

# Changes in the mesozooplankton community associated with the hydrography off the northwestern Iberian Peninsula

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Blanco-Bercial, L., Álvarez-Marqués, F., and Cabal, J. A. 2006. Changes in the mesozooplankton community associated with the hydrography off the northwestern Iberian Peninsula. — ICES Journal of Marine Science, 63: 799–810.

Changes in the mesozooplankton community were investigated along the northwestern coast of the Iberian Peninsula during OMEX II cruises in August 1998, under upwelling conditions, and in October 1999, when there was a saline, warm poleward current flowing along the slope. Six stations, located at both the shelf break and in oceanic waters, were sampled for mesozooplankton by day and by night. Samples were grouped in accordance with their species abundance levels, and the resulting groups were compared with salinity, integrated chlorophyll *a*, and sea surface and average temperatures. The analysis discriminated stations from different cruises into different groups, and detected the influence of hydrographic structures. The abundance of species linked to high concentrations of Chl *a* and low temperature increased during the upwelling session, whereas species related to warmer water were more abundant during the 1999 cruise. Further, the analysis revealed differences in the mesozooplankton composition between coastal and oceanic sites, which were influenced to different degrees by the upwelling and the poleward current.

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Keywords: Iberian Peninsula, mesozooplankton community, poleward current, upwelling.

Received 18 August 2005; accepted 10 March 2006.

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## Introduction

Ocean margins, and the fluxes between shelf areas and open ocean that take place there, are important to the knowledge of the global biogeochemical cycle of carbon, nutrients, and trace elements (Wollast and Chou, 2001; Huthnance *et al.*, 2002; Verity *et al.*, 2002), but the processes are not as well known and understood as they should be. In recent decades many projects have been launched to correct this lack of knowledge, and one of them was the EU's OMEX II Project, focused on the northwestern Iberian Peninsula.

The hydrography NW of the Iberian Peninsula shows marked seasonal variability. Off NW Spain, windstress is directed southwards in summer, and upwelling develops (Tenore *et al.*, 1995; Castro *et al.*, 1997; Teira *et al.*, 2001). The entrance into the euphotic zone of deep, nutrient-rich water associated with this upwelling enhances primary production (Joint *et al.*, 2001b). Coastal systems under the

influence of seasonal upwelling are characterized by changes in the zooplankton coupled to these events (Paffenhöfer *et al.*, 1994; Mackas *et al.*, 2001). Moreover, coastal upwelling can generate displacement of water masses in the form of filaments, exporting the plankton associated with them (Paffenhöfer *et al.*, 1994; Halvorsen *et al.*, 2001; Hitchcock *et al.*, 2002). On the other hand, a warm, saline current flowing polewards along the slope appears to be the main hydrographic feature of the waters off NW Spain during autumn and winter (Frouin *et al.*, 1990; Haynes and Barton, 1990; Pingree and Le Cann, 1990; Huthnance *et al.*, 2002). At the same time, a reversal of the meridional component of the wind to a northward direction induces onshore Ekman transport (Frouin *et al.*, 1990), and primary production decreases (Tenore *et al.*, 1995). Previous studies have investigated the influence of this poleward current on phytoplankton and zooplankton biomass, and on metabolic rates both off NW Spain (Álvarez-Salgado *et al.*, 2003; Huskin *et al.*, 2003; Isla and

Anadón, 2004) and in the central Cantabrian Sea (Fernández and Bode, 1991; Fernández *et al.*, 1993). However, information on the mesozooplankton community composition remains limited. Another important source of seasonal changes comes from the continental freshwater inputs from the Rías Bajas (Álvarez-Salgado *et al.*, 2003).

Changes in the environment affect the composition and structure of plankton communities, and therefore the ecosystem dynamics (Paffenhöfer, 1980; Landry *et al.*, 2001). Consequently, given that mesoscale hydrographic events, and the interactions and exchanges between open ocean and continental shelf waters, affect the spatial distribution and composition of mesozooplankton, environmental changes play an essential role in biogeochemical cycles (Pinca and Dallot, 1995; Pakhomov and Perissinotto, 1997; Grunewald *et al.*, 2002; Siokou-Frangou *et al.*, 2004). Moreover, shelf and oceanic sites have different zooplankton compositions (Siokou-Frangou *et al.*, 1998; Gaard, 1999; Morgan *et al.*, 2003) that can be influenced by hydrographic change to different degrees. The differences in the responses to these changes could be another source of variation.

The objective of this work was to analyse the variations in zooplankton species abundance in response to two different hydrographic conditions: a summer upwelling event and an autumn period when the poleward-flowing current is in evidence. Further, the influence of both on coastal and oceanic areas is analysed, with the purpose of detecting differences in the influence of the hydrographic events close to the coast and farther offshore. The work contributes to knowledge of the mesozooplankton community under different hydrographic conditions in the study area, an area where most earlier studies were carried out during upwelling events.

## Material and methods

### Study area and sampling

The data used for the study were obtained during two oceanographic cruises carried out off NW Spain: OMEX-0898 from 1 to 11 August 1998 onboard RV “Professor Shtokman” and OMEX-1099 from 14 to 20 October 1999 onboard RV “Thalassa”. The same six stations were sampled on each cruise (Figure 1), by day and by night, except for Station 1 in 1998 and Station 16 in 1999, which were only sampled by day.

Continuous profiles of temperature, salinity, and fluorescence were recorded at each station, with a Neil Brown MARK-III CTD probe in 1998 and a SeaBird 25 CTD probe with fluorometer in 1999. Fluorescence measurements were transformed into chlorophyll *a* concentration ( $\text{mg m}^{-3}$ ) according to the fluorescence/Chl *a* relationships obtained by Teira *et al.* (2001) from each cruise.

Zooplankton samples were taken with vertical hauls from 200 m, or from near the bottom in shallower water, to the surface. A triple WP2 net of 200- $\mu\text{m}$  mesh and 40 cm (OMEX-0898) or 60 cm (OMEX-1099) diameter was used. Although different nets were used on the two cruises, we consider that this fact did not influence the results, because both abundance and biomass were higher during OMEX-0898 (40-cm diameter net), when the gear would have been less efficient than if the 60-cm diameter net had been used, as it was during OMEX-1099 (Sameoto *et al.*, 2000). Therefore, if there was any effect, it would have contributed to reducing the differences between both years. No flowmeter was used, assuming the volume of filtered water as the entire column. Samples from one codend were preserved in 4% buffered formalin–seawater solution

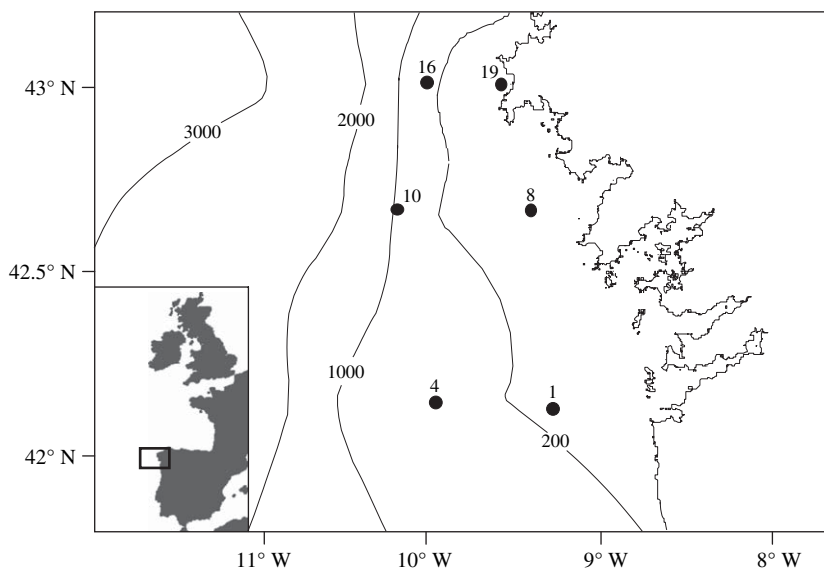


Figure 1. Map of the study area and the stations sampled during both cruises.

for taxon identification. The other codends were set aside for other experiments. In the laboratory, the zooplankton were identified to species level in most cases, and counted under a stereomicroscope. Subsamples taken were no less than 1/10 of the total sample. Abundance was expressed as number  $m^{-2}$ .

