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Sustainable Management of Small Pelagic Fisheries:

A Case Study of Atlantic Chub Mackerel in Madeira

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Abstract

Sustainable fisheries management is of global importance, particularly for vulnerable small pelagic species like sardines, anchovies, and mackerel that require careful monitoring of biological parameters to ensure their long-term conservation. Our study of Atlantic chub mackerel (Scomber colias) in Madeira waters analyzed 50,896 specimens collected between 2002 and 2016, revealing significant changes in life history traits potentially linked to fishing pressure. We observed a concerning reduction in size and age at maturity, with L₅₀ decreasing by 3.40 cm TL and A₅₀ declining by 0.11 years over the study period. The 2016 data showed alarmingly high fishing mortality (1.22 year⁻¹) and exploitation rates (0.70 year⁻¹), with subsequent analysis of the 2014-2016 period confirming unsustainable fishing levels. While maximum yield per recruit was estimated at 23.84 g with corresponding biomass of 59.61 g, the optimal fishing mortality (F_{MAX}) was determined to be just 0.40 year⁻¹, significantly lower than current exploitation rates, estimated at 1.22 year⁻¹. This substantial discrepancy between recommended and actual fishing pressure clearly demonstrates the stock is being overexploited. These findings highlight the urgent need for management intervention in Madeira's purse-seine fishery. Immediate action should focus on reducing fishing effort to sustainable levels, potentially through revised catch limits or seasonal closures. Such measures are crucial not only for stock recovery but also for maintaining the long-term viability of this economically important fishery. Continued monitoring of population parameters will be essential to assess the effectiveness of any management changes implemented.

1. Introduction

Global fisheries face significant challenges with overexploitation, particularly concerning pelagic fish stocks whose health status has become increasingly concerning (Hutchings & Reynolds, 2004). Pelagic species, including highly valuable tuna fisheries, constitute the majority of worldwide catches (FAO, 2012). Small pelagic fishes, such as sardines, anchovies, herring, and mackerel, account for approximately 25% of annual global catches (Alheit et al., 2009), forming the economic foundation for numerous fisheries worldwide (Beare et al., 2004; Sabatés et al., 2006). These ecologically and commercially important species exhibit substantial population fluctuations driven by both fishing pressure and environmental factors that influence recruitment and mortality (Tičina et al., 2005). Their

rapid response to environmental changes stems from remarkable life-history plasticity in growth and survival traits (Alheit et al., 2012). Intensive exploitation has been shown to induce earlier maturation at smaller sizes (De Roos et al., 1992), with profound consequences for population dynamics (Feiner et al., 2015). Environmental extremes may further accelerate this trend, selecting for life-history strategies characterized by early maturation, increased reproductive investment, and reduced lifespan (Winemiller & Rose, 1992).

The Atlantic chub mackerel (*Scomber colias* Gmelin, 1789) represents a widely distributed medium-sized pelagic species inhabiting temperate and subtropical Atlantic waters, including the Mediterranean and southern Black Sea (Collette, 1999). As typical of scombrids, *S. colias* exhibits extensive migratory patterns across continental shelf waters, ranging from surface waters to depths of 300 m (Collette & Nauen, 1983; Collette, 1986). In Madeira's NE Atlantic waters, this species forms part of the traditional "ruama" fishery, a small-scale purse-seine operation targeting mixed pelagic schools, primarily *S. colias* and *Trachurus picturatus*, along the island's southern coast (Vasconcelos et al., 2012). Despite landing 334 tons (5.79% of total landings) in 2016 and maintaining considerable socioeconomic importance, critical knowledge gaps persist regarding the population structure and exploitation levels of *S. colias* in Madeiran waters.

This study investigates fishery-induced impacts on life-history parameters of Atlantic chub mackerel in Madeira by analysing age and length composition of annual catches from 2002-2016. We specifically examine temporal changes in length (L_{50}) and age (A_{50}) at first maturity, while applying yield and biomass per recruit models to assess exploitation patterns throughout this period. These analyses aim to provide crucial baseline data for sustainable management of this ecologically and economically important fishery.

