Short-term meso-scale variability of mesozooplankton communities in a coastal upwelling system (NW Spain)

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Abstract

The short-term, meso-scale variability of the mesozooplankton community present in the coastal upwelling system of the Ría de Vigo (NW Spain) has been analysed. Three well-defined communities were identified: coastal, frontal and oceanic, according to their holoplankton-meroplankton ratio, richness, and total abundance. These communities changed from summer to autumn due to a shift from downwelling to upwelling-favourable conditions coupled with taxa dependent changes in life strategies. Relationships between the resemblance matrix of mesozooplankton and the resemblance matrices of meteorologic, hydrographic and community-derived biotic variables were determined with distance-based linear models (DistLM, 18 variables), showing an increasing amount of explained variability of 6%, 16.1% and 54.5%, respectively. A simplified model revealed that the variability found in the resemblance matrix of mesozooplankton was mainly described by the holoplankton-meroplankton ratio, the total abundance, the influence of lunar cycles, the upwelling index and the richness; altogether accounting for 64% of the total variability. The largest variability of the mesozooplankton resemblance matrix (39.6%) is accounted by the holoplankton-meroplankton ratio, a simple index that describes appropriately the coastal-ocean gradient. The communities described herein kept their integrity in the studied upwelling and downwelling episodes in spite of the highly advective environment off the Ría de Vigo, presumably due to behavioural changes in the vertical position of the zooplankton.

Key words: Mesozooplankton communities, resemblance matrices, coastal upwelling, holoplankton, meroplankton, moon, Ría de Vigo, NW Spain.

1. Introduction

Mesozooplankton (0.2–20 mm) are key components in coastal ecosystems; they link the microbial food web to the classic food chain by feeding on microzooplankton (20–200 μm), which are considered the top predators of microbial food webs (Sherr and Sherr, 2002; Calbet and Saiz, 2005). The importance of mesozooplankton is more remarkable in coastal upwelling areas, where primary production is increased by wind-driven currents that bring nutrient-rich subsurface water up into the photic layer (Bode *et al.* 2003a). Specifically, averaged daily grazing impact on the chlorophyll standing stock by mesozooplankton grazers has been estimated to be 11.7% in the California upwelling system (range 6–18%, Landry *et al.*, 1994), and 6% of primary production in the Galician upwelling (range 2–39%, Bode *et al.*, 2003a).

Galicia (NW Iberian Peninsula, Fig. 1) is at the northern limit of one of the four major eastern boundary upwelling systems of the world ocean (Aristegui *et al.*, 2006). From March–April to September–October, north-easterly winds predominate in the Iberian basin producing coastal upwelling. The rest of the year, the prevailing south-westerly winds produce coastal downwelling. This seasonal cycle explains only about 10% of the variability of the wind regime, whereas >70% of the variability concentrates on periods of 10–20 days (Blanton *et al.*, 1987; Álvarez-Salgado *et al.*, 2002). The hydrographic variability during the upwelling season is coupled with changes in bacteria, phytoplankton, and zooplankton biomasses delayed on the order of a day, days, and weeks, respectively (Tenore *et al.*, 1995).

All physical and biological processes operate at some preferential spatial and temporal scales, generating a multiscale variability in zooplankton communities (Levin, 1992; Clarke and Ainsworth, 1993). In this context, several works have dealt with zooplankton variability in N and NW Spain. Short-term (less than one month) scale changes were studied during upwelling or downwelling events at fixed stations (Valdés *et al.*, 1990; Fusté and Gili, 1991; Tenore *et al.*, 1995; Morgado *et al.*, 2003; Blanco-Bercial *et al.*, 2006; Marques *et al.*, 2006), as well as following the upwelled water through lagrangian experiments (Batten *et al.*, 2001; Halvorsen *et al.*, 2001; Isla and Anadón, 2004). Stable isotopes in mesozooplankton were used to infer the pelagic food web in the Galician coast during spring (Bode *et al.*, 2003b). Interannual variability in mesozooplankton abundance and biomass has been determined at two fixed stations off A Coruña (Bode *et al.*, 1998; 2003a; 2004). Finally, surveys carried out monthly by the Instituto Español de Oceanografía (IEO) since 1987 allowed

67 studying long-term trends in the zooplankton communities off NW and N Spain
68 addressing their link with global warming (Valdés *et al.*, 2007; Bode *et al.*, 2009).
69 However, these studies dealt mainly with zooplankton biomass and abundance, and did
70 not consider the community structure.

71 The Ría de Vigo is a highly dynamic area, which is among the most productive
72 oceanic regions in the world (Blanton *et al.*, 1984). The main driving forces
73 modulating the residual circulation of the Ría de Vigo are the local and shelf winds
74 (Souto *et al.*, 2003), affecting the composition and abundance of phytoplankton
75 (Nogueira *et al.*, 2000; Cermeño *et al.*, 2006; Crespo *et al.*, 2006), microzooplankton
76 (Teixeira *et al.*, 2011) and ichthyoplankton (Ferreiro and Labarta, 1988; Riveiro *et al.*,
77 2004). However, most of the studies dealing with mesozooplankton were centred in the
78 adjacent shelf waters (Valdés *et al.*, 1990; Fusté and Gili, 1991; Tenore *et al.*, 1995;
79 Isla and Anadón, 2004; Blanco-Bercial *et al.*, 2006; Bode *et al.*, 2009) except Valdés *et al.*
80 (2007), who studied long-term trends of zooplankton abundance and biomass east
81 and west of the Cies Islands, at the mouth of the Ría de Vigo (Fig. 1). Nonetheless,
82 there is a lack of studies that characterise mesozooplankton communities inside and
83 outside the Ría de Vigo. So, the aim of this work is to analyse the mesozooplankton
84 variability characterising spatially and temporally the community structure in the Ría
85 de Vigo. Furthermore, we aimed to understand how the physical forcing and
86 environmental variables constrain the integrity of these communities.

87 **2. Material and Methods**

88 Ten surveys to collect zooplankton and hydrographic data were undertaken in the
89 Ría de Vigo (NW Spain, Fig. 1) onboard RV "Mytilus", in the summer (2, 4, 9 and 11
90 July) and autumn (26 September, 1, 3, 9, 10 and 14 October) of 2008. We focused the
91 sampling effort on these periods because they match with the maximum in
92 mesozooplankton biomass (Otero *et al.*, 2008). Each survey was carried out at night in
93 four transects (T2, T3, T4 and T5) parallel to the coast following an onshore-offshore
94 depth gradient with average water depths of 26, 68, 85 and 110 m, respectively. A
95 Seabird 9/11 CTD equipped with a WetLabs ECOFL fluorometer and a Seatech
96 transmissometer, was deployed at the southern part of each transect to obtain vertical
97 profiles of temperature (T°), salinity (Salt), chlorophyll-*a* fluorescence (Chl-*a*),
98 dissolved oxygen and stability of the water column (Stab), calculated as the square of
99 the Brunt –Väisälä frequency. Dissolved oxygen was subtracted from oxygen
100 saturation to obtain the apparent oxygen utilization (AOU), a proxy for the trophic

status of the column: positive values indicate net heterotrophy and negative values net autotrophy.

2.1. Plankton sampling

Mesozooplankton samples were collected with a 750 mm diameter bongo net of 375 μm mesh, equipped with a mechanical flow-meter. The mesh size selected was the same as in Otero *et al.* (2009) to standardize the plankton sampling in the Ría de Vigo. Two samples per transect were collected at a ship speed of 2 knots. The bongo net was first lowered and stabilised near the bottom for a period of 2 min and subsequently hauled up at 0.5 m s^{-1} . Then, it was cleaned onboard and towed in the surface layer during 5 min. Towing times were so short due to the extraordinary abundance of salps. Samples collected near the bottom were considered as integrated water-column samples, because bongo nets spent more time throughout the water column than near the bottom. Plankton samples were fixed with 96% ethanol and stored at -20°C for dietary purposes (Roura *et al.*, 2012).

Salps were counted and removed manually from most samples (200,371 salps) and, then, each sample was divided into an amount suitable for examination using a Folsom splitter (Omori and Ikeda, 1984). The subsample was made up to 300 ml, several aliquots of 3 ml were obtained with a Stempel pipette, then identified and counted until at least 500 individuals were enumerated. Organisms were identified under a binocular (Nikon SMZ800) or inverted microscope (Nikon Eclipse TS100) to the lower taxonomic level possible.

2.2. Oceanographic and meteorological data

Sea surface temperature, wind speed (10 m above sea level) and surface (3 m depth) current speed off the Ría de Vigo were provided by the Seawatch buoy of Puertos del Estado (www.puertos.es) located off Cape Silleiro ($42^{\circ} 7.8'\text{N}$, $9^{\circ} 23.4'\text{W}$; Fig. 1). Continuous records of water temperature and salinity at 4 and 11 m depth at the Rande bridge, in the inner Ría de Vigo ($42^{\circ} 17.4'\text{N}$, $8^{\circ} 39.6'\text{W}$; Fig. 1) were provided by Meteogalicia (www.meteogalicia.es). The sampling area lay between these two observatories, thus providing valuable information of the environmental conditions before, during and after the mesozooplankton surveys. Daily upwelling indices ($-Q_x$, in $\text{m}^3 \text{ s}^{-1} \text{ km}^{-1}$) were calculated from the wind data of the Seawatch buoy following Bakun (1973). The freshwater input to Ría de Vigo is a combination of regulated and natural flows. Daily volume of the Eiras reservoir (which controls 42%

of the drainage basin), was provided by Augas de Galicia (Galician Government). The natural component of the Oitabén-Verdugo river (Fig. 1) flow was estimated according to the empirical method of Rios *et al.* (1992) from the daily precipitation in the drainage basin. Miño river (Fig. 1) discharges were provided by the Confederación Hidrográfica Miño-Sil upon request (station SAIH/SAICA: E033 (1641) Frieira dam).

