

Effect of nursery ground variability on condition of age 0+ years

Merluccius hubbsi

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ABSTRACT

This study examined the southern or Patagonian (41°–55° S) stock of Argentine hake *Merluccius hubbsi*, the more abundant of the two stocks on the Argentinean continental shelf. Pre-recruits (age 0+ year individuals) of this stock settle and grow in the San Jorge Gulf (45°–47° S, 65° 30' W), a complex habitat with large spatial variability in environmental features. Relative condition factor, hepatosomatic index, lipid content and fatty-acid composition of muscle and liver, and diet information were combined with physical and biological data to evaluate: how nutritional status of age 0+ year hake varies spatially within the nursery ground; whether changes in condition are related to environmental factors and feeding; whether the indices are interchangeable metrics of condition. Both morphometric and biochemical indices showed dissimilar spatial trends; enhanced liver-based condition coincided with low salinity nutrient rich waters, higher chlorophyll-*a* values and abundances of *Euphausia* spp., the preferred prey at most stations, suggesting a bottom-up effect on age 0+ year hake condition. Diminished condition at stations where *Thermisto gaudichaudii* was the main prey could derive from lower prey quality in terms of energy density and essential fatty acids content. Coastal waters of the gulf would be essential habitats for *M. hubbsi* pre-recruits. Future monitoring of condition with liver-based indices is encouraged in the gulf, where interannual increasing trends of satellite-derived chlorophyll -*a* values have been observed, which could have implications for recruitment of the species.

KEYWORDS

condition indices, habitat variability, Merluccidae, Patagonian stock, pre-recruits

INTRODUCTION

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For over a century, condition indices have been used to assess the health of fish (Shulman & Love, 1999), appearing as essential indicators for analysing the effects of environmental and human pressures on fish, particularly the exploited ones and for measuring the quality of the environment in which they live (Lloret *et al.*, 2014). Nutritional condition, as an indicator of overall physiological status (Cone, 1989), integrates the heterogeneous set of environmental conditions experienced by the individuals in their habitat. It relates directly with fishes' ability to cope with physical and biological variability at different spatial and time scales. This is critical during the recruitment process, when early stages must achieve high growth rates to minimize vulnerability to size-selective predators (Sogard, 1994). In this sense, studies focused on the age 0+ year individuals (pre-recruits) are of particular interest, since this stage is considered a major determinant of adult fish-stock year-class strength (Hüssy *et al.*, 1997).

Condition can be assessed from a variety of indices, based on length:mass ratio (Fulton's K ; Fulton, 1904; relative condition factor K_n ; Le Cren, 1951), liver mass:body mass ratio (hepato-somatic index I_H ; Lambert & Dutil, 1997) or the biochemical composition of different tissues (*e.g.*, lipids, nucleic acids, proteins; Weber *et al.*, 2003). These indices differ in terms of sensitivity, which refers to the minimum environmental change that can be detected and latency, which is the time required for a given change in the environment to be reflected in the index (Ferron & Leggett, 1994). Previous studies indicate that morphometric and biochemical indices do not always correlate, so do not measure the same aspect of physiological status (McPherson *et al.*, 2011). Crude indices built from morphometric data are the most commonly used. Although they are assumed to be directly proportional to the amount of energy stored in individual fish (Davidson & Marshall, 2010), this is rarely tested using more direct estimates of reserves such as lipid mass and their fatty acid composition.

Lipids are the essential source of metabolic energy for vital processes (Love, 1970) and can add ecological and physiological significance when assessing long-term (weeks to months) growth potential and survival probability of fish early stages (Fonseca *et al.*, 2013). Fish totally or partially deprived of food generally show a decrease in lipid reserves, with the prioritized mobilization of monounsaturated (MUFA) and some saturated (SFA) fatty acids, countered with the preservation of essential polyunsaturated fats (PUFA; Zamal & Ollevier, 1995). In a broader sense, lipids can also be used for assessment of large-scale habitat quality in the context of fisheries management (Lloret *et al.*, 2002), provided they can reveal changes in environmental conditions.

Argentine hake *Merluccius hubbsi* Marini 1933 is one of the most important fishery resources of the Argentinean continental shelf (ACS; Aubone *et al.*, 2000). Of two main stocks, the southern or Patagonian stock (41°–55° S) is the most abundant, accounting for 85% of total hake biomass of the ACS. Age 0+ year *M. hubbsi* of this stock have their nursery and settlement location in the San Jorge Gulf (SJG; Figure 1), where they tend to aggregate in coastal sectors (Álvarez-Colombo *et al.*, 2011), with highest percentages at the south extreme, intermediate values in the central region, drastically diminishing towards the north (Louge *et al.*, 2011; Santos *et al.*, 2012). It has been suggested that this distribution might respond to certain temperature and salinity ranges as well as to zooplankton prey concentrations (Louge *et al.*, 2011). Pre-recruits prey mainly upon euphausiids and amphipods during austral summer, although decapods are included in the diet in a lower proportion (Temperoni *et al.*, 2013). However, the spatial variability of these macrozooplankton prey within the SJG is poorly known (Pérez Seijas *et al.*, 1987; Viñas *et al.*, 1992). Moreover, no attempts have been made hitherto to evaluate the potential effect of biotic and abiotic factors upon age 0+ year *M. hubbsi* condition.

The main objectives of this study were: to determine spatial variations in age 0+ year *M. hubbsi* condition from a variety of indices; to relate these results with environmental factors (temperature, salinity, chlorophyll-*a* concentration, prey abundance) and prey intake; to evaluate whether the selected indices represent interchangeable measures of condition. Results are expected to significantly contribute to *M. hubbsi* recruitment studies in the ACS.

2 | MATERIALS AND METHODS

2.1 | Study area

The San Jorge Gulf is a semi-closed basin located between 45° S (Cape Dos Bahías) and 47° S (Cape Tres Puntas) and between 65° 30' W and the coast (Figure 1a), with a rather deep connection to the open shelf and greatest depths (*c.* 110 m) in the central region (Tonini *et al.*, 2006). It is occupied by shelf waters (salinity 33.4–33.8), modified by the contribution of low salinity coastal waters (< 33.4; Bianchi *et al.*, 1982; Guerrero & Piola, 1997) flowing northwards from the Magellan Strait and Beagle Channel. When reaching the southern tip of the gulf, these cold and less saline waters diverge into two branches, one flows into the SJG along the coast, while the other continues towards the north-east, thus separating the water masses inside the gulf from those located to the east (Palma *et al.*, 2004). Numerical modelling of the gulf has shown the existence of a counter-clockwise gyre throughout the year generated by wind-driven circulation (Palma *et al.*, 2004), as well as a less intense clockwise gyre in the northern area (Tonini *et al.*, 2006). Vertical distribution of speeds shows a two-layered circulation pattern, with a north-east flow in the superficial layer and towards the coast in the deeper layers. This would induce upwelling mechanisms along the south-west coast of the gulf.

