Diel vertical distribution of the larvacean Oikopleura dioica in a North Patagonian tidal frontal system (42°–45°S) of the SW Atlantic Ocean

Mariela Spinelli[ab], Carla Derisio[cd], Patricia Martos[ce], Marcelo Pájaro[c], Graciela Esnal[ab], Hermes Mianzán[ab] & Fabiana Capitanio[ab]

[a] Instituto de Biodiversidad y Biología Experimental y Aplicada, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires, Buenos Aires, Argentina

[b] Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

[c] Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina

[d] Facultad de Ciencias Exactas y Naturales, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

[e] Departamento de Ciencias Marinas, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, UNM, Mar del Plata, Argentina
Published online: 26 Jan 2015.

PLEASE SCROLL DOWN FOR ARTICLE

ORIGINAL ARTICLE

Diel vertical distribution of the larvacean *Oikopleura dioica* in a North Patagonian tidal frontal system (42°–45°S) of the SW Atlantic Ocean

MARIELA SPINELLI[1,2]*, CARLA DERISIO[3,4], PATRICIA MARTOS[3,5], MARCELO PÁJARO[3], GRACIELA ESNAL[1,2], HERMES MIANZÁN[1,2] & FABIANA CAPITANIO[1,2]

[1]*Instituto de Biodiversidad y Biología Experimental y Aplicada, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires, Buenos Aires, Argentina,* [2]*Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina,* [3]*Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina,* [4]*Facultad de Ciencias Exactas y Naturales, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina, and* [5]*Departamento de Ciencias Marinas, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, UNM, Mar del Plata, Argentina*

Abstract

In frontal systems, larvaceans generally comprise a significant fraction of the mesozooplankton. Given the low mobility of these organisms, their vertical distribution is directly influenced by the physical conditions of the water column. The main goal of this study was to investigate the day and night vertical distribution of the larvaceans *Oikopleura dioica* in the different sectors of the Península Valdés tidal front (42°–45°S; SW Atlantic Ocean), focusing on possible causes such as oceanographic conditions (well-mixed, frontal and stratified), feeding activities, reproductive behaviour and predation risks. Day and night samples were collected with a MultiNet of 67 μm and 300 μm mesh size, from two depth layers. Conductivity-temperature-depth (CTD) profiles were also recorded. In the well-mixed waters, the size structure of *O. dioica* was similar in the upper and lower layers both in the day and night samples, probably due to the continuous vertical movement caused by the turbulent mixing of waters. In the frontal and stratified areas, mature animals were found in the upper layers during the night, possibly due to their aggregation in surface waters for synchronized spawning. In these areas, a high percentage of well-fed larvaceans was also found. Principal component analysis showed that, at night, the abundance of potential predators such as chaetognaths, ctenophores and anchovy larvae was correlated with the parameter of stability of the water column (Simpson parameter), and that these were more abundant in the upper layers of the stratified area containing larvaceans. Our results suggest that the degree of stratification of the water column was the main factor affecting the vertical distribution of *O. dioica*.

Key words: *Larvaceans, oceanographic conditions, SW Atlantic Ocean, tidal front, vertical distribution*

Introduction

Larvaceans are considered one of the most abundant mesozooplankton groups in many pelagic environments and their secondary production can even exceed that of copepods in subtropical and tropical areas (Jaspers et al. 2009). Furthermore, their overall abundances are severely underestimated because of the large mesh sizes usually used. Larvaceans capture food by means of a complex external mucous filtering structure secreted by the epidermis, commonly known as the 'house'. The food collected by the house filters passes through the alimentary tract and large numbers of faecal pellets can be produced per day. *Oikopleura* (*Vexillaria*) *dioica* Fol, 1872 is a small-bodied cosmopolitan larvacean, perhaps the best known, characterized by achieving high densities in coastal waters (López-Urrutia et al. 2003). Regarding their reproductive strategy, all larvaceans,

*Correspondence: Dr Mariela Spinelli, Instituto de Biodiversidad y Biología Experimental y Aplicada, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad de Buenos Aires, Intendente Güiraldes 2160, Pabellón 2, 4to. Piso, Laboratorio 34, Ciudad Universitaria, C1428EGA Buenos Aires, Argentina. E-mail: marielaspinelli@bg.fcen.uba.ar

© 2015 Taylor & Francis

except for *O. dioica*, are hermaphrodites. In addition, since they are semelparous organisms with short life cycles, the mechanisms that coordinate the production of mature gametes are strongly related to environmental conditions (Fenaux 1963; Deibel & Lowen 2012). The reproductive strategy of *O. dioica* requires mature individuals to leave their houses and swim to the surface to release their eggs (Lombard et al. 2009). The accumulation of larvaceans in surface waters during the night to spawn has been previously described *in situ* by Alldredge (1982). The generation time of this species varies from 1 day at 27–29°C (Hopcroft & Roff 1995) to 16 days at 10°C (Uye & Ichino 1995).

Frontal systems are generally understood as important zones for pelagic production (Legendre et al. 1986) that influence the spatial and vertical distributions of zooplankton communities, as well as other aspects of their ecology (Lee et al. 2005). The vertical distribution of zooplankton is a complex phenomenon that involves different behaviour that varies from species to species and is moderated by many factors such as abundance of food, predation, competition, reproduction, temperature, salinity, oxygen and nutrients, among others (Morgado et al. 2003, 2006; Marrari et al. 2011; Varpe 2012). Frontal systems are formed through various mechanisms. In shallow waters, tides are the main water-mixing mechanism, and thus these fronts are usually called tidal fronts (Legendre et al. 1986).

In the Patagonian coastal area (Argentine Sea), a tidal front is developed during spring and summer, and extends from 42° to 45°S, from north Península Valdés to Bahía Camarones. Its middle position is oriented NE–SW, closely following the 75–80 m isobaths (Sabatini & Martos 2002). During the cold season, the stratification is destroyed over the mid-shelf by convection and wind mixing and the tidal front disappears (Paparazzo et al. 2010). Circulation occurs at two-layer flows, where the upper layer is directed towards the northeast and the bottom layer moves more slowly in the opposite direction (Palma et al. 2008). The vertical movements of the plankton coupled to the circulation of these two layers have been proposed as a retention mechanism both for zooplankton and for fish larvae (Sinclair 1988). At this front, Álvarez Colombo et al. (2011) proposed that larvae of hake (*Merluccius hubbsi* Marini, 1933) are typically retained by this movement through their migratory behaviour.

