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Influence of a tidal front on zooplankton abundance, assemblages and life histories in Península Valdés, Argentina

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ABSTRACT

The complex biophysical interactions that occur in Península Valdés tidal front offer an appropriate scenario to study how zooplankton species respond to the environmental setting. In that sense, we studied why some zooplankton assemblages come to dominate in certain areas, focusing on the differential use that each life history stage makes on the hydrodynamic regimes. Environmental data and zooplankton samples were taken across the tidal front, covering well-mixed, frontal and stratified waters. Zooplankton abundance, assemblage structure, specific composition and life histories were analyzed in relation to depth, temperature, stratification level of the water column and chlorophyll *a*. Zooplankton-specific composition did not vary across the different zones of the front but, due to differences in relative abundance, three assemblages were detected in coincidence with the three zones analyzed. Most zooplankton adult groups and early life stages were related to the stratification level of the water column. This environmental factor best explained the coupling of the three different zooplankton assemblages with the three zones of the frontal system. This distributional pattern was clearly observed in the copepods group. Despite different copepod species prevailing in different parts of the tidal front, the frontal interface appears to be an important breeding area for all copepod species. The stratification level would be the main factor responsible for the zooplankton distributional pattern across the tidal front, although other physical and biological processes, such as transport, retention and life history strategies could be conditioning the establishment of different zooplankton populations in this complex frontal system.

1. Introduction

Marine fronts are oceanographic features exhibiting strong temperature and/or salinity gradients, occurring at the meeting of two water masses of different physical properties (Mann and Lazier, 2006). The fact that fronts separate different water masses, and thus different plankton populations, is an old idea sustained by several observations at different scales. Physical zonation at fronts, determined by the thermal/haline heterogeneity, leads to variable composition of zooplankton assemblages; for this reason, many fronts seem to act as barriers between very different ecosystems affecting composition, diversity and distributional patterns of plankton (e.g., Berasategui et al., 2006; Gómez-Gutiérrez et al., 2007; Molinero et al., 2008; Moore and Abbott, 2002; Muelbert et al., 2008; Sournia, 1994; Zervoudaki et al., 2006).

Tidal fronts are among the most studied frontal systems worldwide. They are seasonal thermal fronts that are generated, usually, within the same water mass and define the boundary between stratified (offshore) waters and a coastal, vertically mixed body of water. In temperate climates, seasonal thermoclines establish near the surface during late spring and summer. In regions where the rate of tidal energy dissipation is high, the intensity of turbulent mixing is able to continuously overcome the barrier to mixing presented by the stratification (Le Fèvre, 1986; Mann and Lazier, 2006).

In tidal frontal systems, maximum phytoplankton production has been observed on the surface of frontal zones, where optimal environmental conditions for its development are found (e.g., temperature, turbulence, light and nutrients; Mann and Lazier, 2006; Yamamoto et al., 2000). In addition, since fronts are convergence zones, plankton and inert particles are accumulated there, and high food availability promotes zooplankton production; their highest abundances being associated with this area (Genin et al., 2005; Liu et al., 2003; Mann, 2000; Mann and Lazier, 2006; Munk, 1993; Schultes et al., 2013; Uye et al., 1992). For this reason, these fronts are important feeding, spawning and nursery grounds for many fish species (e.g., Hao et al., 2003; Lee et al., 2005; Lough et al., 2006; Munk and Nielsen, 1994), attracting

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many free-swimming organisms (e.g., fish, penguins, marine mammals and turtles) and flying birds that make use of frontal areas for foraging and migration purposes (Olson, 2002; Polovina et al., 2001).

Although it is known that planktonic communities have great variability across tidal fronts, the influence of tidal frontal systems, from the turbulent coastal towards the stratified offshore zones, on zooplankton communities and their life histories is scarcely studied. Unlike other types of fronts (e.g., estuarine, thermo-haline, subtropical shelf and shelf-break), characterized by different zooplankton compositions on each side of the front, tidal fronts do not seem to act as biological barriers (Schultes et al., 2013) and their role in zooplankton composition and diversity across them is still unclear. Given the different hydrographic and food availability conditions across tidal fronts, and following a "bottom-up approach," it would be expected that changes in the environmental setting at these types of fronts could have a paramount role in structuring zooplankton assemblages.

The Península Valdés frontal system is one of the best-known tidal fronts in the northern Patagonian continental shelf. It was first described in relation to a red tide event that killed a couple of fishermen (Carreto et al., 1986). Its reported physical and biological characteristics are typical to what was defined for most tidal fronts. Península Valdés tidal front is an area of high phytoplankton and zooplankton production, and an important spawning and nursery ground for commercially important fishes and squids in the Argentine continental shelf (Acha et al., 2004). Since this frontal system is generated within the same water mass, it is proposed that changes in the environmental setting are strong enough to modulate different zooplankton species prevalence in different parts of the tidal frontal systems. Preliminary information from the area seems to support this statement (Mianzan et al., 2010; Sabatini and Martos, 2002; Viñas and Ramírez, 1996).

Despite considerable research describing zooplankton communities at different zones of the frontal system, there is scarce information about how the transition from a highly turbulent to a more stabilized water column condition influences the establishment of different populations. In this study, a tidal frontal region at the northern Patagonian shelf was sampled during the period of thermal stratification and front occurrence in late spring. The aim of this study was to investigate the influence of environmental forcing on zooplankton assemblages and to understand why certain assemblages come to dominate, focusing on the life histories of the dominant species in the different hydrodynamic regimes.

