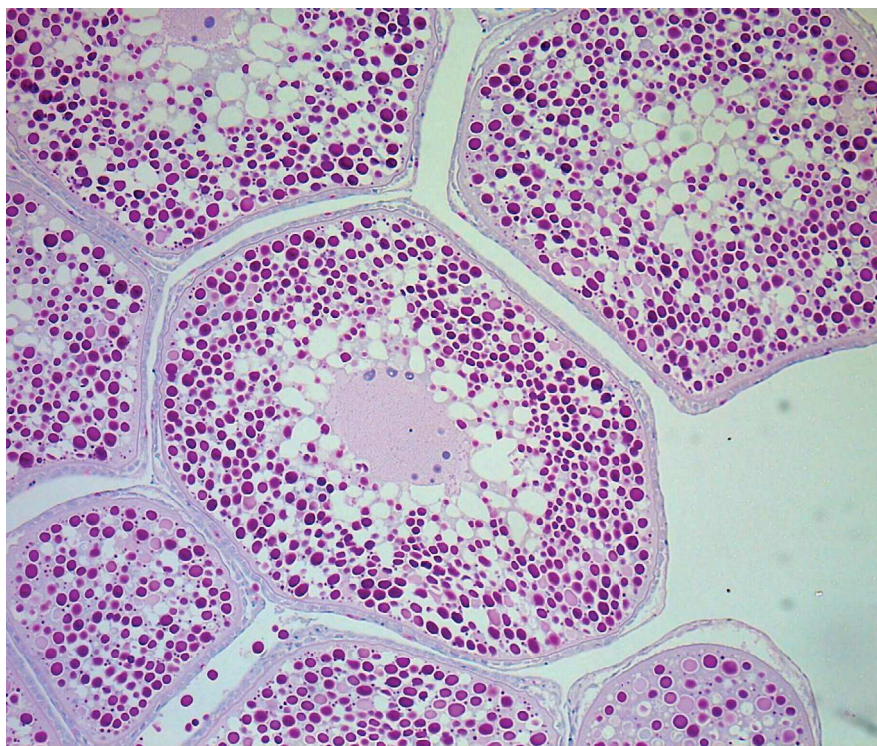


IBEROAMERICAN FISHERIES AND FISH REPRODUCTIVE ECOLOGY

Edited by

Nixon Bahamon, Rosario Domínguez-Petit, Jorge Paramo,
Fran Saborido-Rey and Arturo Acero P.



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08003 Barcelona, Spain
Tel.: +34 932309500.
Fax: +34 932309555
E-mail: scimar@icm.csic.es
www.icm.csic.es/scimar

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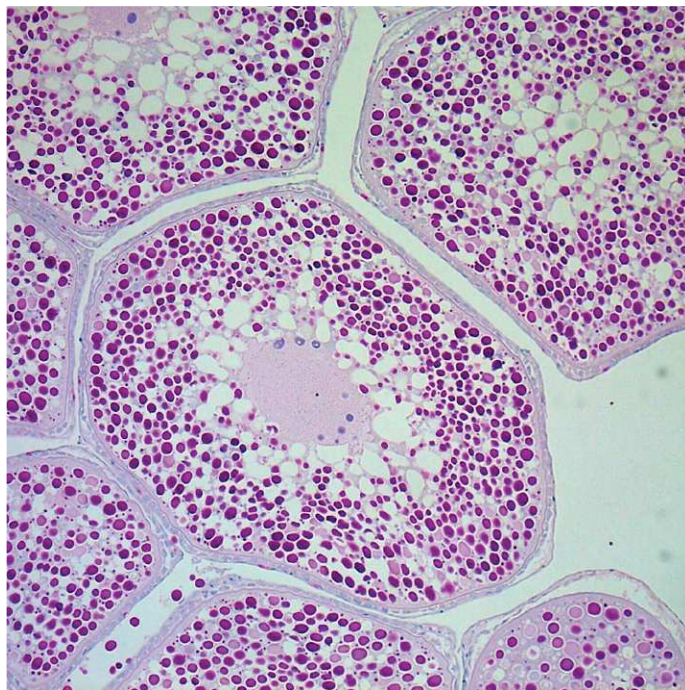
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Foreword

The oceans are facing increasing pressure related to water warming, acidification, pollution, overexploitation and illegal activities, which generate biodiversity loss and ecosystem degradation, placing at risk the provision of goods and services. In order to preserve healthy and resilient marine ecosystems, adaptive scientific tools for the sustainable management of resources are required, as agreed in the Agenda 2030 (UN 2015). Key elements for sustainable social and economic progress worldwide were identified in the Agenda. Under this framework, with humanity's aim to move more efficiently and effectively towards these goals, the UN has designated the period 2021-2030 as the Decade of Ocean Science for Sustainable Development (UN 2017). The focus is placed on i) maintaining a clean, healthy, safe and resilient ocean, ii) developing tools to predict future changes in marine conditions and their impact on society, iii) ensuring the sustainable exploitation of resources, especially food resources, and above all, iv) ensuring transparency and availability of information.

Marine fisheries provide food of high nutritional value for millions of people and are an important economic driver on all continents (FAO 2022). Particularly important is the role that small-scale artisanal fisheries play in the food systems, livelihoods, culture and environment of regions and communities, which are highly vulnerable to environmental and economic perturbations (Chuenpagdee 2011). For this reason, the UN declared 2022 the International Year of Small-scale Fisheries and Aquaculture (UN 2018), with the intention of promoting sustainable small-scale fisheries that ensure food security and poverty eradication.

The current state of fish stocks is alarming, 34% of them being currently exploited at unsustainable levels and 60% at the maximum sustainable level (FAO 2022). It has been predicted that, if current fishing effort is maintained, most fisheries will collapse by 2048 (Worm et al. 2006). While total catches have stabilized since the late 1990s, when they reached the historic maximum, the lack of data from some fisheries and the existence of illegal and unregulated fishing call into question predictions about the future of fisheries (Pauly and Zeller 2015). Pauly and Zeller (2015) estimate global catches at over 100 million t, well above the officially reported 80 million t. Therefore, it is imperative to implement suitable management measures, improve the collection of fisheries information, and expand the knowledge of exploited organisms and marine ecosystems in order to revert to current situation of fisheries exploitation and make them sustainable over time.

Marine ecosystems and fisheries in the Iberian Peninsula and Latin America (i.e. Ibero-America), are no exception to the vulnerabilities and challenges of global fisheries. The wide geographical distribution of the Ibero-American regions entails a high diversity of marine ecosystems (Seeliger and Kjerfve 2013, Cortes et al. 2020), from coral reefs to circumpolar ecosystems, as well as a great diversity of fisheries (Rivero-Rodriguez and González-Fernandez 2021), from the largest industrial fisheries in Peru that exploit pelagic species to the artisanal fisheries in coastal areas of the Caribbean Sea. There is also great variability in the fisheries features and incomes among countries, which hampers the development of appropriate methods for assessment and management (Fig. 1). Fishing in Ibero-America is an important economic activity, generating employment and income for many communities, with more than 1.5 million people working directly in this activity in Latin America and the Caribbean alone (FAO 2022). Fishing activity in Ibero-America focuses on a great diversity of species and ecosystems (Rivero-Rodriguez and González-Fernandez 2021). In fact, this region has some of the largest marine ecosystems on the planet, such as the Humboldt Current System in Chile, Peru and Ecuador, which supports the largest small pelagic fishery in the world, the Patagonian Shelf in Argentina and Uruguay, where one of the most productive demersal fisheries in the world takes place, and the Southern Shelf in Brazil.

There is no facilitating organization in the regions to achieve the objectives of conservation, management and sustainability through coordinated research and assessment of fishery resources, which are often exploited by different countries, including those outside the Ibero-American regions. A particular concern is the lack of knowledge about the resources exploited by artisanal fleets (Olivei-

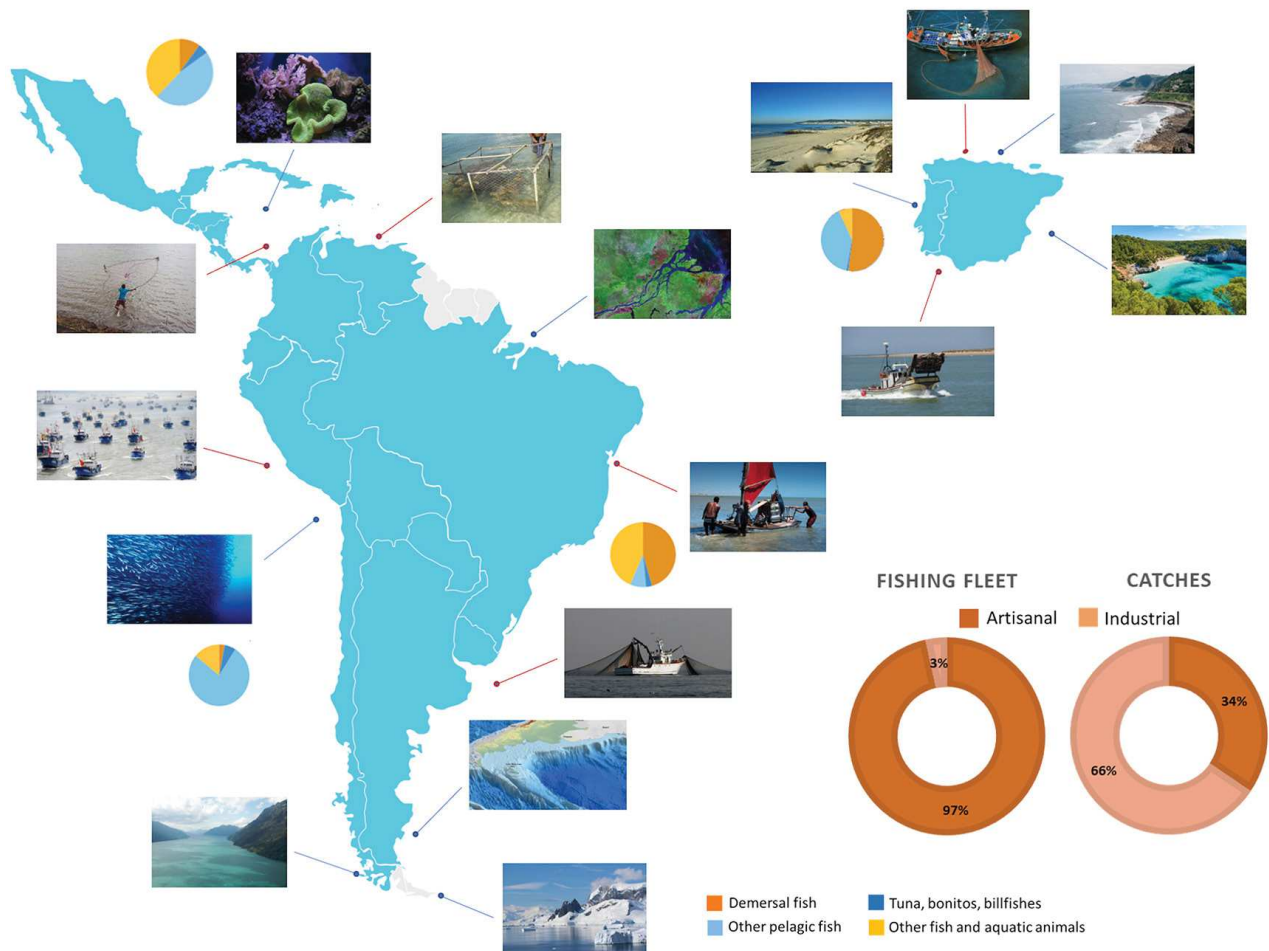


Fig. 1. – Illustrations of the diversity of ecosystems (blue lines) and fisheries (red lines) in Ibero-America. The pie charts represent the major species groups caught in the main Ibero-American fishing areas (FAO 2022). The ring diagrams represent the proportion of vessels and catches from the artisanal and industrial fisheries for the global region of Ibero-America (Pauly and Zeller 2015). Fishing fleet data come from the National Fisheries Statistics of the main fishing countries in the region (Argentina, SPM 2019, Brazil, SISRGP, 2021, Chile, SERNAPESCA 2021, Spain, Pascual-Fernandez et al. 2020 and SGP 2021, Mexico, CONAPESCA 2017 and INEGI 2021, Peru, PRODUCE 2021). Image copyright: Sam Beebe, Ivan Blanco Vilar, Pawel Kazmierczak-Shutterstock, Marco Ramerini, Vitor M. Cabral da Olive, Otávio Nogueira (<https://www.meganoticias.cl>), Diego Delso, El Estrecho Digital, Agencia EFE and Wilfedor.

ra-Leis et al. 2019), despite its great potential for reducing hunger and malnutrition, preserving biodiversity and natural resources and mitigating the impact of climate change.

Research in fisheries ecology and biology contributes greatly to meeting the challenges of today's fisheries. Fish stocks are characterized by their own life history, mainly determined by the traits defining the reproductive potential, growth and natural mortality of individuals and populations (Stearns 1977). These traits are endogenous factors determining the stock dynamics, though stocks are also affected by environmental factors, including fishing (Rochet 1998). For all these reasons, added to the fact that ecological relationships between organisms determine the structure and functioning of the ecosystems, ecosystem-based fisheries management is fundamental for evaluating and regulating the impact of the fishing activity on marine populations, habitats and ecosystems, and ultimately on society (Fig. 2).

Scientific production in the field of fisheries ecology in the Ibero-American regions is extensive, although not always known and accessible. Since its foundation in 2009, the Ibero-American Research Network for the Sustainable Use of Fisheries Resources (RED INVIPESCA) has been working to strengthen Ibero-American fisheries research through collaboration and knowledge exchange between leading institutions and researchers in the field (Rivero-Rodríguez and González-Fernández 2021). This mission is addressed through various activities, including the Ibero-American Symposium on Reproductive Ecology, Recruitment and Fisheries (SIBECORP), of which five editions have already been celebrated in Vigo (Spain) in 2009, Mar del Plata (Argentina) in 2012, Puerto de Galinhas (Brazil) in 2015, Iquique (Chile) in 2018 and Santa Marta (Colombia) in 2021. This special issue of *Scientia Marina* brings together a selection of papers presented at the last edition of SIBECORP in Santa Marta. The programme of this edition, held in hybrid format (face-to-face and online) owing to the COVID-19 pandemic, included four pre- and post-symposium courses, three keynote talks, 48 oral presentations, 48 posters and two workshops.

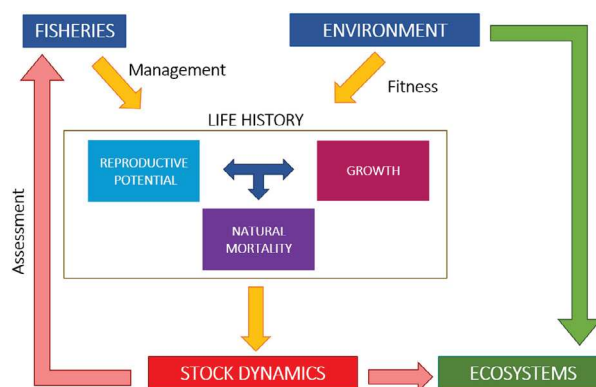


Fig. 2. – Diagram of the main endogenous and exogenous factors involved in the dynamics of exploited fish stocks for consideration in fisheries biology, ecology and management studies.

In contrast to previous editions that were more focused on fish, the fifth SIBECORP included noteworthy communications on reproductive ecology and management of exploited invertebrates. For the first time, some presentations incorporated social and economic perspectives of fisheries, which are essential for a fair and effective management. The symposium was organized around four thematic sessions: i) reproductive strategies of aquatic organisms, ii) reproductive potential and resilience, iii) recruitment and reproductive success and iv) reproductive ecology and fisheries management. The following sections are a review of the main conclusions reached after each session.

Reproductive strategies of aquatic organisms

Exploited aquatic organisms display a large variety of reproductive strategies and associated traits (Saborido-Rey 2016) such as gender, breeding and mating systems, gametogenesis and embryonic development, mode of fertilization, spawning pattern, parental care, distribution of energy resources and behaviour, all of them often showing temporal and spatial variation and defining the reproductive tactics adopted by the different species (Stearns 1992). This variability leads to strong plasticity in life-history traits such as maturation, fecundity and egg size, viability of offspring, growth pattern associated with reproductive dynamics, and mortality (or survival). All these traits define the reproductive potential and govern the annual variability in egg production, which in turn would explain changes in recruitment and reproductive success (see below).

The amount of energy that an individual allocates for growth and reproduction depends on its genetics and physiology, as well on environmentally driven factors. This energy must be balanced in a specific growth and reproduction dynamics and in trade-offs at different time scales of an individual organism: lifetime, annual, intra-seasonal and diel. The lifetime scale refers to attaining sexual maturation, a critical decision that will modify individual fitness, reproductive effort; it has its ultimate goal in egg production and spawning dynamics as a measure of reproductive success. Thus, assessing changes in maturation is an essential goal in fisheries management, as fisheries drastically modify size and age at maturation. They may even induce adaptive changes and changes in maturation alter stock dynamics, sometimes leading to drastic consequences such as stock collapse (Olsen et al. 2004). Lojo et al. (2022) analysed the temporal variability of size at maturity (L_{50}) in European hake (*Merluccius merluccius*), concluding that L_{50} is a good indicator for predicting future population dynamics. The large plasticity in life-history traits implies the existence of local and regional adaptations that will lead to overexploitation if not properly considered in fisheries management. Macal-Lopez et al. (2022) estimated reproductive parameters of the snapper *Lutjanus griseus* on the continental shelf of the Yucatan Peninsula, Mexico, and compared them with other shelves and insular regions in the vicinity, providing data fundamental for stock assessment.

While temporal variation of reproductive traits has often been analysed, spatial variation has received less attention. The spatial patterns of many reproductive traits are known to show great variability, which is being exacerbated by climate change, especially in pelagic fish. Moreno and Claramunt (2022) report that the annual variation in the location and extension of the spawning area of the anchoveta *Engraulis rigens* in Chile shows an interesting strategy of density-dependent use of space related to female size and abundance. However, it is currently difficult to ascertain whether observed spatial patterns in reproductive traits are due to phenotypic plasticity, local adaptation or both, and to determine the role of climate change. Domínguez-Petit et al. (2022b) show a great latitudinal variation in several biological parameters of Atlantic chub mackerel (*Scomber colias*) within a relatively small area, including size at maturity and spawning season. The different strategies observed seem to be related to the thermal tolerance of the subpopulations studied.

Because reproduction has a cost in terms of energy, which may be very high, there is always a trade-off between the number of reproductive events and reproductive outputs (e.g. fecundity and egg size) that the individual can afford. The ultimate goals of reproductive effort are egg production and spawning dynamics as a measure of reproductive success, so fecundity is often considered one of the most important components of a reproductive strategy (Lowerre-Barbieri 2009). Furthermore, studies on fecundity in aquatic organisms are still rare, and long time series

of fecundity are usually not available (Tomkiewicz et al. 2003). Fecundity studies are critical for understanding the temporal variation in reproductive potential and how maternal effects can interact with fecundity, as shown for the Acadian redbfish *Sebastes fasciatus* (González-Carrion and Saborido-Rey 2022).

In summary, there is a critical need for precise knowledge on the reproductive strategies of the managed populations, on the temporal and spatial variation of these strategies, and on life-history traits. These variations have a profound impact on reproductive potential, resilience, recruitment and reproductive success that must be considered in fisheries management, as discussed in the following sections.

Reproductive potential and resilience

Since the concept of reproductive potential of a stock was coined as the capacity to produce viable offspring that are recruited to the fishery (Trippel 1999), many studies have been carried out to understand the endogenous factors, beyond genetics, that regulate this potential (Nissling et al. 1998, Berkeley et al. 2004, Macchi et al. 2018). These factors are called parental effects and refer to the influence that the phenotype and environmental conditions in which individuals develop have on the phenotype of their offspring (Bernardo 1996). To date, the study of parental effects in aquatic organisms has been dominated by research on maternal effects (derived from females), with the role of males being limited to gene transmission (Shama et al. 2014, von Siebenthal et al. 2009). However, an increasing number of studies have demonstrated the existence of paternal effects in aquatic organisms ranging from the direct influence of paternal attributes on offspring quality (Rideout et al. 2004) to the influence of parental behaviour on offspring survival (Stein and Bell 2014) and the impact of the environment on male reproductive success (Beirão et al. 2011, López-Galindo et al. 2019, Thomas et al. 2015). These relationships are not always direct. For example, González-Carrion and Saborido-Rey (2022) report maternal effects on the quantity and quality of eggs of *S. fasciatus* from the Northwest Atlantic. However, these authors observed no effect of maternal attributes on larval characteristics, and questioned whether the maternal effects have a real impact on recruitment of this species. This study also suggests that the assumption that all spawning biomass has the same reproductive potential regardless of the parental attributes and the environmental conditions to which spawners are exposed is insufficient, as there are numerous and complex environment-stock interrelationships that define the long-term reproductive success of a population.

This holistic and transgenerational view is captured in the concept of reproductive resilience coined by Lowerre-Barbieri et al. (2017). The reproductive resilience of a stock is determined by the characteristics of the population's reproductive-recruitment system and the environmental and ecological context in which the population develops. In this theoretical framework, reproductive success is an individual parameter that gives rise to density- and fitness-dependent feedback loops, which act at the population level to maintain reproductive success over time and determine the resilience of the population to external perturbations (Lowerre-Barbieri et al. 2017).

Knowing the spatial structure of the stock is fundamental for determining its reproductive resilience, since this determines the ecological context and the genetic flow between the components of the population. Domínguez-Petit et al. (2022b) present the example of *Scomber colias*, an expanding species in the Northeast Atlantic whose population structure is not yet known, but which shows a gradient in its biological parameters (size, age, condition and maturity) from the core of its distribution in NW African waters to the northern limit of distribution in the Cantabrian Sea, which could lead to differences in the reproductive potential of the species in each area. These authors also postulate the existence of a possible mixing zone in the Gulf of Cadiz, where individuals from the Mediterranean population would converge with those from the Atlantic, demonstrating that studies at different spatial and temporal scales are necessary to understand the functioning of the reproductive-recruitment system.

The study of reproductive resilience is key for a suitable management of fisheries, since it allows us to quantify the sustainability of exploited stocks in the medium and long term under different environmental and exploitation scenarios; however, to achieve this, good quality basic biological information is required. Especially important is the work focused on species for which there is hardly any information, many of which have an important ecological role, inhabit areas sensitive to anthropogenic impact and are exploited by small-scale artisanal or recreational fisheries of great social and economic importance for the communities that depend on them. This is the case of the grey snapper (*Lutjanus griseus*), an important fishing resource in the Atlantic coast of USA and the Gulf of Mexico, whose reproductive traits may vary depending on the area they inhabit. Macal-Lopez et al. (2022) analyse the reproductive strategy of this species in the Yucatan Peninsula, confirming that it shows the typical reproductive pattern of snappers distributed on continental shelves or in shallow water areas. In addition, they highlight the importance of having a good monitoring programme for the species and standardizing the methods for estimating reproductive parameters, as well as considering the reproductive and feeding behaviour of individuals in order to design a suitable monitoring programme.

Recruitment and reproductive success

Stearns (1992) defined reproductive success as the probability that offspring will survive to reproductive age based on egg production, fertilization success and survival of the reproductive output. While in early life stages the environment plays an important role in egg and larval mortality, survival in this period is modulated by paren-

tal effects (Domínguez-Petit et al. 2022). The bigger-is-better hypothesis (Green 2008, Barneche et al. 2018) suggests that larger females produce more and larger eggs from which larger larvae, which are more likely to survive, will hatch (McCormick 2006). It is not just a matter of size: the age and condition of the broodstock also influences the fitness of the offspring (Gall 1974, Marteinsdottir and Steinarsson 1998, Green 2008). This is because larval behaviour and physiology are related to size (Hunter 1981). Similarly, in species such as Atlantic cod (*Gadus morhua*), the size of spawning males has been found to influence fertilization success (Bekkevold 2006) and survival of embryos and larvae (Trippel et al. 2005); while in other species where paternal care of the offspring exist, growth and survival of offspring are related to paternal attributes (Divino and Tonn 2008, Green and McCormick 2005).

Reproductive success depends not only on the quantity and quality of reproductive output, but also on the selection of suitable spawning habitat, i.e. it matters not only how much, but also when and where the fish reproduce. In this regard, it has been observed that female size, closely related to age, affects egg density and thus egg distribution and transport to suitable breeding areas (Kjesbu et al. 1992), while the age of spawners determines the onset and duration of the spawning season (Kjesbu et al. 1990, Macchi et al. 2004) and the ability to reach suitable spawning sites (Macchi et al. 2005, Petitgas et al. 2006). The timing and location of spawning determine the environmental conditions in which offspring must develop, and in the early life stages of fish these factors are key to the survival and thus the reproductive success of the entire population (Marshall 2016). Indeed, in species such as Atlantic cod (Marteinsdottir and Thorarinsson 1998) and Norwegian herring, *Clupea harengus*, (Lambert 1990), recruitment has been shown to be positively correlated with the proportion of older females. Moreover, in species such as *Sander viterus*, populations with low age diversity are more likely to experience mismatches between spawning and optimal environmental conditions, leading to low recruitment (Shaw et al. 2018). This is particularly important in the context of global warming that the oceans are experiencing, as offspring survival will depend on the ability of parents to match adequate spawning location and timing under this changing environment. Puerto et al. (2022) report an expansion of the spawning area of the skipjack tuna, *Katsuwonus pelamis*, in the western Mediterranean, likely associated with the warming of these waters that has been detected in recent decades. This expansion could impact on other tuna species dynamics in the western Mediterranean, which now have to share their spawning area with skipjack tuna.

In summary, recruitment is largely determined during the larval stage (Leggett and Deblois 1994), whose survival is intimately linked to parental effects that ultimately define the reproductive success of the stock. Assessing the factors that determine the reproductive success of a stock is both complex and essential for sustainable fisheries management, as it would reduce uncertainty in recruitment predictions and provide a better insight into population dynamics. A promising tool in this field is the RNA/DNA ratio as an index of larval condition. Using this molecular index, Diaz et al. (2022) demonstrated that the North Patagonian Frontal System is a favourable nursery area for anchovy (*Engraulis anchoita*) and Argentine hake (*Merluccius hubbsi*) and is therefore key in the recruitment in these two commercially important species.

Reproductive ecology and fisheries management

The reproductive ecology of species explains the mechanisms underlying the reproductive success of stocks, and hence their ability to sustain themselves over time. Fisheries are based on the capacity of these populations to maintain themselves at sufficient levels to ensure the profitable capture of individuals without compromising the viability of the population. The ultimate goal of fisheries management is to ensure exploitation levels that guarantee long-term sustainability of both the population and the economic activity.

Fishing activity influences the reproductive success of stocks due to the strong selective impact on populations segments, e.g. large versus small individuals, females versus males, spawners versus juveniles, etc. In turn, the reproductive success of stocks determines the amount of fish available for fishing (Lowerre-Barbieri et al. 2017). In addition, environmental factors and the other species that sharing the ecosystem with the exploited species also impact on their reproductive success (Lowerre-Barbieri et al. 2017). This is the basis of the ecosystem approach to fisheries management (EAFM), which aims to manage marine resources from a holistic perspective, considering the impact of the fishery on the whole ecosystem, including biodiversity (FAO 2003). The EAFM must consider abiotic and biotic components of ecosystems, including human impacts (Garcia and Cochrane 2005) and aim to maintain exploited ecosystems in a healthy, productive and resilient state so that they can provide the services that humans need.

Nursery areas and their associated biodiversity are essential within the EAFM framework, as they contribute to understand the life cycle parameters of fisheries resources (including stock structure, growth, maturity, reproduction, recruitment, mortality and spawning areas and times) and helps to achieve an efficient fisheries management (Hilborn and Walters 1992), while allow protecting and conserving the existing ecosystems (Paramo et al. 2020), e.g. by implementing protected breeding areas, fishing bans, monitoring programmes and conservation strategies, among other management measures.

Knowledge of reproductive ecology, which is the focus of SIBECORP, is still quite limited in many exploited species, especially those targeted by artisanal fisheries, limiting the development and implementation of the EAFM.

The manuscripts published in the present special volume provide important information on the mechanisms that explain the reproductive success of exploited marine species, helping to improve their management. These studies

are based on very diverse research fields such as physiology and bioenergetics (Pauly and Liang 2022), the analysis of spatio-temporal changes in reproductive parameters and parental effects (Domínguez-Petit et al. 2022b, Lojo et al. 2022, Macal-Lopez et al. 2022), and the temporal variation of spawning area location and extension (Moreno and Claramunt 2022, Puerto et al. 2022), in addition to relevant methodologies (Díaz et al. 2022, González-Carrión and Saborido-Rey 2022).

CONCLUSIONS

Fisheries in the Ibero-American region are among the most diverse and productive on the planet, and they contribute significantly to food security, poverty alleviation, development and the stability of rural and coastal communities. However, they face major anthropogenic risks (climate change, pollution, illegal and unregulated fishing and overexploitation), aggravated by a lack of knowledge on the ecology and reproductive potential of many of the exploited species, which in turn determine the resilience of the stocks to external disturbances.

Throughout the different editions of the Ibero-American Symposium on Reproductive Ecology, Recruitment and Fisheries (SIBECORP), the Ibero-American Research Network for the Sustainable Use of Fisheries Resources (RED INVIPESCA) has brought together scientists with expertise in fisheries ecology and assessment in order to identify the main knowledge gaps and needs for future research to implement sustainable management of fisheries resources in the region. To this end, the five editions of SIBECORP have promoted the dissemination of research carried out in the region around four fundamental pillars of fisheries ecology: the study of the reproductive strategies of exploited species; the quantification of reproductive potential and the causes of its variation as a key aspect of reproductive resilience; the influence of reproductive potential on reproductive success and recruitment to the fishery; and the development of management measures to preserve reproductive potential.

Despite the significant progress made in this area, reflected partially in the papers selected for this publication, there is still much work to be done in the region. We must expand and update the knowledge we have on the reproductive potential of exploited species and thoroughly revise globally accepted hypotheses that have proven to be invalid, as is done by Pauly and Liang (2022). These 13 years have only reinforced the idea that forums such as the INVIPESCA Network and the SIBECORP are needed to create a solid scientific basis on which to build a sustainable management system for Ibero-American fisheries to guarantee the achievement of the Sustainable Development Goals of the 2030 Agenda.

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REFERENCES

- Aragón-Noriega E.A., García-Juárez A.R. 2007. Comparison of two methods to determine the maturity period in penaeid shrimps (Decapoda, Penaeidae). *Crustaceana* 80: 513-521. <https://doi.org/10.1163/156854007780765579>
- Barneche D.R., Ross Robertson D., White C.R., Marshall D.J. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360: 642-645. <https://doi.org/10.1126/science.aao6868>
- Beirão J., Soares F., Herráez M.P., Dinis M.T., Cabrita E. 2011. Changes in *Solea senegalensis* sperm quality throughout the year. *Anim. Reprod. Sci.* 126: 122-129. <https://doi.org/10.1016/j.anireprosci.2011.04.009>
- Bekkevold D. 2006. Male size composition affects male reproductive variance in Atlantic cod *Gadus morhua* L. spawning aggregations. *J. Fish Biol.* 69: 945-950. <https://doi.org/10.1111/j.1095-8649.2006.01140.x>
- Berkeley S.A., Hixon M.A., Larson R.J., Love M.S. 2004. Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations. *Fish.* 29: 23-32. [https://doi.org/10.1577/1548-8446\(2004\)29\[23:FSVPOA\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2)
- Bernardo J. 1996. Maternal effects in animal ecology. *Amer. Zool.* 36: 83-105. <https://doi.org/10.1093/icb/36.2.83>
- Chuenpagdee R. 2011. *World Small-scale Fisheries: Contemporary Visions*. Eburon. Delft (The Netherlands). 400 pp. ISBN: 978-90-5972-539-3.
- CONAPESCA. 2017. *Anuario Estadístico de Acuicultura y Pesca 2017*. Comisión Nacional de Acuicultura y Pesca. Secretaría de Agricultura, Ganadería, Desarrollo rural, Pesca y Alimentación. Gobierno de México. https://www.CONAPESCA.gob.mx/work/sites/cona/dgppe/2017/ANUARIO_ESTADISTICO_2017.pdf

- Cortes J., Villamizar A., Nagy G.J., et al. 2020. Coastal marine ecosystems. In Moreno J.M., Laguna-Defior C., V. et al. (eds). Adaptation to climate change risks in Ibero American countries. Mc Grill Hill. Madrid, Spain: 131-160
- Diaz M.V. do Souto M., Cohen S., Macchi G.J. 2022. RNA/DNA and derived condition indices for anchovy and hake larvae as relevant information for comprehensive fisheries management. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). Iberoamerican Fisheries and Fish Reproductive Ecology. Sci. Mar. 86:e 049. <https://doi.org/10.3989/scimar.05288.049>
- Divino J.N., Tonn W.M. 2008. Importance of Nest and Paternal Characteristics for Hatching Success in Fathead Minnow. Copeia 2008: 920-930. <https://doi.org/10.1643/CE-06-245>
- Domínguez-Petit R., García-Fernández C., Leonarduzzi E., Rodrigues K., Macchi G.J. 2022a. Parental effects and reproductive potential of fish and marine invertebrates: Cross-generational impact of environmental experiences. In: Domínguez-Petit R. (ed). Impact of Environmental Stress on Reproductive Processes of Aquatic Animals. Fishes. 7: 188. <https://doi.org/10.3390/fishes7040188>
- Domínguez-Petit R., Navarro M.R., Cousido-Rocha M., et al. 2022b. Spatial variability of life-history parameters of the Atlantic chub mackerel (*Scomber colias*), an expanding species in the northeast Atlantic. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). Iberoamerican Fisheries and Fish Reproductive Ecology. Sci. Mar. 86: e048. <https://doi.org/10.3989/scimar.05296.048>
- FAO. 2003. The ecosystem approach to fisheries. FAO Technical Guidelines for Responsible Fisheries. 4(2). Rome, FAO. 112 pp.
- FAO. 2022. The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation. Rome, FAO. <https://doi.org/10.4060/cc0461en>
- Gall G.A.E. 1974. Influence of size of eggs and age of female on hatchability and growth in rainbow trout. California Fish and Game Journal, 60, 26-35.
- García S., Cochrane K.L. 2005. Ecosystem approach to fisheries: a review of implementation guidelines. ICES J. Mar. Sci. 62: 311-318. <https://doi.org/10.1016/j.jicesjms.2004.12.003>
- Gonzalez-Carrion F., Saborido-Rey F. 2022. Influence of maternal effects and temperature on fecundity of *Sebastes fasciatus* on the Flemish Cap. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). Iberoamerican Fisheries and Fish Reproductive Ecology. Sci. Mar. 86: e050. <https://doi.org/10.3989/scimar.05305.050>
- Green B.S. 2008. Chapter 1 Maternal Effects in Fish Populations. Advances in Marine Biology. Academic Press. 1-105. [https://doi.org/10.1016/S0065-2881\(08\)00001-1](https://doi.org/10.1016/S0065-2881(08)00001-1)
- Green B.S., McCormick M.I. 2005. Maternal and paternal effects determine size, growth and performance in larvae of a tropical reef fish. Mar. Ecol. Prog. Ser. 289: 263-272. <https://doi.org/10.3354/meps289263>
- Hilborn R., Walters C.J. 1992. Quantitative fisheries stock assessment. Choice, Dynamics and Uncertainty. Chapman and Hall. <https://doi.org/10.1007/978-1-4615-3598-0>
- Hunter J. 1981. Feeding Ecology and Predation of Marine Fish Larvae. In R. Lasker (ed), Marine fish larvae: morphology ecology and relation to fisheries. Washington Sea Grant Program, Seattle. 33-77.
- IBAMA. 2009. Estatística da pesca 2007 Brasil: grandes regiões e unidades da federação. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Brasília. 175 pp. <http://www.IBAMA.gov.br/sophia/cnia/livros/estatisticadepescadigital.pdf>
- INEGI. 2021. Pesca y acuicultura: Censos Económicos 2019. Instituto Nacional de Estadística y Geografía. Gobierno de México. vii+58 pp. https://www.INEGI.org.mx/contenidos/productos/prod_serv/contenidos/espanol/bvINEGI/productos/nueva_estruc/702825198978.pdf
- Kjesbu O.S., Krivit H., Sundby S., Solemdal, P. 1992. Buoyancy variations in eggs of cod in relation to chorion thickness and egg size theory and observations. J. Fish Biol. 41: 581-599. <https://doi.org/10.1111/j.1095-8649.1992.tb02685.x>
- Kjesbu O.S., Witthames P.R., Solemdal P., Walker M.G. 1990. Ovulatory Rhythm and a Method to Determine the Stage of Spawning in Atlantic Cod (*Gadus morhua*). Can. J. Fish. Aquatic Sci. 47: 1185-1193. <https://doi.org/10.1139/f90-138>
- Lambert T.C. 1990. The effect of population structure on recruitment in herring. ICES J. Mar. Sci. 47: 249-255. <https://doi.org/10.1093/icesjms/47.2.249>
- Leggett W.C., Deblois E. 1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. 32: 119-134. [https://doi.org/10.1016/0077-7579\(94\)90036-1](https://doi.org/10.1016/0077-7579(94)90036-1)
- Lojo D., Cousido-Rocha M., Cerviño S., et al. 2022. Assessing changes in size at maturity for the European hake (*Merluccius merluccius*) in Atlantic Iberian waters. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). Iberoamerican Fisheries and Fish Reproductive Ecology. Sci. Mar. 86: e046. <https://doi.org/10.3989/scimar.05287.046>
- Lopez-Galindo L., Galindo-Sánchez, C., Olivares A., et al. 2019. Reproductive performance of *Octopus maya* males conditioned by thermal stress. Ecol. Ind. 96: 437-447. <https://doi.org/10.1016/j.ecolind.2018.09.036>
- Lowerre-Barbieri, Susan K. 2009. Reproduction in Relation to Conservation and Exploitation of Marine Fishes. In: Barrie G M Jamieson (ed). Reproductive Biology and Phylogeny of Fishes. 371-94. CRC Press. <https://doi.org/10.1201/b10257-11>
- Lowerre-Barbieri S. K., DeCelles G., Pepin P., et al. 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish Fish. 18: 285-312. <https://doi.org/10.1111/faf.12180>
- Macal-López K.C., Brulé T., Torres-Villegas J.R., et al. 2022. Reproduction of grey snapper (Teleostei: Lutjanidae) in the southern Gulf of Mexico. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). Iberoamerican Fisheries and Fish Reproductive Ecology. Sci. Mar. 86: e047. <https://doi.org/10.3989/scimar.05293.047>
- Macchi G.J., Pajaro M., Ehrlich M. 2004. Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). Fish. Res. 67: 25-38. <https://doi.org/10.1016/j.fishres.2003.08.006>
- Macchi G.J., Pajaro M., Madirolas A. 2005. Can a change in the spawning pattern of Argentine hake (*Merluccius hubbsi*) affect its recruitment? Fish. Bull. 103: 445-452
- Macchi G. J., Rodrigues K., Leonarduzzi E., Diaz M.V. 2018. Is the spawning frequency of Argentine hake, *Merluccius hubbsi*, affected by maternal attributes or physical variables? Fish. Res. 204: 147-155. <https://doi.org/10.1016/j.fishres.2018.02.011>
- Marshall C.T. 2016. Implementing Information on Stock Reproductive Potential in Fisheries Management: The Motivation, Challenges and Opportunities. In: Jakobsen T., Fogarty M.J., Megrey B.A. Moksness E. (eds). Fish Reproductive Biology: Implications for Assessment and Management. Chichester: John Wiley & Sons. 438-464. <https://doi.org/10.1002/9781118752739.ch11>
- Marteinsdottir G., Steinarsson A. 1998. Maternal influence on the size and viability of Icelandic cod *Gadus morhua* eggs and larvae. J. Fish Biol. 52: 1241-1258. <https://doi.org/10.1111/j.1095-8649.1998.tb00969.x>
- Marteinsdottir G., Thorarinnsson K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. Can. J. Fish. Aquatic Sci. 55: 1372-1377. <https://doi.org/10.1139/f98-035>
- McCormick M.I. 2006. Mothers matter: Crowding leads to stressed mothers and smaller offspring in marine fish. Ecol. 87: 1104-1109. [https://doi.org/10.1890/0012-9658\(2006\)87\[1104:MMCLTS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1104:MMCLTS]2.0.CO;2)
- Moreno P., Claramunt G. 2022. Expansion and contraction of the *Engraulis ringens* spawning area in northern Chile. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). Iberoamerican Fisheries and Fish Reproductive Ecology. Sci. Mar. 86: e045. <https://doi.org/10.3989/scimar.05284.045>
- Nissling A., Larsson R., Vallin L., Frohland K. 1998. Assessment of egg and larval viability in cod, *Gadus morhua*: Methods and results from an experimental study. Fish. Res. 38: 169-186. [https://doi.org/10.1016/S0165-7836\(98\)00121-0](https://doi.org/10.1016/S0165-7836(98)00121-0)
- Oliveira Leis M.D., Barragan-Paladines M.J., Saldaña A., et al. 2019. Overview of small-scale fisheries in Latin America and the Caribbean: challenges and prospects. In: Salas S., Barragan-Paladines M.J. and Chuenpagdee R. (eds). Viability and sustainability of

- small-scale fisheries in Latin America and the Caribbean. MARE publication Series. Vol. 19. Springer, Cham. 15-47. https://doi.org/10.1007/978-3-319-76078-0_2
- Olsen E.M., Heino M., Lilly G. R., et al. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428: 932-935. <https://doi.org/10.1038/nature02430>
- Paramo J., Grijalba-Bendeck M., Pérez D., et al. 2020. Conservation strategies for potential new deep-sea crustacean fisheries in the Colombian Caribbean under an ecosystem approach. In: Hendrickx M. (ed). *Deep-Sea Pycnogonids and crustaceans of the Americas*. Cham, Switzerland: Springer. pp. 421-441. https://doi.org/10.1007/978-3-030-58410-8_18
- Pascual-Fernández J.J., Florido-del-Corral D., Cruz-Modino R.D., Villasante S. 2020. Small-scale fisheries in Spain: diversity and challenges. In: *Small-Scale Fisheries in Europe: Status, Resilience and Governance*. Springer, Cham. 253-281. https://doi.org/10.1007/978-3-030-37371-9_13
- Pauly D., Liang C. 2022. A reconceptualization of the interactions between spawning and growth in bony fish. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). *Iberoamerican Fisheries and Fish Reproductive Ecology*. *Sci. Mar.* 86: e044. <https://doi.org/10.3989/scimar.05280.044>
- Pauly D., Zeller D. 2015. Sea Around Us concepts, design and data. www.seaaroundus.org. Accessed 20 October 2022.
- Petitgas P., Reid D., Planque B., et al. 2006. The entrainment hypothesis: an explanation for the persistence and innovation in spawning migrations and life cycle spatial patterns. *ICES Scientific Report*. ICES CM 2006/B:07. <https://www.ices.dk/sites/pub/CM%20Documents/2006/B/B0706.pdf>
- PRODUCE. 2021. Anuario Estadístico Pesquero y Acuicola 2020. Ministerio de la Producción. Gobierno del Perú. 182 pp.
- Puerto M.A., Saber S., Ortiz de Urbina J., et al. 2022. Spawning area of the tropical Skipjack Tuna, *Katsuwonus pelamis* (Scombridae), in the western Mediterranean Sea. In: Bahamon N., Domínguez-Petit R., Páramo J.E., Saborido-Rey F., Acero-Pizarro A. (eds). *Iberoamerican Fisheries and Fish Reproductive Ecology*. *Sci. Mar.* 86: e051. <https://doi.org/10.3989/scimar.05292.051>
- Rideout R. M., Trippel E., Litvak, M. 2004. Relationship between sperm density, spermatocrit, sperm motility and spawning date in wild and cultured haddock. *J. Fish Biol.* 65: 319-332. <https://doi.org/10.1111/j.0022-1112.2004.00451.x>
- Rochet M.J. 1998. Short-term effects of fishing on life history traits of fishes. *ICES J. Mar. Sci.* 55: 371-391. <https://doi.org/10.1006/jmsc.1997.0324>
- Rivero-Rodríguez S., González-Fernández M. 2021. Ecología Reproductiva y Pesquerías en el Contexto Iberoamericano. Red Iberoamericana de Investigación para el Uso Sostenible de los Recursos Pesqueros (RED INVIPESCA). Digital CSIC. Vigo. ISBN: 978-84-09-36793-1. <http://hdl.handle.net/10261/255913.175-215>
- Saborido-Rey, F. 2016. Fish Reproduction. Reference Module in Earth Systems and Environmental Sciences. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-409548-9.09708-6>
- Seeliger U., Kjerfve B. 2013. Coastal marine ecosystems of Latin America. Vol. 144. Springer Science & Business Media. ISBN: 978-3-662-04482-7
- SERNAPESCA. 2021. Anuarios Estadísticos de Pesca y Acuicultura. Ministerio de Economía, Fomento y Turismo. Gobierno de Chile. <http://www.SERNAPESCA.cl/informacion-utilidad/anuarios-estadisticos-de-pesca-y-acuicultura>
- SGP. 2021. La Flota Española: Situación a 31 de diciembre de 2021. Secretaría General de Pesca. Ministerio de Agricultura, Pesca y Alimentación. Gobierno de España. https://www.mapa.gob.es/es/pesca/temas/registro-flota/catalogo-flota-2021_22-2-22_tcm30-609098.pdf
- Shama L. N. S., Strobel A., Mark F. C., Wegner K. M. 2014. Transgenerational plasticity in marine sticklebacks: Maternal effects mediate impacts of a warming ocean. *Funct. Ecol.* 28: 1482-1493. <https://doi.org/10.1111/1365-2435.12280>
- Shaw S.L., Sass G.G., VanDeHey J.A. 2018. Maternal effects better predict walleye recruitment in Escanaba Lake, Wisconsin, 1957-2015: Implications for regulations. *Can. J. Fish. Aquatic Sci.* 75: 2320-2331. <https://doi.org/10.1139/cjfas-2017-0318>
- Shin Y.J., Rochet M.J., Jennings S., et al. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62: 384-396. <https://doi.org/10.1016/j.icesjms.2005.01.004>
- SISRGP. 2021. Painel de Embarcações de Pesca Registradas no Sistema Informatizado do Registro Geral da Atividade Pesqueira. Secretaria de Aquicultura e Pesca. Ministério da Agricultura, Pecuária e Abastecimento. <https://www.gov.br/agricultura/pt-br/assuntos/aquicultura-e-pesca/cadastro-registro-e-monitoramento/registro-de-embarcacoes/embarcacoes-de-pesca-registradas>
- SPM. 2019. Informes de Cadena de Valor. Pesca. 2019. Subsecretaría de Programación Microeconómica. Secretaría de Política Económica. Ministerio de Hacienda. Gobierno de Argentina. ISSN: 2525-0221
- Stein L. R., Bell A. M. 2014. Paternal programming in sticklebacks. *Anim. Behav.* 95: 165-171. <https://doi.org/10.1016/j.anbehav.2014.07.010>
- Stearns S.C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8: 145-171. <https://doi.org/10.1146/annurev.es.08.110177.001045>
- Stearns S.C. 1992. *The Evolution of Life Histories*. Oxford University Press.
- Thomas P., Rahman M. S., Picha M. E., Tan W. 2015. Impaired gamete production and viability in Atlantic croaker collected throughout the 20,000 km² hypoxic region in the northern Gulf of Mexico. *Mar. Poll. Bull.* 101: 182-192. <https://doi.org/10.1016/j.marpolbul.2015.11.001>
- Tomkiewicz J., Morgan M. J., Burnett J. and Saborido-Rey F. 2003. Available information for estimating reproductive potential of Northwest Atlantic groundfish stocks. *J. Northwest Atl. Fish Sci.* 33: 1-21. <https://doi.org/10.2960/J.v33.a1>
- Trippel E.A. 1999. Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *J. Northw. Atl. Fish. Sci.* 25: 61-81. <https://doi.org/10.2960/J.v25.a6>
- Trippel E.A., Kraus G., Köster, F. 2005. Maternal and paternal influences on early life history traits and processes of Baltic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 303: 259-267. <https://doi.org/10.3354/meps303259>
- UN. 2015. A/RES/70/1. Transforming our world: the 2030 Agenda for Sustainable Development. Resolution adopted by the General Assembly of the United Nations on 25 September 2015. https://www.un.org/en/development/desa/population/migration/general-assembly/docs/globalcompact/A_RES_70_1_E.pdf
- UN. 2017. Resolution XXIX-1. International (UN) Decade of Ocean Science for Sustainable Development. Resolution adopted by the IOC Assembly on 29 June 2017. https://en.unesco.org/sites/default/files/ioc_resolution_xxix-1_e.pdf
- UN. 2018. A/RES/72/72. Sustainable fisheries, including through the 1995 Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, and related instruments. Resolution adopted by the General Assembly of the United Nations on 5 December 2017. <https://documents-dds-ny.un.org/doc/UNDOC/GEN/N17/421/83/PDF/N1742183.pdf?OpenElement>
- von Siebenthal B. A., Jacob A., Wedekind C. 2009. Tolerance of whitefish embryos to *Pseudomonas fluorescens* linked to genetic and maternal effects, and reduced by previous exposure. *Fish Shellfish. Immunol.* 26: 531-535. <https://doi.org/10.1016/j.fsi.2009.02.008>
- Worm B., Barbier E.B., Beaumont N., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787-790. <https://doi.org/10.1126/science.1132294>

Rosario Domínguez-Petit, Jorge Enrique Paramo, Fran Saborido-Rey,
Arturo Acero P. and Nixon Bahamon

A reconceptualization of the interactions between spawning and growth in bony fish

Daniel Pauly¹, Cui Liang^{2,3}

¹ *Sea Around Us*, Institute for the Ocean and Fisheries, University of British Columbia, Vancouver, Canada, V6T 2K9.
(DP) (Corresponding author) E-mail: d.pauly@oceans.ubc.ca. ORCID iD: <https://orcid.org/0000-0003-3756-4793>

² CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, P. R. China.

³ Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266237, P. R. China.
(CL) E-mail: liangc@qdio.ac.cn. ORCID iD: <https://orcid.org/0000-0001-6099-4965>

Summary: Among fishery biologists and even ichthyologists, maturation and spawning of fish are viewed as processes that use “energy” that would otherwise be applied to somatic growth, which is supposed to explain why post-maturity growth *in length* tends to decline. This widespread conceptualization may be called the “reproductive drain hypothesis” (RDH). However, when growth is correctly viewed as involving body mass, and is thus expressed *in weight*, post-maturity turns out (in iteroparous bony fish whose maximum length exceeds 10 cm) to accelerate after first maturity, despite its energy cost. This, and other common observations flatly contradict the RDH, and the time has come to withdraw this hypothesis. As a contribution towards this task, we propose an alternative reconceptualization of fish spawning consistent with what is known about fish biology.

Keywords: Von Bertalanffy, reproductive drain, maturation, gill-oxygen limitation theory (GOLT).

Reconceptualización de la interacción entre desove y crecimiento en peces óseos

Resumen: Los biólogos pesqueros e incluso los ictiólogos tienden a ver la maduración y el desove de los peces como procesos que usan “energía” que, de otro modo, sería aplicada al crecimiento somático, lo cual se supone que explica por qué el crecimiento post-maduración, en lo que se refiere a *longitud*, tiende a declinar. Esta popular conceptualización puede ser denominada “Hipótesis del Drenaje Reproductivo” (RDH). Sin embargo, cuando el crecimiento es visto de manera correcta como un proceso que involucra el volumen o masa corporal y, por lo tanto, se expresa *en peso*, la post-maduración (en peces óseos iteróparos cuya longitud máxima supera los 10 cm) se acelera luego de la primera maduración, a pesar de su costo energético. Esta, y otras observaciones comunes, contradicen la RDH y, por lo tanto, ha llegado el momento de jubilar esta hipótesis. Para contribuir con esta tarea, se propone una reconceptualización alternativa del desove en peces, la cual es consistente con el conocimiento existente sobre la biología de los peces.

Palabras clave: Von Bertalanffy, drenaje reproductivo, maduración, Teoría de la Limitación del Oxígeno Branquial (GOLT)

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INTRODUCTION

Fish spawning is a process that fisheries scientists and ichthyologists are familiar with, so much so that for several decades they have failed to re-examine whether their view of this process is compatible with all the specifics we also know about spawning.

Figure 1 illustrates the conventional conceptualization of fish spawning, in which it is perceived as a costly process wherein “energy” is transferred from somatic to gonad growth, thus abruptly impacting on somatic growth (which is strangely and erroneously viewed as a linear process). Thus, depending on the extent of the “energy” transfer, somatic growth is slowed down or even stopped. However, it is generally not appreciated that this conceptualization, of which multiple variants exist (see, e.g., Hubbs 1926, Charnov 2008, Quince et al. 2008), is only a hypothesis which, like all scientific statements about the world, is subject to being rejected if it is incompatible with well-established facts.

The first and perhaps most important reason for the survival of this conceptualization—here called the “reproductive drain hypothesis” (RDH)—is that its outward plausibility rests on the representation of growth as proceeding in length, which it does not, as “energy” certainly does not have the dimension of length. Once somatic growth is—correctly—viewed in terms of mass or weight (Fig. 2), the RDH is refuted. As soon as (iteroparous) fish can reach a maximum weight exceeding a few grams, they tend to reach first maturity at sizes below that at which they experience their highest growth rate.

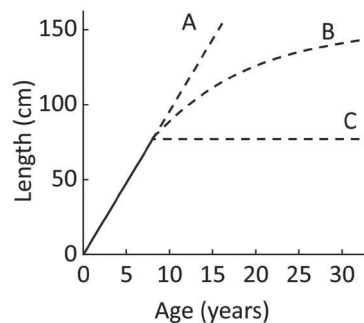


Fig. 1. – Representation of the “reproductive drain hypothesis”, i.e. the notion that reaching the size at first maturity relationship causes previously “linear” growth (line A) to decline due to “energy” previously used for somatic growth being transferred to the elaboration of gonads, with line B implying a small and line C a large transfer of “energy” (modified from Figure 2 in Lester et al. 2004).

Thus, the transition from “energy” transferred from somatic growth to the elaboration of gonads is a case of the post hoc, ergo propter hoc fallacy that considers that an event (1) is the cause of an event (2) simply because event (1) occurred before event (2).

Earlier authors, notably Iles (1974), have also noted that the usual narrative does not make sense. Thus, he wrote, with regard to the age and size at first maturity of fish that “[d]espite the fact that at some time during this stage of the life history large quantities of protein, ultimately derived from the same food sources that sustain body growth, will be newly required for gonad development, there is no indication that the growth pattern is disrupted or disturbed. Indeed, under ‘normal’ con-

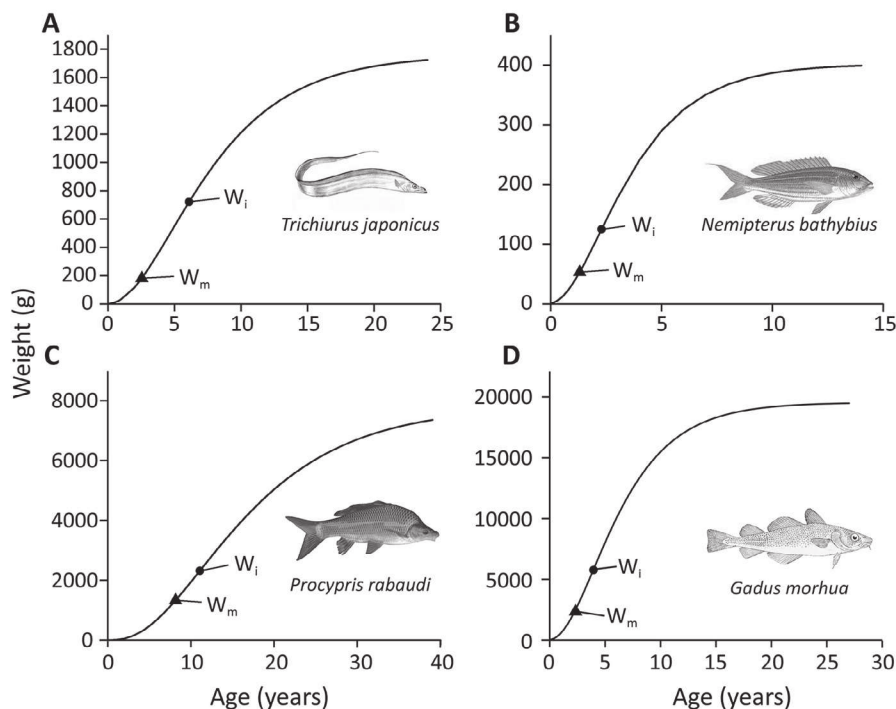


Fig. 2. – Illustrating the fact that, when growth in weight is considered, in fish reaching more than about 10 cm maximum length, the weight at first maturity (W_m) is reached at a size at which growth is accelerating, i.e. well below the weight at which maximum growth rate is attained (at W_i); A, largehead hairtail (*Trichiurus japonicus*), based on data in Shi et al. (2020); B, yellowbelly threadfin bream (*Nemipterus bathybius*), based on data in Li et al. (2009); C, rock carp *Procypris rabaudi*, based on data in Wang et al. (2015); D, Atlantic cod (*Gadus morhua*), based on data in Le Franc (1970).

ditions it appears that it is singularly unaffected by the new physiological and metabolic demands which the fish is called upon to meet. The fact that, for most species of fish, unlike those of mammals and birds, growth continues after the attainment of the adult stage is one of the most characteristic features of the growth of fishes”.

However, the “programme” that he then proposed as an alternative did not explain how fish manage to spawn at the “right” size, i.e. at the size that is a predictable fraction of the maximum size they can reach in a given environment. (Pauly 2019).

In the following, we present a reconceptualization of spawning based on Pauly (2019, 2021a, 2019b) and evidence presented on Chen et al. (2022) and other authors. However, before this can be presented, a brief review of fish growth and related matters is necessary.

MATERIALS AND METHODS

Since Pütter (1920), the growth rate (dW/dt) in fish and other animals is often conceived as a differential equation

$$dW/dt = HW^d - kW \quad (1)$$

where W is the weight (i.e. mass), H is the rate of synthesis of body, $0 < d < 1$ is the exponent of a relationship of the form $S = \alpha \cdot W^d$ which limits protein synthesis, and k is the rate of protein denaturation, or, more precisely, the rate by which denaturation exceeds the refolding of spontaneously unfolding protein.

When $d=2/3$, corresponding to $S=\alpha \cdot L^2$ and $W=a \cdot L^3$, the integration of Equation 1 into a growth curve is the von Bertalanffy Growth Function (VBGF), which for growth in length has the form

$$L_t = L_\infty \cdot (1 - e^{-K \cdot (t-t_0)}) \quad (2)$$

where L_t is the mean length at age t of the animals in question, L_∞ is their asymptotic size, i.e. the mean size attained after an infinitely long time, K is a growth coefficient (here in year⁻¹; with $k=3K$) and t_0 is a parameter adjusting for the fact that the VBGF usually fails to describe the growth of the earliest (larval) stages of fish (see also Table 1).

For growth in weight, this becomes

$$W_t = W_\infty \cdot (1 - e^{-K(t-t_0)})^3 \quad (3)$$

Table 1. – Definitions of the parameters (and their units), symbols and acronyms used in this contribution.

Item (unit)	Definition
α	Proportional to...
α	Multiplicative term in relationship linking gill surface and weight, i.e. $S = \alpha \cdot W^d$
a	Multiplicative term of a length-weight relationship, i.e. $W = a \cdot L^b$
A	Threshold value of $L_{\max}^D / L_m^D \sim 1.35$, corresponding to $Q_m / Q_{\text{maint}} \sim 1.35$
b	Exponent of a length-weight relationship, i.e. $W = a \cdot L^b$
d	Exponent in a relationship linking respiratory surface and weight, i.e. $S = \alpha \cdot W^d$
D	$D = b(1-d)$, used to simplify some equations; note also $D' = 3(1-d)$
dW/dt	Growth rate
H	Coefficient of anabolism, i.e. of protein synthesis
k	Coefficient of catabolism; here: of protein denaturation. Note: $k = 3K$
K (year ⁻¹)	In the VBGF, the rate at which asymptotic size is approached
L (cm)	Any measure of length, with L_t the length at age t
L_∞ (cm)	Asymptotic length in the VBGF, as reached after an infinitely long time
L_m (cm)	Mean length at first maturity in a given population
L_m / L_∞	Reproductive load, usually close to L_m / L_{\max}
L_m / L_{\max}	Reproductive load, usually close to L_m / L_∞
L_{\max} (cm)	Maximum length in a given population; generally close to L_∞
LWR	Length-weight relationship, of the form $W = a \cdot L^b$
Q_m	Weight-specific oxygen consumption at first maturity
Q_{maint}	Weight-specific oxygen consumption at maximum or asymptotic weight
RDH	Reproductive drain hypothesis
RL	Reproductive load, i.e. L_m / L_{\max} or L_m / L_∞
S (cm ²)	A surface; here respiratory surface, i.e. gill surface area, as in $S = \alpha \cdot W^d$
t (year)	Absolute age; relative age = $t - t_0$
t_0 (year)	The usually negative “age” at $L = 0$ predicted by the VBGF
W (g)	Weight (or mass); W_t is weight at age; here fresh, or wet weight
W_∞ (g)	Asymptotic weight in the VBGF, as reached after an infinitely long time
W_i (g)	Inflexion point of a growth curve in weight, i.e. weight at which dw/dt is highest
W_m	Mean weight at first maturity; weight corresponding to L_m

where W_{∞} is the weight corresponding to L_{∞} , all other parameters are defined as above and the exponent ($b=3$) at the right is justified by the fact that it is the most common exponent of the length-weight relationship (LWR) in fish (Froese 2006, Hay et al. 2020, see also FishBase: www.fishbase.org).

Equation (2) has no inflexion point (dL/dt declines linearly with length), but Equation (3) has an inflexion point (W_i , where dW/dt is at a maximum) at $W_i = 0.296 \cdot W_{\infty}$.

Pauly (2019, 2021a) interpreted Pütter's equation in terms of the oxygen required for synthesis of native protein (the first term on the right side of Equation 1) and to replace denatured proteins (the second term on the right side of Equation 1). In this interpretation, d refers to the respiratory surface area of the gills or similar organs, i.e. 2-D structures whose growth cannot keep up with that of a 3-D body requiring oxygen. Hence, $d < 1$ and generally ranges between 0.55 and 0.95 in fish and other metazoans that breathe water (De Jager and Dekker 1974, Pauly 1981).

When $d \neq \frac{2}{3}$, the VBGF is “generalized” and becomes

$$L_t = L_{\infty} \cdot (1 - e^{-K \cdot D(t-t_0)})^{1/D} \quad (4)$$

for length, and

$$W_t = W_{\infty} \cdot (1 - e^{-K \cdot D(t-t_0)})^{b/D} \quad (5)$$

for weight, where $D = b(1 - d)$ and where b is the exponent of an LWR of the form $W = a \cdot L^b$, with b generally 3, or near 3 (see above).

Equation 4 has an inflection point when $D \neq 1$ at age $t_i = t_0 - (\ln(D)/K \cdot D)$ and length $L_i = L_{\infty} \cdot (1 - e^{-(\ln(D))^{1/D}})$, while Equation (5) has an inflection point at age $t_i = t_0 - (\ln(D/b)/K \cdot D)$ and weight $W_i = W_{\infty} \cdot (1 - (D/b))^{b/D}$, which implies

$$W_i / W_{\infty} = (1 - (D/b))^{b/D} \quad (6)$$

In practice, the difference between the standard VBGF (Equations 2 and 3) and the generalized VBGF can be neglected when fitting a set of age-at-length, tagging-recapture, or length-frequency data with a growth curve, especially in fishes where the growth of gill surface area does not differ much from the $\frac{2}{3}$ value assumed in the standard VBGF (i.e. up to $d \approx 0.85$). This is the case for small fishes, e.g. coral fishes and small pelagic fishes, such as herrings, sardines and anchovies, where $d \approx 0.75$, and medium-sized species, e.g. carp or cod, where $d \approx 0.80$ (De Jager and Dekker 1974; see also Fig. 3). Only with higher value does the fit of the standard VBGF became problematic, e.g. in the case of Atlantic bluefin tuna (*Thunnus thynnus*), where $d = 0.90$ (Muir and Hughes 1969), notably because the estimates of asymptotic length (L_{∞}) that are generated by fitting the equation to reliable age-at-length data tend to be much larger than the maximum length (L_{\max}) in a given population, which is not the case when the special VBGF is used (Pauly 2021a). As the overwhelming majority of applications of the VBGF are to species in which d is relatively close to

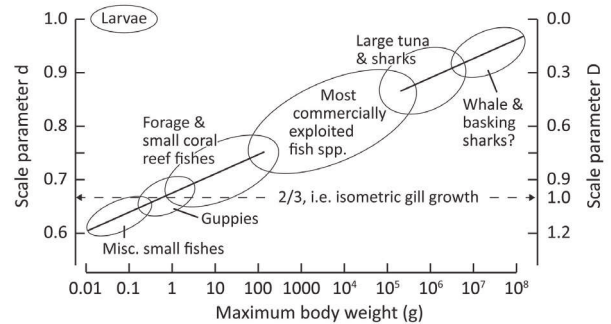


Fig. 3. – Showing that in fish, the parameter d and D are related to the maximum weight reached by various taxa (modified from Figure 2 in Pauly 1981); the straight line is based on the relations $d = 0.674 + 0.0357(\log(W_{\max}))$, with live weight in g.

$\frac{2}{3}$ (see FishBase: www.fishbase.org), the fact that the standard VBGF differs slightly from a physiologically correct equation is usually ignored. This is also what was done here.

It is well-established that the mean length at first maturity (L_m) of the individual in a given population of iteroparous fish is a predictable ratio of the asymptotic length (L_{∞}) or maximum length (L_{\max}) and generally ranges from 0.4 to 0.6 in fish that reach larger sizes and from 0.6 to 0.8 in fish that remain small (Beverton and Holt 1959, Pauly 2021a). Thus, this ratio does not deserve the name “Beverton and Holt invariant” that Charnov (2008) gave it. Rather, we use here the term “reproductive load” for the L_m/L_{∞} (or the similar L_m/L_{\max}) ratio as used by Cushing (1981), which resonates with the RDH mentioned above.

That reproductive loads are not invariant, but vary systematically among fishes of widely different sizes was demonstrated by Froese and Binohlan (2000) who, based on data from 265 fish species from 88 Families and 27 Orders in FishBase (www.fishbase.org), derived the relationships:

$$\log(L_m) = 0.898 \cdot \log(L_{\infty}) - 0.0782 \quad (7)$$

where L_m and L_{∞} are in cm.

This model expresses that fish with $L_{\infty} \approx 10$ cm will have L_m values of 6 to 7 cm, while fish of $L_{\infty} \approx 100$ and 1000 cm will have L_m values near 50 and 400 cm, respectively.

In the following, we present corroborations of the gill-oxygen limitation theory (GOLT; Pauly 2019, 2021a) that result from following up on these considerations.