2. Materials and methods

2.1. Data sampling

Specimens for this study were collected through weekly random sampling from one of three dedicated commercial purse-seine vessels operating in Funchal Port (Madeira) between 2002 and 2016 (Fig. 1). All sagittal otoliths were extracted ventrally, cleaned, and dry-stored in labeled vials for subsequent age determination. Gonadal examination using a five-stage macroscopic maturity scale (I: immature; II:

developing; III: spawning capable; IV: regressing; V: regenerating; following Brown-Peterson et al., 2011) enabled sex and maturity stage assignment. Annual landing statistics were provided by the Regional Fisheries Department (DRP).

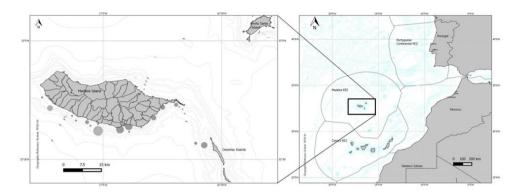


Figure 1 - Map off the southern Atlantic Northeast showing were Atlantic chub mackerel were sampled between 2002 and 2016 (gray spots) off the Madeira archipelago (Source: DRP - Regional Fisheries Department).

2.2. Length and age composition of the landings

Length and age compositions were reconstructed for four temporal periods (2002-2005, 2006-2009, 2010-2013, and 2014-2016) through application of annual age-length keys to the corresponding length-frequency distributions of landings (Holden & Raitt, 1974).

2.3. Length and age at first maturity

Length (L50) and age (A50) at first maturity were calculated using first-semester data (coinciding with the species' spawning season in Madeira; Vasconcelos et al., 2012) following the logistic model described by Jennings et al. (2001).

$$P = \frac{100}{1 + e^{-b(L - L_{50})}} \tag{1}$$

$$P = \frac{100}{1 + e^{-b(A - A_{50})}} \tag{2}$$

where P is the proportion of mature individuals in the size/age class, b is a constant, L the size class in TL (cm) and L_{50} is the size at which 50% of individuals are mature, A is the age group (year) and A_{50} is the age at which 50% of the individuals are mature. Fish classified in maturity stages II through V were considered mature individuals.

2.4. Beverton and Holt's Yield per Recruit and biomass-per-recruit Models

Estimates of yield and biomass per recruit were obtained for the four-time periods using the Beverton and Holt's Yield (3, 4) per Recruit Model (Beverton and Holt, 1957):

$$\frac{Y}{R} = F e^{(-M(T_C - T_T))} W_{\infty} \left[\frac{1}{Z} - \frac{3S}{Z + K} + \frac{3S^2}{Z + 2K} - \frac{S^3}{Z + 3K} \right]$$
(3)

$$S = e^{(-k(t_c - t_0))} \tag{4}$$

where Y/R is the yield per recruit, W_{∞} , K and t_0 are the parameters from VBGF (estimated by Vasconcelos et al., 2011), T_c is the age at first capture (considered as the age of the lowest class landed), T_r is the age at recruitment (assuming as 0), F is the fishing mortality, M the natural mortality and Z the total mortality.

The natural mortality (5) was estimated according to Pauly's method (Pauly, 1980):

$$Log M = 0.0066 - 0.279 Log L_{\infty} + 0.6543 Log K + 0.4634 Log T$$
 (5)

where L_{∞} is the asymptotic length expressed in cm (TL) and K the body growth coefficient from the von Bertalanffy growth function (VBGF) and T the mean annual environmental (seawater) temperature (in °C) that was set at 18°C for the study area. The von Bertalanffy growth parameters used as reference in the estimation of natural mortality were obtained from Vasconcelos et al. (2011).

The total instantaneous mortality rate (Z) was estimated through catch curve analysis (Beverton and Holt, 1957) of the age-structured commercial landings (2002-2016), considering only fully recruited age classes to minimize recruitment variation effects (Everhart et al., 1975; Ricker, 1975). The mortality coefficient was derived as the negative slope of the linear regression between ln-transformed catch numbers and corresponding age classes (Simpfendorfer et al., 2005), following the standard assumption of constant mortality post-recruitment.

Fishing mortality (F) was estimated as the difference between total mortality (Z) and natural mortality (M) according to Beverton and Holt (1957).

The exploitation rate (E) (6) was estimated according to Cushing (1968):

$$E = \frac{F}{Z} \tag{6}$$

Where: F is the fishing mortality and Z the total instantaneous mortality rate.

