

# Factors determining the distribution and betadiversity of mesozooplankton species in shelf and coastal waters of the Bay of Biscay

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In this study, we analysed the factors explaining the distribution and betadiversity of mesozooplankton species in shelf and coastal areas in the Bay of Biscay. Nonparametric multiplicative regression models showed that for 35% of the 26 species analysed, the geographical position was the main factor explaining distribution. The variation partitioning results of the betadiversity analysis indicate that niche adaptation (12–25%) and dispersal limitation (14–15%) influence the distribution of mesozooplankton species equally. Therefore, most of the variance (57–66%) remains unexplained suggesting there are other explaining factors not controlled or that a part of the variability is purely stochastic. A log-normal distribution fitted the species rank-abundance better than Hubbell's neutral model, which also indicates that the mesozooplankton distribution is not the result of pure neutral communities colonizing randomly from a large species pool. Overall, the combination of results suggests that mesozooplankton species have distribution centres that are often associated with geographical features, and from which they disperse randomly.

**KEYWORDS:** mesozooplankton; habitat models; betadiversity; Bay of Biscay

## INTRODUCTION

During the last decades, plankton researchers have worked hard to obtain data at spatial resolutions comparable with those obtained by physical oceanographers. The lack of spatial and temporal resolution has been identified as one of the main limitations to understanding the factors determining zooplankton distribution (Haurly *et al.*, 1978). Based on major distribution patterns (Bary, 1964; Beaugrand *et al.*, 2002), and influenced by the fact that benthic communities are classified in terms of seabed characteristics, it has been suggested that it should be possible to relate plankton species and communities to water masses defined by their temperature

and salinity at lower spatial scales (e.g. Krause *et al.*, 1995; Bonnet and Frid, 2004). Mauchline (Mauchline, 1998) states that “Salinity and salinity-temperature interactions of copepods control their distributions in coastal and estuarine situations”. The definition of plankton as organisms that cannot swim against the current underlies this relationship: plankton are transported along with the surrounding water mass, and the species most adapted to the water mass conditions (niche) will increase in abundance. It has been assumed that these associations have not been properly described due to low sampling resolution and the non-linear nature of these relationships. However, mesozooplankton are not passive organisms,

they can carry out vertical migrations that vary depending on light and predation fields (Ohman, 1990, Pearre, 2000, Irigoien *et al.*, 2004). Transport direction is related to depth (Fiksen *et al.*, 2007), and therefore the dispersion of organisms moving vertically is less likely to be associated with a particular water mass and more likely to be random.

If dispersion is limited and mainly random, the distribution of mesozooplankton species could be explained by the neutral theory of biodiversity instead of niche adaptation (Hubbell, 2001; McGill, 2003; Dornelas *et al.*, 2006; Pueyo, 2006). Despite the fundamental role played by dispersal in structuring populations, there is still little known about the dispersal strategies of many marine species due to the difficulty of tracking the trajectory and fate of propagules (Weersing and Toonen, 2009). In neutral communities, where all individuals are assumed to have the same prospects for reproduction and death, as well as limited dispersal, the variability in relative abundances between species is due entirely to demographic stochasticity or “ecological drift”. Therefore, the similarity of species among sampling sites is expected to decrease logarithmically with increasing geographical distance (Hubbell, 2001). Another concept of the neutral theory of biodiversity is that the frequency of species, in relation to abundance, will follow a Fisher’s log-series distribution (in the case where migration between local community and meta-community is not limited); an example of which is the tintinnids in the Pacific (Dolan *et al.*, 2007).

In the Bay of Biscay, a number of hydrological seascapes have been defined over French shelf areas in relation to water mass characteristics (Planque *et al.*, 2004), which seem to be related to the distribution of mesozooplankton species across a transect (Albaina and Irigoien, 2004). However, in a high spatial resolution analysis of the zooplankton community over a large area of the French shelf, the relation to the water masses was not clear (Albaina and Irigoien, 2007). Further, habitat models for phytoplankton biomass have shown that the geographical position explains a higher percentage of the variability than water mass characteristics in this area (Zarauz *et al.*, 2008). Zarauz *et al.* (Zarauz *et al.*, 2008) argued that this was due to the biomass being related to hydrographical features, such as river plumes, upwellings and fronts, which are persistent structures related to geographical features rather than to physical conditions *per se*.

However, the question remains of whether the same conclusion applies when species rather than biomass is considered. In this paper, we use habitat modelling (Guisan and Zimmermann, 2000; McCune, 2009), betadiversity variance partitioning and species rank-abundance to analyse whether the distribution of

mesozooplankton species is related to water mass characteristics in shelf and coastal areas of the Bay of Biscay, which factors determine the change in species composition, and to what extent the betadiversity fits, if at all, the neutral theory of biodiversity.

