

University of Cape Town

Age, Growth and per-recruit assessment
of the Saldanha and Langebaan stock of
Chelon richardsonii

by

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A thesis submitted in partial fulfillment for the
degree of Masters of Science

in the
Marine Research Institute
and
Department of Biological Sciences

August 2018

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Abstract

Chelon richardsonii are omnivorous, particle feeders found specifically within inshore and estuarine habitats on the west and south coast of South Africa. They are the primary target of the gillnet and beach-seine fishery in this region. Despite being managed through a multifaceted approach of gear restrictions and total allowable effort, the fishery is thought to be oversubscribed and the stock is regarded as being overfished. The social and economic importance of this fishery necessitates an update of the life history parameters of *C. richardsonii* to enable an accurate assessment the current status of the stock.

The fishery in Saldanha and Langebaan was described via investigating changes in sex-ratio, mean length (mm) and standardised catch-per-unit-effort (CPUE). Firstly, exploration of sex ratio indicated a significant switch between the two periods (1998-2002 and 2017), resulting in a predominantly male biased population (1.7 males: 1 female). Secondly, through investigation of three length-frequency distributions of commercial catch of *C. richardsonii* (1998-2002, 2009-2011 and 2017) a reduction in mean total length (TL) of 36.5 mm was observed. Lastly, the standardisation of the Netfishery CPUE for the time series of 2008-2016 through the application of a Generalised Additive Mixed Model (GAMM) showed a reduction of approximately 30% in relative abundance of *C. richardsonii*.

Chelon richardsonii exhibited a fast growth, a maximum age of six and matured relatively early at two years old. Growth was best described using a three parameter von-Bertalanffy growth model; where L_{∞} is the asymptotic length, K is the rate at which L_{∞} is reached and t_0 is the age when the average length is zero. The data collected in 2017 expressed two problems. Firstly, as a result of high gillnet selectivity, smaller individuals within younger age classes were missing. Secondly, due to growth overfishing and/or a small sample size ($n = 353$) older and larger adults were missing. Consequently, this increased K and decreased L_{∞} to biologically implausible values (female original growth: $L_{\infty} = 257.450$ mm, $K = 0.610$ year⁻¹ and $t_0 = -0.040$ year). As a result L_{∞} was fixed in accordance to a historic L_{max} , in order to overcome these issues and produce biologically plausible growth parameters. Growth differed significantly between males and females, hence female growth was subsequently used for the spawner biomass-per-recruit analysis in the proceeding chapter ($L_{\infty} = 347.400$ mm, $K = 0.235$ year⁻¹ and $t_0 = -0.833$ year). Total mortality (Z) and average natural mortality (M) were estimated as 1.466 year⁻¹ and 0.329 year⁻¹, respectively.

Growth and mortality was constant in *Chelon richardsonii* throughout Saldanha and Langebaan and despite potential emigration out of the bay, the sup-population of *C. richardsonii* was considered to be a discrete stock for the purpose of this study. A spawner biomass-pre-recruit model, based on the growth and mortality parameters calculated in Chapter 3, revealed that the stock is heavily depleted and recruitment is likely to be seriously impaired (spawner biomass-per-recruit = 5.5% of pristine levels). It must be acknowledged that the results of a per-recruit stock assessment heavily depend on the growth model parameters. In contrast, the model indicated an optimally exploited stock when the original growth parameters were applied (spawner biomass per-recruit = 76.2% of pristine levels). Considering results from Chapter 2 and the justifications for fixing L_∞ the plausibility of the second scenario being true is less likely. Acknowledging the temporal, spatial and sample size limitations of this study conclusions made will require definitive future examination. Regardless, a reduction in fishing effort and further restrictions in mesh sizes are suggested to facilitate the replenishment and sustainable use of the stock.

Acknowledgements

Firstly, I would like to thank my supervisors, Dr. Sven Kerwath and Dr. Denham Parker. Their mentorship and guidance were integral to the success of this thesis. I couldn't have asked for better teachers for my introduction into stock assessment science. I would also like to also thank Dr. Henning Winker for helping with the statistics and R , and Dr. Stephen Lamberth for providing expert advice and tuition on both the west coast Netfishery and trek-netting.

I would lastly like to thank the crew of marine technicians who took time to help me catch the elusive mullet and although the trips were not a complete success, they were great experiences.

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Chapter 1

General Introduction

1.1 The Fishery

Background

Marine capture fisheries provide important sources of economy and sustenance. Direct global employment through marine fisheries is estimated at 34 million jobs with a total employment as much as 237 million (FAO, 2011; Teh and Sumaila, 2013). To ensure long-term employment, sustainable exploitation of fish stocks is required. In 2011 the FAO reported that 57.4% of global fisheries are optimally exploited, with yields at or around their maximum sustainable yield (MSY) production. An estimated 29.9% of global fisheries are overexploited, which means they have been fished to a point that their yield is lower than that of their full biological and ecological potential (FAO, 2011). Intense overfishing resulting in drastic depletion can cause considerable economic downfalls. Problems further arise from the attempts to rebuild depleted stocks, as intensified fishery management tools such as a reduction in total allowable effort (TAE) and total allowable catch (TAC) diminish economic opportunities (Worm *et al.*, 2009). However, failure to intervene increases the susceptibility of stock collapse resulting ultimately in fishing moratoriums, and radical reductions in job opportunities. The moratorium of the Newfoundland Cod fishery in 1992 is the most well-known example and resulted in a reduction of 30,000 jobs (Schrank, 2005). In 2014 the stock status of the fisheries in South Africa were evaluated by DAFF - 48% of these stocks were considered optimally

exploited and 50% of stocks were of serious concern. The stocks of serious concern were subdivided into two categories: depleted or heavily fished (22%), and heavily depleted and overexploited (28%, DAFF, 2014). The latter category are fish stocks that have been heavily depleted through excessive fishing and are also currently subjected to unsustainable levels of fishing. The South African west coast Netfishery is considered to be within the 28%; heavily depleted and overexploited.

History of the Netfishery

The South African west coast Netfishery operates on the western coast of South Africa from False Bay to Port Nolloth (DAFF, 2014). Southern mullet *Chelon richardsonii* (previously *Liza richardsonii*, Durand and Borsa, 2015) are the predominant target, however regionally specific permits are allocated for the catch and landing of St Joseph sharks *Callorhynchus capensis* and some other species. European colonialists introduced gillnets and beach seines in the early 1800s, enabling commercial exploitation. Consequently, catches rose exponentially to approximately 1.6 million fish annually on the west coast, which was approximately 25% of the national commercial catch at the time (De Villiers, 1987). Following a record breaking reported catch of 14.9 million fish in 1981, management intervened and introduced allocation of permits to control the total allowable effort (TAE). TAE is a common harvest control strategy that indirectly controls the total fishing mortality. After the introduction, the catch remained fairly stable at around 6 million fish per annum.

As a consequence of insufficient data, the allocated TAE between 1981 and 2001 likely exceeded sustainable limits. This resulted in the reported annual catches of approximately 6000 metric tons (t); gillnets contributed 3,250 t and beach seines 1,950 t. Similar to other small-scale fisheries, poor governance and monitoring contributed to overexploitation in the Netfishery (DAFF, 2014). For example, Lamberth *et al.* (1997) assessed and documented substantial levels of non-reporting; catches of up to 80% of the annual total were being unreported (Lamberth *et al.*, 1997). Hutchings and Lamberth (2002) further corroborated these results by postulating that unreported catch was a probable cause of the decreases in reported catch prior to 2001. As a consequence of a decentralised system and lack of governance, growth of illegal gillnetting was enabled. An estimated

400-500 illegal nets were being used annually (DAFF 2014). It is for these reasons that stricter management was necessary to provide suitable protection for the stock.

In 2001 there was a significant reduction in allocated permits. Furthermore, permits were only allocated to bona fide fishers that relied on the fishery as a primary source of income. Beach seine operations were reduced to 28 and gillnet permits were reduced to 162, as shown in Table 1.1 (DAFF, 2014). Additional restrictions were implemented, such as gear restrictions and closed fishing zones, in an attempt to provide relief from recruitment overfishing (DAFF, 2014). In 2008, a new small-scale fisheries policy was created that brought in the production of interim relief (IR) permits. These are short-term permits allocated to small-scale fishers that are directed at their socio-economic needs. There are 17 IR permits currently in the entire fishery.

TABLE 1.1: Total allocation of permits for the West Coast Netfishery.

Area	Permit	Prior 2001	2001	2017
National	Right Holders	450	190	189
	Interim relief	0	0	17
Saldanha and Langebaan	Right Holders	28	14	15
	Interim relief	0	0	3

Current Management

The west coast Netfishery is currently managed by a combination of TAE, gear restrictions and closed areas. The fishery is divided into 15 areas, each with regionally exclusive combinations of TAE and closed fishing areas. During the fishing year of 2017/2018, 27 beach seine and 162 gillnet permits have been allocated within these 15 areas. The current gear restrictions allow a minimum stretched mesh size of 48 mm and a maximum of 64 mm. Each permitted vessel may only use two nets; each one a maximum length of 75 m and depth of 5 m. Each vessel is only entitled to carry two nets at any one time. There are also strict by-catch mitigation measures; vessels may only catch and retain *Chelon richardsonii* and St Joseph shark *Callorhynchus capensis*. Landing of any other species is not permitted and all live by-catch must be returned while dead by-catch must be surrendered to the Local Fishery Control Officer (DAFF, 2017).

Specifically, Langebaan and Saldanha Bay are limited to 15 annual permits, with an additional 3 interim relief concessions. Scientific recommendations state that a reduction in TAE within Langebaan is integral for the replenishment of the *C. richardsonii* stock; as the TAE has been substantially exceeded over the last 5 years (DAFF, 2017). Langebaan Marine Protected Area (MPA) is split into three zones; A, B and C. Currently, fishers are permitted to fish in Zones A and B; with additional gear restrictions in Zone B. Similarly, scientific advice recommends that all TAE within Zone B should be completely withdrawn and redistributed to Zone A, Langebaan and Saldanha (DAFF, 2017).

Status of the stock

The *C. richardsonii* stock has never undergone a formal stock assessment. However, a decline in nominal CPUE suggests that the current fishing mortality is above that required for the maximum sustainable yield (F_{MSY}), and a reduction in effort of up to 60% was recommended in order to rebuild the stock (Hutchings *et al.*, 2002). Areas where these reductions were implemented have shown evidence of recovery. The Berg river estuary, north of Cape Town, experienced notably high levels of gillnet fishing prior to 2003. In 1998, estimations of annual effort exceeded 13,000 gillnet days, producing a total catch of 500 t (Hutchings and Lamberth, 2002b). Concerns about overfishing resulted in a regional moratorium of commercial gillnetting within the estuary (Hutchings *et al.*, 2008). Post moratorium CPUE and length-frequency data were investigated to determine its success. An increase in CPUE and abundance of larger individuals indicated partial stock recovery (Hutchings *et al.*, 2008), attributable to the absence of fishing.

Regional overexploitation of *C. richardsonii* remains a problem. Annual CPUE trends for St Helena and Saldanha Bay depict a short periods of high CPUE followed by a prolonged period of low CPUE. The high periods coincided with the lowest effort, hence, it suggests that fishers are removing the replenished stock from the previous winter (Hutchings and Lamberth, 2002b). Furthermore, illegal, unreported and unregulated (IUU) fishing is increasing. Illegal fishing in the Berg River escalated rapidly post-moratorium, accumulating annual catches of 400 t (Hutchings *et al.*, 2008).

The *C. richardsonii* stock is facing a multitude of pressures and with uncertainty regarding the current stock status, it is a prime candidate for assessment. In addition to existing fishing pressure there are initiatives to expand and provide more permits under the Marine Living Resources Act 1998. Gillnets are seen as a good method to increase access to the resources by impoverished communities, as they have relatively low investment and low operating costs compared to other fisheries (Grant, 1981). Yet, the Netfishery is already oversubscribed, with little room for expansion (Hutchings and Lamberth, 2002a). Furthermore, with the large amounts of unreported catch, there is uncertainty surrounding the actual total catch.

Socio-economic considerations

A study by Hutchings *et al.* (2002) looked at the socio-economic characteristics of the Netfishery. During the study period, the authors estimated that 2,700 people were directly or indirectly employed by the Netfishery. Economic stability and viability varied considerably between jobs and evidence suggested that, on average, gillnet fishers marginally covered their investment and operation costs (Hutchings *et al.*, 2002). This is the primary consequence of the low market value of the fish, a poor value chain and repeated equipment replacement. Fishers also raised concern of decreasing catches and were hesitant to the possibility of introducing more permits (Hutchings *et al.*, 2002).

Lastly, there has been conflict between Netfishers, and commercial and recreational linefishers, as it is suspected that nets are removing all fish from the inshore zones, either indirectly by limiting baitfish or directly via removing target fish through by-catch (DAFF, 2014). *Chelon richardsonii* are common prey for numerous angling species, such as garrick *Lichia amia*, silver kob *Argyrosomus inodorus*, dusky kob *Argyrosomus japonicus* and elf *Pomatomus saltatrix* (Heemstra and Heemstra, 2004). The removal of prey species such as harder was regarded to be the cause of a decrease in the abundance of predators. Furthermore, due to the mesh sizes used in the Netfishery, juvenile fishes tend to also get caught as by-catch (Lamberth, *et al.*, 1995); another argument by both recreational and commercial linefishers to decrease the number of active Netfish permits.

1.2 Southern mullet *Chelon richardsonii*

Southern mullet *C. richardsonii* are omnivorous particle feeders that are found within inshore and estuarine habitats around the west and south coast of Southern Africa. There are 5 genera within Mugilidae found in Southern African waters, of which 8 are known species within the genus *Chelon* (Smith, 1986). First described in 1846 (Smith, 1846) as *Mugil richardsonii*, it went under taxonomic reclassification following the description of the genus *Liza* by Jordan and Swain (1884). More recently, the genus underwent re-reclassification and is now described within the genus *Chelon* (Durand and Borsa, 2015). Its geographical range stretches from Lobito, Angola to the subtropical waters of the East Coast of South Africa, but is rarely found at the extremes of its geographical range (DAFF, 2014).

Chelon richardsonii express an ontogenetic shift in environmental residency, from brackish to marine. Juveniles have a higher tolerance for low salinities enabling them to take refuge in estuaries, whereas, adults are more permanent residents in marine systems, specifically surf zones (Clark *et al.*, 1994; Naesje *et al.*, 2007; Mann *et al.*, 2013). *C. richardsonii* are non-migratory, however they are commonly found in single species shoals (Mann *et al.*, 2013). They are available all year round, though their variability in abundance tends to be seasonal. As for many other species, abundance and distribution of prey items likely governs their distribution. Their east coast residency synchronises with the abundance of phytoplankton within the surf zone during the summer months, and individuals then tend to disperse during the autumn and winter (Lamberth *et al.*, 1995). Similar behaviour was observed within False Bay. Abundance was associated with patches of diatoms, which form due to the onshore winds and wave patterns within the summer months (Lamberth *et al.*, 1995). *C. richardsonii* have developed a specialised crop instead of a stomach, similar to the gizzard of a bird, to cope with its omnivorous diet (Naesje *et al.*, 2007). Their bioenergetic demands are primarily met through a combination of diatoms and detritus (Masson and Marais, 1975).

It is thought that sexes exhibit similar somatic growth until maturation, where after females continue and males cease to increase in size (Lasiak, 1983). As a consequence, females have a tendency to be larger. Maximum length recorded was a 430 mm (total length, TL) female from Saldanha (Lamberth and Hutchings, unpublished data).

Length-at-50% maturity was estimated between 210-215 mm (fork length, FL), which corresponds to 3 years (Nepgen as cited in De Villiers, 1987). The spawning season is extended, occurring during spring and summer, though peak spawning is within the summer months (Lasiak, 1983).

Saldanha Bay is not a typical estuary. Yet, Whitfield (2005) referred to it as a coastal embayment type of estuary as it shares many common properties such as wave shelter and shallow, warm, nutrient rich waters. Estuaries are important ecosystems for many different species. It's sheltered, warm and nutrient enriched waters provide a productive environment which facilitates rapid growth for resident species (Wallace, 1975; Whitfield and Kok, 1992). Predation is often limited by gape size of the predator, consequently a faster growth rate in prey reduces its overall lifetime predation rate (Arendt, 1997). It is for these reasons that estuarine environments are dominated by juveniles (Potter *et al.*, 1990). Juvenile *C. richardsonii* are important estuarine species, contributing as much as 76% of the teleost biomass (Clark *et al.*, 1994). They can tolerate a wide range of environmental conditions (Naesje *et al.*, 2007; Mann *et al.*, 2013). As a consequence of their densities and accessibility, aggregations of juvenile *C. richardsonii* in estuaries are easily exploited (Clark *et al.*, 1994). The Berg River estuary, before its gillnetting ban in 2003, was subjected to approximately 17 230 net-days year⁻¹ (Lamberth and Turpie, 2003). These nurseries provide excellent conditions for the development of juvenile *C. richardsonii* and the removal of immature fish hampers the recruitment potential of the stock.

1.3 Study site

Saldanha Bay is a sheltered inlet located roughly 100 km north of Cape Town (Figure 1.1). As a consequence of its location and protection, it provides favourable conditions for certain commercial species. Similarly, it has become an attractive location for large commercial activities such as industrial fishery and metal ore operations. These unique environmental properties have led to the evolution of highly diverse flora and fauna, motivating the establishment of a no-take MPA in the southern area of Langebaan lagoon (Kerwath *et al.*, 2009). Saldanha bay exhibits similar thermohaline and biological properties to that of the Benguela current, however during summer months

higher temperatures increase evaporation resulting in increased sea surface temperatures and salinity (Shannon and Stander, 1977). These characteristics enable high primary production within the bay, phytoplankton densities regularly reach 885 mg/m^3 during the summer (Henry *et al.*, 1977). This highly productive, sheltered inlet has therefore been referred to as a coastal embayment type of estuary (Whitfield, 2005) and as a consequence is a favourable environment for a large number of juvenile teleost species (Day, 1959).

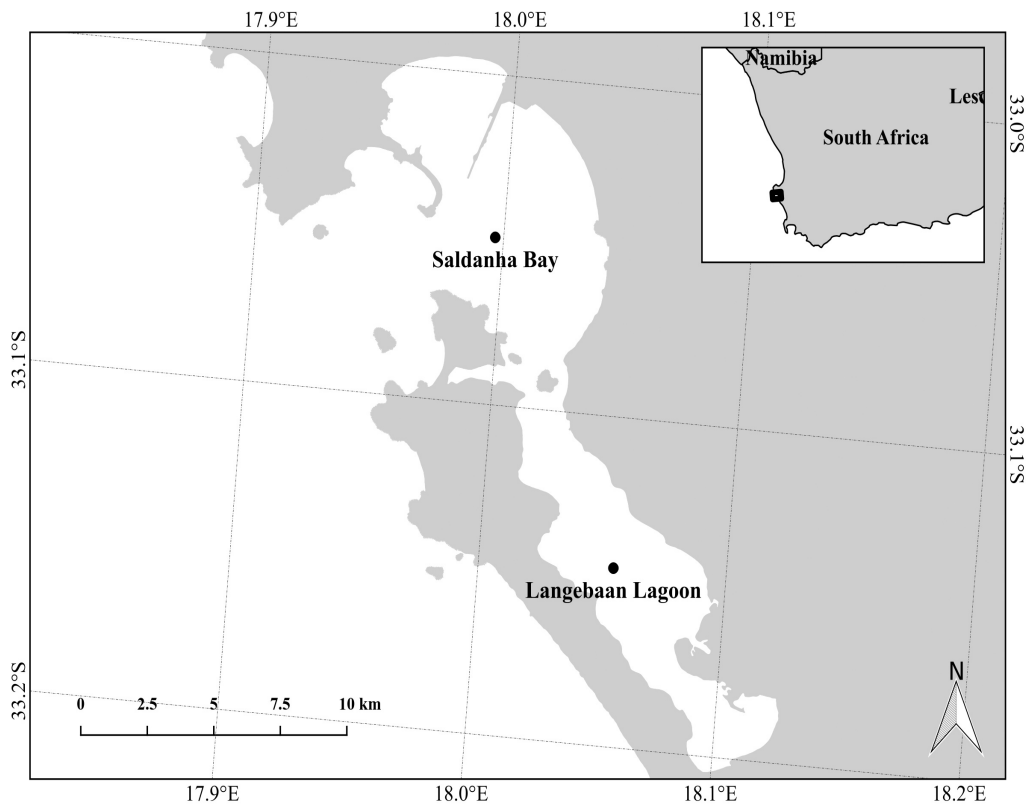


FIGURE 1.1: A map of the study site displaying its location in terms of South Africa

The bay is under considerable pressure both from commercial fishing and industrial pollutants. There is a high water residency time observed in the bay (Shannon and Stander, 1977), which catalyses the effects of the added pollutants (Beckley, 1981; Jackson and McGibbon, 1991). *Chelon richardsonii* dominate the diversity of teleosts numerically in the bay (Clark, 1997), which makes the bay attractive to fishers within the commercial Netfishery.