RESULTS

Because their gill surface area, with $d < 1$, which supplies oxygen to their growing bodies, cannot keep up with their weight, and hence with their oxygen demand, relative oxygen supply declines with body weight. This decline of relative oxygen supply has its limit when $HW^d - kW = 0$, i.e. when the oxygen supply meets only the requirements for maintenance (Q_{maint}), with nothing left for further somatic growth. Pauly

(2019) and Pauly and Liang (2022) elaborate on the seasonal trade-off allowing the elaboration and release of reproductive products under these conditions.

It is evident that gonads, which require oxygen for their synthesis, will have to be elaborated when fish are smaller than L_{\max} and hence their relative oxygen supply higher, i.e. $Q_m > Q_{\text{maint}}$, where Q_m is the relative oxygen supply at first maturity. Also, it can be shown that, given LWR of the form $W = a \cdot L^b$ and gill surface area-body weight relationship of the form $S = \alpha \cdot W^d$, the ratio L_{\max}^D / L_m^D is equivalent to the ratio Q_m / Q_{maint} (Pauly 1984).

Numerous studies covering hundreds of species suggest that in growing iteroparous bony fishes maturation and spawning is initiated when a threshold ratio $L_{\max}^D / L_m^D \sim 1.35$ is reached, as was first demonstrated for 56 populations of marine fish in 34 species by Pauly (1984) and confirmed for 51 populations in 3 freshwater salmonid species by Meyer and Schill (2021), for 41 populations in 7 species of cichlids by Amarasinghe and Pauly (2021) and for 241 populations in 132 freshwater and marine species by Chen et al. (2022). This established that the threshold ratio $L_{\max}^D / L_m^D \sim 1.35$ acts as a heuristic (*sensu* Budaev *et al.* 2019) which individual fish can rely on (Pauly 2021b) and which is compatible with life-history theory (Morbey and Pauly 2022). We shall use the label $A = L_{\max}^D / L_m^D \sim 1.35$ because it signifies a beginning (in German *Anfang*—the letters of the English alphabet are exhausted).

Given its definition and LWRs, $A = (W_{\max}^{1/b} / W_m^{1/b})^D$ and its inverse A^{-1} is:

$$A^{-1} = (W_m^{1/b} / W_{\infty}^{1/b})^D \quad (8)$$

Thus, $A^{-1} = (W_m / W_{\infty})^{D/b}$ or

$$W_m = W_{\infty} (1/A)^{b/D} \quad (9)$$

By combining equation (6) and (9), we obtain

$$W_i / W_m = (1 - (D/b))^{b/D} / A^{-b/D} \quad (10)$$

When $W_i > W_m$, we also have:

$$(1 - (D/b))^{b/D} > A^{-b/D} \quad (11)$$

which implies $(1 - (D/b)) > A^{-1}$. Now, given the definition of $D = b \cdot (1 - d)$, we have

$$d > A^{-1} \text{ implies } W_i > W_m \quad (12a)$$

$$d \approx A^{-1} \text{ implies } W_i \approx W_m \quad (12b)$$

$$d < A^{-1} \text{ implies } W_i < W_m \quad (12c)$$

Thus, while for $d < 1/1.35$ (i.e. 0.74, generally occurring in small, short-lived and often semelparous fishes; see Fig. 3) spawning occurs after their growth rate (dW/dt) has started to decline, this is not the case in larger iteroparous, longer-lived fish in which $d > 0.75$. This explains why, e.g., the maturity of cod and similarly large species occurs well before these fish have spawned (Fig. 2), thus refuting the RDH.

As, an alternative, we propose a new framework for understanding the concept of a “spawning season”. For

simplicity’s sake, we shall here assume one spawning season per year, occurring in the spring (Pauly and Liang 2022), as the extension of the conceptualization presented would here would require further elaboration to account for autumn spawning in temperate fish (Warlen and Burke 1990) or monsoonal spawning in fishes of the Indo-Pacific (Longhurst and Pauly 1987).

This new framework should explain the processes taking place such that various aspects of fish spawning, which had remained unexplained or been treated as anomalies, can be straightforwardly accounted for, i.e. without ad hoc hypotheses. This requires a second heuristic, the “cusp catastrophe”.

The cusp catastrophe, or “cusp”, is one of the seven topological entities which, as shown by Thom (1975), are sufficient to describe *qualitatively* the transitions among a maximum of four “control factors”, and to distinguish areas where the transitions would be smooth from areas where they would be sudden (thus the term “catastrophe”, the cause of many misunderstanding). With its two control factors, the cusp can easily be used to represent sudden transitions between, e.g., two biologically relevant variables (Woodcock and Davis 1980). Our use of the cusp is illustrated by the example of a growth curve in Figure 4, whose insert represents a cusp and the two control factors that adapt it to maturation and spawning events. Thus, our cusps have body size and time (here one year, given one spring spawning season per year) as control factors.

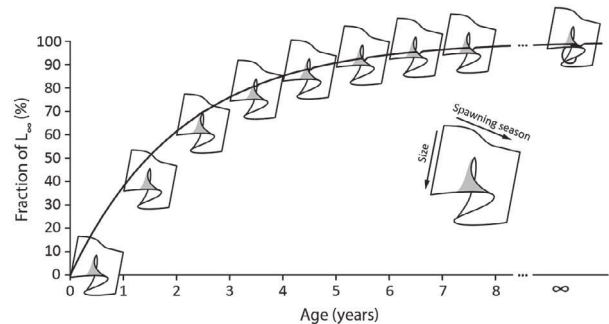


Fig. 4. – A representation of fish growth as a succession of cusps, with the young fish being too small to enter the region (shaded grey) where spawning occurs. This region is approached in pre-adults which may undergo an (abortive) maturation, but fail to spawn. In the year following, however, their size will be higher than that associated with $Q_m / Q_{\text{maint}} \sim 1.35$, and maturation and spawning can proceed. In the following years, size increases are associated with a spawning season that starts earlier and ends later, until maximum size is approached, when spawning often occurs repeatedly, and the body weight is reset at a lower value, which allows growth to be re-initiated.

Young fish (age 1 and 2 in Fig. 4) are too small for their A-ratio to have fallen to 1.35, so they entirely avoid the region of the cusp where maturation and spawning occurs. At 3 years, the largest fish of a cohort will mature and spawn, the smallest will not, and the fish of intermediate size may undergo an abortive maturation, i.e. elaborate production of gonads which, however, are resorbed and not shed (Iles 1974; review in Rideout et al. 2005).

This “skipped spawning”, performed “more often by young and small fish” and often when food is scarce

(Jørgensen et al. 2006), is therefore neatly explained without requiring elaborate models of trade-offs between reproductive output, growth and survival, which individual fish could not use as heuristic to “decide” whether to spawn or not.

Subsequent growth in year 4 and beyond pushes the fish deeper onto the shaded areas of the cusps in Figure 4, implying that the maturation of larger (older) fish should start earlier than that of smaller fish, and end later in the season, while smaller (younger) fish mature (and spawn) only during the peak of the season. This is confirmed by numerous authors, such as Rijnsdorp (1989) for plaice *Pleuronectes platessa* in the North Sea, and Trippel et al. (1997), who summarized their review by stating that “[t]he importance of female size to recruitment success is reinforced by the observation that large females commonly start spawning earlier in the season [...], continue for longer and produce larger eggs with higher viability than smaller females.”

The cusp often implies that once a phase transition has occurred, the system displays “hysteresis”, wherein the behaviour in question (in this case spawning) loops repeatedly at the highest age in Figure 4, above the ∞ symbol. As it happens, this is precisely the behaviour of large, old fish, which may spawn repeatedly during a spawning season, while small adults usually spawn only once, or even skip spawning. The interpretation of this behaviour is as follows: once a large fish has spawned, i.e., lost some of the tissues that it has to supply with oxygen, it has a higher gill area/body weight than before spawning, and hence it can in principle return to its usual activities, including feeding. This leads to increased body weight, and thus renewed lowering of the gill area/body weight ratio, which can (at least in large individuals) cause rapid re-maturation and repeated spawning (Trippel et al. 1997). This cycle can repeat itself within a spawning season until the temperatures drops and the respiratory stress declines, at which point the reproductive season ends.

DISCUSSION

The case made above was that a heuristic determines the overall readiness of fish to mature and spawn as a function of their metabolic rate (Q) relative to their maintenance metabolism (Q_{maint}). Specifically, in longer-lived iteroparous fish this heuristic readies them to perceive seasonal (i.e. within-year) environmental maturation and spawning stimuli only when the threshold A is reached (see Table 1 and the above equation for the definition and properties of A) and not earlier (Pauly 2021b).

Another heuristic, the cusp, then provides a graphic metaphor for spawning. Indeed, the cusp links three phenomena which to date had not been tied to a common explanatory framework (skipped spawning, size-dependent reproductive seasons and spawning hysteresis). Figure 4 thus represents an integrated view of the life of a long-lived fish as a succession of cusps, each “entered” at another size (corresponding to successive ages), thus implying a different set of responses by the individual fish.

Obviously, maturation and spawning are more complicated than is presented in this account. Notably, these processes involve the release of numerous hormones in response to environmental stimuli (Pankhurst 2016). However, as shown in Pauly (2021b), based on multiple long-lived fish species that fail to respond to such seasonal stimuli during many years (even decades) of pre-adulthood during which they could perceive these stimuli, the “hormonal cascade” leading to maturation and spawning is not self-starting. What is required for such maturation and spawning is an internal state that is related to the size of the fish (Fig. 4), i.e. to their relative oxygen supply.

Finally, the reconceptualization presented here implies that, rather than being, in analogy to humans, the life-threatening and often debilitating event that giving birth is, spawning in fish is a seasonally liberating event, which frees females from a quivering mass of eggs that must be supplied with scarce oxygen and thus enables them to grow again.

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REFERENCES

- Amarasinghe U.S., Pauly D. 2021. The relationship between size at maturity and maximum size in cichlid populations corroborates the Gill- Oxygen Limitation Theory (GOLT). *Asian Fish. Sci.* 34: 14-22.
<https://doi.org/10.33997/j.afs.2021.34.1.002>
- Beverton R.J.H., Holt S.J. 1959. A Review of the Lifespans and Mortality Rates of Fish in Nature, and Their Relation to Growth and Other Physiological Characteristics. In: Wolstenhome G.E.W., Maeve O’Conner B.A. (eds), *Ciba Foundation Symposium - The Lifespan of Animals (Colloquia on Ageing)*. John Wiley & Sons Ltd, pp. 142-180.
<https://doi.org/10.1002/9780470715253.ch10>
- Budaev S., Jørgensen C., Mangel M., et al. 2019. Decision-making from the animal perspective: bridging ecology and subjective cognition. *Front. Ecol. Evol.* 7: 164.
<https://doi.org/10.3389/fevo.2019.00164>
- Charnov E. 2008. Fish growth: Bertalanffy k is proportional to reproductive effort. *Environ. Biol. Fishes.* 83: 185-187.
<https://doi.org/10.1007/s10641-007-9315-5>
- Chen Z., Bigman J., Xian W., et al. 2022. The ratio of length at first maturity to maximum length in marine and freshwater fish. *J. Fish Biol.*
<https://doi.org/10.1111/jfb.14970>
- Cushing D.H. 1981. *Fisheries Biology: as Study in Population Dynamics*, 2nd edition. University of Wisconsin Press, Madison, 295 pp.
- De Jager S., Dekkers W.J. 1974. Relations Between Gill Structure and Activity in Fish. *Neth. J. Zool.* 25: 276-308.
<https://doi.org/10.1163/002829675X00290>
- Froese R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J. Appl. Ichthyol.* 22: 241-253.
<https://doi.org/10.1111/j.1439-0426.2006.00805.x>
- Froese R., Binohlan C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *J. Fish Biol.* 56: 758-773.
<https://doi.org/10.1111/j.1095-8649.2000.tb00870.x>
- Hay A., Xian W., BaillyN., Liang C. and Pauly D. 2020. The

- why and how of determining length-weight relationships of fish from preserved museum specimens. *J. Appl. Ichthyol.* 36: 373-379.
<https://doi.org/10.1111/jai.14014>
- Hubbs C.L. 1926. The structural consequence and modifications of the development rate in fishes, considered in reference to certain problems of evolution. *Am. Nat.* 60: 57-81.
<https://doi.org/10.1086/280071>
- Iles T.D. 1974. The tactics and strategy of growth in fishes. In: Harden Jones E.R. (ed), *Sea Fisheries Research*. Elek Science, London, pp. 331-345.
- Jørgensen C., Ernande B., Fiksen Ø., Dieckman U. 2006. The logic of skipped spawning in fish. *Can. J. Fish. Aquat. Sci.* 63: 200-211.
<https://doi.org/10.1139/f05-210>
- Le Franc G. 1970. Biologie de la morue du Sud de la mer du Nord et de la Manche Orientale. *Rev. Trav. Inst. Pêches Marit.* 34: 277-296.
- Lester N.P., Shuter B.J., Abrams P.A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proc. R. Soc. B: Biol. Sci.* 271: 1625-1631.
<https://doi.org/10.1098/rspb.2004.2778>
- Li Z.-L., Lu H.-S., Gan X.-P., Jing X. 2009. Growth and mortality of bottom threadfin bream *Nemipterus bathybius* in the mouth of Beibu Gulf, South China Sea. *Fish. Sci.* 28: 556-562. [In Chinese with English abstract]
- Longhurst A., Pauly D. 1987. *Ecology of Tropical Oceans*. Academic Press, San Diego, 407 pp.
<https://doi.org/10.1016/B978-0-12-455562-4.50010-0>
- Meyer K.A., Schill D.J. 2021. The Gill-Oxygen Limitation Theory and size at maturity/maximum size relationships for salmonid populations occupying flowing waters. *J. Fish Biol.* 98: 44-49.
<https://doi.org/10.1111/jfb.14555>
- Morbey Y.E. and D. Pauly. 2022. Juvenile-to-adult transition invariances in fishes: perspectives on proximate and ultimate causation. *J. Fish Biol.* 1-11.
<https://doi.org/10.1111/jfb.15146>
- Muir B.S., Hughes G.M. 1969. Gill Dimensions for Three Species of Tunny. *J. Exp. Biol.* 51: 271-285.
<https://doi.org/10.1242/jeb.51.2.271b>
- Pankhurst N.W. 2016. Reproduction and development. In: Schreck C.B., Tort L., Farrell A.P., Brauner C.J. (eds), *Fish Physiology* Vol. 35. Elsevier, Amsterdam, pp. 295-331.
<https://doi.org/10.1016/B978-0-12-802728-8.00008-4>
- Pauly D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Berichte der Deutschen wissenschaftlichen Kommission für Meeresforschung* 28: 251-282.
- Pauly D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *J. Cons. Int. Explor. Mer* 41: 280-284.
<https://doi.org/10.1093/icesjms/41.3.280>
- Pauly D. 2019. Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals - 2nd Edition. International Ecology Institute, Oldendorf/Luhe, Germany, 279 pp.
- Pauly D. 2021a. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Sci. Adv.* 7: 2.
<https://doi.org/10.1126/sciadv.abc6050>
- Pauly D. 2021b. Why do fish reach first maturity when they do? *J. Fish Biol.*
<https://doi.org/10.1111/jfb.14902>
- Pauly D., Liang C. 2022. Temperature and the early maturation of fish: a simple sine-wave model for predicting spring spawning. *Environ. Biol. Fish.*
<https://doi.org/10.1007/s10641-022-01212-0>
- Pütter A. 1920. Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten. *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere* 180: 298-340.
<https://doi.org/10.1007/BF01755094>
- Quince C., Abrams P.A., Shuter B.J., Lester N.P. 2008. Biphasic growth in fish I: Theoretical foundations. *J. Theor. Biol.* 254: 197-206.
<https://doi.org/10.1016/j.jtbi.2008.05.029>
- Rideout R.M., Rose G.A., Burton M. 2005. Skipped spawning in female iteroparous fish. *Fish Fish.* 6: 50-62.
<https://doi.org/10.1111/j.1467-2679.2005.00174.x>
- Rijnsdorp A.D. 1989. Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *ICES J. Mar. Sci.* 46: 35-51.
<https://doi.org/10.1093/icesjms/46.1.35>
- Shi D.F., Zhang K., Cai Y.C., Geng P., Xu Y.W., Sun M.S., Chen Z.Z. 2020. Population structure of *Trichiurus japonicus* in northern South China Sea and parameters of its growth, mortality and maturity. *South China Fisheries Science* 16: 51-59.
- Thom R. 1975. Structural stability and morphogenesis: an outline of a general theory of models. Translated by D.H. Fowler. Benjamin-Cummings, Reading, MA, 348 pp.
- Trippel E.A., Kjesbu O.S., Solemdial P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers R.C., Trippel E.A. (eds), *Early life history in fish populations*. Chapman & Hall-Kluwer, Dordrecht, pp. 31-61.
https://doi.org/10.1007/978-94-009-1439-1_2
- Wang T., Gao X., Wang J., Jakovlić I., Dan S.G., Liu H.Z. 2015. Life history traits and implications for conservation of rock carp *Procypris rabaudi* Tchang, an endemic fish in the upper Yangtze River, China. *Fish. Sci.* 81: 515-523.
<https://doi.org/10.1007/s12562-015-0872-9>
- Woodcock A., Davis M. 1980. Catastrophe theory: a new way of understanding how things change. Penguin Books, Harmondsworth, 152 pp.
- Warlen S.M., Burke J.S. 1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. *Estuaries* 13: 453-461.
<https://doi.org/10.2307/1351789>

Expansion and contraction of the *Engraulis ringens* spawning area in northern Chile

Paola Moreno ^{1,2}, Gabriel Claramunt ²

¹ Programa Magister en Ciencias Aplicadas mención Biología Pesquera, Facultad de Recursos Naturales Renovables, Universidad Arturo Prat, Avenida Arturo Prat 2120, Iquique, Casilla 121, Chile.

(PM) E-mail: paolmorenogon@gmail.com. ORCID ID: <https://orcid.org/0000-0002-1041-4632>

² Facultad de Recursos Naturales Renovables, Universidad Arturo Prat, Avenida Arturo Prat 2120, Iquique, Casilla 121, Chile.

(GC) E-mail: gclaramu@gmail.com. ORCID ID: <https://orcid.org/0000-0003-0490-6734>

Summary: Many studies have considered the temporal patterns of reproduction of *Engraulis ringens*, but little attention has been given to the spatial patterns of reproduction (spawning areas), which have shown great variability in both location (geographical position) and extent (the area covered by positive stations), without a satisfactory explanation. Along the Chilean coast, the daily egg production method (DEPM) has been used for several years to estimate spawning biomass in the northern Chile *E. ringens* population, with 24 surveys being carried out from 1992 to 2020. The most fluctuating parameters estimated in the DEPM have been the location and extent of the spawning area and the average female weight. In the last few years the eggs were distributed near the coast, whereas in the first few years they showed a more oceanic distribution. The average female weight has fallen from 30 g in the 1990s to 11 g in the last few years. In the present study, we analysed the relationship of the location and extent of spawning areas with female size and abundance in *E. ringens* from northern Chile. According to the results, periods of high abundance of eggs are positively correlated with larger females that spawn in more oceanic zones and to the south, expanding the spatial egg distribution and increasing the egg density. By contrast, in years with low abundance of eggs, the spawning was located north and towards the coast, with a smaller spawning area and smaller female size.

Keywords: anchovy; reproduction; spawning areas.

Expansión y contracción del área de desove de *Engraulis ringens* en el norte de Chile

Resumen: Han habido muchos estudios sobre los patrones temporales en la reproducción de *Engraulis ringens*, sin embargo, se ha prestado poca atención a los patrones espaciales de reproducción (áreas de desove), que han mostrado una gran variabilidad tanto en la ubicación (posición geográfica) como en la extensión (área cubierta por estaciones positivas), sin tener explicación satisfactoria. A lo largo de la costa chilena, el método de producción diaria de huevos (MPDH) se ha utilizado durante varios años para estimar la biomasa desovante de *E. ringens* del norte de Chile, con 24 aplicaciones desde 1992 hasta 2020. Los parámetros más fluctuantes estimados en el MPDH han sido la zona de desove, tanto en localización como en extensión y el peso medio de las hembras. En los últimos años los huevos se han distribuido cerca de la costa en contraste con los primeros años con una distribución más oceánica. El promedio del peso de las hembras se ha reducido de 30 g en la década de los 90 a 11 g en los últimos años. En el presente estudio analizamos la relación entre la ubicación y extensión de las áreas de desove, con el peso de las hembras y su abundancia en *E. ringens* del norte de Chile. Según los resultados, los períodos de alta abundancia de huevos se correlacionan positivamente con hembras más grandes que desovan en zonas más oceánicas y hacia el sur, expandiendo la distribución espacial de huevos y aumentando la densidad de huevos. Por el contrario, en años donde se registró baja abundancia de huevos, el desove se ubicó al norte y hacia la costa con menor área de desove y menor tamaño de las hembras.

Palabras clave: anchoveta; reproducción; áreas de desove.

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INTRODUCTION

The anchoveta, *Engraulis ringens* Jenyns 1842, from northern Chile has a short life cycle, a fast growth rate and therefore a naturally high mortality rate (Cubillos and Arancibia 1993, Cubillos et al. 2001). Juveniles typically recruit to the fisheries around five months after hatching (Castillo and Plaza 2016). The spawning season of the species tends to occur in winter (Southern Hemisphere) and extends from July to September with a peak between August and September (Claramunt et al. 2014). Many studies have considered the temporal patterns of reproduction of the anchoveta (Cubillos and Claramunt 2009, Claramunt et al. 2014, Hernández et al. 2013), but little attention has been given to the spatial patterns of reproduction (spawning areas), which have shown great variability in both location (geographical position) and extent (the area covered by positive stations), without a satisfactory explanation. According to Castillo-Jordán et al. (2007), GAM models indicate that in southern Chile egg density distribution is better explained by a bivariate function of longitude and latitude together with bottom depth. However, since in this case egg densities depend exclusively on parameters that are not directly sensitive for fish, the results are not satisfactory from a biological point of view (Castillo-Jordán et al. 2007). For northern populations there is no explanation yet for the changes in the location or extent of their spawning areas. In a study of spawning habitat preferences, Claramunt et al. (2012) concluded that chlorophyll concentration could be a relevant variable in female spawning habitat selection, but this does not explain interannual expansion and contraction of the spawning area.

Along the Chilean coast, the daily egg production method has been used for several years to estimate spawning biomass in the northern Chile *E. ringens* population, with 24 surveys being carried out from 1992 to 2020. One of the great advantages of this method is that in addition to abundance estimates it provides valuable information about the reproductive biology of the stocks, through intensive sampling of the ichthyoplankton and adult females (Claramunt et al. 2019, Claramunt et al. 2012). The most fluctuating parameters estimated in the daily egg production method have been location and extent of the spawning area and the average female weight. In the spawning area, changes occurred in latitude and coast-ocean directions. In the last few years the eggs were distributed near the coast, whereas the first few years they showed a more oceanic distribution. The average female weight has fallen from 30 g in the 1990s to 11 g in the last few years. In the present study, we analysed the relationship of the location and extent of the spawning areas with female size and abundance in *E. ringens* from northern Chile.

MATERIALS AND METHODS

This study used information found in the database of the daily egg production method programme, which consisted of research cruises carried out during the peak spawning season from 1992 to 2020, except the

years 1993, 1994, 1998 and 2010, making a total of 25 cruises (Table 1). The study area covered the northern region of Chile, from 18°20'S (Arica) to 26°03'S (Carizalillo), and from the coast to 60 or 80 nautical miles (nm) seaward, with transects every 10 nm and stations every 5 nm. At every station, eggs were collected using a CalVET plankton net with a 0.05 m² mouth area equipped with a 250 µm mesh size net. Simultaneously purse-seine boats were used for annual adult surveys, which sampled a minimum of 30 females in each of the 40 hauls.

For the purpose of exploring the changes in the location of the spawning areas, the centre of gravity for each year was calculated using the following equation.

$$CG = \frac{\sum h * Lat}{\sum h}$$

where h is the number of eggs at a given station and Lat is the position of the station in either latitude or longitude (Bez 1997, Gutierrez et al. 2012). The egg density was calculated as the average number of eggs per 0.05 m² at the positive stations (i.e. at least one egg).

For each survey the area regarded as the main spawning area encompassed all positive stations (i.e. with anchovy eggs) as well as negative stations embedded between positive stations. All negative stations outside the positive area were omitted from the area estimate. To overcome interannual differences in the total amount of surveyed area, the spawning area was standardized by the ratio with the total area of each survey: spawning area/survey area (Table 1).

The annual catch (Table 1) was used as an abundance index for the stock. The database of industrial fleet landing was obtained from the national fisheries service (SERNAPESCA; www.SERNAPESCA.cl).

The relationships between variables were tested by means of multiple and simple linear regressions and the significance of the coefficients by t test.

RESULTS

In the northern zone a high variability in both location (geographical position) and extent (the area covered by positive stations) of the spawning area was observed (Fig. 1). In terms of locations, changes occurred in latitude and coast-ocean directions. In some years (e.g. 2015, 2017 and 2019) the eggs were distributed near the coast, whereas in others (2000, 2002) they showed a more oceanic distribution. Latitudinally within the spawning area in northern Chile, in some years (e.g. 2013) the main spawning zones were north of 20°S, while in other years (e.g. 2011, 2015) they were south of 21°S.

Female length frequency distribution shows a clear reduction pattern (Fig. 2). In the first years the mode is centred near 16 cm, falling to 12 cm in the last years. The extent of the spawning area is correlated with annual landings (Fig. 3A, Table 2), latitude (Fig. 3B) and longitude (Fig. 3D, Table 2). An expansion of the

Table 1. – Information used in the study. Stations (+): number of stations with anchovy eggs. CG, centre of gravity in latitude (°S) and longitude (°W); A, survey area; A(+), spawning area; A(+)/A, spawning area/survey area.

	Stations	Stations (+)	Egg density	Survey area	Spawning area	A(+)/A	Female weight	CG Latitude	CG Longitude	Annual catch
Year	N°	N°	N°/0.05 m ²	mn ²	mn ²		g	°S	°W	t*1000
1992	542	212	20.2	18341.8	9966.5	0.54	21.0	19.94	70.61	954
1995	578	209	13.3	18794.6	8710.3	0.46	29.0	22.40	70.76	1482
1996	752	176	8.9	19668.5	6422.9	0.33	30.0	21.10	70.66	840
1997	800	209	10.1	28713.7	10328.2	0.36	21.7	21.92	70.72	1317
1999	598	132	12.7	28018.7	7182.8	0.26	23.0	21.72	70.53	809
2000	502	212	20.9	20186.8	10212.8	0.51	30.9	21.59	70.64	1154
2001	514	60	14.5	25630.9	3481.3	0.14	32.4	21.93	70.33	640
2002	589	310	31.0	29947.1	17781.3	0.59	21.3	21.43	70.60	1216
2003	537	129	17.2	26799.6	7498.3	0.28	25.2	21.18	70.42	418
2004	649	211	19.1	32006.8	11694.9	0.37	23.6	20.78	70.59	1394
2005	658	215	25.9	32581.1	12239.6	0.38	23.0	21.33	70.77	1008
2006	799	226	14.3	40771.6	14804.0	0.36	22.5	20.89	70.52	513
2007	799	113	5.9	38206.6	7611.9	0.20	21.7	19.40	70.64	745
2008	717	136	14.4	34860.3	8912.6	0.26	21.8	21.24	70.33	648
2009	773	41	6.1	38234.8	3036.6	0.08	18.0	19.47	70.30	440
2011	730	292	19.1	35033.2	17316.6	0.49	23.4	21.34	70.51	958
2012	564	211	19.1	34823.7	18326.2	0.53	20.1	21.72	70.51	710
2013	770	201	8.2	35874.6	11141.7	0.31	24.5	20.37	70.50	691
2014	632	128	11.8	29581.5	6937.7	0.23	17.0	19.82	70.41	729
2015	659	150	9.4	31814.3	9689.9	0.30	13.2	21.12	70.41	633
2016	791	64	7.6	41102.6	4175.2	0.10	11.5	18.89	70.46	243
2017	819	108	5.4	42508.7	7095.8	0.17	15.7	19.63	70.51	530
2018	799	203	16.9	40732.0	12783.0	0.31	15.9	20.84	70.48	751
2019	782	117	14.3	41757.0	8366.0	0.20	11.1	20.28	70.35	516
2020	789	52	5.4	39272.9	3890.8	0.10	11.7	19.79	70.29	268

spawning area is associated with an increase in egg density (Fig. 3C, Table 2).

The eggs' centres of gravity show a trend over time to be located north and towards the coast (Fig. 4A). The years with centres of gravity located south and towards the ocean are associated with high annual landings (Fig. 4B). Low landings are associated with centres of gravity located north and towards the coast. A multiple linear regression of annual landings as a function of centres of gravity in latitude and longitude was adjusted (Table 3), resulting in an equation with predicted values very close to the observed ones (Fig. 5).

Female size is correlated with centre of gravity in latitude and longitude (Fig. 6, Table 2). Larger females spawn in more oceanic areas and southwards. Summarizing the results, years with high catch are associated with larger females that spawn in more oceanic zones and to the south, expanding the eggs' spatial distribution.

DISCUSSION

According to the results, years with high annual catches of anchovy show high egg density, an extended spawning area and a good range of female size distribution, with females over 31 g or 16 cm. By contrast, years with low annual catches show lower egg density, the spawning area is restricted to the coastal zone and the female size distribution is restricted to smaller females (<31 g or 16 cm).

The egg distribution area could be used as a proxy for the adult fish distribution area, as tested by Barange et al. (2009), indicating that if the eggs samples are taken during the peak period of the species' spawning season, the distribution area of the eggs is proportional (but not equivalent) to that of the adults, thus validating the use of either eggs or adults to estimate the relationship between distribution area and stock size (Barange et al. 2009). Therefore, we can postulate that spawning area is a proxy of adult distribution, so the expansion and contraction of the spawning area of the anchoveta

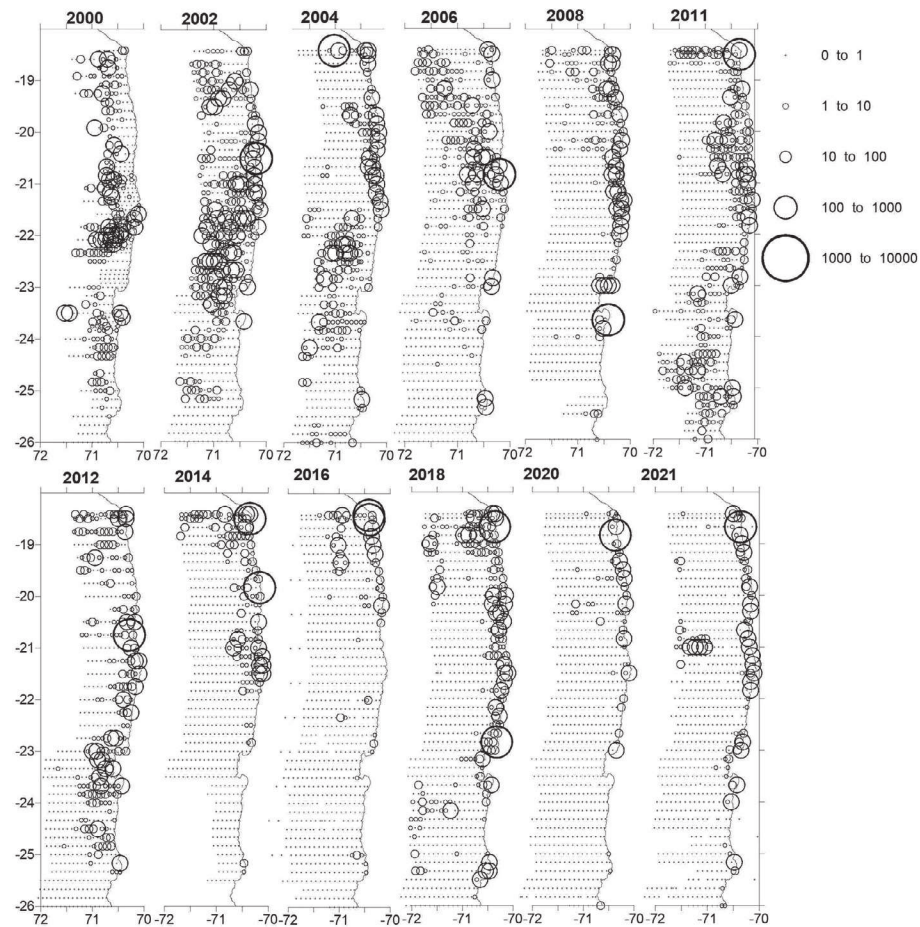


Fig. 1. – Anchovy egg distribution from 2000 to 2021. Diameter of the circles are proportional to the eggs numbers ($N^{\circ}/0.05 \text{ m}^2$). Circles in eggs number/ 0.05 m^2 .

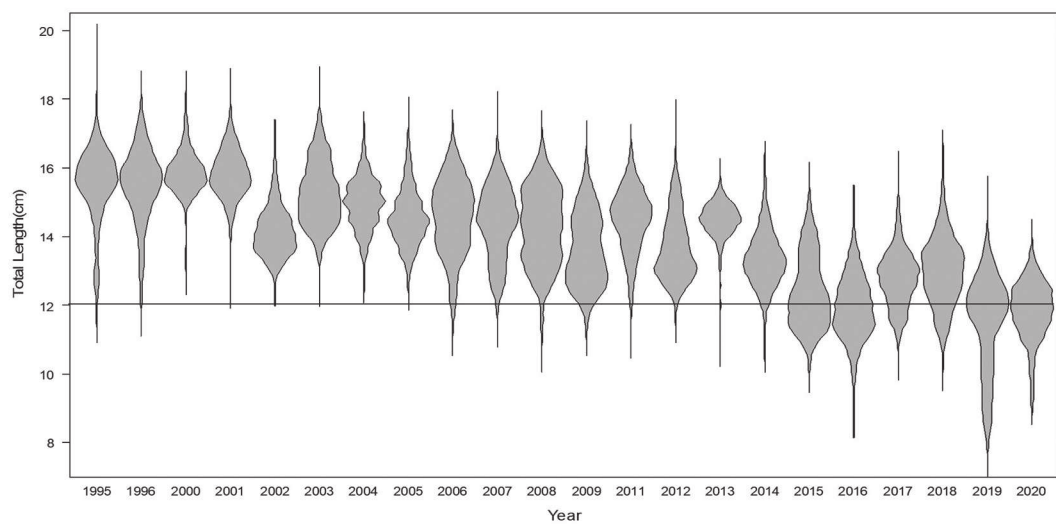


Fig. 2. – Distribution of female total length (cm). Horizontal line indicates 12 cm total length (maturity).

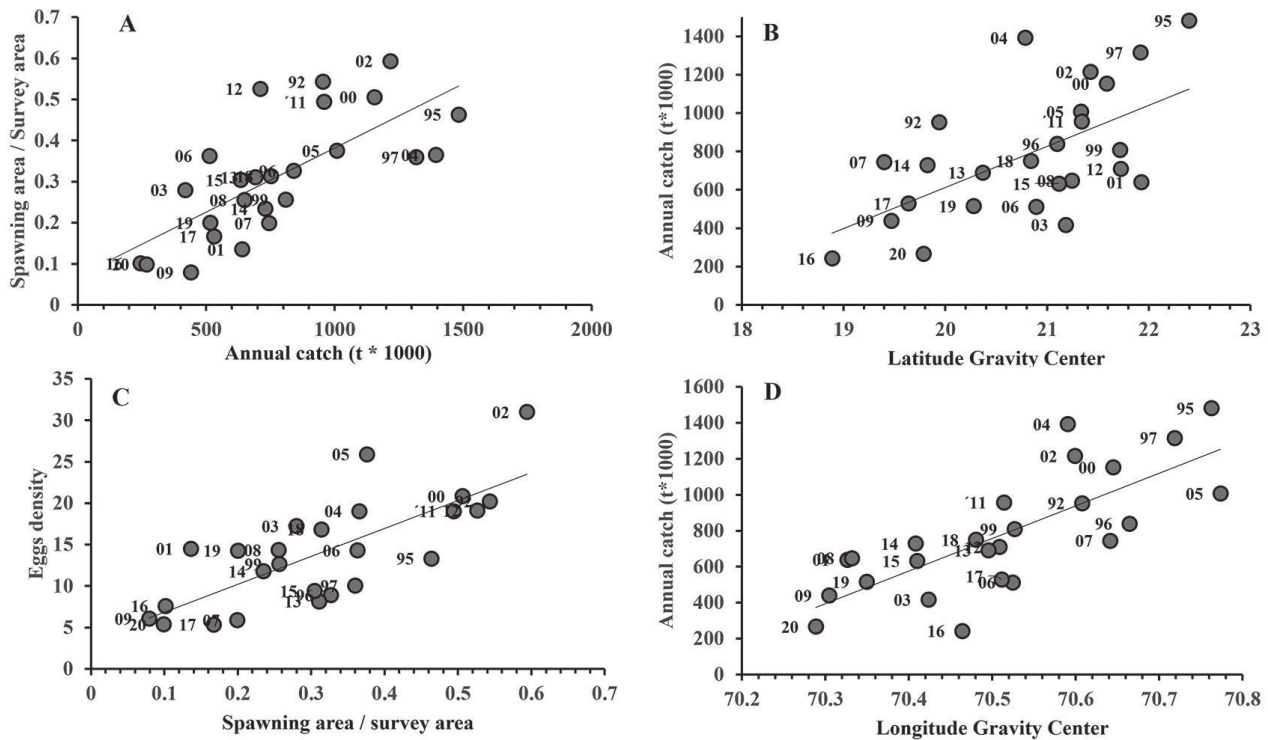


Fig. 3. – Relationship between annual catch and spawning area (as a proportion of the survey area) (A). Egg distribution latitude ($^{\circ}$ S), centre of gravity and annual catch (B). Spawning area and egg density ($N^{\circ}/0.05 \text{ m}^2$) (C). Egg distribution longitude ($^{\circ}$ W), centre of gravity and annual catch (D). Numbers indicate year.

Table 2. – Results of the linear regressions between independent (X) and dependent (Y) variables. CG, Gravity Centre; a, Intercept; b, slope; Sa and Sb, standard error. Prob, probability parameter = 0.

Independent	Dependent	a	Sa	Prob	b	Sb	Prob	R ²	n
Annual catch	Spawning area	0.069	0.055	0.219	0.0003	10^{-5}	$7.08 \cdot 10^{-5}$	0.50	25
Spawning area	Egg density	3.47	2.11	0.114	33.7	6.11	$1.30 \cdot 10^{-5}$	0.57	25
GC latitude	Annual catch	-3672	1250	0.007	214	60.04	0.0016	0.36	25
GC longitude	Annual catch	-127179	22658	$1.03 \cdot 10^{-5}$	1814.7	321.3	$9.50 \cdot 10^{-6}$	0.58	25
GC latitude	Average female weight	-62.9	21.27	0.007	4.04	1.02	0.0006	0.41	25
GC longitude	Average female weight	-1343	550.2	0.023	19.4	7.80	0.021	0.21	25

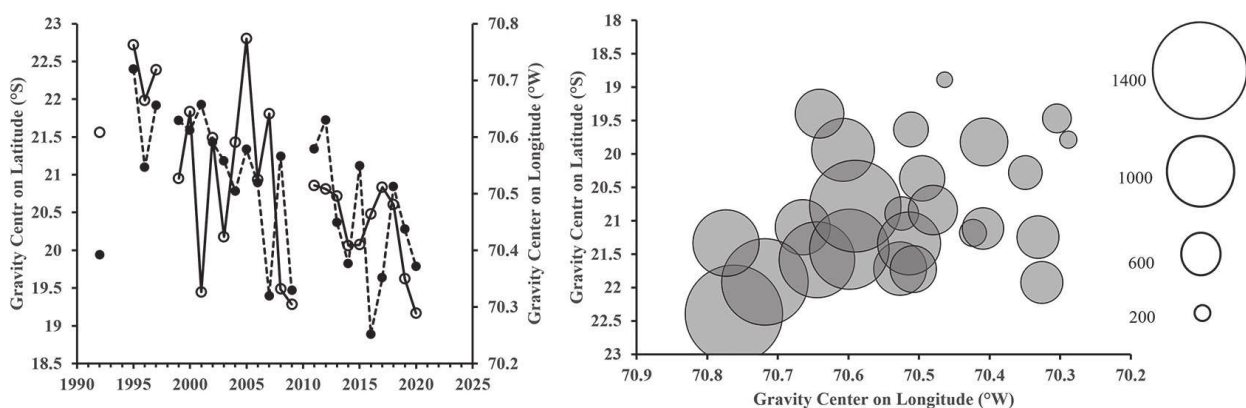


Fig. 4. – A, centre of gravity of egg distribution. B, centre of gravity of egg distribution and annual catch (diameter of the circles).

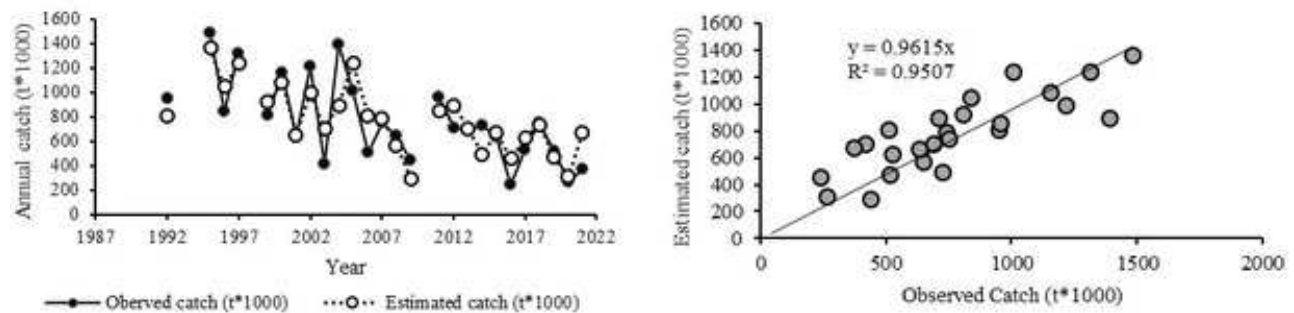


Fig. 5. – Left: Observed annual catch from 1992 to 2020 and estimated annual catch (t*1000) by a multiple linear regression with egg distribution centre of gravity in latitude (°S) and longitude (°W). Right: Linear regression between observed and estimated annual catch.

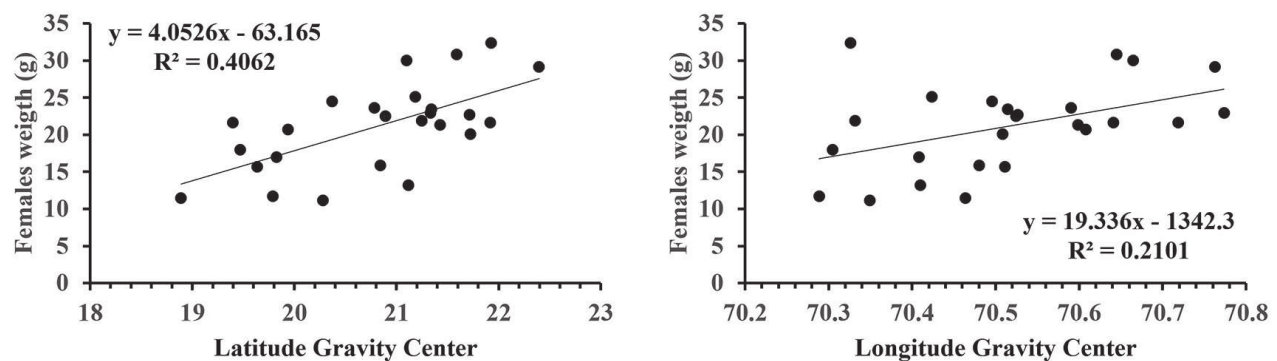


Fig. 6. – Relationship between average female weight and latitude (°S) and longitude (°W) of the centre of gravity of egg distribution.

Table 3. – Results of the linear multiple relationship between annual catch and centre of gravity in longitude (CGLong) and latitude (CGLat). SD, standard deviation.

Coefficient	SD	Probability
Intercept	-107329.9	3.6758E-05
CGLong	1494.4	5.568E-05
CGLat	131.5	0.0082
r^2	0.84	
n	25	

in the northern region of Chile follow the changes in abundance of eggs to adults.

The results show that the spawning area location is influenced by female weight distribution. Bigger females have a more oceanic and southward spawn, expanding the egg distribution. These results contrast with the proposal of Schwartzman et al. (2008) that the Peruvian stock of anchoveta is restricted to the cold waters of coastal upwelling, regardless of their abundance. Barange et al. (2009) suggest that in anchoveta the available habitat determines the size of the stock of the anchoveta. The causes of female size reduction in the northern anchovy population are as yet unknown. Natural and fishery mortality and changes in growth rate could be involved.

Three basic models describe the relationship between stock size, distribution area and local density (Petitgas 1998, Barange et al. 2009): (i) the constant density model, in which density stays constant and the

area covered by the stock varies with abundance; (ii) the proportional model, in which the area occupied stays constant and local density varies proportionally to abundance; and (iii) the basin model, in which density and area vary with abundance. According to our results, anchovy off northern Chile shows a type (iii) model, density and area varying with abundance.

Although the mechanisms and environmental aspects that cause fluctuations in anchoveta populations have received considerable attention around the world (Alheit and Bakun 2010, Alheit et al. 2019, McCall 2009), these studies have not yet been sufficient to determine the environmental aspects or mechanisms that regulate the changes in abundance and the density-dependent processes that might be involved. In fishes, changes in time and space in reproduction, namely, changes in spawning periods and spawning areas, affect growth and early stage survival because they also determine the kind of environment in which the fish populations will develop (Secor 2007). In the Japanese pacific, fluctuations in the abundance of the stock of *Sardinops melanosticus* were followed by changes in the spawning period (Itoh et al. 2009, Takahashi et al. 2008, Watanabe et al. 1996, 1997), which in turn changed the environment encountered by the early stages (i.e. temperature, food availability and predator evasion), which affects early growth.

This strategy of a density-dependent use of space could be a mechanism for avoiding cannibalism upon

their own eggs. This also signifies that, if the appropriate conditions are met in more oceanic sites, the population could undergo a phase of expansion. Something similar happens with the anchoveta *Engraulis encrasicolus* in the Adriatic Sea, where apparently they seem to change their spawning centres during the reproductive period according to the favourable environmental conditions, beginning the spawning process in the northern and more shallow part of the Adriatic, where they first find the appropriate conditions for survival of the early stages of life (Zorica et al. 2018). Examples of periodic habitat expansion and contraction are reported in the literature for small pelagic populations in different ecosystems (Bakun 2005, 2006, Barange et al. 2009). These expansions have been linked to predator-prey interactions or competitive advantages, which determine or are determined by an increase in population size (Bakun 2006, Barange et al. 2009). This density-dependent relationship assumes that the number of progenies recruited to a fishery is proportional to the number of eggs spawned until an environmental carrying capacity is reached. Departures from this relationship are density-independent and attributed to the environment. Implicitly, the stock-recruit relationship does not account for climate variability and change, although environmental terms can be added to expand this type of model (Checkley et al 2017).

In conclusion, the expansion and contraction of spawning areas in *E. ringens* of northern Chile depend on the abundance and size of females. Abundance is more related to extent and female size to the location of the spawning areas.

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REFERENCES

- Alheit J., Bakun A. 2010. Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical-biological linkage mechanisms. *J. Mar. Syst.* 79: 267-285. <https://doi.org/10.1016/j.jmarsys.2008.11.029>
- Alheit J., Lorenzo E. D., Rykaczewski R. R., Sundby S. 2019. Drivers of dynamics of small pelagic fish resources: environmental control of long-term changes. *Deep Sea Res. Part II.* 159: 1-3. <https://doi.org/10.1016/j.dsr2.2018.12.005>
- Bakun A. 2005. Regime Shifts. In: Robinson A.R., Brink K. (eds), *The Sea*, vol. 13. Harvard University Press, Cambridge, MA, pp.971-1018 (Chapter 24).
- Bakun A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. *Prog. Oceanogr.* 68: 271-288. <https://doi.org/10.1016/j.pocean.2006.02.004>
- Barange M., Coetzee J., Takasuka A., et al. 2009. Habitat expansion and contraction in anchovy and sardine populations. *Prog. Oceanogr.* <https://doi.org/10.1016/j.pocean.2009.07.027>
- Bez N. 1997. Statistiques individuelles et géostatistique transitive en écologie halieutique. Thèse, Ecole Nationale Supérieure des Mines de Paris, 303 pp.
- Castillo-Jordán C., Cubillos L., Paramo J. 2007. The spawning spatial structure of two co-occurring small pelagic fish off central southern Chile in 2005. *Aquat. Living Resour.* 20: 77-84. <https://doi.org/10.1051/alr:2007018>
- Castillo F., Plaza G. 2016. Daily growth patterns of juveniles and adults of the Peruvian anchovy (*Engraulis ringens*) in northern Chile. *Mar. Freshw. Res.* 67: 899-912. <https://doi.org/10.1071/MF15032>
- Checkley D.M., Asch R.G., Rykaczewski R.R. 2017. Climate, Anchovy, and Sardine. *Ann. Rev. Mar. Sci.* 9: 469-493. <https://doi.org/10.1146/annurev-marine-122414-033819>
- Claramunt G., Castro L.R., Cubillos L., et al. 2012. Variaciones interanuales en aspectos reproductivos y preferencias por el sitio de desove en *Engraulis ringens* del norte de Chile. *Rev. Biol. Mar. Oceanogr.* 47: 227-243. <https://doi.org/10.4067/S0718-19572012000200006>
- Claramunt G., Cubillos L., Castro L., et al. 2014. Variation in the spawning periods of *Engraulis ringens* and *Strangomera bentincki* off the coasts of Chile: A quantitative analysis. *Fish. Res.* 160: 96-102. <https://doi.org/10.1016/j.fishres.2013.09.010>
- Claramunt, G., Cubillos, L., Herrera, G., Díaz E. 2019. Spawning marker patterns of *Engraulis ringens* of northern Chile. *Fish. Res.* 219: 105306. <https://doi.org/10.1016/j.fishres.2019.06.004>
- Cubillos L., Arancibia H. 1993. Análisis de la pesquería de sardina común (*Strangomera bentincki*) y anchoveta (*Engraulis ringens*) del área de Talcahuano, Chile. *Invest. Mar., Valparaíso* 21: 3-21.
- Cubillos L.A., Claramunt G. 2009. Length-structured analysis of the reproductive season of anchovy and common sardine off central southern Chile. *Mar. Biol.* 156: 1673-1680. <https://doi.org/10.1007/s00227-009-1202-5>
- Cubillos L., Arcos D., Bucarey D., Canales M. 2001. Seasonal growth of small pelagic fish off Talcahuano (37°S-73°W), Chile: a consequence of their reproductive strategy to seasonal upwelling? *Aquat. Living Resour.* 14: 115-124.
- Gutierrez M., Castillo R., Segura M., et al. 2012. Tendencias espacio-temporales en la distribución de la biomasa de anchoveta peruana y de otros peces pelágicos pequeños entre 1966 y 2009. *Lat. Am. J. Aquat. Res.* 40: 633-648.
- Hernández C., Perez-Mora G., Díaz-Ramos E., Bohm-Stoffel G. 2013. Análisis de indicadores macro y microscópicos para establecer el periodo de máxima intensidad de desove de la anchoveta *Engraulis ringens* en la zona norte de Chile. *Rev. Biol. Mar. Oceanogr.* 48: 451-457. <https://doi.org/10.4067/S0718-19572013000300004>
- Itoh S., Yasuda I., Nishikawa H., et al. 2009. Transport and environmental temperature variability of eggs and larvae of the Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*) in the Western North Pacific estimated via numerical particle-tracking experiments. *Fish. Oceanogr.* 18: 118-133. <https://doi.org/10.1111/j.1365-2419.2009.00501.x>
- McCall A. D. 2009. Mechanisms of low-frequency fluctuations in sardine and anchovy populations. In Checkley D., Alheit J. et al. (eds), *Climate change and small pelagic fish* (pp. 45-63). Cambridge, UK: Cambridge University Press.
- Petitgas P. 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves - ICES Journal of Marine Science 55: 443-453. <https://doi.org/10.1006/jmsc.1997.0345>
- Secor D.H. 2007. The year-class phenomenon and the storage effect in marine fishes. *J. Sea Res.* 57(2-3 SPEC. ISS.), 91-103. <https://doi.org/10.1016/j.seares.2006.09.004>
- Servicio Nacional de Pesca y Agricultura (SERNAPESCA). www.SERNAPESCA.cl
- Swartzman G., Bertrand A., Gutiérrez M., et al. 2008. The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983 to 2005. *Progress In Oceanography* 79: 228-237. <https://doi.org/10.1016/j.pocean.2008.10.021>
- Takahashi M., Nishida H., Yatsu A., Watanabe Y. 2008. Year-class strength and growth rates after metamorphosis of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific Ocean during 1996-2003. *Can. J. Fish. Aquat. Sci.* 65: 1425-1434. <https://doi.org/10.1139/F08-063>

- Watanabe Y., Zenitani H., Kimura R. 1996. Offshore expansion of spawning of the Japanese sardine, *Sardinops melanostictus*, and its implication for egg and larval survival. Can. J. Fish. Aquat. Sci. 53: 55-61.
<https://doi.org/10.1139/f95-153>
- Watanabe Y., Zenitani H., Kimura R. 1997. Variations in spawning ground area and egg density of the Japanese sardine in Pacific coastal and oceanic waters. Fish. Oceanogr. 6: 35-40.
<https://doi.org/10.1046/j.1365-2419.1997.00024.x>
- Zorica B, Čikeš Keč V, Pešić A, et al. 2018. Spatiotemporal distribution of anchovy early life stages in the eastern part of the Adriatic Sea in relation to some oceanographic features. J. Mar. Biol. Ass. U.K. 99: 1205-1211.
<https://doi.org/10.1017/S0025315418001145>

Assessing changes in size at maturity for the European hake (*Merluccius merluccius*) in Atlantic Iberian waters

Davinia Lojo¹, Marta Cousido-Rocha², Santiago Cerviño², Rosario Dominguez-Petit²,
María Sainza², Maria Grazia Pennino²

¹ Centro Tecnológico del Mar-Fundación CETMAR, C/Eduardo Cabello s/n, 36208 Vigo, Pontevedra, Spain.
(DL) (Corresponding author) E-mail: Dlojo@cetmar.org. ORCID iD: <https://orcid.org/0000-0003-1145-9776>

² Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Vigo, Subida a Radio Faro, 50-52.
36390 Vigo, Pontevedra, Spain.

(MB) E-mail: marta.cousido@ieo.es. ORCID iD: <https://orcid.org/0000-0002-4587-8808>

(SC) E-mail: santiago.cervino@ieo.es. ORCID iD: <https://orcid.org/0000-0003-4146-0890>

(RD) E-mail: rosario.dominguez@ieo.es. ORCID iD: <https://orcid.org/0000-0003-1731-6848>.

(MS) E-mail: maria.sainza@ieo.es. ORCID iD: <https://orcid.org/0000-0003-1432-1123>

(MGP) E-mail: grazia.pennino@ieo.es. ORCID iD: <https://orcid.org/0000-0002-7577-2617>

Summary: European hake (*Merluccius merluccius*) is a commercially important resource in Iberian Atlantic waters. Despite the recovery plan implemented in 2006 and the multiannual management plan for western waters, fishing mortality is still higher than that corresponding to the maximum sustainable yield for the southern European hake stock. The biological processes underlying the dynamics of this stock and its life history traits are essential for assessing population productivity and resilience, making them basic information for management. We analysed the temporal variability of size at maturity (L_{50}) of this species and the main factors influencing it in Atlantic Iberian waters from 1982 to 2019. The annual variability of L_{50} for each sex was modelled with generalized additive models, considering explanatory environmental variables (Atlantic Multidecadal Oscillation, North Atlantic Oscillation and sea surface temperature) and biological variables (biomass, spawning biomass at length and relative condition factor). The results showed that the L_{50} of males decreased by a total of 12.9 cm and L_{50} of females decreased by a total of 10.9 cm from 1982 to 2019. For females the significant explanatory variables were year, spawning biomass at length, biomass and the North Atlantic Oscillation, while for males only year was an explanatory variable. These results are important for understanding the status of the European hake population, signalling that L_{50} is a good indicator for predicting future population dynamics.

Keywords: North Atlantic Oscillation, life history, reproductive traits, relative condition factor, southern European stock.

Evaluación de los cambios en la talla de madurez de la merluza europea (*Merluccius merluccius*) en las aguas atlánticas ibéricas

Resumen: La merluza europea (*Merluccius merluccius*) es un recurso comercialmente importante en aguas Atlánticas Ibéricas. A pesar del plan de recuperación puesto en marcha en 2006 y del plan de gestión plurianual de las aguas occidentales, la mortalidad por pesca sigue siendo superior a la correspondiente al rendimiento máximo sostenible de la población de merluza del sur de Europa. Comprender los procesos biológicos que subyacen a la dinámica de este stock y proporcionar información sobre los rasgos de la historia de vida es fundamental para evaluar la productividad y la resiliencia de la población, convirtiéndolos en información básica para la gestión. Analizamos la variabilidad temporal de la talla de madurez (L_{50}) y los principales factores que influyen en ella, desde 1982 hasta 2019 en aguas Atlánticas Ibéricas. La variabilidad anual de L_{50} para cada sexo se modeló con Modelos Aditivos Generalizados considerando variables ambientales explicativas (Oscilación Multidecadal del Atlántico, Oscilación del Atlántico Norte y Temperatura Superficial del Mar), y variables biológicas (biomasa, biomasa reproductora por talla y factor de condición relativo). Los resultados mostraron que la de los machos disminuyó en un total de 12,9 cm y la L_{50} de las hembras disminuyó en un total de 10,9 cm de 1982 a 2019. Para las hembras las variables explicativas significativas fueron año, biomasa de desove por talla, biomasa y NAO, mientras que para los machos solo el año. Estos resultados son importantes para comprender el estado de la población de merluza europea, lo que destaca que la L_{50} es un buen indicador para predecir la dinámica futura de la población.

Palabras clave: Oscilación del Atlántico Norte; historia de vida; rasgos reproductivos; factor de condición relativa; población del sur de Europa.

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INTRODUCTION

Life history parameters, and in particular reproductive traits such as spawning cycle, size and age at maturity, fecundity and spawning potential are the basis for assessing the productivity and resilience of fish stocks, making them essential information for stock assessment and management (Dominguez-Petit et al. 2008). The estimation of the size at which 50% of individuals are mature (L_{50}) can be used to define the minimum legal landing size for exploited stocks. However, in most stock assessments the causes of L_{50} variability are not analysed, though there are intrinsic and extrinsic factors affecting maturity that may act at a temporal scale (Lorenzen and Camp 2019). Size and age at maturity are especially sensitive to population abundance (Dominguez-Petit et al. 2008, Lorenzen and Camp 2019) owing to density-dependent effects. When stock size decreases, individuals tend to mature at large sizes and early ages because of compensatory growth (Ali et al. 2003). However, some environmental and anthropogenic drivers, including high rates of fishing mortality, may also impact on size at maturity (Pepin 2015). Moreover, when the effects of these drivers are intense and/or sustained over a long period of time, they could lead to evolutionary changes because of the selection of certain genotypes (Hollins et al. 2018). Subsequently, understanding mechanisms driving maturity variability within species could provide preliminary evidence of the species's adaptability to climate change (Dalglish et al. 2010), habitat degradation (Öckinger et al. 2010) and overfishing (Hobday et al. 2011).

Barot et al. (2004) identified a downward shift in size at maturity in the Georges Bank Atlantic cod (*Gadus morhua*) that supports the hypothesis that an evolutionary change, likely caused by high fishing mortality, is partially responsible for the observed decline in age and size at maturity in these cod stocks (Olsen et al. 2005). Regardless of the causes of variation in maturation, size and age at maturity can have significant effects on the reproductive performance of the stock by regulating its reproductive potential. For example, fecundity and the quality and viability of eggs and larvae are directly related to the size of spawning females (Trippel et al. 1997, Marteinsdottir and Begg 2002). The extent to which these effects may extend over several generations and affect the adaptive capacity of populations is not yet well understood, although understanding these processes is critical to comprehending stock dynamics.

European hake (*Merluccius merluccius*) is a resource of great commercial importance in Atlantic Iberian waters. This species is assessed by the International Council for the Exploration of the Sea (ICES) in two units: the northern and the southern stocks (ICES 2021). The southern stock, which is the object of this

study, is distributed in the Atlantic Iberian waters that correspond to ICES divisions 27.8.c and 27.9.a. Though this stock has been subjected to a recovery plan since 2006 and the multiannual management plan for Western Waters, fishing mortality is still above that corresponding to the maximum sustainable yield (F_{msy}) (ICES 2021). For this stock, the main indicator of stock status is the spawning stock biomass, which is calculated as numbers, mean weight and proportion of mature fish. The proportion of mature fish was established for the entire study period (1982-2019) by estimating annual maturity ogives for both sexes combined based on macroscopic observations of hake specimens, although a time-constant female-only maturity ogive was used from 2020 onwards owing to the change of the assessment model. The impact of using different reproductive potential metrics (combined vs only female) was evaluated by Cerviño et al. (2013) for this stock, showing that, although the absolute values change, their impact on the management recommendations is slight because the reference points also change in the same direction.

Several studies have analysed the size at maturity of this stock (Dominguez-Petit et al. 2008, Murua 2010), but generally only for females and never for the two sexes separated. The objective of this study was to provide information on size at maturity for the period 1982-2019 in order to corroborate the decreasing trend of the L_{50} in this stock for each sex and to determine which factors explain this trend. Understanding which factors influence the size at maturity of the southern European hake stock can contribute to better assessment and management. To this end, we first estimated the size at maturity of the European hake for each sex in Atlantic Iberian waters from 1982 to 2019. Second, the variability of the L_{50} for each sex was modelled with generalized additive models, considering as explanatory variables environmental factors (Atlantic Multidecadal Oscillation, North Atlantic Oscillation and sea surface temperature), and biological variables (biomass, spawning biomass at length and relative factor condition) to test density-dependent effects and the year to assess the interannual variations.

MATERIALS AND METHODS

European hake data

Length and weight measurements were taken from historical records collected by the commercial sampling programme of the Spanish Institute of Oceanography (IEO) on a monthly basis between 1982 and 2019 from bottom trawlers that operate in the Atlantic Iberian waters, ICES divisions 27.8.c and 27.9.a. A total of 27692 hake specimens were sampled, from which individuals' length and weight (total and gutted), maturity stage and sex were recorded. Both maturity and sex,

were assessed based on macroscopic observations. Of the 27692 hake specimens, the majority (56%) were females. In addition, the majority of the specimens sampled (54%) were mature. Cross-referencing these variables (sex and maturity stage), the data indicate that 63% of the males and 46% of the females were mature.

In addition, 90% of the hake specimens were caught in division 27.9.a versus 10% in 27.8.c, which indicates that the data were not proportional by area. Also, data are not available in certain months for each year throughout the study period (For more details, see Table S1), which makes monthly analysis difficult. To avoid influence of these biases on analyses results, both areas (27.8.c and 27.9.a) were considered together and year was used as a temporal variable.

Owing to its complexity, dealing with a large amount of data coming from different sources of information is not exempt from human error. To avoid this, a thorough review of the matrix was carried out to ensure data consistency. Finally, to test for density-dependent effects, we included data on the total biomass (in tonnes) and spawning stock biomass (SSB, in tonnes) at length of the European hake for the study period, obtained from the data compiled by the ICES Working Group for the Bay of Biscay and the Iberian Waters Ecoregion (WGBIE) (ICES 2019) for assessment purposes.

Size at maturity

The percentage of mature females for every length class was fitted to a logistic equation as described by Ashton (1972):

$$PL = \frac{1}{1 + e^{-(\beta_0 + \beta_1 L)}},$$

where PL is the probability of an individual being mature at a given length, β_0 the intercept and β_1 the slope of the curve. These parameters are estimated by iteratively reweighted least squares, assuming a binomial distribution (mature-immature).

The length at which 50% of specimens were mature (L_{50} , size at maturity) was estimated as

$$L_{50} = -\frac{\hat{\beta}_0}{\hat{\beta}_1},$$

where $\hat{\beta}_0$ and $\hat{\beta}_1$ are the intercept and slope estimates, respectively, estimated using the *SizeMat* (Torre-jón-Magallanes 2020) package of the R software (R Core Team 2021).

In addition, the classical logistic models including and not including sex as a covariable and were compared through a Chisq likelihood-ratio test (P-value < 0.05) to check whether a partial effect of sex existed.

It should be noted that the lack of observations of immature male individuals for the years 2014 and 2015 owing to a reduction in the sampling prevented the size at maturity of males from being estimated in these years. To address this handicap, missing values were calculated using moving averages with a window of four (eight observations were taken into account; four

on the left and four on the right) using the *imputeTS* package (Moritz and Bartz-Beielstein 2017, see details in the supplementary materials).

Le Cren's condition factor

Body condition is a key indicator of the health status of fish since it is closely related to important fitness variables such as growth, reproduction, behaviour and survival. Consequently, the body condition can partially explain the L_{50} variability. Among the several indices proposed to measure body condition, Le Cren's relative condition factor (Kn) (Le Cren 1951) was selected. Le Cren's factor is defined as the observed weight of an individual divided by its predicted weight, which is obtained from the linear regression of the length-weight relationship (after linearizing using logarithms).

$$Kn = \frac{W}{\hat{a}L^{\hat{b}}},$$

where W is the total weight (g), L the total length (cm), the constant estimate and the exponent estimate usually between 2.5 and 4. The \hat{a} and \hat{b} length-weight relationship parameters were estimated using the *lm* function of the R software through the linear regression model $\log(W) = \log(a) + b \log(L)$. Guttled weight was missing for a large percentage of the individuals, so total weight was used instead. However, the presence of missing values of total weight prevented us from estimating the relative condition factor for males between 1998 and 2001 and for females between 1999 and 2001. These missing values were calculated by moving averages with a window of four using the *imputeTS* package (Moritz and Bartz-Beielstein 2017).

Environmental data

In order to analyse the effect of the environmental conditions on the L_{50} , we used the sea surface temperature (SST in °C) as a local environmental index and the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) as large-scale climate indices representative of sea level pressure patterns. The AMO and NAO indices were included because large-scale climatic events affect not only temperature but also ocean masses and circulation, which affect plankton and zooplankton (Nye et al. 2009, 2014). These indices have disproportionate effects on the early life stages of fishes because of alterations in food sources and temperature (Nye et al. 2009, 2014). SST was included because it affects the fish community through thermal tolerance and species migration (Marshall and Elliott 1998). The AMO and NAO annual-times series were downloaded from the US National Oceanic and Atmospheric Administration (NOAA, <http://www.noaa.gov/>). For SST, annual averages covering the entire study period (1982-2019) and sampling area were extracted from the NOAA NCDC platform (<https://www.ncdc.noaa.gov/oisst>), which provides a global 1/4° gridded dataset of the advanced very high-resolution radiometer.