2. Methods

2.1. Sampling procedure

Field sampling was carried out by the German R/V *Meteor* during December 1989, representing the highest vertical resolution dataset ever obtained from a tidal front in the region. Environmental data and plankton samples were taken across the Península Valdés tidal front, at six stations along a transect (Fig. 1). This transect was planned in order to cross the thermal front, which had been previously identified from real-time satellite imagery and a physical transect (see Alheit et al., 1991). Stations were close to each other and sampling was performed at well-mixed, frontal and stratified waters during a continuous sampling designed for day and night. All stations had similar weather conditions; therefore, the major factors that influence zooplankton assemblages and specific composition would be hydrographic rather than meteorological. Environmental profiles of the water column (temperature, salinity and fluorescence) were obtained at each station using a CTD-Fluorescence-Sonde (Fig. 1). Fluorescence values were transformed to chlorophyll *a* data (Chl-*a*, mg m^{-3}) using the equation proposed by Alheit et al. (1991).

Plankton samples were collected at different depth strata using two net types with multiple opening–closing mechanisms. A Biomoc net (1 m^2 mouth opening, 300 μm of mesh size and nine nets) was used

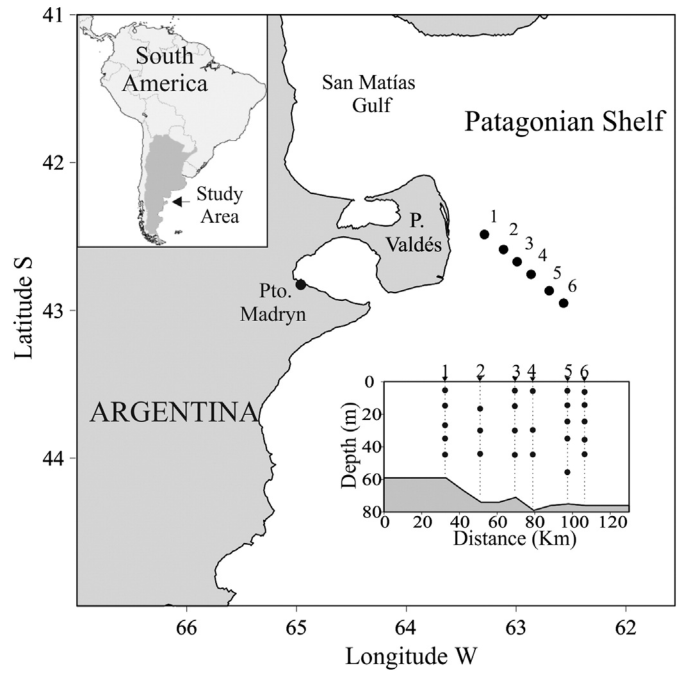


Fig. 1. Study area at the Argentine continental shelf. Transect location and sampling vertical section across Península Valdés tidal front, Argentina. Insert: vertical distribution of sampling stations showing CTD's profiles (dotted line from surface to bottom) and plankton samples at different depths (black dots).

for macrozooplankton groups and a Multinet (0.25 m^2 mouth opening, 64 μm of mesh size and five nets) for micro and mesozooplankton groups. Plankton samples were taken between 5 and 60 m depth, above, in and below the thermocline. When the water column was homogeneous, samples were taken in different depths throughout the water column. Zooplankton samples were preserved in 4% buffered formaldehyde. In the laboratory, specimens were identified to the lowest taxonomic level and counted using binocular stereomicroscope or microscope. The zooplankton samples included immature and adult stages of different groups. For the different zooplankton groups, identification appropriate literature was consulted (e.g., Boltovskoy, 1999; Ramírez, 1970), achieving the species level only in juveniles and adults. Zooplankton abundance, expressed as individuals per volume (ind m^{-3}) was determined for each depth of a station along the transect.

2.2. Data analysis

2.2.1. Environmental data

The stratification parameter value was used to determine the level of stratification of the water column. The different zones of the frontal system (mixed, frontal and stratified) were identified using the stratification parameter value ($\Phi = \text{J m}^{-3}$; Simpson, 1981) and temperature pattern, considering: (a) mixed zone when $\Phi < 10$ and temperature was vertically homogeneous; (b) frontal interface, that is, the front itself when $10 < \Phi < 90$, and a strong horizontal temperature gradient and a weak thermocline were present; and (c) stratified zone when $\Phi > 90$ and a strong thermocline was present. Chl-*a* distribution pattern was described according to the different zones of frontal system. Data was plotted as mean ± standard deviation.

2.2.2. Zooplankton community

The zooplankton community was analyzed to study the influence of the tidal front on its abundance, assemblages, specific composition and dominant life histories. Particular attention was paid on the copepod group because of its abundance, its key role in the marine trophic web

(Lenz, 2000) and because it is one of the richest and taxonomically best-known groups in the region (Bradford-Grieve et al., 1999).

