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Age, growth and per-recruit stock assessment of southern mullet *Chelon richardsonii* in Saldanha Bay and Langebaan Lagoon, South Africa

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The southern mullet *Chelon richardsonii* (Mugilidae) is the main target species of the inshore net fishery (gillnet and beach-seine) on the west coast of South Africa. The stock has displayed symptoms of overfishing, with a 28% reduction in the standardised catch per unit effort (CPUE) between 2008 and 2016, and a 36.5-mm reduction in mean total length (TL) of fish in the commercial catch between 1998 and 2017. The socioeconomic importance of the inshore net fishery and concern regarding stock status necessitated an assessment of the *C. richardsonii* stock. This work presents an update of the life-history parameters and the first stock assessment of *C. richardsonii* at the centre of its distribution—Saldanha Bay and Langebaan Lagoon—using CPUE standardisation and per-recruit analysis. The sexes exhibited distinctive growth, with females growing larger, and their length-at-first-maturity was estimated at 205 mm TL, corresponding to age 2 years. Estimated natural mortality was 0.718 y⁻¹, total mortality was 1.599 y⁻¹, and fishing mortality was 0.881 y⁻¹. Current spawner-biomass-per-recruit was estimated at 24.5% of the pristine (unfished) levels, indicating a stock at risk of recruitment failure. An increase in the minimum stretched mesh size of the gillnets to 51 mm and a reduction in fishing mortality to 0.60 y⁻¹ (approximately 30%) would facilitate the recovery of the spawner biomass to the target of 40% of pristine (SB₄₀).

Keywords: CPUE, fishery management, gillnets, life history, mortality, Mugilidae, spawner biomass

Introduction

The southern mullet or ‘harder’ *Chelon richardsonii* (Smith, 1846) is an omnivorous particle-feeder endemic to inshore habitats from Lobito, Angola, to the subtropical waters of the east coast of South Africa (DAFF 2016). This fish is particularly abundant on the south and west coasts of South Africa, from the Orange River estuary to Cape Agulhas (Smith and Heemstra 1986; Lamberth and Whitfield 2013). Juveniles frequent estuarine and surf-zone nursery habitats, whereas adults become more-permanent residents of inshore marine systems, specifically sandy beach surf-zones (Clark et al. 1994; Næsje et al. 2007; Lamberth and Whitfield 2013). Spawning occurs during austral spring and summer, with early and late summer peaks (Lasiak 1983; Lamberth and Whitfield 2013).

The South African west coast inshore net fishery, operating from Port Nolloth to False Bay, is a multinet and multispecies fishery (DAFF 2016). *Chelon richardsonii* is the primary target, especially within the gillnet sector. Currently managed under a combination of gear restrictions, total allowable effort (TAE) and closed areas, this net fishery reports a total catch of approximately 1 500 tonnes (t) per annum, of which at least half is *C. richardsonii*. Prior to 2001, annual catches consistently above 6 000 t catalysed strict management measures, yet the current TAE remains excessively high

(Hutchings and Lamberth 2002; Hutchings et al. 2002; Hutchings et al. 2008). Diagnoses of regional overfishing have resulted in areas of complete closure (Hutchings and Lamberth 2002; Hutchings et al. 2008).

Located in the middle of the species’ distribution, Saldanha Bay and Langebaan Lagoon provide essential nursery grounds and refugia for both juveniles and adults of *C. richardsonii*. Langebaan Lagoon is a marine protected area (MPA) with three management zones: A, B and C, denoting ‘controlled’, ‘restricted’ and ‘sanctuary’ zones, respectively. Currently, fishers are permitted to fish in Zones A and B, although there are additional gear restrictions in Zone B (Figure 1). Regardless of scientific recommendations, the TAE has been exceeded here by a substantial margin since 2012 (DAFF 2017). Scientific advice has included recommendations to (a) substantially reduce all TAE within Saldanha Bay, and (b) redistribute fishing effort in the Langebaan MPA by removing all effort from Zone B and redistributing it to Zone A (DAFF 2017). Decreases in the mean size of fish (Hutchings and Lamberth 2002) and fisher perceptions of declining catches (Hutchings et al. 2002) suggested that the *C. richardsonii* stock in Saldanha Bay and Langebaan Lagoon had experienced overfishing, the magnitude of which was unknown.

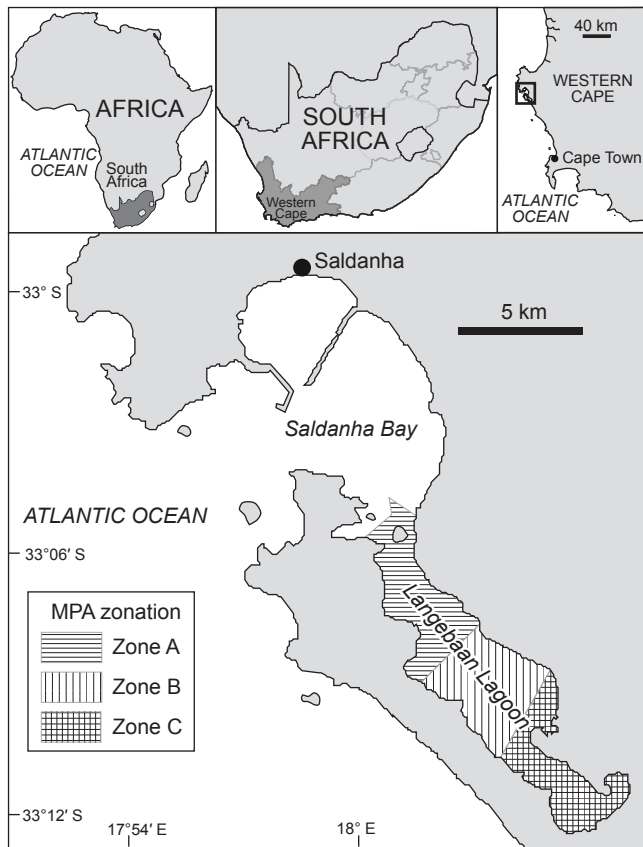


Figure 1: Map of the study area showing localities mentioned in the text as well as the different management zones of the Langebaan Marine Protected Area (MPA). Zones A, B and C are controlled, restricted and sanctuary areas, respectively

Despite the fishery's socioeconomic importance, there is a lack of accurate, holistic studies focusing on the life-history parameters of *C. richardsonii* and its retrospective stock assessment (Lasiak 1983; De Villiers 1987; CS de V Nepgen pers. comm., in De Villiers 1987). A few studies have monitored the state of the fishery through trends in catch per unit effort (CPUE), highlighting regional stress (Lamberth et al. 1997; Hutchings and Lamberth 2002), yet a quantitative assessment is needed.

