

Comparison of mesozooplankton assemblages across quasi-synoptic oceanographic features on the north-western Iberian shelf break

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Abstract The mesozooplankton community at the north-western Iberian shelf break was studied among adjacent oceanographic regimes (including upwelling, stratification and anticyclonic eddies) during 17 days in autumn 2009. Zooplankton sampling locations were determined in situ, after identifying the oceanographic regimes from CTD profiles performed over the continental shelf and upper slope. Zooplankton samples were sorted indentifying taxonomically the main zooplankton groups, from phylum to subclass. Copepods were the most abundant group (ind m⁻³) in all stations, followed by appendicularians, doliolids and siphonophores. The mesozooplankton community was significantly different amongst oceanographic conditions. Meroplankton abundance was higher in upwelling stations; particularly lamellibranchia, polychaeta and bryozoan larvae abundance, and decreased from

early to late upwelling conditions. Medusae and chaetognata were found exclusively under the latter oceanographic regime. However, dissimilarity between the oceanographic conditions was mostly based on the varying contribution of the four most common groups.

Keywords Mesozooplankton · Community structure · Meroplankton–holoplankton rate · Mesoscale oceanography · Upwelling

Introduction

The pelagic system over the shelf break area is a complex environment acting as a transition zone between the productive shelf and the oligotrophic waters of the open ocean (Huthnance, 1995). Interactions between these two systems are particularly relevant in coastal margins with narrow shelves and wind-driven upwelling (Morales et al., 2010) such as the north-western Iberian shelf break during the summer–autumn transition (Gil, 2008). In this area, the trade winds blowing southwards along the Portuguese coast during summer favour upwelling on the western Iberian slope, while in winter, the area is characterised by a poleward slope current (Gil, 2008). Our study was carried out in the transition period between these two situations, when mesoscale features dominate the regional oceanography. The

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biological composition of mesoscale structures is originally determined by the source water mass; however, its evolution (isolation of eddies, warming and mixing for upwelled waters) affects community composition by modifying species abundance and biomass (Strzelecki et al., 2007). Although it is widely acknowledged that mesoscale features promote ocean production due to the existence of deep water upwelling and the formation of oceanographic discontinuities such as fronts and filaments, the evolution of communities from recently upwelled waters to stratification and anticyclonic eddy conditions has not drawn as much scientific attention. Several studies have focused on the mesozooplankton community at the species level in our study area covering multiple aspects from its distribution, including spatial and temporal trends (Valdes et al., 1990; Gonzalez-Quirós et al., 2003; Blanco-Bercial et al., 2006; Valdés et al., 2007; Bode et al., 2009; Sobrinho-Gonçalves et al., 2013). We propose, however, a different approach aimed at discerning differences in mesozooplankton community structure among singular oceanographic structures. Using quasi-synoptic sampling in a set of adjacent oceanographic conditions, we test the hypothesis that the evolution of upwelled waters is closely followed by the zooplankton community abundance and structure.

Materials and methods

Sampling was performed during daylight between 23rd September and 10th October 2009 along the north-western continental shelf and shelf break of the Iberian Peninsula on board the International Bottom Trawl Survey 'DEMERSALES'. In this oceanographic survey, the sampling locations follow a randomly stratified design covering the continental shelf and shelf break between 70 and 500 m depth with some special sampling points over 500 m depth (for details see Sanchez & Serrano, 2003). In each sampling station, we also obtained a CTD profile (using a CTD SBE-25) for characterising the water column. We examined the CTD data in situ to identify typical profiles of upwelling, eddy or stratification structures. Stratification conditions were identified by the strong temperature gradient in the upper 50–100 m

of the water column (Fig. 1a), while anticyclonic eddies displayed high and constant temperature up to the bottom of the eddy, when a sharp decrease in temperature occurred (Fig. 1c). In contrast, upwelling areas showed low temperatures at the sea surface and no temperature gradient in the upper water column (Fig. 1b). Early, medium and late upwelling could be distinguished by the distinct temperature gradient between the sea surface and 50 m depth; thus, early upwelling showed low surface temperatures and no gradient in depth (Fig. 1b), while medium and late upwelling the gradient became increasingly noticeable. Additionally, comparing the profiles to the surrounding temperature fields at 10 and 50 m depth (Figs. 1, 2a, b), we were able to corroborate the initial assessment carried out on board. Satellite images from the NOAA MODIS sensor (<http://oceancolor.gsfc.nasa.gov/>) focused on the study area were visually analysed to assess if the hydrography measures could be appreciated on the chlorophyll surface field, and the image from 28th September with low cloudiness is used for results and discussion (Fig. 3).

