MISS BRENDA TEMPERONI (Orcid ID : 0000-0003-1580-221X)

DR. MARINA MARRARI (Orcid ID : 0000-0002-3806-8356)

Article type      : Original Article

# SEASONAL AND SPATIAL VARIABILITY IN CONDITION OF AGE-0+ ARGENTINE HAKE *MERLUCCIUS HUBBSI* MARINI, 1933 IN THE SAN JORGE GULF (ARGENTINA): A BOTTOM-UP PERSPECTIVE

Running title**:** Age-0+ *Merluccius hubbsi* condition

BRENDA TEMPERONI [1,2] *, AGUEDA E. MASSA [1,2], PATRICIA MARTOS [3], MARINA MARRARI [4,5]

[1] Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N° 1, B7602HSA, Mar del Plata, Argentina

[2] Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMdP-CONICET, Rodríguez Peña 4046, B7602GSD, Mar del Plata, Argentina

[3] Departamento de Ciencias Marinas, Facultad de Ciencias Exactas y Naturales, UNMdP. Deán Funes 3350, B7602AYL Mar del Plata, Argentina

[4] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Godoy Cruz 2290, C1425FQB, Buenos Aires, Argentina

[5] Departamento de Oceanografía, Servicio de Hidrografía Naval (SHN), Av. Montes de Oca 2124, C1270ABV, Buenos Aires, Argentina

*Corresponding author: btemperoni@inidep.edu.ar

ABSTRACT AND KEYWORDS

In the north Patagonian region of the Argentinean Continental Shelf, the San Jorge Gulf (SJG; 45°-47°S, 65°30'-67°30'W) is the main nursery ground of age-0+ Argentine hake *Merluccius hubbsi* Marini, 1933, one of the most important fishery resources in Argentina. The gulf exhibits strong seasonal and spatial fluctuations in environmental features, which might affect survival of age-0+ individuals and recruitment to the adult population. Our main goal was to evaluate the seasonal and spatial dynamics of their nutritional status within the SJG in winter 2016, spring 2016, and summer 2017. Condition indices (relative condition factor $K_n$, hepatosomatic index HSI and liver lipid content %L) and diet information (feeding incidence, relative importance of prey) were combined with physical (temperature, salinity) and biological (satellite chlorophyll-*a* concentration; chl-*a*) data. Age-0+ condition indices and prey intake showed significant seasonal variations, with minimum values in winter, intermediate in summer and maximum in spring, strongly coupled to the mean chl-*a* concentration in each season. Herbivorous euphausiids *Euphausia* spp. were the preferred prey along the study period. A bottom-up effect on condition of age-0+ hake is suggested, manifested as lower condition values in winter, the less productive season. Spatially, better conditioned individuals matched sectors of the gulf where chl-*a* concentrations were higher, coupled to the presence of frontal systems. Monitoring age-0+ hake nutritional status is relevant in the current global change scenario, which might modify phytoplankton biomass and composition and, consequently, the herbivorous zooplankton abundances.

Merlucciidae; prerecruits; Argentine shelf; Patagonian stock; nutritional condition; seasonality; spatial patterns

# 1. INTRODUCTION

Fish survival at early life stages depends on the temporal and spatial overlap with prey resources, following the match-mismatch hypothesis (Cushing, 1990). In temperate ecosystems, variability in physical and biological features such as the onset of stratification, light availability and the occurrence of phytoplankton blooms, affects the seasonal and spatial patterns of zooplankton abundance, which further influences the feeding success of planktivorous fish. Adequate feeding translates into energy reserves stored within individuals, which reflect their well-being or physiological condition to accomplish essential biological processes such as growth and reproduction (Lloret et al., 2002). This is critical during the recruitment process, when fish early stages must achieve high growth rates to minimize vulnerability to size-selective predators (Sogard, 1997). In this sense, condition studies focused on fish prerecruits (age-0+ year individuals) are of particular interest, since this stage is considered a major determinant of adult fish stocks year-class strength (Hüssy et al., 1997). Ultimately, identification of links between fish nutritional status, ocean conditions and productivity could provide a mechanistic framework for predicting the effects of climate change on temperate marine food webs, as well as improve ecosystem-based models that are under development for fisheries management (Litz et al., 2010).

Fish condition can be assessed from a variety of indices, which differ in terms of sensitivity - referring to the minimum environmental change that can be detected- and latency -the time required for a given change in the environment to be reflected in the index- (Ferron & Leggett, 1994). Morphometric indicators are based on length and mass ratios, such as the relative condition factor $K_n$ (Le Cren, 1951), while physiological types give information about fish energy reserves, such as those mainly concentrated in the liver through the hepatosomatic index HSI (Lambert & Dutil, 1997). These indices provide essential criteria for assessing fish condition. However, despite being commonly used and easy to calculate, several reviews have highlighted their statistical deficiencies (Cone, 1989; Hayes & Shonkwiler, 2001). On the other hand, biochemical indices are based on determining different components in fish tissues, such as lipid content (Fonseca et al., 2013). Previous studies indicate that morphometric, physiological and biochemical indices do not always correlate, indicating they do not measure the same aspect of the nutritional status (McPherson et al., 2011). Morphometric indicators encompass shorter response time to nutritional stress, while lipids have been pointed out as more accurate indicators of long-term (weeks to months) growth potential and

survival probability of fish early stages (Weber et al., 2003; Fonseca et al., 2013). Thus, to gain further insight into fish nutritional status, condition should ideally rest upon a multi-index approach.

Argentine hake *Merluccius hubbsi* Marini, 1933, is one of the most important fishery resources in the Argentinean continental shelf (ACS) (Irusta et al., 2016). Of two main stocks, the southern or Patagonian one (41º-55ºS) is the most abundant, accounting for 85% of total hake biomass. Within the north Patagonian shelf (NPS), hake fishery overlaps in time and space with another fishery targeting Argentine red shrimp *Pleoticus muelleri* (Góngora et al., 2012). *M. hubbsi* is a batch spawner with indeterminate annual fecundity (Macchi et al., 2004) that reaches maturity at a size of ~32-35 cm (ages between 2.6 and 2.8, respectively) (Irusta et al., 2016). Prior to the onset of spawning (October), adults move from deeper waters towards the coast (near the 50 m isobath) where reproduction takes place. Spawning occurs during austral spring and summer (from November to March) with a peak in January, in the Isla Escondida sector of the NPS (IE; 43°-45°30'S) (Pájaro et al., 2005) (Figure 1a). The San Jorge Gulf (SJG; 45°-47°S, 65°30'-67°30'W) is the main nursery and settlement location of hake prerecruits (age-0+ individuals; 10-13 cm total length) (Álvarez-Colombo et al., 2011). These individuals access the gulf from the spawning sector in IE by the end of summer, probably favored by the circulation patterns in the region (Álvarez Colombo et al., 2011), remaining there until age 2. Both age 0 and age 1 (14-23 cm total length) groups are found between the coast and the 100 m isobath with concentrations at 43°30'S-47°S and maximum yields within the SJG. Distribution of the age 2 (24-32 cm total length) group is similar, but extended to 200 m, while individuals age 3 and over distribute from the shelf to the slope (Renzi et al., 2003). During daylight hours, age-0+ hake form dense aggregations separated 15-20 m from the bottom in winter and 10-15 m in summer (Álvarez Colombo et al., 2014). At night, they perform vertical migrations towards the upper layers, following the movements of their preferred zooplankton prey, mainly euphausiids and hyperid amphipods (Temperoni et al., 2013). These individuals, as well as spawners, are protected by year-round areas closed to fishing in the NPS (~42°-48°S, 60°-65°W) (Irusta et al., 2016). In addition, within the SJG, temporal restrictions to fishing are established by provincial authorities from Chubut and Santa Cruz provinces (Góngora et al., 2012). Despite the use of selectivity devices (Ercoli et al., 2000) recommended in hake and red shrimp fisheries, juvenile *M. hubbsi* by-catch and discards occur, which have the largest impact on the age 1 group (Irusta et al., 2016 and references).

In recent years, studies on age-0+ hake condition using morphometric, physiological and biochemical indicators have intensified in the main nursery areas of both stocks in the ACS

(Temperoni et al., 2018a; b). For the Patagonian population, results evidenced a strong spatial coupling between nutritional status of the individuals and phytoplankton biomass in the SJG during summer. Hence, a bottom-up effect was suggested to be the main driver of such coupling, mediated by age-0+ hake consumption of herbivorous euphausiids. However, whether this effect on prerecruits condition occurs in periods other than summer remains to be explored. In this context, the main goal of this study is to assess the seasonal and spatial changes in age-0+ hake condition within the SJG in relation to the environmental variability (temperature, salinity, chlorophyll-*a* concentration) and prey intake (feeding incidence, relative importance of prey), during winter 2016-summer 2017. We hypothesize that a year-round bottom-up effect on age-0+ hake condition occurs within the San Jorge Gulf, manifested as a poorer nutritional condition in less productive seasons (i.e. winter and summer) with respect to spring, when the main phytoplankton bloom occurs. Results are expected to significantly contribute to *M. hubbsi* recruitment studies in the Argentinean continental shelf.