Generalized additive models

Generalized additive models (GAMs, Wood 2017) were implemented to test the influences of temporal (year), environmental (SST, AMO and NAO) and biological (relative condition factor, biomass, and spawning biomass at length) variables on the L_{50} .

GAMs are semi-parametric extensions of generalized linear models (GLMs) for which the strictly linear predictor

$$g(\mu(\mathbf{X})) = \beta_0 + \beta_1 X_1 + \dots + \beta_p X_p,$$

where $\mathbf{X} = (X_1, \dots, X_p)$ are covariables, $\mu(X) = E(Y|X)$ is the conditional expectation of the response variable Y , g is the link function (explained below) and $\beta_0, \beta_1, \dots, \beta_p$ are the unknown parameters, is replaced by

$$g(\mu(\mathbf{X})) = \beta_0 + f_1(X_1) + \dots + f_p(X_p), \quad (1)$$

where $f_j(X_j)$ is the unknown smooth partial effect of X_j on the predictor. Hence, GAMs avoid the assumption of a linear relation between the response variable and the covariables, thus providing a more flexible model. Note that GLMs are an extension of linear models for which the distribution of the response variable can be other than Gaussian. For this reason, in the previous models a link function g is applied to $\mu(X)$. In this study, it was assumed that the Gaussian distribution correctly fits the response variable size at maturity (L_{50}).

Standardized data exploration techniques were used to identify any outliers and any correlation and collinearity between the explicative variables (Zuur et al. 2010). In particular, correlation among variables was checked using a Pearson's correlation test with the *corrplot* package (Wei et al. 2017) of the R software. In particular, correlation among variables was checked by performing a Pearson's correlation test with the *corrplot* package (Wei et al. 2017) of the R software. By calculating the generalized variance inflation factors (GVIF), which are the values of VIF corrected for the number of degrees of freedom of a predictor variable (Fox and Weisberg 2019), collinearity was tested. GVIF was evaluated using the *corvif* function in R software. In particular, as both the Pearson's correlation ($\rho > 0.70$) and the GVIF (> 3) were high between the year and AMO, the latter was not further considered in models for avoiding collinearity (see more details in supplementary materials).

Covariables were selected with a backward stepwise procedure based on the Akaike information criterion (AIC) and an adjusted R-square. The best (and most parsimonious) model was finally chosen based on the compromise between low AIC values, a high adjusted R-square and significant predictors.

Cubic regression splines basis were used for explanatory variables, restricting the dimension of the basis (k) to four to allow a high degree of flexibility without overfitting problems. When a spline was not required, the variable was considered a linear effect.

For each final GAM, a diagnosis of the model assumptions was carried out, among which the independence of the residuals was verified using the autocorrelation (ACF) and partial autocorrelation (PACF)

functions and the Ljung-Box test (Wood 2006). Additionally, results of Jarque-Bera and Shapiro-Wilk tests (normality assumption), a Dickey-Fuller test (stationarity assumption) and a Student t-test (zero mean assumption) were also explored.

The GAMs were performed using the *mgcv* package (Wood 2011) of the R software. The R code for the applied models can be found on the GitHub repository (<https://github.com/Lojamodav/PAPER.git>).

RESULTS

Size at maturity estimates

Firstly, a single value of the size at maturity of European hake was estimated for the whole period 1982-2019 and for both sexes combined, resulting in $L_{50} = 37.5$ cm. European hake shows sexual dimorphism, hence the was also estimated by sex in this period. The data exploration analysis showed that the estimate was 44.4 cm and 31.8 cm for females and males, respectively (Fig. 1). In conclusion, the partial effect of the sex covariable was significant.

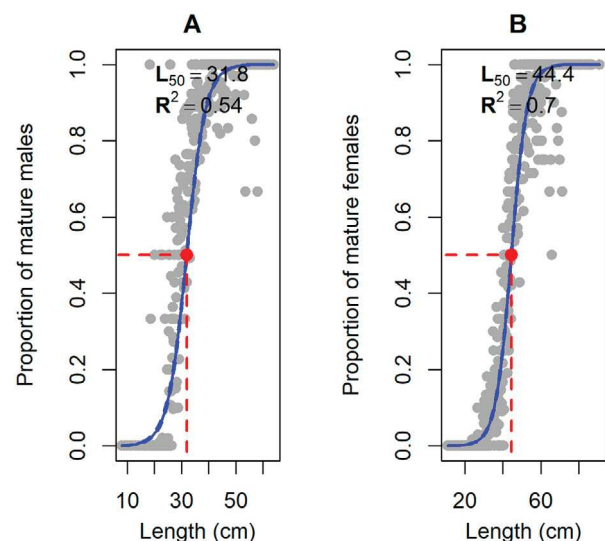


Fig. 1. – Maturity ogive for (A) males and (B) females of European hake in the period 1982-2019. The grey dots represent the observations, the blue line is the fitted model and the red line represents the size at maturity.

Secondly, sex-specific size at maturity was also estimated for each year of the time series (Fig. 2). The male L_{50} time series showed a decreasing trend over the whole period (Fig. 2A), while the female L_{50} time series showed two trends (Fig. 2B): an increasing trend starting in 1990 and reaching its highest value of 56.2 cm in 1996, followed by a decreasing trend in the L_{50} for the remaining years. The male L_{50} in 1982 was 36.1 cm and reached the lowest value of 23.2 cm in 2019, which is a decrease of 19.2 cm (40.6% in relative terms) with respect to the mean value for male L_{50} . However, the female L_{50} started at 49.7 cm in 1982 and declined to 38.8 cm at the end of the series, which represented a

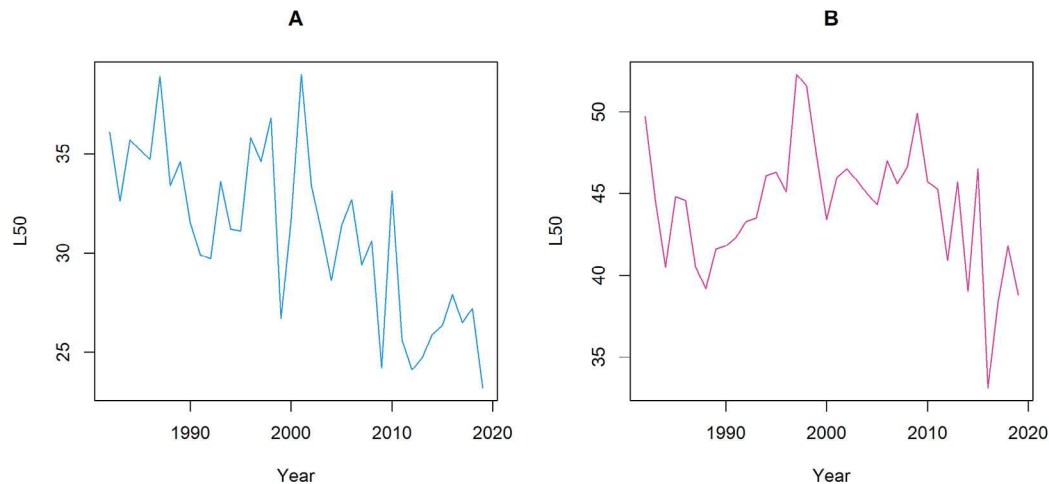


Fig. 2. – Temporal variability of size at maturity (L_{50}) during the time series (1982-2019) for (A) males and (B) females of European hake.

decrease of 24.5% in relative terms with respect to the mean value for female L_{50} .

Relative condition factor estimates

For the whole period 1982-2019 the relative condition factor of European hake was $Kn=0.88$ for both sexes combined, 0.61 for males and 1.10 for females. When Kn was estimated by year, it was observed that males showed a decreasing trend from the beginning of the time series until 1993, from which an increase in Kn was observed (Fig. 3B). Likewise, female Kn followed the same pattern as male Kn . In particular, the lowest Kn value for males and females was 0.37 and 0.35, respectively, recorded in 1993. This translates into a decrease in Kn of 39% and 68.2% (with respect to the mean) for males and females, respectively. In contrast, the highest Kn value was 0.87 (2014) and 2.48 (1998) for males and females, respectively, an increase of 42.6% and 125.45% for males and females in 1998, respectively. It should be noted that the high Kn value

for females in 1998 was due to a bias in the sample because only 15 mature hakes showed very high weights.

Analysis of temporal variability of L_{50}

The final GAM for European hake males derived from the backward stepwise procedure included only the year as a significant covariable (Tables 1 and S4).

The model results show that 55.3% of the L_{50} variability of European hake males was explained by the temporal covariable year. Figure 4 shows estimated smoother effect of year of the fitted GAM, which showed a negative relationship with the L_{50} estimates.

For European hake females, in addition to the temporal year covariable, the final GAM included the biological covariables, biomass and spawning biomass at length, and the NAO environmental covariable (Tables 2 and S5). This model explained 76.8% of the variability of the size at maturity of female hake.

In particular, year showed a dome-shaped relationship with L_{50} estimates (Fig. 5). Density-dependent ef-

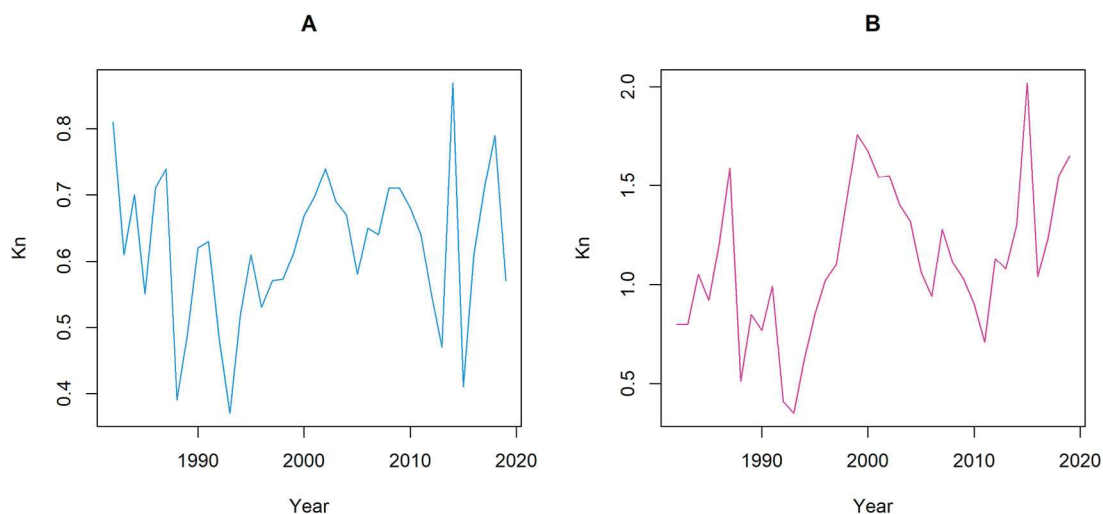


Fig. 3. – Temporal variability of the relative condition factor (Kn) of European hake from 1982 to 2019 for (A) males and (B) females.

Table 1. – Coefficient estimates of the final GAM for the size at maturity of European hake males.

	Parametric coefficients			
	Estimate	se	t value	Pr (> t)
$\hat{\beta}_0$	31.0263	0.4684	66.24	<2e-16 ***
	Significance of smooth functions			
	Edf	Ref. df	F	P-value
\hat{f} (year)	1.616	1.969	22.77	1.1e-06 ***

Table 2. – Coefficient estimates of the final GAM for size at maturity (L_{50}) of European hake females.

	Parametric coefficients			
	Estimate	Std error	t value	Pr (> t)
$\hat{\beta}_0$	44.4441	0.3035	146.4	<2e-16 ***
	Significance of smooth functions			
	Edf	Ref. df	F	P-value
\hat{f} (year)	2.595	3.245	2.541	0.04783 *
\hat{f} (biomass)	3.198	3.634	4.992	0.00474 **
\hat{f} (Spawning biomass at length)	2.249	2.788	7.734	0.00144 **
\hat{f} (NAO)	1.000	1.000	8.094	0.00821 **

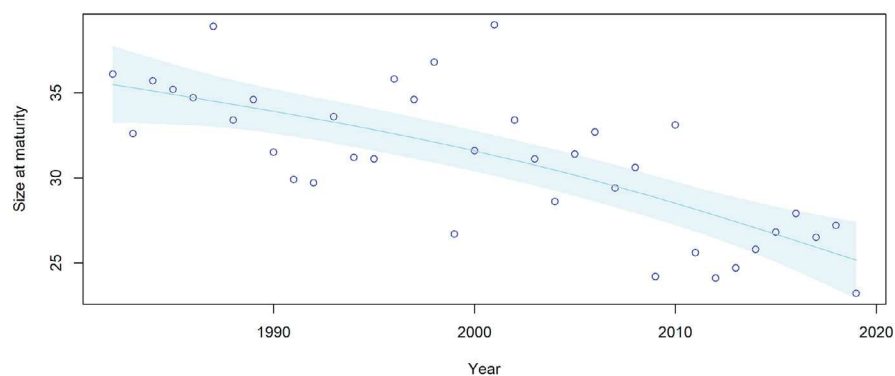


Fig. 4. – Estimated smoother effect of year for the GAM size at maturity (L_{50}) for males of the European hake for the time series (1982-2019). The blue circles represent the estimated annual values and the blue shading represents the 95% confidence intervals of the year's smooth component.

fects were detected. The results showed a positive relationship of biomass with L_{50} estimates and a negative relationship of spawning biomass at length with L_{50} estimates (Fig. 5). Finally, the NAO index also showed a slight positive relationship with L_{50} (Fig. 5).

In both GAMs all the theoretical assumptions were respected, and the results of the autocorrelation (ACF) and partial autocorrelation (PACF) functions and the Ljung-Box test of the residuals are presented in the supplementary material.

DISCUSSION

Understanding biological processes underlying southern hake stock dynamics in Atlantic Iberian waters

can help to improve their assessment and management. The overall aim of this study was to assess changes in the size at maturity (L_{50}) of both sexes in the period 1982-2019 and determine the potential drivers of its variation.

It should be mentioned that the data used in this study were limited to the northern part of the southern stock distribution and that, owing to the missing data and the way the data were compiled, these results should be interpreted with caution. However, our results highlight the importance of understanding the factors affecting the balance between the energy invested in reproduction, maintenance and growth and the interannual variability of this trade-off. This is the only way to understand how environmental pressures influence the population dynamics of this species at a regional scale.

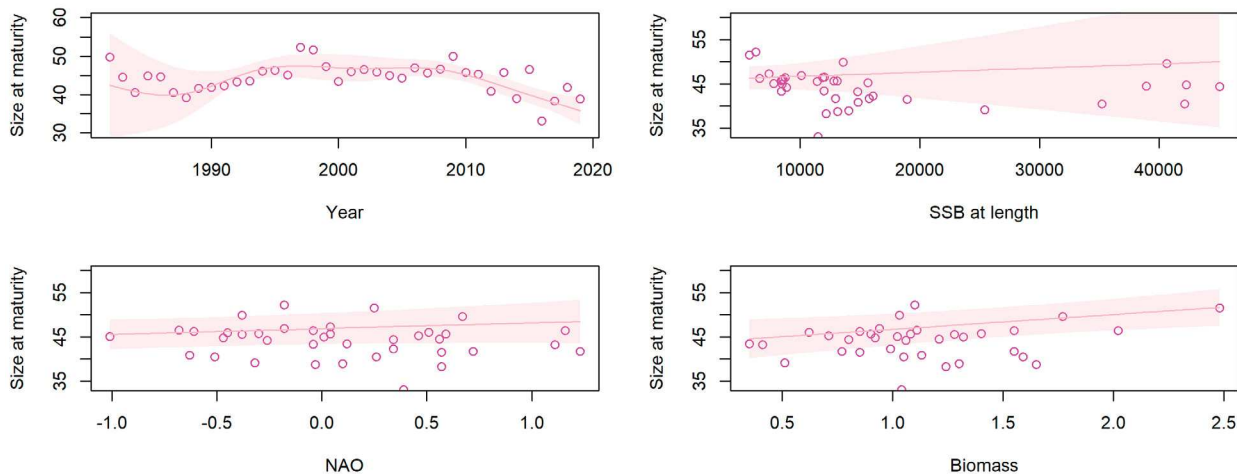


Fig. 5. – Estimated smooth effects of year, spawning biomass at length, NAO and biomass for the GAM size at maturity (L_{50}) for females of European hake during the time series (1982–2019). The pink circles represent the estimated annual values and the pink shading represents the 95% confidence intervals of the smooth components.

The results of this study showed that differentiated long-term patterns were observed for the two sexes, with major long-term declines for male hakes. For males, the size at maturity decreased by 12.9 cm over the study period, from 36.1 cm in 1982 to 23.2 cm, the lowest observed value, in 2019. However, for females two trends in L_{50} can be distinguished: an increasing trend starting in 1990 and reaching its highest value of 56.2 cm in 1996, followed by a decreasing trend for the rest of the time series, reaching a value of 38.8 cm in 2019.

In relation to Kn , both sexes showed the same structure, that is, a tendency to increase from 1993 onwards, in which year both males and females reached the minimum values of 0.37 and 0.35, respectively. This translates into a decrease in Kn of 39% for males and 68.2% for females with respect to the mean. In contrast, the highest Kn value was 0.87 in 2014 for males and 2.48 in 1998 for females, which is an increase of 42.6% and 125.45% percentage points, respectively. It should be noted that the high Kn value for females in 1998 is due to a bias in the sample, as only 15 mature hakes showed very high weights. This can be explained by the fact that when total weight (heavily influenced by gonad size/maturity stage and stomach size/repletion stage) is used to calculate Kn , these weights can fluctuate markedly because of factors unrelated to the actual physiological condition of the hake specimen.

From the above, it can be deduced that though both sexes follow the same pattern for Kn , male and female maturity responded differently to over time, likely linked to external drivers, including fishing pressure.

The reproductive system of fish reacts to any changes in life conditions, so variations in growth and reproduction dynamics of fish populations substantially affects fish production not only quantitatively but also qualitatively (Godø and Haug 1999, Oven 2004). When fishing pressure removes old and large individuals from the spawning stock, it may favour density-dependent growth, leading to an increase in size at maturity (Olsen et al. 2004); however, if fishing pressure

is too intense and maintained for a long time, it can remove the fast-growth or large-size genotypes from the stock, resulting in a decrease of size at maturity and even causing evolutionary changes in the stock (Trippel 1995, Jørgensen et al. 2007, Hidalgo et al. 2012).

In Iberian Atlantic waters, European hake has been exploited beyond safe biological limits since the 1990s, with the largest landings being recorded in this period, but in 2004 it was declared in a critical state because of overfishing (Dominguez-Petit 2007, Korta et al. 2010). Currently, the stock is considered to be in a relatively healthy status but still shows reduced reproductive capacity, according to the annual observed recruitment. It is still intensely exploited (in 2018, $F=0.60$), exceeding the rate of fishing mortality for the maximum sustainable yield ($F_{msy}=0.25$) but not above the precautionary limits ($F_{pa}=0.75$) (ICES 2019). In addition, European hake is the target of mixed fisheries delivered by the industrial and artisanal fleets with different gears: gillnet, longline and different trawl gears (Korta et al. 2015, ICES 2019) targeting medium-large specimens (<40cm). Gillnets and longlines, have accounted for 16% and 13% of catches during the last decade, respectively, targeting hake adults (especially longliners that target large hake). However, Dominguez-Petit (2007) and Korta et al. (2015), reported a decrease in the mean hake size in the landings in the last few decades independently of the gear type used, supporting the perception of overexploitation.

In line with the above, fishing pressure has been widely reported as a selection factor for larger individuals with an effect that is especially problematic when the oldest and largest individuals of the population are removed (Law 2000), because the size/age truncation of the stock leads to a decrease in reproductive potential (Hixon et al. 2014). However, no proxy for fishing effort was considered in our models (for both males and females) owing to the lack of detailed and reliable fleet information (with the same spatial and temporal coverage) that could support this hypothesis. On the

contrary, biological (biomass, spawning biomass at length and K_n) and environmental factors (NAO and SST) were considered as drivers of the variations in the decrease of L_{50} for each sex.

Several studies have addressed the changes in the maturity ogives in different species (Haug and Tjemsland 1986, Junquera et al. 1999, Marteinsdottir and Begg 2002, Engelhard and Heino 2004). In particular, Dominguez-Petit et al. (2008) studied these changes for European hake, although males were not considered in their study. They observed for the southern stock that the size at maturity increased even when total biomass and spawning biomass continued to decrease, which is contrary to the compensatory theory, probably as a consequence of environmental drivers such as NAO and upwelling. However, their results indicate that the pattern of the size at maturity in the Bay of Biscay (northern stock) was different, as a steady decline was observed throughout the study period.

For male hake, both environmental and biological factors failed to explain the trend towards decreasing L_{50} for our entire study period. This may well be explained by the fact that fishing pressure has eliminated larger individuals (mostly females), which could lead to a clear alteration of growth rates, causing profound changes in L_{50} , either because fishing intensity has caused a regime shift, which has caused the main drivers of maturation/growth to change, or even because there has been a regime shift in the fishery itself, so fishing pressure has lost influence relative to other drivers. Considering the above, fishing pressure and behaviour of the trawl fleet could explain the decline, but further work is required because males and females do not show the same response.

In the case of female hake, the reduction in stock biomass, usually as a consequence of high fishing exploitation, leads to a reduction in size at maturity. The results showed a negative relationship between biomass and size at maturity for female hake, which is to be expected in a density-dependent relationship. The higher the biomass, the greater the intraspecific competition, the lower the growth and the lower the L_{50} . However, the results showed a positive relationship between biomass at spawning and L_{50} , which is contrary to the compensatory theory. The lack of compensatory response is known as depensation. According to Liermann and Hilborn (2001), there are four mechanisms of depensation: i) reduced probability of fertilization, ii) altered group dynamics, iii) environmental influences and iv) predator saturation. These four mechanisms are responsible for the lack of a compensatory response, although population density and intraspecific competition decrease.

Major observed declines in L_{50} are usually explained by unfavourable environmental conditions that reduce growth or by high fishing pressure (or a combination of both) as a mechanism to maximize fitness (Albo-Puigserver et al. 2021). L_{50} is expected to be more variable than other traits, particularly in heterogeneous environments (Hidalgo et al. 2014).

The only significant environmental variable included in our model for European hake females was

the NAO index, which showed a positive relationship with the L_{50} . The NAO is the most important source of variability in the North Atlantic region. The NAO index acts as an integrator of several environmental factors that can have a synergistic effect on fisheries dynamics. NAO impacts on air temperature, wind and precipitation regime and on large water mass distribution and flow, with the subsequent influence that all these factors have on marine ecosystems (Greene and Pershing 2000, Köster et al. 2005). Effects of the NAO ripple influence life history traits and population dynamics and do so across trophic levels from primary production to predators (Ottersen et al. 2001). In fact, many examples show that NAO drives the life history and dynamics of many fish populations (Ottersen et al. 2001, Hjermann et al. 2004, Sullivan and Cowen 2005) and in particular of the European hake stocks (Meiners-Mandujano 2007, Dominguez-Petit et al. 2008, Goikoetxea and Irigoien 2013). Similarly, Drinkwater (2005) showed that NAO explains approximately 50% of the variability in the growth increase of northern cod between ages three and five in Newfoundland, which is undoubtedly a determinant of L_{50} , as these are the ages at which cod mature in this area. For female hake something similar may occur: positive NAO values imply higher growth, which implies higher L_{50} . The NAO index may influence the maturation process of hake indirectly through alterations in ecosystem composition and resource availability (Köster et al. 2005, Kell et al. 2005).

CONCLUSIONS

The size at maturity of the southern European hake stock has declined in both sexes in the last few decades. The present results show that the maturation of southern hake is influenced by a combination of demographic, anthropogenic and environmental factors, leading to a deeper understanding of the factors explaining the annual decrease in L_{50} for both sexes, which was the objective of this study.

However, determining which variables explain the decreasing trends in L_{50} for both sexes requires applying more complex models than an overall linear trend to all the data, because there are much more complex relationships between L_{50} and the factors that may explain the variability in L_{50} .

Total biomass, spawning biomass at length and the NAO partially explain the decline in the L_{50} of females, but for males no relevant factor was found among the analysed ones that could explain this drastic decline. Overall, life history traits that rapidly respond to external changes, such as L_{50} , might be good indicators to anticipate further declines in populations and require close monitoring and evaluation. That is why this study reiterates the need for a posteriori studies to confirm the hypothesis of fishing pressure as a maturity driver in order to have a better understanding of the underlying dynamics of this stock. Additionally, the impact of the reduction in the L_{50} in males on the reproductive potential of the stock should be also investigated as paternal effects have proved to be more important than

previously thought in stock dynamics (Dominguez-Petit et al. 2022).

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REFERENCES

- Albo-Puigserver M., Pennino M.G., Bellido J.M., et al. 2021. Changes in life history traits of small pelagic fish in the western Mediterranean Sea. *Front. Mar. Sci.* 8: 1197. <https://doi.org/10.3389/fmars.2021.570354>
- Ali M., Nicieza A., Wootton R.J. 2003. Compensatory growth in fishes: a response to growth depression. *Fish. Fish.* 4: 147-190. <https://doi.org/10.1046/j.1467-2979.2003.00120.x>
- Ashton W.D. 1972. The logit transformation with special reference to its uses in bioassay. Haffner Publishing Co., INC., New York, 88 pp.
- Barot S., Heino M., O'Brien L., Dieckmann U. 2004. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evol. Ecol. Res.* 6: 659-678.
- Cervino S., Dominguez R., Jardim E., et al. 2013. Impact of egg production and stock structure on MSY reference points. Implications for Southern hake management. *Fish. Res.* 138: 168-178. <https://doi.org/10.1016/j.fishres.2012.07.016>
- Dalglish H.J., Koons D.N., Adler P.B. 2010. Can life-history traits predict the response of populations to changes in climate variability? *J. Ecol.* 98: 209-217. <https://doi.org/10.1111/j.1365-2745.2009.01585.x>
- Dominguez-Petit R. 2007. Study of reproductive potential of *Merluccius merluccius* in the Galician shelf. Doctoral Thesis. University of Vigo, Spain.
- Dominguez-Petit R., Korta M., Saborido-Rey F., et al. 2008. Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environmental regimes. *J. Mar. Syst.* 71: 260-278. <https://doi.org/10.1016/j.jmarsys.2007.04.004>
- Dominguez-Petit R., Garcia-Fernandez C., Leonarduzzi E., et al. 2022. Parental effects and reproductive potential of fish and marine invertebrates: Cross-generational impact of environmental experiences. In: Dominguez-Petit R. (ed). *Impact of Environmental Stress on Reproductive Processes of Aquatic Animals*. Fishes 7: 188. <https://doi.org/10.3390/fishes7040188>
- Drinkwater K.F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J. Mar. Sci.* 62: 1327-1337. <https://doi.org/10.1016/j.icesjms.2005.05.015>
- Engelhard G.H., Heino M. 2004. Maturity changes in Norwegian spring spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* 272: 245-256. <https://doi.org/10.3354/meps272245>
- Fox J., Weisberg S. 2019. *An R Companion to Applied Regression* (Third). SAGE Publications Inc, pp. 608.
- Godø O.R., Haug T. 1999. Growth rate and sexual maturity in cod (*Gadus morhua*) and Atlantic halibut (*Hippoglossus hippoglossus*). *J. Northwest Atl. Fish. Sci.* 25: 115-123. <https://doi.org/10.2960/J.v25.a10>
- Goikoetxea N., Irigoien X. 2013. Links between the recruitment success of northern European hake (*Merluccius merluccius* L.) and a regime shift on the NE Atlantic continental shelf. *Fish. Oceanogr.* 22: 459-476. <https://doi.org/10.1111/fog.12033>
- Greene C.H., Pershing A.J. 2000. The response of *Calanus finmarchicus* populations to climate variability in the North-west Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. *ICES J. Mar. Sci.* 57: 1536-1544. <https://doi.org/10.1006/jmsc.2000.0966>
- Haug T., Tjemsland T. 1986. Changes in size and age distribution and age at sexual maturity in Atlantic Halibut, *Hippoglossus hippoglossus*, caught in North Norwegian waters. *Fish. Res.* 4: 145-155. [https://doi.org/10.1016/0165-7836\(86\)90039-1](https://doi.org/10.1016/0165-7836(86)90039-1)
- Hidalgo M., Rouyer T., Bartolino V., et al. 2012. Context-dependent interplays between truncated demographics and climate variation shape the population growth rate of a harvested species. *Ecography* 35: 637-649. <https://doi.org/10.1111/j.1600-0587.2011.07314.x>
- Hidalgo M., Rouyer T., Molinero J.C., et al. 2014. Contrasting evolutionary demography induced by fishing: The role of adaptive phenotypic plasticity. *Ecol. App.* 24: 1101-1114. <https://doi.org/10.1890/12-1777.1>
- Hixon M.A., Johnson D.W., Sogard S.M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71: 2171-2185. <https://doi.org/10.1093/icesjms/fst200>
- Hjermann D.O., Stenseth N.C., Ottersen G. 2004. Indirect climatic forcing of the Barents Sea capelin: a cohort effect. *Mar. Ecol. Prog. Ser.* 273: 229-238. <https://doi.org/10.3354/meps273229>
- Hobday A.J., Smith A.D.M., Stobutzki I.C., et al. 2011. Ecological risk assessment for the effects of fishing. *Fish. Res.* 108: 372-384. <https://doi.org/10.1016/j.fishres.2011.01.013>
- Hollins J., Thambithurai D., Koeck B., et al. 2018. A physiological perspective on fisheries-induced evolution. *Evol. Appl.* 11: 561-576. <https://doi.org/10.1111/eva.12597>
- ICES. 2019. Working Group for the Bay of Biscay and the Iberian Waters Ecoregion (WGBIE). *ICES Sci. Rep.* 1: 31.
- ICES. 2021. Working Group for the Bay of Biscay and the Iberian Waters Ecoregion (WGBIE). *ICES Sci. Rep.* 3: 48.
- Jørgensen C., Enberg K., Dunlop E.S., et al. 2007. Ecology: Managing Evolving Fish Stocks. *Sci.* 318: 1247-1248. <https://doi.org/10.1126/science.1148089>
- Junquera S., Roman E., Paz X., Ramilo G. 1999. Changes in Greenland halibut growth, condition and fecundity in the Northwest Atlantic (Flemish Pass, Flemish Cap and southern Grand Banks). Variations in maturation, growth, condition and spawning stock biomass production in groundfish. *J. Northwest Atl. Fish. Sci.* 25: 17-28. <https://doi.org/10.2960/J.v25.a2>
- Kell L.T., Pilling G.M., O'Brien C.M. 2005. Implications of the climate change for the management of North Sea cod (*Gadus morhua*). *ICES J. Mar. Sci.* 62: 1483-149. <https://doi.org/10.1016/j.icesjms.2005.05.006>
- Korta M., Dominguez-Petit R., Murua H., Saborido-Rey F. 2010. Regional variability in reproductive traits of European hake *Merluccius merluccius* L. populations. *Fish. Res.* 104: 64-72. <https://doi.org/10.1016/j.fishres.2009.03.007>
- Korta M., García, D., Santurtún M., et al. 2015. "European Hake (*Merluccius merluccius*) in the North-east Atlantic," in *Hakes: biology and Exploitation*, ed. H. Arancibia (Hoboken: John Wiley & Sons, Ltd), 1-37. <https://doi.org/10.1002/9781118568262.ch1>
- Köster F.W., Möllmann C., Hinrichsen H.H., et al. 2005. Baltic cod Recruitment - the impact of climate variability on key processes. *ICES J. Mar. Sci.* 62: 1408-1425. <https://doi.org/10.1016/j.icesjms.2005.05.004>
- Law R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57: 659-668. <https://doi.org/10.1006/jmsc.2000.0731>
- Le Cren E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch. *J. Anim. Ecol.* 2: 201-219. <https://doi.org/10.2307/1540>
- Liermann M., Hilborn R. 2001. Depensation: evidence, models and implications. *Fish. Fish.* 2: 33-58. <https://doi.org/10.1046/j.1467-2979.2001.00029.x>
- Lorenzen K., Camp E.V. 2019. Density-dependence in the life history of fishes: when is a fish recruited? *Fish. Res.* 217: 5-10. <https://doi.org/10.1016/j.fishres.2018.09.024>

- Marshall S., Elliott M. 1998. Environmental influences on the fish assemblage of the Humber estuary. U.K. Estuar. Coast. Shelf Sci. 46:175-184.
<https://doi.org/10.1006/ecss.1997.0268>
- Marteinsdottir G., Begg G.A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 235:235-256.
<https://doi.org/10.3354/meps235235>
- Meiners-Mandujano C.G. 2007. Importancia de la variabilidad climática en las pesquerías y biología de la merluza europea *Merluccius merluccius* (Linnaeus, 1758) de la costa Noroccidental Africana. PH.D. Thesis. Universitat Politècnica de Catalunya (UPC) (Spain). 207 pp.
- Moritz S., Bartz-Beielstein T. 2017. Imputets: Time Series Missing Value Imputation in R. R J. 9: 207-218.
<https://doi.org/10.32614/RJ-2017-009>
- Murua H. 2010. The biology and fisheries of European hake, *Merluccius merluccius*, in the north-east Atlantic. Adv. Mar. Biol. 58: 97-154.
<https://doi.org/10.1016/B978-0-12-381015-1.00002-2>
- Nye J.A., Link J.S., Hare J.A., Overholtz W.J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar. Ecol. Prog. Ser. 393, 111-129.
<https://doi.org/10.3354/meps08220>
- Nye J. A., Baker M.R., Bell R., et al. 2014. Ecosystem effects of the Atlantic Multidecadal Oscillation. J. Mar. Syst. 133, 103-116.
<https://doi.org/10.1016/j.jmarsys.2013.02.006>
- Öckinger E., Schweiger O., Crist T.O., et al. 2010 Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. 13: 969-979.
<https://doi.org/10.1111/j.1461-0248.2010.01487.x>
- Olsen E.M., Heino M., Lilly G.R., et al. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature. 428: 932-935.
<https://doi.org/10.1038/nature02430>
- Olsen EM, Lilly GR, Heino M, et al. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 62:811-823.
<https://doi.org/10.1139/f05-065>
- Ottersen G., Planque B., Belgrano A., et al. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia. 128: 1-14.
<https://doi.org/10.1007/s004420100655>
- Oven L.S. 2004. Resorption of Vitellogenic Oocytes as an Indicator of the State of the Black Sea Fish Populations and Their Environment. Journal of Ichthyology, 44: 115-119.
- Pepin P. 2015. Reconsidering the impossible - linking environmental drivers to growth, mortality, and recruitment of fish. Can. J. Fish. Aquat. Sci. 73: 205-215.
<https://doi.org/10.1139/cjfas-2015-0091>
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Version 4.1.2. Vienna, Austria.
- Sullivan M.C., Cowen R.K., Steves B.P. 2005. Evidence for atmosphere-ocean forcing of yellowtail flounder (*Limanda ferruginea*) recruitment in the Middle Atlantic Bight. Fish Oceanogr. 14: 386-399.
<https://doi.org/10.1111/j.1365-2419.2005.00343.x>
- Torrejón-Magallanes E.J. 2020. sizeMat: Estimate Size at Sexual Maturity. R package version 1.1.2.
- Trippel E.A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience. 45:759-771.
<https://doi.org/10.2307/1312628>
- Trippel E.A., Kjesbu O.S., Solemdal P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In Chambers R.C., Trippel E.A. (eds), Early life history and recruitment in fish populations. Chapman and Hall, London, U.K, pp. 31-62.
https://doi.org/10.1007/978-94-009-1439-1_2
- Wei T., Simko V., Levy M., et al. 2017. Package 'corrplot'. J. Am. Stat. 56: 316-324.
- Wood S.N. 2006. Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC. Series: Chapman & Hall/CRC. Texts in Statistical Science.
- Wood S.N. 2011. MgcV: GAMs with GCV/AIC/REML smoothness estimation and GAMMs by REML/PQL.
- Wood S.N. 2017. Generalized Additive Models: An Introduction with R (2nd edition). Chapman and Hall/CRC, New York, 496 pp.
- Zuur A.F., Ieno E.N., Elphick C.S. 2010. A protocol for data exploration to avoid common statistical problems. Methods. Ecol. Evol. 1: 3-14.
<https://doi.org/10.1111/j.2041-210X.2009.00001.x>

SUPPLEMENTARY MATERIAL

Table S1. – Number of hake samples per month and year.

	1	2	3	4	5	6	7	8	9	10	11	12
1980	0	0	0	0	177	115	333	0	97	0	0	99
1981	50	0	0	0	0	0	0	0	0	0	0	0
1982	81	43	152	61	31	30	33	0	0	0	0	0
1983	0	93	49	151	0	24	0	0	0	0	0	0
1984	22	142	302	232	0	0	48	22	0	119	122	0
1985	167	168	21	50	252	245	328	294	0	277	155	251
1986	63	181	45	0	0	0	0	103	0	93	0	0
1987	0	0	0	0	0	5	165	0	0	0	3	0
1988	0	76	0	0	0	462	240	231	91	0	0	0
1989	0	29	290	57	345	230	38	198	0	0	0	0
1990	0	98	130	43	14	66	0	142	0	34	58	0
1991	58	0	35	77	332	25	41	74	0	0	0	0
1992	0	26	134	0	0	0	0	0	0	0	0	0
1993	0	0	0	38	32	135	0	0	0	0	0	33
1994	0	83	60	0	143	36	0	0	12	20	117	35
1995	0	81	154	175	0	94	67	32	10	0	80	0
1996	0	5	227	8	83	152	71	199	201	16	41	18
1997	12	73	101	8	47	119	0	143	0	110	0	0
1998	0	0	101	0	162	0	23	0	5	0	0	0
1999	0	76	83	51	34	0	2	0	0	2	0	3
2000	31	43	7	50	0	40	22	0	76	0	55	0
2001	10	14	42	0	22	0	0	0	0	0	0	0
2002	0	0	0	0	74	177	133	0	35	40	27	12
2003	95	280	164	159	323	298	358	146	48	103	195	140
2004	272	162	284	164	200	281	80	165	140	63	318	64
2005	138	198	260	75	272	3	215	419	0	0	286	0
2006	248	116	80	348	0	33	224	0	0	0	0	52
2007	162	39	258	161	116	143	118	78	148	52	0	109
2008	152	225	25	246	65	75	84	157	0	0	76	153
2009	140	21	29	100	27	0	0	169	0	0	0	0
2010	147	106	66	112	48	0	151	0	41	0	11	25
2011	0	0	286	0	20	0	62	112	0	0	106	0
2012	44	71	121	0	0	0	0	0	0	0	0	0
2013	0	30	0	98	47	97	0	0	56	0	0	36
2014	0	51	0	23	110	0	0	0	0	0	0	18
2015	0	73	0	0	18	0	0	0	0	0	0	0
2016	0	76	95	37	79	49	0	0	0	0	0	0
2017	0	0	0	20	270	0	50	0	0	0	42	38
2018	0	65	0	0	72	15	0	0	0	0	43	0
2019	46	46	0	56	119	0	0	0	0	0	0	0

Missing values

In this section, a graphical analysis is presented to illustrate the data for size at maturity (for males and females) and the relative condition factor (for males and females) during the study period before imputing missing values.

Missing values for size at maturity

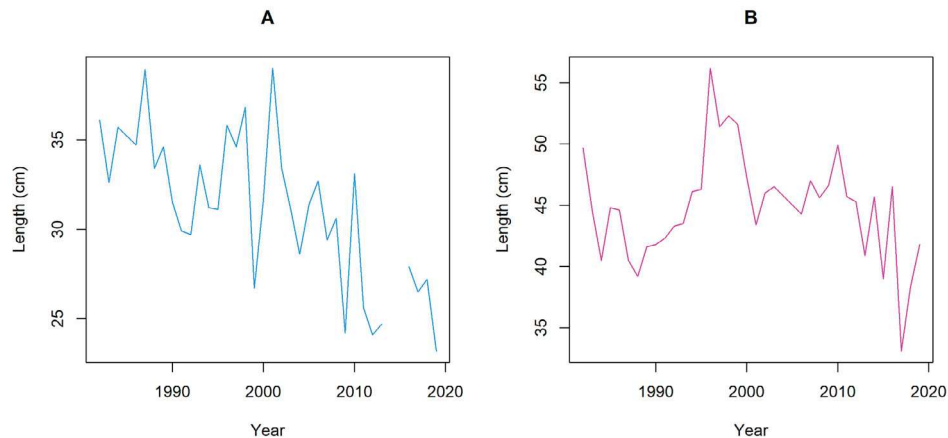


Fig. S1. – Annual variation of the size at maturity for male (A) and female (B) hakes before imputation of missing values.

Missing values for relative condition factor

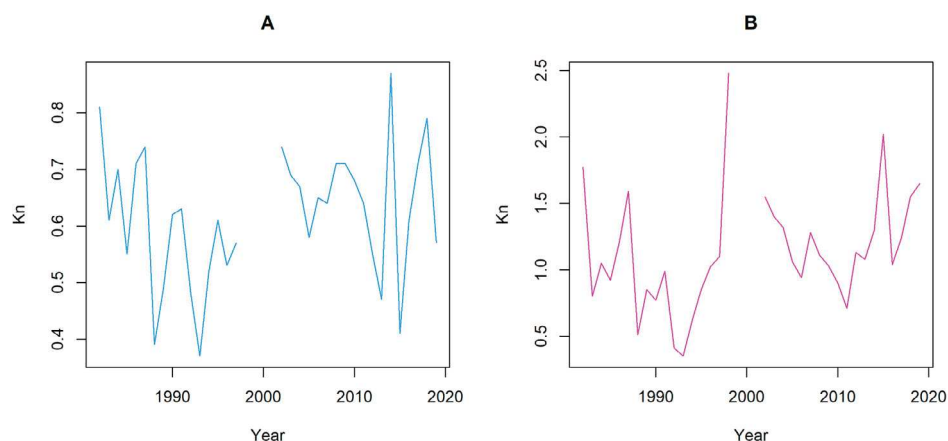


Fig. S2. – Annual variation of the relative condition factor for male (A) and female (B) hakes before imputation of missing values.

Correlation and multicollinearity analysis

In this section, data exploration techniques were presented to identify possible correlation and collinearity between the explanatory variables (Zuur et al. 2010) used for males and females in L_{50} GAM models. In particular, correlation among variables was checked by performing a Pearson correlation test with the *corrplot* package (Wei et al. 2017) of the R software. Collinearity was tested by computing the GVIFs, which are the VIF values corrected by the number of degrees of freedom of a predictor variable (Fox and Weisberg 2017).

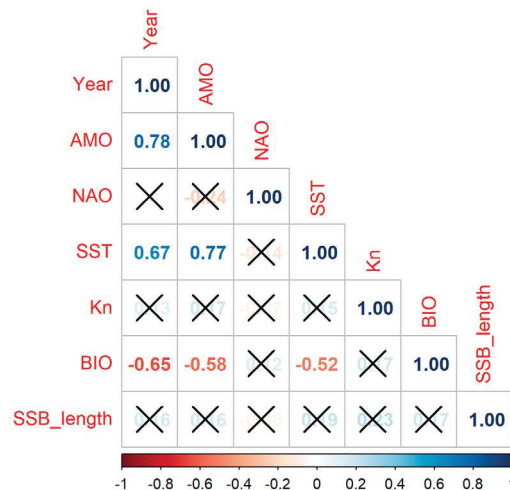
European hake males

Fig. S3. – Correlation matrix between predictor variables using regression for male L_{50} with Pearson correlation coefficients (*corrplot* package; Wei et al. 2017). Colour intensity (light to dark) and size of circles are proportional to Pearson correlation coefficients; positive correlations are represented in blue and negative correlations in red. Significant values are shown ($p < 0.05$). NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation; SST, sea surface temperature; SSB, spawning stock biomass at length; BIO, biomass; Kn, relative condition factor.

Table S2. – Checking for multicollinearity predictors variables using regression for male L_{50} with generalized variance inflation factors (GVIF). GVIF values < 3 demonstrate an absence of collinearity issues. NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation; SST, sea surface temperature; SSB_length, spawning stock biomass at length; BIO, biomass; Kn, relative condition factor.

Predictor variables	GVIF
Year	2.944590
AMO	3.234100
NAO	1.135156
SST	2.432250
Kn	1.161385
BIO	2.366113
SSB_length	1.304750

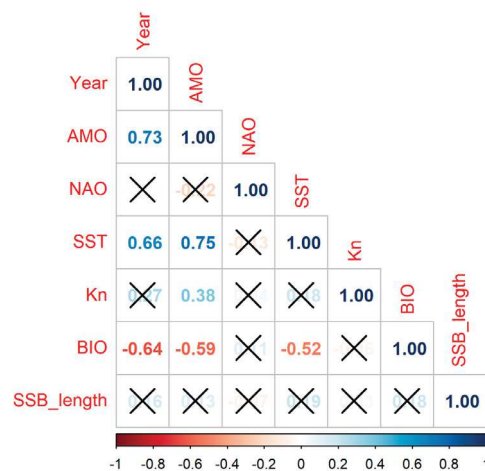
European hake females

Fig. S4. – Correlation matrix between predictor variables using regression for female L_{50} with Pearson correlation coefficients (*corrplot* package; Wei and Simko, 2017). Colour intensity (light to dark) and size of circles are proportional to Pearson correlation coefficients; positive correlations are represented in blue and negative correlations in red. Significant values are shown ($p < 0.05$). NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation; SST, sea surface temperature; SSB, spawning stock biomass at length; BIO, biomass; Kn, relative condition factor.

Table S3. – Checking for multicollinearity predictor variables using regression for female L_{50} with generalized variance inflation factors (GVIF). GVIF values <3 demonstrate an absence of collinearity issues. Variables acronyms are: NAO, North Atlantic Oscillation; AMO, Atlantic Multidecadal Oscillation; SST, sea surface temperature; SSB_length, spawning stock biomass at length; BIO, biomass; Kn, relative condition factor.

Predictors variables	GVIF
Year	3.278021
AMO	3.436279
NAO	1.130783
SST	2.499691
Kn	1.494685
BIO	2.304125
SSB_length	1.459627

Backward procedure of models

Covariables for each final GAM were selected with a backward stepwise procedure based on the AIC and adjusted R-square. The best (and most parsimonious) model was finally chosen based on the compromise between low AIC values, high adjusted R-square and significant predictors.

European hake males

Table S4. – Comparison between the generalized additive models of the L_{50} of European hake males during the study period (1982-2019). NAO, North Atlantic Oscillation; SST, sea surface temperature; SSB_length, spawning stock biomass at length; BIO, biomass; Kn, relative condition factor; D2 (%), deviance explained; AIC, Akaike information criterion. With respect to the model, s() indicates smooth function. bs specifies the type of function we are going to approximate, in this case we select “cr” cubic regression; K indicates the degree of the polynomial of the curve; and REML is the restricted maximum likelihood used to estimate these parameters.

Models	D2 (%)	AIC
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 6) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SST}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SSB_length}, \text{bs} = \text{“cr”}, k = 6) + s(\text{BIO}, \text{bs} = \text{“cr”}, k = 6) + s(\text{Kn}, \text{bs} = \text{“cr”}, k = 6), \text{method} = \text{“REML”}, \text{data} = L_{50}\text{mb})$	63.8%	195.07
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 6) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SSB_length}, \text{bs} = \text{“cr”}, k = 6) + s(\text{Kn}, \text{bs} = \text{“cr”}, k = 6), \text{method} = \text{“REML”}, \text{data} = L_{50}\text{mb})$	61.6%	191.94
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 6) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SSB_length}, \text{bs} = \text{“cr”}, k = 6), \text{method} = \text{“REML”}, \text{data} = L_{50}\text{mb})$	59.8%	191.71
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 7) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 7), \text{method} = \text{“REML”}, \text{data} = L_{50}\text{mb})$	57.5%	191.75
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 5), \text{method} = \text{“REML”}, \text{data} = L_{50}\text{mb})$	55.3%	193.65

European hake females

Table S5. – Comparison between the generalized additive models of the L_{50} of European hake females during the study period (1982-2019). NAO, North Atlantic Oscillation; SST, sea surface temperature; SSB_length, spawning stock biomass at length; BIO, biomass; Kn, relative condition factor; D2 (%), deviance explained; AIC, Akaike information criterion. With respect to the model, s() indicates smooth function. bs = specifies the type of function we are going to approximate, in this case we select “cr” = cubic regression; K indicates the degree of the polynomial of the curve; and REML is the restricted maximum likelihood used to estimate these parameters.

Models	D2 (%)	AIC
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SSB_length}, \text{bs} = \text{“cr”}, k = 6) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SST}, \text{bs} = \text{“cr”}, k = 6) + s(\text{BIO}, k = 6, \text{bs} = \text{“cr”}) + s(\text{Kn}, k = 6, \text{bs} = \text{“cr”}), \text{method} = \text{“REML”}, \text{data} = L_{50})$	76.8%	172.31
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 6) + s(\text{SSB_length}, \text{bs} = \text{“cr”}, k = 6) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 6) + s(\text{BIO}, k = 6, \text{bs} = \text{“cr”}) + s(\text{Kn}, k = 6, \text{bs} = \text{“cr”}), \text{method} = \text{“REML”}, \text{data} = L_{50})$	76.8%	170.49
$m \sim \text{gam}(L_{50} \sim s(\text{Year}, \text{bs} = \text{“cr”}, k = 7) + s(\text{SSB_length}, \text{bs} = \text{“cr”}, k = 7) + s(\text{NAO}, \text{bs} = \text{“cr”}, k = 7) + s(\text{BIO}, k = 7, \text{bs} = \text{“cr”}), \text{method} = \text{“REML”}, \text{data} = L_{50})$	76.8%	169.21

Residual analysis for generalized additive models

This section presents the contrasts of the basic hypotheses on the residuals of the GAMs addressed in this study to explain the annual variability of the size at maturity for male and female European hakes.

European hake males

Table S6. – Tests of the hypotheses on the residuals of the model for the size at maturity of males.

Test	Hypotheses	P-value
Jarque-Bera	Normality	0.587
Shapiro-Wilk	Normality	0.5972
Dickeye-Fuller	Stationarity	0.01
Student's t	Zero mean	1

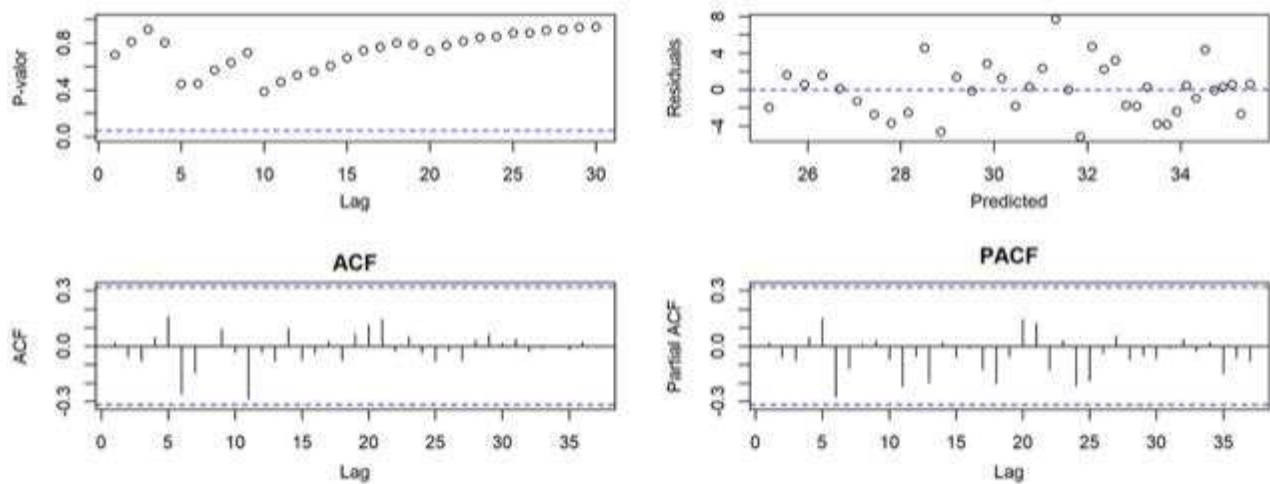


Fig. S5. – Graphical contrasts on the model residuals. The upper left corresponds to the P-values of the Ljung-Box. The upper left-hand side is the p-value of the Ljung-Box independence contrast and the upper right-hand side is the sign of the homoscedasticity of the model residuals. The lower graphs represent the simple and partial correlations of the residuals.

European hake females

Table S7. – Tests of the hypotheses on the residuals of the model for the size at maturity of females.

Test	Hypotheses	P-value
Jarque-Bera	Normality	0.9266
Shapiro-Wilk	Normality	0.9836
Dickeye-Fuller	Stationarity	0.01
Student's	Zero mean	1

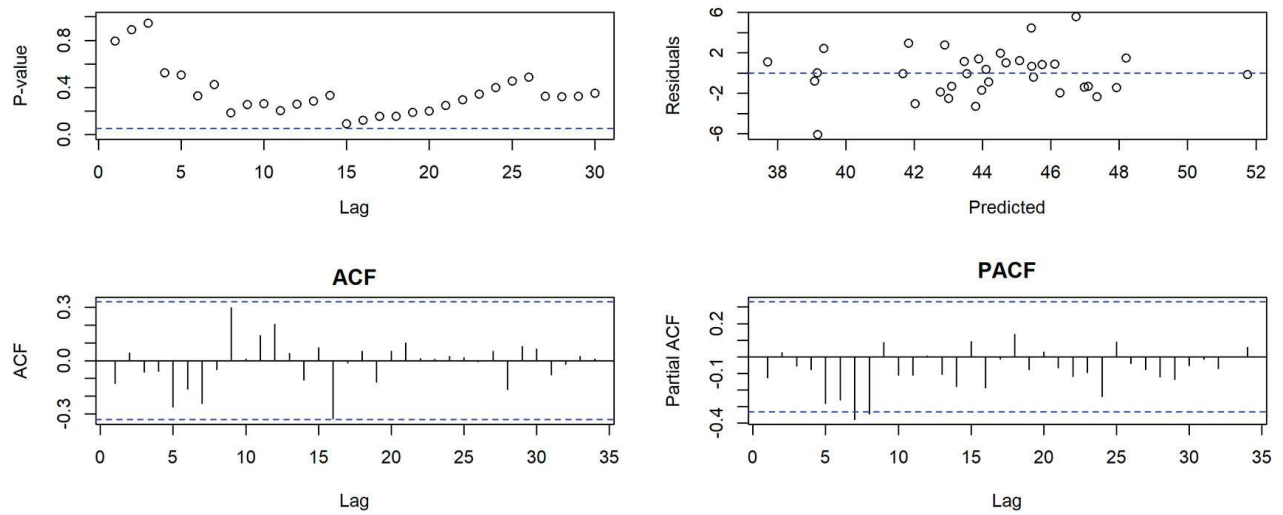


Fig. S6. – Graphical contrasts on the model residuals. The upper left-hand side is the p-value of the Ljung-Box independence contrast and the upper right-hand side is the sign of the homoscedasticity of the model residuals. The lower graphs represent the simple and partial correlations of the residuals.

Reproduction of grey snapper (Teleostei: Lutjanidae) in the southern Gulf of Mexico

Karina del C. Macal-López¹, Thierry Brulé¹, Julián René Torres-Villegas²,
Teresa Colás-Marrufo¹, Virginia Elena Noh-Quñones¹

¹Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Departamento de Recursos del Mar, Unidad Mérida, Antigua Carretera a Progreso Km. 6, A.P. 73, Cordemex, 97310, Mérida, Yucatán, México.
(KM-C) (Corresponding author) E-mail: karina.macal@cinvestav.com. ORCID-iD: <https://orcid.org/0000-0001-6036-6002>
(TB) E-mail: tbrule@cinvestav.mx. ORCID-iD: <https://orcid.org/0000-0002-0691-8934>
(TCM) E-mail: tcolas@cinvestav.mx. ORCID-iD: <https://orcid.org/0000-0002-3955-7696>
(VEN-Q) E-mail: vicky_01_3@hotmail.com. ORCID-iD: <https://orcid.org/0000-0002-9048-605>

²Centro Interdisciplinario de Ciencias Marinas del Instituto Politécnico Nacional, Departamento de Pesquerías y Biología Marina, Avenida Instituto Politécnico Nacional s/n, Colonia Playa Palo de Santa Rita, 23096 La Paz, Baja California Sur, México.
(JRT-V) E-mail: jvillega@ipn.mx. ORCID-iD: <https://orcid.org/0000-0002-6691-3393>

Summary: Snappers exhibit reproductive trait plasticity in response to habitat distribution. *Lutjanus griseus* is among the most economically important snappers in the western Central Atlantic but has received limited study in the region. Data on the reproductive biology of the *L. griseus* population were collected on the continental shelf of the Yucatan Peninsula, Mexico. Over a nineteen-month period, 1236 specimens were captured monthly in three Yucatan artisanal fishing fleet operational areas. Data were grouped by month to generate an annual analysis. Individual sex and maturation status were identified by gonad histology. Median size did not differ between females (33.2 cm fork length [FL]) and males (33.3 cm FL), and the sex ratio was balanced (F:M=0.98:1.00). Size at maturity was 24.2 cm FL for females (38% of maximum size reported for the species) and 22.8 cm FL for males (36% of maximum size), and the spawning season ran from May to September. The results confirm that this population exhibits the typical reproductive pattern of snappers distributed on continental shelves or in shallow water areas and provide critical data for stock assessment and implementation of management measures for *L. griseus* stock in the southern Gulf of Mexico.

Keywords: sex ratio; sexual maturity; spawning season; Lutjanidae; Mexico.

Reproducción del pargo gris (Teleostei: Lutjanidae) en el sur del Golfo de México

Resumen: Los pargos exhiben plasticidad en sus rasgos reproductivos según su hábitat de distribución. *Lutjanus griseus* es uno de los pargos de mayor interés económico en el Atlántico Central Occidental, pero ha sido poco estudiado en esta región. Este trabajo analiza la biología reproductiva de la población de *L. griseus* de la plataforma continental de la Península de Yucatán, México. En un periodo de un año y medio natural se capturaron 1236 especímenes en tres áreas operativas de la flota pesquera artesanal de Yucatán. Los datos fueron agrupados por meses para generar un análisis anual. El sexo y el estado de maduración de cada individuo fueron determinados mediante el análisis histológico de sus gónadas. No se observó una diferencia significativa entre las medianas de las tallas de las hembras (33.2 cm LF) y de los machos (33.3 cm LF), y la proporción sexual fue equilibrada (H:M=0.98:1.00). Los datos obtenidos sobre las tallas de madurez fueron de 24.2 cm LF para las hembras (38% de la talla máxima de la especie) y de 22.8 cm LF (36% de la talla máxima) para los machos y la temporada de desove ocurrió entre mayo y septiembre. Estas características confirmaron que la población presenta el patrón de reproducción típico de los pargos distribuidos en plataformas continentales o en zonas de agua somera. Estos resultados proporcionan datos críticos para la evaluación y la aplicación de medidas de gestión de la población de *L. griseus* del sur del Golfo de México.

Palabras clave: proporción sexual; madurez sexual; temporada de desove; Lutjanidae; México.

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INTRODUCTION

Snappers (Lutjanidae) are mainly restricted to tropical and subtropical regions. They are commercially important fish species throughout their geographical range, especially for local artisanal fisheries (Allen 1985). Snapper populations in the Gulf of Mexico are distributed over extensive continental platforms, while those of the Caribbean Sea are essentially insular (Allen 1985, Bannerot et al. 1987). The grey snapper *Lutjanus griseus* (Linnaeus, 1758) is widely and continuously distributed from Massachusetts in the United States to the Caribbean coast of Venezuela (Lindeman et al. 2016). It is one of the most abundant reef fish in many areas of the Caribbean Sea. In Florida, it represents a major portion of recreational snapper catches; indeed, the *L. griseus* recreational fishery in this region exceeds its commercial fishery in terms of catch (Allen 1985, Lindeman et al. 2016). Although the International Union for Conservation of Nature (IUCN) Red List classifies *L. griseus* as of least concern, Lindeman et al. (2016) argue that its populations in Cuba, Puerto Rico and along the US Atlantic coast show signs of decline. In the northern Gulf of Mexico, the US stock is not considered to be overfished but has exhibited signs of overfishing since 1976 (SEDAR 2018). In the southern Gulf of Mexico, *L. griseus* is one of the main snapper species exploited by artisanal fishers in the state of Yucatan, Mexico (Monroy-García et al. 2019). Snapper fisheries have become increasingly important in Yucatan in response to sharp declines in populations of red grouper *Epinephelus morio* (Valenciennes, 1828), the region's main fishery. In addition, large decreases have been observed in the population of Mexican red snapper *Lutjanus campechanus* (Poey, 1860) since early 1990 (SAGARPA 2018). Both trends have helped make *L. griseus* one of the most exploited snappers in the waters of the Yucatan Peninsula (Monroy-García et al. 2019).

In response to their distribution habitat, snappers generally show a certain plasticity in some of their reproductive traits. Following Grimes' (1987) concept, reproductive seasonality and size at maturity in snappers are more dependent on habitat types than on latitude. Species or populations that inhabit continental shelves or shallow waters (<91 m) have a restricted spawning season centred in summer and a sexual maturity which occurs at 41% (continental shelves) or 43% (shallow waters) of species maximum size. Conversely, species or populations from insular regions or deep reef zones (>91 m) reproduce year-round with spawning pulses in spring and autumn, and experience sexual maturity at 51% (insular regions) or 49% (deep reef zones) of species maximum size (Grimes 1987). For example, the population of silk snapper *Lutjanus vivanus* (Cuvier, 1828) from North Carolina and South Carolina has a restricted spawning season (June to August) and matures at 36% (female) or 41% (male) of its maximum size, whereas in Jamaica the same species spawns year-round and matures at 85% (female) or 73% (male) of its maximum size. In the Antilles and the Bahamas, deepwater (120-180 m

depth; Allen 1985) black snapper *Apsilus dentatus* (Guichenot, 1853) mature at 74% (female) or 79% (male) of its maximum size (Grimes 1987). However, Grimes (1987) also mentions that in various snapper populations around the world, sexual maturity and/or reproductive season are not strictly dictated by habitat type. For example, populations of red snapper *L. campechanus* and yellowtail snapper *Ocyurus chrysurus* (Bloch, 1791) from the continental shelf of the Yucatan Peninsula are reported to have an extended seasonal reproductive pattern: February to November for *L. campechanus* (Brulé et al. 2010) and January to September for *O. chrysurus* (Trejo-Martínez et al. 2011). This is more typical of insular snapper species and populations.

The reproductive biology of *L. griseus* has been investigated in populations in Florida (Starck 1971, Domeier et al. 1996, Allman and Grimes 2002), Cuba (González et al. 1979, Báez et al. 1982, Claro 1983), Guatemala (Andrade and Santos 2019) and Venezuela (Guerra-Campos and Bashirullah 1975), but not in the southern Gulf of Mexico. Therefore, the present study analysed the main reproductive characteristics (sex-size distribution, sex ratio, size at maturity and spawning seasonality) of *L. griseus* from the continental shelf of the Yucatan Peninsula (i.e. Campeche Bank). The objective was to assess whether this population exhibits the pattern of sexual maturity and reproductive seasonality typical of continental snapper species and populations.

MATERIALS AND METHODS

Study area

In the southern Gulf of Mexico, Campeche Bank corresponds to the northern extension of the Yucatan Peninsula continental shelf (Fig. 1). Bottoms are sandy, coral and limestone substrates and, to a lesser degree, mud (García and Gómez 1974). Macrobenthos biomass estimates suggest Campeche Bank harbours a great abundance of zoobenthos that is likely to be the dietary basis of various demersal fish species, such as snappers (Spichak and Formoso 1974). All continental freshwater outflows into the sea at Campeche Bank originate from the terrestrial aquifer in the form of point-specific submarine discharges along the Peninsula coast (Aranda-Cirerol et al. 2006). In the northeastern Campeche Bank, in spring and summer, there is a temporary massive upwelling of cold (22.5°C), nutrient-rich water from the depths of the Caribbean Sea which flows east-to-southwest across the continental slope of Campeche Bank (Merino 1997). During the autumn and winter, the region experiences atmospheric cold fronts from the northwest, while in the summer prevailing winds are from the south and southeast, with occasional cyclones during the summer and early autumn (Kornicker and Boyd 1962, Logan 1969). Mean sea surface temperature during the study period fluctuated from 26.8°C in February to 29.3°C in September (Gutiérrez et al. 2021).

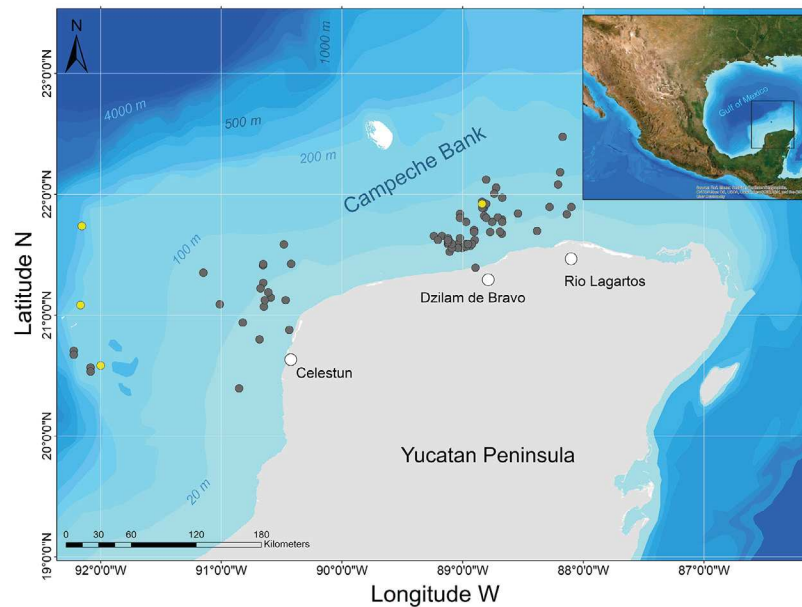


Fig. 1. – Sample sites of *Lutjanus griseus* caught from Campeche Bank, southern Gulf of Mexico, between January 2018 and September 2019. Yellow dots indicate sampling sites where females in actively spawning or past-spawner reproductive subphases were captured.

Sampling and specimen analysis

Specimens were collected monthly between January 2018 and September 2019 in three areas of Campeche Bank near the fishing ports of Celestún (20°52'N, 88°45'W), Dzilam de Bravo (21°30' N, 88°45'W) and Río Lagartos (21°40'N, 88°10'W) (Fig. 1). The collections were made by fishers from the Mexican artisanal fleet using fibreglass boats (22-26 feet long) equipped with an outboard motor (40 to 150 HP) (Monroy-García et al. 2019). The snappers were caught at 1 to 44 m depth using free diving or hookah harpoon, hook and line, shrimp net and/or cast net (for juveniles). Global positioning system points were recorded for each sampling site.

For each individual, measurements were taken of total length (TL; nearest 0.1 cm), fork length (FL; nearest 0.1 cm), standard length (SL; nearest 0.1 cm), whole-body weight (WW; nearest 1 g), gutted weight (GW; nearest 1 g), and fresh gonad weight (gW; nearest 0.01 g).