Here, we provide the first comprehensive assessment of the *C. richardsonii* stock in Saldanha Bay and Langebaan Lagoon. Specifically, we (i) update the species' life-history parameters from current and historical catch-and-effort data and samples; (ii) produce an abundance index based on standardised CPUE; and (iii) develop an age-structured per-recruit model. In doing so we aim to provide management recommendations for a sustainable fishery.

Materials and methods

Fishery trends

Length-frequency trends

Length-frequency data for three periods, 1998–2002, 2009–2011 and 2017, for *C. richardsonii* from Saldanha Bay and Langebaan Lagoon, were obtained from four

separate data sources (Table 1). Potential differences between the mean total length (TL, mm) among the three time-series were tested by means of ANOVA.

Catch and effort

Catch-and-effort data were obtained from obligatory catch reports of commercial net fishers (i.e. the DAFF Netfish System). The initial dataset consisted of 39 515 entries from the gillnet sector of the entire west-coast inshore net fishery between January 2008 and December 2016, and included the catch (weight [kg] by species) per fisher per net-day. Fishing localities were also recorded. The dataset was refined to include only outing records of *C. richardsonii* from specifically Saldanha Bay and Langebaan Lagoon, resulting in 11 640 entries from 17 frequently active fishers. Fishers were permitted to operate a maximum of two 75 m × 5 m gillnets with minimum and maximum stretched mesh sizes of 48 mm and 64 mm; however, fishers each used primarily one 48-mm net and one 51-mm net. CPUE was calculated as the weight (kg) of fish caught per trip (kg trip⁻¹), in which a trip was a fishing outing reported by the fisher.

The long-term CPUE trend (2008–2016) was analysed using generalised additive mixed models (GAMMs) with a quasi-Poisson error distribution and a log-link function (Hastie and Tibshirani 1995). A quasi-Poisson error distribution was chosen because the data were moderately zero-inflated and over-dispersed. Final model selection was performed on the basis of percentage deviance explained, and significant predictors were determined by *F*-tests. The final GAMM included three fixed effects: Year, Area and Month, with Month fitted as a continuous variable with a cyclic cubic spline. Individual fishers were included as a random effect, with the assumption that fishing ability and average daily effort would vary among fishers, but that each fisher would exhibit some level of behavioural consistency. Fisher as a random effect assumes that the variation around the intercept is normally distributed with an undefined mean of variation ($N(0, \sigma^2)$). Accordingly:

$$C_{it} = \beta_1 + \text{Year} + s(\text{Month}) + \text{Area} + \alpha \text{Fisher} + \varepsilon_i \quad (1)$$

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

where C_{it} 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 αFisher denotes the fisher as a random effect, and ε_i is the unexplained variation in the model. These residuals are expected to be normally distributed, with a variance of σ^2 .

Length–weight relationship

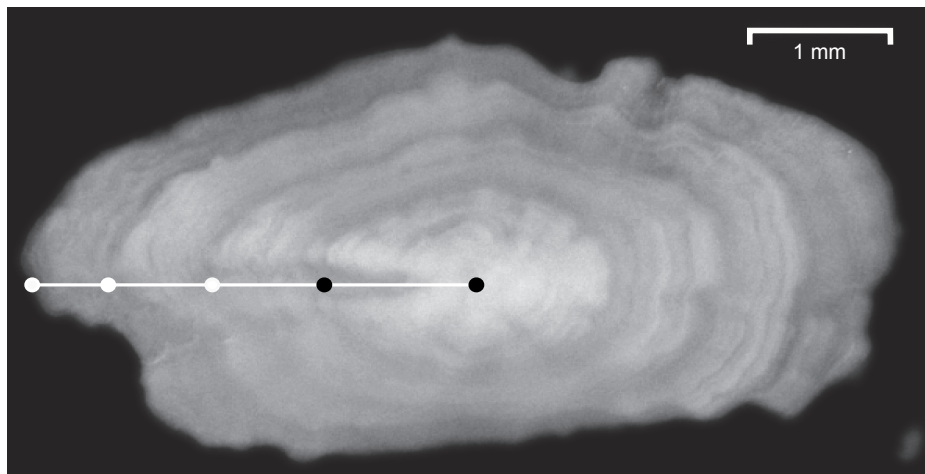
A total of 353 *C. richardsonii* caught from Saldanha Bay and Langebaan Lagoon in September 2017, by both gillnet and beach-seine, were used to calculate the length–weight relationship. The relationship between TL (mm) and weight (g) was described using a log-linear regression.

Age and growth

In total, 435 whole otoliths of *C. richardsonii* (one otolith per fish), from a region of the west coast (Yzerfontein to

Table 1: Description of datasets used for the length-frequency analysis of *Chelon richardsonii* in the net fishery at Saldanha Bay/Langebaan Lagoon, South Africa. DAFF = Department of Agriculture, Forestry and Fisheries

Time period	Source	Number of entries	Sampling trips	Mesh size (mm)	Protocol
1998–2002	DAFF, unpublished data	285	12	48	Fish lengths sampled from catches of commercial fishers
1998–2002	Hutchings and Lamberth (2003)	434	12	44, 48, 51	Fishery-independent survey implementing a commercial-fishing protocol
2009–2011	Net-fishery observer programme	16 702	184	44, 48	Fish lengths sampled from catches of commercial fishers
2017	Commercial catch	301	1	48, 51	Fish lengths sampled from the catch of a commercial fisher

**Figure 2:** Sagittal otolith of a 3-year-old female *Chelon richardsonii* caught in the commercial net fishery at Saldanha Bay/Langebaan Lagoon, South Africa. Black dots indicate the centre and edge of the otolith nucleus, and white dots indicate translucent annuli