Zooplankton vertical distributions have been examined in different areas of the world's ocean with the main goal of understanding the physical and biological processes that control the patterns observed, as well as of investigating the ecological interactions between taxa (Marrari et al. 2011).

Höffle et al. (2013) have suggested that the vertical movements of fish larvae are related to the concurrent needs of feeding in the upper water column during the night and of hiding from visual predators at deeper layers during the day.

Several authors have studied the spatial and vertical distributions of zooplankton at the frontal system of Península Valdés. Abundance of eggs and nauplii of copepods are highest in the frontal area, while that of adults and of the larvacean *O. dioica* is at a maximum in stratified waters, associated with the highest concentration of chlorophyll *a* at the thermocline layer (Viñas & Ramirez 1996; Capitanio & Esnal 1998; Sabatini & Martos 2002). Considering the mesozooplankton size fractions, the smallest fraction (< 500 μm) is more abundant at well-mixed areas, coincident with peaks of abundance of first feeding larvae of *Engraulis anchoita* (Hubbs & Marini, 1935), while the largest fraction (> 500 μm) predominates at the stratified area, coincident with the highest abundance of anchovy eggs (Spinelli et al. 2012). At 'El Rincón' (39°–41°S), another coastal frontal area, a higher density and biomass of *O. dioica* has been found mainly in stratified surface waters in summer, coinciding with the highest concentration of chlorophyll *a* and the highest abundances of *E. anchoita* (Spinelli et al. 2013). Although prey selectivity is often attributed to prey size, other factors such as prey swimming behaviour, conspicuousness and availability in the water column also seem to be important (Duró & Saiz 2000). It is known that adults of *E. anchoita* and juveniles of other engraulid species prey upon larvaceans (Capitanio et al. 1997; Morote et al. 2010; Chicharo et al. 2012). Ctenophores and chaetognaths are also predators of larvaceans (Purcell et al. 2005), but at this frontal system, although these organisms are very abundant (e.g. Mianzán & Guerrero 2000), these trophic relationships are still unknown.

The main goal of the present study was to investigate the day and night vertical distribution of *O. dioica* in the different sectors of the Península Valdés tidal front, testing the hypotheses that the mixing process prevents a vertical distribution pattern in coastal waters and that the stratified condition favours it. In this context, we focused on the possible causes of the pattern observed in relation to oceanographic conditions, reproductive behaviour, feeding activities and predation risks, discussing the main implications for larvaceans living in a coastal frontal system.

Materials and methods

Continuous conductivity-temperature-depth (CTD) profiles were recorded with a Seabird SBE 19 CTD

at 15 oceanographic stations, both during the day and during the night in spring (14–19 December) of 2008 along a transect crossing the Península Valdés tidal front (42°–45°S; SW Atlantic Ocean). Zooplankton samples were also taken at five of the stations (St. 1, 2, 5, 12 and 13) (Figure 1a).

A total of 40 samples (day and night) were collected with a Hydrobios MultiNet of 67 μm and 300 μm mesh size (0.25 m² mouth opening) at two depth layers: from the bottom to the thermocline layer (lower layer) and from the thermocline to the surface layer (upper layer). The samples were fixed on board with 2% formaldehyde. The depth of the sampling was decided by establishing the thermocline position with a CTD. At the well-mixed area, both depth layers were obtained by dividing the total depth into two equal depth layers. At all stations, to quantify the stratification at the front, we used the parameter of stability (Simpson 1981) in J m⁻³, which is defined as

$$\Phi = g \times h - h \times \int 0(\rho - \rho_0) \times Z \times dz,$$

where g is the acceleration of gravity, h is the total depth, ρ is the density of sea water, ρ_0 is the average density of the water column and Z is the depth. A Φ value of about 40 J m⁻³ was used to separate well-mixed and stratified waters (Martos & Sánchez

1997), thereby defining the middle position of the frontal area. Temperature profiles were analysed at each station using Ocean Data View. The surface concentration of chlorophyll a (Chl-a) was obtained from satellite images of a MODIS sensor with a resolution of 1 km provided by the ANTARES network (original data from NASA).

The larvacean *Oikopleura dioica* (obtained from the 67 μm plankton samples), the chaetognath *Sagitta* sp., the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 and larvae of the anchovy *Engraulis anchoita* (obtained from the 300 μm plankton samples) were separated and identified in the laboratory using a stereoscopic microscope, estimating their densities for the day and night samplings. *Oikopleura dioica* size (determined by the trunk length, TL) was measured using an ocular micrometer. Samples were organized in a size frequency distribution, grouping the larvaceans in 100 μm TL size intervals. Larvaceans were classified as either juvenile or mature, using available literature (Capitanio et al. 1995). Larvaceans with pellets in their digestive tracts were quantified and the percentages of well-fed larvaceans, defined as actively feeding animals with three pellets inside their digestive tracts (López-Urrutia & Acuña 1999), were estimated.

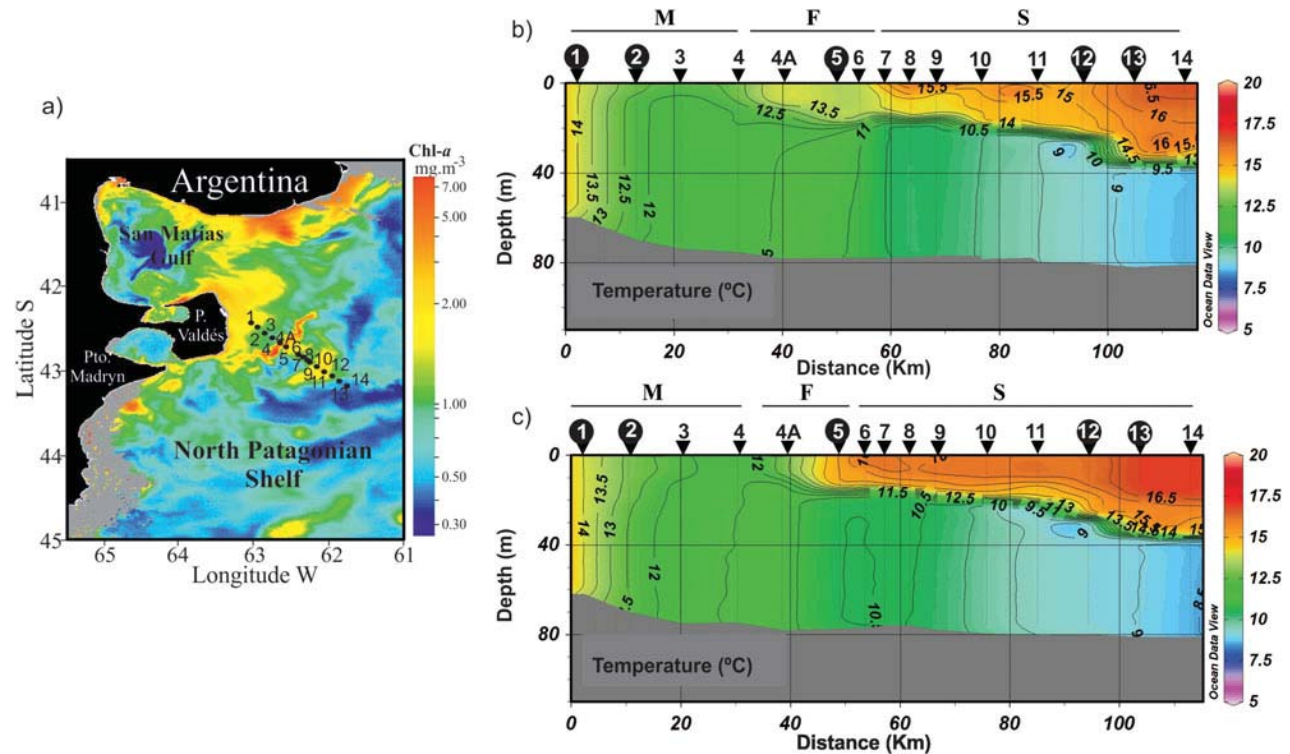Densities of larvaceans were compared between the upper and lower layers for the day and night