In *L. griseus*, oocytes develop homogeneously during the spawning season, regardless of the ovary lobe and lobe zone (Macal-López et al. in press). For histological examination, a sample obtained from the central portion of one lobe from each gonad was preserved in Bouin's fixative (Gabe 1968) for an average of four days. After fixation, gonad samples were rinsed in 70% ethanol to remove excess fixative, dehydrated in graded ethanol baths (96% and 100%), treated with CitriSolv as an alternative to xylene or benzene, and impregnated in Paraplast baths (melting point: 56°C) following standard histological techniques (Gabe 1968). The blocks containing the samples were sectioned with a microtome (6 µm), and the sections were stained with haematoxylin/eosin (Martoja and Martoja-Pierson 1967).

After sex definition by gonad histological analysis, each female and male was classified into established reproductive phases or subphases (Brown-Peterson et al. 2011): immature, developing (including the early developing subphase), spawning capable (including the actively spawning and past-spawner subphases for females), regressing and regenerating. Males in the actively spawning subphase were identified macroscopically following the criteria of Brown-Peterson et al. (2011). Except for immature individuals, all specimens in any of these phases or subphases were considered sexually mature. All individuals in the spawning capable phase and the actively spawning or past-spawner subphases were considered reproductively active specimens and representative of the mature spawning population (Lowerre-Barbieri et al. 2009).

Size and sex ratio

Size frequency distributions for each sex were established by applying Sturge's rule (Scherrer 1984) to identify the number and size class interval to be analysed. Median sizes of females and males were compared with the Kruskal-Wallis test. The Kolmogorov-Smirnov test was applied to compare the size frequency distributions of individuals between sexes (Sokal and Rohlf 1997). All statistical analyses were run with the R software (R Core Team 2020) using the FSA library (Mangiafico 2016, Ogle et al. 2021).

Overall and size class sex ratios were calculated considering the number of females per male (F:M). The Pearson chi-square (χ^2) goodness-of-fit statistical test was applied to determine whether the observed sex ratio differed from a balanced sex ratio (1:1) (InfoStat software, Di Rienzo et al. 2014).

Sexual maturity

Minimum size at sexual maturity (L_{min}), corresponding to the smallest adult individual captured during the study was established for both sexes. In snappers, size at maturity increases linearly relative to the maximum size reported for a species or a population (Grimes 1987). The percentage of the maximum size at sexual maturity for females and males was calculated ($L_{min}/L_{max} \times 100$), considering L_{max} as the largest individual observed in this population, irrespective of sex. The size at which 50% of individuals reached sexual maturity (L_{50}) was estimated for both sexes using a logistic regression model ($L_{50} = e^z \times [1 + e^z]^{-1}$, where $z = a + b \times \log_{10} FL$), adjusted by the maximum likelihood method (SYSTAT 13.1; SYSTAT Software, Inc., San Jose, California). For this analysis, regenerating females were distinguished histologically from immature females by the presence of morphological structures in their ovaries indicative of earlier reproductive activity (i.e. muscle bundle, connective tissue and surrounding blood vessels) (Shapiro et al. 1993, Rhodes and Sadovy 2002). However, this distinction between the two reproductive phases is sometimes uncertain in some species, mainly owing to variability in the time of disappearance from the ovaries of morphological structures indicative of previous reproductive activity (Brown-Peterson et al. 2011, Lowerre-Barbieri et al. 2011). To compensate for this possibility, the reliability of the regenerating and immature female classifications was estimated by comparing median sizes of immature and regenerating females with a Kruskal-Wallis test and their length-frequency distributions using a Kolmogorov-Smirnov test (R Core Team 2020, Mangiafico 2016, Ogle et al. 2021).

Sexual cycle

Sexual cycle was characterized by analysing monthly mean variations in the gonadosomatic index ($GSI = 100 \times [gW/GW]$) and in the relative proportion of individuals in each reproductive phase or subphase. To run a calendar year analysis, individuals (excluding immatures) were grouped by month of capture.

Presumed *L. griseus* spawning sites on Campeche Bank were identified based on actively spawning female spatial distribution (i.e. ovaries showing oocyte maturation [OM]) or past-spawner subphases (i.e. ovaries showing vitellogenic oocytes and postovulatory follicles) (Fig. 2). The first subphase indicates that females are in an imminent spawning stage, while the second indicates recently past spawning (Brown-Peterson et al. 2011).

Data for TL and SL from previous snapper reproduction studies were converted to FL using the equations $FL = 0.943 \times TL + 0.157$ ($r^2 = 0.984$; $n = 1236$) and $FL = 1.151 \times SL + 0.957$ ($r^2 = 0.993$; $n = 1226$), based on TL, FL and SL data from the present study.

All measurements are presented as mean \pm standard error (se), and all statistical analyses were run using an α level of 0.05.

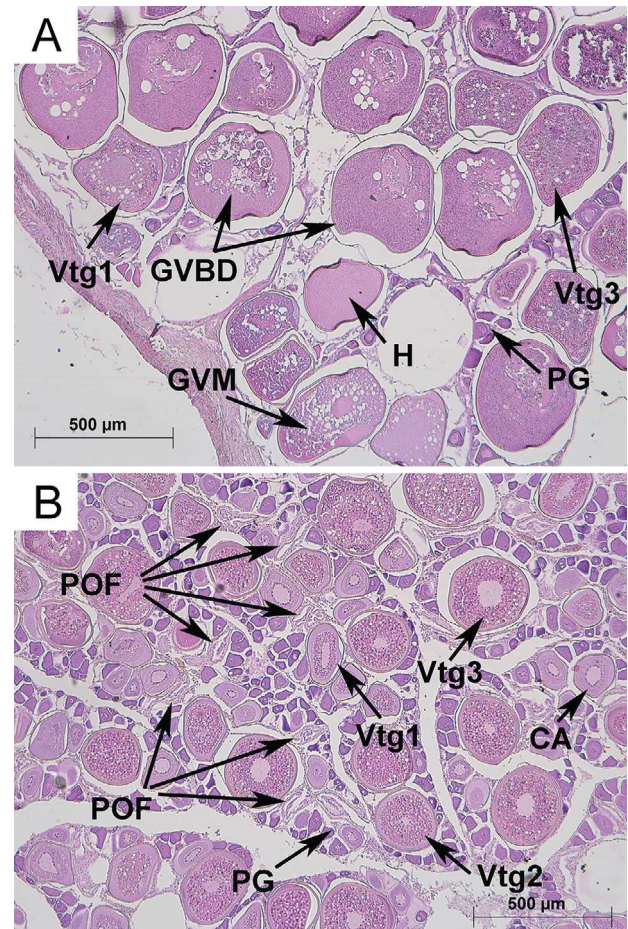


Fig. 2. – Histological sections of ovaries from female *Lutjanus griseus* caught from Campeche Bank, southern Gulf of Mexico, between January 2018 and September 2019. A, actively spawning females; B, past-spawner females. CA, cortico alveolar oocyte; GVBD, germinal vesicle breakdown; GVM, germinal vesicle migration; H, hydrated oocyte; PG, primary growth oocyte; POF, postovulatory follicle; Vtg1, primary vitellogenic oocyte; Vtg2, secondary vitellogenic oocyte; Vtg3, tertiary vitellogenic oocyte (haematoxylin-eosin staining).

RESULTS

Size frequency and sex ratio

A total of 1236 individuals were captured (610 females, 626 males) (Appendix 1). Individual length and weight ranges for sexually mature females ($n = 322$) ranged from 24.2 to 63.9 cm FL (mean = 37.2 ± 0.4 cm FL), and 250 to 4248 g WW (mean = 917 ± 35 g WW). Sexually mature males ($n = 544$) ranged from 22.8 to 63.2 cm FL (mean = 35.5 ± 0.3 cm FL), and 113 to 3876 g WW (mean = 794 ± 23 g WW). Length and weight of immature females ($n = 288$) ranged from 14.7 to 46.0 cm FL (mean = 30.6 ± 0.4 cm FL) and from 57 to 2906 g WW (mean = 522 ± 19 g WW). Immature males ($n = 82$) ranged from 15.5 to 42.5 cm FL (mean = 27.5 ± 0.7 cm FL) and from 64 to 1236 g WW (mean = 359 ± 24 g WW). Median size did not differ between females (33.2 cm FL) and males (33.3 cm FL) (Kruskal-Wallis test $H = 0.2224$, $df = 1$, $P = 0.6372$), and neither did the size frequency distributions (Kolmogorov-Smirnov test $KS = 0.069244$, $P = 1.397e-05$).

Sex ratio (0.98:1.00) did not differ from a balanced value (1:1) (Pearson=0.16, df=1, P=0.69) (Table 1) and remained balanced regardless of size class. The one exception was the 15 to 20 cm FL size class, in which the sex ratio was biased towards females (2.30:1.00; Pearson =5.12, df=1, P<0.02) (Table 1). No males smaller than 15.5 cm FL were captured (Appendix 1).

Table 1. – Sex ratio by fork length(FL)-class for *Lutjanus griseus* from Campeche Bank, southern Gulf of Mexico. F:M=number of females per male; χ^2 , Pearson goodness-of-fit statistic; p, significance value. *: significant differences from a ratio of 1:1.

FL-class (cm)	Number		Sex ratio (F:M)	χ^2 value	p
	Females	Males			
10.1 – 15.0	1	0	-	-	-
15.1 – 20.0	23	10	2.30:1.00	5.120	0.0236*
20.1 – 25.0	29	34	0.85: 1.00	0.400	0.5287
25.1 – 30.0	144	162	0.89: 1.00	1.060	0.3035
30.1 – 35.0	163	154	1.06: 1.00	0.260	0.6132
35.1 – 40.0	125	124	1.01: 1.00	0.004	0.9405
40.1 – 45.0	74	92	0.80: 1.00	1.950	0.1624
45.1 – 50.0	31	31	1.00: 1.00	0.000	0.9999
50.1 – 55.0	12	11	1.09: 1.00	0.040	0.8348
55.1 – 60.0	5	7	0.71: 1.00	0.330	0.5637
60.1 – 65.0	3	1	3.00: 1.00	1.000	0.3173
Total	610	626	0.97: 1.00	0.210	0.6490

Sexual maturity

The L_{min} was 24.2 cm FL for sexually mature females (individual in regeneration phase), and 22.8 cm FL for sexually mature males (individual in regression phase). The L_{max} recorded for *L. griseus* on Campeche Bank was 63.9 cm FL for females and 63.2 cm FL for males; therefore, the percentage of maximum size at which females reached maturity was 38% and that for males was 36%. For females, L_{50} was 32.2 cm FL (31.0-33.5 cm FL limits, 95% confidence interval) and for males it was 22.0 cm FL (20.0-23.6 cm FL limits, 95% confidence interval) (Fig. 3).

Median sizes of immature females (30.3 cm FL) were significantly lower than median sizes of regenerating females (36.6 cm FL) (Kruskal-Wallis test H=94.91, df=1, P<2.2e-16). The length-frequency distribution of immature females differed from that of regenerating females (Kolmogorov-Smirnov test KS=0.0617, P=0.0355) (Fig. 4). These results confirm the accuracy of discrimination between immature and regenerating females based on ovary histology in the present study.

Sexual cycle

Monthly evolution of the GSI for females and males throughout a calendar year showed that repro-

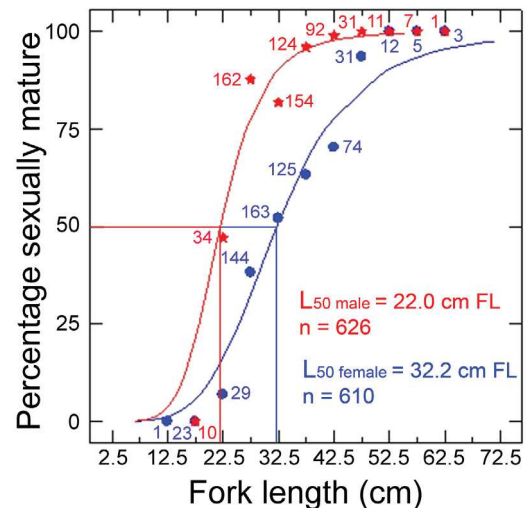


Fig. 3. – Percentage in relation to fork length of sexually mature female and male *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019. The proportion of sexually mature fish within each size class was plotted using a binary logistic regression. Vertical lines indicate the length at which 50% of individuals were mature (L_{50}). Numbers indicate sample size for each size class. Sexually mature fish are early developing, developing, spawning capable, actively spawning, past-spawner (only for females), regressing and regenerating individuals.

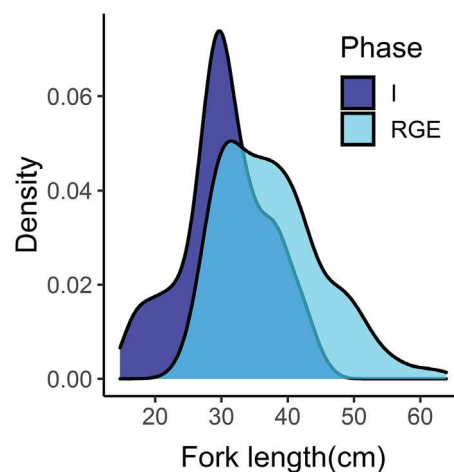


Fig. 4. – Size-frequency distributions for immature (I) and regenerating (RGE) female *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019.

ductive activity in *L. griseus* begins in May and ends in September (Fig. 5). Maximum mean GSI values were observed in June for males ($1.01 \pm 0.14\%$) and in August for females ($1.38 \pm 0.34\%$). The low mean GSI values observed between October and April for both females ($0.33 \pm 0.02\%$ and $0.46 \pm 0.05\%$, respectively) and males ($0.13 \pm 0.01\%$ and $0.12 \pm 0.01\%$, respectively) indicate that they were reproductively inactive during this period.

Annual monthly variation in the percentage of individuals in different reproductive phases and subphases confirmed the GSI analysis observations (Fig. 6). Re-

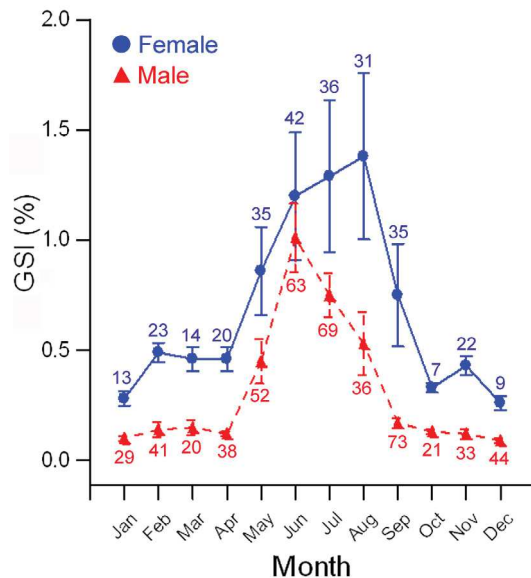


Fig. 5. – Seasonal variation of the Gonadosomatic index (GSI; mean \pm se) for female and male *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019. Numbers indicate sample size for each pooled sampled month.

productively active females ($n=47$; 15% of captured females) were observed between May and September and reached a maximum percentage of captures in July (36%; $n=13$). The highest percentage of spawning capable females was recorded in June (29%; $n=12$), that for actively spawning females in August (6%; $n=2$), and that for past-spawning females in July (14%; $n=5$). From May to September, regenerating females represented between 24% and 77% of females captured monthly. Few regressing females were observed in monthly captures (range: 2-9%; $n=1-3$). Between October and April, all or most (96% in November) captured females were in the regenerating phase. Although males were reproductively active during a slightly longer time than females (April to October), their seasonal peak in reproductive activity was very similar to that of females (Fig. 6). The highest percentages of spawning capable and actively spawning males were observed between May and August (range=47-89%; $n=17-58$). The highest percentages of actively spawning males were observed in June (34%; $n=22$) and July (38%; $n=26$). The percentages of regenerating males were lowest between May and August (range=0-28%; $n=0-10$) and highest between December and March (range=57-93%; $n=26-38$).

DISCUSSION

The use of different fishing gears to capture *L. griseus* specimens on Campeche Bank generated a sample consisting of individuals distributed over a wide range of representative lengths (14.7-63.9 cm FL). This snapper species is reported to reach a maximum size of 89 cm TL (=84 cm FL), although the most frequent size is 40 cm TL (=38 cm FL) (Allen 1985). However, in this study juveniles smaller than 14.0 cm FL were not

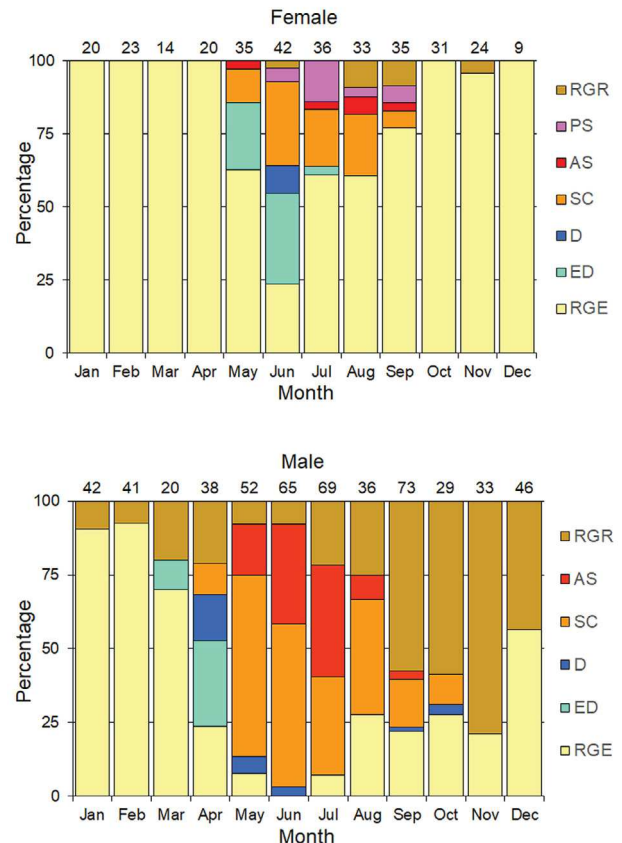


Fig. 6. – Seasonal variation of the percent frequency of female and male *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019, classified according to reproductive phases and subphases over a single year (RGE, regenerating; ED, early developing; D, developing; SC, spawning capable; AS, actively spawning; PS, past-spawner; RGR, regressing). Numbers indicate sample size for each pooled sampled month.

collected, probably because the fishing area covered by the artisanal fleet in Yucatan excludes estuaries, coastal lagoons and the coastal margin, which are nursery habitats for *L. griseus* (Starck 1971, Claro and Lindeman 2004, Faunce and Seafy 2007). The median sizes and length-frequency distributions for both sexes on Campeche Bank were identical, as previously reported for *L. griseus* populations in Florida (Starck 1971, Domeier et al. 1996). According to Domeier et al. (1996), this demographic trait could result from this species's gonochoric-type sexuality pattern.

Grimes (1987) states that snappers can exhibit a slightly female-biased sex ratio in larger size classes because of differences in growth and mortality between sexes. Moreover, the overall sex ratio in *L. griseus* populations frequently favours females, as reported in the west Florida Keys (Domeier et al. 1996), Cuba (Báez et al. 1982, Claro 1983) and Venezuela (Guerra-Campos and Bashirullah 1975) (Table 2). However, the sex ratio observed here in the Campeche Bank population was balanced, as previously observed in populations in the Everglades National Park and the Florida Keys (Crocker 1962, Starck 1971), the west coast of Florida (Allman and Goetz 2009) and the coast of Guatemala (Andrade and Santos 2019) (Table 2). Interpopulational variation

Table 2. – Fork length (FL) at maturity, sex ratio and reproductive season reported for *Lutjanus griseus* populations from the Gulf of Mexico and the Caribbean Sea (F, female; M, male; L_{\min} , minimum size at which individuals became sexually mature; L_{\max} , maximum size observed in the sample; L_{\min}/L_{\max} , length at first maturity expressed as a percentage of maximum length; L_{50} , length at which 50% of individuals were mature). ^a, standard length (SL, cm) data converted to FL (cm) using the formula $FL=0.957+1.151 \times SL$ ($r^2=0.993$, $n=1226$), calculated from data of the present study. ^b, total length (TL, cm) data converted to FL (cm) using the formula $FL=0.157+0.943 \times TL$ ($r^2=0.984$, $n=1236$), calculated from data of the present study. ^c, pooled sex data. ^d, more accurate estimate of maturity. ^e, peak spawning.

Fork length (cm) at maturity							Sex ratio F:M	Reproductive season	Reference
Sex	L _{min}	L _{max}	L _{min} /L _{max} ×100 (%)	L ₅₀					
United States (Florida)									
-	-	-	-	-	1.10:1.00	-	Croker (1962)		
F	23.4 ^a	57.2 ^a	40.9	-	0.87:1.00	Apr-Sept (Jun-Aug) ^e	Starck (1971)		
M	22.3 ^a		40.0	-					
F	23.7 ^a	58.2 ^a	40.7	-	1.20:1.00	May-Sept (Jun-Aug) ^e	Domeier et al. (1996)		
M	21.9 ^a		37.6	-					
-	-	--	-	-	-	May-Sept (Jul) ^e	Allman and Grimes (2002)		
-	-	-	-	-	1:00:0.99	-	Allman and Goetz (2009)		
-	-	-	-	23.9-28.8 30.0 ^d	1.00:1.00	-	SEDAR (2018)		
Mexico (Yúcatan)									
F	24.2	63.9	37.9	32.2	0.97:1.00	May-Sept (Jun; Aug) ^e	Present study		
M	22.8		35.7	22.0					
Cuba									
F	24.6	53.0	46.4	-	1.58:1.00	Jun-Sept (Jul-Aug) ^e	Báez et al. (1982)		
M	22.9		43.2	-					
F	21.0	51.0	41.2	-	1.30:1.00	Jun-Sept (Jul-Aug) ^e	Claro (1983)		
M	18.0		35.3	-					
Guatemala									
F	26.1 ^b	52.0 ^b	50.2	29.4 ^{b, c}	1.00:1.00	Apr-Sept (Jun-Jul) ^e	Andrade and Santos (2019)		
M	19.6 ^b		37.7						
Venezuela (Isla de Cubagua)									
-	-	62.4 ^b	-	-	1.96:1.00	Apr-Sept (Jun-Jul) ^e	Guerra-Campos and Bashirullah (1975)		

in sex ratio in *L. griseus* may occur in response to certain spatial-temporal factors such as habitat type and climatic season (Claro and Lindeman 2004).

On Campeche Bank, male *L. griseus* reach sexual maturity at a smaller size than females, as reported for other populations (Table 2). The percentages of maximum size at sexual maturity in females (38%) and males (36%) show that the Campeche Bank population exhibits a typical maturity pattern for snapper populations distributed on continental shelves or in shallow waters (mature at about 41% and 43% of maximum size, respectively), as defined by Grimes (1987). Similar results have been reported for Florida continental shelf populations: 40% for females and 37% to 38% for males (Starck 1971, Domeier et al. 1996). On the Guatemalan coast, however, the maximum size at sexual maturity percentage for *L. griseus* was higher in females (50%) than in males (38%) (Table 2); the female value was similar to those established by Grimes

(1987) for snapper populations in insular or deep-water regions (mature at about 51% and 49% of maximum size, respectively). In Cuba, by contrast, the maximum size at sexual maturity percentages reported for *L. griseus* females (41%-46%) and males (35%-43%) were more typical of species and populations distributed on continental shelves (Báez et al. 1982, Claro 1983) (Table 2). Differences between observed values and those proposed by Grimes (1987) may be explained by errors in calculating L_{\min} in females and males and/or L_{\max} for the studied populations. For example, Báez et al. (1982), Claro (1983) and Andrade and Santos (2019) calculated L_{\min} for both sexes by macroscopic examination of gonads, which is considered the least accurate method (Murua et al. 2003, Lowerre-Barbieri et al. 2011). The L_{\max} values reported by these authors were lower (51-53 cm FL and 55 cm TL [=52 cm FL]) than the L_{\max} observed in the present study. Another possible explanation for discrepancies is that Grimes's

(1987) proposed values are not generally applicable to all snapper species and populations. For example, populations of lane snapper *Lutjanus synagris* (Linnaeus, 1758) from Cuba, Puerto Rico, Jamaica and Trinidad have an atypical sexual maturity pattern characteristic of continental shelf areas, while the population off Venezuela has an atypical pattern characteristic of island regions (Trejo-Martínez et al. 2021).

Two previous reports containing L_{50} data for *L. griseus* are for the populations of the northern Gulf of Mexico (SEDAR 2018) and off the Guatemalan coast (Andrade and Santos 2019) (Table 2). For the northern Gulf of Mexico population, the more recent calculation of female length at 50% maturity is between 23.9 and 28.8 cm FL, with 90% of individuals being mature at 36.2 cm FL. However, if based on female GSI values, a significant contribution to the spawning stock is not achieved until 30.0 cm FL, a size considered a more accurate estimate of L_{50} for *L. griseus* (SEDAR, 2018). Combining data from both sexes, Andrade and Santos (2019) estimated an L_{50} of 31.1 cm TL (=29.5 cm FL) for the Guatemalan population. The values from both studies are between those observed for females and males in the present study. In contrast, a study of *L. griseus* off Florida over 25 years ago found that 90% of individuals (females and males combined) were mature at 20 cm SL (=24 cm FL) and 100% at 24 cm SL (=29 cm) (Domeier et al. 1996). Compared with the L_{50} data values reported for the northern Gulf of Mexico (SEDAR 2018) and Guatemala (Andrade and Santos 2019), and those in the present study, these values seem to be serious underestimates and are difficult to explain. Perhaps the number of specimens analysed by Domeier et al. (1996) by means of histological preparation of gonads was too small ($n=122$), and/or mistakes were made in identification of the microscopic stages of gonadal maturation.

Spawning season for the Campeche Bank *L. griseus* population occurs from May to September, with probable spawning pulses between June and August, which are typical of snapper species and populations from continental shelves (Grimes 1987). These results coincide with those for *L. griseus* populations from other continental shelf regions such as Florida (Starck 1971, Domeier et al. 1996, Allman and Grimes 2002) and Guatemala (Andrade and Santos 2019) (Table 2). However, *L. griseus* populations from insular regions such as Cuba (Báez et al. 1982, Claro 1983) and Cubagua Island in Venezuela (Guerra-Campos and Bashirullah 1975) also display a restricted spawning season centred in summer, a spawning season pattern characteristic of continental shelf populations (Table 2). Thus, as previously noted by Grimes (1987), insular *L. griseus* populations do not always exhibit reproductive seasons strictly in accordance with their habitat type.

Collection sites for two of the actively spawning females ($n_{\text{total}}=6$) and three of the past-spawner females ($n_{\text{total}}=10$) analysed in the present study could not be placed confidently. But it is known that the others (four actively spawning and seven past-spawner females) were caught at three collection sites west of Celestún (range=29–44 m deep) and one north of Dzilam de Bra-

vo (22 m deep), suggesting that these may be *L. griseus* spawning areas. Actively spawning and past-spawner females were captured within seven days before and two days after the full moon phase. Only one actively spawning female was caught five days after the new moon. This would coincide with a report that in Cuba *L. griseus* spawners migrate to waters 20 to 30 m deep to reproduce at night near the full moon (Claro 1983, Claro and Lindeman 2003). Larger movements by grey snapper are related to spawning migration and it is probable that this species aggregates at offshore spawning sites (SEDAR 2018). However, *L. griseus* spawning aggregations have not yet been fully validated (Domeier and Colin 1997, Lindeman et al. 2000; Binder et al. 2021). The Campeche Bank *L. griseus* population exhibits an asynchronous ovarian organization and is a batch spawner (Macal-López et al. in press). However, spawning frequency/spawning interval was not calculated in this study because there were insufficient numbers of reproductively active females in the sample. In the northern Gulf of Mexico, it has been estimated that the *L. griseus* spawning season is 137 days long and encompasses 37 spawns within that period (SEDAR 2018). Using these values provides an estimated spawning interval of 3.7 days for this snapper.

Despite a paucity of reproductively active females, particularly those in the active spawning and past-spawner subphases, the present data were sufficient to characterize sexual maturity and spawning season for *L. griseus* on Campeche Bank. This is an ongoing challenge in the study of *L. griseus* (Starck 1971, Rutherford et al. 1983, Domeier et al. 1996), because maturing adults migrate from shallow coastal waters to spawning grounds in deeper reef areas during the spawning season (Starck, 1971, Domeier et al. 1996, SEDAR 2018). Collection for the present study was done mainly in shallow waters, which may have caused the scarcity of reproductively active females in the collections. However, high percentages of reproductively active males (range=19%–89%), including various in the actively spawning subphase (range=3%–38%), were caught every month of the spawning season (May–September). Mature *L. griseus* decrease feeding activity during the spawning season (Claro 1983), and thus reproductively active females may have been less accessible than males to the fishing gear used during the spawning season, especially to passive techniques such as hook and line. Another possible explanation is that most reproductively active females start migrating to offshore spawning grounds earlier in the season than reproductively active males, and/or that most reproductively active males make continuous movements during the spawning season between offshore spawning sites and inshore feeding sites.

The present results for the Campeche Bank *L. griseus* population corroborate Grimes's (1987) concept regarding continental reproductive pattern in snappers. For this continental population, sexual maturation occurred at a smaller size in males than in females, and between 36% and 38% of the maximum size for both sexes. The spawning season was centred around summer, with spawning peaks observed between June and

August. This study generates new data on core aspects of the reproductive strategy of *L. griseus*, one of the least-studied snappers in the western Central Atlantic. It expands knowledge on the life history of a species vital to tropical marine ecosystem ecology and provides data fundamental to stock assessment and to defining the fisheries management policies most appropriate to specific snapper populations.

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REFERENCES

- Allen G.R. 1985. FAO Species Catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. 125: 208 p.
- Allman R.J., Goetz L.A. 2009. Regional variation in the population structure of gray snapper, *Lutjanus griseus*, along the west Florida shelf. *Bull. Mar. Sci.* 84: 315-330.
- Allman R.J., Grimes C.B. 2002. Temporal and spatial dynamics of spawning, settlement and growth of gray snapper (*Lutjanus griseus*) from the west Florida shelf as determined from otolith microstructures. *Fish. Bull.* 100: 391-403.
- Andrade H., Santos J. 2019. Life history of the gray snapper at the warm edge of its distribution range in the Caribbean. *Mar. Coast. Fish.* 11: 315-327. <https://doi.org/10.1002/mcf2.10087>
- Aranda-Cirerol A., Herrera-Silveira J.A., Comín F.A. 2006. Nutrient water quality in a tropical coastal zone with groundwater discharge, northwest Yucatán, Mexico. *Estuar. Coast. Shelf Sci.* 68: 445-454. <https://doi.org/10.1016/j.ecss.2006.02.015>
- Báez M.I., Alvarez-Lajonchere L.S., Ojeda-Serrano E. 1982. Reproducción del caballerote, *Lutjanus griseus* (Linnaeus) en Tunas de Zaza, Cuba. *Rev. Invest. Mar.* 3: 43-86.
- Bannerot S., Fox W.W., Powers J.E. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf on Mexico and Caribbean. In: Polovina J. and Ralston S. (eds), *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, Colorado, pp. 561-603.
- Binder B.M., Taylor J.C., Gregg K., Boswell K.M. 2021. Fish spawning aggregations in the southeast Florida Coral Reef Ecosystem Conservation Area: A case study synthesis of user reports, literature, and field validation efforts. *Front. Mar. Sci.* 8: 671477. <https://doi.org/10.3389/fmars.2021.671477>
- Brown-Peterson N.J., Wyansky D.M., Saborido-Rey F., et al. 2011. A Standardized terminology for describing reproductive development in fishes. *Mar. Coast. Fish.* 3: 52-72. <https://doi.org/10.1080/19425120.2011.555724>
- Brulé T., Colás-Marrufo T., Pérez-Díaz E., Sámamo-Zapata J.C. 2010. Red Snapper reproductive biology in the southern Gulf of Mexico. *Trans. Am. Fish. Soc.* 139: 957-968. <https://doi.org/10.1577/T09-125.1>
- Claro R. 1983. - Ecología y ciclo de vida del caballerote, *Lutjanus griseus* (Linnaeus), en la plataforma cubana. I. Identidad, distribución y hábitat, nutrición y reproducción. *Rep. Invest. Inst. Oceanol., Acad. Cien. Cuba* 7: 1-30.
- Claro R., Lindeman K.C. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and serranidae) on the insular shelf of Cuba. *Gulf Caribb. Res.* 14: 91-106. <https://doi.org/10.18785/gcr.1402.07>
- Claro R., Lindeman K.C. 2004. Biología y manejo de los pargos (Lutjanidae) en el Atlántico occidental. CITMA, Cuba, 472 pp. En CD-ROM, ISBN 878-959-298-011-2. <http://www.redciencia.cu/cdoceano>
- Crocker R.A. 1962. Growth and food of the gray snapper, *Lutjanus griseus*, in Everglades National Park. *Trans. Amer. Fish. Soc.* 91: 379-383. [https://doi.org/10.1577/1548-8659\(1962\)91\[379:GAFOT-G\]2.0.CO;2](https://doi.org/10.1577/1548-8659(1962)91[379:GAFOT-G]2.0.CO;2)
- Di Rienzo J.A., Casanoves F., Balzarini M.G., et al. 2014. InfoStat versión 2014. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Domeier M.L., Colin P.L. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bull. Mar. Sci.* 60: 698-726.
- Domeier M.L., Koenig C., Coleman F. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other western Atlantic snappers (Lutjanidae). In: Arreguin-Sanchez F., Munro J.L., Balgos M.C., Pauly D. (eds), *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM, pp. 189-201.
- Faunce C.H., Seafy E.J. 2007. Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. *Bull. Mar. Sci.* 80: 473-495.
- Gabe M. 1968. *Techniques histologiques*. Masson et Cie, Paris. 1113 pp.
- García C., Gómez J.A. 1974. Carta preliminar de fondos del Banco de Campeche., *Res. Invest., INP* 1: 37-38.
- González E., Damas T., Millares N., Borrero M. 1979. Desove inducido en el caballerote (*Lutjanus griseus* Linné, 1758), en condiciones de laboratorio. *Rev. Cub. Investig. Pesq.* 4: 43-64.
- Grimes C.B. 1987. Reproductive biology of the Lutjanidae: a review. In Polovina J.J., Ralston S. (eds), *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, Colorado. 239-294 pp.
- Guerra-Campos A., Bashirullah A.K.M. 1975. Biología del pargo *Lutjanus griseus* (Linn.) de la isla de Cubagua, Venezuela. II. Maduración sexual y Fecundidad. *Bol. Inst. Oceanogr. Univ. Oriente* 14: 109-116.
- Gutiérrez J.M., Jones R.G., Narisma G.T., et al. (eds), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press: Cambridge. Available online: <http://interactive-atlas.ipcc.ch/> (accessed on 1 March 2022).
- Kornicker L.S., Boyd D.W. 1962. Shallow-water geology and environments of Alacran reef complex, Campeche Bank, Mexico. *Bull. Am. Assoc. Pet. Geol.* 46: 640-673. <https://doi.org/10.1306/BC743851-16BE-11D-7-8645000102C1865D>
- Lindeman K.C., Pugliese R., Waugh G.T., Ault J.C. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bull. Mar. Sci.* 66: 929-956.
- Lindeman K. C., Anderson W., Carpenter K.E., et al. 2016. - *Lutjanus griseus*. The IUCN Red List of Threatened Species 2016: e.T192941A2180367.
- Logan B.W. 1969. Coral reefs and banks, Yucatán shelf, Mexico. *Bull. Am. Assoc. Pet. Geol.* 11: 129-198.
- Lowerre-Barbieri S.K., Henderson N., Llopiz J., et al. 2009. Defining a spawning population (spotted seatrout *Cynoscion nebulosus*) over temporal, spatial, and demographic scales. *Mar. Ecol. Prog. Ser.* 394: 231-245. <https://doi.org/10.3354/meps08262>
- Lowerre-Barbieri S. K., Ganas K., Saborido-Rey F., et al. 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Mar. Coast. Fish.* 3: 71-91. <https://doi.org/10.1080/19425120.2011.556932>
- Macal-López K.C., Brulé T., Torres-Villegas J.R., et al. In press. Oocyte distribution, ovarian organization, and spawning pat-

- tern in *Lutjanus griseus*. Cybium.
- Mangiafico S.S. 2016. Summary and Analysis of Extension Program Evaluation in R, version 1.19.10. rcompanion.org/handbook/. (Pdf version: rcompanion.org/documents/RHandbookProgramEvaluation.pdf.)
- Martoja R., Martoja-Pierson M. 1967. Initiation aux techniques de l'histologie animale. Masson et Cie, Paris. 345 pp.
- Merino M., 1997. Upwelling on the Yucatan Shelf: hydrographic evidence. J. Mar. Syst. 13: 101-121.
[https://doi.org/10.1016/S0924-7963\(96\)00123-6](https://doi.org/10.1016/S0924-7963(96)00123-6)
- Monroy-García C., Gutiérrez-Pérez C., Medina-Quijano H., et al. 2019. La actividad pesquera de la flota ribereña en el estado de Yucatán: pesquería de escama. Primera edición, Instituto Nacional de Pesca y Acuicultura, Ciudad de México, México. 102 pp.
- Murua H., Kraus G., Saborido-Rey F., et al. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. J. Northwest Atl. Fish. Sci. 33: 33-54.
<https://doi.org/10.2960/J.v33.a3>
- Ogle D.H., Wheeler P., Dinno A. 2021. FSA: Fisheries Stock Analysis. R package version 0.8.32,
<https://github.com/drOglenc/FSA>
- R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rhodes K.L., Sadovy, Y. 2002. Reproduction in the camouflage grouper (Pisces: Serranidae) in Pohnpei, Federate States of Micronesia. Bull. Mar. Sci. 70: 851-869.
- Rutherford E.S., Thue E.B., Buker D.G. 1983. Population structure, food habits, and spawning activity of gray snapper, *Lutjanus griseus*, in Everglades National Park. S. Fla. Res. Cent. Rep. SFRC-83/02. 41 pp.
- Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA). 2018. Acuerdo por el que se da a conocer la actualización de la carta nacional pesquera. In López-González A. (ed), Diario Oficial de la Federación, Tomo DCCLXXVII 10 (segunda sección). Secretaría de Gobernación, Ciudad de México, pp. 1-112.
- Scherrer B. 1984. Biostatistique. Gaëtan Morin Editeur, Boucherville, Québec. 850 pp.
- Southeast Data, Assessment, and Review (SEDAR). 2018. - SEDAR 51 Gulf of Mexico gray snapper Final Stock Assessment Report. SEDAR: North Charleston SC.
- Shapiro D.Y., Sadovy Y., McGehee M.A. 1993. Periodicity of sex change and reproduction in the red hind *Epinephelus guttatus*, a protogynous grouper. Bull. Mar. Sci. 53: 1151-1162.
<https://doi.org/10.2307/1447138>
- Sokal R.R., Rohlf F.J. 1997. Biometry: the principles and practice of statistics in biological research. Third Edition. W.H. Freeman and Co., New York. 880 pp.
- Spichak S.K., Formoso M. 1974. Distribución cuantitativa del zoobentos alimenticio en el banco de Campeche (primavera). INP/CIP Cuba, Res. Invest. 1: 88-92.
- Starck W.A. II. 1971. Biology of the Gray Snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. In: Starck W.A., II, Schroeder R.E. (eds), Investigations on the gray snapper, *Lutjanus griseus*. Stud. Trop. Oceanogr. Miami 10: 11-150.
<https://doi.org/10.2307/1442662>
- Trejo-Martínez J., Brulé T., Mena-Loría A., et al. 2011. Reproductive aspects of the yellowtail snapper *Ocyurus chrysurus* from the southern Gulf of Mexico. J. Fish Biol. 79: 915-936.
<https://doi.org/10.1111/j.1095-8649.2011.03062.x>
- Trejo-Martínez J., Brulé T., Morales-López N., et al. 2021. Reproductive strategy of a continental shelf lane snapper population from the Southern Gulf of Mexico. Mar. Coast. Fish. 13: 140-156.
<https://doi.org/10.1002/mcf2.10142>

APPENDIX

Appendix 1 – Sex, number of individuals (n), mean±se, and range of fork length and whole-body weight of *Lutjanus griseus* sampled between January 2018 and September 2019 on Campeche Bank, southern Gulf of Mexico.

Month	n	Female				n	Male			
		Fork length (cm)		Whole-body weight (g)			Fork length (cm)		Whole-body weight (g)	
		Mean	Range	Mean	Range		Mean	Range	Mean	Range
January	36	38.7±0.9	27.4-50.6	948±68	348-2100	46	40.9±1.0	27.2-56.6	1115±87	116-2701
February	41	39.4±1.8	20.1-63.9	1182±146	132-4248	53	41.6±1.4	17.4-59.3	1311±110	85-3081
March	55	29.7±1.1	16.9-46.6	500±51	80-1562	44	29.7±1.3	16.5-46.4	504±61	76-1703
April	41	32.6±1.8	14.7-56.7	746±105	57-3146	46	33.6±1.2	15.5-51.0	701±59	64-1931
May	51	36.0±0.9	19.7-53.2	875±85	123-2906	52	34.7±0.7	24.8-45.5	693±45	260-1727
June	74	32.4±0.6	21.9-45.4	584±35	167-1537	66	32.0±0.7	21.2-45.6	567±41	154-1799
July	61	34.2±0.8	22.5-51.2	681±51	205-2118	71	34.7±0.7	22.8-52.5	718±50	194-2145
August	46	34.4±0.6	27.5-46.9	670±38	323-1644	36	35.5±0.9	26.5-49.7	747±61	282-1888
September	66	33.7±0.7	25.5-52.0	677±46	240-2042	75	33.1±0.6	23.6-47.1	618±34	113-1666
October	58	31.9±0.6	19.0-43.6	541±35	116-1428	56	32.0±0.6	26.0-48.4	545±39	291-1778
November	44	40.7±1.3	29.1-61.0	1246±126	391-3489	34	40.3±1.3	29.0-63.2	1191±124	402-3876
December	37	28.4±0.4	23.0-36.4	375±16	235-765	47	28.1±0.5	23.5-37.7	375±22	210-936
Total	610	34.1±0.3	14.7-63.9	730±22	57-4248	626	34.4±0.3	15.5-63.2	737±21	64-3876

Spatial variability of life-history parameters of the Atlantic chub mackerel (*Scomber colias*), an expanding species in the northeast Atlantic

Rosario Domínguez-Petit¹, María Rosario Navarro², Marta Cousido-Rocha¹,
Jorge Tornero³, Fernando Ramos³, Alba Jurado-Ruzafa⁴, Cristina Nunes⁵, Carmen Hernández²,
Andreia V. Silva⁵, Jorge Landa²

¹ Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Vigo, Spain.
(RD-P) (Corresponding author) E-mail: rosario.dominguez@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0003-1731-6848>
(MC-R) E-mail: marta.cousido@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0002-4587-8808>
² Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Santander, Spain.
(MRN) E-mail: charo.navarro@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0002-0651-2491>
(CH) E-mail: carmen.hernandez@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0002-0786-582X>
(JL) E-mail: jorge.landa@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0002-0786-582X>
³ Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Cádiz, Spain.
(JT) E-mail: jorge.tornero@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0002-8723-3354>
(FR) E-mail: fernando.ramos@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0001-9591-7214>
⁴ Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Canarias, Santa Cruz de Tenerife, Spain.
(AJ-R) E-mail: alba.jurado@ieo.csic.es. ORCID-iD: <https://orcid.org/0000-0003-4562-045X>
⁵ Instituto Português do Mar e da Atmosfera (IPMA), Portugal.
(AS) E-mail: avsilva@ipma.pt. ORCID-iD: <https://orcid.org/0000-0002-5768-5827>
(CN) E-mail: cnunes@ipma.pt. ORCID-iD: <https://orcid.org/0000-0003-1116-8274>

Summary: Atlantic chub mackerel is a pelagic species present in the Atlantic Ocean that in recent decades has expanded northwards in the eastern Atlantic. Fish samples were collected in scientific surveys and commercial catches between 2011 and 2019. We analysed the geographical variation of the biological parameters (age, length, weight and condition), as well as the length-weight relationship, maturity-at-length and spawning season onset and duration in five geographical areas (from south to north): the Canary Islands, Gulf of Cadiz, western Portuguese coast, northwestern Spanish coast and Cantabrian Sea. The influence of sea surface temperature (SST) on fish length was modelled as a potential driver of geographical variability. All biological parameters increased progressively northwards, while the spawning season was delayed and prolonged with increasing latitude, from January in the Canary Islands to May-August in the Cantabrian Sea, when SST was between 15°C and 19°C. SST had a positive effect on length in three study areas and a negative one in two of them, suggesting that each group is at a different position within their thermal tolerance range. Deviance from the geographical pattern of some biological parameters in the Gulf of Cadiz suggests that it could be a hinge or mixing zone between Atlantic African, Mediterranean and Atlantic Iberian population components.

Keywords: growth; maturity; condition; reproductive phenology; climate change.

Variabilidad espacial de los parámetros de historia vital del estornino (*Scomber colias*), una especie en expansión en el Atlántico noreste

Resumen: El estornino es una especie pelágica presente en el océano Atlántico que en las últimas décadas se ha expandido hacia el norte en el Atlántico Oriental. Se recogieron muestras de peces procedentes de campañas científicas y capturas comerciales entre 2011 y 2019. Se analizó la variación geográfica de los parámetros biológicos (edad, longitud, peso y condición), así como la relación longitud-peso, la talla de madurez y el inicio y la duración de la temporada de desove en cinco áreas geográficas (de sur a norte): las islas Canarias, el Golfo de Cádiz, la costa occidental portuguesa, la costa noroccidental española y el mar Cantábrico. Se modeló la influencia de la SST en la talla de los peces como posible causa de la variabilidad geográfica. Todos los parámetros biológicos aumentaron progresivamente hacia el norte, mientras que la temporada de desove se retrasó y prolongó con el aumento de la latitud, desde enero en las islas Canarias hasta mayo-agosto en el mar Cantábrico, cuando la SST estaba entre 15°C y 19°C. La SST tuvo un efecto positivo sobre la talla en tres áreas de estudio y negativo en dos de ellas, lo que sugiere que cada grupo se encuentra en una posición diferente dentro de su rango de tolerancia térmica. La desviación del patrón geográfico de algunos parámetros biológicos en el Golfo de Cádiz, sugiere que podría ser una zona bisagra o de mezcla entre componentes poblacionales atlánticos africanos, mediterráneos e ibéricos.

Palabras clave: crecimiento; madurez; condición; fenología reproductiva; cambio climático.

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INTRODUCTION

Distribution shifts of marine fishes towards polar areas due to global warming have been reported or predicted in the northeast (Perry et al. 2005, Rijnsdorp et al. 2009) and northwest Atlantic (Murawski 1993), in Australian waters (Cheung et al. 2012 and references therein) and in the Pacific Ocean (Alabia et al. 2018, Cheung et al. 2015). Moreover, changes in marine biodiversity have been foreseen as a result of climate change (Cheung et al. 2009). Variations in temperature, pH and oxygen dissolved in the ocean affect the physiology and dynamics of all marine organisms (Pörtner et al. 2005, Rijnsdorp et al. 2009, Ottersen et al. 2010) and, together with distributional shifts, alter trophic structures, the composition of marine communities and thus ecosystem balances (Vergés et al. 2014). While any alteration in marine ecosystems will have a major impact on the services they provide, it is especially evident that changes affecting species exploited by fisheries will have a direct impact on the economy and human health because of the importance of fisheries in the economic development of coastal communities and in the provision of healthy food (Hollowed et al. 2013).

Atlantic chub mackerel (*Scomber colias*, Gmelin, 1789) is a medium-sized migratory coastal pelagic fish distributed in warm and temperate waters on both sides of the Atlantic Ocean (Castro and Santana 2000), including the Macaronesian archipelagos and reaching the Mediterranean and southern Black seas (Collette and Nauen 1983, Whitehead et al. 1984, Collette et al. 2011). Although for many years the Atlantic chub mackerel was considered the same species as the Indo-Pacific chub mackerel (*Scomber japonicus*, Houttuyn 1789), morphologic and genetic studies carried out in the first decade of the 20th century demonstrated that they are two different species (Infante et al. 2007, Catanese et al. 2010, Cheng et al. 2011).

In the Canary Islands (FAO area 34.1.2), small pelagic fish are targeted by the artisanal purse-seine fleet, and the Atlantic chub mackerel is the species most commonly caught all year around (FAO 2020a). In the Gulf of Cadiz (FAO area 27.9.a.s), Atlantic chub mackerel is jointly with anchovy and sardine one of three target species fished by the purse seine fleet operating in this area. Additionally, a specifically dedicated seasonal purse-seine fishery targets the species during the second and third quarters of the year, supplying the regional canning industry and providing food for caged bluefin tuna. On the western Portuguese coast (FAO area 27.9.a.c), the northwestern Spanish coast (FAO area 27.9.a.n) and the Cantabrian Sea (FAO area

27.8.c), Atlantic chub mackerel has gained economic importance in recent decades, becoming an important resource for the fishing fleet, especially purse seiners, which are responsible for the bulk of the total landings of this species (ICES 2020, 2021a). In these last three areas, increasing landings of Atlantic chub mackerel have coincided with the decrease in European sardine (*Sardina pilchardus*) landings and restrictions on Atlantic mackerel (*Scomber scombrus*) catches.

Despite its wide distribution, 90% of the Atlantic chub mackerel catches in the northeast Atlantic proceed from northwest African waters (FAO 2020b). More northerly, in the Atlantic Iberian waters, landings have increased significantly in the most recent years (ICES 2020). This increase has been associated with a higher availability of the fish, as it has expanded its distribution northwards (Martins et al. 2013, Punzón et al. 2016, ICES 2020). This phenomenon has been suggested to be probably driven by the increase in the sea temperature (Costoya et al. 2015, Jurado-Ruzafa et al. 2019) as a result of climate change (Tasker 2008, Reid and Valdés 2011). This distribution expansion makes Atlantic chub mackerel an interesting case study for the analysis of the impact of climate change on exploited species. In fact, Atlantic chub mackerel could compete in the new habitats with other important commercial pelagic species such as the congener Atlantic mackerel (*S. scombrus*), horse mackerel (*Trachurus trachurus*), sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) (Bachiller and Irigoien 2015, Garrido et al. 2015a, b, Veiga-Malta et al. 2019), especially in areas where its presence has increased recently. This competition could affect the fishing yields as well as the pelagic ecosystem balance.

Genetic, morphologic and parasite studies have shown significant differences between Atlantic chub mackerel from the western Atlantic and the eastern Atlantic (Scoles et al. 1998, Roldán et al. 2000, Costa et al. 2011), supporting the existence of two different populations at either side of the Atlantic Ocean. However, whether this species constitute a single stock or not in the eastern Atlantic is still unknown, as the studies performed in this area provide conflicting results (Scoles et al. 1998, Mele et al. 2014, Muniz et al. 2020). The information available on the northeast Atlantic suggests that in both African and European waters the species migrates from the wintering areas (mainly located in Mauritanian waters, southern Portugal and the inner part of the Bay of Biscay) towards northern waters in summertime and, in the case of the Bay of Biscay, towards the western Iberian Peninsula (ICES 2021a). However, knowledge regarding population dynamics,

life-history traits, migration patterns and connectivity of Atlantic chub mackerel in the northeast Atlantic and environmental drivers of their variation is scarce and fragmented. Therefore, large-scale studies such as the present one are essential to understand not only the population structure of Atlantic chub mackerel in the eastern Atlantic but also the influence of climate change on the dynamics of this expanding commercial species and, subsequently, on the ecosystems it colonizes and the fisheries targeting it.

The aim of this study was to analyse the spatial variation of the biological parameters of Atlantic chub mackerel between the traditional areas of distribution (Canary Islands and Gulf of Cadiz) and those of recent expansion further north on the Atlantic coast of the Iberian Peninsula (W Portuguese Coast, NW Spanish waters and Cantabrian Sea), as well as the role of sea surface temperature (SST) as a climate change-linked driver of life-history traits. The results of the present work will be useful for the future assessment of the species in European Atlantic waters, which has been promoted by ICES (2020).

MATERIAL AND METHODS

The study area covered most of the distributional range of Atlantic chub mackerel in the northeast Atlantic (Fig.1), from the Canary Islands (FAO area 34.1.2) to the Cantabrian Sea (FAO area 27.8.c). Table 1 contains information about the characteristics of the sampling procedures in each study area.

The Spanish Institute of Oceanography (IEO, CSIC, Spain) and the Instituto Português do Mar e da Atmosfera (IPMA, Portugal) collect biological data of Atlantic chub mackerel (length, weight and maturity) in the Atlantic Iberian waters from regular (monthly or quarterly) sampling of the commercial fleet (including landings, observers on board and biological sampling in the laboratory), as well as from the acoustic and demersal research surveys carried out within the EU Data Collection Framework. In the Canary Islands, the IEO monitors fleet activity and collects biological information on Atlantic chub mackerel monthly from

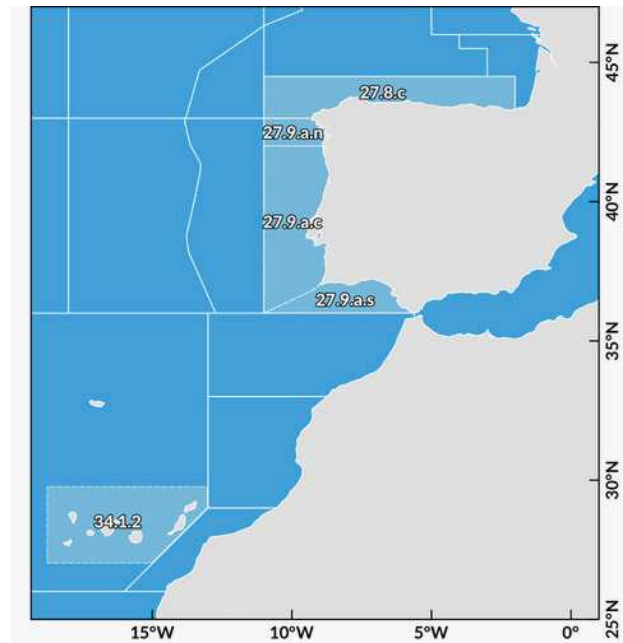


Fig. 1. – Map of the study area including the FAO subdivisions considered in the present analyses. 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea

commercial landings exclusively. For the present study, biological information on Atlantic chub mackerel collected between 2011 and 2019 from the monitoring programmes mentioned above was analysed.

For all collected specimens, total length (TL), total weight (TW) and sex were recorded. TL was recorded to the nearest 0.1 cm and TW to the nearest 0.1 g in the Canary Islands, 0.01 g for laboratory sampling and 0.5 g for scientific surveys in the remaining areas. Maturity stages were determined through macroscopic examination of the gonads in all areas. In the Canary Islands, maturity classification was based on the Holden and Raitt (1974) maturity key (I, immature; II, maturing virgin or resting; III, maturing; IV, spawning; V, spent), while in the remaining ar-

Table 1. – Description of the dataset used in the present study, including study area, Subdivision, FAO code of the study areas; Period, range of sampled years; N, number of sampled specimens (number of females); Length range, total length range of sampled specimens (cm); Age range, age range of sampled specimens (years); Origin, C-commercial landings; S-scientific surveys; n.a., not available.

Study area	Subdivision	Period	N	Length range	Age range	Origin
Cantabrian Sea	27.8.c.	2011-2019	10173 (4888)	11-51	0-14	C-S
NW Spanish Coast	27.9.a.n	2011-2019	3979 (2018)	12-42	0-6	C-S
W Portuguese waters	27.9.a.c	2011-2019	15075 (7458)	13-54	0-10	C-S
Gulf of Cadiz	27.9.a.s	2011-2019	12318 (5263)	11-40	0-7	C-S
Canary Islands	34.1.2	2013-2019	6778 (3426)	13-43	n.a.	C

as it was determined according to the Walsh et al. (1990) maturity key (I, immature; II, maturing; III, mature; IV, spawning; V, partial post-spawning; VI, final post-spawning).

More detailed information about the sampling schedules is provided in the supplementary material, including quarterly length distribution of sampled individuals in each study area (Table S1, Fig. S1).

In all study areas otoliths were collected from both males and females. Whole otoliths were mounted on black plastic slides, concave side up, covered with transparent resin and observed with a binocular microscope under reflected light for age estimation. Age readings from otoliths sampled from fish caught in the Canary Islands did not provide consistent results, so Canary data were not considered in the analyses involving age.

Since no sexual dimorphism has been found in this species (Techetach et al. 2019), all analyses were performed for both sexes combined, except for the study of the onset and duration of the spawning season (see details below).

Length-weight relationship

The length-weight (TL-TW) model used was

$$TW_i = aTL_i^b, i = 1, \dots, N,$$

where TW_i and TL_i are the total weight and length of the individual i , respectively, N the total number of individuals, and a and b the parameters to be estimated. The model was linearized taking logarithms (with base 10) on both sides, $\log_{10}(TW_i) = \log_{10}(a) + b\log_{10}(TL_i)$, for fitting in R software (R Core Team 2021) using the common function *lm* for linear models.

In addition to TL, other covariables can be included in the model predictor. In particular, the TL-TW parameters a and b can be specific for each of the K categories of a factor (Note this K has not any relationship with Fulton's condition factor). Then the model including the interaction between length and the factor is formulated as follows.

$$\begin{aligned} \log_{10}(TW_i) = & \log_{10}(a_1)I_1 + \log_{10}(a_2)I_2 + \dots \\ & + \log_{10}(a_K)I_K + b_1\log_{10}(TL_i)I_1 \\ & + b_2\log_{10}(TL_i)I_2 + \dots + b_K\log_{10}(TL_i)I_K \end{aligned}$$

where a_j and b_j are the a and b estimates, respectively, for category j ($j=1, \dots, K$) of the factor covariable, and the variables $I_j, j=1, \dots, K$ are binary dummy variables which take the value of 1 if individual i corresponds to category j . Then, the model leads to a and b specific estimates for each category of the factor covariable. In the current analysis, the model has been implemented for estimating a specific TL-TW relationship in each study area.

Condition

Condition was approached using Fulton's K condition index (Fulton 1902) to facilitate comparison with previous studies that used this proxy of condition.

Spawning season

The spawning period was determined for each area based on maturity stage data of females, as males sampled for the present study were in the spawning capable stage almost all year around. Furthermore, the existence of spawning capable females is the limiting factor for effective breeding. For the analysis, the proportion of spawning capable over the total number of mature females was the selected index. In the case of the Canary Islands, only females in stage IV (Holden and Raitt's scale) were considered as spawning capable females, whereas in the rest of areas, they corresponded to females in stages IV and V (Walsh's maturity scale). Spawning season was defined as the period of consecutive months when the proportion of spawning capable females was higher than 25%.

Length at maturity

The percentage of mature females at length class was fitted to the logistic equation:

$$\hat{P} = \frac{1}{1 + e^{-(a+bTL)}}$$

where \hat{P} is the predicted mature proportion, a and b the estimated coefficients of the logistic equation and TL the total length.

The length at which 50% of specimens are mature (length at first maturity, L_{50}) was estimated as the minus ratio of the coefficients ($-a/b$). All maturity ogive parameters were estimated using the *sizeMat* (Torrejon-Magallanes 2020) package of the R software (R Core Team, 2021), applying a frequentist generalized linear model with 500 iterations in the bootstrap resampling.

Modelling

Geographical variability

Comparisons of length, age, weight and condition between study areas were delivered by the Kruskal-Wallis rank sum test (Kruskal and Wallis 1952; *kruskal.test* function of the R software), because variances were not homogeneous between areas.

For post hoc comparisons between group levels, the Wilcoxon pairwise Rank sum Test was used (*pairwise.wilcox.test* function of the R software) with the Benjamini and Hochberg (1995) method for multiple testing corrections. These functions are from the *stats* R package (R Core Team, 2021).

Temperature effects

To explain the potential geographical differences in biological parameters between study areas, SST was chosen as an explanatory environmental variable because it is directly linked to global warming. SST data for the study areas were downloaded from the *SST Aqua MODIS, NPP, 4km, Daytime (11 microns)*,

2003-2019 (Monthly Composite) dataset at NOAA West Coast Regional Node ERDDAP data server (<https://coastwatch.pfeg.noaa.gov/erddap>). After data download, a 0.25×0.25-degree grid was used to average the SST, and subsequently the monthly averaged SST was assigned to the centroid of each grid cell. The R script for data download and averaging replication is available at <https://git.csic.es/jtornero/erddap-sst-download>.

A correlation analysis showed that TL and TW were highly correlated and that the condition factor, K, was also correlated with both length and weight (Fig. S2). We used generalized linear models (GLMs; Wood 2017) to model the effect of SST and geographical distribution (study area) on TL exclusively, assuming that their variability would be reflected directly in TW and partially in K, because these variables were correlated.

GLMs are an extension of linear models for which the distribution of the response variable can be other than Gaussian. For this reason, a link function, g , is required between the linear predictor and the conditional expectation of the response variable Y , $\mu(X)=E(Y|X)$, and the GLM is formulated as

$$g(\mu(X)) = \beta_0 + \beta_1 X_1 + \dots + \beta_p X_p$$

where $X=(X_1, \dots, X_p)$ are the covariables, $\mu(X)=E(Y|X)$ is the conditional expectation of the response variable Y , g is a link function between $\mu(X)$ and the linear predictor, and $(\beta_0, \beta_1, \dots, \beta_p)$ are the unknown model parameters.

A GLM assumes that the response variable follows a distribution belonging to the exponential distribution

family; in our analysis, it is assumed that our response variable (i.e. TL) follows a Gamma distribution with a natural logarithm link because it is a strictly positive continuous variable.

In GLM, the effects of categorical variables are considered fork-1 of the J factor levels, with the remaining one being considered the base level. Hence the estimated coefficient of each factor level will indicate the deviation from the value of the base level.

The presence of influence points, outliers that greatly affect the regression estimates, was checked using the *influence* function of the *mgcv* package (Wood 2011), which was also used to perform the GLMs.

All statistical analyses were performed with R v.4.0.5 (R Core Team 2021) and RStudio v.1.4.1717 (RStudio Team 2021). In all analyses, results were considered statistically significant when the p-value was <0.01. All figures were plotted using the *ggplot2* R package (v.3.3.5. Wickham 2016).

RESULTS

The TL of specimens collected for this study ranged between 11 and 54 cm (between 6 and 1498 g TW), corresponding to estimated ages between 0 and 14 years (Table 1). The largest and oldest specimens were collected on the western Portuguese coast and the Cantabrian Sea.

Results of the Kruskal-Wallis test demonstrated that the medians of all biological parameters (age, TL, TW and Fulton's K) were significantly different between the study areas ($p<0.01$, Fig. 2). In fact, the Wilcoxon test revealed that all variables differed significantly be-

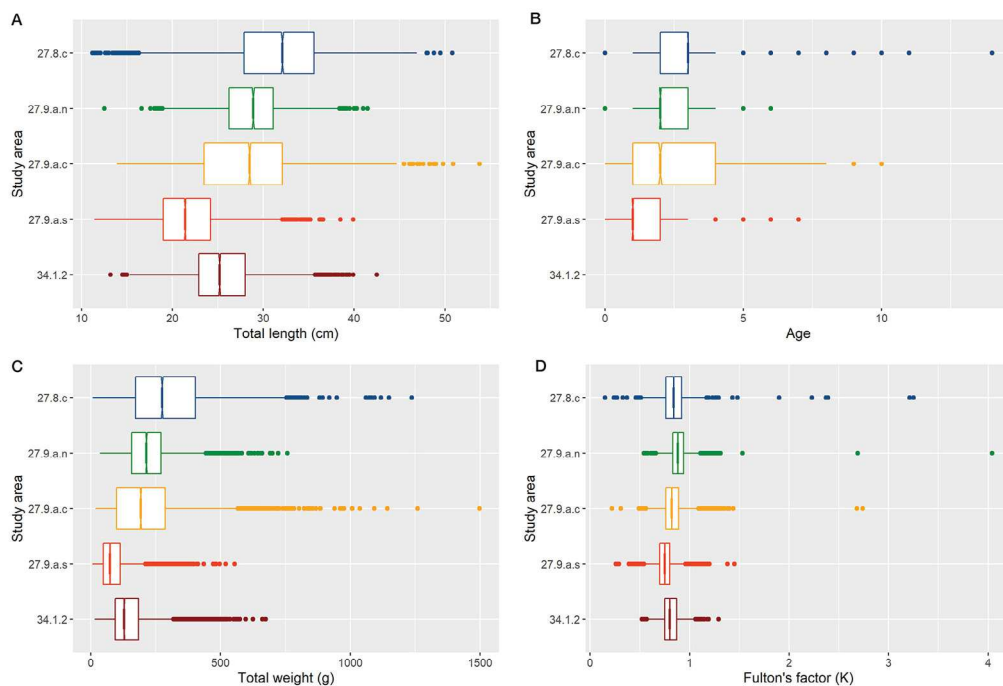


Fig. 2. – Boxplot of biological parameters by study area. A, total length; B, age (years); C, total weight and D, Fulton's condition factor (K). Geographical study areas from south to north are 34.1.2, Canary Islands (red); 27.9.a.s, Gulf of Cadiz (orange); 27.9.a.c, W Portuguese coast (yellow); 27.9.a.n, NW Spanish coast (green); and 27.8.c, Cantabrian Sea (blue). Vertical line within the boxes represents the median, boxes represent the inter-quartile range (IQR) or distance between the first (25%) and third (75%) quartiles, the notch represents the 95% confidence interval of the median, the whiskers represent $\pm 1.5 * IQR$ and dots represent the outliers.

Table 2. – Descriptive statistics of variables analysed in each study area. N, number of specimens; sd, standard deviation; min, minimum; max, maximum; se, standard error. Study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, Portuguese W coast; 27.9.a.n, NW Spanish coast; 27.8.c, Cantabrian Sea. SST, sea surface temperature; totL, total length (cm); totW, total weight (g); K, Fulton's condition factor; gonW, gonad weight (g). N in SST refers to the number of values extracted from the NOAA database according to the procedure explained in the Material and methods section (one value per day and cell of the 0.25x0.25-degree grid).