Velddrif) that included the study site, were analysed to model growth. Of these, 301 fish caught in 2017 were provided by a commercial gillnet fisher, 52 fish collected in 2017 came from research seine-net sampling (Horton 2018), and 82 fish were caught in 1998–2002 and were provided by the local management authority (DAFF, unpublished data). No sampling design was used to select the fish used for ageing, and all 435 fish were aged. Whole otoliths submerged in methyl salicylate and viewed under reflected light against a black background adequately displayed growth increments of *C. richardsonii*. Otoliths were viewed using a Nikon SMZ800 microscope under a magnification of 2×, and photographs of each otolith were taken using a Canon EOS 650D camera. De Villiers (1987) recorded the sequential deposition of translucent annuli during the spring and summer, and opaque annuli during the autumn and winter, for *C. richardsonii* younger than 3 years. Furthermore, Ellender et al. (2012) showed that growth-zone deposition was annual in both flathead grey mullet *Mugil cephalus* and freshwater mullet *Pseudomyxus capensis* in South Africa. Consequently, we assumed that *C. richardsonii* expresses the same deposition rate (Figure 2). The photographs were read by three independent readers; each reader aged every otolith once. If two or more of the readings agreed, this was taken as the

age; if there was disagreement between all three readings, the otolith was discarded. To determine the accuracy and precision of the age determination, the average percent error (APE) and the coefficient of variation (CV) were calculated (Beamish and Fournier 1981; Campana 2001). Ages expressed as integers can underestimate the actual biological age, especially when sample collection varies temporally. To overcome this, a biological age was calculated for each fish relative to *C. richardsonii*'s peak spawning month.

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

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}) \quad (3)$$

where L_t is the total length (TL) of fish 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 was applied to test for a significant difference between the growth rates of male and female *C. richardsonii*.

Per-recruit assessment

Gillnet selectivity

Gillnet selectivity was calculated using data from a long-term monitoring study in the Orange River estuary on the west coast (van Niekerk et al. 2016). A total of 2 790 *C. richardsonii* were caught, using four different monofilament mesh sizes: 44, 48, 51 and 54 mm. Using the SELECT method, developed by Millar and Holst (1997), whereby log-linear models were applied to length-frequency data of fish caught by known mesh sizes, the gillnet size-at-selectivity (S_L) for the study in the Orange River estuary was calculated (Millar and Holst 1997). Subsequently, it was assumed that the S_L of the current study was equal to the product of those of nets of mesh sizes 48 mm and 51 mm used in the Orange River study.

Total mortality

The 2017 gillnet length-frequency ($n = 301$) was corrected for gillnet selectivity by calculating the expected length-frequency = observed length frequency/ S_L . The new expected length-frequency was then converted to the expected age-frequency using a normalised age-length key. The calculation of instantaneous total mortality (Z) was then calculated via the Chapman and Robson (1960) equation:

$$Z = \ln \left(1 + \left(\frac{1}{\bar{a} - a_f} \right) \right) \quad (4)$$

where a_f is the age at full recruitment into the fishery, and \bar{a} is the mean age of all fish fully recruited in the sample ($\bar{a} \geq a_f$).

Natural mortality

The instantaneous rate of natural mortality (M) was calculated by obtaining an average from the following three methods: Chen and Watanabe (1989), Hoenig (1983) and Jensen (1996). The method of Chen and Watanabe (1989) is as follows:

$$M = \frac{K}{G} \quad (5)$$

where K is the von Bertalanffy parameter, and G is the growth measure. G can be represented as follows:

$$G = \begin{cases} 1 - e^{-K(t-t_0)} & t \leq t_M \\ a_0 + a_1(t-t_M) + a_2(t-t_M)^2 & t > t_M \end{cases} \quad (6)$$

where a_0 , a_1 , a_2 and t_M are expressed as:

$$\begin{cases} a_0 = 1 - e^{-K(t_M-t_0)} \\ a_1 = K e^{-K(t_M-t_0)} \\ a_2 = -\frac{1}{2} K^2 e^{-K(t_M-t_0)} \end{cases} \quad (7)$$

$$t_M = -\frac{1}{2} \ln |1 - e^{K t_0}| + t_0 \quad (8)$$

and where t_0 is the age of fish at zero length, and t_M is the age at maturity.

Second, the method of Hoenig (1983) is as follows:

$$\ln(M) = 1.46 - 1.01 \ln(t_{\max}) \quad (9)$$

where t_{\max} is the maximum age of the fish.

Third, the method of Jensen (1996) is:

$$M = 1.63K \quad (10)$$

where K is the von Bertalanffy parameter. Lastly, the current fishing mortality (F_{curr}) was obtained by subtracting M from Z .

Per-recruit analysis

Due to time constraints, macroscopic aging of gonads was not possible. Hence, age-at-first-maturity was estimated from the smallest ripe female within the dataset and was assumed to be knife-edged. Spawner-biomass-per-recruit (SBR) was calculated as a function of fishing mortality (F) and the gillnet selectivity of a fish at age a (S_a):

$$\text{SBR}(S_a, F) = \sum_{a=0}^{t_{\max}} W_a \tilde{N}_a \psi_a \quad (11)$$

when ψ_a is the proportion of mature fish at age a , W_a is the weight (g) at age a , S_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 as follows:

$$\tilde{N}_a = \begin{cases} 1 & a = 1 \\ \tilde{N}_{a-1} e^{-M-S_{a-1}F} & 1 < a < t_{\max} \\ \frac{\tilde{N}_{a-1} e^{-M-S_{a-1}F}}{e^{-M-S_aF}} & a = t_{\max} \end{cases} \quad (12)$$

Owing to substantial fishing-induced age truncation, $a = t_{\max}$ is a plus group. To account for the difficulty of accurately estimating the natural mortality rates of exploited populations, the sensitivity of the per-recruit model was assessed by investigating SBR under varying scenarios of M . Three levels of natural mortality were applied: (i) M , the natural mortality as estimated above; (ii) $M_{0.9}$, 90% of the estimated M ; and (iii) $M_{1.1}$, 110% of the estimated M .

Results

Fishery trends

Length frequency

All analyses were performed using the statistical platform R 3.4.1 (R Core Team 2017). There has been a clear and consistent reduction in the mean TL of *C. richardsonii* caught by the west-coast net fishery at Saldanha Bay and Langebaan Lagoon (Figure 3). The mean TL of individuals decreased significantly, from 257.1 mm TL (SD 23.3) in 1998–2002 to 215.6 mm TL (SD 14.45) in 2017 (ANOVA; $F = 95.98$, $df = 2$, $p < 0.05$). *Post hoc* testing revealed a significant reduction in mean TL between all three time periods (Tukey HSD; $p < 0.05$).

Catch and effort

Annual catch decreased from 127.4 t to 90.5 t between 2008 and 2016 in Saldanha Bay and Langebaan Lagoon, whereas effort declined marginally during the same period, from 1 481 days y^{-1} to 1 228 days y^{-1} (Figure 4a).

