

Stock assessment

Red cod

(Salilota australis)

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Natural Resources

Fisheries

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Introduction

Red cod (*Salilota australis*, Moridae) is a demersal gadiform inhabiting shelf waters around the southern tip of South America (Arkhipkin et al. 2010). Red cod consume a diversity of fish and crustacean prey (Arkhipkin et al. 2001), and are eaten by predators including fish (Payá 1992, Arkhipkin et al. 2003), penguins (Raya Rey and Schiavini 2005), dolphins (Schiavini et al. 1997), and sea lions (Muñoz et al. 2013). For the Falkland Islands economy, red cod is a minor commercial species taken in mixed-finfish trawls (Barton 2002) that has yielded between 2.4% and 6.4% of finfish catches over the past 10 years (FIG 2018). However last year, 2017, has been the lowest catch year since 1987 with 1387 tonnes (Figure 1). For Argentina, red cod represents a similarly small component of commercial fishery catches (Sánchez et al. 2012, Navarro et al. 2014). Argentina's catch of 1520 tonnes in 2017 was the lowest since 1994 (Figure 1).



Figure 1. Commercial catches of red cod reported in Falkland Islands (dark blue) and Argentine (light blue) fisheries, 1985 to 2017.

Red cod aggregations are dispersed over the Patagonian shelf in summer, and in winter move to spawn around upwelling areas south-west of the Falkland Islands (Arkhipkin et al. 2010, 2012). The species' migratory behaviour results in Falklands and Argentinean fisheries both taking catches from the same population, and therefore both fisheries must be accounted for stock assessment. Because effort data of Argentine fisheries are not currently available, a comprehensive relative biomass index cannot be derived for tuning a production model. Instead, stock assessment for red cod examined two recent approaches developed for data-poor species: OCOM, by Zhou et al. (2018), and CMSY, by Froese et al. (2017).

Methods

OCOM

OCOM (optimized catch-only method) uses time series of catches and priors for population growth rate and stock saturation (Zhou et al. 2018), optimized on the Schaefer surplus production model (Schaefer 1954):

$$B_{y+1} = B_y + r \cdot B_y \left(1 - \frac{B_y}{K}\right) - C_y$$

For red cod assessment, catches per year (C_y) were entered as the reported annual catches of the Falkland Islands + Argentina. Population growth rate r was calculated from the generalized empirical relationship for gadiforms (Zhou et al. 2012):

$$r = 2 \cdot F_{MSY} = 2 \cdot 1.014 \cdot M$$

where M is natural mortality. M, in turn, was calculated from several published empirical life-history equations, below. Given the uncertainties in estimating M (Kenchington 2014), it is recommended to examine multiple estimators (Gunderson et al. 2003, Zhang and Megrey 2006, Brodziak et al. 2011).

$M = 4.899 \cdot t_{max}^{-0.916}$	(Then et al. 2015)
$M = 4.118 \cdot k^{0.73} \cdot L_{\infty}^{-0.33}$	(Then et al. 2015)
$M = 1.82 \cdot k$	(Charnov et al. 2013)
$M = \frac{1.65}{t_{mat}}$	(Jensen 1996)
$M = \frac{4.3}{t_{max}}$	(Kenchington 2014)

Parameters are t_{max} = maximum age, L_{∞} = asymptotic length, k = rate by which L_{∞} is approached, and t_{mat} = age at maturity. Age-length data from the FIFD database were used to determine t_{max} and estimate L_{∞} and k from the von Bertalanffy equation:

$$\mathbf{L} = \mathbf{L}_{\infty} \cdot \left(1 - \mathbf{e}^{-\mathbf{k}(\mathbf{t} - \mathbf{t}_0)} \right)$$