## MATERIAL AND METHODS

### Zooplankton samples and CTD

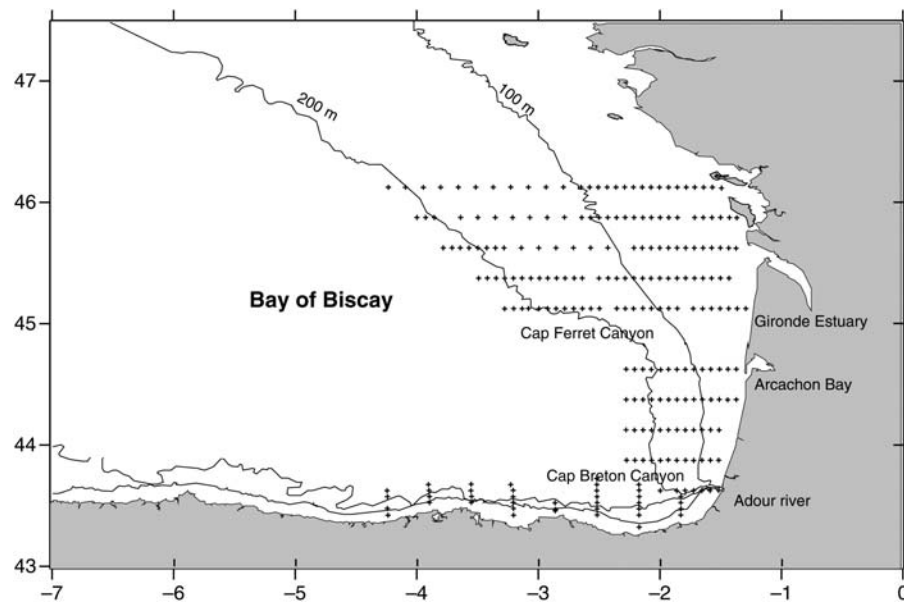
The collection and identification of zooplankton samples are described fully by Albaina and Irigoien (Albaina and Irigoien, 2007). Briefly, zooplankton samples were collected from 2 to 16 May 2004, in a grid of 267 stations. Consecutive stations were 3 nautical miles (nm) apart located in transects spaced 15 nm apart covering the Bay of Biscay from 43.32°N to 46.12°N and from 1.29°W to 4.31°W (Fig. 1). Samples were collected using vertical hauls of a 150  $\mu$ m PAIROVET net (double CalVET, Wiebe and Benfield, 2003) fitted with a flowmeter and lowered to a maximum depth of either 100 m, or 5 m above the bottom at shallower stations. Net samples were preserved immediately after collection with 4% borax-buffered formaldehyde. The qualitative and quantitative analyses of zooplankton were carried out under a stereoscopic microscope and identification was made to species or genus level in the majority of the holoplanktonic groups, and to general categories in meroplanktonic forms. In each sample, a minimum of 200 individuals (all categories included) was counted.

The sampling is continuous during day and night and therefore parts of the survey are covered at different times of the day. This could have an effect on the observed distribution of vertically migrating species. However, with the sampling to 100 m, in a large part of the area the whole water column is sampled. Further, Albaina and Irigoien (Albaina and Irigoien, 2007) did not observe day/night differences in mesozooplankton density, suggesting that the bias due to missing vertical migrators in the stations sampled at day was minor.

The nets were also fitted with a Conductivity, Temperature and Depth data logger (CTD; model RBR XR-420) with a fluorescence sensor (Seapoint Chlorophyll Fluorometer; Seapoint Sensors, Inc.).

### Habitat models

Habitat models were built using non-parametric multiplicative models implemented in Hyperniche (NPMR, McCune, 2009). The model selected was a Gaussian weighting function with a local mean estimator.



**Fig. 1.** Study area showing the sampled stations.

The percentage improvement for including new predictors into the model was set at 5%. The goodness of fit is expressed in terms of a cross validated  $R^2$  ( $xR^2$ ). In NPMR models, tolerance corresponds to the smoothing parameter for each quantitative parameter. Sensitivity evaluates the importance of individual variables by evaluating the effects of changing the value of a variable in the final output of the model. A value of 1 implies that nudging the predictor results in a modification of the output of the same magnitude, and 0.5 implies that the response is half the magnitude of the change in the predictor. The notation of the sensitivity analysis and details can be found in McCune (McCune, 2009).

### Selected taxonomic categories for habitat models

Based on the categories outlined by Albaina and Irigoien (Albaina and Irigoien, 2007), habitat maps were produced for the specimens identified to species level or genus level when one species was dominant in the area (e.g. *Centropages typicus* and *Centropages chierchiae*). As a general rule, only those groups that were present in more than 40% of the sampled stations were considered for habitat modelling (Table I). The 40% limit was decided after regressing the percentage of occupied stations against the  $xR^2$  of the habitat model (Supplementary data, Fig. A3). When species that appeared in less than 40% of the stations were included, there was a significant relation between the percentage of positive stations for the species and the amount of

variability explained by the model. However, this relation did not hold for groups present in more than 40% of the stations (Supplementary data, Fig. A4). We used the Shannon index of diversity and considered the copepods identified at least to the genus level as the biodiversity descriptor (see Supplementary data, Table A1).