Figure 1. Location of CTD samplings (Sts 1 to 14); plankton stations (Sts 1, 2, 5, 12 and 13) and spatial distribution of satellite Chl-a concentration (a), profiles of temperature during day (b) and night (c) at the Peninsula Valdés frontal system. M: well-mixed area; F: frontal area; S: stratified area.

samplings by using the Wilcoxon test. At each day and night sampling, size structures of *O. dioica* were compared between the upper and lower layers at the different sectors of the front using the chi-square test. The Pearson correlation test was used to correlate the abundances of larvaceans (upper + lower layers) with Chl-*a* concentration. A principal component analysis (PCA) was applied to establish relationships between the Simpson parameter and abundances (upper + lower layers) of *O. dioica*, chaetognaths, ctenophores and anchovy larvae for the day and night samplings. Statistica 6.0 and InfoStat packages were used for data analysis.

Results

Temperature changed along the transect, from coastal homogeneously mixed to offshore well-stratified areas, with higher surface concentration of Chl-*a* in the frontal zone (Figure 1a). The frontal zone (St. 4A and St. 6) separated the well-mixed coastal area (St. 1 to St. 4) from the stratified off-shore stations (St. 7 to St. 14). The thermocline was situated at 20 m depth at station 4A, sinking to 40 m depth at offshore stations. In well-mixed waters, the temperature varied from 14°C to 12°C during the day and the night. In frontal and stratified waters, temperature varied from 13.5°C to 16.5°C during the day and from 15°C to 16.5°C during the night in the upper layers, and from 11.5°C to 9°C both during the day and during the night in the lower layers (Figure 1b-c).

Oikopleura dioica inhabited the whole sampled area (Figure 2). During the day, its densities were significantly different between the upper and lower layers (Wilcoxon test, $P = 0.014$), particularly at the frontal area where densities were higher in the upper layer (St. 5: 724 Ind. m^{-3}). During the night, *O. dioica* densities were similar in the upper and lower layers (Wilcoxon text, $P = 0.4$).

The differences in the size structure of this species between the upper and lower layers in the well-mixed, frontal and stratified areas are shown in Figure 3 and Table I. In the well-mixed area, no differences in size structure were found during the day or during the night. In the frontal area, there was a different vertical pattern during the night, with larger *O. dioica* (1100–1400 µm TL) occurring in the upper layer. In the stratified area, the vertical pattern was significantly different between day and night samples, trunk sizes being larger in the upper layer at night and in the lower layer during the day.

In the well-mixed area, no individuals with completely mature gonads were found and immature individuals dominated. In the frontal and stratified areas, mature specimens were found with a higher proportion in the upper layer at night (up to 90%). In the frontal area, mature larvaceans were found only in the lower layers during the day, whereas in the stratified area, larvaceans were equally distributed between the upper and lower layers. The abundance of *O. dioica* was positively correlated with surface Chl-*a* concentration (Pearson correlation: 0.9, $P < 0.05$). The highest concentration of Chl-*a* was found in the frontal area. Remarkably, the highest percentage of well-fed larvaceans was found mainly in the upper levels of this area both during the day and during the night. In contrast, in the well-mixed area, a lower percentage of well-fed larvaceans was recorded both in the upper and lower layers (Table II).

Figure 4 shows the vertical distribution of the potential predators (*Sagitta* sp., *Mnemiopsis leidyi* and *Engraulis anchoita* larvae) during the day and during the night. *Sagitta* sp. was found only in the lower layers during the day but was more abundant in the upper layers during the night, particularly in stratified stations both during the day and during the night. Larvae of *E. anchoita* were more abundant in the lower layers in the daytime and in the upper
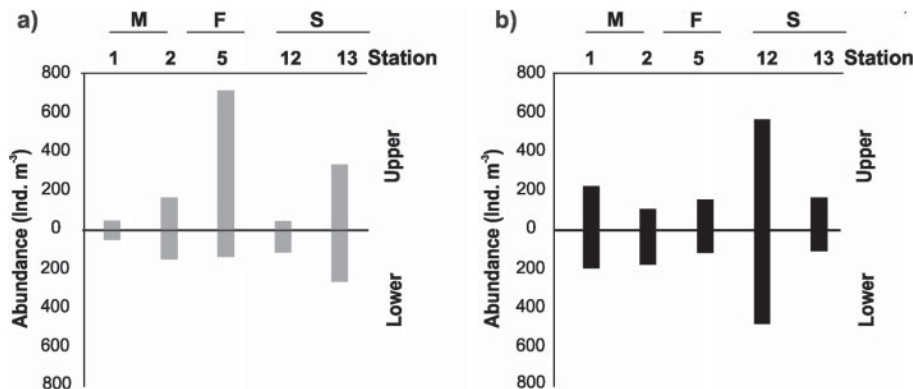

