



Spatial patterns of copepod biodiversity in relation to a tidal front system in the main spawning and nursery area of the Argentine hake *Merluccius hubbsi*



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ABSTRACT

Copepods play an important role in marine ecosystems as a direct link of energy transfer between primary producers and higher trophic level consumers, such as fish. In the Argentine Sea, the Patagonian stock of Argentine hake *Merluccius hubbsi* spawns from late austral spring (December) to early autumn (April) in the northern Patagonian shelf region (43°–45°30'S), in association with a highly productive tidal front system. Since hake larvae prey mainly upon copepods, the objective of this study was to assess the spatial variability in the abundance and diversity of these potential food items in different sectors of the front, as one of the possible factors affecting hake recruitment success. Two complementary mesh sizes (67 and 300 μm) were used to accurately target the entire copepod size spectrum. The copepod community was dominated by developmental stages < 1 mm in total length (eggs, nauplii, copepodites of cyclopoids and calanoids), and adults of the species *Oithona helgolandica*, *Microsetella norvegica*, *Ctenocalanus vanus* and *Drepanopus forcipatus*. Their spatial distribution was highly influenced by the across-shelf characteristics of the tidal front system, highlighting the impact of environmental features, mainly bottom temperature and salinity, in shaping the community. Abundances were higher in the transitional relative to the stratified sector of the system. Such sector would provide the appropriate conditions to sustain *M. hubbsi* larval growth resulting from high availability of adequate prey, the suitable thermal ranges, and the existence of retention mechanisms.

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1. Introduction

Copepods are the most abundant component of marine zooplankton, playing an important role in marine ecosystems as a direct link of energy transfer between primary producers and higher trophic level consumers (Mauchline, 1998). Temporal and spatial variability in copepod diversity, size composition, and abundance has been shown to influence the species/size composition of associated fish larvae communities (Cass-Calay, 1997), since these crustaceans constitute their main food source in nature (Hunter, 1981). However, there is still a gap between zooplankton and fisheries research, mainly due to differences in spatial scales, which result in a lack of appropriate biological information on the prey field for adult fish and their offspring. As a

result, relevant questions as to whether larval survival and recruitment are limited by food often remain unanswered (Irigoin et al., 2009).

Argentine hake (*Merluccius hubbsi*) is one of the most abundant fish resources in the Argentine Sea (Cousseau and Perrota, 1998), with two different stocks identified: a northern stock located between 34° and 41°S, and a southern or Patagonian stock between 41° and 55°S (Bezzi et al., 1995). The Patagonian stock is the most important commercially, including ~85% of the total biomass (Aubone et al., 2000) and a spawning biomass of around 400,000 t (Villarino et al., 2012). Spawning occurs in the inner sector of the northern Patagonian shelf, between Isla Escondida (43°S) and Bahía Camarones (45°30'S) (Pájaro et al., 2005), during late austral spring (December) and early autumn (April) with a peak in January–February, when a highly productive tidal front system develops (Carreto et al., 1981). As a consequence of overexploitation in the last decade (Pérez et al., 2000), spawner biomass decreased drastically and the spawning pattern was affected. The main reproductive aggregations coincided spatially during 2001–2004; however, after 2005, spawning expanded into deeper waters and a new spawning

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group was detected in the outer sector of the northern Patagonian shelf in proximity of the 100 m isobath (Macchi et al., 2010). The observed changes in the spawning pattern lead to the occurrence of larvae in areas with different environmental conditions to those found close to frontal zones, which are probably less favorable for larval development (Díaz et al., 2014). Thus, a comparative study of the copepod community structure in both spawning sectors in relation to the environmental conditions is needed to elucidate the influence on the growth and survival of the recently hatched hake larvae.

Previous studies investigating the environmental factors partially responsible for hake population fluctuations in the spawning area have focused mainly on the adult fraction (Macchi et al., 2009; Pájaro et al., 2005). Hence, the critical larval phase, when food availability is one of the factors controlling survival (Houde and Scheckter, 1981), remains to be examined in detail. Since various stages of small- and medium-sized copepods are the main prey for *M. hubbsi* larvae (Ciechomski and Weiss, 1974; Temperoni and Viñas, 2013; Viñas and Santos, 2000), the assessment of their spatial variability during the reproductive season is essential to improve our understanding of one of the main factors affecting recruitment success of Argentine hake. The copepod community associated with the frontal structure in the northern Patagonian shelf has been previously described (Sabatini and Martos, 2002; Santos and Ramírez, 1995; Viñas et al., 1992); however, in most of these studies the finest mesh size used was 150 μm , with a resulting underestimation of small and medium-sized copepods (Antacli et al., 2010; Di Mauro et al., 2009). In addition, information on the small-scale distribution patterns of copepods is limited. Thus, the primary objective of this study was to investigate the diversity, abundance, and distribution patterns of copepods in the main spawning area of the Patagonian hake stock. The particular objectives were: 1) to analyze the spatial variability and temporal progression (monthly during the reproductive season) of copepod biodiversity, 2) to identify key species, 3) to determine the size structure of the copepod community, 4) to relate the observed patterns to the structure of the tidal front and 5) to identify favorable sectors within the spawning area for hake larvae survival. We hypothesize that the spatial and temporal environmental heterogeneity of the northern Patagonian shelf structures the copepod community.

2. Methods

2.1. Study area

The northern Patagonian shelf (43°–45°30'S) is characterized by two main water masses: Sub Antarctic Shelf Waters (salinities between 33.4–34), which occupy most of the shelf, and Magellan Strait Waters (<33.4), present in the inner and mid-shelf as a low-salinity surface tongue associated with the discharge of the Magellan Strait (Guerrero and Piola, 1997; Palma et al., 2008). During austral spring and summer, the most important feature in the area is a marked tidal front system that extends southward from Península Valdés (42°30'S) along the Patagonian coast to 45°S (Carreto et al., 1981, 2007; Glorioso, 1987; Sabatini and Martos, 2002). The front is located 80 km offshore in the northern part of the study area and approximately 50 km off the coast towards the south. The formation of this front is controlled by tidal currents and winds, and enhanced by inshore headlands. It starts developing during spring as the seasonal thermocline originates offshore and persists until autumn when stratification weakens. The system is characterized by a strong horizontal temperature gradient as the thermocline intersects the surface and bottom layers, separating vertically homogeneous waters from stratified (two-layered) waters (Sabatini and Martos, 2002). The front is usually strongest at the bottom but can also involve a surface component (Sabatini and Martos, 2002; Spinelli et al., 2012). In consequence, three sectors can be identified within the tidal front system: a vertically homogeneous (i.e. mixed) coastal sector, a transitional or frontal sector characterized by the

maximum horizontal bottom temperature gradient, and a stratified sector with a two-layer structure. Concentrations of Argentine hake spawners have been reported in coincidence with the bottom signal of the frontal system (Macchi et al., 2010; Pájaro et al., 2005), while high phytoplankton (Carreto and Benavides, 1989) and microzooplankton production have been reported in the transitional sector of the front (Sabatini and Martos, 2002; Viñas and Ramírez, 1996).

Numerical modeling of the vertical circulation structure in the spawning area indicates the presence of a two-layered flow, with an upper layer flowing offshore towards the northeast and a bottom layer flowing slowly towards the coast (Palma et al., 2008). In austral spring and summer, an intensification of the circulation is expected, with a near surface fast-flowing jet above the bottom temperature gradient and below the thermocline (Tonini, 2010). Moreover, cross-isobathic tidal excursion of the frontal zone (up to 10 km) between neap-spring tides was also demonstrated by the model. A vertical migratory behavior coupled to this circulation pattern has been proposed as a plausible retention mechanism for Argentine hake larvae (Álvarez Colombo et al., 2011). Such frontal features could both enhance horizontal transport and influence the spatial heterogeneity of the ecosystem, as reported for similar wide tidally-energetic continental shelves worldwide (Hill et al., 2008).

2.2. Collection and analysis of samples

Stock assessment cruises were conducted monthly in the spawning ground of hake Patagonian stock during the reproductive season: 3–13 December 2008 (D, EH-04/08), 10–27 January 2009 (J, EH-01/09) and February 28–March 11 2009 (FM, OB-02/09), by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), which provided an adequate platform to collect environmental data and zooplankton samples simultaneously (Fig. 1).

