REVIEW

Recruitment of the Argentine hake, *Merluccius hubbsi*, from Patagonian stock: a review of main features affecting the reproductive potential and survival during early life stages

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ABSTRACT. Understanding the causes that generate variability of recruitment in marine populations constitutes one of the greatest challenges in fishery science. Our predictive capacity to explain these variations is relatively low, due to the interaction of exogenous and endogenous factors, which vary across time and space within populations. In order to gain information on recruitment fluctuations of the Argentine hake (*Merluccius hubbsi*) from Patagonian stock, we reviewed the results obtained analyzing the reproductive ecology, trophic and energetic dynamics during different stages of development of this species, and its relationship with environmental variables. We observed that the reproductive potential is strongly influenced by characteristics of the parental stock, particularly females, in terms of their size, age and condition. This feature, called 'maternal effect', suggests that the spawning stock biomass, commonly used as an index of productivity in fishery assessment, is a poor predictor of recruitment. We also observed that survival during hake early life is affected by the spatial coincidence with the North Patagonian Frontal System, characterized by a high concentration of nutrients, high productivity, and food availability. Physical conditions and larval density in the nursery area affected the nutritional state and mortality of hake, mainly by competition for food or predation. It was observed that the transition of juveniles from pelagic to demersal habitat occurs over a longer period than previously recognized for this species, stressing the importance of using acoustic information to complement data from bottom trawls. This is one of the main topics to be further developed in order to estimate new recruitment indices for Argentine hake, along with other research items proposed to improve stock assessment.

Key words: Southwest Atlantic Ocean, maternal effect, north Patagonian Frontal System, larval survival.

Reclutamiento de la merluza argentina, *Merluccius hubbsi*, del *stock* patagónico: una revisión de las principales características que afectan el potencial reproductivo y la supervivencia durante las primeras etapas de la vida

RESUMEN. Comprender las causas que generan la variabilidad del reclutamiento en las poblaciones marinas constituye uno de los mayores desafíos de la ciencia pesquera. Nuestra capacidad

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predictiva para explicar estas variaciones es relativamente baja, debido a la interacción de factores exógenos y endógenos, que varían en el tiempo y el espacio dentro de las poblaciones. Con el fin de obtener información sobre las fluctuaciones en el reclutamiento de la merluza argentina (*Merluccius hubbsi*) del *stock* patagónico, revisamos los resultados obtenidos analizando la ecología reproductiva, la dinámica trófica y energética durante las diferentes etapas de desarrollo de esta especie y su relación con variables ambientales. Observamos que el potencial reproductivo está fuertemente influenciado por las características parentales, particularmente de las hembras, en cuanto a su tamaño, edad y condición. Esta característica, denominada "efecto materno", sugiere que la biomasa de la población reproductora, comúnmente utilizada como índice de productividad en la evaluación de pesquerías, es un predictor deficiente del reclutamiento. También observamos que la supervivencia durante los primeros años de vida de la merluza se ve afectada por la coincidencia espacial con el Sistema Frontal Norpatagónico, caracterizado por una alta concentración de nutrientes, alta productividad y disponibilidad de alimento. Las condiciones físicas y la densidad larvaria en la zona de crianza afectaron el estado nutricional y la mortalidad de la merluza, principalmente por competencia por alimento o depredación. Se observó que la transición del hábitat pelágico al demersal en los juveniles se produce durante un período más extenso que el reconocido anteriormente para esta especie, lo que destaca la importancia de utilizar los registros acústicos para complementar la información de las redes de arrastre de fondo. Este es uno de los principales temas a desarrollar para estimar nuevos índices de reclutamiento de merluza argentina, junto con otras líneas de investigación propuestas para mejorar la evaluación del *stock*.

Palabras clave: Océano Atlántico Sudoccidental, efecto maternal, Sistema Frontal Norpatagónico, supervivencia larval.

INTRODUCTION

The reproductive strategy adopted by fish is associated with the availability of energy resources and with the physical conditions in the environment. These are key factors that determine the survival of the progeny and affect the incorporation of new individuals into the population, a process known as recruitment. For this reason, knowing and understanding the causes that generate variability of this process in marine populations, and identifying the factors that determine changes in the abundance of individuals constitutes one of the greatest challenges in fisheries biology (Marshall et al. 1998). Recruitment is affected both by exogenous environmental factors and by those endogenous or intrinsic to the population. Among the first are physical variables in the breeding area, such as temperature, salinity, stratification and dissolved oxygen, as well as food availability, intra- and interspecific competition and predation (Houde 2009). Endogenous factors are mainly associated with parental stock features including abundance, size/age composition, physiological condition, or genetic diversity (Jakobsen et al. 2009).

Regardless of the characteristics of the life cycle of the species, the relationship between parental stock and recruitment (S-R) occupies a central role in the study of population dynamics and management of marine resources. The S-R models developed by Beverton and Holt (1957) and Ricker (1954) originally used the term fecundity, but it was later replaced by Spawning Stock Biomass (SSB) as a proxy of stock productivity (Rothschild and Fogarty 1989). In such cases, it is assumed that a given adult biomass has the same probability to generate the same level of recruitment, independent of the age or size composition of the population (Marshall et al. 2003). However, during the last years, it was demonstrated that there are few examples of fisheries showing good fits in the S-R relationships (Vert-pre et al. 2013). At the end of 90's, an alternative term to SSB was introduced, the Stock Reproductive Potential (SRP), which more accurately represents the stock's ability to produce viable eggs and larvae that may eventually be recruited to the population (Trippel 1999). This term includes parental factors that influence the early life stages of fish related to recruitment processes. Given that the set of individual characteristics will determine the reproductive success of the population, special attention has been paid to the structure and age diversity of the stocks (Marteinsdottir and Begg 2002; Scott et al. 2005; Mehault et al. 2010) or the proportion of primiparous spawners (Evans et al. 1996; Trippel 1998), since they can influence the resilience of an overexploited population (Rijnsdorp et al. 2010).

The link between reproductive potential and recruitment is established through the selective survival of eggs and larvae based on parental characteristics. In other words, egg production is not a sufficient mechanism to ensure certain recruitment. It has been shown that some factors, especially maternal, greatly influence the survival of offspring, particularly in their interaction with the environment (Marteinsdottir and Steinarsson 1998; Lambert et al. 2003). For example, egg quality as a function of maternal characteristics, such as size/age and nutritional condition (Marteinsdottir and Steinarsson 1998; Saborido-Rey et al. 2003; Macchi et al. 2013), could affect the rate of development or the larval size (Miller et al. 1995; Pepin et al. 1997). In general, it is assumed that larger larvae have a better chance of getting food, so they would have better chances of survival during this critical life phase and could give rise to higher recruitments (Rijnsdorp and Vingerhoed 1994; Trippel 1998). Many studies on the early life history of fish suggest that larger females would have a positive effect on the fecundity and quality of eggs produced, generating more significant recruitments, which has led to the BOFFFF hypothesis (Big, Old, Fat, Fecund Female Fish) proposed by Berkeley et al. (2004). In species subjected to intense fishing exploitation, the extractive activity is mainly focused on larger individuals, so it can generate changes in the size/age structure of stocks. Thus, the disappearance or decrease of large spawners would directly affect the reproductive potential and therefore the population recruitment.

The nutritional condition of spawners is another trait that influences the reproductive potential of stocks, affecting both fecundity and the quality of eggs produced. For this reason, it is important to consider the strategy of energy allocation of fish, particularly in those species that accumulate reserves prior to spawning (capital breeding), since this process can be decisive for reproductive success, and also act as a recruitment proxy (Marshall et al. 1999; Wuenschel et al. 2013).

Since a higher egg production generated by the spawning stock does not ensure good recruitment in the future, it is important to consider also the interaction of the early life stages with the environment. The effect of oceanographic variables, such as temperature, salinity, or the vertical stratification of the water column, determine the availability of nutrients, and therefore the productivity of the system (Bakun 1996). Frontal zones, for example, can be advantageous as retention areas for larvae or act negatively due to the accumulation of predators (Bailey and Houde 1989). A central point in the theory of recruitment is occupied by various hypotheses about the critical period in the early life of fish, which arose from Hjort's postulate (1914), such as 'Match-Mismatch', 'Stable Ocean' and 'Member/ Vagrant' (Houde 2009). These hypotheses, in general, converge on the idea that larval phases must coincide in time and space with a series of optimal ecological circumstances for their maximum survival (retention, greater production and concentration of food or little competition). At this point, it has also been shown that the structure of the parental stock and its demography determine the timing, duration and place of spawning, and therefore have a profound effect on larval survival (Lowerre-Barbieri et al. 2009, 2011; Wright and Trippel 2009). In summary, recruitment success would depend on the result of complex physical and trophodynamic processes acting on different temporal and spatial scales throughout the pre-recruit life stage (Houde 2008). New approaches in recruitment theories point to complementing the traditional S-R relationship, which mainly considers the productivity of stocks determined by the abundance of parents and their fecundity, by an S-R system where different aspects of the reproductive strategy of the species operate, and that define the reproductive resilience of populations (Lowerre-Barbieri et al. 2016).

Merluccius hubbsi (Argentine hake) is one of the main fishing resources of Argentina, with biomass estimates close to 1,315,000 t (Irusta et al. 2022; Santos and Villarino 2022). This species is distributed over the continental shelves of Uruguay and Argentina, mainly at depths between 50 and 400 m from 35° S to 54° S (Otero et al. 1982), but the highest concentrations are found up to 48° S. *Merluccius hubbsi* reaches 21° S in Brazilian waters in response to the upwelling of sub-Antarctic waters, but abundance in this region is very low (Vaz-dos-Santos et al. 2009). On the Argentine continental shelf, there are two main fishing stocks separated by parallel 41° S, whose reproductive cycles are spatially and temporally out of phase. The southern or Patagonian stock, which is the object of the present review, is the most abundant population of this species and represents 90% of its total biomass, with an annual catch of 260,000 t reported in 2022 (MAGyP 2022). This stock reproduces during the austral spring and summer, between November and April, with the main peak in January (Macchi et al. 2004; Pájaro et al. 2005). During the 1990s, the intense fishing activity of different commercial fleets on the Argentine hake produced a sharp drop in the abundance of this resource, resulting in the implementation of a permanent closure area in waters of Patagonia since 1997 (Irusta et al. 2016). At present, this stock is assessed annually through age-structured models (VPA-XSA and ECE) using SSB as the most important biological reference point (Santos and Villarino 2022). The S-R model obtained during the assessment of Patagonian population showed high variability, which increased studies on the recruitment process in this fishing stock. For this reason, starting in 2008, the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) generated a research project called Recruitment of Patagonian Hake Stock (REC), whose main objective was to determine the physical and biological variables affecting the abundance of hake individuals recruited to the population in the first year of life. The project focused on the study of factors that influence the reproductive potential of hake during the adult phase and on the analysis of the processes that affect the survival of eggs, larvae, and juveniles, until their recruitment at the age-1 class.