optimized in R package 'fishmethods' (Nelson 2015). Age-maturity data from the FIFD database were used to determine t_{mat} as the age corresponding to 50% of sampled fish classified as mature. Observers assign a stage from the FIFD maturity scale to specimens that are sampled for sex, length and weight. However, gonadal maturity is cyclical as fish pass through pre- to post-spawning phases. For red cod, definitive assignments of maturity can only be made that stages ≤ 1 are always juveniles and stages ≥ 3 are always adult (H. Randhawa, FIFD, personal communication). Therefore, maturity assignment was simplified to a dichotomous classification of juvenile (0 - 1) or adult (3+), omitting stage 2, and modelled vs. age on a binomial distribution. Age of 50% maturity was then extracted from the logistic function of the binomial model. Age determinations in the FIFD database have mostly been carried out by the Sea Fisheries Institute in Gdynia, Poland. Recent quality controls have raised concerns about the accuracy of Gdynia's age determinations (H. Randhawa, FIFD, personal communication). A parallel estimate of t_{mat} was calculated by

averaging published lengths of maturity for red cod (averaged to 45 cm; from Brickle et al. 2011, Chong Follert et al. 2017) and inverting the von Bertalanffy equation. Red cod have sexually dimorphic growth (Brickle et al. 2011, Chong Follert et al. 2017), but as commercial catch data are not distinguished by sex, calculations were simplified to averages of both males and females. For all equations uncertainty of growth rate r (σ_r^2) was set by the empirical estimates in Zhou et al. (2018): measurement error of M $\sigma_M^2 = 0.23$ and process error of the relationship between M and $F_{MSY} \sigma_e^2 = 0.0012$; $\sigma_r^2 = \sigma_M^2 + \sigma_e^2$.

LBB

Saturation S = the ratio of stock biomass over carrying capacity (B_y/K), was derived from a different approach for evaluating data-poor stocks; the length-based Bayesian biomass estimation method (LBB) (Froese et al. 2018). LBB is based on the principle of calculating relative rates of natural mortality over somatic growth (M/k), and fishing mortality over somatic growth (F/k), which cancel out absolute values of time and biomass; reducing the data requirements to lengths only. M/k and F/k are then used to derive indices of yield per recruit with and without fishing, and the ratio of these indices estimates current exploited biomass relative to unexploited biomass $B_{current}/B_0$ (Froese et al. 2018). LBB was run with the Gibbs sampler JAGS (sourceforge.net/projects/mcmc-jags/files/JAGS/4.x) through R package 'R2jags' (Su and Yajima 2015). Uncertainty of the ratio B/B₀ was calculated from the MCMC of the Gibbs sampler (Froese et al. 2018).

Red cod length measurements are archived in the FIFD database, and include data from research surveys as well as observer sampling in the commercial fisheries. Research data may be higher resolution (taken with smaller-mesh trawls) and selected surveys are synchronous from one year to another, whereas data from the commercial fisheries may be coarser but have broader coverage. The LBB method was tested on two alternate sets of red cod length data, one set using research data and the other set using commercially sampled observer data. Research data were taken from the series of surveys that were instigated to estimate first biomass of rock cod, then finfish biomass in general. These surveys were all held in February, and covered the finfish zone including the known spawning grounds of red cod (Arkhipkin et al. 2010). Commercial observer data were taken from measurements that had been selected randomly, and for consistency, were restricted to grids that are open to either finfish (A, G, W) or calamari (C, X) licenses by current regulation, including September / October variances. Data from autumn (April, May, June) were excluded entirely as red cod biomass is minimal in Falkland waters during autumn (Arkhipkin et al. 2012). Again to maintain consistency, data from winter, spring, and summer were weighted to equality by year for finfish grids, as there was no pattern of which season was sampled more from year to year, and data from calamari grids were weighted to $3.5 \times$ more in 2^{nd} (X) season than in 1^{st} (C) season, as this represented the approximate proportion by which more samples were taken in 2nd than 1st season over the past five years. Weighting consisted of assigning a multiplication factor to seasons that had fewer samples, and fractional parts of the multiplication factor were assigned randomly among the samples. Thus the weighting algorithm was partly stochastic. Finally, finfish vs. calamari lengths were re-weighted so that 85% of lengths were from finfish each year; the approximate average proportion over the past five years.