The north and south lowest depth (*c.* 30 m) extremes of the gulf are influenced by the presence of two frontal systems that differ from each other in their main forcing, as well as in their temporal and spatial scales (Bogazzi *et al.*, 2005). The northern extreme is influenced by the highly productive Northern Patagonian Frontal System (NPFS; Sabatini & Martos, 2002; Figure 1a), which develops during austral spring and summer *c.* 42° 30'–5° 00' S. It is forced by seasonal thermal stratification and high tidal energy dissipation typical of the area (Glorioso, 1987; Sabatini & Martos 2002; Bogazzi *et al.*, 2005). The southern extreme is characterized by the permanent thermohaline Southern Patagonian Frontal System (SPFS; Guerrero & Piola, 1997), which represents the transition between tidally mixed nutrient-rich low-salinity coastal waters (Guerrero & Piola, 1997; Bogazzi *et al.*, 2005) and seasonally stratified more saline waters of the continental shelf. The influence of low-salinity coastal waters within the gulf has been verified in the deeper layers of the stratified area (Krock *et al.*, 2015). The area is also characterized by enhanced energy dissipation associated with a prominent shoal (contouring the 80 m isobath; Figure 1a) around Cape Tres Puntas (Bogazzi *et al.*, 2005). The highly dynamic physical oceanography of the nursery ground translates into nutrient enrichment and retention mechanisms of ecological importance to phyto and zooplankton growth at the base of the food web.

2.2 | Sampling

An *M. hubbsi* stock assessment cruise (EH-01/14) was carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) in the SJG during austral summer of 2014 (01-19-2014 to 02-07-2014), on board the R.V. *Eduardo Holmberg* and provided the opportunity to collect environmental data, zooplankton prey and *M. hubbsi* pre-recruits simultaneously.

Surface temperature and salinity measures were taken from 60 conductivity–temperature–depth (CTD) casts, using a Seabird SBE-19 profiler (Sea-Bird Scientific; www.seabird.com; Figure 1a), while *in vivo* active fluorescence (Fl) was measured by a Seapoint fluorometer (www.seapoint.com) attached to the CTD. 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 4.7.10 (Schlitzer, 2016). The position of the frontal systems within the gulf was determined based on the Simpson's stability index (Φ ; Simpson, 1981), considering a mean value of $\Phi = 40 \text{ J m}^{-3}$ as the limit between homogeneous and stratified waters (Sabatini & Martos, 2002; Bogazzi *et al.*, 2005). At 11 stations (Figure 1a), water samples were collected using a bucket for *in situ* quantification of chlorophyll-*a* concentration by fluorometry. The surface chlorophyll-*a* field and vertical profiles were estimated from the ratio chlorophyll-*a* :Fl (chlorophyll-*a* concentration *v. in vivo* fluorescence), as described by Lutz *et al.* (2010).

Zooplankton samples were collected at 13 sampling stations (Figure 1b) with a Bongo net (300 μm mesh) fitted with a flowmeter (Hydrobios; www.hydrobios.de), by oblique tows from near the bottom to the surface. Samples were fixed in a 5% formalin–seawater solution. Once in the laboratory, abundance of the common prey of age 0+ year *M. hubbsi* was estimated at each sampling station as individuals m^{-3} , from the counts of each species or taxon under a Wild M5 stereoscopic microscope (www.wild-heerbrugg.com) and the volume of filtered water.

Age 0+ year *M. hubbsi* were collected during daylight (02-01-2014 to 02-04-2014) with a bottom trawl (100 mm cod-end mesh with an intranet cover of 20 mm mesh size, headrope of 35 m and footrope of 50 m) in eight sampling stations (Figure 1b). Speed and

time of the fishing trawls was about 7 km h^{-1} for 30 min. Fish ($n = 5$ per trawl) were frozen at -20°C to minimize lipolytic enzyme activity quickly following catch.

2.3 | Size and condition indices

Age 0+ year *M. hubbsi* were thawed and the following measures were taken: total length (L_T , cm, from the tip of the snout to the end of the caudal fin; range 10.00–14.50 cm), total mass (M_T , g; range 6.53–19.96 g), somatic mass (M_S , g, representing total mass without head, gonads and stomach content *sensu* Lambert & Dutil (1997); range 4.08–18.28 g) and liver mass (M_H , g; range 0.15–0.71 g). Then, the relative condition factor (K_n), as the ratio of the observed M_S and the expected M_S , predicted by the relationship between M_S and L_T for the population from which age 0+ year *M. hubbsi* were sampled (in this case, $M_S = 0.0011L_T^{3.5968}$, $R^2 = 0.77$, $n = 40$) and the hepato-somatic index (I_H), expressed as $I_H = 100M_HM_S^{-1}$, were calculated.

Muscle and liver total lipid content (%L, $\text{g } 100 \text{ g}^{-1}$ of wet mass) were determined gravimetrically from 1 g of muscle and the whole liver of each individual, following Bligh & Dyer (1959). Then, fatty-acid composition of both tissues was determined by gas chromatography following transesterification to fatty-acid methylesters (FAME), based on ISO 12966-2 (ISO, 2017) with some modifications. Briefly, 60 mg of lipid sample were mixed with 2 ml hexane and 0.3 ml of KOH–MeOH reagent in a glass test tube. Sample was mixed vigorously (1 min) with a vortex. Then, 2 ml of NaCl and 2 ml of hexane were added and mixed again for 1 min. The sample was allowed to stand for 5 min and the upper hexane layer was separated and transferred to a clean tube. FAME were determined with a Shimadzu GC-2010 gas chromatograph (Shimadzu Corp.; www.ssi.shimadzu.com), equipped with a flame-ionization detector (260°C) and capillary column (30 m x 0.32 mm; 0.25 μm film thickness; Omegawax 320; Sigma-Aldrich; www.sigmaaldrich.com). GC stings were split

rate 50, injector temperature 250°C, column temperature 120°C with nitrogen as a carrier gas. The oven temperature was increased to 240°C at a rate of 5°C min⁻¹ and held for 5 min. A volume of 1 µl of sample was manually injected and peaks were identified by comparison of their retention times with those of external reference standards (Supelco FAME Mix C₄-C₂₄ + PUFA N°1 Marine Source; Sigma-Aldrich). Individual fatty acids were reported as % peak area of the total FAME area.

2.4 | Feeding analysis

Stomachs were dissected from each individual and prey items were identified to the lowest possible level. Feeding incidence (I_F) was calculated as the percentage of age 0+ year *M. hubbsi* with at least one prey item in the gut contents (Arthur, 1976). The contribution of each prey category (i) to the diet was examined through its frequency of occurrence (% O_i) and percentage in number (% N_i). Both variables were integrated in an index of relative importance (I_{RI}) (Pinkas *et al.*, 1971), calculated as $I_{RIi} = \%O_i\%N_i$ and expressed as $\%I_{RI} = 100I_{RI}(\sum I_{RI})^{-1}$ (Cortés, 1997).

