Mesozooplankton size-fractionated metabolism and feeding off NW Spain during autumn: effects of a poleward current

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Two consecutive cruises were carried out off NW Spain in October 1999 in an attempt to obtain information on the poleward current that affects the hydrodynamics of this area during autumn and winter. The stations sampled were divided into three zones: coastal (C), between the saline intrusion and the coast; poleward current (P), where salinity at 100-m depth was >35.85; and oceanic (O), outside the poleward current. Phytoplankton biomass, integrated through the photic zone, was similar for the three zones. Conversely, mesozooplankton biomass showed high spatial variation, with the lowest values associated with the high-salinity current. There was a decreasing trend in the relative importance of the biomass of the largest size class (>1000 μm) from coastal to oceanic zones. The lowest percentages of both Chl a and primary production ingested daily by copepods were measured at the poleward current stations. Specific metabolic rates were not significantly different between zones. The total amount of carbon respired and the NH_4 and PO_4 released were highest in coastal areas and lowest within the poleward current, in agreement with the pattern observed for mesozooplankton biomass. Diel vertical migrations were more marked in the coastal areas, decreasing gradually towards the oceanic stations. The role of mesozooplankton in promoting the flux of carbon, nitrogen, and phosphorus followed the same spatial distribution. Overall, the contribution of mesozooplankton to biogeochemical cycles seems to be minor in the poleward current compared to the other two zones, possibly as a consequence of the low biomass associated with this current.

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Introduction

During autumn and winter, the hydrodynamics of the NW Iberian Peninsula is characterized by the presence of a warm and high-salinity current flowing northward along the continental slope (Frouin et al., 1990; Haynes and Barton, 1990). The physical properties of this current have been analysed in detail (Frouin et al., 1990; Haynes and Barton, 1990; Pingree and Le Cann, 1990; van Aken, 2002). Studies concerning the biogeochemical features of the poleward current have mainly focused on microplankton (Fernández et al., 1991, 1993; Castro et al., 1997; Álvarez-Salgado et al., 2003), whereas the larger zooplankton has been ignored in most cases. The poleward current has been regarded as a mechanism of passive transport for some zooplankton species (Villate et al., 1997; Valdés and Moral, 1998). Furthermore, zooplankton accumulations have been observed at the thermohaline front that generally forms between the current and the coastal waters (Fernández et al., 1993; González-Quirós et al., 2003). However, information on the role of zooplankton in elemental fluxes, grazing impact, or trophic structure under the influence of the poleward current remains scarce. Our main goal was to investigate these aspects in order to contribute to the knowledge of the biogeochemical cycles in the area.

Mesoscale hydrographic variability affects both community structure (e.g. Gaard, 1999; Halvorsen and Tande, 1999) and physiological properties (Gaudy and Youssara, 2003) of mesozooplankton. In this article, we investigate the effects of the warm saline current on the distribution and metabolism of mesozooplankton. The wedge-like shape of the intrusion, a decreasing trend in salinity and the thickness of the saline core in its northward flow (Teira et al., 2001; Huskin et al., 2003), as well as SST images and ADCP data

(R. Torres, pers. comm.), confirm that during the study the area was affected by an initial phase of saline intrusion. On the other hand, freshwater run-off from the Rias is normally at its maximum by October−November (Álvarez-Salgado *et al.*, 1999). So, during the study period, a saline front was well developed in the shelf break area separating the poleward current from coastal zones. As a result, three different zones were considered within the sampling area: coastal, inside the poleward current, and oceanic.

The combination of results on the size-structure, grazing, and metabolic rates may provide valuable information on the role of mesozooplankton on food web functioning. Finally, the importance of zooplankton in the downward export of organic matter is examined by analysing the active flux mediated by mesozooplankton diel vertical migrations (DVM). Our results are compared with those obtained by Huskin *et al.* (2003) on salp distribution and grazing during the Gigovi-1099 cruise. The relative importance of salps and mesozooplankton in the overall grazing

impact is discussed, as is the potential mechanism of interaction of these two groups with the poleward current.