OCOM + LBB

Time series of annual red cod biomass were calculated by randomly drawing values of growth rate r and biomass ratio $B_{current}/B_0$ from their distributions (as above), and minimizing

the difference between $B_{opt. current} / B_{current}/B_0$ and carrying capacity K in the Schaefer production model. Minimization was carried out in two steps. First, K was fixed equal to biomass in the first year of the time series (B₁). This commonly used assumption (Punt 1990) sets K as the single parameter to be optimized, which can therefore be searched efficiently over a wide range. Second, the initial optimized value of K was input as the prior for both K and B₁ in a Schaefer model with K and B₁ parameterized independently, and this model was optimized again. The second step was implemented because commercial fishing occurred in both Falklands and Argentine waters before regular catch reporting, and K = B₁, while plausible, cannot be explicitly verified for the time series. Random draws of r and B_{current}/B₀ were iterated and optimized 10000× (Zhou et al. 2018), and the medians and 95% confidence intervals computed for parameters r, K, B₁, B_{current} and MSY (maximum sustainable yield); defined from a Schaefer production model as (Hilborn and Walters 1992):

$$MSY = \frac{r \cdot K}{4}$$

Medians and 95% confidence intervals were weighted inverse to the optimum fit value (i.e., proportional to the likelihood) of each iteration.

CMSY

CMSY (catch – MSY), similarly to OCOM, uses catch time series and parameter priors to estimate fish populations on a Schaefer production model (Froese et al. 2017). Rather than empirically computed priors for growth rate r, however, CMSY sets broadly categorical prior ranges based on species' resilience (Martell and Froese 2013, Froese et al. 2017), where resilience is defined by the spawning stock biomass per recruit that corresponds to replacement fishing mortality (Musick 1999). The prior for carrying capacity K is based on the ratio of highest catch in the time series over growth rate r. Rather than optimizing r and K, CMSY uses a Monte Carlo algorithm to search pairs of r and K that do not crash the stock or exceed projected maximum biomass levels in relation to depletion criteria shown by the catch time series. Median biomass levels and confidence intervals are derived from the validated r and K pairs.

CMSY + BSM

CMSY may be further expanded to a Bayesian state-space implementation of the Schaefer production model (BSM), if the parameters can be fit to an index of biomass or relative biomass (e.g., CPUE) (Froese et al. 2017). For red cod, BSM implementation was applied to biomass estimates from the finfish surveys (Table 1). While these survey estimates are not a comprehensive index, given the absence of Argentinean data, the assumption was tested that if red cod migrate back to the same area yearly in the same time period, their relative biomasses would represent a stationary proportionality. BSM was also calculated in the Gibbs sampler JAGS, and in addition to the r and K priors, above, used a prior range for the catchability coefficient q that was defined by the average biomass index multiplied by the geometric mean and maximum r, divided by the average catch.

Length-frequency and maturity time series

For comparative evaluation, length-frequency modes were determined in each year by LOESS (degree = 2, span = 0.75) from the weighted commercial length distributions, to

mitigate sampling fluctuations. 50% maturities-at-age from the binomial logistic regressions were also examined in each year. The aggregates of length-frequency modes and 50% maturities were plotted against years and their linear regressions calculated.

Results

Total commercial fishery catches from the Falkland Islands and Argentina were examined for the years 1985 to 2017. As the first year of substantial reported catches was 1988 (Figure 1), the assessment time series was started from 1988. Red cod catches in earlier years were likely higher than recorded, but not specifically reported.

OCOM + LBB



Figure 2. Red cod von Bertalanffy age-length relationship.

The von Bertalanffy age-length relationship was calculated from 17022 age and length samples taken between 1988 and 2017. Of these samples, 16637 were aged in Gdynia, 79 in the FIFD, and 306 did not identify source of age measurement. Maximum age was 24 years. The age-length relationship (Figure 2) gave parameters: $L_{\infty} = 95.66$ cm, k = 0.1018, and $t_0 = -0.543$ years. Empirical life-history mortality calculations thus gave:

$M = 4.899 \cdot t_{max}^{-0.916}$	= 0.2666
$M = 4.118 \cdot k^{0.73} \cdot L_{\infty}^{-0.33}$	= 0.1725
$M = 1.82 \cdot k$	= 0.1853

$$M = \frac{1.65}{t_{mat}} = 0.4761 \qquad t_{mat} = 3.47 \text{ years (binomial distribution)}$$
$$M = \frac{1.65}{t_{mat}} = 0.2895 \qquad t_{mat} = 5.70 \text{ years (publ. } L_{mat} = 45 \text{ cm})$$
$$M = \frac{4.3}{t_{max}} = 0.1792$$

A total of 24095 red cod lengths were sampled in the six February finfish surveys (Table 1). B/B₀ ratios according to the LBB calculations varied from 0.1009 in 2016 to 0.2661 in 2011 (Figure 3). 2017 was retained as the most recent year of completed data, $B_{current}/B_0 = B_{2017}/B_0 = 0.1799$ with a 95% confidence interval = (0.0954, 0.2773) (Figure 3), and standard deviation = 0.0566.