## 2. MATERIALS AND METHODS

### 2.1. STUDY AREA

The San Jorge Gulf (45°-47°S, 65°30′-67º30'W) is a semi-closed basin (maximum depth ~ 100 m) with a rather deep connection to the open shelf (Figure 1a). As a spawning and nursery ground for commercial fisheries such as *M. hubbsi* and *P. muelleri* (Góngora et al., 2012), it has been identified as a priority strategic area by Argentina's federal government program "Pampa Azul" (2014). The gulf is occupied by a mixture of Shelf Water (salinity 33.4 to 33.8) and Low-Salinity Coastal Water (LSCW; salinity <33.4; Bianchi et al., 2005) that flow northwards from the Magellan Strait and Beagle Channel transported by the Patagonian Current. When reaching the southern tip of the gulf, LSCW diverge into two branches. One branch flows into the SJG along the coast, while the other continues towards the northeast, thus separating water masses inside the gulf from those located at east by an outer thermal front (Matano & Palma, 2018; Palma et al., 2020). Numerical modeling has shown the existence of wind-driven upwelling mechanisms along the south and southwest coast, which have also been identified by lower in situ temperature and salinities (Tonini et al., 2006; Rivas & Pisoni, 2010; Pisoni et al., 2018). The shallowest areas in the northern and southern gulf (~ 30 m) are characterized by frontal systems. At the northern end, a highly productive Northern Patagonian Frontal System (NPFS) (42º30'-45ºS) develops during austral spring and summer, forced by seasonal thermal stratification and high tidal energy dissipation typical of the area (Sabatini & Martos 2002; Bogazzi et al., 2005). In the south, the permanent thermohaline Southern

Patagonian Frontal System (SPFS) represents the transition between tidally mixed, nutrient-rich LSCW (Guerrero & Piola, 1997; Bogazzi et al., 2005) and seasonally stratified, more saline waters of the continental shelf. Associated with these fronts, maximum phytoplankton concentrations occur from spring (diatom-dominated) until the end of the summer (dinoflagellate-dominated), with a secondary maximum in autumn and a minimum in winter (diatom-dominated) (Akselman, 1996; Glembocki et al., 2015). Following the seasonal and spatial patterns in chlorophyll-*a* values and water column stability, a rather diverse zooplankton community develops. The micro and mesozooplankton fractions are dominated by calanoid copepods and appendicularians, while the macrozooplankton is mostly represented by early stages and adults of euphausiids (*Euphausia* spp.: *E. lucens* + *E. vallentini*), hyperid amphipods (*Themisto gaudichaudii*) and decapods (*Munida gregaria* and *Peisos petrunkevitchi*) (Cepeda et al., 2018 and references therein).

## 2.2. SAMPLING

Age-0+ hake were captured during daylight at a variable number of sampling stations during three research cruises carried out in the SJG in austral winter (September 2016), spring (November 2016) and summer (January 2017) (Figure 1b; Table 1). Winter and summer cruises were carried out onboard the R/V "*Eduardo Holmberg*" (Instituto Nacional de Investigación y Desarrollo Pesquero, INIDEP), and individuals were collected with a bottom trawl net Engel (100 mm mesh at codend with an intranet cover of 20 mm mesh size, headrope of 35 m and footrope of 50 m). The spring cruise was performed onboard the R/V "*ARA Puerto Deseado*" (Pampa Azul program), and prerecruits were captured with a Pilot net (50 mm mesh at codend with an intranet cover of 10 mm mesh size). These are appropriate gears for sampling age-0+ hake, since they reside on or close to the bottom during daytime (Álvarez Colombo et al., 2014). Fish were frozen at -20ºC to minimize lipolytic enzyme activity quickly following catch.

## 2.3. SIZE AND CONDITION INDICES

In the laboratory, 3-10 individuals (depending on availability) were randomly selected from every sampling station of each cruise (Table 1). Age-0+ hake were thawed and total length ($L_T$, in cm; from the tip of the snout to the end of the caudal fin) and total mass ($M_T$, in g) were measured for a total of 120 individuals (winter 2016 n = 45; spring 2016 n = 40; summer 2017 n = 35). After dissecting the liver (preserved at -80ºC), the stomach (preserved in 5% formaldehyde) and the

remaining viscera, measurements of somatic mass ($M_s$, representing total mass without head, gonads and stomach content) and liver mass ($M_H$, in g) were taken.

From these measures, two condition indices were calculated: the relative condition factor ($K_n$), as the ratio of the observed $M_s$ and the expected $M_s$ predicted by the $L_T$–$M_s$ relationship; and the hepatosomatic index (HSI), as HSI = ($M_H$/$M_s$) * 100. As a biochemical index, total liver lipid content (%L, expressed as g 100 $g^{-1}$ of wet mass) was determined gravimetrically (in duplicate), following Folch et al. (1957) (from 0.1-0.5 g of liver homogenate of each individual, processed with a glass potter). Liver was selected as the target organ to determine lipids since it is the main energy storage tissue in juvenile gadoids (Lambert & Dutil, 1997).

## 2.4. FEEDING ANALYSIS

Feeding incidence was calculated as the percentage of age-0+ hake with at least one prey item in their stomach (Arthur, 1976). Prey items were identified to the lowest possible level. The contribution of each prey category to the diet was examined through its frequency of occurrence (%F) and numerical abundance (%N). Both parameters were integrated in an index of Relative Importance (RI) (Laroche, 1982), calculated by multiplying the %F and %N of each prey, and expressed as %RI.

## 2.5. ENVIRONMENTAL VARIABLES

Temperature and salinity measures were taken from CTD casting of Seabird profilers (winter 2016: n = 42, SBE-19; spring 2016: n = 86, SBE 911; summer 2017: n = 83, SBE 25). Oceanographic data were processed using standard Seasoft routines (Sea-Bird Electronics, 1997) and stored in "Base Regional de Datos Oceanográficos (BaRDO)-INIDEP" (Baldoni et al., 2008). Data were visualized and plotted with Ocean Data View Software (ODV-version 4.7.10; Schlitzer, 2016). For statistical analyses, bottom temperature and salinity were selected, considering the vertical distribution of age-0+ hake during daylight (Álvarez Colombo et al., 2014). For each cruise, the position of the frontal systems was determined with the Simpson's stability index ($\phi$, J $m^{-3}$) (Simpson, 1981), considering values of $\phi$ = 30-40 J $m^{-3}$ as the limit between homogeneous and stratified waters (Sabatini & Martos, 2002; Bogazzi et al., 2005). As a proxy of phytoplankton biomass, monthly averages of MODIS Aqua surface chlorophyll-*a* concentrations (chl-*a*; mg $m^{-3}$) with a spatial resolution of 2 km $pixel^{-1}$ were obtained for each cruise (data distributed by NASA Goddard Space Flight Center, http://oceancolor.gsfc.nasa.gov).

## 2.6. DATA ANALYSES

For the statistical analyses, age-0+ hake condition indices ($K_n$, HSI, %L) and the relative importance of *Euphausia* spp. in the diet (%$RI_{euph}$) were considered as response variables, while total length ($T_L$), bottom temperature ($T_B$), bottom salinity ($S_B$), chlorophyll-*a* concentration (chl-*a*), season (winter, spring and summer) and sampling station were included as explanatory variables. For the spatial analyses, sampling stations within each season were grouped following pre-defined areas (*sensu* Glembocki et al., 2015), which these authors determined based on preliminary analysis of surface temperature, satellite chl-*a* and basin topography of the gulf. Four areas were considered: Northern (NA), Central Coastal (CCA), Central (CA), and Southwestern (SWA) (Figure 1b).

To evaluate the relationship between (1) condition indices and $T_L$ of individuals (as estimates of these indicators can be biased by size effects) and (2) morphometric ($K_n$), physiological (HSI) and biochemical (%L) indices, Spearman's correlations were used. Seasonal variability in $T_L$ and the environmental variables was explored by means of Generalized Linear Models (GLMs), since assumptions of normality (Shapiro test) and homogeneity of variance (Bartlett test) were not fulfilled. GLMs were also used to test for variability in condition indices and the relative importance of *Euphausia* spp. in the diet, considering season (winter, spring, summer), area (NA, CCA, CA, SWA), $T_B$, $S_B$ and chl-*a* as explanatory variables. Both season and station were included as factors in the models. A gamma family error distribution (log link function) was assumed (with the exception of %$RI_{euph}$, were a negative binomial distribution was chosen), and a stepwise forward regression procedure was applied to select for the best model, considering the lowest Akaike's information criterion (AIC), which was compared with the AIC of the null model (without any explanatory variables). Analyses were performed with the R software version 4.0.1 (R Development Core Team, 2014), setting significance at $P < \alpha = 0.05$.