### Data analysis

Rare species (those in <10% of the samples) were excluded from the analysis. The structure of the mesozooplankton community was examined by multivariate techniques using the PRIMER software package (Clarke and Warwick, 1994). Both classification and ordination procedures were employed to group samples with similar zooplankton composition.

Prior to analysis, all data were transformed using the function  $X' = X^{1/4}$  to reduce the weighting of abundant species. Cluster analysis was based on the Bray–Curtis similarity measure and average linkage classification. Similarity level was adjusted to obviously meaningful groupings, rather than forcing clusters to a fixed level (Hunt *et al.*, 2002). Moreover, the similarity matrix was ordinated using non-metric multidimensional scaling (NMDS) in a two-axis ordination. A combination of clustering and ordination analysis allows evaluation of the adequacy and mutual consistency of both representations (Clarke and Warwick, 1994). The ordination scores of the NMDS, which summarize the zooplankton community in terms of the abundance data, were regressed against sea surface temperature, average temperature, average salinity, and integrated Chl *a* concentration, to determine the effect of these variables on community structure.

The percentage contribution of each species to within- and between-group dissimilarity was determined using the similarity percentages (SIMPER) procedure within the PRIMER software. The abundance of the taxa responsible for most of the similarity (within groups) and dissimilarity (between groups) was tested against the environmental variables by regression analysis, to check the affinity of the taxa for different environmental conditions.

Differences in average temperature between groups were tested using one-way ANOVA and a *post hoc* Tukey test ( $\alpha = 0.05$ ). Assumptions of ANOVA were checked using a Kolmogorov–Smirnov test for normality and a Levene test for homogeneity of variances. Differences between particular groups in sea surface temperature, integrated Chl *a* concentration, and salinity were checked by applying *t*-tests owing to the heterogeneity of variances. When multiple tests were carried out, sequential Bonferroni correction was applied (Rice, 1989).

## Results

Hydrographic conditions, phytoplankton size structure, and chlorophyll *a* concentration and distribution during OMEX-0898 and OMEX-1099 are described in Teira *et al.* (2001).

During OMEX-0898, upwelling conditions prevailed, the upper water column being cooler near the coast than at oceanic stations. Coastal waters were slightly fresher than oceanic waters, so there was a thermohaline stratification. Chl *a* concentration was higher at coastal stations, with

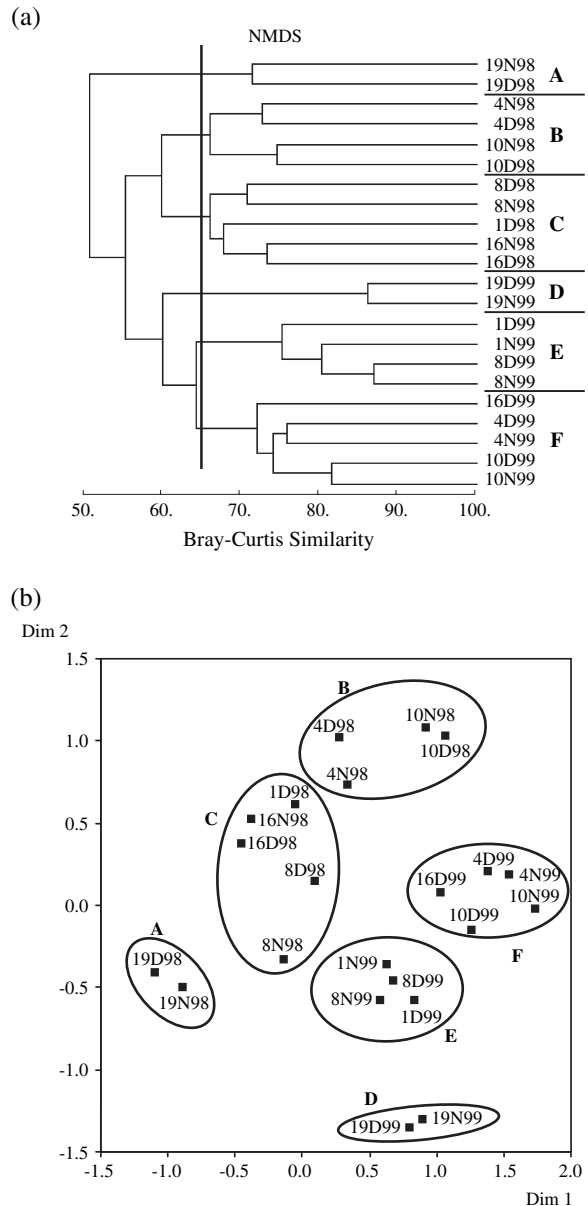


Figure 2. Groups of samples obtained from the similarity matrix based on zooplankton abundance data, represented as: (a) Dendrogram. Axes indicate the distance between clusters using a Bray–Curtis similarity index. Station groups selected for the analysis are indicated. (b) NMDS plot (stress = 0.10). Station groupings are indicated in agreement with groups from dendrogram. Samples are indicated by the number of the station, D(day)/N(night), and year of sampling.

Table 1. Mean (number m<sup>-2</sup>) abundance of zooplankton taxa in each group. Asterisks indicate species that were not included in the similarity matrix.