In order for CPUE to constitute an index of abundance, either catchability should be constant, or factors influencing catchability should be included in the model to remove their effect on the index. *Chelon richardsonii* displayed significant variation in both seasonal [s(Month)] and spatial (area) abundance (Table 2). The standardised CPUE (kg trip⁻¹) of *C. richardsonii* decreased from 114.54 kg trip⁻¹ in 2008 to 82.78 kg trip⁻¹ in 2016, a decline of approximately 30% (Figure 4b).

Length–weight

The relationship between length (TL) and weight (*W*) for the combined sexes was $W \text{ (g)} = 0.0000009 \times TL \text{ (mm)}^{3.05}$ ($r^2 = 0.991$).

Age and growth

Of the 435 fish sampled, 307 otoliths (68%) were read and 128 otoliths (32%) were rejected because of a failure to interpret the annuli or owing to otolith damage (Table 3). The APE index calculated for the three age determinations was 13.9%, with a CV of 18.5%.

The von Bertalanffy growth equation provided an adequate fit to the age–length data, and post-model validation illustrated normal, homoscedastic residuals. A model was fitted to each sex successfully (Figure 5) and results from the likelihood-ratio test showed that there was a significant difference in growth between sexes ($df = 1$, $\chi^2 = 59.178$, $p < 0.05$), with females exhibiting slower growth and attaining larger sizes. Sex-specific and combined-sex growth parameters are presented in Table 4.

Per-recruit assessment

Selectivity

The SELECT model adequately described the unimodal selectivity of the four sizes of monofilament gillnets used within the Orange River estuary and was able to explain 99% ($r^2 = 0.99$) of the variation seen within the data (Figure 6).

The main mesh sizes used within the current study were 48 mm and 51 mm. Therefore, the selectivity parameter (S_L) was calculated as the product of the selectivity curves for mesh sizes of 48 mm and 51 mm (Figure 7). Applying the normalised age–length key, the S_L was converted to the S_a for the age classes in this study.

Mortality

The methods of Chen and Watanabe (1988), Jensen (1996) and Hoenig (1983) provided M estimates of 1.190–0.514 y⁻¹ ($\bar{x} = 0.680$ y⁻¹, 0.748 y⁻¹ and 0.727 y⁻¹, respectively). Hence, the average M estimated for females of *Chelon richardsonii* was 0.718 y⁻¹. The estimate for Z was 1.599 y⁻¹, and F_{curr} was 0.881 y⁻¹.

Per-recruit analysis

Age-at-first-maturity was estimated as 2 years (205 mm TL); using the parameters estimated in the previous sections (Table 5), the resulting SBR estimated for *C. richardsonii* from Saldanha Bay and Langebaan Lagoon was 24.5% of the pristine (unfished) level.

Although SBR is sensitive to changes in both F and mesh size, at F_{curr} the SBR is seemingly more responsive to changes in mesh size (Figure 8). The isopleth shows that at small mesh sizes, a correspondingly low F is required to

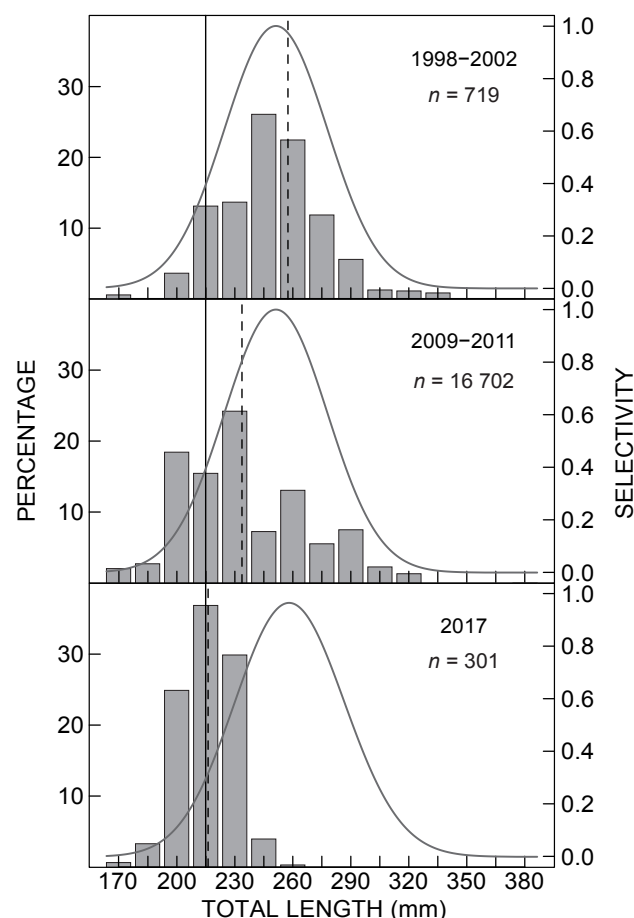


Figure 3: Length-frequency distributions of *Chelon richardsonii* landed by the commercial net fishery fleet at Saldanha Bay/Langebaan Lagoon, South Africa, for three time periods. Data were obtained from four separate data sources (see Table 1). The solid vertical line represents length at first maturity (205.1 mm TL), and the dotted vertical lines represent mean TL. The gillnet selectivity is illustrated by the bell-shaped selection curves

maximise the SBR. However, as the mesh size increases, increasing F has a reduced influence on SBR.

The results from the analysis of SBR sensitivity to differing levels of M demonstrated the expected response: under scenarios of lower estimated M , SBR would be lower (Table 6; Figure 9). Relative to the current estimated level of SBR the associated response is minimal and, under any scenario, a substantial reduction of F would be necessary to achieve the target reference point of F_{SBR0} (Table 6).

Discussion

The Saldanha Bay and Langebaan Lagoon stock of *Chelon richardsonii* has displayed symptoms of overfishing, with a 28% reduction in standardised CPUE from 2008 to 2016, and a 36.5-mm reduction in mean TL of fish in the commercial catch between 1998 and 2017. Current spawner-biomass-per-recruit (SBR) was estimated at 24.5% of the unfished level, indicating a stock at risk of recruitment failure, warranting immediate management action.