1.4 Aims

Commercial Netfishery catch returns and independent catch monitoring data suggests a decrease in *C. richardsonii* abundance in Saldanha and Langebaan. However, the magnitude of population decline is unknown and a quantitative assessment is required. The objectives of this study were to (1) track relative abundance of *C. richardsonii* in Saldanha and Langebaan, (2) update the life history parameters relevant for assessment and (3) assess the current depletion status of the *C. richardsonii* stock in Saldanha and Langebaan. The analysis is in two components:

Chapter 2 provides insight into the changes in *C. richardsonii* stock characteristics in terms of CPUE, sex-ratio and length-frequency distribution, highlighting features that are indicative of overfishing.

Chapter 3 investigates relevant life history parameters of *C. richardsonii*. Ageing of individuals enables the estimation of growth, maturity and mortality. These parameters are then included in a spawner biomass-per-recruit model (SBR), facilitating the production of accurate and useful management recommendations corresponding to fishing effort and mesh size.

This thesis will be concluded in Chapter 4. This chapter will discuss the findings and then provide further management recommendations for the sustainable exploitation of the *C. richardsonii* stock in Saldanha and Langebaan.

Chapter 2

Catch trends and life history changes of exploited *Chelon richardsonii* in Saldanha and Langebaan

2.1 Introduction

Gulland (1992) described the steps of length-based assessments in the following stages; (1) determination that the fishery is in stress, (2) quantitative predictions, and (3) management inferences. Determination of a stock in poor condition or under considerable stress can be detected by observing changes in fish abundance or composition (Gulland, 1992). Compositional changes within a population can be useful predictors of excessive fishing effort (Cushing, 1972; Ricker, 1981; Gulland, 1992; Hutchings and Lamberth, 2002b).

As a consequence of the selective nature of fishing gear, especially gill nets, fishing mortality is not homogenous across the fish population. Individuals display varying lengths, ages, maturation and even behaviours, which can cause heterogeneity in susceptibility to fishing (Rowe and Hutchings, 2003). It is widely accepted that excessive size selective fishing reduces the abundance of larger, older fish (Cushing, 1972; Gulland,

1992). Cushing (1972) coined this as growth overfishing, where overfishing decreases the stocks average individual weight. Applying this principle, assuming that everything else remains constant, a reduction in mean length of fish can therefore be attributable to fishing. Investigation of dynamic length-frequency data of *C. richardsonii* caught in the commercial fishery, will therefore enable estimates on the level of fishing. There are obvious problems with drawing conclusions on stock condition from length-frequencies, as fish stocks are not static, closed systems. There are other variables that contribute to variation such as recruitment (Gulland, 1992) and migration. Nevertheless, important scientific advice can be offered to aid management methods such as minimum landing sizes (MLS) and mesh sizes.

Changes in a population's sex-ratio can be used as an indicator of the level of exploitation on a stock (Griffiths *et al.*, 1999). As just mentioned, intense fishing pressures customarily decrease the abundance of larger adults within the population (Gulland, 1992) hence in populations with sexual size dimorphism the larger sex will be reduced first (Kendall and Quinn, 2012). Sexual size dimorphism was observed in *C. richardsonii*. Both Lasiak (1983) and De Villiers (1987) documented differential maximum lengths between male and female *C. richardsonii*. Females dominated the larger size classes. From the data collected by Lasiak (1983), 12% of the male sample was larger than 300 mm TL and approximately 58% of females were greater than 300 mm. Similar characteristics were found by De Villiers (1987).

True abundance of fish is difficult to determine, and ideally should be calculated through fishery-independent data. However, this can be extremely time consuming and expensive, which renders impracticable for less economically important fisheries. The small pelagic fishery of South Africa, which is the largest national fishery in terms of landed mass, calculates relative abundance of fish via annual hydro-acoustic surveys (Coetzee and Badenhorst, 2012; DAFF, 2014). In contrast, for many small-scale fisheries calculations of relative abundance rely upon fishery dependent information primarily in the form of catch and effort data (Punt *et al.*, 2000).

Catch-per-unit of effort (CPUE) is the most commonly used index of abundance, and is assumed to be linearly proportional to the true abundance such that:

$$CPUE = \frac{C}{E} = \frac{aqB}{A} \quad (2.1)$$

where C is the total catch, E is the total fishing effort, B is the true abundance of fish, A is the area, a is the availability of the fish population to the fishery and q is the catchability coefficient (Campbell, 2004). Therefore, if the raw catch is proportional to the true abundance of fish, then the availability and catchability of the fish must remain constant over time (Campbell, 2004), inferring that any changes in CPUE over time must be intimately linked to changes in actual fish abundance. There are obvious issues that arise with this simplistic method, as there are variations in catch that cannot be attributed to changes in true abundance, such as changes in fishing gears, fish behaviour and effort allocation (Campbell, 2004; Maunder and Punt, 2004). CPUE standardisation attempts to minimise the influence of such factors.

Early methods of standardisation realised notable differences in fishing power between vessels within a fishery (Beverton and Holt, 1957; Robson, 1961; Kimura, 1981), therefore in addition to effort, vessel fishing power was used as an additional factor. Currently the most widely used method of CPUE standardisation is using generalised linear models (GLMs) and generalised additive models (GAMs). These allow the inclusion of multiple explanatory variables that help explain the additional variation that isn't attributable to the changes in fish abundance (Maunder and Punt, 2004).

Alternatively, generalised linear mixed effect models (GLMMs) and generalised additive mixed effect models (GAMMs) are having increasing ecological and fishery applications (Swartzman *et al.*, 1992, 1995; Bigelow *et al.*, 1999). The addition of random variables becomes useful in the standardisation of CPUEs in small-scale fisheries; when a fishery has a relatively large and diverse fishing fleet (Helser *et al.*, 2004) and the individual fishing power of the vessel cannot be categorised. The west coast Netfishery has had 173 individual operational vessels over the last 8 years. This justifies the use of GAMMs for standardising the Netfishery CPUE.

In this Chapter sex-ratios and length-frequencies from different time periods were compared to investigate the effects of fishing on the size and sex composition of the *C. richardsonii* stock in Saldanha and Langebaan. The selectivity of the gillnets used in these different periods were calculated to enable further comments on the dynamic

length-frequencies. Lastly, the change in catch-per-unit-effort of the Netfishery in Saldanha and Langebaan between 2008 and 2016 was explored as a measure of relative abundance. The CPUE within the time series was standardised by applying GAMMs.

2.2 Methods

Data

Data for this chapter were derived from five sources: (1) a Netfishery observer programme; (2) Netfishery catch records; (3) the commercial catch from a Saldanha fisher; (4) the Department of Agriculture, Forestry and Fisheries (DAFF) *C. richardsonii* sampling data; and (5) Length-frequency data from a study performed by Naesje *et al.* (2007) in the Orange River estuary.

Sex-ratio and Length-frequency

Historical *C. richardsonii* length-frequency and sex-ratio data for 1998-2002 were obtained from two sources. The management authority (DAFF, unpublished data) provided the first data set which was reduced to only contain length-frequency and sex-ratio records caught from Langebaan, Church Haven and Saldanha (sex-ratio = 225, length-frequency = 285, Table 2.1). The size of the gillnets deployed were 48 mm stretched mesh. The second data set was obtained from a study performed by Hutchings and Lamberth (2003). The total length of 434 *C. richardsonii* from Saldanha and Langebaan caught between 1998-2002 were used for the length-frequency analysis (Hutchings and Lamberth, 2003, Table 2.1). The size of the gillnets deployed were 44, 48 and 51 mm stretched mesh.

Length-frequency data for 2009-2011 were obtained from the Netfishery scientific observer programme (DAFF, unpublished data). The data consisted of a total of 16,702 individually measured fish from Saldanha (7919 fish) and Langebaan (8783 fish) from 2009-2011 (Table 2.1). The size of the gillnets deployed were 44 and 48 stretched mesh.

TABLE 2.1: Description of data sets used for sex ratio and length-frequency analysis.

Time Period	Source	Original data set		Refined data set			
		Number of Entries	Fields	Included records	Sex ratio	Number of Entries	Length frequency
1998 - 2002	DAFF, unpub- lished data	4833	<ul style="list-style-type: none"> • Date • Locality • Capture method • Total length (mm) • Weight (g) • Sex • Maturity stage • Gonad weight (g) • Condition factor • Age estimation 	<ul style="list-style-type: none"> • Langebaan • Saldanha • Church Haven 	225	285	12
1998 - 2002	Hutchings and Lamberth (2003)	434	<ul style="list-style-type: none"> • Date • Locality • Capture method • Total length (mm) • Sample number 	<ul style="list-style-type: none"> • All 	-	434	12
2009 - 2011	Netfishery Observer Programme	16 702	<ul style="list-style-type: none"> • Date • Locality • Capture method • Fisher • Total length (mm) 	<ul style="list-style-type: none"> • All 	-	16 702	184
2017	Commercial catch and beach-seine trip sampling	353	<ul style="list-style-type: none"> • Date • Locality • Weight (g) • Fisher • Total length (mm) • Sex • Capture method 	<ul style="list-style-type: none"> • Sexed • Gillnetted en- tries 	313	301	4

Length-frequency and sex-ratio data for the current period (2017) were obtained from two sources. Length-frequency data were collected by measuring catch from a commercial fisher from a normal fishing outing. The fish were caught on the 6/09/2017 in Saldanha Bay and Langebaan Lagoon (zones A and B). The fisher used two nets; one 75 m x 5 m net of 48 mm stretched mesh and one 75 m x 5 m net of 51 mm stretched mesh. The total length (mm) was measured for 301 fish in total. An additional 52 fish were caught from 3 beach-seine sampling trips within Langebaan and Saldanha between 1/09/2017 and 24/10/2017 (Table 2.1).

Commercial catch

It is obligatory for permitted commercial fishers to submit reports of each fishing trip and its associated catch. This dataset was provided by DAFF. The initial dataset comprised of 39,515 entries between 01/01/2008 to 31/12/2016. It comprised of the (1) Number of individual fish, (2) Weight (kg) of the total fish caught per fishing trip taken by the individual permit holder per species, (3) Date, (4) Location, (5) Fisher and (6) Species caught. For the purpose of this study, the data were refined to include only catch records of *C. richardsonii* from Saldanha and Langebaan. In circumstances where only either (1) numbers caught or (2) weight (kg) was entered, the missing value was estimated using the average weight (kg) of an individual caught that month by that fisher. Entries were removed if there were equipment malfunctions that hindered the fishers from fishing. Following refinement, the data comprised of 11,640 entries with a total of 17 active fishers within Saldanha and Langebaan.

Selectivity

Different stretched mesh sized gillnets were deployed for the three time periods, therefore the specific individual selectivity for each was estimated in order to compare length-frequencies. Gillnets are passive methods of fishing, requiring fish to swim into the net and becoming gilled, snagged or tangled. Unlike other fishing methods where the selectivity is represented by logistic functions, gillnets are represented by bell shaped selection curves as a function of the mesh size. The ascending slope of the curve represents smaller fish successfully gilled and the descending slope represents the larger fish tangled

in the mesh (Hamley, 1975). The SELECT method proposed by Millar and Holst (1997) was used to assess the selectivity. SELECT is based on the assumption that for a given length class, L , the number of fish, Y_{Lj} , that encounter gillnet, j , is represented as a Poisson distribution:

$$Y_{Lj} \sim Po(p_j \gamma_L) \quad (2.2)$$

where the expected count, $p_j \gamma_L$, is the product of the number of fish in length class L , γ_L , by the relative fishing power of gillnet j , p_j (Millar and Holst, 1997). The amount of fish that encounter the gillnet j of a specific mesh size m_i that are actually caught, C_{Li} , can be expressed as the a random Poisson probability by multiplying by the gillnet retention probability, denoted as $r_j(L)$:

$$C_{Lj} \sim Po(p_j \gamma_L r_j(L)) \quad (2.3)$$

For ease of calculation, this form can be log-linearized, which then represents the catch of length L (mm) fish by gillnet j in the following way:

$$\ln(C_{Lj}) = \ln(p_j) + \ln(\gamma_L) + \ln(r_j(L)) \quad (2.4)$$

where,

$$\ln(r_j(L)) = \beta_0 + \beta_1 x_{Lj} + \beta_2 x_{Lj}^2 \quad (2.5)$$

where,

$$\begin{cases} \beta_0 = -\frac{K_1^2}{2K_2} \\ \beta_1 = \frac{K_1}{K_2} \\ \beta_2 = \frac{1}{2K_2} \end{cases} \quad (2.6)$$

and,

$$x_{Lj} = \frac{L}{m_i} \quad (2.7)$$

when k_1 and k_2 are scaling parameters for the selectivity curves. If we then assume that the selection curve is normally distributed, the selectivity S_{ti} of the mesh size m_i can be given as:

$$S_{ti} = \exp\left(-\frac{(L - \mu_i)^2}{2\sigma_i^2}\right) \quad (2.8)$$

where the mean μ_i is denoted as a linear function of the mesh size, m_i , and the spread σ_i is proportional to the mesh size, m_i , via the following: $\mu_i = k_1 \times m_i$ and $\sigma_i = m_i\sqrt{k_2}$. Due to multiple mesh sizes being used the selectivity of a multimesh gillnet catching a fish of size L can be formulated as

$$S_{GN}(L) = \sum S_{ti}(L) \quad (2.9)$$

In order to interpret the goodness of fit that the SELECT model explains the data, a pseudo-coefficient of determination (r^2) was calculated in the following way:

$$r^2 = 1 - \left(\frac{\text{Residual deviance}}{\text{Null deviance}}\right) \quad (2.10)$$

A study of *C. richardsonii* using monofilament gillnets was performed in the Orange River Estuary (Naesje *et al.*, 2007). A total of 2,790 fish were caught using different mesh sizes (44, 48, 51 and 54 mm). Consequently, the SELECT method was applied to this data. A combination of the selectivity of the mesh sizes 44, 48 and 51 mm were used to model the selectivity of the nets used in each of the time periods.

Sex-ratio and Length-frequency

Sex-ratios observed in 1998-2002 and 2017 were compared through a contingency table, to investigate whether the sex ratio was uniform over the years.

Potential differences between the mean TL (mm) of the three time series (1998-2002, 2009-2011 and 2017) were tested using an ANOVA. The assumptions of normal distribution of errors and equal variance were tested for *a priori*. In the circumstance of significant results, a Tukey-test (HSD) was applied to determine the underlying significant differences (Tukey, 1949).

Catch-per-unit-effort

Effort, in terms of time fished, of each fishing trip was not specified. It was therefore assumed that each fisher applied equivalent effort for all fishing days:

$$E = e_{ft} \quad (2.11)$$

where e_{ft} is the effort of each fisherman f , of each trip t . Therefore the unstandardised CPUE is the daily catch C_{ft} divided by the effort E .

$$CPUE_{ft} = \frac{C_{ft}}{e_{ft}} \quad (2.12)$$

where $CPUE_{ft}$ is the daily catch of *Cheloni richardsonni* (fish. trip⁻¹. fisher⁻¹).

The long-term CPUE trend was analysed between 2008 and 2016 using GAMMs with a quasi-Poisson error distribution and a log-link function. A quasi-Poisson error distribution was chosen as it better fitted the data structure than Poisson and Negative Binomial - the data were moderately zero-inflated and over-dispersed. Final model selection was performed on the basis of percentage deviance explained. Significant contributions were determined by F -tests.

The final fitted GAMM included three fixed effects; *year*, *area* and *month*, with *month* as a continuous variable with a cyclic spine. Individual *fishers* was introduced as a random effect with the assumption that there would be differences in fishing ability and average daily effort between *fishers*. *Fisher* as a random effect assumes that the variation around the intercept is normally distributed with an undefined mean of variation ($N(0, \sigma^2)$).

$$C_{ft} = \beta_1 + year + month + area + \alpha fisherman + \epsilon_i \quad (2.13)$$

$$\epsilon_i \sim N(0, \sigma^2) \quad (2.14)$$

where C_{ft} is the estimated catch (kg) of an individual fisher per fishing trip, *year*, *month* and *area* are all fixed effects. *Month* is smoothed by a cyclic cubic spline. The variable α_{fisher} denotes the fisher as a random effect, and finally ϵ_i is the unexplained variation in the model. These residuals are expected to be normally distributed with a variance of σ^2 .

2.3 Results

Selectivity

The SELECT model adequately described the selectivity of the four sizes of monofilament gillnets used within the Orange River Estuary. The model explained 99% of the variation seen within the data ($r^2 = 0.99$, Table 2.2). The scaling parameters, k_1 and k_2 , were estimated from the model (Table 2.2), and then used to estimate the mean (μ) TL (mm) and the standard deviation (σ) of each of the selection curves of each mesh size (Table 2.3 and Figure 2.1).

TABLE 2.2: The parameter estimates from the log-linear SELECT method, based on a normally distributed selection curve (Millar and Holst, 1997).

Parameter	k_1	k_2	Residual deviance	Null Deviance	df	r^2
Estimates	5.01	0.33	206.23	19721.84	94	0.99

TABLE 2.3: The mean (μ , mm) and standard deviation (σ , mm) of each normally distributed selection curves estimated for *Chelon richardsonii*.

Parameter	44 mm	48 mm	51 mm	54 mm
μ	220.45	240.49	255.52	270.55
σ	25.22	27.51	29.23	30.95

TABLE 2.4: The selectivity towards *C. richardsonii* of 75 m long monofilament gillnets used within the west coast Netfishery in the Orange River.

Fish Length (mm, TL)	44 mm	48 mm	51 mm	54 mm
80	0	0	1	0
90	0	0	0	1
100	0	0	1	0
110	1	0	0	0
120	1	1	0	0
130	0	0	0	0
140	0	0	2	0
150	1	0	0	0
160	1	0	1	0
170	0	0	0	0
180	11	2	0	0
190	44	14	1	3
200	108	56	6	8
210	175	115	22	20
220	158	165	78	43
230	159	182	119	86
240	115	124	160	98
250	43	75	113	92
260	23	40	47	80
270	11	18	17	45
280	6	10	10	24
290	1	6	6	13
300	2	3	5	6
310	1	1	0	2
320	0	1	0	1
330	0	1	0	1
340	0	0	0	1
350	0	0	0	1
360	0	0	0	0
370	0	0	0	0
380	0	0	0	0
390	0	0	0	1
Total	861	814	589	526

The selectivity parameter ($S_{GN}(L)$) was then calculated in accordance of the mesh size used during each time period (Figure 2.2).