Figure 2. Upper and lower densities of *Oikopleura dioica* at the Peninsula Valdés front during day (a) and night (b) samplings. M, well-mixed area; F, frontal area; S, stratified area.
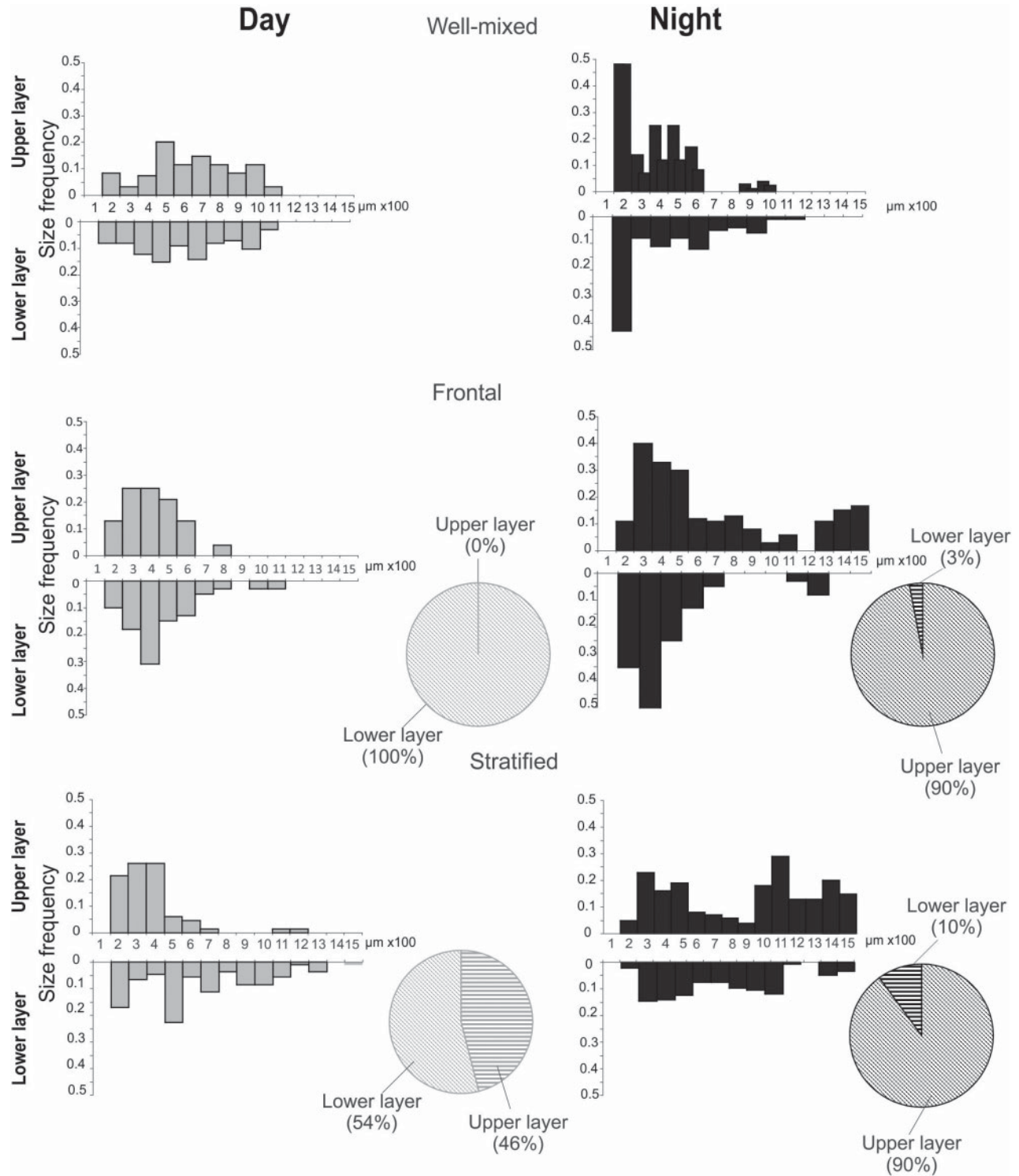
Figure 3. Upper and lower trunk length structure (TL, μm) of *Oikopleura dioica* at different sectors of the Península Valdés front during day and night. Percentages of mature specimens at day/night upper and lower layers at frontal and stratified waters are indicated.

layers at night time. The principal component analysis (PCA) of the Simpson parameter, as well as the abundance of *O. dioica*, chaetognaths, ctenophores and anchovy larvae both during the day and during the night, are shown in Figure 5. At night, the abundance of chaetognaths, ctenophores and anchovy larvae were correlated with the Simpson parameter ($r = 0.81$; 0.94; 0.75; $P < 0.05$, respectively). *Oikopleura dioica* abundance was positively correlated with chaetognath abundance ($r = 0.79$, $P < 0.05$) during the night. Abundances of chaetognaths and anchovy larvae during the day were

Table I. *Oikopleura dioica* size structure comparison between upper and lower layers during day and night samplings at the different sectors of the Península Valdés front.

	Day		Night	
	χ^2	P	χ^2	P
Well-mixed	8.80	0.72	15.19	0.09
Frontal	3.43	0.94	44.89	**<0.05**
Stratified	55.75	**<0.05**	77.09	**<0.05**

Note: Significant differences where indicated, in bold. χ^2: statistical value.

Table II. Percentage of well-fed *Oikopleura dioica* larvaceans in day/night upper and lower layers at the Península Valdés tidal front.

		Upper layer	Lower layer
Well-mixed	Day	11.50	12.90
	Night	23	18.50
Frontal	Day	70.60	30.30
	Night	43.40	38.50
Stratified	Day	29.70	14.85
	Night	54.15	28.50

positively correlated ($r = 0.98$, $P < 0.05$). PCA showed that the Simpson parameter was mainly correlated with PC1 (Table III), separating the stations according to stratification. Biological variables (abundances of groups) were grouped according to samples taken during the day or during the night (see Figure 5). The abundance of chaetognaths and ctenophores during the night were mainly associated with PC1, whereas abundance of *O. dioica* (day and night samples) and ctenophores during the day were correlated with PC2.