## 3. RESULTS

### 3.1. AGE-0+ SIZE

Mean total length of age-0+ hake varied significantly among seasons (Table 1), with smaller individuals in spring than in winter and summer (Table 2). On the contrary, no significant differences were recorded in $T_L$ among areas within each season ($P > 0.05$). Correlations between total length and condition indices $K_n$, HSI and %L were not significant ($P > 0.05$).

### 3.2. AGE-0+ CONDITION AND FEEDING

A positive and significant relationship was observed between HSI and %L ($rs$ = 0.65; $R^2$ = 0.42; $P$ < 0.0001). Values of $K_n$, HSI and %L ranged from 0.8 to 1.3 (1.0 ± 0.1), 0.9 to 7.4 (3.4 ± 1.1) and 2.0 to 27.4 (10.6 ± 6.7), respectively. Feeding incidence was 75% considering all data from the three seasons, with euphausiids *Euphausia* spp. as the preferred prey item in terms of relative importance (%RI>75) (Figure 2). The diet also included other euphausiids (*Nematoscelis megalops*), the decapods *Peisos petrunkevitchi* and *Munida gregaria*, the hyperid amphipod *Themisto gaudichaudii*, misidaceans and non-identified crustaceans, although with lower relative importance with respect to *Euphausia* spp.

### 3.2.1. Seasonal variability

In the selected GLMs of $K_n$, HSI, %L, and %RI$_{euph}$, the variable season was statistically significant (Table 2). Minimum $K_n$ values were recorded in summer (0.98 ± 0.10) and spring (0.99 ± 0.08) with respect to winter (1.05 ± 0.10), while for HSI and %L, values increased from winter (HSI: 3.1 ± 0.8; %L: 4.7 ± 1.4) to summer (3.2 ± 1.2; 10.6 ± 5.1) and spring (4.1 ± 1.1; 17.2 ± 5.2) (Figure 3). Feeding incidence and %RI$_{euph}$ followed a similar seasonal trend (Table 3), exhibiting higher percentages in spring and summer. In the models of %L and %RI$_{euph}$, the environmental variables chl-*a* and T$_B$ were also selected. Both features showed a significant increase from winter to summer (Table 4) with a marked seasonal signal (Table 5), while this was not observed for bottom salinity.

### 3.2.2. Spatial variability (within-season)

In winter, models for $K_n$ (Figure 4a), HSI (Figure 4b) and %L (Figure 4c) did not show significant spatial variations between areas. However, $K_n$ was positively related to chl-*a* concentration (Table 6). Higher condition values were observed in NA, CCA and SWA with respect to CA, concurrent with the highest chlorophyll-*a* records (Table 4; Figure 5a). These areas exhibited similar bottom temperatures (Figure 5b), while bottom salinities were higher in NA and CA and minimum at SWA (Figure 5c). Opposite to condition indices, area was selected as a significant variable in the %RI$_{euph}$ model, together with chl-*a* (Table 6); higher relative importance of this prey occurred in NA with respect to CA and SWA (Table 3).

In spring, no significant spatial variations were observed in $K_n$ (Figure 4a) and %RI$_{euph}$ (Table 3). This condition index was again explained by chl-*a* concentration, but the relationship was negative (Table 6). Chlorophyll-*a* concentration was high in most areas of the gulf during this season, but particularly at CCA (Figure 5a). On the other hand, area was a significant variable in HSI (Figure

4b) and %L (Figure 4c) models (Table 6). Both indices indicate a similar spatial trend, with minimum values in NA, CA and SWA with respect to CCA. Maximum spring values of $T_B$ occurred in NA and CA (Figure 5b), where the onset of stratification was evident ($\Phi > 30$ J m$^{-3}$). Horizontal thermal gradients indicate the incipient formation of the NPFS in the north end of the gulf. Maximum bottom salinities were also observed in these areas (Figure 5c) and, at the south end, the presence of the SPFS was evident from thermal and saline gradients.

In summer, area was selected as a significant variable in the %L model (Table 6), while this was not observed for $K_n$ (Figure 4a) and HSI (Figure 4b). Lipid-based condition values were higher in CA (Figure 4c), corresponding to the highest values of chl-*a* (Figure 5c). Chlorophyll-*a* values followed a spatial distribution strongly linked to the bottom temperature field (Figure 5b). Water column stratification was maximum in summer ($\Phi > 40$ J m$^{-3}$), with strong gradients in the north end, indicating the NPFS. On the other hand, bottom salinity was selected as a significant variable in the HSI and %RI$_{euph}$ models. Values were higher in CA, concurrent with a weak stratification in the $S_B$ field (32.9 to 33.57 at the surface (figure not shown; 33.03 to 33.5 at the bottom) and the input of low salinity coastal waters in the south end of the gulf, indicating the SPFS (Figure 5c).

## 4. DISCUSSION

This paper examines the seasonal and spatial variability in age-0+ *M. hubbsi* condition within their main nursery ground in the north Patagonian shelf, in relation to environmental features and by means of different indices. Results represent an improvement with respect to previous studies on the Patagonian stock (Temperoni et al., 2018a), which only explored spatial patterns of age-0+ condition during austral summer. Here, further exploration of the seasonal dynamics on the nutritional well-being of the individuals, as well as the spatial variability during winter and spring periods was carried out. It should be noted that the cruises from which samples were collected were not specifically designed to evaluate *M. hubbsi* condition, but rather were assessment and/or oceanographic cruises in which age-0+ hake samplings occurred opportunistically and were not fixed. This represented a constraint with respect to the number of sampling stations available per cruise as well as a comparable design among seasons, which most likely impacted our ability to conclude about within-season spatial patterns. In spite of this, interesting links between age-0+ condition and environmental variables arose, which set the basis for future sampling oriented to more thoroughly explore such variability.

Age-0+ hake lipid-based nutritional status and prey intake (mainly the euphausiid *Euphausia* spp.) showed clear seasonal changes, increasing from winter to summer, which resembled the

significant trend recorded in chl-*a* concentration as well as the increase in stratification of the water column and the formation of frontal systems within the gulf. Similar results have been obtained in related gadoid species such as *Theragra chalcogramma* (Brodeur et al., 2000; Kooka et al., 2009) and *Merluccius merluccius* (Hidalgo et al., 2008). In temperate ecosystems, juvenile fish generally accumulate energy as lipids to overcome winter (Sogard, 1997), being these reserves more elevated in the previous season. In age-0+ hake, minimum liver lipids observed in winter may reflect the depletion of the energetic reserves during the previous months (autumn-early winter). The latter lipid accumulation during chl-*a* peaks in spring and summer could be considered as a storage strategy to face the following winter. Lower lipid reserves during winter could also be related with prey availability. Abundances of *Euphausia* spp. in the SJG are known to be lower in winter (0.62 ± 0.64 ind m$^{-3}$; Belleggia et al., 2019) than spring (12.94 ± 19.39 ind m$^{-3}$; Temperoni & Derisio, 2018) and summer (4.85 ± 6.49 ind m$^{-3}$; Derisio & Martos, 2018). These euphausiids are mainly herbivorous species (Stuart, 1989; Gurney et al., 2002) that can benefit from nutrient resuspension and elevated chl-*a* values to sustain their populations and build energetic reserves, especially during spring and summer. In this sense, the bottom-up effect upon age-0+ hake condition that was suggested for the summer by Temperoni et al. (2018a), in which the available phytoplankton energy was transferred to the prerecruits through consumption of herbivorous euphausiids, would also be occurring in spring and winter, modulated by prey abundance. Corroborating our hypothesis, the bottom-up effect was manifested as a poorer condition, in winter, when local productive and feeding conditions were less favorable. This also suggests that the potential time-lag in the chl-*a* effect on condition, which was previously observed in other gadoids (Hidalgo et al., 2008; Rueda et al., 2015), would not be occurring in the gulf. This lag is attributed to the energy transfer efficiency of the trophic cascade as well as to the complexity of the food web. The lack of such lag in the SJG might respond to the properties of the local phytoplankton blooms. For instance, in spring, the bloom is known to last for an average of 110 days (Marrari et al., 2019), which is considerably longer than bloom periods reported for other areas of the NPS.