Taxon	A	B	C	D	E	F
<b>Copepods</b>	—	—	—	—	—	—
Calanoid copepodite*	200	—	152	16 095	—	—
<i>Calanus helgolandicus</i>	956	330	4 524	2 297	1 933	265
<i>Mesocalanus tenuicornis</i>	244	1 613	349	265	252	1 433
<i>Calanoides carinatus</i>	1 276	241	6 682	4 987	2 375	213
<i>Nannocalanus minor</i>	4	293	70	21	3	52
<i>Neocalanus gracilis</i>	4	—	13	—	—	13
<i>Subeucalanus monachus</i>	—	208	96	—	—	1
<i>Eucalanus crassus</i>	52	4	301	2	3	1
<i>Rhincalanus nasutus</i>	—	—	3	—	—	1
<i>Paracalanus parvus</i>	8 480	19 929	9 408	35 512	33 739	12 203
<i>Calocalanus styliremis</i>	—	1 937	421	53	80	1 025
<i>Ischnocalanus tenuis</i>	—	—	112	—	—	—
<i>Pseudocalanus elongatus</i>	1 108	951	350	282	3 003	165
<i>Microcalanus pusillus</i>	—	70	—	141	28	666
<i>Clausocalanus arcuicornis</i>	40	527	158	212	205	666
<i>C. jobei</i>	320	6 880	6 000	88	248	449
<i>C. pergens</i>	1 000	11 556	918	371	386	5 507
<i>C. lividus</i>	—	96	—	269	30	406
<i>Clausocalanus</i> spp.	—	4 374	1 465	4 152	2 405	10 789
<i>Ctenocalanus vanus</i>	—	2 134	527	147	3 456	5 503
<i>Spinocalanus</i> sp.*	—	—	—	—	—	1
<i>Aetidus armatus</i>	—	70	155	—	—	116
<i>A. giesbretchti</i> *	—	—	—	—	—	1
<i>Gaetanus minor</i>	—	38	—	—	—	1
<i>Euchirella curticauda</i>	—	28	—	—	1	69
<i>Chirundia streeti</i> *	—	—	—	—	—	4
<i>Chiridius</i> sp.*	—	30	—	—	—	—
<i>Undeuchaeta major</i>	—	—	—	—	—	28
<i>U. plumosa</i>	—	—	—	4	—	30
<i>Euchaeta hebes</i>	204	38	1 791	5	790	833
<i>Euchaeta</i> sp.	204	2	1 643	53	2 278	125
<i>E. norvegica</i>	—	41	370	—	2	2
<i>E. tonsa</i>	—	—	6	—	—	1
<i>Scolecithricella dentata</i>	—	—	—	—	—	16
<i>S. minor</i>	—	—	—	—	—	21
<i>Scolecithricella</i> sp.*	—	—	—	—	—	35
<i>Scaphocalanus echinatus</i>	—	2	—	—	—	129
<i>S. robustus</i>	—	—	—	—	—	73
<i>Scaphocalanus</i> sp.*	—	—	—	—	—	4
<i>Temora longicornis</i>	560	—	272	1 555	508	43
<i>T. stylifera</i>	44	287	1 249	184	4	9
<i>Metridia lucens</i>	200	1 345	920	12	169	1 640
<i>Pleuromamma robusta</i>	—	12	6	—	—	97
<i>P. gracilis</i>	—	1 477	336	42	83	89
<i>Pleuromamma</i> sp.	—	—	—	—	—	177
<i>Centropages chierchiae</i>	244	3 099	1 152	4 664	1 268	276
<i>C. typicus</i>	880	677	640	—	—	520
<i>Isias clavipes</i>	—	—	—	2 336	—	—
<i>Heterorhabdus spinifrons</i>	—	120	32	—	—	2
<i>H. papilliger</i>	—	159	—	—	—	—
<i>H. robustus</i> *	—	—	48	—	—	—
<i>Heterorhabdus</i> sp.*	8	—	—	—	—	—
<i>Heterostylites longicornis</i> *	—	—	13	—	—	—
<i>Phyllopus impar</i> *	—	2	—	—	—	—
<i>P. helgae</i>	—	—	—	—	—	10
<i>Candacia armata</i>	—	63	27	—	55	16
<i>Acartia clausi</i>	11 148	19 771	3 614	7 156	8 618	4 386
<i>Oithona helgolandica</i>	7 000	14 085	9 392	1 625	2 259	7 948

Table 1 (continued)

Taxon	A	B	C	D	E	F
<i>O. nana</i>	—	—	—	10 247	3 000	2 035
<i>O. plumifera</i>	16	1 007	1 117	—	472	1 383
<i>Microsetella rosea</i>	—	—	—	—	45	56
<i>Microsetella norvegica</i>	—	—	10	—	—	—
<i>Euterpina acutifrons</i>	800	100	—	124	27	42
<i>Clytemnestra rostrata</i>	—	—	80	17	133	110
<i>Oncaea media</i>	9 048	979	6 085	989	270	526
<i>Sapphirina opalina</i> *	—	—	—	—	—	2
<i>S. angusta</i>	—	—	—	2	—	18
<i>S. ovatolanceolata</i> *	—	—	—	—	—	4
Corycaeidae	200	252	464	71	82	52
<i>Monstrilla</i> sp.*	—	—	—	—	1	—
Copepod nauplii	400	339	415	5 353	352	744
<b>Other holoplankton</b>						
Phoraminiophera	8	420	1 088	—	—	—
Hydromedusae	1 140	122	104	2 043	179	26
<i>Phialidium</i> spp.	—	—	—	97	56	14
<i>Obelia</i> spp.	4	—	97	355	53	—
<i>Liriope</i> spp.	24	2	261	9	595	35
Siphonophora	—	—	—	—	—	—
Calicophorae	—	—	—	6 621	1 198	134
Phisophoridae	84	4	386	32	11	42
Ctenophora larvae	—	—	—	18	—	—
<i>Cavolinia inflexa</i>	—	—	—	150	24	515
<i>Limacina</i> spp.	—	—	143	143	39	157
Pteropoda larvae	—	212	—	—	—	—
Cephalopoda	—	—	—	—	1	1
Polychaeta	408	104	96	1 273	73	25
<i>Podon intermedius</i>	—	—	—	301	—	23
<i>Evadne spinifera</i>	284	—	—	230	1	288
<i>Evadne nordmanni</i>	—	—	—	1 415	—	—
Ostracoda	—	255	31	478	9	55
Euphausiacea	40	20	1 288	—	735	1
Metanauplius larvae	—	522	663	—	103	—
Calyptopsis larvae	1 256	189	2 744	184	648	81
Furcilia larvae	600	—	121	341	165	19
Mysidacea	—	—	3	4	197	—
Amphipoda	56	12	—	—	2	1
Amphipoda hyperiidae	—	20	—	7	18	6
<i>Phronima</i> spp.	—	—	—	—	81	1
<i>Sagitta friderici</i>	—	46	381	3 206	1 793	397
Salpida	—	—	—	587	—	354
<i>Salpa fusiformis</i>	—	—	—	4	2 023	905
<i>Thalia democratica</i>	—	—	—	—	—	23
Doliolida	320	2	1 613	193	119	55
Appendicularia	16	5 381	1 751	35 156	264	1 980
<i>Branchiostoma lanceolatum</i>	2 608	—	128	—	7	2
<b>Meroplankton</b>						
Gastropoda larvae	—	110	320	2 384	943	778
Bivalvia larvae	—	—	64	5 298	2 054	1 493
Briozoa larvae	—	—	383	1 436	433	319
Cirripedia larvae	7 480	80	294	10 098	9	24
Stomatopoda larvae	—	—	—	—	1	—
Decapoda larvae	116	12	382	592	176	27
Pluteus larvae	520	100	16	283	—	10
Myctophidae larvae	—	4	48	—	2	—
<i>Trachurus</i> sp. larvae	—	—	—	16	—	—
<i>Trachurus</i> sp. eggs	—	4	64	30	—	6

>2- $\mu\text{m}$  phytoplankton cells accounting for >80% of total Chl *a*, while at open ocean stations, the subsurface Chl *a* maximum (50–80 m deep) was composed of small particles containing Chl *a*. In autumn 1999 (OMEX-1099), the thermohaline structure was characterized by the warm, saline poleward current flowing over the upper slope, at depths of 60–120 m. There was a nucleus of warm water (17°C) in the upper 50 m over the core of the poleward current. Freshwater inputs were higher than in the summer 1998 cruise, affecting the entire water column at some stations. Chl *a* concentration was lower than during upwelling. The poleward current favoured accumulation of phytoplankton biomass in the upper 60 m at shelf and shelf break stations, and a subsurface maximum (40–50 m deep) was found at oceanic stations. The relative contribution of >2- $\mu\text{m}$  Chl *a* was generally <70% in the upper 40 m, and the proportion of large cells increased with depth. Pico-plankton dominated the upper layer of the onshelf stations of the south transect, representing >60%.