2.3. Statistical analysis

Mesozooplankton community structure was examined with multivariate techniques using the software packages PRIMER6 & PERMANOVA+ (Anderson *et al.*, 2008). Prior to analysis, the database was screened to select those taxa that appeared at least in 10% of the samples. Afterwards the abundance was transformed using the function $\log(x + 1)$ to normalize the data (Legendre and Legendre, 1998). The Bray-Curtis similarity matrix, which reflects changes in relative abundance as well as in species composition, was used to calculate the resemblance matrix among samples.

A principal coordinate analysis (PCO) ordination was used to visualise the natural groupings of the samples using 2D and 3D plots. The PCO output is an unconstrained plot (i.e., does not include *a priori* hypothesis) where samples are projected onto axes that maximize the variance found in the resemblance matrix. The natural groupings emerging from the PCO plot were analysed with PERMDISP, based on distances to centroids, to examine the dispersion among groups. Subsequently, a non-parametric permutational ANOVA (PERMANOVA) analysis was used to test for statistical differences in the location of natural groupings in the multidimensional space. Furthermore, PERMDISP was used on compositional dissimilarity (Bray-Curtis on presence/absence data matrix) to test for similarity in β -diversity (i.e., the variability in species composition among sampling units for a given area at a given spatial scale) among the natural groupings (Anderson, 2006). The species contributing most to similarities within and dissimilarities among the natural groupings, were determined using the program SIMPER (Warwick and Clarke, 1991) with a two-way crossed analysis. Organisms with a high average contribution and large ratio of average contribution to standard deviation of contribution were considered good discriminating organisms (Clarke, 1993).

Finally, relative abundance of single species (p_i) in the natural groupings was used to calculate species diversity, homogeneity and dominance using the Shannon-Weaver index ($H' = -\sum_i p_i \ln p_i$), the Evenness Index ($J' = H' / \ln S$) and the Simpson's

index ($\lambda = \sum p_i^2$), respectively (Omori and Ikeda, 1984). We calculated also the species richness (S) of each natural grouping by counting the different taxa and the Margalef's index ($d = (S-1)/\log N$), which is an index of the number of species for a given number of individuals. The total abundance (N), as well as holoplankton and meroplankton abundances (all expressed in individuals per 1000 m⁻³) were calculated for each natural grouping. Non-parametric analysis using Mann-Whitney U test (STATISTICA v6 software, StatSoft Inc., Tulsa, USA) was subsequently conducted to test if these biotic variables varied significantly between natural groupings.

Three set of variables were considered to model the mesozooplankton community structure: i) meteorologic variables: upwelling index (-Qx), fresh water inputs from the rivers Oitabén-Verdugo (QrOi) and Miño (QrMi) and the moon, which was codified as a categorical variable, dividing the lunar cycle into 4 periods following Hernández-León *et al.* (2001); ii) hydrographic variables obtained from the CTD casts and Silleiro and Rande observatories; and iii) biotic variables obtained from the natural groupings: total abundance (N), holoplankton-meroplankton ratio (H/M), richness (S), diversity (H'), homogeneity (J'), dominance (λ) and Margalef's index (d). Prior to modelling, all variables were tested for collinearity (Spearman correlation matrix) and those with determination coefficients (R^2) higher than 0.9 were omitted. The retained variables were then transformed to compensate for skewness. Given that variables were measured in different units, they were standardized prior to calculate the resemblance matrix using Euclidean distance.

RELATE analysis was carried out to test if the spatial pattern of each set of variables matched with the spatial pattern of the mesozooplankton samples, by correlating the matching entries of the resemblance matrices based on the Spearman rank correlation (ρ). Relationships between the resemblance matrix of mesozooplankton and environmental-biotic variables were modelled with distance-based linear models (DistLM). In order to assign the contribution of the different sets of variables (meteorologic, hydrographic and biotic) to the total variability found in the mesozooplankton resemblance matrix, a step-wise selection procedure was carried out using the adjusted R^2 as selection criterion. The output of the fitted model in multi-dimensional space was visualized with distance-based redundancy analysis (dbRDA) (McArdle and Anderson, 2001).

Finally, all significant variables were introduced in the model with the "best" procedure of the DistLM model, using the bayesian information criterion (BIC),

because it includes a more severe penalty for the inclusion of new predictor variables than Akaike's information criterion (AIC). Such a procedure allowed us to generate the simplest model that explained the highest variability found in the mesozooplankton resemblance matrix. Finally, the output of the fitted model in multi-dimensional space was visualized with distance-based redundancy analysis (dbRDA).

3. Results

3.1. Hydrography and dynamics

The main forcing variables affecting the hydrography of the Ría de Vigo and adjacent shelf are presented in Fig. 2 and the CTD profiles of innermost transect 2 (T2) and outermost transect 5 (T5) shown in Fig. 3. Surveys 1 to 4 (from July 2 to 11) were conducted under wind relaxation/downwelling conditions, characterised by weak winds of variable direction and a monotonic increase of SST (Fig. 2a, b, d), with the exception of the strong downwelling-favourable winds recorded on July 4 (Fig. 2a, b) resulting in a strong northward current (Fig. 2c). The downwelling/relaxation event gradually warmed the surface layer, increasing the stratification (Fig. 3a, b), leading to the deepening of the Chl-*a* maximum and posterior dispersion through the water column (Fig. 3c).

Surveys 5 to 10, conducted from September 26 to October 14, were characterised by upwelling-favourable winds (Fig. 2a, b) that cooled the surface layer sharply (Fig. 2d). The dynamics were more complex during these surveys with four well-defined periods: i) from September 25 to 28 weak winds of variable direction prevailed, accompanied by surface layer warming and stratification (Figs. 2a, d, 3a, b); ii) from September 29 to October 4 upwelling-favourable winds resulted in strong south-westward currents and a sharp cooling of the water column, that uplifted the Chl-*a* maximum close to the surface, with Chl-*a* levels being twice as much in T2 than in T5 (Fig. 2a, c, 3c); iii) from October 5 to 8 sustained south-southwestward winds reversed the circulation pattern and warm oceanic surface water was advected to the coast increasing the stratification (Figs. 2a, c, d, 3a); and iv) from October 9 to 13, north-eastward winds favoured coastal upwelling resulting in strong westward currents, water column cooling and Chl-*a* maximum export to the ocean (Figs. 2a, c, d, 3a, c). The last survey (October 14) was dominated by weak winds of variable direction and a reversal of the circulation pattern that warmed the water increasing the stratification and lowering Chl-*a* (Figs. 2a, c, d, 3a, c).

In summary, whilst surveys 1 to 4 (July) occurred under predominantly summer-downwelling conditions with similar Chl-*a* levels inside and outside the Ría de Vigo, autumn-upwelling conditions prevailed during surveys 5 to 10 (September - October) with higher Chl-*a* levels in the coastal (T2) than in the mid-shelf (T5) domains. Autotrophy prevailed in the upper 10 m throughout the surveys, except on July 11 and October 3, when heterotrophy was dominant (Fig. 3d).

3.2. Mesozooplankton communities

It should be noted that the net used in this study could bias the mesozooplankton size range (0.2 - 20 mm) towards relatively large-size animals. However, the high abundance of phytoplankton in the samples clogged the net avoiding this bias, thus capturing animals of less than 375 μm as harpacticoid copepods or foraminifera.

The PCO plot (Fig. 4) shows three well-defined groups across the PCO1 axis, which accounted for 47.3% of the variability of the resemblance matrix. The samples at the extremes of that axis corresponded to T5 and T2 respectively, with T5 having negative values and oceanic fauna (as hyperiids or adults of euphausiids), while T2 had positive values and larval stages of coastal species. Samples in between the oceanic and coastal domains (between -25 and +5 in the PCO1 axis) grouped together with a large dispersion and were considered collectively as frontal samples. Therefore, the PCO1 axis reflected the gradient from oceanic to coastal stations, with transition frontal stations among them.

The PCO2 axis explained 14.2 % of the variability of the resemblance matrix and it was strongly related with the two sampling periods: summer-downwelling (positive values of PCO2) and autumn-upwelling (negative values of PCO2). Within the summer-downwelling frontal group there were three outliers (PCO2 values around +40) that corresponded to samples with high abundances of calyptopis stages (1260-3090 ind m^{-3}).

Based on the PCO plot (Fig. 4) and the previous analysis of the hydrography and dynamics of the study area, samples were grouped according to two factors (sampling period/hydrographic characteristics and coast-ocean gradient) into 6 communities: summer-downwelling coastal (SC), summer-downwelling frontal (SF), summer-downwelling oceanic (SO), autumn-upwelling coastal (AC), autumn-upwelling frontal (AF) and autumn-upwelling oceanic (AO).