2.5 | Statistical Analyses

Pearson's correlations were used: to evaluate the relationship between condition indices and L_T of age 0+ year *M. hubbsi*, as estimates of these indicators can be biased by size effects; to test whether morphometric (K_n , I_H) and biochemical (% L and fatty acids in muscle and liver) indices represent interchangeable metrics of condition; to explore how environmental variables and condition indices relate to each other. The station-related variability in size (L_T and M_T) and condition (K_n , I_H , % L) of the individuals were evaluated with one-way ANOVA,

using a *post hoc* Tukey test as pair-wise multiple comparisons procedure. Spatial variations in feeding data were analysed by building generalized linear models (GLM), with feeding incidence (binomial-error distribution) and numerical abundance of prey (negative-binomial distribution) as response variables. All the analyses were performed with R 3.3.3 (www.r-project.org), setting significance at $P < 0.01$.

For fatty acids data of muscle and liver, multivariate statistical analyses were carried out using PRIMER 6.1.13 (Clarke & Gorley, 2006) with PERMANOVA+ 1.0.3 (Anderson *et al.*, 2008). Only those representing $> 1\%$ of the total as well as essential PUFA were analysed. The data were left untransformed following Cook *et al.* (2010) to prevent an excessive weighting to fatty acids with a low contribution to the profiles. Permutational multivariate analysis of variance (PERMANOVA) performed on Bray–Curtis similarity matrix was used to assess differences in fatty-acid composition based on two main factors (fixed): tissues (two levels) and stations (eight levels). The significance of PERMANOVA analysis (set at $P < 0.01$) was determined using permutation of residuals under a reduced model (4999 permutations) with Type III sums of squares (Anderson *et al.*, 2008). If significant, data were compared through *a posteriori* pair-wise comparison using 4999 random permutations to obtain P -values. The similarity percentages (SIMPER) routine was used to identify fatty acids that contributed most to observed differences in the profiles. Data were visualized with multidimensional scaling (MDS) and the stress value represented the goodness of fit for the ordination. Stress values < 0.2 were considered to be acceptable, while plots with stress values > 0.2 are close to random (Clarke & Gorley, 2006). To aid in data interpretation, fatty acids were represented in the MDS with vectors of relative length corresponding to their strength (*i.e.*, magnitude of change and variability) in sample positioning. Correlation coefficients (Pearson's r) of the fatty acids and the MDS 1 and MDS 2 were also calculated.

3 | RESULTS

3.1 | Environmental setting

During the cruise, most of the gulf was occupied by shelf waters, which were evident from the highest surface temperature (16.8°C; Figure 2a) and salinity (33.55; Figure 2b) values at the northern and central stations, respectively. On the other hand, lower temperature (12.3°C) and salinity (33.1) values in coastal and southern stations indicated the presence of low-salinity coastal waters. Bottom temperatures were lower (7.6–14.7°C) than at the surface, while no differences were observed in salinities (data not shown). Water masses are further illustrated by a temperature–salinity diagram (Figure 2c) of selected stations where biological samplings (zooplankton and age 0+ year *M. hubbsi*) were available. Within low-salinity coastal waters, Stations 120, 121 and 122 corresponded to well-mixed waters, while Stations 109, 119, 110, 104 and 117 were located in the frontal area. The remaining stations were stratified, with shelf waters in the upper layers and cold and less saline water in the deeper layers. Position of the fronts within the gulf, determined by the critical $\Phi = 40 \text{ J m}^{-3}$ (Figure 1a) showed coastal homogeneous waters in the north and south extremes of the gulf, separated from stratified waters in the central and external regions of the area. The presence of the South Patagonian Frontal System was also evident from maximum gradients in surface temperature and salinity fields, while the North Patagonian Frontal System was less marked since its maximum development occurs at the bottom. *In situ* surface chlorophyll-*a* values ranged from 0.82 to 2.79 mg C m^{-3} (mean \pm SD = $1.52 \pm 0.77 \text{ mg C m}^{-3}$). Most of the gulf exhibited values $< 2 \text{ mg C m}^{-3}$, particularly in the central region (*e.g.*, St. 102; Figure 2d), while in coastal waters around 45°–46° S, values $> 2 \text{ mg C m}^{-3}$ predominated (*e.g.*, Stations

110, 114 and 99). Particularly, in Stations 110, values ranging 2–4 mg C m⁻³ were recorded in the first 15 m of the water column.

The macrozooplankton community in the gulf was dominated by the euphausiids *Euphausia* spp. (91.84%), including the species *Euphausia lucens* and *Euphausia vallentini* (*sensu* Ramírez, 1971). Other taxa present were the hyperiid amphipod *Themisto gaudichaudii* (2.08%) and non-identified gammarids (0.58%), the decapods *Munida gregaria* (0.19%) and *Peisos petrunkevitchi* (0.38%) and non-identified species of mysids (4.92%). Spatially, higher abundances of euphausiids (mean total abundance \pm SD = 4.85 \pm 6.49 ind. m⁻³) were recorded at Stations 98, 110 and 104, while lower values occurred at Stations 119, 120, 121 and 122 (Figure 3). In contrast, decapods (0.29 \pm 0.59 ind. m⁻³) were particularly dominant at Station 71 north of the gulf, while non-identified mysids (0.26 \pm 0.63 ind m⁻³) and amphipods (0.11 \pm 0.18 ind m⁻³) prevailed south of the gulf (Stations 119, 120, 121 and 122).

3.2 | Age 0+ year *M. hubbsi* condition and feeding

Mean \pm SD L_T of age 0+ year *M. hubbsi* was 12.82 \pm 1.16 cm, while M_T was 13.10 \pm 3.85 g. No significant differences in length and mass of age 0+ year *M. hubbsi* were observed among stations ($P > 0.01$; Figure 4). Condition indices K_n and I_H ranged from 0.69 to 1.32 (mean \pm SD = 0.98 \pm 0.17) and 1.54 to 5.53 (3.43 \pm 0.93), respectively, while %L in muscle and liver ranged from 0.18 to 1.37 (mean \pm SD = 0.73 \pm 0.30) and 1.34 to 24.64 (10.15 \pm 5.38), respectively. Station-related variability was recorded for most of these indices (Table 1; Figure 5). K_n showed two groups of stations with significantly higher (Stations 99, 101, 107, 109 and 117) and lower (Stations 94, 102 and 115) condition values. I_H and %L in liver followed a similar spatial trend, with significantly higher values in coastal Stations 99, 109

and 115 and lower values in central stations of the gulf (Stations 101, 102 and 107). On the contrary, lipids in muscle were higher in central waters (Station 101), with intermediate values in coastal Stations 99, 109 and 117.

