marine Science* 29: 247-252.
- Ortega-Garcia, S., Klett-Traulsen, A. and Ponce-Diaz, G. 2003. Analysis of sportfishing catch rates of striped marlin (*Tetrapturus audax*) at Cabo San Lucas, Baja California Sur, Mexico and their relation to sea surface temperature. *Marine and Freshwater Research* 54: 483-488.

- Ortega-Garcia, S., Ponce-Diaz, G., O'Hara, R. and Merila, J. 2008. The relative importance of lunar phase and environmental conditions on striped marlin (*Tetrapturus audax*) catches in sport fishing. *Fisheries Research* 93: 190-194.
- Ortiz, M., Legault, C. M. and Ehrhardt, N. M. 2000. An alternative method for estimating bycatch from the US shrimp trawl fishery in the Gulf of Mexico, 1972-1995. *Fisheries Bulletin* 98: 583-599.
- Panella, G. 1980. Growth patterns in fish sagittae. In: Rhoads, D. C. and Lutz, R. A. (Eds.), *Skeletal Growth of Aquatic Organisms*. Plenum Press, New York.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science* 39: 175-192.
- Pauly, D. 1984. Length-converted catch curves, a powerful tool for fisheries research in the tropics (Part II). *Fishbyte* 2: 17-19.
- Penney, A. J., Mann-Lang, J. B., van der Elst, R. P. and Wike, C. G. 1999. Long-term trends in catch and effort in the KwaZulu-Natal nearshore linefisheries. *South African Journal of Marine Science* 21: 51-76.
- Pillai, N. G. K., Pillai, P. P., Said Koya, K. P. and Sathianandan, T. V. 1996. Assessment of the stock of kingseer, *Scomberomorus commerson* (Lacepede), along the west coast of India. *Expert consultation on Indian Ocean tunas. 6th Session*. Colombo, Sri Lanka, 25-29 September 1995.
- Pulfrich, A. and Griffiths, C. L. 1988. The fishery for hottentot *Pachymetapon blochii* in the south-western Cape. *South African Journal of Marine Science* 7: 227-241.
- Punt, A. E., Garratt, P. A. and Govender, A. 1993. On an approach to applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysoblephus puniceus* (Pisces: Sparidae). *South African Journal of Marine Science* 13: 109-119.
- Punt, A. E., Smith, D. C., Thompson, R. B., Haddon, M., He, X. and Lyle, J. M. 2001. Stock assessment of the blue grenadier *Macruronus novaezelandiae* resource off south-eastern Australia. *Marine and Freshwater Research* 52: 701-717.
- Punt, A. E., Walker, T. I., Taylor, B. L. and Pribac, F. 2000. Standardization of catch and effort data in a spatially-structured shark fishery. *Fisheries Research* 45: 129-145.
- Quinn, T. J. and Deriso, R. B. 1999. *Quantitative fish dynamics*. Oxford University Press. New York.
- R Development Core Team. 2003. R: a language and environment for statistical computing. R Foundation for statistical computing. Vienna. Austria. <http://www.r-project.org/>.