This paper is an up-to-date review of the main results obtained for the REC project to date, addressing aspects of the Argentine hake life cycle in Patagonian waters, from the spawning to the juvenile phase, passing through larval stages. The study includes the analysis of the reproductive ecology, trophic and energetic dynamics during different stages of development, and its relationship with environmental variables. We also include information on new lines of research that are being developed in the project and its future perspectives. The importance of an integrative comprehension of the species' life traits, considering the reproductive strategy and early development, is highlighted in order to improve the recruitment indices.

PHYSICAL CHARACTERISTICS OF THE SPAWNING AND NURSERY AREAS

Characteristic large tide ranges from the Patagonian region lead to high-energy dissipation rates. The interaction of this energy with the bottom topography and the stratification generated by surface heating favors the formation of frontal zones (Simpson and Bowers 1981; Rivas and Piola 2002). This type of hydrographic structure is characteristic of the 'North Patagonian Frontal System' (NPFS) in the north Patagonian region between 41° S and 45° S (Sabatini and Martos 2002), where a seasonal thermocline between 30 and 50 m depth begins to develop in early spring due to increasing solar radiation (Figure 1). This thermocline defines a two-layered structure where the lower layer is under the influence of colder waters from the middle shelf. While in the coastal region the effect of tides homogenizes the water column, in the stratified zone conditions are more stable and the mixture between water masses is relatively weaker, prevailing an increase in temperature at the surface (Simpson and Hunter 1974; Acha et al. 2015). During this process, three main sectors are defined: homogeneous, frontal, and stratified. In this sense, the frontal zone represents the transition between the homogeneous coastal region and the more deeply stratified one. In the cold season, the middle shelf stratification begins to break by convection and wind-driven mixing, and the frontal structure disappears. The position of the tidal front has been determined by hydrographic observations that allowed estimating the stability parameter (Simpson 1981), establishing a 40 J m^{-3} reference value that separates homogeneous and stratified regions (Martos and Sánchez 1997). From a series of *in situ* data, the mean position of the NPFS was estimated (Figure 1 A) approximately on the 70 m isobath, with a NE-SW direction following the bathymetry (Sabatini and Martos 2002). The front

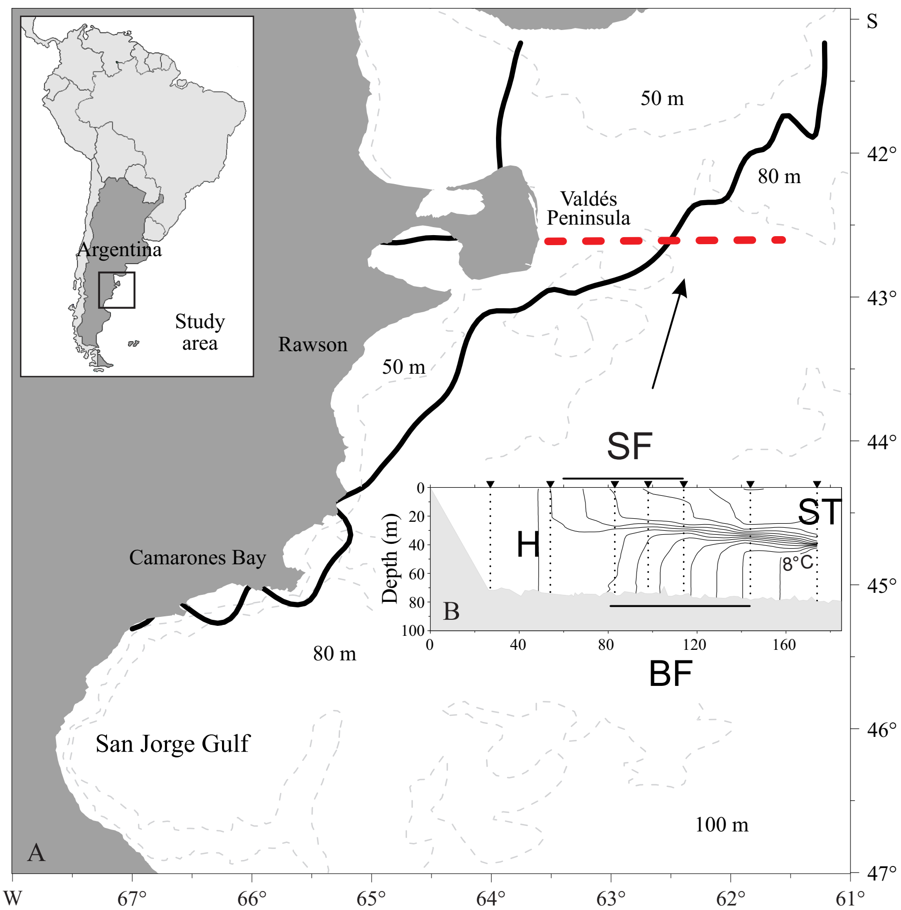

Figure 1. A) Mean location of the North Patagonian Frontal System (black line) as determined from the Simpson parameter (Value 40 J m^{-3}). B) Vertical section of temperature along the transect located near the Valdés Peninsula (red dotted line), showing the homogeneous (H) and stratified (ST) zone, and the surface (SF) and bottom thermal front (BF). The numbers on the abscissa in panel B represent the distances in km. Modified from Sabatini and Martos (2002).

is present both on the surface and on the bottom, showing the intersection of the thermocline in both places with different thermal gradients depending on the region (Figure 1 B). The physical structure and location of the front show latitudinal differences related to variations of main hydrometeorological forces, tide and wind, being located further from the coast in front of Valdés Peninsula and closer to it further south.

Circulation in frontal areas is affected by differences in water masses density, which generates convergence zones both at surface and bottom (Largier 1993; Mann and Lazier 1996). High amount of nitrates produced by phytoplankton blooms and large copepod aggregations characterize tidal fronts, which are typical of regions with high biological productivity (Derisio et al. 2014; Temperoni et al. 2014). A clear transition of nitrate concentrations has been observed through the thermocline in the front stratified sector, and relatively high values throughout the water column in the homogeneous zone (Carreto et al. 1985). Another characteristic of this type of front, generated by the mix of turbulent tides, is that variability in their position and structure is partially associated with the transition between syzygy and square tides, which may contribute to a greater flow of nutrients through the front (Pisoni et al. 2015). This scenario creates an ideal habitat for spawning and development of early life stages of many species (Sánchez and Ciechomski 1995; Acha et al. 2015). This is partly due to the physical conditions generated by the differential stratification of water masses, in addition to nutrient enrichment, which has led to postulating one of the best-known hypotheses on the variability of recruitment in marine populations, such as the 'fundamental Bakun triad' (1996). The hypothesis postulates that some frontal areas are essential for fish survival during their first life stages since they have three main characteristics: 1) the nutrient-rich upwelling of deeper waters that enrich superficial layers; 2) the concentration of planktonic organisms that constitute the main food source for fish larvae, and 3) the retention of fish eggs and larvae in these favorable areas. Elements of this triad have been described for the NPFS during spring and summer; particularly, high concentrations of chlorophyll and microzooplankton have been reported in the transitional zone of the front, which favors a higher biological production (Viñas and Santos 2000; Temperoni et al. 2014). Although little information is available on direct current measurements in that region, retention seems to be a key feature in the hake spawning and nursery area of the Patagonian stock (Piola and Rivas 1997). Recently, as part of the Cassis-Malvinas Project (http://www.cima.fcen.uba.ar/malvinascurrent/es/), a current meter deployment was carried out in a transect located at the latitude of Camarones Bay (Figure 1 A) from the coast to greater depths, whose information has been partially analyzed by Lago (2022). In any case, numerical models suggest the existence of circulation patterns in the north Patagonian region that varies with depth (Palma et al. 2008), and that could support the existence of retention mechanisms in the nearness of the thermocline during the summer (Álvarez Colombo et al. 2011). This area is coincident with the main spawning site of hake, where the highest densities of herbivorous calanoid copepods, the preferred larval food, occur (Derisio 2012).

South of this region, the San Jorge Gulf (45° S-47° S) is considered to be the main nursery area for young-of-the-year juvenile hake (YOY or age-0 group) of Patagonian stock (Álvarez Colombo et al. 2014; Irusta et al. 2016). According to studies carried out in this area, the influence of tidal fronts led to high chlorophyll-*a* (Chl-*a*) concentrations south of the gulf's mouth (Romero et al. 2006). On the other hand, various authors (Tonini et al. 2006; Torres et al. 2018; Pisoni et al. 2020) have observed that coastal upwelling events in the SW of the gulf generate changes in nutrient availability (especially nitrates), boosting primary productivity (Papparazzo et al. 2021). In the NE sector of the gulf, there is a high biodiversity associated with the mesoscale circulation generated by the interaction of tidal currents with the islands and topographic features of the coastal zone (Gagliardini et al. 2004). In addition to influencing the availability of nutrients and primary productivity, these circulation patterns generate a series of relevant processes for the development of communities, particularly those affecting the dispersal and transport of planktonic larvae.

REPRODUCTIVE CYCLE AND SPAWNING

The first papers on the biology of the Argentine hake suggested the existence of two reproductive periods for the species in waters of the Argentine continental shelf: the main one during spring-summer, and a secondary one in autumn-winter (Angelescu and Gneri 1958; Christiansen and Cousseau 1971). The spring-summer spawning corresponds to the Patagonian hake stock, which takes place mainly in coastal waters of Chubut Province, south of Valdés Peninsula (Ciechomski et al. 1983). More recent papers based on the macroscopic and histological analysis of gonads and on the evaluation of the spatial distribution and abundance of ichthyoplankton, allowed adjusting the extension of the reproductive season and determining variations in spawning intensity during this period (Macchi et al. 2004; Ehrlich et al. 2019). In addition, monitoring the hake reproduction from research surveys carried out throughout the spawning period has made it possible to determine movements of pre- and post-spawning aggregations, providing additional information on the behavior and migrations of hake during reproduction (Macchi et al. 2007).