### Hydrographic explanatory variables

The depth of the CTD casts was 100 or 5 m above the bottom. Salinity, temperature and fluorescence profiles were smoothed for each 2 m interval. Seawater density ( $\sigma$  and  $\sigma$ -t) was estimated using the equation of state of sea-water (Fofonoff and Millard, 1983). From these measurements, we derived the following descriptors of the water column: temperature, salinity and density at the surface and bottom, the difference in density between the surface and bottom and the maximum Brunt–Väisälä frequency in the vertical profile (Supplementary data, Fig. A1).

### Biological explanatory variables

As explanatory variables representing food we used integrated fluorescence (0–100 m or to the bottom if less), depth of the maximum fluorescence and level of fluorescence at the maximum of fluorescence. We also included indexes of abundance of some predators derived from the net samples as potential explanatory variables: chaetognath abundance, jellyfish abundance and fish egg abundance (Supplementary data, Fig. A2).

Table I: NPMR models for the selected species and the Shannon diversity index for copepods

Species	% stations present	xR <sup>2</sup>	Explanatory variable 1	Tolerance	Sensitivity	Explanatory variable 2	Tolerance	Sensitivity	Explanatory variable 3	Tolerance	Sensitivity	Explanatory variable 4	Tolerance	Sensitivity
1 <i>Calanoides carinatus</i>	41	0.14	Latitude	0.28	0.61	Density bottom	0.29	1.34						
2 <i>Calanus helgolandicus</i>	90	0.62	Latitude	0.28	0.35	Depth	741.30	0.05	Density bottom	0.44	0.16	Density difference	0.22	0.16
3 <i>Mesocalanus tenuicornis</i>	40	0.78	Latitude	0.42	0.07	Longitude	0.30	0.48	Depth	864.85	0.06			
4 <i>Eucalanus</i> sp.	41	0.37	Latitude	0.28	0.48	Longitude	0.30	0.53	Chaetognaths abundance	9.07	0.10			
5 <i>Calocalanus</i> sp.	46	0.48	Longitude	0.44	0.29	Depth	741.30	0.16	Density surface	0.29	1.51			
6 <i>Paracalanus parvus</i>	84	0.34	Latitude	0.42	0.30	Salinity surface	0.37	1.36	Salinity bottom	0.32	0.40			
7 <i>Clausocalanus</i> sp.	81	0.09	Density bottom	0.29	1.53	Jellyfish abundance	83.04	0.31						
8 <i>Pseudocalanus elongatus</i>	55	0.66	Brunt-Väisälä frequency	3.49	1.00	Temperature surface	0.28	0.49	Fish eggs abundance	3.17	1.46			
9 <i>Ctenocalanus vanus</i>	62	0.37	Latitude	0.42	0.28	Salinity surface	0.37	1.12	Fluorescence maximum	1.09	0.12			
10 <i>Temora longicornis</i>	93	0.71	Latitude	0.28	0.19	Brunt-Väisälä frequency	1.74	0.59	Salinity surface	0.37	0.55			
11 <i>Centropages</i> sp.	91	0.57	Brunt-Väisälä frequency	1.74	1.82	Salinity bottom	0.16	1.12	Fluorescence maximum	3.82	0.01			
12 <i>Acartia clausi</i>	90	0.62	Latitude	0.42	0.19	Brunt-Väisälä frequency	3.49	0.21	Temperature bottom	0.29	0.17	Depth of fluorescence maximum	14.10	0.11
13 <i>Oithona helgolandica</i>	100	0.75	Latitude	0.14	0.50	Longitude	1.03	0.03	Brunt-Väisälä frequency	1.74	0.76			
14 <i>Oithona nana</i>	92	0.69	Brunt-Väisälä frequency	1.74	1.91	Salinity surface	2.60	0.05	Salinity bottom	0.16	1.27	Temperature bottom	0.59	0.06
15 <i>Oithona plumifera</i>	75	0.83	Latitude	0.28	0.16	Longitude	0.30	0.44	Depth	741.30	0.05			
16 <i>Corycaeus</i> sp.	81	0.66	Latitude	1.26	0.04	Longitude	0.15	0.76	Brunt-Väisälä frequency	1.74	0.79	Fluorescence maximum	1.91	0.04
17 <i>Oncaea</i> sp.	100	0.78	Longitude	0.15	0.59	Brunt-Väisälä frequency	1.74	0.68	Temperature bottom	0.39	0.08	Fluorescence maximum	2.46	0.02
18 <i>Euterpina acutifrons</i>	62	0.67	Salinity surface	1.86	0.10	Salinity bottom	0.32	0.47	Density bottom	0.88	0.06	Depth of fluorescence maximum	4.70	0.23
19 <i>Microsetella</i> sp.	75	0.23	Latitude	0.28	0.62	Depth	617.75	0.10	Density surface	0.29	0.97			