Conductivity–temperature–depth (CTD) profiles were obtained at all stations with a CTD Seabird SBE-19 profiler. Surface and bottom temperature and salinity fields were calculated for the area. In addition, vertical profiles were produced following inshore–offshore transects perpendicular to the coastline (T_D , T_J , T_{FM} ; Fig. 1). Sectors within the tidal front system (homogenous, transitional and stratified) were identified based on the Simpson's stability index ϕ (J m^{-3}) (Simpson, 1981). This parameter provides a measure of the energy needed to homogenize the water column and was calculated at each station, considering a mean value of $\phi = 40 \text{ J m}^{-3}$ as the limit between homogeneous and stratified waters (Martos and Sánchez, 1997). SeaWiFS surface chlorophyll *a* concentrations (chl-*a*) with a spatial resolution of 9 km pixel⁻¹ were obtained for each cruise (data distributed by NASA Goddard Space Flight Center, <http://oceancolor.gsfc.nasa.gov>).

Zooplankton samples were collected by oblique tows with two different nets. Bongo sampling (300 μm mesh) covered the whole spawning area between the coast and the 100 m isobath during the season, while additional Minibongo sampling (67 μm mesh) focused on the inner (~50–85 m depth) and outer (~90–100 m depth) sectors of the shelf where spawning was known to occur (Fig. 1). This fine mesh was incorporated to accurately target the smallest fraction of the copepod community that represents a main prey for hake larvae in the area. Samples were fixed immediately after collection in a 5% formalin–seawater solution and were inspected in the laboratory under a Wild M5 stereoscopic microscope. Previously, each sample was homogenized in a glass beaker to ensure a random distribution of the organisms. Then, subsamples of variable volume were obtained from each sample to include at least 100 individuals of the dominant copepod species or stage. Abundance (individuals per cubic meter) was estimated from the counts of each species/stage and the volume of filtered water, which was estimated by a Hydrobios flowmeter placed in the mouth of the nets. Adult copepods were identified to species using appropriate taxonomic references, while immature stages were classified as eggs, nauplii, or copepodites. Copepodites were sorted considering four categories of total length,

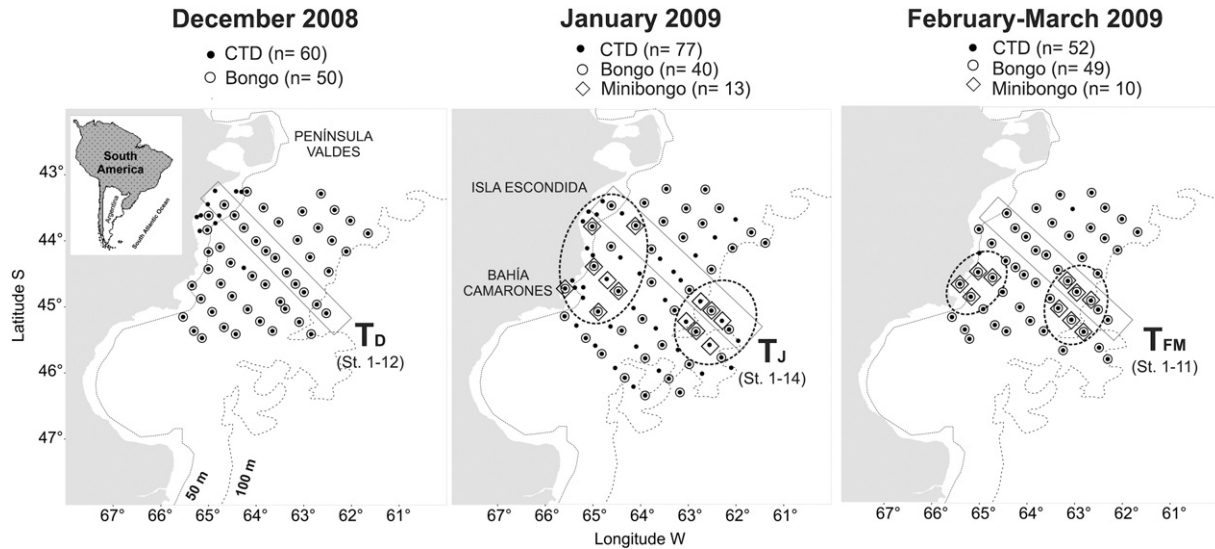


Fig. 1. Location of the environmental (CTD) and zooplankton (Minibongo and Bongo nets) sampling stations in the northern Patagonian shelf during *M. hubbsi* reproductive season. Dashed ovals indicate the inner and outer spawning sectors. Inshore–offshore transects for the vertical section ($T_{D,J,FM}$) with the number of CTD stations in brackets, are shown for December, January, and February–March.

which included mostly members of the more common copepod species in the area (Ramírez, 1970; Viñas et al., 1992) as follows: cyclopoids < 1 mm, *Oithona helgolandica* (syn. *Oithona similis*); calanoids < 1 mm, early copepodites of Clausocalanidae (*Drepanopus forcipatus* and *Ctenocalanus vanus*); calanoids 1–2 mm, late copepodites of Clausocalanidae and early copepodites of *Calanoides carinatus*, and calanoids > 2 mm, late copepodites of *C. carinatus*.

2.3. Data analysis

Spatial and temporal patterns of the copepod community structure were analyzed by multivariate analyses, considering the $\log(x + 1)$ -transformed abundances of the adults (females and males) sampled with the Bongo net, which provided the highest spatial and temporal coverage of the spawning area during the reproductive season. Rare species, i.e. occurring in <5% of samples, were excluded. Cluster analyses were done using weighted group-average linkage based on the Bray–Curtis similarity matrices of species abundances (Field et al., 1982), and used to identify natural assemblages (= groups) of sampling stations based on similarity in copepod community structure. The matrices were ordinated using a non-metric multidimensional scaling analysis (NMDS) (Kruskal and Wish, 1978) to verify cluster results. An interpretable NMDS map was defined by goodness of fit with a stress value <0.2 (Clarke and Gorley, 2001). The significance of differences between station groups was evaluated by one-way ANOSIM (analysis of similarities), obtaining a global R value and considering groups as highly separated if $R > 0.75$, overlapped if $R > 0.5$ and poorly separated if $R < 0.25$. Typical species (i.e. those that contributed most to similarities within groups) were recognized by the SIMPER test (similarity percentages) from relatively larger ratios between the species contribution to the average similarity within a group (SIM) and the standard deviation (SD) of their contribution (SIM/SD; Clarke and Gorley, 2001). Furthermore, a Kruskal–Wallis non-parametric test (significance level set at 5%) was performed to evaluate differences in the total abundance of the adult copepods sampled with the Bongo net between months (December, January and February–March).

To determine which environmental parameter could best explain the copepods grouping, the NMDS ordination scores (independent variables) were multi-regressed against environmental data (dependent variables), including surface (T_s) and bottom (T_b) temperature, surface (S_s) and bottom (S_b) salinity and satellite chlorophyll *a* concentration (chl-*a*). Regression lines and their directions were plotted in the

NMDS graphs according to Kruskal and Wish (1978). More details and discussion of the advantages of the method are provided in Somarakis et al. (2002). Prior to regression analyses, Pearson correlations were performed between the parameters and from a pair that displayed a simple correlation > 0.8, one was excluded. All multivariate analyses were performed with the *vegan* package (Oksanen, 2013) in the R statistical software, version 3.0.1 (<http://www.r-project.org/>).

Complementary to the multivariate analyses, both spawning sectors within the north Patagonian shelf were compared on the basis of copepods biodiversity, abundance and size structure estimated with the Minibongo net, to evaluate differences in food availability for larvae. Mann–Whitney non-parametric tests (significance level set at 5%) were performed to evaluate differences in the total abundance of copepods and abundance of each developmental stage and species (adults) between months (January and February–March) and sectors (Inner–Outer). In addition, Pearson correlations were calculated between biological (abundances of stages and adults) and environmental variables (S_s , S_b , T_s , T_b , chl-*a*).

3. Results

3.1. Environmental setting

Sea surface temperature showed a similar pattern in the three cruises, increasing from south to north, while bottom temperature evidenced an offshore decrease (Fig. 2). A clear warming was apparent in surface values from December to February–March, while bottom values remained similar (Table 1; Figs. 2 and 4). No monthly variations were observed in surface and bottom salinities (Table 1; Fig. 2), which showed a similar distribution, with a tongue of minimum values (<33.4) in the southern and central area typical of Magellan Strait Waters, and increasing values northwards and offshore, corresponding to Sub-Antarctic Shelf Waters (33.4–34).

During the reproductive season, most of the spawning area was characterized by the transitional and stratified sectors of the tidal front system, since few inshore stations with a vertically homogenous water column ($\phi < 40 \text{ J m}^{-3}$) were identified in December 2008 and January 2009 (Fig. 3). The range of ϕ values for the transitional sector in December was 40–120 J m^{-3} while in January and February–March 2009 such range was wider (ϕ between 40–200 J m^{-3}), due to a monthly increase in the strength of the stratification observed towards offshore waters.