At the beginning of the austral spring (October), adult fish at latitudes 43° S-44° S move from shelf waters (> 100 m depths) towards the coast in order to reproduce (Macchi et al. 2007). This analysis showed that hake spawning intensifies in December, mainly in the south of Valdés Peninsula, reaching the peak in January when the spawning area extends between 43° S and 45° S, from the 50 m isobath up to approximately 80 m depth (Figure 2). Dense hake shoals have been observed in December, mainly in the coastal area called Isla Escondida, near Rawson city (Macchi et al. 2005), coinciding with the first reproductive aggregation. In February, the abundance of hake in the spawning area decreases as a consequence of offshore displacements of the species after spawning (Figure 2). By the end of summer, the abundance of spawning-capable-individuals decreases even more, and the presence of females in regression or post-spawning phase increases, reaching the maximum of this stage at the beginning of autumn, when very few specimens are in reproductive activity (Macchi et al. 2004). Both direct trawl captures and acoustic methods have

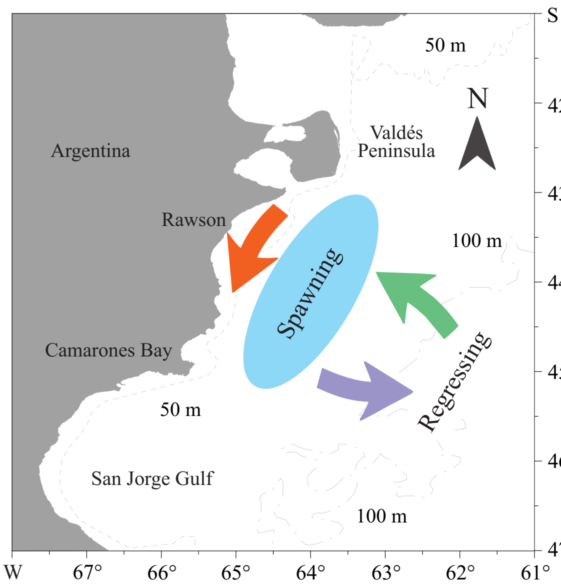

Figure 2. Spawning cycle of *Merluccius hubbsi* in the north Patagonian area. Arrows represent movements of hake individuals in different periods: October-November (green), December-January (orange) and February-March (violet). The oval shows the main spawning site during summer and the regressing or post-spawning area offshore near the 100 m isobath. Modified from Macchi et al (2007).

been used to determine variations in the abundance of parental stock during the reproductive period. The comparative analysis has shown that trends obtained with both methods are very similar, giving greater certainty to the estimations (Álvarez Colombo et al. 2006).

AGE/SIZE COMPOSITION AND CONDITION OF THE SPAWNING STOCK

Spatial variations observed in the parental stock of hake during the reproductive season are also reflected in the size composition of spawning shoals. Analysis of length distributions made it possible to determine that smallest females (< 50 cm TL) finished spawning earlier, moving outside the main reproductive area, which was also reflected in the age structure of the reproductive stock (Macchi et al. 2004). On the contrary, larger and older females (> 5-year-old) showed longer spawning periods, allowing them to stay longer in the breeding area. Males, as discussed for other species, also tend to remain active for longer, even after the reproductive activity has ended (Macchi et al. 2004). This is probably due to the lower energy investment by males during reproduction compared to that derived for the development of female gametes. This feature coupled with the migration of females to deeper waters after spawning, causes male-biased proportions in coastal areas at the end of the reproductive season (Pájaro et al. 2005). Moreover, a high proportion of males is recorded in areas where hake females are ovulating, suggesting the possible existence of courtship mechanisms or competition between males before egg fertilization (Pájaro et al. 2005; Macchi et al. 2007).

During some years, it was possible to detect the presence of small groups of females spawning in deeper waters, near the 100 m isobath, far from the main reproductive aggregations of hake (Macchi et al. 2010). These shoals were mainly composed of larger females (> 50 cm TL) near the regression stage, with evidence of having made several spawning events during the reproductive season. Some of these females, particularly the larger ones, were still in spawning-capable condition, but migrated into deeper waters to feed and recover energy reserves (Figure 2). This suggests that Argentine hake may incorporate energy during the reproductive season, responding to an energy allocation strategy typical of an income breeding species (Macchi et al. 2013; Leonarduzzi 2018), as has also been reported for the European hake *M. merluccius* (Domínguez-Petit and Saborido-Rey 2010).

Traditional indices (hepatosomatic and K factor) and analysis of proximal composition of different tissues (liver, gonad, and muscle) used to study the nutritional condition of the Argentine hake revealed that females primarily store energy in the liver as lipids, but they would also use proteins from the muscle as they matured (Leonarduzzi 2018). This author observed that larger females (> 50 cm TL) showed a better energetic condition compared to smaller ones, characterized by larger livers and high lipid content, which could be associated with both feeding frequency and quality of the prey available for larger individuals, such as squid and anchovy.

FEEDING OF THE SPAWNING STOCK

The trophic ecology of the Argentine hake from Patagonian stock has been extensively studied through the classical analysis of stomach contents during the last years. The diet of this species exhibits regional and seasonal variations, which would be related to prey availability. During summer, it feeds on zooplanktonic crustaceans such as the white shrimp *Peisos petrunkevitchi* in Escondida Island (Ruiz and Fondacaro 1997), squid (*Illex argentinus*) and Argentine anchovy (*Engraulis anchoita*) in the reproductive area south of Valdés Peninsula (Belleggia et al. 2014). Conversely, during winter, Argentine hake feed on euphausiids (mainly *Euphausia lucens*) and amphipods (*Themisto gaudichaudii*) in San Jorge Gulf and surrounding area, making vertical nictemeral migrations (Belleggia et al. 2014; 2019), and on myctophids and squids in the shelf break region (Angelescu and Cousseau 1969; Belleggia et al. 2014). From zooplankton crustaceans during early life stages of hake to fish and cephalopods in the adult phase, growth-associated ontogenetic dietary changes were also observed (Belleggia et al. 2014).

Since 2008, and more intensely in 2011, there have been changes in the diet of hake from San Jorge Gulf, with an increased consumption of the lobster krill *Munida gregaria* (Belleggia et al. 2017). The decrease in the abundance of predators of *M. gregaria*, such as the pink cusk eel *Genypterus blacodes*, Argentine seabass *Acanthistius patachonicus* and Rajidae skates (*Zearaja brevicaudata*, *Psammobatis* spp. and *Sympterygia bonapartii*) can be considered among the biological factors explaining the expansion of the lobster krill population and the increased biomass in San Jorge Gulf (Belleggia et al. 2017).

The Argentine hake is considered a facultative opportunist, because although the general proportion of prey consumed and that present in the environment is similar, the species is able to select under certain circumstances high-energy-density prey (i.e. lobster krill *M. gregaria*) to satisfy their energetic and nutritional requirements, disregarding less caloric content food items even when they are abundant in the environment (Belleggia et al. 2019). However, despite that since 2011 it has fed mainly on this crustacean, preliminary studies carried out with stable carbon and nitrogen isotopes revealed that the 'new' prey is not efficiently assimilated into hake's muscle (Belleggia et al. 2022a). These analyses showed that euphausiids, particularly *E. lucens*, were the main food item assimilated in the San Jorge Gulf region (Belleggia et al. 2022a).

Cannibalism occurs in Argentine hake as a denso-independent process (Belleggia et al. 2019), influenced by the proximity of YOY individuals to the demersal habitat (Belleggia et al. 2022b). During daylight hours, YOY hake in the San Jorge Gulf nursery area distributes in the pelagic layers, while the age-1+ group is found close to the bottom in the demersal layer (Álvarez-Colombo et al. 2014; Belleggia et al. 2022b). The vertical spatial segregation of hake life stages in different layers of the water column in San Jorge Gulf may reduce trophic overlap, diminish intraspecific competition and limit cannibalism (Belleggia et al. 2022b). Pelagic YOY hake are more abundant and are located more distant from the bottom during the cold season, thus, cannibalism is less during winter (Belleggia et al. 2022b).

REPRODUCTIVE POTENTIAL OF THE STOCK

The Argentine hake from Patagonian stock reaches sexual maturity at 2-3 years old, showing differences between sexes (Macchi et al. 2017). The length at maturity (L_{50}) has been estimated close to 33-35 cm TL for females and between 26 and 28 cm TL for males (Macchi et al. 2007; 2021). This is an important parameter for the assessment and management of fisheries, being considered when establishing catch limits by size for many species to reduce the mortality of juveniles in the population. The length at maturity model, also estimated with age, is commonly called maturity ogive, and is relevant for the stock assessment, since it is used to estimate the SSB (Mace and Sissenwine 1993). Seasonal variations of L_{50} in the hake from Patagonian stock characterized by higher values of this parameter at the end of the reproductive period were also observed (Pájaro et al. 2005). A similar pattern was registered when L_{50} was estimated with samples collected in autumn-winter during the resting phase of the maturity cycle (Macchi et al. 2017).

Regarding the interannual variations of L_{50}, comparisons made using samples collected during the reproductive peak (January) of this stock between 2001 and 2018, have not shown trends indicating changes in the length or age at maturity during that period (Macchi et al. 2021).

A recently recorded phenomenon in the Patagonian hake stock that affects the estimation of the maturity ogive, is skipped spawning (Macchi et al. 2016). This is the interruption of the spawning process in a fraction of the parental population during the annual reproductive cycle. It has been observed that during the spawning peak, a proportion of adult females remain in the resting stage, with no evidence of oocyte development or recent ovulation (Macchi et al. 2016). These authors observed that skipped spawning occurred mostly in young adult females, and that it could be related to a poorer nutritional condition of these individuals in comparison to older specimens as a strategy of female hake to conserve energy reserves. This 'irregularity' in the reproductive cycle would have consequences for the estimation of the SSB, since not every adult fish would contribute to the annual reproductive potential of the population. In fact, it was estimated that skipped spawning could cause a reduction in the annual egg production of hake between 4% and 12% (Macchi et al. 2017).

The Argentine hake is a multiple spawner with an indeterminate annual fecundity, meaning that unyolked oocytes continuously mature and are spawned throughout the reproductive season (Hunter et al. 1992). The number of eggs produced by batch (batch fecundity, BF) increases with total length, weight and age of females (Figure 3 A). Relative fecundity (RF), which represents the number of eggs per unit of female weight, may also evidence positive relationships with the size of spawners, although models obtained in this case showed great variability (Figure 3 B). A comparative analysis of these variables between different months of the spawning season showed a decrease in the number of oocytes produced towards the end of this period, which is possibly associated with a depletion of energy reserves used for reproduction (Macchi et al. 2004).