Table 1. Summary of red cod length-frequency data from research surveys, used to fit an LBB model, and biomass estimates used to fit the BSM implementation.

Year	Survey Dates	N Stations	N Lengths	Biomass T	Reference
2010	30/01 - 22/02	60	3310	103566.0	Brickle & Laptikhovsky 2010
2011	31/01 - 23/02	56	4185	161707.1	Arkhipkin et al. 2011
2015	02/02 - 22/02	70	4486	140540.4	Gras et al. 2015
2016	02/02 - 22/02	79	4933	136964.0	Gras et al. 2016
2017	04/02 - 25/02	79	3821	75978.8	Gras et al. 2017
2018	03/02 - 24/02	86	3360	78797.3	Gras et al. 2018



Figure 3. Time series of B / $B_0 \pm 95\%$ confidence intervals, calculated from finfish survey data according to the LBB model (Froese et al. 2018). 2017 is underlined in grey.

Year	N Stations	N Lengths	W Lengths	Year	N Stations	N Lengths	W Lengths
		-	-				
1988	53	2168	3626	2004	107	3720	5359
1989	13	979	2860	2005	126	1873	5933
1990	34	1649	2444	2006	114	3230	5652
1991	13	636	1773	2007	86	3329	6309
1992	45	2375	6051	2008	79	1935	2801
1993	54	2382	6026	2009	101	4051	5678
1994	12	210	210	2010	50	2021	5150
1995	12	332	1299	2011	117	5251	10351
1996	13	956	956	2012	55	2750	6818
1997	27	2677	4122	2013	69	2174	5760
1998	12	1213	3011	2014	57	2234	2645
1999	8	784	993	2015	68	3192	5283
2000	38	2571	3942	2016	78	4128	6155
2001	4	382	498	2017	85	1340	5093
2002	67	2247	4348	2018	14	691	691
2003	74	1342	2962				

Table 2. Summary of red cod length-frequency data from observer data in the commercial fisheries, used to fit an LBB model. W Lengths: numbers of lengths after re-weighting.



Figure 4. Time series of B / $B_0 \pm 95\%$ confidence intervals, calculated from commercial fishery data according to the LBB model (Froese et al. 2018). 2017 is underlined in grey.

A total of 64822 red cod lengths were sampled randomly in commercial fisheries on Falklands finfish or calamari grids (Table 2). B/B_0 ratios according to the LBB calculations showed high margins of uncertainty and high inter-annual variability over much of the time

series since 1988 (Figure 4), underscoring the difficulty of assessing a stock that has never been the primary target in a mixed fishery with shifting species composition (Laptikhovsky et al. 2013, FIG 2018). Years since 2014 have followed a smoother trend, and the B_{2017}/B_0 ratio was 0.0976 with a 95% confidence interval = (0.0612, 0.1525) (Figure 4), and standard deviation = 0.0260.

Given its smoother inter-annual trend and simpler assumptions, B_{2017}/B_0 from the February finfish surveys was retained for inclusion in the OCOM. Accordingly, prior distributions for saturation S and growth rate r were:

$$S \sim \text{norm} (\mu_{\text{B2017/B0}}, \sigma_{\text{B2017/B0}}) = \text{norm} (0.1799, 0.0566)$$

r ~ exp(norm (log(\mu_r), \sigma_r)) = exp(norm (log(2 \cdot 1.014 \cdot M), sqrt(0.2312)))

for each value M above. Results of the 10000 iterated Schaefer model optimizations are summarized in Table 3.