The test for dispersions among communities with PERMDISP revealed statistical differences in summer between SF-SC ($p < 0.05$) and in autumn between AF-AO and

AC-AO ($p < 0.05$). PERMANOVA tests revealed that all the communities were statistically different in a multidimensional space (Table 1). However, such a difference can be in species composition and/or abundance. Variability in species composition (β -diversity) revealed that in summer-downwelling conditions, the coastal community differed significantly ($p < 0.001$) from the oceanic and frontal communities, which were similar in composition between them. Autumn-upwelling communities displayed also compositional differences between coastal and frontal-oceanic communities, but marginally significant ($p = 0.07$). Besides, coastal communities varied in composition between sampling periods ($p = 0.001$), but the frontal and oceanic communities did not. PERMANOVA tests revealed no significant differences ($p = 0.375$) between the surface and oblique hauls. However, samples were not merged together because certain species did vary between the two strata. In fact, in some cases the surface and column samples obtained in the same transect belonged to different communities (Fig. 5, day 4).

Average abundances of the taxa that contributed most to the within-group similarity, i.e. the discriminating species, appear in Table 2 as well as the different taxa within each community that are summarised in Annexe 1. In summer, coastal waters were dominated by copepods (24 species), larval stages of the euphausiid *Nyctiphanes couchii*, echinoderm larvae and appendicularians. Frontal waters were dominated by larval stages of the euphausiid *N. couchii*, copepods (17 species), and salps. In contrast, oceanic waters were dominated by salps, copepods (18 species) and euphausiids (13% adults). In autumn, coastal waters differed markedly from summer with echinoderm larvae, larval stages of *N. couchii*, appendicularians, copepods (25 species), cirripeds and decapods contributing the most. Frontal waters were dominated by larval stages of *N. couchii*, copepods (20 species), salps and chaetognaths. Finally, oceanic waters were dominated by salps, copepods (18 species), euphausiids (49% adults) and chaetognaths (Fig. 6).

The species that contributed most to discriminate between pairs of communities are presented in Table 3. Spatial dissimilarities among communities were consistent through summer and autumn, with the highest dissimilarity between coastal and oceanic samples (the most distant communities), then coastal and frontal samples and, finally, the lower dissimilarity was found between frontal and oceanic communities. Discriminating species present in the upper part of Table 3 are good indicators of changes in space due to water body preferences (meroplankton present in the coastal

domain versus holoplankton present in the oceanic domain). In contrast, temporal dissimilarities among communities showed that coastal and oceanic communities changed less with time (38.78 and 37.71%, respectively) than the frontal community (45.96%). Discriminating species between both sampling periods give an idea of the zooplankton succession due to different life cycle strategies and/ or due to the different upwelling/downwelling situations.

It is noticeable the contrasting levels of similarity found for the holoplankton and meroplankton components within each community (Table 4). While the holoplankton was quite similar across the communities, with the frontal community showing the lowest values; the meroplankton was more variable showing a decreasing gradient of similarity from coastal to oceanic communities. Comparisons between communities revealed that the holoplankton component changed less spatially and temporally than the meroplankton. The later showed enormous differences between coastal and oceanic samples, as well as a marked change in the frontal and oceanic communities of both sampling periods.

The biotic indices obtained from the different communities are presented in Table 5 and their spatial and temporal non-parametric comparisons are summarized in Table 6. In summer, there was a marked gradient between the coastal and the frontal-oceanic domains: the coastal community had the highest diversity and abundance, with many species almost homogenously distributed and the lowest ratio between holoplankton and meroplankton, due to the high abundance of larval stages of coastal species (Table 5, Fig. 6). The frontal community was very similar to the oceanic one but with significant differences in richness and abundance (3-fold in the frontal than in the oceanic samples). In the oceanic community, there was a remarkable decline of meroplankton, with almost all the animals present in the oceanic sample being holoplankton. In autumn, there were less significant differences between coastal and frontal-oceanic communities, except in total abundance and richness that followed the previously described coastal-frontal-oceanic gradient (Fig. 6, Table 6).

Coastal waters underwent larger changes between sampling periods, with less richness, diversity and, consequently, lower evenness and higher dominance in autumn than in summer. However, there was no statistical difference between meroplankton and holoplankton although there was more meroplankton in the autumn coastal community (Fig. 6). The structure of frontal and oceanic communities did not vary

much between both periods, except for a marked decrease in autumn abundance for both communities, mainly due to a decrease in holoplankton.

The significant relationships of the correlations between CTD variables and the discriminating taxa are summarized in Table 7. Species more abundant in coastal waters (i.e. *Pisidia longicornis* zoea, echinoderm zoea, cirripedia zoea, processidae zoea, appendicularians) showed negative correlations with Salt and positive correlations with Stab, common features of coastal areas influenced by continental runoff. Frontal communities (i.e. *brachyura megalopa*, *Calanus helgolandicus*, *Calanoides carinatus*, *Acartia clausi*) correlated negatively with AOU, related with higher phytoplankton activity. Conversely, oceanic communities (i.e. salps, mysidacea, *Paraeuchaeta hebes*, hyperiids) correlated positively with T° and Salt and negatively with Chl-*a* and Stab.

3.3. Linking environmental and biotic variables with mesozooplankton communities

The ordination scores of the PCO 1 and 2 axes on each station were regressed against the meteorologic, hydrographic and dynamic variables obtained from the Silleiro and Rande observatories to determine the relative importance of each forcing factor and the delay of the response of the community structure. All variables showed better correlations with the scores of the PCO2 axis and the delay intervals varied depending on the variable (Table 8). These correlation coefficients were used to weight the effect of the forcing variables recorded at the Silleiro and Rande observatories on each sampling station. Eighteen variables were retained based on collinearity analysis. The variables Chl-*a*, Stab, N and H/M were log transformed to compensate for skewness.

The retained variables were then run with the “best” procedure of the DistLM model, using the Bayesian information criterion (BIC). As a result, only five variables were retained by the model, together accounting for 64% of the variability found in the mesozooplankton resemblance matrix (Table 9, Fig. 7). Three of the five fitted variables were biotic: log (H/M), log (N) and S, the fourth was -Qx and the fifth was the moon. The first two dbRDA axes accounted with 88.3% of the fitted variability, corresponding to 55.4% of the total variability of the resemblance matrix. This model based only on five variables clearly represented the community patterns shown in the unconstrained PCO plot of Fig. 4 (RELATE analysis $\rho = 0.58$, $p < 0.001$), demonstrating that the main structuring forces of the data cloud were included in the model. Thus, attending to the variable vectors overlaid in Fig. 7 it can be concluded

that the most important variables involved in originating the coastal–oceanic gradient, were log (H/M) inversely and log (N) together with S directly (also shown in Table 5). Such a gradient was a consequence of very rich, abundant and meroplankton-dominated coastal waters facing poor, less abundant and holoplankton-dominated oceanic waters. On the other hand, the sampling period/hydrographic characteristics found in the Y axis were directly related with the moon and log (N) and negatively with -Qx, because summer waters were dominated by high-abundance downwelled waters while autumn waters were dominated by low-abundance upwelled waters with higher contribution of meroplankton. The last quarter of the moon (waning crescent) was directly related with increased abundances of mesozooplankton in summer, while the first three quarters were correlated with autumn waters. The first and third quarters (waxing crescent and waning gibbous) were correlated with high abundance autumn coastal communities and the second quarter (waxing gibbous) was correlated with autumn frontal and oceanic communities, where less abundance was found.

RELATE analysis showed that the spatial patterns based on the meteorologic ($\rho = 0.174$, $p < 0.01$), hydrographic ($\rho = 0.285$, $p < 0.01$), and biotic data ($\rho = 0.67$, $p < 0.001$) were significantly related to the patterns found in the mesozooplankton resemblance matrix, with the optimal match (largest Spearman ρ) corresponding to biotic data. The output of marginal tests on each set of variables showed that biotic data accounted for 54.5%, hydrography for 48.8% and meteorology for 39.9% of the variability (Table 10). However, when fitted into the step-wise model grouping the variables according to the three sets of variables, the DistLM model revealed that the variability found in the mesozooplankton resemblance matrix was better described by the biotic variables (54.5%), followed by the hydrography (16.1%) and finally the meteorology (6.0%); altogether accounting 76.6% of the total variability found in the mesozooplankton resemblance matrix (Fig. 8).

The same analyses were performed splitting the mesozooplankton data matrix in holoplankton and meroplankton components to filter out the main descriptor of the community. PCO analysis revealed that while the holoplankton shared almost the same structuring forces as found for the mesozooplankton (41.7% corresponding to the coast-ocean gradient and 18.1% corresponding to sampling period/hydrographic characteristics, $\rho = 0.956$, $p < 0.001$), the meroplankton did it to a lesser extent (only 30.6% corresponding to the coast-ocean gradient and 11.9 % to the sampling period/hydrographic characteristics, $\rho = 0.703$, $p < 0.001$). Furthermore, the spatial

patterns based on the resemblance matrix of the explicative variables (meteorologic, hydrographic, and biotic without log (H/M)), were significantly better represented by the resemblance matrix of holoplankton ($\rho = 0.454$, $p < 0.001$) than that of the meroplankton ($\rho = 0.261$, $p < 0.01$). DistLM model run with the “step-wise” procedure and BIC as selection criterion revealed that while the variability found in the holoplankton resemblance matrix was better described by five variables (log (N) 28.2%, d 12.3%, -Qx 10.4%, moon 4 4.9% and Salt 2.8%, altogether accounting with 58.6%) the meroplankton was better described by three variables (S 19%, log (N) 9.2% and -Qx 4.5% altogether accounting with 32.7%).