Continued

Species	% stations present	xR <sup>2</sup>	Explanatory variable 1	Tolerance	Sensitivity	Explanatory variable 2	Tolerance	Sensitivity	Explanatory variable 3	Tolerance	Sensitivity	Explanatory variable 4	Tolerance	Sensitivity
20 <i>Fritillaria</i> sp.	76	0.69	Latitude	0.28	0.19	Longitude	0.44	0.22	Depth	617.75	0.05	Integrated fluorescence	50.57	0.09
21 <i>Oikopleura</i> sp.	61	0.80	Brunt–Väisälä frequency	3.49	1.03	Difference density	0.22	1.11	Integrated fluorescence	37.93	0.68	Integrated fluorescence	50.57	0.07
22 <i>Appendicularia</i> sp.	58	0.58	Latitude	0.56	0.07	Longitude	0.30	0.23	Temperature surface	0.56	0.08	Integrated fluorescence	50.57	0.07
23 <i>Noctiluca scintillans</i>	97	0.57	Latitude	0.56	0.11	Longitude	0.30	0.44	Density surface	0.29	0.66	Integrated fluorescence	50.57	0.07
24 <i>Solmundella bitentaculata</i>	49	0.29	Latitude	0.42	0.42	Longitude	0.30	0.38	Depth of fluorescence maximum	23.50	0.13	Integrated fluorescence	50.57	0.07
25 <i>Podon</i> sp.	75	0.31	Latitude	2.10	0.03	Brunt–Väisälä frequency	3.49	0.40	Depth of fluorescence maximum	18.80	0.31	Fish eggs abundance	3.17	1.62
26 <i>Evadne nordmani</i>	62	0.39	Latitude	0.28	0.26	Depth	741.30	0.07	Temperature surface	0.14	0.52	Integrated fluorescence	50.57	0.07
H diversity index copepods		0.60	Latitude	0.28	0.44	Longitude	0.30	0.67	Salinity surface	1.11	0.19	Depth of fluorescence maximum	1.90	0.07

### Betadiversity

In order to determine the relative contribution of environmental factors and geographical distance to biodiversity (the rate of change in species composition), we calculated similarity matrices and used Mantel tests and variation partitioning of the mesozooplankton composition across sites. Given the set of  $n = 237$  stations and  $m = 24$  species (those most abundant, i.e. present in at least 10% of stations), we computed an  $n \times n$  species similarity matrix. Each entry  $(i, j)$  of the similarity matrix is an index that measures the pairwise compositional similarity between station  $i$  and station  $j$ . Two indices were used in this study. The Jaccard similarity index (for presence–absence data) is the number of species shared between the two plots, divided by the total number of species observed. The Bray–Curtis similarity index (for abundance data) is defined by  $2W/(A + B)$ , where  $W$  is the sum of the minimum abundances of all species (i.e. number of individuals) between two stations where the species were sampled, and  $A$  and  $B$  are the sums of the abundances of all species at the two stations.

We used Mantel tests (Legendre and Legendre, 1998) to determine the correlation between species similarity matrices and environmental similarity matrices, and geographical distance. This test computes a statistic  $r_M$  which measures the correlation between two matrices and results from the cross product of the matrix elements after normalizing them. The statistic  $r_M$  is bounded between  $-1$  and  $+1$ , and behaves like a correlation coefficient. Since similarity and distance matrix entries are not independent, the Mantel statistic is tested by a non-parametric permutation test (999 permutations were computed for each test). Before performing the Mantel test, we converted both similarity measures (Jaccard and Bray–Curtis) to a distance measure ( $1 - \text{similarity}$ ). The distance matrices for environmental variables were defined as the Euclidean distance between values at two stations. The geographical distance among sampling sites was also measured with the Euclidean distance.

We partitioned the variance of the mesozooplankton composition across sites to determine the relative contribution of environmental factors and geographical distance. The total inter-site variation in species abundances was decomposed into four components: pure effect of environment, pure effect of geographical distance, combined variation due to the joint effect of environment and geographical distance and unexplained variation. The variance partitioning analysis has two steps. For environmental variables, we used the *vegan* package (Oksanen *et al.*, 2006) implemented in the R language to select the best subset of environmental

variables so that the Euclidean distances of scaled environmental variables have the maximum correlation with community dissimilarities. As we considered 15 environmental variables (bottom depth, temperature, salinity and density at the surface and bottom, the difference in density between the surface and bottom, Brunt–Väisälä frequency, integrated fluorescence, depth of the maximum fluorescence, level of fluorescence at the maximum of fluorescence and the abundances of chaetognaths, jellyfish and fish eggs), 32 767 possible subsets were compared. A partial Mantel test was then carried out to determine the relative contribution of environmental distance (after selection) and geographical distance to species variation.