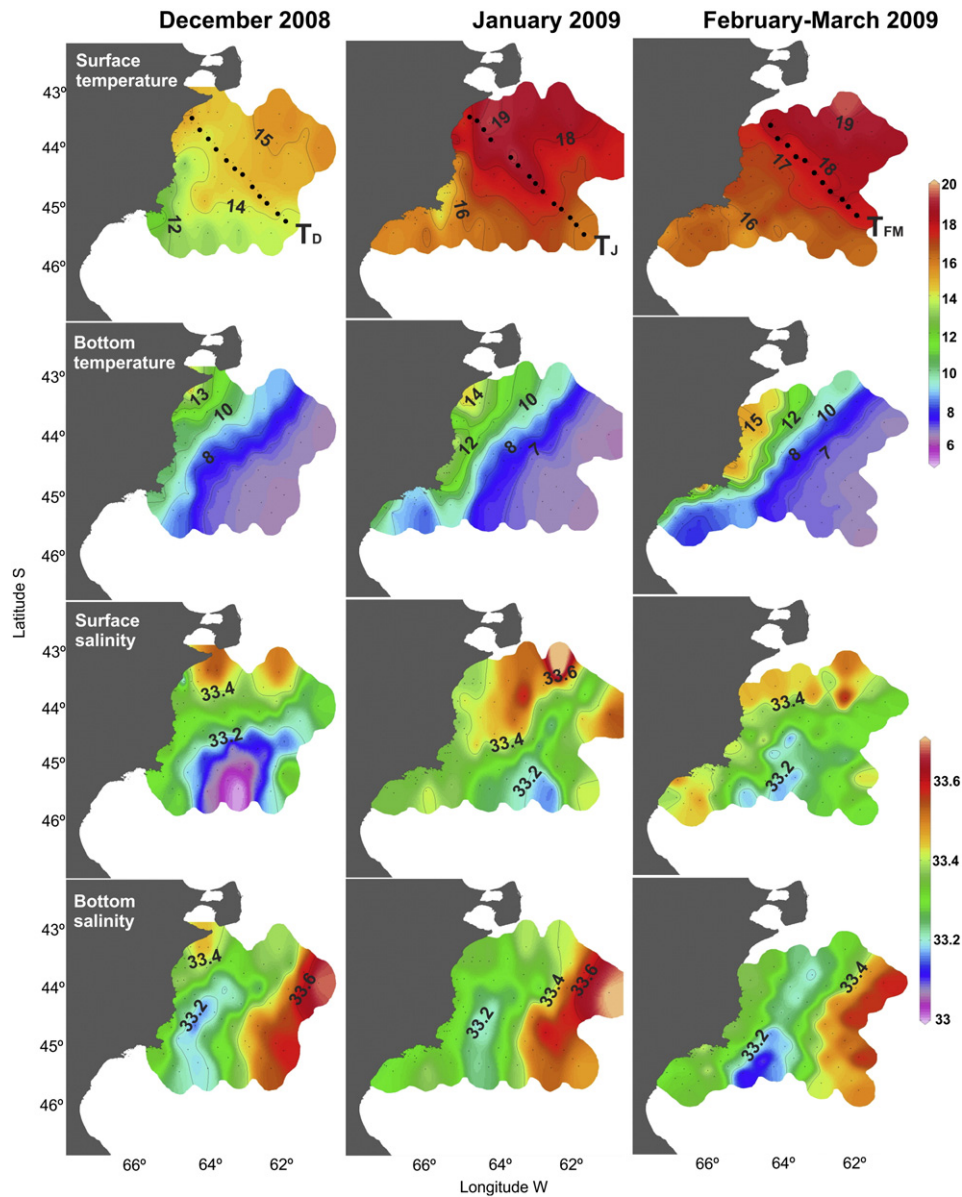


Fig. 2. Surface and bottom temperature and salinity fields in the northern Patagonian shelf during *M. hubbsi* reproductive season. Inshore–offshore transects used for the vertical sections (T_D , T_J , T_{FM}) are indicated. Temperature data reported in °C.

The different sectors of the tidal front were also evident in the vertical temperature section across the inshore–offshore transects (Fig. 4). A weak surface frontal signal was detected in December 2008, being

undetected in January 2009 and February–March 2009, while a rather extended strong bottom signal was always present (Table 1). An offshore stratified two-layered structure was observed during the three

Table 1
Environmental variables recorded in the northern Patagonian shelf during *M. hubbsi* spawning season.

	December 2008	January 2009	February–March 2009
Horizontal surface T° (°C)	11.7–15.5	12.0–19.0	15.0–19.0
Horizontal bottom T° (°C)	6.4–13.5	6.5–14.0	7.0–13.5
Horizontal surface salinity	33.0–33.5	33.1–33.6	33.2–33.5
Horizontal bottom salinity	33.2–33.6	33.1–33.6	33.2–33.5
Surface layer T° (°C)	14.0–15.0	15.5–19.0	16.5–18
Bottom layer T° (°C)	6.5–7.0	6.5–7.5	7.0–8.0
Thermocline depth inshore (m)	20–30	20–30	30–40
	($\Delta T = 0.23$ °C m^{-1})	($\Delta T = 0.31$ °C m^{-1})	($\Delta T = 0.6$ °C m^{-1})
Thermocline depth offshore (m)	40	35–50	30–60
	($\Delta T = 0.21$ °C m^{-1})	($\Delta T = 0.28$ °C m^{-1})	($\Delta T = 0.3$ °C m^{-1})
Frontal surface signal (°C km^{-1})	0.027	Not observed	Not observed
Frontal bottom signal (°C km^{-1})	0.07 (40 m)	0.06 (40–70 m)	0.07 (60–80 m)
Chl- <i>a</i> concentration (mg m^{-3})	0.5–4.5	0.4–5.6	0.4–2.6

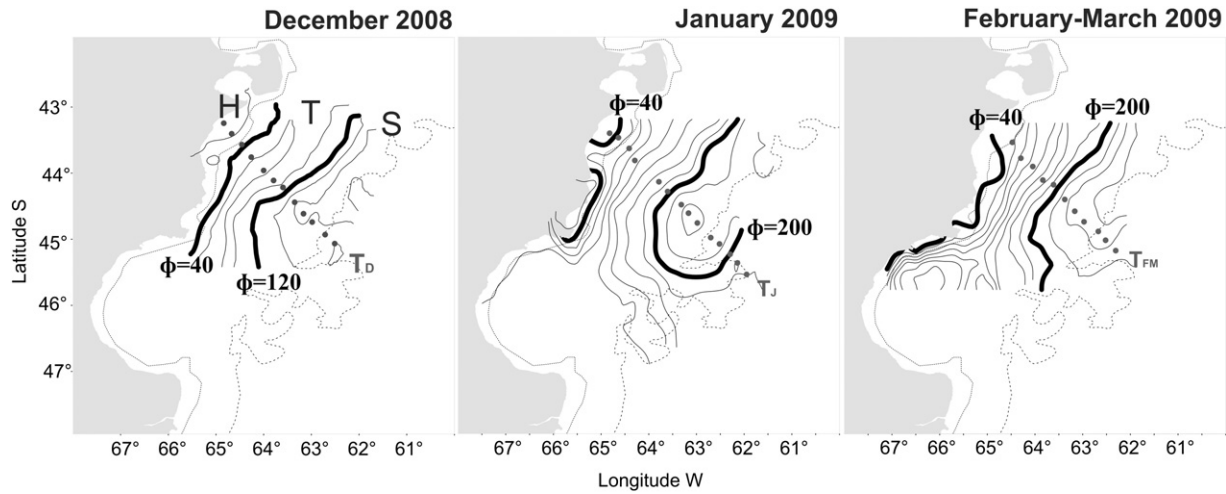


Fig. 3. Horizontal distribution of Simpson's stability index (ϕ) in the northern Patagonian shelf during *M. hubbsi* reproductive season. Thicker black lines indicate ϕ values delimiting the homogeneous (H), transitional (T), and stratified (S) sectors of the tidal front. Inshore–offshore transects used for the vertical sections (T_D , T_J , T_{FM}) are indicated with gray dots.

months, separated by a thermocline of varying depth and width (Table 1). The salinity section showed little changes in the vertical (Figure not shown) with a similar pattern during the season; minimum values were registered in transitional waters closely coupled to the bottom signal of the front, while higher values occurred both at the surface and the bottom in nearshore and offshore waters. Chl-*a* concentrations showed a similar distribution during the season (Fig. 5) with higher values in the transitional sector than in the stratified sector.