In the nine selected sampling locations, spanning along the shelf break at depths ranging from 200 to 600 m depth, mesozooplankton was sampled with a 40-cm-diameter bongo net with 200 μ m mesh size in double-oblique hauls up to 100 m. Samples were stored in 4% buffered formalin immediately after collection. In the laboratory, samples were identified and classified into the main taxonomic groups, including several holoplankton and meroplankton categories. Abundance data were log-transformed prior to the statistical analysis, in order to down-weight the contribution of both very dominant and rare groups. Non-metric multidimensional scaling (NMDS analysis) was performed on the log-transformed data set to investigate the assemblage similarities amongst sampling stations and oceanographic conditions, applying the Bray-Curtis distance metric. To assess differences in the assemblages amongst oceanographic conditions an ANOSIM analysis based on the abundance data matrix was performed. Additionally, we used SIMPER analysis to evidence the main taxonomic groups which characterised the mesozooplankton community amongst oceanographic regimes and assess the dissimilarity between groups based on their zooplankton assemblage.

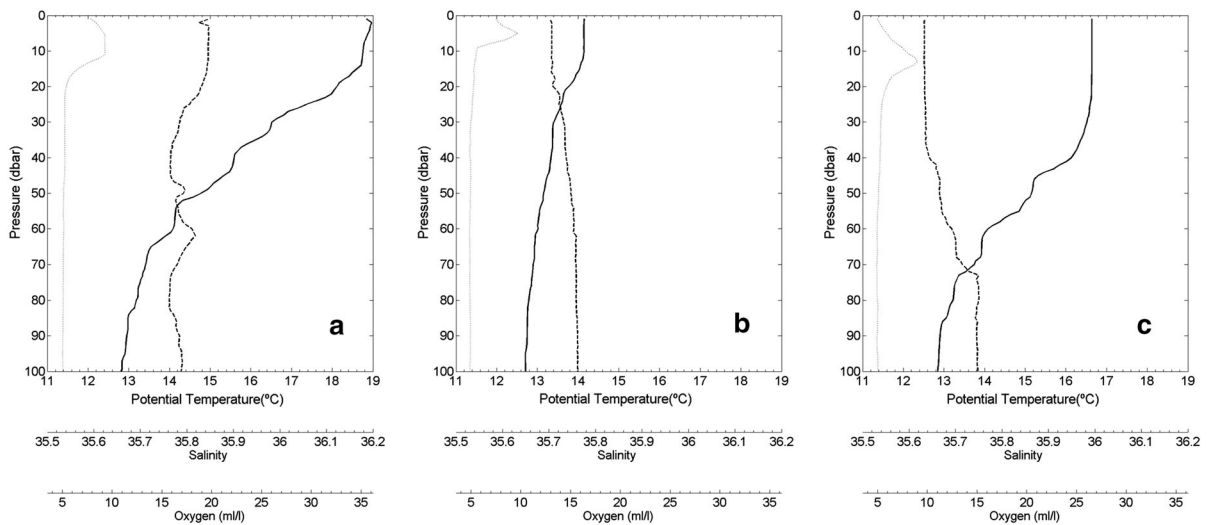


Fig. 1 Typical profile of **a** water column stratification, **b** recent upwelling event and **c** anticyclonic eddy, featuring temperature (black solid line), salinity (black dashed line) and dissolved oxygen concentration (grey pointed line)