4. Discussion

4.1. Mesozooplankton communities

Mesozooplankton communities have been characterised at the short-time (< 1 wk) and spatial (< 11 km) scale for the first time in the Ría de Vigo. A total of six mesozooplankton communities were identified according to their species composition and abundance, together with the influence of the meteorology and hydrography of the Ría de Vigo and adjacent shelf. As a consequence of the circulation pattern during upwelling/downwelling events (Souto *et al.*, 2003), part of the biomass produced inside (outside) the Ría de Vigo is transported offshore (onshore) by the surface ocean ward (coastal ward) current (Álvarez-Salgado *et al.*, 2002, Spyarakos *et al.*, 2011). Therefore, the communities present in the Ría de Vigo might be disrupted and mixed by this highly advective coastal upwelling/downwelling environment (González *et al.*, 2005). Indeed, such an effect can be tracked in our samples. Following the time-course of the mesozooplankton community found at T3, it is clear how it changed in parallel with the meteorology: On July 9, the mesozooplankton collected in surface waters (Fig. 5a, number 3) belonged to the coastal community. On July 10, southerly winds transported surface warm oceanic waters onshore (Figs. 2a, c, d, 3a), thus changing the surface sample collected on July 11 to an oceanic community (Fig. 5a). At the same time, the water column sample of July 11 (Fig. 5b) belonged to the frontal community, due to the diminishing effect of the wind stress with depth. So, there were two different communities in the same transect at different depths, although the methodology used in this study (bongo sampling) was not the optimal to explore such differences.

The large dispersion found in frontal communities (Fig. 4) is a consequence of their location between the coastal and oceanic domains and the continuous intrusions of animals from both communities forced by the upwelling/downwelling currents.

Nonetheless, such intrusions did not lead to a continuous gradient between coastal and oceanic realms caused by the mixing of the three communities. Intriguingly, the persistence of the three communities suggests specific mesozooplankton responses, like behavioural distribution patterns coupled with the residual circulation of the Ría de Vigo (Marta-Almeida *et al.*, 2006; Queiroga *et al.*, 2007), that would allow the return of advected animals to their community of origin.

4.2. Coastal-oceanic gradient

The natural groupings represented in the PCO plot (Fig. 4) clearly differentiate coastal from frontal and oceanic waters. The latter were not different in species composition but in abundance (more than 3-fold in the frontal than in the oceanic samples) in both seasons (Table 5). Coastal waters differed from oceanic waters, because neritic holoplankton species such as *Temora longicornis*, *Acartia clausi*, *Pseudocalanus elongatus*, *Paracalanus parvus* (Peterson, 1998; Gaard, 1999) coexist with meroplankton near the coast, therefore increasing notably the abundance of coastal communities (Fusté and Gili, 1991; Bode *et al.*, 1998, 2009; Blanco-Bercial *et al.*, 2006). Indeed, the largest mesozooplankton abundance occurred in the coastal domain, both in summer and autumn, with meroplankton contributing 31.7 and 47.2%, respectively. Coastal waters act as nursery areas in the Ría de Vigo, as found in long-term studies off Galicia (Bode *et al.*, 2009). The meroplankton contribution clearly declined in the frontal (2.3 and 3.6% on each sampling period) and even more in the oceanic community (only 0.6 and 0.4%). Furthermore, a decreasing similarity from coastal to oceanic communities (Table 4) was coupled with this decline in meroplankton abundance. Therefore, it can be concluded that the coastal-oceanic gradient was mainly due to a gradient in holoplankton/meroplankton abundance, as shown in Fig. 7 and reinforced by the high contribution of this ratio (39.6%) describing the overall variability found in the mesozooplankton resemblance matrix (Table 9).

The ratio (H/M) is proposed as an index for mesozooplankton community studies in coastal and shelf areas. Indeed, there is a need for a consensus between the taxonomists involved with data acquisition to avoid the difficulties inherent when comparing zooplankton time series (Perry *et al.*, 2004; Valdés *et al.*, 2007). The adoption of the ratio (H/M) as a consensus index is supported by the following advantages: i) the easiness of obtaining the data due to its independency on the degree of taxonomic expertise (the recognition of meroplankton and holoplankton groups is an easy task, even with plankton-imaging software as in Benavides *et al.* (2010)); ii) its

high power describing the variability found in mesozooplankton communities (39.6% against 9.7% explained by Shannon's diversity index, H' , which deeply depends on the taxonomic expertise); iii) less time and effort for obtaining data; iv) its independency on the biomass given that is a ratio of individuals. Furthermore, the ratio (H/M) may be used to place other people's works into mesozooplankton coastal-oceanic community gradients, as well as to track mesozooplankton communities advected by mesoscale oceanographic events like filaments, gyres, upwelling/downwelling (Relvas *et al.*, 2007).

4.3. Short-term changes in mesozooplankton communities

There was a noticeable change between summer and autumn communities, originated by contrasting oceanographic conditions coupled with zooplankton life strategies. Summer surveys were carried out under downwelling-relaxation conditions. The predominant southerly winds pushed onshore warm and salty surface waters of subtropical origin (Souto *et al.*, 2003; Spyrakos *et al.*, 2011), carrying oceanic species positively correlated with Salt and T° and negatively correlated with Chl-*a* (salps, mysids, hyperiids, *Paraeuchaeta hebes*), as found in other works (Valdés *et al.*, 1990; Blanco-Bercial *et al.*, 2006). These subtropical waters had less richness and abundance than coastal waters, with the salps *Salpa fusiformis* and *Thalia democratica* dominating the samples (Huskin *et al.*, 2003; Boero *et al.*, 2008). The frontal community was similar in composition to the oceanic, but differed in abundance due to the onshore advection that piled up oceanic species in the front, with *N. couchii* larval stages dominating the samples (Fig. 6). Discriminating taxa found in frontal waters were negatively correlated with AOU (brachyuran megalopae, *Calanus helgolandicus*, *Calanoides carinatus*, *A. clausi*), suggesting that these animals were present in waters with high primary production as found by Blanco-Bercial *et al.* (2006). Coastal waters were dominated by species positively correlated with Stab and Chl-*a* and negatively correlated with Salt as appendicularians (Acuña and Anadón, 1992), meroplankton (cirriped, echinoderm, crustacean, polychaete and gastropod larvae), and cladocerans, which are species specialized to feed on small particles (Blanco-Bercial *et al.*, 2006). The copepod *A. clausi* was exceptionally abundant in coastal waters far followed by *T. longicornis* (Bode *et al.*, 2009).

Autumn surveys occurred under dominant upwelling conditions, which resulted in less difference between coastal and frontal communities, because coastal waters were advected offshore against the frontal community. Species found in the coastal

community correlated positively with AOU, Stab (meroplankton, siphonophores and appendicularians) and Chl-*a* (*Oithona plumifera*). This community showed marked changes in their composition compared with summer, with increased numbers of siphonophores, chaetognaths, echinoderm larvae and *O. plumifera*, which is an upwelling indicative species (Blanco-Bercial *et al.*, 2006); and decreased numbers of cladocerans (*Podon intermedius* and *Evadne nordmanni*) and the copepods *A. clausi*, *T. longicornis*, *Centropages chierchei* and *Clausocalanus* spp. The frontal community was characterised by animals negatively correlated with AOU and positively correlated with Chl-*a* and Stab as chaetognaths, siphonophores, *N. couchii* larvae, gastropods, and the copepods *C. carinatus*, *C. helgolandicus*, *P. parvus* and *A. clausi*, that are considered coastal upwelling species (Peterson, 1998). Increased abundances of chaetognaths, mysidaceans, *P. parvus* and *Paraeuchaeta* spp. were found in autumn frontal communities; while decreased numbers of brachyuran zoea and megalopa, gastropods, furcilia stages of *N. couchii* and the copepods *P. hebes*, *C. helgolandicus* and *C. carinatus* were found in autumn compared with summer. Finally, oceanic waters showed an increase in autumn abundances of *N. couchii* adults and larval stages, chaetognaths, mysidaceans and *P. parvus*; while a marked decrease in salps, *P. hebes*, *P. spp.*, *C. carinatus* and *C. helgolandicus* was noted compared to the summer oceanic community. These seasonal changes are in agreement with previous works (Valdés *et al.*, 1990; Bode *et al.*, 1998, 2004; Blanco-Bercial *et al.*, 2006; Huskin *et al.* 2006).

Huge numbers of *N. couchii* calyptopis (ranging from 282-3090 ind m⁻³) found in the frontal community of July 2 (transects 3 and 4) coincided with the highest aggregation of adults (170 ind m⁻³, dominated by mature females carrying fully developed eggs) at the outer transect number 5. Furthermore, *N. couchii* adult aggregations were found again in autumn frontal communities on October 9 and 10 (139 and 123 ind m⁻³ respectively), coinciding with calyptopis abundances ranging from 540-2395 ind m⁻³. This spatial distribution of larvae mainly in the coastal and frontal domains coupled with the high abundance of mature adults in the frontal and oceanic domains, suggest a breeding aggregation of adults through the upwelling season, which coincides with the reproductive ecology of this species (Mauchline, 1984).