- Rao, K. S. 1962. Observations on the food and feeding habits of *Scomberomorus guttatus* (Bl. & Schn.) and juveniles of *S. lineolatus* (Cuv. & Val.) and *S. commerson* (Lac.) of the Waltair Coast. Marine biological association of India, Proceedings: *Symposium on Scombrid fishes. Part II*: 591-598.
- Richards, L. J. and Schnute, J. T. 1986. An experimental and statistical approach to the question: Is CPUE and index of abundance. *Canadian Journal of Fisheries and Aquatic Science* 43: 1214-1227.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*.
- Ricker, W. E. 1979. Growth rates and models. In: Hoar, W. S., Randall, D. J. and Brett, J. R. (Ed.) *Fish Physiology, Vol. VIII. Bioenergetics and Growth*. Academic Press, New York, pp. 677-743.
- Robillard, E., Reiss, C. S. and Jones, C. M. 2009. Age-validation and growth of bluefish (*Poatomus saltatrix*) along the East Coast of the United States. *Fisheries Research* 95: 65-75.
- Rodriguez-Martin, E., Arrizabalage, H., Ortiz, M., Rodriguez-Cabello, C., Moreno, G. and Kell, L. T. 2003. Standardization of Bluefin tuna, *Thunnus thynnus*, catch per unit effort in the baitboat fishery of the Bay of Biscay (Eastern Atlantic). *ICES Journal of Marine Science* 60: 1216-1231.
- Russ, G. R., Lou, D. C., Higgs, J. B. and Ferreira, B. P. 1998. Mortality rate of a cohort of the coral trout, *Plectropomus leopardus*, in zones of the Great Barrier Reef Marine Park closed to fishing. *Australian Journal of Marine and Freshwater Research* 49: 505-511.
- Schaefer, K. M. 1987. Reproductive biology of black skipjack, *Euthynnus lineatus*, an eastern Pacific tuna. *Inter-American Tropical Tuna Comission Bulletin No. 19*, 260pp.
- Schnute, J. T. 1981. A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1128-1140.
- Shepherd, J. G. and Pope, J. G. 2002. Dynamic pool models 2: Short-term and long-term forecasts of catch and biomass. In: Hart, P. J. B. and Reynolds, J. D. (Eds.) *Handbook of fish biology and fisheries Volume 2: Fisheries*. United Kingdom: Blackwell Publishing.
- Shojaei, M. G., Motlagh, S. A. T., Seyfabadi, J., Abtahi, B. and Dehghani, R. 2007. Age, growth and mortality rate of the narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepede, 1800) in coastal waters of Iran from length frequency data. *Turkish Journal of Fisheries and Aquatic Science* 7: 115-121.
- Shoji, J. and Tanaka, M. 2003. Larval abundance, growth, and recruitment of Japanese Spanish mackerel *Scomberomorus niphonius* in the Seto Inland Sea, Japan. In: Browman, H. I. and Skiftesvik, A. B. (Eds.). *The big fish bang*. Institute of Marine Research, Bergen, pp 395-404.

- Shoji, J. and Tanaka, M. 2006. Growth-selective survival in piscivorous larvae of Japanese Spanish mackerel *Scomberomorus niphonius*: early selection and significance of ichthyoplankton prey supply. *Marine Ecology Progress Series* 321: 245-254.
- Shono, H. 2008. Application of the Tweedie distribution to zero-catch data in CPUE analysis. *Fisheries Research* 93: 154-162.
- Siddeek, M. S. M. 1996. Review of fisheries biology of *Scomberomorus* and *Acanthocybium* species in the Western Indian Ocean (FAO Area 51). *Department of fisheries science and technology, College of Agriculture*. Sultan Qaboos University. Sultanate of Oman.
- Sink, K. J., Branch, G. M. and Harris, J. M. 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. *African Journal of Marine Science* 27: 81-96.
- Sissenwine, M. P. and Shepherd, J. G. 1987. An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 913-918.
- Smale, M. J. and Punt, A. E. 1991. Age and growth of the red steenbras *Petrus rupestris* (Pisces: Sparidae) on the south east coast of South Africa. *South African Journal of Marine Science* 10: 131-139.
- Smith, D. 2008. Movement, growth and stock assessment of the coastal fish *Lichia amia* (Teleostei: Carangidae) off the South African coast. MSc. Thesis. Oceanographic Research Institute. University of Natal.
- Smith, M. M. and Heemstra, P. C. 1986. *Smiths' sea fishes*. Macmillan South Africa (Pty) Ltd. Johannesburg.
- Sosa, N. O. 1998. Historical review of the billfish management in the Mexican Pacific. *Ciencias Marinas* 24: 95-111.
- Sturn, M. G. and Salter, P. 1990. Age, growth, and reproduction of the king mackerel, *Scomberomorus cavalla* (Cuvier) in Trinidad waters. *Fisheries Bulletin of the United States* 88: 361-370.
- Su, N., Sun, C., Punt, A. E., Yeh, S. and diNardo, G. 2011. Modelling the impacts of environmental variation on the distribution of blue marlin. *ICES Journal of Marine Science* 68: 1072-1080.
- Teo, S. L. H. and Block, B. A. 2010. Comparative influence of ocean conditions on Yellowfin and Atlantic Bluefin Tuna catch from longlines in the Gulf of Mexico. *PLoS One* 5: e10756.
- Tobin, A. and Mapleston, A. 2004. Exploitation dynamics and biological characteristics of the Queensland east coast Spanish mackerel (*Scomberomorus commerson*) fishery. *CRC Reef Research Centre Technical Report No 51*, CRC Reef Research Centre, Townsville.
- Townend, J. 2002. *Practical statistics for environmental and biological scientists*. John Wiley & Sons Ltd: West Sussex.