With respect to fatty acids, the PERMANOVA test indicated significant differences in composition of the profiles in muscle and liver (sums of squares = 3047.2, mean square = 3047.2, pseudo- $F = 83.11$, $P[\text{perm}] < 0.001$). Similarity within both tissues was high (> 90% in SIMPER test; Table 2), with the PUFA 22:6n3 (docosahexaenoic acid), the MUFA 18:1n9 (oleic acid) and the SFA 16:0 (palmitic acid) as the highest contributors to similarity. However, DHA dominated in muscle, while 16:0 prevailed in liver. Despite these differences, dissimilarity between tissues was rather low (15.18%). Minor fatty acids contributing to the profiles in both tissues were 18:0, 18:1n7, 22:1n9, 18:2n6, 18:3n3 and 20:5n3. Accordingly, MDS revealed a clear differentiation in the spatial ordination of muscle and liver samples, mainly along MDS 1, with a rather strong goodness of fit (stress value: 0.08; Figure 6). Fatty acids with the highest effect on the sample ordination, based on Pearson's correlation, were 22:6n3 ($r_s = 0.90$), 18:0 ($r_s = 0.83$), 18:1n7, 22:1n9 and 18:2n6 ($r_s = -0.87$ in all three fatty acids) in the MDS 1 and 16:0 ($r_s = 0.84$) in the MDS 2. This showed higher proportions of SFA and PUFA in muscle, with MUFA predominating in liver. PERMANOVA also showed significant differences in fatty acids composition among stations (sum of squares = 1268.1, mean square = 181.2, pseudo- $F = 4.94$, $P[\text{perm}] < 0.001$). In muscle, pair-wise comparisons indicated significantly higher proportions of 22:6n3 at Stations 107 and 101 and lower values at Stations 99 and 115 and an opposite spatial trend in 16:0 percentages (Table 1). In liver, Stations 99 and 109 were significantly different from the rest and exhibited lower 22:6n3 values, but higher 18:1n9 percentages.

Condition indices were independent of L_T of the individuals within the size range used in this study ($P > 0.01$). The morphometric relative condition index K_n was not significantly

correlated with any of the other indices. On the other hand, the hepato-somatic index I_H was significantly correlated ($P < 0.01$) with the content of lipids ($r_s = 0.61$) and fatty acids in the liver (18:1n9 $r_s = 0.62$, 22:6n3 $r_s = -0.54$) and the muscle (22:6n3 $r_s = -0.45$), indicating that these indices followed the same general trend. Per cent lipid in the liver correlated positively with 18:1n9 ($r_s = 0.62$) and negatively with 22:6n3 ($r_s = -0.62$) in the same tissue. In fact, both 18:1n9 and 22:6n3 were strongly and negatively correlated in liver ($r_s = -0.79$), with a less strong relationship in muscle ($r_s = -0.50$). Moreover, in muscle, 22:6n3 correlated negatively with 16:0 ($r_s = -0.85$). With respect to correlations among indices and the environmental variables, some strong coefficients were observed between I_H and %L in liver with surface temperature ($r_s = -0.49$ and -0.65 , respectively), as well as between K_n and %L in muscle with chlorophyll-*a* ($r_s = 0.66$ and 0.52 , respectively). However, these correlations were not significant ($P > 0.01$).

Stomach contents analyses revealed a mean \pm SD feeding incidence of $85 \pm 28\%$, with significantly lower values in Stations 99, 101 and 109 (GLM model: $P < 0.01$; $AIC_{\text{best model}} = 31.01$, $AIC_{\text{null model}} = 35.82$; Figure 7). *Euphausia* spp. were the main prey consumed at most stations, followed by *T. gaudichaudii*. Other items such as *P. petrunkevitchii* and non-identified gammarids were also found occasionally. The numerical abundance of *Euphausia* spp. in the diet did not vary spatially ($P > 0.01$), although lower values were observed at Stations 101 and 102. An opposite trend was observed for *T. gaudichaudii*, with significantly higher values at these last stations (GLM model: $P < 0.01$; $AIC_{\text{best model}} = 87.17$, $AIC_{\text{null model}} = 127.03$). In agreement, %Ni of *Euphausia* spp. and *T. gaudichaudii* in the stomachs were significantly and negatively correlated ($r_s = -0.99$, $n = 8$, $P < 0.01$)

4 | DISCUSSION

4.1 | General considerations

Results on condition of age 0+ year *M. hubbsi* are presented for the first time for the Patagonian stock of the species within their main nursery ground in the Argentinean continental shelf, by a combination of different indices. Data are novel, considering that condition studies of exploited species in the ACS have focused either on *Engraulis anchoita* Hubbs & Marini 1935 larvae (Díaz *et al.*, 2011), or *M. hubbsi* larvae (Díaz *et al.*, 2014) and adults (Macchi *et al.*, 2013; Leonarduzzi *et al.*, 2014), with only a previous record for age 0+ year *M. hubbsi* solely based on morphology (Prenski & Angelescu, 1993). Despite the lack of previous local data to establish a comparison, our estimations closely agree with results on related age 0+ year gadoid species. For instance, Ferraton *et al.* (2007) estimated K_n values ≈ 1.0 for juvenile *Merluccius merluccius* (L. 1758), while Grant & Brown (1999) indicated I_H values from 2 to 4 for age 0 year *Gadus morhua* L. 1758. With respect to biochemical indices, our data set is the first regarding lipids and fatty acids in muscle and liver of age 0+ year *M. hubbsi* in the ACS. Lipids in age 0+ year *M. hubbsi* were stored mainly in the liver, following the known trend in Gadidae (Lambert & Dutil, 1997) and the previous studies performed on adult females of the species (Leonarduzzi *et al.*, 2014). They were characterized by fatty acids 16:0, 18:1n9 and 22:6n3 (DHA), which are among the most common in marine organisms' lipids (Arts *et al.*, 2009). These compositional values fairly agree with those mentioned for pre-recruits of *G. morhua* (Olsen *et al.*, 1991; Lambert & Dutil, 1997), *Gadus macrocephalus* Tilesius 1810 (Van Pelt *et al.*, 1997; Copeman *et al.*, 2013) and *M. merluccius* (Küçükgülmez *et al.*, 2008).

Total length and mass of age 0+ year *M. hubbsi* in the San Jorge Gulf exhibited a limited and spatially homogenous size range, which was expected considering that the present work was directed at a particular life stage (age 0+ years). Length, in particular, was

not significantly correlated with any of the condition indices used in this study, suggesting that there are very weak effects of *M. hubbsi* size on the condition estimates within the size range used. Consequently, the use of these indices is allowed without a bias from the effect of size, as stated by Bolger & Connolly (1989). Similar results were reported in juvenile gadoids such as *G. morhua* (Lambert & Dutil, 1997) and *M. merluccius* (Lloret *et al.*, 2008). Most measures of condition are vulnerable to length dependence, provided body, liver, gonad and digestive tract masses increase as the fish grow (Lloret *et al.*, 2002). This is probably because larger fish with greater demand on their resources lay down greater energy reserves. However, energy storage strategies differ through ontogeny as individuals shift their energy allocation from growth to storage (*e.g.*, in preparation for reproduction; Lloret *et al.*, 2014). In this sense, age 0+ year *M. hubbsi* are probably allocating energy to somatic growth, with intensive protein synthesis that promotes increases both in length and mass (Lloret *et al.*, 2014). This isometric growth was also evident from the *b* slope of the length–mass regression, which was ~ 3.0 , as proposed for the species (Prenski & Angelescu, 1993) and observed in age 0 year gadoids (Lambert & Dutil, 1997; Hidalgo *et al.*, 2008).