Cluster analysis (Figure 2a) grouped samples from the same years, discriminating samples from the different cruises into two groups, except for samples from Station 19, which were grouped separately from other samples. The NMDS plot (Figure 2b) reflects the same grouping of samples. Average abundances of the mesozooplanktonic taxa within each group are shown in Table 1.

The analysis identified six groups of samples at approximately a 65% level of similarity. Within-group similarities of groups B and C were each 66.3%, and the rest of the groups had within-group similarities >70%. Group A contained samples from Station 19 in 1998. At that station, close to the coast and with a bottom depth of 39 m, the upwelled water reached the surface. Group B included the oceanic stations (4, 10) sampled during OMEX-0898. These stations were located in or outside the upwelling front, where water was more saline and warmer than in the upwelling area, and slightly stratified. Group C comprised samples influenced directly by the summer upwelling of 1998, inshore of the upwelling front. Therefore, those samples were collected in the coolest average temperatures and the highest Chl *a* concentrations of the study (Table 2). Groups D, E, and F corresponded to the OMEX-1099 cruise. Group D included samples from Station 19, which was close to the coast, so its main characteristics then were a low salinity (owing to the continental freshwater inputs, affecting the entire column) and a high average temperature. Group E contained continental shelf samples, under the influence of the run-off from the Rías Bajas. Group F comprised slope and oceanic samples. Samples of that group came from Stations 4, 10, and 16 (Figures 2a, b). The main features of those stations during October 1999 were the presence of a nucleus of warm water in the upper 50 m, and the high salinity core of the poleward slope current found at depth.

Values of the environmental variables for each group are shown in Table 2. Groups differed significantly in average

temperature ( $F_{5,16} = 128.8$ ;  $p < 0.001$ ), which were ranked  $C = A < B = F < E < D$  by the *post hoc* Tukey test. Surface temperatures were significantly higher in D vs. A ( $p = 0.004$ ) and E vs. C ( $p = 0.003$ ), but were not different between C and B ( $p = 0.105$ ) nor between F and E ( $p = 0.114$ ). Integrated salinity was significantly higher in group B than in group C ( $p < 0.001$ ), and in group E it was significantly lower than in group F ( $p = 0.04$ ). Integrated Chl *a* in group C was significantly higher than in groups E and B ( $p = 0.002$  and  $p = 0.049$ , respectively). The regression analysis between environmental variables and the ordination scores of the NMDS showed that Chl *a* explained 49% of the variation in zooplankton abundance data, salinity explained 63.8%, surface temperature accounted for 71.8%, and average temperature accounted for 58.9% of the variation (Table 3).

Only taxa with the greatest contribution to within- and between-group dissimilarity (Table 4) were studied in detail. Group C, where during OMEX-0898 the upwelled waters caused low temperatures and high integrated salinity and Chl *a*, was characterized by the dominance of species linked to high phytoplankton concentrations: *Calanus helgolandicus*, *Calanoides carinatus*, *Oithona helgolandica*, and *Oncaea media*. On the other hand, during October 1999 (group E), the density of species specialized to feed on small particles such as appendicularians, *Salpa fusiformis*, and *Oithona nana*, increased. This group was also characterized by higher densities of gastropod and bivalve larvae. Meroplankton taxa, such as polychaetes and cirripede larvae, and pluteus, bivalve, and gastropod larvae, appear as indicators of very shallow water (groups A and D) in both cruises. Appendicularians, *Sagitta friderici*, and *O. nana* were scarce during upwelling, attaining their greatest densities in October 1999. Conversely, coastal upwelling indicator species such as *O. helgolandica* and *O. media* dominated during OMEX-0898. At open ocean stations (B and F), there were oceanic indicator copepods, such as *Calocalanus styliremis*, *Mesocalanus tenuicornis*, *Metridia lucens*, *Pleuromamma gracilis*, and *Clausocalanus peregins* during both cruises, and their abundance peaked in those groups of samples (Table 1). In general, such species were positively related to salinity (Table 5). In general, temporal changes at those stations were mainly due to the input of continental shelf species (Table 4). Whereas the populations of species related to upwelling, such as *O. helgolandica*, increased during OMEX-0898, taxa such as *O. nana* and bivalve larvae, which are typically found near-shore, were at their greatest density in October. Conversely, the densities of oceanic species did not change significantly between cruises (Table 1).

The significance of the regression analyses carried out with average and sea surface temperatures, integrated Chl *a*, and salinity against the species indicated by the SIMPER analysis (Table 5) reflects the link between the main species involved in the groupings (indicated by the SIMPER analysis) and the hydrographic variables. Species

Table 2. Mean and standard deviation of integrated Chl *a*, salinity, and average and sea surface temperatures (°C) for each group.

Group	Average temperature (°C)		Sea surface temperature (°C)		Chlorophyll <i>a</i> (mg m <sup>-2</sup> )		Salinity	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
A*	12.99	—	13.97	—	56.25	—	35.74	—
B	14.00	0.08	17.33	2.07	62.11	35.23	35.82	0.01
C	12.68	0.19	14.98	0.48	114.01	30.51	35.75	0.02
D	16.06	0.08	16.13	0.18	9.00	1.97	35.55	0.01
E	14.64	0.32	16.72	0.73	25.53	9.18	35.69	0.13
F	14.03	0.08	17.52	0.14	17.69	3.51	35.80	0.02

\*Only one measurement for both samples.

related positively with Chl *a* and/or colder waters were representative of upwelling samples (group C): *C. helgolandicus*, *O. helgolandica*, *O. media*, *Clausocalanus jobei*, whereas the species indicators of samples from the autumn cruise were related to warmer water and low values of Chl *a* (*S. fusiformis*, *O. nana*, some groups of meroplankton; Tables 4 and 5). A positive relationship with salinity was an indicator of taxa related to open ocean waters, i.e. groups B and F (*C. styliremis*, *M. lucens*, *P. gracilis*, *C. pergens*), whereas taxa linked to shelf break conditions (meroplankton taxa, appendicularians, *S. friderici*, *Paracalanus parvus*) were negatively related to this factor (Tables 4 and 5).

## Discussion

The study showed the influence of the two main hydrographic features off the NW Iberian Peninsula on the composition of the zooplankton community. The high phytoplankton biomass generated by upwelling (Teira *et al.*, 2001) would explain the dominance of species associated with highly productive systems near the coast in OMEX-0898, whereas the influence of the poleward current on the environment played a crucial role in determining the zooplankton community during October 1999.