Area:	27.8.c						
	N	mean	sd	median	min	max	se
SST	10055	15.85	3.02	14.4	10.88	21.95	0.03
totL	10173	31.31	5.99	32.1	11.2	50.8	0.06
totW	10163	295.46	166.07	275	8	1237	1.65
K	10163	0.84	0.12	0.84	0.15	3.25	0
gonW	2828	4.46	9.92	1.51	0.01	128.2	0.19
Age	8084	2.75	1.37	3	0	14	0.02
Area:	27.9.a.n						
	N	mean	sd	median	min	max	se
SST	3979	16.38	2.15	16.05	12.84	20.7	0.03
totL	3979	28.4	4	28.9	12.5	41.5	0.06
totW	3977	218.45	95.89	214.34	35.6	757.71	1.52
K	3977	0.89	0.11	0.88	0.54	4.04	0
gonW	1454	1.39	2.76	0.78	0.01	66.48	0.07
Age	2356	2.28	1.02	2	0	6	0.02
Area:	27.9.a.c						
	N	mean	sd	median	min	max	se
SST	14899	18.04	2.32	18.36	13.65	22.36	0.02
totL	15074	27.94	5.46	28.5	13.9	53.8	0.04
totW	15072	207.56	127.54	192.55	18.14	1497.92	1.04
K	15072	0.82	0.11	0.82	0.22	2.74	0
gonW	10662	2.49	5.01	1.02	0.01	124.45	0.05
Age	6072	2.71	1.76	2	0	10	0.02
Area:	27.9.a.s						
	N	mean	sd	median	min	max	se
SST	12318	21.05	1.7	21.74	16.08	22.84	0.02
totL	12318	21.75	3.87	21.4	11.4	39.9	0.03
totW	12318	88.22	57.12	74	6.5	554	0.51
K	12318	0.75	0.09	0.75	0.26	1.45	0
gonW	1418	1.46	2.77	1	0.04	32.9	0.07
Age	3008	1.51	0.96	1	0	7	0.02
Area:	34.1.2						
	N	mean	sd	median	min	max	se
SST	6721	22.1	1.81	22.1	18.73	25.66	0.02
totL	6778	25.65	3.81	25.2	13.2	42.5	0.05
totW	6778	150.06	80.44	128.9	15.4	674.1	0.98
K	6778	0.82	0.09	0.8	0.52	1.29	0
gonW	6778	1.7	4.2	0.5	0.1	89.5	0.05
Age	0	NA	NA	NA	NA	NA	NA

tween all areas ($p < 0.01$; Fig. S3). In general, age, TL and TW progressively increased northwards from the Canary Islands to the Cantabrian Sea, with the exception of the Gulf of Cadiz, where the values were lower than expected according to the geographical pattern mentioned above. Mean age increased by 86.6% from the Gulf of Cadiz (1.5 years) to the Cantabrian Sea (2.8 years); mean TL decreased by 21.8% from the Canary Islands (25.7 cm) to the Gulf of Cadiz (21.8 cm) and then increased by 43.6% from Cadiz to the Cantabrian Sea (31.3 cm; by 21.8% compared with the Canary Islands); finally, mean TW decreased by 70.2% from Canary Islands (150.1 g) to the Gulf of Cadiz (88.2 g) and increased by 335% from here to the Cantabrian Sea (2955 g; by 96.9% compared with the Canary Islands). Table 2 shows the basic descriptive statistics of the biological variables analysed in this study.

The condition factor K ranged between 0.15 and 4.04. Individuals in the best condition were observed in the northern areas (NW Spanish waters and the Cantabrian Sea), but the geographical trend in K was not as clear as that observed in age, TL and TW. Similar mean K values were obtained in Atlantic chub mackerel from the Cantabrian Sea (27.8.c), the western Portuguese coast (27.9.a.c) and the Canary Islands (34.1.2) (\bar{K} between 0.82 and 0.84). The highest ($\bar{K}=0.89$) and lowest ($\bar{K}=0.75$) mean values were found on the northwestern Spanish coast (27.9.a.n) and the Gulf of Cadiz (27.9.a.s), respectively (Table 2). As expected, TW increased with TL and the values fitted to a power relationship, but this relationship differed significantly between study areas ($p < 0.01$, Fig. 3), even when only the overlapping size range was considered. Though the intercept and slope was significantly different between all study areas ($p < 0.01$; Fig. S4), the length-weight relationship was more similar among the groups from the Cantabrian Sea, the western Portuguese coast and the Canary Islands than for the groups from the northwestern Iberian Peninsula and the Gulf of Cadiz, which were more similar to each other, as observed in the condition factor. The final model predicts that the largest specimens from the northwestern Spanish waters and the Gulf of Cadiz are heavier than those from the other three areas.

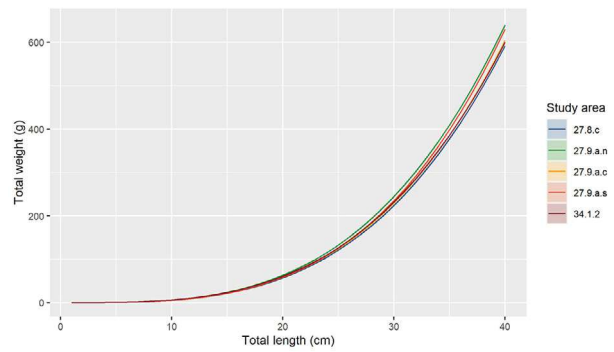


Fig. 3. – Plot of the modelled relationship between the total length (cm) and the total weight (g) by study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Shadow area, 95% confidence intervals.

Spawning activity was detected in all study areas based on monthly variability in the proportion of actively spawning females, although on the northwestern Spanish coast it was negligible ($< 25\%$) compared with the remaining areas. In the Canary Islands the peak of spawning activity was recorded in January, when 58% of females were active. In the Gulf of Cadiz a peak of 70% was recorded in February, on the western Portuguese coast a peak of 61% was recorded in March, on the northwestern Spanish coast a peak of 20% was recorded in April-May, and in the Cantabrian Sea a peak of 27% was recorded in May. Assuming that spawning period corresponds to the consecutive months when the proportion of actively spawning females is greater than 25%, a certain prolongation of the spawning season is also observed towards the north. While in the Canary Islands spawning is concentrated in a single month (January), in the Gulf of Cadiz it lasts three months (February-April) and on the western Portuguese coast it lasts six months (January-June). Spawning activity on the northwestern Spanish coast did not reach the threshold established in this study and in the Cantabrian Sea. Though spawning females were detected from January to September, their proportion was less than 25% only in May and July (Fig. 4). In summary, the peak of spawning was delayed and the spawning season extended northwards.

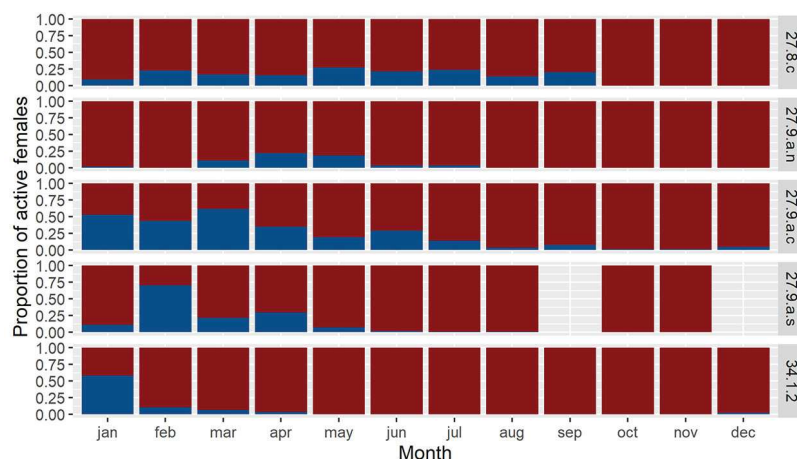


Fig. 4. – Monthly proportion of sexually active (blue) and inactive (red) females in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

Regarding size at first maturity, significant differences in the maturity ogive were detected between areas in both the intercept and the slope ($p < 0.01$, Fig. 5). Maturity ogives were estimated based on macroscopic maturity classification of ovaries, so a certain degree of inaccuracy is expected owing to the difficulty in distinguishing macroscopically between immature and recovering ovaries. The best fit of maturity ogives was obtained in the Cantabrian Sea ($R^2 = 0.73$), while in the remaining areas the goodness of fit was lower ($R^2 < 0.42$), especially in the Gulf of Cadiz (Table 3). However, the proportion of mature specimens was significantly related to length in all areas and fitted to the logistic model ($p < 0.01$), although the adjustment can only be considered really good in the Cantabrian Sea.

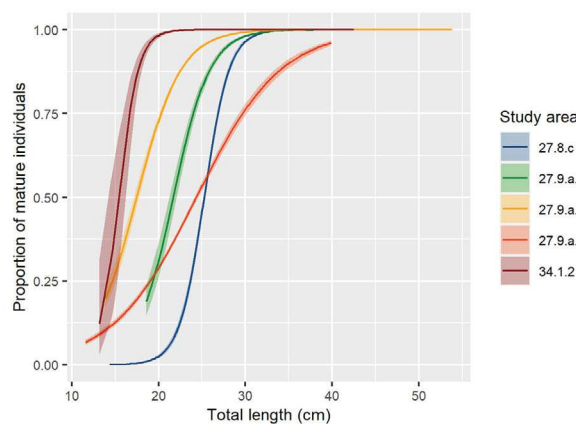


Fig. 5. – Estimated proportion of mature females at length in each study area based on macroscopic maturity classification of ovaries. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Shaded area, 95% confidence intervals.

Table 3. – Parameters of maturity ogives obtained in each study area. 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

Study area	a	b	L_{50}	R^2
27.8.c	-17.84	0.71	25.23	0.73
27.9.a.n	-10.21	0.47	21.70	0.41
27.9.a.c	-6.91	0.40	17.49	0.36
27.9.a.s	-5.71	0.24	23.98	0.19
34.1.2	-13.98	0.90	15.49	0.38

All these limitations imply that the results should be interpreted with caution. However, according to our analysis, a progressive increase in the L_{50} towards the north was observed, from 15.5 cm in the Canary Islands to 25.2 cm in the Cantabrian Sea, with the exception, once again, of the Gulf of Cadiz ($L_{50} = 24$ cm).

The SST in the study areas fluctuated between 10.9°C and 25.7°C (Table 2), with a significant and progressive decrease in mean SST from the Canary Islands (22.1°C) to the Cantabrian Sea (15.9°C) ($p < 0.01$,

Fig. S5). Spawning season was detected to take place between 14°C and 21°C in all study areas. More specifically, mean SST during the spawning season decreased progressively from the Canary Islands (20.5°C) to northwestern Spanish waters (14.6°C), increasing again in the Cantabrian Sea (18.1°C). Our results demonstrated that SST influences total fish length. In fact, our model, which includes the study area, mean annual SST and interaction between them as covariates, explains 33.3% of TL deviance (Table 4). In the Atlantic Iberian waters, the SST-TL relationship showed a positive slope in the Cantabrian Sea (mean SST = 15.8°C), which decreased and became negative southwards, coinciding with the increase in SST: 16.4°C on the northwestern Spanish coast, 18°C on the western Portuguese coast and 21°C in the Gulf of Cadiz. Whereas in the Cantabrian Sea and on the northwestern Spanish coast the slope was positive, on the western Portuguese coast and in the Gulf of Cadiz it was negative. On the other hand, in the Canary Islands, with the highest mean annual SST (22.1°C), the SST-TL relationship showed the steepest slope (Fig. 6).

Table 4. – Parameters and coefficients of the total length model. 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

	Estimate	Std. Error	t value	p-value
Intercept	3.34	0.009	348.8	< 0.01
27.9.a.n	-0.07	0.024	-2.93	< 0.01
27.9.a.c	0.01	0.015	0.721	0.47
27.9.a.s	-0.03	0.022	-1.174	0.24
34.1.2	-0.42	0.029	-14.834	< 0.01
SST	0.01	0.001	10.655	< 0.01
27.9.a.n:SST	-0.001	0.001	-1.264	0.21
27.9.a.c:SST	-0.01	0.001	-8.795	< 0.01
27.9.a.s:SST	-0.02	0.001	-15.648	< 0.01
34.1.2:SST	0.01	0.001	6.184	< 0.01
R^2	0.329		Dev.Expl.	33.3%

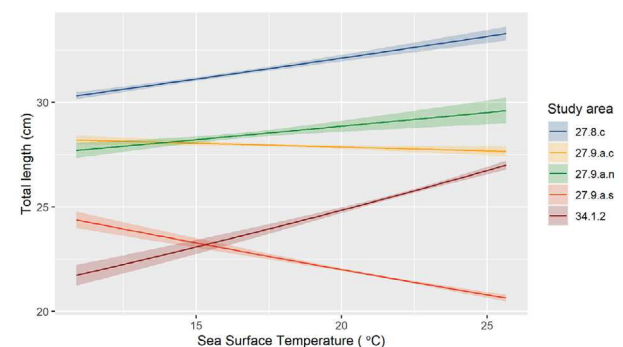


Fig. 6. – Predicted effect of sea surface temperature on total length in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Shaded area, 95% confidence intervals.

DISCUSSION

Our results show a clear latitudinal gradient of biological parameters of Atlantic chub mackerel from the Canary Islands (division 34.1.2) to the Cantabrian Sea (27.8.c), with the exception of the Gulf of Cadiz (27.9.a.S), where the estimated values in general break this trend. Both the age range and mean age increase northwards, leading to an increase not only in length and weight, but also in length at first maturity and condition factor, though in the latter case the progression is not as evident as for the other parameters. The smallest, lightest and youngest specimens were collected in the Gulf of Cadiz. Growth was not estimated in this work because age data were not available for all study areas. However, the differences in length suggest that the age structure in Canary waters is likely to be biased towards younger ages than in the Iberian Peninsula groups (with the exception of the Gulf of Cadiz). Although the sampling in the Gulf of Cadiz was biased towards the second half of the year (Fig. S1), the lengths of the specimens caught in this area were smaller than in the other areas in all quarters of the year, so these differences were not due to sampling bias but rather to the biological attributes of this component of the north-east Atlantic population of Atlantic chub mackerel, as we discuss below.

The increase in size with latitude coincides with Bergman's rule (Bergmann 1847). Several works have attempted to verify Bergman's rule on ectothermic species, with contradictory results for fishes (Belk and Houston 2002 and references therein). Rypel (2014) suggested that the expression of Bergman's rule in fishes is linked to the species' thermal niches and is only applicable to coldwater species. However, Atlantic chub mackerel is a temperate species (Castro and Santana 2000), so our results suggest that Rypel's hypothesis could also be extended to this type of species or, at least, to those with a wide distribution range, such as Atlantic chub mackerel (Whitehead et al. 1984). Recent studies show that pelagic fish, including Atlantic mackerel, also belonging to the genus *Scomber*, follow Bergmann's rule, confirming that temperature is one of the most important determinants of body size (Hattab et al. 2021). Similarly, latitudinal differences in length at maturity have been observed in the horse mackerel (*Trachurus trachurus*) in the Mediterranean Sea (Ferrer et al. 2019), which some authors have associated with primary production and temperature (Bonanno et al. 2016; Basilone et al. 2017). Pörtner et al. (2005) concluded that eurytherms are able to dynamically adjust the range of their tolerance windows according to temperature fluctuations, so adapted eurytherms show better fitness than native stenotherm species. These authors further suggested that natural selection should favour the adapted eurytherm species, which are energy-efficient, grow fast and reproduce successfully. These results are especially relevant when one considers global warming and its combined impact with fisheries exploitation, as the most commonly exploited pelagic species have shown a drastic decline in growth, condition and size (Van Beveren et al. 2014; Brosset et

al. 2017). Given the wide distribution of Atlantic chub mackerel, it can be considered a highly adaptive eurytherm, so its ability to colonize new habitats is likely to be high, and it may continue to expand northwards as long as water becomes warmer within its temperature tolerance or preference, so it is able to adapt to global warming even better than native species.

This type of geographical gradients of life-history traits has been reported in other species from both freshwater and marine habitats (Vila-Gispert et al. 2002, Blanck and Lamouroux 2006), as well as different life stages, from early ones (Castro et al. 2002, Takahashi et al. 2012) to adults (Huret et al. 2019). Hughes et al. (2017) relate the latitudinal gradient of life-history traits to temperature, while other authors relate it to other environmental processes such as upwelling events (Gertseva et al. 2017), meso- and large-scale oceanographic processes (Castro et al. 2009, Stocks et al. 2014), fishing pressure (Gertseva et al. 2010), food quality and availability (Perrotta et al. 2005) or a combination of several of them (Huret et al. 2019). The reality is that energy trade-offs in fish are complex and depend on the balance between energy inputs and the metabolic costs of maintenance, growth or maturity. Additionally, all these metabolic processes are strongly influenced by the physical and biological environment in which individuals develop their life stages (Kooijman 2009) and by their life strategies. Because of this, linking geographical clines of biological parameters to specific environmental drivers is difficult, especially in widely distributed species such as the Atlantic chub mackerel.

In the case of pelagic fish, latitudinal changes of biological parameters have been documented in several life-history traits. For example, in *Arripis trutta* from Australia the number of large and old fish was reported to increase northwards, from the cold waters of Tasmania to the warm waters of southern Queensland, although the initial growth rate was higher in the southern areas (Hughes et al. 2017). Furthermore, Huret et al. (2019) observed an increase in growth rate, body size and length at maturity with latitude in European anchovy, and suggested a combination of factors (food availability, maintenance costs, environmental seasonality and temperature) as drivers of these latitudinal gradients.

The present study demonstrates that geographical differences in age and length structure, condition, spawning and maturity of NE Atlantic chub mackerel are significant, showing a clear latitudinal gradient with small and early maturing individuals in the south (the Canary Islands). As the maturity classification was based on macroscopic staging, the results for this parameter must be interpreted with caution; however, considering that we found significant differences between areas in the other biological parameters, the differences in length at first maturity detected in this study can be expected to be real. Latitudinal gradient is also detected in reproductive phenology, with earlier, shorter and more intense spawning activity in the southern study areas than in the northern ones. Latitudinal variability of reproductive season onset and duration has been re-

ported in other fish species too. Huret et al. (2019) reported a delay and shortening of the reproductive season of European anchovy in more northern latitudes, linked to seasonal variability of temperature and food availability and the ability of individuals to accumulate energy reserves. Barbee et al. (2011) found that, in the diadromous fish *Galaxias maculatus*, spawning season onset occurred earlier at high latitude (New Zealand), where spawning fish were older and larger than on the south coast of Australia. These authors linked this geographical variability of life-history traits to key environmental parameters that vary seasonally, such as temperature, day-light duration and productivity. In our case, latitudinal differences in reproductive phenology could be related not only to temperature and food availability, but also to population structure. However, more analyses are required to corroborate this hypothesis.

The maximum length observed in the present study was between 40 and 54 cm (mean between 21.8 and 31.3 cm), while the maximum age recorded was between 6 and 14 years (mean between 1.5 and 2.8 years). These results are in accordance with the observations of previous studies (Velasco et al. 2011, Jurado-Ruzafa et al. 2021, Navarro et al. 2021b).

Mean Fulton's K ranged between 0.82 and 0.89 considering all study areas, except in the Gulf of Cadiz, where K was slightly lower (mean = 0.75). In Atlantic chub mackerel, condition factor is significantly related to TL (Fig. S6). Therefore, the low values observed in the Gulf of Cadiz may be due to the small size of specimens from this area. Fulton's K values between 0.7 and 1.1 have been reported for the Atlantic chub mackerel from the Atlantic Portuguese coast (Alves 2016, Santos et al. 2017, Barboza et al. 2020), suggesting that the mean condition indices obtained in the study period and areas are in the lower part of this range. Fish body condition is closely related to feeding, metabolic rates and the capacity to store energy reserves, i.e. to energetic trade-offs (Saborido-Rey and Kjesbu 2005), all of which are modulated by environmental factors such as temperature or prey availability and diversity, i.e. marine community biodiversity. Changes in the pelagic ecosystem induced by global warming, fishing pressure or any other environmental driver may lead to a decrease in the health status of native pelagic fishes (Shephard et al. 2014, Muhling et al. 2017).

The biological characteristics of Atlantic chub mackerel from the Gulf of Cadiz (young, small and low-condition specimens) should be also addressed from the environmental-induced point of view. In this area, there has been an increase in landings of Atlantic chub mackerel since 2007. While this increase coincides with the recent expansion of the species throughout Ibero-Atlantic waters, it also coincides with the decline of the Ibero-Atlantic sardine stock, which led to severe restrictions on fishing opportunities for this species. These limitations may have led to a change in the behaviour of the fleet, which may have redirected its effort towards Atlantic chub mackerel to compensate for the decline in sardine catches (ICES 2021a). This increase in fishing effort could be behind the juvenescence of Atlantic chub mackerel in this area. However,

as explained below, the Gulf of Cadiz could also be either a mixing area between the Atlantic and Mediterranean populations or a hinge area in the latitudinal and longitudinal biological gradient observed for Atlantic chub mackerel in the NE Atlantic and Mediterranean.

Regarding the onset and duration of the spawning season, most of the existing studies of Atlantic chub mackerel are based on the analyses of the monthly prevalence of active females and the gonado-somatic index, showing some variability among regions. The spawning season in North African waters has been reported from December to March in Morocco (Tchetchach et al. 2010, Wahbi et al. 2011) and from January to March in Mauritania and Senegal (ICES 2020). In the Atlantic islands the spawning season of Atlantic chub mackerel has been reported from November/December to March in the Canary Islands (Lorenzo and Pajuelo 1996, Jurado-Ruzafa et al. 2021), from January to April in Madeira (Vasconcelos et al. 2012) and from March to July/August in the Azores (Carvalho et al. 2002). Finally, in the Atlantic Iberian waters spawning season has been reported from December to March in waters of southern Portugal waters (ICES 2020), from December to May in western Portuguese waters (Nunes et al. 2019) and, lastly, from March to July on the northwestern Spanish coast and the Cantabrian Sea (Villamor et al. 2017, Navarro et al. 2021a). The spawning period of Atlantic chub mackerel in the Mediterranean Sea has been reported from April to August (Rizkalla 1998, Cengiz 2012, Allaya et al. 2013). Our results show a clear latitudinal gradient of spawning season onset and duration that matches with previous studies. Reviewing all this information together, there seems to be a latitudinal trend from the Strait of Gibraltar towards the poles, but also a longitudinal one from the Strait of Gibraltar towards the Mediterranean Sea and the central Atlantic. Changes in reproductive phenology are usually associated with environmental drivers (Rogers and Dougherty 2019, Slesinger et al. 2021), although they could be related to the age structure of populations, as spawning season onset and duration may change depending on the age of reproductive specimens (Lambert 1987, Wright and Trippel 2009). However, with the available data we cannot distinguish whether the phenological differences observed in this study are due to environmental drivers or to the differences in the population structure of each study area. This is especially important in the context of global warming, which is leading to distribution shifts of fish species because reproductive phenology affects population resilience (Lowerre-Barbieri et al. 2017), and more attention should be paid to this issue in the near future.

Regarding the size at first maturity (L_{50}) of Atlantic chub mackerel, our results based on macroscopic observations showed a latitudinal trend, with the lowest value in the Canary Islands (15.5 cm) and increasing progressively towards the north (17.5 cm on the western Portuguese coast and 25.2 cm in the Cantabrian Sea). Once again, the L_{50} values for the Gulf of Cadiz (24 cm) break with this trend, despite the fact that in general the individuals in this area are the smallest. Previous studies reported higher values in the Bay of

Biscay ($L_{50}=29$ cm; Lucio 1997) and in Portuguese waters ($L_{50}=27$ cm; Martins 1996), although more recent investigations showed L_{50} values in the Bay of Biscay similar to those reported here (25 cm; Villamor et al. 2017, Navarro et al. 2021a). In western Portuguese waters, Nunes et al. (2019) reported an L_{50} equal to 22.6 cm and 19.2 cm for females and males, respectively; while Gonçalves et al. (2016) in southern Portugal reported an L_{50} for both sexes combined of 18.6 cm. These Portuguese values are slightly higher than our estimations (17.5 cm). In the case of the Canary Islands, our estimate of L_{50} is the smallest one and lower than previous estimations reported in the same area (18–19 cm; Lorenzo and Pajuelo 1996, Jurado-Ruzafa et al. 2021). This difference is likely due to differences in the data used to calculate the L_{50} , which in previous studies included post-spawning and spawning specimens collected exclusively during the spawning period. In Atlantic Moroccan waters, L_{50} values increased from 23 cm in the north (Techetach et al. 2010) to 25 to 27.5 cm in the south (Wahbi et al. 2017). High values of L_{50} were reported in the Azores (27.8 cm; Carvalho et al. 2002), followed by Madeira (22 cm; Vasconcelos et al. 2012) and the Mediterranean Sea (16.8 and 19 cm; Cengiz 2012, Cikeš and Zorica 2012, Techetach et al. 2019). Spatial patterns of size at first maturity do not seem to be as clear as spawning onset and duration, although the L_{50} values presented here should be interpreted with caution, as stated above. Nevertheless, certain latitudinal and longitudinal trends of maturity patterns can be glimpsed and should be corroborated by histological studies. In any case, the spatial differences observed in size and age structure and condition suggest the existence of different life-history patterns, so spatial differences in maturation can also be expected. This aspect would be especially relevant for stock assessment purposes.

The spatial population structure of the Atlantic chub mackerel in the eastern Atlantic, the migration processes through the distribution range and the connectivity, including the Mediterranean Sea, remain unknown (ICES 2021a). The geographical differences in life-history traits estimated in this and previous studies suggest that there may be at least two population components: one in the Canary Islands and one in the Iberian Peninsula. Furthermore, the Iberian unit could include two subcomponents in the Cantabrian Sea (Bay of Biscay) and the Portuguese coast, whose degree of connection could vary depending on the abundance and migration intensity of Atlantic chub mackerel in each area (ICES 2020 and references therein). Additionally, the Gulf of Cadiz could be considered a hinge area, or even a mixing area between the northeast and central east Atlantic populations of Atlantic chub mackerel as well as between the northeast Atlantic and Mediterranean stocks, as suggested by ICES (2021a). The results of the growth analysis carried out by Velasco et al. (2011) support the hypothesis of a mixing area, as they found no differences in growth between the Gulf of Cadiz and the Alboran Sea, suggesting that the Strait of Gibraltar is not a geographical barrier for this species. However, in general, results of studies targeting

the stock structure of Atlantic chub mackerel in the northeast Atlantic and the Mediterranean Sea show differences depending on the methodological approach. Some genetic studies showed no significant differences between the Atlantic chub mackerel from the Mediterranean and eastern Atlantic areas (Scoles et al. 1998, Zardoya et al. 2004). However, significant regional differences have been found between smaller areas in the east Atlantic Ocean, including the Mediterranean Sea and Macaronesian islands, based on the analysis of morphology, meristic characteristics (Allaya et al. 2016, Bouzzammit and El Ouizgami 2019, Muniz et al. 2020) and associated parasites (Mele et al. 2014). Muniz et al. (2020), based on otolith morphology analysis, suggested the existence of one group in the northeast Atlantic islands (Azores, Madeira and the Canary Islands) and another one on the Iberian Portuguese coast. Correia et al. (2021), according to microchemical analysis of the same otoliths, suggested the existence of at least four stock components in the northeast Atlantic (Azores, Madeira, Canary Islands and Iberian Portuguese coast). There is no information on the migratory behaviour of this species in the study area, although by analogy with the previous study on the species in northwest African waters (García 1982), we assume that the Atlantic chub mackerel performs annual reproductive migrations all along its distributional range. If so, connectivity between the different population components may exist, but the extent of this migration and therefore the degree of potential connectivity remain unknown. Many of these studies have been approached on a local or regional scale, and thus lack the global vision required to investigate the population structure of a species as widely distributed as the Atlantic chub mackerel. Jansen et al. (2013) proposed for the northeast Atlantic mackerel (*S. scombrus*) that the population structure is more a dynamic cline rather than connected contingents, and this could also be the case of the Atlantic chub mackerel. However, more studies targeting migration behaviour, genetics, morphometry and meristic characterization from a global perspective should be carried out to confirm meaningful biological management units for assessment purposes.

Considering that the increase in abundance of Atlantic chub mackerel in the Atlantic Iberian waters is assumed to be a relatively recent event (Villamor et al. 2017), it is striking that individuals in the northernmost (i.e. most recently occupied) study areas show the greatest diversity of age and size and the best condition. There are two possible explanations for this: a) the presence of older and larger individuals of Atlantic chub mackerel could be due to the fact that they have a greater capacity for movement and therefore a greater capacity for expansion to new suitable habitats in a global warming scenario; and/or b) fishing pressure or predation could be less intense in the north than in northwest African waters, reducing the presence of larger and older individuals in this area. With the information available, we cannot determine the causes of the age and size structure observed in each study area. According to Saunders and Tarling (2018), greater body size in mesopelagic fishes is a necessary attri-

bute to reach colder regions, which supports our first hypothesis that the largest individuals are those with the greatest migratory capacity.

In most studied fish species, great size, age and condition are associated with high reproductive potential owing to the existence of maternal effects (Green 2008). In addition, a prolonged reproductive season increases the probability of offspring finding optimal environmental windows for their development, thus increasing their survival (Mertz and Myers 1994). Given the biological characteristics of the groups analysed in this study and the duration of the reproductive season in each area, the geographical variability of the reproductive potential of this species and its impact on stock resilience should be analysed in the future. This variability may be a mechanism of adaptation to the environmental conditions (temperature, productivity and turbulence) that could favour or jeopardize offspring survival and hence recruitment.

Our model indicates that SST does indeed play a relevant role in the size of Atlantic chub mackerel and, presumably, on its growth. While on the western Portuguese coast and the Gulf of Cadiz this effect is negative, in the remaining areas it is positive. The rates of physiological processes usually increase with temperature up to a certain limit, above which the temperature effect becomes negative. This temperature effect is also observed in the growth of fish, so at low temperatures growth increases as temperature increases until a tipping point (optimum temperature) when growth decreases with increasing temperature (Jobling 1995). The temperature range at which fish populations exhibit this behaviour changes geographically owing to acclimation mechanisms (Sunday et al. 2011). Therefore, growth is expected to increase with temperature in areas that are below their optimum temperature and to decrease in areas that have exceeded this threshold. Assuming the total length as a proxy of the growth rate of Atlantic chub mackerel for each study area, and based on the slope of the SST-TL relationship, we could conclude that *S. colias* in the Cantabrian Sea and on the northwestern Spanish coast is farther from its optimum temperature than it is on the western Portuguese coast, where it is slightly above it, and in the Gulf of Cadiz, where it is clearly above it. In the Canary Islands, where mean annual SST is considerably higher than in the rest of the study areas, the effect of SST on the TL of Atlantic chub mackerel was the most markedly positive. We do not know the reasons behind this relationship but it could be related to the comparatively small specimens of Atlantic chub mackerel inhabiting the Canary waters. Further knowledge of this relationship between SST and growth would help to better understand the dynamics and population structure of Atlantic chub mackerel in the northeast Atlantic in order to properly calibrate the assessment and manage this resource adequately under future global warming scenarios.

Many fish species have been reported to be moving to higher latitudes as a consequence of climate change (Perry et al. 2005, Rijnsdorp et al. 2009). One of the most emblematic cases in recent decades is that of the Atlantic mackerel (*S. scombrus*), whose distribution

has expanded northwards and westwards in the NE Atlantic Ocean, reaching the waters of Svalbard and Iceland (Berge et al. 2015) driven by stock size and temperature (Astthorsson et al. 2012, Olafsdottir et al. 2019). Similarly, landings of Atlantic chub mackerel in the Atlantic Iberian waters have increased during the last few decades (Martins et al. 2013, Villamor et al. 2017, ICES 2020), likely associated with an increase in stock size and its northward expansion linked to global warming. The arrival of new species in ecosystems can have a major impact on trophic balances and the dynamics of other species (Cheung et al. 2009, Hollowed et al. 2013, Muhling et al. 2017). The Atlantic chub mackerel is an opportunistic pelagic species that feeds mainly on euphausiids and decapod crustaceans, but also significantly on eggs, larvae and juveniles of other pelagic and demersal fish species (Torres et al. 2013). In fact, Garrido et al. (2015a) identified sardine eggs as an important component of the diet of Atlantic chub mackerel and reported a considerable overlap in the prey spectrum between European sardine and juvenile chub mackerel. Taking this into account, it is probable that the expansion of Atlantic chub mackerel in Atlantic Iberian waters played an important role in the decline of Iberian sardine populations observed in the same period. To corroborate this hypothesis, the trends of both species in the Atlantic Iberian waters in the coming years should be monitored, especially when the sardine population has started to recover (ICES 2021b). Another question that would be worth investigating further is whether the change in the distribution of *S. scombrus* could have reduced the occupation of certain pelagic niches in Atlantic Iberian waters, which could be being occupied by warmer-water species such as the Atlantic chub mackerel. Furthermore, its expansion in Atlantic Iberian waters may also impact on predators, as it has been reported as an important prey for other commercial species such as European hake, sharks, bluefin tuna and marine mammals (Torres et al. 2013, Varela et al. 2013, Giménez et al. 2017).

This paper outlines the population structure of the Atlantic chub mackerel in the northeast Atlantic from a broad geographical perspective and provides information on the regional variability of key biological parameters commonly required for assessment, such as length-weight relationships, the maturity ogive and size composition. However, there are still many gaps to be filled. In relation to population structure, it would be desirable to extend the study to North African and western Mediterranean waters in order to carry out not only analyses of life-history parameters such as growth and maturation, but also other stock identification studies such as genetic, morphometric and parasite analyses with a wider perspective. Similarly, it would be necessary to analyse how the biological differences detected between the study areas affect the productivity and resilience of the species. This would require time series of fecundity, egg and larval quality and recruitment. Additionally, analysing biodiversity changes in the pelagic ecosystem of the study areas would allow us to understand the impact of new species arrivals on fisheries yields. Ulti-

mately, from an ecological point of view, this species is a promising case study for monitoring the impact of climate change on pelagic ecosystems.

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REFERENCES

- Alabía I.D., García Molinos J., Saitoh S.I., et al. 2018. Distribution shifts of marine taxa in the Pacific Arctic under contemporary climate changes. *Divers Distrib.* 24: 1583-1597. <https://doi.org/10.1111/ddi.12788>
- Allaya H., Hattour A., Hajjej G., Trabelsi M. 2013. Biologic characteristics of *Scomber japonicus* (Houttuyn, 1782) in Tunisian waters (Central Mediterranean Sea). *Afr. J. Biotechnol.* 12: 3040-3048. <https://doi.org/10.5897/AJB12.2723>
- Allaya H., Zrelli S., Hajjej G. 2016. Identification of Atlantic Chub mackerel *Scomber colias* population through the analysis of body shape in Tunisian waters. *Cah. Biol. Mar.* 57: 195-207
- Alves M.F. 2016. Survey of parasites of Atlantic Chub Mackerel (*Scomber colias*) with economic and public health impact: MSc thesis. 1-37.
- Astthorsson O.S., Valdimarsson H., Gudmundsdottir A., Óskarsson G.J. 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *ICES J. Mar. Sci.* 69: 1289-1297. <https://doi.org/10.1093/icesjms/fss084>
- Bachiller E., Irigoien X. 2015. Trophodynamics and diet overlap of small pelagic fish species in the bay of biscay. *Mar. Ecol. Prog. Ser.* 534: 179-198. <https://doi.org/10.3354/meps11375>
- Barbee N.C., Hale R., Morrongiello J., et al. 2011. Large-scale variation in life history traits of the widespread diadromous fish, *Galaxias maculatus*, reflects geographic differences in local environmental conditions. *Mar. Freshw. Res.* 62: 790-800. <https://doi.org/10.1071/MF10284>
- Barboza L.G.A., Lopes C., Oliveira P., et al. 2020. Microplastics in wild fish from North East Atlantic Ocean and its potential for causing neurotoxic effects, lipid oxidative damage, and human health risks associated with ingestion exposure. *Sci. Total. Environ.* 717: 134625. <https://doi.org/10.1016/j.scitotenv.2019.134625>
- Basilone G., Mangano S., Pulizzi M., et al. 2017. European anchovy (*Engraulis encrasicolus*) age structure and growth rate in two contrasted areas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas. *Mediterr. Mar. Sci.* 18: 504-516. <https://doi.org/10.12681/mms.2059>
- Belk M.C., Houston D.D. 2002. Bergmann's Rule in Ectotherms: A Test Using Freshwater Fishes. *Am. Nat.* 160: 803-808. <https://doi.org/10.1086/343880>
- Benjamini Y., Hochberg Y. 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *J. R. Stat. Soc. Ser. B.* 57: 289-300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Berge J., Heggland K., Lønne O.J., et al. 2015. First Records of Atlantic Mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with Possible Explanations for the Extensions of Its Distribution, Arctic 68: 54-61. <https://doi.org/10.14430/arctic4455>
- Bergmann C. 1847. Über die Verhältnisse der Wärme ökonomie der Thiere zu ihrer Grösse. *Göttinger Stud.* 3: 595-708.
- Blanck A., Lamouroux N. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. *J. Biogeogr.* 34: 862-875. <https://doi.org/10.1111/j.1365-2699.2006.01654.x>
- Bonanno A., Barra M., Basilone G., et al. 2016. Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. *Fish. Oceanogr.* 25: 471-490. <https://doi.org/10.1111/fog.12166>
- Bouzzammit N., El Ouizgani H. 2019. Morphometric and meristic variation in the Atlantic chub mackerel *Scomber colias* Gmelin, 1789 from the Moroccan coast. *Indian J. Fish.* 66: 8-15. <https://doi.org/10.21077/ijf.2019.66.2.78488-02>
- Brosset P., Fromentin J.M., Van Beveren E., et al. 2017. Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas, *Prog. Oceanogr.* 151: 149-162. <https://doi.org/10.1016/j.pocean.2016.12.002>
- Carvalho N., Perrotta R.G., Isidro E. 2002. Age, growth and maturity in the chub mackerel (*Scomber japonicus* Houttuyn, 1782) from the Azores. *Life Mar. Sci.* 19A: 93-99.
- Castro J.J., Santana A.T. 2000. Synopsis of Biological Data on The Chub Mackerel (*Scomber japonicus* Houttuyn, 1782). *FAO Fish Synopsis.* 39: 1-77.
- Castro L.R., Llanos A., Blanco J., et al. 2002. Influence of Latitude Variations in Spawning Habitat Characteristics on the Early Life History Traits of the anchoveta, *Engraulis ringens*, off northern and central Chile. In: Van der Lingen C.D., Roy C., Fréon P., Barange M., Castro L., Gutierrez M., Nykjaer L. and Shillington F. (eds). Report of a GLOBEC-SPACC/IDYLE/ENVIFISH workshop on spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas. *GLOBEC Report* 16: 42-45.
- Castro L., Claramunt G., Krautz M., et al. 2009. Egg trait variation in anchoveta *Engraulis ringens*: a maternal response to changing environmental conditions in contrasting spawning habitats. *Mar. Ecol. Prog. Ser.* 381: 237-248. <https://doi.org/10.3354/meps07922>
- Catanese G., Machado M., Infante C. 2010. Evolutionary relatedness of mackerels of the genus *Scomber* based on complete mitochondrial genomes: Strong support to the recognition of Atlantic *Scomber colias* and Pacific *Scomber japonicus* as distinct species. *Gene.* 452: 35-43. <https://doi.org/10.1016/j.gene.2009.12.004>
- Cengiz Ö. 2012. Age, growth, mortality and reproduction of the chub mackerel (*Scomber japonicus* Houttuyn, 1782) from Saros Bay (Northern Aegean Sea, Turkey). *Turkish J. Fish. Aquat. Sci.* 12: 799-809. https://doi.org/10.4194/1303-2712-v12_4_08
- Cheng J., Gao T., Miao Z., Yanagimoto T. 2011. Molecular phylogeny and evolution of *Scomber* (Teleostei: Scombridae) based on mitochondrial and nuclear DNA sequences. *Chinese J. Oceanol. Limnol.* 29: 297-310. <https://doi.org/10.1007/s00343-011-0033-7>
- Cheung W.W.L., Lam W.V.Y., Sarmiento J.L., et al. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish. Fish.* 10: 235-251. <https://doi.org/10.1111/j.1467-2979.2008.00315.x>
- Cheung W.W.L., Meeuwig J.J., Feng M., et al. 2012. Climate-change induced tropicalisation of marine communities in Western Australia. *Mar. Freshw. Res.* 63: 415-427. <https://doi.org/10.1071/MF11205>
- Cheung W.W.L., Brodeur R.D., Okey T.A., Pauly D. 2015. Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. *Prog. Oceanogr.*

- 130: 19-31.
<https://doi.org/10.1016/j.pocean.2014.09.003>
- Cikeš Keč V., Zorica B. 2012. The reproductive traits of *Scomber japonicus* (Houttuyn, 1782) in the Eastern Adriatic Sea. J. Appl. Ichthyol. 28: 15-21.
<https://doi.org/10.1111/j.1439-0426.2011.01893.x>
- Collette B.B., Nauen C.E. 1983. FAO Species Catalogue Vol. 2 Scombrids of the world an annotated and illustrated catalogue of Tunas, Mackerels, Bonitos and related species know to date
- Collette B., Amorim A.F., Boustany A., et al. 2011. *Scomber colias*. The IUCN Red List of Threatened Species 2011: e.T170357A6767497.
<https://doi.org/10.2305/IUCN.UK.2011-2.RLTS.T170357A6767497.en>
- Correia A.T., Moura A., Triay-Portella R., et al. 2021. Population structure of the chub mackerel (*Scomber colias*) in the NE Atlantic inferred from otolith elemental and isotopic signatures. Fish. Res. 234: 105785.
<https://doi.org/10.1016/j.fishres.2020.105785>
- Costa G., Cavallero S., D'Amelio S., et al. 2011. Helminth parasites of the Atlantic chub mackerel, *Scomber colias* Gmelin, 1789 from Canary Islands, Central North Atlantic, with comments on their relations with other Atlantic regions. Acta Parasitol. 56: 98-104.
<https://doi.org/10.2478/s11686-011-0006-1>
- Costoya X., de Castro M., Gómez-Gesteira M., Santos F. 2015. Changes in sea surface temperature seasonality in the Bay of Biscay over the last decades (1982-2014). J. Mar. Syst. 150: 91-101.
<https://doi.org/10.1016/j.jmarsys.2015.06.002>
- FAO. 2020a. Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa. Casablanca, Morocco, 8-13 July 2019. Casablanca, Morocco.
- FAO. 2020b. Fisheries and aquaculture software. FishStatJ - software for fishery statistical time series. In: FAO Fish. Aquac. Dep. <https://www.fao.org/fishery/statistics/software/fishstatj/en>
- Ferreri R., McBride R.S., Barra M., et al. 2019. Variation in size at maturity by horse mackerel (*Trachurus trachurus*) within the central Mediterranean Sea: Implications for investigating drivers of local productivity and applications for resource assessments. Fish. Res. 211, pp.291-299.
<https://doi.org/10.1016/j.fishres.2018.11.026>
- Fulton T. W. 1902. The rate of growth of fishes. 20th Annual Report of the Fishery Board of Scotland 1902 (3): 326-446.
- García S. 1982. Distribution, migration and spawning of the main fish resources in the Northern CECAF Area. Rome
- Garrido S., Ben-Hamadou R., Santos A.M.P., et al. 2015a. Born small, die young: Intrinsic, size-selective mortality in marine larval fish. Sci. Rep. 5: 17065.
<https://doi.org/10.1038/srep17065>
- Garrido S., Silva A., Pastor J., et al. 2015b. Trophic ecology of pelagic fish species off the Iberian coast: Diet overlap, cannibalism and intraguild predation. Mar. Ecol. Prog. Ser. 539: 271-286.
<https://doi.org/10.3354/meps11506>
- Gertseva V.V., Cope J.M., Matson S.E. 2010. Growth variability in the splitnose rockfish *Sebastes diploproa* of the northeast Pacific Ocean: pattern revisited. Mar. Ecol. Prog. Ser. 413: 125-136.
<https://doi.org/10.3354/meps08719>
- Gertseva V., Matson S.E., Cope J. 2017. Spatial growth variability in marine fish: example from Northeast Pacific groundfish. ICES J. Mar. Sci. 74: 1602-1613.
<https://doi.org/10.1093/icesjms/fsx016>
- Giménez J., Marçalo A., Ramírez F., et al. 2017. Diet of bottlenose dolphins (*Tursiops truncatus*) from the Gulf of Cadiz: Insights from stomach content and stable isotope analyses. PLoS One 12: e0184673.
<https://doi.org/10.1371/journal.pone.0184673>
- Gonçalves J.M.S., Blanc N., Brandão C., et al. 2016. Valorização de recursos pesqueiros: Cavala Algarvia. Relatório final. Universidade do Algarve, CCMAR, Faro. 44pp.+Anexos.
<http://hdl.handle.net/10400.1/8699>
- Green B.S. 2008. Chapter 1: Maternal Effects in Fish Populations. Adv. Mar. Biol. 54: 1-105.
[https://doi.org/10.1016/S0065-2881\(08\)00001-1](https://doi.org/10.1016/S0065-2881(08)00001-1)
- Hattab T., Gucu A., Ventero A., et al. 2021. Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. Mediterr. Mar. Sci. 22(4): 800-811.
<https://doi.org/10.12681/mms.26525>
- Holden M.J., Raitt D.F.S. 1974. Manual of fisheries science. Part 2: Methods of resource investigation and their application. FAO Fish. Tech. Rep. 115:
- Hollowed A.B., Barange M., Beamish R.J., et al. 2013. Projected impacts of climate change on marine fish and fisheries. ICES J. Mar. Sci. 70: 1023-1037.
<https://doi.org/10.1093/icesjms/fst081>
- Hughes J.M., Stewart J., Lyle J.M., et al. 2017. Influence of latitudinal variation in environmental gradients and population structure on the demography of a widespread pelagic fish, *Arripis trutta* (Forster, 1801). Environ. Biol. Fishes. 100: 121-135.
<https://doi.org/10.1007/s10641-016-0565-y>
- Huret M., Tsiaras K., Daewel U., et al. 2019. Variation in life-history traits of European anchovy along a latitudinal gradient: a bioenergetics modelling approach. Mar. Ecol. Prog. Ser. 617-618: 95-112.
<https://doi.org/10.3354/meps12574>
- ICES. 2020. Workshop on Atlantic chub mackerel (*Scomber colias*) (WKCOLIAS).
<https://doi.org/10.17895/ICES.PUB.5970>
- ICES. 2021a. Second Workshop on Atlantic Chub Mackerel (*Scomber colias*) (WKCOLIAS2).
<https://doi.org/10.17895/ICES.PUB.8142>
- ICES. 2021b. Working Group on Southern Horse Mackerel Anchovy and Sardine (WGHANSA).
- Infante C., Blanco E., Zuasti E., et al. 2007. Phylogenetic differentiation between Atlantic *Scomber colias* and Pacific *Scomber japonicus* based on nuclear DNA sequences. Genetica. 130: 1-8.
<https://doi.org/10.1007/s10709-006-0014-5>
- Jansen T., Gislason H., Goldstien S.J. 2013. Population Structure of Atlantic Mackerel (*Scomber scombrus*). PloS One. 8(5): e64744.
<https://doi.org/10.1371/journal.pone.0064744>
- Jobling M. 1995. The influence of environmental temperature on growth and conversion efficiency in fish. 1995: 1-26.
- Jurado-Ruzafa A., González-Lorenzo G., Jiménez S., et al. 2019. Seasonal evolution of small pelagic fish landings index in relation to oceanographic variables in the Canary Islands (Spain). Deep Res. Part II Top Stud. Oceanogr. 159: 84-91.
<https://doi.org/10.1016/j.dsr2.2018.07.002>
- Jurado-Ruzafa A., Sotillo B., Hernández E., et al. 2021. The Atlantic chub mackerel (*Scomber colias*) in the Canary Islands (Spain), Fishery and Biological data Update. Second Workshop on Atlantic chub mackerel (*Scomber colias*) Second Workshop on Atlantic Chub Mackerel (*Scomber colias*) (WKCOLIAS2). ICES Working Documents WD3. ICES Sci. Rep. 2(20): 148-164.
- Kooijman S.A.L.M. 2009. Dynamic energy budget theory for metabolic organisation, third edition. Cambridge University Press.
<https://doi.org/10.1017/CBO9780511805400>
- Kruskal W.H., Wallis W.A. 1952. Use of Ranks in One-Criterion Variance Analysis. J. Am. Stat. Assoc. 47: 583-621
<https://doi.org/10.1080/01621459.1952.10483441>
- Lambert T.C. 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. Mar. Ecol. Prog. Ser. 39: 209-220.
<https://doi.org/10.3354/meps039209>
- Lorenzo J.M., Pajuelo J.G. 1996. Growth and reproductive biology of chub mackerel *Scomber japonicus* off the Canary Islands. Southafrican J. Mar. Sci. 17: 275-280.
<https://doi.org/10.2989/025776196784158635>
- Lowerre-Barbieri S., De Celles G., Pepin P., et al. 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish. Fish. 18: 285-312.
<https://doi.org/10.1111/faf.12180>
- Lucio P. 1997. Biological aspects of Spanish chub mackerel (*Scomber japonicus*, Houttuyn, 1782) in the Bay of Biscay from the Basque Country catches. ICES CM 1997/BB: 10. 31 pp.
https://www.ICES.dk/sites/pub/CM%20Documents/1997/BB/1997_BB10.pdf
- Martins M. 1996. New biological data on growth and maturity of Spanish Mackerel (*Scomber japonicus*) off the Portuguese coast (ICES Division IXa). ICES CM 1996/H: 23, 17 pp.

- Martins M.M., Skagen D., Marques V., et al. 2013. Changes in the abundance and spatial distribution of the Atlantic chub mackerel (*Scomber colias*) in the pelagic ecosystem and fisheries off Portugal. *Sci. Mar.* 77: 551-563.
<https://doi.org/10.3989/scimar.03861.07B>
- Mele S., Pennino M.G., Piras M.C., et al. 2014. Parasites of the head of *Scomber colias* (Osteichthyes: Scombridae) from the western Mediterranean Sea. *Acta Parasitol.* 59: 173-183.
<https://doi.org/10.2478/s11686-014-0207-5>
- Mertz G., Myers R.A. 1994. Match/mismatch predictions of spawning duration versus recruitment variability. *Fish. Oceanogr.* 3: 236-245.
<https://doi.org/10.1111/j.1365-2419.1994.tb00101.x>
- Muhling B., Lindegren M., Clausen L.W., et al. 2017. Impacts of Climate Change on Pelagic Fish and Fisheries. *Clim. Chang. Impacts Fish. Aquat.* 771-814.
<https://doi.org/10.1002/9781119154051.ch23>
- Muniz A.A., Moura A., Triay-Portella R., et al. 2020. Population structure of the chub mackerel (*Scomber colias*) in the North-east Atlantic inferred from otolith shape and body morphometrics. *Mar. Freshw. Res.* 72: 341-352.
<https://doi.org/10.1071/MF19389>
- Murawski S.A. 1993. Climate Change and Marine Fish Distributions: Forecasting from Historical Analogy. *Trans. Am. Fish. Soc.* 122: 647-658.
[https://doi.org/10.1577/1548-8659\(1993\)122<0647:C-CAMFD>2.3.CO;2](https://doi.org/10.1577/1548-8659(1993)122<0647:C-CAMFD>2.3.CO;2)
- Navarro M.R., Domínguez-Petit R., Landa J., et al. 2021a. Preliminary observations on sexual maturity of chub mackerel (*Scomber colias*) in the Northern Iberian Atlantic waters (ICES Divisions 27.8.c and 27.9.aN). Second Workshop on Atlantic chub mackerel (*Scomber colias*) (WKCOLIAS2). 11 pp.
- Navarro M.R., Landa J., Villamor B., et al. 2021b. First approach to the growth and age corroboration of Northeast Atlantic chub mackerel (*Scomber colias*) in Northern Iberian waters. *Estuar. Coast. Shelf. Sci.* 107433.
<https://doi.org/10.1016/j.ecss.2021.107433>
- Nunes C., Silva A.V., Feijó D., et al. 2019. Atlantic chub mackerel (*Scomber colias*) growth and reproduction off the Portuguese coast in relation to the population dynamics. *Front. Mar. Sci. Conference Abstract: XX Iberian Symposium on Marine Biology Studies (SIEBM XX)*.
<https://doi.org/10.3389/conf.fmars.2019.08.00022>
- Olafsdottir A.H., Utne K.R., Jacobsen J.A., et al. 2019. Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. *Deep Sea Res. Part II Top Stud. Oceanogr.* 159: 152-168.
<https://doi.org/10.1016/j.dsr2.2018.05.023>
- Ottersen G., Kim S., Huse G., et al. 2010. Major pathways by which climate may force marine fish populations. *J. Mar. Syst.* 79: 343-360.
<https://doi.org/10.1016/j.jmarsys.2008.12.013>
- Perrotta R.G., Carvalho N., Isidro E. 2005. Comparative study on growth of Chub Mackerel (*Scomber japonicus* Houttuyn, 1782) from three different regions: NW Mediterranean, NE and SW Atlantic*. *Rev. Investig. y Desarr. Pesq.* 17: 67-79
- Perry A.L., Low P.J., Ellis J.R., Reynolds J.D. 2005. Climate Change and Distribution Shifts in Marine Fishes. *Science* 308: 1912-1915.
<https://doi.org/10.1126/science.1111322>
- Pörtner H.O., Storch D., Heilmayer O. 2005. Constraints and trade-offs in climate-dependent adaptation: energy budgets and growth in a latitudinal cline. *Sci. Mar.* 69: 271-285.
<https://doi.org/10.3989/scimar.2005.69s2271>
- Punzón A., Serrano A., Sánchez F., et al. 2016. Response of a temperate demersal fish community to global warming. *J. Mar. Syst.* 161: 1-10.
<https://doi.org/10.1016/j.jmarsys.2016.05.001>
- Reid P.C., Valdés L. 2011. ICES status report on climate change in the North Atlantic. ICES Cooperative Research Report No. 310. 262. Copenhagen
- Rijnsdorp A.D., Peck M.A., Engelhard G.H., et al. 2009. Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* 66: 1570-1583.
<https://doi.org/10.1093/icesjms/fsp056>
- Rizkalla S. 1998. Some biological characters of chub mackerel (*Scomber japonicus*, Houttuyn, 1782) from the Mediterranean waters of Egypt. *Egypt J. Aquat. Biol. Fish.* 2: 101-116.
<https://doi.org/10.21608/ejabf.1998.1627>
- Rogers L.A., Dougherty A.B. 2019. Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Glob. Chang. Biol.* 25: 708-720.
<https://doi.org/10.1111/gcb.14483>
- Roldán M.I., Perrotta R.G., Cortey M., Pla C. 2000. Molecular and morphologic approaches to discrimination of variability patterns in chub mackerel, *Scomber japonicus*. *J. Exp. Mar. Bio. Ecol.* 253: 63-74.
[https://doi.org/10.1016/S0022-0981\(00\)00244-6](https://doi.org/10.1016/S0022-0981(00)00244-6)
- Rypel A.L. 2014. The cold-water connection: Bergmann's rule in North American freshwater fishes. *Am. Nat.* 183: 147-156.
<https://doi.org/10.1086/674094>
- Saborido-Rey F., Kjesbu O.S. 2005. Growth and maturation dynamics. 26 pp.
<http://hdl.handle.net/10261/47150>
- Santos M.J., Castro R., Cavaleiro F., et al. 2017. Comparison of anisakid infection levels between two species of Atlantic mackerel (*Scomber colias* and *S. scombrus*) off the Atlantic Portuguese coast. *Sci. Mar.* 81: 179-185.
<https://doi.org/10.3989/scimar.04552.26A>
- Saunders R.A., Tarling G.A. 2018. Southern ocean mesopelagic fish comply with Bergmann's Rule. *Am. Nat.* 191: 343-351.
<https://doi.org/10.1086/695767>
- Scoles D.R., Collette B.B., Graves J.E. 1998. Global phylogeography of mackerels of the genus *Scomber*. *Fish. Bull.* 96: 823-842.
- Shephard S., Rindorf A., Dickey-Collas M., et al. 2014. Assessing the state of pelagic fish communities within an ecosystem approach and the European Marine Strategy Framework Directive. *ICES J. Mar. Sci.* 71: 1572-1585.
<https://doi.org/10.1093/icesjms/fsu005>
- Slesinger E., Jensen O.P., Saba G. 2021. Spawning phenology of a rapidly shifting marine fish species throughout its range. *ICES J. Mar. Sci.* 78: 1010-1022.
<https://doi.org/10.1093/icesjms/fsaa252>
- Stocks J.R., Gray C.A., Taylor M.D. 2014. Synchrony and variation across latitudinal gradients: The role of climate and oceanographic processes in the growth of a herbivorous fish. *J. Sea Res.* 90: 23-32.
<https://doi.org/10.1016/j.seares.2014.03.002>
- Sunday J.M., Bates A.E., Dulvy N.K. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B Biol. Sci.* 278: 1823-1830.
<https://doi.org/10.1098/rspb.2010.1295>
- Takahashi M., McCormick M.I., Munday P.L., Jones G.P. 2012. Influence of seasonal and latitudinal temperature variation on early life-history traits of a coral reef fish. *Mar. Freshw. Res.* 63: 856-864.
<https://doi.org/10.1071/MF11278>
- Tasker M.L. 2008. The effect of climate change on the distribution and abundance of marine species in the OSPAR Maritime Area. *ICES Coop. Res. Rep.*, 293. 45 pp.
- Team R.C. 2021a. R: A language and environment for statistical computing.
- Team Rs. 2021b. RStudio: Integrated Development for R. RStudio.
- Techetach M., Hernando-Casal J.A., Saoud Y., Benajiba M.H. 2010. Reproductive biology of chub mackerel *Scomber japonicus* in Larache area, Moroccan North Atlantic coast. *Cybiurn* 34: 159-165.
- Techetach M., Ajana R., Saoud Y. 2019. Reproductive parameters of Atlantic chub mackerel *Scomber colias* in M'diq Bay, Morocco. *J. Mar. Biol. Assoc. United Kingdom.* 99: 957-962.
<https://doi.org/10.1017/S0025315418000930>
- Torrejón-Magallanes J. 2020. sizeMat: Estimate Size at Sexual Maturity.
<https://cran.r-project.org/web/packages/sizeMat/sizeMat.pdf>
- Torres M.A., Coll M., Heymans J.J., Christensen V., Sobrino I. 2013. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecol. Modell.* 265: 26-44.
<https://doi.org/10.1016/j.ecolmodel.2013.05.019>
- Van Beveren E., Bonhommeau S., Fromentin J.M., et al. 2014. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Mar. Biol.* 161: 1809-1822.
<https://doi.org/10.1007/s00227-014-2463-1>

- Varela J.L., Rodríguez-Marín E., Medina A. 2013. Estimating diets of pre-spawning Atlantic bluefin tuna from stomach content and stable isotope analyses. *J. Sea Res.* 76: 187-192. <https://doi.org/10.1016/j.seares.2012.09.002>
- Vasconcelos J., Afonso-Dias M., Faria G. 2012. Atlantic chub mackerel (*Scomber colias*) spawning season, size and age at first maturity in Madeira waters. *Life Mar. Sci.* 29: 43-51
- Veiga-Malta T., Szalaj D., Angélico M.M., et al. 2019. First representation of the tropic structure and functioning of the Portuguese continental shelf ecosystem: insights into the role of sardine. *Mar. Ecol. Prog. Ser.* 617-618: 323-340 <https://doi.org/10.3354/meps12724>
- Velasco E.M., del Arbol J., Baro J., Sobrino I. 2011. Edad y crecimiento del estornino *Scomber colias* del sur de España: una comparación entre muestras procedentes del Atlántico NE y del SW Mediterráneo. *Rev. Biol. Mar. Oceanogr.* 46: 27-34. <https://doi.org/10.4067/S0718-19572011000100004>
- Vergés A., Steinberg P.D., Hay M.E., et al. 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc. R. Soc. B Biol. Sci.* 281(1789): 20140846. <https://doi.org/10.1098/rspb.2014.0846>
- Vila-Gispert A., Moreno-Amich R., García-Berthou E. 2002. Gradients of life-history variation: An intercontinental comparison of fishes. *Rev. Fish. Biol. Fish.* 12: 417-427. <https://doi.org/10.1023/A:1025352026974>
- Villamor B., Carrera P., Castro J., et al. 2017. The Chub Mackerel (*Scomber colias*) in the Atlantic Spanish Waters (ICES divisions 8.c and 9.a): Biological, fishery and survey data. Report of the Working Group on Widely Distributed Stocks (WGWISE). ICES Working Document WD XVI. ICES CM 2017/ACOM: 23. 873-934.
- Wahbi F. 2017. Bio-écologie de *Trachurus trachurus* (Linnaeus, 1758) et de *Scomber colias* Gmelin, 1789 dans l'écosystème pélagique de la zone atlantique sud marocaine (21°N - 26°30'N). PhD thesis, Univ. Hassan II, Faculté des Sciences Ain Chock, Casablanca. 230 pp.
- Wahbi F., Errhif A., Ettahiri O. 2011. Cycle de reproduction et variabilité du régime alimentaire du maquereau *Scomber japonicus* (Houttuyn, 1782) débarqué au port de Casablanca. In: Garcia S., Tandstad M., Caramelo A.M. (eds) Science and Management of Small Pelagic Fisheries and Aquaculture proceedings. FAO, pp 127-138
- Walsh M., Hopkins P., Witthames P.R., et al. 1990. Estimation of total potential fecundity and atresia in the western mackerel stock in 1989. ICES Document CM. 1990/H: 31. 22 pp.
- Whitehead P.J.P., Bauchot M.L., Hureau J.C., et al. 1984. Scombridae. In: Fishes of the North-eastern Atlantic and the Mediterranean. UNESCO, Paris. 981-997. ISBN: 92-3-002308-6 (v.2)
- Wickham H. 2016. ggplot2: Elegant graphics for data analysis. 2nd edition. Springer International Publishing, Cham. 260 pp. <http://dx.doi.org/10.1007/978-3-319-24277-4>
- Wood S.N. 2011. MgcV: GAMs with GCV/AIC/REML smoothness estimation and GAMMs by REML/PQL
- Wood S.N. 2017. Generalized additive models: An introduction with R. 2nd edition. CRC Press, New York. 496 pp. <https://doi.org/10.1201/9781315370279>
- Wright P.J., Trippel E.A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish. Fish.* 10: 283-304. <https://doi.org/10.1111/j.1467-2979.2008.00322.x>
- Zardoya R., Castilho R., Grande C., et al. 2004. Differential population structuring of two closely related fish species, the mackerel (*Scomber scombrus*) and the chub mackerel (*Scomber japonicus*), in the Mediterranean Sea. *Mol. Ecol.* 13: 1785-1798. <https://doi.org/10.1111/j.1365-294X.2004.02198.x>

SUPPLEMENTARY MATERIAL

Table S1. – Detailed description of all samples considered in the present study, including study area (subdivision), sampling source (S, research cruise; C, commercial vessels), scientific survey name, survey methodology, sampling dates, number of samples (samples), number of individuals in each sample (n), size range of sampled specimens (cm), and maturity key used for macroscopic maturity staging (Mat. Scale). Attached as a separate PDF file.