The abundance of each zooplankton group (mean ± standard deviation) was analyzed in relation to the different frontal zones, and only the most frequent zooplankton groups were plotted. Then, the zooplankton assemblage structures at different stations across the front were analyzed using multivariate analysis on the abundance of those adults and juveniles identified at the species level (PRIMER 5 software package; Clarke and Warwick, 2001). Data were transformed [$\log_{10}(x+1)$] to reduce the influence of the most abundant species, and a Bray–Curtis similarity matrix were constructed on the abundance data followed by cluster analysis and non-metric multidimensional scaling (NMDS). The stress coefficient (s) of the NMDS ordination indicates excellent representation ($s < 0.05$), adequate ordination ($s < 0.2$) or arbitrary ordination ($s > 0.3$; Clarke and Warwick, 2001). The species most responsible for the multivariate pattern observed were identified using a similarity percentages analysis (SIMPER) on zooplankton abundance data. This method compares average abundances and examines the contributions of each species to similarities within a given group or dissimilarities between groups (Clarke and Warwick, 2001).The BIO-ENV procedure was used to relate environmental data with zooplankton assemblage structure.

To investigate the influence of the tidal front on zooplankton-specific composition, mean species richness (species number) was calculated and analyzed at each zone of the frontal system. To evaluate the null hypothesis of no difference in richness between different frontal zones, analysis of variance was used (ANOVA; Zar, 1999). Also, as suggested by Koleff et al. (2003), beta diversity (B sim; Lennon et al.,

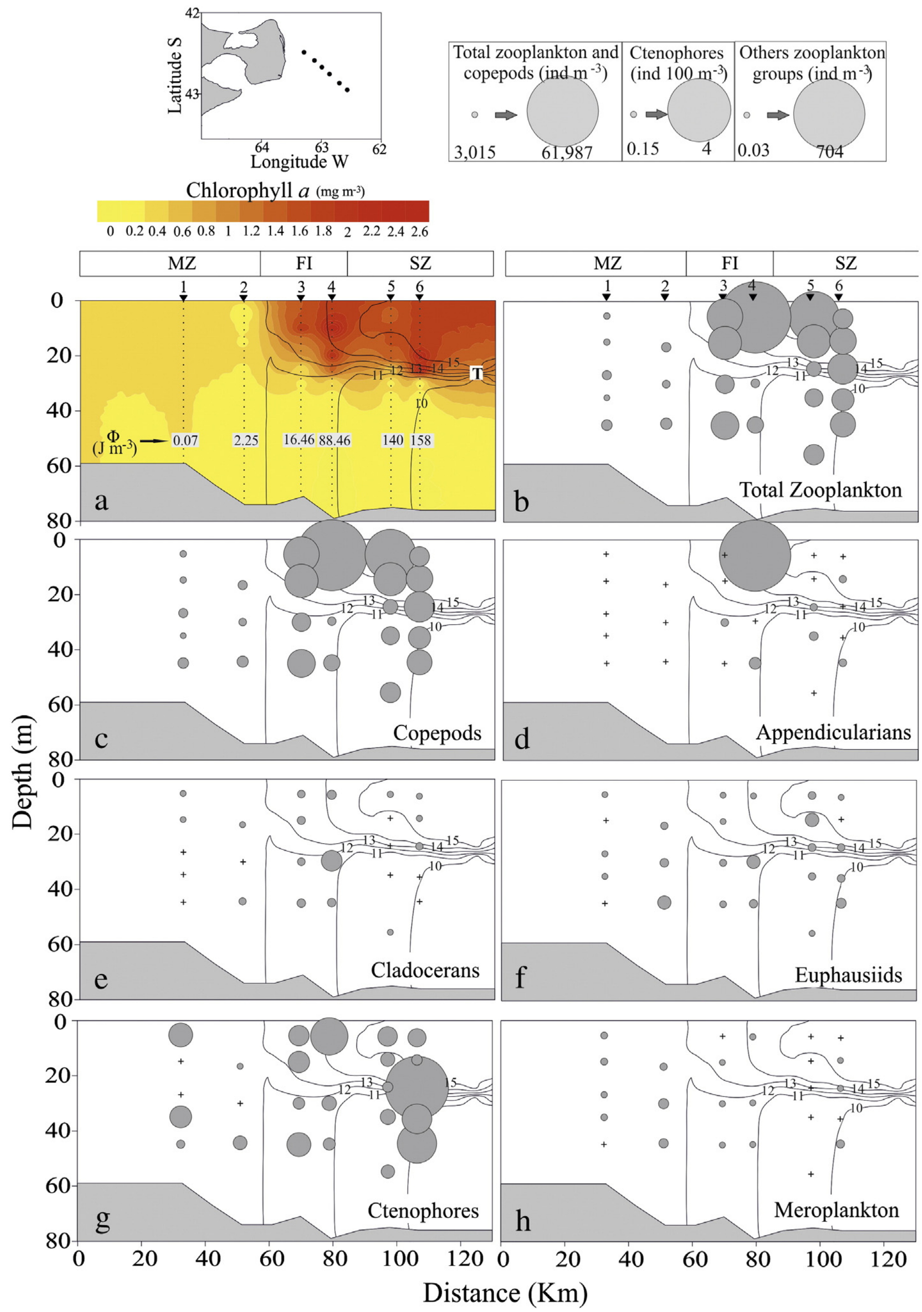


Fig. 2. Vertical section showing isotherms that define the three zones analyzed across the Península Valdés tidal front: mixed zone (MZ), frontal interface (FI) and stratified zone (SZ). (a) Chlorophyll *a* distributional pattern (color scale) and values of the stratification parameter (Φ) for each sampling station; T = thermocline. (b–h) Abundance pattern (circles; individuals per volume, ind m^{-3} or ind 100 m^{-3}) of each zooplankton group. The (+) symbol indicates zooplankton absence.