In the well-mixed area, *O. dioica* percentages were similar during the day and during the night in both layers. In the frontal area, 60–100% of *O. dioica* occurred in the upper layer both during the day and during the night, whereas in the stratified area, it was more abundant in the upper layer only during the night (Figure 6a). In the well-mixed area, chaetognaths (Figure 6b) were least abundant in the upper layers both during the day and during the night, whereas in the frontal and stratified areas, they were more abundant in the upper layers during the night. The percentage of ctenophores in the upper layer (Figure 6c) was similar (80–100%) in frontal and stratified sections both during the day and during the night. About 60–80% of *E. anchoita* larvae were found in the upper layer in the well-mixed area both during the day and during the night, whereas in the frontal and stratified areas, 60–80% were found in the upper layer during the night (Figure 6d). Overall, in the frontal and stratified areas, the distribution of larvaceans and ctenophores was similar during the day, with most occurring in the upper layer, in contrast to anchovy larvae and chaetognaths, which occurred mainly in the lower layer. During the night, all groups, including larvaceans, were found mainly in the upper layer.
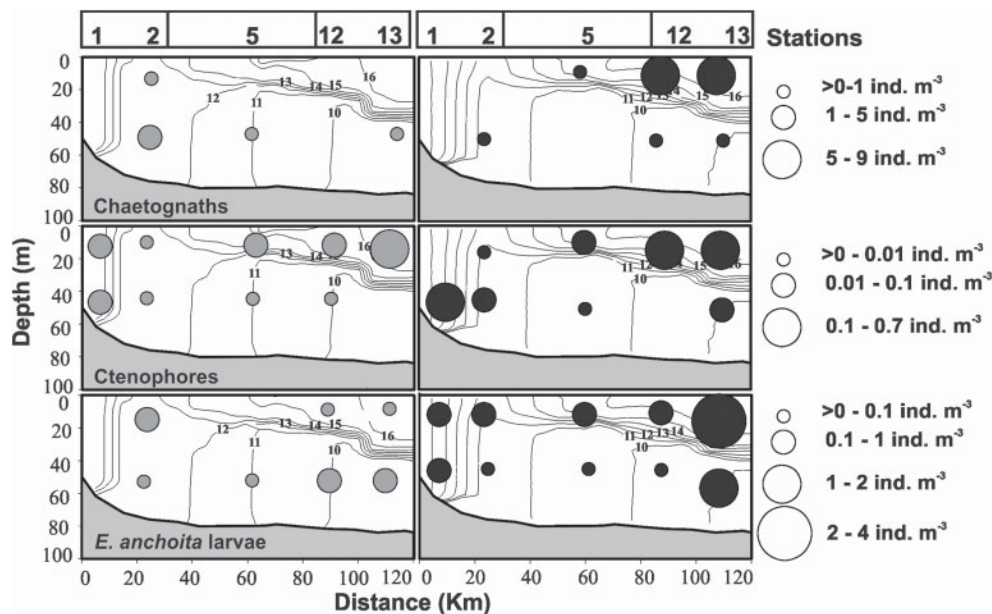

Figure 4. Day and night vertical abundance distribution of *Sagitta* sp. chaetognaths, *Mnemiopsis leidyi* ctenophores and *Engraulis anchoita* anchovy larvae at the Península Valdés front.
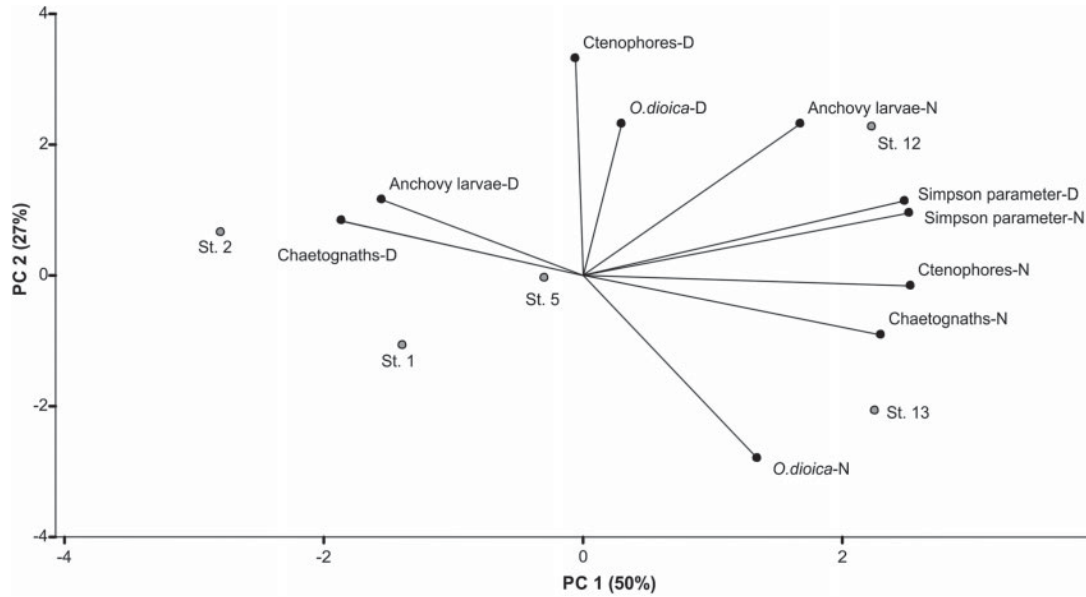
Figure 5. Principal component analysis (PCA) between Simpson parameter and abundance of *Oikopleura dioica*, chaetognaths, ctenophores and anchovy larvae at day (D) and night (N) at Península Valdés tidal front. Stations (Sts 1, 2, 5, 12 and 13) are indicated.

Table III. Results of the PCA, eigenvectors (evc), eigenvalues percent of the variance explained by the original dataset (r^2), and correlation (r) of the original variables with the first two principal components (PC1 and PC2).

	PC1		PC2	
	r	evc	r	evc
Simpson parameter-N	0.95	0.43	0.27	0.16
Oikopleura dioica-N	0.51	0.23	−0.78	−0.47
Chaetognaths-N	0.87	0.39	−0.26	−0.16
Ctenophores-N	0.96	0.43	−0.04	−0.03
Anchovy larvae-N	0.64	0.29	0.65	0.39
Simpson parameter-D	0.94	0.42	0.32	0.19
Oikopleura dioica-D	0.11	0.05	0.65	0.39
Chaetognaths-D	−0.71	−0.32	0.23	0.14
Ctenophores-D	−0.02	−0.01	0.93	0.56
Anchovy larvae-D	−0.59	−0.26	0.33	0.2
r^2		50		27

N, night; D, day.

Discussion

The day and night vertical distribution patterns of *Oikopleura dioica* differed according to the proximity to the frontal system of Península Valdés. In frontal and stratified areas, the largest individuals were found above the thermocline during the night. In the well-mixed area, the pattern of sizes was similar at both levels of the water column both during the day and during the night, the degree of stratification being the main factor affecting the vertical distribution of this species. In the well-mixed area, no vertical distribution pattern was observed, probably because of the continuous vertical movement caused

by the turbulent mixing of waters and the strong kinetic energy dissipation rates (over 5 W m^{-2}) at the northeast coast of Península Valdés (Glorioso & Simpson 1994; Mianzán et al. 2010). High turbulence in the water column can drastically affect planktonic communities because motility is compromised. Thus, patches of phytoplankton are more difficult to find and the ability to escape from visual predators is decreased (Peters & Marrasé 2000; Zervoudaki et al. 2006).