Results

We sampled nine stations (Fig. 2) whose CTD profiles unambiguously corresponded to early (St. 3 and 4), medium (St. 2 and 5) or late upwelling (St. 6 and 7), eddy (St. 8 and 9) and stratification (St. 1). Temperature was the variable better characterising these structures (Fig. 2a, b) aided by dissolved oxygen (Fig. 2e, f), since the peak of dissolved oxygen was shallower in upwelling stations (Fig. 1). The salinity pattern did not greatly contribute to identifying the oceanographic regimes; salinity was higher than expected in the southern part of the study area which is otherwise commonly affected by the discharge of freshwater from neighbouring rivers. Salinity variations were smaller than 0.5‰. The geographical distribution of surface chlorophyll in the area was patchy, mirroring the mesoscale structuring of the regional oceanography (Fig. 3). High production possibly associated with upwelling conditions is easily identifiable in several spots along the coast, as well as a low productivity area which can be identified in the southwest of our study region (Fig. 3), where we found stratification conditions. Nevertheless, the eddies we identified from the CTD profiles have apparently no parallel in the chlorophyll image. Mesozooplankton abundance (ind m^{-3}) was higher in the north-western edge of the study site, during medium and late upwelling conditions (Table 1;

Fig. 4). The stratification regime had the lowest mesozooplankton abundance (Table 1; Fig. 4), followed by eddy conditions, early upwelling, late upwelling and medium upwelling (Table 1). Regarding the proportion of meroplankton and holoplankton in the different regimes, upwelling conditions showed the highest proportion of meroplankton, decreasing from early upwelling (12%) to late upwelling (3%) (Table 1). Copepods were the most abundant group throughout the study area, followed by doliolids, appendicularians and siphonophores (Fig. 5).

For subsequent analyses, we eliminated the four zooplankton taxa which were present in only one station; these were pteropods (eddy conditions, abundance 0.34 ind m^{-3}), amphipods (stratification, abundance 0.03 ind m^{-3}), adult euphausiids (early upwelling, abundance 0.23 ind m^{-3}) and annelid larvae (late upwelling, abundance 0.78 ind m^{-3}). The NMDS results clearly differentiated the four oceanographic regimes considered based on the mesozooplankton assemblage (Fig. 5). Indeed, the analysis of similarities (ANOSIM) on the communities' structure identified these domains as statistically different ($P < 0.05$, 999 permutations). The associative pattern displayed in Fig. 5 clearly relates larval stages (meroplankton) with the upwelling conditions, as well as other zooplankton groups as medusae and chaetognaths, only found under upwelling conditions (Figs. 5, 6). Doliolids, despite their widespread