2001) was used to locate zones of maximum zooplankton species turnover between each pair of stations along a transect.

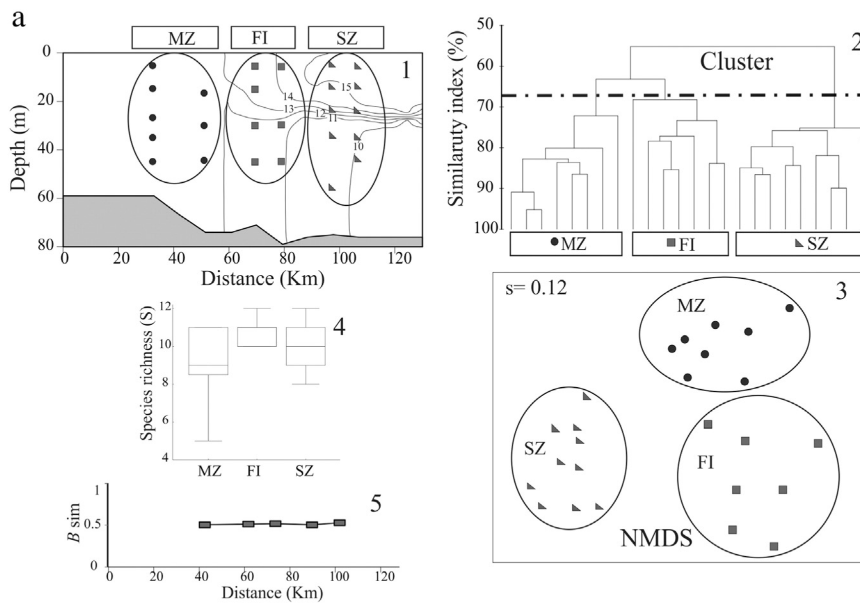
To assess the effect of the different zones of the frontal system on life histories, abundance data of copepods and euphausiids were used because they were the only zooplankton groups exhibiting early life stages and adult stage in the samples. In this study, benthic invertebrate larvae (meroplankton) were also included. The dominance of these groups in the different frontal zones was analyzed based on what is reported about the life history characteristics of the dominant species in the general literature, and our data on the physical setting of each zone.

Finally, all zooplankton groups and development stages were analyzed in relation to environmental data (depth, temperature, stratification parameter of the water column and Chl-*a* concentration) using Spearman's correlations (Zar, 1999).

3. Results

3.1. Environmental data

The typical zones of a tidal front (mixed, frontal interface and stratified) were identified in the study area (Fig. 2a). Temperature values showed a wide range (9.9 °C to 15.4 °C; mean = 12.7 °C ± 1.6) while salinity was uniform across the front (33.5–33.8; mean = 33.6 ± 0.08). The stratified zone showed a well-marked thermocline at 20–30 m depth, with temperatures of 14.7 °C–15.4 °C above the thermocline and of 9.9 °C–10.3 °C below it. The stratification parameter value (Φ) increased towards the stratified zone, indicating greater stability in the water column; Φ values in the range 16.4–88.5 characterized the frontal interface (Fig. 2a).



b

		MZ Ind/m^3	MZ %	FI Ind/m^3	FI %	SZ Ind/m^3	SZ %
	Copepods						
Cal	*Calanus australis*	13	<9	0	0	356	18
Cal	*Calanoides carinatus*	14	<9	25	<6	101	10
Cal	*Ctenocalanus vanus*	18	<9	156	17	551	17
Cal	*Paracalanus parvus*	265	22	446	13	347	7
Cal	*Drepanopus forcipatus*	404	15	1,058	14	5,899	72
Cal	*Centropages brachiatus*	0	0	58	<6	7	<4
Cal	*Clausocalanus brevipes*	2	<9	0	0	14	<4
Cycl	*Oithona helgolandica*	179	15	779	15	477	13
Cycl	*Oithona nana*	90	10	542	14	202	6
Harp	*Microsetella norvegica*	801	26	1,524	24	422	17
Harp	*Euterpina acutifrons*	1,170	28	438	15	3	<4
	Appendicularians						
	Oikopleura dioica	0	0	113	<6	8	<4
	Cladocerans						
	Evadne nordmanni	0	0	37	11	3	<4
	Podon leuckarti	0	0	1	<6	0	0
	P. intermedius	2	<9	8	<6	0	0
	Euphausiids						
	Euphausia lucens	0	0	0	0	0.16	<4
	Ctenophores						
	Mnemiopsis leidy	0.004	<4	0.009	<6	0.01	<4
	Hyperiid Amphipods						
	Themisto gaudichaudii	0	0	0	0	0.06	<4
	Chaetognaths						
	Sagitta sp.	0.04	<4	0	0	0.06	<4

Fig. 3. Analyses of zooplankton assemblages at the three different zones of the tidal front. (a) (1–3) Three zooplankton assemblages in coincidence with each zone of the frontal system. Round, square and triangular symbols represent the mixed zone (MZ), the frontal interface (FI) and the stratified zone (SZ) respectively. (1) Assemblages distribution. (2) Cluster (dotted line indicates the similarity percentage). (3) Non-metric multidimensional scaling (NMDS) where s = stress coefficient. (4) Box plot of species richness in each zone. (5) B diversity values (B sim) across the front. (b) SIMPER analysis: abundance contribution of each zooplankton species (%) in different zones and the species most responsible for the multivariate pattern in each zone (gray highlighted). Cal = calanoids; Cycl = cyclopoids; Harp = harpacticoids. Mean zooplankton abundance (ind m^{-3}).