The spawning frequency (S) is another necessary parameter to determine the reproductive potential of a species, since it represents the time elapsed between egg batches and is an estimator of the number of spawning events carried out by females during the reproductive season (Hunter and Goldberg 1980). For the Patagonian stock, the estimated value of S at the beginning of the spawning season was close to 13 d, but during the reproductive peak (January) the time elapsed between spawning events was shorter, reaching up to 7 d (Macchi et al. 2018). Spawning frequency is generally estimated as an average value for the population, although differences associated with the size-age of females have been reported (Claramunt et al. 2007). In fact, for the Patagonian stock, the number of days between spawning events decreases as the size/age of females increases (Figure 3 C), e.g. older spawners would have a higher number of spawning events during the reproductive season (Macchi et al. 2018). The combination of batch fecundity, spawning frequency and abundance of mature females by size class is necessary to estimate the potential egg production of the stock. This parameter, in the case of the Patagonian hake population, is characterized by a significant contribution of larger females (Rodrigues et al. 2015).

The third component to consider when evaluating the reproductive potential of stocks is the quality of oocytes produced, since it is a factor that can influence the survival of first life stages. The size and weight of oocytes are variables commonly used to assess egg quality in fish, since both are associated with the amount of nutritive substances available in the yolk (Brooks et al. 1997). The most accurate parameter for hake was the estimated oocyte dry weight during the hydration phase, just before ovulation. Analysis of this variable during the reproductive season of Patagonian stock has shown that the quality of eggs

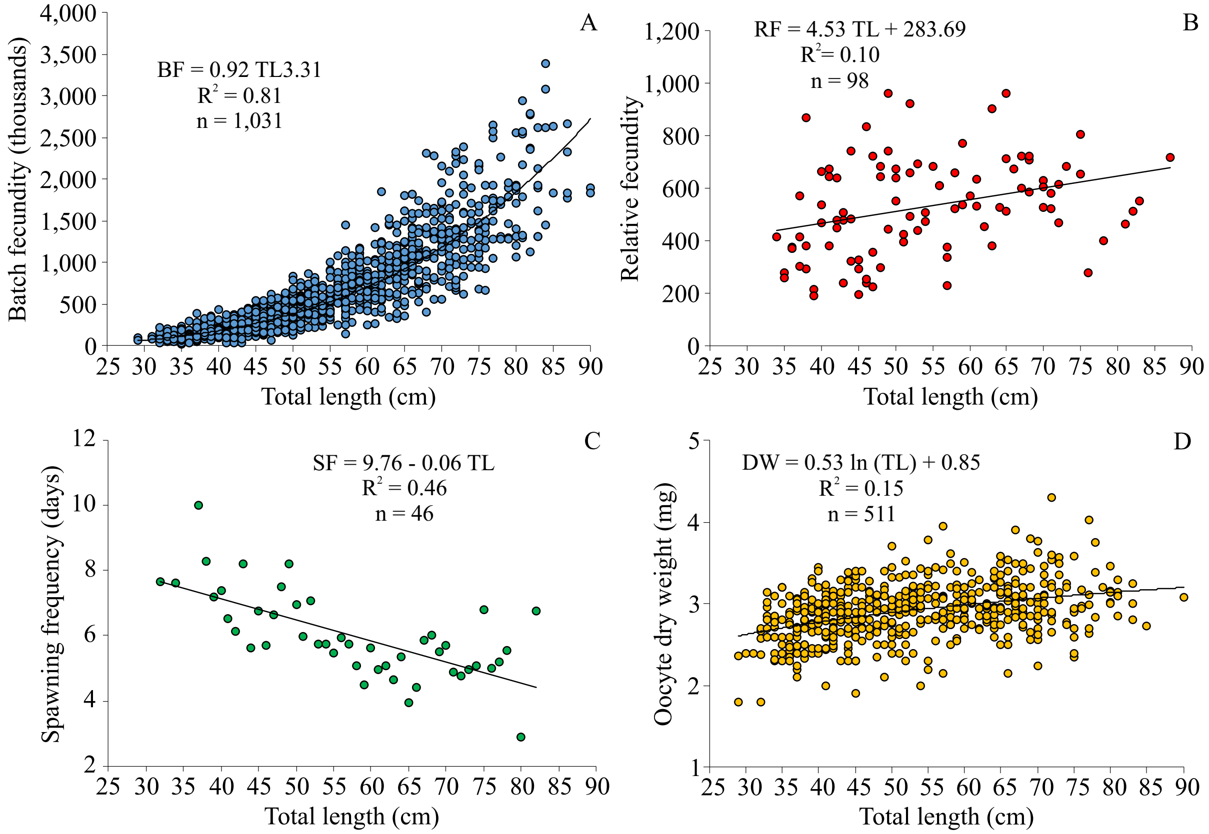

Figure 3. Influence of maternal size on the reproductive potential of *Merluccius hubbsi* from the Patagonian stock determined by the relationships between batch fecundity (A), relative fecundity (B), spawning frequency in days (C), and oocyte dry weight (n = 100 hydrated oocytes) (D) with female total length. All data correspond to the spawning peak of the Patagonian stock (January) and were obtained from Macchi et al. (2013, 2018).

produced decreases towards the end of this period, coupled with the reduction of batch and relative fecundity (Macchi et al. 2006).

Regarding the relationship between oocyte quality and maternal characteristics in hake, studies showed that both the dry weight of hydrated oocytes and the size of the oily droplet increase with total length (Figure 3 D), weight and age of females (Macchi et al. 2006, 2013; Rodrigues et al. 2018). These results suggest that eggs produced by largest females would have a greater amount of stored reserves, giving rise to larger larvae, having a positive effect on survival rates during this critical phase of early development (Hinckley 1990; Rijnsdorp and Vingerhoed 1994). Female condition, as determined from the hepatosomatic index (HSI) and gonadosomatic index (GSI), has also shown positive relationships with oocyte quality (Macchi and Leonarduzzi 2022). However, the analysis of proximal composition carried out with female hake did not show a direct relationship between the lipid content in the liver and muscle and the lipid content in the ovaries (Leonarduzzi 2018). This is probably due to the energy allocation strategy of hake, which shows a very dynamic exchange between food intake and organs involved in energy storage during reproduction, or that the level of oocyte quality is independent of liver reserves available at the time of spawning.

In summary, characteristics of the parental stock, particularly size, age, and condition of females, have a significant impact on the reproductive potential of this population. This characteristic, called 'maternal effect', suggests that SSB, commonly used as an index of productivity in fishery assessment, is a poor predictor of recruitment for hake. Therefore, in order to preserve a level of egg production that allows a higher rate of larval survival, it is convenient to preserve a population structure that ensures the presence of large females, as they have longer reproductive periods with higher fecundities and major quality eggs. As a result, it was decided to include a goal of reaching a SSB composed of at least 16-18% of large individuals (age-5+) in the assessment of the Patagonian stock since 2013 (Santos and Villarino 2013). These percentages arose from analyzing the population structure of hake obtained from research surveys carried out since the early 1990s, and from the information resulting from commercial catches carried out during years prior to the overexploitation of this resource.

EARLY LIFE STAGES (EGGS, LARVAE AND YOUNG-OF-THE-YEAR)

Abundance and spatial distribution

Studies of ichthyoplankton in the Argentine hake were based on developmental stages described by Ehrlich (1998) and Betti et al. (2009). In general, highest densities of eggs and larvae occur within the main spawning area of the stock, between 42° S and 45° S from the coast to 100 m depth. During summer research surveys conducted in this region from 2009 to 2018, a wide distribution of hake ichthyoplankton was observed. Eggs were found in 50-82% of stations and larvae were found in 28-60% of plankton trawls (Ehrlich et al. 2019). When evaluation the presence of hake ichthyoplankton during the whole reproductive season, it was discovered that smaller larvae were typically found during the first spawning events in December, while the size range increased and abundance reached its highest values in January (Machinandiarena et al. 2004a, 2004b). Acoustic records obtained during monthly cruises throughout the reproductive season also reflected this, showing that hake larvae dispersed southwards by the end of summer (Álvarez Colombo et al. 2011).

Analysis of hake ichthyoplankton during the last 20 years showed inter-annual variations in the spatial distribution and density of egg and larval aggregations in the north Patagonian area, which could be associated with movements made by hake spawners during the reproductive season or with environmental aspects (Macchi et al. 2013, 2021). In general, sampling stations with maximum egg and larval records were characterized by a strong thermocline. The thermal variability observed at surface and bottom allowed us to confirm that hake larvae are resilient to temperature changes, at least within a range of 3-4 °C during the larval phase (Ehrlich et al. 2019). Acoustic records in the nursery area showed that larvae with swim bladder (> 4 mm TL) performed vertical migrations during the daily cycle, locating near the bottom during daylight hours and near the thermocline during the night (Álvarez Colombo et al. 2011). These authors suggest that the migratory behavior could be associated with the two-layered circulation pattern with an opposite flow described for the area by Palma et al. (2008) in summer, allowing the larvae to remain retained in that area with optimal survival conditions.

As the reproductive season progresses the hake larval nursery area in the north Patagonian region provides recruits to the stock. This fact has been verified by the displacement and size increase of post-larvae and juveniles towards San Jorge Gulf, which is the main aggregation area for YOY specimens (Machinandiarena et al. 2006; Álvarez Colombo et al. 2011). This group includes juveniles that span the developmental stage between larval metamorphosis and the first year of life, generally overlapping with the settlement of the species to the demersal environment. Settlement refers to the acquisition of the habit of settling near the bottom, which in the case of hake is mostly observed during daylight hours. This habitat change between larvae and juveniles can be studied by analyzing the microstructure of otoliths with the formation of accessory growth cores (Campana 1984). In *M. hubbsi* from Patagonian stock it was observed that the transition to demersal habit began at approximately 50 days of life (15 mm LT) and ended at 80 days (30 mm LT). The average age of settlement was estimated at 66.7 ± 8.6 days (Buratti and Santos 2010). However, as detailed further in this review, new evidence on the vertical distribution of YOY individuals obtained from acoustic records suggests that the final settlement would occur later, possibly at the end of age-0 stage (35-150 mm TL). Studies on the characteristics of benthic communities associated with hake pre-recruits suggested a preference for boulder and sponge bottoms during this phase of the life cycle (Giberto et al. 2014, 2015).

Growth

Knowledge of the processes that act generating mortality during early life stages is fundamental to understanding inter-annual variability in the recruitment (Houde 1987). As larvae grow, they are less vulnerable to mortality due to predation, so an accelerated growth increases larval survival rate by decreasing the residence time of early stages (Legget and Deblois 1994; Houde 2008). In addition, the growth of fish larvae and juveniles is a metabolic indicator that provides information on the potential of nursery areas, which could be relevant for the management of a fishery resource. The most commonly used method for determining the age and daily growth of fish larvae is the analysis of daily increments of *sagitta* otoliths (Jones 1992; Houde 2008). The daily pattern of otolith increments deposition in the Argentine hake larvae was adopted according to criteria established by other authors for larvae of the Genus *Merluccius* such as *M. productus* (Bailey 1982) and *M. merluccius* (Arneri and Morales-Nin 2000; Morales-Nin et al. 2005).