Not only phytoplankton availability but also its composition could explain the observed seasonal changes in age-0+ hake condition. Fish nutritional status usually benefits more from diatom-based food webs (St John & Lund, 1996) than from more heterotrophic food chains supported by flagellates and ciliates, since the latter are less efficient in energy transfer (Cushing, 1989). In this context, higher condition values observed in spring might respond to diatom dominance within the gulf (Segura & Silva, 2017), most likely responsible for the elevated satellite chl-*a*

concentrations, while by the end of spring and during summer, dinoflagellates predominate and chl-*a* values diminish (Akselman, 1996). In spring, not only *Euphausia* spp. but also the decapod *Munida gregaria* contributed to elevated feeding incidences, season in which condition of age-0+ hake was higher. This might respond to the notorious input of its pelagic zoea and decapodite stages to the zooplankton community, which matches the phytoplankton spring peak and the reproductive period of the species that begins in August (Varisco, 2013). Particularly, in recent years the presence of the pelagic morphotype of the species (*M. gregaria*) in relation to an increase in chl-*a* concentration that would favor its prevalence over the benthic morphotype (*M. subrugosa*) (Ravalli et al., 2013; Varisco, 2013). The preference for euphausiids over other prey items was mentioned in previous studies, which mostly corresponded to summer records (Temperoni et al., 2013 and references therein), as well as the increasing importance of *M. gregaria* in *M. hubbsi* diet, particularly since 2011 (Belleggia et al., 2017). The positive selection of both prey by age-0+ hake, irrespective of the season, could be related with their better nutritional quality in energetic terms over other available prey such as amphipods or other decapods, as observed by Temperoni & Derisio (2018) in spring.

Within each season, spatial heterogeneity was also recorded in local productivity and the degree of stratification of the water column, which was manifested as changes in age-0+ condition. The best conditioned individuals inhabited areas of high chl-*a*, a pattern that was previously observed in other gadoids. For instance, in *M. merluccius* from the Balearic Islands, Hidalgo et al. (2008) compared recruit condition in two locations with different oceanographic conditions, attributing the observed patterns to differential productivity of water masses. Despite the low number of sampling stations in each cruise and the fact that they were not fixed, consistent spatial trends in condition were also revealed here. For instance, in spring, prerecruits in better condition were observed in CCA, were upwelling occurs (Tonini et al., 2006; Rivas & Pisoni, 2010; Pisoni et al., 2018), while in summer, enhanced nutritional status was observed in CA, where stratified inner waters encounter vertically mixed water from the southeast (Glembocki et al., 2015; Matano & Palma, 2018; Palma et al., 2020). Accordingly, in summer, higher relative importance of *Euphausia* spp. in the diet was observed in CA. In this sense, this mainly herbivorous prey would act as an intermediary in the energy transfer from primary producers to age-0+ hake. In winter, on the contrary, the spatial pattern was less clear and in the southern end of the gulf, where chl-*a* values peaked, no samples were available to evaluate condition. However, due to the presence of a permanent thermohaline front it this area, a spatial effect upon condition of age-0+ hake could be expected, which deserves further exploration in future cruises. Identifying spatial patterns at local scale is

relevant, provided that effects of environmental drivers on fish condition that might be considered for assessment and management could be ignored when searching for general responses at large scales (Rueda et al., 2015).

Results indicate that morphometric and biochemical condition indices were not interchangeable metrics of age-0+ *M. hubbsi* nutritional status. For instance, $K_n$ was not correlated with %L, which was also observed in *G. morhua* (Pardoe et al., 2008). In addition, this index showed a non-consistent correlation with chl-*a* values in winter and spring, which was not observed for the other indices. On the other hand, significant correlation between the physiological index HSI and the biochemical %L indicates that the former is a good indicator of the energetic condition of hake prerecruits. Similar results were observed in other gadoids (Lambert & Dutil, 1997; Lloret et al., 2008) and in *M. hubbsi* females (Leonarduzzi et al., 2014). In this sense, HSI is easier to obtain from liver mass, and could be regularly used as an indicator of hake physiological status, reflecting the lipid reserves stored in such tissue. Typically, the higher the organization level of the index, the longer it takes to respond to an environmental change for a given developmental stage, species, and specific nutritional status of the individual in a given season. Suthers (1998) postulated that the difference in temporal responses of the indices to environmental factors, i.e., latency, is one of the reasons why several condition indices derived from the same individual are poorly correlated to each other. For instance, low sensitivity of $K_n$ to short-term events has been highlighted, since mass changes require longer to be perceived (Ferron & Leggett, 1994). In contrast, liver-based indices are known to respond more rapidly to external changes (McPherson et al., 2011), particularly in Gadidae such as *M. hubbsi* that store most of their lipid reserves in this organ (Lambert & Dutil, 1997). In addition, assessment of condition variability depended on the index used, as previously observed by other authors (e.g. Schloesser & Fabrizio, 2016). For instance, HSI and %L revealed clear seasonal trends that $K_n$ did not. Liver-based indices exhibited similar trends, reinforcing their accuracy to reveal seasonal and spatial shifts in condition, as previously suggested for prerecruits (Temperoni et al., 2018a; b) and adults (Leonarduzzi et al., 2014) of *M. hubbsi*, and for other gadoids (e.g. juvenile polllock; Kooka et al., 2009). It is also worth mentioning that these indices were not significantly correlated with total length, suggesting a very weak effect of *M. hubbsi* size on the condition estimates within the size range used. Consequently, their use is allowed without a bias from the effect of size, as stated by Bolger and Connolly (1989). Similar results were reported in juvenile gadoids such as *G. morhua* (Lambert & Dutil, 1997) and *M. merluccius* (Lloret et al., 2008). Ultimately, differential patterns observed for each index suggest that, as previously discussed by

several studies (e.g. Lloret et al., 2002; McPherson et al., 2011), a multi-index approach can provide a more accurate understanding of age-0+ hake energy-storage strategies.

Aside from physical and biological variables affecting age-0+ hake condition within the San Jorge Gulf that were explored in the present study, other non-tested potential factors that might be affecting their well-being should be considered. For instance, in terms of fishing pressure, vulnerability to fishing gear may be increased when hake prerecruits are in poor condition, affecting competency of swimming behavior. On the other hand, age-0+ individuals in poor condition may be able to escape through the fishing mesh while rounder, better condition conspecifics are retained (Dutil et al., 1995). In this sense, being in good condition does not necessarily mean higher chances of survival. Predatory pressure upon hake prerecruits could also affect their condition and persistence. Within the gulf, age-0+ hake are important prey items in the diet of demersal fish (Sánchez & Prenski, 1996; García de la Rosa & Sánchez, 1997; Sánchez & García de la Rosa, 1999), birds (Yorio et al., 2010; 2017), and marine mammals (Koen Alonso et al., 2000; Loizaga de Castro et al., 2016). Predation from settled age 1 and age 2 conspecifics is also of major importance (Sánchez & García De la Rosa, 1999), and is most likely the factor governing age-0+ individuals' vertical segregation (Álvarez Colombo et al., 2014). For the SJG ecosystem, Belleggia et al. (2017) suggested a top-down trophic dynamic system controlled by predators. While predation may be an important cause of mortality, the measurement of its direct impact in the field is exceptionally difficult and presently no data are available to appropriately test its effect. Finally, the potential effect of density-dependent mechanisms upon condition should also be mentioned. Competition among age-0+ individuals when searching for zooplankton prey may alter food availability, which in turn would translate into a lesser amount of energy available and, ultimately, into a lower lipid-based condition. This could probably be a factor of potential concern in winter, when euphausiid abundances in the gulf are lower. As discussed by Rueda et al. (2015), despite the environmental, anthropogenic, and local density-dependent influence on fish condition, general patterns are often elusive. Hence, all these variables deserve further exploration in future studies, to gain a full picture of *M. hubbsi* prerecruits condition and survival while nursing in the gulf.

CONCLUSIONS

Age-0+ hake liver lipid reserves reflected the seasonal and spatial environmental variability of the San Jorge Gulf. A regular monitoring of their nutritional status is relevant to understand the growth progression of this life stage in the nursery area, addressing how the environment can

modulate their energy depots, which are crucial for survival and consequent recruitment of the species. Investigating lipids provides insight into physiological mechanisms that determine how intra- and interannual changes in the ocean environment alter the availability (to higher trophic levels) of energy from primary production (Litz et al., 2010). This is particularly true in the current global change context. For the San Jorge Gulf, average annual increases of 2% and 0.34ºC in satellite chl-*a* concentration and surface temperature anomalies since ~1982, respectively, have been described (Marrari et al. 2016, 2019). Facing these increasing trends, that will most likely affect the availability and composition of herbivorous prey, changes in age-0+ hake lipid reserves are expected, which can ultimately have an effect upon survival. Moreover, since age-0+ hake play a key trophic role as prey item of upper level predators within the gulf, evaluating their lipid dynamics are of major importance to a better comprehension of how energy flows within the San Jorge Gulf food web.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest and that the research meets the required ethical guidelines.