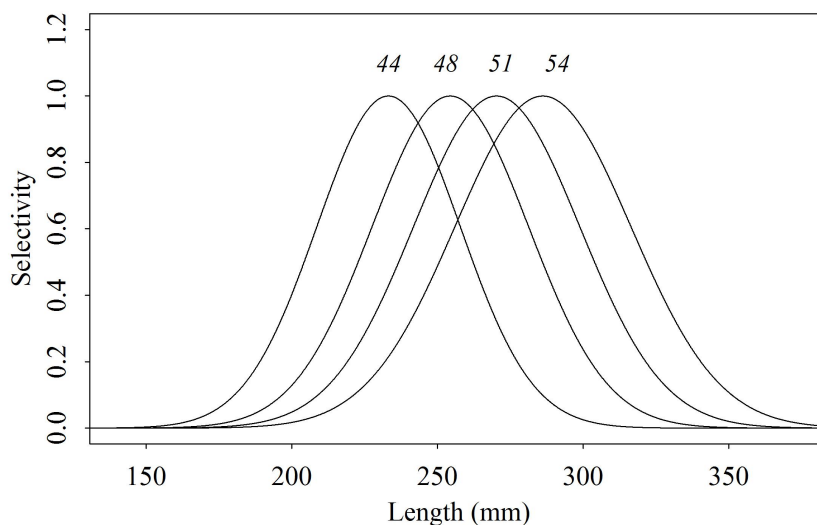


FIGURE 2.1: The *Chelon richardsonii* selectivity ($S_{GN}(L)$) of 44 mm (length at full selectivity, $L_f = 233.24$ mm), 48 mm ($L_f = 254.45$ mm), 51 mm ($L_f = 270.35$ mm) and 54 mm ($L_f = 286.25$ mm) monofilament gillnets (75 m per net) calculated from the gillnet fishery data in the Orange River.

Sex-ratio and Length-frequency

Of the total sampled fish ($n = 353$) in 2017, 40 were classified as immature (unsexed), 196 as male and 117 as female (Table 2.5). During the sampling period 1998-2001, 59 fish were classified as immature, 104 as male and 122 as female ($n = 285$, Table 2.5). A chi-squared test revealed a significant difference between the sex-ratios among the two periods ($\chi^2 = 13.992$, $df = 1$, $p\text{-value} < 0.05$). As such, the null hypothesis that the occurrence of males and females is independent of the year that they were collected was rejected, inferring a shift to a predominantly male based sex-ratio.

TABLE 2.5: Observed sex-ratios for male and female fish sampled from Saldanha and Langebaan, Western Cape South Africa, during 1998-2002 and 2017.

Year	Male	Female	Ratio	Sampling events
1998-2002	103	122	1 : 1.2	12
2017	196	117	1.7 : 1	4

There has been a clear and consistent reduction in the mean length of *C. richardsonii* caught by the west coast Netfishery in Saldanha and Langebaan (Figure 2.2). The mean TL (mm) of fish in 1998-2002 was 257.1 mm (SD = 23.3 mm), this decreased to 234.7 mm (SD = 32.6 mm) in the period of 2009-2011. A further decrease was observed in 2017 to a mean TL of 215.6 mm (SD = 14.5 mm). The results from the ANOVA corroborate this, showing that there was a significant decrease in mean TL (mm) since 1998-2002 (F value = 69.30, df = 2, p value < 0.005). Results from the Tukey-test (HSD) showed significant differences between all three time periods (Table 2.7). It must be taken into account that selectivity of nets used between all three time periods differed slightly, the selectivity of each period is represented by the selectivity curve in Figure 2.2, calculated from $S_{GN}(L)$.

TABLE 2.6: Summary statistics of the length-frequency data from all three periods.

Year	Mean (mm)	Median (mm)	Range (mm)	n	Sampling events
1998 - 2002	257.1	250	170 - 330	718	24
2009 - 2011	234.7	230	170 - 320	16,702	184
2017	215.6	215	170 - 245	301	1

TABLE 2.7: The results of a Tukey-test (HSD) on the mean TL (mm) of *Chelon richardsonii* between the three time periods.

Period	Difference (TL, mm)	LCI	UCI	P value
2009/2011 - 1998/2002	-22.91	-31.18	-14.64	<0.001
2017 - 1998/2002	-41.34	-49.63	-33.05	<0.001
2017 - 2009	-18.43	-26.67	-10.18	<0.001

Additionally, there is a depletion of mature individuals (> 205.1mm TL). In 2000, the catch was dominated by mature individuals (98% > 205.1mm) which decreased in proportion through the time series. By 2017 only 70.8% of the sampled fish were mature (Figure 2.2).

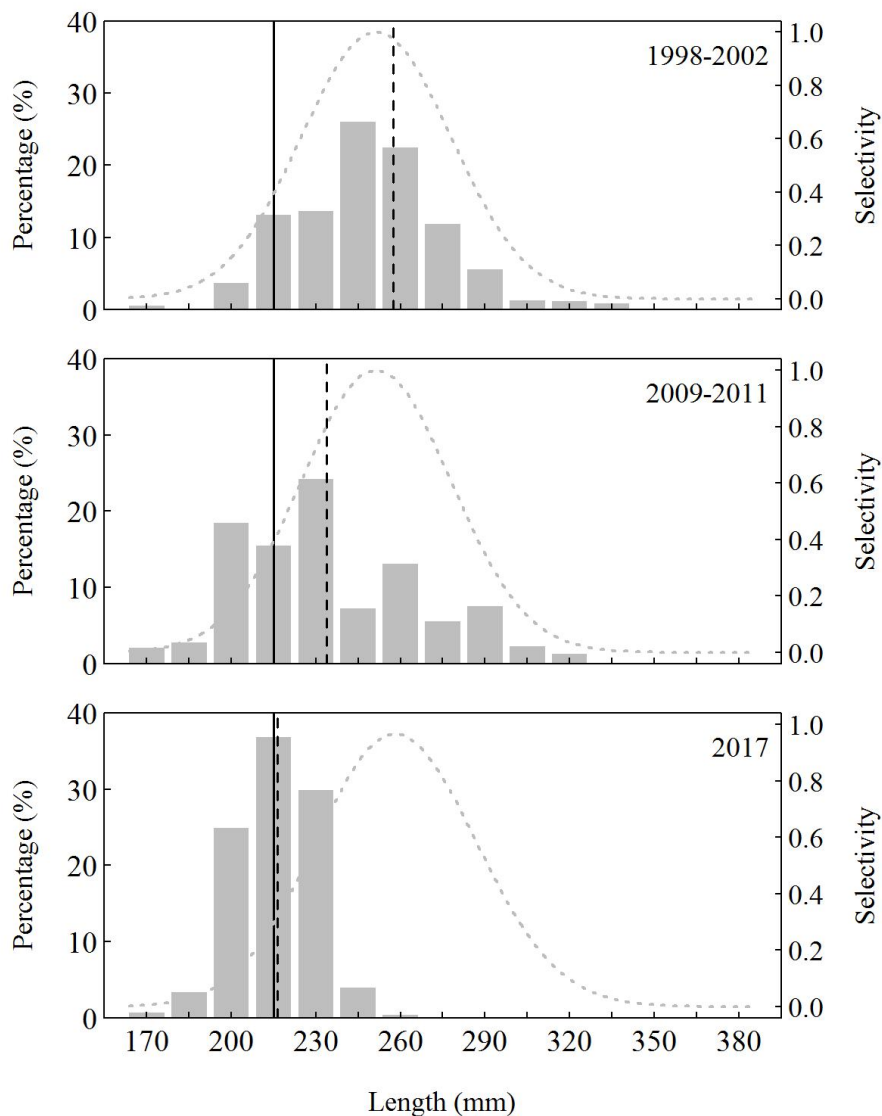


FIGURE 2.2: Length-frequency distributions of *Chelon richardsonii* caught by the commercial Netfishery fleet using the same mesh size for three different time periods. The solid vertical line represents length-at-50% maturity (205.1 mm) and the dotted vertical line is the mean TL (mm) for that length-frequency series. The bell shaped selection curve is the selectivity of the gillnets that were deployed during that particular time series.

Catch and long term CPUE

There has been a steady decrease in annual catch (t) from 2008 to 2016. In 2008, the annual catch within Saldanha and Langebaan was 127.4 t, which subsequently decreased to 77.5 t in 2016 (Figure 2.3). This equates to an approximate 40% decrease in annual catch over 8 years. Within the same period, total effort reduced slightly - in 2008, 1481

days were fished and in 2016 1228 days were fished.

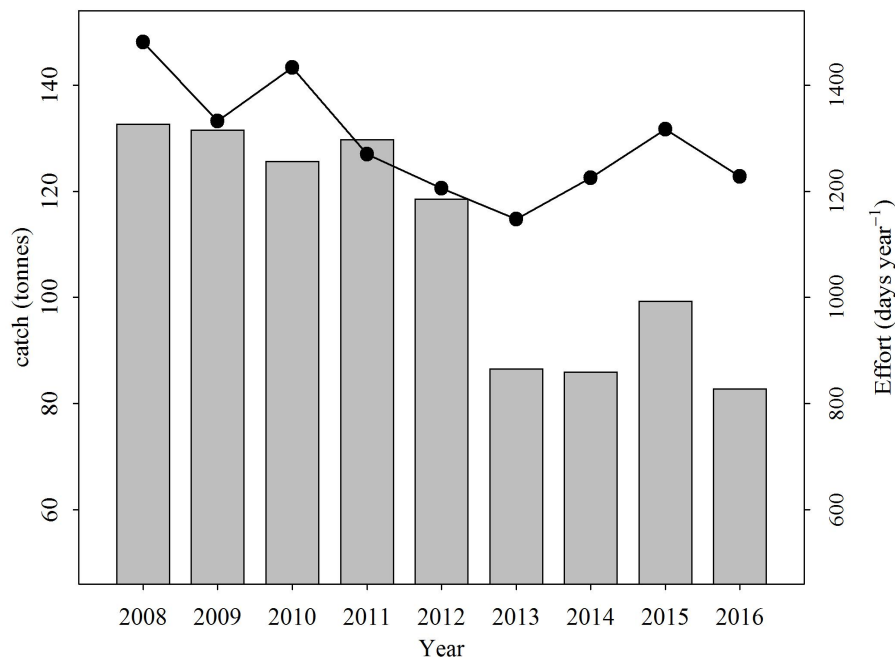


FIGURE 2.3: The annual catch (tonnes) and fishing effort (days) of *Chelone richardsonii* by the commercial Netfishery in Saldanha and Langebaan derived from mandatory commercial catch return logbooks.

The decrease in catch was accompanied by a similar declining trend in standardised CPUE (kg trip⁻¹) between 2008 and 2016. The average standardised CPUE in 2008 was estimated at 114.54 kg trip⁻¹, which declined to 82.78 kg trip⁻¹ by 2016, which equates to an approximate decrease of 30% in less than 10 years (Figure 2.4). There was a slight increase in standardised CPUE between the years of 2009 and 2011 peaking in 2011 at 126.59 kg trip⁻¹, before steeply declining. All fixed effects in the model contributed a significant percentage of deviance explained within the model, with the most variation explained by the addition of *area* (Table 2.8).

TABLE 2.8: Model statistics for all of the fixed variables within the final selected GAMM. Showing the degrees of freedom (df), the residual deviance, the change in residual deviance (Δ Deviance), the percentage of variation explained (% explained) and the F and corresponding P values.

Model	df	Residual Deviance	Δ Deviance	% explained	F	$P(\chi^2)$
Null	2	761833.2	0	0	0	0
+ Year	10	739802.1	-22031.1	6.3	34.1	<0.001
+ Month	21	737036.5	-2765.6	7.4	3.4	<0.001
+ Area	22	693555.8	-43480.6	19.1	5.6	<0.001

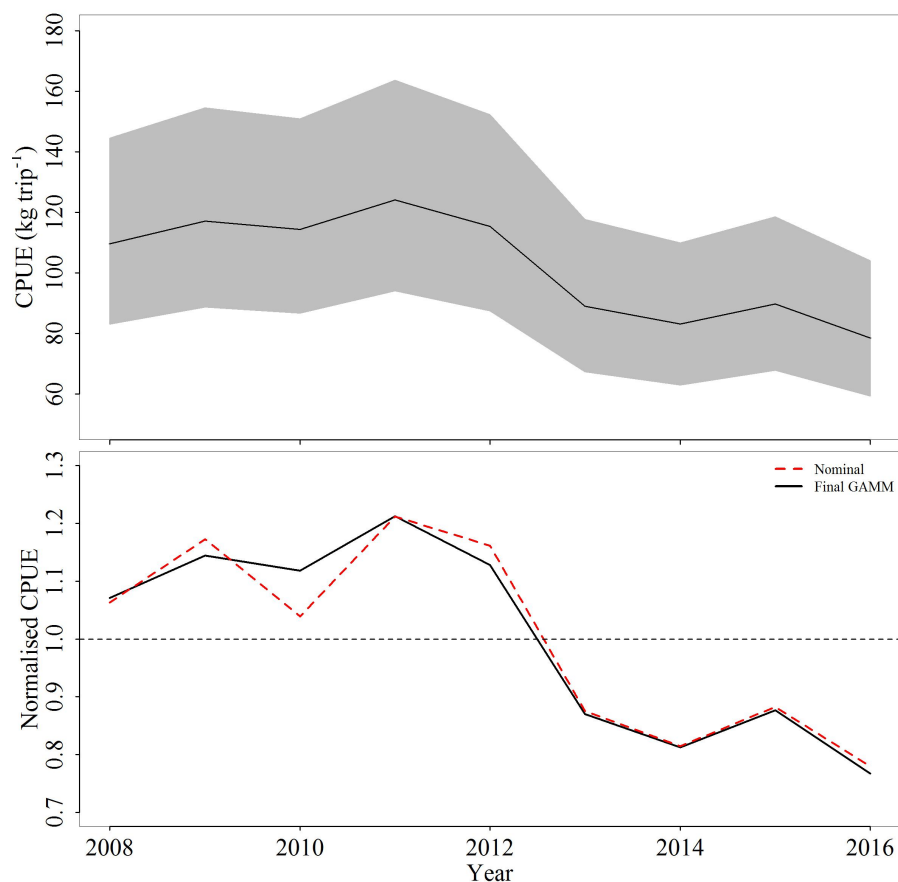


FIGURE 2.4: Annual CPUE (kg trip⁻¹) estimates ($\pm 95\%$ CI) of the commercial *Chelon richardsonii* Netfishery in Saldanha and Langebaan between 2008 and 2016 based on the GAMM (top panel). The normalised CPUE of both the final GAMM and the nominal CPUE is compared in the bottom panel.

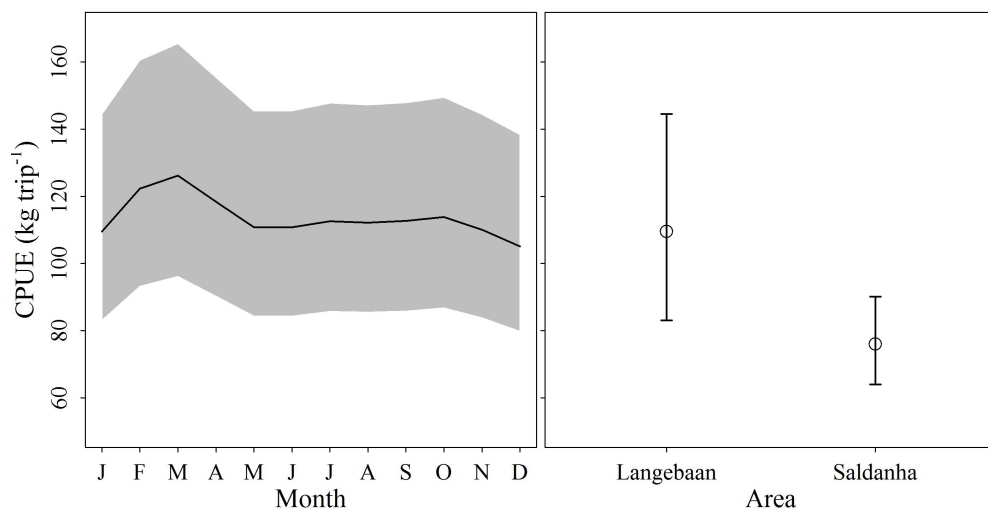


FIGURE 2.5: The influence of the fixed effects *month* and *area* on the standardised CPUE of the west coast Netfishery in Saldanha and Langebaan, modelled by a GAMM.

There is a steady standardised CPUE during winter months (May-November, approximately 110 kg fish⁻¹), followed by a small decline in spring (November-December) and then a slight spike during the summer (January-May), peaking in March at 126 kg trip⁻¹ (Figure 2.5). Furthermore, standardised CPUE is larger in Langebaan in comparison to Saldanha (Figure 2.5). Average standardised CPUE in Langebaan is 109.5 kg trip⁻¹ and in Saldanha is 76.0 kg trip⁻¹. Yet, it is not significant due to overlapping confidence intervals.

2.4 Discussion

Analysis of long term CPUE provides evidence of a declining stock of *C. richardsonii* within Saldanha and Langebaan. The CPUE has depreciated by approximately 30% over a period of 8 years (Figure 2.4). Assuming that CPUE is linearly proportional to the true abundance of *C. richardsonii*, there is strong indication that the stock has been subjected to excess fishing effort, resulting in a decline in abundance. Caution must be exercised when making inferences that assume linearity between CPUE and true abundances. Harley *et al.* (2001) provided evidence that CPUEs are not always reliable indices of abundance.

There are certain obstacles that may limit using CPUE as a reliable index for true abundance. The relationship between true abundance and CPUE can be described on a scale between hyperstability and hyperdepletion (Prince and Hilborn, 1998; Harley *et al.*, 2001). CPUEs exhibiting stability whilst true abundance decreases are classified as hyperstable, while the opposite effect is referred to as hyperdepletion. Results from a meta-analysis of CPUEs performed by Harley *et al.* (2001) provided evidence suggesting CPUEs exhibiting hyperstability were more common. Previous to this, Clark (1982) described fish stocks in reflection of their naturally occurring densities, these were classified as concentration profiles that ranged from uniform to highly aggregative. CPUE does not behave consistently across all concentration profiles. Aggregative species (type IV concentration profile), such as schooling fish, exhibit hyperstable CPUEs (Clark, 1982; Prince and Hilborn, 1998). This is of particular importance in accordance with the Netfishery due to the fishing technique and schooling behaviour of the fish. Nets are seldom set without identifying activity of schooling fish. Furthermore, *C. richardsonii*

are found in aggregations within estuarine and surf zone habitats. Consequently, this would suggest that the standardised CPUE calculated in this study would reflect that of a type IV concentration profile, hyperstable. A trait of hyperstability is that following a prolonged period of stability, there is a final period of substantial decrease, reflecting a heavily depleted stock on the verge of collapse. The standardised CPUE shows a sharp decline within the last 5 years. Therefore, it is possible that the *C. richardsonii* fishery is following this trend.

There has been an overall decrease in effort (days year⁻¹) of 20% between 2008 and 2016. Between 2012 and 2013 there was a 40% decline in catch, however the same period presented a 5% reduction in days fished. Considering nets are only deployed when shoals of fish are observed, this decline suggests a lack of fish found and/or smaller fish shoals. This is further corroborated by the number of days fished with zero catches. In 2012 there was one day with a catch of zero and in 2013 there was a total of 96 days with zero catches. Consequently, this corroborates references made to the reduction of true abundance of *C. richardsonii* within Saldanha and Langebaan.