Materials and methods

Two consecutive cruises were conducted off NW Spain in autumn 1999, on board RV "Thalassa": Omex-1099 (14−20 October) and Gigovi-1099 (20 October to 7 November). On each cruise, stations were distributed along three transects perpendicular to the coast (Figure 1). An additional Lagrangian sampling exercise was carried out during the second cruise, following a drifting drogue deployed at 100-m depth, at the core of the poleward current. This Lagrangian component resulted in a transect parallel to the coast (Stations 98−105). Station 34 was not included in any transect, because it is clearly outside the shelf break area. The sampling area was divided into three zones: coastal (C), between the saline intrusion and the coast;
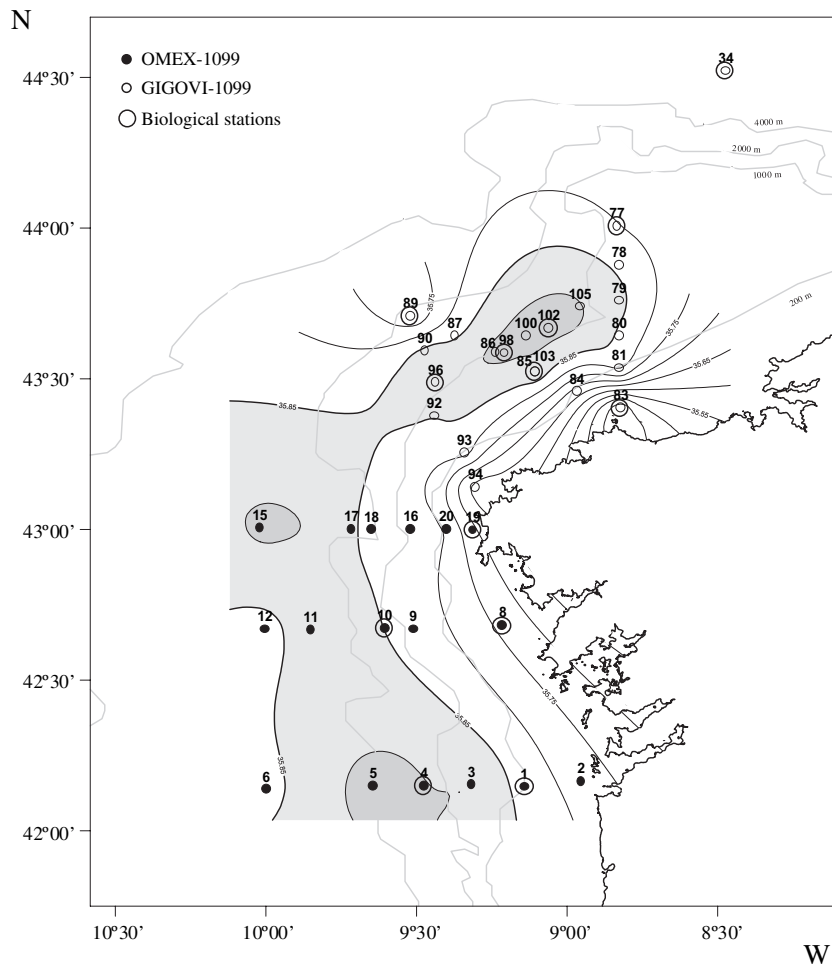

Figure 1. Map of the study area with the stations sampled during Omex-1099 (filled dots) and Gigovi-1099 (open dots). Biological stations are marked as circled dots. Isolines represent salinity at 100-m depth. The grey areas (salinity > 35.85) correspond to the zone considered as inside the poleward current.

poleward current (P), where salinity at 100-m depth was >35.85; and oceanic (O), outside the poleward current.