### Species abundance distributions

Different models of community organization according to species-rank abundance were fitted to test whether the mesozooplankton community follows the neutral theory of random colonization from a large species pool. Species log-rank abundance curves for the overall mesozooplankton assemblage were constructed and hypothetical models were fitted using the *vegan* (Oksanen *et al.*, 2006) and *untb* (Hankin, 2007) packages implemented in the R language. We used all identified species (i.e. 51) in order to take into account the relevant information from rare species. We fitted four different models of community organization (reviewed in Hubbell, 2001): (i) MacArthur's broken-stick distribution, which represents a random community assembly as a result of randomly apportioned limiting resources; (ii) the geometric series distribution [called the “pre-emption niche” model by Motomura and determined by Whittaker (Whittaker, 1972)], which is conceptually similar to the broken-stick model except that the partitioning of limiting resources is set by hierarchical dominance; (iii) Fisher's log-series distribution, which represents the result of random dispersal from a larger community in Hubbell's neutral theory, it is characterized by the widely used Fisher's  $\alpha$  parameter (coincident with the biodiversity number  $\theta$  generated by spatially implicit neutral theory); and (iv) Preston's log-normal distribution, which is one of the most common distributions found in nature. How exactly this last distribution comes about remains unexplained as it could arise from multiplicative interactions between many random processes that affect population growth, or it could arise from relationships between a large number of species with independent population dynamics. The best model was selected using the root mean squared error (RMSE), which was determined as the root of the mean of squared deviations between the observed and

predicted  $\ln$  (abundance) for all ranked  $S$  species. The lower the calculated RMSE value, the better the fit.

## RESULTS

The habitat models were able to predict species distribution ranges from an  $xR^2$  value of 0.09 for *Clausocalanus* sp. to 0.83 for *Oithona plumifera* (Table I). The value for *Clausocalanus* sp. probably indicates that it is part of a species complex because it appears as an outlier in terms of model performance. Examples of the observed and predicted distribution can be seen in Fig. 2. The whole set of figures of observed versus predicted results is available in the Supplemental Material.

In 9 out of the 26 species analysed (35%), latitude and longitude are the first variables selected to explain distribution (Table I). Latitude and depth and latitude and Brunt–Väisälä frequency are the following most common pairs with three cases each (11%). The only other pair of explanatory variables that are repeated is latitude and surface salinity (occurs twice, 7%). The interpretation is clear for some of the remaining cases, such as the relation between salinity and *Euterpina acutifrons* or between vertical stability and *Oikopleura* sp.; however, for the rest, there seems to be a component of coastal affinity expressed in terms of Brunt–Väisälä frequency, salinity and depth (Table I).

The NPMR models predict copepod biodiversity well (Table I).

In the betadiversity analysis, the Jaccard index ranged from 0.15 to 1.00 among pairs of sites (mean = 0.58), and the Bray–Curtis index from 0.04 to 0.96 among pairs of sites (mean = 0.50), evidencing the high similarity among plots in average and high variability. The best subsets of environmental variables selected to explain the maximum variation in the similarity of species were (Table II): Brunt–Väisälä frequency, surface salinity, the density at the bottom and jellyfish abundance for the Bray–Curtis index and the temperature at the bottom, the density at the surface and bottom and fish abundance for the Jaccard index. The two similarity indices correlate best with water density and predator abundance. The Bray–Curtis index showed a higher correlation with environmental factors than with geographical distance, while the Jaccard index had a slightly higher correlation with geographical distance (Table II). When abundance is taken into account, the variation partitioning indicates that the mesozooplankton composition is determined more by the environment (25%) than by geographical distance (13.5%) (Fig. 3); however, when the presence of species is considered, the geographical distance is slightly more