Chl-*a* values varied between 0.2 and 2.6 mg m^{-3} (mean = 0.8 ± 0.7). The highest values were found in and above the thermocline of the frontal interface and the stratified zones (1.2–2.6 mg m^{-3}; mean = 1.8 ± 0.4). Lower values of Chl-*a* were registered along the entire water column of the mixed zone (0.2–0.5 mg m^{-3}; mean = 0.4 ± 0.08) and the lowest values were observed below the thermocline of the frontal interface and the stratified zones (0.2–0.3 mg m^{-3}; mean = 0.24 ± 0.04; Fig. 2a).

3.2. Zooplankton community

3.2.1. Abundance and specific composition

Zooplankton abundance was very high in the whole study area (3,015–61,987 in. m^{-3}; mean = 17,165 ± 13,779). Maximum abundances were observed above the thermocline of the frontal interface and the stratified zones, in coincidence with the highest Chl-*a* values (Fig. 2a,b). Copepods were the dominant group with an abundance percentage of >95%, mainly composed by Calanoid (*Calanus australis*, *Calanoides carinatus*, *Ctenocalanus vanus*, *Paracalanus parvus*, *Drepanopus forcipatus*, *Centropages brachiatus* and *Clausocalanus brevipes*), Cyclopoid (*Oithona helgolandica* and *O. nana*) and Harpacticoid groups (*Microsetella norvegica* and *Euterpina acutifrons*). The rest of the zooplanktonic groups were represented by appendicularians (*Oikopleura dioica*), cladocerans (*Evadne nordmanni*, *Podon leuckarti* and *P. intermedius*), euphausiids (*Euphausia lucens*), ctenophores (*Mnemiopsis leidyi*), meroplanktonic larvae (decapod, barnacles and bryozoans), hyperiid amphipods (*Themisto gaudichaudii*) and chaetognaths (*Sagitta* sp.).

Maximum values of copepods abundance (3,004–61,241 in. m^{-3}; mean = 17,088 ± 13,690) were found above the thermocline of the frontal interface and the stratified zones (Fig. 2c). Appendicularians (0–704 in. m^{-3}; mean = 35 ± 140) and cladocerans (0–159 in. m^{-3}; mean = 14 ± 32) were more abundant in the frontal interface, but the former with higher abundances above the thermocline (Fig. 2d,e). Euphausiids abundance (0–82 in. m^{-3}; mean = 19 ± 25) was similar across all the transect (Fig. 2f). Ctenophores abundance (0–0.03 in. m^{-3}; mean = 0.009 ± 0.008) increased towards the stratified zone, although their abundance was comparatively low (Fig. 2g). Meroplanktonic larvae (0–47 in. m^{-3}; mean = 7 ± 12) were more abundant in the mixed zone (Fig. 2h). Hyperiid amphipods (0–0.56 in. m^{-3}; mean = 0.02 ± 0.11) and chaetognaths (0–0.56 in. m^{-3}; mean = 0.03 ± 0.12) appeared in few stations and in low abundance, with hyperiid amphipods being more abundant below the thermocline of the stratified zone and chaetognaths not showing a clear distributional pattern.

Zooplankton assemblages at the Península Valdés tidal front were determined by the relative abundance of the groups, mainly copepod