AUTHOR CONTRIBUTION

B. Temperoni planned sampling, performed nutritional condition analysis, made the statistical analysis of the data and wrote the manuscript. A. Massa supervised nutritional condition analysis. P. Martos and M. Marrari processed and analyzed the oceanographic and satellite chl-*a* data, respectively. P. Martos, A. Massa and M. Marrari critically revised the drafted paper.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Akselman, R. (1996). Estudios ecológicos en el golfo San Jorge y adyacencias (Atlántico Sudoccidental). Distribución, abundancia y variación estacional del fitoplancton en relación a factores físico-químicos y la dinámica hidrológica. *PhD dissertation*. Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Buenos Aires, 234 pp.

Álvarez Colombo, G.L., Dato, C., Macchi, G., Palma, E., Machinandiarena, L., Christiansen, H. E., Betti, P., Derisio, C., Martos, P., Castro-Machado, F., Brown, D., Ehrlich, M., Mianzan, H. & Acha, E. M. (2011). Distribution and behavior of argentine hake larvae: evidences of a biophysical mechanism for self-recruitment in the northern patagonian shelf waters. *Ciencias Marinas*, 37, 633-657. doi:10.7773/cm.v37i4B.1777

Álvarez-Colombo, G.L., Dato, C. V, Machinandiarena, L., Castro-Machado, F. & Betti, P. (2014). Daylight vertical segregation of young-of-the-year Argentine hake *Merluccius hubbsi*: Advances in assessment of juvenile abundance with acoustic methods. *Fisheries Research*, 160, 85-95. doi:10.1016/j.fishres.2014.03.014

Arthur, D. K. (1976). Food and feeding of larvae of three fishes occurring in the California current: *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. *Fishery Bulletin U.S.*, 74, 517-530.

Baldoni, A., Molinari, G., Guerrero, R. & Kruk, M. (2008). Base Regional de Datos Oceanográficos (BaRDO) INIDEP. *Informe de Investigación INIDEP*, 13, 1-25.

Belleggia, M., Alves, N. M., Leyton, M. M, Álvarez-Colombo, G., Temperoni, B., Giberto, D. & Bremec, C. (2019). Are hakes truly opportunistic feeders? A case of prey selection by the Argentine hake *Merluccius hubbsi* off southwestern Atlantic. *Fisheries Research*, 214, 166174. doi:10.1016/j.fishres.2019.02.008

Belleggia, M., Giberto, D. & Bremec, C. (2017). Adaptation of diet in a changed environment: Increased consumption of lobster krill *Munida gregaria* (Fabricius, 1793) by Argentine hake. *Marine Ecology*, 38, e12445. doi:10.1111/maec.12445

Bogazzi, E., Baldoni, A., Rivas, A., Martos, P., Reta, R., Orensanz, J. M. (Lobo), Lasta, M., Dell'Arciprete, P. & Werner, F. (2005). Association between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the Southwestern Atlantic. *Fisheries Oceanography*, 14, 359–376. doi:10.1111/j.1365-2419.2005.00340.x

Bolger, T. & Connolly, P. L. (1989). The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology*, 34, 171–182. doi:10.1111/j.1095-8649.1989.tb03300.x

Brodeur, R. D., Wilson, M. T. & Ciannelli, L. (2000). Spatial and temporal variability in feeding and condition of age-0 walleye pollock (*Theragra chalcogramma*) in frontal regions of the Bering Sea Richard. *ICES Journal of Marine Science*, 57, 256–264. doi:10.1006/jmsc.1999.0525

Cepeda, G. D., Temperoni, B., Sabatini, M. E., Viñas, M. D., Derisio, C. M., Santos, B. A., Antacli, J. C. & Padovani, L. N. (2018). Zooplankton Communities of the Argentine Continental Shelf (SW Atlantic, ca. 34°-55°s), An Overview. In M. Hoffmeyer, M. E. Sabatini, F. Brandini, D. Calliari & N. H. Santinelli (Eds.), *Plankton ecology of the Southwestern Atlantic. From the Subtropical to the Subantarctic Realm*. pp. 171-199. Springer. doi:10.1007/978-3-319-77869-3

Cone, R. S. (1989). The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society*, 118, 510-514.

Cushing, D. H. (1989). A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *Journal of Plankton Research*, 11, 1-13.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26, 249-293.

Derisio, C. & Martos, P. (2018). Distribución y abundancia de la comunidad zooplanctónica en relación a las características oceanográficas en la zona de cría de larvas y juveniles de la merluza del efectivo sur (verano 2011-2014). *INIDEP Informe Investigación*, 139, 1-22.

Dutil, J.D., Lambert, Y., Chouinard, G. A. & Fréchet, A. (1995). Fish condition: what should we measure in cod (*Gadus morhua*)? *DFO Atlantic Fisheries Research Document*, 95(11), 1-26.

Ercoli, R., García, J., Aubone, A., Salvini, L. & Bertelo, R. (2000). Escape de juveniles de merluza (*Merluccius hubbsi*) en las redes de arrastre de fondo, mediante la aplicación del dispositivo de selectividad DEJUPA con diferentes distancias entre varillas, utilizando un diseño especial de copo de retención en la grilla. *Informe Técnico INIDEP*, 33, 1-16.

Ferron, A., & Leggett, W. C. (1994). An appraisal of condition measures for marine fish larvae. *Advances in Marine Biology*, 30, 217–303. doi:10.1016/S0065-2881(08)60064-4

Folch, J., Lees, M., & Sloane-Stanley, G. H. (1957). A Simple Method for the Isolation and Purification of Total Lipides from Animal Tissues. *The Journal of Biological Chemistry*, 226, 497–509.

Fonseca, V. F., Narciso, L. & Cabral, N. H. (2013). Lipid-based indicators of nutritional condition in juvenile sole *Solea solea*. *Journal of Applied Ichthyology*, 29, 154-162. doi:10.1111/jai.12000

García de la Rosa, S. B. & Sánchez, F. (1997). Alimentación de *Squalus acanthias* y predación sobre merluza *Merluccius hubbsi* en el Mar Argentino entre 34º-47'-47ºS. *Revista de Investigación y Desarrollo Pesquero*, 11, 119–133.

Glembocki, N. G., Williams, G. N., Góngora, M. E., Gagliardini, D. A. & Orensanz, J. M. (Lobo). (2015). Synoptic oceanography of the San Jorge Gulf (Argentina): A template for Patagonian red shrimp (*Pleoticus muelleri*) spatial dynamics. *Journal of Sea Research*, 95, 22-35. doi:10.1016/j.seares.2014.10.011

Góngora, M. E., González-Zevallos, D., Pettovello, A. & Mendia, L. (2012). Caracterización de las principales pesquerías del Golfo San Jorge Patagonia, Argentina. *Latin American Journal of Aquatic Research*, 40(1), 1–11. doi:10.4067/S0718-560X2012000100001

Guerrero, R. A. & Piola, A. R. (1997). Masas de agua en la plataforma continental. In E. E. Boschi (Ed.), *El Mar Argentino y sus Recursos Pesqueros, Tomo I: Antecedentes históricos de las exploraciones en el mar y las características ambientales*. pp. 107-119. Mar del Plata: INIDEP.

Gurney, L. J., Froneman, W., Pakhomov, E. A. & Mc Quaid, C. D. (2002). Diel feeding patterns and daily ration estimates of three subantarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep Sea Research Part II: Topical Studies in Oceanography*, 49, 3207-3227. doi:10.1016/S0967-0645(02)00079-6

Hayes, J. P. & Shonkwiler, J. S. (2001). Morphometric indicators of body condition: worthwhile or wishful thinking? In J. R. Speakman (Ed.), *Body Composition Analysis of Animals* (pp. 8–38). Cambridge: Cambridge University Press.

Hidalgo, M., Massutí, E., Moranta, J., Cartés, J. E., Lloret, J., Oliver, P., & Morales-Nin, B. (2008). Seasonal and short spatial patterns in European hake (*Merluccius merluccius* L.) recruitment process at the Balearic Islands (NW Mediterranean): The role of the environment on distribution and condition. *Journal of Marine Systems*, 71, 367–384. doi:10.1016/j.jmarsys.2007.03.005

Hüssy, K., St. John, M. A. & Böttcher, U. (1997). Food resource utilization by juvenile baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? *Marine Ecology Progress Series*, 155, 199-208. doi:10.3354/meps155199

Irusta, G., Macchi, G., Louge, E., Rodrigues, K., D'Atri, L., Villarino, M. F., Santos, B. & Simonazzi, M. (2016). Biology and fishery of the Argentine hake (*Merluccius hubbsi*). *Revista de Investigación y Desarrollo Pesquero*, 28, 9-36.

Koen-Alonso, M., Crespo, E. A., Pedraza, S. N, García, N. A & Coscarella, M. A. (2000). Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin*, 98, 250–263.