A suite of different condition indices was selected in this work to evaluate whether they represented interchangeable metrics of physiological status of age 0+ year *M. hubbsi*. Considering the morphometric K_n , this hypothesis should be rejected, provided it does not correlate with any other, as previously reported for *G. morhua* (Pardoe *et al.*, 2008). On the other hand, significant correlation between I_H and the liver lipid content indicates that the hepato-somatic index is a good indicator of the energetic condition of age 0+ year *M. hubbsi*. Similar results were observed in other gadoids (Lambert & Dutil, 1997; Lloret *et al.*, 2008) and in *M. hubbsi* females (Leonarduzzi *et al.*, 2014). 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) and the same is expected for lipids in muscle, which are usually more stable fat stores (Lovern & Wood, 1937). In contrast, liver-based indices are known to respond more rapidly to external changes (Love, 1970), particularly in Gadidae such as *M. hubbsi* that store most of their lipid reserves in this organ (Lambert & Dutil, 1997). Within-liver lipids, interplay was observed between MUFA and PUFA proportions, with the preservation of the latter in stations where condition was lower. Accordingly, the concurrent mobilization of MUFA in low-condition age 0+ year *M. hubbsi* might respond to their use as an energy source during lipolysis, especially oleic (18:1n9) and palmitic (16:0) acids (Lloret *et al.*, 2014), which were dominant in pre-recruit profiles. These facts highlight the potential of lipids and fatty acids as indicators of spatial changes in age 0+ year *M. hubbsi* nutritional status, despite the specific and laborious laboratory analysis they require. Ultimately, a set of indicators gives a fuller picture of condition variability and energy-storage strategies than the one provided by a single index. This is particularly true based on our results, since spatial patterns among condition indices were not congruent. Thus, the combined use of liver-based morphometric and biochemical indices is encouraged for future studies focusing on age 0+ year *M. hubbsi*.

4.2 | Spatial changes in condition

From an oceanographic point of view, the northern and central sectors of the San Jorge Gulf during the cruise were characterized by shelf waters, while in coastal and southern areas, low-

salinity coastal waters prevailed. The presence of the typical frontal structures described for the region and season (Bianchi *et al.*, 1982; Glorioso, 1987; Guerrero & Piola, 1997; Sabatini & Martos, 2002; Bogazzi *et al.*, 2005) was observed, with a stratified water column in most of the stations analysed. Chlorophyll-*a* values found in the gulf were in agreement with previous records for the region in austral summer derived from field (Segura & Cucchi Colleoni, 2015) and remote sensing (Marrari *et al.*, 2016) data. Higher values were observed in the coastal area around 45°–46° S, 67° W, coincident with cold and nutrient-rich low-salinity coastal waters. These waters would correspond to coastal upwelling processes that have been observed by numerical modelling (Tonini *et al.*, 2006). A decrease in temperature and salinity values recorded in this coastal area also suggests a weak upwelling, as found by Rivas and Pisoni (2010). With respect to macrozooplankton, species found in this study had been previously described for the gulf in summer, with similar abundance ranges (Pérez Seijas *et al.*, 1987; Viñas *et al.*, 1992). Particularly for euphausiids, higher abundances were recorded in coincidence with the highest chlorophyll-*a* values and in the southern extreme of the gulf, probably associated with the dynamics of the Southern Patagonian Frontal System. This latter fact could also explain higher mysid and amphipod abundances in this sector.

The heterogeneity observed in the environment of the San Jorge Gulf was reflected in the nutritional status of age 0+ year *M. hubbsi*, which showed clear spatial variability. Maximum chlorophyll-*a* values and lower temperatures around 45°–46° S, 67° W concurrent with highest *Euphausia* spp., which were the preferred pre-recruit prey according to diet analyses, coincided with their enhanced condition in this sector. Accordingly, K_n and lipids in muscle were positively correlated with chlorophyll-*a*, while I_H and lipids in liver were negatively correlated with surface temperature. Since euphausiids are mostly herbivorous (Stuart, 1989; Gurney *et al.*, 2002), a positive bottom-up effect upon age 0+ year *M. hubbsi* condition can be suggested. A similar effect was observed in age 0 year *T. chalcogramma* in

the eastern Bering Sea, where productivity in the pelagic environment as well as consumption of euphausiids was suggested to favour condition during summer (Moss *et al.*, 2009).

Chlorophyll *a* concentration also played a key role in determining body condition of gadoids in the Balearic Islands (Rueda *et al.*, 2015). In the southern extreme of the gulf, under the influence of the South Patagonian Frontal System, a similar process might be occurring. Even though no fish trawls were available for this area of the SJG, the high zooplankton abundances observed could have a positive effect upon pre-recruit condition. This bottom-up effect upon age 0+ year *M. hubbsi* condition could favour their growth and survival and deserves future monitoring, considering that chlorophyll-*a* values in the SJG derived from a > 17 year time series of multi-sensor data show increasing trends since 1997 (Marrari *et al.*, 2016). This is particularly relevant in a global climate change scenario that will unpredictably alter the present interactions between biotic and abiotic drivers (Heintz *et al.*, 2013) and could change the duration of suitable feeding conditions for fish (Lloret *et al.*, 2014).

Another factor that might be moderating age 0+ year *M. hubbsi* condition is prey quality. In stratified central waters of the gulf, where liver-based condition was lower, *T. gaudichaudii* dominated the diet. Preliminary results indicate that lipid-derived energy density (kJ g⁻¹) is significantly higher in *Euphausia* spp. (mean ± SD = 1.28 ± 0.54 kJ g⁻¹) than in *T. gaudichaudii* (0.94 ± 0.42 kJ g⁻¹; B. Temperoni, unpubl. data). Accordingly, in age-0 *T. chalcogramma* and *M. merluccius*, the consumption of high-quality prey improved their growth and nutritional condition, reducing energy deficits and leading to increased survival (Harmelin-Vivien *et al.*, 2012; Heintz *et al.*, 2013). Ferraton *et al.* (2007) observed an interannual decline in the relative condition factor of age 0+ year *M. merluccius* in the Gulf of Lions, probably deriving from the energetic content of the prey, while Grant & Brown (1999) reported a rapid response of small 0-group *G. morhua* condition to the consumption of lipid-rich copepods. Also, the input of essential PUFA from prey should be

considered. PUFA usually cannot be biosynthesized *de novo* by most fish, being first synthesized by primary producers and then incorporated unchanged into the tissues of secondary consumers (Dalsgaard *et al.*, 2003). Particularly, DHA affects fish condition through its role in cell membrane fluidity, development of neural function and the production of compounds involved in a wide range of metabolic processes (Dalsgaard *et al.*, 2003). While herbivorous euphausiids in the gulf can probably prey upon DHA-rich dinoflagellates (Mansour *et al.*, 1999) that are dominant in summer (Akselman, 1996; Krock *et al.*, 2015), *T. gaudichaudii* has a carnivorous behaviour (Sheader & Evans, 1975). Hence, it would provide age 0+ year *M. hubbsi* with a lower DHA input. Ongoing research on age 0+ year *M. hubbsi* prey quality within the San Jorge Gulf will allow us to either confirm or reject this hypothesis. This is relevant considering that climate shifts could also change the production of PUFA, either by changing phytoplankton species composition or by changing their production within phytoplankton taxa (Litzow *et al.*, 2006).