2.5. Analysis

The normality of size and age distributions was assessed using the Kolmogorov-Smirnov test, while homogeneity of variance was evaluated through Levene's statistics. For all subsequent analyses of variance, the Brown-Forsythe F-test was employed when data violated homogeneity assumptions. Differences in size and age structure of *S. colias* across study periods were examined using one-way ANOVA, with this parametric approach being implemented after verification of the underlying statistical assumptions.

The length (L_{50}) (1) and age (A_{50}) (2) at first maturity along the periods were tested using a general linear model (GLM). Covariates examined were: period; number of individuals per age and length class; fishing mortality; and the relevant measure of temperature. Sea surface temperature (SST) for each period was estimated as the average of the 6 month prior to spawning. SST data was obtained from https://data.giss.nasa.gov/gistemp/.

All statistical analyses were performed using SPSS v. 20.0 (IBM Corp., Armonk, NY). For all tests, statistical significance was considered when p < 0.05.

3. Results

The study analyzed 50,896 Atlantic chub mackerel (*S. colias*) specimens collected between January 2002 and December 2016, with sagittal otoliths from 8,611 individuals used for age determination. Landings revealed a total length range of 10.00-47.00 cm, showing a progressive decrease in mean size from 26.62 cm TL (2002-2005) to 24.54 cm TL (2014-2016). Biological sampling demonstrated greater size variability (13.50-49.60 cm TL), with the smallest specimen being a 13.50 cm male and the largest a 49.60 cm female, both recorded during 2006-2009.

The population exhibited a broad weight distribution (19.42-1,184.94 g) across seven age classes (0-6 years), reflecting the species' growth plasticity under fishing pressure. These morphometric patterns suggest potential fishery-induced changes in population structure over the 15-year study period.

The size (Z= 4.02, p<0.05) and age (Z = 17.47, p < 0.05) frequency showed that the sampled data had a normal distribution. However, size (W = 662.93, p < 0.05) and age (W = 126.40, p < 0.05) did not exhibit homogeneous variance. Significant differences were found in the mean length (F = 586.72, p < 0.05) and in the mean age (F = 42.43, p < 0.05) along the four periods.

3.1. Length and age composition of landings

The estimated annual length landings composition (in number), for the study period, is represented in Fig. 2a. A decreasing trend in the mean length can be observed from 2006-2009 to 2014-2016 periods.

From the application of the annual age-length keys, estimated by direct reading of otoliths, to the length compositions in number of the annual landings resulted the annual age compositions. The estimated age compositions in number per period are represented in Fig. 2b. Catches are based on very young individuals, aged between 0 and 3 years, being the modal age in the last period of 1 year.

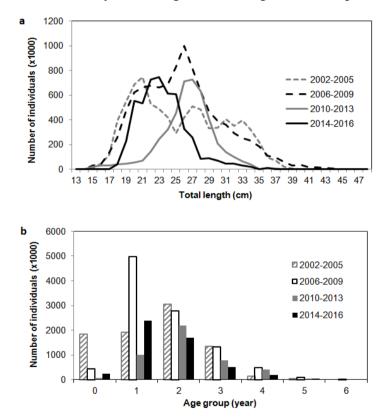


Figure 2 - Length (a) and age (b) composition of the annual catches of *S. colias* sampled in the four study periods (2002-2005, 2006-2009, 2010-2013 and 2014-2016) off Madeira archipelago.

3.2. Length and age at first maturity

The length at first maturity decreased from 21.90 cm TL in 2002-2005 to 18.50 cm TL in 2014-2016. The age at first maturity decreased from 0.95 in 2002-2005 to 0.84 for 2014-2016 (Table 1). Figures 3a and 3b represents length and age at maturity obtained for *S. colias* caught off Madeira between 2002 and 2016.

Table 1 – General linear models (GML) of size (L_{50}) and age (A_{50}) at first maturity for *S. colias* in Madeira by study periods (2002-2005, 2006-2009, 2010-2013, 2014-2016).