3.2. Copepod community structure

Mean total abundance of adult copepods sampled with the 300 μm mesh decreased from a maximum in December (532 ind m^{-3}) to a minimum in February–March (339 ind m^{-3}) (Table 2, Fig. 6), although such difference was not significant (Kruskal–Wallis test $H(2, n = 139) = 5.3, p = 0.07$). Values were highest in the transitional sector of the tidal front system. A total of 11 species belonging to 9 genera and 6 families were identified. Both *D. forcipatus* and *C. vanus* were overwhelmingly abundant during the season, representing 50–60% of the adult copepods.

Cluster and NMDS analyses identified similar station assemblages during the reproductive season; 4 groups were identified in December 2008 (A_D, B_D, C_D, D_D ; 60% similarity; stress value = 0.14), and January 2009 (A_J, B_J, C_J, D_J ; 48%; stress value = 0.4), while only 3 groups were recorded in February–March 2009 (E_{FM}, BC_{FM}, D_{FM} ; 60%; stress value = 0.13) (Fig. 7). BC_{FM} included stations that belonged to groups B_D – C_D in December and B_J – C_J in January, while E_{FM} represented a new assemblage. Overall, groups were highly different from each other (ANOSIM test; Global $R_D = 0.81$, Global $R_J = 0.78$, Global $R_{FM} = 0.81$). In December, group A_D included stations within the homogeneous sector of tidal front, while B_D and C_D were located in the transitional sector and D_D included stations from the stratified sector offshore (Figs. 7, 4). A similar pattern was observed in January (A_J and B_J : transitional sector; C_J and D_J : stratified sector) and February–March (E_{FM} and BC_{FM} : transitional sector; D_{FM} : stratified sector). Typical species (SIM/SD ratio > 3 in SIMPER output, results not shown) of station groups located in the transitional sector were *D. forcipatus* and *C. vanus*, while *Oithona atlantica* and *Calanus simillimus*, only found offshore (depths > 90 m), were characteristic of stations from the stratified sector (see Fig. 6).

Bottom temperature and salinity were the main environmental variables determining station groups during the season (Fig. 8). In general, assemblages within the transitional sector had higher bottom temperature than those within the stratified sector, while an inverse trend for bottom salinity values was observed (see Fig. 2). Surface temperature

and salinity also explained part of the variation in the NMDS ordinations, but were only significant for groups E_{FM} (salinities > 33.4) and B_D (salinities between 33.3–33.4), while chlorophyll *a* concentration mainly explained the definition of groups B_D , B_J , and BC_{FM} , with higher chl-*a* values in the transitional sector of the tidal front.

3.3. Comparison of both spawning sectors

Mean total abundance of the copepod community sampled with the 67 μm mesh was higher in the inner spawning sector, within the transitional sector of the tidal front, both in January and February–March (Table 3), although the difference between sectors was not significant (Mann–Whitney test, $Z = 0.7, p = 0.5$). On the other hand, mean total abundance was significantly different between months, with higher values in February–March ($Z = -3.6, p < 0.001$). A total of 14 species belonging to 11 genera and 8 families were identified, including four species that were absent or undersampled in the samples from the 300 μm : *Oithona nana*, *O. helgolandica*, *Microsetella norvegica* and *Euterpina acutifrons*. Copepod developmental stages smaller than 1 mm (eggs, nauplii, cyclopoid and calanoid copepodites) were numerically dominant in the community. *O. helgolandica* and *M. norvegica* were the dominant species in this size category, while *D. forcipatus* and *C. vanus* were the most abundant ones in the 1–2 mm size range (Fig. 9). The comparison of the abundance of the latter species from both sampling meshes (Tables 2 and 3) showed that they were best sampled by the 67 μm mesh.

Abundances of copepod eggs ($Z = 3.1, p < 0.01$) (Fig. 9) and adults of *C. carinatus* ($Z = 2.6, p < 0.01$) (Table 3) were significantly higher in the inner spawning sector, whereas adults of *O. atlantica* ($Z = -2.5, p = 0.013$) and *C. simillimus* ($Z = -3, p < 0.01$) were more abundant in the outer sector (Table 3). The abundances of nauplii ($Z = -3.5, p < 0.001$), cyclopoid copepodites ($Z = -4, p < 0.001$), calanoid copepodites < 1 mm ($Z = -3.2, p < 0.01$), *O. helgolandica* ($Z = -3.9, p < 0.001$), *M. norvegica* ($Z = -2.8, p < 0.01$), *D. forcipatus* ($Z = -2.8, p < 0.01$) and *C. vanus* ($Z = -3.5, p < 0.001$) were significantly higher in February–March (Fig. 9). In addition, abundances of calanoid copepodites < 1 mm (Pearson correlation = 0.58; $p = 0.02$) and adults of *D. forcipatus* (Pearson correlation = -0.56; $p = 0.02$) were significantly correlated to bottom temperature and surface salinity, respectively.

A strong correspondence was observed between the distribution of copepod species from both nets. In January as well as in February–March, the outer spawning sector (67 μm Minibongo sampling) coincided spatially with groups D_J and D_{FM} determined by multivariate analysis (300 μm Bongo sampling). In fact, *O. atlantica* and *C. simillimus*, species

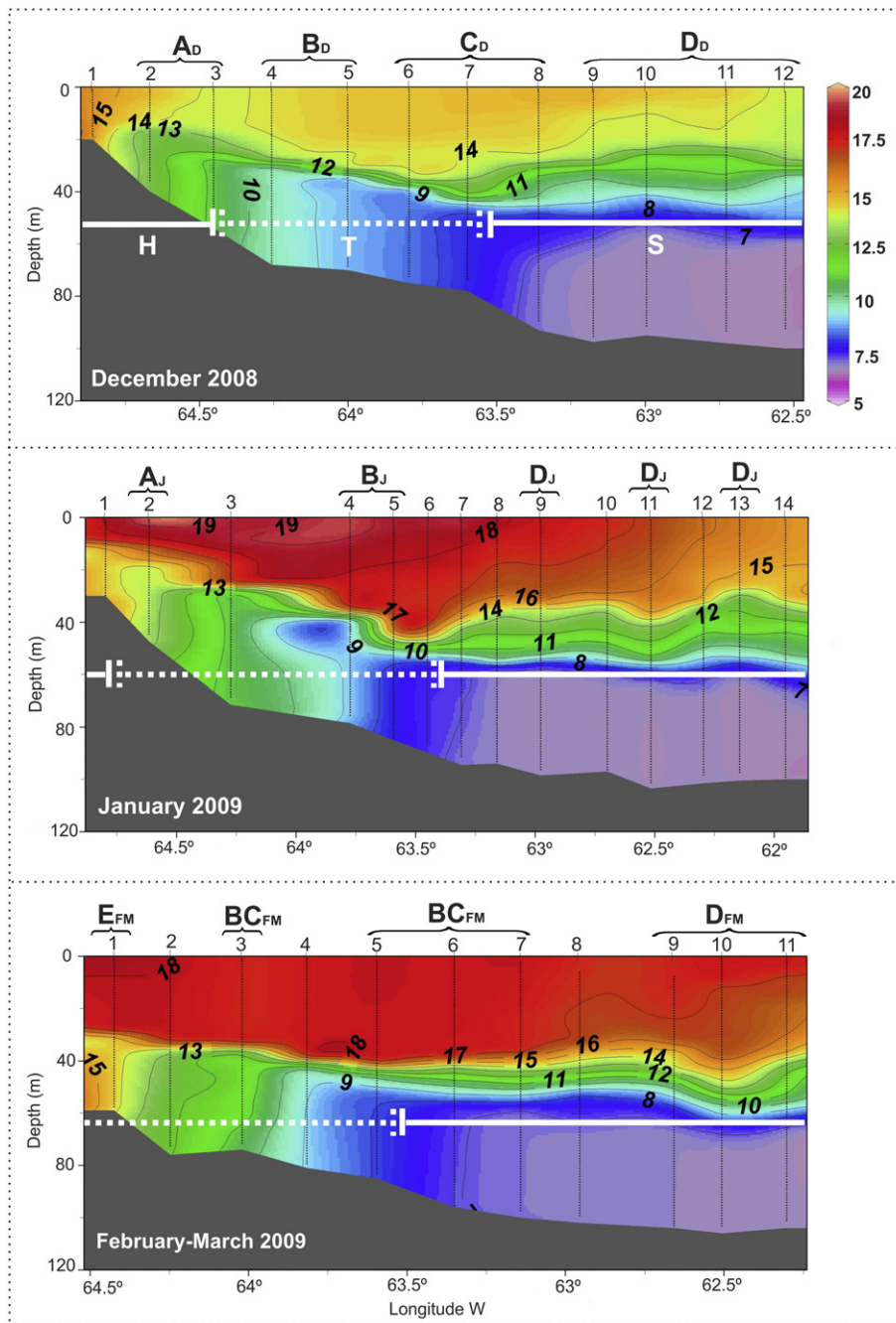


Fig. 4. Vertical sections of temperature along the T_D , T_J and T_{FM} transects in the northern Patagonian shelf during *M. hubbsi* reproductive season. Corresponding cluster copepod groups are indicated (see Fig. 7). H: homogeneous sector, T: transitional sector, S: stratified sector. Temperature data reported in °C.

characteristic of such assemblages, had higher mean abundances in the outer spawning sector and had lower abundances or were absent from the inner sector (Table 3). The inner spawning sector closely corresponded with BC_{FM} (Bongo net) in February–March, whereas during January it included stations from A_J and C_J , with some correspondence of species; BC_{FM} and C_J were characterized by the presence of *D. forcipatus* and *C. vanus*, species that dominated both spawning sectors, while A_J was typified by *C. carinatus*, which showed higher abundances in the inner spawning sector.