Condition, like most essential biological traits, is very sensitive to the spatial changes in environmental factors occurring in marine ecosystems, with individuals of several species displaying different levels of condition according to areas, seas, oceans, depths and habitats (Lloret *et al.*, 2014). The observed variability in fish condition in temperate locations, such as the San Jorge Gulf, inhabited by age 0+ year hake would be related to food availability, where the best conditioned individuals inhabit the areas of high productivity (and food abundance), such as upwelling systems and coastal waters (Lloret *et al.*, 2002; Lloret & Planes, 2003). This was particularly evident from our data set and was also observed in *M. hubbsi* larval stages within their Patagonian spawning ground, north of the Gulf (43°–45° S) (Díaz *et al.*, 2014). Similar results have also been obtained in related gadoid species. For instance, Brodeur *et al.* (2000) found that age-0 walleye pollock *Gadus chalcogrammus* Pallas 1814 located offshore of a tidal front in the Bering Sea have significantly higher

condition than those found inshore. This was attributed to a bioenergetic advantage of individuals in stratified waters that migrate into the surface layer to feed upon energetically profitable prey. 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. The identification of spatial patterns is of essential interest, because local effects of environmental drivers on fish condition that might be considered for assessment and management (Rueda *et al.*, 2015) could be ignored when searching for general responses at large scales. In this sense, and considering the key role that age 0+ year individuals play in *M. hubbsi* fisheries recruitment in the ACS, studies linking their condition with the environment are essential to understanding the influence of bottom-up factors on the recruitment levels of the species and should continue in the future

Following the “ideal free distribution” hypothesis (Fretwell & Lucas, 1970), age 0+ year *M. hubbsi* should have distributed within the San Jorge Gulf in a way that equalizes feeding incidence, resulting in spatially-uniform condition, but results indicate otherwise. Although the habitats most conducive to growth are clearly preferred, fishes may occupy suboptimal areas due to transport, avoidance of competition, or predation (Sogard, 1994). Because condition may characterize components of the environment in which fish exist (*e.g.*, prey availability, competition), observed spatial variability in fish condition can reveal changes in environmental conditions and can therefore be used as an indicator of environmental status (Lloret *et al.*, 2014). In this sense, present results on age 0+ year *M. hubbsi* condition during austral summer could provide an indication of the quality of the SJG as a nursery habitat, as observed in other Gadidae (Chouinard & Swain, 2001). Coastal waters of this gulf could be postulated as high-quality or essential habitats to sustain the Patagonian *M. hubbsi* stock (*sensu* Lloret *et al.*, 2002). However, it should also be considered

that patterns of juvenile fish habitat quality can show considerable temporal variation both within and between years (Ciotti *et al.*, 2013). This is probable in the San Jorge Gulf, a highly dynamic habitat controlled by physical features such as different water masses, topography and the presence of frontal systems. Nutrient-rich waters, upwelling mechanisms and circulation cells seem to have a considerable effect upon phyto and zooplankton growth. Also, the flow directed towards the coast in deeper layers of the water column would favour the access of pre-recruits to high quality feeding grounds. Hence, temporal monitoring of age 0+ year *M. hubbsi* condition in relation to environmental conditions is encouraged. Work in progress, particularly focused on spring and winter scenarios within the gulf, will provide further insight into this topic.

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FIGURE CAPTIONS

Figure 1. Sampling stations (numbered) in the San Jorge Gulf during austral summer of 2014 for: (a) conductivity–temperature–depth (CTD) casts (●) and water samples for *in situ* chlorophyll-*a* determination (●); (b) plankton bongo-net tows (▲) and fish trawls (■). —, Mean position of the Northern (NPFS) and Southern (SPFS) Patagonian Frontal Systems (critical Simpson parameter $\Phi = 40 \text{ J m}^{-3}$).

Figure 2 (a) Surface temperature ($^{\circ}\text{C}$) distribution, (b) surface salinity distribution, (c) temperature–salinity diagram of conductivity–temperature–depth (CTD) casts and (d) estimated surface chlorophyll-*a* concentration (mg m^{-3}) distribution in the San Jorge Gulf during austral summer of 2014. In (c), numbers correspond to the bongo-net and fish-trawl stations (Figure 1b); |, separation between groups of stations located in well-mixed, frontal and stratified waters.

Figure 3 Spatial distribution of macrozooplankton abundances ($n \text{ m}^{-3}$) in the San Jorge Gulf during austral summer of 2014. NI: non-identified.

Figure 4. Mean total length (L_T) and total mass (M_T) of age-0+ year *Merluccius hubbsi* in eight stations in the San Jorge Gulf during austral summer of 2014. Boxes indicate mean \pm 95% CI, and vertical bars indicate mean \pm 2SD.

Figure 5. Spatial variability in morphometric relative condition factor (K_n) and hepatosomatic index (I_H) and biochemical liver lipid indices in muscle ($\%L_{\text{muscle}}$) and liver ($\%L_{\text{liver}}$) of age 0+ year *Merluccius hubbsi* in the San Jorge Gulf during austral summer of 2014.

Figure 6. Non-metric multidimensional scaling (MDS) ordination on fatty acids composition of age 0+ year *Merluccius hubbsi* comparing muscle (M; black symbols) and liver (L; grey symbols) per sampling station (St.).

Figure 7. Spatial variability in the index of relative importance (% I_{RI}) of diet composition (*Euphausia* spp., *Thermisto gaudichaudii* and *Peisos petrunkevitchi*) of age-0+ year *Merluccius hubbsi* in the San Jorge Gulf during austral summer of 2014. Numbers indicate feeding incidence (%) at each station.