-At-maturity	Covariate	F-value	P-value
Size	Fishing mortality	47462.30	< 0.05
	Temperature	9185.38	< 0.05
	Number of individuals	12.25	< 0.05
Age	Fishing mortality	1614.73	< 0.05
	Temperature	325.38	< 0.05
	Number of individuals	2.50	>0.05

GLM analysis of the relationship between the length and age at first maturity of Atlantic chub mackerel in each period and identified covariates (period, number of fish by length and age class, fishing mortality and the relevant measure of temperature) showed a significant relationship between both length and age at maturity and all covariates, being positively related, except for number of fish by age class and age at maturity (Table 1).

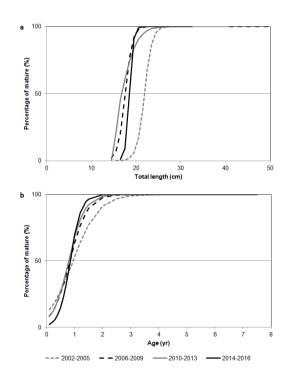


Figure 3 - Length (a) and age maturity (b) obtained for *S. colias* caught off Madeira archipelago for the study periods: a) 2002-2005: P = 100/1+e-(-25.36)(L-21.90), 2006-2009: P = 100/1+e-(-22.25)(L-17.57), 2010-2013: P = 100/1+e-(-10.10)(L-16.78), 2014-2016: P = 100/1+e-(-42.60)(L-18.50); b) 2002-2005: P = 100/1+e-(-2.10)(A-0.95), 2006-2009: P = 100/1+e-(-2.70)(A-0.84), 2010-2013: P = 100/1+e-(-2.80)(A-0.79), 2014-2016: P = 100/1+e-(-4.32)(A-0.84).

GLM analysis also showed that the length (F = 5.25×10^{17} , p < 0.05) and age (F = 7.65×10^{17} , p < 0.05) at first maturity values have been steadily decreasing year by year throughout the study period (2002-2016).

3.3. Beverton and Holt's yield-per-recruit model

Figure 3 presents the results of the yield per recruit model applied to each of the four time-periods. A decreasing trend in the maximum Y/R can be seen from the first (2002-2005) to the last period (2014-2016) with values of 26.61 g and 23.84 g respectively, corresponding to a F_{MAX} of 0.4 year⁻¹.

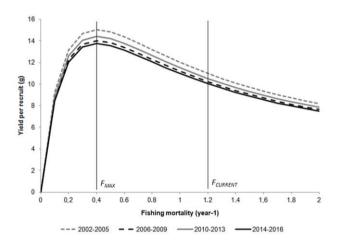


Figure 4. Curve of production (capture) and biomass per recruit for *S. colias* off Madeira archipelago. The parameters used: W = 2002-2005=1320.20; g; W = 2006-2009=1202.27 g; W = 2010-2013=1244.10 g; W = 2014-2016=1183.11 g;

According to Pauly's equation, natural mortality was estimated at 0.52 year⁻¹. In 2016, the estimated total mortality was 1.74 years⁻¹. Fishing mortality and exploitation rate estimated values for 2016 were 1.22 and 0.70 year⁻¹, respectively.

4. Discussion

Biological data on growth and mortality are fundamental for effective stock assessment and fisheries management (Cadima, 2000). Prior to implementing management measures, fisheries managers must evaluate population dynamics to identify critical issues and prevent stock collapse (Pope

et al., 2010). Age-length key analysis of landing compositions is a widely used approach for assessing exploited fish populations, providing insights into the size and age structure underpinning fishery productivity (Bellido et al., 2000).

The findings reveal a concerning trend in Madeira's Atlantic chub mackerel (*S. colias*) fishery, with an increasing reliance on smaller, younger individuals. By 2014–2016, approximately 80% of landings consisted of fish under 25 cm total length (TL), predominantly from age groups 1 and 2. This shift toward smaller size classes has led to a decline in juvenile availability, raising significant conservation concerns. Furthermore, the proportion of mature individuals in landings has decreased steadily over the past two decades, with the current fishery dominated by immature specimens, highlighting unsustainable exploitation patterns.

The observed reduction in adult body size aligns with global patterns reported in exploited fish stocks (Pauly et al., 1998; Levin et al., 2006). Such size-selective declines can trigger cascading ecological effects, including altered trophic interactions, increased predation mortality, reduced post-fishing biomass, and ultimately diminished stock productivity, introducing substantial uncertainty in fisheries management (Audzijonyte et al., 2015).