Several research cruises were conducted along the Patagonian coast in the summers of 2001, 2005, and 2009, with a wide spatiotemporal coverage, including most of the reproductive season of hake. In 2001, hake larvae were collected in a size range between 2 and 11 mm TL, their ages were determined and a linear growth model was fitted (Brown et al. 2004). The growth rate (0.156 mm day^{-1}) was quite similar to values obtained by other authors for larvae of the same genus, such as *M. products*: 0.16 mm day^{-}1 (Bailey 1982) and 0.156 mm day^{-1} (Butler and Nishimoto 1997), and *M. bilinearis*, 0.17 mm day^{-1} (Jeffrey and Taggart 2000).

Different types of nets were used in subsequent studies to better characterize the growth and size range of the larvae caught (Betti et al. 2014). These authors analyzed hake larvae in a size range from 2 to 24 mm TL, and established two exponential growth models in 2005 and 2009, which were statistically different from each other. Mean daily growth values were 0.22 mm day^{-1} in 2005 and 0.31 mm day^{-1} in 2009, similar to values recorded for other hake larvae of the genus (Brown et al. 2004; Álvarez and Cotano 2005; Palomera et al. 2005; Grote et al. 2012). During the 2009 spawning season, variations in the daily growth of hake larvae were detected, which were attributed to different availability of copepods during that time (Betti et al. 2014).

The hatching dates distribution curve could provide information about periods of high mortality or good survival of different cohorts of larvae. Hatching dates of larvae born in 2001 ranged from 11 December to 20 February, with a maximum between 21 and 31 January. The hatching period for larvae caught in 2005 ranged from 11 November to 20 February, with a peak between 1 and 10 January, while in 2009 it ranged from 11 December to 31 March, with a peak between 21-31 December. Although several cohorts of hake larvae were observed in the same spawning season (Figure 4), as a general trend, all larvae hatched within the spawning period reported for this species in the north Patagonian area (Macchi et al. 2004, 2010).

With respect to juvenile hake, studies of daily growth have been carried out on specimens captured in autumn and winter of 2001, ranging between 26 and 190 mm TL (Santos et al. 2005). Results from the analysis of back-calculated spawning dates revealed that the highest number of births would have occurred between January and mid-February 2001. This result was conditioned to the sampling time; therefore, the period was not necessarily the moment of the greatest spawning. Estimates of juvenile growth rates showed values of ca. 0.60 mm d^{-1} for individuals captured in May, born between December 2000 and April 2001 (ca. 150 and 70 days, respectively). Highest growth rates (0.70 mm d^{-1}) corresponded to individuals born in January and February, while the lowest (0.40 mm d^{-1}) to those born at the beginning of spawning, between September and October. These data are similar to those estimated by Hollowed (1992) and lower than those found by Woodbury et al. (1995) for *M. productus*. From these studies, it was possible to corroborate that specimens born in late winter/spring would have slower growth rates than those born in summer, and that individuals captured in Camarones Bay showed higher growth rates than those from San Jorge Gulf and shelf waters.

Mortality

Most fish suffer high mortality rates during early life stages, which in the case of marine teleosts exceed 99% during the egg and larval stages (Bailey and Houde 1989; Houde 2008). The classic methodology used to determine fish larval mortality is the construction of survival curves (Houde 2002), which seek to rebuild the decline in numbers of a cohort of larvae from the age-specific abundances of individuals. For this purpose, an exponential extinction model is fitted to the averages of larval abundances by age class, expressed as densities.

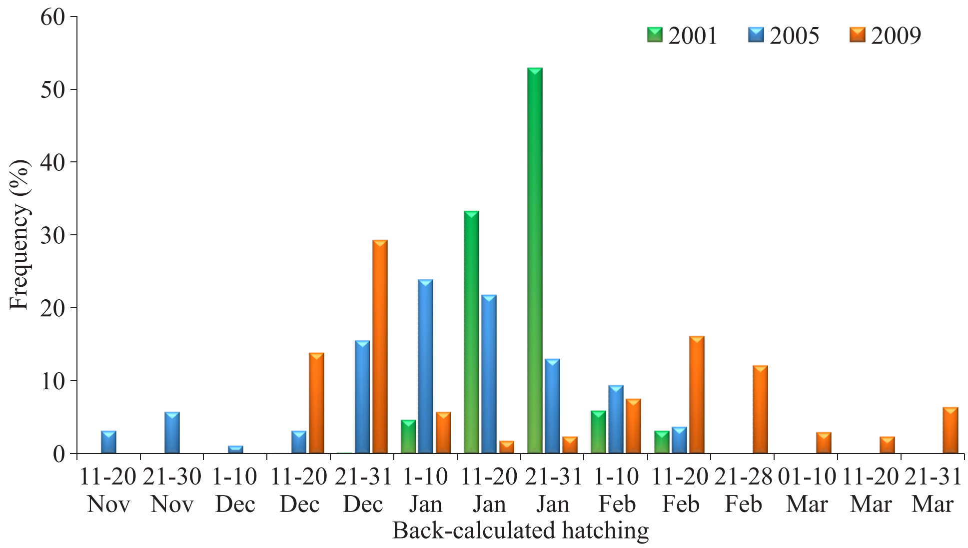

Figure 4. Back-calculated hatching dates of *Merluccius hubbsi* larvae from the Patagonian stock captured during reproductive seasons 2001, 2005 and 2009. Data from Brown et al. (2004, 2009, 2013).

Estimates of daily mortality rates for hake larvae (Table 1) were obtained from eight research surveys conducted along the north Patagonian area during different months of reproductive seasons 2001, 2004-2005, 2009 and 2010 (Brown et al. 2004, 2009, 2013). Except for the value of 0.27 in January 2001, which was associated with a very high density of larvae at age-0, reflecting a recent spawning pulse (Brown et al. 2004), mortality coefficients ranged from 0.062 to 0.12. Although it has commonly been associated with predation (Houde 2008) or with competition for food, as recently suggested for hake larvae from Patagonian stock by analyzing the relationship between egg production, larval abundance in the nursery area and their nutritional condition (Diaz et al. 2020; Macchi et al. 2021), it is particularly challenging to establish the causes of mortality in fish larvae.

Feeding

The traditional gut content analysis was used to conduct trophic studies on larvae and YOY individuals of hake from Patagonian stock (Ciechomski and Weiss 1974; Viñas and Santos 2000; Moriondo 2002). Coupled with these studies, a large amount of information has been gathered on the availability of their zooplanktonic prey in the environment, which has allowed determining their preference and/or selectivity and the implications of such choices upon recruitment.

The larval diet was analyzed in the warm period covering the size range from the onset of exogenous feeding (< 5 mm TL) to early (5-10 mm TL) and advanced stages (10-25 mm TL) (Temperoni and Viñas 2013). With increasing length, a higher number of preys consumed was observed, which highlights the ability of hake lar-

Table 1. Daily growth models and comparison of number of individuals at age-0 (N_0) and natural mortality (M) of hake larvae estimated during different months of the reproductive seasons 2001, 2004-2005, 2009 and 2010. N = number of sampled larvae; DM = daily mortality percentage; R^2 = coefficient of determination. From Brown et al. (2004, 2009, 2013).

Reproductive seasons	Month	N	Size range (mm)	Age range (days)	Growth model	N_0	M	DM
2001	January	2,343	2.00-6.50	1-35	$L(t) = 0.136\ t + 1.76$ ($R^2 = 0.86$)	880.07	0.270	23.67
	February	305	2.50-11.00	3-59	$L(t) = 0.153\ t + 1.95$ ($R^2 = 0.87$)	72.24	0.120	11.30
2004-2005	December	190	1.92-5.68	0-36	$L(t) = 2.08exp(0.04t)$ ($R^2 = 0.923$)	12.077	0.092	8.83
	January	339	2.92-14.00	9-67	$L(t) = 2.06exp(0.04t)$ ($R^2 = 0.889$)	121.15	0.092	8.79
	February	516	1.92-16.17	0-40	$L(t) = 2.06exp(0.03t)$ ($R^2 = 0.916$)	32.394	0.087	8.31
2009	January	454	2.00-12.00	1-44	$L(t) = 2.147exp(0.04t)$ ($R^2 = 0.71$)	79.34	0.062	6.01
	March	2,359	2.00-20.00	1-59	$L(t) = 2.662exp(0.034t)$ ($R^2 = 0.931$)	103.40	0.105	9.97
2010	January	1,520	1.40-8.20	0-57	$L(t) = 1.95exp\ (0.042\ t)$ ($R^2 = 0.88$)	111.70	0.080	7.70

vae to pursue, capture and handle prey items along ontogeny, as well as the higher energetic requirements as they grow and develop. Larvae capture small prey at the onset of exogenous feeding that are replaced with larger items as their body increases in size, increasing the diversity of their diet. While first feeding larvae selected adult stages of *Drepanopus forcipatus* and calanoid copepodites ranging in size 1-2 mm and < 1 mm (despite being less abundant in the environment than other available prey), early and advanced larvae exclusively predated upon adult stages of *Calanoides carinatus* and *D. forcipatus*, even when their abundances were very low in the zooplanktonic community (Temperoni and Viñas 2013). Hake larvae probably preferred these preys considering their intermediate size, reflecting an optimal balance between the energetic profit and the cost of their capture. On the other hand, the high incidence of calanoid copepods in the larval diet might relate to their nutritional benefit in terms of the high amount of polyunsaturated fatty acids (Temperoni et al. 2019a).

The 'fatty acid trophic markers (FATM)' approach was also used to investigate the diet of hake larvae (Temperoni et al. 2019a), identifying prey specific signatures in their tissues. While the gut content analysis provides a 'snapshot' of the recent diet, FATM integrates the diet on longer time scales by analyzing the assimilated food items in the tissues. As expected, a high overlap in the fatty acids profile between hake larvae and calanoid copepods was observed, especially by means of markers 22:1n9 and 22:1n11. Moreover, signatures typical of bacteria (15:0, 17:0) were identified, suggesting a microbial input at the base of the food web in the hake spawning ground, as well as those from dinoflagellates (18:4n3, 22:6n3) that probably act as intermediaries towards the larvae. FATM also suggested possible direct predation of hake larvae upon protozoans, which cannot be easily detected in the gut content analysis, thus broadening the information gathered from the traditional approach. Information on the available prey field for hake larvae was improved in recent years (Derisio et al. 2014, 2021; Temperoni et al. 2014; Cepeda et al. 2019) by the incorporation of a finer sampling mesh (e.g. 67 µm). This allowed expanding the knowledge on the zooplankton community with respect to older studies (e.g. Santos and Ramírez 1995) that only properly characterized meso (0.2-20 mm) and the macro (2-20 cm) zooplanktonic fractions. Since hake larvae consume mostly individuals from the microzooplankton (20-200 µm) fraction, this information has been key to better establishing their prey selectivity.