TABLES

Table 1 Mean values (SD) of morphometric indices relative condition factor (K_n) and hepatosomatic index (I_H), liver lipid content (%L) and fatty-acid content in muscle and liver (%FAME; only those accounting >10% shown) of age 0+ year *Merluccius hubbsi* in the San Jorge Gulf, Argentina, during austral summer of 2014

Sampling station	Muscle					Liver				
	K_n	%L	22:6n3	18:1n9	16:0	I_H	%L	22:6n3	18:1n9	16:0
94	0.8 (0.1) ^a	0.4 (0.1) ^b	27.8 (9.4)	14.9 (1.4)	27.3 (4.5)	3.5 (0.6)	7.3 (2.8) ^a	24.6 (1.5)	11.3 (1.7)	25.7 (4.1)
99	1.1 (0.1) ^b	0.9 (0.2) ^a	24.3 (2.5)	12.9 (0.4)	27.2 (1.8)	4.2 (0.6) ^b	18.3 (4.7) ^b	14.8 (1.7)	14.2 (1.0)	22.2 (1.1)
101	1.0 (0.1) ^b	1.2 (0.1) ^a	31.2 (2.6)	14.5 (1.8) ^b	24.2 (0.9)	2.3 (0.5) ^a	4.8 (4.2) ^a	26.0 (4.0)	10.3 (3.1)	24.3 (1.5)
102	0.7 (0.1) ^a	0.7 (0.2) ^b	29.7 (3.2)	13.0 (0.9)	25.6 (2.1)	3.4 (1.2)	8.8 (4.9) ^a	19.1 (4.2)	11.6 (1.7)	27.4 (4.0)
107	1.2 (0.1) ^b	0.5 (0.1) ^b	33.3 (3.0)	11.9 (0.6)	23.8 (0.9)	2.7 (0.3) ^a	7.1 (1.6) ^a	22.0 (4.1)	11.1 (1.7)	22.5 (0.9)
109	1.1 (0.1) ^b	0.8 (0.1) ^a	30.6 (3.0)	12.5 (0.6)	26.0 (1.7)	3.9 (0.2) ^b	13.8 (4.8) ^b	17.2 (1.6)	14.6 (0.9)	22.7 (0.8)
115	0.9 (0.1) ^a	0.5 (0.3) ^b	26.0 (3.4)	13.6 (1.3)	27.1 (2.1)	4.5 (1.0) ^b	10.8 (4.7)	22.0 (1.7)	11.9 (1.4)	23.4 (1.2)
117	1.1 (0.04) ^b	0.9 (0.2) ^a	28.7 (6.3)	12.6 (1.2)	24.8 (2.8)	3.1 (0.2) ^a	10.4 (1.9)	18.2 (2.1)	11.9 (1.1)	22.8 (0.9)
ANOVA $F_{7,32}$	19.9*	9.4*	—	—	—	6.7*	5.9*	—	—	—

*, $P < 0.01$; ^{a,b}, significant differences from *post hoc* Tukey test.

Table 2 Similarity percentages (SIMPER) analysis showing major fatty acids contributing to the average similarity within and to the average dissimilarity between muscle and liver of age 0+ year *Merluccius hubbsi*.

	Fatty acids	Contribution (%)	Cumulative contribution (%)
Mean similarity within groups			
Muscle 93.10	22:6n-3	32.80	32.80
	16:0	30.42	63.23
	18:1n-9	15.68	78.90
	22:1n-9	8.28	87.19
	18:0	5.47	92.66
Liver 92.71	16:0	31.68	31.68
	22:6n-3	26.14	57.82
	18:1n-9	15.62	73.43
	22:1n-9	14.19	87.62
	18:1n-7	5.31	92.93
Mean dissimilarity between groups			
Muscle & Liver 15.18	22:6n-3	37.34	37.34
	22:1n-9	16.66	54.00
	16:0	12.68	66.68
	18:0	12.35	79.03
	18:1n-9	8.74	87.77
	18:2n-6	4.44	92.21

Figure 1

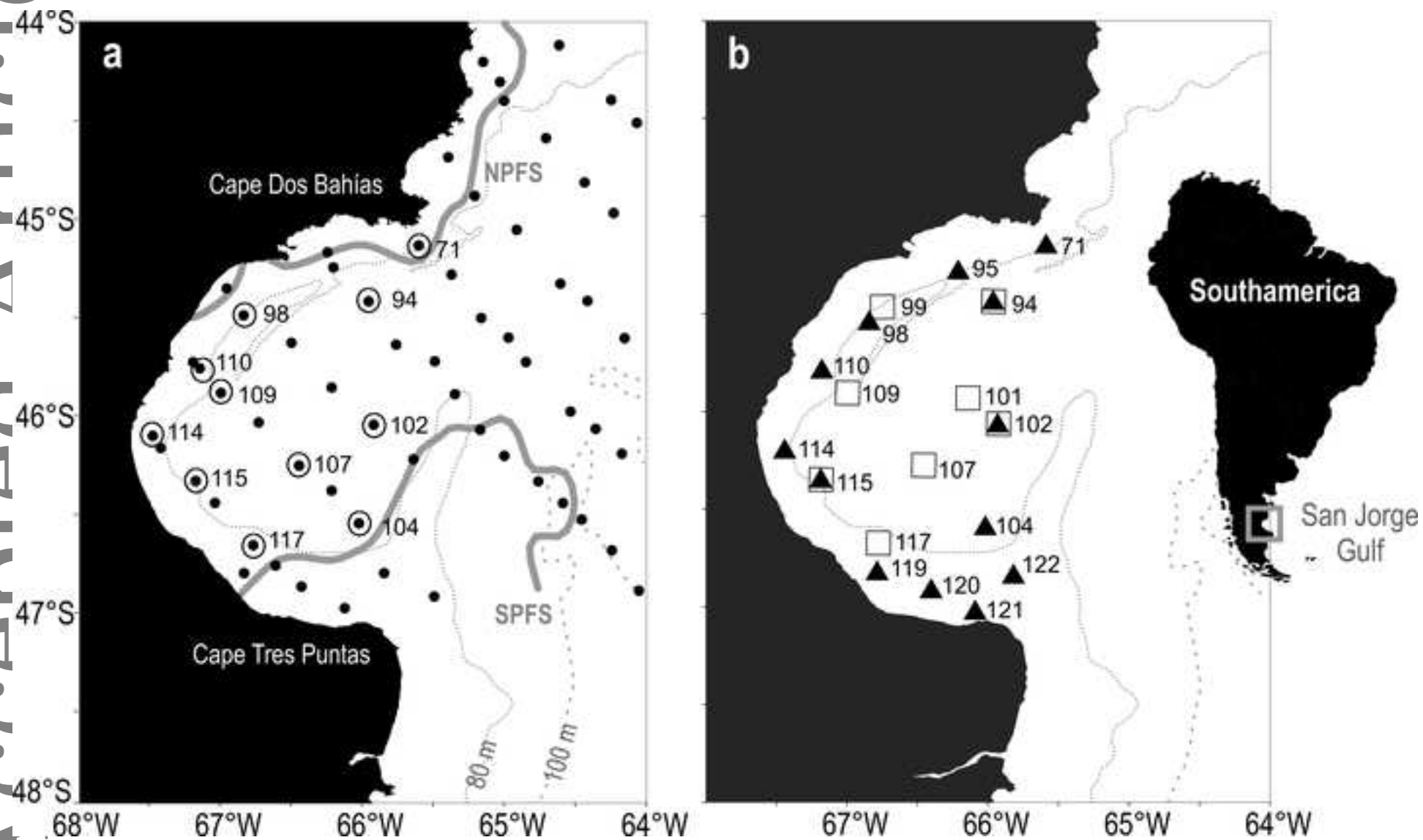
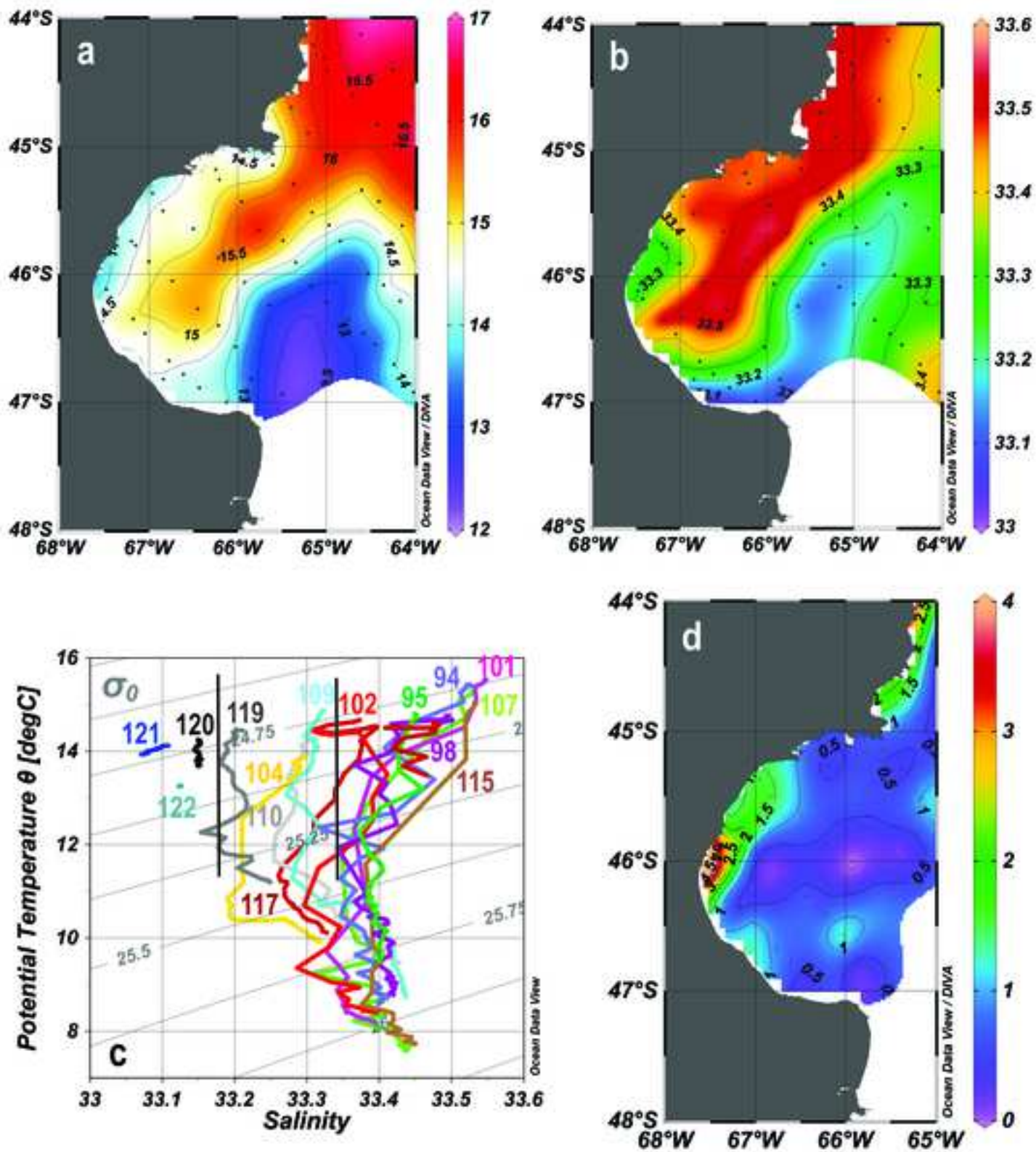