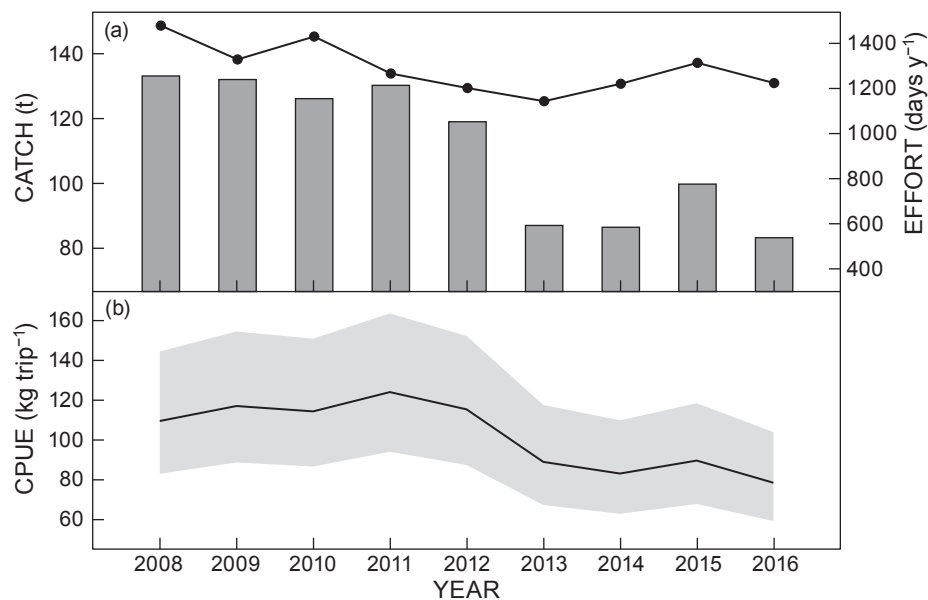


Figure 4: (a) Annual total catch and fishing effort for *Chelone richardsonii* in the commercial net fishery at Saldanha Bay and Langebaan Lagoon, South Africa, and (b) the standardised CPUE estimates (with 95% confidence intervals, grey area) derived from mandatory catch records kept between 2008 and 2016

Table 2: Model statistics for all fixed variables within the final selected generalised additive mixed models applied to CPUE of *Chelone richardsonii* caught in the net fishery at Saldanha Bay and Langebaan Lagoon, South Africa, 2008–2016, summarising the degrees of freedom (df), the residual deviance, the changes in residual deviance (Δ deviance), the percentage of the total reduction in deviance explained by the factors (% explained), the *F*-test statistic and the corresponding *p*-values

Model	df	Residual deviance	Δ deviance	% explained	<i>F</i>	<i>p</i> -value
Null	2	761 833.2				
+ Year	10	739 802.1	–22 031.1	6.3	34.1	<0.05
+ Month	21	737 036.5	–2 765.6	7.4	3.4	<0.05
+ Area	22	693 555.8	–43 480.6	19.1	5.6	<0.05

Fishery trends

Investigation of the dynamic length-frequency data indicates a reduction of approximately 20% in the mean size (TL) of fish in the population in recent years. Hutchings and Lamberth (2002) diagnosed similar symptoms in the inshore net fishery, where regions with high effort showed reductions in mean TL in comparison with regions with low effort. This reduction in the abundance of larger fish, especially females, in Saldanha Bay and Langebaan Lagoon has the potential to impair the stock's recruitment.

Owing to logistical constraints, length-frequency data collected in 2017 were limited to a small sample size ($n = 301$ fish) and one sampling event, increasing the likelihood of shoal-bias. Individuals prefer to shoal with familiar individuals, and common discriminations of conspecifics can be length-based (Krause 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). Therefore, the 2017 data might illustrate the length-frequency distribution of discrete shoals and not the entire stock. It is noteworthy, however, that multiple nets were set during the single sampling event, implying multiple shoals were sampled (MH pers. obs.). Furthermore, the same decreasing trend was also observed between the periods 1998–2002 and 2009–2011, both of which had considerably more sampling events, at 24 and 184, respectively, minimising the potential for a shoal-bias effect (Table 1).

The abundance of *C. richardsonii* decreased overall in Saldanha Bay and Langebaan Lagoon over the study period, with the lowest mean annual CPUE recorded in 2016. The fishery exhibited relative stability in CPUE between 2008 and 2012, followed by a sharp decline. The decline coincided with two events that led to a significant increase in the number of fishers. The first was a management decision to allow unrestricted access by existing fishers to the restricted zone of the Langebaan MPA, and the second was a court judgement that allowed an additional 15 fishers, over and above the TAE of 10, to fish within the Langebaan MPA (DAFF 2017). The net result, in terms of fisher numbers, was a two-fold increase in potential gillnet effort in the Langebaan-Saldanha area. Notwithstanding the above, there was an overall decrease of 20% in reported effort (days fished y⁻¹) between 2008 and 2016. Between 2012 and 2013 there was a 40% decline in catch but only a 5% reduction in days fished. During this period the total number of days fished with zero catches increased from 1 to 96. This reduced catch forced permitted fishers to source additional means of income to support boat maintenance and equipment upkeep (MH pers. obs.). This had the synergistic effect of reducing the available income and days fished, likely increasing selectivity by fishers for

Table 3: Sex-specific age–length key produced from whole-otolith readings of *Chelon richardsonii* from Saldanha Bay and Langebaan Lagoon, South Africa ($n = 307$). Values in regular font denote females (F), and values in italics denote males (M)

Total length (mm)	Age (y)																	
	0		1		2		3		4		5		6		7		8	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
80	11	11																
90	6	6																
100	1	1																
110																		
120																		
130																		
140																		
150																		
160																		
170			1	1														
180			1	1			1	1										
190			1	2		2		1										
200			2		9	9	4	11		1								
210				1	7	16	9	20	2	5								
220					5	10	4	17	1	4		2						
230					5	6	9	13	3	8	1	1						
240							11	2	4	4	2	1	1					
250							1		3		3	4	1		2			
260							1		1	1	3	3	3		2	1		2
270									2		4	1			1	2	1	1
280									3	1	1		2		3	1		
290							1		1		2						1	
300															1		1	
310									1				2					
320									1									
330													1					

days fished where the probability of catches was higher. These effects are probable contributors to the observed reduction in reported effort—despite an increase in the number of permitted fishers.

Age and growth

Based on preliminary analysis, the submersion of whole otoliths in methyl salicylate was considered the best method of discriminating growth bands. However, under recommended threshold values (<7.6% CV and <5.5% APE; Campana 2001) it rendered relatively imprecise readings (CV = 18.2%, APE = 13.9%). Large amounts of discrepancy originated from younger and older individuals. Locating the nucleus edge and the first annulus increment was relatively difficult in whole otoliths of *C. richardsonii*, resulting in frequent reader disagreement for younger fish. Furthermore, there was low conformity in the older fish, which implies that superimposition of annuli is a factor to take into account. It is important to note that APE is an index of precision, and therefore reproducibility, but not accuracy. Age validation was not possible in this study but, given published findings for similar species (De Villiers 1987; Ellender et al. 2012), the assumption of one band representing 1 year of somatic growth is considered reasonable.