During upwelling, species linked to high phytoplankton biomass were in increased numbers close to the coast; *O. helgolandica* and *O. media* are linked to coastal upwelling events or to spring blooms (Paffenhöfer, 1980;

Turner and Granéli, 1992; Atkinson and Shreeve, 1995). *C. helgolandicus* can take advantage of spring blooms in temperate latitudes (Laabir *et al.*, 1998; Weikert *et al.*, 2001), and *C. carinatus* develops in seasonal upwelling areas (Verheye and Field, 1992; Verheye *et al.*, 1992; Hitchcock *et al.*, 2002) and during summer along the Atlantic coast of the Iberian Peninsula (Williams and Conway, 1988; Ceballos *et al.*, 2004). The results of the regression analyses supported these results; such species are negatively related to temperature (a consequence of upwelling) and/or positively to Chl *a* (Tables 1 and 5). Although other species such as *P. parvus* and *Acartia clausi* were abundant everywhere during upwelling, their importance was less close to the coast, where Chl *a* concentrations and phytoplankton composition (mainly >2- $\mu$ m cells; Teira *et al.*, 2001) favoured other species adept at taking advantage of phytoplankton blooms and feeding on large phytoplankton cells (Table 1). In shallower water, the upwelled water reached the surface, but the Chl *a* concentrations and the >2- $\mu$ m phytoplankton contribution were less than over the continental shelf, so the contribution of the larger “upwelling” species (*C. helgolandicus* and *C. carinatus*) was less important, even less than during OMEX-1099. The other two species associated with upwelling (*O. helgolandica* and *O. media*) could also feed on small phytoplankton, and they were present in great numbers. Head *et al.* (2002) also found communities dominated by *Oithona* spp. and *Oncaea* spp. wherever flagellates and picoplankton accounted for ca. 85% of phytoplankton

Table 3. Regressions of environmental variable against NMDS ordination scores (Dim 1, Dim 2).

Variable	Regression coefficients					
	Dim 1	Dim 2	$r^2$	Adjusted $r^2$	$F_{2,19}$	$p$
Integrated temperature	0.794	-0.759	0.628	0.589	16.053	<0.001
Surface temperature	1.626	0.555	0.745	0.718	27.775	<0.001
Salinity	0.005	0.108	0.673	0.638	19.532	<0.001
Chlorophyll <i>a</i>	-36.543	22.852	0.539	0.490	11.093	0.001

Table 4. Taxa with the greatest contribution to differences between pairs of groups (indicated in the first row). The percentage contribution to between-group dissimilarity is indicated.

Spatial changes					
A–C	A–B	B–C	D–E	D–F	E–F
<i>A. clausi</i> 9.91%	<i>A. clausi</i> 13.85%	<i>A. clausi</i> 14.37%	Appendicularia 23.44%	Appendicularia 20.44%	<i>P. parvus</i> 22.07%
Cirripedia larvae 9.03%	<i>P. parvus</i> 11.00%	<i>P. parvus</i> 11.33%	<i>P. parvus</i> 19.01%	<i>P. parvus</i> 14.73%	<i>Clausocalanus</i> spp. 11.07%
<i>O. media</i> 8.84%	<i>C. pergens</i> 9.58%	<i>C. pergens</i> 9.63%	Cirripedia larvae 6.91%	Cirripedia larvae 6.33%	<i>O. helgolandica</i> 6.99%
<i>C. jobei</i> 7.88%	<i>O. media</i> 8.22%	<i>O. helgolandica</i> 7.76%	<i>O. nana</i> 5.20%	<i>O. nana</i> 5.18%	<i>A. clausi</i> 6.49%
<i>O. helgolandica</i> 6.71%	<i>C. jobei</i> 7.11%	<i>C. carinatus</i> 5.86%	<i>A. clausi</i> 4.49%	<i>Clausocalanus</i> spp. 4.43%	<i>C. pergens</i> 6.24%
<i>C. carinatus</i> 6.53%	Cirripedia larvae 6.98%	<i>C. jobei</i> 5.13%	Calicophorae 3.55%	<i>O. helgolandica</i> 3.93%	<i>C. vanus</i> 4.33%
<i>P. parvus</i> 4.69%	<i>O. helgolandica</i> 6.62%	<i>O. media</i> 4.72%	Copepod naup. 3.50%	Calicophorae 3.73%	<i>O. nana</i> 2.91%
<i>C. helgolandicus</i> 4.49%	Appendicularia 4.99%	<i>Clausocalanus</i> spp. 4.58%	Bivalvia larvae 2.66%	<i>C. vanus</i> 3.31%	<i>C. carinatus</i> 2.59%
Calyptopis euphausiacea 3.28%	<i>Clausocalanus</i> spp. 4.72%	<i>C. helgolandicus</i> 3.67%	<i>C. chierchiaie</i> 2.63%	<i>C. pergens</i> 3.29%	<i>P. elongatus</i> 2.31%
<i>B. lanceolatum</i> 3.12%	<i>B. lanceolatum</i> 2.46%	Appendicularia 3.67%	<i>Clausocalanus</i> spp. 1.90%	<i>C. carinatus</i> 3.06%	<i>S. fusiformis</i> 2.29%
Temporal changes					
A–D	B–F		C–E		
Appendicularia 22.16%	<i>A. clausi</i> 16.32%		<i>P. parvus</i> 20.52%		
<i>P. parvus</i> 16.54%	<i>P. parvus</i> 12.77%		<i>O. helgolandica</i> 8.20%		
<i>O. nana</i> 6.54%	<i>Clausocalanus</i> spp. 9.90%		<i>C. jobei</i> 6.91%		
<i>O. media</i> 5.33%	<i>O. helgolandica</i> 8.16%		<i>A. clausi</i> 6.53%		
Cirripedia larvae 4.24%	<i>C. jobei</i> 8.02%		<i>C. carinatus</i> 5.33%		
Calicophorae 3.89%	<i>C. pergens</i> 7.96%		<i>O. media</i> 5.01%		
<i>A. clausi</i> 3.78%	Appendicularia 4.39%		<i>C. helgolandicus</i> 3.79%		
<i>O. helgolandica</i> 3.64%	<i>C. vanus</i> 4.07%		<i>S. fusiformis</i> 3.03%		
Bivalvia larvae 3.60%	<i>C. chierchiaie</i> 2.92%		<i>C. vanus</i> 2.63%		
Copepod nauplii 3.22%	<i>O. nana</i> 1.94%		Calyptopis euphausiacea 2.57%		

standing stock. Another characteristic of such samples, which distinguished them from continental shelf or shelf break samples, was the great abundance of species linked to lower salinity, such as *A. clausi* and meroplankton, which are quite common inshore (Gislason and Asthorsson, 1995; Gaard, 1999).

In general, small copepods (<500 µm) dominated the offshore community during August 1998 (Table 1), and Chl *a* concentrations were less than near the coast and the subsurface Chl *a* maximum was formed largely by cells <2 µm (Teira et al., 2001). These conditions restricted the numbers of larger copepods (>500 µm) linked to coastal upwelling, which specialize on feeding on larger cells. The small size of phytoplankton would also explain the relative abundance of appendicularians in oceanic waters

compared with close to the coast (Tables 1 and 4) during OMEX-0898. Oceanic indicator species were characterized by their positive relationship with salinity, a feature observed for *C. styliremis* and *M. lucens*, which had higher densities at these stations (Tables 1 and 5) than close to the coast.