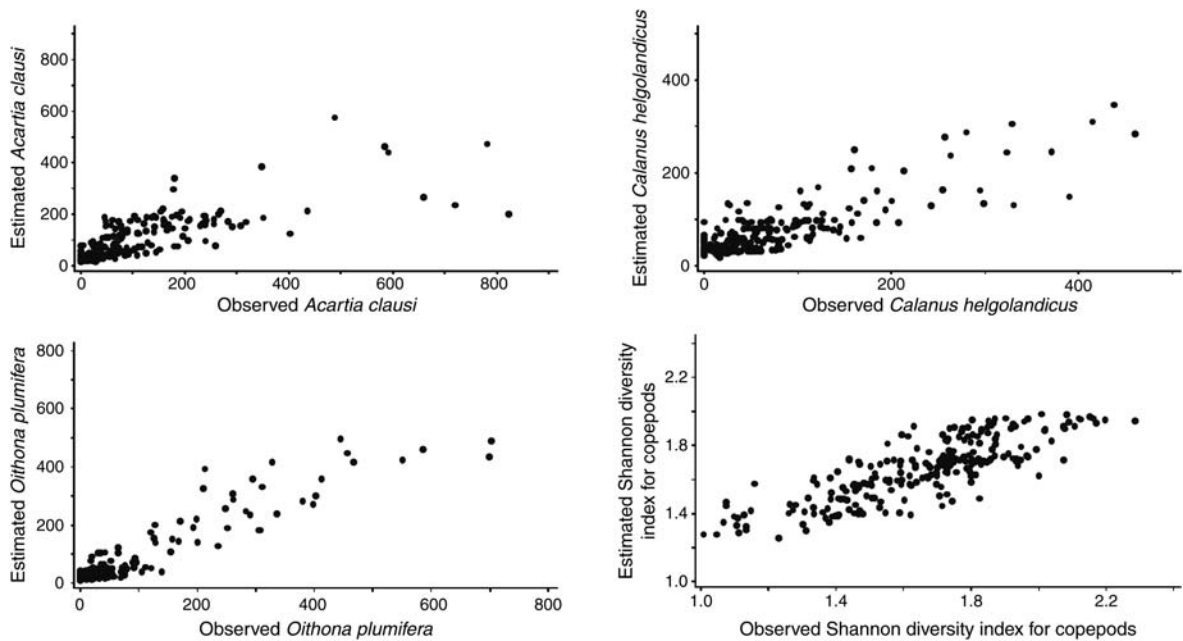


Fig. 2. Examples of the NPMR estimated abundances compared with observed abundances (ind. m<sup>-3</sup>) and diversity. From left to right and top to bottom *Oithona plumifera*, *Calanus helgolandicus*, *Acartia clausi* and Shannon diversity index for copepods.

Table II: Mantel and partial Mantel correlation coefficient between species similarity (Bray–Curtis and Jaccard) and environmental variables, and geographical distance

	Mantel <i>r</i>	<i>P</i> -value	Terms selected for environmental variables
Bray–Curtis × environment	0.54	0.001	Brunt–Väisälä frequency, salinity at surface, density at bottom, jellyfish abundance
Bray–Curtis × distance	0.43	0.001	
Bray–Curtis × environment (distance partially out)	0.50	0.001	
Jaccard × environment	0.44	0.001	Temperature at bottom, density at surface and at bottom, fish abundance
Jaccard × distance	0.47	0.001	
Jaccard × environ selec (distance partially out)	0.34	0.001	

The *P*-value of the significance test was obtained by computing 999 permutations.

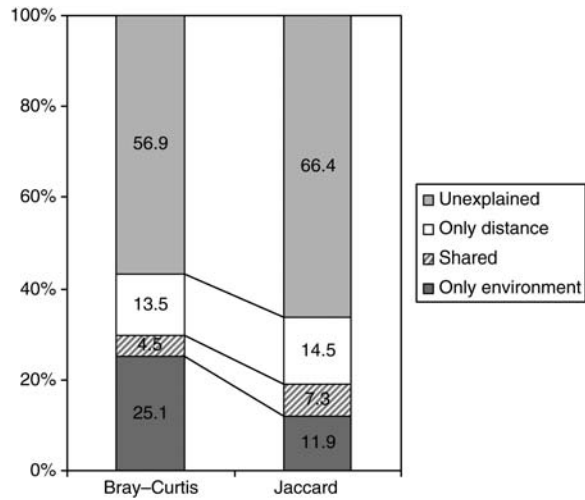
important (14.5 compared to 11.9%). In both cases, the shared explained variation is low and a high percentage of variation (60–66%) remains unexplained (Fig. 3).

Despite the small differences between the results that take into account abundance or presence–absence data, in both cases the role of geographical distance is significant. This implies that dispersal limitation affects the distribution of mesozooplankton species assemblages. This is illustrated in Fig. 4, in which the species similarity decreases with distance. In the Bray–Curtis index, a strong decay in similarity with the geographical distance is found at small scales (below ~120 km), followed by a nearly constant average value between 120 and 270 km. Beyond this threshold, the similarity decreases again with the geographical distance, which suggests that two spatial scales affect the assemblage compositions.