Compared with previous growth studies (Ratte 1977; De Villiers 1987), this study estimated faster growth and a substantially smaller L_{∞} (Table 7). Restricted to a limited representation of age classes, historical studies may have overestimated the growth of older age classes (age

>6 years), as there is a substantial decrease in growth after age 6 (Figure 5). This study used nine age classes, and thus a reduced L_{∞} is not surprising. Furthermore, it is likely that the Saldanha–Langebaan stock has been subject to extensive size-selective net fishing.

Females exhibit slower growth and attain larger sizes. The number of ova produced by female *C. richardsonii* is proportional to their size (CS de V Nepgen pers. comm., in De Villiers 1987), and females attaining a larger size than males can be interpreted as a selective response for increased individual fitness (hence, lifetime reproductive output).

Per-recruit

The per-recruit assessment estimated SBR at 24.5% of pristine levels. The risk of stock collapse and recruitment failure is significantly increased when the spawner biomass falls to less than 25% of the unfished level (SBR_{25}) (Griffiths et al. 1999), implying that this particular stock is at high risk of recruitment failure and is currently being fished at unsustainable levels.

Applying the minimum mesh size (48 mm) results in an age-at-first-capture of 2 years (205.6 mm TL), which is equivalent to the estimated age-at-first-maturity of this study and previous studies (CS de V Nepgen pers. comm., 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, protecting stocks by setting age-at-first-capture to age-at-50%-maturity is

not necessarily effective in protecting spawner biomass (Griffiths 1997). Therefore, applying this management measure must be performed with caution. Approximately 30% of the current commercial catch consists of immature fish (Figure 3), leading to an increase in growth overfishing, and thereby decreasing the resilience of the stock to fishing pressure. This is confirmed by the sensitivity of SBR to mesh size. As mesh size is increased such that age-at-first-capture is above the age-at-first-maturity, the stock becomes increasingly resilient to larger fishing mortalities (Figure 8). Accordingly, this stock would benefit greatly from increasing the age-at-recruitment into the fishery. Macroscopic staging of gonads was not performed in this study, and the estimated

age-at-first-maturity for the Saldanha–Langebaan stock of *C. richardsonii* should be verified.

Life-history parameters in exploited populations show pronounced changes in response to intense fishing (Buxton 1993; Biro and Post 2008; Enberg et al. 2012); consequently, estimating M from these parameters will result in inaccuracies (Vetter 1988; Hilborn and Walters 1992; James et al. 2004). The sensitivity of SBR as a function of M showed that underestimating M will lead to an overestimate of SBR. However, regardless of potential inaccuracies, the sensitivity analysis supports the conclusion that the stock requires a substantial reduction in TAE and further gear restrictions (i.e. increased mesh size).

Management inferences

The use of target reference points in the application of per-recruit models has become commonly accepted for recommending optimum levels of fishing (Mace 1994). It has been recommended that SB_{40} would be an appropriate target of spawner biomass (Punt 1993; Mace 1994). A combination of further restrictions in TAE and gear would be beneficial in rebuilding spawner biomass towards this target level. Similar to recommendations made by Griffiths et al. (1999) for the South African linefishery, the *C. richardsonii* fishery warrants drastic management action, and potentially complete closure. However, it is important to acknowledge that compliance by fishers is integral to the success of fishery management. Therefore, consideration of further fishery restrictions should take into account fisher perceptions and attitudes towards management. More-lenient but well-managed restrictions may have higher efficacy in this fishery.

Current gear restrictions allow the use of two 75 m × 5 m monofilament nets with a stretched mesh of between 48 mm and 64 mm. Selectivity-at-age (mesh-size) analysis illustrated a positive population response to applying additional gear restrictions. An increase of the minimum stretched mesh size to 51 mm would delay recruitment into the fishery to an age of ~2.5 years (227.5 mm TL), which would enable recently matured individuals to spawn prior to capture (age-at-first-maturity = 2 years, 205 mm TL). Additionally, it is critical to reduce the total fishing mortality from the current estimated 0.88 y^{-1} . With an increase in minimum mesh size to 51 mm, a reduction in fishing mortality to 0.60 y^{-1} (implying a decrease in effort of approximately 30%) would facilitate the recovery of spawner biomass to the target of SB_{40} .

Historically, the majority of Saldanha–Langebaan fishers relied solely on the inshore net fishery as their source of income (Hutchings et al. 2002). More recently, fishers have

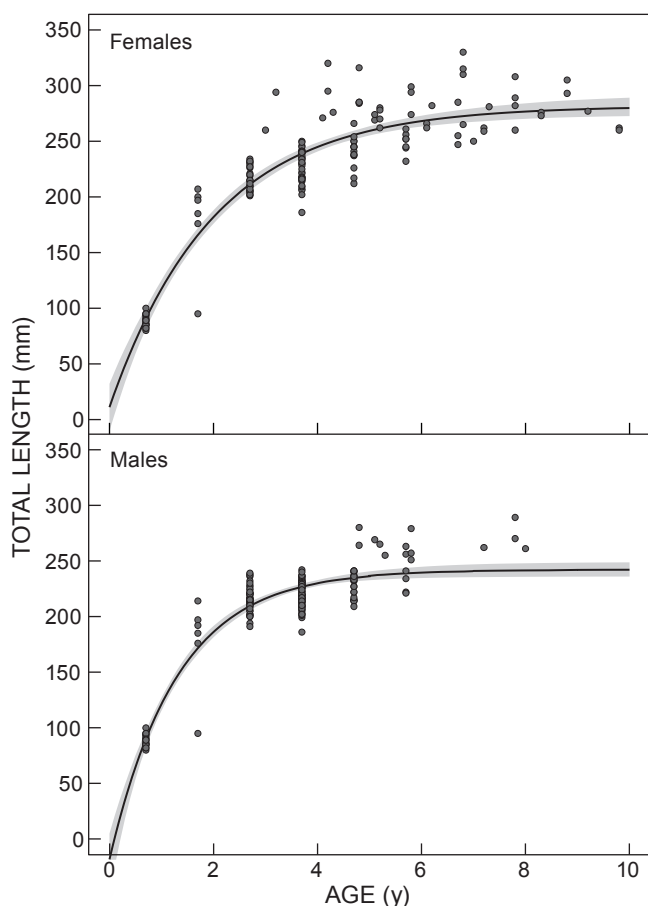


Figure 5: The sex-disaggregated age–length relationships of *Chelon richardsonii* from Saldanha Bay and Langebaan Lagoon, South Africa, described by von Bertalanffy growth curves, with 95% confidence intervals fitted by parametric bootstrapping