Picoplankton dominated the phytoplankton community during OMEX-1099 (Teira et al., 2001), agreeing with the findings of Fernández et al. (1993), Castro et al. (1997), and Álvarez-Salgado et al. (2003), who found that the phytoplankton community in the poleward current was dominated by small autotrophic flagellates. Species such as appendicularians (Acuña and Anadón, 1992), *Salpa fusiformis* (Calbet et al., 2001), and *Oithona nana* (Nielsen and Sabatini, 1996; Nielsen and Andersen, 2002) are



Table 5. Significant results of the regressions of average and sea surface temperatures, integrated Chl *a*, and salinity against the taxa with highest contribution to the dissimilarity between groups.

Taxon	Variable	<i>B</i>	<i>r</i> <sup>2</sup>	<i>F</i> <sub>1,20</sub>	<i>p</i>
<i>Calanus helgolandicus</i>	Surface temperature	−0.83	0.37	11.7	<0.01
	Salinity	−11.95	0.27	7.3	<0.05
	Chlorophyll <i>a</i>	0.02	0.32	9.2	<0.01
<i>Calanoides carinatus</i>	Surface temperature	−0.92	0.34	10.1	<0.01
	Salinity	−16.07	0.36	11.0	<0.01
<i>Paracalanus parvus</i>	Average temperature	1.30	0.32	9.5	<0.01
	Salinity	−15.34	0.35	10.8	<0.01
<i>Calocalanus styliremis</i>	Salinity	13.63	0.26	7.1	<0.05
<i>Clausocalanus jobei</i>	Average temperature	1.29	0.22	5.5	<0.05
	Chlorophyll <i>a</i>	0.04	0.32	9.6	<0.01
<i>Clausocalanus pergens</i>	Surface temperature	1.26	0.42	14.6	<0.01
	Salinity	17.43	0.29	8.0	<0.05
<i>Ctenocalanus vanus</i>	Surface temperature	1.48	0.43	15.2	<0.01
	Chlorophyll <i>a</i>	−0.04	0.21	5.2	<0.05
<i>Euchaeta hebes</i>	Chlorophyll <i>a</i>	0.02	0.19	4.6	<0.05
<i>Temora stylifera</i>	Average temperature	−1.02	0.20	4.9	<0.05
	Chlorophyll <i>a</i>	0.04	0.51	21.1	<0.01
<i>Metridia lucens</i>	Salinity	16.20	0.40	16.2	<0.01
<i>Pleuromamma gracilis</i>	Surface temperature	0.93	0.38	12.4	<0.01
	Salinity	16.33	0.41	13.9	<0.01
<i>Oithona helgolandica</i>	Average temperature	−1.05	0.29	8.1	<0.05
	Salinity	13.47	0.37	11.8	<0.01
	Chlorophyll <i>a</i>	0.02	0.21	5.4	<0.05
<i>Oithona nana</i>	Average temperature	3.01	0.58	28.0	<0.01
	Salinity	−29.48	0.44	15.7	<0.01
	Chlorophyll <i>a</i>	−0.06	0.40	13.2	<0.01
<i>Oncaea media</i>	Average temperature	−1.44	0.26	6.9	<0.05
	Surface temperature	−1.29	0.15	16.6	<0.01
	Chlorophyll <i>a</i>	0.04	0.31	9.1	<0.01
<i>Sagitta friderici</i>	Average temperature	1.23	0.21	5.4	<0.05
	Salinity	−18.73	0.39	12.6	<0.01
<i>Salpa fusiformis</i>	Average temperature	1.24	0.18	4.5	<0.05
	Surface temperature	0.94	0.23	6.1	<0.05
	Chlorophyll <i>a</i>	−0.04	0.41	13.8	<0.01
Appendicularia	Average temperature	1.58	0.24	6.2	<0.05
Gastropoda larvae	Average temperature	1.58	0.34	10.4	<0.01
	Salinity	−16.04	0.28	7.7	<0.05
Bivalvia larvae	Average temperature	2.45	0.52	21.4	<0.01
	Salinity	−25.52	0.44	15.6	<0.01
	Chlorophyll <i>a</i>	−0.05	0.33	10.0	<0.01
Cirripedia larvae	Salinity	−20.62	0.25	6.6	<0.05

related to warm water (a characteristic of the poleward current), and are specialized to feed on small particles. Halvorsen *et al.* (2001) detected relatively high densities of *O. nana* during the OMEX-0898 cruise in an off-shelf

upwelled filament, where the phytoplankton community also consisted of picophytoplankton, which accounted for 61–65% of the total carbon fixation (Joint *et al.*, 2001a). Huskin *et al.* (2003) found high concentrations of salps

NW of Spain during November 1999 in the poleward intrusion, and the relatively high temperature and salinity observed in the poleward current would also favour *S. fusiiformis* because this species seems to have an affinity for warm saline water (Lavaniegos *et al.*, 2002). Another feature of the OMEX-1099 cruise was the densities of gastropod and bivalve larvae, findings which support the increase in meroplankton already reported in the study zone at the end of summer and during autumn by Valdés *et al.* (1990). However, groups of stations during OMEX-1099 had distinguishing characteristics. Shallower stations were dominated by species linked to warm and/or low-salinity water, such as meroplankton, *S. friderici*, and *O. nana*. *S. friderici* and *O. nana* prefer shallow water, low salinity, and high temperature (Gibbons, 1994; Marazzo and Nogueira, 1996; Jamet *et al.*, 2001; Richard and Jamet, 2001), and peaked in October 1999, when freshwater inputs were at their maximum (Teira *et al.*, 2001). Moreover, the increased densities of small phytoplankton during OMEX-1099 favoured *O. nana* and particle-feeders such as appendicularians, which also favour warmer temperatures. These results are also supported by the relationships found (positive for temperatures, negative for salinity; Table 5) for these species. The abundances of *C. helgolandicus* and *C. carinatus* remained high during OMEX-1099, even higher than during the upwelling period. Over the continental shelf, the abundance of those species was lower than during OMEX-0898, but they were still relatively high. Both species can maintain relatively high abundance during October, because the upwelling season extends from March to October (Álvarez-Salgado *et al.*, 2002). As a consequence, Ceballos *et al.* (2004) pointed out that *C. carinatus* could follow a conservative strategy to extend its reproductive season beyond the end of the upwelling season.

Oceanic waters were indicated by the presence of ocean indicator species, positively related to salinity (*M. lucens*, *P. gracilis*, *C. styliremis*). Moreover, offshore sites were indicated during OMEX-1099 by the presence of *Scolecithriella dentata* (Table 1). This copepod is a tropical/subtropical species (Bradford-Grieve *et al.*, 1999), which would likely prefer the warm, saline poleward current that was found there. Finally, during OMEX-1099, the contribution of coastal plankton such as *O. nana* (Böttger-Schnack, 1995) and bivalve larvae (Gislason and Asthorsson, 1995; Gaard, 1999) offshore was greater than during the August 1998 cruise, indicating a possible displacement of coastal waters offshore.

The trends described here agree with the findings of Isla *et al.* (2004) and Isla and Anadón (2004), who based their analyses on the same data series. Isla *et al.* (2004) described a herbivorous foodweb close to the coast and an omnivorous one offshore during upwelling. Similarly, our community was dominated by large (>1000 µm) herbivorous species close to the coast, while offshore the dominant species belonged to the 200–500-µm and

500–1000-µm fractions, with their ability to feed on small phytoplankton cells and some of them usually described as omnivorous, or were large carnivorous copepods. Offshore, however, Isla and Anadón (2004) hypothesized the presence of an omnivorous foodweb (protein-orientated metabolism). Likewise, we found that the abundance of relatively small omnivorous species, particle-feeders, and meroplankton larvae increased in comparison with the upwelling cruise.