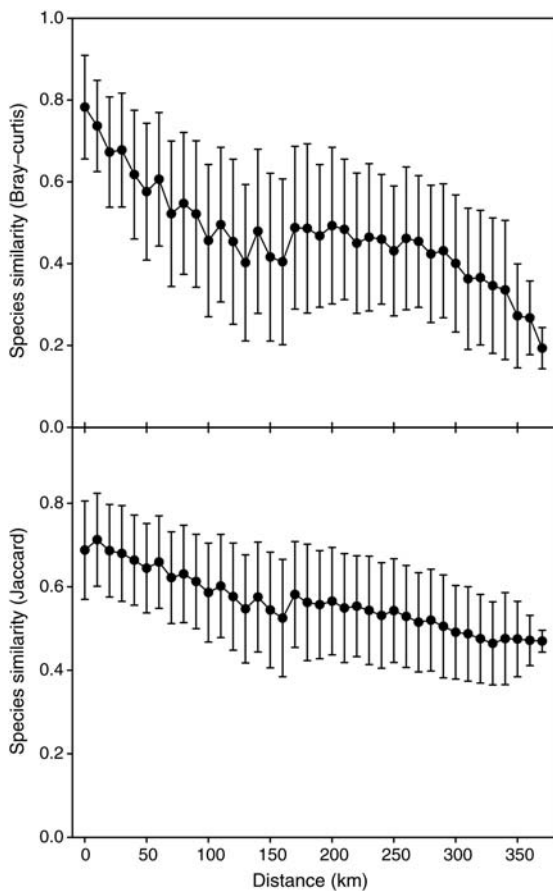
The best model fitted to the observed species rank in abundance is the log-normal distribution according to the RMSE value (0.35), followed by the log-series (RMSE = 0.82). The geometric and brokenstick models were clearly the two worst models (AIC of 3.25 and 4.54, respectively). Figure 5 shows graphically the good fit of the log-normal distribution, while the geometric and brokenstick models diverge, especially for rare species. The log-series model, with a Fisher’s  $\alpha$  of 3.9, has an intermediate fit to the observed data.

## DISCUSSION

One of the most interesting results of this study is that mesozooplankton species distribution has only a very limited relation to temperature and salinity contrary to

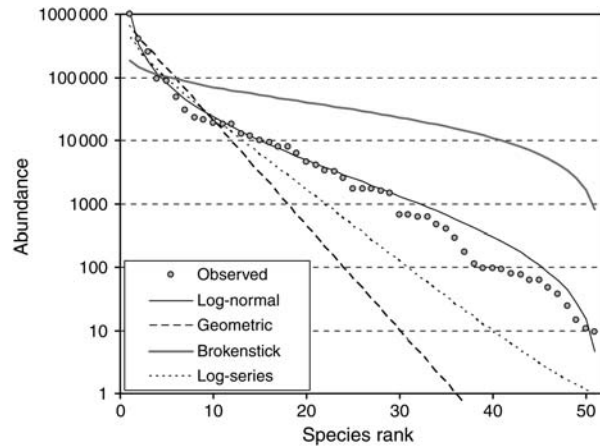


**Fig. 3.** Variation partitioning of species composition according to geographical distance and environmental determinants, based on the two similarity indices.



**Fig. 4.** Species similarity indices against geographical distance.

what is commonly expected (see as an example Fig. 5 in Albaina and Irigoien, 2007). Actually, these results challenge the previous interpretation of the species



**Fig. 5.** Species rank-abundance models fitted to the overall assemblage of mesozooplankton.

distribution where a procedure to select and discard explanatory factors was not used and position was not included as an explanatory factor (Albaina and Irigoien, 2007). That when included, spatial position has a higher explanatory power than water mass characteristics, raises the question of their respective role. It is clear that at large spatial scales, temperature (and salinity) plays a major role in the distribution of species (e.g. Brinton, 1962; Beaugrand *et al.*, 2002; Reygondeau and Beaugrand, 2010). Furthermore, temperature and salinity (like other variables) should determine distribution when species are at the limit of their distribution range with respect to these variables, and therefore sensitive to variations in temperature and salinity that could exceed the values of their preferred niche (Holste and Peck, 2006). However, our study shows that at regional scales, without strong gradients, factors other than the water masses play a more relevant role in the species distribution. Spatial position, coastal influence and vertical structure are basically the main factors that determine distribution. The influence of the coast and vertical structure is not so surprising because several species are coastal and have adapted life cycle features, such as resting eggs (e.g. *Acartia clausi*) or an affinity for estuarine waters (e.g. *Euterpina acutifrons*). For most species, vertical structure and mixing are also likely to be greatly related to their feeding modes and their ability to stay in preferred layers, and therefore these variables would also influence the life cycles of species (Visser and Stips, 2002). As an example in this area, *Oikopleura* sp. is generally more abundant in coastal stratified waters (Albaina and Irigoien, 2004) and periods (Lopez Urrutia *et al.*, 2005). This may be due to lower growth efficiencies at high turbulences (Peters *et al.*, 2002) or to higher overall efficiency in areas dominated



by small phytoplankton (Tiselius *et al.*, 2003) such as the stratified waters in the Bay of Biscay (Labry *et al.*, 2002).