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
Cantabrian Sea (27.8.c)	S	PELACUS0411	Acoustic-trawl	mar/11	11	364	192-469	Walsh et al. (1990)
	S	DEMERSALES2011	Bottom-trawl	oct/11	1	9	127-175	Walsh et al. (1990)
	S	PELACUS0412	Acoustic-trawl	mar/12	16	186	166-425	Walsh et al. (1990)
	S	DEMERSALES2012	Bottom-trawl	oct/12	9	20	147-177	Walsh et al. (1990)
	S	PELACUS0313	Acoustic-trawl	mar-apr/13	13	202	144-437	Walsh et al. (1990)
	S	PELACUS0314	Acoustic-trawl	mar-apr/14	17	255	176-444	Walsh et al. (1990)
	S	DEMERSALES2014	Bottom-trawl	oct/14	8	37	145-195	Walsh et al. (1990)
	S	PELACUS0315	Acoustic-trawl	mar-apr/15	22	461	185-431	Walsh et al. (1990)
	S	DEMERSALES2015	Bottom-trawl	oct/15	13	140	112-261	Walsh et al. (1990)
	S	PELACUS0316	Acoustic-trawl	mar/16	11	287	174-381	Walsh et al. (1990)
	S	DEMERSALES2016	Bottom-trawl	sep-oct/16	15	68	146-400	Walsh et al. (1990)
	S	PELACUS0317	Acoustic-trawl	mar-apr/17	9	216	181-391	Walsh et al. (1990)
	S	DEMERSALES2017	Bottom-trawl	sep-oct/17	32	335	142-488	Walsh et al. (1990)
	S	PELACUS0318	Acoustic-trawl	mar-apr/18	10	288	171-406	Walsh et al. (1990)
	S	DEMERSALES2018	Bottom-trawl	sep-oct/18	16	124	167-320	Walsh et al. (1990)
	S	PELACUS0319	Acoustic-trawl	mar-apr/19	13	348	180-368	Walsh et al. (1990)
	S	DEMERSALES2019	Bottom-trawl	oct/19	6	10	169-362	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/11	1	97	241-344	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/11	1	92	250-381	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/11	1	100	299-384	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/11	1	85	316-420	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/11	2	95	293-395	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/11	1	71	330-480	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/11	1	93	330-410	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/11	1	52	365-402	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/11	1	65	316-410	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/11	3	123	286-418	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/11	1	69	325-405	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/12	1	99	262-430	Walsh et al. (1990)
	C	Commercial	Gillnet	feb/12	1	67	336-411	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/12	2	152	254-411	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/12	1	71	359-422	Walsh et al. (1990)
	C	Commercial	Gillnet	may/12	2	105	307-385	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/12	2	94	287-469	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/12	1	35	297-392	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/12	1	18	321-353	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/12	1	64	330-452	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/12	2	61	343-428	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/12	2	101	341-465	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/12	1	82	373-453	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/12	1	100	277-435	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/13	1	94	337-435	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Gillnet	feb/13	1	39	320-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/13	1	92	357-441	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/13	1	68	349-411	Walsh et al. (1990)
	C	Commercial	Gillnet	may/13	2	105	292-430	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/13	1	76	342-508	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/13	1	39	237-286	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/13	1	100	270-329	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/13	1	100	355-429	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/13	1	127	312-438	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/13	1	50	317-422	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/13	1	39	276-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/13	2	117	272-495	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/13	1	12	244-300	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/14	1	99	273-357	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/14	1	100	264-351	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/14	1	80	304-495	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/14	1	54	275-340	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/14	1	84	325-430	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/14	1	20	327-409	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/15	1	95	302-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	abr/15	1	2	335-342	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/15	2	100	266-400	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/15	1	67	295-367	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/15	1	31	265-339	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/15	1	70	314-420	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/16	1	85	317-428	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/16	2	102	183-412	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/16	1	100	282-387	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/16	2	138	278-382	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/16	1	86	287-369	Walsh et al. (1990)
	C	Commercial	Gillnet	ago/16	1	101	311-379	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/16	2	183	270-377	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/17	1	105	303-401	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/17	1	100	222-340	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/17	1	112	261-382	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/17	1	100	215-295	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/17	1	64	268-402	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/18	1	6	258-278	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/18	1	100	276-393	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/18	1	100	227-310	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/18	2	189	242-391	Walsh et al. (1990)
	C	Commercial	Gillnet	ago/18	1	100	293-388	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/18	1	100	280-356	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/18	1	100	264-346	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/19	1	120	260-405	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/19	1	98	256-328	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/19	1	99	254-341	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/19	1	90	296-356	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
NW Spanish Coast (27.9.a.n)	C	Commercial	Purse-seine	jul/19	1	94	269-320	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/19	1	104	280-366	Walsh et al. (1990)
	C	Commercial	Gillnet	ago/19	1	83	302-418	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/19	1	100	258-314	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/19	2	95	292-373	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/19	1	118	281-442	Walsh et al. (1990)
	Total			317	10173	112-495		
	S	PELACUS0315	Acoustic-trawl	mar/15	4	31	238-350	Walsh et al. (1990)
	S	PELACUS0317	Acoustic-trawl	mar/17	5	129	125-276	Walsh et al. (1990)
	S	DEMERSALES2017	Bottom-trawl	sep/17	1	10	232-263	Walsh et al. (1990)
	S	PELACUS0318	Acoustic-trawl	apr/18	6	70	190-292	Walsh et al. (1990)
	S	PELACUS0319	Acoustic-trawl	apr/19	4	17	249-285	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/11	1	20	207-279	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/11	1	100	241-373	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/11	1	90	262-380	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/11	1	100	257-336	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/11	1	100	282-376	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/11	2	125	218-326	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/11	1	100	275-353	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/11	2	92	279-415	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/12	1	96	284-335	Walsh et al. (1990)
	C	Commercial	Gillnet	feb/12	1	95	269-372	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/12	1	89	288-328	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/12	2	176	193-384	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/12	1	92	289-356	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/12	2	101	166-355	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/12	2	113	205-344	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/12	1	110	190-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/12	1	140	186-255	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/12	1	100	310-403	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/13	1	100	191-245	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/13	1	91	210-351	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/13	1	61	252-335	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/13	1	113	245-320	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/13	1	100	248-325	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/13	2	183	220-375	Walsh et al. (1990)
	C	Commercial	Gillnet	dic/13	1	111	261-378	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/14	2	150	250-326	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/14	1	75	254-324	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/14	1	120	254-343	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/15	1	97	261-356	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/15	2	105	268-387	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/18	1	99	214-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/18	1	89	276-356	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dic/18	1	90	259-360	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/19	2	200	248-320	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	jul/19	1	99	240-331	Walsh et al. (1990)
	Total			64	3979	125-415		
W Portuguese Coast (27.9.a.c)	S	IBTS11	Bottom-trawl	oct/11	3	195	176-312	Walsh et al. (1990)
	S	PELAGO13	Acoustic-trawl	apr-may/13	6	308	176-278	Walsh et al. (1990)
	S	JUVESAR13	Acoustic-trawl	nov/13	4	46	186-314	Walsh et al. (1990)
	S	IBTS13	Bottom-trawl	oct/13	5	210	182-318	Walsh et al. (1990)
	S	PELAGO14	Acoustic-trawl	apr-may/14	5	166	187-281	Walsh et al. (1990)
	S	IBTS14	Bottom-trawl	oct/14	2	135	205-322	Walsh et al. (1990)
	S	PELAGO15	Acoustic-trawl	apr-may/15	3	89	217-326	Walsh et al. (1990)
	S	IBTS15	Bottom-trawl	oct/15	1	46	192-259	Walsh et al. (1990)
	S	PELAGO16	Acoustic-trawl	apr/16	1	6	294-328	Walsh et al. (1990)
	S	JUVESAR16	Acoustic-trawl	dec/16	2	109	153-267	Walsh et al. (1990)
	S	IBTS16	Bottom-trawl	nov-oct/16	9	172	143-325	Walsh et al. (1990)
	S	PELAGO17	Acoustic-trawl	apr/17	1	39	162-215	Walsh et al. (1990)
	S	PELAGO_N17	Acoustic-trawl	aug/17	5	363	170-269	Walsh et al. (1990)
	S	JUVESAR17	Acoustic-trawl	dec/17	2	97	188-258	Walsh et al. (1990)
	S	PELAGO17	Acoustic-trawl	may/17	6	266	150-311	Walsh et al. (1990)
	S	IBTS17	Bottom-trawl	nov-oct/17	11	357	167-287	Walsh et al. (1990)
	S	IBTS18	Bottom-trawl	dec/18	3	52	183-307	Walsh et al. (1990)
	S	PELAGO18	Acoustic-trawl	may/18	8	538	172-309	Walsh et al. (1990)
	S	IBERAS18	Acoustic-trawl	nov/18	4	293	176-310	Walsh et al. (1990)
	S	IBTS18	Bottom-trawl	nov-oct/18	5	119	171-265	Walsh et al. (1990)
	S	PELAGO19	Acoustic-trawl	apr/19	1	61	203-294	Walsh et al. (1990)
	S	MPDO19	Bottom-trawl	feb/19	3	110	178-273	Walsh et al. (1990)
	S	PELAGO19	Acoustic-trawl	may/19	2	98	174-340	Walsh et al. (1990)
	S	IBERAS19	Acoustic-trawl	sep/19	6	228	181-300	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/11	1	62	256-399	Walsh et al. (1990)
	C	Commercial	Purse-seine	jan/11	2	218	286-395	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/11	1	68	255-402	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/11	1	84	276-348	Walsh et al. (1990)
	C	Commercial	Trammelnet	mar/11	1	26	264-336	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/11	1	82	198-397	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/11	1	45	233-298	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/11	1	69	253-381	Walsh et al. (1990)
	C	Commercial	Purse-seine	apr/11	2	98	286-429	Walsh et al. (1990)
	C	Commercial	Gillnet	may/11	2	91	277-414	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/11	1	59	283-338	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/11	1	99	216-416	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/11	1	57	264-337	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/11	1	59	254-385	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/11	1	49	275-348	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/11	2	117	273-372	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/11	1	76	283-378	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/11	2	127	271-357	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/11	2	94	270-362	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Bottom trawl	sep/11	2	127	283-365	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/11	1	41	302-362	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/11	2	121	277-352	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/11	1	48	258-401	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/11	2	124	283-364	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/11	1	67	312-355	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/11	2	63	305-391	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/11	1	63	286-413	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/12	2	122	264-406	Walsh et al. (1990)
	C	Commercial	Trammelnet	feb/12	1	36	314-429	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/12	1	37	254-356	Walsh et al. (1990)
	C	Commercial	Trammelnet	mar/12	2	109	263-382	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/12	1	57	325-396	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/12	1	58	245-330	Walsh et al. (1990)
	C	Commercial	Gillnet	may/12	2	80	255-398	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/12	1	40	293-342	Walsh et al. (1990)
	C	Commercial	Hook and Line	jun/12	2	51	331-418	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/12	1	70	288-365	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/12	1	120	221-349	Walsh et al. (1990)
	C	Commercial	Gillnet	aug/12	1	34	307-393	Walsh et al. (1990)
	C	Commercial	Hook and Line	sep/12	1	24	345-406	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/12	2	102	171-267	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/12	1	59	279-353	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/12	1	61	292-376	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/12	2	109	250-384	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/12	1	35	290-405	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/13	2	120	282-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/13	2	127	237-421	Walsh et al. (1990)
	C	Commercial	Purse-seine	apr/13	1	45	329-411	Walsh et al. (1990)
	C	Commercial	Drift longline	may/13	1	32	313-388	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/13	1	69	260-347	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/13	2	125	240-345	Walsh et al. (1990)
	C	Commercial	Trammelnet	jul/13	1	21	310-396	Walsh et al. (1990)
	C	Commercial	Drift longline	jul/13	1	12	422-538	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/13	1	52	247-323	Walsh et al. (1990)
	C	Commercial	Gillnet	aug/13	1	16	414-490	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/13	1	55	243-375	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/13	1	77	218-283	Walsh et al. (1990)
	C	Commercial	Bottom trawl	sep/13	2	101	253-363	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/13	1	48	220-290	Walsh et al. (1990)
	C	Commercial	Longline	oct/13	1	16	372-462	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/13	1	81	273-354	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/13	1	38	267-365	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/13	1	74	251-316	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/13	1	21	292-387	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/14	1	49	257-335	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/14	1	50	233-292	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/14	1	49	252-355	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Bottom trawl	apr/14	1	99	240-337	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/14	1	50	254-351	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/14	1	30	302-416	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/14	1	31	268-351	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/14	1	66	264-367	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/14	1	51	312-412	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/14	1	45	224-300	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/14	1	59	284-372	Walsh et al. (1990)
	C	Commercial	Bottom trawl	sep/14	1	52	307-376	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/14	1	57	208-280	Walsh et al. (1990)
	C	Commercial	Drift longline	oct/14	1	41	253-365	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/14	1	38	312-355	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/14	2	117	203-435	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/14	1	52	244-309	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/14	1	62	257-346	Walsh et al. (1990)
	C	Commercial	Trammelnet	jan/15	1	31	302-392	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/15	2	67	233-368	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/15	2	110	274-386	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/15	1	53	210-296	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/15	1	38	225-270	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/15	1	47	237-299	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/15	2	150	257-433	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/15	1	30	321-375	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/15	1	49	268-354	Walsh et al. (1990)
	C	Commercial	Trammelnet	jul/15	1	24	311-349	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/15	2	95	239-347	Walsh et al. (1990)
	C	Commercial	Trammelnet	aug/15	1	25	335-418	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/15	1	42	266-326	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/15	1	41	276-359	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/15	1	52	272-364	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/15	2	86	270-344	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/15	1	63	241-320	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/15	1	26	264-329	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/15	1	31	322-404	Walsh et al. (1990)
	C	Commercial	Purse-seine	dec/15	2	114	244-373	Walsh et al. (1990)
	C	Commercial	Gillnet	jan/16	1	58	307-399	Walsh et al. (1990)
	C	Commercial	Trammelnet	jan/16	1	32	313-379	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/16	2	77	248-384	Walsh et al. (1990)
	C	Commercial	Trammelnet	mar/16	2	120	239-440	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/16	1	50	239-303	Walsh et al. (1990)
	C	Commercial	Gillnet	may/16	2	55	267-393	Walsh et al. (1990)
	C	Commercial	Trammelnet	jun/16	1	28	320-382	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/16	1	76	266-353	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/16	1	32	312-385	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/16	2	123	219-342	Walsh et al. (1990)
	C	Commercial	Trammelnet	aug/16	1	52	230-318	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/16	2	109	238-367	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/16	2	72	260-365	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	sep/16	1	34	139-229	Walsh et al. (1990)
	C	Commercial	Trammelnet	oct/16	2	81	150-323	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/16	1	52	286-393	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/16	2	60	242-345	Walsh et al. (1990)
	C	Commercial	Longline	nov/16	1	27	354-403	Walsh et al. (1990)
	C	Commercial	Gillnet	dec/16	1	52	237-373	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/16	1	56	166-224	Walsh et al. (1990)
	C	Commercial	Trammelnet	jan/17	1	17	297-404	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/17	1	48	287-348	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/17	1	67	259-355	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/17	1	55	276-364	Walsh et al. (1990)
	C	Commercial	Gillnet	apr/17	1	49	218-392	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/17	1	55	263-359	Walsh et al. (1990)
	C	Commercial	Gillnet	may/17	1	57	272-394	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/17	1	13	191-239	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/17	1	26	332-377	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/17	1	24	306-377	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/17	1	70	257-335	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/17	1	46	281-359	Walsh et al. (1990)
	C	Commercial	Trammelnet	jul/17	1	28	284-369	Walsh et al. (1990)
	C	Commercial	Trammelnet	aug/17	1	10	405-483	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/17	1	57	266-360	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/17	1	50	208-286	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/17	2	77	185-363	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/17	4	118	180-405	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/17	1	28	290-336	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/17	1	48	192-273	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/17	1	87	256-365	Walsh et al. (1990)
	C	Commercial	Trammelnet	nov/17	1	77	181-303	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/17	2	49	237-360	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/17	1	48	253-337	Walsh et al. (1990)
	C	Commercial	Purse-seine	jan/18	1	57	228-361	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/18	2	104	227-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	apr/18	1	27	291-386	Walsh et al. (1990)
	C	Commercial	Gillnet	may/18	1	31	317-394	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/18	1	55	247-335	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/18	1	68	231-343	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/18	1	23	281-377	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/18	1	32	296-363	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/18	1	51	195-257	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/18	1	55	214-268	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/18	1	49	254-379	Walsh et al. (1990)
	C	Commercial	Bottom trawl	sep/18	1	51	246-315	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/18	1	45	258-312	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/18	1	17	291-355	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/18	1	57	228-325	Walsh et al. (1990)
	C	Commercial	Gillnet	dec/18	2	76	238-389	Walsh et al. (1990)
	C	Commercial	Gillnet	jan/19	1	28	271-380	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Bottom trawl	jan/19	1	54	273-355	Walsh et al. (1990)
	C	Commercial	Gillnet	feb/19	1	39	256-343	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/19	1	45	250-376	Walsh et al. (1990)
	C	Commercial	Gillnet	apr/19	1	54	189-302	Walsh et al. (1990)
	C	Commercial	Gillnet	may/19	1	29	334-395	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/19	1	52	252-332	Walsh et al. (1990)
	C	Commercial	Longline	jun/19	1	25	327-362	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/19	1	41	218-258	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/19	1	26	307-359	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/19	1	51	217-279	Walsh et al. (1990)
	C	Commercial	Gillnet	aug/19	1	62	274-396	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/19	1	44	285-368	Walsh et al. (1990)
	C	Commercial	Pots and Traps	sep/19	1	14	309-381	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/19	1	74	282-402	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/19	3	114	221-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/19	1	55	222-298	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/19	2	65	227-321	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/19	1	53	250-333	Walsh et al. (1990)
	C	Commercial	Gillnet	dec/19	1	5	260-300	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/19	1	53	264-345	Walsh et al. (1990)
	Total			326	15074	139-538		
Gulf of Cadiz (27.9.a.s)	S	BOCADEVA 0711	GoC anchovy DEPM	22/07-02/08/2011	16	560	137-300	WKSPMAT 2008
	S	ECOCADIZ 0813	Acoustic-trawl	02 – 13/08/2013	11	4549	194-332	WKSPMAT 2008
	S	ECOCADIZ 2014-07	Acoustic-trawl	24/07 – 06/08/2014	15	525	167-300	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2014-10	Acoustic-trawl	13 – 31/10/2014	13	363	201-302	WKSPMAT 2008
	S	ECOCADIZ 2015-07	Acoustic-trawl	28/07 – 10/08/2015	13	346	178-315	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2015-10	Acoustic-trawl	10-29/10/2015	14	362	185-335	WKSPMAT 2008
	S	ECOCADIZ 2016-07	Acoustic-trawl	29/07 – 12/08/15	26	1212	114-364	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2016-10	Acoustic-trawl	16/10-03/11/2016	11	476	116-307	WKSPMAT 2008
	S	ECOCADIZ 2017-07	Acoustic-trawl	31/07-13/08/2017	21	832	159-349	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2017-10	Acoustic-trawl	12-24/10/2017	4	151	180-315	WKSPMAT 2008
	S	ECOCADIZ 2018-07	Acoustic-trawl	31/07-13/08/2018	24	970	157-283	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2018-10	Acoustic-trawl	10-29/10/2018	24	835	165-318	WKSPMAT 2008
	S	ECOCADIZ 2019-07	Acoustic-trawl	31/07-13/08/2019	24	739	132-343	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2019-10	Acoustic-trawl	09-30/10/2019	18	564	182-323	WKSPMAT 2008

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
Canary Islands (34.1.2)	S	ECOCADIZ 2020-08	Acoustic-trawl	01-14/08/2020	26	1198	163-388	Walsh et al. (1990)
	S	ECOCADIZ-RE-CLUTAS 2020-10	Acoustic-trawl	02-20/10/2020	18	688	177-396	Walsh et al. (1990)
	C	Commercial	Purse-seine	14/03/2019	1	100	222-309	WKSPMAT 2008
	C	Commercial	Purse-seine	15/05/2019	1	100	283-348	WKSPMAT 2008
	C	Commercial	Purse-seine	27/06/2019	1	100	268-315	WKSPMAT 2008
	C	Commercial	Purse-seine	25/07/2019	1	100	281-366	WKSPMAT 2008
	C	Commercial	Purse-seine	09/09/2020	1	100	257-323	Walsh et al. (1990)
	Total			283	14870	114-396		
	C	Commercial	Purse-seine	ene-13	1	81	215-287	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-13	1	111	173-219	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-13	1	111	175-223	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-13	1	52	264-331	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-13	1	59	256-331	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-13	1	44	279-339	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-13	1	89	217-295	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-13	1	37	270-352	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-13	1	34	294-381	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-13	1	111	229-339	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-13	1	93	199-273	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-13	1	52	261-346	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-14	1	81	212-270	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-14	2	59	237-383	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-14	1	95	230-285	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-14	1	81	191-283	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-14	1	155	197-361	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-14	1	72	213-290	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-14	1	60	252-313	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-14	1	100	174-299	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-14	1	43	282-337	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-14	1	100	193-254	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-14	1	100	197-235	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-15	1	100	187-272	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-15	1	100	185-269	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-15	1	50	217-350	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-15	1	50	267-336	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-15	1	94	203-274	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-15	1	100	198-282	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-15	1	78	223-288	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-15	1	56	179-326	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-15	1	72	236-292	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-15	1	100	195-264	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-15	1	99	150-260	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-16	1	39	269-348	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-16	1	100	190-277	Holden and Rait (1974)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	mar-16	1	100	203-280	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-16	1	88	212-270	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-16	1	93	215-275	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-16	1	65	232-302	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-16	1	42	259-326	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-16	1	74	232-296	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-16	2	94	167-375	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-16	1	109	145-305	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-16	1	106	216-279	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-17	1	87	206-332	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-17	1	104	198-284	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-17	2	231	185-270	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-17	2	154	177-329	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-17	1	64	245-310	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-17	2	111	217-363	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-17	2	139	210-346	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-17	1	62	234-305	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-17	1	53	253-312	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-17	1	102	202-275	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-17	1	84	212-291	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-17	1	100	208-251	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-18	1	69	227-312	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-18	1	98	212-283	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-18	1	100	212-283	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-18	1	53	259-320	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-18	2	98	209-354	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-18	2	109	193-387	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-18	1	89	239-342	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-18	1	45	261-307	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-18	1	79	145-281	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-18	1	44	242-319	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-18	2	174	207-353	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-18	1	95	153-277	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-19	1	76	214-293	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-19	1	66	239-296	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-19	2	103	168-399	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-19	2	73	132-425	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-19	2	105	226-344	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-19	1	48	231-337	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-19	1	67	270-388	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-19	2	78	258-365	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-19	2	96	147-342	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-19	1	36	280-370	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-19	1	57	233-320	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-20	1	47	164-343	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-20	2	106	224-386	Holden and Rait (1974)
Total				97	6931	132-425		

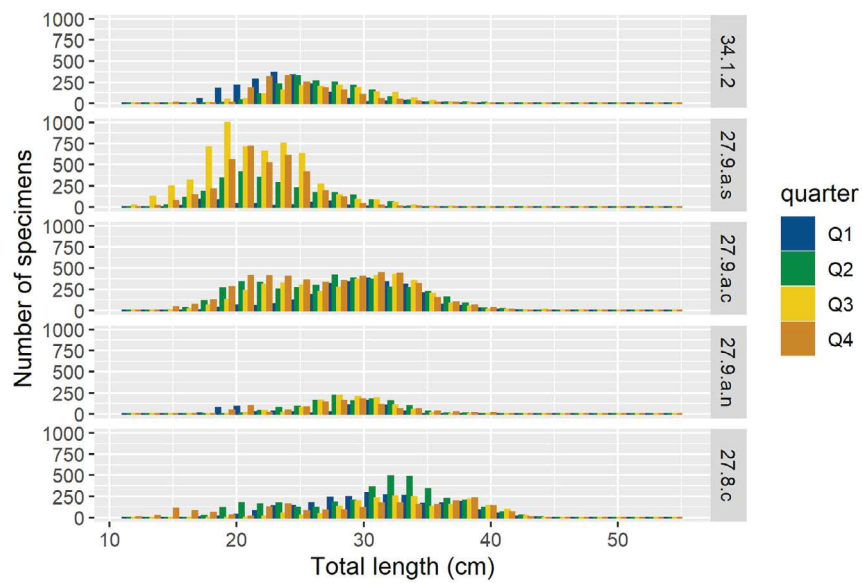


Fig. S1. – Total length distribution of sampled fish per quarter in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

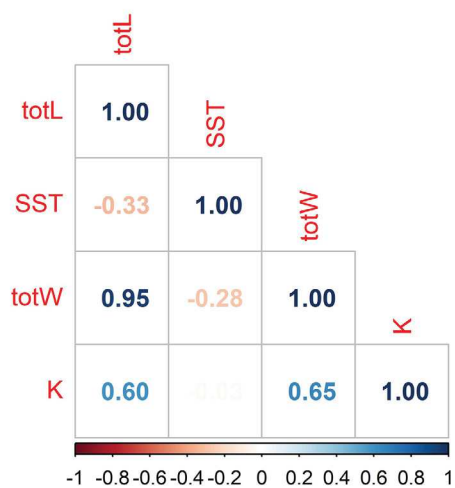


Fig. S2. – Correlation plot among variables. totL, total length (cm); totW, total weight (g); SST, sea surface temperature (°C); and K, Fulton's condition factor.

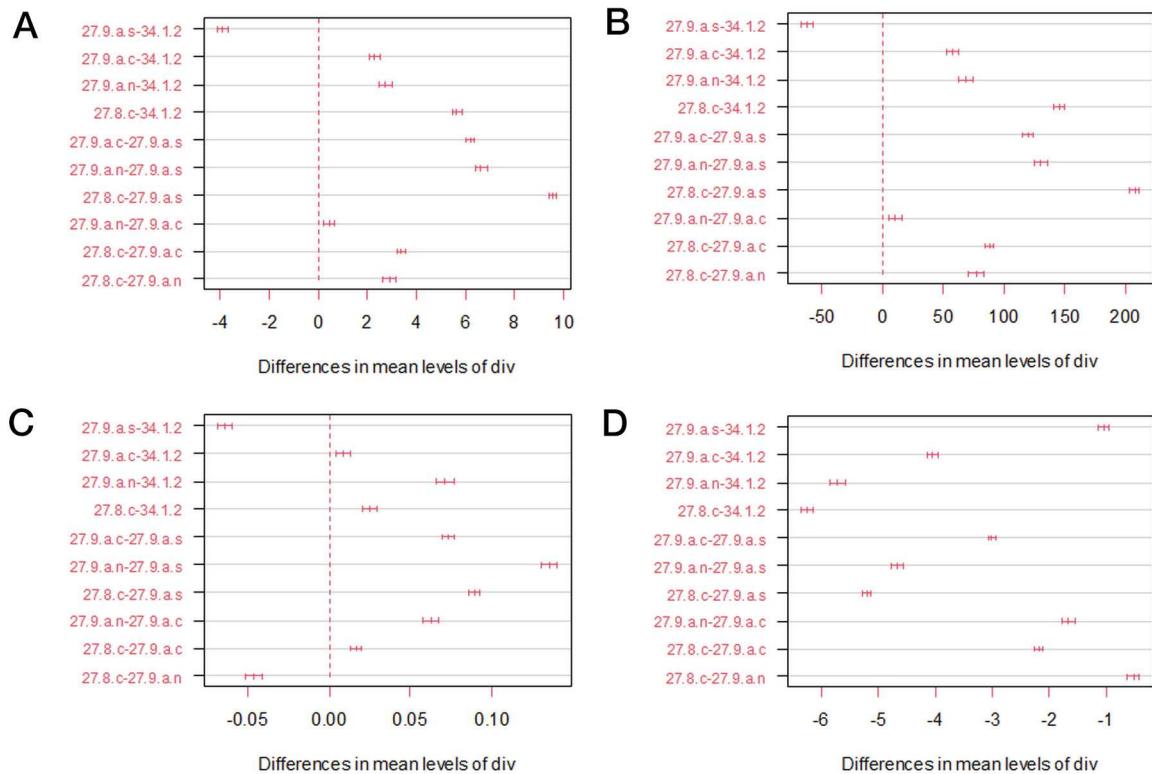


Fig. S3. – Plots of the estimated differences in mean levels of pairwise comparison between study areas. A) total length (cm); B) total weight (g); C) Fulton's condition factor (K); D) sea surface temperature (°C). Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Whiskers, 95% confidence interval. Results are highlighted in red when pairwise comparison is significant.

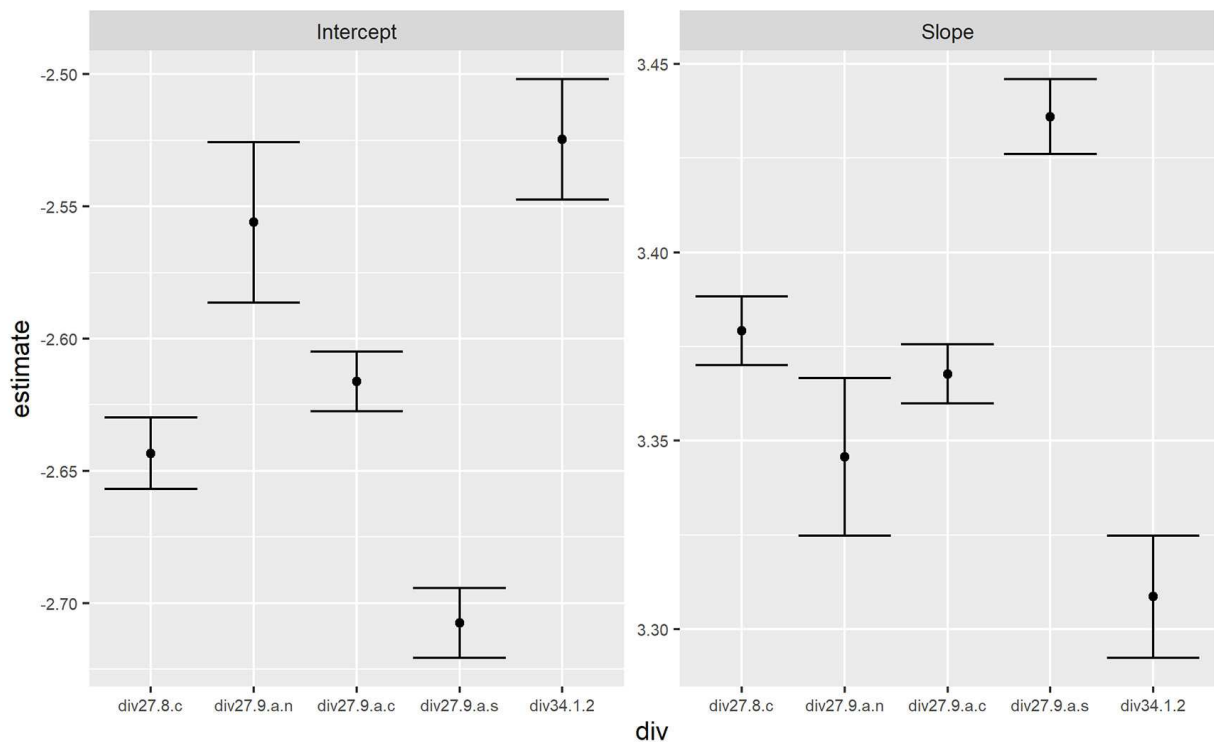


Fig. S4. – Estimations of the intercept and slope of the relationship between total length (cm) and total weight (g) in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Dots represented the mean value; whiskers represented the standard error.

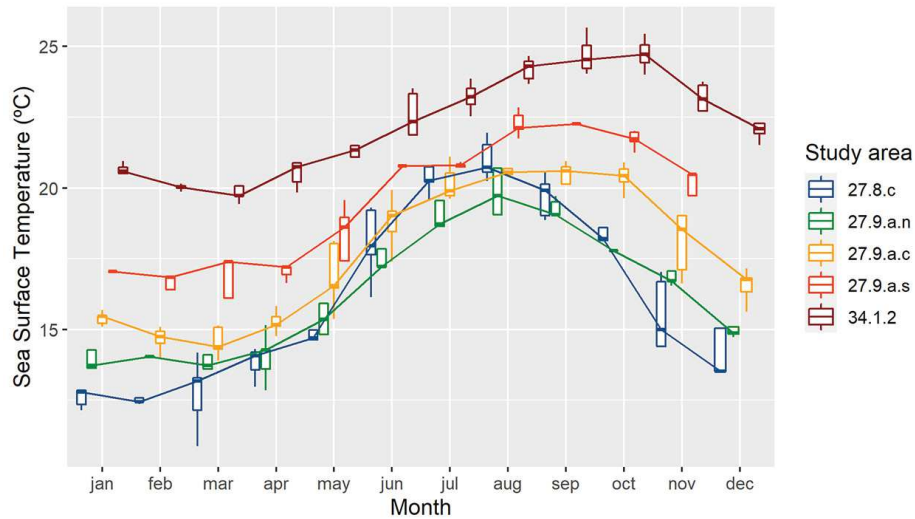


Fig. S5. – Monthly variability of sea surface temperature (SST) in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Horizontal line within the boxes represents the median, boxes represent the inter-quartile range (IQR) or distance between the first (25%) and third (75%) quartiles, whiskers represent $\pm 1.5 * \text{IQR}$ and solid line connect the medians.

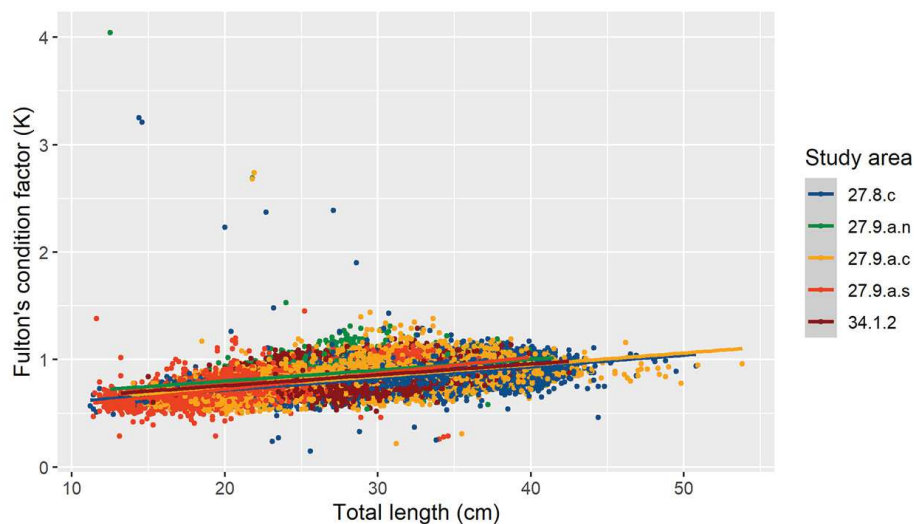


Fig. S6. – Relationship between Fulton's condition factor (K) and Atlantic chub mackerel total length (cm) in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

RNA/DNA and derived condition indices for anchovy and hake larvae as relevant information for comprehensive fisheries management

Marina V. Diaz, Marina Do Souto, Stefanía Cohen, Gustavo J. Macchi

Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMDP-CONICET, Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo V. Ocampo s/n Mar del Plata BsAs, Argentina.
(MVD) E-mail: mdiaz@inidep.edu.ar. ORCID-iD: <https://orcid.org/0000-0002-2912-5232>
(MDS) E-mail: mdo@inidep.edu.ar. ORCID-iD: <https://orcid.org/0000-0002-2259-0115>
(SC) Corresponding author: E-mail: stefaniacohen@gmail.com. ORCID-iD: <https://orcid.org/0000-0001-5872-7091>
(GJM) E-mail: gmacchi@inidep.edu.ar. ORCID-iD: <https://orcid.org/0000-0003-1821-5491>

Summary: The nutritional condition of anchovy and Argentine hake larvae in the Northern Patagonian Frontal System (NPFS) area was studied in the austral spring of 2018. We hypothesized that this area provides adequate features for larval growth and survival. The RNA/DNA index (RD) and its derived index of growth performance were employed. A critical RD value for starvation was calculated. The percentage of individuals under starvation and in optimal growth conditions was calculated. Because the period of study was the beginning of the hake spawning period, a limited number of larvae of this species were collected. The RD index showed a significant increase throughout larval ontogeny for anchovy larvae, being 1.84 ± 1.39 (N=739) and 2.77 ± 1.50 (N=220) in the pre-flexion and flexion stages respectively. These values were significantly higher at stations close to the NPFS and at the upper level of the water column. No differences were observed throughout the day. The area inside the NPFS showed a lower proportion of starved anchovy and a higher proportion of individuals in optimal growth, standing as a favourable nursing area. For hake larvae, the average RD was 1.64 ± 0.55 (N=15). The great sensitivity of the RD index makes it a powerful tool for assessing the probability of larval survival and posterior recruitment into fisheries and allowing the identification of favourable rearing areas for these important species for fisheries.

Keywords: nutritional condition; RNA/DNA index; ichthyoplankton; *Engraulis anchoita*; *Merluccius hubbsi*; North Patagonian Frontal System.

ARN/ADN e índices de condición derivados de larvas de anchoíta y merluza como información relevante para la gestión integral de las pesquerías

Resumen: Se estudió el estado nutricional de larvas de anchoíta y merluza argentina en la zona del Sistema Frontal Norpatagónico (SFNP) (primavera austral 2018). Nuestra hipótesis fue que esta área proporciona características adecuadas para el crecimiento y la supervivencia de las larvas. Se empleó el índice de ARN/ADN (RD) y su índice derivado denominado *performance* de crecimiento. Se calculó un valor crítico de RD para la inanición. Se determinó el porcentaje de individuos en inanición y en condiciones óptimas de crecimiento. Debido a que el período de estudio fue al inicio del período de desove de la merluza, se recolectó un número limitado de larvas de esta especie. El índice RDs mostró un aumento significativo a lo largo de la ontogenia para las larvas de anchoíta; siendo 1.84 ± 1.39 (N=739) y 2.77 ± 1.50 (N=220) en preflexión y flexión respectivamente. Estos valores fueron significativamente más altos en las estaciones cercanas a SFNP y en el nivel superior de la columna de agua. No se observaron diferencias a lo largo del día. El área al interior del SFNP presentó una menor proporción de anchoíta en inanición y una mayor proporción de individuos en óptimo crecimiento, destacándose como un área favorable para la crianza. Para las larvas de merluza, el RD promedio fue de 1.64 ± 0.55 (N=15). La gran sensibilidad del índice RDs lo convierte en una poderosa herramienta para evaluar la probabilidad de supervivencia de las larvas y posterior reclutamiento en las pesquerías; permitiendo la identificación de áreas de cría favorables para estas especies con relevancia pesquera.

Palabras clave: condición nutricional; índice ARN/ADN; ictioplancton; *Engraulis anchoita*; *Merluccius hubbsi*; Sistema Frontal Norpatagónico.

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INTRODUCTION

The Argentine anchovy, *Engraulis anchoita* (Hubbs and Marini, 1935), represents the pelagic resource with the highest biomass in the southwest Atlantic Ocean, with a total catch of approximately 9000 t reported in 2021 (Ministry of Agroindustry 2022). Its high densities and wide distribution make it the most ecologically important fish in the Argentine Sea. It plays a key role in the food web, sustaining several species of commercial value within this region (Angelescu 1982, Hansen 2004). Two populations of anchovy are separated by the 41°S parallel (Sánchez and Ciechomski 1995). The spawning and breeding areas of this species are related to upwelling regions, estuarine, tidal and shelf break fronts characteristic of the Argentine continental shelf. The reproductive activity of the Patagonian stock, distributed south of 41°S, begins in November and shows maximum spawning in December (Sánchez and Ciechomski 1995). The Argentine hake *Merluccius hubbsi* is one of the most important fishing resources for the Argentine bottom trawling fleet, with a total catch of approximately 287000 t reported in 2021 (Ministry of Agroindustry 2022). It inhabits the waters of the southwest Atlantic Ocean between Cabo Frio in Brazil (22°S) and southern Argentina (55°S), at depths between 50 and 500 m (Cousseau and Perrotta 1998). There are two main fishing stocks in Argentina, north, and south of 41°S. Owing to the increase in fishing pressure in recent decades, a decrease in spawning biomass has been observed in this species, as well as variations in the age structure of the parental stock and the location of spawning schools (Macchi et al. 2005, 2021). The reproductive activity of the southern or Patagonian stock, which is the one with the highest population abundance, occurs on the North Patagonian shelf mainly between November and April and peaks in January (Ehrlich 1998, Macchi et al. 2004, Macchi et al. 2007).

As in other fish species, variability in the recruitment of both anchovy and hake is affected by processes that operate on different spatial and temporal scales. This variability depends on physical and thermodynamic factors that determine survival during the early stages of life (Houde 2008). The study of larval nutritional condition allows us to evaluate the individual physiological state, which at the same time reflects the environmental context to which the larvae have been exposed (Chícharo and Chícharo 2008). It is also a useful instrument for determining favourable breeding areas (Diaz and Pájaro 2012). Various nutritional condition indices have been used to estimate mortality due to starvation in marine fish larvae (Buckley 1984, Clemmesen 1994). The RNA/DNA ratio (RD) stands as one of the best indicators of the nutritional status of various marine organisms (Clemmesen 1994, Folkvord et al. 1996) and is currently the biochemical index most widely used as an indicator of the nutritional condition of fish larvae (Chícharo and Chícharo 2008). The RD ratio varies with age, developmental stage and size under different environmental conditions (Bulow 1970). It has also been shown to respond to changes in the

concentration of available prey (McGurk et al. 1992, Chícharo and Chícharo 1995) among other factors. The monitoring of the larval state in situ over time could be a useful tool for determining favourable breeding areas for the species and for developing a time series to assess the effects of climate change in these areas. Detecting these favourable areas and periods for larval survival makes a valuable contribution to the comprehensive management of a population subjected to fishing exploitation (Viladrich et al. 2016).

The northern Patagonia region is hydrographically characterized by the existence of a tidal front, the Northern Patagonian Frontal System or NPFS (Guerero et al. 1997, Martos and Sánchez 1997, Sabatini and Martos 2002). This system is characterized by the formation of a seasonal thermocline, particularly during the austral summer, which gives rise to a homogeneous coastal zone and an increasing stratification towards the offshore zone. Figure 1 depicts three typical vertical temperature profiles observed in this area during summer: coastal homogeneous stations (Fig. 1D-F), frontal stratified stations (Fig. 1G) and stratified offshore stations (Fig. 1H-I). The dynamic that characterizes the frontal system causes a high availability of nutrients that are mainly due to upwelling and concentration and favour primary and secondary productivity (Bakun and Parrish 1991, Bakun 1997), generating major phytoplankton blooms (Carreto and Benavídez 1990) and large aggregations of copepods (Derisio et al. 2014, Temperoni et al. 2014, Temperoni and Viñas 2015), in addition to a great diversity of other zooplanktonic organisms (Mianzan and Guerrero 2000, Schiariti 2008, Schiariti et al. 2015). The water circulation in this area also favours the retention of the first stages of life of both fish and invertebrates (Álvarez Colombo et al. 2011). The NPFS is therefore a propitious area for the reproduction and breeding of many species during spring and summer, including important fishing resources such as the Patagonian stocks of hake and anchovy (Hansen et al. 2001, Macchi et al. 2004, Pájaro et al. 2005). Given that the survival during the first phases of life of these species is affected by the existence of the NPFS, the spatial and temporal coincidence of these organisms with this tidal front during the larval stage could be one of the most important factors that explain the observed variability in recruitment. Because of the importance of the NPFS for the conservation and management of major fishery resources and the aforementioned hydrographic characteristics, part of this area is currently under study for the implementation of a new marine protected area (MPA). For this reason, it is essential to carry out a comprehensive analysis of the NPFS, covering the environmental and biological aspects of this region.

In December 2018, a research survey was carried out to analyse the oceanographic and biological conditions in the NPFS region within the project “Strengthening the Management and Protection of Coastal Biodiversity Marine in Key Ecological Areas and the Application of the Ecosystem Approach to Fisheries” (GEF-FAO). Within the framework of this survey, our main objective was to evaluate the nutritional condition

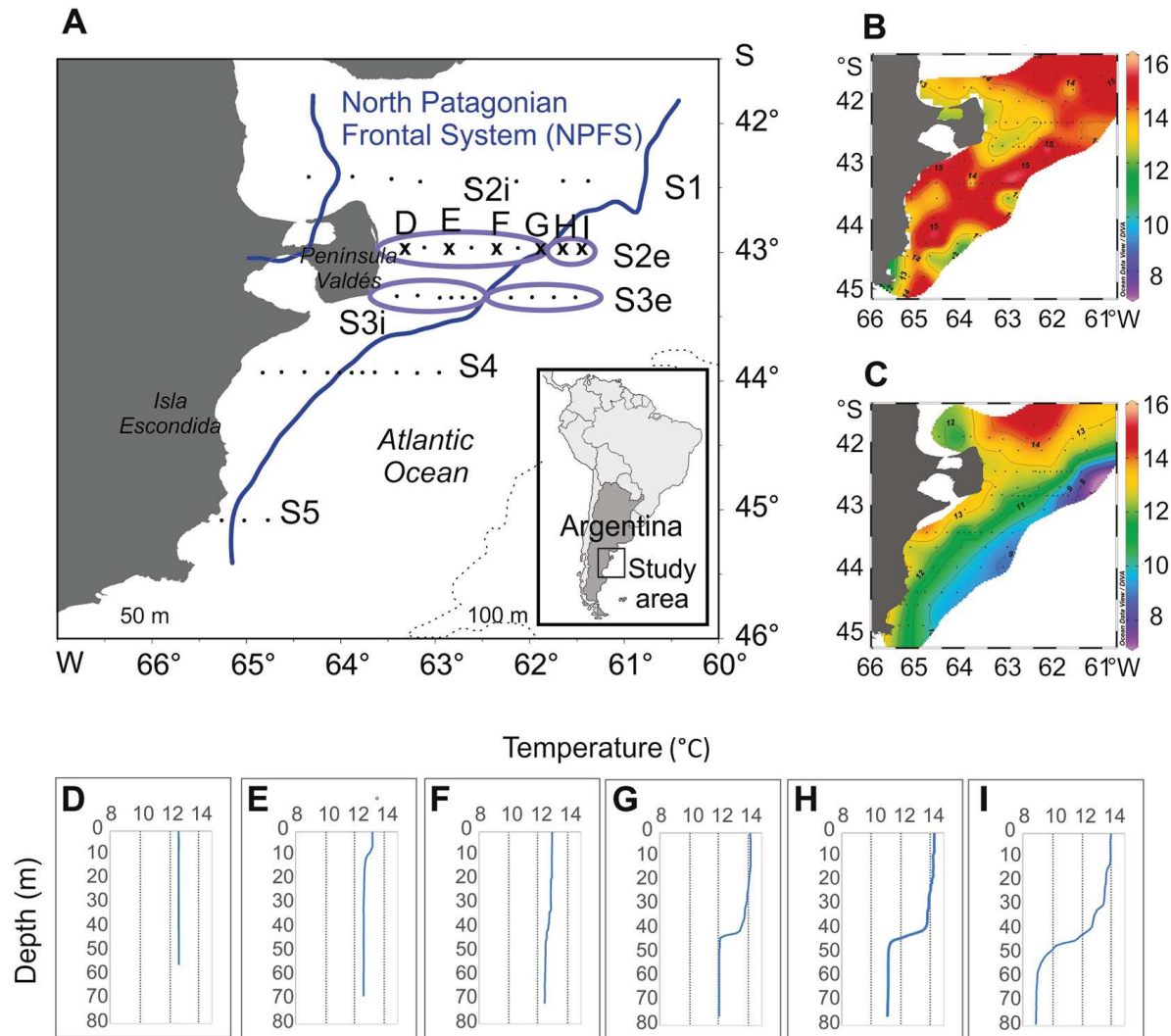


Fig. 1. – Spatial distribution of the sampling stations. (A) Five transects or oceanographic sections (S1–S5) were made. The schematic position of the Northern Patagonian Frontal System (NPFS) during December 2018 is indicated in blue (calculated according to Simpson 1981; by Martos and collaborators, INIDEP Physical Oceanography Office). For the analysis, the stations of sections S2 and S3 were grouped in relation to the position of the NPFS: the stations in the homogeneous zone of the front or internal zone (S2i, S3i) and the stations of the stratified offshore or external zone (S2e, S3e). (B) Horizontal isolines of temperature (°C) at the surface and (C) at the bottom are indicated. The vertical gradients of temperature (°C) with respect to depth (m) are indicated in the stations with an “x” in Section 2 (S2), (D–I) from coast to offshore stations. Data obtained from the BaRDO-INIDEP regional oceanographic database. Dotted lines indicate 50 and 100 m isobaths.

of *E. anchoita* and *M. hubbsi* larvae during the beginning of the austral summer in the northern Patagonia region and to analyse the spatial variation of this parameter. Because the sampling was performed early in the spawning period for hake, a small number of larvae of this species were collected. Thus, the study is mainly based on anchovy larvae, with some additional information on the nutritional condition of initial larval stages of hake. We hypothesized that the presence of the NPFS provides adequate features for larval growth and survival evidenced in a better nutritional condition of anchovy and hake larvae than that observed in the offshore area. To test this hypothesis, we assessed the RD index and a derived index of growth performance. The proportion of individuals in starvation and in optimal growth conditions was estimated. Larval condition was mapped in the study area to determine the exist-

ence of favourable areas for growth and larval survival in relation to the NPFS.

MATERIALS AND METHODS

Sample collection

The samples were taken during a research survey carried out on board the vessel *Victor Angelescu* of the National Institute for Fisheries and Development (INIDEP) in the northern Patagonia area between 4 and 16 December 2018 (Fig. 1). At each station, temperature and salinity measurements were made using the CTD Seabird Electronics system. The data collected by the staff of the Physical Oceanography Office of INIDEP are part of the BaRDO database. A stratified plankton sampling was performed with the HydroBios

Model Midi Multinet (0.5×0.5 m), equipped with three opening and closing nets (300 µm pore size) and soft collectors. Oblique trawls were carried out at different levels in the water column. The towing speed during the ascent was maintained between 2 and 3 knots, with a duration that varied between 5 and 7 minutes per sampling strata. When the station was in the homogeneous area the nets were operated covering strata of equal width, while in the frontal and stratified regions the nets were operated above, on and below the thermocline. Five transects or oceanographic sections were made (Fig. 1: S1-S5). The stations of sections S2 and S3 were grouped for the analysis in relation to the position of the frontal system: the stations in the homogeneous or internal zone (Fig. 1: S2i, S3i) and the stations of the stratified offshore or external zone (Fig. 1: S2e, S3e). Larvae were not found in section S5.

Once the plankton samples (N=126) were obtained, they were inspected on board to detect and separate anchovy and hake larvae. These were extracted from the sample and placed in labelled cryotubes and then stored in an ultrafreezer (−80°C) for studies of nutritional condition and growth. A representative larval sample was taken at each sampling station with a maximum of 100 larvae in those where anchovy larvae were very abundant, including all sizes present in the entire sample. In total, 1045 anchovy larvae were collected from 29 stations, and 16 hake larvae were obtained from four hauls. The rest of the plankton sample was fixed in 5% formalin in seawater to be later analysed under a binocular stereoscope in the INIDEP laboratories.

Sample processing

Anchovy and hake larvae were identified and classified under a Carl Zeiss stereoscopic microscope equipped with the Axio Vision software. According to Betti et al. (2009) and Alheit et al. (1991), a developmental stage was assigned to each larva: (a) pre-flexion, (b) flexion and (c) post-flexion. Before the determination of nucleic acid content, the larvae were photographed and the standard length of each larva was measured. The head and digestive tract were dissected according to Olivar et al. (2009). The heads were preserved in 96% ethyl alcohol for later age studies, and the digestive tubes in 5% formalin for stomach content studies. The muscle trunks were individually lyophilized and weighed to the microgram using a Sartorius microbalance.

The protocol used for the analysis of nutritional condition was the one described by Caldarone et al. (2001), partially modified by Diaz and Pájaro (2012) to maximize the detection of nucleic acids in a 1 mL volume instead of microplates. This method is based on the quantification of total nucleic acids (TNA) by spectroluminescence, RNA digestion by adding a specific enzyme (RNase) and subsequent determination of the resulting DNA fluorescence. Thus, the fluorescence due to RNA is determined by difference: $[RNA] = [TNA] - [DNA]$. The DNase step was not performed in the protocol because residual fluorescence was negligible. The concentrations of nucleic acids cor-

responding to the fluorescences obtained were determined by comparing with a calibration curve obtained from a series of standards of known concentrations of ultrapure DNA and RNA. The results were expressed as µg DNA/mg dry weight (DW), µg RNA/mg DW, and RD. The minimum mass from which reliable RD ratios were obtained was 33 µg DW. Reported RD indices correspond to individual muscle trunks. Of the total hake and anchovy larvae processed, 15 and 959 reliable determinations were respectively obtained.

Data analysis

The RD values obtained in this study were standardized (RDs) according to Caldarone et al. (2006), using 2.4 as the reference value for the slope of the calibration curves of ultrapure DNA and RNA standards. This procedure allows direct comparison with other published RDs results, avoiding inter-laboratory differences caused by analytical protocols. The average value for the slope of the calibration curves obtained in the present study was 2.19 (±0.71 SD).

Growth rate (G) was estimated for each larva using the RDs-T-G model developed by Buckley et al. (2008). For hake larvae, the model developed by Buckley for gadiform fish was used, and the general multi-specific model was used to determine the instantaneous growth of anchovy larvae according to the following expressions:

$$G = 0.0254 \times RDs + 0.0037 \times T \times RDs - 0.0873 \text{ (hake)} \quad (1)$$

$$G = 0.0145 \times RDs + 0.0044 \times T \times RDs - 0.0780 \text{ (anchovy)} \quad (2)$$

where G is the instantaneous growth rate and T is the temperature measured at the sampling site, which corresponds to the average of the stratum in which the larvae were collected.

A critical value of the RD index was determined assuming null larval growth (CRD), that is $G=0$. The percentage of larvae below the CRD was calculated, and it was assumed that these specimens were in starvation (% starvation, Fig. 2A).

In addition, the growth performance (Gpf) was determined as a derived condition index. This index represents the quotient of the observed G and a reference growth (Gref) rate achieved by a larva under optimal environmental and feeding conditions. Due to the lack of a Gref for the studied species, larval growth rates were compared with a Gref that was calculated according to Houde and Zastrow (1993), who established a multi-specific model based on 80 marine and estuarine species:

$$G_{ref} = 0.0106 \times T - 0.0203 \quad (3)$$

Larvae with Gpf higher than or equal to 1 were assumed to be in optimal growth condition. The percentage of larvae with Gpf higher than 1 (optimal %, Fig. 2B) was calculated. A Student t-test was used to compare mean RD values of pre-flexion and flexion anchovy larvae. ANOVA was used to compare mean RD values of each size class of anchovy larvae. Analyses

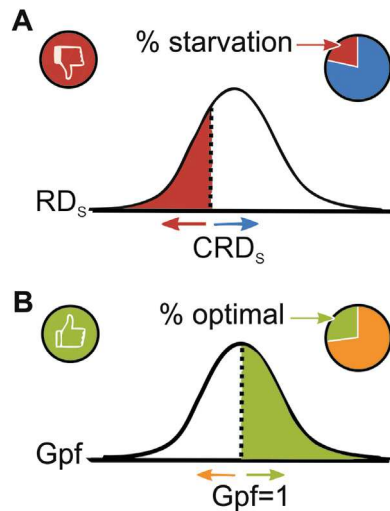


Fig. 2. – Theoretical distribution for (A) RNA/DNA index (RD) and (B) growth performance (Gpf) values for fish larvae. (A) The curve corresponding to RD shows a critical value (CRD_s) used to detect starving larvae: above this value, the larvae are not in starvation (white colour) and below it they are in starvation (red colour). (B) The Gpf curve represents the growth performance being the quotient between the observed growth rate and the larval growth rate under optimal environmental and feeding conditions. Values greater than 1 (green colour) indicate more than optimal growth, and values less than 1 (white colour) indicate less than optimal growth. Modified from Alves et al. (2022).

were performed to evaluate variability in the position of the frontal system (calculated according to Simpson (1981), see Fig. 1), time of the day and depth where the larvae were collected. The mean values of RD and Gpf obtained for the larvae were compared by ANCOVA, using the standard length of the specimens as a co-variable. When significant differences were found, a Tukey test was performed. The results are then expressed according to oceanographic section (S1-S4), oceanographic section grouping the internal and external stations in relation to the position of the tidal front (S1, S2i, S2e, S3i, S3e, S4), time of day (M, morning; A, afternoon; N, night), and depth (B, bottom; T, thermocline; S, surface).

RESULTS

A large number of the anchovy larvae obtained ($N=959$) were classified in pre-flexion ($SL < 8$ mm) and in flexion (8–12.9 mm) and a small proportion in post-flexion ($SL > 12.9$ mm). The RD index showed a significant increase throughout the anchovy larval ontogeny, with an average value of 1.84 ± 1.39 ($N=739$) and 2.77 ± 1.50 ($N=220$) in pre-flexion and flexion, respectively (t -test, T ($N=957$) = 8.54; $p < 0.0001$). A small number of *Merluccius hubbsi* larvae were collected ($N=15$) and classified in pre-flexion ($SL < 6.49$ mm), and the RD obtained was 1.64 ± 0.55 .

The mean values of the RD index for size class showed a positive trend in both species. For anchovy larvae, the mean RD by size class also showed an increase towards the post-flexion stage (Fig. 3A), but no significant differences were observed when the mean values were compared by size class, except for the

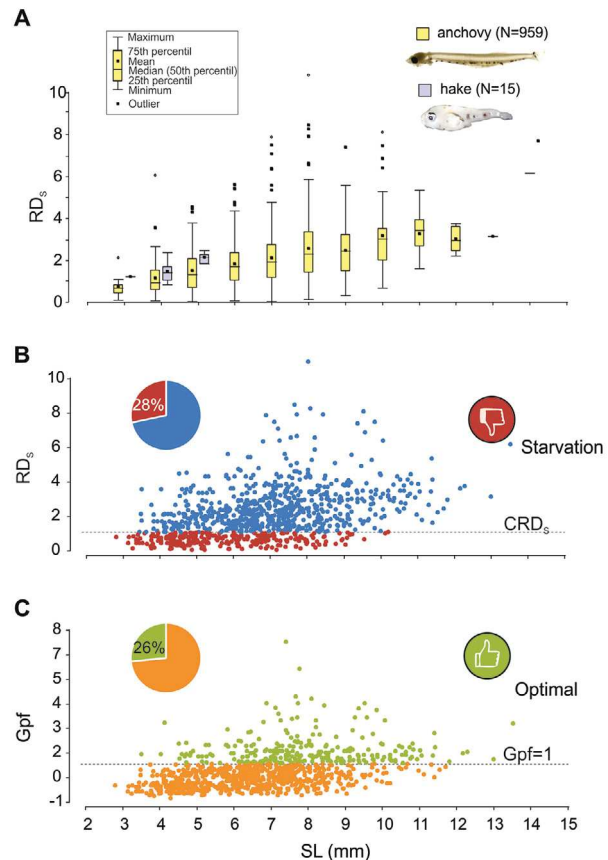


Fig. 3. – (A) Box plot of the standardized RD index as a function of standard length (SL, mm) class for larvae of anchovy *Engraulis anchoita* and hake *Merluccius hubbsi*. Dispersion graph of the (B) standardized RNA/DNA index (RD) and (C) growth performance (Gpf) as a function of the SL of larvae of anchovy *Engraulis anchoita*. The dotted line in (B) indicates the critical value of the RD index (CRD_s), the individuals in starvation ($RD < CRD_s$) are indicated in red, and the individuals in good nutritional condition are indicated in blue. The dotted line in (C) indicates optimal growth performance ($Gpf=1$); the individuals in optimal growth ($Gpf > 1$) are indicated in green, and the individuals that showed less than optimal growth are shown in orange.

class 14 mm (ANOVA, F (11, 947) = 15.47; $p < 0.0001$); however, only one larva of this size class was collected.

The scatterplot of the RD indices as a function of the standard length (SL, mm) of the anchovy larvae shows the proportion of individuals below the critical RD index (28%), that is, in starvation (Fig. 3B), and the proportion of individuals with a growth performance (Gpf) above one (26%), that is, in optimal growth (Fig. 3C).

Significant differences were observed in the mean RD values in the oceanographic sections for anchovy larvae. A co-variance analysis was performed using the SL of the specimens as a co-variable (Fig. 4, Table 1), and differences were observed when the stations were grouped according to the position of the NPFS. The larvae from the internal stations of the frontal system showed higher condition indices than the larvae from the external stations. (Fig. 4 and 5A-B, Table 2). A better nutritional condition was observed in the larvae collected in the upper stratum (surface), but no differences were observed at the different times of the day (Fig. 4, Table 3).

Table 1. – Analysis of variance of mean values of the standardized RNA/DNA index (RD) for *Engraulis anchoita* larvae collected in different oceanographic sections (S1-S4) in December 2018. Standard length was used as a co-variable (ANCOVA). SS, Sum of squares; MS, Mean squares

	SS	df	MS	F	p-value	Coeff.
Model	339.14	4	84.78	47.25	<0.0001	
Section	43.31	3	14.44	8.04	<0.0001	
SL (mm)	251.78	1	251.8	140.32	<0.0001	0.30
Error	1711.81	954	1.79			
Total	2050.95	958				

Table 2. – Analysis of variance to compare the mean values of the standardized RNA/DNA index (RD) between the oceanographic sections zone grouping the internal and external stations in relation to the position of the tidal front (S1, S2i, S2e, S3i, S3e, S4) for *Engraulis anchoita* larvae collected in December 2018. Standard length was used as a co-variable (ANCOVA).

	SS	df	MS	F	p-value	Coeff.
Model	349.92	6	58.32	32.64	<0.0001	
Zone	54.09	5	10.82	6.05	<0.0001	
SL (mm)	162.79	1	162.79	91.11	<0.0001	0.27
Error	1701.03	952	1.79			
Total	2050.95	958				

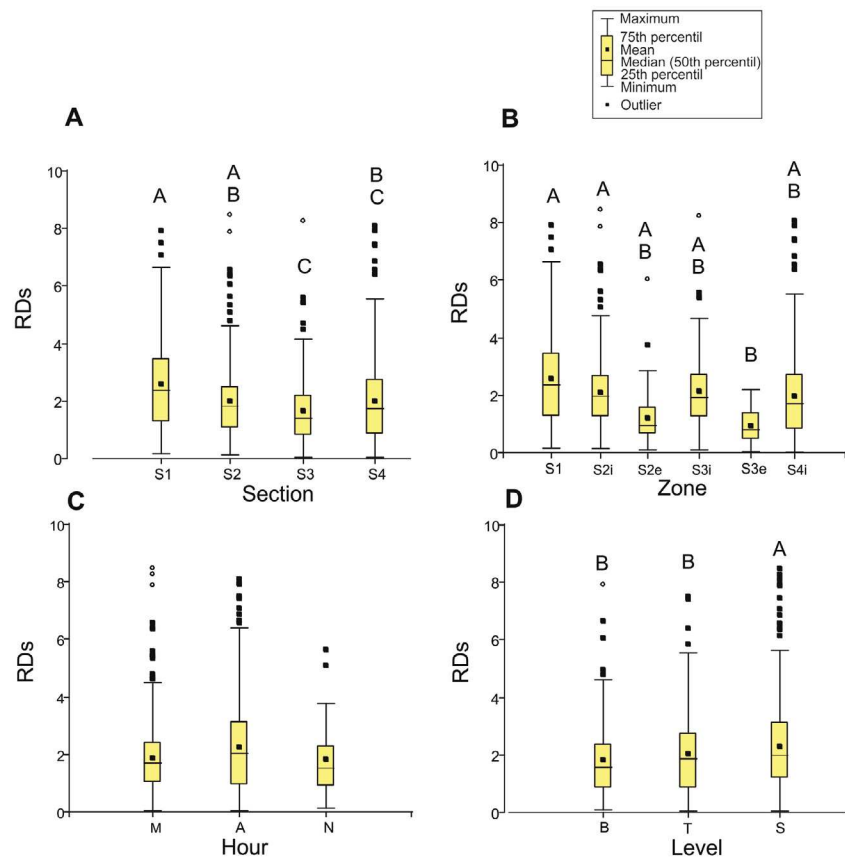


Fig. 4. – Box plot of the standardized RNA/DNA index (RD) for larvae of the anchovy *Engraulis anchoita*, according to (A) oceanographic section (S1-S4), (B) oceanographic section grouping the internal and external stations in relation to the position of the tidal front (S1, S2i, S2e, S3i, S3e, S4), (C) time of day (M, morning; A, afternoon; N, night), (D) depth (B, bottom; T, thermocline; S, surface). Different letters on the bars indicate significant differences in Tukey comparisons.

Table 3. – Two-way analysis of variance to compare the mean values of the standardized RNA/DNA index between time of day and depth for *Engraulis anchoita* larvae collected in December 2018. Standard length was used as a covariate (ANCOVA).

	SS	df	MS	F	p-value	Coeff.
Model	343.61	5	68.72	38.36	<0.0001	
Depth	37.19	2	18.60	10.38	<0.0001	
Time of day	38.01	2	19.01	10.61	<0.0001	
SL (mm)	268.40	1	268.40	149.82	<0.0001	0.30
Error	1707.34	953	1.79			
Total	2050.95	959				

Finally, the percentage of larvae in starvation (RDs<CRDs) and the percentage of specimens in optimal growth (Gpf>1) were mapped in both species. A higher percentage of anchovy larvae in starvation was observed at the stations outside the position of the NPFS, and a higher percentage of larvae in optimal growth was detected at the internal stations (Fig. 5C-F, Table 4). It was observed that between 18% and 32% of anchovy larvae were in starvation and between 24% and 44% above optimal growth inside the NPFS. At offshore stations between 59% and 66% of the anchovy larvae were in starvation and the percentage above optimal growth was low (0% to 6%). Of the hake larvae, it was observed that 25% were in starvation and 12.5% above optimal growth.

DISCUSSION

Little information is available on the nutritional condition of the anchovy southern stock, so the results presented here are highly important. Somewhat lower RD values were observed than those previously reported in the study area (Díaz et al. 2016, Do Souto et al. 2019), and a large percentage of anchovy larvae were recorded below the critical value of the RD index in the zone external to the NPFS. The internal area of the NPFS showed a lower proportion of individuals under starvation and a higher incidence of individuals showing optimal growth.

Because the survey research was carried out during the beginning of the reproductive period of the Argentine hake, the number of hake larvae analysed was very low (Macchi et al. 2004), and was also reflected in the small size of the larvae. However, the RD values obtained for the nutritional condition of this species were similar to those recorded in previous studies, as were the percentages of hake larvae in starvation and in optimal growth conditions (Díaz et al. 2014, Cohen et al. 2021).

Various studies have inferred the importance of the NPFS as a nursery area for the southern anchovy stock (Bakun and Parrish 1991, Díaz et al. 2016, Do Souto et al. 2018), with better feeding conditions for anchovy and hake larvae in the area associated with the NPFS (Viñas and Ramírez 1996, Temperoni et al. 2014). Our results support this idea of better feeding conditions towards the NPFS.

Within the analysed area, the internal zone to the position of the tidal front seems to respond to the

Table 4. – Percentage of *Engraulis anchoita* larvae in starvation (RD<CRD) and above optimal growth (Gpf>1) in each oceanographic section (S) grouping the internal (i) and external (e) stations in relation to the position of the tidal front (S1, S2i, S2e, S3i, S3e, S4).

Section	n	% starvation	% optimal
S1	209	22	44
S2i	262	19	24
S2e	50	66	6
S3i	110	18	25
S3e	75	59	0
S4i	255	32	27

“Bakun triad” hypothesis (Bakun and Parrish 1991) in that the frontal structure would guarantee the stability of the water column as a result of vertical stratification, nutrient enrichment and retention of spawning products within a favourable habitat. It is evident that frontal systems play a fundamental role in the ecological processes of the ocean because they allow a high primary production, they are suitable areas for the reproduction and feeding of many nektonic species, they offer a suitable breeding environment for the feeding of the early stages of fish development, and they act as retention zones (Acha et al. 2004). NPFS could also be an area with a high concentration of prey, predators and competitors of anchovy and hake eggs and larvae (Mianzan and Guerrero 2000, Álvarez-Colombo et al. 2003, Díaz et al. 2016, 2020).

Regarding daily variations in nucleic acid content, the available information is not consistent: some authors have found differences in the RD ratio throughout the day, and others have observed no detectable pattern (Buckley et al. 1999). For example, Rooker and Holt (1996) while studying croaker larvae, found a marked daily pattern in the RD values. These authors observed that the RD values were higher during the day and lower at night and suggested that this phenomenon was due to differences in metabolic rates throughout the day, food requirements or food digestion. In this study, we observed an increase during the afternoon hours, but no statistically significant differences were observed during the morning and night. Previous studies have reported that *E. anchoita* larvae feed during daylight hours (Viñas and Ramírez 1996), which could

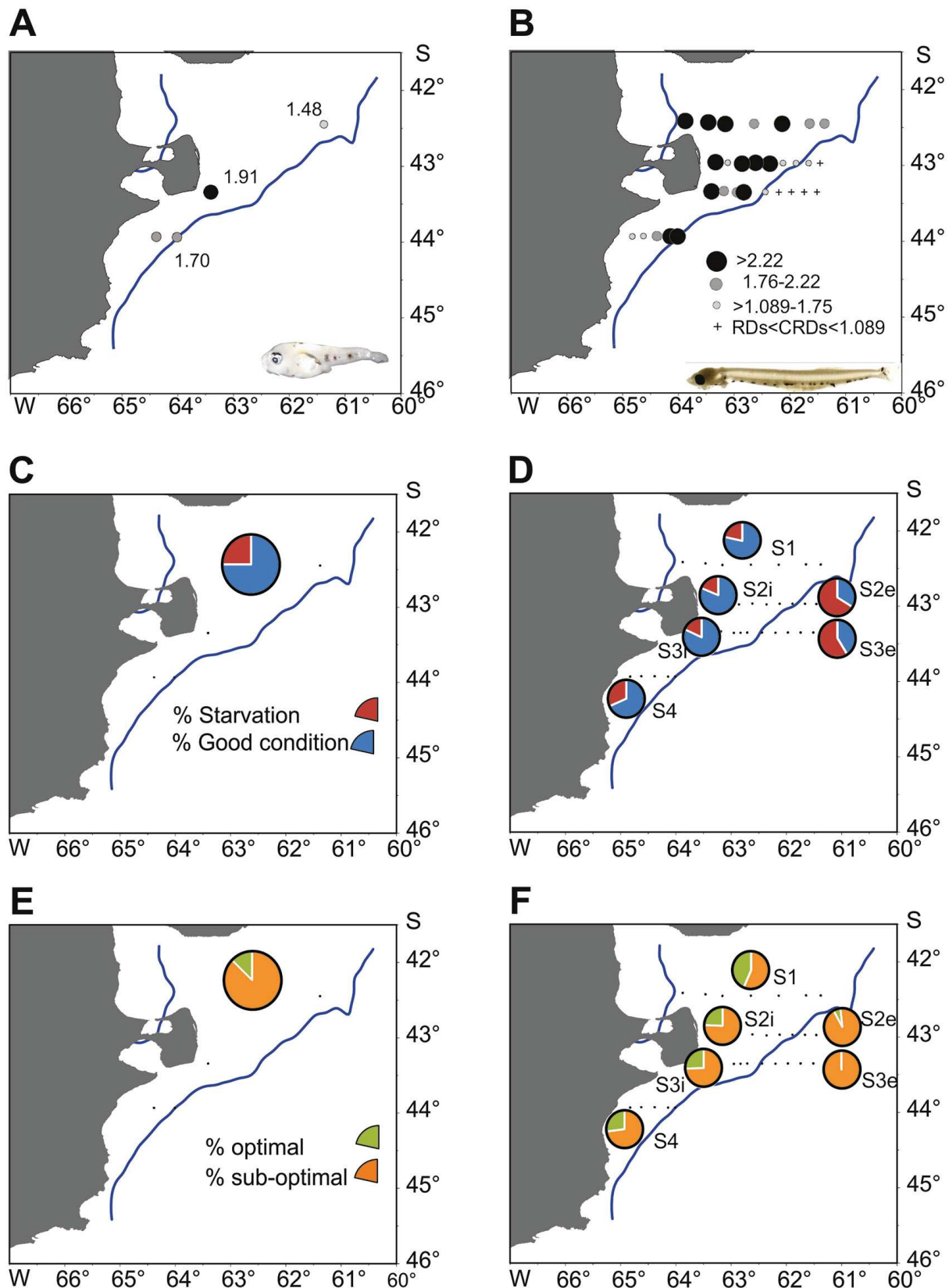


Fig. 5. –Average standardized RNA/DNA index (RD) obtained for each station studied for larvae of the hake *Merluccius hubbsi* (A) and the anchovy *Engraulis anchoita* (B). The size of the circles is proportional to the RD values obtained. Spatial distribution of the percentages of individuals below the critical standardized RNA/DNA index (CRD), i.e. in starvation, in red for (C) *Merluccius hubbsi* larvae and (D) *Engraulis anchoita* larvae and the percentage of individuals above the optimal Gpf ($Gpf > 1$) in green, that is, in sub-optimal condition, for (E) hake *Merluccius hubbsi* larvae and (F) anchovy *Engraulis anchoita* larvae. Dots in (C) to (F) indicate the stations where the fish larvae were caught. S1, S2i, S2e, S3i, S3e, S4: oceanographic sections grouping the internal and external stations in relation to the position of the tidal front (blue line).

explain the increase in the RD values during the afternoon hours.