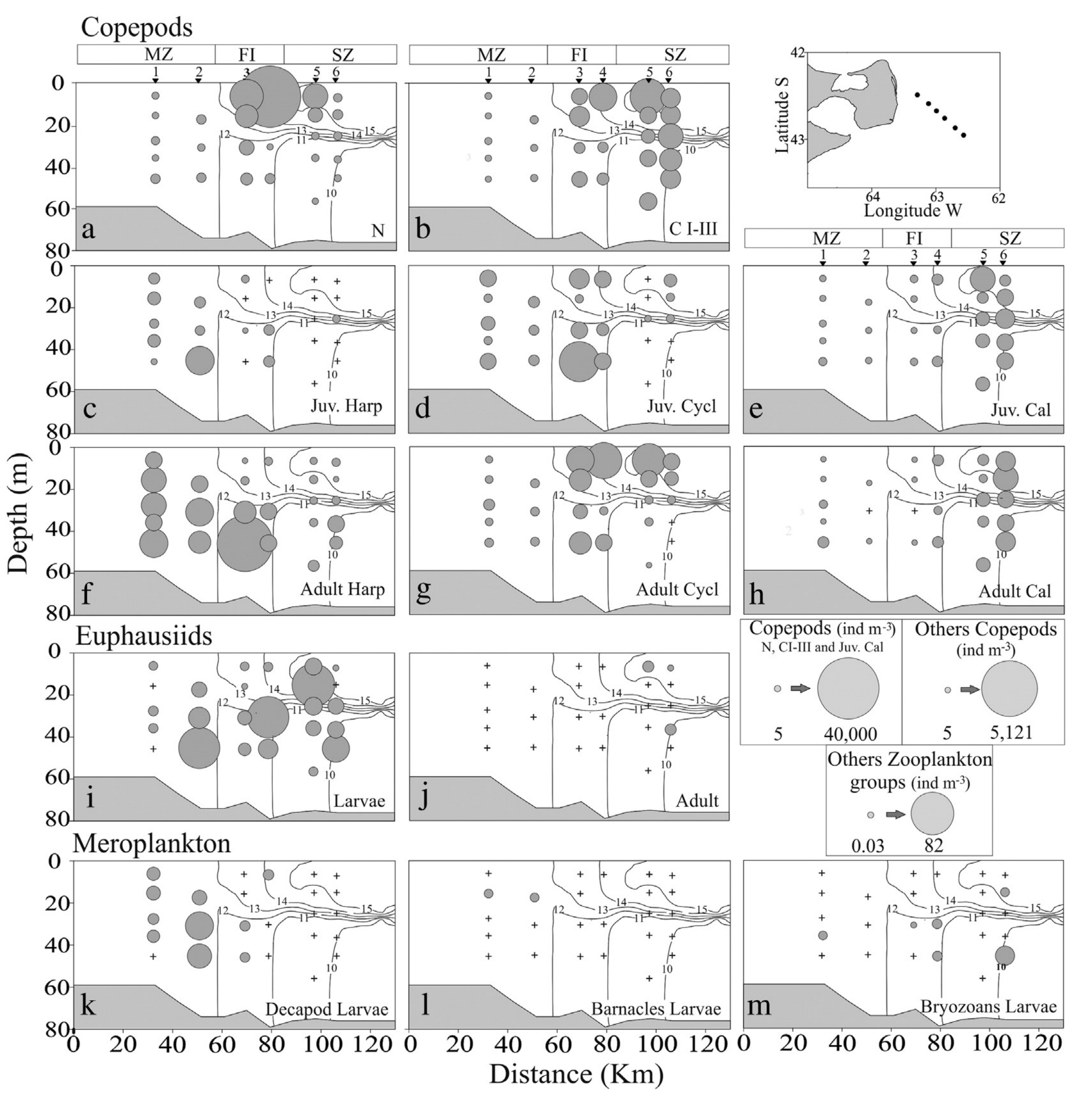


Fig. 4. Vertical section showing the abundance pattern (circles; individuals per volume, ind m^{-3}) of life stages of different zooplankton groups across the tidal front. Mixed zone (MZ), frontal interface (FI) and stratified zone (SZ). N = nauplii; CI–III = copepodites (I–III); Juv. = juvenile. The (+) symbol indicates zooplankton absence.

species, and not by the specific composition. Three different assemblages were identified across the transect in correspondence with each frontal zone analyzed (Fig. 3a, 1–3). High similarity percentages within each zone (81%–82%) and low dissimilarity percentages between zones (<37%) were observed. This is because the species that have contributed to the total abundance were present in the three zones, differing only in their relative abundance. The mixed zone was dominated by the harpacticoid copepod *E. acutifrons*; the frontal interface by cyclopoid copepods, the harpacticoid copepod *M. norvegica* and by the cladoceran *E. nordmanni*; and the stratified zone by calanoid copepods (Fig. 3b). Species richness did not differ between zones and beta diversity (Fig. 3a, 4–5) did not vary between stations because the same zooplankton species were present all along the transect. Thus, specific composition did not change along the transect.

3.2.2. Life histories

All development stages of copepods and euphausiids were found, being dominant the immature stages; however, the distributional patterns of immature and adults were different (Fig. 4a–j). Copepod nauplii were more abundant in the upper layer of the frontal interface (Fig. 4a) while copepodites (I–III) were more abundant toward the stratified zone (Fig. 4b). Juvenile (copepodites IV–V) and adult stages of different copepod groups were more abundant in different zones, in coincidence with the pattern observed in the assemblage analysis (see Fig. 3b). So, the harpacticoid group was more abundant towards the mixed zone (Fig. 4c,f), with *E. acutifrons* being the dominant species in the mixed zone whereas *M. norvegica* was dominant below the thermocline in the frontal interface (see Figs. 3b and 4f). The cyclopoid group was more abundant towards the frontal interface, with the adult stage being more abundant in the upper layer of the front and towards the stratified zone (Fig. 4d,g). The calanoid group was more abundant towards the stratified zone (Fig. 4e,h). In the euphausiids group, adults were only present in the stratified zone, with low abundances (Fig. 4i, j), although the larval stages were present and with high abundances in the three zones analyzed.

Regarding meroplankton, decapod and barnacle larvae, they were more abundant in the mixed zone, (Fig. 4k,l). On the other hand, bryozoans larvae were more abundant below the thermocline of the frontal interface and the stratified zones (Fig. 4m).

3.2.3. Influence of environmental factors on zooplankton distribution

The stratification level of the water column was the environmental factor that best correlated with most zooplankton groups and its development stages (Table 1). Moreover, this variable was the one that best explained the three zooplankton assemblages defined (Spearman's rank correlation, rs = 0.65, BIO-ENV analysis), which coincided with the three zones of the frontal system (see Fig. 3). Although the spatial pattern of some zooplankton groups were observed in relation to depth (above or below the thermocline; see Figs. 2 and 4), which could be related to different Chl-*a* and/or temperature values, only cyclopoid and harpacticoid adults were correlated with these variables (see Table 1). Therefore, differences in stratification level would be the main factor responsible for the zooplankton spatial pattern across the Valdés tidal front.