The really interesting aspect is the role geographical position plays in species distribution. Zarauz *et al.* (Zarauz *et al.*, 2008) confirmed this result to species level with observations for different large taxonomic groups of plankton (diatoms, ciliates, mesozooplankton). In coastal and shelf areas, topography (e.g. rivers, shelf-break) is the main cause of the permanent hydrographical features, such as plumes, internal waves or fronts, and therefore the position of a topographical feature causes different water conditions. An example is the position of a river that determines the plume rather than the absolute salinity value. Actually, in some cases, hydrographical features may not even be involved; it is the presence of a canyon that allows oceanic species to enter coastal areas, resulting in increased biodiversity. A terrestrial ecology simile could be made with an insect whose distribution is determined by the distance to a river, not because of the effect of the river on the surrounding vegetation but because the need for fresh water for larval growth determines the location of the insect's distribution centre. We also find species that are related to topographic features. Some of these topographic features enhance primary production (shelf-break or river plumes), but the species do not respond to increased phytoplankton biomass in different places but to the specific places themselves. Therefore, there must be factors that act at a different level (such as the local population) than physiology (e.g. temperature, salinity or food) which make such places suitable. The factors affecting the local population (by inducing changes in the extinction and colonization processes) are components of the heterogeneity of the surrounding environment. This is a scale-dependent concept because it must be referenced to a spatial scale (distance, area, volume) (Chust *et al.*, 2003), and has been studied extensively in terrestrial habitat fragmentation research (e.g. Fahrig, 2003). Here, the geographical position is a proxy of the distance to geographical features. Potential candidates for these factors that merit further research are the vertical lift in the shelfbreak areas due to internal waves (Rodríguez *et al.*, 2001), the need for deep waters for vertical migration or overwintering in oceanic species (Williams and Conway, 1988), and the lower susceptibility to predation of small organisms in turbid coastal waters (Utne-Palm, 2002).

The rate of change in species composition in relation to geographical distance, i.e. the betadiversity analysis results, also suggests that species have distribution centres and random dispersion occurs around these centres. If dispersion is related to water mass transport, we would expect environmental variables that trace

water masses, such as salinity and temperature, to explain most of the betadiversity variance. However, we found that distance in a random direction explains a non-negligible part of the betadiversity variance (13.5%) when abundance is considered, and a higher percentage than environmental factors when species presence (14.5%) is considered. The community variance explained by niche adaptation and dispersal limitation in our analysis is about equal. However, it has to be considered that a high percentage of the variation remains unexplained (57–66%). Two main factors may contribute to that variation. First, we have to consider that the factors we have used to define niches are limited. There is a range of other factors defining niche space that are either unknown or difficult to quantify (e.g. resting stages, differences in vulnerability, density effects; see Planque *et al.*, 2004). The not measured niche space could account for a considerable of the unexplained variance increasing therefore the role of the niche respect to the dispersal limitation. On the other hand, the system we are considering is dynamic, there are a number of physical processes other than currents interacting (e.g. tides, internal waves) and contributing to randomly mix mesozooplankton. Further, the distribution we observe is not a fixed picture but the result of the interaction between the cruise track, the physical forcing factors and the organism migrations. Therefore, part of the percentage of unexplained variation could be attributed to stochastic processes.

The neutral model fit to species-rank abundance (i.e. Fisher's log-series distribution) was not as good as to the log-normal distribution, which also indicates that the distribution of mesozooplankton is not the result of pure neutral communities colonizing randomly from a large species pool. Using a data set of Mediterranean and Caribbean marine phytoplankton, Pueyo (Pueyo, 2006) illustrated that both neutral and non-neutral mechanisms can coexist in nature, although they seem to have different weights in different groups of organisms. Dolan *et al.* (Dolan *et al.*, 2007) found that a log-series often showed the best fit to the tintinnid rank-abundance distributions in the Pacific. Raybaud *et al.* (Raybaud *et al.*, 2009) found that a log-normal distribution fitted the *Ceratium* (as Pueyo, 2006) and copepod (as in the present work) species distribution better, whereas a log-series distribution showed a better fit for tintinnids. These results confirm that neutral and non-neutral mechanisms could have different weights in different groups.

In summary, our results indicate that a large part of the mesozooplankton betadiversity variance in the Bay of Biscay remains unexplained by dispersal limitation or by the factors commonly expected to define the niche such as temperature, salinity, vertical structure or food.

This implies on one side that there probably are remaining explanatory factors that we do not know or we can not quantify and on the other that communities in the Bay of Biscay are probably subjected to a high degree of environmental and/or demographic stochasticity. The habitat models indicate that mesozooplankton species are associated with distribution centres. These centres are not defined by the water mass characteristics but rather by geographical features. Even if the mechanism underlying the relation of each species to the geographical features is not always clear, it can be seen that a niche exists. This explains why variance partitioning and species rank-abundance analysis do not fit the neutral theory predictions completely. However, as can be expected for plankton, dispersal limitation still plays a role in species distribution, which was estimated at about 14–15% of the variance partitioning. The niche and neutral theories are complementary, not conflicting (Chave, 2004).

## SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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