Continuous profiles of temperature, salinity, density, and fluorescence were recorded using a Neil Brown MARK-III CTD. Chl *a* concentration was estimated from CTD fluorescence, whereas primary production was estimated using the NaH $^{14}CO_3$ inoculation method, as described in Teira *et al.* (2001). Incubations for primary production estimates were made at all stations labelled as ''biological'' during the Omex cruise, and only at Stations 89 and 96 during the Gigovi cruise. Mesozooplankton samples for biomass and abundance estimates and for copepod gut contents were taken at all stations. Biological stations were sampled during both daytime and night-time, whereas the rest of the stations were sampled only once (generally during daytime). Incubations to estimate mesozooplankton respiration and excretion, as well as gut evacuation experiments, were performed at the biological stations sampled at night. Sampling hauls were made with a modified triple WP-2 net, with 60-cm ⌀ rings, 200-µm mesh, and filtering cod-ends. The net was towed vertically, from 200 m (or close to the bottom in the case of shallower stations) to the surface at ca. 0.5 m s^{-1}. Cod-end contents were sieved sequentially through 1000-µm, 500-µm, and 200-µm meshes to separate the mesozooplankton into large, medium, and small size fractions. Samples for abundance and taxonomic identification were preserved in 4% borax-buffered formalin–seawater solution. Biomass samples were filtered through pre-weighed Whatman GF/A filters and then stored at −20°C. Filters were dried at 60°C for about 24 h before weighing. Carbon and nitrogen analyses were performed with a Perkin–Elmer 2400 Elemental Analyser.

Given the high numerical dominance of copepods (86.5%, 94.2%, and 97.5% of total abundance in coastal, poleward current, and oceanic zones, respectively), their herbivorous activity was considered to provide a good estimation of the grazing impact of the whole mesozooplankton community. The ingestion rate of copepods was estimated using the gut pigment method (Mackas and Bohrer, 1976). Copepods were gathered on shark-skin filters immediately after size fractionation and stored at −20°C in complete darkness until laboratory analysis. The numbers of individuals picked for gut fluorescence measurements were 75, 30–50, and 5–15 for the small, medium, and large fractions, respectively. Three sub-replicates were taken in each case. Gut pigments were extracted in 6 ml of 90% acetone, overnight at 4°C and in darkness. Fluorescence was measured with a Turner Designs 10-005R fluorometer. No corrections for Chl *a* destruction were applied. To estimate gut evacuation rates, size-fractionated mesozooplankton was transferred to a cool box with 0.2 µm filtered surface seawater. Subsamples were taken at consecutive time intervals (0, 2, 5, 8, 10, 15, 20, 30, and 40 min) and processed as described for gut pigment measurement. At the biological stations, diurnal and nocturnal samples were compared to test for diel variations in gut contents. The relationship obtained between

nocturnal and diurnal values was used to recalculate daily ingestion at the stations that were sampled only once. A different relationship was considered for each cruise (Figure 2) because of the highly significant differences observed between the slopes (test of parallelism, $F_{1,34} = 26.1$; $p < 0.0001$). Within the same cruise, the night:day relationships did not differ between size fractions (ANCOVA test, $p > 0.1$ on both cruises).