Fishing pressure typically depletes larger size classes (Conover & Munch, 2002), and in Madeira waters, the disappearance of bigger *S. colias* specimens (2002-2016) likely reflects either direct fishery depletion or behavioral shifts toward deeper waters or nearby seamounts. While no operational changes in fishing depth or location were documented, similar habitat shifts have been reported for *T. picturatus* in this region (Vasconcelos, 2017).

Despite accounting for 15% and 9% of Madeira's total landings (by weight and value, respectively) over the past decade, this small pelagic fishery requires urgent management interventions. Sustainable exploitation demands precise knowledge of stock structure, mortality rates, and fishing effort, deficiencies in which may precipitate overfishing and stock collapse, particularly for less productive populations (Begg et al., 1999).

Fishing mortality acts as a powerful evolutionary force, driving reductions in size-at-age and earlier maturation in exploited stocks (Heino & Gødo 2002; Trippel 1995). The Madeira population of *S. colias* demonstrated this phenomenon clearly between 2002-2016, with length at 50% maturity (L₅₀) decreasing by 3.4 cm (21.9 to 18.5 cm TL) and age at maturity declining correspondingly (Hunter et al. 2015). These changes likely represent either an adaptive response to maintain reproductive output in a

declining population or direct fisheries-induced evolution favoring smaller, earlier-maturing phenotypes (Trippel 1995).

Mortality is essential to understand population dynamics (Lorenzen and Enberg, 2002). The optimal scenario for a population is when the fishing mortality equals natural mortality. In this case, fishery exploit the portion of the population which is lost anyway by natural mortality. With the knowledge of mortality rates, it is possible to model population dynamics, and estimate sustainable exploitation rates and permit the optimum catch whilst saving the reproductive proportion of the population (Simpfendorfer et al., 2005; Kec and Zorica, 2013). The natural mortality of 0.52 year⁻¹ herein estimated was much higher than the observed in Azores (0.19 year⁻¹) (Carvalho et al. 2002), and in the Adriatic Sea (0.35 year⁻¹) (Kec and Zorica, 2013). Observed differences on natural mortality could be influenced by age, sex, size, density, disease, parasites, predation, water temperature and fishing pressure (Vetter, 1998).

According to Patterson (1992) fishing mortalities >2/3 M are mostly related to the decline of the stock while recovery stocks show lower mortality rates. The estimated value for *S. colias* in Madeira, for 2016 was much higher than 2/3 M (0.35) suggesting that this species is presently facing high levels of exploitation, probably is overexploited. This declining trend observed in fish length and weight of the landings is in agreement with Vasconcelos (2017) that states that current *T. picturatus* populations of Madeira are also being exploited above the optimum levels. In 2010 the local government made an adjustment plan to reduce fishing effort in the Madeira purse seine fleet that resulted in the definitive cessation of activity of 2 of the 5 purse seine vessels in the local fleet. This management measure lead to a decrease in the fishing mortality for *S. colias* and *T. picturatus* since 2011, but in 2016 there was an abrupt increase of this rate (1.22 year⁻¹) that is not suitable with the management strategy of S. *colias* in Madeira.

The yield per recruit model provides information on the biological and/or economic effects of the fishing activity on the stocks to the fishery resources managers (Sparre and Venema, 1997b), allowing exploitation at fishing levels in which maximum production is achieved on a sustainable basis, without compromising the stock and future catches. Considering the current value of maximum yield per recruit (Y/R = 23.84 g) and the corresponding fishing mortality (Fmax = 0.4 Year⁻¹), obtained by the Beverton and Holt's yield per recruit model, and the current exploitation rate of 0.70 per year, the stock is clearly being exploited beyond its optimal limit. As the current F value (1.22 year⁻¹) is substantially higher than the Fmax, any increase in fishing effort should be discouraged in order to advert a stock

collapse. However, the yield per recruit results must be taken with caution since landings could reflect mainly the immature fraction of the population.