The oceanographic situation found in this study, i.e. downwelling in summer and upwelling in autumn, was opposite to the main oceanographic pattern off NW Spain,

where coastal winds describe a seasonal cycle, favour upwelling from March-April to September-October and downwelling for the rest of the year (Wooster *et al.*, 1976; Blanton *et al.*, 1987). However, more than 70% of the wind variability concentrates on periods of 10-20 days, thus allowing the frequent occurrence of downwelling events during the upwelling season (Álvarez-Salgado *et al.*, 2002). Therefore, the downwelling event experienced during summer samplings may account for the unexpected massive amounts of salps found in the oceanic community (maximum of 995 salps m⁻³), although their natural cycle place these animals at the end of the upwelling season, occurring along the offshore edge of the shelf break salinity fronts (Huskin *et al.*, 2003; Blanco-Bercial *et al.*, 2006; Huskin *et al.*, 2006; Deibel and Paffenhöfer, 2009) when high salinity water flows poleward along the Portuguese and Galician coasts (Haynes and Barton, 1990; Castro *et al.*, 1997). Furthermore, the presence of the warm-water copepod *Temora stylifera* (Villate *et al.*, 1997; Valdés *et al.*, 2007; Bode *et al.*, 2009) in summer oceanic waters reinforces the unusual oceanographic conditions experienced during July samplings. Hence, we would like to point out that the mesozooplankton community composition found in summer samplings may be distorted by the unusual oceanographic conditions and the abundance of salps (Huskin *et al.*, 2003).

4.4. Linking mesozooplankton communities to environment: to what extent?

The relationship between environment and plankton is difficult to generalise, because the environmental factors interact at different temporal scales (Bode *et al.* 2009; Nogueira *et al.* 2011) aside from indirect interactions canalized through the food web that gradually diminish along the trophic levels resulting in a weakening effect (Micheli, 1999). In this work, only two days were enough to change the community present in the surface sample of T3 from coastal to oceanic (Fig. 5a, day 4). Such a quick change contrast with the delay of weeks found between the time series and the zooplankton response by Tenore *et al.* (1995), or the lack of apparent response of plankton to climate forcing found at mid latitudes compared to boreal locations (Beaugrand *et al.*, 2000). Although, coastal communities shifted to oceanic due to wind-driven currents produced the same day and the day before, the coastal-ocean gradient was better explained by the biotic variables (log (H/M), 39.6%) than those directly related with surface currents (u and v, altogether explaining 10.8%) or indirectly related (-Qx, 8.3%). This large difference between the explanatory power of biotic and environmental variables may play some part in the delays obtained by other

authors (Tenore *et al.*, 1995; Bode *et al.* 2009; Nogueira *et al.*, 2011) or even the lack of response (Beaugrand *et al.*, 2000).

Another complication that may mask the link between environment and plankton is that the environmental conditions are more tightly linked with the holoplankton than with the meroplankton. This difference may be produced by the low abundance and the high variability found in the meroplankton samples of the frontal and oceanic communities (Table 4). However, the contrasting life-history characteristics of both planktonic components may play some part in their link with the environment given that the holoplankton spends their entire life in the pelagic realm, and the meroplankton spends but a part of their life in the water column.

An interesting finding was the significant contribution of the moon describing the mesozooplankton variability. Although there are few samplings to reveal how the moon is influencing the zooplankton abundance, we find that the different moon periods affect unequally the holoplankton and meroplankton components. We ignore whether the zooplankton reproductive strategies are coupled with specific moon periods by means of its light intensity and/or with the tidal currents (Tankersley *et al.*, 2002; Queiroga *et al.*, 2007) and requires further study. However, we discard the moon effect through the predatory influence of diel vertical migrators (Hernández-León *et al.*, 2001), because such predators are not present in the study area but in pelagic open ocean environments.

5. Conclusions

Three well-defined mesozooplankton communities named as coastal, frontal and oceanic were defined by means of their abundance and specific composition in the Ría de Vigo. These communities changed from summer to autumn due to a shift in coastal upwelling/downwelling conditions coupled with taxa dependent changes in life cycle strategies. The main factor responsible of the coastal-oceanic gradient was the ratio between holoplankton and meroplankton, which was increasing from coastal to the oceanic community. This ratio has been proposed as a consensus index for coastal-shelf zooplankton community studies due to its explicative power and easiness of identification. The episodic upwelling/downwelling events off the Ría de Vigo create an advective environment where zooplankton faces forcible removal from the ecosystem. However, the communities kept their integrity throughout the upwelling season in spite of being displaced by the offshore/onshore currents, presumably due to behavioural changes in their vertical position. This study brings light into the

traditionally overlooked mesozooplankton fraction of the Ría de Vigo, an essential component of the pelagic realm that channels the high productivity of the Ría de Vigo up to higher trophic levels.

Acknowledgements

We are indebted to the captain, crew and technicians of R/V “Mytilus” (IIM, CSIC Vigo), for their assistance in collecting the zooplankton samples and hydrographic data. We acknowledge the enormous patience of Félix Álvarez, which sorted by hand every single salp out of the samples, as well as Mariana Rivas. We would like to thank Silvia Piedracoba, Francisco de la Granda and to Puertos del Estado, MeteoGalicia, Augas de Galicia and the Confederación Hidrográfica Miño-Sil for providing the meteorological and hydrographic data. The authors thank the three anonymous reviewers for their effort, which improved the quality and clarity of the manuscript. This study was supported by the projects CAIBEX (Spanish Ministry of Innovation and Science CTM2007-66408-C02) and LARECO (CTM2011-25929), FEDER Funds and the first author by a JAE-pre grant (CSIC) cofinanced with Fondo Social Europeo (ESF) funds.

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Table 1. Results from multivariate PERMANOVA analysis testing differences in zooplankton communities. PERMANOVA full factor test for differences between sampling periods (summer and autumn), coast-ocean gradient (coast, front and ocean) and interaction between these factors. Data log (x+1) transformed.

Factor	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Sampling periods (SP)	1	8708	8708	14.439	0.0001	9939
Coast-ocean gradient (CO)	2	44727	22364	37.081	0.0001	9935
SP x CO	2	2940.4	1470.2	2.4377	0.0008	9881
Residual	73	44027	603.11			
Total	78	104880				

Table 2. Mean abundance (ind 1000 m⁻³) of the ten most discriminating species of each community and averaged similarity of each community (as percentage).

Coastal 70.55%	Summer Frontal 62.35%	Oceanic 70.27%	Coastal 64.82%	Autumn Frontal 61.66%	Oceanic 71.74%
<i>Nyctiphanes couchii</i> calyptopis 199067	<i>Calanoides carinatus</i> 126273	<i>A. clausi</i> 6499	Appendicularia 222062	Chaetognatha 32060	<i>Paraeuchaeta</i> spp. 20097
<i>Pisidia longicornis</i> zoea 22775	<i>N. couchii</i> calyptopis 426896	<i>P. hebes</i> 14187	Ophiuroidea larvae 641873	<i>N. couchii</i> furcilia 58139	Salpida 61479
Appendicularia 185072	<i>N. couchii</i> furcilia 259331	<i>Paraeuchaeta</i> spp. 23423	Chaetognatha 76318	<i>N. couchii</i> calyptopis 235948	Chaetognatha 16781
Brachyura zoea 60756	<i>Acartia clausi</i> 101237	Salpida 213747	<i>N. couchii</i> calyptopis 249736	<i>A. clausi</i> 39961	<i>N. couchii</i> adults 15486
Gastropoda larvae 19417	Brachyura zoea 12760	<i>C. carinatus</i> 62404	<i>N. couchii</i> furcilia 158338	<i>C. carinatus</i> 24567	<i>A. clausi</i> 14914
<i>Centropages chierchiae</i> 8683	<i>C. helgolandicus</i> 51451	Mysidacea 2190	Cirripedia larvae 135229	<i>Paraeuchaeta</i> spp. 12939	<i>P. hebes</i> 7891
<i>N. couchii</i> furcilia 182578	Salpida 119867	<i>C. helgolandicus</i> 36756	Brachyura zoea 29979	<i>C. helgolandicus</i> 11233	Mysidacea 3692
<i>Podon intermedius</i> 68166	<i>Paraeuchaeta hebes</i> 14135	<i>N. couchii</i> calyptopis 6626	<i>Oithona plumifera</i> 12044	Mysidacea 2669	<i>N. couchii</i> calyptopis 12151
<i>Calanus helgolandicus</i> 14331	<i>C. chierchiae</i> 20464	Chaetognatha 2838	Siphonophora 38073	<i>Paracalanus parvus</i> 6829	<i>N. couchii</i> furcilia 3981
<i>Evadne nordmanni</i> 28669	<i>N. couchii</i> adults 21720		Salpida 24927	Salpida 32756	<i>P. parvus</i> 1621

Table 3. Taxa with the highest contributions to spatial and temporal differences among communities (averaged dissimilarity for each pair of communities in parenthesis), their percentage contributions to between group dissimilarity, their discriminate power in bold and the community where their abundance was higher. Community abbreviations: SC, summer coast; SF, summer front; SO, summer ocean; AC, autumn coast; AF, autumn front; AO, autumn ocean.