Animals collected for respiration and excretion incubations were size-fractionated in a cool box filled with surface seawater and transferred at once, without being exposed to air, to 3-litre jars filled with 0.2 µm filtered seawater, where they were kept for about 2 h for acclimation. Mixed crustaceans were then introduced in 1-litre glass bottles filled with 0.2 µm filtered seawater. Gelatinous zooplankton was not used because of the high mortality rates observed in previous incubations. Three control bottles without animals and three experimental replicates for each size fraction were incubated for ca. 20 h under dim light conditions. Incubations were performed on a rotating wheel kept in a water bath at the temperature of the deep Chl *a* maximum (±0.1°C). At the end of the incubation, the health of the animals was checked by ensuring that they were swimming actively in the bottles, and then two subsamples for oxygen analysis and another two for NH_4 and PO_4 analyses were taken by siphoning water through a 200-µm mesh. Dissolved oxygen concentrations were measured on board by the Winkler titration method with a 721 NET Titrino. Samples for the determination of NH_4 and PO_4 were frozen at −20°C for subsequent analysis in the laboratory, according to Grasshoff *et al.* (1983), using a Technicon AAII Autoanalyzer. After subsampling, the animals incubated were recovered on Whatman GF/A filters and frozen until analysis for carbon and nitrogen content, as mentioned for the biomass samples. Respired oxygen was converted to carbon assuming a respiratory quotient of 0.97 (Omori and Ikeda, 1984). Active fluxes of carbon respired, as well as of NH_4 and PO_4 excreted, to the mesopelagic zone were estimated as in Zhang and Dam (1997), by applying the equation $F = B \times M \times T$, where B is the diel migrating
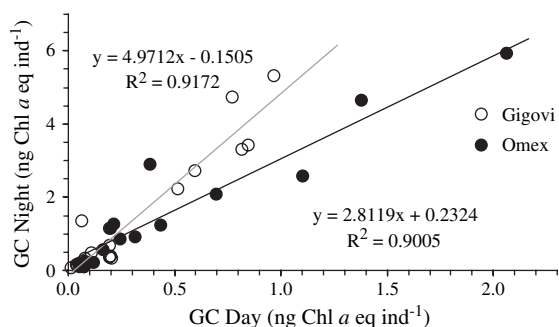

Figure 2. Relationships between nocturnal and diurnal copepod gut contents (GC) in Omex-1099 and Gigovi-1099. Given that these relationships did not differ between fractions (see Materials and methods), the three size classes were pooled for each cruise.

mesozooplankton calculated as the difference in biomass (mg C m^{-2}) between day and night samples in the top 200 m, M is the hourly metabolic rate, and T is the number of hours per day (13 h in this case), during which migrating mesozooplankton stay below the euphotic zone.

Results

A detailed description of the hydrographic conditions during Omex-1099 and Gigovi-1099 can be found in Teira *et al.* (2001) and Huskin *et al.* (2003). Both studies reveal the presence of the saline current flowing northward along the continental slope, with a high-salinity core (> 35.85) located between ca. 60- and 130-m depth. Phytoplankton biomass integrated through the photic zone was virtually identical for the three zones considered (Figure 3), with values of ∼ 17 mg Chl *a* m^{-2}. Conversely, mesozooplankton biomass showed large spatial variations (one-way ANOVA, $F_{2,33} = 4.01$; $p = 0.028$). A post hoc Tukey HSD test for unequal samples revealed significant differences only between coastal and poleward zones ($p = 0.049$). Total mesozooplankton biomass ranged from 0.27 ± 0.04 (mean $\pm$ s.e.) g C m^{-2} in the poleward, to 0.53 ± 0.10 g C m^{-2} at the coastal area. Mesozooplankton C:N ratio showed a slight variation between zones (Figure 4), with differences statistically significant only for the medium size class (one-way ANOVA, $F_{2,34} = 5.23$; $p = 0.01$). For the three size classes, the highest C:N ratios were detected in the poleward current. There was a decreasing trend in the relative importance in the biomass of the higher size class (> 1000 μm) from the coastal to the oceanic zone (Figure 5a).