Oikopleura dioica is an excellent model to study food flow through the digestive system because of its transparency and limited motility and because faecal pellets move along the digestive system in an orderly sequence which can be easily timed. Experimentally, López-Urrutia & Acuña (1999) and Lombard et al. (2009) observed up to three faecal pellets in the digestive tracts of *O. dioica* at high food concentrations. This is consistent with our results from samples in the upper frontal and stratified waters of Península Valdés, where many individuals exhibited three pellets inside their guts. Thus, we inferred active feeding of *O. dioica* in the upper layers. At the Ushant front (Iroise Sea, North Atlantic Ocean), Schultes et al. (2013) found that larvaceans were more abundant in the upper layer where Chl-*a* concentration was highest. Similar results were found in Toyama Bay (Japan Sea) by Tomita et al. (2003), where the larvacean *Oikopleura (Coecaria) longicauda* (Vogt, 1854) was mainly found around the 50 m surface layer, associated with the highest concentration of Chl-*a*.
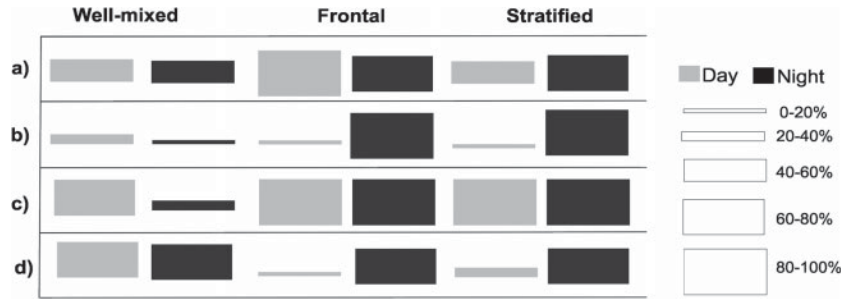
Figure 6. Day and night abundance of *Oikopleura dioica* larvaceans (a), *Sagitta* sp. chaetognaths (b), *Mnemiopsis leidyi* ctenophores (c) and *Engraulis anchoita* anchovy larvae (d) at upper layer, expressed as percentage of abundances (%), in the different sectors of the Península Valdés front. Five percentage categories were defined.

Larvaceans have one reproductive episode during their life cycle (Deibel & Lowen 2012), so it would be more advantageous to spawn in an area with more favourable conditions for the survival and development of their progeny. Our observation of more mature specimens being found near the surface during the night may be related to a reproductive strategy to release their eggs in the upper layers. Larvaceans stop producing new houses prior to reproduction, becoming free swimmers (Alldredge 1982). Mature individuals in culture often swim to the surface before reproduction. However, this swimming strategy, combined with the peculiar colouration of gonads (males have bright orange gonads clearly distinguished from female gonads, which are a grey blue or pink colour; Gorsky & Palazzoli 1989; Fenaux 1998), also implies that they are more easily detected by predators. Moreover, large larvaceans are more prone to adjust their own depth in the water column than smaller ones (Lombard, 2006). In our study, smaller individuals (100–600 μm TL) were found in both the upper and lower layers and both during the day and during the night, whereas larger individuals (> 800 μm TL) were more frequently found in the lower layers during the day in frontal and stratified areas. This might be considered as a possible strategy to reduce their detection by visual predators. On the other hand, the size of the organisms is related to the temperature. When temperature increases the trunk length at maturity and fecundity decreases (Uye & Ichino 1995; Lombard et al. 2009). This is because there seems to be a strong positive relationship between egg production and trunk length (Wyatt 1973; Lombard et al. 2009). Although it may be possible to find differences in *in situ* growth due to the existence of different temperatures in the water column, we do not consider this an important factor in determining the differences observed in the size structure. If vertical differences in growth had occurred, we would expect larger sizes in the deeper layers both during the day and during the night, where

temperatures are lower and organisms take more time to reach maturity and have lower growth rates.

Diel vertical migration has long been recognized as a potentially important mechanism determining the position in the water column of planktonic organisms (Hill 1991), generally regarded as a trade-off between feeding opportunities and predation risk caused by changes in light intensity (Cohen & Forward 2009; Ringelberg 2010). Thus, while light is the main factor for the diel migration of zooplankton, influencing the vertical distribution and time of migration (Ringelberg & Van Gool 2003), the distribution of food and predation risk are regarded as the main drivers (Neilson & Perry 1990; Sutton & Hopkins 1996). The predominance of chaetognaths and anchovy larvae in the upper layers (above the thermocline) at night may control the population of larvaceans (top-down control). Chaetognaths detect prey by sensing movements, so the distinct beating of the tails of larvaceans may make them susceptible to detection when they are free swimming animals without their houses, mainly during spawning (Feigenbaum 1991; Tonnesson & Tiselius 2005). Also, it is well known that adults of *E. anchoita* feed mostly on zooplankton during their lifespan and that they prey on larvaceans together with their houses by filtering them (Capitanio et al. 1997). In the Black Sea, Shiganova (2005) observed that the abundance of *O. dioica* declined drastically after invasion by the ctenophore *Mnemiopsis leidyi*. Although ctenophores feed on larvaceans, in the present study they showed no vertical distribution pattern.

In experimental studies, some authors have noted that the abundance of larvaceans is inversely related to the abundance of copepod species such as *Calanus helgolandicus* (Claus, 1863), *Candacia armata* (Boeck, 1872), *C. bipinnata* (Giesbrecht, 1889), *Centropages typicus* (Krøyer, 1849), *Temora longicornis* (O. F. Müller, 1785) and *Subeucalanus crassus* (Giesbrecht, 1888), due to their ability to prey on eggs and younger stages of larvaceans (Sommer et al. 2003;

López-Urrutia et al. 2004; Stibor et al. 2004). In this study, no data on copepods are available, but previous studies performed at this front have shown that small species such as *Paracalanus parvus* (Claus, 1863), *Drepanopus forcipatus* (Giesbrecht, 1888), *Ctenocalanus vanus* (Giesbrecht, 1888), *Centropages brachiatus* (Dana, 1849) and *Oithona* sp. are dominant (Sabatini & Martos 2002; Spinelli et al. 2012). However, it is known that these small species of copepods do not prey on eggs and juvenile stages of *O. dioica*. Some species of copepods have been shown to undergo reverse diel migration to avoid predators (e.g. Ohman et al. 1983; Bollens & Frost 1989). Although we cannot determine whether the diel vertical migration of predators affects the distribution pattern of *O. dioica*, daily vertical migration of both predators and *O. dioica* may facilitate the maintenance of position in this highly productive system, favouring their reproductive cycles as well as their recruitment processes. Importantly, the Península Valdés tidal front is also a reproduction area for other predators such as hake, which could be feeding on chaetognaths and anchovy larvae (Macchi et al. 2007; Betti et al. 2009), and may influence the abundances of these potential predators of *O. dioica* both during the day and during the night (see Figure 5).