Table 4: Estimates of von Bertalanffy growth parameters using age–length data for females, males and the sexes combined, for *Chelon richardsonii* from the west coast of South Africa

Sex	L_{∞} (mm) (95% CI)	K (y^{-1}) (95% CI)	t_0 (y) (95% CI)
Females	281.69 (273.37, 292.66)	0.49 (0.42, 0.58)	−0.08 (−0.27, 0.07)
Males	242.15 (235.97, 249.01)	0.77 (0.66, 0.91)	0.09 (−0.03, 0.21)
Sexes combined	271.75 (264.43, 279.96)	0.51 (0.45, 0.58)	−0.15 (−0.32, −0.01)

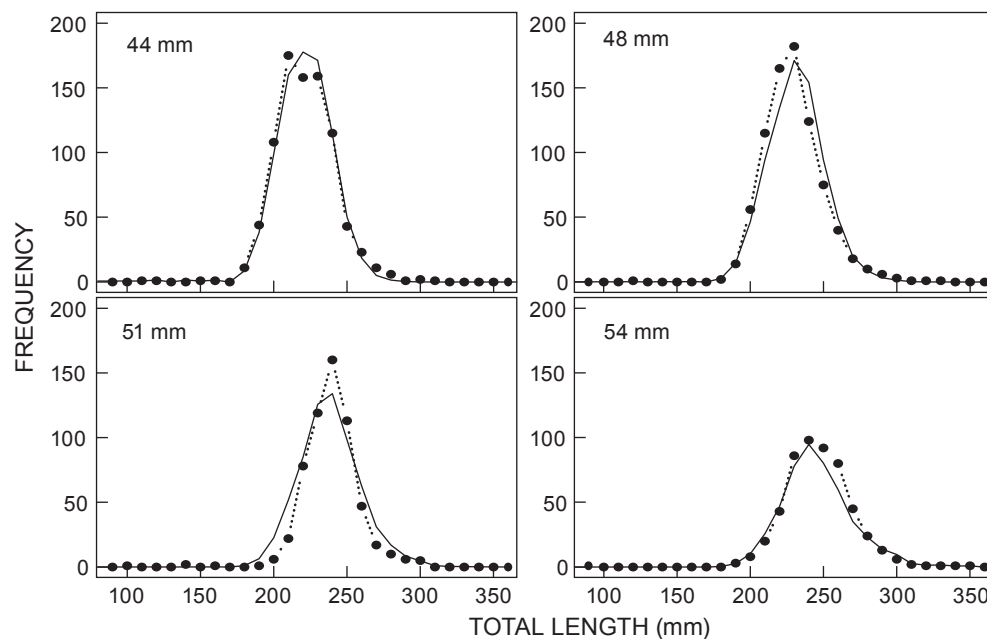


Figure 6: The observed (points and dotted lines) and SELECT-model-predicted (solid lines) distributions of catches of *Chelone richardsonii* caught in the Orange River estuary with gillnets of four different mesh sizes

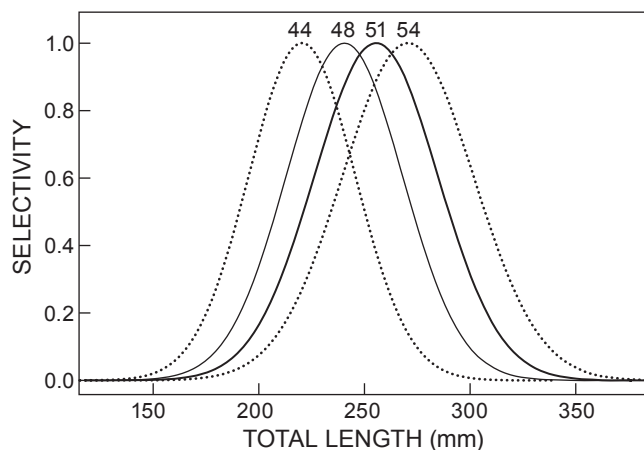


Figure 7: The relative gillnet-selectivity curves estimated for *Chelone richardsonii*, following the method of Millar and Holst (1997). The mean selectivity of 48-mm and 51-mm gillnets was used in this study

been participating in a range of additional fisheries and other employment pursuits to offset the reduction in catch. Consequently, the proposed new management measures might not affect the income of fishers as greatly as would previously have been the case. Regardless, stricter fishery management will likely cause an immediate reduction in yield and consequently in economic gain (Overholtz et al. 1993; Punt 1993; Worm et al. 2009), which might result in increased illegal, unreported and unregulated fishing activity and hence contribute further to stock collapse. Illegal netting is already a problem (Hutchings et al. 2008), a situation that has the potential to be exacerbated by further restrictions. Therefore,

Table 5: Estimates of the parameters used in the spawner-biomass-per-recruit (SBR) analysis of the Saldanha–Langebaan stock of *Chelone richardsonii*

Parameter	Description	Estimate
L_{∞}	Asymptotic length (mm)	281.690
K	Growth coefficient (y^{-1})	0.496
t_0	Age when average length was 0 (y)	-0.081
t_1	Known minimum age (y)	0
t_2	Known maximum age (y)	11
M	Natural mortality (y^{-1})	0.718
F	Fishing mortality (y^{-1})	0.881
t_{max}	Observed maximum age (y)	6
a	Length–weight regression parameter	0.000009
b	Length–weight regression parameter	3.051
ψ	Age-at-first-maturity (y)	2
S_a	Multipanel gillnet selectivity	0–1.930*

*Range of values for parameter with independent values per age class

alternative management techniques might be required, such as distributing effort elsewhere by providing access to other fisheries, including local aquaculture initiatives, via the developing fishery cooperatives (RSA 2012).