A higher CPUE was estimated within Langebaan (CPUE = 109.5 kg trip⁻¹) than Saldanha (CPUE = 76.0 kg trip⁻¹). The efficacy of MPAs with regard to fishery conservation is a highly debated topic (Attwood *et al.*, 1997; Hilborn *et al.*, 2004; da Silva *et al.*, 2013; Kerwath *et al.*, 2013). The spill-over effect is a commonly mentioned benefit of MPAs (McClanahan and Mangi, 2000; Kerwath *et al.*, 2013), where individuals through emigration or exportation of larvae stock neighbouring fishing zones. Although the results presented here are not significant it gives an indication that the Langebaan MPA represents a refuge for *C. richardsonii*. Thus, increased fishing further into Zone B and C within Langebaan MPA has the potential to hamper catches within both Langebaan and Saldanha. It is worth mentioning that there may be other contributing factors that weren't applied within the model, hence the observed difference in true abundance may be attributable to additional unknown factors and not changes in abundance.

In the last 20 years there has been a significant change in sex-ratio to a male dominated population within Saldanha and Langebaan. This observed change would suggest that either (a) females are being removed from the stock faster than males through increased migration or mortality, or (b) due to insufficient data sampling in both time periods, females were completely missed. Regarding the former, due to sexual size dimorphism

observed in *C. richardsonii*, the larger females within the stock would have been removed due to excessive size selective fishing pressures. This theory of size selective fishing is further corroborated by the results of the dynamic length-frequency data. In 1998-2002, more than 50% of the fish caught by the Netfishery were larger than 250 mm. By 2017, there was complete absence of this size class (Figure 2.2). The larger size classes are dominated by females (Lasiak, 1983; De Villiers, 1987) and it is therefore likely that this absent size class would have been predominantly female - effectively explaining the observed change in the sex-ratio.

It is however, most likely that the observed change in sex-ratio is an artefact of insufficient sampling. Phenotypic assortment within shoals has been widely documented, concluding that the phenotypic variation is smaller within than between shoals of fish (Ranta *et al.*, 1994). Individuals prefer to shoal with familiar individuals and common discrimination's of conspecifics can be length-based (Krausse *et al.*, 1996, Griffiths and Magurran, 1997, Peuhkuri *et al.*, 1997, Croft *et al.*, 2003) or sex-based, especially during reproductive periods (Bracciali *et al.*, 2014). This limits the extent to which the conclusions from the sex-ratio analysis can be interpreted, as the number of shoals sampled for the periods 1998-2002 and 2017 were minimum. Shoal bias could have been an issue, hence increased sampling is needed to solidify any conclusions made in this study. In addition, restricted data collection in 2017 may have lead to missing potential temporal variation in female abundance. Consequently, the switch in sex-ratio may have been a product of incomprehensive data instead of the theories posed above.

Investigation of the dynamic length-frequency data indicates an approximate 20% reduction in the mean size of fish in the population, indicating possible over fishing. Similar symptoms of excessive fishing were diagnosed in the Netfishery in 2002 by Hutchings and Lamberth (2002b) where regions with high effort, such as Saldanha Bay and the Berg River, showed reductions in mean TL (mm) in comparison to regions with low effort, such as Langebaan. The mean TL of the Berg River catch was 217 mm in 1999 and the mean TL of Saldanha and Langebaan in 2017 was 215.6 mm (Hutchings and Lamberth, 2002b). Shortly after observing symptoms of growth overfishing in the Berg River, a moratorium was implemented on all gillnetting in the estuary to facilitate replenishment of *C. richardsonii* (Hutchings *et al.*, 2008). There is a general consensus that areas exhibiting comparable concerning problems should follow similar management

changes.

Growth overfishing (Cushing, 1972; Ricker, 1981) as a product of intensive overfishing has been widely documented (Law, 1991; Boehlert, 1996; Hutchings and Lamberth, 2002a; Ottersen, 2008). Contraire to common thought, growth overfishing has the potential to impair recruitment (Beamish *et al.*, 2006), as size is commonly synchronous with reproductive potential in fish (Trippel *et al.*, 1997; Birkeland and Dayton, 2005; Hixon *et al.*, 2014) - a reduction in size would reduce an individuals reproductive output. Considering that female size in *C. richardsonii* is directly proportional to the number of ova produced (De V Nepgen as cited in De Villiers, 1987), the reduction in abundance of the larger females has potential to hamper the stocks recruitment. Consequently, the synergistic effect of high fishing mortality and hampered recruitment will further increase the rate of depletion.

It must be noted that due to temporal restrictions of this project, 2017 length-frequency data were limited to a small sample size ($n = 301$ fish) and sampling was only conducted during September 2017. As such, inferences derived from these data must be made with caution. As previously mentioned, fish prefer to shoal with characteristically similar conspecifics, commonly similar sized individuals. Therefore, the 2017 data likely shows the length-frequency distribution of one shoal and not the entire stock. Yet, the same decreasing trend was observed between 1998-2002 and 2009-2011 both of which had considerably more sampling events (1998-2002 = 24, 2009-2011 = 184), minimising the shoal bias effect. Further sampling is needed to verify any conclusion made on the length-frequency of the current stock. Nevertheless, a decrease in length-frequency occurred between 1998-2002 and 2009-2011 despite the large reduction in right-holders (Table 1.1).

To conclude, catch (kg) and CPUE (kg year^{-1}) within the Netfishery in Saldanha and Langebaan has depreciated considerably in the past 8 years. Fishing effort remains relatively high despite declining annual catches. Furthermore, the population sex-ratio has undergone a pronounced change over the last 20 years and the removal of females has resulted in a predominantly male stock in Saldanha and Langebaan (1.7 males : 1 female). Lastly, the dynamic length-frequency data corroborates the hypothesis of growth overfishing - there has been a significant reduction in mean TL (mm) within the last 20 years. Individually, these results could suggest alternative reasons other than

excessive overfishing. However, together the results substantiate the theory of an unsustainably fished stock that requires management intervention. Thus, the undertaking of a full quantitative stock assessment to facilitate the implementation of a new correct management framework is imperative for the sustainability of the future stock.

Chapter 3

Age, growth and the application of a spawner biomass-per-recruit model to *Chelon richardsonii* in Saldanha and Langebaan

3.1 Introduction

The life history of an organism refers to the temporal events that contribute to the chronological framework of its life. These, are essentially birth, maturity and death. These traits are governed by trade-offs between growth, reproduction and survival in order to maximise the fitness of the organism, which in turn are determined and constrained by environmental forces and natural selection (Stearns, 1976). Additional anthropogenic forces such as fishing can also contribute to modifications in life history traits. Fishing pressures may have created selection forces that favour the development of alternative life history strategies; such as increased somatic growth rate and decreased age at maturity (Rijnsdorp, 1993; Rochet, 1998; Law, 2000; Olsen *et al.*, 2004). Consequently, exploited populations may exhibit differential life history traits to an unexploited population.

The r - K selection theory (MacArthur and Wilson, 1967), trilateral continuum (Wine-miller and Rose, 1992) and further developments of these (Kawasaki, 1980; McCann and Shuter, 1997) are biological concepts that attempt to categorise these life history traits. These theories can provide valuable information a stocks behaviour. In some cases, species grouped with similar species as a result of their life history strategies may allow the production of management frameworks in the absence of fishery data (King and McFarlane, 2003). Previous studies have explored the reproduction and maturity exhibited by *C. richardsonii* (Lasiak, 1983; De Villiers, 1987). *Chelon richardsonii* are highly fecund isochronal broadcast spawners, with relatively small eggs and no parental care (De Villiers, 1987). Ripe females can carry up to 369,000 eggs (De Villiers, 1987), however it is postulated that only half of these eggs are viable oocytes (Lasiak, 1983). The combined sex length-at-50% maturity was calculated to be between 210-215 mm FL (De V Neppen as cited in De Villiers, 1987), which corresponds to an age-at-50% maturity of 3 years. This evidence suggests that *C. richardsonii* exhibits a life history strategy commensurate with the r -type, highly fecund, early maturation and no parental care. In a fisheries context, r -selected species theoretically show higher resilience to increased fishing intensity (Adams, 1980).

A pre-requisite for elucidating the life history parameters of a fish, is to determine age. This can be achieved via exploiting the regular growth and deposition of annular rings within calcified hard parts such as scales and otoliths (Royce, 2013).

The use of scales for age determination is attractive due to the accessibility and the amount of scales per specimen. However, age is commonly underestimated when using scales due to absorption, regeneration, growth delay and compression of calcium increments (Beamish, 1987). As age estimates are intricately linked to growth and mortality, underestimation can overestimate the growth. This error has historically led to mismanagement of fisheries through the implementation of excessive catch and effort quotas (Ashford *et al.*, 2001; Yule *et al.*, 2008). In contrast, otoliths do not suffer from such issues and have two particular traits that makes them advantageous for age estimation. The membranes that encase the calcium structures are far more regulatory than blood. This property means that when environmental conditions fluctuate, the regular growth increments do not vary significantly in comparison to other hard structures (Campana, 1999). Fish grow to an asymptotic length, once reached, somatic growth

ceases which makes age determination past this age difficult. Unlike scales and bones, otoliths continually grow regardless of asymptotic length being reached (Maillet and Checkley, 1990).

There are processing errors associated with ageing fish by examining hard structures such as otoliths and scales. Not all hard calcium structures form uniform increments at regular intervals across all axes (Beamish, 1979). For instance, as fish reach asymptotic length, otoliths tend to grow wider rather than longer. Furthermore, not all species or age-groups within species share the same periodic formation of growth rings (Beamish and McFarlane, 1985); hence it is necessary to validate the temporal deposition of sequential growth increments in order to verify the specific ageing technique used (Campana, 2001). There are also interpretation errors that arise from the preparation and interpretation of the structures by the examiner (Boehlert, 1985). Underestimation of age through these errors can be detrimental to the status of the stock, and in some circumstances, like the orange roughy, can cause stock collapse (van den Broek, 1983). Therefore it is essential to minimize these errors.

Annuli (annual calcium increments) of otoliths can be assessed visually by studying the whole or sectioned otoliths. Conducting age estimation with sectioned otoliths has comprehensively shown increased reliability of estimates (Beamish, 1979; Hyndes *et al.*, 1992; Griffiths, 1996). Yet, inaccuracy of age estimation is primarily observed in fishes exhibiting higher longevities (Beamish, 1979; Griffiths, 1996). As individuals reach their asymptotic length, growth decelerates and the length of growth annuli shortens, ending in superimposition (Beamish, 1979; Hyndes *et al.*, 1992). However, *C. richardsonii* have a much smaller age range, enabling the use of whole otoliths for age estimation, as shown successfully in previous Mugilidae studies (Moura and Serrano Gordo, 2000; Gonzalez Castro *et al.*, 2009).

Stock assessments are intimately linked to the quality of data provided. Conclusions drawn from assessments produced from a foundation of poor data can have erroneous outcomes for the stock in question. Fishery independent data, such as annual surveys, provide the most robust form of data. Investment costs, both economic and labour, are notably high for the production of fishery independent data. Thus, large scale fisheries that are economically more valuable, such as the demersal trawl- and the small pelagic purse-seine fishery in South Africa, are assessed with the aid of fishery independent

surveys (DAFF, 2014). Contrastingly, small-scale fisheries such as the Netfishery, which has a much lower economic value, only provides fishery dependent records. Given fishery dependent data, there are favourable assessment methods that can be applied when no survey time series is available. The Netfishery has high levels of non-reported catch (Lamberth *et al.*, 1997) and the effort documented was rudimentary only days, not soaked net times. Therefore, a per-recruit analysis was favoured over surplus production models.

Per-recruit models, developed by Beverton and Holt (1957), have been essential tools for fishery managers. Regardless of Sparre and Venema (1998) doubting the future application of these models, they have been widely applied to data poor fisheries. In cases with a lack of robust data and knowledge of the spawner-biomass and recruit relationship, Butterworth *et al.* (1987) recommended per-recruit analyses to be appropriate. In South Africa, they have been widely applied and accepted as methods to assess the data poor linefish stocks (Smale and Punt, 1991; Bennett, 1993; Griffiths, 1996; Booth and Buxton, 1997). It is postulated that the *C. richardsonii* stock has been subject to recruitment overfishing. Recruitment overfishing is the reduction of the stock population to the point that the stock-recruitment relationship becomes linear (Walters and Martell, 2004). This is difficult to diagnose, as to ascertain the stock-recruitment relationship with any confidence is challenging (Hilborn and Walters, 1992). The spawner biomass-per-recruit model is a tool that requires no prior knowledge of this relationship.

Spawner biomass-per-recruit (SBR) and yield per-recruit (YPR) are both steady state models that estimate the response of a stock in relation to mortality, recruitment and growth. Due to the assumption of temporal uniformity, inaccurate estimates of relative yield and biomass can be calculated (Griffiths, 1996). Furthermore the model assumes that recruitment remains uniform independent of the spawner-biomass or fecundity. This is important to note, as Saldanha Bay is not a closed system so recruitment and migration may not remain constant. Regardless of *C. richardsonii* spawning in inshore and surf zone habitats it is likely that they spawn with stocks outside of the bay. Implying that the number of recruits would be dependent of a larger, national population and not the stock within Saldanha and Langebaan. These limitations must be kept in mind. Nevertheless, it does facilitate the investigation of the response of the yield and spawner-biomass as a function of the instantaneous fishing mortality (F) and age-at-first capture

(t_c) (Booth and Buxton, 1997). These parameters, F and t_c , are intimately linked to fishing effort and net mesh size, respectively. Thus, knowledge of how combinations of these can be manipulated to alter the SBR of a stock is valuable information to fishery scientists (Booth and Buxton, 1997). This will allow the development of management recommendations for TAE and minimum mesh size (Booth and Buxton, 1997).

This Chapter aims to determine the life history traits expressed by the Saldanha and Langebaan *C. richardsonii* stock. Age, and subsequently growth and mortality, was explored via age determination using whole otoliths. Age-based curves facilitated the estimation of total instantaneous mortality (Z). Using the estimated life history components a spawner biomass-per-recruit analysis was conducted to assess the stock status of *C. richardsonii* in Saldanha and Langebaan in the west coast Netfishery. By investigating SBR through different fishing mortalities (F) and combinations of mesh sizes, the study provided a synthesis of a favourable management framework that facilitates the replenishment and sustainable use of the stock.

3.2 Methods

Length-weight relationship

Relationships between fork length (FL, mm) and total length (TL, mm), and FL and weight (g) were explored using linear regression. For the length-weight relationship both weight and FL were natural-log transformed. The significance of the relationship was described by r^2 . Fultons Condition Factor (1904) was also calculated (Fulton, 1904):

$$K = \frac{W}{FL^3} \quad (3.1)$$

where K is the condition factor and W is the weight in g. A student t-test was applied in order to test the null hypothesis which there is no difference between the mean condition factor between males and females.

Ageing

After preliminary investigation, growth increments were adequately displayed in whole otoliths. Thus, whole otoliths were used for age determination over sectioned otoliths. Whole otoliths submerged in methyl-salicylate and viewed under reflected light against a black background adequately displayed annual growth increments of *C. richardsonii*. Otoliths were viewed using a Nikon SMZ800 microscope under a magnification of 2X. Photographs of each otolith were taken using a Canon EOS 650D camera. The microscope eyepiece was removed and the camera (without a lens) was attached to the eyepiece sleeve. The photos were then read by 3 independent readers. Due to the temporal restraints of this study, an age validation study was not performed. However, De Villier's (1987) recorded the sequential deposition of translucent annuli during the spring and summer and opaque annuli during the autumn and winter in fish younger than 3 in *C. richardsonii*. Furthermore, Ellender *et al.* (2012) showed that growth zone deposition was annual in both *Mugil cephalus* and *Myxus capensis*. Consequently I have assumed that *C. richardsonii* expresses the same deposition rate. Each reader aged every otolith once. If two or more of the readings agreed, this was taken as the age, if there was no agreement between all three readings the otolith was discarded. To determine the accuracy and precision of the age determination, the Average Percentage Error (APE) and the Coefficient of Variation (CV) was calculated (Beamish and Fournier, 1981; Campana, 2001):

$$APE_j = 100\% \times \frac{1}{R} \sum_{i=1}^R \frac{|x_{ij} - x_j|}{x_j} \quad (3.2)$$

where, x_{ij} is the i^{th} age determination of the j^{th} fish, x_j is the mean age determination of the j^{th} fish, and R is the number of times that each fish was aged. This will be averaged across all fish aged, resulting in an index APE.

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^R \frac{(x_{ij} - x_j)^2}{R-1}}}{x_{ij}} \quad (3.3)$$

where, CV_j is the age precision estimate for the j^{th} fish. CV_j will be averaged over all the fish used, resulting in a mean CV.

Growth

Using both combined and sex-specific age-length data, the growth of *C. richardsonii* was modelled with the three parameter von Bertalanffy growth equation:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (3.4)$$

where L_t is the total length (TL) at time t , L_∞ is the asymptotic length where the growth rate is zero, K is the rate at which L_∞ is reached and t_0 is the age of fish at zero length (Beverton and Holt, 1957). The variability of the parameter estimates was estimated by a parametric bootstrapping technique, with 1000 bootstraps (Efron, 1981). A Likelihood Ratio Test (LRT) was applied in order to test for a significant difference between the growth rates of male and female *C. richardsonii*.

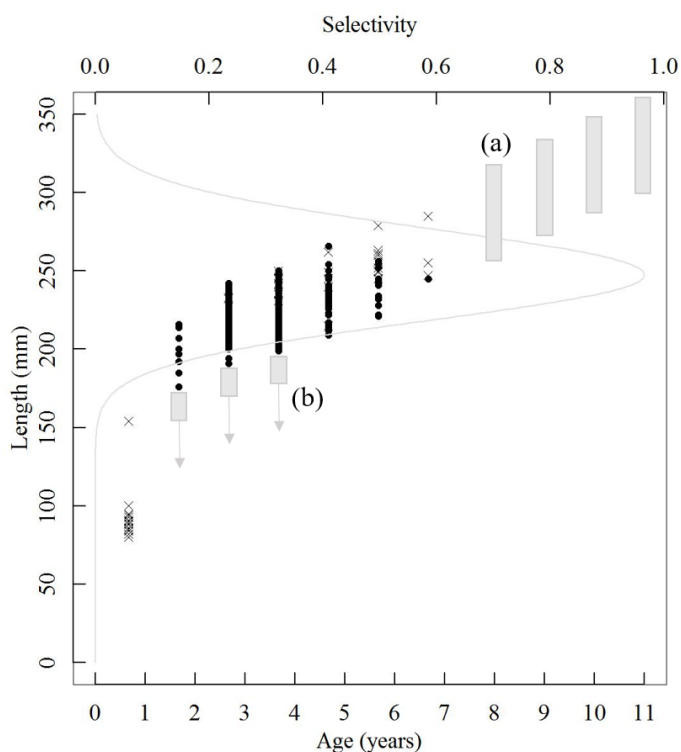


FIGURE 3.1: A conceptual diagram of the assumed absent data due to (a) either sampling effort or completely absent older individuals and, (b) gillnet selectivity. The ● represent the fish caught by gillnets (48 and 51 mm) and the X represent fish caught by beach seine. Lastly, the size selectivity of the gillnets is denoted by the grey curve.