Table 3. OCOM + LBB Schaefer production model parameters for different estimates of M, and resulting calculations of year 2017 red cod biomass and MSY. Medians, and 95% confidence intervals in parentheses. $B_{1988} = B_1$ and $B_{2017} = B_{current}$.

М	r	Κ	B ₁₉₈₈	B ₂₀₁₇	MSY
0.2666	0.543	65333	65386	11427	8883
	(0.215 - 1.265)	(34491 - 125451)	(35719 - 125477)	(3869 - 26930)	(6716 -10912)
0.1725	0.350	90784	90855	15529	7935
	(0.136 - 0.887)	(44979 - 161661)	(44843 - 161519)	(5035 - 35687)	(5473 - 9943)
0.1853	0.376	86218	86224	14906	8103
	(0.145 - 0.947)	(42627 - 155951)	(42929 - 155830)	(4670 - 34895)	(5652 - 10109)
0.4761	0.922	43660	44443	7740	9843
	(0.361 - 2.029)	(0 - 91245)	(30166 - 92825)	(0 - 19312)	(0 - 11767)
0.2895	0.585	61850	61802	10841	9032
	(0.222 - 1.340)	(33119 - 123216)	(34220 - 123015)	(3540 - 26004)	(6818 - 11083)
0.1792	0.365	88151	88014	15218	8041
0.1792	(0.142 - 0.926)	(43519 - 157657)	(43411 - 157729)	(4998 - 34970)	(5610 - 10054)

CMSY + BSM

Red cod is reported as a medium resilient species (Froese and Pauly 2018), corresponding to an r prior range of 0.2 to 0.8 (Froese et al. 2017). Red cod was likewise considered a medium depleted species; with a final-year catch approximately 31% of the maximum 3-year moving average catch, giving a prior range for B/K (relative ending biomass) of 0.2 to 0.6 (Froese et al. 2017). The prior range for K was accordingly max._{catch 3}/0.8 to 4× max._{catch 3}/0.2 = 18665.0 to 298640.4. The catchability q prior was avg _{bio index} × 0.5 × geo mean _r/ avg _{catch} to avg _{bio index} × max _r / avg _{catch} = 0.417·10⁻⁴ to 1.668·10⁻⁴. Results of the CMSY and BSM Schaefer model realizations are summarized in Figure 5 and Table 4.

Figure 5 [next page]. Median and 95% confidence intervals of annual red cod biomass estimated from the CMSY (black lines), and BSM implementations (green error bars) of the Schaefer production model.



Figure 5. Median and 95% confidence intervals of annual red cod biomass estimated from the CMSY (black lines), and BSM implementations (green error bars) of the Schaefer production model.

Table 4. CMSY and BSM Schaefer production model parameters, and resulting calculations of year 2017 red cod biomass and MSY. Medians, and 95% confidence intervals in parentheses.

Method	r K		B ₁₉₈₈	B ₂₀₁₇	MSY
CMSY	0.521	74355	23216	37539	9680
	(0.385 - 0.772)	(46445 - 108535)	(13470 - 35926)	(16345 - 58572)	(8331 - 11248)
+BSM	0.495	46799		12166	5742
	(0.425 - 0.552)	(32614 - 83238)	-	(6840 - 17458)	(3964 - 10216)

Length-frequency and maturity time series

Red cod adult length modes obtained a significantly decreasing linear trend over the time series 1988 to 2018 (p < 0.001), of approx. 0.7 cm per year (Figure 6). Within the overall decrease, three sequences were evident of length modes increasing for 6-7 year periods; from 1990 to 1996, 1997 to 2002, and 2003 to 2008. Correspondingly, ages of 50% adulthood showed a marginally significant decreasing trend over the time series (p = 0.059) of approx. 0.046 years per year (Figure 7). Length-frequency and age of 50% adulthood distributions of all individual years are plotted in Appendix Figures A1 and A2.

Figure 6 [next page]. Yearly modes of red cod lengths in the Falkland Islands, and linear regression from 1988 to 2018 (red line; regression weighted by the inverse RMSD of each year's LOESS function): $R^2 = 0.381$, p < 0.001.





Figure 7. Ages corresponding to 50% adulthood in the Falkland Islands, and linear regression from 1988 to 2017 (red line; weighted by the coefficient of deviation of each year's logistic function): $R^2 = 0.122$, p = 0.059.