Kooka, K., Yamamura, O., Ohkubo, N. & Honda, S. (2009). Winter lipid depletion of juvenile walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan. *Journal of Fish Biology*, 75, 186-202. doi:10.1111/j.1095-8649.2009.02279.x.

Lambert, Y. & Dutil, J. D. (1997). Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 104-112. doi:10.1139/f96-149

Laroche, J. L. (1982). Trophic patterns among larvae of five species of sculpins (family: Cottidae) in a Maine estuary. *Fishery Bulletin*, 80, 827–840.

Le Cren, E. D. (1951). The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology*, 20, 201–219.

Leonarduzzi, E., Rodrigues, K. & Macchi, G. J. (2014). Proximate composition and energy density in relation to Argentine hake females (*Merluccius hubbsi*) morphometrics and condition indices. *Fisheries Research*, 160, 33-40. doi:10.1016/j.fishres.2014.04.017

Litz, M. N. C., Brodeur, R. D., Emmett, R. L., Heppell, S. S., Rasmussen, R. S., O'Higgins, L. & Morris, M. S. (2010). Effects of variable oceanographic conditions on forage fish lipid content and fatty acid composition in the northern California Current. Marine *Ecology Progress Series*, 405, 71-85. doi:10.3354/meps08479

Lloret, J., Gil de Sola, L., Souplet, A. & Galzin, R. (2002). Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. *ICES Journal of Marine Science*, 59, 1215-1227. doi:10.1006/jmsc.2002.1294

Lloret, J., Demestre, M. & Sánchez-Pardo, J. (2008). Lipid (energy) reserves of European hake (*Merluccius merluccius*) in the north-western Mediterranean. *Vie et Milieu-Life and Environment*, 58, 75-85.

Loizaga de Castro, R., Saporiti, F., Vales, D. G., García, N. A., Cardona. L. & Crespo, E. A. (2016). Feeding ecology of dusky dolphins *Lagenorhynchus obscurus*: evidence from stable isotopes. *Journal of Mammalogy*, 97, 310-320. doi:10.1093/jmammal/gyv180

Macchi, G. J., Pájaro, M. & Ehrlich, M. (2004). Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research*, 67, 25–38. doi:10.1016/j.fishres.2003.08.006

Marrari, M., Piola, A. R., Valla, D. & Wilding, J.G. (2016). Trends and variability in extended ocean color time series in the main reproductive area of the Argentine hake, *Merluccius hubbsi*

(Southwestern Atlantic Ocean). *Remote Sensing of Environment*, 177, 1-12. doi:10.1016/j.rse.2016.02.011

Marrari, M., Macchi, G. J., Santos, B. & Leonarduzzi, E. (2019). Influence of environmental conditions on the reproductive success and recruitment of the Argentine hake *Merluccius hubbsi* (southwestern Atlantic Ocean). *Fisheries Oceanography*, 28, 66-81. doi:10.1111/fog.12387

Matano, R. P. & Palma, E. D. (2018). Seasonal variability of the oceanic circulation in the Gulf of San Jorge, Argentina. *Oceanography*, 31, 16–24. doi:10.5670/oceanog.2018.402

McPherson, L. R., Slotte, A., Kvamme, C., Meier, S., & Marshall, C. T. (2011). Inconsistencies in measurement of fish condition: A comparison of four indices of fat reserves for Atlantic herring (*Clupea harengus*). *ICES Journal of Marine Science*, 68, 52–60. doi:10.1093/icesjms/fsq148

Pájaro, M., Macchi, G. J. & Martos, P. (2005). Reproductive pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research*, 72, 97-108.

Palma E. D., Matano, R. P., Tonini, M. H., Martos, P. & Combes V. (2020). Dynamical Analysis of the Oceanic Circulation in the Gulf of San Jorge, Argentina*. Journal of Marine Systems*, 203. doi:10.1016/j.jmarsys.2019.103261

Pampa Azul (2014). Ministerio de Ciencia, Tecnología e Innovación Productiva de la Nación-Programa Nacional de Investigación e Innovación Productiva en Espacios Marítimos Argentinos, Ley PROMAR Nº 27.167.

Pardoe, H., Thórdarson, G. & Marteinsdóttir, G. (2008). Spatial and temporal trends in condition of Atlantic cod *Gadus morhua* on the Icelandic shelf. *Marine Ecology Progress Series*, 362, 261-277. doi:10.3354/meps07409

Pisoni, J. P., Rivas, A. L., & Tonini, M. H. (2018). Surgencia costera en el Golfo San Jorge. *Libro de resúmenes X Jornadas Nacionales de Ciencias del Mar*, p. 120, ISBN 978-987-42-9493-7.

R Development Core Team. (2014). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ravalli, C., De la Garza, J. & López Greco, L. (2013). Distribución de los morfotipos *gregaria* y *subrugosa* de la langostilla *Munida gregaria* (Decapoda, Galatheidae) en el Golfo San Jorge en la campaña de verano AE-01/2011. Integración de los resultados con las campañas 2009 y 2010. *Revista de Investigación y Desarrollo Pesquero*, 22, 29-41.

Rivas, A. L., & Pisoni, J. P. (2010). Identification, characteristics and seasonal evolution of surface thermal fronts in the Argentinean Continental Shelf. *Journal of Marine Systems*, 79, 134-143. doi:10.1016/j.jmarsys.2009.07.008

Renzi, M., Santos, B. & Simonazzi, M. (2003). Estructura por edad y sexo de la población de merluza. In: L. S. Tringali & S. I. Bezzi (Eds.), *Aportes para la evaluación del recurso merluza (Merluccius hubbsi) al sur de los 41° S. Año 1999. INIDEP Informe Técnico*, 51, 57- 76.

Rueda, L., Moranta, J., Abelló, P., Balbín, R., Barberá, C., Fernández de Puelles, M. L., Olivar, M. P., Ordines, F., Ramón, M., Torres, A. P., Valls, M. & Massutí, E. (2014). Body condition of the deep water demersal resources at two adjacent oligotrophic areas of the western Mediterranean and the influence of the environmental features. *Journal of Marine Systems*, 138, 194–202. doi:10.1016/j.jmarsys.2013.11.018

Rueda, L., Massutí, E., Alvarez-Berastegui, D. & Hidalgo, M. (2015). Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid's body condition. *Ecosphere*, 6(10), 1-17. doi:10.1890/ES15-00087.1

Sabatini, M. & Martos, P. (2002). Mesozooplankton features in a frontal area off northern Patagonia (Argentina) during spring 1995 and 1998. *Scientia Marina*, 66, 215–232. doi:10.3989/scimar.2002.66n3

Sánchez, F. & Prenski, L. B. (1996). Ecología trófica de peces demersales en el Golfo San Jorge. *Revista de Investigación y Desarrollo Pesquero*, 10, 57–71.

Sánchez, F. & García de la Rosa, S. B. (1999). Alimentación de *Merluccius hubbsi* e impacto del canibalismo en la región comprendida entre 34º50'-47ºS del Atlántico Sudoccidental. *Revista de Investigación y Desarrollo Pesquero*, 12, 77-93.

Schlitzer, R. (2016). Ocean Data View. http://odv.awi.de.

Schloesser, R. W. & Fabrizio, M. C. (2016). Temporal dynamics of condition for estuarine fishes in their nursery habitats. *Marine Ecology Progress Series*, 557, 207-291. doi:0.3354/meps11858

Segura, V. & Silva, R. (2017). Producción primaria y su relación con los grupos fitoplanctónicos en el periodo de primavera en el Golfo San Jorge y área adyacente, Argentina. *INIDEP Informe de Investigación*, 30, 1-33.

Simpson, J. H. (1981). The shelf-sea fronts: implications of their existence and behavior. *Philosophical Transactions Royal Society of London A*, 302, 531-546.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science*, 60, 1129–1157.

St John, M. A. & Lund, T. (1996). Lipid biomarkers: linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. *Marine Ecology Progress Series*, 131, 75–85.

Stuart, V. (1989). Observations on the feeding of *Euphausia lucens* on natural phytoplankton suspensions in the southern Benguela upwelling region. *Continental Shelf Research*, 9, 1017-1028. doi:10.1016/0278-4343(89)90005-8

Suthers, I. M. (1998). Bigger? Fatter? Or is faster growth better? Considerations on condition in larval and juvenile coral-reef fish. *Australian Journal of Ecology*, 23, 265–273.

Temperoni, B., Viñas, M. D. & Buratti, C. (2013). Feeding strategy of juvenile (age-0+ year) Argentine hake (*Merluccius hubbsi*) in the Patagonian nursery ground. *Journal of Fish Biology*, 83, 1354-1370. doi:10.1111/jfb.12238

Temperoni, B. & Derisio, C. (2018). Abundancia y calidad nutricional de presas zooplanctónicas para los prerreclutas de *Merluccius hubbsi* en el Golfo San Jorge. In A. M. Parma, N. Sánchez-Carnero & L. Venerus (Eds.), *V Seminario "Golfo San Jorge: avances y retos futuros"*. Puerto Madryn: CESIMAR. ISSN 2618-5334.