Spatial changes			Summer			Autumn					
SC – SF (50.56%)	SC – SO (66.08%)	SF – SO (46.17%)	AC – AF (51.76%)	AC – AO (66.73%)	AF – AO (42.84%)						
<i>Pisidia longicornis</i> zoea 3.91% - 3.06 - SC Appendicularians 6.41% - 2.61 - SC <i>Calanoides carinatus</i> 4.73% - 2.39 - SF <i>Podon intermedius</i> 4.50% - 2.24 -SC Cirripedia larvae 3.65% - 2.16 - SC Ophiouroidea larvae 5.77% - 2.04 - SC Paguridae zoea 2.41% - 1.99 - SC Echinoidea larvae 4.45% - 1.87 - SC <i>Evadne nordmanni</i> 3.44% - 1.85 - SC Brachyura zoea 2.79% - 1.83 - SC Gastropoda 2.88% - 1.78 - SC	<i>Pisidia longicornis</i> zoea 4.01% - 5.2 - SC Brachyura zoea 4.9% - 4.09 –SC Gastropoda 3.76% - 3.84 - SC <i>Podon intermedius</i> 4.86% - 3.21 – SC Appendicularia 5.88% - 2.74 - SC <i>Temora longicornis</i> 4.67% - 2.7 - SC Paguridae zoea 2.69% - 2.57 – SC Cirripedia larvae 3.54% - 2.53 - SC <i>Acartia clausi</i> 4.22% - 2.49 – SC <i>N. couchii</i> calyptopis 4.29% - 2.44 – SC Ofiuroidae larvae 5.28% - 2.11 - SC	<i>Acartia clausi</i> 6.68% - 2.17 – SF Brachyura zoea 4.91% - 1.94 – SF <i>N. couchii</i> furcilia 8.92% - 1.74 – SF Mysidacea 2.36% - 1.58 – SO <i>Paraeuchaeta sp.</i> 5.11% - 1.57 – SO Salpida 5.75% - 1.5 – SO <i>Paraeuchaeta hebes</i> 3.27% - 1.47 – SO Brachyura megalopa 3.16% - 1.45 – SF <i>N. couchii</i> calyptopis 6.95% - 1.44 – SF Chaetognatha 2.9% - 1.44 – SO <i>Calanus helgolandicus</i> 4.34% - 1.35 - SF	Ofiuroidae larvae 7.8% - 2.82 - AC Appendicularia 6% - 2.69 - AC <i>Oithona plumifera</i> 3.4% - 2.55 - AC Brachyura zoea 3.53% - 2.12 - AC Cirripedia larvae 4.95% - 2.07 - AC Siphonophora 3.59% - 1.68 - AC Gastropoda 2.49% - 1.66 - AC <i>Acartia clausi</i> 3.17% - 1.6 - AF <i>Calanoides carinatus</i> 2.98% - 1.6 - AF <i>Clausocalanus spp.</i> 1.86% - 1.53 - AC <i>N. couchii</i> furcilia 2.99% - 1.52 - AC	Appendicularia 7.37% - 5.62 - AC Ofiuroidae larvae 8.1% - 5.15 - AC Cirripedia larvae 5.75% - 3.49 - AC Brachyura zoea 3.99% - 3.47 - AC <i>Oithona plumifera</i> 3.16% - 2.6 - AC <i>N. couchii</i> adult 3.55% - 2.52 - AO <i>N. couchii</i> furcilia 4.6% - 2.23 - AC Siphonophora 3.69% - 2.16 - AC Gastropoda 2.9% - 1.98 – AC <i>N. couchii</i> calyptopis 4% - 1.8 – AC <i>Clausocalanus spp.</i> 1.85% - 1.75 - AC	<i>Calanoides carinatus</i> 6.36% - 1.87 - AF <i>N. couchii</i> adult 5.68% - 1.67 - AO <i>Calanus helgolandicus</i> 4.38% - 1.61 - AF Chaetognatha 3.62% - 1.56 - AF <i>Paracalanus parvus</i> 3.57% - 1.53 - AF <i>N. couchii</i> furcilia 6.32% - 1.51 - AF <i>Acartia clausi</i> 4.97% - 1.5 - AF Gastropoda 2.37% - 1.45 - AF <i>N. couchii</i> calyptopis 6.76% - 1.31 - AF <i>Paraeuchaeta hebes</i> 3.65% - 1.26 - AO Siphonophora 2.43% - 1.25 - AF						
Temporal changes			Coastal			Frontal			Oceanic		
			SC – AC (38.78%)			SF – AF (45.96%)			SO – AO (37.71%)		
			<i>Centropages chierchiae</i> 2.86% - 1.99 - SC Siphonophora 3.57% - 1.7 - AC <i>Temora longicornis</i> 4.3% - 1.65 - SC Chaetognatha 2.71% - 1.61 - AC <i>Oithona plumifera</i> 2.5% - 1.57 - AC <i>Podon intermedius</i> 3.7% - 1.53 - SC <i>Calanoides carinatus</i> 2.35% - 1.5 - AC Ofiuroidae larvae 4.01% - 1.47 - AC <i>Acartia clausi</i> 4.17 % - 1.46 - SC <i>Evadne nordmanni</i> 2.91% - 1.46 - SC <i>Clausocalanus spp.</i> 2% - 1.46 - SC				Chaetognatha 5.25% - 1.93 - AF <i>Paracalanus parvus</i> 3.91% - 1.77 - AF Brachyura zoea 3.52% - 1.61 - SF Mysidacea 2.17% - 1.51 - AF <i>Paraeuchaeta hebes</i> 3.55% - 1.5 - SF <i>Calanoides carinatus</i> 4.45% - 1.45 - SF Brachyura megalopa 2.71% - 1.42 - SF Gastropoda 2.18% - 1.41 - SF <i>Paraeuchaeta sp.</i> 3.74% - 1.4 - AF <i>N. couchii</i> furcilia 4.44% - 1.38 - SF <i>Calanus helgolandicus</i> 4.14% - 1.36 - SF				<i>Paracalanus parvus</i> 4.25% - 2.21 - AO <i>Calanoides carinatus</i> 12.13% - 1.99 – SO <i>N. couchii</i> adult 9.78% - 1.99 – AO <i>Paraeuchaeta hebes</i> 5.23% - 1.64 – SO <i>Paraeuchaeta sp.</i> 4.37% - 1.58 – SO <i>Calanus helgolandicus</i> 9.1% - 1.56 - SO <i>N. couchii</i> calyptopis 5.45% - 1.52 – AO <i>N. couchii</i> furcilia 5.11% - 1.45 – AO Salpida 6.21% - 1.36 – SO Chaetognatha 7.19% - 1.35 – AO Mysidacea 2.84% - 1.34 - AO

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846 **Table 4.** Percentages of similarity found in the holoplankton and meroplankton
847 samples of each community (abbreviated as in Table 3), as well as their spatial and
848 temporal comparisons.

	SC	SF	SO	AC	AF	AO
Holo	72.4	65.8	72.55	66.4	66	73
Mero	66.8	44.1	15.6	61.5	31.3	17.5
Spatial						
Holo	SC – SF 57.1	SC – SO 44.8	SF – SO 58.7	AC – AF 55.4	AC – AO 43.1	AF – AO 61.6
Mero	SC – SF 30.2	SC – SO 5.2	SF – SO 16.1	AC – AF 27.3	AC – AO 3.2	AF – AO 10.1
Temporal						
Holo	SC – AC		SF – AF		SO – AO	

	62.2	58.5	63.8
Mero	SC – AC 58.3	SF – AF 26.7	SO – AO 14

Table 5. Biotic indices of the different communities expressed as mean values of the Shannon diversity index (H'), species richness (S), Margalef's index (d), Simpson's index (λ), Pielou's evenness index (J'), total abundance (N) and the ratio between holoplankton and meroplankton (H/M).

	Coastal	Summer Frontal	Oceanic	Coastal	Autumn Frontal	Oceanic
Diversity (H')	2,25	1,61	1,31	1,98	1,85	1,70
Richness (S)	42	26	21	36	30	21
Margalef's index (d)	13	9	8	11	11	9
Simpson's index (λ)	0.19	0.33	0.44	0.25	0.29	0.28
Evenness (J')	0.42	0.34	0.30	0.38	0.38	0.39
Total abundance (ind 1000 m ⁻³)	1665502	1314714	387248	1952373	538493	168932
Holoplankton/meroplankton (H/M)	4,27	51,71	557,31	2,74	47,40	418,66

Table 6. Non-parametric analysis (Mann-Whitney U Test) of the biotic indices (abbreviations defined in Table 5) plus meroplankton (mero) and holoplankton (holo) showing the spatial and temporal relationships between the different communities (abbreviations defined in Table 3). Asterisks indicate significant differences at levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s.: $p > 0.05$.

		H'	S	d	λ	J'	N	Mero	Holo
Spatial differences in summer	SC-SF	C>F ***	C>F ***	C>F ***	C<F **	C>F *	n.s.	C>F ***	n.s.
	SC-SO	C>O ***	C>O ***	C>O ***	C<O ***	C>O *	C>O ***	C>O ***	C>O ***
	SF-SO	n.s.	F>O *	n.s.	n.s.	n.s.	F>O **	F>O ***	F>O **
Spatial differences in autumn	AC-AF	n.s.	C>F **	n.s.	n.s.	n.s.	C>F ***	C>F ***	C>F **
	AC-AO	C>O *	C>O ***	C>O *	n.s.	n.s.	C>O ***	C>O ***	C>O ***
	AF-AO	n.s.	F>O **	n.s.	n.s.	n.s.	F>O **	F>O ***	F>O **
Temporal differences	SC-AC	S>A *	S>A ***	S>A *	S<A *	S>A *	n.s.	n.s.	n.s.
	SF-AF	n.s.	n.s.	S<A *	n.s.	n.s.	S>A **	n.s.	S>A *
	SO-AO	n.s.	n.s.	n.s.	n.s.	n.s.	S>A *	n.s.	S>A *

Table 4. Significant results of the regressions between environmental variables (averaged values in surface and column) against the taxa with highest contribution to the dissimilarity between communities.