Discussion

The different versions of data-poor methods resulted in wide disparities of parameter and biomass estimates. OCOM with LBB was highly sensitive to the input value of M, with a significant (p = 0.001) negative correlation between M and MSY among the six variants (Table 3). Further, median MSY values for OCOM with LBB were all >50% of the estimated 2017 biomass, a questionable outcome as 2017 biomass estimates were themselves <18% of carrying capacity K (consistent with the optimizing parameter B_{current}/B₀ = 0.1799).

CMSY and CMSY + BSM were more conservative with MSY / B_{2017} ratios of 25.8% and 47.2% respectively (Table 4). However, CMSY and CMSY + BSM gave outcomes substantially different from each other in carrying capacity and current biomass. The biomass time series estimated by CMSY showed an undulating but non-significant trend (Figure 5).

Data-poor assessments are typical for high uncertainty, as 'data poor' (sparsely reported) stocks often concur with 'poor data' (low quality) (Jiao et al. 2011, Bentley et al. 2015). Length-based methods assume equilibrium conditions that may not apply (Rudd and Thorson 2017). With the uncertainties in this assessment, it is recommended as a precautionary default for red cod to accept the lowest absolute MSY calculated by any of the model versions: 5742 tonnes (CMSY + BSM, Table 4). A threshold of 5742 tonnes is higher than the combined Falkland and Argentinean catches of any of the past three years (Figure 1): 5645.6 t in 2015, 5166.2 t in 2016, 2907.1 t in 2017. All combined catches between 2006 and 2014 were greater than 5742 t, indicative that the stock is not currently overfished but has been in recent years. For the stock to be sustainable at its current levels of fishing suggests high productivity of the species. Median growth rates r of the CMSY and CMSY + BSM methods were comparatively similar at 0.521 and 0.495 (Table 4), and r = 0.495 means that the population is intrinsically capable of increasing by $e^{0.495} - 1 = 64.0\%$ per year. Consistent with high productivity, red cod are known to have high fecundity (Arkhipkin et al. 2010, Brickle et al. 2011).

Furthermore, biological evidence suggests that the red cod population may have adapted to fishing pressure by decreasing size and possibly age of maturation through plasticity in the species' life-history traits (Bianchi et al. 2000, Hutchings 2004, Shin et al. 2005). As catches have declined in the past few years, in both Argentina and the Falkland Islands, abundance and biological trends are likely to continue changing.

References

- Arkhipkin, A., Brickle. P., Laptikhovsky, V., Butcher, L., Jones, E., Potter, M., Poulding, D. 2001. Variation in the diet of the red cod with size and season around the Falkland Islands (south-west Atlantic). Journal of the Marine Biological Association of the UK 81: 1035-1040.
- Arkhipkin, A., Brickle. P., Laptikhovsky, V. 2003. Variation in the diet of the Patagonian toothfish, *Dissostichus eleginoides* (Perciformes: Nototheniidae), with size, depth and season around the Falkland Islands (Southwest Atlantic). Journal of Fish Biology 63: 428–441.
- Arkhipkin, A., Brickle. P., Laptikhovsky, V. 2010. The use of island water dynamics by spawning red cod, *Salilota australis* (Pisces: Moridae) on the Patagonian Shelf (Southwest Atlantic). Fisheries Research 105: 156-162.
- Arkhipkin, A., Bakanev, S., Laptikhovsky, V. 2011. Rock cod biomass survey Cruise Report ZDLT1-02-2011. Falkland Islands Government Department of Natural Resources, 37 p.