Given the low motility of larvaceans, their migratory behaviour would be directly influenced by the physical conditions of the water column. In the well-mixed area, we found no differences in the vertical distribution. Our observations on the vertical distribution of *O. dioica* in the frontal and stratified waters of the Península Valdés tidal front suggest different life-history strategies to be successful for inhabiting this system with a two-layered circulation pattern.

Acknowledgements

Funding

References

Alldredge AL. 1982. Aggregation of spawning appendicularians in surface windrows. Bulletin of Marine Science 32:250–54.

Álvarez Colombo G, Dato C, Macchi GJ, Palma E, Machinandiarena L, Christiansen HE, et al. 2011. Distribution and behavior of Argentine hake larvae: Evidence of a biophysical mechanism for self-recruitment in northern Patagonian shelf waters. Ciencias Marinas 37:633–57.

Betti P, Machinandiarena L, Ehrlich MD. 2009. Larval development of Argentine hake *Merluccius hubbsi*. Journal of Fish Biology 74:235–49.

Bollens SM, Frost BW. 1989. Predator-induced diel vertical migration in a planktonic copepod. Journal of Plankton Research 5:1047–65.

Capitanio F, Esnal G. 1998. Vertical distribution of the maturity stages of *Oikopleura dioica* (Tunicata, Appendicularia) in the frontal system off Valdés Peninsula, Argentina. Bulletin of Marine Science 63:531–39.

Capitanio F, Marschoff E, Esnal G. 1995. Distribution and characterization of the maturity stages of *Oikopleura dioica* (Tunicata, Appendicularia) in the area off Valdés Peninsula, Argentina. Iheringia, Série Zoologia 79:59–66.

Capitanio F, Pájaro M, Esnal G. 1997. Appendicularians (Chordata, Tunicata) in the diet of anchovy (*Engraulis anchoita*) in the Argentine Sea. Sciencia Marina 61:9–15.

Chícharo MA, Amaral A, Faria A, Morais P, Mendes C, Piló D, et al. 2012. Are tidal lagoons ecologically relevant to larval recruitment of small pelagic fish? An approach using nutritional condition and growth rate. Estuarine, Coastal and Shelf Science 112:265–79.

Cohen JH, Forward Jr RB. 2009. Zooplankton diel vertical migration: A review of proximate control. Oceanography and Marine Biology 47:77–110.

Deibel D, Lowen B. 2012. A review of the life cycles and life–history adaptations of pelagic tunicates to environmental conditions. ICES Journal of Marine Science 69:358–69.

Duró A, Saiz E. 2000. Distribution and trophic ecology of chaetognaths in the western Mediterranean in relation to an inshore-offshore gradient. Journal of Plankton Research 22:339–61.

Feingenbaum DL. 1991. Food and feeding behaviour. In: Bone Q, Kapp H, Pierrot-Bults AC, editors. The Biology of Chaetognaths. Oxford: Oxford University Press, p 45–55.

Fenaux R. 1963. Ecologie et biologie des Appendiculaires méditerranéens (Villefranche-sur-Mer). Vie et Milieu 16 (Suppl. 8):1–142.

Fenaux R. 1998. Life history of the Appendicularia. In: Bone Q, editor. The Biology of Pelagic Tunicates. Oxford: Oxford University Press, p 151–60.

Glorioso PD, Simpson JH. 1994. Numerical modelling of the tide on the northern Patagonian Shelf. Continental Shelf Research 14:267–78.

Gorsky G, Palazzoli I. 1989. Aspects de la biologie de l'appendiculaire *Oikopleura dioica* Fol. 1872 (Chordata: Tunicata). Oceanis 15:39–49.

Hill AE. 1991. A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. Marine Biology 111:485–92.

Höffle H, Nash RDM, Falkenhaug T, Munk P. 2013. Differences in vertical and horizontal distribution of fish larvae and zooplankton, related to hydrography. Marine Biology Research 9:629–44.

Hopcroft R, Roff J. 1995. Zooplankton growth rates: Extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. Journal of Plankton Research 17:205–20.

Jaspers C, Nielsen TG, Carstensen J, Hopcroft RR, Møller EF. 2009. Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of larvaceans. Journal of Plankton Research 31:525–40.

Lee O, Nash RDM, Danilowicz BS. 2005. Small-scale spatio-temporal variability in ichthyoplankton and zooplankton distribution in relation to a tidal-mixing front in the Irish Sea. ICES Journal of Marine Science 6:1021–36.

Legendre L, Demers S, Lefaivre D. 1986. Biological production at marine ergoclines. In: Nihoul JCJ, editor. Marine Interfaces Ecohydrodynamics. New York: Elsevier, p 1–30.

Lombard F. 2006. Etude expérimentale et modélisation de l'écophysiologie de l'appendiculaire *Oikopleura dioica*. Doctoral Thesis. Université Pierre et Marie Curie, Paris VI. 284 pages.

Lombard F, Renaud F, Sainsbury C, Sciandra A, Gorsky G. 2009. Appendicularian ecophysiology I. Food concentration dependent clearance rate, assimilation efficiency, growth and reproduction of *Oikopleura dioica*. Journal of Marine Systems 78:606–16.

López-Urrutia A, Acuña JL. 1999. Gut throughput dynamics in the appendicularian *Oikopleura dioica*. Marine Ecology Progress Series 191:195–205.

López-Urrutia A, Acuña JL, Irigoien X, Harris RP. 2003. Food limitation and growth in temperate epipelagic appendicularians (Tunicata). Marine Ecology Progress Series 252:143–57.

López-Urrutia A, Harris RP, Smith T. 2004. Predation by calanoid copepods on the appendicularian *Oikopleura dioica*. Limnology and Oceanography 49:303–07.

Macchi GJ, Pájaro M, Dato C. 2007. Variaciones espaciales de los cardúmenes desovantes de merluza común (*Merluccius hubbsi* (Marini, 1933)) en el área de Patagonia durante una estación reproductiva. Revista de Biología Marina y Oceanografía 42:345–56.