There was an absence of fish larger than 280 mm (Figure 3.1(a)) and fish smaller than the

gill-net selectivity (Figure 3.1(b)) in the catch data collected in 2017. It was assumed that the large fish were either missed due to insufficient sampling or that they were totally absent from the population. Any growth model applied to this data would not truly reflect the stocks growth. Consequently, an additional growth model was estimated using an estimated L_∞ from the historical L_{max} of the commercial catch in 1998. The aim was to overcome the potential problems arising from this missing data and to produce a more realistic representation of the growth and natural mortality of *C. richardsonii*.

Pauly (1984) suggested that the relationship between L_{max} and L_∞ can be described in the following way (Pauly, 1984):

$$L_\infty = \frac{L_{max}}{0.95} \quad (3.5)$$

where L_{max} is the maximum length within the observed sample. Historical catch data suggests that female *C. richardsonii* grows to an L_{max} of 330 mm and males 280 mm, from which L_∞ was estimated. L_∞ was fixed within the model and the two parameters, t_0 and K , were fitted to the 2017 age-length data. For ease of delineation, this growth model will be referred to as the fixed model and the original model will be referred to as the original model.

Due to the selective nature of gillnets, the sample was dominated by 2 and 3 year old fish, which caused artificial inflation of samples within these age groups. Consequently, the model emphasised these age groups over the poorly represented age groups. Brouwer and Griffiths (2005) determined the minimal sample sizes needed to retain precision and accuracy of growth models. A minimum of 10 fish per 20 mm size class was agreed upon (Brouwer and Griffiths, 2005). Due to the reduced range of sizes observed in *C. richardsonii* (80 mm-285 mm), a minimum of 15 fishes per 10 mm was used and fish were selected randomly within each 10 mm size class.

Mortality

Total

The calculation of instantaneous total mortality (Z) was calculated via the method outlined by Butterworth *et al.* (1989). The commercial catch length-frequency data was transformed to an age-frequency distribution using the normalised age-length key. This age-frequency data was then natural-log transformed. Z was then estimated as the negative gradient of the linear model applied to the descending limb of the distribution. The linear regression was applied to the age (a) that exceeds and includes the a at full recruitment (a_f), this tends to be when the selectivity of this age is equal to 1, and also the peak of the age distribution (Butterworth *et al.*, 1989). This equation is as follows:

$$Z = \ln\left(1 + \frac{1}{(\bar{a} - a_f)}\right) \quad (3.6)$$

where \bar{a} is the mean age of all fish full recruited in the sample ($a \geq a_f$). The age-frequency distribution was then adjusted to represent a more realistic sample using the selectivity parameter ($S_{GN}(L)$) calculated later in this study.

Natural

Natural instantaneous mortality (M) was calculated by applying the three following methods: Chen and Watanabe (1988), Hoenigs (1983) and Jensens (1996). Paulys (1980) method was left out as equation was derived from tropical species. Firstly, Chen and Watanabe (1988) is as follows:

$$M = \frac{K}{G} \quad (3.7)$$

where K is the von Bertalanffy parameter which is the rate that L_∞ is reached and G is the growth measure. G can be represented as follows:

$$G = \begin{cases} 1 - e^{-K(t-t_0)}, & t \leq t_M \\ a_0 + a_1(t - t_M) + a_2(t - t_M)^2, & t \geq t_M \end{cases} \quad (3.8)$$

where a_0 , a_1 , a_2 and t_M can be expressed as follows:

$$\begin{cases} a_0 = 1 - e^{-K(t_M-t_0)} \\ a_1 = Ke^{-K(t_M-t_0)} \\ a_2 = -\frac{1}{2}K^2e^{-K(t_M-t_0)} \end{cases} \quad (3.9)$$

and

$$t_M = -\frac{1}{2} \ln|1 - e^{Kt_0}| + t_0 \quad (3.10)$$

where t_0 is the age of fish at zero length, t_M is the age at maturity (Chen and Watanabe, 1989). Secondly, Hoenig's (1983) is estimated as follows:

$$\ln(M) = 1.46 - 1.01 \ln(t_{max}) \quad (3.11)$$

where t_{max} is the maximum age of the fish (Hoenig, 1983). Lastly, Jensen's (1996):

$$M = 1.63K \quad (3.12)$$

where K is the von Bertalanffy parameter which is the rate at which L_∞ is reached.

Selectivity

Using the selectivity parameter ($S_{GN}(L)$) calculated in Chapter 2, the selectivity of the gillnets used in this study (48 and 51 mm) was calculated as outlined in equation 2.9.

Per-recruit

Parameter estimates for mortality, maturity and length-weight relationships (Table 3.1) were incorporated into a spawner biomass-per-recruit (SBR) model to estimate the status of the stock in terms of fishing mortality (F) and age-at-selectivity ($S_{GN}(a)$ as calculated in Chapter 2) in the following way:

$$SBR(S_{GN}(a), F) = \sum_{a=0}^{t_{max}} W_a \tilde{N}_a \psi_a \quad (3.13)$$

when ψ_a is the proportion of mature fish at age a , W_a is the weight (g) at age a , $S_{GN}(a)$ is the selectivity of each fish at age a , F is the instantaneous rate of fishing mortality, M is the instantaneous rate of natural mortality, t_{max} is the maximum age of the observed sample and \tilde{N}_a is the number of fish at age a calculated by the following:

$$\tilde{N}_a = \begin{cases} 1 & \text{if, } a = 1 \\ \tilde{N}_{a-1} e^{-M-S_{GN}a-1F} & \text{if, } 1 < a < t_{max} \\ \frac{\tilde{N}_{a-1} e^{-M-S_{GN}a-1F}}{e^{-M-S_{GN}aF}} & \text{if, } a = t_{max} \end{cases} \quad (3.14)$$

TABLE 3.1: Estimates of the parameters that were used in the spawner biomass-per-recruit analyses for *Chelon richardsonii*.

Parameters	Description	Fixed model	Original model
L_∞	Asymptotic length	347.40	245.40
K	Growth rate coefficient	0.23	0.85
t_0	Age when average length was 0	-1.03	-0.07
t_1	Known minimum age	0	0
t_2	Known maximum age	11	11
M	Asymptotic natural mortality rate	0.26 - 0.62*	0.88 - 1.42*
F	Asymptotic fishing mortality rate	0.93 - 1.29*	0.04 - 0.60*
t_{max}	Observed maximum age	11	6
a	Length-weight regression parameter	0.000009	0.000009
b	Length-weight regression parameter	3.05	3.05
ψ	Length-at-50% maturity	205.10	205.10
$S_{GN}(L)$	The multipanel gillnet selectivity	0 - 1.89*	0 - 1.90*

*range of values for parameters with independent values per age class

The depletion level of the stock population was investigated by exploring three biological reference points as different rates of instantaneous fishing mortality (F). These points

were $F_{0.1}$, the fishing mortality rate that will relate to a stock that has been fished 10% of its pristine unfished levels (Gulland and Boerema, 1972). Secondly, F_{SB25} , which is the F when the spawner biomass is at 25%. Below this threshold it is assumed that the stock is at serious risk of recruitment failure (Griffiths *et al.*, 1999). Lastly, F_{SB40} which is F when the spawner biomass is at 40% of unfished levels, which translates to an optimally exploited population (Griffiths *et al.*, 1999).

3.3 Results

Morphometrics and population structure

The relationship between FL and TL can be described by $TL (mm) = 1.109 FL (mm) - 1.659 (mm)$ ($r^2 = 0.991$). Additionally, the length-weight relationship for the combined sexes is described by $Wt (g) = 0.0000009 FL (mm)^{3.05}$ ($r^2 = 0.954$, Figure 3.2).

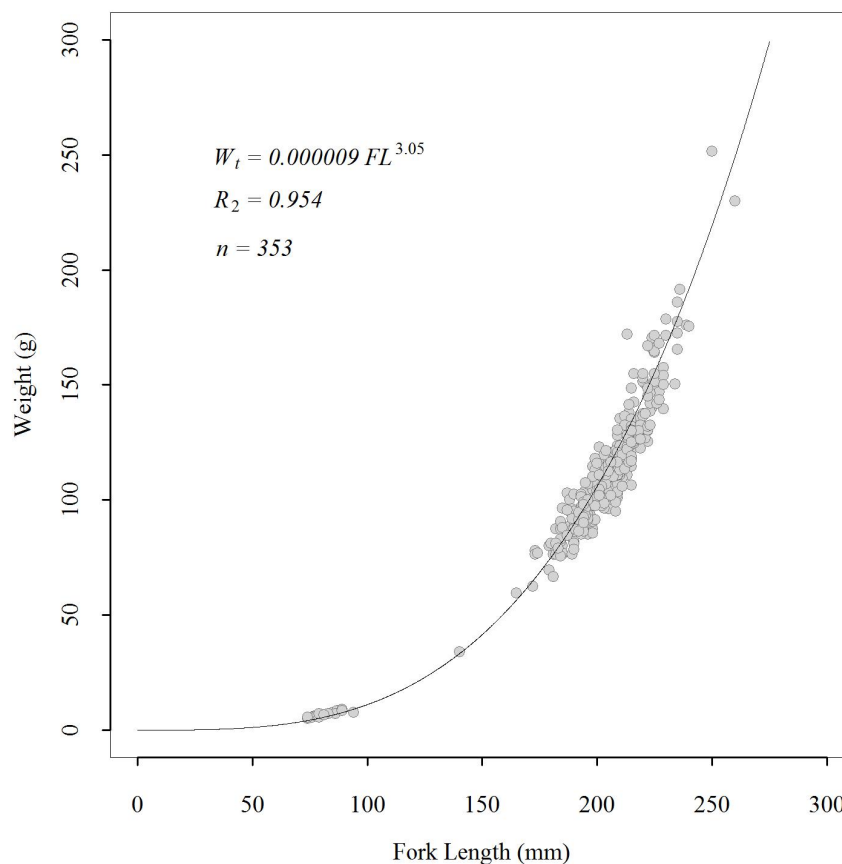


FIGURE 3.2: Length-weight relationship of *Cheloniidae* sampled from Saldanha and Langebaan, Western Cape South Africa.

There was no significant difference between the conditions factors of male and female ($t = -0.814$, $df = 202.22$, $p \text{ value} = 0.4164$).

Ageing

Of the 353 sampled fish, 240 (68%) otolith readings were accepted, while 113 (32%) were rejected due to inability to interpret annuli and breaking. The IAPE calculated for the three age determinations was 13.9% with a CV of 18.4%.

TABLE 3.2: The mean total length (TL, mm) and the Index of Average Percentage Error of each age class of all *Chelon richardsonii* caught in Saldanha and Langebaan (2017).

Age	Mean (TL, mm)	IAPE	n
0	92.15	0	18
1	200.11	34.07	9
2	218.00	10.90	65
3	225.44	10.92	96
4	234.35	13.89	36
5	248.71	12.29	13
6	261.67	23.33	3

The largest disagreement between readers occurred within younger and older individuals. Age estimation for medium sized individuals was relatively consistent among readers (Table 3.2). The maximum age within the sample was 6 years old, with a minimum age of 0. The most commonly aged class in the data was 3 years old (225.44 mm TL, Table 3.2). The age-length key produced from the age readings is illustrated in Table 3.3.

Growth

The von Bertalanffy growth model provided an adequate fit to the age-length data, and post model validation illustrated normal residuals and homoscedasticity. The model was fitted to both sexes successfully. Results from the LRT show that there was a significant difference in growth between sexes ($df = 3$, $\chi^2 = 59.178$, $p \text{ value} < 0.001$). Model estimates for all six models (original and fixed models), including confidence intervals produced by parametric bootstrapping, can be found in Table 3.4.

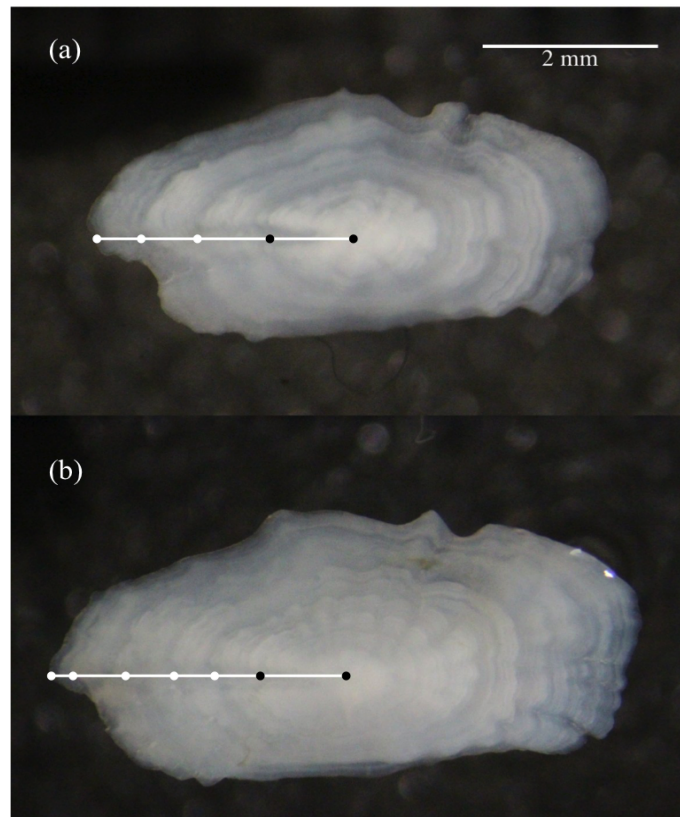


FIGURE 3.3: Whole otoliths submersed in methyl-salicylate and viewed under a dissection microscope using reflected light with a dark background. In each photo (white ●) represents each year (a pair of translucent and opaque bands) and (black ●) represents the centre and edge of the nucleus. Photo (a) is a 3 year old individual, and (b) is a 5 year old individual.

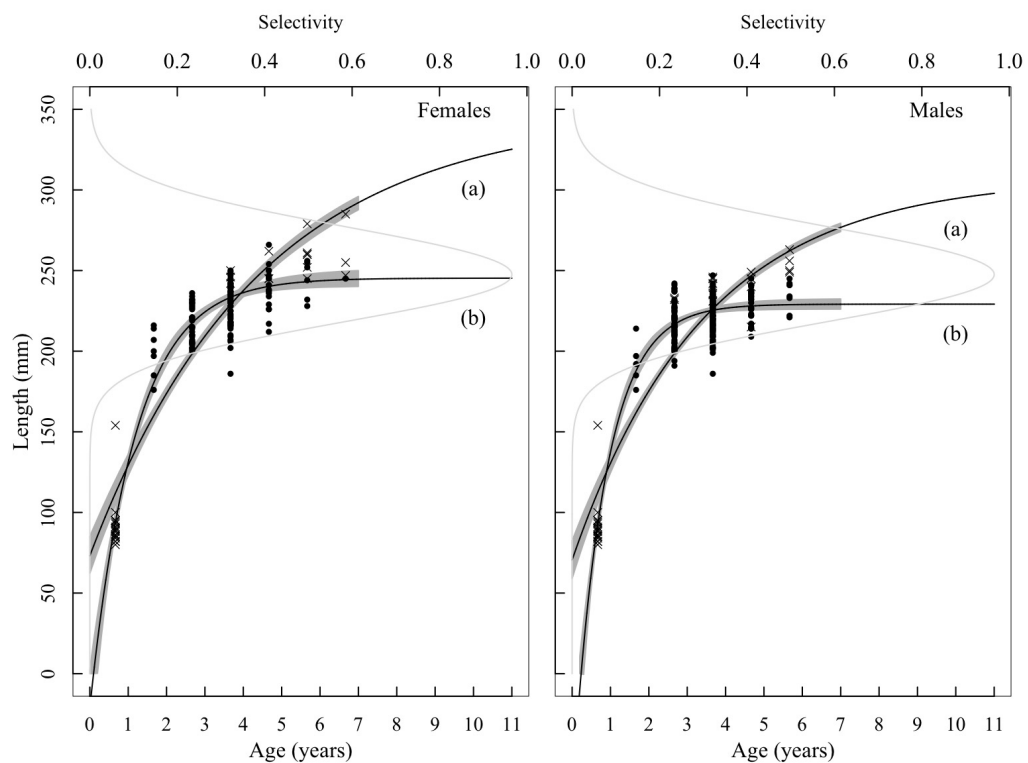


FIGURE 3.4: The separate sex length age relationship of *Chelonia richardsonii* from Saldanha and Langebaan (2017) described by a von Bertalanffy growth curve ($n = 353$, females = 157, males = 236), with the 95% confidence intervals fitted by parametric bootstrapping, (a) represents the fixed model and (b) represents the original model. The ● represent the fish caught by gillnets (48 and 51 mm) and the X represent fish

TABLE 3.3: The age-length key produced from the whole otolith readings for the combined sexes of *Chelon richardsonii* sampled from Saldanha and Langebaan (2017, n = 240).

Total Length (mm)	Number of fish in each age class						
	0	1	2	3	4	5	6
80	11						
90	6	1					
100	1						
110							
120							
130							
140							
150							
160							
170		1					
180		1		1			
190		2	2	1			
200		2	15	12	1		
210		2	22	27	7		
220			14	21	6	2	
230			11	22	11	2	
240			1	11	8	3	1
250				1	2	4	1
260					1	2	
270							
280							1
Total	18	9	65	96	36	13	3

As a consequence of the missing data outlined in Figure 3.1, the original growth model (represented as *(b)* in Figure 3.3) showed an increase in growth and a decrease in L_{∞} (Table 3.4). As smaller individuals within the age classes one - four were missing K was increased. As a consequence of the missing older, larger fish, L_{∞} was significantly reduced (Table 3.4). Somatic growth ceased for both males and females at approximately 5 years of age. The growth models fitted using a fixed L_{∞} (as shown as *(a)* in Figure 3.3) displayed a slower growth and a larger L_{∞} (Table 3.4). Compared to previous growth studies of *C. richardsonii* (Table 3.5) the fixed model provided a more realistic representation of the growth. Thus, the estimates of growth from the female fixed model (Table 3.4) were used for the subsequent sections of the study.

TABLE 3.4: Point estimates and summary statistics from the von-Bertalanffy growth model fitted separately to males, females then combined of *Chelon richardsonii* sampled from Saldanha and Langebaan (CV = coefficient of variation, CI = the lower and upper 95% confidence intervals).

		Parameter	Point Estimate	CV	95% CI
Original	Male	L_∞	229.18	0.01%	226.151 : 232.51
		K	1.20	0.07%	1.03 : 1.40
		$n = 236$	t_0	0.23	0.04%
	Females	L_∞	245.40	0.01%	240.34 : 251.02
		K	0.85	0.08%	0.73 : 0.98
		$n = 157$	t_0	-0.07	0.71%
	Combined	L_∞	236.32	0.01%	233.49 : 239.70
		K	1.00	0.06%	0.90 : 1.12
		$n = 353$	t_0	0.16	0.23%
Fixed	Male	L_∞	307.40	-	-
		K	0.29	0.03%	0.27 : 0.31
		$n = 236$	t_0	-0.89	0.12%
	Females	L_∞	347.40	-	-
		K	0.23	0.03%	0.22 : 0.24
		$n = 157$	t_0	-1.03	0.12%
	Combined	L_∞	347.40	-	-
		K	0.19	0.03%	0.18 : 0.20
		$n = 353$	t_0	-1.79	0.09%

TABLE 3.5: von Bertalanffy growth parameters of *Chelon richardsonii* from different studies and localities.