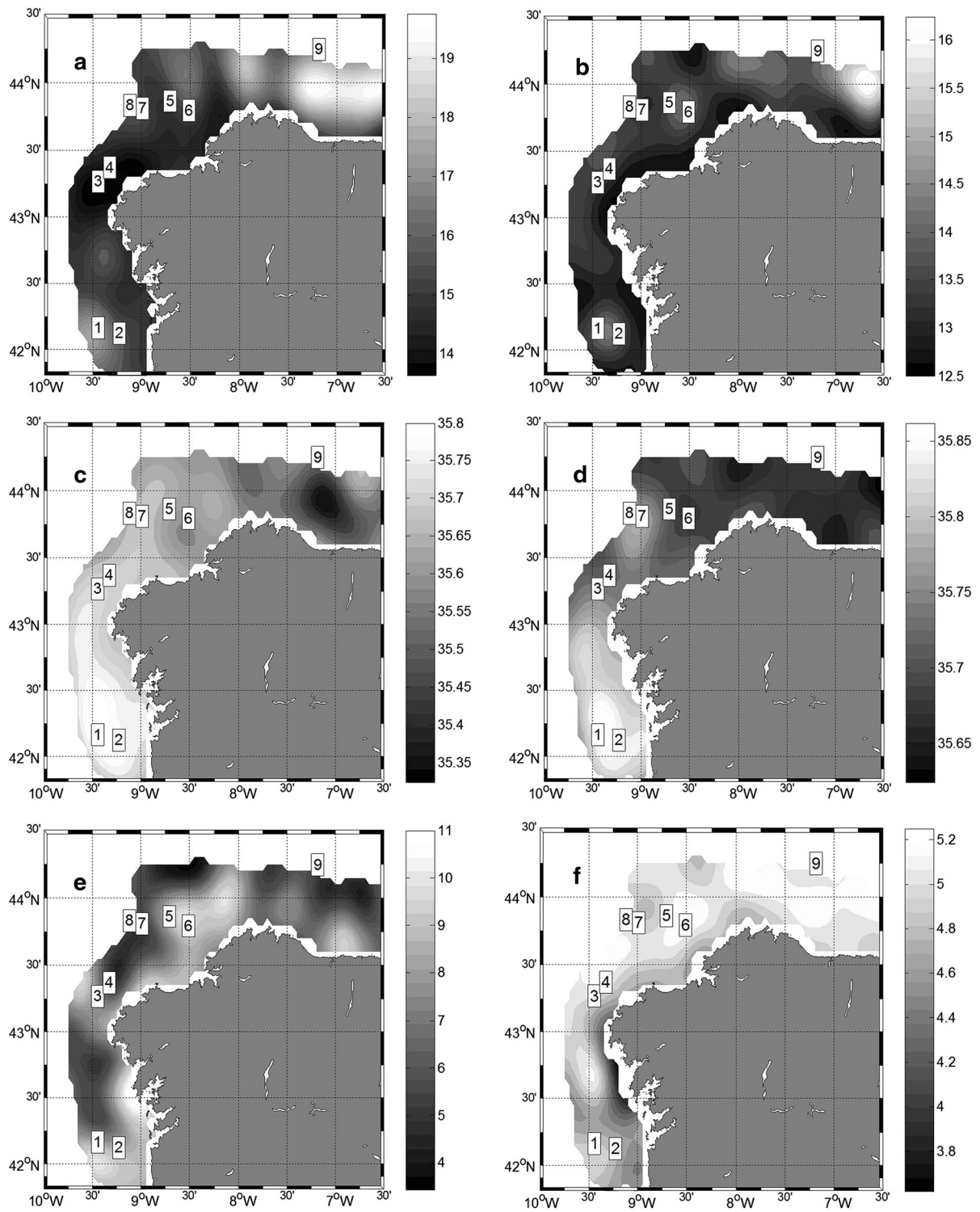


Fig. 2 In situ temperature field at **a** 10 and **b** 50 m, salinity field at **c** 10 m depth and **d** 50 m depth and dissolved oxygen at **e** 10 m depth and **f** 50 m depth. Numbers correspond to the sampling stations

presence, showed relatively higher abundances in upwelling conditions (Figs. 5, 6). Early upwelling stations differed from other upwelling phases by their lower proportion of appendicularians and relative high lamellibranchs larvae abundance. However, no group could be directly associated with stratification or anticyclonic eddy conditions (Fig. 5). Ostracods, foraminifera and appendicularians which apparently relate to anticyclonic eddies (Fig. 6) were frequently found under the other oceanographic regimes considered (Fig. 5).

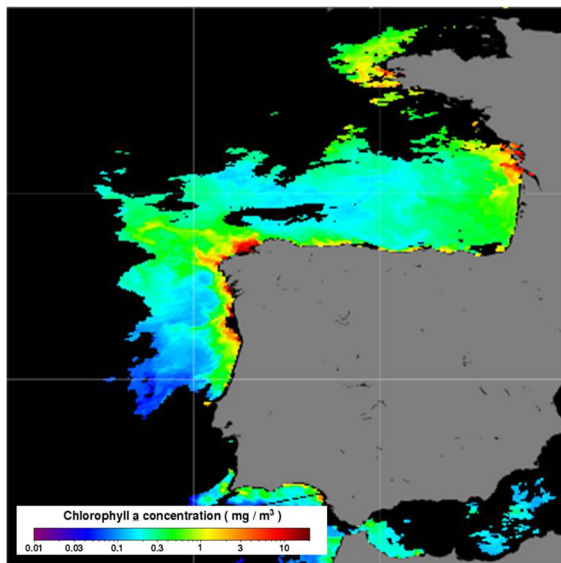


Fig. 3 Surface chlorophyll measured on 28th September 2009 from the NOAA MODIS sensor (<http://oceancolor.gsfc.nasa.gov/>)

Simper analysis allowed recognising the mesozooplankton groups paramount in discerning amongst oceanographic regimes (Table 2). Average dissimilarity was lower between the different stages of upwelling (<40%). The stratification was unlike other oceanographic regimes; it displayed high average dissimilarities with all others (>50%), although these