- Arkhipkin, A., Brickle, P., Laptikhovsky, V., Winter, A. 2012. Dining hall at sea: feeding migrations of nektonic predators to the eastern Patagonian Shelf. Journal of Fish Biology 81: 882-902.
- Barton, J. 2002. Fisheries and fisheries management in Falkland Islands Conservation Zones. Aquatic Conservation: Marine and Freshwater Ecosystems 12: 127-135.
- Bentley, N. 2015. Data and time poverty in fisheries estimation: potential approaches and solutions. ICES Journal of Marine Science 72: 186-193.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand–Heileman, S., Payá, I., Sainsbury, K., Sanchez, F., Zwanenburg, K. 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES Journal of Marine Science 57: 558–571.
- Brickle, P., Laptikhovsky, V. 2010. Rock cod biomass survey Cruise Report ZDLT1-02-2010. Falkland Islands Government Department of Natural Resources, 31 p.
- Brickle, P., Laptikhovsky, V., Arkhipkin, A. 2011. The reproductive biology of a shallow water morid (*Salilota australis* Günther, 1878), around the Falkland Islands. Estuarine, Coastal and Shelf Science 94: 102-110.
- Brodziak, J., Ianelli, J., Lorenzen, K., and R.D. Methot Jr., R.D. (eds). 2011. Estimating natural mortality in stock assessment applications. US Dept. Commerce, NOAA Tech. Memo. NMFS-F/SPO-119, 38 p.
- Charnov, E. L., Gislason, H., Pope, J. G. 2013. Evolutionary assembly rules for fish life histories. Fish and Fisheries 14: 213-224.
- Chong Follert, L., Contreras M., F., Quiroz, J.C. 2017. Biología reproductiva y aspectos poblacionales de la brótula (*Salilota australis*) en la zona sur-austral de Chile: consideraciones para el manejo de la pesquería. Latin American Journal of Aquatic Research 45:787-796.
- Falkland Islands Government (FIG). 2018. Fisheries Department Fisheries Statistics, Volume 22, 2017. Directorate of Natural Resources, Falkland Islands Government, 100 p.
- Froese, R., Demirel, N., Coro, G., Kleisner, K.M., Winker, H. 2017. Estimating fisheries reference points from catch and resilience. Fish and Fisheries 18: 506-526.
- Froese, R., Pauly, D. (eds.) 2018. FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2018).
- Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A.C., Dimarchopoulou, D., Scarcella, G., Probst, W.N., Dureuil, M., Pauly, D. 2018. A new approach for estimating stock status from length frequency data. ICES Journal of Marine Science doi:10.1093/icesjms/fsy078.
- Gras, M., Blake, A., Pompert, J., Jürgens, L., Visauta, E., Busbridge, T., Rushton, H., Zawadowski, T. 2015. Rock cod biomass survey ZDLT1-02-2015. Falkland Islands Government Department of Natural Resources, 45 p.
- Gras, M., Pompert, J., Blake, A., Boag, T., Grimmer, A., Iriarte, V., Sánchez, B. 2016. Finfish and rock cod biomass survey Cruise Report ZDLT1-02-2016. Falkland Islands Government Department of Natural Resources, 81 p.

- Gras, M., Pompert, J., Blake, A., Busbridge, T., Derbyshire, C., Keningale, B., Thomas, O. 2017. Ground Fish Survey Cruise Report ZDLT1-02-2017. Falkland Islands Government Department of Natural Resources, 83 p.
- Gras, M., Randhawa, H., Blake, A., Busbridge, T., Chemshirova, I., Guest, A. 2018. Groundfish survey Cruise Report ZDLM3-02-2018. Falkland Islands Government Department of Natural Resources, 81 p.
- Gunderson, D.R., Zimmermann, M., Nichol, D.G., Pearson, K. 2003. Indirect estimates of natural mortality rate for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*). Fishery Bulletin 101: 175-182.
- Hilborn, R., Walters, C.J. 1992. Quantitative Fisheries Stock Assessment. Chapman and Hall, New York, 570 p.
- Hutchings, J. A. 2004. Chapter 7; Life histories of fish. In Handbook of Fish Biology and Fisheries, Vol. 1 (Hart, P. J. B. & Reynolds, J. D., eds), pp. 149–174. Oxford: Blackwell Science Ltd..
- 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: 820–822.
- Jiao, Y., Cortés, Andrews, K., Guo, F. 2011. Poor-data and data-poor species stock assessment using a Bayesian hierarchical approach. Ecological Applications 21: 2691-2708.
- Kenchington, T.J. 2014. Natural mortality estimators for information-limited fisheries. Fish and Fisheries 15: 533-562.
- Laptikhovsky, V., Arkhipkin, A., Brickle, P. 2013. From small bycatch to main commercial species: Explosion of stocks of rock cod *Patagonotothen ramsayi* (Regan) in the Southwest Atlantic. Fisheries Research 147: 399-403.
- Martell, S., Froese, R. 2013. A simple method for estimating MSY from catch and resilience. Fish and Fisheries 14: 504-514.
- Muñoz, L., Pavez, G., Quiñones, R.A., Oliva, D., Santos, M., Sepúlveda, M. 2013. Diet plasticity of the South American sea lion in Chile: stable isotope evidence. Revista de Biologia Marina y Oceanografia 48: 613-622.
- Musick, J.A. 1999. Criteria to define extinction risk in marine fishes: The American Fisheries Society initiative. Fisheries 24: 6-14.
- Navarro, G., Rozycki, V., Monsalvo, M. 2014. Estadísticas de la pesca marina en la Argentina. Evolución de los desembarques 2008-2013. Ministerio de Agricultura, Ganaderia y Pesca de la Nación. Buenos Aires, 144 p.
- Nelson, G.A. 2015. Package 'fishmethods': Fishery Science Methods and Models in R. R package version 1.10-4.
- Payá, I. 1992. The diet of Patagonian hake *Merluccius australis polylepis* and its daily ration of Patagonian grenadier *Macrouronus magellanicus*. South African Journal of Marine Science 12: 753-760.