Taxon	Variable	B	p	Taxon	Variable	B	p
<i>Pisidia longicornis</i>	Salinity	-0.48	<0.05	Appendicularia	Stability	0.31	<0.05

zoea	Stability	0.72	<0.00001				
Salpida	Temperature	0.61	<0.0001	Siphonophora	AOU	0.53	<0.001
	Fluorescence	-0.23	<0.05		Stability	0.53	<0.00001
	Stability	-0.28	<0.01				
Brachyura zoea	Stability	0.54	<0.0001	Cnidaria	Salinity	-0.4	<0.001
					Stability	0.57	<0.00001
Brachyura megalopa	Temperature	-0.36	<0.05	Amphipoda	Temperature	0.58	<0.001
Gasteropoda	AOU	-0.41	<0.05	Hyperidea	Stability	-0.38	<0.01
	Stability	0.25	<0.05	<i>Acartia clausii</i>	Fluorescence	-0.28	<0.05
					AOU	-0.63	<0.001
Ofiuroidea larvae	Stability	0.58	<0.0001	<i>Calanus helgolandicus</i>	Temperature	1.59	<0.05
Echinoidea larvae	Stability	0.30	<0.05	<i>Calanoides carinatus</i>	AOU	-0.66	<0.001
					Salinity	0.48	<0.001
Cirripedia larvae	Salinity	-0.26	<0.05	<i>Centropages chiercheai</i>	AOU	-0.73	<0.0001
	Stability	0.40	<0.001		Temperature	-2.2	<0.05
Paguridae zoea	Fluorescence	0.37	<0.01	<i>Oithona plumifera</i>	Salinity	0.73	<0.05
	Stability	0.25	<0.05		Fluorescence	0.29	<0.05
Processidae zoea	Salinity	-0.25	<0.05	<i>Paracalanus parvus</i>	AOU	0.50	<0.05
	Stability	0.67	<0.00001		Temperature	-0.37	<0.05
<i>Podon intermedius</i>	Stability	0.34	<0.001	<i>Paraeuchaeta hebes</i>	Salinity	-0.49	<0.001
					Temperature	0.34	<0.05
					Salinity	0.29	<0.05
					Fluorescence	-0.24	<0.05
Mysidacea	Fluorescence	-0.26	<0.05	<i>Paraeuchaeta spp.</i>	Fluorescence	-0.3	<0.05
Chaetognatha	Salinity	-0.45	<0.001	<i>Temora longicornis</i>	Salinity	0.28	<0.05
	Fluorescence	0.25	<0.05		Stability	0.27	<0.05

Table 5. Multiple regression coefficients of PCO2 scores on each station sampled (T: transect; C: integrated column sample; S: surface samples) against continuous variables delayed up to 4 days (lag numbers 0 to 4). Only significant coefficients ($p < 0.05$; $n = 10$) are shown. Abbreviations. Ano11.3 m: anomaly of density at 11.3 m; QrMi: outflow from Miño river; QrOi: outflow from Oitabén-Verdugo river; -Qx: upwelling index; SST: Sea surface temperature; T° 4.3m: temperature at 4.3 m; u: east-west surface current direction; v: north-south surface current direction.

		lag	T5C	T5S	T4C	T4S	T3C	T3S	T2C	T2S
-Qx	β	0	-0.75	-0.62	-0.48	-0.91	-0.43	-0.64	-0.42	-0.30
		1			-0.34		-0.37		-0.38	-0.56
		R ²	0.57	0.38	0.60	0.82	0.57	0.41	0.58	0.65
QrMi	β	0					0.26		0.49	0.36
		1	0.58	0.65	0.59	0.42	0.38	0.53		
		R ²	0.34	0.43	0.35	0.18	0.33	0.32	0.24	0.13
QrOi	β	1	16.13	8.44	13.04	22.26	12.31	13.18	12.34	11.78
		3	3.86	1.64	2.61	5.01	2.48	3.11	2.24	2.86
		R ²	0.31	0.15	0.18	0.30	0.16	0.14	0.19	0.22
Ano11.3m	β	0				0.41		0.49		
		1		1.30						10.11
		2		4.00						29.70
		3								10.05
		4	0.73		0.86	2.19	0.92	2.25	0.92	
		R ²	0.73	0.81	0.93	0.88	0.93	0.82	0.92	0.84
T° 4.3m	β	1	18.32	7.10	6.20	11.76	4.28	7.46	0.85	4.00
		2	25.30	8.73	6.25	9.74	3.35	9.68	4.20	
		3	1.77	6.25	6.27	2.12	6.35	5.71	6.35	
		4		3.43	4.42	1.91	6.05	4.04		2.16
		R ²	0.91	0.88	0.95	0.88	0.92	0.84	0.88	0.83
SST	β	3	-0.67	-0.76	-0.81	-0.73	-0.8	-0.63	-0.92	-0.72
		R ²	0.44	0.57	0.65	0.54	0.65	0.40	0.85	0.52

u	β	0	0.82	0.65	0.63	0.88	0.42	0.71	0.72
		1	0.42	0.36	0.35	0.30	0.31	0.15	0.51
		2	0.50	0.44	0.46	0.58	0.38	0.29	0.74
	R^2		0.34	0.20	0.18	0.28	0.09	0.03	0.24
v	β	0			0.26	0.45	0.32	0.32	0.50
		1			0.31	0.41	0.38	0.39	0.58
		2	0.58	0.64	0.35		0.34	0.39	0.54
		3							0.40
	R^2		0.34	0.41	0.50	0.45	0.62	0.71	0.66

Table 9. Results of DISTLM model showing the marginal tests on each variable, with the proportion of variability explained for each variable (Prop.), as well as the results of the model obtained with “best” selection procedure on the basis of BIC selection criterion.

Variable	Marginal tests			Sequential test			
	Pseudo-F	P-value	Prop.	Pseudo-F	P-value	Prop.	Cumulative
log (H/M)	50.435	0.0001	0.396	50.435	0.0001	0.396	0.396
log (N)	33.865	0.0001	0.305	13.859	0.0001	0.093	0.489
Moon	3.440	0.0005	0.121	3.5564	0.0001	0.065	0.554
-Qx	8.235	0.0001	0.083	11.556	0.0001	0.062	0.616
S	30.54	0.0001	0.284	4.8639	0.0001	0.025	0.640

Table 10. Results of DISTLM model obtained with “step-wise” selection procedure on the basis of adjusted R^2 as selection criterion, showing the marginal tests on each variable, with the significance (p-value), the proportion of variability explained for each variable (Prop), and the total variation explained for each set of variables (% Var).

Set	Variables	Marginal tests		
		p-value	Prop	% Var
Biotic	log(H/M)	0.001	0.396	54.5
Biotic	log(N)	0.001	0.305	
Biotic	S	0.001	0.284	
Biotic	H'	0.003	0.097	
Biotic	d	0.001	0.093	
Hydrographic	T°4.3m	0.001	0.249	47.7
Hydrographic	log(fluo)	0.001	0.105	
Hydrographic	Ano 11.3m	0.001	0.087	
Hydrographic	Salt	0.001	0.078	
Hydrographic	v	0.001	0.074	
Hydrographic	log(stab)	0.001	0.069	
Hydrographic	SST	0.004	0.063	
Hydrographic	AOU	0.018	0.049	
Hydrographic	u	0.046	0.034	
Hydrographic	T°	0.231	0.016	
Meteorologic	QrMi	0.001	0.161	39.9
Meteorologic	-Qx	0.001	0.083	
Meteorologic	Moon 4	0.004	0.057	
Meteorologic	Moon 2	0.022	0.039	
Meteorologic	Moon 3	0.029	0.034	
Meteorologic	Moon 1	0.107	0.024	
Meteorologic	QrOi	0.67	0.008	

Fig. 1. Sampling area showing the transects where mesozooplankton samples were collected and CTD casts marked with an asterisk (Ría de Vigo, NE Atlantic Ocean), as well as the location of the Silheiro and Rande observatories on the inset.

899 **Fig. 2.** (a) Wind speed and direction (m s^{-1}); (b) upwelling index ($-Q_x$, $\text{m}^3 \cdot \text{s}^{-1} \cdot \text{km}^{-1}$);
900 and (c) surface currents (cm s^{-1}) recorded at the Silleiro Seawatch buoy; (d) sea surface
901 temperature (SST, $^{\circ}\text{C}$) from the Silleiro Seawatch buoy ($42^{\circ} 7.8' \text{N}$, $9^{\circ} 23.4' \text{W}$) and
902 Rande observatories ($42^{\circ} 17.4' \text{N}$, $8^{\circ} 39.6' \text{W}$); (e) daily average discharge from Miño
903 and Oitabén-Verdugo rivers (Q_r in $\text{m}^3 \text{s}^{-1}$). Vertical bars mark the sampling days.

Fig. 3. Profiles of temperature, salinity, Chl-*a* fluorescence and apparent oxygen utilization (AOU) recorded at transects number 2 (30 m depth) and 5 (95 m depth) throughout the sampling days.

Fig. 4. Ordination PCO plot with superimposed cluster grouping samples according to coastal-ocean gradient (PCO1) and sampling period / hydrographic characteristics (PCO2). Symbols represent the different communities identified: SC, summer coastal; SF, summer frontal; SO, summer oceanic; AC, autumn coastal; AF, autumn frontal; AO, autumn oceanic.