Marrari M, Daly KL, Timonin A, Semenova T. 2011. The zooplankton of Marguerite Bay, western Antarctic Peninsula – Part II: Vertical distributions and habitat partitioning. Deep-Sea Research Part II 58:1614–29.

Martos P, Sánchez RP. 1997. Caracterización oceanográfica de regiones frontales en la plataforma Patagónica en relación con áreas de desove y cría de la anchoíta (*Engraulis anchoita*). In: Abstracts Coloquio Argent. Oceanografía. IAPSO–IADO (Conicet), Bahía Blanca, Argentina, 4–5 de septiembre. 30 pages.

Mianzán HW, Guerrero RA. 2000. Environmental patterns and biomass distributions of gelatinous macrozooplankton. Three study cases in the Southwestern Atlantic Ocean. Scientia Marina 64:S215–24.

Mianzán HW, Martos P, Costello JH, Guerrero RA. 2010. Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina. Hydrobiologia 645:113–24.

Morgado FM, Melo R, Queiroga H, Sorbe JC. 2003. Zooplankton abundance in a coastal station off the Ria de Aveiro inlet (north-western Portugal): Relation with tidal and day/night cycles. Acta Oecologica 24:175–81.

Morgado FM, Pastorinho MR, Quintaneiro C, Ré P. 2006. Vertical distribution and trophic structure of the macrozooplankton in a shallow temperate estuary (Ria de Aveiro, Portugal). Scientia Marina 70:177–88.

Morote E, Olivar MP, Villate F, Uriarte I. 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. ICES Journal of Marine Science 5:897–908.

Neilson JD, Perry RI. 1990. Diel vertical migrations of marine fishes: An obligate or facultative process? Advances in Marine Biology 26:115–68.

Ohman MD, Frost BW, Cohen EB. 1983. Reverse diel vertical migration: An escape from invertebrate predators. Science 220:1404–47.

Palma ED, Matano RP, Piola AR. 2008. A numerical study of the Southwestern Atlantic Shelf circulation: Stratified ocean response to local and offshore forcing. Journal of Geophysical Research 113:1–22.

Paparazzo FE, Bianucci L, Schloss IR, Almandoz GO, Solís M, Esteves JL. 2010. Cross-frontal distribution of inorganic nutrients and chlorophyll-a on the Patagonian Continental Shelf of Argentina during summer and fall. Revista de Biología Marina y Oceanografía 45:107–19.

Peters F, Marrasé C. 2000. Effects of turbulence on plankton: An overview of experimental evidence and some theoretical considerations. Marine Ecology Progress Series 205:291–306.

Purcell JE, Sturdevant MV, Galt CP. 2005. A review of appendicularians as prey of invertebrate and fish predators. In: Gorsky G, editor. Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians. Paris: Editions Scientifiques, p 360–435.

Ringelberg J. 2010. Diel Migration of Zooplankton in Lakes and Oceans: Causal Explanations and Adaptive Significances. London: Springer. 472 pages.

Ringelberg J, Van Gool E. 2003. On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. Hydrobiologia 491:85–90.

Sabatini M, Martos P. 2002. Mesozooplankton features in a frontal area off northern Patagonia (Argentina) during spring 1995 and 1998. Scientia Marina 66:215–32.

Schultes S, Sourisseau M, Le Masson E, Lunven M, Marié L. 2013. Influence of physical forcing on mesozooplankton communities at the Ushant tidal front. Journal of Marine Systems 109:191–202.

Shiganova TA. 2005. Changes in appendicularian *Oikopleura dioica* abundance caused by invasion of alien ctenophores in the Black Sea. Journal of the Marine Biological Association of the United Kingdom 85:477–94.

Simpson JH. 1981. The shelf-sea fronts: Implications of their existence and behaviour. Philosophical Transactions of the Royal Society of London A 302:531–46.

Sinclair M. 1988. Marine Populations. An Essay on Population Regulation and Speciation. Seattle: Washington Sea Grant. 252 pages.

Sommer F, Hansen T, Feuchtmayr H, Santer B, Tokle N, Sommer U. 2003. Do calanoid copepods suppress apendicularians in the coastal ocean? Journal of Plankton Research 25:869–71.

Spinelli M, Pájaro M, Martos P, Esnal G, Sabatini M, Capitanio F. 2012. Potential zooplankton preys (Copepoda and Appendicularia) for *Engraulis anchoita* in relation to early larval and spawning distributions at the Patagonian frontal region (SW Atlantic Ocean). Scientia Marina 76:39–47.

Spinelli M, Guerrero R, Pájaro M, Capitanio F. 2013. Distribution of *Oikopleura dioica* (Tunicata, Appendicularia) associated with a coastal frontal system (39°–41°S) of the SW Atlantic Ocean in the spawning area of *Engraulis anchoita* anchovy. Brazilian Journal of Oceanography 61:141–48.

Stibor H, Vadstein O, Lippert B, Roederer W, Olsen Y. 2004. Calanoid copepods and nutrient enrichment determine population dynamics of the appendicularian *Oikopleura dioica*: A mesocosm experiment. Marine Ecology Progress Series 270:209–15.

Sutton TT, Hopkins TL. 1996. Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: Strategies, selectivity and impact of a top mesopelagic predator. Marine Biology 127:179–92.

Tomita M, Shiga N, Ikeda T. 2003. Seasonal occurrence and vertical distribution of appendicularians in Toyama Bay, southern Japan Sea. Journal of Plankton Research 25:579–89.

Tonnesson K, Tiselius P. 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. Marine Ecology Progress Series 289:177–90.

Uye S, Ichino S. 1995. Seasonal variations in abundance, size composition, biomass and production rate of *Oikopleura dioica* (Fol) (Tunicata: Appendicularia) in a temperate eutrophic inlet. Journal of Experimental Marine Biology and Ecology 189:1–11.

Varpe O. 2012. Fitness and phenology: Annual routines and zooplankton adaptations to seasonal cycles. Journal of Plankton Research 34:267–76.

Viñas MD, Ramírez FC. 1996. Gut analysis of first-feeding anchovy larvae from Patagonian spawning area in relation to food availability. Archive of Fishery and Marine Research 43:231–56.

Wyatt T. 1973. The biology of *Oikopleura dioica* and *Fritillaria borealis* in the Southern Bight. Marine Biology 22:137–58.

Zervoudaki S, Nielsen TG, Christou ED, Siokou-Frangou I. 2006. Zooplankton distribution and diversity in a frontal area of the Aegean Sea. Marine Biology Research 2:149–68.

Editorial responsibility: David McKinnon