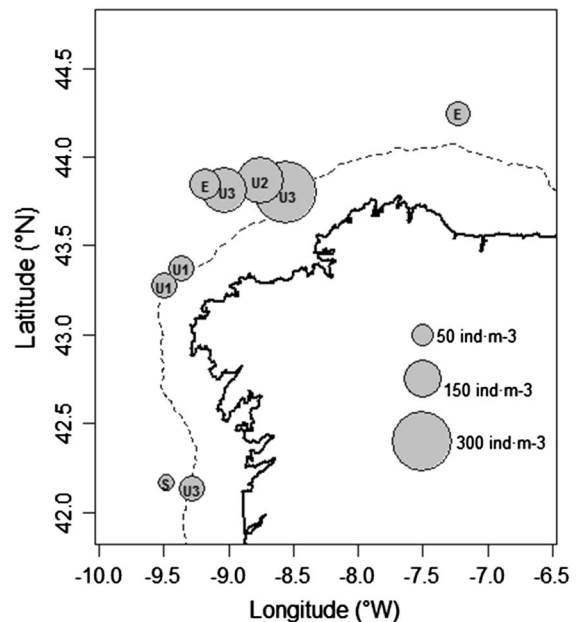
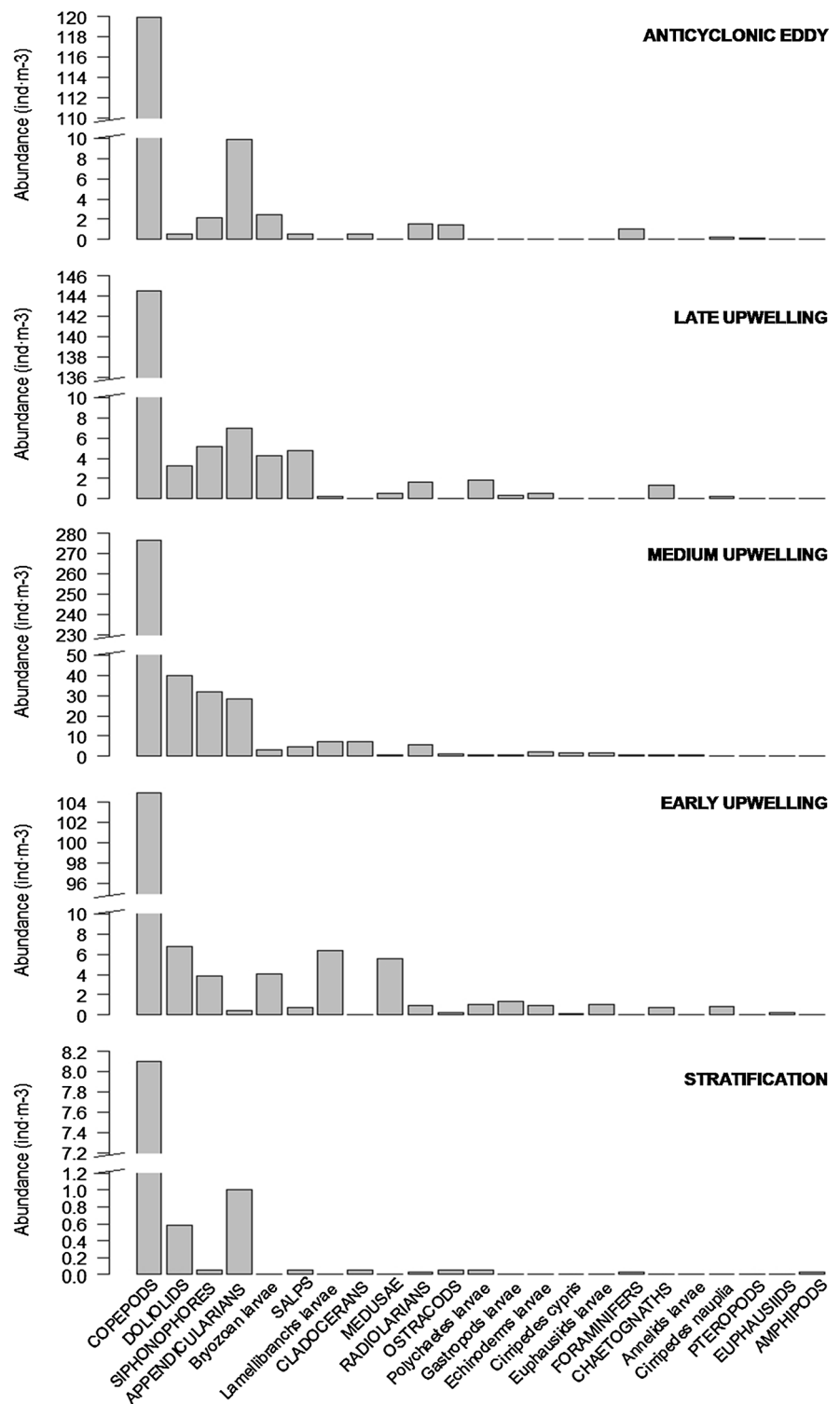