Copepod gut contents did not show any pattern associated with the three zones (Table 1). Gut evacuation rates increased slightly with size (0.0243, 0.0316, and 0.0329 min^{-1} for small, medium, and large fractions, respectively), although the differences were not statistically significant (test of parallelism, $F_{2,224} = 1.50$; $p > 0.1$). The percentage of Chl *a* ingested daily was lowest in the poleward current (Table 1). However, the ANOVA test did not reveal differences between zones ($F_{2,33} = 2.01$; $p = 0.15$). The
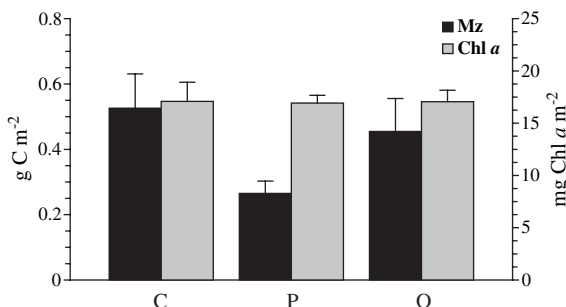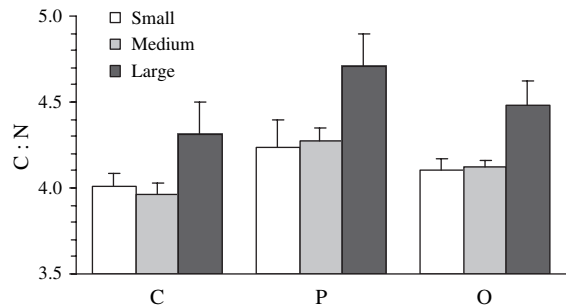

Figure 4. C:N ratios of size-fractionated mesozooplankton in each zone. Error bars indicate s.e.

differences observed reflect mainly the variation in the numerical abundance of copepods. The contribution of the different size classes to the total grazing impact was similar in the coastal and the oceanic areas, whereas the impact of the small fraction was higher in the poleward current than in the other two zones (Figure 5b), but there were no significant differences between zones (one-way ANOVA, $F_{2,32} = 0.58$; $p > 0.1$). The percentage of primary production ingested daily by copepods was also lowest at the stations located within the poleward current (Table 1). It is noteworthy that the percentage reported for the outer area is that of Station 89, the only oceanic station where primary production was measured. Assuming an assimilation efficiency of 70% (Conover, 1966), and a C:Chl *a* ratio of 50, the total phytoplankton ingested failed to fulfil the minimum metabolic requirements of mesozooplankton (Table 2). Specific
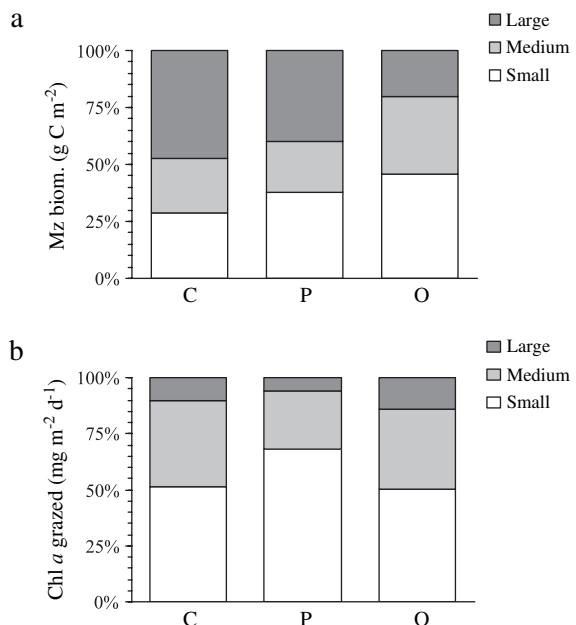
Figure 5. Contribution to total mesozooplankton biomass (Mz biom.) of large, medium, and small fractions (a), and relative importance of each size class of copepods to total Chl *a* grazed daily by copepods (b).

Figure 3. Mesozooplankton (Mz) and phytoplankton (Chl *a*) biomass at coastal (C), poleward (P), and oceanic (O) zones. Units are g C m^{-2} and mg Chl *a* m^{-2} for Mz and Chl *a*, respectively. Error bars indicate s.e.

Table 1. Mean values $\pm$ s.e. of gut contents (GC) of small, medium, and large copepods, percentage of phytoplankton standing stock (% Chl *a* grazed), and primary production (% Pp grazed) ingested daily by the sum of the three size classes. Grazing impact by salps was calculated from Table 2 in Huskin *et al.* (2003), and corresponds only to the cruise Gigovi-1099.