Management measures should focus on effort reduction through fishing day limitations (20% reduction with 48-hour weekly closures), gear modifications (increased mesh size to 18mm and deeper fishing minimums), and spawning season protection (January-March closures) (DGRM 2012). Such measures mirror successful strategies implemented in Iberian small pelagic fisheries (Vasconcelos 2017) and would help rebuild the stock while maintaining economic viability. The predominance of immature fish in landings (80%) underscores the urgency of these actions to prevent stock collapse and ensure long-term sustainability of this ecologically and economically important fishery (Begg et al. 1999; Lorenzen & Enberg 2002).

References

Alheit J, Pohlmann T, Casini M, et al., 2012. Climate variability drives anchovies and sardines into the North and Baltic Seas. Prog. Oceanogr. 96, 128–139.

Alheit, J., Roy, C., Kifan, S., 2009. Decadal-scale variability in populations, in: Checkley, D.M., Alheit, J.R., Oozeki, Y., Ry, C. (Eds), Climate change and small pelagic fish. Cambridge University Press, Cambridge, pp. 64–87.

Audzijonyte, A., Fulton E.A., Kuparinen, A., 2015. The impacts of fish body size changes on stock recovery: a case study using an Australian marine ecosystem model. ICES J. Mar. Sci., 72(3), 782–792.

Beare, D., Burns, F., Jones, E., Portilla, E., Greig, T., McKenzie, E., Reid, D., 2004. An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. Glob. Chang. Biol. 10, 1209–1213.

Beddington, J.R., Kirkwood G.P., 2005. The estimation of potential yield and stock status using life-history parameters. Phil. Trans. R. Soc. B. 360, 163–170.

Begg, G.A., Friedland, K.D., Pearce, J.B., 1999. Stock identification and its role in stock assessment and fishery management: an overview. Fish. Res. 43, 1–8.

Bellido, J., Pierce, G., Romeno, J., Millán, M., 2000. Use of frequency analysis methods to estimate growth of anchovy (*Engraulis encrasicolus* L. 1758) in the Gulf of Cadiz (SW Spain). Fish. Res. 48, 107–115.

Beverton, R., Holt, S., 1957. On the Dynamics of Exploited Fish Populations. Springer Science + Business Media, B.V, London.

Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewicz, B.J., Lowerre-Barbieri, S.K., 2011. A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish.: Dyn. Manage. Ecosyst. Sci. 3, 52–70.

Cadima, E., 2000. Manual de avaliação de recursos pesqueiros. Documento Técnico sobre as pescas. FAO Fish. Tech. Pap. 393, 10–125.

Carvalho, N., Perrota, N.G., Isidro, E.J., 2002. Age, growth and maturity in the chub mackerel (*Scomber japonicus* Houttuyn, 1782) from the Azores. Arquipelago - Life Earth Sci. 19A, 93–99.

Collette, B.B., 1986. Scombridae, in: Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the Northeastern Atlantic and the Mediterranean, Volume II. Unesco, Paris, pp. 981–997.

Collette, B.B., 1999. Mackerels, molecules, and morphology, in: Proceedings of the 5th Indo-Pacific Fish Conference, 3-8 November 1997. Soc. Fr. Ichtyo, pp. 149–164.

Collete, B.B., Nauen, C., 1983. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Species Catalogue. FAO Fisheries Synopsis No 125(2).

Conover D.O., Munch S.B., 2002. Sustaining Fisheries Yields Over Evolutionary Time Scales. Science 297, 94–96.

De Roos, A.M., Boukal, S.D., Persson, L., 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. Proc. R. Soc. B. Biol. Sci. 273, 1873–1880.

DGRM. 2012. Sardine Fishery Management plan. https://www.dgrm.mm.gov.pt/web/guest/plano-de-gestao-da-sardinha?inheritRedirect=true (accessed 18 February 2018).

Everhart, W., Eipper, A., Youngs, W.D., 1975. Principles of Fishing Science. Cornel University Press Ltd, London.

FAO, 2012. The state of world fisheries and aquaculture (SOFIA). Food and Agriculture Organization of the United Nations (FAO), Rome (Italy).

Feiner, S.Z., Bunnell, B.D., Höök, Ö.T., Madenjian, P.C., Warner, M.D., Collingsworth, D.P., 2015. Non-stationary recruitment dynamics of rainbow smelt: the influence of environmental variables and variation in size structure and length-at-maturation. J. Great. Lakes Res. 41(1), 246–258.