Fig. 4 a Map area showing the sampling locations and the oceanographic condition at each of them (*S* stratification, *U1* early upwelling, *U2* medium upwelling, *U3* late upwelling, *E* anticyclonic eddy). The radiuses of the pies are proportional to the total abundance (N/m^3) in the sample, with minimum being $10.02 \text{ ind } m^{-3}$ and maximum $311.04 \text{ ind } m^{-3}$. The dotted line indicates the 200-m isobath

Table 1 Summary of mesozooplankton (holoplankton and meroplankton) average abundance values across the different oceanographic regimes considered

Oceanographic regime	Abundance ($\text{ind } m^{-3} \pm \text{SE}$)		
	Holoplankton	Meroplankton	Total
Upwelling	155.21 ± 37.44	9.64 ± 2.62	164.84 ± 38.54
Early upwelling	82.55 ± 0.96	11.97 ± 4.46	94.52 ± 3.50
Medium upwelling	199.69	13.32	213.01
Late upwelling	188.82 ± 65.99	6.85 ± 4.45	195.67 ± 70.09
Stratification	9.97	0.05	10.02
Anticyclonic eddy	85.59 ± 18.74	1.43 ± 1.26	87.01 ± 20.00
Total	123.60 ± 29.94	6.75 ± 2.24	130.35 ± 31.34

Fig. 5 Average community composition in each of the oceanographic conditions considered, i.e. stratification, early upwelling, medium upwelling, late upwelling and anticyclonic eddy



results should be taken cautiously due to the presence of only one sampling point under stratification. The highest contribution to dissimilarity amongst

oceanographic regimes was based on the proportion of the most common taxa, i.e. copepods, appendicularians, doliolids and siphonophores. The results of

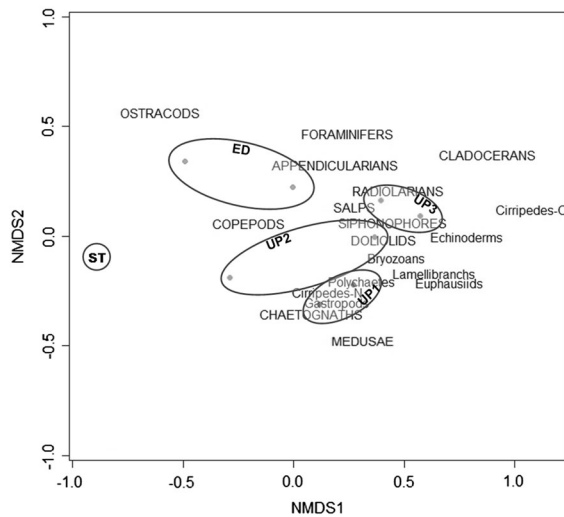


Fig. 6 Results from the NMDS analysis on the log-transformed mesozooplankton abundance data. Capital letters are used for adults and lower case for larvae. ‘-N’ and ‘-C’ stand for nauplius and cypris larvae of cirripedes, respectively. Ellipses encircling the sampling points characterised by different oceanographic conditions are drawn for easing the interpretation

SIMPER analysis agreed with the NMDS analysis in identifying lamellichanchia, bryozoan and polychaeta larvae as the main meroplankton groups, which discriminated upwelling stations from eddy and stratification conditions (Table 2; Fig. 6).