4. Discussion

During the reproductive season, the *M. hubbsi* spawning area was mostly characterized by a stratified water column with a two-layer

structure. Both the transitional and the stratified sectors of the front were observed during the three cruises, while the homogeneous sector was only detected at a few stations in December and January. An increase in the stability of the tidal front system was observed from December to February–March, as previously described (Sabatini and Martos, 2002).

The copepod community was dominated by the <1 mm fraction, which included eggs, nauplii, cyclopid and calanoid copepodites, and adults of the species *D. forcipatus*, *C. vanus*, *O. helgolandica* and *M. norvegica*. Dominance of these species has been previously observed in relation to the tidal front system in the study area (Derisio, 2012; Sabatini and Martos, 2002; Santos and Ramírez, 1995; Spinelli et al., 2012; Viñas et al., 1992). The overwhelming predominance not only of copepod stages smaller than 1 mm but also of adults of small copepod

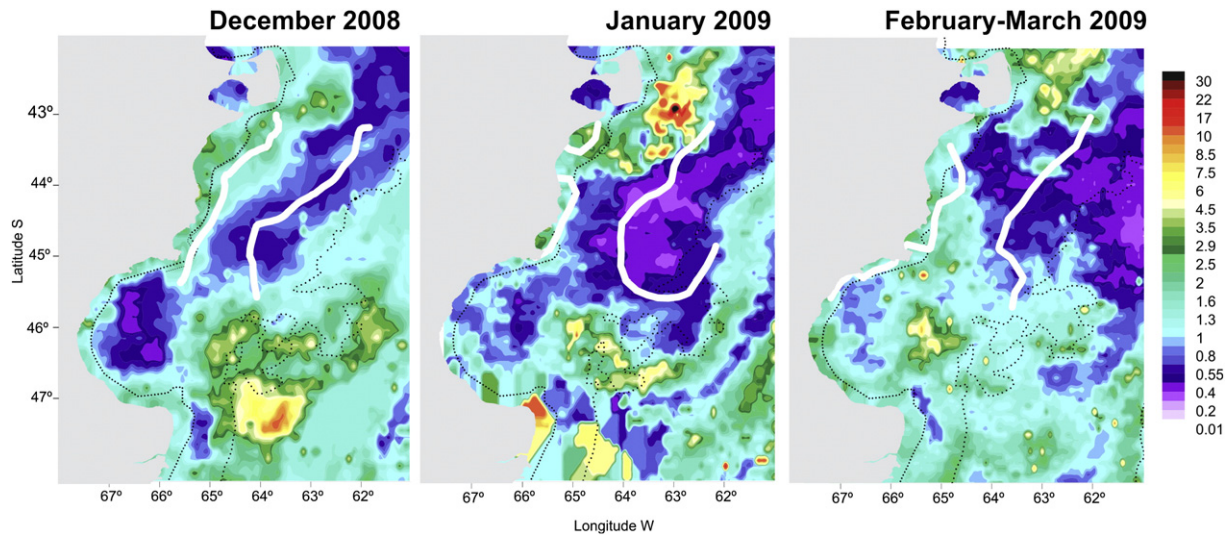


Fig. 5. Surface satellite chlorophyll *a* concentrations (SeaWiFS, 9 km pixel⁻¹, mg m⁻³) in the northern Patagonian shelf during *M. hubbsi* reproductive season (data correspond to 2–9 December 2008, 17–24 January 2009 and 28 February–5 March 2009). Isolines (white tick lines) of Simpson's stability index () delimiting homogeneous, transitional, and stratified sectors of the tidal front are shown. See also Fig. 3.

species was only evident from additional sampling with the 67 μm-meshed net. The high contribution (in terms of abundance and biomass) of the smaller fraction of the copepod community has been increasingly reported worldwide in the last years (Gallienne and Robins, 2001; Turner, 2004) and particularly in some sectors of the Argentine Sea (Antacli et al., 2010; Di Mauro et al., 2009; Spinelli et al., 2012; Viñas et al., 2013). However, this fraction had been historically underestimated in the study area due to the sampling mostly with >150 μm meshes (Ramírez, 1970, 1981; Sabatini and Martos, 2002; Santos and Ramírez, 1995; Viñas et al., 1992). Thus, future studies of the copepod community in the hake spawning area should include fine meshes to adequately sample their full size spectrum and species diversity.

D. forcipatus, *C. vanus*, *O. helgolandica* and *M. norvegica*, in addition to *O. atlantica* and *C. simillimus*, may be regarded as the most significant planktonic copepods in the food web of the northern Patagonian shelf. *D. forcipatus* and *C. vanus*, which characterized the transitional sector of the tidal front, have been reported as conspicuous components of the shelf mesozooplankton communities in subtropical, temperate, and subantarctic regions (Antacli, 2011; Hulzemann, 1991; Mauchline,

1998; Pakhomov et al., 1997; Sabatini and Martos, 2002; Sabatini et al., 2012). Both species usually produce very large populations due to their ability to survive under a wide range of environmental conditions (Antacli, 2011; Cornils et al., 2007). Considering their preferentially herbivorous behavior and similar food type preference (Atkinson, 1994; Hopkins, 1987), we suggest that both species might be occupying different depth layers of the water column in order to minimize competition, which agrees with previous studies in the southern Patagonian shelf (Antacli, 2011; Sabatini, 2008) that reported *C. vanus* at greater depths than *D. forcipatus*, which was observed above the thermocline. On the other hand, *C. simillimus* and *O. atlantica*, species that are known to prefer colder and stratified waters (Kattner et al., 2012; Ramírez, 1970; Ramírez and Sabatini, 2000; Sabatini et al., 2012), were typical of the stratified sector of the tidal front. Their presence greatly contributed to an increase in the copepod community biodiversity towards offshore waters, as has been previously reported for this region (Sabatini and Martos, 2002) and the southern Patagonian shelf (Sabatini, 2008). Although not identified as typical species in the SIMPER analysis, *O. helgolandica* and *M. norvegica* were also highly abundant in the spawning area. *O. helgolandica*, a broadly distributed species in the Argentine Sea between 34° and 55°S (Cepeda, 2012; Ramírez, 1981), was more abundant in the transitional sector of the tidal front, in agreement with previous studies in the area (Derisio, 2012; Sabatini and Martos, 2002). *M. norvegica* is widely distributed in subtropical, temperate, and boreal waters of the world ocean, often representing one of the numerically dominant copepods in inshore waters (Uye et al., 2002). In this study, abundances were very similar in the transitional and stratified sectors, although they have been reported to be more concentrated in the bottom layer of the transitional sector (Derisio, 2012).

Our findings suggest that the spatial and temporal variability in the across-shelf structure of the tidal front system clearly impacts copepod distributions, including adults and stages that represent key prey for hake larvae. Bottom temperature and salinity were the main environmental features structuring the copepod community, thus corroborating our initial hypothesis. Accordingly, both variables have been previously mentioned as the main factors explaining copepod distributions in the northern limit of the spawning area (Península Valdés; Spinelli et al., 2012) and the southern Patagonian shelf (Sabatini et al., 2012). There was evidence of cross-frontal transport and cross-isobathic tidal excursion, previously suggested for the area (Tonini, 2010), since most of the identified station assemblages were

Table 2
300 μm-meshed Bongo net. Mean abundance (ind m⁻³ ± standard deviation) of adult copepods in the northern Patagonian shelf during *M. hubbsi* spawning season.