	GC (ng Chl *a* eq ind $^{-1}$)			% Chl *a* grazed		
	Small	Medium	Large	Copepods	Salps	% Pp grazed
Coastal	0.24 $\pm$ 0.06	0.69 $\pm$ 0.16	1.60 $\pm$ 0.32	6.6 $\pm$ 1.9	6.5 $\pm$ 4.0	8.9 $\pm$ 5.4
Poleward	0.25 $\pm$ 0.05	0.63 $\pm$ 0.09	2.90 $\pm$ 0.42	3.1 $\pm$ 0.6	11.8 $\pm$ 7.5	7.5 $\pm$ 3.3
Oceanic	0.15 $\pm$ 0.02	0.51 $\pm$ 0.09	2.47 $\pm$ 0.64	4.9 $\pm$ 1.3	5.1 $\pm$ 2.1	12.4

metabolic rates decreased from the smaller to the larger size classes (Table 3), in agreement with the widely reported allometric relationship between metabolic rate and body size. There were no significant differences between zones in respiration rates, or in NH_4 and PO_4 excretion rates. Data were analysed using an ANCOVA for each size class and metabolic rate, with incubation temperature as covariate. A sequential Bonferroni test was then applied. The total amount of carbon respired, as well as the NH_4 and PO_4 released, was highest in the coastal areas and lowest in the poleward current (Table 2), following the same spatial pattern observed for mesozooplankton biomass. The percentage of phytoplankton nitrogen requirements met through mesozooplankton NH_4 excretion ranged from 10.9% (poleward current) to 24.7% (open ocean). PO_4 excretion accounted for between 16.5% (poleward current) and 37.3% (open ocean) of the total phosphorus demand of the primary producers (Table 2). Phytoplankton nutrient requirements were estimated by applying Redfield ratios, i.e. C : N : P = 106 : 16 : 1 (Redfield *et al.*, 1963).

Diel vertical migrations were more marked in the coastal areas and decreased gradually towards the oceanic stations (Table 2). As a consequence, the importance of mesozooplankton in the active flux of carbon, nitrogen, and phosphorus followed this same spatial distribution. Most of the migrant biomass was attributed to the largest size class. Differences between diurnal and nocturnal biomass were statistically significant only for this size fraction (t-test for paired samples, t $= -3.85$; p $= 0.004$; n $= 10$).

Discussion

Given that high values of zooplankton biomass are normally associated with fronts, especially fronts located within shelf break areas (Mann and Lazier, 1996 and references therein), this pattern might be expected at the saline front that developed between the poleward current and the coastal waters. The shelf break front originating from this poleward current leads to an enhancement in phytoplankton, zooplankton, and ichthyoplankton biomass in the southern Bay of Biscay during the spring (Fernández *et al.*, 1993; González-Quirós *et al.*, 2003). Likewise, the maximum concentrations of salps during the Gigovi-1099 cruise were

Table 2. Total carbon respired and ammonium and phosphate excreted daily by mesozooplankton are summarized for the three zones. Resp. C flux, excr. NH_4 flux, and excr. PO_4 flux indicate the amount of these products that are released below 200 m during night-time by diel vertical migrators, and represent the active flux driven by mesozooplankton within the biological pump. C ing./C req.: percentage of mesozooplankton carbon requirements for metabolism that is supported by phytoplankton carbon ingested. In C ing. corr./C req., ingestion was corrected by assuming a 33% of Chl *a* destruction during digestion. NH_4 excr./N req. and PO_4 excr./P req.: percentages of nitrogen and phosphorus required by primary producers resupplied by mesozooplankton through their excretory activity. All the values are presented as average $\pm$ s.e.