There is also conflicting evidence in the literature about the variability observed in the nutritional condition of larvae in the water column. Grønkjær et al. (1997) found that protein growth rates of *Gadus morhua* larvae were significantly higher for all age groups of larvae in the upper layers. In contrast, Dänhardt et al. (2007), studying different indicators of nutritional condition in *Sprattus sprattus* larvae, did not find a better nutritional condition in the superficial layers, although this was not the case in all the condition indicators used. Palomera (1991) observed that *E. encrasicolus* larvae mainly occurred above the level of the thermocline, and the highest abundances were recorded in the first 10 m of the water column. The thermocline could function as an upper or lower barrier for larval distribution, favouring the permanence in superficial layers with greater availability of prey associated with the depth of the thermocline (Smith and Suthers 1999). In our work, we found differences in anchovy larvae condition at different levels with respect to the vertical stratification of the water column. This fact should be considered in the future in designing the collection of samples and making comparisons of larvae condition. However, it is not easy to make comparisons between different studies because these aspects are very dependent on variables such as the zone, period, prey availability and species.

Although the anchovy is currently a low-exploitation species, it has a key position in the food web, regulating the systems towards lower and higher levels (Do Souto et al. 2018). Changes in the annual abundances and mean lengths of this species have recently been recorded, so studying its life traits during its early ontogeny is important for understanding the variability of its recruitment (Orlando et al. 2019). Currently, with a continuous increase in fishing effort, many of the main resources are exploited to the limit of their possibilities. The impact of fishing on ecosystems leads to a decline in commercial and non-commercial species. There is a clear need for an integrated vision for the correct management of fishing resources, including both commercial and non-commercial species in the analysis (Coll and Palomera 2007, Pauly 2009). Therefore, the measures adopted must consider integral care of the ecosystem, including zonation of the oceans and the generation of new MPAs (Pauly 2009).

Previous studies have shown that the application of MPAs has positively influenced the nutritional condition of fish species of commercial interest (Viladrich et al. 2016). The RD index and its derivatives are highly sensitive, which has made it possible to map the larval condition and establish favourable areas in relation to the NPFS. Studying nutritional condition allows us to estimate the probabilities of survival of the organisms and their potential recruitment to fisheries. The results presented here are relevant as a baseline for future studies that consider the evolution of the larval condition of these two species and evaluate the potential of areas as MPAs. The RD index is a simple and useful tool that provides complementary information to that provided

by indicators of diversity and abundance usually used in strategies aimed at ensuring the conservation and comprehensive management of these fishery resources in the Argentine Sea.

In conclusion, the results presented herein are of great importance because little information is available on the nutritional condition of *E. anchoita* larvae from the southern stock. In this species, lower RD values were observed than those previously recorded in the study area. Nevertheless, as was hypothesized, the larvae collected in the areas influenced by the NPFS showed a good nutritional condition. The area inside the NPFS showed a lower proportion of individuals in starvation and a higher proportion of individuals in optimal growth, whereas the area outside the NPFS showed a high percentage of anchovy larvae below the critical value of the RD index. It was also observed that the hake RD values and the percentages of larvae in starvation at the beginning of the spawning period in the austral summer of 2018 were similar to those recorded in previous studies. Finally, the RD ratio and its derived index are highly sensitive, making it possible to “map” the larval condition and establish the most favourable areas for survival during the early phases of the life cycle.

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REFERENCES

- Acha E.M., Mianzan H.W., Guerrero R.A., et al. 2004. Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *J. Mar. Syst.* 44: 83-105. <https://doi.org/10.1016/j.jmarsys.2003.09.005>
- Alheit J., Ciechomski J.D., Djurfeldt L., et al. 1991. SARP studies on Southwest Atlantic anchovy, *Engraulis anchoita*, off Argentina, Uruguay and Brazil. *ICES, France*, 46: 1-32.
- Álvarez-Colombo G., Dato C., Macchi G., et al. 2011. Distribution and behavior of Argentine hake larvae: Evidence of a biophysical mechanism for self-recruitment in northern Patagonian shelf waters. *Cienc. Mar.* 37, 633-657. <https://doi.org/10.7773/cm.v37i4B.1777>
- Álvarez-Colombo G., Mianzan H., Madirolas A. 2003. Acoustic characterization of gelatinous-plankton aggregations: four case studies from the Argentine Continental shelf. *ICES J. Mar. Sci.* 60: 650-657. [https://doi.org/10.1016/S1054-3139\(03\)00051-1](https://doi.org/10.1016/S1054-3139(03)00051-1)
- Alves N.M., Braverman M.S., Temperoni B. et al. 2022. Primeros estudios de condición nutricional en juveniles de *Mi-*

- cropogonias furnieri* en Bahía Samborombón durante dos temporadas del año (cálida y fría). Inf. Inv. INIDEP N°67, Mar del Plata, 18 pp.
- Angelescu V. 1982. "Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*). Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema." Contr. INIDEP. 409: 1-83.
- Bakun A. 1997. Patterns in the ocean: ocean processes and marine population dynamics. Oceanogr. Lit. Rev. 5: 530.
- Bakun A., Parrish R.H. 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the Southwestern Atlantic. ICES J. Mar. Sci. 48: 343-361.
<https://doi.org/10.1093/icesjms/48.3.343>
- Betti P., Machinandiarena L., Ehrlich M.D. 2009. Larval development of argentine hake *Merluccius hubbsi*. J. Fish Biol. 74: 235-249.
<https://doi.org/10.1111/j.1095-8649.2008.02136.x>
- Buckley B.A., Caldaroni E.M., Ong T.L. 1999. RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia 401: 265-277.
<https://doi.org/10.1023/A:1003798613241>
- Buckley B.A., Caldaroni E.M., Clemmesen C.M. 2008. Multi-species larval fish growth model based on temperature and fluorometrically derived RNA/DNA ratios: results from a meta-analysis. Mar. Ecol. Prog. Ser. 371: 221-232.
<https://doi.org/10.3354/meps07648>
- Buckley L. 1984. RNA/DNA ratio: an index of larval fish growth in the sea. Mar. Biol. 80: 291-298.
<https://doi.org/10.1007/BF00392824>
- Bulow F.J. 1970. RNA-DNA ratios as indicators of recent growth rates of a fish. J. Fish. Res. Board Can. 27: 2343-2349.
<https://doi.org/10.1139/f70-262>
- Caldaroni E.M., Wagner M., St. Onge-Burns J., Buckley L.J. 2001. Protocol and guide for estimating nucleic acids in larval fish using a fluorescence microplate reader. Reference Document 01-11, Northeast Fisheries Science Center.
- Caldaroni E.M., Clemmesen C.M., Berdalet E., et al. 2006. Inter-calibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. Limnol. Oceanogr.-Meth. 4: 153-163.
<https://doi.org/10.4319/lom.2006.4.153>
- Carreto J.L., Benavidez H.R. 1990. Synopsis on the reproductive biology and early life of *Engraulis anchoita*, and related environmental conditions in Argentine waters. Phytoplankton. IOC. Worksh. Rep. 65. Annex V: 2-5.
- Chícharo L., Chícharo M.A. 1995. The RNA/DNA ratio as a useful indicator of the nutritional condition in juveniles of *Ruditapes decussatus*. Sci. Mar. 59 (suppl. 1): 95-101.
- Chícharo M.A., Chícharo L. 2008. RNA: DNA ratio and other nucleic acid derived indices in marine ecology. Int. J. Mol. Sci. 9: 1453-1471.
<https://doi.org/10.3390/ijms9081453>
- Clemmesen C. 1994. The effect of food availability, age or size on the RNA/DNA ratio of individually measured herring larvae: laboratory calibration. Mar. Biol. 118: 377-382.
<https://doi.org/10.1007/BF00350294>
- Cohen S., Díaz A.O., Diaz M.V. 2021. Morphological and biochemical approaches to assess the nutritional condition of the Argentine hake *Merluccius hubbsi* larvae from two different nursery areas. J. Fish Biol. 98: 132-141.
<https://doi.org/10.1111/jfb.14563>
- Coll M., Palomera I. 2007. Hacia el estudio y la gestión pesquera basada en los ecosistemas. Ecología política 21: 87-89.
- Cousseau M.B., Perrota R.G. 1998. Peces marinos de Argentina. Biología, distribución y pesca. INIDEP, Mar del Plata, 163 pp.
- Dänhardt A., Peck M.A., Clemmesen C.M., Temming, A. 2007. Depth-dependent nutritional condition of sprat *Sprattus sprattus* larvae in the central Bornholm Basin, Baltic Sea. Mar. Ecol. Prog. Ser. 341: 217-228.
<https://doi.org/10.3354/meps341217>
- Derisio C., Alemany D., Acha E.M., Mianzan H.W. 2014. Influence of a tidal front on zooplankton abundance, assemblages and life histories in Península Valdés, Argentina. J. Mar. Syst. 139: 475-482.
<https://doi.org/10.1016/j.jmarsys.2014.08.019>
- Diaz M.V., Pájaro M. 2012. Protocolo para la determinación de las concentraciones de ácidos nucleicos en larvas de peces. Inf. Inv. INIDEP N°20, Mar del Plata, 9 pp.
- Diaz M.V., Olivar M.P., Macchi G.J. 2014. Larval condition of *Merluccius hubbsi* (Marini, 1933) in the northern Patagonian spawning ground. Fish. Res. 160: 60-68.
<https://doi.org/10.1016/j.fishres.2013.11.009>
- Diaz M.V., Do Souto M., Peralta M., et al. 2016. Comer o ser comido: factores que determinan la condición nutricional de larvas de *Engraulis anchoita* de la población patagónica de la especie. Ecología Austral 26:120-133.
<https://doi.org/10.25260/EA.16.26.2.0.71>
- Diaz M.V., Do Souto M., Betti P., et al. 2020. Evaluating the role of endogenous and exogenous features on larval hake nutritional condition. Fish Oceanogr. 29: 584-596.
<https://doi.org/10.1111/fog.12497>
- Do Souto M., Spinelli M., Brown D.R., et al. 2018. Benefits of frontal waters for the growth of *Engraulis anchoita* larvae: The influence of food availability. Fish. Res. 204: 181-188.
<https://doi.org/10.1016/j.fishres.2018.02.019>
- Do Souto M., Brown D.R., Leonarduzzi E., et al. 2019. Nutritional condition and otolith growth of *Engraulis anchoita* larvae: the comparison of two life traits indexes. J. Mar. Syst. 193: 94-102.
<https://doi.org/10.1016/j.jmarsys.2019.01.008>
- Ehrlich M.D. 1998. Los primeros estadios de vida de la merluza *Merluccius hubbsi*, Marini 1933, en el Mar Argentino como aporte al conocimiento de su reclutamiento y estructura poblacional. Doctoral thesis, Univ. Buenos Aires, 318 pp.
- Folkvord A., Ystanes L., Moksness E. 1996. RNA:DNA ratios and growth of herring (*Clupea harengus*) larvae reared in mesocosms. Mar. Biol. 126: 591-602.
<https://doi.org/10.1007/BF00351326>
- Grønkjær P., Clemmesen C.M., St. John M. 1997. Nutritional condition and vertical distribution of Baltic cod larvae. J. Fish Biol. 51: 352-369.
<https://doi.org/10.1111/j.1095-8649.1997.tb06108.x>
- Guerrero R.A., Acha E.M., Framiñan M.B., Lasta C.A. 1997. Physical oceanography of the Río de la Plata Estuary, Argentina. Cont. Shelf Res. 17: 727-742.
[https://doi.org/10.1016/S0278-4343\(96\)00061-1](https://doi.org/10.1016/S0278-4343(96)00061-1)
- Hansen J.E. 2004. Anchoíta (*Engraulis anchoita*). In: Sánchez R.P., Bezzi S.I., Boschi E.E. (eds), El mar argentino y sus recursos pesqueros. Publicaciones especiales INIDEP: 101-115.
- Hansen J.E., Martos P., Madirolas A. 2001. Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. Fish. Oceanogr. 10: 193-206.
<https://doi.org/10.1046/j.1365-2419.2001.00166.x>
- Houde E.D. 2008. Emerging from Hjort's Shadow. J. Northwest Atl. Fish. Sci. 41: 53-70.
<https://doi.org/10.2960/J.v41.m634>
- Houde E.D., Zastrow C.E. 1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. Bull. Mar. Sci. 53: 290-335.
- Macchi G.J., Pájaro M., Ehrlich M. 2004. Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). Fish. Res. 67: 25-38.
<https://doi.org/10.1016/j.fishres.2003.08.006>
- Macchi G.J., Pájaro M., Madirolas A. 2005. Can a change in the spawning pattern of Argentine hake (*Merluccius hubbsi*) affect its recruitment? Fish. Bull. 103: 445-452.
- Macchi G.J., Pájaro M., Dato C. 2007. Spatial variations of the Argentine hake (*Merluccius hubbsi*) spawning shoals in the Patagonian area during a reproductive season. Rev. Biol. Mar. Oceanogr. (Chile). 42: 345-356.
<https://doi.org/10.4067/S0718-19572007000300013>
- Macchi G.J., Diaz M.V., Leonarduzzi E., et al. 2021. Temperature, maternal effects and density-dependent processes during early life stages of Argentine hake as relevant recruitment drivers. Fish. Res. 238: 105898.
<https://doi.org/10.1016/j.fishres.2021.105898>
- Martos P., Sánchez R. 1997. Caracterización oceanográfica de regiones frontales en la plataforma patagónica en relación con áreas de desove y cría de la anchoíta (*Engraulis anchoita*). 10° Coloquio Argentino de Oceanografía, 4-5 Septiembre, IADO-CONICET, Bahía Blanca.
- McGurk M.D., Warburton H.D., Galbraith M., Kusser W.C. 1992. RNA-DNA ratio of herring and sand lance larvae from Port Moller, Alaska: Comparison with prey concentration and temperature. Fish. Oceanogr. 1: 193-207.
<https://doi.org/10.1111/j.1365-2419.1992.tb00038.x>
- Mianzan H.W., Guerrero R.A. 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three

- study cases in the Southwestern Atlantic Ocean. *Sci. Mar.* 64: 215-224.
<https://doi.org/10.3989/scimar.2000.64s1215>
- Ministry of Agroindustry. 2022. https://www.magyp.gob.ar/sitio/areas/pesca_maritima/desembarques/
- Olivar M.P., Diaz M.V., Chicharo M.A. 2009. Tissue effect on RNA: DNA ratios of marine fish larvae. *Sci. Mar.* 73S1: 171-182.
<https://doi.org/10.3989/scimar.2009.73s1171>
- Orlando P., Buratti C., Garciarena A.D. 2019. Diagnóstico de la población de anchoita bonaerense (*Engraulis anchoita*) y estimación de captura biológicamente aceptable durante el año 2019. *Inf. Téc. INIDEP N° 24*, Mar del Plata, 29 pp.
- Pájaro M., Macchi G.J., Martos P. 2005. Reproductive pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fish. Res.* 72: 97-108.
<https://doi.org/10.1016/j.fishres.2004.09.006>
- Palomera I. 1991. Vertical distribution of eggs and larvae of *Engraulis encrasicolus* in stratified waters of the western Mediterranean. *Mar. Biol.* 111: 37-44.
<https://doi.org/10.1007/BF01986343>
- Pauly D. 2009. Beyond duplicity and ignorance in global fisheries. *Sci. Mar.* 73: 215-224.
<https://doi.org/10.3989/scimar.2009.73n2215>
- Rooker J.K., Holt G.J. 1996. Application of RNA:DNA ratios to evaluate the condition and growth of larval and juvenile red drum (*Sciaenops ocellatus*). *Mar. Freshw. Res.* 47: 283-290.
<https://doi.org/10.1071/MF9960283>
- Sabatini M.E., Martos P. 2002. Mesozooplankton features in a frontal area off northern Patagonia (Argentina) during spring 1995 and 1998. *Sci. Mar.* 66: 215-232.
<https://doi.org/10.3989/scimar.2002.66n3215>
- Sánchez R.P., Ciechowski J.D. 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. *Sci. Mar.* 59: 455-478
- Schiariti A. 2008. Historia de vida y dinámica de poblaciones de *Lychnorhiza lucerna* (Scyphozoa) ¿un recurso pesquero alternativo? Doctoral thesis, Univ. Buenos Aires, 220 pp.
- Schiariti A., Betti P., Dato C., et al. 2015. Medusas y ctenóforos de la región norpatagónica I: diversidad y patrones de distribución. *Inf. Inv. INIDEP N°21*, Mar del Plata, 16 pp.
- Simpson J.H., Bowers D. 1981. Models of stratification and frontal movement in shelf seas. *Deep-Sea Res.* 28: 727-738.
[https://doi.org/10.1016/0198-0149\(81\)90132-1](https://doi.org/10.1016/0198-0149(81)90132-1)
- Smith K.A., Suthers I.M. 1999. Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf. *Mar. Ecol. Prog. Ser.* 176: 49-62.
<https://doi.org/10.3354/meps176049>
- Temperoni B., Viñas M.D. 2015. Disponibilidad de presas zooplanctónicas para larvas de *Merluccius hubbsi* en el área de desove. Resultados de la campaña EH-01/14. *Inf. Inv. INIDEP N°50*, Mar del Plata, 15 pp.
- Temperoni B., Viñas M.D., Martos P., Marrari M. 2014. Spatial patterns of copepod biodiversity in relation to a tidal front system in the main spawning and nursery area of the Argentine hake *Merluccius hubbsi*. *J. Mar. Syst.* 139: 433-445.
<https://doi.org/10.1016/j.jmarsys.2014.08.015>
- Viladrich N., Rossi S., Lopez-Sanz A., Orejas C. 2016. Nutritional condition of two coastal rocky fishes and the potential role of a marine protected area. *Mar. Ecol.* 37: 46-63.
<https://doi.org/10.1111/maec.12247>
- Viñas M.D., Ramírez F.C. 1996. Gut analysis of first-feeding anchovy larvae from Patagonian spawning area in relation to food availability. *Arch. Fish. Mar. Res.* 43: 231-256.

Influence of maternal effects and temperature on fecundity of *Sebastes fasciatus* on the Flemish Cap

Francisco González-Carrión, Fran Saborido-Rey

Instituto de Investigaciones Marinas (IIM), CSIC, Vigo, Spain.

(FG-C) (Corresponding author) E-mail: fgonzalez@iim.csic.es. ORCID-iD: <https://orcid.org/0000-0002-7574-9820>
(FS-R) E-mail: fran@iim.csic.es. ORCID-iD: <https://orcid.org/0000-0002-2760-8169>

Summary: The conservation of a sufficient reproductive potential of an exploited stock is one of the goals of fisheries management, as it ensures sustainable productivity. However, there is evidence that spawning stock biomass (SSB) does not represent well the variation in stock reproductive potential, often leading to impaired stock-recruitment relationships. In this study we show that fecundity of *Sebastes fasciatus* on Flemish Cap is not proportional to SSB and shows temporal fluctuation influenced by maternal effects. Females were collected in 23 research surveys between 1996 and 2020. An autodiametric calibration model was developed for *S. fasciatus* for the first time to estimate fecundity. Mean potential fecundity was estimated as 36000 oocytes and mean relative fecundity as 79 oocytes g⁻¹. Potential fecundity varied significantly with female length, age, condition index, gonadosomatic index and environmental variability. Mixed-effect linear models were fitted to assess the effect of maternal traits and bottom temperature on fecundity. Fecundity increased significantly with condition factor and sea bottom temperature. Relative fecundity also increased significantly with length, age and gonadosomatic index, indicating that older, larger and better-conditioned females produce more eggs per female gram. This suggests that SSB is not a good proxy to stock reproductive potential so it is unsuitable for use in stock assessment and scientific advice. Considering that *S. fasciatus* is a viviparous species, future research should focus on maternal effects on offspring and on building time series of reproductive potential indexes that take into account maternal effects.

Keywords: reproductive potential; fish condition; life history; autodiametric method.

Influencia de los efectos maternos y la temperatura en la fecundidad de *Sebastes fasciatus* en Flemish Cap

Resumen: La conservación de un potencial reproductivo suficiente de una población explotada es uno de los objetivos de la gestión pesquera, ya que garantiza la consecución de una productividad sostenible. El establecimiento de relaciones fiables stock-reclutamiento es esencial para lograr este objetivo, pero la biomasa reproductora (SSB) se utiliza a menudo como índice poblacional, mientras que hay evidencias de que no representa bien la variación del potencial reproductivo de la población, lo que da lugar a relaciones stock-reclutamiento deficientes. En este estudio mostramos que la fecundidad de *Sebastes fasciatus* en Flemish Cap no es proporcional a la SSB y que tiene una fluctuación temporal influida por los efectos maternos. Se recogieron hembras en 23 campañas oceanográficas realizadas entre 1996 y 2020. Por primera vez, se desarrolló un modelo autodiamétrico para *S. fasciatus* para estimar la fecundidad. La fecundidad potencial media se estimó en 36000 ovocitos y la fecundidad relativa en 79 ovocitos g⁻¹. La fecundidad potencial varió significativamente con la talla de la hembra, la edad, el factor de condición, el índice gonadosomático y la variabilidad ambiental. Se ajustaron modelos lineales mixtos para evaluar los efectos de los rasgos maternos y la temperatura del fondo marino sobre la fecundidad. Los resultados mostraron que la fecundidad aumentó significativamente con el factor de condición y la temperatura del fondo. La fecundidad relativa también incrementó significativamente con la talla, la edad y el GSI, lo que indica que las hembras más longevas, más grandes y con mejor condición producen más huevos por gramo de hembra. Esto implica que la biomasa de la población reproductora (SSB) no es un buen indicador del potencial reproductivo de la población, lo que pone en peligro su uso en la evaluación de la población y el asesoramiento científico. Teniendo en cuenta que *S. fasciatus* es una especie vivípara, la investigación futura debería centrarse en los efectos maternos sobre las crías y en la creación de series temporales de índices de potencial reproductivo que tengan en cuenta los efectos maternos.

Palabras clave: potencial reproductivo; condición; historia vital; método autodiamétrico.

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INTRODUCTION

Changes in spawning dynamics, size or age at maturity, size structure and poor condition can increase the variability of recruitment (Marteinsdottir and Thorarinsson 1998, Blanchard et al. 2003, Anderson et al. 2008), reduce the resilience and capacity of populations to dampen environmental changes (Hsieh et al. 2006) and increase the impact of climate change (Cheung et al. 2009). Fisheries management will considerably benefit from a better understanding of how maternal features affect offspring phenotypes (the so-called maternal effect) and hence of how stock reproductive potential determines population productivity and recruitment.

Consequently, fecundity studies are critical for understanding the reproductive potential of fish populations (Tomkiewicz et al. 2003, Lambert et al. 2003, Saborido-Rey and Trippel 2013) and how maternal effects can interact with fecundity (Thorsen and Kjesbu 2006). Fecundity is a highly temporal and geographically sensitive variable that changes drastically with attributes of the individual spawners, including length, age and condition factor (Murua and Saborido-Rey 2003, Rideout and Morgan 2010). In consequence, the population's egg production is highly dependent on adult stock demography and factors affecting demography, such as growth, maturation schedules, fishing pressure, environmental conditions and disease (McElroy et al. 2013, Chang et al. 2021). Moreover, in many teleosts, significant differences have revealed proportionally positive relationships between potential fecundity and fish length (Stafford et al. 2014, Love et al. 2002), age and condition (Thorsen et al. 2006, Lambert 2008), highlighting the importance of maternal effects. Several studies have shown that in Pacific rockfish species maternal effects are determined by release off-spring date and seasonal changes in the productivity of the California current, so offspring quality is directly affected (Fisher et al. 2007).

Monitoring of fecundity, as reported in the literature, can be used in stock assessment and fisheries management (Yoneda and Wright 2004, Lambert 2008, McElroy et al. 2013), especially under the climate change scenario in species with a strong maternal influence, such as those showing viviparity. However, long time series of fecundity are usually not available, as reported by Tomkiewicz et al. (2003), and the situation has not improved over time. The difficulty of estimating fecundity is likely the main hindrance to regular and routine estimation. In this regard, the autodiametric method developed by Thorsen and Kjesbu (2001) must facilitate fecundity estimations.

In this study, for the first time we applied the autodiametric method to estimate fecundity in *S. fasciatus* on the Flemish Cap bank to build a unique long time series of fecundity data of 20 years from 1996 to 2020. We analysed the maternal influence on several reproductive traits and tested whether water temperature influences fecundity. Our overall aim was to improve our understanding of the effects of maternal influence and climate variability on the productivity of *S. fasciatus*,

following the hypothesis that spawning stock biomass (SSB) and other stock indexes do not represent well the variation in stock reproductive potential, often leading to impaired stock-recruitment relationships. Our results highlight the importance of building time series of reproductive potential variables other than SSB, such as fecundity.

MATERIALS AND METHODS

Study area

The study was carried out on the Flemish Cap in the northwest Atlantic, between 46°N and 49°N and 44°W and 46°W (Fig. 1). It is separated from the Newfoundland shelf by the Flemish Pass, a channel with depths in excess of 1100 m, which hinders the migration to and from the Grand Bank for most of the fish species inhabiting the Flemish Cap, including *S. fasciatus*. The Flemish Cap is a dome-shaped, deep-water mountain, with a total area of 17,000 square miles up to 1460 m and 10,555 square miles up to 730 m, with the shallowest part of the bank (120 m depth) located in the southeastern quadrant.

Data collection, histology and ovarian processing

Ovaries of *S. fasciatus* were collected from the EU Flemish Cap survey conducted annually in June/July since 1988 as part of the European Union sampling programme with the participation of Spain and Portugal. For each fish, fork length (FK), total weight (TW), gutted weight (GW) and maturity stage were recorded on board. Otoliths were removed for further age determination.

Ovaries were preserved in 4% buffered formaldehyde and then weighed in the laboratory. Ovary sections of 0.5 cm thickness from the central portion of the gonad were embedded in paraffin based on conventional histological processing. Sections of 3 µm were stained with haematoxylin and eosin protocol. The ovarian developmental phase, as described in Brown-Peterson et al. (2011), was determined under a microscope.

Bottom temperature was obtained from the Copernicus Marine Environment Monitoring service (<https://doi.org/10.48670/moi-00021>) for the Flemish Cap area (between 45°N to 49°N and 47°W to 43°W) for July within the period 1996-2020 and for sampling depths between 300 and 600 m.

Fecundity estimation and image analyses

Fecundity was estimated in ovaries with the presence of advanced vitellogenic oocytes and no signs of postovulatory follicles and/or fertilization. Because *Sebastes* species are group-synchronous with a determinate oocyte recruitment mode, this single leading cohort of oocytes is considered representative of the potential fecundity (Murua and Saborido-Rey 2003). A total of 281 ovaries were selected according to the above criteria between 1996 and 2020 (Table 1). Ovary weight was recorded and subsamples

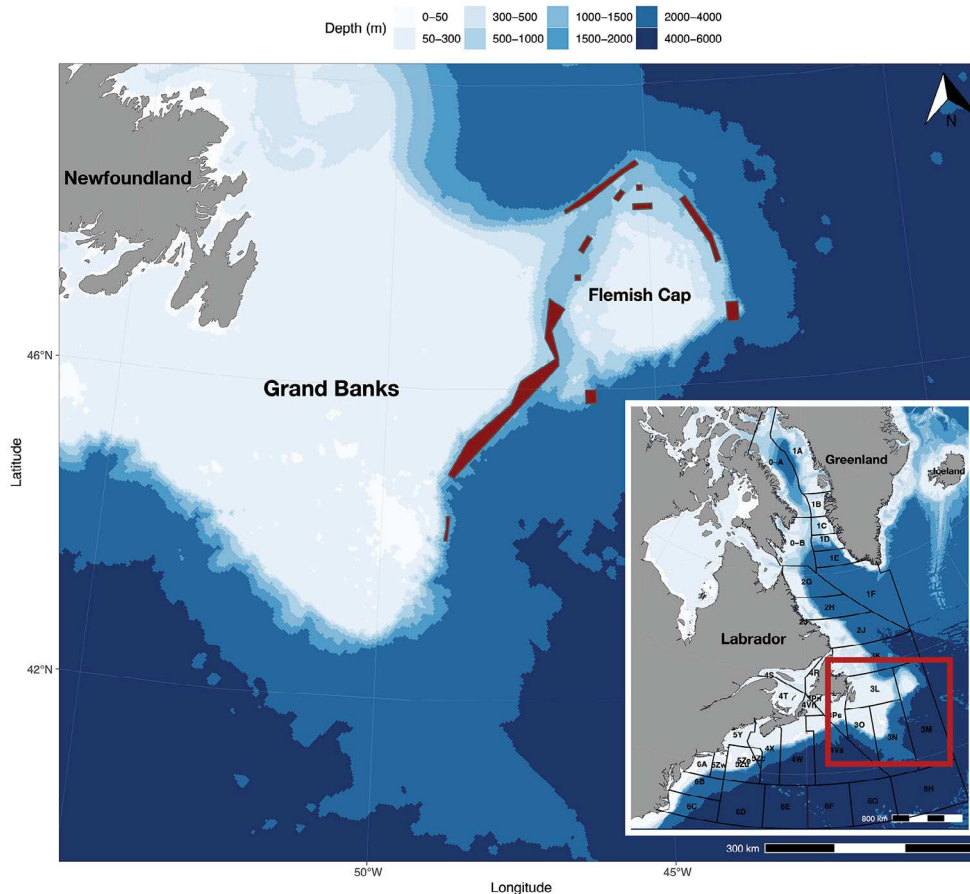


Table 1. – Summary statistics of the female *S. fasciatus* maternal traits: age, fork length, gutted weight (GW) and condition factor. Numbers indicate the average \pm standard deviation, with ranges shown in parentheses. Years with merged data required to increase sampling size are indicated with asterisks and correspond to the year label used in the figures.

Year	n	Age (years)	Length (cm)	GW (g)	Condition factor
1996	14	8.43 \pm 2.53 (6-14)	29.29 \pm 2.53 (25-39)	381.54 \pm 169.99 (240-820)	1.43 \pm 0.08 (1.3-1.57)
1997	12	11.36 \pm 3.93 (7-21)	30 \pm 3.3 (25-35)	428.75 \pm 133.04 (220-640)	1.53 \pm 0.06 (1.41-1.61)
1998	5	8.4 (7-10)	25.8 (24-28)	269 (235-340)	1.56 (1.45-1.7)
1999	10	11.7 \pm 4 (6-16)	30.6 \pm 4.97 (21-36)	436.1 \pm 168.62 (140-659)	1.45 \pm 0.18 (1.27-1.78)
2000	16	12.88 \pm 2.22 (10-17)	32.44 \pm 2.9 (27-37)	503.44 \pm 112.68 (320-720)	1.46 \pm 0.1 (1.28-1.63)
2001	29	11.23 \pm 3.28 (6-16)	28.9 \pm 2.81 (22-35)	351.14 \pm 97.17 (140-610)	1.42 \pm 0.11 (1.23-1.74)
2002	4	11.75 \pm 3.86 (6-14)	28.25 \pm 3.1 (24-31)	328.25 \pm 109.59 (188-445)	1.41 \pm 0.06 (1.36-1.49)
2004 (2003-2004)*	13	12.44 \pm 2.92 (7-17)	30.31 \pm 2.14 (27-33)	399.08 \pm 77.77 (291-580)	1.43 \pm 0.14 (1.22-1.61)
2005	32	12.31 \pm 3.45 (6-19)	29.28 \pm 2.45 (24-34)	364.12 \pm 91.35 (230-530)	1.43 \pm 0.12 (1.07-1.67)
2006	12	11.08 \pm 3.48 (7-16)	28.83 \pm 2.37 (24-32)	354.58 \pm 95.38 (180-500)	1.44 \pm 0.11 (1.3-1.63)
2008	5	12 \pm 4.47 (6-18)	30.8 \pm 3.7 (26-36)	384 \pm 110.59 (240-510)	1.3 \pm 0.14 (1.09-1.48)
2010 (2009-2010)*	7	10.86 \pm 2.79 (7-16)	31.14 \pm 2.97 (26-34)	431.29 \pm 116.45 (260-580)	1.4 \pm 0.13 (1.25-1.61)
2011	3	12.33 \pm 3.79 (8-15)	32.67 \pm 4.51 (28-37)	523 \pm 213.19 (293-714)	1.44 \pm 0.12 (1.33-1.56)
2013	13	14.85 \pm 6.03 (7-25)	32.77 \pm 4.9 (26-40)	565.08 \pm 219.82 (272-975)	1.55 \pm 0.16 (1.32-1.81)
2014	12	13.92 \pm 3.12 (9-20)	32.58 \pm 2.84 (28-36)	508.92 \pm 117.7 (325-653)	1.45 \pm 0.14 (1.25-1.66)
2015	8	15.25 \pm 7.15 (6-24)	35 \pm 6.85 (22-44)	672 \pm 352.8 (198-1190)	1.46 \pm 0.2 (1.13-1.86)
2016	21	14.13 \pm 4.12 (9-25)	31.75 \pm 1.96 (29-35)	432.43 \pm 85.97 (270-560)	1.3 \pm 0.09 (1.11-1.44)
2018 (2017-2018)*	35	14.76 \pm 4.02 (8-28)	33.06 \pm 3.34 (27-41)	518.09 \pm 148.81 (316-950)	1.41 \pm 0.16 (1.22-2.05)
2019	15	16.73 \pm 3.2 (10-22)	35.27 \pm 3.53 (28-40)	675.13 \pm 172.18 (360-940)	1.52 \pm 0.13 (1.3-1.83)
2020	15	14.4 \pm 4 (8-20)	34.07 \pm 4.77 (27-44)	630.47 \pm 259.34 (323-1230)	1.53 \pm 0.13 (1.25-1.81)
Total	281	271	280	280	280

Maternal traits

The Fulton condition index (K) and the gonadosomatic index (GSI) were calculated as follows:

$$K = \left(\frac{GW}{FL^3} \right) \times 100 \quad (3)$$

$$GSI = \left(\frac{OW}{GW} \right) \times 100 \quad (4)$$

where GW represents gutted weight (g) and FL is fork length (cm) recorded for each female. Age (yr) and GW (g) were also recorded for each female for further analyses as an explanatory variable in the models and to estimate relative fecundity.

Statistical analysis

Generalized linear models (GLM) were fitted to examine the relationships between the reproductive investment (absolute and relative potential fecundity) and maternal traits (length, age and fish condition).

When bottom water temperature was included, generalized linear mixed models (GLMM) were used to analyse the effect of female traits on their reproductive output. Models were fitted using length, age, K and GSI as fixed effects, haul as a random effect and water temperature as a random slope to allow the relationship with bottom temperature to differ by year. Water temperature data were unavailable for numerous coordinate-year combinations, hindering possible water bottom temperature effects on potential fecundity relationships. However, a dataset covering 15 years was obtained. The reproductive output was analysed as follows:

$$\text{Reproductive output}_{ti} = \alpha + FL \text{ or } A + K + GSI + \text{TBTM} + a_i + \varepsilon_{ti}$$

where reproductive output is the absolute and relative potential fecundity in year i and haul j , α is the intercept, FL is the fork length, A is age, K is Fulton's condition factor, GSI is the gonadosomatic index, TBTM is the bottom temperature at deep habitat range (300–600 m), a_i is the random intercept allowing for variation between years, and b_i is the random intercept allowing for variation between hauls. The residuals ε_{ti} are a normally distributed random error with mean 0 representing the within-year and haul variation.

To avoid collinearity due to fish length and age correlation, they were used in separate models: the models were fitted for absolute and relative fecundity using age and length separately. Haul and Year were included as random effects to correct for the non-independence of reproductive output from the same year and haul. Thus, we evaluated the effects of how these maternal traits and water bottom temperature affect potential fecundity. GLMM were fitted using negative binomial mean variance with a “log” link function. Diagnostic plots testing residual homogeneity, independence and normality and the Akaike information criterion (AIC) were used for model validation (Supplementary material,

Tables S1, S2). We avoided transforming the response variable as long as possible using a negative binomial distribution. First, Poisson distribution was used in all the models because of the nature of the response variable (count data). However, high overdispersion values were obtained, so negative binomial distribution was used to avoid overdispersion problems (Zuur and Ieno 2013). Variance inflation factor was calculated in each model to test for collinearity between independent covariates. All statistical analyses were performed with the statistical software R4.0.1 (R Core Team 2020) and using the glmmTMB package (Brooks et al. 2017).

RESULTS

The autodiametric method

The estimated autodiametric relationship between *S. fasciatus* oocyte density (n/g) and mean OD was significant ($p < 0.001$, $r^2 = 0.80$, $n = 108$). No significant difference was detected ($df = 255$, $P = 0.133$) between the autodiametric curves of *S. fasciatus* on the Flemish Cap, *S. norvegicus* in Iceland and *S. mentella* in Iceland and the Irminger Sea (Fig. 2). The autodiametric curve with all species combined ($p < 0.001$, $r^2 = 0.88$, $n = 256$) was the following:

$$\text{Oocyte density (n/g)} = \exp(1.068 \times 10 - (3.234 \times 10^{-3}) \times \text{OD} (\mu\text{m})) \quad (5)$$

We then used this curve to estimate the potential fecundity from OD and ovary weight for *S. fasciatus* on the Flemish Cap.

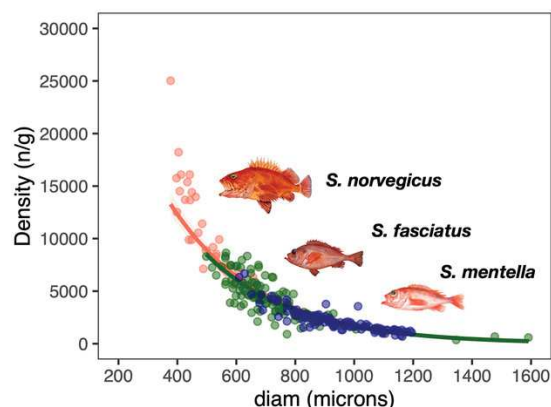


Fig. 2. – Relationship between oocyte diameter and oocyte density (number of oocytes/g) for species of the genus *Sebastes* sampled on the Flemish Cap bank (*S. fasciatus* with green dots) and in the Irminger Sea and Iceland (*S. norvegicus* and *S. mentella* with coral and blue dots, respectively). No significant differences were observed between areas.

Potential fecundity

Influence of female traits on fecundity

Four maternal traits (fork length, age, GSI and K) were used to study their influence on fecundity. To avoid using age and length together, two separate

models were built. The resulting two GLM models explained 75% and 62% of potential fecundity (Table 2) using length and age, respectively. In the case of relative fecundity, the two models explained 47% and 50% of the variation (Table 2). Our results show that potential fecundity increased significantly with age and size. Interestingly, relative fecundity also increased with those female traits, indicating a disproportionately higher fecundity at larger sizes and older ages (Fig. 3).

Females with higher K and constant GSI (1.58, the average value of the time series) had a higher potential fecundity than fish with lower K (Fig. 3). For example, for a length of 34 cm (the average of the mature stock), the potential fecundity varied between 33707 oocytes with a K=1.2 compared with 47512 oocytes with a K=1.6 and 56409 oocytes with a K=1.8, i.e. an increase of 41% and 67%, respectively (Fig. 3A). Similarly, for a female at 15 years old, the predicted potential fecundity for all three scenarios of K was 34544 oocytes for K=1.2, 40739 oocytes for K=1.6 and 44242 oocytes for K=1.8 (Fig. 3B). Thus, potential fecundity of females in poorer condition was notably lower.

However, relative fecundity did not increase significantly with condition. For a fixed length of 34 cm, the relative fecundity was 71 oocytes g⁻¹ body weight for K=1.2, 76 oocytes g⁻¹ body weight for K=1.6 and 79 oocytes g⁻¹ body weight for K=1.8, i.e. a difference of 7% and 11%, respectively. Moreover, for a fixed age of 15 years, relative fecundity was 72 oocytes g⁻¹ body weight for K=1.2, 76 oocytes g⁻¹ body weight for K=1.6 and 78 oocytes g⁻¹ body weight for K=1.8, i.e. a difference of barely 5% and 8% (Fig. 3C and D).

Interannual variation of fecundity

Interannual variation in potential fecundity was examined by comparing potential relationships between fecundity and maternal traits between 1996 and 2020 (Fig. 4). Fork length and age showed a significant effect on potential fecundity in all years analysed ($p < 0.001$), and the optimal model showed a significant year effect ($p < 0.001$). However, the post hoc Tukey test showed that the fecundity variation between years was caused by only a few years (Tables S3, S4), mostly 2010, a year with a low sample size.

Figure 5 shows the fecundity variation for a 34 cm female. Potential fecundity showed generally higher values at the beginning of the time series, an average of 48500 oocytes between 1996 and 2001 and four years with fecundity above 50 thousand oocytes. Later, fecundity decreased to an average of 42000 oocytes for the rest of the times series (except 2010). During this period, fecundity was below 45000 oocytes in all years except 2010, with particularly low values in the latest years (2015-2019). The year with the highest (2000) fecundity for a fixed size of 34 cm and age of 15 years showed 1.8-fold greater fecundity rates on average than the year with the lowest fecundity (2015) (not considering 2010).

The analyses with relative fecundity yielded similar results to those with absolute potential fecundity. Optimal models included length, age and year, which explained 22% and 34%, respectively (Supplementary Table 5 and Supplementary Table 6). For a 34 cm female, relative fecundity ranged between 62 and 139 oocytes g⁻¹, showing a very similar pattern to potential fecundity, with higher values before 2002 (mostly above 90 oocytes g⁻¹) and lower values thereafter (mostly below 80 oocytes g⁻¹).

Table 2. – Summary of GLM negative binomial models fitted to estimate the effect on potential and relative fecundity of the maternal traits fork length, age, condition factor (K) and gonadosomatic index (GSI) of *S. fasciatus* on the Flemish Cap.

Models	Response variable	n	R ²	Variable	Coeffs	SE	z value	Pr(> z)
1	Potential fecundity	252	0.75	α	4.862	0.278	17.491	<0.001
				Length	0.113	0.005	22.216	<0.001
				K	0.858	0.142	6.028	<0.001
				GSI	0.445	0.033	13.654	<0.001
2	Potential fecundity	252	0.62	α	7.917	0.276	28.732	<0.001
				Age	0.093	0.006	14.852	<0.001
				K	0.424	0.175	2.421	<0.05
				GSI	0.405	0.042	9.767	<0.001
3	Relative fecundity	252	0.47	α	2.905	0.251	11.588	<0.001
				Length	0.016	0.005	3.367	<0.001
				K	0.096	0.112	0.857	0.39138
				GSI	0.436	0.031	14.187	<0.001
4	Relative fecundity	244	0.50	α	3.257	0.188	17.301	<0.001
				Age	0.023	0.005	4.685	<0.001
				K	0.042	0.108	0.391	0.696
				GSI	0.413	0.038	13.437	<0.001

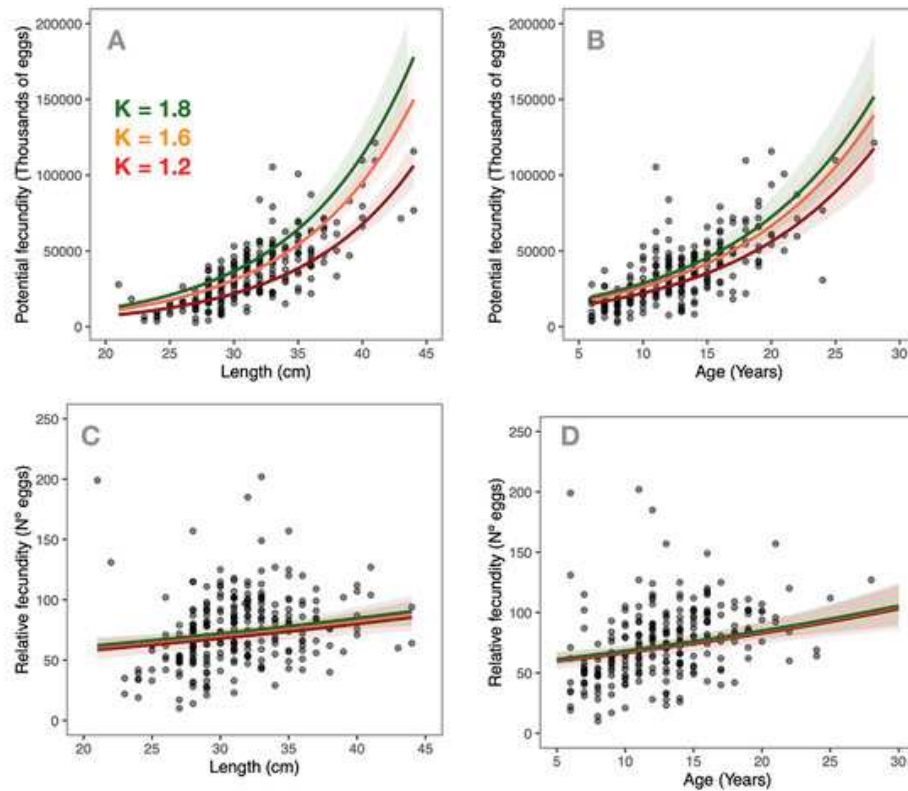


Fig. 3. – Relationship and fitted curves between potential fecundity by length (A) and age (B), and between relative fecundity by length (C) and age (D) of *S. fasciatus* on the Flemish Cap between 1996 and 2020. Data were fitted for three different values of condition factor ($K=1.2$, $K=1.6$ and $K=1.8$)

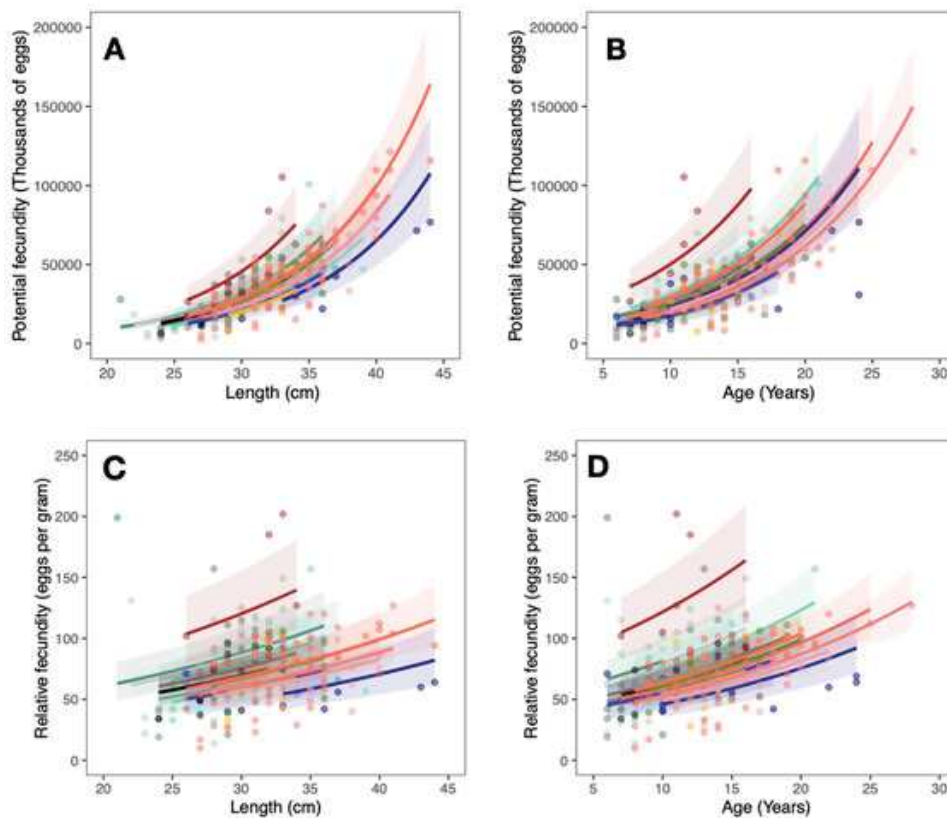


Fig. 4. – Interannual variation of the relationships between potential fecundity by length (A) and age (B), and between relative fecundity by length (C) and age (D) of *S. fasciatus* on the Flemish Cap between 1996 and 2020.

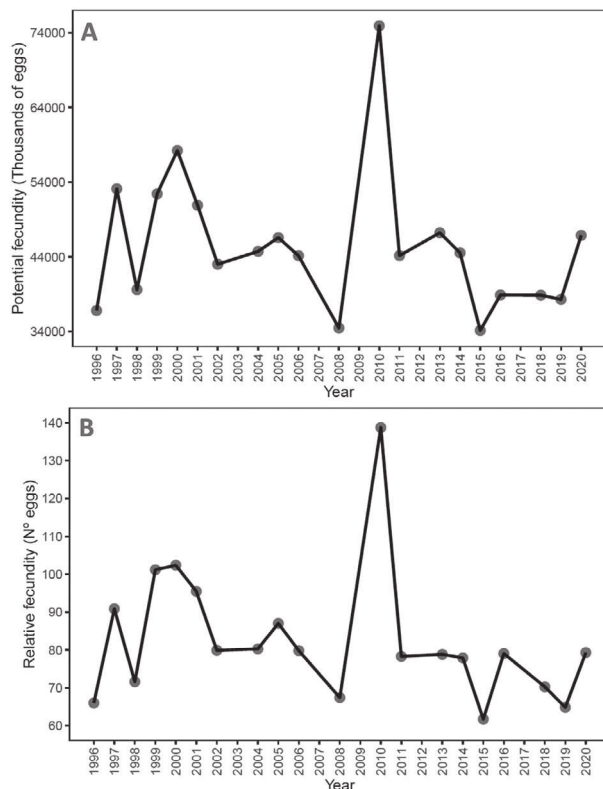


Fig. 5. – Temporal variation in potential fecundity (A) and relative fecundity (B) between 1996 and 2020 for a 34 cm *S. fasciatus* female.

The role of bottom water temperature in fecundity

The range of bottom temperature in which females were sampled varied between 3°C and 5°C, with the highest frequencies in a narrow range between 3.5°C

and 4°C, i.e. 70% of females were sampled in a range of 0.5°C (Fig. 6). Because samples were randomly taken during the survey, this result likely reflects the distribution of females in advanced stage of vitellogenesis.

The potential and relative fecundity increased per degree of bottom temperature water (Fig. 6 A, B). The median of potential fecundity increased from 30743 oocytes in 3°C to 45000 oocytes in 4.5°C, i.e. by 31%. Similarly, relative fecundity increased from 64 oocytes g⁻¹ body weight at 3°C to 85 oocytes g⁻¹ body weight at 4°C, i.e. an increase of 24%. The two GLMMs fitted (using length and age) showed that fecundity-at-length and at-age increased with temperature (Fig. 6C, D). However, only the model using age showed a significant positive relationship between bottom temperature and potential fecundity in the age model (Table 3 and Table 4).

DISCUSSION

Our findings provide empirical evidence of autodiometric curve stability, indicating that the autodiometric method for estimating fecundity originally developed in cod (Thorsen and Kjesbu 2001) can be applied in North Atlantic *Sebastes* species.

This study demonstrated no significant differences in autodiometric curves between three species of *Sebastes* on the Flemish Cap, in Iceland and in the Irminger Sea. Likewise, no significant differences were obtained between autodiometric curves from different stocks in the northeast Arctic, the northern Gulf of St. Lawrence and Georges Bank (Thorsen and Kjesbu 2001, Lambert 2008, Alonso-Fernández et al. 2009). For example, for a fixed diameter size of 800 µm, the oocyte density varied between 3174 oocytes in the Flemish Cap autodiometric curve and 3303 oocytes in the Irminger Sea autodiometric curve, a difference of 4%. Lambert (2008) found a similar difference of less

Table 3. – Parameters of the optimal GLMM using potential fecundity as the response variable and including length, condition factor (K), gonadosomatic index (GSI) and bottom temperature from 21 years (N=280 observations) as explanatory variables. SD, standard deviation; SE, standard error. R²LMM(m) describes the proportion of variance explained by fixed effects alone and R²LMM(c) describes the proportion of variance explained by fixed and random effects combined.

Fixed effects	Parameter estimate	SE	z value	Pr(> z)
Intercept	3.764875	0.490177	7.68	<0.001
Length	0.125494	0.007794	16.10	<0.001
K	0.971214	0.188958	5.14	<0.001
GSI	0.526113	0.05054	10.41	<0.001
Sea bottom temperature	0.107033	0.07218	1.48	0.138
Random effects (SD)				
Year	0.00971			
Haul	0.01133			
Metric				
R ² _{LMM(m)}	0.813			
R ² _{LMM(c)}	0.858			

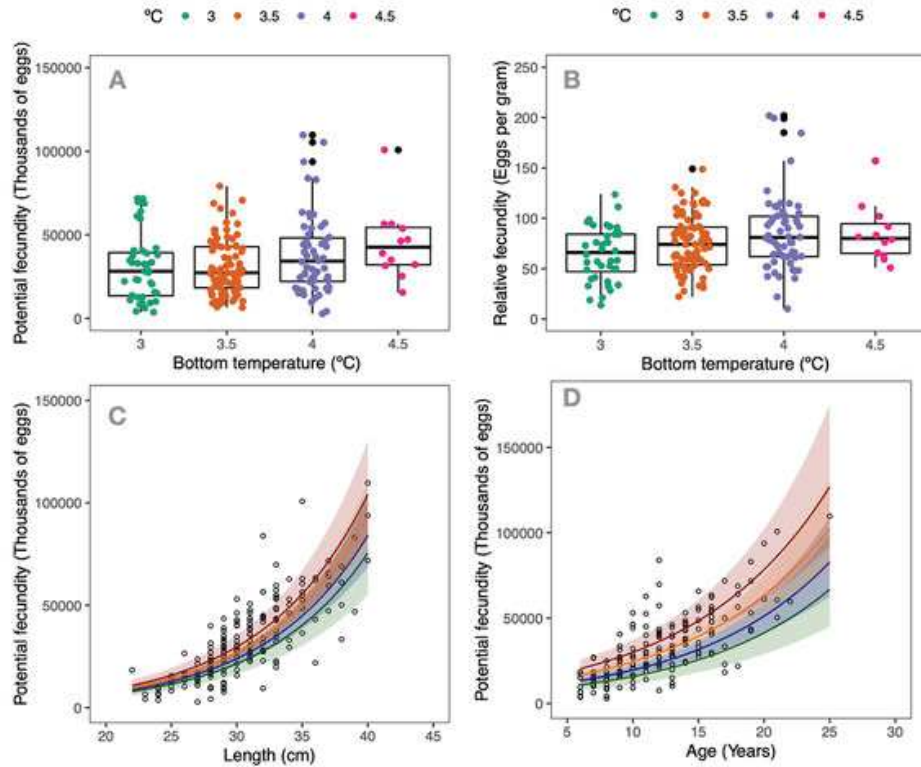


Fig. 6. – Boxplots displaying the relationship of sea bottom temperature with potential fecundity (A) and relative fecundity (B) of *S. fasciatus* on the Flemish Cap. The relationships of potential fecundity at four different temperatures are shown in C) for length and in D) for age.

Table 4. – Parameters of the optimal GLMM using potential fecundity as the response variable and including age, condition factor (K), gonadosomatic index (GSI) and bottom temperature from 21 years (n=280 observations) as explanatory variables. SD, standard deviation; SE, standard error. R²LMM(m) describes the proportion of variance explained by fixed effects alone and R²LMM(c) describes the proportion of variance explained by fixed and random effects combined.

Fixed effects	Parameter estimate	SE	z value	Pr(> z)
Intercept	7.413802	0.439226	16.879	<0.001
Age	0.090452	0.007516	12.035	<0.001
K	0.334705	0.200544	1.669	0.135
GSI	0.418751	0.057942	7.227	<0.001
Sea bottom temperature	0.166456	0.082827	2.010	<0.05
Tandom effects (SD)				
Year	0.009952			
Haul	0.026120			
Metric				
R ² _{LMM(m)}	0.677			
R ² _{LMM(c)}	0.778			

than 6.5% in oocyte density estimated with different calibration curves for two cod stocks, concluding that they were essentially the same curve.

The use of OPD and the success of the autodiometric method could vary between areas, stocks and species (Dominguez-Petit et al. 2018) spatial differences in the autodiometric calibration curve were observed in

the Northwest Atlantic, but did not translate into differences in fecundity at length. This is the first time that spatial differences between ACCs of the same species have been reported, what could be the result of (i, for reasons such as energy allocation and preservation techniques (Friedland et al. 2005). Thus, fecundity estimations could be inaccurate when published calibra-

tion curves not estimated for the species or a stock of interest are used (Witthames et al. 2009).

In this paper, we have studied the fecundity of *S. fasciatus* on the Flemish Cap for the first time, building a twenty-year time series between 1996 and 2020; such long time series in fecundity are rarely seen in the literature. Mean potential fecundity and mean relative fecundity were 36000 oocytes per female and 78.17 oocytes/gram female respectively. These results are in accordance with the fecundity reported for *S. mentella* in the Irminger Sea (Saborido-Rey et al. 2015). Our study shows annual changes in potential fecundity between several years of the time series, as other reported in species of the genus *Sebastes* (Beyer et al. 2015).

We have shown that larger, older and better-conditioned fish produced more offspring in both absolute and relative terms than smaller individuals. Therefore, SSB may not be an accurate metric for the reproductive potential of stocks with a different demographic composition. The relative fecundity-age relationship suggests that there is a significant effect of repeat spawners in *S. fasciatus* stocks and highlights the importance of maintaining a strong length/age population structure. Similar results have been reported in several species, such as cod (Blanchard et al. 2003, Yoneda and Wrieth. 2004, Mion et al. 2018). We have also shown significant variation in fecundity between years. It is well known that fecundity, like many other life-history traits, is highly variable between stocks, geographic areas and/or years (Kraus et al. 2000, Marteinsdottir and Begg 2002, McElroy et al. 2013). Nevertheless, fecundity is still mostly ignored in the monitoring programmes. As a consequence, population egg production is rarely estimated for assessment purposes, or if estimated a constant fecundity-at-length or at-age relationship is used.

An increase in potential fecundity with female size was observed in other *Sebastes* species, including *Sebastes melanops*, *S. goodei*, *S. entomelas*, *S. flavidus* and *S. atrovirens* (Berkeley et al. 2004, Sogard et al. 2008, Dick 2009). However, our results show an increase in reproductive potential with size and age and the importance of using indexes other than SSB to measure stock reproductive potential. This finding has been reported in *S. mentella* and *S. norvegicus* (Saborido-Rey et al. 2015), where the exponent of the fecundity-length power function differed significantly from 3. It is important to highlight that we used females with ovaries showing advanced vitellogenic stages, as down-regulation of fecundity has been shown to drastically modify fecundity during the course of vitellogenesis (Saborido-Rey et al. 2015). This process is likely driven by fish condition and environment factors (Murua et al. 2003, Armstrong and Witthames 2012).

In line with length and age, Fulton's condition factor and the GSI were only significantly related to potential but not to relative fecundity in our study. In addition, other studies have demonstrated that fish condition has a high influence on potential fecundity, with the result that fish in better nutritional status had a higher fecundity than fish in poorer conditions (Thorsen et al. 2006, Kennedy et al. 2007, Lambert 2008).

In this paper, explained variance of fecundity was high when K and GSI were included. The GLM model using fish length, condition factor and GSI as a dependent variable explained 75% of the variability in fecundity, in agreement with an earlier study carried out in cod (Lambert et al. 2008). Considering that the effect of the condition factor can be related to the fact that it intervenes in the final part of oocyte recruitment, i.e. during this phase fish will feed and therefore the condition factor will be a key maternal trait determining fish fecundity. However, a recent study (Beyer et al. 2015) showed that the hepatosomatic index (HSI) was significantly related in four studied species, whereas K was significant in one species. This finding suggests that a more accurate index of fish condition, such as HSI, lipid concentration or muscle water content and prey availability index (Kraus et al. 2002), should be included in future research into maternal effects on fecundity.

In this study, we found a positive relation between potential fecundity and bottom water temperature. Several studies have described water temperature as an important factor that can play a direct or indirect key role in fecundity variation in fish (Kjesbu et al. 1998, Kraus et al. 2000, Lambert et al. 2008). Moreover, bottom temperature, which has been increasing on the Flemish Cap since the 1990s (Colbourne et al. 2018), could generate changes in the way in which *S. fasciatus* allocates energy to reproduction during the whole time series. For example, Yoneda and Wright (2004) describe spatial and temporal fecundity variation as changes in energy allocation that influence maternal condition. The increasing temperature reported on the Flemish Cap may be one of the causes of the sharp increase in *S. fasciatus* abundance after several strong year-classes in 2002-2006 (González-Troncoso et al. 2022). Although recruitment was poor thereafter, it produced a shift in dominance on the Flemish Cap, where the traditionally more abundant *S. mentella* declined in favour of *S. fasciatus*, traditionally considerably less abundant. It is important to highlight that *S. mentella* has a distribution towards more northern and colder waters than *S. fasciatus*. Reproduction of other aquatic species can also be affected by variability of environmental factors such as sea surface temperature, which plays an important role in regulating brooding activity in crustaceans (Chang et al. 2021) and barnacles (Román et al. 2022) through the primary productivity.

Potential implications and future directions

Firstly, our findings provide for the first time an autodiometric calibration curve between oocyte mean diameter and ovarian oocyte density in *S. fasciatus*, which can be applied to estimate potential fecundity in North Atlantic for species of the genus *Sebastes*. Secondly, our study shows that potential fecundity varies interannually in *S. fasciatus*, probably a response of maternal effects of individual females to varying combinations of biological and environmental factors. Because maternal effects have been reported in a number of exploited species, we suggest that annual variations in fecundity should be monitored regularly. This would

improve stock reproductive indexes and increase our understanding of the processes affecting reproductive success. Our results suggest that developing a better understanding of how maternal effects impact on offspring quality may help to understand recruitment processes, enhance stock assessment models, and ultimately improve our capacity to achieve a sustainable fisheries management.