With respect to the YOY individuals, older studies compiled by Temperoni (2015) were mostly qualitative and included a low number of samples. More recently, research was expanded to include individuals from 100 to 150 mm TL that are going through their first year of life (Temperoni et al. 2013, 2018, 2020b). The preferred prey of this group were crustaceans from the macrozooplankton fraction, mainly hyperiid amphipods (*Themisto gaudichaudii*) and euphausiids (*Euphausia* spp.), and to a lesser extent decapods (*Peisos petrunkevitchi* and pelagic stages of *Munida gregaria*). The capture of these preys involves a lower energetic cost associated with searching, handling and ingestion compared to more mobile prey such as fish, which probably explains their great incidence in YOY individuals. In the context of these trophic studies, and given the advanced decomposition of some prey items in the gut content, equations were developed to estimate the size of *T. gaudichaudii* and *Euphausia* spp. from their remains that resist digestion (such as carapaces or eyes), to obtain an estimate of their individual weight from length-weight relationships (Temperoni et al. 2013).

It should be mentioned that, asides from the traditional gut content approach, the stable isotope analysis has been applied to determine the trophic niche and position of hake larvae (from the spawning ground) to juveniles until age-2 (in the nursery ground) (Botto et al. 2019). Hake occupies different trophic niches along ontogeny. Larvae (8-34 mm TL) mostly ate copepods, while age-0 individuals (35-150 mm TL) exhibited a rather diverse diet with consumption of amphipods and euphausiids, as well as epibenthic prey (mysidaceans and *P. petrunkevitchi*). The older (150-320 mm TL) and already settled individuals showed an almost exclusively epibenthic diet.

Within the nursery ground in San Jorge Gulf, high availability of prey items for YOY hake has been described, most likely guaranteeing their development and survival. First studies described horizontal spatial and temporal patterns in the distribution of the main groups, such as copepods, euphausiids and hyperiid amphipods (Pérez Seijas et al. 1987; Viñas et al. 1992; Fernández Aráoz 1994). More recent analyses have shown the importance of the macrozooplankton fraction in terms of abundance within the gulf when compared with adjacent areas further north (Derisio and Martos 2018; Derisio 2020, 2021). Representative species are euphausiids *Euphausia lucens* and *Nematoscelis megalops*, hyperiid amphipod *Themisto gaudichaudii* and squat lobster *Munida gregaria*. Particularly for the euphausiids, studies on their vertical distribution pattern have been performed by means of net samplings and video plankton recorder data in summer (Nocera et al. 2021). A classical diel vertical migratory pattern was observed, with individuals ascending in the water column during dawn (~ 18:30 h) and descending at dusk (~ 06:30 h), remaining as dense aggregates near the bottom during the day. In agreement, studies performed in the cold season combining acoustic and net samplings allowed to describe a similar migratory pattern for both euphausiids and copepods (Menna et al. 2022).

Carbon sources and trophic structure in San Jorge Gulf have been evaluated by means of stable isotope analysis (Giménez et al. 2018). Feeding regimes indicated that zooplankton items could be either herbivorous, carnivorous or omnivorous, with appendicularians located at the base of the food web, while copepods occupied an intermediate position and chaetognaths at the top. An enrichment in carbon isotopes was observed from north to south of the gulf, indicating that the main carbon source would not be the same in every sector of the nursery ground.

Nutritional condition

The study of nutritional condition allows the evaluation of the individual physiological state of fish larvae and juveniles, which is a reflection of environmental features to which they have been exposed. Nutritional condition indices have been widely used to determine the importance of starvation in the early stages of fish, and to estimate their survival probabilities, thus making it possible to detect high mortality events during ontogenetic development or to characterize breeding areas. Different criteria have been developed to estimate larval condition based on the effects of starvation on body shape, condition factor, cell constituents, or characteristics of their tissues (Ferron and Leggett 1994). Currently, the standardized RNA/DNA (RDs) ratio is the most widely used biochemical index to assess the nutritional condition of fish larvae (Chícharo and Chícharo 2008). Cohen et al. (2020) used morphometric variables and RDs to compare the condition of hake larvae from northern and southern stocks. Both indicators showed a better condition for larvae from the southern stock, but statistically significant differences could only be detected using the RDs, indicating that RDs are more sensitive than morphometrical indicators. However, previous studies using morphometric variables such as body height and weight have also shown to be reliable indicators of condition for hake larvae of the Patagonian stock (Diaz et al. 2014a). Since the effect of fixation causes the larval body to shrink, one of the drawbacks presented by these techniques is the necessity of establishing shrinkage indices prior to their application (Diaz et al. 2015).

Studies based on the RDs of hake larvae and early juveniles (2-72 mm SL) from the Patagonian stock that were collected during the austral summer season between 2010 and 2021 (Diaz et al. 2014b, 2020; Rodriguez et al. 2023), have shown variations in nucleic acid concentrations during the early ontogeny of the species at different developmental stages (Figure 5 A). The RDs showed a significant decrease during the beginning of ontogeny in the larval preflexion stage (3-4 mm SL) and in the postflexion stage (15-16 mm SL). The highest values of the RDs and the greatest variability were observed at the beginning of the transformation toward the juvenile stages. After that, indices decreased toward the initial juvenile stage (60-70 mm). The ontogenetic pattern of the RDs was similar to that observed in *M. paradoxus* and *M. capensis* larvae by Grote et al. (2012). At least two stages of great vulnerability are observed by reductions registered in the RDs: one coinciding with the start of exogenous feeding and another during the transition from the postflexion stage to the larval transformation stage, when settlement occurs and the trophic niche abruptly changes. These periods represent critical moments with a significant reduction in the abundance of individuals and their condition.

The RDs indices showed spatial variations in the nutritional condition of hake larvae. Cohen et al. (2020) observed differences between larvae from northern and southern stocks (Figure 5 B). For the Patagonian hake stock, spatial changes in adult reproductive activity caused an expansion in the spawning area and variability in larval condition outside the traditional breading area (Figure 5 C). Larvae hatched in disadvantageous areas for development are less likely to survive and therefore a reduction in subsequent recruitment will probably be observed (Diaz et al. 2014a, 2020). Diaz et al. (2020) indicated that variables regulating the larval condition of the Patagonian hake stock are larval length, temperature, and larval density. Both temperature and larval density presented negative coefficients, indicating that lower temperatures favor larval condition and the existence of density-dependent mechanisms at high larval densities. These results coincide with those previously mentioned, in that highest larval densities are associated with the presence of marked water stratification. The presence of the NPFS would favor the aggregation of larvae and their potential food, although at high densities it could cause a detriment to the larval condition due to competition for food. Future studies integrating endogenous and environmental variables will provide in-depth knowledge of parameters that determine the larval condition of hake, influencing their survival and subsequent recruitment.

Contamination by microplastics (MPs) has recently been incorporated as a determining factor of the nutritional condition of specimens, given that MPs accumulate in areas with oceanographic discontinuities and would have an overlap in size with potential preys (Di Mauro et al. 2022). Efforts are currently focused on the development of models including all available variables that allow explaining the nutritional condition of larvae of this species of great fishing relevance.

First studies to assess the condition of YOY hake were carried out by Prenski and Angelescu (1993) using the Fulton index. In more recent analyses, information on lipids stored in the liver (hepatosomatic index HSI, and lipid percentage %L) was incorporated as a proxy of condition (Temperoni et al. 2018, 2020a). Both indices showed significant seasonal and spatial variations, being maximum in spring and minimum in winter, with intermediate values in summer, associated with variations of Chl-*a* concentration from satellite measures. Hence, the existence of a bottom-up type control upon YOY nutritional condition mediated by the consumption of herbivorous euphausiids, which are the preferred prey throughout the year was suggested. In this sense, the simultaneous evaluation of lipid and fatty acid composition of their main zooplanktonic prey (Temperoni et al. 2019b, 2020c, 2022;