Table 1
Spearman's correlation coefficient between environmental factors and abundance of different zooplankton groups and its developmental stages across the Península Valdes tidal front. T = temperature; Φ = stratification parameter; Chl a = chlorophyll a; Juv. = juvenile; Harp = harpacticoids; Cycl = cyclopoids; Cal = calanoids.

Zooplankton group	Environmental factors			
	Depth (m)	T (°C)	Φ (J m^{-3})	Chl a (mg m^{-3})
Copepods				
Nauplii	−0.140	0.191	0.074	0.251
Copepodites I–III	−0.070	0.099	***0.718**	0.213
Juv. Harp	0.044	−0.037	***−0.771**	−0.215
Adult Harp	***0.553**	***−0.593**	***−0.602**	***−0.549**
Juv. Cycl	−0.097	0.072	***−0.569**	0.035
Adult Cycl	−0.272	***0.413**	0.087	*0.428
Juv. Cal	−0.007	0.099	***0.819**	0.191
Adult Cal	0.183	0.009	***0.705**	0.095
Appendicularians	0.107	−0.178	0.333	−0.096
Cladocerans	−0.179	0.129	−0.051	0.241
Euphausiids				
Larvae	0.022	−0.065	0.243	−0.143
Adults	−0.168	0.105	***0.440**	0.127
Ctenophores	−0.089	0.014	***0.409**	0.081
Chaetognaths	0.178	−0.154	−0.145	−0.194
Amphipod hyperiid	0.170	−0.312	0.287	−0.298
Meroplankton				
Decapod larvae	0.099	−0.224	***−0.702**	−0.376
Bernacle larvae	−0.162	−0.013	−0.328	−0.056
Bryozoan larvae	−0.174	0.305	0.318	0.348

* Significant correlation marked correlations in bold are significant at $p < 0.05$.

4. Discussion

Tidal fronts, such as that occurring in Península Valdés surroundings, represent a good scenario to study the role of certain environmental variables in structuring zooplankton communities. Given that the front occurs within the same water mass, species composition did not vary across the different zones of the frontal system but relative abundance of zooplankton groups led to differences in assemblages' structure among zones. We showed that the stratification level of the water column had an important relationship with the zooplankton distribution pattern. Within the copepods group, which represented up to 95% of the total zooplankton abundance, harpacticoids numerically dominated the mixed zone, cyclopoids the frontal interface and calanoids the stratified zone. However, all copepods groups seem to share the frontal interface as a breeding area, as its nauplii maximum abundances were observed there.

As occur in many tidal fronts (e.g., Liu et al., 2003; Perry et al., 1993; Schultes et al., 2013), the lowest zooplankton abundance and Chl-*a* values were found in the mixed zone. Although this zone is characterized by the presence of suspension detritus (Carreto et al., 1986; Li et al., 2007) and high nutrient concentrations, which are resuspended from the bottom to the surface by the effect of the strong tidal mixing (Mann and Lazier, 2006), the success of many planktonic organisms would be difficult because of the mechanical stress due to turbulence (e.g., Carreto et al., 1986; Liu et al., 2003; Mianzan et al., 2010; Munk, 1993; Sabatini and Martos, 2002). Despite the low phytoplankton abundance registered in this area, it is known that the tidal mixing favors diatom development while dinoflagellates develop better in less turbulent waters (Carreto et al., 1986; Franks, 1992; Kiϕrboe et al., 1990). Although diatoms are considered a high-quality food for many zooplankton groups (Mauchline, 1998; Youssara and Gaudy, 2001), in the mixed zone, they are diluted along most of the water column with the consequence that their concentration is not enough to support large zooplankton abundances. Moreover, in highly turbulent environments, zooplankton would not only be limited by food availability but also by its swimming ability, affected by the strong mixing effect that in turn diminish predator–prey encounters (e.g., Prairie et al., 2012; Saiz and Kiϕrboe, 1995; Zervoudaki et al., 2006).

Despite turbulent conditions, our results show that adults and juveniles of harpacticoid copepods seem to do better shoreward, in the mixed zone and below the thermocline of the frontal interface. Harpacticoid copepods reached their highest abundances at the mixed zone, being the dominant zooplanktonic group. Those harpacticoids found in the present study are of coastal habits (Viñas and Gaudy, 1996); their success in the mixed zone could be favored for some characteristics of their life strategies; females of those species carry the eggs in sacks instead of releasing them freely in the water (Turner, 2004) diminishing their dispersion in this strongly turbulent environment. Furthermore, these copepods do not depend on phytoplankton for survival because they feed mainly on small particles associated with the microplankton community (Uye et al., 2002), which usually grows on suspended detritus (Kepkay et al., 1990; Li et al., 2007) that characterizes this zone (Carreto et al., 1986). Meroplanktonic larvae, mainly of decapod and barnacles, were also observed in the mixed zone, although bryozoan larvae were more abundant below the thermocline of the stratified zone. Meroplanktonic larvae are usually concentrated and retained at fronts (McEdward, 1995; Zervoudaki et al., 2006), but their patterns could also be affected by the distribution of the benthic populations from where they were released. There is not enough knowledge on the benthos of the region as to compare with our results on benthic larvae.