Adults	December 2008	January 2009	February–March 2009
Oithonidae			
<i>Oithona helgolandica</i> ^a	3 ± 7	10 ± 20	5 ± 15
<i>Oithona atlantica</i>	59 ± 95	66 ± 127	7 ± 15
Calanidae			
<i>Calanoides carinatus</i>	18 ± 38	37 ± 100	31 ± 74
<i>Calanus simillimus</i>	7 ± 13	8 ± 17	4 ± 8
<i>Calanus australis</i>	0.1 ± 0.3	0.2 ± 0.7	3 ± 8
Centropagidae			
<i>Centropages brachiatus</i>	90 ± 196	37 ± 61	56 ± 80
Clausocalanidae			
<i>Clausocalanus brevipes</i>	22 ± 40	41 ± 85	17 ± 50
<i>Drepanopus forcipatus</i>	231 ± 330	105 ± 152	70 ± 127
<i>Ctenocalanus vanus</i>	85 ± 119	134 ± 284	141 ± 183
Acartiidae			
<i>Acartia tonsa</i>	17 ± 34	6 ± 18	4 ± 9
Paracalanidae			
<i>Paracalanus parvus</i>	0.1 ± 0.3	2 ± 8	–
Total	532 ± 452	447 ± 531	339 ± 334

^a *Oithona helgolandica* (syn. *O. similis*).

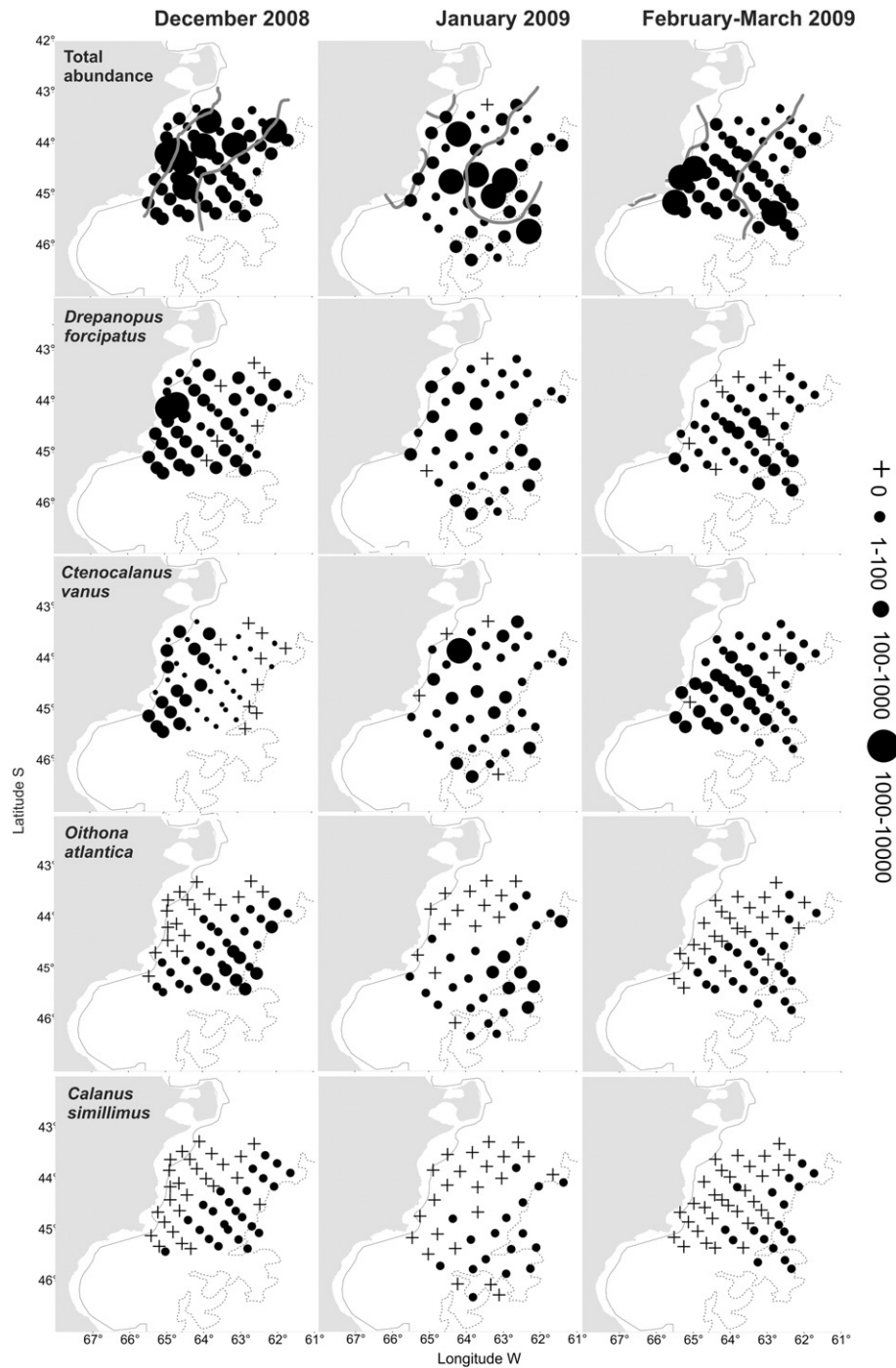


Fig. 6. 300 μm -meshed Bongo net. Mean total abundance (ind m^{-3}) of copepods and abundance of typical species (derived from SIMPER analysis) in the northern Patagonian shelf during *M. hubbsi* reproductive season. Isolines (gray tick lines) of Simpson's stability index (ϕ) delimiting homogeneous, transitional, and stratified sectors of the tidal front are shown.

characterized by the same species (*C. vanus* and *D. forcipatus*), although abundances varied. Copepods were most likely being transported to different locations as the water masses were moved either inshore or offshore by tidal currents, providing evidence for tidal advection. This highlights how frontal features can contribute to the observed heterogeneity of the community, as previously pointed out for this frontal system further north (Derisio, 2012) and for similar tidal fronts worldwide (Brylinski and Aelbrecht, 1993; Wishner et al., 2006).

The highest abundance of the adult copepods was observed in the transitional sector of the front throughout the spawning season, in coincidence with higher temperatures and maximum chlorophyll *a* concentrations both at surface (this study; Carreto et al., 2007) and at

the thermocline level (Viñas and Ramírez, 1996). This chl-*a* maximum in the transitional sector results from a greater stability of the water column coupled with the input of nutrients from the mixed sector favored by strong tidal mixing (Carreto and Benavides, 1989; Carreto et al., 2007). Egg production (based on the observed highest abundance of copepods eggs), was likely enhanced in this transitional sector because of the favorable influence of these factors on the reproductive rates of species of Clausocalanidae (Derisio, 2012; Sabatini and Martos, 2002) and Oithonidae (Cepeda, 2012) in the study area. Accordingly, the highest abundances of copepod eggs and nauplii have been reported at the depth of the thermocline and below it in the transitional sector (Derisio, 2012; Viñas and Ramírez, 1996). Thus, this sector would