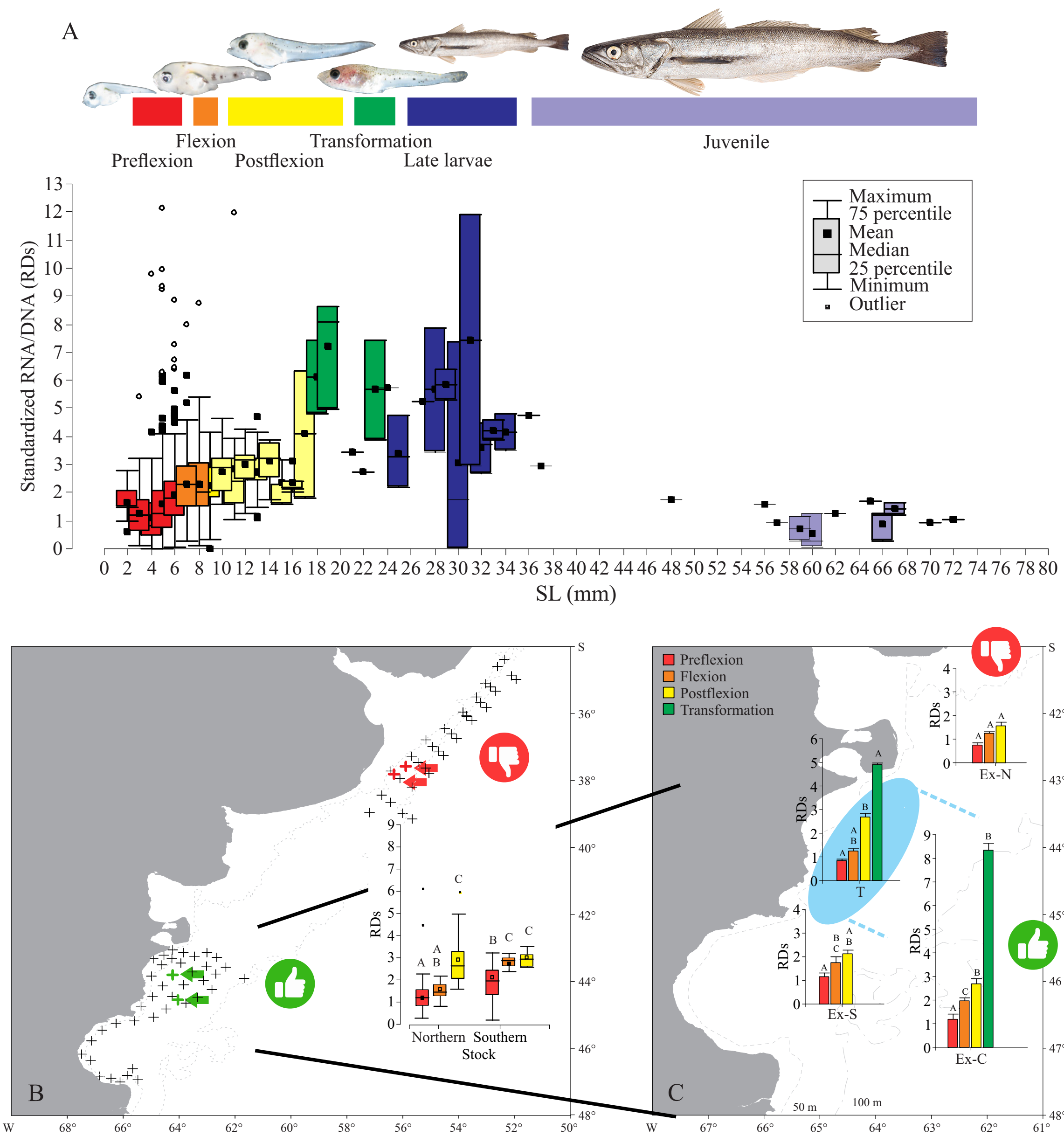

Figure 5. A) Box-plot diagram of standardized RNA/DNA ratio (RDs) obtained for each size class of *Merluccius hubbsi* larvae. Developmental stages are indicated. B) Box-plot diagram of RDs obtained for each hake larvae developmental stage from northern and southern stocks. Crosses indicate position of sampling stations; arrows indicate where hake larvae for RDs ratio analysis were collected for stock comparisons. Different letters indicate significant mean value differences ($p < 0.05$) of RDs in Tukey's post hoc comparisons by the two-way ANOVA (stock and stage of development). C) Box-plot diagram of standardized RDs ratio obtained for each hake larvae developmental stage from different areas of the southern stock. In light blue: schematic delimitation of the Traditional spawning grounds (from Álvarez Colombo et al. 2011). T: traditional spawning area. Ex-N: external northern area. Ex-C: external central area. Ex-S: external southern area. Different letters indicate significant differences ($p < 0.05$) in mean values of the RDs in Tukey's post hoc comparisons of the two-way ANOVA (area and stage of development). Modified from Diaz et al. (2014a, 2020), Cohen et al. (2020) and Rodriguez et al. (2023).

Temperoni and Massa 2021), provides a fundamental perspective to understand the food preferences of YOY individuals in terms of their nutritional quality and energy intake. For instance, in summer, low condition values observed in the central region of San Jorge Gulf were associated with the consumption of *T. gaudichaudii*, that has a lower nutritional value in comparison to euphausiids, due to the lower amount of polyunsaturated fatty acids (PUFA). In this area, it was observed that YOY hake retain essential PUFAs and mobilize monounsaturated ones, such as 16:0 palmitic and 18:1n-9 oleic acids to obtain energy (Temperoni et al. 2018).

Predation and competition

In terms of predation pressure within the spawning area, a high horizontal overlap between hake eggs and larvae and adult specimens of the ctenophore *Mnemiopsis leidyi* was observed (Mianzan 1999; Mianzan and Guerrero 2000). It has been suggested that ctenophores may affect fish recruitment by direct predation of eggs and larvae and/or through competition for food with the larvae (Purcell and Arai 2001, and references therein). In this context, the existence of a high overlap and an inverse correlation between the mean abundance of *M. leidyi* and hake larvae suggests a potential risk for *M. hubbsi* recruitment in the north Patagonian area. However, this approach needs to be complemented as recent studies describe the low clearance rate of ctenophores on fish eggs and larvae (Jaspers et al. 2011). Furthermore, despite the horizontal overlap, they could be occupying different vertical strata.

As a prey, YOY hake in San Jorge Gulf nursery area constitutes an important food source for several demersal fish such as *Squalus acanthias*, *Zearaja brevicaudata*, *Genypterus blacodes* and *G. brasiliensis* (Sánchez and Prenski 1996; García de la Rosa and Sánchez 1997). The energy density deriving from proteins and lipids stored in muscle and liver, as a food quality proxy for these predators, show that the YOY hake has a low or moderate quality compared to other available prey in the nursery area, such as *E. anchoita*, mollusks (e.g. squid) and some crustaceans (e.g. shrimps) (Temperoni et al. 2020b).

ENVIRONMENTAL VARIABILITY AND RECRUITMENT

There are few studies that analyze the influence of the interannual variability of physical factors on the reproduction and recruitment of the Argentine hake. Temperature is generally considered among the most important variables affecting the maturation and spawning process of fish, also influencing growth rates during early life stages (Houde 2009). Salinity may be another significant variable for fish reproduction; however, in the case of hake from the Patagonian stock, values obtained in the spawning area in general show little variation ranging between 33.40 and 33.60 near the bottom (Macchi et al. 2010). In this area, maturation of hake may occur in a wide temperature range from 7 °C to 15 °C, but females in ovulation were mainly recorded at temperatures between 9 °C and 13 °C (Macchi et al. 2021). Areas with a higher abundance of eggs and larvae of hake are coincident with the location of main spawning groups of this species (Álvarez Colombo et al. 2011); thus, the thermal range is similar to that observed for females in ovulation (Macchi et al. 2021). Based on this information, optimal areas for the spawning and nursery of hake have been defined, whose dimensions showed interannual variations, depending on the position of the bottom thermal front (Macchi et al. 2021). These authors observed that years characterized by a reduced optimal spawning area and higher larval density resulted in lower recruitments, which could be associated with higher mortality rates due to density-dependent processes.

Satellite analysis of Chl-*a* concentration in the north Patagonian area during spring and summer of 1997 to 2015, showed that years with the highest values of Chl-*a* had a positive influence on the recruitment of hake one year later (Marrari et al. 2019). These results suggest that higher primary productivity during the spawning season could lead to higher larval survival rates, probably due to greater availability of food in the nursery area. In any case, the relationships obtained were weaker than those reported for other species, such as *Engraulis anchoita* from Buenos Aires area (Marrari et al. 2013), possibly due to values of Chl-*a* concentration estimated in the north Patagonian region during November-January (average 1.84 mg m^{-3}) remain relatively high compared to other areas (Marrari et al. 2019).

Information on the variability of surface temperature (ST) in the north Patagonian area for the same period, showed that lower surface temperatures by the end of the spawning season (April) could be beneficial for larval survival, generating higher recruitments one year later (Marrari et al. 2019). These authors also demonstrated that physical variables analyzed (Chl-*a* and ST) showed a positive trend in the area during the last two decades. These findings are significant in the current context of climate change because of their potential impact on the reproductive success and recruitment of many species, including the Argentine hake.

ADVANCES IN THE ESTIMATION OF RECRUITMENT INDICES

The assessment model used to diagnose the state of the Patagonian hake stock (VPA-XSA and ECE) allows obtaining estimates of recruitments during the period under exploitation. The model is based on catch-at-age data adjusted with catch per unit effort (CPUE) indices and abundance indices independent of fishing activity, derived from research surveys (Santos and Villarino 2022). During the last years, attempts have been made to include new indices derived from advances in the knowledge of the life history of hake, such as the abundance of YOY juveniles per swept area and estimates of reproductive potential during the spawning peak of the stock. However, this new information did not evidence a significant improvement in the S-R relationship estimated by the assessment model.

The YOY juvenile abundance estimates were obtained by bottom net trawls of reduced dimensions (~ 4 m horizontal and ~ 0.8 m vertical opening) called 'pilot net', assuming that hake juveniles adopt demersal habits during the settlement process, shortly after the end of the metamorphosis process from larval stages, thus becoming available for capture with bottom trawls. This hypothesis on the vertical distribution of early juveniles in the nursery area was mainly based on knowledge of the size and timing of settlement of different hake species (Papaconstantinou and Stergiou 1995; Payne and Punt 1995; Auster et al. 1997), including *M. hubbsi* (Ehrlich 1998; Machinandiarena et al. 2006; Buratti and Santos 2010). Nevertheless, during research surveys carried out to assess the abundance of juvenile hake of the Patagonian stock, it was observed that catches with the Pilot net were inefficient for assessing smallest juveniles (Castrucci et al. 2003). The acoustic information demonstrated that the transition from pelagic to demersal habitat of YOY hake takes longer than previously recognized for this species, which may explain their low catchability with bottom trawls (Álvarez Colombo et al. 2014). These last authors observed a diurnal pelagic behaviour of hake juveniles through acoustic records, which was later validated by the capture with pelagic nets. The assessment of YOY juvenile (A-0) with acoustic methods provided for the first time estimates of abundance in orders of magnitude compatible with recruitments obtained one year later, represented by the age-1 group (A-1). Information from research surveys carried out in the winters of

2011, 2012 and 2016 showed a large difference between the A-0 estimates obtained from acoustic data with those derived from bottom trawling with the Engel net (Figure 6 A). However, values obtained in 2011 and 2012 from acoustic records were compatible with the abundance of survivors in the following year (A-1) estimated from the swept area method (Figure 6 B). Acoustic estimates of A-0 juveniles were combined with estimates from annual modelling assessments of other age groups to get a complete picture of the stock structure in different years (Figure 7), revealing that 2011 and 2012 cohorts turned out to be very similar based on the acoustic data and model results. Acoustics from 2016 indicated a strong cohort during this year that was later confirmed by the model information (Santos and Villarino 2022). While these results are promising, the possibility of using an acoustic index of YOY juveniles should rely on data from a larger number of research surveys, allowing the evolution of a larger number of cohorts to be analysed. In any case, acoustics could provide a valid recruitment index for the Patagonian hake stock based on direct field observations, considering the expected level of natural mortality of fully developed juveniles, as opposed to the reduced survival of eggs and larvae of the species. These results show the importance of the information obtained with echo sounders, which is complementary to estimations made by swept area with bottom trawls. In other gadoid fisheries, such as cod and haddock, acoustic and swept area indices of abundance are combined in an estimate of absolute abundance (Godø and Wespestad 1993; Guttormsen et al. 2003; Hjellvik et al. 2003; Fleischer et al. 2005), providing a broader framework for understanding the sources of variability associated with such estimates.