Discussion

Mesoscale structures such as eddies, fronts and filaments are commonly associated to coastal margins with narrow shelves and wind-driven upwelling (Barth & Wheeler, 2005). The coexistences of these mesoscale structures with upwelling and stratification areas configure a highly heterogeneous environment originating a variety of habitats in the pelagic realm (Keister et al., 2009), which are widely recognised as a major source of variability for plankton distribution and population dynamics. In situ identification of these oceanographic domains through T–S profiles is proven to be a reliable method for identifying these oceanographic structures, which typically last 10–30 days (Cury et al., 2008) and are difficult tracked by other means. In our study area, three of these features are commonly present after the strong summer upwelling: (i) a cold water layer on the shelf originated by the

upwelling—considered a mesoscale process presenting local peculiarities (Gil, 2008), (ii) a warm and stratified water column off the shelf break, and (iii) an intermediate zone or front area characterised by anticyclonic warm-core eddies over the shelf break (Gil, 2003). Due to advection of productive slope water, cold-core eddies and upwelling areas have generally higher productivity than warm-core eddies, where nutrients get quickly depleted. However, the origin of the water masses might have a crucial importance in determining the productivity inside the eddy (Strzelecki et al., 2007). We could not identify low productivity in association with the anticyclonic eddies we sampled, but since these structures are short lived and the image corresponds to one snapshot, the eddies might not have developed by the time the satellite image was captured.

We found the highest abundance values in our study area on the upwelling stations, increasing as the upwelling aged. Upwelling areas favouring primary production allow the development of grazing organisms within few days, particularly those with faster development rates as salps and doliolids (Andersen et al., 1998; Deibel & Paffenhoefer, 2009). Studies on cyclonic eddies of the Sargasso Sea (Goldthwait & Steinberg, 2008) and the vicinity of the Canary Islands (Hernández-Leon et al., 2001) show that the initial higher phytoplankton productivity in the centre might drift to the periphery deepening the chlorophyll maximum and favouring accumulation of large motile zooplankton, such as euphausiids, in the outer boundary area. These large eddies, which can persist for several months (McGillicuddy et al., 2007), cover the generation time of copepods and euphausiids being able to alter their population dynamics (Huntley et al., 2000). Although the anticyclonic eddies which commonly get formed in our study area have shorter life spans, these structures also favour zooplankton cohesiveness linked to frontal zones (Molinero et al., under review; Molinero & Nival, 2004). We did not find, however, any particular mesozooplankton taxa that could be unambiguously associated to only this oceanographic regime. Regarding the mesozooplankton groups distribution, we found larger amounts of meroplankton in upwelling stations, particularly lamellibranchia, bryozoan and polychaeta larvae, which helped characterising this oceanographic regime. Blanco-Bercial et al. (2006) linked meroplankton to very shallow habitats, but we found that they also

Table 2 Average dissimilarity between groups (DI) as resulting from the Simper analysis specifying the mesozooplankton groups with a higher contribution (given as a percentage) to intergroup dissimilarity

	Early upwelling	Medium upwelling	Late Upwelling	Stratification
Medium upwelling	DI = 33.15			
	Appendicularians	19.40%		
	Salps	13.74%		
	Lamellibranchs larvae	10.35%		
	Bryozoan larvae	7.35%		
Late upwelling	DI = 38.33	DI = 33.61		
	Appendicularians	Bryozoan larvae	12.73%	
	Doliolids	Appendicularians	10.57%	
	Medusae	Doliolids	9.05%	
	Lamellibranchs larvae	Salps	8.67%	
	Siphonophores	Siphonophores	7.73%	
	Radiolarians	Polychaetes larvae	7.41%	
Stratification	DI = 68.06	DI = 71.53	DI = 67.44	
	Copepods	Copepods	Copepods	18.01%
	Lamellibranchs larvae	Bryozoan larvae	Siphonophores	15.38%
	Medusae	Salps	Appendicularians	11.05%
	Bryozoan larvae	Appendicularians	Doliolids	10.88%
	Doliolids			
Eddy	DI = 49.03	DI = 45.86	DI = 46.58	DI = 52.00
	Lamellibranchs larvae	Salps	Doliolids	Copepods
	Doliolids	Bryozoan larvae	Siphonophores	29.66%
	Appendicularians	Siphonophores	Appendicularians	13.61%
	Medusae	Doliolids	Radiolarians	Ostracods
	Bryozoan larvae	Polychaetes larvae	Lamellibranchs larvae	10.83%
				5.75%