Figure 2



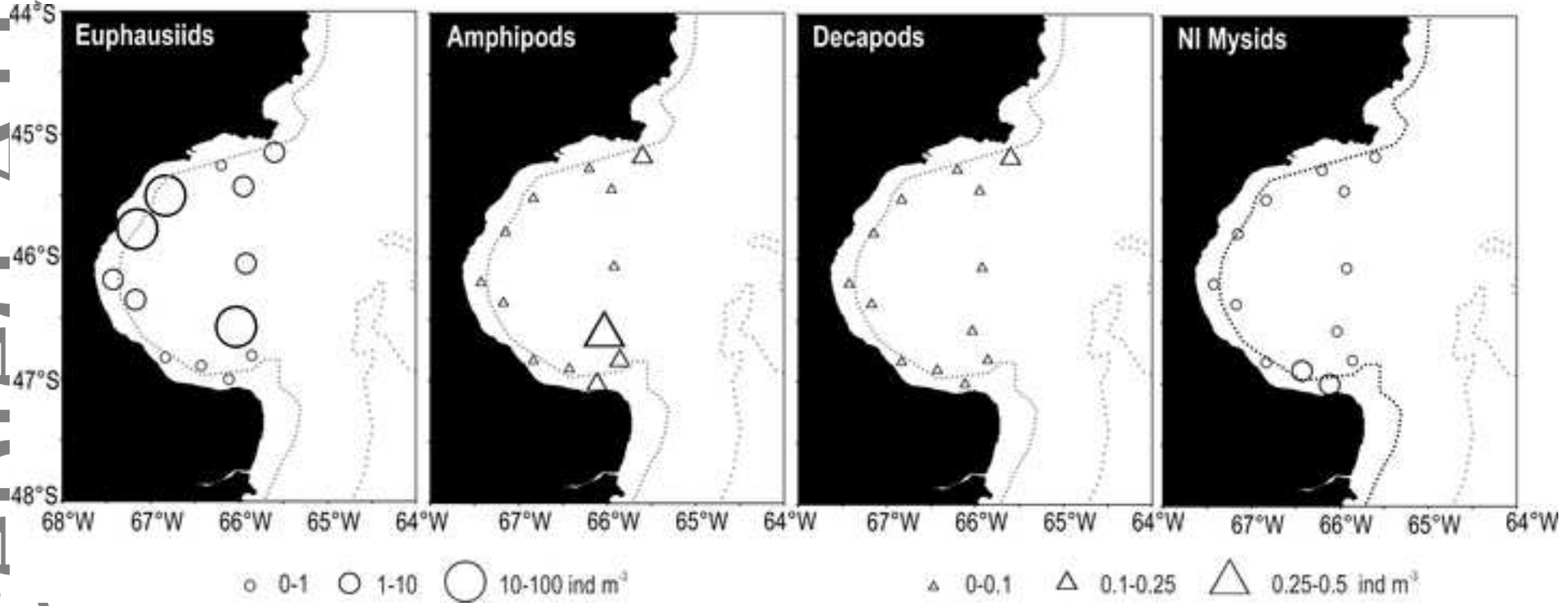


Figure 4

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□ L_T (cm) □ ● T_M (g)