Species	K	L_∞	t_0	Sex	Locality	Study
<i>C. richardsonii</i>	0.228	347	-1.033	Female	Saldanha	Current (2017)
<i>C. richardsonii</i>	0.256	359	0.255	Combined	False Bay	Ratte (1977)
<i>C. richardsonii</i>	0.287	352	0.240	Combined	False Bay	De Villiers (1987)

Selectivity

The mesh sizes used within this study were 48 mm and 51 mm. Therefore, the selectivity parameter ($S_{GN}(L)$) of the commercial fishery in Saldanha and Langebaan was the product of the selectivity curves; 48 mm and 51 mm (Figure 3.5) as outlined in equation 2.9. This was then used to adjust the observed age-frequency catch curve to the adjusted age-frequency (Figure 3.7) used to calculate the total mortality (Z) in the next section.

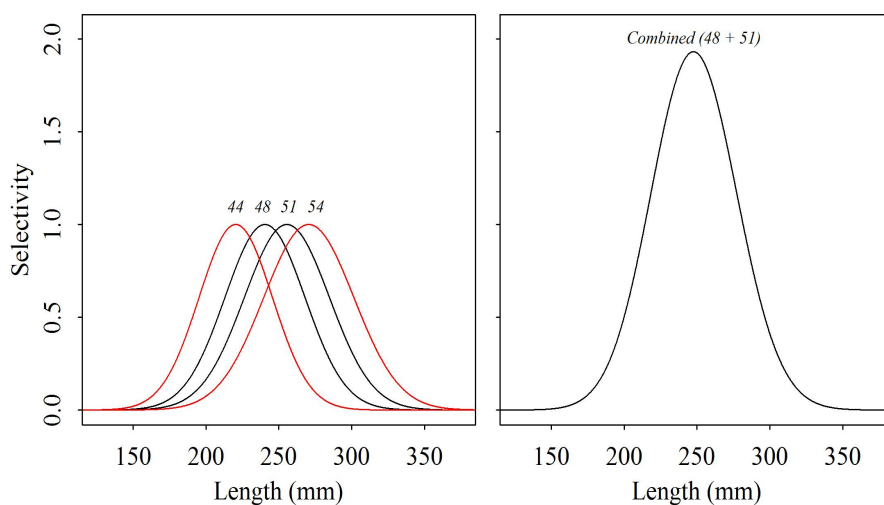


FIGURE 3.5: The *Chelone richardsonii* selectivity of 48 mm (length at full selectivity, $L_f = 240.5$ mm) and 51 mm ($L_f = 255.5$ mm) monofilament gillnets (75 m per net) calculated from the gillnet fishery data in the Orange River. Combined selectivity was calculated for the use in this study ($S_{GN}(L)$).

Mortality

Natural mortality

Chen and Watanabes (1988) method of natural mortality estimation was chosen as it does not assume uniform mortality across all age groups and consequently produces a much more realistic natural mortality estimate. The natural mortality for each age class (0 - 11 years) is compared against Jensen's (1996) and Hoenig's (1983) in Figure 3.6.

Total mortality

The instantaneous total mortality (Z) was estimated at 1.466 year^{-1} . Length-frequency data was transformed using the SELECT method, to get a more realistic representation of age classes (Figure 3.7).

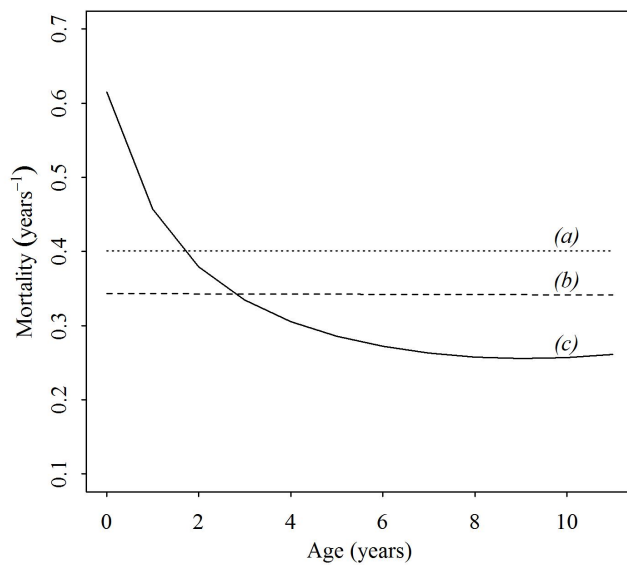


FIGURE 3.6: The instantaneous natural mortality estimate for all age classes represented by *Chelonia richardsonii* in Saldanha and Langebaan (2017). Natural mortality was calculated using three methods; (a) Hoenig's (1983), (b) Jensen's (1996), and (c) Chen and Watanabe's (1988).

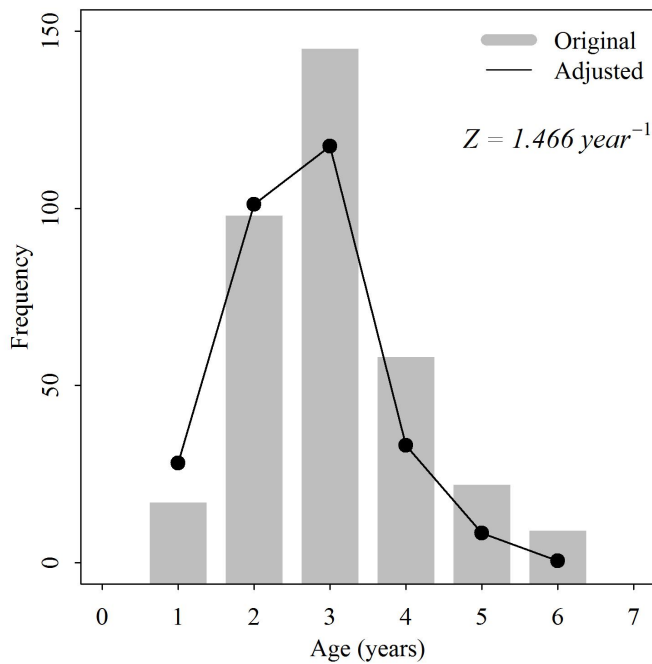


FIGURE 3.7: The SELECT converted normalised age-frequency distribution of females used to estimate the instantaneous total mortality (Z) via applying the technique outlined by Butterworth *et al.* (1989).

Per-recruit

Using the parameters estimated in the previous sections (Table 3.1) the resulting SBR estimated for Saldanha and Langebaan was 5.5% of pristine unfished levels.

TABLE 3.6: The calculated fishery target reference points ($F_{0.1}$, F_{SB40} and F_{SB25}) for *C. richardsonii* for three varying levels of natural mortality (M), based on the Chen and Watanabe (1992) estimate, for both the fished and unfished growth models.

Natural Mortality	Original growth				Fixed growth			
	$F_{current}$	$F_{0.1}$	F_{SB40}	F_{SB25}	$F_{current}$	$F_{0.1}$	F_{SB40}	F_{SB25}
$M_{0.9}$	0.56	0.97	3.59	228.85	1.17	0.17	0.13	0.23
M	0.46	1.07	4.67	734.06	1.14	0.20	0.14	0.26
$M_{1.1}$	0.37	1.18	6.13	1187.55	1.10	0.22	0.16	0.29

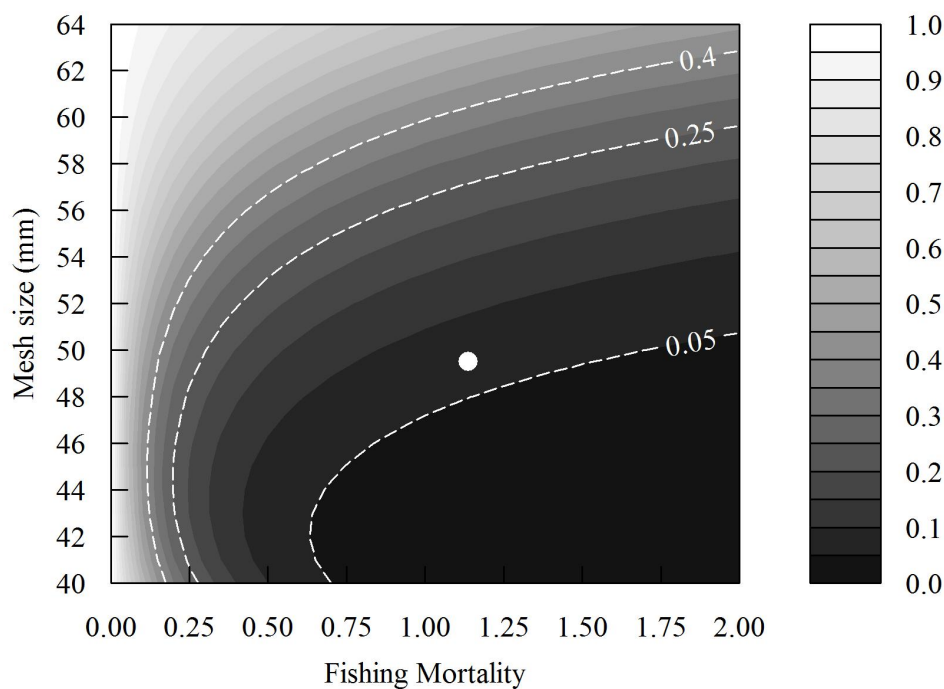


FIGURE 3.8: An isopleth illustrating the response of the spawner biomass-per-recruit (SBR) of *Chelonia richardsonii* according to varying levels of fishing mortality (F) and different combinations of mesh sizes (mm). Critical reference depletion points (SB_{40} , SB_{25} and SB_5) are represented by dashed white lines. The current SBR is denoted by the white dot; SBR depletion = 0.052, $F_{current} = 1.137 \text{ year}^{-1}$.

The effect on SBR under different combinations of TAE and gear restrictions was investigated by producing isopleths as a function of mesh size and fishing mortality. Although SBR is sensitive to changes in both F and mesh size, at the current state it is slightly more responsive to changes in mesh size (mm, Figure 3.8). The isopleth shows that at low mesh sizes then correspondingly low F is required in order to maximise the SBR. However, as mesh size increases, increasing F has a reduced influence on the SBR.

The results from the sensitivity analysis of SBR to differing levels of instantaneous natural mortality (M) illustrated the expected response; under scenarios of lower estimated M , SBR would be lower (Figure 3.9). However, relative to the current estimated level of SBR the response is minimal (Figure 3.8b). Therefore, it displayed a relative insensitivity towards M . This was investigated further through biological target reference points (F_{max} , $F_{0.1}$, F_{SB40} and F_{SB25}). If M is underestimated, then stricter management of TAE may be inferred to achieve F_{SB40} . However, under any scenario, a reduction of F by more than 100% would be necessary to achieve F_{SB40} (Table 3.6).

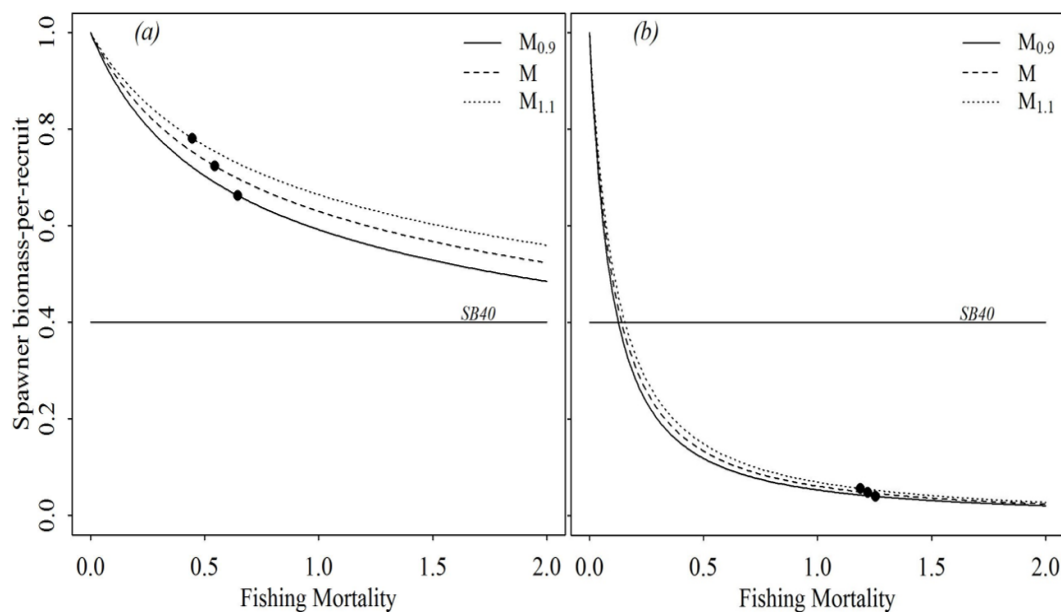


FIGURE 3.9: The sensitivity of the SBR model to varying instantaneous natural mortality rates. M is the estimated natural mortality by the Chen and Watanabe (1992) method, $M_{0.9}$ is the mortality rate corresponding to 90% of the original M estimate and $M_{1.1}$ is the mortality rate corresponding to 110% of the original M estimate. The (•) correspond to the current SBR at the respective M . Plot (a) represents the SBR calculated from the female original growth model, (b) represents the fixed growth model.

Exploration of the sensitivity of spawner biomass-per-recruit to growth parameters calculated from heavily fished populations was investigated by estimating SBR using both the fixed and original von Bertalanffy growth parameters. The SBR from the original model was estimated at 76.2% (fixed SBR = 5.5%). Comparisons between the two results were investigated by exploring different target reference points (Table 3.6 and Figure 3.9). Estimates calculated from the original model parameters were overly enthusiastic. Under the original model scenario, $F_{current}$ would have to be increased by 4.21 year⁻¹ to achieve the target reference of F_{SB40} .

3.4 Discussion

Chelon richardsonii is a fast growing species with a short life span. Observed individuals did not exceed 6 years old, a pronounced reduction from the maximum recorded age of 11 (Lamberth and Hutchings, unpublished data). Yet, similar age classes were documented by comparable studies performed in False Bay and Saldanha (Ratte, 1977; De Villiers, 1987; Lamberth, unpublished data).

Life History

This study has shown that the use of whole otoliths as a method of age determination for *C. richardsonii* provides fairly imprecise readings (IAPE = 13.9%, CV = 18.4%). Following review of 131 ageing studies, Campana (2001) recommended threshold values of precision of < 7.6% CV and < 5.5% IAPE, implying imprecise age determination of *C. richardsonii*. Problems in age precision tend to stem from young and old fish as a consequence of difficulties delineating between the nucleus edge and superimposition of annuli (Campana, 2001). The results suggest that in whole otoliths of *C. richardsonii* locating the nucleus edge and the first annuli increment is relatively difficult. Lastly, low conformity of older fish implies that superimposition in *C. richardsonii* is an issue. It is important to note that IAPE is an index of precision and therefore reproducibility, not accuracy. However, a comparative study between sectioned and whole otoliths is advised for future studies.

The observed age-length structure estimated from otolith readings in this study (Table 3.2) shows significantly different growth compared to De Villiers (1987) and Ratte (1977). Younger age classes were substantially larger (length, mm) compared to De Villiers (1987). This either implies a faster growth rate, underestimation of age or an artefact of the gear used. Ageing errors and inaccuracies have negative implications on the management outcomes from per-recruit assessments (Lin Lai and Gunderson, 1987; Tyler *et al.*, 1989; Reeves, 2003). Under ageing or "smearing" appreciates the weight and subsequently the somatic growth of younger age classes, suggesting a highly productive stock (Tyler *et al.*, 1989; Beamish and McFarlane, 1995; Reeves, 2003). This corresponds to overly enthusiastic F and t_c estimates, consequently leading to overfishing (Lin Lai and Gunderson, 1987; Beamish and McFarlane, 1995). This error could have potentially occurred. Further age validation studies would be required in order to corroborate the age accuracy of this study.

Gillnets are highly selective, therefore fish too small or big will elude the nets. This is evident in the age-length structure of this study (Figure 3.1). Very few fish were caught smaller than length-at-50%-selection (214.5 mm). This is likely to increase the mean length at each age, as the smaller individuals within the age classes are not caught. The consequence of such would over estimate growth and increase K . This can be seen in the von Bertalanffy models fitted to the data prior to fixing L_∞ (Figure 3.4). Hence, it is more likely that the larger age classes observed in this study is due to the selectivity of the fishing nets used.

Age-truncation is a common artefact in fisheries exposed to excessive size selective fishing (Rowe and Hutchings, 2003; Hixon *et al.*, 2014). This structural change creates difficulties for the accurate estimation of unfished growth. This study provides evidence to support this. Historic data shows that *C. richardsonii* were commonly caught larger than 300 mm (Chapter 2, Figure 2.2) with a maximum age of 11, yet, the largest and oldest individual caught in this study was 285 mm at 6 years old. The implications of this meant that the estimated asymptotic length was severely stunted in comparison to historic estimates (Table 3.5). It is acceptable to infer that *C. richardsonii* has the potential to grow larger, but large individuals are absent due to excessive fishing pressure or insufficient sampling effort. Additionally, K was increased due to larger average age

classes (especially 2-4 year olds) due to net selectivity. This amalgamated into a predicted growth similar to that of a highly productive species, such as pilchards *Sardinops ocellata* (Baird, 1970; Thomas, 1985; Musick, 1999). The author acknowledges that these are also potential issues arising from an insufficient sample size, however within the temporal constraints of this study manipulating L_{∞} to represent similar asymptotic growth of historic populations has provided a quick method to overcome these potential problems.

Per-recruit analysis

The per-recruit assessment estimated SBR at 5.5% of pristine levels. The use of target reference points in the application of per-recruit models has become commonly accepted as targets for recommending optimum levels of fishing mortality (Gulland and Boerema, 1972; Clark, 1991; Mace, 1994; Anderson *et al.*, 2008). Following revision of previous recommended optimal levels of F , Mace (1994) recommended that a F_{SB40} would be an appropriate target (Clark, 1991; Punt, 1993; Mace, 1994), anything below this point is debatably overexploited. This would suggest that the *C. richardsonii* stock in Saldanha and Langebaan is heavily overexploited, confirming earlier suspicions ($SBR < SB_{40}$). The risk of stock collapse and recruitment failure is significantly increased when the spawner biomass falls to less than 25% of unfished levels (F_{SB25})(Griffiths *et al.*, 1999); implying that this particular stock is at high risk of recruitment failure and is still being fished at unsustainable levels.

Currently, the minimum mesh size used (48 mm) facilitates the fishing of immature individuals. Recruitment into the fishery is currently at an age of 2 years old (205.6 mm). Age-at-50% maturity was also estimated at 2 years old in this study, which is a year younger than previously estimated (De V Nepgen as cited in De Villiers, 1987). Restricting age-at-first capture to at least the age-at-50% maturity is a common fishery management tool in the South African linefishery (Punt, 1993; Griffiths, 1997; Brouwer and Griffiths, 2005). However, despite having the age-at-first capture set at age-at-50% maturity for silver kob *Argyrosomus inodorus*, the stock became seriously depleted (3-12% SBR reduction) in 1997 (Griffiths, 1997). Therefore, protecting stocks by setting age-at-first capture to age-at-50% maturity must be applied with caution.

Approximately 30% of the current commercial catch is immature fish (Figure 2.2). The opportunity to spawn and therefore contribute to the population is removed, increasing recruitment overfishing and decreasing SBR. A stock with a weaker SBR is less resilient to excessive fishing. This is confirmed by the sensitivity of SBR to mesh size (mm). As mesh size is increased above the age-at-50% maturity, the stock becomes increasingly resilient to larger fishing mortalities (Figure 3.8). Hence, the stock would benefit greatly from increasing the age-at-recruitment into the fishery. Unfortunately, macroscopic staging of gonads was not performed in this study, thus the age-at-50% maturity may not be accurate. Further assessment needs to be conducted to verify this conclusion.