Heino, M., Godø, O.R., 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bull. Mar. Sc. 70, 639–656.

Holden, M., Raitt, D., 1974. Manual of fisheries science, Part 2 – Methods of resource investigation and their application. FAO, Roma.

Hunter, A., Speirs, D.C., Heath, M.R., 2015. Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde. Fish. Res. 170, 14–23.

Hutchings, J.A., Reynolds, J.D., 2004. Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk. BioScience 54(4), 297–309.

Jennings, S., Kaiser, M., Reynolds, J., 2001. Marine Fisheries Ecology. Blackwell Science, Oxford.

Jobling, M., 1996. Biology of fishes. Chapman and Hall, London.

Kec, V.C., Zorica, B., 2013. Length-weight relationship, age, growth and mortality of Atlantic chub mackerel *Scomber colias* in the Adriatic Sea. J. Mar. Biol. Assoc. U.K 93(2), 341–349.

Levin, P.S., Holmes, E.E., Piner, K.R., Harvey, C.J., 2006. Shifts in a Pacific Ocean fish assemblage: the potential influence of exploitation. Conserv. Biol. 20(4), 1181–1190.

Lorenzen, K., Enberg, K., 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. Lond. B 269, 49–54.

Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., Smith, P.E., 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8, 195–205.

Misund, O., 1994. Swimming behaviour of fish schools in connection with capture by purse seine and pelagic trawl, in: Fernö, A., Olsen, S. (Eds.) Marine fish behaviour in capture and abundance estimation. Fishing News Books, Oxford, pp 84–106.

Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. Rev. Fish. Biol. Fisher. 2(4), 321–338.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39, 175–192.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food web. Science, 279: 860–863.

Pope, K.L., Lochmann, S.E., Young, M.K., 2010. Methods for Assessing Fish Populations. Nebraska: Nebraska Cooperative Fish & Wildlife Research Unit.

Ralston, S., 1987. Mortality rates of snappers and groupers, in: Polovina, J.J., Ralston, S. (Eds.), Tropical snappers and groupers. Biology and fisheries management. Ocean Resour. Mar. Policy Ser. Westview Press, Inc., London, pp. 375–404.

Ricker, W., 1975. Computation and interpretation of biological statistics of fish populations. J. Fish. Res. Board Can. 191, 1–382.

Sabatés, A., Martín, P., Lloret, J., Raya, V., 2006. Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. Glob. Chang. Biol. 12, 2209–2219.

Simpfendorfer, C., Bonfil, R., Latour, R. (2005) Mortality estimation. In: Musick, J., Bonfil, R. (Eds.), Management techniques for elasmobranch fisheries. FAO Fish. Tech. Pap. 474. FAO, Rome, pp. 127–142.

Sutherland, W.J., Orafen, A., Harvey, H.P., 1986. Life history correlations and demography. Nature 320, 88.

Tičina, V., Katavić, I., Dadić, V., Grubišić, L., Franičević, M., Tičina, V.E., 2005. Acoustic estimates of small pelagic fish stocks in the eastern part of the Adriatic Sea: September 2004. GFCM – SAC – SCSA, Rome, 26–30.

Trippel, E.A., 1995. Age at maturity as a stress indicator in fisheries. BioScience 45, 795-771.

Vasconcelos, J., Afonso-Dias, M., Faria, G., 2011. Age and growth of the Atlantic chub mackerel *Scomber colias* Gmelin, 1789 off Madeira Island. Arquipélago - Life Earth Sci. 28, 57–70.

Vasconcelos, J., Afonso-Dias, M., Faria, G., 2012. Atlantic chub mackerel (*Scomber colias*) spawning season, size and age at first maturity in Madeira waters. Arquipélago - Life Earth Sci. 29, 43–51.

Vasconcelos, J., 2017. Estrutura populacional do Chicharro, *Trachurus picturatus* do Atlântico Nordeste. Tese de Doutoramento submetido à Universidade da Madeira, Funchal, 277pp. http://hdl.handle.net/10400.13/1502

Vetter, E., 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. 86, 25-43.

Winemiller, K.O., Rose, K.A., 1992. Patterns of life history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49, 2196–2218.