Fig. 5. PCO plot showing the temporal variation of mesozooplankton samples collected at transect 3 along the ten surveys (1 to 10) at a) surface and b) column.

Fig. 6. Holoplankton and meroplankton abundances (ind m^{-3}), together with the relative importance of the principal mesozooplankton groups found in the different communities. Community abbreviators as defined in Fig. 5.

Fig. 7. Distance-based redundancy (dbRDA) plot illustrating the DistLM model based on the mesozooplankton assemblage data and selected variables under BIC criterion. Symbols represent the different communities. log(H/M): holoplankton-meroplankton ratio logarithm; log(N): mesozooplankton total abundance logarithm; Moon 1-4: four moon phases; -Qx: upwelling index; S: richness.

Fig. 8. Flow diagram showing the sources of variability (as percentages) affecting the resemblance matrix of mesozooplankton samples collected in the Ría de Vigo.

944 **Annexe 1.** Mean abundance (ind 1000 m⁻³) of zooplankton taxa in each community.

945 Asterisks indicate species that were not included in the multivariate analysis.

Taxon	Summer			Autumn		
	Coastal	Frontal	Oceanic	Coastal	Frontal	Oceanic
Meroplankton						
Fish larvae	3857.2	1775.0	125.0	1456.3	169.5	76.5
Fish eggs	1092.3	207.7	106.0	4840.3	200.9	-
Isopoda Aegidae	21.4	1.6	0.9	33.7	26.6	10.5
Isopoda Cyrolanidae*	-	-	-	7.9	1.6	-
Isopoda Gnathiidae*	-	-	0.5	-	-	-
Cumacea	205.2	89.3	46.4	110.6	88.8	8.1
Cirripedia larvae	25626.2	1332.8	-	135228.7	5161.1	59.2
Brachyura zoea	60756.3	12760.3	557.0	29978.6	1990.8	85.6
Brachyura megalopa	2748.9	4907.2	335.4	1108.4	259.0	26.3
Brachyura juvenile	14.8	64.8	25.9	2.3	2.6	1.7
Galatheid zoea	1536.5	48.3	-	585.4	631.0	31.6
<i>Pisidia longicornis</i> zoea	22775.2	865.2	116.4	23186.1	-	-
<i>Pisidia longicornis</i> megalopa	1149.2	-	-	897.4	-	-
<i>Porcellana platycheles</i> zoea	4547.4	182.2	194.0	32032.7	184.2	-
Galatheid megalopa*	56.1	154.1	-	-	-	-
Paguridae zoea	8681.0	982.5	-	5730.8	1375.2	60.4
Paguridae megalopa*	-	649.7	-	252.6	-	-
<i>Scyllarus arctus</i> *	52.1	-	40.2	-	-	-
Crangonidae zoea	375.4	85.3	-	698.9	26.8	-
Crangonidae megalopa*	-	-	-	15.4	50.1	-
Palaemonidae zoea	907.0	-	76.8	630.2	29.8	-
Processidae zoea	1445.6	318.9	121.6	3973.9	370.8	51.2
Hippolitidae zoea	353.1	-	-	1046.9	168.6	87.6
Alpheidae zoea	1792.4	1273.0	79.0	525.6	173.4	52.3
<i>Jaxea nocturna</i> *	571.3	-	-	64.7	-	-
Penaeidae zoea*	52.1	-	-	-	140.7	-
<i>Meiosquilla desmaresti</i>	0.4	240.1	147.8	-	-	5.2
<i>Platysquilla eusebia</i>	-	117.8	-	-	-	-
Briozoa larvae*	-	-	-	478.5	-	-
Amphipoda Gammaridea	311.6	115.0	86.5	562.1	255.9	88.6
Amphipoda Caprellidea	5.7	-	-	5.2	13.6	20.9
Tanaidacea*	0.5	-	-	-	-	-
Ophiuroidea larvae	290802.4	103.9	-	641873.0	6596.4	-
Equinoidea larvae	78566.2	-	-	14267.9	129.3	-
<i>Octopus vulgaris</i>	8.7	4.2	1.9	19.2	59.5	3.6
Loliginidae	5.3	15.3	-	7.2	4.5	2.0
<i>Sepiella atlantica</i>	5.2	3.7	0.2	1.8	3.5	-
Ommastrephidae paralarvae*	-	-	-	0.2	-	-
Bivalvia larvae	867.5	-	-	161.4	-	-
Nudibranchia larvae*	0.1	-	-	-	-	-
<i>Lamellaria perspicua</i> *	0.3	-	-	-	-	-
Gastropoda larvae	19417.2	3711.1	219.4	21447.4	1440.9	12.5
Polychaeta larvae	495.6	2.8	25.4	137.3	18.1	35.3
Holoplankton						
Siphonophora	8748.4	1206.5	117.9	38073.4	2328.1	588.2
Cnidaria	1185.0	220.9	-	13469.6	701.5	110.6
Pteropoda*	469.1	-	27.9	-	-	-
Trematoda digenea	860.4	115.0	-	363.0	32.3	25.5
<i>Tomopteris</i> spp.	-	-	-	231.4	323.2	71.4
Chaetognatha	11020.9	4384.5	2838.0	76317.7	32060.3	16780.6
Salpida	45102.1	119867.2	213747.0	24926.6	32755.7	61478.5
Appendicularia	185071.6	397.5	54.5	222062.0	8101.2	-
Doliolida*	812.2	-	-	56.1	-	-
<i>Branchiostoma lanceolatum</i> *	76.5	-	-	-	-	-
<i>Evadne nordmanni</i>	28669.1	1003.4	220.2	22643.5	519.3	-
<i>Podon intermedius</i>	68166.0	2887.5	354.5	17058.5	96.9	-
Ostracoda	56.1	-	-	-	-	-
<i>Nyctiphanes couchii</i> calyptopis	199067.0	426896.2	6626.3	249736.0	235947.8	12151.3
<i>N. couchii</i> furcilia	182578.5	259331.2	9476.6	158338.2	58138.7	3981.0
<i>N. couchii</i> adults	100.3	21720.3	2491.0	346.1	32262.3	15485.6

<i>Solenocera membranacea</i> *	56.1	-	-	-	19.3	-
Mysidacea	4284.9	3189.0	2190.3	1400.6	2668.7	3691.8
Amphipoda Hyperiidea	4.6	113.6	168.7	28.6	38.7	183.0
Copepods						
<i>Calanus helgolandicus</i>	14330.5	51450.6	36756.1	5678.5	11233.4	2681.1
<i>Mesocalanus tenuicornis</i>	212.0	-	-	144.7	176.3	235.3
<i>Pseudocalanus elongatus</i>	1976.0	891.6	23.2	1356.6	3143.9	247.9
<i>Subeucalanus crassus</i> *	-	-	-	38.7	-	14.0
<i>Paracalanus parvus</i>	-	795.0	40.2	12847.4	6828.5	1621.2
<i>Clausocalanus</i> spp.	10289.8	2538.6	483.7	4760.37	4823.9	268.1
<i>Ctenocalanus vanus</i>	-	600.2	-	697.5	53.0	137.5
<i>Calanoides carinatus</i>	7050.1	126273.3	62403.6	12795.9	24566.5	4143.6
<i>Centropages chierchiae</i>	8683.0	20464.0	1513.0	5393.2	871.2	145.1
<i>C. typicus</i>	200.7	-	-	1664.9	212.8	-
<i>Paraeuchaeta hebes</i>	7244.3	14135.4	14186.8	2401.6	5409.2	7891.2
<i>Paraeuchaeta</i> spp.	18785.0	23369.0	23422.6	11334.0	12938.8	20097.2
<i>Aetideus armatus</i> *	-	-	23.2	15.4	-	-
<i>Temora longicornis</i>	69319.9	99413.6	979.1	23221.4	1480.2	44.2
<i>T. stylifera</i> *	-	-	61.2	-	-	-
<i>Acartia clausi</i>	231558.7	101237.6	6499.2	106228.1	39961.0	14914.3
<i>Scolecithricella</i> spp.*	465.9	204.3	-	-	-	-
<i>Metridia lucens</i>	945.6	322.7	224.0	896.7	287.0	976.4
<i>Pleuromamma gracilis</i>	-	-	54.5	44.9	-	-
<i>Candacia armata</i>	443.5	24.1	40.2	40.0	-	-
<i>Parapontella brevicornis</i> *	1863.4	-	-	-	-	-
<i>Isias clavipes</i>	4015.9	1030.2	-	1837.8	184.2	-
<i>Diaxis pygmaea</i> *	-	-	174.7	-	-	12.5
<i>Oithona nana</i>	371.7	-	-	666.3	19.3	-
<i>O. similis</i> *	690.3	-	-	-	-	-
<i>O. plumifera</i>	2415.7	-	-	12044.2	193.0	124.6
<i>Corycaeus</i> spp.	152.9	-	-	94.8	347.6	-
Sapphirinidae*	-	-	0.5	-	-	-
Siphonostomatoida*	0.1	-	-	-	-	-
Monstrilloida*	-	-	-	518.7	-	-
Harpacticoida	1362.3	484.7	1.2	405.5	53.0	2.6
<i>Euterpina acutifrons</i> *	16770.9	-	-	-	-	-
Calanoid copepodit	424.0	115.0	-	824.1	151.6	188.3