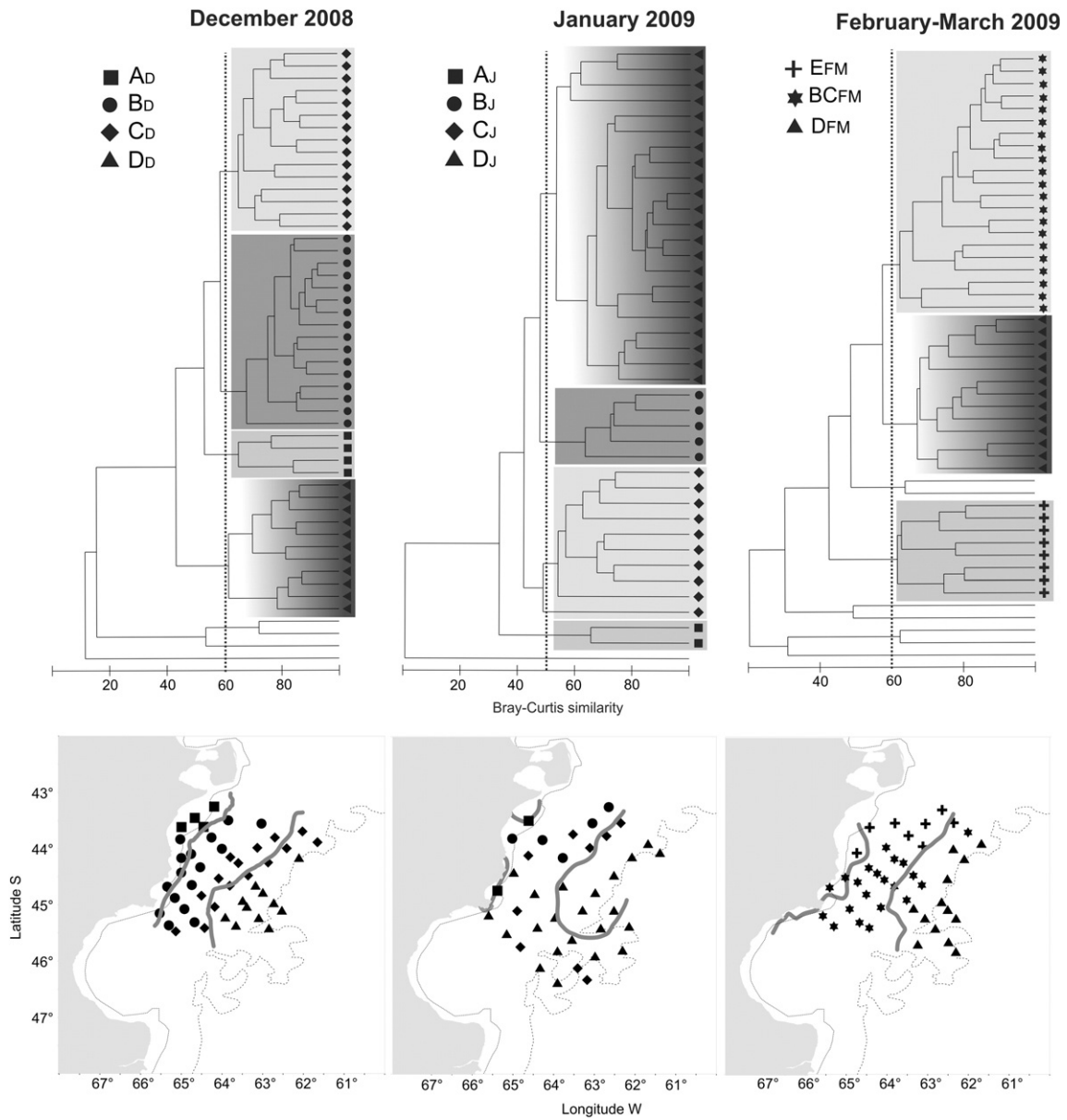


Fig. 7. Copepod groups identified by cluster analysis (Bray–Curtis similarity index) in the northern Patagonian shelf during *M. hubbsi* reproductive season. Upper panels: dendrograms, lower panels: geographic location of each group. Isolines (gray tick lines) of Simpson's stability index (ϕ) delimiting homogeneous, transitional, and stratified sectors of the tidal front are shown.

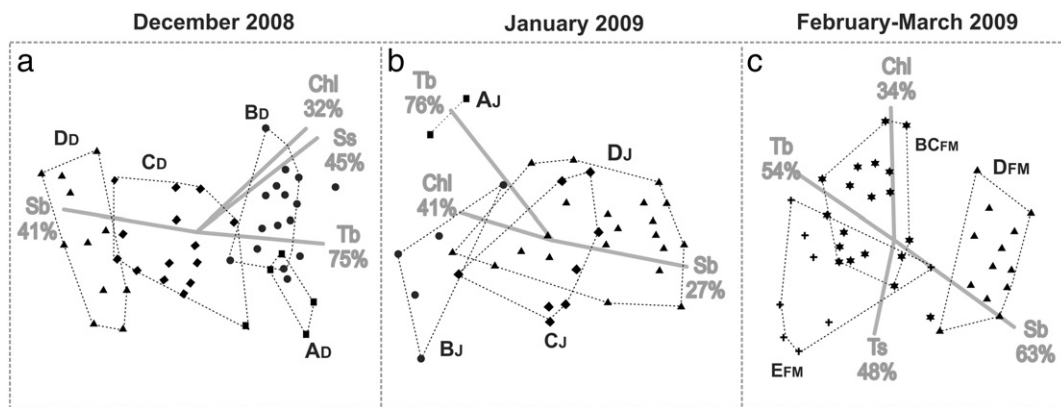


Fig. 8. Ordination plots of the comparison of samples using NMDS and Bray–Curtis similarity index in the northern Patagonian shelf during *M. hubbsi* reproductive season. Respective cluster groups of copepods are superimposed (black dashed lines). Significant multiple regressions between ordination scores and environmental parameters are also shown, as well as the percentage of the variance of the copepod data explained by the parameters. Stress values: (a) 0.14, (b) 0.16 and (c) 0.16. S_s : surface salinity, S_b : bottom salinity, T_s : surface temperature, T_b : bottom temperature, Chl: chl-*a* concentration.

Table 3
67 μm -meshed Minibongo net. Mean abundance (ind $\text{m}^{-3} \pm$ standard deviation) of adults and developmental stages of copepods in two sectors (inner–outer) within the spawning area of *M. hubbsi* in January and February–March 2009.

Adults	Size	January 2009		February–March 2009	
		Inner	Outer	Inner	Outer
Oithonidae					
<i>Oithona nana</i>	<1	52 \pm 79	27 \pm 25	6 \pm 13	0
<i>Oithona helgolandica</i>	<1	171 \pm 177	177 \pm 88	1376 \pm 761	445 \pm 123
<i>Oithona atlantica</i>	1–2	20 \pm 32	63 \pm 28	0	44 \pm 77
Calanidae					
<i>Calanoides carinatus</i>	>2	173 \pm 235	19 \pm 39	49 \pm 45	0
<i>Calanus simillimus</i>	>2	0	53 \pm 73	0	14 \pm 23
<i>Calanus australis</i>	>2	0	10 \pm 14	0	0
Centropagidae					
<i>Centropages brachiatus</i>	1–2	7 \pm 13	24 \pm 43	223 \pm 120	138 \pm 81
Clausocalanidae					
<i>Clausocalanus brevipipes</i>	1–2	22 \pm 36	27 \pm 36	64 \pm 49	61 \pm 56
<i>Drepanopus forcipatus</i>	1–2	219 \pm 314	16 \pm 18	200 \pm 131	178 \pm 48
<i>Ctenocalanus vanus</i>	1–2	224 \pm 333	23 \pm 17	553 \pm 293	552 \pm 265
Acartiidae					
<i>Acartia tonsa</i>	1–2	0	0	73 \pm 47	0
Paracalanidae					
<i>Paracalanus parvus</i>	<1	8 \pm 13	0	215 \pm 154	38 \pm 63
Ectinosomatidae					
<i>Microsetella norvegica</i>	<1	100 \pm 87	78 \pm 105	119 \pm 44	256 \pm 185
Euterpinidae					
<i>Euterpina acutifrons</i>	<1	17 \pm 46	0	6 \pm 13	0
Developmental stages					
Eggs	<1	1994 \pm 1802	99 \pm 135	1901 \pm 1067	545 \pm 241
Nauplius larvae	<1	2750 \pm 3395	2450 \pm 2295	8652 \pm 4975	2938 \pm 1619
Cyclopoid copepodites	<1	826 \pm 525	725 \pm 471	7559 \pm 1718	9888 \pm 4574
Calanoid copepodites < 1 mm		680 \pm 624	155 \pm 124	5375 \pm 2877	1058 \pm 535
Calanoid copepodites 1–2 mm		580 \pm 667	116 \pm 40	1293 \pm 860	1074 \pm 607
Calanoid copepodites > 2 mm		111 \pm 157	67 \pm 93	427 \pm 239	151 \pm 153
Total		441 \pm 316	229 \pm 187	1404 \pm 2609	966 \pm 406

represent a highly productive area for the dominant copepods, with a constant bulk of potential prey for hake larvae during the reproductive season.

Encounter between copepods and *M. hubbsi* larvae in stratified waters might be favored by several factors (Fig. 10). Maximum chlorophyll *a* concentrations have been reported at the thermocline level (Viñas and Ramírez, 1996), where high concentrations of calanoid copepodites and adults of *D. forcipatus*, *C. vanus* and *C. carinatus*, which are the preferred prey for hake larvae in the spawning area (Temperoni and Viñas, 2013; Viñas and Santos, 2000), also have been reported (Derisio, 2012). These copepod species are known to display diel vertical migrations ascending at night to the chlorophyll-rich thermocline level, and descending to the bottom during daylight hours, when predation risk due to increased visibility is higher (Guglielmo et al., 2011; Verheye and Field, 1992). Hake larvae could gain access to these prey items by increased retention within stratified waters, which occurs through the coupling of circulation and behavior (Álvarez Colombo et al., 2011). Circulation in the region likely involves a two-layered flow, with a surface layer moving offshore and a bottom layer directed onshore (Palma et al., 2008). The smaller larvae (<5 mm) are scarce or absent in the surface layer due to the strong currents that can advect them offshore, but are highly concentrated in the bottom layer, where a low motion level develops. Once they grow, a functional swimming bladder allows the larger individuals (>5 mm) to perform daily vertical migrations from near the bottom to the thermocline level at night. Hence, migratory behavior allows the larvae not only to follow the copepod migrations ensuring a successful and efficient foraging throughout the day while diminishing prey searching costs, but also to counteract the advective horizontal forces of the frontal system by moving towards the bottom layer during the day.