Natural mortality (M) has forever been difficult to estimate accurately, which can cause significant problems as a result of its intimacy with per-recruit assessments. Primarily, inaccuracies of M originate from life history traits estimated from exploited populations (Vetter, 1988; Hilborn and Walters, 1992). Life history parameters in exploited populations show pronounced changes corresponding to intense fishing (Buxton, 1993; Biro and Post, 2008; Boukal *et al.*, 2008; Enberg *et al.*, 2012), consequently estimating M from these will create inaccuracies (James *et al.*, 2004). It is important to understand how miscalculations of M can lead to inaccurate management recommendations, hence the sensitivity of SBR as a function of M was explored. As expected, underestimating M overestimates the SBR. However, regardless of inaccuracies, the outcome still remains that the stock requires heavy reduction in TAE and further gear restrictions due to the heavy depletion status of *C. richardsonii*.

To highlight the sensitivity of spawner biomass-per-recruit model to parameters calculated from inaccurate data, the SBR was calculated from the female original growth model (Table 3.4). Under the scenario of calculating SBR from the original growth model parameters, the estimated SBR of the stock was 76.2% of unfished, pristine conditions, a substantially different outcome compared to the current outcome of 5.5%. Therefore, management inferences based on this outcome would recommend that F could be increased by 640% in order to achieve an optimally exploited stock F_{SB40} . Whereas, the current scenario recommends an approximate 88% reduction in F to achieve the desired goal. This provides evidence of the importance of accurately estimating the input parameters of per-recruit models. Temporal restrictions causing insufficient sampling lead to a lack of comprehensive data that fully represented the stock. Making it difficult

to accurately estimate the growth, and subsequently the mortality, of *C. richardsonii* in Saldanha and Langebaan. It is advised that future studies should increase sampling effort in order to increase the sample in size and temporal scale. Further investigation into the accurate growth of this species is stressed. As a consequence, it is recommended that the actual SBR lies between the two estimates (76.2% and 5.5%) but closer to the latter.

In order to achieve the desired SBR of 40% under the current scenario there are two management options. Firstly, F would have to be solely reduced to at least 0.155 year^{-1} . Secondly, age-at-first capture would have to be increased corresponding to a stretched mesh size of at least 61 mm or greater. The results of this stock assessment suggest that the *C. richardsonii* stock in Saldanha and Langebaan is heavily overexploited as a cause of high F and small mesh sizes used, therefore new management regulations are recommended.

Conclusion

In the absence of robust long term catch data and knowledge of stock-recruit relationship, per-recruit analysis provides a favourable assessment method. With reference to the Netfishery, the results from this Chapter have provided quantitative recommendations for replenishment of a currently overfished stock. A drastic reduction in fishing effort coupled with an increase in mesh size (mm) is needed for the rebuilding of the *C. richardsonii* stock.

Chapter 4

General Discussion

4.1 Introduction

Sustainable fishing is often an idealistic theory that is challenging to implement due to contradicting demands from an intricate network of stake holders. Although uncertainty surrounds fishery assessments, they provide the most favourable evaluation that offers the opportunity for sustainable fishing. The Marine Living Resource Act (1998) in South Africa manifests sustainable and optimal use of marine resources in the first two principles (MLRA, 1998). *Chelon richardsonii* is a commercial species on the west coast of South Africa that despite evidence for overexploitation has been allocated excessive fishing effort and thus unsustainable fishing (Lamberth, 2017, pers. comm.). This study has provided substantial findings through assessment methods that validate motivations for reduced number of permits and fishing access.

The west coast Netfishery relies on the annual availability of *Chelon richardsonii*. Previous suspicions of excessive fishing created demand for assessment (Hutchings and Lamberth, 2002a, 2002b). The estimation of accurate life history parameters was integral for both understanding the biology of the species and the per-recruit assessment. Accuracy was dependent on two things; firstly, accurate age determination and secondly, accurate estimation of unfished growth. Previous studies produced age estimates from sectioning otoliths of *C. richardsonii* (Lamberth, unpublished data). This study's findings showed that whole otoliths submerged in methyl-salicylate provided a fairly imprecise method of age determination in *C. richardsonii* (Chapter 3). Growth was distinct between males

and females, with females growing larger. The asymptotic length within the final growth model was fixed to a historic maximum with the objective to overcome structural issues observed in fished populations such as age truncation and reduced growth (Cooke *et al.*, 2007; Hixon *et al.*, 2014).

Calculating life history parameters from exploited stocks has the potential to create inaccuracies in the results from stock assessments (Hilborn and Walters, 1992). This study provided empirical evidence on the severity of outcomes when estimating life history parameters from heavily fished stocks. Due to excessive fishing, the *C. richardsonii* stock exhibits severe age-truncation (Chapter 2), causing a decreased longevity and increased a growth rate in growth estimates. Per-recruit results based on these parameters enthusiastically estimated the current SBR at 76.2%. In accordance to commonly accepted fishery reference points, it would have been an underexploited stock (Gulland and Boerema, 1972; Clark, 1991; Mace, 1994). In actual fact, the SBR is closer to 5.5% of pristine conditions (Chapter 3). This extreme dichotomy of results from a simple fishing artefact could have considerably damaging outcomes through recommendations of mismanagement (Boyer *et al.*, 2001).

The *C. richardsonii* stock in Saldanha and Langebaan is currently heavily overexploited. The multifaceted diagnostic approach as performed here highlights several characteristics of overfishing. Together, the change in sex-ratio and reduction in both CPUE and mean TL (mm), characterise a fishery in distress (Gulland, 1992; Griffiths *et al.*, 1999; Kendall and Quinn, 2012). These trends were previously documented (Hutchings and Lamberth, 2002a, 2002b), yet, were rendered as insufficient to convince management authorities (High Court of South Africa, 2016; Lamberth, 2017, pers. comm.). This study provides further evidence of a heavily depleted stock through per-recruit analyses. The current estimated SBR is at 5.5% of pristine levels. With a SBR of 5.5% ($<F_{SB25}$) the regional stock is at high risk of recruitment failure and stock collapse. Current fishing pressure (1.14 year^{-1}) is approximately four times larger than that of a highly productive stock (Musick, 1999; ICES, 2015). Regional stocks of *C. richardsonii* exhibiting similar reductions in mean TL (mm) and CPUEs required complete regional closure or a 60% reduction in effort (Hutchings *et al.*, 2008, 2010). The stock within Saldanha and Langebaan requires drastic reductions in effort and further gear restrictions.

4.2 Management Inferences

A combination of further restrictions in TAE and gear would be the most beneficial method. Current gear restrictions allow the use of two 75 m by 5 m monofilament nets with a minimum stretched mesh of 48 mm and maximum of 64 mm. The age-at-selectivity (mesh size) analysis performed outlined the positive population response to applying increasing gear restrictions. An increase of stretched mesh size to 57 mm would delay recruitment into the fishery to an age of 5 years (247.5 mm TL), which would enable recently matured individuals the opportunity to spawn for 3 years prior to capture (age-at-50% maturity = 2 years, 205 mm TL). Additionally, it is critical to reduce the total fishing mortality. Currently at 1.14 year^{-1} it is unsustainably high. With an increase in net size to 57 mm, a reduction in fishing mortality to 0.45 year^{-1} (approximately 60%) would facilitate the opportunity to replenish spawner-biomass to the target of F_{SB40} . An option to explore, is to instead of reducing allocation of permits, is to reduce the length of nets used. Theoretically, if each vessel was only permitted to use one 75 x 5 m gillnet the total effort would effectively be halved, without reduction of permits.

An important notion to remember is that compliance of the fisher is integral to the successfulness of fishery management. Therefore, consideration of further fishery restrictions in terms of the user must be acknowledged. Following implementation of stricter fishery management is likely to cause immediate reduction in yield and consequently economic gain (Overholtz *et al.*, 1993; Punt, 1993; Worm *et al.*, 2009). Enforcing these new restrictions would have a drastic reduction in catch for the immediate future. Theoretically, shortcomings of yield will only be observed for two to three years, until younger cohorts grow to recruitment size. Yield will be greater as individuals will be larger (Overholtz *et al.*, 1993; Punt, 1993). However, the majority Saldanha and Langebaan fishers rely solely on the Netfishery as their primary source of income (Hutchings *et al.*, 2010), meaning that a substantial reduction in catch has the potential to financially devastate the fishers, which might result in increased IUU activity and contribute further to stock collapse.

There is a substantial volume of literature on the problems that can arise when small scale fisheries are forced to adhere to traditional, centralised top-down management

(e.g. Berkes, 2001, 2003; Salas *et al.*, 2007). Small scale fisheries are inherently different in comparison to large scale fisheries; high quantities of independent fishers, a lack of monitored supply chain and a decentralised system creates difficulties in efficient management (Castilla and Fernandez, 1998; Isaacs, 2013). Fishery management tools such as Total Allowable Catch are harder to enforce (Worm *et al.*, 2009). The Netfishery is currently managed with effort and gear regulations, as outlined in Chapter 1. Illegal netting is already an issue (Hutchings *et al.*, 2008) and has the potential to be further enhanced with harsher restrictions. Hence, development of alternative management techniques may be required.

Fishers within Saldanha and Langebaan would not cope with a prolonged substantial reduction in catch. Thus, alternative solutions must be developed to mitigate these future problems. Avenues that account for these include schemes such as buybacks, alternative livelihoods and value-adding. Buyback schemes are commonly used government tools that address overcapacity and overexploitation (Squires, 2010), with the objective of resource conservation (Holland *et al.*, 1999). They are of particular benefit to fisheries in stock crisis, as funding can be directed at the vessels that have the most successful catch history effectively reducing the fishing power quickly (Holland *et al.*, 1999). Development of alternative livelihoods is key for long-term reduction in fishing effort, as buybacks have a tendency to only be short-term (Holland *et al.*, 1999). The growing mussel and oyster industry within Saldanha has the potential to create a further 2,500 jobs within the area (Olivier *et al.*, 2013), thus producing alternative sources of financial income for Netfishers. Lastly, *C. richardsonii* are low value fish that are commonly salted and dried (Hutchings *et al.*, 2010), yet through the improvement of the supply chain there is the opportunity to add value; such as producing frozen fish, thereby increasing income of fishers (Bn and Heck, 2005; DAFF, 2012).

4.3 Future Research

De Villiers (1987) demonstrated the chronological deposition of opaque and translucent annual growth bands, however quantitative validation was not performed. Hence, further examination of age validation would be recommended (Campana, 2001), in order to confirm the feasibility of using whole otoliths for *C. richardsonii* age determination.

The importance of stock identification for accurate fishery management is well known (Begg *et al.*, 1999). Populations with multiple separate spawning stocks are likely to exhibit different life history parameters and mortalities (Begg and Waldman, 1999), hence if fishing mortality was uniform the less productive stock may be removed (Ricker, 1958). It has been proposed that there are multiple spatially explicit stocks of *C. richardsonii* (Lamberth, unpublished data). Consequently, future research for stock identification within the west coast *C. richardsonii* population is imperative for the accurate management.

Lastly, considering that per-recruit assessments are short term predictors of stock condition and fish stocks are dynamic, re-assessment would be recommended in 3 years (the observed half life span of *C. richardsonii*).

References

- (2014). Status of the South African Marine Fishery Resources, 2014. Technical report, DAFF.
- Adams, P. (1980). Life history patterns in Marine Fishes and their consequences for Fisheries Management. *Fishery Bulletin*, **78**(1):1 –12.
- Anderson, C. N. K., Hsieh, C.-h., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., and Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, **452**(7189):835 – 839.
- Ashford, J., Wischniowski, S., Jones, C., Bobko, S., and Everson, I. (2001). A comparison between otoliths and scales for use in estimating the age of *Dissostichus eleginoides* from South Georgia. *CCAMLR Science*, (8):75 – 92.
- Attwood, C., Mann, B., Beaumont, J., and Harris, J. (1997). Review of the state of Marine protected areas in South Africa. *African Journal of Marine Science*, **18**:341 – 361.
- Baird, D. (1970). *Age and growth of the South African pilchard, Sardinops ocellata*. PhD thesis.

-
- Beamish, R. (1987). Current trends in age determination methodology. In Summerfelt, R. and Hall, G., editors, *Age and Growth of Fish*, pages 15–42. Iowa State University Press.
- Beamish, R. and McFarlane, G. (1995). A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. In Sector, D., Campana, S., and Dean, J., editors, *Recent developments in fish otolith research*, pages 545 – 565. University of South Carolina Press, Columbia, South Carolina.
- Beamish, R., McFarlane, G., and Benson, A. (2006). Longevity overfishing. *Progress in Oceanography*, **68**(2 - 4):289 – 302.
- Beamish, R. J. (1979). Differences in the Age of Pacific Hake (*Merluccius productus*) Using Whole Otoliths and Sections of Otoliths. *Journal of the Fisheries Board Canada*, **36**(2):141 – 151.
- 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 Sciences*, **38**(8):982–983.
- Beckley, L. E. (1981). Marine benthos near the Saldanha Bay iron-ore loading terminal. *African Zoology*, **16**(4):269 – 271.
- Beddington, J. R., Agnew, D. J., and Clark, C. W. (2007). Current Problems in the Management of Marine Fisheries. *Science*, **316**(5832):1713 – 1716.
- Begg, G. A., Friedland, K. D., and Pearce, J. B. (1999). Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research*, **43**(1 - 3):1 – 8.
- Begg, G. A. and Waldman, J. R. (1999). An holistic approach to fish stock identification. *Fisheries Research*, **43**(1 - 3):35 – 44.
- Béné, C. and Heck, S. (2005). Fish and Food Security in Africa. *NAGA, WorldFish Center Quarterly*, **28**(3 - 4):8 – 13.
- Bennett, B. (1993). The fishery for white steenbras *Lithognathus lithognathus* off the Cape coast, South Africa, with some considerations for its management. *South African Journal of Marine Science*, **13**(1):1–14.

-
- Berkes, F. (2001). *Managing Small-scale Fisheries: Alternative Directions and Methods*. IDRC, first edition.
- Berkes, F. (2003). Alternatives to conventional management: lessons from small-scale fisheries. *Environments*, **31**(1):5 – 19.
- Beverton, R. and Holt, S. (1957). *On the Dynamics of Exploited Fish Populations*. First edition.
- Bigelow, K., Boggs, C., and He, X. (1999). Environmental effects on swordsh and blue shark catch rates in the US North Pacific longline fishery. *Fisheries Oceanography*, **8**(3):178 – 198.
- Birkeland, C. and Dayton, P. K. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution*, **20**(7):356 – 358.
- Biro, P. A. and Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences*, **105**(8):2919 – 2922.
- Boehlert, G. (1996). Biodiversity and the sustainability of Marine Fisheries. *Oceanography*, **9**(1):28 – 35.
- Boehlert, G. W. (1985). Using objective criteria and multiple regression models for age determination in fishes. *Fishery Bulletin*, **83**(2):103 – 117.
- Booth, A. J. and Buxton, C. D. (1997). Management of the panga *Pterogymnus laniarius* (Pisces: Sparidae) on the Agulhas Bank, South Africa using per-recruit models. *Fisheries Research*, **32**(1):1 – 11.
- Boukal, D. S., Dunlop, E. S., Heino, M., and Dieckmann, U. (2008). Fisheries-induced evolution of body size and other life history traits: the impact of gear selectivity. *ICES*.
- Boyer, D. C., Kirchner, C. H., McAllister, M. K., Staby, A., and Staalesen, B. I. (2001). The orange roughy fishery of Namibia: lessons to be learned about managing a developing fishery. *African Journal of Marine Science*, **23**:205 – 221.
- Bracciali, C., Piovano, S., Sarà, G., and Giacoma, C. (2014). Seasonal changes in size, sex-ratio and body condition of the damselfish *Chromis chromis* in the central Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, **94**(5):1053 – 1061.

-
- Brouwer, S. L. and Griffiths, M. H. (2005). Influence of sample design on estimates of growth and mortality in *Argyrozona argyrozona* (Pisces: Sparidae). *Fisheries Research*, **74**(1 - 3):44 – 54.
- Butterworth, D., Punt, A., Borchers, D., Pugh, J., and Hughes, G. (1989). *A manual of mathematical techniques for linefish assessment*. Foundation for Research Development: CSIR.
- Buxton, C. (1993). Life-history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes*, **36**(1):47 – 63.
- Campana, S. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series*, **188**:263 – 297.
- 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**(2):197 – 242.
- Campbell, R. (2004). CPUE standardisation and the construction of indices of stock abundance in a spatially varying fishery using general linear models. *Fisheries Research*, **70**(2 - 3):209 – 227.
- Castilla, J. C. and Fernandez, M. (1998). Small-Scale Benthic Fisheries in Chile: On Co-Management and Sustainable Use of Benthic Invertebrates. *Ecological Applications*, **8**(1):124 – 132.
- Chen, S. and Watanabe, S. (1989). Age Dependence of Natural Mortality Coefficient in Fish Population Dynamics. *Nippon Suisan Gakkaishi*, **55**(2):205 – 208.
- Clark, B. (1997). Variation in Surf-zone Fish Community Structure Across a Wave-exposure Gradient. *Estuarine, Coastal and Shelf Science*, **44**(6):659 – 674.
- Clark, B. M., Bennett, B. A., and Lamberth, S. J. (1994). A comparison of the ichthyofauna of two estuaries and their adjacent surf zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. *South African Journal of Marine Science*, **14**(1):121 – 131.
- Clark, C. (1982). Concentration Profiles and the Production and Management of Marine Fisheries. In Eichhorn, W., Henn, R., Neumann, K., and Shephard, R., editors, *Economic Theory of Natural Resources*, pages 97 – 112. Physica, Heidelberg.

-
- Clark, W. (1991). Groundfish Exploitation Rates Based on Life History Parameters. *Canadian Journal Fisheries and Aquatic Science*, **48**(5):734 – 750.
- Coetzee, J. and Badenhorst, A. (2012). Status and management of the South African small pelagic fishery 2012. Technical report, Oceana Group Limited, Cape Town.
- Cooke, S. J., Suski, C. D., Ostrand, K. G., Wahl, D. H., and Philipp, D. P. (2007). Physiological and Behavioral Consequences of Long-Term Artificial Selection for Vulnerability to Recreational Angling in a Teleost Fish. *Physiological and Biochemical Zoology*, **80**(5):480 – 490.
- Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I., and Krause, J. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, **100**(3):429 – 438.
- Cushing, D. H. (1972). A History of Some of the International Fisheries Commissions. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, **73**:361 – 390.
- DAFF (2012). Policy for the small-scale fisheries sector in South Africa. Technical report, DAFF, Cape Town.
- DAFF (2017). Recommendation of the Linefish Scientific Working Group for management of sustainable beach-seine and gillnet (smallnet/driftnet) Fisheries for the period 2017/2018. Technical report.
- De V Nepgen, C. (1987). Personal Communication with De Villiers, G. In De Villiers, G., editor, *Harvesting harders *Liza richardsonii* in the Benguela upwelling region*. South African Journal of Marine Science.
- De Villiers, G. (1987). Harvesting harders *Liza richardsoni* in the Benguela upwelling region. *South African Journal of Marine Science*, **5**(1):851 – 862.
- DEA (1998). Marine Living Resources Act. *Government Gazette number 19148, Notice number 747*.
- Dietz, T., Ostrom, E., and Stern, P. (2003). The Struggle to Govern the Commons. *Science*, **302**(5652):1907 – 1912.