Our results emphasize the essential role that hydrographic conditions play in structuring the mesozooplankton community along the NW Iberian Peninsula.

## Acknowledgements

We thank the captains and crews of RV “Professor Shtokman” and RV “Thalassa”, and the participants of cruises OMEX-0898 and OMEX-1099, for their support. We are also grateful for the comments on an earlier draft made by S. Ceballos and J. A. Isla, which helped to improve the manuscript. LB-B is financially supported by a PhD grant of the “III Plan Regional de I+D+I del Principado de Asturias”. The work was supported by the EU in the framework of the Mast 3 Programme, contract number MAS3-CT97-0076 (OMEX II project).

## References

- Acuña, J. L., and Anadón, R. 1992. Appendicularian assemblages in a shelf area and their relationship with temperature. *Journal of Plankton Research*, 14: 1233–1250.
- Álvarez-Salgado, X. A., Beloso, S., Joint, I., Nogueira, E., Chou, L., Pérez, F. F., Groom, S., Cabanas, J. M., Rees, A. P., and Elskens, M. 2002. New production of the NW Iberian shelf during the upwelling season over the period 1982–1999. *Deep-Sea Research I*, 49: 1725–1739.
- Álvarez-Salgado, X. A., Figueiras, F. G., Pérez, F. F., Groom, S., Nogueira, E., Borges, A. V., Chou, L., Castro, C. G., Moncoiffé, G., Ríos, A. F., Miller, A. E. J., Frankignoulle, M., Savigde, G., and Wollast, R. 2003. The Portugal coastal counter current off NW Spain: new insights on its biogeochemical variability. *Progress in Oceanography*, 56: 281–321.
- Atkinson, A., and Shreeve, R. S. 1995. Response of the copepod community to a spring bloom in the Bellingshausen Sea. *Deep-Sea Research II*, 42: 1291–1311.
- Böttger-Schnack, R. 1995. Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoid copepods. *Marine Ecology Progress Series*, 118: 81–102.
- Bradford-Grieve, J. M., Markhaseva, E. L., Rocha, C. E. F., and Abiahy, B. 1999. Copepoda. *In* South Atlantic Zooplankton, vol. 2, pp. 869–1098. Ed. by D. Boltovskoy. Backhuys Publishers, Leiden. 837 pp.
- Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., and Duarte, C. M. 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *Journal of Plankton Research*, 23: 319–331.
- Castro, C. G., Álvarez-Salgado, X. A., Figueiras, F. G., Pérez, F. F., and Fraga, F. 1997. Transient hydrographic and chemical conditions affecting microplankton populations in the coastal transition zone of the Iberian upwelling system (NW Spain) in September 1986. *Journal of Marine Research*, 55: 321–352.

- Ceballos, S., Cabal, J. A., and Álvarez-Marqués, F. 2004. Reproductive strategy of *Calanoides carinatus* and *Calanus helgolandicus* during a summer upwelling event off NW Spain. *Marine Biology*, 145: 739–750.
- Clarke, K. R., and Warwick, R. M. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Environmental Research Council, Cambridge. 138 pp.
- Fernández, E., and Bode, A. 1991. Seasonal patterns of primary production in the central Cantabrian Sea (Bay of Biscay). *Scientia Marina*, 55: 629–636.
- Fernández, E., Cabal, J., Acuña, J. L., Bode, A., Botas, A., and García-Soto, C. 1993. Plankton distribution across a slope current-induced front in the southern Bay of Biscay. *Journal of Plankton Research*, 15: 619–641.
- Frouin, R., Fiúza, A. F. G., Ambar, I., and Boyd, T. J. 1990. Observations of a poleward surface current off the coasts of Portugal and Spain during winter. *Journal of Geophysical Research*, 95: 679–691.
- Gaard, E. 1999. The zooplankton community structure in relation to its biological and physical environment on the Faroe shelf, 1989–1997. *Journal of Plankton Research*, 21: 1133–1152.
- Gibbons, M. J. 1994. Diel vertical migration and feeding of *Sagitta friderici* and *Sagitta tasmanica* in the southern Benguela upwelling region, with a comment on the structure of the guild of primary carnivores. *Marine Ecology Progress Series*, 111: 225–240.
- Gislason, A., and Astthorsson, O. S. 1995. Seasonal cycle of zooplankton southwest of Iceland. *Journal of Plankton Research*, 17: 1959–1976.
- Grunewald, A. C., Morales, C. E., González, H. E., Sylvester, C., and Castro, L. R. 2002. Grazing impact of copepod assemblages and gravitational flux in coastal and oceanic waters off central Chile during two contrasting seasons. *Journal of Plankton Research*, 24: 55–67.
- Halvorsen, E., Hirst, A. G., Batten, S. D., Tande, K. S., and Lampitt, R. S. 2001. Diet and community grazing by copepods in an upwelled filament off the NW coast of Spain. *Progress in Oceanography*, 51: 399–421.
- Haynes, R., and Barton, E. D. 1990. A poleward flow along the Atlantic coast of the Iberian Peninsula. *Journal of Geophysical Research*, 95: 11425–11441.
- Head, R. N., Medina, G., Huskin, I., Anadón, R., and Harris, R. P. 2002. Phytoplankton and mesozooplankton distribution and composition during transects of the Azores Subtropical Front. *Deep-Sea Research II*, 49: 4023–4034.
- Hitchcock, G. L., Lane, P., Smith, S., Luo, J., and Ortner, P. B. 2002. Zooplankton spatial distributions in coastal waters of the northern Arabian Sea, August, 1995. *Deep-Sea Research II*, 49: 2403–2423.
- Hunt, B. P. V., Pakhomov, E. A., and McQuaid, C. D. 2002. Community structure of mesozooplankton in the Antarctic polar frontal zone in the vicinity of the Prince Edward Islands (Southern Ocean): small-scale distribution patterns in relation to physical parameters. *Deep-Sea Research II*, 49: 3307–3325.
- Huskin, I., Elices, M. J., and Anadón, R. 2003. Salp distribution and grazing in a saline intrusion off NW Spain. *Journal of Marine Systems*, 42: 1–11.
- Huthnance, J. M., Van Aken, H. M., White, M., Barton, E. D., Le Cann, B., Coelho, E. F., Alvarez Fanjul, E., Miller, P., and Vitorino, J. 2002. Ocean margin exchange – water flux estimates. *Journal of Marine Systems*, 32: 107–137.
- Isla, J. A., and Anadón, R. 2004. Mesozooplankton size-fractionated metabolism and feeding off NW Spain during autumn: effects of a poleward current. *ICES Journal of Marine Science*, 61: 526–534.
- Isla, J. A., Ceballos, S., and Anadón, R. 2004. Mesozooplankton metabolism and feeding in the NW Iberian upwelling. *Estuarine, Coastal and Shelf Science*, 61: 151–160.
- Jamet, J-L., Bogé, G., Richard, S., Geneys, C., and Jamet, D. 2001. The zooplankton community in bays of Toulon area (northwest Mediterranean Sea, France). *Hydrobiologia*, 457: 155–165.
- Joint, I., Inall, M., Torres, R., Figueiras, F. G., Álvarez-Salgado, X. A., Rees, A. P., and Woodward, E. M. S. 2001a. Two Lagrangian experiments in the Iberian upwelling system: tracking an upwelling event and an off-shore filament. *Progress in Oceanography*, 51: 221–248.
- Joint, I., Rees, A. P., and Woodward, E. M. S. 2001b. Primary production and nutrient assimilation in the Iberian upwelling in August 1998. *Progress in Oceanography*, 51: 303–320.
- Laabir, M., Poulet, S. A., Harris, R. P., Pond, D. W., Cueff, A., Head, R. N., and Ianora, A. 1998. Comparative study of the reproduction of *Calanus helgolandicus* in well-mixed and seasonally stratified coastal waters of the western English Channel. *Journal of Plankton Research*, 20: 407–421.
- Landry, M. R., Al-Mutairi, H., Selph, K. E., Christensen, S., and Nunnery, S. 2001. Seasonal patterns of mesozooplankton abundance and biomass at Station ALOHA. *Deep-Sea Research II*, 48: 2037–2061.
- Lavaniegos, B. E., Jiménez-Pérez, L. C., and Gaxiola-Castro, G. 2002. Plankton response to *El Niño* 1997–1998 and *La Niña* 1999 in the southern region of the California Current. *Progress in Oceanography*, 54: 33–58.
- Mackas, D. L., Thomson, R. E., and Galbraith, M. 2001. Changes in the zooplankton community of the British Columbia continental margin, 1985–1999, and their covariation with oceanographic conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 685–702.
- Marazzo, A., and Nogueira, C. S. R. 1996. Composition, spatial and temporal variations of Chaetognatha in Guanabara Bay, Brazil. *Journal of Plankton Research*, 18: 2367–2376.
- Morgan, C. A., Peterson, W. T., and Emmett, R. L. 2003. Onshore–offshore variations in copepod community structure off the Oregon coast during the summer upwelling season. *Marine Ecology Progress Series*, 249: 223–236.
- Nielsen, T. G., and Andersen, C. M. 2002. Plankton community structure and production along a freshwater-influenced Norwegian fjord system. *Marine Biology*, 141: 707–724.
- Nielsen, T. G., and Sabatini, M. 1996. Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. *Marine Ecology Progress Series*, 139: 79–93.
- Paffenhöfer, G-A. 1980. Zooplankton distribution as related to summer hydrographic conditions in Onslow Bay, North Carolina. *Bulletin of Marine Science*, 30: 819–832.
- Paffenhöfer, G-A., Atkinson, L. P., Lee, T. N., Blanton, J. O., Sherman, B. K., and Stewart, T. B. 1994. Variability of particulate matter and abundant zooplankton off the southeastern United States during spring of 1984 and 1985. *Continental Shelf Research*, 14: 629–654.
- Pakhomov, E. A., and Perissinotto, R. 1997. Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa. *Journal of Plankton Research*, 19: 675–691.
- Pinca, S., and Dallot, S. 1995. Meso- and macrozooplankton composition patterns related to hydrodynamic structures in the Ligurian Sea (Trophos-2 experiment, April–June 1986). *Marine Ecology Progress Series*, 126: 49–65.
- Pingree, R. D., and Le Cann, B. 1990. Structure, strength and seasonality of the slope currents in the Bay of Biscay Region. *Journal of the Marine Biological Association of the UK*, 70: 857–885.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, 43: 223–225.
- Richard, S., and Jamet, J-L. 2001. An unusual distribution of *Oithona nana* Giesbrecht (1982) (Crustacea: Cyclopoida) in a bay: the case of Toulon Bay (France, Mediterranean Sea). *Journal of Coastal Research*, 17: 957–963.