Conclusions

The multifaceted, diagnostic approach performed here highlights several characteristics of overfishing and all evidence indicates that the *C. richardsonii* stock in Saldanha Bay and Langebaan Lagoon is currently overexploited. The risk of recruitment failure and subsequent stock

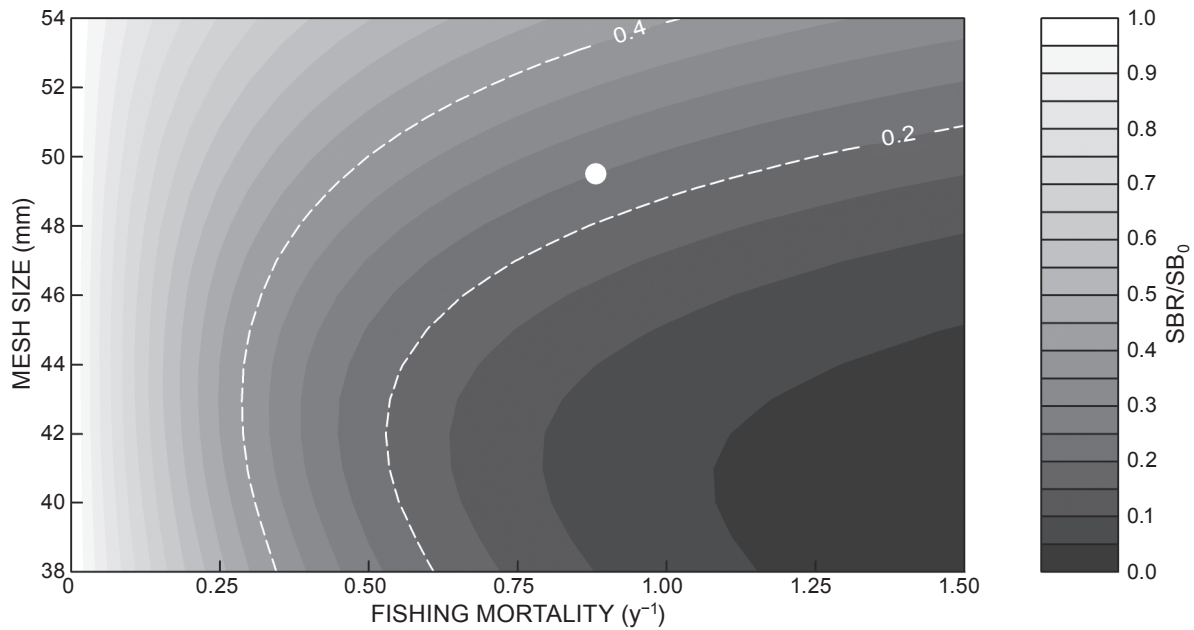


Figure 8: An isopleth illustrating the response of the percentage of spawner-biomass-per-recruit (SBR) to the unexploited level of spawner biomass (SB_0) of *Chelon richardsonii*, according to varying levels of fishing mortality and different combinations of mesh sizes in the net fishery at Saldanha Bay/Langebaan Lagoon, South Africa. Critical reference depletion points (i.e. SB_{40} and SB_{20} , denoting 40% and 20% of the pristine [unfished] level, respectively) are represented by dashed white lines; the current SBR is denoted by a circle ($F_{curr} = 0.881 \text{ y}^{-1}$; SBR depletion = 0.245)

Table 6: Calculated spawner biomass per recruit (SBR) and fishery target reference points ($F_{0.1}$, F_{SB40} and F_{SB25} , denoting the fishing mortality required for a marginal yield, and to reduce spawner biomass to 40% and 25% of the pristine [unfished] level, respectively) for *Chelon richardsonii*, from the west coast of South Africa, for three levels of natural mortality. M = estimated natural mortality in this study; $M_{0.9}$ = mortality rate corresponding to 90% of the original M estimate; $M_{1.1}$ = mortality rate corresponding to 110% of the original M estimate

$M \text{ (y}^{-1}\text{)}$	SBR	$F_{curr} \text{ (y}^{-1}\text{)}$	$F_{0.1}$	F_{SB40}	F_{SB25}
$M_{0.9}$	0.21	0.95	0.60	0.41	0.78
M	0.25	0.88	0.67	0.46	0.86
$M_{1.1}$	0.28	0.81	0.74	0.51	0.94

collapse is significant. To avoid this, an appropriate and timeous management intervention is required. This study identified the most-appropriate management measures as a 30% decrease in total fishing effort and an increase in the minimum net mesh size to 51 mm. Despite decreased catches in recent years, *C. richardsonii* remains an economically important resource to the largely underprivileged Saldanha Bay net-fishing community. However, it is unlikely that this fishery will remain viable under the current trajectories and, notwithstanding the proposed introduction of improved management measures, alternative sources of income might continue to be required to supplement that derived from decreasing catches.

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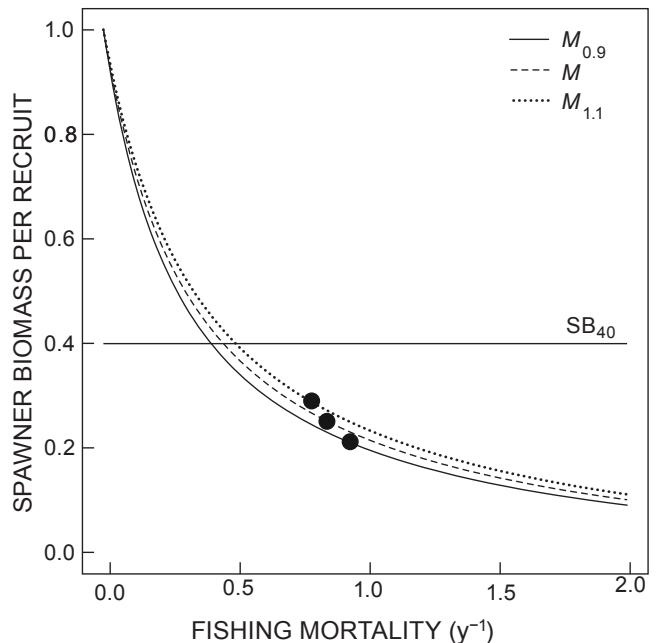


Figure 9: Sensitivity of the spawner-biomass-per-recruit (SBR) model to varying instantaneous natural mortality rates. M = estimated natural mortality calculated in this study; $M_{0.9}$ = mortality rate corresponding to 90% of the original M estimate; $M_{1.1}$ = mortality rate corresponding to 110% of the original M estimate. Black dots indicate SBR at the respective M value


Table 7: The von Bertalanffy growth parameters of *Chelon richardsonii* from different studies undertaken in the Western Cape Province, South Africa

Locality	K (y^{-1})	L_{∞} (mm)	t_0 (y)	Age classes (y)	Sex	Study
Saldanha and Langebaan	0.490	282	−0.080	0–9	Females	Current (2019)
False Bay	0.256	359	0.255	1–4	Sexes combined	Ratte (1977)
False Bay	0.287	352	0.240	1–6	Sexes combined	De Villiers (1987)

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