-
- Durand, J.-D. and Borsa, P. (2015). Mitochondrial phylogeny of grey mullets (Acanthopterygii: Mugilidae) suggests high proportion of cryptic species. *Comptes Rendus Biologies*, **338**(4):266 – 277.
- Fitzsimmons, K. (2008). Tilapia product quality and new product for international markets. *8th International Symposium on Tilapia in Aquaculture*, pages 1 – 10.
- Fulton, T. (1904). The rate of growth of fishes. *Twenty-second Annual Report*, pages 141 – 241. Technical report.
- González Castro, M., Abachian, V., and Perrotta, R. G. (2009). Age and growth of the striped mullet, *Mugil platanus* (Actinopterygii, Mugilidae), in a southwestern Atlantic coastal lagoon (37°32'S-57°19'W): a proposal for a life-history model. *Journal of Applied Ichthyology*, **25**(1):61 – 66.
- Götz, A., Kerwath, S. E., Attwood, C. G., and Sauer, W. H. H. Effects of fishing on population structure and life history of roman *Chrysoblephus laticeps* (Sparidae). *Marine Ecology Progress Series*, **362**:245 – 259.
- Griffiths, M., Attwood, C., and Thompson, R. (1999). New management protocol for the South African linefishery. In Mann, B., editor, *Proceedings of the Third Southern African Marine Linefish Symposium*, pages 145 – 156. South African Network for Coastal and Oceanic Research Occasional Report Series.
- Griffiths, S. W. and Magurran, A. E. (1997). Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour*, **53**(5):945 – 949.
- Gulland, J. and Boerema, L. (1972). Scientific advice on catch levels. *Fishery Bulletin*, **71**(2):325 – 336.
- Gulland, J. A. (1992). A review of length-based approaches to assessing fish stocks. *FAO*, pages 100.
- Hamley, J. M. (1975). Review of Gillnet Selectivity. *Journal of the Fisheries Research Board of Canada*, **32**(11):1943 – 1969.
- Harley, S. J., Myers, R. A., and Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Science*, **58**(9):1760 – 1772.

-
- Heemstra, P. and Heemstra, E. (2004). *Coastal Fishes of Southern Africa*. NISC (Pty) Ltd.
- Helser, T. E., Punt, A. E., and Methot, R. D. (2004). A generalized linear mixed model analysis of a multi-vessel fishery resource survey. *Fisheries Research*, **70**(2 -3):251 – 264.
- Henry, J. L., Mostert, S. A., and Christie, N. D. (1977). Phytoplankton production in Langebaan Lagoon and Saldanha Bay. *Transactions of the Royal Society of South Africa*, **42**(3 - 4):383 – 398.
- High Court of South Africa (2016). Coastal Links Langebaan and others vs. the Minister of Agriculture Forestry and Fisheries and others. Technical report, Western Cape.
- Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K. L., Garcia, S., Hall, S. J., Kirkwood, G. P., Sainsbury, K., Stefansson, G., and Walters, C. (2004). When can marine reserves improve fisheries management? *Ocean & Coastal Management*, **47**(3- 4):197 – 205.
- Hilborn, R. and Walters, C. J. (1992). *Quantitative fisheries stock assessment : choice, dynamics and uncertainty*. Kluwer Academic, Boston.
- Hixon, M. A., Johnson, D. W., and Sogard, S. M. (2013). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, **71**(8):2171 – 2185.
- Hoenig, J. (1983). Empirical Use of Longevity Data to Estimate Mortality Rates. *Fishery Bulletin*, **82**(1):898 – 903.
- Holland, D., Gudmundsson, E., and Gates, J. (1999). Do fishing vessel buyback programs work: A survey of the evidence. *Marine Policy*, **23**(1):47 – 69.
- Hutchings, K., Clark, B., Atkinson, L., and Attwood, C. (2008). Evidence of recovery of the linefishery in the Berg River Estuary, Western Cape, South Africa, subsequent to closure of commercial gillnetting. *African Journal of Marine Science*, **30**(3):507 – 517.
- Hutchings, K. and Lamberth, S. (2002a). Bycatch in the gillnet and beach-seine fisheries in the Western Cape, South Africa, with implications for management. *African Journal of Marine Science*, **24**:227 – 241.

-
- Hutchings, K. and Lamberth, S. (2002b). Catch-and-effort estimates for the gillnet and beach-seine fisheries in the Western Cape, South Africa. *African Journal of Marine Science*, **24**:205 – 225.
- Hutchings, K., Lamberth, S., and Turpie, J. (2002). Socio-economic characteristics of gillnet and beach-seine fishers in the Western Cape, South Africa. *African Journal of Marine Science*, **24**:243 – 262.
- Hutchings, K. and Lamberth, S. J. (2003). Likely impacts of an eastward expansion of the inshore gill-net fishery in the Western Cape, South Africa: implications for management. *Marine and Freshwater Research*, **54**(1):39 – 56.
- Hyndes, G. A., Potter, I. C., and Loneragan, N. R. (1992). Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fishery Bulletin*, **90**(2):276–284.
- ICES (2016). *ICES Advice on fishing opportunities, catch, and effort Bay of Biscay and the Iberian Coast Ecoregion*. 7th edition.
- Isaacs, M. (2013). Small-scale Fisheries Governance and Understanding the Snoek (*Thyrsites atun*) Supply Chain in the Ocean View Fishing Community, Western Cape, South Africa. *Ecology and Society*, **18**(4).
- Jackson, L. F. and McGibbon, S. (1991). Human activities and factors affecting the distribution of macrobenthic fauna in Saldanha Bay. *Southern African Journal of Aquatic Science*, **17**(1 - 2):89 – 102.
- James, N., Mann, B., and Radebe, P. (2004). Mortality estimates and biological reference points for the Natal stumpnose *Rhabdosargus sarba* (Pisces: Sparidae) in KwaZulu-Natal, South Africa. *African Journal of Aquatic Science*, **29**(1):67 – 74.
- Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**(4):820 – 822.
- Jordan, D. and Swain, J. (1884). A review of the American species of Marine Mugilidae. *Proceedings of the United States National Museum*, pages 261 – 275.
- Kawasaki, T. (1980). Fundamental relations among the selections of life history in the marine teleosts. *Bulletin of the Japanese Society for the Science of Fish*, **46**:289 – 293.

-
- Kendall, N. and Quinn, T. (2012). Size-selective fishing affects sex ratios and the opportunity for sexual selection in Alaskan sockeye salmon *Oncorhynchus nerka*. *Oikos*, **122**(3):411 – 420.
- Kerwath, S., Götz, A., Attwood, C., and Sauer, W. (2008). The effect of marine protected areas on an exploited population of sex-changing temperate reef fish: an individual-based model. *African Journal of Marine Science*, **30**(2):337 – 350.
- Kerwath, S. E., Thorstad, E. B., Naesje, T. F., Cowley, P. D., Økland, F., Wilke, C., and Attwood, C. G. (2009). Crossing Invisible Boundaries: the Effectiveness of the Langebaan Lagoon Marine Protected Area as a Harvest Refuge for a Migratory Fish Species in South Africa. *Conservation Biology*, **23**(3):653 – 661.
- Kerwath, S. E., Winker, H., Götz, A., and Attwood, C. G. (2013). Marine protected area improves yield without disadvantaging fishers. *Nature Communications*, **4**(2347).
- Kimura, D. K. (1981). Standardized measures of relative abundance based on modelling $\log(c.p.u.e.)$, and their application to Pacific ocean perch (*Sebastes alutus*). *Journal of Marine Science*, **39**(3):211 – 218.
- King, J. and McFarlane, G. (2003). Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology*, **10**(4):249 – 264.
- Krause, J. and Godin, J.-G. J. (2010). Shoal Choice in the Banded Killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae): Effects of Predation Risk, Fish Size, Species Composition and Size of Shoals. *Ethology*, **98**(2):128 – 136.
- Kuparinen, A. and Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, **22**(12):652 – 659.
- Lamberth, S. J., Bennett, B. A., and Clark, B. M. (1995a). The vulnerability of fish to capture by commercial beach-seine nets in False Bay, South Africa. *South African Journal of Marine Science*, **15**(1):25 – 31.
- Lamberth, S. J., Clark, B. M., and Bennett, B. A. (1995b). Seasonality of beach-seine catches in False Bay, South Africa, and implications for management. *South African Journal of Marine Science*, **15**(1):157 – 167.

-
- Lamberth, S. J., Sauer, W. H. H., Mann, B. Q., Brouwer, S. L., Clark, B. M., and Erasmus, C. (1997). The status of the South African beach-seine and gill-net fisheries. *South African Journal of Marine Science*, **18**(1):195 – 202.
- Lamberth, S. J. and Turpie, J. K. (2003). The Role of Estuaries in South African Fisheries: Economic Importance and Management Implications. *African Journal of Marine Science*, **25**(1):131 – 157.
- Lasiak, A. T. (1983). Aspects of the reproductive biology of the southern mullet, *Liza richardsoni*, from Algoa Bay, South Africa. *South African Journal of Zoology*, **18**(2):89 – 95.
- Law, R. (1991). On the Quantitative Genetics of Correlated Characters under Directional Selection in Age-Structured Populations. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **331**(1260):213 – 223.
- Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, **57**(3):659 – 668.
- Lin Lai, H. and Gunderson, D. R. (1987). Effects of ageing errors on estimates of growth, mortality and yield per recruit for walleye pollock (*Theragra chalcogramma*). *Fisheries Research*, **5**(2 - 3):287 – 302.
- MacArthur, R. H. and Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.
- Mace, P. M. (1994). Relationships between Common Biological Reference Points Used as Thresholds and Targets of Fisheries Management Strategies. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**(1):110 – 122.
- Maillet, G. and Checkley, D. (1990). Effects of Starvation on the Frequency of Formation and Width of Growth Increments in Sagittae of Laboratory-Reared Atlantic Menhaden *Brevoortia tyrannus* Larvae. *Fishery Bulletin*, **88**(1):155 – 165.
- Mann, B., Kistnasamy, N., and Hattingh, D. (2013). Southern African Marine linefish species profiles. Technical report, Southern African Marine linefish species profiles, Durban.

-
- Marconato, A., Shapiro, D. Y., Petersen, C. W., Warner, R. R., and Yoshikawa, T. (1997). Methodological analysis of fertilization rate in the bluehead wrasse *Thalassoma bifasciatum*: pair versus group spawns. *Marine Ecology Progress Series*, **161**:61–70.
- Martell, S. J., Walters, C., and Sumaila, U. R. (2009). Industry-funded fishing license reduction good for both profits and conservation. *Fish and Fisheries*, **10**(1):1 – 12.
- Masson, J. and Marais, H. (1975). *Stomach content analysis of mullet from the Swartkop Estuary*, volume **10**. NISC (Pty) Ltd.
- Maunder, M. and Punt, A. (2004). Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, **70**(2 - 3):141 – 159.
- McCann, K. and Shuter, B. (1997). Bioenergetics of life history strategies and the comparative allometry of reproduction. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**(6):1289 – 1298.
- McClanahan, T. R. and Mangi, S. (2000). Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications*, **10**(6):1792 – 1805.
- Millar, R. and Holst, R. (1997). Estimation of gillnet and hook selectivity using log-linear models. *ICES Journal of Marine Science*, **54**(3):471 – 477.
- Møller, A. P. and Legendre, S. (2001). Allee Effect, Sexual Selection and Demographic Stochasticity. *Oikos*, **92**(1):27 – 34.
- Moura, I. M. and Serrano Gordo, L. (2000). Abundance, age, growth and reproduction of grey mullets in Óbidos Lagoon, Portugal. *Bulletin of Marine Science*, **67**(2):677 – 686.
- Mousseau, T. A. and Roff, D. A. (1987). Natural selection and the heritability of fitness components. *Heredity*, **59**(2):181 – 197.
- Musick, J. A. (1999). Criteria to Define Extinction Risk in Marine Fishes. *The American Fisheries Society Initiative*, **24**(12):6 – 14.
- Naesje, T. F., Hay, C. J., Nickanor, N., Koekemoer, J., Strand, R., and Thorstad, E. B. (2007). Fish populations, gill net catches and gill net selectivity in the Lower Orange River, Namibia, from 1995 to 2001. Technical report, Norsk institutt for naturforskning.

-
- Olivier, D., Heineken, L., and Jackson, S. (2013). Mussel and oyster culture in Saldanha Bay, South Africa: potential for sustainable growth, development and employment creation. *Food Security*, **5**(2):251 – 267.
- Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., Dieckmann, U., and Hordijk, L. (2004). Maturation Trends Suggestive of Rapid Evolution Preceded the Collapse of Northern Cod. Technical report, International Institute for Applied Systems Analysis, Laxenburg.
- Ottersen, G. (2008). Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian cod (*Gadus morhua*) and possible consequences for recruitment. *Canadian Journal of fisheries and Aquaculture science*, **65**(3):523 – 534.
- Overholtz, W., Edwards, S., and Brodziak, J. (1993). Strategies for rebuilding and harvesting New England groundfish resources. Technical report, Alaska Sea Grant College Program, Anchorage.
- Pauly, D. (1984). *Fish Population Dynamics in Tropical Waters: A Manual for Use with programmable calculators*. WorldFish, 8th edition.
- Peuhkuri, N., Ranta, E., and Seppä, P. (2010). Size-assortative Schooling in Free-ranging Sticklebacks. *Ethology*, **103**(4):318 – 324.
- Potter, I. C., Beckley, L. E., Whitfield, A. K., and Lenanton, R. C. J. (1990). Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environmental Biology of Fishes*, **28**(1 - 4):143 – 178.
- Prince, J. and Hilborn, R. (1998). Concentration profiles and invertebrate fisheries management. *Canadian Special Publication of Fisheries and Aquatic Science*, **125**:187 – 196.
- Punt, A. (1993). The use of spawner-biomass-per-recruit in the management of line-fisheries. In Beckley, L. and Van der Elst, R., editors, *Proceedings of the Second South African Marine Linefish Symposium*, pages 80 – 89.
- Punt, A., Walker, T., Taylor, B., and Pribac, F. (2000). Standardization of catch and effort data in a spatially-structured shark fishery. *Fisheries Research*, **45**(2):129 – 145.

-
- Ranta, E., Peuhkuri, N., and Laurila, A. (1994). A theoretical exploration of antipredatory and foraging factors promoting phenotype-assorted fish schools. *Écoscience*, **1**(2):99 – 106.
- Ratte, T. W. (1977). Age and growth of the mullet *Mugil richardsonii* (Smith) in the Berg River Estuary. Technical report, Department of Nature and Environmental Conservation.
- Reeves, S. (2003). A simulation study of the implications of age-reading errors for stock assessment and management advice. *ICES Journal of Marine Science*, **60**(2):314 – 328.
- Ricker, W. E. (1958). Maximum Sustained Yields from Fluctuating Environments and Mixed Stocks. *Journal of the Fisheries Research Board of Canada*, **15**(5):991 – 1006.
- Rijnsdorp, A. D. (1993). Fisheries as a Large-Scale Experiment on Life-History Evolution: Disentangling Phenotypic and Genetic Effects in Changes in Maturation and Reproduction of North Sea Plaice, *Pleuronectes platessa* L. *Oecologia*, **96**(3):391 – 401.
- Robson, D. S. (1961). Estimation of the relative fishing power of individual ships. Technical report, Biometrics Unit Technical Reports.
- Rochet, M. (1998). Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science*, **55**(3):371 – 391.
- Rowe, S. and Hutchings, J. A. (2003). Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology & Evolution*, **18**(11):567 – 572.
- Royce, W. F. (1996). *Introduction to the practice of fishery science*. Elsevier Science, revised ed edition.
- Sadovy, Y. (2001). The threat of fishing to highly fecund fishes. *Journal of Fish Biology*, **59**:90 – 108.
- Salas, S., Chuenpagdee, R., Seijo, J. C., and Charles, A. (2007). Challenges in the assessment and management of small-scale fisheries in Latin America and the Caribbean. *Fisheries Research*, **87**(1):5 – 16.
- Shannon, L. V. and Stander, G. H. (1977). Physical and chemical characteristics of water in Saldanha Bay and Langebaan Lagoon. *Transactions of the Royal Society of South Africa*, **42**(3 - 4):441 – 459.

-
- Smale, M. and Punt, A. (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**(1):131 – 139.
- Smith, J. (1986). *Smiths' Sea Fishes*. Macmillan publishers, first edition.
- Squires, D. (2010). Fisheries buybacks: a review and guidelines. *Fish and Fisheries*, **11**(4):366 – 387.
- Stearns, S. C. (1976). *Life-History Tactics: A Review of the Ideas*, volume **51**. The University of Chicago Press.
- Swartzman, G., Huang, C., and Kaluzny, S. (1992). Spatial Analysis of Bering Sea Groundfish Survey Data Using Generalized Additive Models. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**(7):1366 – 1378.
- Swartzman, G., Silverman, E., and Williamson, N. (1995). Relating trends in walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to environmental factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**(2):369 – 380.
- Teh, L. C. L. and Sumaila, U. R. (2013). Contribution of marine fisheries to worldwide employment. *Fish and Fisheries*, **14**(1):77 – 88.
- Thomas, R. (1985). *Age studies on pelagic fish in the south-east Atlantic, with particular reference to the South West African pilchard, *Sardinops ocellate**. Doctoral thesis, University of Cape Town.
- Trippel, E. A. (1995). Age at Maturity as a Stress Indicator in Fisheries. *BioScience*, **45**(11):759 – 771.
- Trippel, E. A., Kjesbu, O. S., and Solemdal, P. (1997). Effects of adult age and size structure on reproductive output in marine fishes. In Chambers, R. and Trippel, E., editors, *Early Life History and Recruitment in Fish Populations*, pages 31 – 62. Springer, Dordrecht.
- Tukey, J. W. (1949). Comparing Individual Means in the Analysis of Variance. *Biometrics*, **5**(2):99 – 114.
- Tyler, A., Beamish, R., and McFarlane, G. (1989). Implications of Age Determination Errors to Yield Estimates. *Canadian Special Publication of Fisheries and Aquatic Sciences*, **108**:27 – 35.

-
- Uusi-Heikkilä, S., Wolter, C., Klefoth, T., and Arlinghaus, R. (2008). A behavioral perspective on fishing-induced evolution. *Trends in Ecology & Evolution*, **23**(8):419 – 421.
- Van Den Broek, W. L. F. (1983). Ageing deepwater fish species: report of a visit to the United Kingdom, September-November 1982. Technical report.
- Vetter, E. (1988). Estimation of natural mortality in fish stocks: A review. *Fishery Bulletin*, **86**(1):25 – 43.
- Wallace, J. (1975). The estuarine fishes of the East Coast of South Africa. I: Species composition and length distribution in the estuarine and marine environments. II. Seasonal abundance and migrations. Technical report.
- Walters, C. J. and Martell, S. J. D. (2004). *Fisheries Ecology and Management*. Princeton University Press, New Jersey.
- Weninger, Q. and McConnell, K. E. (2000). Buyback programs in commercial fisheries: efficiency versus transfers. *Canadian Journal of Economics*, **33**(2):394 – 412.
- Whitfield, A. and Kok, H. (1992). Recruitment of Juvenile Marine Fishes into Permanently Open and Seasonally Open Estuarine Systems on the Southern Coast of South Africa. *Ichthyological Bulletin*, **57**.
- Winemiller, K. and Rose, K. (1992). Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation. *Canadian Journal of Fisheries and Aquaculture Science*, **49**(10):2196 – 2218.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., Watson, R., and Zeller, D. (2009). Rebuilding Global Fisheries. *Science*, **325**(5940):578 – 585.
- Yule, D. L., Stockwell, J. D., Black, J. A., Cullis, K. I., Cholwek, G. A., and Myers, J. T. (2008). How Systematic Age Underestimation Can Impede Understanding of Fish Population Dynamics: Lessons Learned from a Lake Superior Cisco Stock. *Transactions of the American Fisheries Society*, **137**(2):481 – 495.