- Trent, L., Fable Jr, W. A., Russel, S. J., Bane, G. W. and Palko, B. J. 1987. Variations in size and sex ratio of king mackerel, *Scomberomorus cavalla*, off Louisiana, 1977-85. *Marine Fisheries Review* 49: 91-97.
- Trent, L., Palko, B. J., Williams, M. L. and Brusher, H. A. 1987. Abundance of king mackerel, *Scomberomorus cavalla*, in the Southeastern United States based on CPUE data from Charterboasts, 1982-85. *Marine Fisheries Review*: 78-90.
- Trent, L., Williams, R. O., Taylor, R. G., Saloman, C. H. and Monooch, C. S. III. 1983. Size, sex ratio, and recruitment in various fisheries of king mackerel, *Scomberomorus cavalla*, in the south-eastern United States. *US National Marine Fisheries Service Fishery Bulletin* 81: 709-721.
- Van der Elst, R. P. 2003. *A guide to the common sea fishes of southern Africa*. Struik Publishers. Cape Town.
- Van der Elst, R. P. Groeneveld, J. C. Baloi, A. P. Marsac, F. Katonda, K. I. Ruwa, R. K. and Lane, W. L. 2009. Nine nations, one ocean: A benchmark appraisal of the South West Indian Ocean Fisheries Project (2008-2012). *Ocean and Coastal Management* 52: 258-267.
- Van Herwerden, L., McIlwain, J., Al-Oufi, H., Al-Amry, W. and reyes, A. Development and application of microsatellite markers for *Scomberomorus commerson* (Perciformes; Teleostei) to a population genetic study of Arabian Peninsula stocks. *Fisheries Research* 79: 258-266.
- Venables, W. N. and Dichmont, C. M. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research* 70: 319-337.
- Vetter, E. F. 1988. Estimation of natural mortality in fish stock: a review. *Fisheries Bulletin* (US) 86: 25-43.
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Human Biology* 10: 181-213.
- Weatherley, A. H. 1972. *Growth and Ecology of Fish Populations*. Academic Press, London, 293 pp.
- Welsh, D. J., Hoyle, S. D., McPherson, G. R. and Gribble, N. A. 2002. Preliminary assessment of the Queensland east coast Spanish mackerel fishery. *Information Series QI02110*. Queensland Government, Department of Primary Industries. Cairns.
- Williams, R. E. and Lester, R. J. G. 2006. Stock structure of Spanish mackerel *Scomberomorus commerson* along the Australian east coast deduced from parasite data. *Journal of Fish Biology* 68: 1707-1712.
- Winker, H., Kerwath, S. E. and Attwood, C. G. 2013. Comparison of two approaches to standardize catch-per-unit-effort for targeting behaviour in a multispecies hand-line fishery. *Fisheries Research* 139: 118-131.
- WIOFISH. 2011. Western Indian Ocean Fisheries Database: A catalogue of small-scale fisheries.

- Ye, Y. 2011. Western Indian Ocean: FAO statistical area 51. In: Review of the state of world fishery resources. *FAO Fisheries and aquaculture technical paper*, No. 569. Rome, 334 pp.
- Ye, Y., Al-Husaini, M. and Al-Baz, A. 2001. Use of generalized linear models to analyse catch rates having zero values: the Kuwait driftnet fishery. *Fisheries Research* 53: 151-168.
- Zar, H. J. 1999. *Biostatistical analysis* 4th Ed. Prentice Hall, Inc. New Jersey.
- Zischke, M. T., Griffiths, S. P. and Tibbetts, I. R. 2012. Catch and effort from a specialized recreational pelagic sport fishery off eastern Australia. *Fisheries Research* 127-128: 61-72.
- Zuniga Flores, M. S., Otega-Garcia, S. O. and Klett-Traulsen, A. 2008. Interannual and seasonal variation of dolphinfish (*Coryphaena hippurus*) catch rates in the southern Gulf of California, Mexico. *Fisheries Research* 94: 13-17.