Temperoni, B., Massa, A. E., Derisio, C., Martos, P., Berghoff, C. & Viñas, M. D. (2018a). Effect of nursery ground variability on condition of age-0+ year *Merluccius hubbsi* Marini 1933. *Journal of Fish Biology*, 93, 1090-1101. doi:10.1111/jfb.13816

Temperoni, B., Derisio, C., Massa, A. E. & Viñas M. D. (2018b). Condición nutricional de prerreclutas (edad 0) de *Merluccius hubbsi* del efectivo bonaerense: relación con la disponibilidad e ingesta de presas. *INIDEP Informe de Investigación*, 137, 1-12.

Tonini, M., Palma, E. D. & Rivas, A. L. (2006). Modelo de alta resolución de los Golfos Patagónicos. *Mecánica Computacional*, XXV, 1441–1460.

Varisco, M. A. (2013). Biología de *Munida gregaria* (Crustacea Anomura): bases para su aprovechamiento pesquero en el Golfo San Jorge, Argentina. *PhD dissertation*. Universidad Nacional de la Plata, Facultad de Ciencias Exactas y Museo, La Plata, 171 pp.

Weber, L. P., Higgins, P. S., Carlson, R. I. & Janz, D. M. (2003). Development and validation of methods for measuring multiple biochemical indices of condition in juvenile fishes. *Journal of Fish Biology*, 63, 637-658. doi:10.1046/j.1095-8649.2003.00178.x

Yorio, P., Quintana, F., Dell'Arciprete, P. & González-Zevallos, D. (2010). Spatial overlap between foraging seabirds and trawl fisheries: implications for the effectiveness of a marine protected

area at Golfo San Jorge, Argentina. *Bird Conservation International*, 20, 320–334. doi:10.1017/S0959270910000286

Yorio, P., González-Zevallos, D., Gatto, A., Biagioni, O. & Castillo, J. (2017). Relevance of forage fish in the diet of Magellanic penguins breeding in northern Patagonia, Argentina. *Marine Biology Research*, 13(6), 1-15. doi:10.1080/17451000.2016.1273529

FIGURE LEGENDS

Figure 1. (a) Map of the north Patagonian region (42°-48°S) showing *Merluccius hubbsi* spawning (Isla Escondida) and nursery (San Jorge Gulf, SJG) areas. Dashed black line corresponds to the federal/provincial jurisdictions boundary. The dotted black line at 46°S represents the limit between Chubut and Santa Cruz provinces jurisdictions (Góngora et al., 2012) (b) Sampling stations (coded by number) performed in the SJG during three consecutive seasons: winter 2016 (September), spring 2016 (November) and summer 2017 (January) to collect age-0+ *M. hubbsi*. In dashed lines, areas considered for spatial analyses (*sensu* Glembocki et al., 2015): Northern (NA), Central Coastal (CCA), Central (CA), and Southwestern (SWA).

Figure 2. Relative importance (%) of prey items in the diet of age-0+ *Merluccius hubbsi* in the San Jorge Gulf in winter 2016 (September), spring 2016 (November) and summer 2017 (January). NI: non identified.

Figure 3. Mean (± 095 confidence interval; SD: standard deviation; SE: standard error) values of condition indices ($K_n$, HSI and %L) of age-0+ *Merluccius hubbsi* in the San Jorge Gulf in winter 2016 (September), spring 2016 (November) and summer 2017 (January).

Figure 4. Spatial variability in condition indices (a) $K_n$, (b) HSI and (c) %L of age-0+ *Merluccius hubbsi* in the San Jorge Gulf in winter 2016 (September), spring 2016 (November) and summer 2017 (January). In dashed lines, areas considered for spatial analyses (*sensu* Glembocki et al., 2015): Northern (NA), Central Coastal (CCA), Central (CA), and Southwestern (SWA).

Figure 5. (a) Satellite chlorophyll-*a* concentration (mg m$^{-3}$) (MODIS Aqua monthly average, spatial resolution of 2 km pixel$^{-1}$), (b) bottom temperature (ºC), and (c) bottom salinity fields in the San Jorge Gulf in winter 2016 (September), spring 2016 (November) and summer 2017 (January). Thick black lines in (b) and (c) indicate the average position (critical Simpson parameter φ = 30 J m$^{-3}$) of the Northern (NPFS) and Southern (SPFS) Patagonian Frontal Systems, respectively. In dashed lines, areas considered for spatial analyses (*sensu* Glembocki et al., 2015): Northern (NA), Central Coastal (CCA), Central (CA), and Southwestern (SWA).

**Table 1.** Details of the samplings performed in the San Jorge Gulf during three seasons to collect age-0+ hake *Merluccius hubbsi*.

| Season | Date | Cruise | St. | Area | n | Size range |
|---|---|---|---|---|---|---|
| **Winter 2016** | September | EH-01/16 | 1 | CA | 5 | 11.6 - 13.4 |
| | (9/12-9/15/16) | *R/V Eduardo Holmberg* | 2 | CA | 5 | 11.1 - 13.7 |
| | | | 3 | NA | 5 | 13.5 - 14.7 |
| | | | 4 | CCA | 5 | 13.5 - 14.5 |
| | | | 5 | CA | 5 | 12.9 - 14.5 |
| | | | 6 | SWA | 5 | 12.0 - 14.2 |
| | | | 7 | CCA | 5 | 12.0 - 13.5 |
| | | | 8 | CA | 5 | 11.5 - 14.0 |
| | | | 9 | CA | 5 | 10.0 - 12.0 |
| | | | | | | **12.8 ± 1.1** |
| **Spring 2016** | November | PA-GSJ-2016 | 10 | SWA | 6 | 11.0 - 14.1 |
| | (11/13-11/21/16) | *R/V ARA Puerto Deseado* | 11 | CA | 10 | 9.6 - 12.5 |
| | | | 12 | CCA | 10 | 9.4 - 15.0 |
| | | | 13 | NA | 6 | 11.5 - 15.3 |
| | | | 14 | NA | 5 | 11.0 - 14.5 |
| | | | 15 | CA | 3 | 9.6 - 14.1 |
| | | | | | | **12.2 ± 1.7** |
| **Summer 2017** | January | EH-01/17 | 16 | CA | 5 | 13.4 - 14.4 |
| | (01/16-01/20/17) | *R/V Eduardo Holmberg* | 17 | CA | 5 | 10.4 - 14.1 |
| | | | 18 | CCA | 5 | 12.6 - 14.0 |
| | | | 19 | CA | 5 | 13.1 - 14.6 |
| | | | 20 | CA | 5 | 11.0 - 14.0 |
| | | | 21 | NA | 5 | 12.7 - 14.8 |
| | | | 22 | NA | 5 | 12.5 - 13.9 |
| | | | | | | **13.4 ± 1.0** |

*Note:* Date, cruise, station (St.) number, area, number of individuals (n) analyzed per St., size range (cm) per St., and mean total length (± standard deviation) per season are indicated. Areas (*sensu* Glembocki et al., 2015): Northern (NA), Central Coastal (CCA), Central (CA), Southwestern (SWA).

**Table 2.** Generalized Linear Models for the seasonal (winter 2016, spring 2016 and summer 2017) variability in total length ($T_L$), condition indices ($K_n$, HSI, %L) and the relative importance of *Euphausia* spp. in the diet (%RI$_{euph}$) of age-0+ *Merluccius hubbsi*.

| | Estimate | Std. Error | t value | Pr (>\|t\|) | |
|---|---|---|---|---|---|
| **$T_L$** | | | | | |
| Intercept | 0.08 | 0.001 | 64.93 | $<2e^{-16}$ | *** |
| SEASON (spring) | 0.004 | 0.002 | 2.19 | 0.0306 | * |
| **$K_n$** | | | | | |
| Intercept | 0.96 | 0.013 | 73.23 | $<2e^{-16}$ | *** |
| SEASON (spring) | 0.05 | 0.019 | 2.54 | 0.0126 | * |
| SEASON (summer) | 0.06 | 0.020 | 2.95 | 0.0038 | *** |
| **HSI** | | | | | |
| Intercept | 0.33 | 0.015 | 22.08 | $<2e^{-16}$ | *** |
| SEASON (spring) | -0.09 | 0.019 | -4.68 | $7.64e^{-06}$ | *** |
| **%L** | | | | | |
| Intercept | 0.22 | 0.012 | 17.76 | $<2e^{-16}$ | *** |
| SEASON (spring) | -0.14 | 0.012 | -11.75 | $<2e^{-16}$ | *** |
| SEASON (summer) | -0.11 | 0.013 | -8.14 | $5.09e^{-13}$ | *** |
| chl-*a* | -0.01 | 0.004 | -2.29 | 0.0236 | * |
| **%RI$_{euph}$** | | | | | |
| Intercept | 5.91 | 0.120 | 48.87 | $<2e^{-16}$ | *** |
| SEASON (spring) | 0.23 | 0.031 | 7.40 | $1.34e^{-13}$ | *** |
| SEASON (summer) | 0.63 | 0.032 | 19.25 | $<2e^{-16}$ | *** |
| $T_B$ | -0.21 | 0.014 | -15.44 | $<2e^{-16}$ | *** |

*Note:* Significance levels: *** 0.001, ** 0.01, * 0.05. chl-*a*: chlorophyll-*a* concentration, $T_B$: bottom temperature.