Transitional waters of the tidal front (= inner spawning sector) would provide optimal and better trophic conditions to sustain *M. hubbsi* larval growth and development than the stratified waters offshore (= outer spawning sector). Accordingly, Díaz et al. (2014) found a good nutritional condition in individuals hatched inshore. Highly

abundant copepod species in the transitional sector, such as *D. forcipatus*, *C. vanus* and *C. carinatus*, the preferred prey for *M. hubbsi* larvae, might represent a nutritional benefit in terms of caloric content for larvae due to their elevated levels of highly unsaturated fatty acids (Cripps and Atkinson, 2000; Verheye et al., 2005; Vogedes et al., 2010). On the other hand, the stratified sector might expose the larvae to higher abundances of potential predators and/or competitors, such as the amphipod *Themisto gaudichaudii*, which is less concentrated in inshore waters at this latitude (Viñas et al., 1992). The intensified northward circulation in the offshore sector of the northern Patagonian shelf (Palma et al., 2008) may be an additional factor preventing hake larvae from successfully developing. Once advected offshore, individuals would be trapped in an unfavorable environment and eventually die (Álvarez Colombo et al., 2011). Moreover, the outer spawning group is mainly composed of females which are laying their last batches of eggs before moving outside of the reproductive area (Macchi et al., 2009); thus, spawning is known to be usually less intense and of lower quality (Macchi et al., 2006). Since bottom temperatures in the outer spawning sector were lower than the optimal spawning temperature range for *M. hubbsi* (10–13 °C; Macchi and Pájaro, 2003), these eggs might not be viable. In fact, few larvae were observed during austral summer months in this sector (Álvarez Colombo et al., 2011).

5. Conclusions

The present study provided, for the first time, a quantitative and intensive small-scale monitoring of the copepod community in the spawning and nursery area of the Patagonian stock of *M. hubbsi* during its reproductive season. Detailed information on the abundance, biodiversity, size structure, and distribution patterns of the dominant species and stages sampled with two complementary mesh sizes (67 and 300 μm) was provided. A distinct spatial pattern of the copepod community across the tidal front system was identified, highlighting the great influence of hydrography in shaping the community, with more

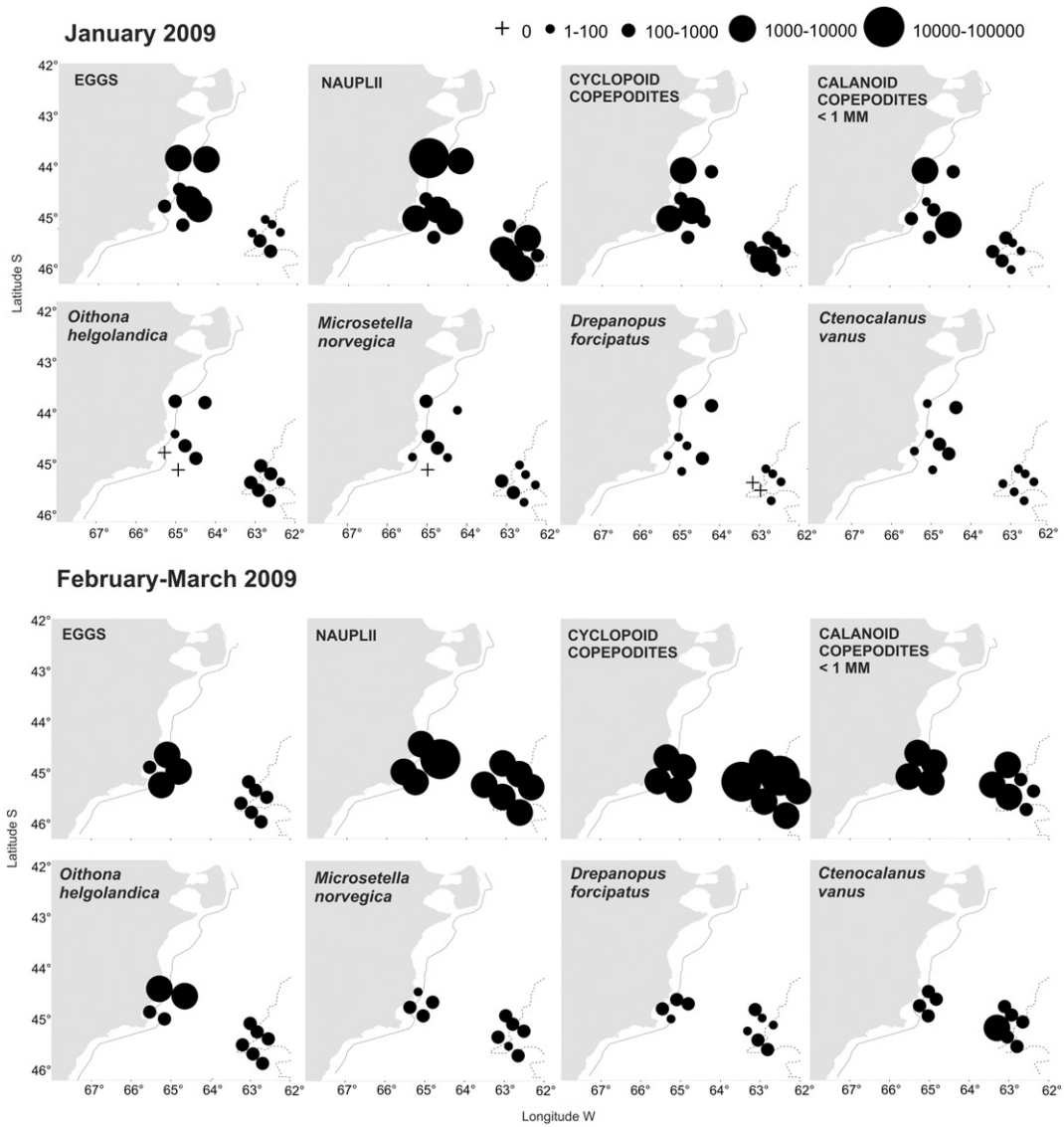


Fig. 9. 67 μm -meshed Minibongo net. Abundance (ind m^{-3}) of dominant copepod developmental stages and adults in the northern Patagonian shelf in January and February–March 2009.

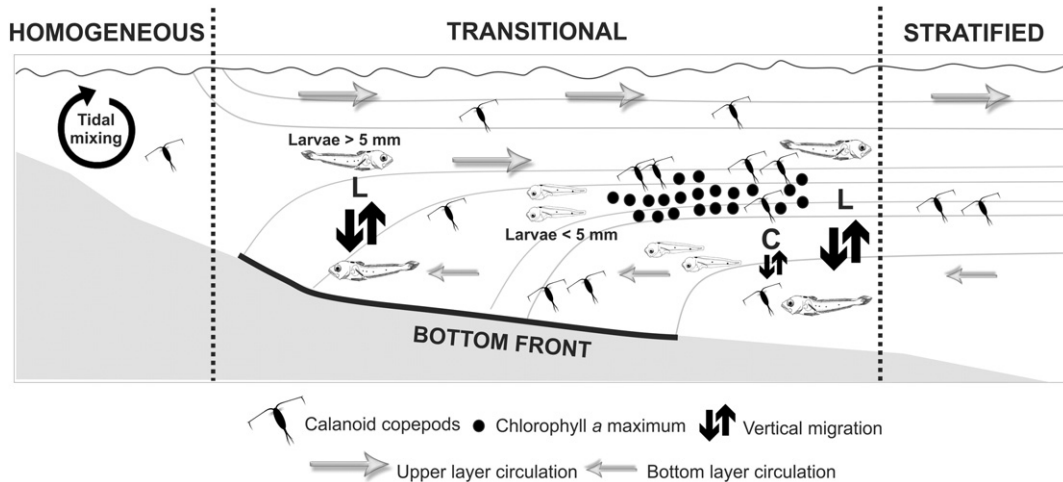


Fig. 10. Schematic drawing showing the vertical movements of *M. hubbsi* larvae (L) and their copepod prey (C) coupled to the two-layered circulation pattern and the chlorophyll *a* maximum in the transitional sector of the tidal front system (see text for further details).

abundant prey for hake larvae within the transitional sector. As a consequence, this sector would be more suitable for a successful development of hake larvae due to the availability of adequate food, the appropriate thermal ranges, and the existence of retention mechanisms. Given the observed strong link between the physical and biological features of the frontal system, further studies are needed for a better understanding of the processes involved. In particular, future work should focus on the vertical distribution of the copepod community to accurately assess their spatial patterns and vertical migration behavior in relation to the structure of the tidal front and the circulation patterns of the study area.

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