constitute an important part of the community over the shelf break. It has been traditionally thought that larval dispersion might be importantly affected by cross-shelf transport. Strong upwelling events are thought to sweep offshore larval stages with reduced swimming abilities which are thus ‘wasted’, prevented from settlement in their native environment. Several results seem to support this hypothesis, as the study of Garland et al. (2002) on crab zoea, bivalve, gastropoda and polychaeta larvae. The distribution found by these authors was best explained by cross-shelf transport of single or multitaxa larval patches. However, this traditional view on meroplankton dispersion has been recently challenged as meroplankton is able to adjust their position on the shelf by performing active vertical migrations. Shanks & Brink (2005) demonstrated that slow-swimming bivalve larvae remained within 5 km from the coast notwithstanding upwelling nor downwelling events, where current speeds reached velocities two or three order of magnitude higher than that of the larvae swimming speed. By changing their preferred depth and swimming up- or down-wards in circadian cycles or influenced by pressure fields, larvae would be able to return to the original site taking advantage of cross-shelf currents (Shanks & Shearman, 2009; Yoshinaga et al., 2010), as vertical current speeds are lower than horizontal ones. These two views on larval dispersion in upwelling areas are, nevertheless, not exclusive. Even if meroplankton has the ability to maintain its spatial distribution by adjusting its preferred depth, a certain loss might occur from the high-density nucleus.

Other organisms, as gelatinous zooplankton, are also able to perform pronounced vertical migrations (Andersen et al., 1992; Riandey et al., 2005); however, their lack of complex physiognomy and weak swimming abilities can distance them from the most productive area, following divergent cell currents (Molinero et al., under review). Filter feeders such as appendicularians, with high success in areas dominated by small phytoplankton (Lopez-Urrutia et al., 2003) predominate in anticyclonic gyres and generally in areas of low productiveness, thus are also predicted to achieve their highest densities within warm-core eddies, as found in this study, Euphausiids larvae, which had been associated to anticyclonic eddies in the Ligurian front (Pinca & Dallot, 1995), were found exclusively in upwelling stations in our study area.

The high zooplankton abundances found in upwelling stations probably respond to the increased nutrient load in these areas, breaking the stratification during the summer–autumn. These upwelling events are strongly associated with the development of anticyclonic eddies (Gil, 1995) and thus to the support of juvenile demersal fish recruitment patches in the area (Sanchez & Gil, 2000). However, the prevalence of upwelling events throughout the summer and autumn seems to be declining both in duration and intensity contributing to surface water warming on the continental shelf (Llope et al., 2006; Bode et al., 2009), contrarily to the predicted intensification of wind-driven upwelling in eastern boundary currents (Bakun et al., 2010). These results point out the need for multidisciplinary research to study the relation between declining upwelling events and anticyclonic eddies, the zooplankton abundance and community structure and its effect on the recruitment of demersal fish.

Our study draws general conclusions on the relative abundances of several zooplankton taxa over the shelf-slope break across a set of mesoscale oceanographic conditions based on synchronous CTD profiles for capturing mesoscale variability and highlighting the higher meroplankton/holoplankton ratio in upwelling stations. However, two main limitations impeded deepening the conclusions of this work, i.e. the relatively low number of stations and the identification of large taxa aggregating different species. A more detailed taxonomic identification would allow considering not only morphological traits but also phenological and physiological ones, which are essential to achieve a deep understanding of zooplankton dynamics in short-lived oceanographic structures. In addition to the mesozooplankton community structure, other factors might also vary under changing oceanographic conditions such as species size distributions (Blanco-Bercial et al., 2006), the ratio amongst carnivores-detritivorous and herbivorous organisms (Thibault et al., 1994; Hernandez-Leon et al., 2002; Gaudy & Youssara, 2003) and physiological rates of the mesozooplankton communities. An increased sampling effort is thus a necessary condition for effectively determining the implications of mesoscale oceanography for mesozooplankton ecology.

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