**Table 3.** Feeding incidence (FI; %), relative importance (%RI) and number of individuals per stomach (N) of *Euphausia* spp. in stomach contents of age-0+ hake *Merluccius hubbsi* per area in each season.

| Season | Area | FI | %RI | N |
|---|---|---|---|---|
| **Winter 2016** | NA | 80 | 96 | 32 |
| | CCA | 60 | 0 | 0 |
| | CCA | 80 | 50 | 6 |
| | CA | 80 | 0 | 0 |
| | CA | 80 | 67 | 2 |
| | CA | 60 | 78 | 9 |
| | CA | 40 | 100 | 13 |
| | CA | 60 | 95 | 7 |
| | SWA | 40 | 38 | 3 |
| Mean value | | 64 | 58 | 8 |
| **Spring 2016** | NA | 83 | 97 | 57 |
| | NA | 60 | 0 | 0 |
| | CCA | 80 | 87 | 22 |
| | CA | 100 | 98 | 15 |
| | CA | 100 | 0 | 0 |
| | SWA | 100 | 99 | 93 |
| Mean value | | 87 | 64 | 31 |
| **Summer 2017** | NA | 80 | 100 | 18 |
| | NA | 80 | 79 | 11 |
| | CCA | 100 | 95 | 32 |
| | CA | 40 | 89 | 4 |
| | CA | 60 | 100 | 4 |
| | CA | 100 | 0 | 0 |
| | CA | 40 | 100 | 30 |
| Mean value | | 71 | 80 | 14 |

*Note:* Areas (*sensu* Glembocki et al., 2015): Northern (NA), Central Coastal (CCA), Central (CA), Southwestern (SWA).

**Table 4.** Generalized Linear Models for the seasonal (winter 2016, spring 2016 and summer 2017) variability in the environmental variables bottom temperature ($T_B$), and chlorophyll-*a* concentration (chl-*a*) in the San Jorge Gulf.

|  | Estimate | Std. Error | t value | Pr (>\|t\|) | |
|---|---|---|---|---|---|
| **$T_B$** | | | | | |
| Intercept | 0.11 | 0.0014 | 81.31 | $<2e^{-16}$ | *** |
| SEASON (spring) | -0.013 | 0.0019 | -6.98 | $1.92e^{-10}$ | *** |
| SEASON (summer) | -0.017 | 0.0019 | -8.97 | $5.82e^{-15}$ | *** |
| **chl-*a*** | | | | | |
| Intercept | 0.77 | 0.04 | 19.58 | $<2e^{-16}$ | *** |
| SEASON (spring) | -0.28 | 0.05 | -6.09 | $1.5e^{-08}$ | *** |
| SEASON (summer) | -0.27 | 0.05 | -5.39 | $3.8e^{-07}$ | *** |

*Note:* Significance level: *** 0.001

**Table 5.** Mean (± standard deviation) and range of variation of environmental variables recorded in the San Jorge Gulf during three seasons.

| Season | chl-*a* | $T_B$ | $S_B$ |
|---|---|---|---|
| **Winter 2016** | 1.29 ± 0.19 | 8.73 ± 0.29 | 33.37 ± 0.07 |
| | 1.12 - 1.73 | 8.09 - 9.06 | 33.18 - 33.43 |
| **Spring 2016** | 2.06 ± 0.43 | 9.90 ± 0.92 | 33.35 ± 0.07 |
| | 1.54 - 2.77 | 8.64 - 11.07 | 33.23 - 33.41 |
| **Summer 2017** | 1.96 ± 1.12 | 10.31 ± 1.13 | 33.34 ± 0.10 |
| | 0.61 - 3.67 | 9.18 - 11.82 | 33.16 - 33.44 |

*Note:* chl-*a*: chlorophyll-*a* concentration (mg m$^{-3}$), $T_B$: bottom temperature (°C), $S_B$: bottom salinity.

**Table 6.** Generalized Linear Models for the spatial (within-season) variability in condition indices ($K_n$, HSI, %L) and relative importance of *Euphausia* spp. (%RI$_{euph}$) in the diet of age-0+ *Merluccius hubbsi*.

| | | | Estimate | Std. Error | t value | Pr (>\|t\|) | |
|---|---|---|---|---|---|---|---|
| **Winter 2016** | **$K_n$** | Intercept | 1.17 | 0.083 | 14.02 | $<2e^{-16}$ | *** |
| | | chl-*a* | -0.16 | 0.063 | -2.56 | 0.0142 | * |
| | **%RI$_{euph}$** | Intercept | 46.93 | 6.727 | 6.98 | $3.04e^{-12}$ | *** |
| | | Area (CA) | -5.71 | 0.973 | -5.87 | $4.43e^{-09}$ | *** |
| | | Area (NA) | 3.94 | 0.672 | 5.86 | $4.64e^{-09}$ | *** |
| | | Area (SWA) | 2.62 | 0.629 | 4.17 | $3.11e^{-05}$ | *** |
| | | chl-*a* | -32.54 | 5.083 | -6.40 | $1.54e^{-10}$ | *** |
| **Spring 2016** | **$K_n$** | Intercept | 0.81 | 0.059 | 13.61 | $3.47e^{-16}$ | *** |
| | | chl-*a* | 0.09 | 0.028 | 3.28 | 0.00223 | ** |
| | **HSI** | Intercept | 0.18 | 0.011 | 16.87 | $<2e^{-16}$ | *** |
| | | Area (CA) | 0.12 | 0.019 | 6.33 | $2.51e^{-07}$ | *** |
| | | Area (NA) | 0.06 | 0.018 | 3.68 | 0.000754 | *** |
| | | Area (SWA) | 0.09 | 0.023 | 3.78 | 0.000576 | ** |
| | **%L** | Intercept | 0.09 | 0.0064 | 14.11 | $8.98e^{-16}$ | *** |
| | | Area (CA) | -0.03 | 0.0073 | -3.76 | 0.000640 | *** |
| | | Area (NA) | -0.05 | 0.0068 | -7.29 | $1.92e^{-08}$ | *** |
| | | Area (SWA) | -0.03 | 0.0077 | -3.99 | 0.000332 | *** |
| **Summer 2017** | **HSI** | Intercept | -13.01 | 5.267 | -2.47 | 0.0188 | * |
| | | $S_B$ | 0.40 | 0.158 | 2.53 | 0.0164 | * |
| | **%L** | Intercept | 0.17 | 0.028 | 6.02 | $1.15e^{-06}$ | *** |
| | | Area (CA) | -0.04 | 0.019 | -2.12 | 0.04174 | * |
| | | chl-*a* | -0.02 | 0.006 | -3.42 | 0.00168 | ** |
| | **%RI$_{euph}$** | Intercept | -107.52 | 8.514 | -12.63 | $<2e^{-16}$ | *** |
| | | $S_B$ | 3.34 | 0.254 | 13.14 | $<2e^{-16}$ | *** |
| | | chl-*a* | 0.18 | 0.019 | 9.22 | $<2e^{-16}$ | *** |

*Note:* Significance levels: *** 0.001, ** 0.01, * 0.05. chl-*a*: chlorophyll-*a* concentration, $S_B$: bottom salinity. Areas (*sensu* Glembocki et al., 2015): Northern (NA), Central Coastal (CCA), Central (CA), Southwestern (SWA).

Relative importance (%) by season showing *Euphausia* spp., *M. gregaria*, NI crustaceans, *N. megalops*, *P. petrunkevitchi*, *T. gaudichaudii*, and Misidaceans for Winter 2016, Spring 2016, and Summer 2017.

Winter 2016 | Spring 2016 | Summer 2017

NA | CA | CCA | SWA

(a) $K_n$
- 0.90 - 0.98
- 0.98 - 1.06
- 1.06 - 1.15

(b) HSI
- 2.5 - 3.5
- 3.5 - 4.5
- 4.5 - 5.5

(c) %L

Winter
- 3 - 5
- 5 - 7
- 7 - 14

Spring - Summer
- 7 - 14
- 14 - 19
- 19 - 24