- Sameoto, D., Wiebe, P., Runge, J., Postel, L., Dunn, J., Miller, C., and Coombs, S. 2000. Collecting zooplankton. In *ICES Zooplankton Methodology Manual*, pp. 55–81. Ed. by R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley. Academic Press, London. 648 pp.
- Siokou-Frangou, I., Papathanassiou, E., Lepretre, A., and Frontier, S. 1998. Zooplankton assemblages and influence of environmental parameters on them in a Mediterranean coastal area. *Journal of Plankton Research*, 20: 847–870.
- Siokou-Frangou, I., Shiganova, T., Christou, E. D., Kamburska, L., Gubanov, A., Konsulov, A., Musaeva, E., Skryabin, V., and Khoroshilov, V. 2004. Mesozooplankton communities in the Aegean and Black Seas: a comparative study. *Marine Biology*, 144: 1111–1126.
- Teira, E., Serret, P., and Fernández, E. 2001. Phytoplankton size-structure, particulate and dissolved organic carbon production and oxygen fluxes through microbial communities in the NW Iberian coastal transition zone. *Marine Ecology Progress Series*, 219: 65–83.
- Tenore, K. R., Alonso-Noval, M., Álvarez-Ossorio, M. T., Atkinson, A., Cabanas, J. M., Cal, R. M., Campos, H. J., Castillejo, F., Chesney, E. J., González, N., Hanson, R. B., McClain, C. R., Miranda, A., Roman, M. R., Sánchez, J., Santiago, G., Valdés, J. L., Varela, M., and Yoder, M. 1995. Fisheries and oceanography off Galicia, NW Spain: mesoscale spatial and temporal changes in physical processes and resultant patterns of biological productivity. *Journal of Geophysical Research*, 100: 10943–10996.
- Turner, J. T., and Granéli, E. 1992. Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden. *Journal of Experimental Marine Biology and Ecology*, 157: 19–31.
- Valdés, J. L., Roman, M. R., Álvarez-Ossorio, M. T., Gauzens, A. L., and Miranda, A. 1990. Zooplankton composition and distribution off the coast of Galicia, Spain. *Journal of Plankton Research*, 12: 629–643.
- Verheye, H. M., and Field, J. G. 1992. Vertical distribution and diel vertical migration of *Calanoides carinatus* (Kroyer, 1849) developmental stages in the southern Benguela upwelling region. *Journal of Experimental Marine Biology and Ecology*, 158: 123–140.
- Verheye, H. M., Hutchings, L., Huggett, J. A., and Painting, S. J. 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. *South African Journal of Marine Science*, 12: 561–584.
- Verity, P. G., Bauer, J. E., Flagg, C. N., DeMaster, D. J., and Repeta, D. J. 2002. The Ocean Margins Program: an interdisciplinary study of carbon sources, transformations, and sinks in a temperate continental margin system. *Deep-Sea Research II*, 49: 4273–4295.
- Weikert, H., Koppelman, R., and Wiegatz, S. 2001. Evidence of episodic changes in deep-sea mesozooplankton abundance and composition in the Levantine Sea (eastern Mediterranean). *Journal of Marine Systems*, 30: 221–239.
- Williams, R., and Conway, D. V. P. 1988. Vertical distribution and seasonal numerical abundance of the Calanidae in oceanic waters to the south-west of the British Isles. *Hydrobiologia*, 167/168: 259–266.
- Wollast, R., and Chou, L. 2001. Ocean Margin EXchange in the Northern Gulf of Biscay: OMEX I. An introduction. *Deep-Sea Research II*, 48: 2971–2978.