Recent advances from specific hake recruitment surveys using an Engel net have shown that A-0 juveniles vary their vertical distribution pattern (Álvarez Colombo et al. 2021). These authors observed that highest concentrations in San Jorge Gulf remain pelagic during the day, but occasionally approached to the bottom beyond the range of echo sounders, effectively being captured by bottom trawls. On-going studies on the effect of marine circulation, as well as other environmental and habitat structure factors and survey designs in the nursery sector of the species, may explain part of the variability detected in the respective abundance estimates.

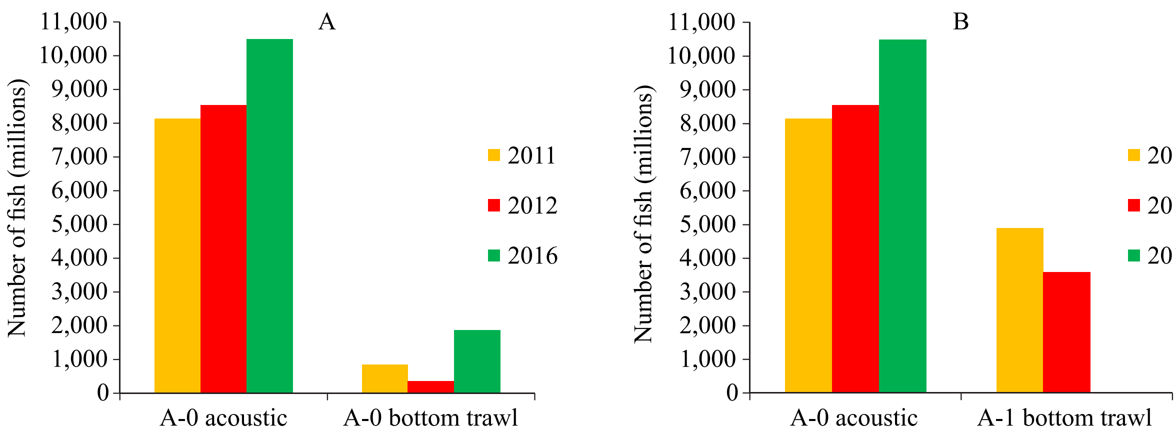

Figure 6. A) Absolute abundance of *Merluccius hubbsi* age-0 group from Patagonian stock estimated using acoustic (A-0 acoustic) and bottom trawl swept area (A-0 bottom trawl) methods during 2011, 2012 and 2016. B) Abundance of age-0 group estimated by acoustic (A-0 acoustic) in 2011, 2012 and 2016, and survivors in the following year estimated from swept area method (A-1 bottom trawl) corresponding to 2011 and 2012 cohorts. Data from Álvarez Colombo (2021) and Santos and Villarino (2022).

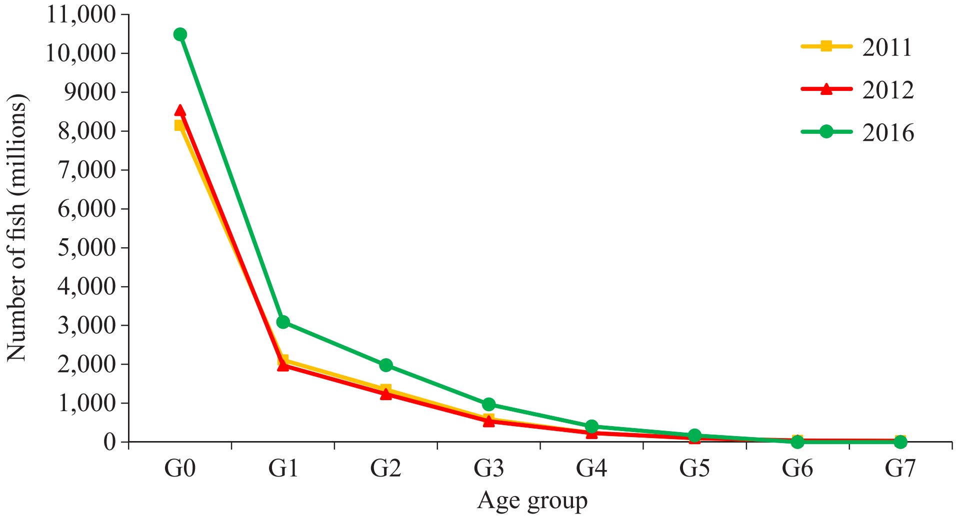

Figure 7. Abundances of 2011, 2012 and 2016 cohorts of *Merluccius hubbsi* from Patagonian stock estimated by combining the age-0 group (G0) obtained by using the acoustic method, with the rest of the age groups (G1-G7) obtained with the assessment model. Data from Álvarez Colombo (2021) and Santos and Villarino (2022).

PERSPECTIVES AND FUTURE CHALLENGES

Several research lines may contribute to the understanding of recruitment variability of the Patagonian hake stock. Future studies may focus on male characteristics and their influence on the reproductive success and recruitment of hake, which is the influence of the 'parental effect' on the offspring. This topic has rarely been studied in most species, since information on reproductive potential has generally focused on females. However, the contribution of males to ensure the reproductive success of fish, beyond eggs fertilization, has reached greater relevance in recent years (Domínguez-Petit et al. 2022). For example, it is important to analyze the influence of male characteristics (size, age and nutritional condition) on sperm quality, or to establish how the sex ratio and the size/age composition of males may affect fertilization rates or larval survival. It is essential to plan experimental studies in order to evaluate these aspects as well as to corroborate the maternal effect hypothesis. With the help of these studies, it may be possible to establish whether there is a correlation between parental characteristics and those of their offspring (larval size, condition or survival rates).

The selection of spawning sites and environmental factors that trigger maturation and ovulation of this species are currently the subject of research. In this regard, reproductive ecophysiology studies involving sex steroids (testosterone, estradiol, progesterone) during the maturation cycle are being developed in order to evaluate hormonal profiles of specimens depending on environmental conditions (Elisio et al. 2021). Since the Patagonian stock reproduces in a transition zone within the NPFS, where temperature exhibits strong horizontal and vertical gradients, the main hypothesis suggests that temperature is the variable that determines ovulation. However, mechanisms underlying this process are unknown.

Further studies on the nutritional condition are important to complement traditional analysis on the feeding of the Argentine hake with the measurement of stable C and N isotopes, in order to build the trophic web and analyze the energy flow and its role in survival and reproductive success.

Stomach content studies provides a 'snapshot' of an individual's diet, while stable isotope analysis use Bayesian mixing models to fit values of $\delta 13C$ and $\delta 15N$ from tissues to estimates of prey assimilated rather than ingested. This point is highly relevant, since recently observed changes in the diet of the Patagonian hake stock related to the increase of *Munida gregaria* in that region, could affect the condition and reproductive potential of the species. In addition, further studies on the composition of fatty acids, both in hake and their prey, could serve not only to evaluate the condition of specimens but also as food web biomarkers. This is particularly relevant in the current scenario of changes for the north Patagonian ecosystem, since variations in the *de novo* production of fatty acids at the base of the food web could move towards YOY hake with implications for recruitment success (Jónasdóttir 2019).

In the case of hake larvae, it should be highlighted the importance of carrying out laboratory experiments keeping specimens under controlled conditions, in order to compare with individuals captured in the field. These studies would make it possible to infer the survival potential of larvae and eventually estimate the probability that these individuals will survive the critical period and be recruited to the fishery. In this sense, some attempts have been made to keep specimens alive in INIDEP aquaria (Betti et al. 2013; Radonic et al. 2013; Suárez et al. 2013), but experiments did not exceed 20 days of larval survival. Recently, some studies showed the existence of density-dependent mortality processes in the Argentine hake larvae from the north Patagonian area, which could affect the recruitment of this stock (Diaz et al. 2020; Macchi et al. 2021). This would be reflected in both the nutritional condition and survival rates during early stages of larval life, either due to competition for food between individuals of the same species or with other organisms. For this reason, studies are currently being carried out to evaluate the role of macrozooplankton, particularly ctenophores, as a competitor of hake larvae. The aim is to complement field observations with experimental studies, which allow corroborating whether the abundance of ctenophores has a significant effect on the survival of hake eggs and larvae, acting either as a predator or as competitor of this species.

One of the most relevant results obtained within the REC project was the observation and recording of pelagic aggregations of YOY hake during daylight hours (Álvarez Colombo et al. 2014). This finding was first made acoustically and later corroborated by the capture of specimens with pelagic nets. The relevance of these results lies in the fact that, until then, it was thought that once the Argentine hake settled near the bottom, it maintained an exclusively demersal behavior during the day and only migrated towards the pelagic region at night. For this reason, to assess the abundance of the juvenile fraction, demersal trawls have traditionally been used during the day, whose vertical opening does not exceed one meter from the bottom (Álvarez Colombo et al. 2014). As was mentioned in the previous item, this means that abundance values obtained with this capture method actually represent a small fraction of juveniles to be evaluated. This situation raises the need to generate new methodologies that allow estimating abundance indices for the age-0 group of hake in a more appropriate way. A possibility with great potential for the future is to use information from acoustic transects to obtain abundance indices that estimate the real magnitude of pelagic groups of hake. This methodology would not only allow obtaining more realistic estimates, but would also provide a synoptic overview of the distribution of juveniles of the species, both in horizontal and vertical dimensions.

The distribution of the Argentine hake in the north Patagonian area shows spatial changes during its life cycle. As already mentioned, hatching and development of early stages of this species take place mostly in coastal and shelf waters between 43° S and 45° S; however, highest abundances of the YOY individuals, particularly pelagic aggregations, occur towards the south of this region, in San Jorge Gulf (Álvarez Colombo et al. 2014). Preliminary results suggest that the early larvae remain retained in the main spawning area, and that later post-larvae and early juveniles (< 9 cm TL) drift towards San Jorge Gulf at the end of the reproductive period (Álvarez Colombo et al. 2011). To support this hypothesis, it is necessary to model the current flow in the involved areas. This will help to understand how the retention process works in the breeding zone and how it relates to the juvenile zone. At present, there are little data on coastal currents from the north Patagonian area, so it is necessary to increase this information in order to contribute to the development of new models that allow explaining how circulation at different depths affects hake recruitment. Studies with satellite monitoring of drifting buoys are also required to detect drift routes for hake eggs and larvae. Such studies should be related to the directionality and intensity of currents at different spatial and temporal scales.

Finally, a relevant aspect for the future is the need to develop new recruitment models allowing the incorporation of biological and environmental information in order to generate greater reliability in the stock assessment. This would be a fundamental advance compared to traditional models, since it would make it possible to broaden the spectrum of variables associated with the process of incorporating new individuals into the population, improving understanding of the dynamics of the stock-recruitment system and, consequently, increasing the predictive capacity of models (Lowerre-Barbieri et al. 2016).

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