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REFERENCES

- Alonso-Fernández, A., Vallejo, A. C., Saborido-Rey, F., et al. 2009. Fecundity estimation of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) of Georges Bank: Application of the autodiometric method. *Fish. Res.* 99: 47-54.
<https://doi.org/10.1016/j.fishres.2009.04.011>
- Anderson C.N.K., Hsieh C.H., Sandin S.A. et al. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452: 835-839.
<https://doi.org/10.1038/nature06851>
- Armstrong M.J., Witthames P.R. 2012. Developments in understanding of fecundity of fish stocks in relation to egg production methods for estimating spawning stock biomass. *Fish. Res.* 117/118: 35-47.
<https://doi.org/10.1016/j.fishres.2010.12.028>
- Berkeley S.A., Bobko S.J. 2004. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fish. Bull.* 102: 418-429.
- Beyer S.G., Sogard S.M., Harvey C. J., Field J.C. 2015. Variability in rockfish (*Sebastes* spp.) fecundity: species contrasts, maternal size effects, and spatial differences. *Environ. Biol. Fish.* 98: 81-100.
<https://doi.org/10.1007/s10641-014-0238-7>
- Blanchard J.L., Frank K.T., Simon J.E. 2003. Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci.* 60: 321-332.
<https://doi.org/10.1139/f03-024>
- Brown-Peterson N.J., Wyanski D.M., Saborido-Rey F., et al. 2011. A standardized terminology for describing reproductive development in fishes. *Mar. Coast. Fish.* 3: 52-70.
<https://doi.org/10.1080/19425120.2011.555724>
- Brooks M. E., Kristensen K., van Benthem K. J., et al. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9: 378-400.
<https://doi.org/10.32614/RJ-2017-066>
- Chang H. Y., Richards R. A., Chen Y. 2021. Effects of environmental factors on reproductive potential of the Gulf of Maine northern shrimp (*Pandalus borealis*). *GECCO* 30: e01774.
<https://doi.org/10.1016/j.gecco.2021.e01774>
- Cheung W. Lam W. L., Sarmiento V.W.Y., et al. 2009. Projecting global marine biodiversity impacts under climate Change scenarios. *Fish Fish.* 10: 235-251.
<https://doi.org/10.1111/j.1467-2979.2008.00315.x>
- Colbourne E., Perez-Rodriguez A., Cabrero A., Gonzalez-Nuevo G. 2018. Ocean Climate Variability on the Flemish Cap in NAFO Subdivision 3M during 2017 June.
- Dick E. J. 2009. University of California Santa Cruz modeling the reproductive potential of rockfishes, 299 pp.
- Dominguez-Petit R., Rideout R.M., Garabana D., et al. 2018. Evaluating the use of the autodiometric method for estimating fecundity of *Reinhardtius hippoglossoides*, a species with an unusual oocyte development strategy. *ICES J. Mar. Sci.* 75: 831-839.
<https://doi.org/10.1093/icesjms/fsx162>
- Fisher R., Sogard S.M., Berkeley S.A. 2007 Trade-offs between size and energy reserves reflect alternative strategies for optimizing larval survival potential in rockfish. *Mar. Ecol. Prog. Ser.* 344: 257-270.
<https://doi.org/10.3354/meps06927>
- Friedland K.D., Ama-Abasi D., Manning M., et al. 2005. Automated egg counting and sizing from scanned images: Rapid sample processing and large data volumes for fecundity estimates. *J. Sea. Res.* 54: 307-316.
<https://doi.org/10.1016/j.seares.2005.06.002>
- Hsieh C.H., Reiss C.S., Hunter J.R., et al. 2006. Fishing elevates variability in the abundance of exploited species. *Nature* 443: 859-862.
<https://doi.org/10.1038/nature05232>
- González-Troncoso D., Garrido I. Rábade S., et al. 2022. Results from Bottom Trawl Survey on Flemish Cap of June-July 2021. NAFO SCR Doc. 22/004.
- Kennedy J., Witthames P.R., Nash R.D.M. 2007. The concept of fecundity regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning populations. *Can. J. Fish. Aquat. Sci.* 64: 587-601.
<https://doi.org/10.1139/f07-034>
- Kraus G., Müller A., Trella K., Köster F.W. 2000. Fecundity of Baltic cod: Temporal and spatial variation. *J. Fish. Biol.* 56: 1327-1341.
<https://doi.org/10.1111/j.1095-8649.2000.tb02146.x>
- Kraus G., Tomkiewicz J., Köster F.W. 2002. Egg production of Baltic cod (*Gadus morhua*) in relation to variable sex ratio, maturity, and fecundity. *Can. J. Fish. Aquat. Sci.* 59:1908-1920.
<https://doi.org/10.1139/f02-159>
- Lambert Y. 2008). Why should we closely monitor fecundity in marine fish populations? *J. Northwest. Atl. Fish. Soc.* 41: 93-106.
<https://doi.org/10.2960/J.v41.m628>
- Lambert Y., Yaragina N. A., Kraus G., et al. 2003. Using environmental and biological indices as proxies for egg and larval production of marine fish. *J. Northwest. Atl. Fish. Soc.* 33: 115-159.
<https://doi.org/10.2960/J.v33.a7>
- Marteinsdottir G., Begg G. A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 235: 235-256.
<https://doi.org/10.3354/meps235235>
- Marteinsdottir G., Thorarinnsson K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Can. J. Fish. Aquat. Sci.* 55: 1372-1377.
<https://doi.org/10.1139/f98-035>
- McElroy W.D., Wuenschel M.J., Press Y.K., et al. 2013. Differences in female individual reproductive potential among three stocks of winter flounder, *Pseudopleuronectes americanus*. *J. Sea. Res.* 75: 52-61.
<https://doi.org/10.1016/j.seares.2012.05.018>
- Mion M., Thorsen A., Vitale F., et al. 2018. Effect of fish length and nutritional condition on the fecundity of distressed Atlantic cod *Gadus morhua* from the Baltic Sea. *J. Fish. Biol.* 92: 1016-1034.
<https://doi.org/10.1111/jfb.13563>
- Murua H., Saborido-Rey F. 2003. Female Reproductive Strategies of Marine Fish Species of the North Atlantic. *J. Northwest. Atl. Fish. Soc.* 33: 23-31.
<https://doi.org/10.2960/J.v33.a2>
- Nichol D.G., Acuna E.I. 2001. Annual and batch fecundities of yellow fin sole, *Limanda aspera*, in the Eastern Bering Sea. *Fish. Bull. U.S.* 99: 108-122.
- R Core Team. 2020 R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rideout R.M., Morgan M.J. 2010. Relationships between maternal body size, condition and potential fecundity of four northwest Atlantic demersal fishes. *J. Fish. Biol.* 76: 1379-1395.
<https://doi.org/10.1111/j.1095-8649.2010.02570.x>

- Román S., Weidberg N., Muñiz C., et al. 2022. Mesoscale patterns in barnacle reproduction are mediated by upwelling-driven thermal variability. *Mar. Ecol. Prog. Ser.* 685: 153-170.
<https://doi.org/10.3354/meps13992>
- Saborido-Rey F., Domínguez-Petit R., Garabana D., Sigurðsson Þ. 2015. Fecundity of *Sebastes mentella* and *Sebastes norvegicus* in the Irminger Sea and Icelandic waters. *Sci. Mar.*, 41: 107-124.
<https://doi.org/10.7773/cm.v41i2.2500>
- Saborido-Rey F., Trippel E.A. 2013. Fish reproduction and fisheries. *Fish. Res.* 138: 1-4.
<https://doi.org/10.1016/j.fishres.2012.11.003>
- Sogard S. M., Berkeley S.A., Fisher R. 2008. Maternal effects in rockfishes *Sebastes* spp.: A comparison among species. *Mar. Ecol. Prog. Ser.* 360: 227-236.
<https://doi.org/10.3354/meps07468>
- Stafford D.M., Sogard S.M., Berkeley S.A. 2014. Maternal influence on timing of parturition, fecundity, and larval quality in three shelf rockfishes (*Sebastes* spp.). *Aquat. Biol.* 21: 11-24.
<https://doi.org/10.3354/ab00564>
- Thorsen A., Kjesbu O.S. 2001. A rapid method for estimation of oocyte size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. *J. Sea. Res.* 46: 295-308.
[https://doi.org/10.1016/S1385-1101\(01\)00090-9](https://doi.org/10.1016/S1385-1101(01)00090-9)
- Thorsen A., Marshall C.T., Kjesbu O.S. 2006. Comparison of various potential fecundity models for north-east Arctic cod *Gadus morhua*, L. using oocyte diameter as a standardizing factor. *J. Sea. Res.* 69: 1709-1730.
<https://doi.org/10.1111/j.1095-8649.2006.01239.x>
- Tomkiewicz J., Morgan M.J., Burnett J. Saborido-Rey F. 2003. Available information for estimating reproductive potential of northwest Atlantic groundfish stocks. *J. Northwest. Atl. Fish. Soc.* 33: 1-21
<https://doi.org/10.2960/J.v33.a1>
- Witthames P.R., Thorsen A., Murua H., et al. 2009. Advances in methods for determining fecundity: application of the new methods to some marine fishes. *Fish. Bull.* 107: 148-164.
- Yoneda M., Wright P.J. 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. *Mar. Ecol. Prog. Ser.* 276: 237-248.
<https://doi.org/10.3354/meps276237>
- Zuur A.F., Ieno E.N. 2013. Mixed effects Models and Extensions in Ecology with R. In *Journal of Chemical Information and Modeling*. 53(9).

SUPPLEMENTARY MATERIAL

Table S1. – Selection of random effects for GLMM fitted with potential fecundity as a dependent variable. First, optimal random effects were tested. The covariates in all models (i.e. fixed structure) are the maternal traits length/age, condition factor (K), gonadosomatic index (GSI) and sea bottom temperature.

Model	Fixed effects	Random effects	AIC	BIC	logLik	P-value
1	Length, K, GSI, Btm temperature	Year	3860.1	3882.6	–1923.0	0.2532
2	Length, K, GSI, Btm temperature	Year and Haul	3860.8	3886.6	–1922.4	
3	Age, K, GSI, Btm temperature	Year	3769.4	3791.7	–1877.7	
4	Age, K, GSI, Btm temperature	Year and Haul	3761.4	3786.9	–1872.7	<0.001

Table S2. – Selection of random effects with potential fecundity as a dependent variable. First, optimal random effects were tested AIC, Akaike information criterion. Note: The covariates in all these models (i.e. the fixed structure) are the fork length, condition factor (K), gonadosomatic index (GSI) and bottom temperature. The Δ AIC of random intercept and slope model is lower compared with random intercepts. However, the likelihood ratio test was performed to compare models.

Model	Random effects	Correlation	Parameters	AIC	Δ AIC
1	Year intercept and bottom temperature slope by year	None	10	3852.178	0
2	Intercept varying between Year and Haul	None	8	3916.77	71.72

Table S3. Summary of the multiple regression models for potential fecundity against length and interannual variation (years) of *S. fasciatus* on the Flemish Cap bank. GLM NB, negative binomial generalized linear.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(> z)	Post hoc Tukey HSD test																			
GLM NB Potential fecundity	α	0.62	6.340897	0.222047	28.557	<0.001	1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019	
	Length		0.122727	0.006775	18.116	<0.001	1996																			
	1997		0.366615	0.14684	2.497	<0.05	1997	0.5864																		
	1998		0.073197	0.195804	0.374	0.708533	1998	1	0.9964																	
	1999		0.353864	0.154717	2.287	<0.05	1999	0.7438	1	0.9986																
	2000		0.458608	0.138183	3.319	<0.001	2000	0.1001	1	0.9175	1															
	2001		0.324362	0.121439	2.671	<0.01	2001	0.45	1	0.9983	1	0.9999														
	2002		0.155521	0.211627	0.735	0.46241	2002	1	1	1	1	0.9971	1													
	2004		0.194977	0.143856	1.355	0.175303	2004	0.9987	0.9999	1	1	0.9431	1	1												
	2005		0.235417	0.119544	1.969	<0.05	2005	0.9151	1	1	1	0.9317	1	1	1											
	2006		0.181792	0.146795	1.238	0.215567	2006	0.9996	0.9997	1	1	0.9335	0.9999	1	1	1										
	2008		-0.065257	0.194633	-0.335	0.737413	2008	1	0.8166	1	0.8812	0.4011	0.8297	1	0.999	0.9827	0.9996									
	2010		0.710836	0.173143	4.105	<0.001	2010	<0.01	0.926	0.3023	0.9249	0.9955	0.624	0.6866	0.2605	0.2081	0.2477	<0.05								
	2011		0.1821	0.238438	0.764	0.445034	2011	1	1	1	1	0.9998	1	1	1	1	1	0.8806								
	2013		0.24921	0.145613	1.711	0.086997	2013	0.9779	1	1	1	0.995	1	1	1	1	1	0.9896	0.4781	1						
	2014		0.190639	0.148449	1.284	0.19907	2014	0.9994	0.9999	1	1	0.9435	1	1	1	1	1	0.9993	0.2726	1	1					
	2015		-0.075086	0.169813	-0.442	0.65837	2015	1	0.5489	1	0.6688	0.1103	0.5179	1	0.9907	0.8878	0.9963	1	<0.01	1	0.9298	0.9925				
	2016		0.055175	0.129799	0.425	0.670775	2016	1	0.7361	1	0.867	0.1195	0.6011	1	1	0.9796	1	1	<0.01	1	0.9961	1	1			
	2018		0.054424	0.120708	0.451	0.652079	2018	1	0.609	1	0.7875	<0.05	0.3842	1	0.9999	0.9351	1	1	<0.01	1	0.9889	0.9999	1	1		
	2019		0.039704	0.144431	0.275	0.783391	2019	1	0.8029	1	0.895	0.1845	0.7658	1	1	0.9906	1	1	<0.05	1	0.9961	1	1	1	1	
	2020		0.241787	0.142364	1.698	0.089438	2020	0.9796	1	1	1	0.9886	1	1	1	1	1	0.9907	0.4066	1	1	1	0.9258	0.9962	0.9875	0.9958

Table S4. Summary of the multiple regression models for potential fecundity against age and interannual variation (years) of *S. fasciatus* on the Flemish Cap bank. GLM NB, negative binomial generalized linear model.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(> z)	Post hoc Test TukeyHSD																			
GLM NB	α	0.61	8.999869	0.114758	78.425	<0.001	1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019	
Potential fecundity	Age		0.111031	0.006379	17.407	<0.001	1996																			
	1997		0.232985	0.153979	1.513	0.1303	1997	0.9946																		
	1998		-0.342318	0.197644	-1.732	0.0833	1998	0.9749	0.3556																	
	1999		0.096701	0.158439	0.61	0.5416	1999	1	1	0.8563																
	2000		0.35734	0.141687	2.522	<0.05	2000	0.5665	1	0.0472	0.9791															
	2001		-0.065619	0.127014	-0.517	0.6054	2001	1	0.8079	0.9956	0.9999	0.0583														
	2002		-0.357145	0.216111	-1.653	0.0984	2002	0.9849	0.4551	1	0.894	0.0868	0.9973													
	2004		-0.127733	0.164081	-0.778	0.4363	2004	1	0.8501	1	0.9993	0.1961	1	1												
	2005		-0.205216	0.124054	-1.654	0.0981	2005	0.9847	0.1052	1	0.8033	<0.001	0.9981	1	1											
	2006		-0.193367	0.150191	-1.287	0.1979	2006	0.9993	0.4337	1	0.9658	<0.05	1	1	1	1										
	2008		-0.280005	0.198942	-1.407	0.1593	2008	0.9978	0.5785	1	0.9602	0.1126	0.9999	1	1	1	1									
	2010		0.71477	0.176272	4.055	<0.001	2010	<0.01	0.4841	<0.001	0.1042	0.8706	<0.001	<0.001	<0.01	<0.001	<0.001	<0.01								
	2011		0.13418	0.24261	0.553	0.5802	2011	1	1	0.9777	1	1	1	0.98	1	0.9958	0.9989	0.9953	0.7905							
	2013		-0.023449	0.151732	-0.155	0.8772	2013	1	0.9867	0.9919	1	0.4446	1	0.9937	1	0.9969	0.9999	0.9994	<0.01	1						
	2014		0.007224	0.153278	0.047	0.9624	2014	1	0.9976	0.9787	1	0.6505	1	0.9841	1	0.9852	0.9993	0.9975	0.0143	1	1					
	2015		-0.068408	0.17366	-0.394	0.6936	2015	1	0.9803	0.9996	1	0.5198	1	0.9996	1	1	1	1	0.0118	1	1	1				
	2016		-0.26184	0.145587	-1.799	0.0721	2016	0.9632	0.1171	1	0.7322	<0.001	0.9911	1	1	1	1	1	<0.001	0.9852	0.9843	0.9561	0.9998			
	2018		-0.195491	0.12706	-1.539	0.1239	2018	0.9933	0.1348	1	0.8472	<0.001	0.9994	1	1	1	1	1	<0.001	0.9971	0.9981	0.9902	1	1		
	2019		-0.149036	0.150588	-0.99	0.3223	2019	1	0.6043	1	0.9925	<0.05	1	1	1	1	1	1	<0.001	0.9998	1	1	1	1	1	
	2020		0.170095	0.146018	1.165	0.2441	2020	0.9998	1	0.5308	1	0.9985	0.9407	0.6135	0.95	0.1628	0.624	0.7413	0.1765	1	0.9988	0.9999	0.9972	0.1732	0.1774	0.7412

Table S5. – Summary of the multiple regression models for relative fecundity against length and interannual variation (years) of *S. fasciatus* in Flemish Cap bank. GLM NB, negative binomial generalized linear model.

Response variable	Vari-able	R2	Parameter estimate	SE	z value	Pr(> z)	Post hoc Tukey HSD test																						
GLM NB Relative fecundity	a	0.22	3.004153	0.216123	13.9	<0.001	1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019				
	Length		0.034865	0.006489	5.373	<0.001	1996																						
	1997		0.32001	0.142844	2.24	<0.05	1997	0.7753																					
	1998		0.081475	0.191604	0.425	0.67067	1998	1	0.9996																				
	1999		0.42751	0.149608	2.858	<0.01	1999	0.3167	1	0.9734																			
	2000		0.439153	0.134197	3.272	<0.01	2000	0.1143	1	0.9397	1																		
	2001		0.3693	0.119615	3.087	<0.01	2001	0.1872	1	0.9862	1	1																	
	2002		0.191255	0.204729	0.934	0.35021	2002	1	1	1	0.9999	0.9996	1																
	2004		0.195788	0.14048	1.394	0.1634	2004	0.9981	1	1	0.9921	0.9549	0.9964	1															
	2005		0.276552	0.117999	2.344	<0.05	2005	0.7036	1	0.9999	0.9998	0.9957	1	1	1														
	2006		0.19001	0.143549	1.324	0.18562	2006	0.999	1	1	0.9919	0.9593	0.9962	1	1	1													
	2008		0.02129	0.18925	0.112	0.91043	2008	1	0.9915	1	0.8667	0.7468	0.9022	1	1	0.9959	1												
	2010		0.743227	0.165104	4.502	<0.001	2010	<0.001	0.5465	0.1649	0.9545	0.9294	0.5517	0.596	0.0946	0.1384	0.1033	0.0603											
	2011		0.170889	0.228625	0.747	0.45478	2011	1	1	1	0.9999	0.9997	1	1	1	1	1	1	0.6958										
	2013		0.177755	0.141809	1.253	0.21003	2013	0.9995	1	1	0.9822	0.9084	0.9905	1	1	1	1	1	0.0682	1									
	2014		0.165809	0.144438	1.148	0.25099	2014	0.9999	1	1	0.9757	0.8904	0.9858	1	1	1	1	1	0.0636	1	1								
	2015		-0.067009	0.165361	-0.405	0.68531	2015	1	0.7113	1	0.293	0.1153	0.2624	0.9999	0.9889	0.6994	0.9939	1	<0.001	1	0.9942	0.9975							
	2016		0.180599	0.13871	1.302	0.19292	2016	0.9992	1	1	0.9809	0.9012	0.9885	1	1	1	1	1	0.0617	1	1	1	0.9925						
	2018		0.062649	0.118983	0.527	0.59851	2018	1	0.8342	1	0.311	<0.05	0.107	1	0.9999	0.6855	1	1	<0.001	1	1	1	1						
	2019		-0.017752	0.140948	-0.126	0.89977	2019	1	0.6719	1	0.2193	<0.05	0.1335	1	0.9933	0.5875	0.9971	1	0.0005	1	0.997	0.999	1	0.9957	1				
	2020		0.183641	0.138597	1.325	0.18517	2020	0.999	1	1	0.9823	0.8973	0.9907	1	1	1	1	1	0.0612	1	1	1	0.989	1	0.9999	0.9926			

Table S6. – Summary of the multiple regression models for relative fecundity against age and interannual variation (years) of *S. fasciatus* on the Flemish Cap bank. GLM NB, negative binomial generalized linear model.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(> z)	Post hoc Test TukeyHSD																									
GLM NB Relative fecundity	<i>α</i>	0.34	3.609169	0.1034872	34.875	<0.001	1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019							
	Age		0.0493357	0.0054966	8.976	<0.001	1996																									
	1997		0.2150357	0.1351951	1.591	0.11171	1997	0.9902																								
	1998		-0.0407179	0.1752052	-0.232	0.81623	1998	1	0.9973																							
	1999		0.2960636	0.1384885	2.138	<0.05	1999	0.8373	1	0.9503																						
	2000		0.3222687	0.1243912	2.591	<0.01	2000	0.5122	1	0.8457	1																					
	2001		0.2021966	0.1129256	1.791	0.07337	2001	0.9648	1	0.9954	1	0.9998																				
	2002		-0.0319896	0.1893652	-0.169	0.86585	2002	1	0.9993	1	0.98	0.9271	0.999																			
	2004		0.0848131	0.1439403	0.589	0.55571	2004	1	1	1	0.9976	0.9705	1	1																		
	2005		0.072853	0.1106353	0.658	0.51022	2005	1	0.9995	1	0.9364	0.5641	0.995	1	1																	
	2006		0.027246	0.1329194	0.205	0.83759	2006	1	0.9983	1	0.9285	0.6846	0.9937	1	1	1																
	2008		-0.0910626	0.1751269	-0.52	0.60308	2008	1	0.9755	1	0.8263	0.6161	0.958	1	1	1	1															
	2010		0.6991852	0.151583	4.613	<0.001	2010	<0.001	0.1671	<0.05	0.5345	0.4987	<0.05	<0.05	<0.05	<0.001	<0.001	<0.001														
	2011		0.0835729	0.2104391	0.397	0.69127	2011	1	1	1	1	0.9998	1	1	1	1	1	1	0.3842													
	2013		-0.0265995	0.133847	-0.199	0.84247	2013	1	0.9639	1	0.7002	0.3061	0.8885	1	1	1	1	1	<0.001	1												
	2014		-0.0008873	0.1349319	-0.007	0.99475	2014	1	0.9907	1	0.8399	0.4958	0.968	1	1	1	1	1	<0.001	1	1											
	2015		-0.1920493	0.1533378	-1.252	0.2104	2015	0.9995	0.4671	1	0.1697	<0.05	0.2738	1	0.9753	0.8946	0.997	1	<0.001	0.9996	0.9999	0.9994										
	2016		-0.0404102	0.1310346	-0.308	0.75778	2016	1	0.9274	1	0.5898	0.2039	0.7903	1	1	1	1	1	<0.001	1	1	1	1									
	2018		-0.1300531	0.1132962	-1.148	0.25101	2018	0.9999	0.2212	1	<0.05	<0.001	<0.05	1	0.9724	0.5959	0.9979	1	<0.001	0.9999	1	0.9998	1	1								
	2019		-0.2279436	0.1329839	-1.714	0.08652	2019	0.9775	0.0939	1	<0.05	<0.001	<0.05	1	0.7757	0.316	0.9216	1	<0.001	0.9951	0.9878	0.9666	1	0.9935	1							
	2020		0.0453156	0.1286718	0.352	0.7247	2020	1	0.9992	1	0.9414	0.6756	0.9962	1	1	1	1	1	<0.01	1	1	1	0.9848	1	0.9741	0.7477						

Spawning area of the tropical Skipjack Tuna, *Katsuwonus pelamis* (Scombridae), in the western Mediterranean Sea

Miguel Angel Puerto¹, Samar Saber^{1,2}, José María Ortiz de Urbina¹, María José Gómez-Vives¹,
Salvador García-Barcelona¹, David Macías¹

¹ Centro Oceanográfico de Málaga, Instituto Español de Oceanografía, (IEO-CSIC), Puerto pesquero s/n, 29640 Fuengirola, Málaga, Spain.

(P-MA) (Corresponding autor) E-mail: mapuerto@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0003-4937-1569>

(OU) E-mail: urbina@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0002-9525-6783>

(GV_MJ) E-mail: maco.gomez@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0002-2108-8685>

(GB-S) E-mail: salvador.g.barcelona@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0002-5747-582X>

(MD) E-mail: david.macias@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0003-3054-2858>

² Centro Oceanográfico de Murcia, Singular Scientific and Technical Infrastructure for Atlantic Bluefin Tuna Aquaculture, ICTS-ICAR (IEO-CSIC), Ctra. de La Azohía s/n, 30860 Puerto de Mazarrón, Murcia, Spain.

(SS) E-mail: samar.saber@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0002-3863-2949>

Summary: Skipjack is an important commercial species with a tropical distribution, although captures in the Mediterranean Sea have been recorded for decades. The western Mediterranean Sea, specifically the Balearic Sea, is a spawning area for several tuna species. We hypothesized that the western Mediterranean warming in the last few decades could lead to the expansion of skipjack tuna spawning areas from tropical areas to the Mediterranean Sea. We analysed 454 individuals (41.8–81 cm straight fork length) caught by sport fishing vessels in offshore trolling championships in Spanish Mediterranean waters during summer months from 2014 to 2019. Analysis of the gonadosomatic index and microscopic examination of the ovaries (n=192) showed that the skipjack is reproductively active in the western Mediterranean, particularly in the Balearic Sea. These results indicate that the skipjack has expanded its distribution and spawning area from tropical waters to the Mediterranean, probably owing to the gradual warming detected in the area in the last few decades. This new spawning activity in the area should be monitored in the near future to study the possible impact on other tuna species that share the distribution range and spawning area with skipjack tuna in the western Mediterranean.

Keywords: Skipjack; reproductive biology; spawning season; sexual maturity; gonadosomatic index; Mediterranean.

Área de puesta del listado, *Katsuwonus pelamis* (Scombridae), en el Mediterráneo occidental

Resumen: El listado (*Katsuwonus pelamis*) es una especie muy importante a nivel comercial. Aunque su distribución es tropical, desde hace décadas se registran capturas en el Mediterráneo. El Mediterráneo occidental, concretamente el mar Balear, es zona de puesta de varias especies de túnidos. Este trabajo planteó la hipótesis de que el calentamiento registrado en las últimas décadas en el Mediterráneo occidental podría producir la expansión de las áreas de puesta del Listado desde las zonas tropicales hasta el mar Mediterráneo. Analizamos 454 ejemplares (41,8–81 cm SFL) capturados por embarcaciones de pesca recreativa en campeonatos de curricán de altura durante los meses de verano de 2014 a 2019 en aguas del Mediterráneo español. El análisis del Índice Gonadosomático y el análisis microscópico de los ovarios (n=192) mostraron que la especie es reproductivamente activa en el Mediterráneo occidental, particularmente en el mar Balear. Estos resultados indican que el Listado ha ampliado su área de distribución y puesta desde aguas tropicales hasta el Mediterráneo, probablemente debido al calentamiento gradual detectado en la zona en las últimas décadas. Además, es de interés realizar un seguimiento de esta nueva actividad de puesta en un futuro próximo para estudiar el posible impacto sobre otras especies de túnidos con las que comparte tanto área de distribución como zona de puesta en el Mediterráneo occidental.

Palabras clave: atún listado; biología reproductiva; época de puesta; madurez sexual; índice gonadosomático; Mediterráneo.

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INTRODUCTION

The skipjack tuna *Katsuwonus pelamis* (Linnaeus, 1758), hereafter referred to as SKJ, is a cosmopolitan, migratory species distributed in tropical and subtropical waters of all oceans, including the Mediterranean Sea. Its geographical limits are 55–60°N and 45–50°S and it is more abundant in the equatorial region throughout the year (Collete and Nausen 1983, Matsu-moto et al. 1984). The SKJ is a commercially important species, being the third species in terms of captures for the eleventh consecutive year, with 2.8 million t in 2020 (FAO 2022). Its catches in the Mediterranean Sea are common, especially in recent decades. In the western Mediterranean Sea, the first catches were recorded in 1968, and the average landing of the last six years (2015–2020) is 168 t (ICCAT 2021). The main Spanish catches come from the traps located in Ceuta (Strait of Gibraltar) and longline surface fisheries targeting albacore tuna. The SKJ is also caught by Spanish recreational offshore trolling fisheries in the Alboran Sea during the summer months, mainly in August and September, and in the Balearic Sea in June and July, coinciding with the reproductive season for tunas in the area (Saber et al. 2015, 2020).

The SKJ has been classified as a multiple batch spawner fish with asynchronous oocyte development (Goldberg and Au 1986, Schaefer 2001a, Grande et al. 2012). Its reproductive potential is considered high because it reaches sexual maturity at around one year of age and spawns opportunistically throughout the year in large areas of the ocean (ICCAT 2019). Knowledge of the biology of the species is required for stock assessment, so it is important to know the reproductive characteristics and phenology of the species.

In the Atlantic Ocean SKJ spawn in two main areas: one in the western Atlantic Ocean, where it spawns over two subtropical areas off the coast of South America, and its migration is influenced by season (Andrade and Santos 2004, Benevenuti et al. 2019); and one in the eastern Atlantic Ocean, where it spawns year-round in the equatorial area, from the Gulf of Guinea to 20–30°W. In the tropical area, spawning occurs only in the warm season (Andrade and Santos 2004). In the Indian Ocean two spawning seasons have been identified, one coinciding with the northeast monsoon and one with the southwest monsoon (Stequert and Ramcharrun 1996, Grande et al. 2014). Though the Balearic Sea is an important spawning area for several tuna species (Alemany et al. 2010), there is no information about the reproduction of SKJ in the area, except for a study in which a few spawning females were recorded (Saber et al. 2012). Temperature is a very important factor determining the distribution of both adult top predators and larvae (Worm et al. 2005, Reglero et al. 2014). An increase in water temperatures before and during spawning is needed for the adult tunas to release eggs (Margulies et al. 2007). The SKJ, like other tunas, breeds at a sea surface temperature (SST) exceeding 24°C, and its spawning season varies according to locality (Cayre and Farrugio 1986, Schaefer 2001b). Geographical differences in the reproductive traits of the SKJ probably

occur because the spawning depends on oceanographic conditions (Ashida 2020), and especially on SST (Margulies et al. 2007).

Global warming will directly affect the phenology and spatial distribution of marine organisms and have indirect effects on the productivity and structure of marine ecosystems with important consequences for fisheries. Future changes in the marine environment are expected to affect the physiological rates (reproduction, growth), geographical distribution and migration of SKJ with consequences for their life history. Vargas-Yañez et al. (2010, 2019) analysed trends in different temperature time series in Spanish Mediterranean waters and found warming in intermediate, deep and surface waters from the middle of the last century. We hypothesized that the western Mediterranean warming in the last decades could lead to the expansion of skipjack tuna spawning areas from tropical areas to the Mediterranean Sea. To study the reproductive status of SKJ in the western Mediterranean, we used the gonadosomatic index, microscopic analysis of ovaries and estimates of the daily spawning fraction.

MATERIALS AND METHODS

Study areas and data collection

Specimens of SKJ were obtained from sport fishery during fishing tournaments targeting large pelagic species (mainly albacore *Thunnus alalunga*, skipjack, dolphinfish *Coryphaena hippurus* and Mediterranean spearfish *Tetrapturus belone*) from June to September 2014–2019. Sampling areas located in the western Mediterranean Sea were divided into two areas based on the oceanographic features: (i) the Balearic Sea (Area I) and (ii) the Alboran Sea (Area II) (Fig. 1). The fishing grounds extended 50 to 60 nautical miles around six base ports. Fishes were caught during daylight hours using rod and reel gear by trolling, which consists of fishing lines with hooks and artificial lures, targeting fish in surface waters between 0 and 5 m approximately.

A total of 454 SKJ were randomly collected for sampling collection. Immediately after landing, the round weight (RW, kg), the straight fork length (to the nearest 0.1 cm) and the gonad weight (GW, to the nearest g) were measured. Sex was determined by visual inspection and the sex ratio was calculated as the ratio of females to males. Assuming no systematic differences in ovarian homogeneity throughout the whole ovary, including between the two ovarian lobes (Otsu and Uchida 1959, Stequert and Ramcharrun 1995), a full cross section (2–3 cm wide) from the central part of one of the lobes was fixed in Bouin's fluid for 4 h and then preserved in 70% ethanol for later analysis.

The gonadosomatic index (GSI) was calculated as the ratio of GW to fish gonad-free weight (RW-GW) times 10². GW and RW were both measured in grams for males and females to examine monthly changes. The equation of Gibson and Ezzi (1980) was used:

$$\text{GSI} = \text{GW} / (\text{RW} - \text{GW}) \times 100$$

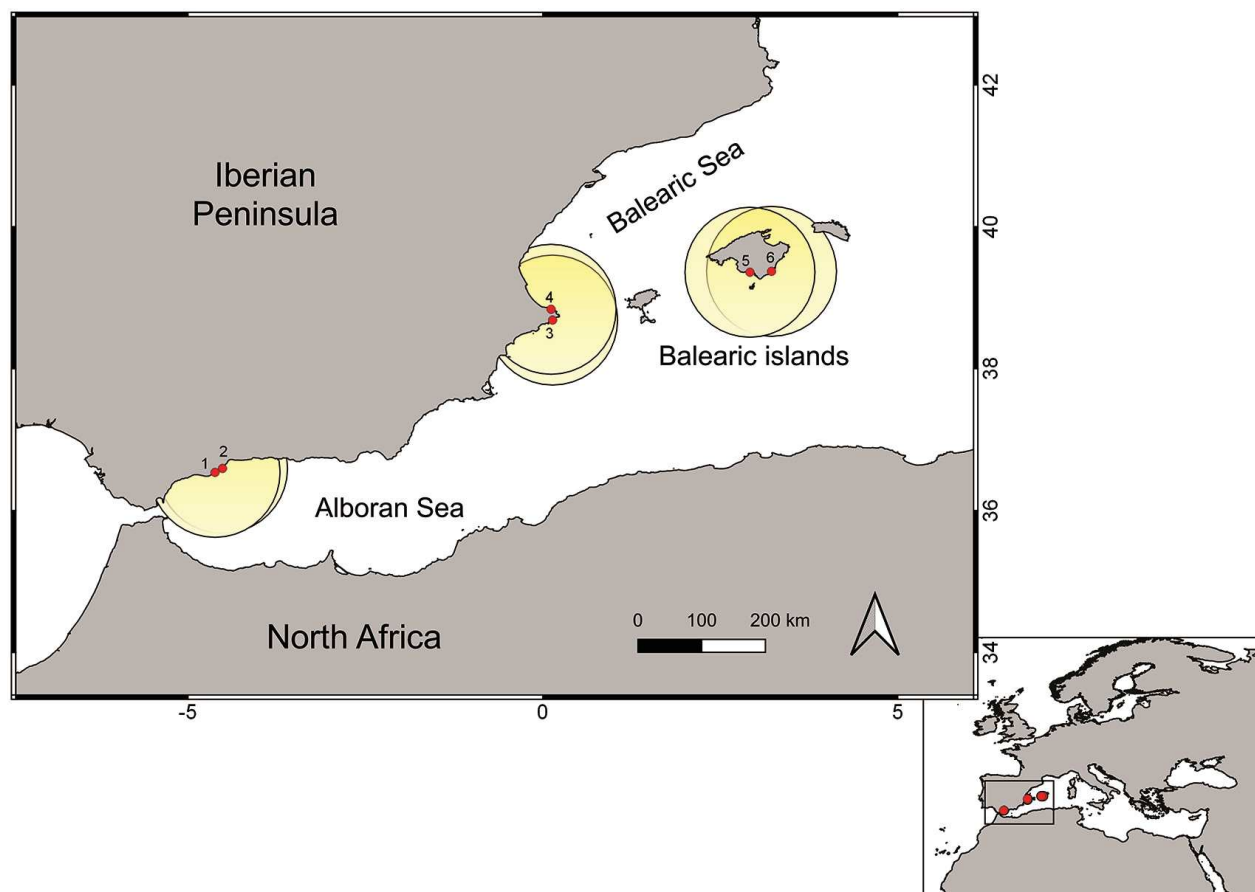


Fig. 1. – The western Mediterranean Sea showing the fishing grounds of recreational fishery (circles around the base ports) during the fishing tournaments. Base ports. Alboran Sea (Area 2): 1, Fuengirola; 2, Benalmadena. Balearic Sea (Area 1): 3, Moraira; 4, Denia; 5 S'Estanyol; 6, Cala D'Or.

An exploratory analysis showed that the relationship between GSI, length and month was non-linear, so generalized additive models (GAM) were used to model the relationships between months, specimen length and monthly means of GSI:

$$\text{GSI} = \alpha + s(\text{FL}, \text{month}) + \epsilon$$

All statistical analyses and graphs were performed using R software (R Core Team 2017). For the GAM, the *mgcv* (Wood 2017) and *ggplot2* packages were particularly useful (Wickham 2016).

Histological procedures and microscopic classification of ovaries

A sub-sample was taken from each ovary, including the area from the tunica albuginea to the ovarian lumen. These representative sub-samples were then dehydrated through increasing concentrations of ethanol series, embedded in Paraplast Plus® (paraffin), sectioned at a thickness of 10 µm and, stained with Mallory's trichrome stain. A total of 192 ovaries were analysed microscopically.

The oocytes were classified into six developmental stages using the terminology of Brown-Peterson et al. (2011) and Ashida et al. (2017): primary growth, cor-

tical alveolar, early or primary vitellogenic, advanced (secondary or tertiary) vitellogenic, germinal vesicle migration and hydrated oocytes. The microscopic maturity scale for skipjack females (Table 1) was based on a modification of the criteria of Schaefer (1998), Farley et al. (2013) and Saber et al. (2015). Each ovary was examined to record the most advanced group of oocytes, the presence of both postovulatory and atretic follicles (alpha and beta stages) and maturity markers. The maturity markers were well-defined muscle bundles and numerous Brown bodies (Farley et al. 2013) and the relative thickness of the gonad wall (Schaefer and Fuller 2019). Ovaries of mature females were classified into one of four ovarian phases, namely: developing, spawning capable, spawning and postspawning (including regressing and regenerating phases).

Data on SST come from the Earth System Research Laboratory, Physical Science Division NOAA (National Oceanic and Atmospheric Administration, www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html, Reynolds et al. 2022).

Spawning frequency

Postovulatory follicles of SKJ can be observed in the ovary for one day or less after ovulation (Schaefer and

Table 1. – Microscopic classification criteria for females based on a modification of Schaefer (1998), Farley et al. (2013) and Saber et al. (2015).

Female Maturity stage	Microscopic characteristics
1. Immature (virgin)	Only oogonia; primary growth or cortical alveolar oocytes present. No atresia. Absence of post-ovulatory follicles (POFs). Thin ovarian wall and little space between oocytes.
2. Developing	Early vitellogenic oocytes present as the most advanced group of oocytes (MAGO). Some atretic follicles may be present. Absence of POFs. Little space between oocytes.
3. Spawning capable	Advanced vitellogenic oocytes present as the MAGO. Atresia can be present. Absence of POFs.
4. Spawning	POFs present and/or migratory nucleus or hydrated oocytes present as the MAGO. Atresia, when present at all, only in limited amounts.
5a. Regressing	Cortical alveolar or early vitellogenic oocytes as the MAGO. Abundant alpha and/or beta atresia. Absence of POFs. Disorganization of ovary structures, with spaces. Thick and/or wrinkled gonad wall is observed (in some ovaries).
5b. Regenerating	Only primary growth oocytes as the MAGO or cortical alveolar oocytes present, with some spaces between oocytes. Absence of POFs. Late stages of atresia. Maturity markers. Thick and/or wrinkled gonad wall is observed (in some ovaries).

Fuller 2019). Spawning female frequency was estimated as the inverse of the spawning fraction for individuals collected in Area I. The spawning fraction was estimated following the postovulatory follicles method (Hunter and Macewicz 1985) as the ratio between the active spawning

females (females with postovulatory follicles) and the total mature active females (females whose ovaries are either in the spawning capable or spawning stage). Female mature specimens whose ovaries were reproductively inactive (regressing or regenerating) were not included.

Table 2. – Sampled individuals by year, zone, fishing sport and month in offshore trolling championships.

Year	Area	Fishing port	Month	Sampled individuals
2014	Balearic Sea	Cala D'Or	June	30
	Alboran Sea	Benalmádena	August	6
2015	Balearic Sea	S'Estanyol	June	9
		Cala D'Or	July	37
	Alboran Sea	Benalmádena	August	7
2016	Balearic Sea	Moraira	June	4
		S'Estanyol		6
		Cala D'Or	July	32
		Dénia		2
	Alboran Sea	Benalmádena	August	13
		Fuengirola	September	10
2017	Balearic Sea	S'Estanyol	June	8
			July	7
		Cala D'Or		18
	Alboran Sea	Benalmádena	August	41
		Fuengirola	September	26
2018	Balearic Sea	S'Estanyol	June	2
		Cala D'Or	July	37
	Alboran Sea	Benalmádena	August	101
		Fuengirola	September	26
2019	Balearic Sea	S'Estanyol	June	4
		Cala D'Or	July	28

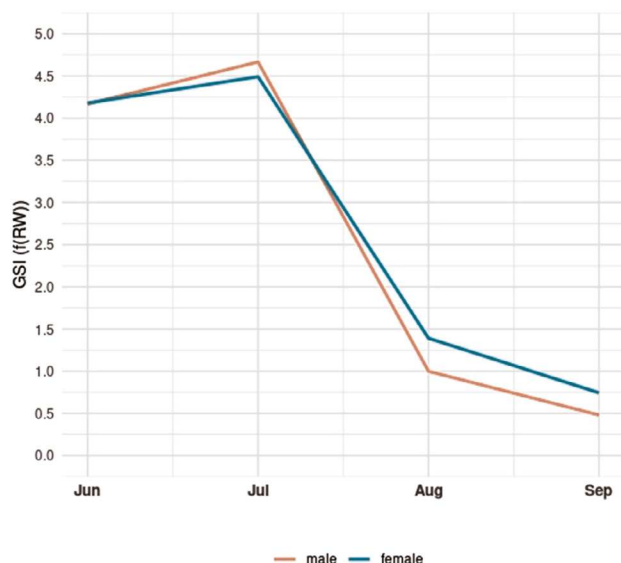


Fig. 2. – Monthly average of GSI as a function of round weight (RW): females (blue line) and males (red line).

RESULTS

Between 2014 and 2019 we attended a total of 21 sport fishing championships. A total of 224 SKJ were sampled in the Balearic Sea (Area I) and 230 in the Alboran Sea (Area II). For more detail of the number of individuals sampled per year, month or fishing port, see Table 2.

The straight fork length of 233 females ranged between 41.8 and 76 cm (mean \pm sd=61.5 \pm 6.2 cm) and the weight between 9.6 and 1.54 kg (5.4 \pm 1.7 kg). The sizes of 221 males ranged between 46.5 and 81 cm (61.2 \pm 6.3 cm) and the weight between 2.1 and 12.1 kg (5.4 \pm 1.8 kg). The sex ratio was 1:0.98 (F:M). Females were more abundant than males in the study sample. However, using a binomial test we concluded that there were no significant differences in the population analysed ($p=0.6057$, $p>0.05$). The SKJ belonging to Area I were slightly larger than those in Area II in both size (65.2 \pm 5.1 cm versus 57.7 \pm 5.0 cm) and weight (6.5 \pm 1.5 kg vs 4.3 \pm 1.3 kg).

We used total weight to calculate the GSI. The Balearic Sea samples had the highest mean GSI values (4.46 \pm 1.04 vs 1.04 \pm 0.66). In general, females always showed slightly higher values than males (2.81 \pm 1.8 vs 2.64 \pm 2.04). The highest GSI value for females was 7.82 (56.5 cm, 4.3 kg) and that for males was 7.44 (67 cm, 6.8 kg), both found in spawning individuals sampled in July in Balearic waters.

The mean monthly GSI was calculated for both males and females (Fig. 2). In June, a slight increase was observed until the maximum was reached at the beginning of July. After that date, the mean GSI decreased rapidly until it reached the minimum values in September. The monthly evolution showed a similar trend in both sexes, suggesting that the spawning season for SKJ in western Mediterranean occurs between June and August. Mean GSI showed an increasing

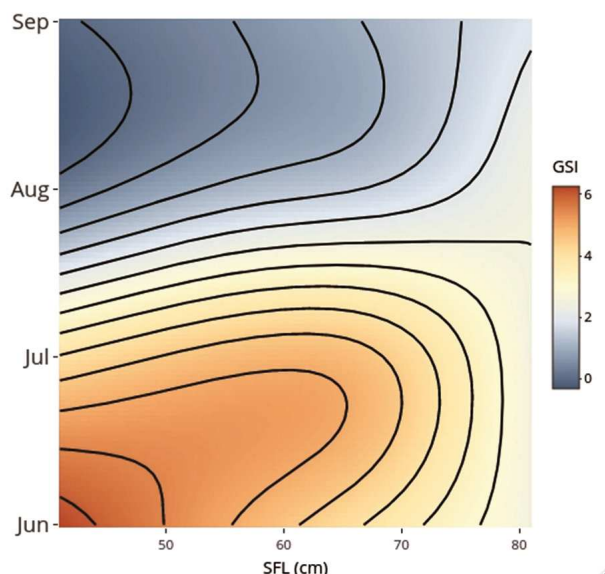


Fig. 3. – Contour plot of the fitted GAM for the GSI as a function of months and size. Straight fork length on the x-axis, month on the y-axis and the response values (GSI) given by the isolines (gray colour indicates the lowest and orange the highest GSI values).

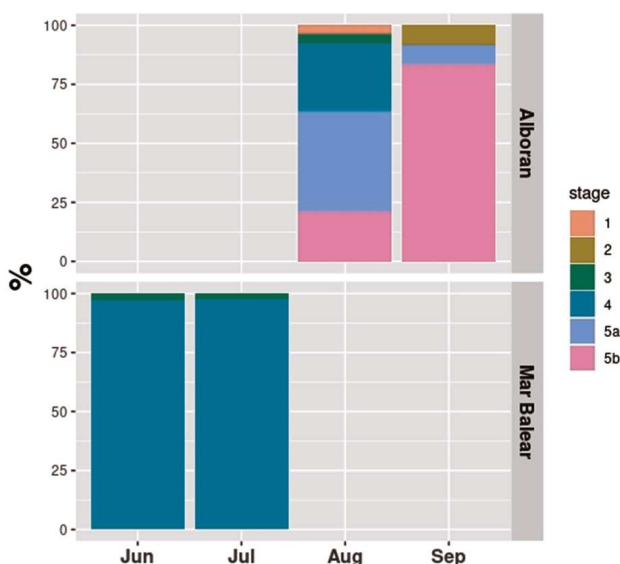


Fig. 4. – Monthly relative frequency of ovarian stages found by microscopic examination in the Alboran Sea and the Balearic Sea.

trend during the maturation progress. The immature females showed the lowest GSI values, followed by developing and postspawning ones. The spawning capable females followed by spawning females showed the highest values. The GAM analysis (Fig. 3) revealed that larger-sized individuals showed the highest GSI values in June and July and the lowest in August and September.

The monthly frequencies of gonad stages by area are shown in Figure 4. Regarding the ovaries analysed, 76 females belonged to fishing championships in the Alboran Sea and 116 to ones in the Balearic Sea. The majority ($n=113$) of the samples from the Balearic Sea

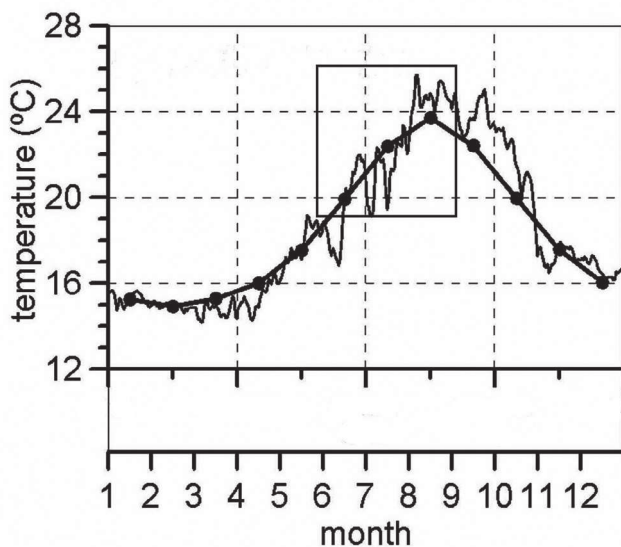


Fig. 5. – Mean daily SST for the northern zone of the Alboran Sea in 2018 and monthly mean values for the period 1981-2021 (line with points). The rectangle highlights the biological sample (June to September).

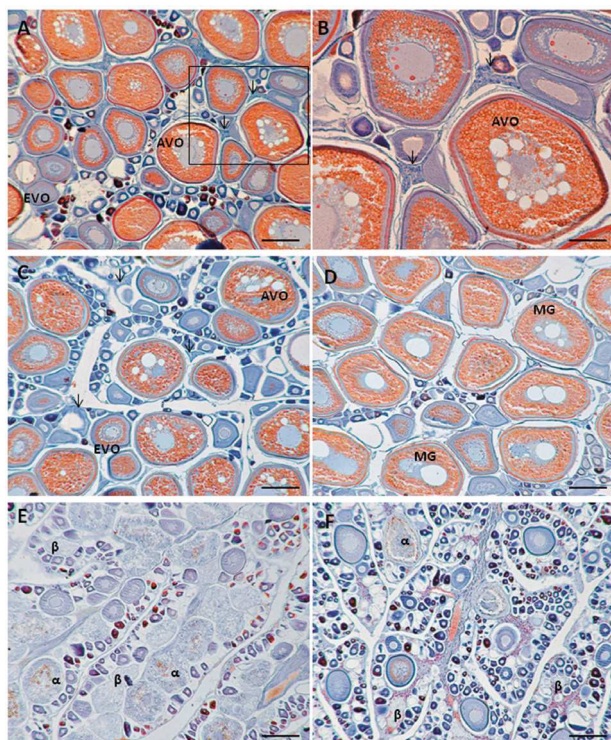


Fig. 6. – Microphotographs of spawning females. A. Ovary with early (EVO) and advanced (AVO) vitellogenic oocytes; arrows point to postovulatory follicles. B. Squared area in A, detail of postovulatory follicles (arrows show POFs) and AVOs. C. Ovary with vitellogenic oocytes and POFs. D. Ovary with migratory oocyte nucleus (MG). E and F. Ovary in regression after spawning, α and β atresia. Bar on images A, C, D and F=250 μ m and on image B=100 μ m.

were spawning females and the rest were spawning capable. We consistently found spawning females in the Balearic Sea throughout the study period. The ovaries collected in the Alboran Sea showed greater variability

in all possible gonad stages: two immature individuals, two specimens in the developing stage, two in the spawning capable stage, 15 in the spawning stage, 24 in the regressing stage and 31 in the regenerating stage. In 2018 all spawning capable and spawning females were captured in the Benalmadena sport fishing championship. This unusual episode was recorded for the first time.

Figure 5 shows the mean daily SST in 2018 for northern zone of the Alboran Sea (5°W to 2°W and 36.4°N to 37°N) and the monthly mean values for the period 1981-2021. A few days before the sport championship, an SST peak occurred there (25.4°C), with higher temperatures than expected for these dates ($23.7 \pm 0.94^{\circ}\text{C}$).

Figure 6 shows microphotographs of ovaries in spawning and postspawning phases, confirming the reproduction of the species in the western Mediterranean. The spawning female fraction calculated considering the proportion of spawning females ($n=116$) to all active females ($n=119$, that is, the spawning capable and spawning stages) was 0.97, and the mean spawning frequency was 1.03 days. Therefore, SKJ from the Balearic Sea are capable of spawning every day.

DISCUSSION

Though the SKJ is of great economic importance and several studies have been carried out on it worldwide, there is a lack of knowledge about its biology and migrations in the Mediterranean Sea.

An upward trend in the CPUE of SKJ was observed in the Balearic Sea, where the specimens caught were slightly larger than in the Alboran Sea. Catches in the Alboran Sea also showed an upward trend in CPUE. However, this trend is more irregular than in the Balearic Sea (Saber et al. 2012, 2015, 2020). Our results on CPUE trends agree with those reported by Saber et al. (2015), which indicate an increase in the abundance, weight and average size of individuals caught in the area during the study period.

The sex ratio we found was close to 1:1. However, in Atlantic waters Cayré and Farrugio (1986) identified a global sex ratio in favour of males. In the Indian Ocean, Stequert and Ramcharrun (1996) and Timohina and Romanov (1996) observed the same for larger fishes.

The estimated length at which 50% of the female population of the species reached maturity (L_{50}) is below the sizes sampled in our study. The minimum size at which SKJ reached maturity in the western Mediterranean was at least 53.5 cm straight fork length. This finding agrees with studies in the Indian Ocean, where the L_{50} reaches 41 to 43 cm in females, corresponding to 1.5 years (Stequert and Ramcharrun 1996, Hartaty et al. 2020). In the southwest Atlantic L_{50} was estimated at 45.6 cm for both sexes, 43.2 cm for females and 46.2 cm for males (Benevenuti et al. 2019). Grande et al. (2014) used cortical alveolar oocytes as an indicator of maturation in the western Indian Ocean and the L_{50} of the female population that reached maturity was 39.9 cm. When these authors used advanced vitellogenic oocytes as an indicator, the L_{50} was similar to that in

other areas and estimated as 43.5 cm. In our study, the lack of small-sized and immature specimens did not allow us to calculate the L_{50} in the western Mediterranean. We will have to resolve this lack of information in further studies.

The monthly variation of the mean GSI values for males and females and the results obtained from the GAM indicated that the western Mediterranean is a spawning area for SKJ. GAM results indicated that larger specimens reached their maximum GSI earlier than smaller specimens, suggesting that larger specimens start their spawning period earlier than smaller ones. Our results agree with those of other studies conducted on other tuna species in the western Mediterranean Sea (e.g. Macías et al. 2005, Saber et al. 2018). These results were confirmed by histological analysis. The majority of the females sampled in Area I in June and July were spawning females. SKJ spawned in the Mediterranean in the summer months when the environmental conditions were suitable. Several tuna larval surveys carried out by Alemany et al. (2010) and Reglero et al. (2012) have demonstrated that the Balearic Sea is an important spawning ground for tuna species. Moreover, Alemany et al. (2010) and Reglero et al. (2014) reported larvae of SKJ around the Balearic Islands, confirming this area as a spawning ground for the species in the western Mediterranean Sea.

Schaefer and Fuller (2019) found that SKJ spawning in the eastern Pacific Ocean occurred from 24°C to 30°C. The optimal temperatures for tuna spawning are only reached in the Balearic Sea precisely on the dates when spawning SKJ were found in this study. For more details on the oceanography of the western Mediterranean Sea, see Vargas-Yañez et al. (2010, 2019). Our results confirm the preliminary study carried out by Saber et al. (2012) showing spawning-stage fish in the Balearic Sea.

SKJ from the Balearic Sea were capable of spawning every day (spawning frequency=1.03 d) during the spawning season. This result is slightly less than that found by Schaefer and Fuller (2019) in the eastern Pacific Ocean (spawning frequency=1.18 d) and by Ashida (2020) in the western Pacific Ocean (spawning frequency ranged from 4.38 d in the Kuroshio-Oyashio transition area to 2.16 d in the Nasei Islands area).

Given the subtropical and tropical distribution of the species and its high plasticity, the increasing presence of SKJ in the western Mediterranean and the new spawning area detected in the Balearic Sea could be related to the trend towards an increase in SST in the region. Vargas-Yañez et al. (2010, 2019) analysed a long-term time series of temperature generated by the monitoring programmes supported by the Spanish Oceanography Institute in Spanish Mediterranean Waters, complemented with meteorological information from the Spanish Meteorological Agency (AEMET), satellite data from the NOAA and data from meteorological stations to assess the possible impact of climate change. All the areas analysed by these authors, including the Alboran Sea and the Balearic Sea, show a trend to increase in temperature. Analysing the in-

termediate and deep waters, the same authors detected an increase since the mid-20th century of between 0.13 and 0.3°C/100 years. The increasing temperature trend was confirmed in surface waters, and at a higher rate since 1970. According to Ashida (2020), the reproductive investment of spawning fish in high-latitude areas of the western Indian Ocean may be lower than in tropical and subtropical zones because of shorter durations of favourable oceanographic conditions. These results agree with our results in the western Mediterranean, where the reproductive season only occurs in the summer months.

The specimens caught in the Balearic Sea were reproductively active, while those captured in the Alboran Sea were reproductively inactive and would be migrating towards the Atlantic at the end of the summer once the spawning season was over and SST in the western Mediterranean was decreasing. The exceptional SST conditions in the Alboran Sea in August 2018 could explain the unusual presence of spawning females in Area II. Using NOAA data, we saw that a few days before the championship there was an SST peak maintaining higher temperatures than expected for these dates. However, it must be taken into consideration that the SST in 2018 were above the historical monthly means, a phenomenon that may be related to global warming (Vargas-Yañez M., pers. com. 13/03/2022). This information could be related to changes in the oceanographic conditions (mainly temperature) or changes in the migratory behaviour of the species. Varela et al. (2019) found that SKJ feeds actively between the two areas in our study. This result supports the “income breeding strategy” described for the species. Spawning individuals can adjust their reproductive investment in response to environmental factors, indicating that higher investments in reproduction can be made when food resources are available (McBride et al. 2015) and when they have optimal environmental conditions.

As shown above, SST is of high importance for the highly migratory species, as it impacts spawning activity (Medina et al. 2002), and climate change will directly affect the physiology and spatial distribution of marine organisms, and is expected to affect SKJ. Dueri et al. (2014) projecting the impacts of climate change on SKJ abundance and spatial distribution, found that under present climatic conditions, the biomass peaks at the Equator. In addition, the model projected an increase of biomass at the latitudes 10°N and 10°S for 2050 and a displacement of the biomass peak from the Equator to 10°N. The reproduction rate showed a temporal trend similar to biomass abundance. Our study confirms that the Balearic Sea is a new spawning ground for this species in the western Mediterranean Sea and agrees with the expanding habitats projected for the species in the future.

The presence of a new reproductive species in the study area could be affecting the larval ecology and recruitment of local tuna species. This issue must be studied in the near future to assess its implications for tuna management and conservation in the region.

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REFERENCES

- Aleman F., Quintanilla L., Velez-Belchi P., et al. 2010. Characterization of the spawning habitat of Atlantic bluefin tuna and related species in the Balearic Sea (Western Mediterranean). *Progr. Oceanogr.* 86: 21-38.
<https://doi.org/10.1016/j.pocan.2010.04.014>
- Andrade H.A., Santos J.A.T. 2004. Seasonal trends in the recruitment of skipjack tuna (*Katsuwonus pelamis*) to the fishing ground in the southwest Atlantic. *Fish. Res.* 66: 185-194.
[https://doi.org/10.1016/S0165-7836\(03\)00199-1](https://doi.org/10.1016/S0165-7836(03)00199-1)
- Ashida H. 2020. Spatial and temporal differences in the reproductive traits of skipjack tuna *Katsuwonus pelamis* between the subtropical and temperate western Pacific Ocean. *Fish. Res.* 221: 105352.
<https://doi.org/10.1016/j.fishres.2019.105352>
- Ashida H., Tanabe T., Suzuki N. 2017. Difference on reproductive trait of skipjack tuna *Katsuwonus pelamis* female between schools (free vs FAD school) in the tropical western and central Pacific Ocean. *Environ. Biol. Fish.* 100: 935-945.
<https://doi.org/10.1007/s10641-017-0621-2>
- Benevenuti J., Monteiro-Neto C., Rodrigues M., et al. 2019. Size structure, reproduction, and growth of skipjack tuna (*Katsuwonus pelamis*) caught by the pole-and-line fleet in the southwest Atlantic. *Fish. Res.* 212: 136-145.
<https://doi.org/10.1016/j.fishres.2018.12.011>
- Brown-Peterson N.J., Wyanski D.M., Saborido-Rey F., et al. 2011. A Standardized Terminology for Describing Development in Fishes. *Mar. Coast. Fish.* 3(1): 52-70.
<https://doi.org/10.1080/19425120.2011.555724>
- Cayre P., Farrugio H. 1986. Biologie de la reproduction du listao (*Katsuwonus pelamis*) del ocean Atlantique. In: Symmons P.E.K., Miyake P.M., Sahagawa G.T. (eds), Proc. ICCAT Conf. Int. Skipjack Year Program, Int. Comm. Conser. Atl. Tunas, Madrid, Spain, pp. 252-272.
- Collette B.B., Nausen C.E. 1983. FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. Rome: FAO. FAO Fish. Synop. 125: 1-137.
- Dueri S., Bopp L., Maury O. 2014. Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. *Global Change Biol.* 20: 742-753.
<https://doi.org/10.1111/gcb.12460>
- FAO. 2022. El estado mundial de la pesca y la acuicultura 2022. Hacia la transformación azul. Roma, FAO.
<https://doi.org/10.4060/cc0461es>
- Farley J.H., Williams A.J., Hoyle S.D., et al. 2013. Reproductive dynamics and potential annual fecundity of South Pacific albacore tuna (*Thunnus alalunga*). *PloS ONE* 8(4): e60577.
<https://doi.org/10.1371/journal.pone.0060577>
- Gibson R.N., Ezzi I.A. 1980. The biology of the scaldfish, *Arnoglossus laterna* (Walbaum) on the west coast of Scotland. *J. Fish Biol.* 17: 565-575.
<https://doi.org/10.1111/j.1095-8649.1980.tb02788.x>
- Goldberg S.R., Au D.W. 1986. The spawning of skipjack tuna from the southern Brazil as determined from histological examination of ovaries. In: Symmons P.E.K., Miyake P.M., Sahagawa G.T. (eds), Proc. ICCAT Conf. Int. Skipjack Year Program, Int. Comm. Conser. Atl. Tunas, Madrid, Spain, pp. 277-284.
- Grande M., Murua H., Zudaine I., Korta M. 2012. Oocyte development and fecundity type of the skipjack *Katsuwonus pelamis*, in the Western Indian Ocean. *J. Sea Res.* 73: 117-284.
<https://doi.org/10.1016/j.seares.2012.06.008>
- Grande M., Murua H., Zudaine I., et al. 2014. Reproductive timing and reproductive capacity of the Skipjack Tuna (*Katsuwonus pelamis*) in the western Indian Ocean. *Fish. Res.* 156: 14-22.
<https://doi.org/10.1016/j.fishres.2014.04.011>
- Hartaty H., Setyadi B., Fahmi Z. 2020. Reproductive biology of Skipjack Tuna (*Katsuwonus pelamis*) in Indonesian Exclusive Economic Zone. IOTC-2020-WPTT22(AS)-8.
- Hunter J.R., Macewicz B.J. 1985. Measurement of spawning frequency in multiple spawning fishes. In: Lasker R., (ed) An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rept. NMFS 36, pp. 79-94.
- ICCAT. 2021. International Commission for the Conservation of Atlantic Tunas - Access to ICCAT statistical databases. Task I.
<https://iccat.int/en/accessingdb.html>
- ICCAT. 2019. International Commission for the Conservation of Atlantic Tunas - Report of the Standing Committee on Research and Statistics (SCRS). 459 pp.
- Macías D., Gómez-Vives M.J., García S., Ortiz de Urbina J.M. 2005. Reproductive characteristics of Atlantic Bonito (*Sarda sarda*) from the south-western Spanish Mediterranean. *Col. Vol. Sci. Pap. ICCAT* 58: 470-483.
- McBride R.S., Somarakis S., Fitzhugh G.R., et al. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish. Res.* 16: 23-57.
<https://doi.org/10.1111/faf.12043>
- Margulies D., Suter J.M., Hunt S.L., et al. 2007. Spawning and early development of captive yellowfin tuna (*Thunnus albacares*). *Fish. Bull.* 105: 249-265.
- Matsumoto W.M., Skillman R.A., Dixon A.E. 1984. Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis*. U.S. Nat. Mar. Fish. Serv. Nat. Oceanic Atmos. Adm. Tech. Rep. NMFS Circ., vol 451. U.S. Department of Commerce.
- Medina A., Abascal F.J., Megina C., García A. 2002. Stereological assessment of the reproductive status of female Atlantic northern bluefin tuna during migration to Mediterranean spawning grounds through the Strait of Gibraltar. *J. Fish Biol.* 60: 217-230.
<https://doi.org/10.1111/j.1095-8649.2002.tb02398.x>
- Otsu T., Uchida R. 1959. Study for age determination by hard parts of albacore from central Pacific and Hawaiian waters. *U.S. Fish. Bull.* 59: 353-363.
- R Core Team. 2017. R: A language and environment for analysis computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reglero P., Ciannelli L., Álvarez-Berasategui D., et al. 2012. Geographically and environmentally driven spawning distributions of tuna species in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 463: 273-284.
<https://doi.org/10.3354/meps09800>
- Reglero P., Titteser D.P., Álvarez-Berasategui D., et al. 2014. Worldwide distributions of tuna larvae: revising hypotheses on environmental requirements for spawning habitats. *Mar. Ecol. Prog. Ser.* 501: 207-224.
<https://doi.org/10.3354/meps10666>
- Reynolds R.W., Rayner N.A., Smith T.M., et al. 2002. An improved in situ and satellite SST analysis for climate. *J. Climate* 15: 1609-1625.
[https://doi.org/10.1175/1520-0442\(2002\)015<1609:AIISAS>2.0.CO;2](https://doi.org/10.1175/1520-0442(2002)015<1609:AIISAS>2.0.CO;2)
- Saber S., Gómez-Vives M.J., García-Barcelona S., et al. 2012. Recreational catch rates and biology of Skipjack tuna from the western Mediterranean Sea. In: Morris E.P., Mañanes R., Fernández M.C., Gómez J. (eds), Libro de resúmenes del III Simposio Internacional de Ciencias del Mar (ISMS12), Cádiz, ISBN: 978-84-695-1394-1, p. 112.

- Saber S., Muñoz P., Ortiz de Urbina J., et al. 2015. Análisis de las tendencias de las capturas de atún listado *Katsuwonus pelamis* (Linnaeus, 1758) de la pesca deportiva en el Mediterráneo occidental (2006-2014). In: Díaz del Río V., Bárcenas P., Fernández-Salas L.M., et al. (eds), Volumen de Comunicaciones presentadas en el VIII Simposio sobre el Margen Ibérico Atlántico (MIA15). Málaga, Spain, 21-23 September 2015, Ediciones Sia Graf, Málaga, pp. 517-520.
- Saber S., Ortiz de Urbina J., Lino P.G., et al. 2018. Biological aspects of little tunny *Euthynnus alletteratus* from Spanish and Portuguese waters. Collect. Vol. Sci. Pap. ICCAT. 75: 95-110.
- Saber S., Macías D., Gómez-Vives M.J., et al. 2020. Standardized catch rates of Skipjack from the Mediterranean Spanish recreational fishery (2006-2018). Collect. Vol. Sci. Pap. ICCAT 76(6): 867-873.
- Schaefer K.M. 1998. Reproductive biology of yellowfin tuna (*Thunnus albacores*) in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 21: 205-272.
- Schaefer K.M. 2001a. Assessment of skipjack tuna, *Katsuwonus pelamis* spawning activity in the eastern Pacific Ocean. Fish. Bull. 99: 343-350.
- Schaefer K.M. 2001b. Reproductive biology of tunas. In: Block B.A., Stevens E.D. (eds), Tuna physiology, ecology and evolution. Academic Press, San Diego, CA, pp. 225-272. [https://doi.org/10.1016/S1546-5098\(01\)19007-2](https://doi.org/10.1016/S1546-5098(01)19007-2)
- Schaefer K.M., Fuller D.W. 2019. Spatiotemporal variability in the reproductive dynamics of skipjack tuna (*Katsuwonus pelamis*) in the eastern Pacific Ocean. Fish. Res. 209: 1-13. <https://doi.org/10.1016/j.fishres.2018.09.002>
- Steuert B., Ramcharrun B. 1995. The fecundity of skipjack tuna (*Katsuwonus pelamis*) from the western Indian Ocean. Aquat. Liv. Res. 8: 79-89. <https://doi.org/10.1051/alr:1995006>
- Steuert B., Ramcharrun B. 1996. La reproduction du listao (*Katsuwonus pelamis*) dans le bassin ouest de l'océan Indien. Aquat. Liv. Res. 9: 235-247. <https://doi.org/10.1051/alr:1996027>
- Timohina O.I., Romanov E.V. 1996. Characteristics of ovogenesis and some data on maturation and spawning of skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), from the western part of the equatorial zone of the Indian Ocean. Indian Ocean Tuna Commission 24.
- Varela J.L., Cañavate J. P., Medina A. Mourente G. 2019. Inter-regional variation in feeding patterns of skipjack tuna (*Katsuwonus pelamis*) inferred from stomach content, stable isotope and fatty acid analyses. Mar. Env. Res. 152: 104821. <https://doi.org/10.1016/j.marenvres.2019.104821>
- Vargas-Yañez M., García M.C., Moya F., et al. 2010. Cambio Climático en el Mediterráneo español. Segunda edición. Instituto Español de Oceanografía. 176 pp.
- Vargas-Yañez M., García M.C., Moya F., et al. 2019. Estado de los ecosistemas marinos en el Mediterráneo español en un contexto de cambio climático. Instituto Español de Oceanografía. 284 pp.
- Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag. New York.
- Wood S.M. 2017. Generalized Additive Models: An Introduction with R (2nd ed.) Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>
- Worm B., Sandow M., Oschlies A., et al. 2005. Global patterns of predator diversity in the open oceans. Science 309: 1365-1369. <https://doi.org/10.1126/science.1113399>