- Punt, A. E. 1990. Is B1 = K an appropriate assumption when applying an observation error production-model estimator to catch-effort data? South African Journal of Marine Science 9: 249-259.
- Raya Rey, A., Schiavini, A. 2005. Inter-annual variation in the diet of female southern rockhopper penguin (*Eudyptes chrysocome chrysocome*) at Tierra del Fuego. Polar Biology 28: 132-141.
- Rudd, M.B., Thorson, J.T. 2018. Accounting for variable recruitment and fishing mortality in lengthbased stock assessments for data-limited fisheries. Canadian Journal of Fisheries and Aquatic Sciences75: 1019-1035.
- Sánchez, R., Navarro, G., Rozycki, V. 2012. Estadísticas de la pesca marina en la Argentina. Evolución de los desembarques 1898-2010. Ministerio de Agricultura, Ganaderia y Pesca de la Nación. Buenos Aires, 528 p.
- Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bulletin of the IATTC 1: 27-56.
- Schiavini, A.C.M., Goodall, R.N.P., Lescrauwaet, A.-K., Koen Alonso, M. 1997. Food habits of the Peale's dolphin, *Lagenorhynchus australis*; review and new information. Report of the International Whaling Commission 47: 827-834.
- Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J. G., Gislason, H. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science 62: 384–396.
- Su, Y.-S., Yajima, M. 2015. Package 'R2jags': Using R to Run 'JAGS'. R package version 0.5-7.
- Then, A. Y., Hoenig, J. M., Hall, N. G., Hewitt, D. A. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES Journal of Marine Science 72: 82-92.
- Zhang, C.-I., Megrey, B. 2006. A revised Alverson and Carney model for estimating the instantaneous rate of natural mortality. Transactions of the American Fisheries Society 135: 620-633.
- Zhou, S., Yin, S., Thorson, J.T., Smith, A.D.M., Fuller, M. 2012. Linking fishing mortality reference points to life history traits: an empirical study. Canadian Journal of Fisheries and Aquatic Sciences 69: 1292-1301.
- Zhou, S., Punt, A.E., Smith, A.D.M., Ye, Y., Haddon, M., Dichmont, C.M., Smith, D.C. 2018. An optimized catch-only assessment method for data poor fisheries. ICES Journal of Marine Science 75: 964-976.

Appendix

Figure A1. Length-frequency distributions by year with LOESS smooths (black line) and the mode (vertical red line). The summary of modes corresponds to Figure 6.





Figure A1, continued.



Figure A1, continued.



Figure A1, concluded.

Figure A2. Juvenile (0) or adult (1) maturity vs. age, by year from observer measurements. Grey circles: scaled to numbers of samples. Black lines: binomial function GLMs. Red lines: Age intercept of 50% adulthood. The summary of 50% adulthood intercepts corresponds to Figure 7.





Figure A2, continued.



Figure A2, continued.



Figure A2, concluded.