The highest abundances of copepod nauplii were observed at the surface of the frontal interface of the Península Valdés tidal system. Although the specific identification of nauplii stages cannot be reached in the present work, we might suggest that this area could be an important breeding zone for all copepod species that inhabit this frontal system. As this frontal interface is a convergence area (Mann and Lazier, 2006), copepod nauplii could be transported from other zones of the system and concentrate at the frontal interface because of physical forcing. Furthermore, as this zone is characterized by a high and constant nutrient supply, which are provided from the mixed zone, it is an optimal area for phytoplankton production (e.g., Mann and Lazier, 2006; Yamamoto et al., 2000), which is in turn food for copepods. The highest copepod eggs production rates and egg concentrations occurred at the frontal interface (Liu et al., 2003; Sabatini and Martos, 2002; Uye et al., 1992; Viñas and Ramírez, 1996), indicating that the front is also a favorable area for increases of secondary production. Copepod nauplii, unlike copepodites and adults, have limited energy reservoirs and inefficient feeding appendages, and given that its survival depends on high concentrations of phytoplankton (Uye et al., 1992 and references therein), they could achieve high survival rates in the frontal interface where the highest Chl-*a* values are registered. Although in this study we could not detect a correlation between copepod nauplii and Chl-*a*, a positive association has been previously reported (e.g., Liu et al., 2003; Sabatini and Martos, 2002; Viñas and Ramírez, 1996). The frontal interface is also characterized by the dominance of cyclopoid copepods, whose juvenile and adult abundances have a tendency to increase towards this zone. Other zooplankton groups with high abundances in the frontal interface were appendicularians and cladocerans. All the groups that dominated in abundance at the frontal interface feed on phytoplankton (although only cyclopoids were correlated with Chl-*a*) and they also take advantage of microplankton as a food source (Capitanio and Esnal, 1998; Caron et al., 1995; Hopcroft et al., 1998; Morales et al., 1991; Ramirez, 1981; Turner, 2004; Viñas et al., 2007), which is also more abundant at fronts (e.g., Kepkay et al., 1990; Li et al., 2007; Santoferrara and Alder, 2009). Thus, convergence processes that occur in the frontal interface could benefit the survival of these zooplankton groups, given the high concentration and varied availability of food there.

The stratified zone showed the highest abundances of copepodites (I–III), juveniles and adults of calanoid copepods. These groups could succeed better in this zone, where high Chl-*a* values were detected above thermocline, given that they are preferably herbivores in eutrophic environments (e.g., Mauchline, 1998 and references therein). Moreover, their ability to search for food, encounter mates and predator detection is favored in areas with high water column stability (McManus et al., 2013; Zervoudaki et al., 2006), as occurred at the stratified zone of the tidal system. Ctenophores and amphipods hyperiid, considered as main copepods predators (Pakhomov and Perissinotto, 1996; Waggett and Costello, 1999), were found in the stratified zone but in very low abundances at the study time. However, it is common to find high ctenophore densities in this zone (Mianzan et al., 2010) as well as other zooplankton predators such as fish larvae (e.g., Pájaro et al., 2005; Viñas and Ramírez, 1996; Viñas and Santos, 2000). These organisms could have a negative impact on copepods' abundance. Moreover, very low euphausiid adults' abundances were found in the stratified zone, this could be explained by the preference of this group for more oceanic habitats (Ramírez, 1971). However, their larvae were highly abundant across the tidal front, which suggests the use of the tidal frontal system as a reproduction and/or nursery area for this group.

Despite all zooplankton species, mainly copepods, would perform better in different zones of the Península Valdés tidal front, the frontal interface appears to be an important breeding area for all copepod species. Nauplii of all copepod groups could be transported to the frontal interface and there retained by physical processes (e.g., convergence), but it is not clear how juveniles and adults of the different copepods species are then transported from the interface zone to the other zones, where better conditions for their development seem to exist. It has been shown that small hake larvae are retained in the stratified zone of a tidal front through a vertical migratory behavior, taking advantage of the existence of a two-layer water flow that would allow horizontal transport (Álvarez-Colombo et al., 2011). This behavior has been observed in several zooplankton organisms that are retained in highly productive systems such as fronts (Andersen et al., 2004; Morgan et al., 1997; Naylor, 2010; Perry et al., 1993; Schmitt et al., 2011). In that sense, it could be expected that a similar behavior of copepods would be the main mechanism responsible for the movement of this group to the different zones of the tidal frontal system, allowing them to explore zones profitable for its development.

In conclusion, abundance, distributional patterns and life histories of zooplankton appear to be strongly influenced by differences in the stratification level of the water column across the Península Valdés tidal front, although no differences were detected in the specific composition of the assemblages. The formation of the tidal front controls the food supply in the different zones, offering different physical and feeding scenarios for zooplankton groups, which respond differently to the environmental settings varying from a highly turbulent to a stratified and stable condition. The different zooplankton groups prevailing in different parts of the tidal frontal system could also be related to physical processes such as transport and retention and also to their life history strategies. Furthermore, the existence of zooplankton vertical migrations coupled to a two-layer water flow could be playing an important role in the distribution of different organisms.

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