	Coastal	Poleward	Oceanic
Migrant biomass (g C m^{-2} d^{-1})	0.36 $\pm$ 0.07	0.27 $\pm$ 0.21	0.03 $\pm$ 0.01
Total C resp. (mg m^{-2} d^{-1})	96.9 $\pm$ 16.1	48.0 $\pm$ 14.8	59.4 $\pm$ 15.3
Resp. C flux (mg m^{-2} d^{-1})	30.3 $\pm$ 1.9	10.4 $\pm$ 6.3	2.2 $\pm$ 0.3
Total NH_4 excr. (μmol m^{-2} d^{-1})	1 094.6 $\pm$ 292.2	628.9 $\pm$ 150.1	1 035.3 $\pm$ 344.9
Excr. NH_4 flux (μmol m^{-2} d^{-1})	353.3 $\pm$ 78.6	159.6 $\pm$ 61.6	48.1 $\pm$ 17.4
Total PO_4 excr. (μmol m^{-2} d^{-1})	40.3 $\pm$ 10.1	20.2 $\pm$ 5.0	40.7 $\pm$ 16.3
Excr. PO_4 flux (μmol m^{-2} d^{-1})	12.7 $\pm$ 2.3	2.8 $\pm$ 0.7	1.2 $\pm$ 0.5
C ing./C req. (%)	24.4 $\pm$ 7.1	30.7 $\pm$ 3.2	38.8 $\pm$ 16.0
C ing. corr./C req. (%)	36.6 $\pm$ 10.7	46.1 $\pm$ 6.7	58.3 $\pm$ 23.9
NH_4 excr./N req. (%)	20.8 $\pm$ 3.4	10.9 $\pm$ 2.2	24.7
PO_4 excr./P req. (%)	32.1 $\pm$ 15.2	16.5 $\pm$ 4.5	37.3

Table 3. Mean ± s.e. values of metabolic rates and O:N atomic ratios of small, medium, and large mesozooplankton at coastal (C), poleward (P), and oceanic (O) zones.

	μmol O$_2$ μmol C^{-1} d^{-1}			μmol NH$_4$ μmol C^{-1} d^{-1}			μmol PO$_4$ μmol C^{-1} d^{-1}			O:N		
	C	P	O	C	P	O	C	P	O	C	P	O
Small	0.29 ± 0.24	0.25 ± 0.12	0.22 ± 0.11	0.042 ± 0.016	0.042 ± 0.013	0.031 ± 0.004	0.0015 ± 0.0006	0.0015 ± 0.0005	0.0016 ± 0.0001	13.8	11.9	14.2
Medium	0.15 ± 0.06	0.17 ± 0.05	0.16 ± 0.09	0.023 ± 0.008	0.036 ± 0.010	0.034 ± 0.006	0.0009 ± 0.0004	0.0009 ± 0.0002	0.0010 ± 0.0001	13.0	9.4	9.4
Large	0.12 ± 0.07	0.09 ± 0.05	0.09 ± 0.01	0.022 ± 0.007	0.014 ± 0.007	0.024 ± 0.006	0.0007 ± 0.0003	0.0004 ± 0.0002	0.0007 ± 0.0001	10.9	12.9	7.5

found associated with the saline front (Huskin *et al.* 2003). However, no such accumulations were observed for meso-zooplankton biomass (Figure 6a). The discrepancy between the spatial distribution of the salps and that of the meso-zooplankton could be due to a higher affinity of salps for warm and saline waters (Lavaniegos *et al.*, 2002). In addition, the phytoplankton community inside the poleward current was dominated by small cells (Fernández *et al.*, 1993; Castro *et al.*, 1997; Álvarez-Salgado *et al.*, 2003), which are adequate food for salps but not for copepods. Unlike the situation described by Fernández *et al.* (1993) for the central Cantabrian Sea, during our study phytoplankton did not accumulate at the slope front, and biomass maxima were instead observed at the coastal stations (Figure 6b).

Differences in the elemental composition of mesozoo-plankton between zones were not marked. Nevertheless, the pattern of variation was consistent for the three size fractions, with similar ratios recorded in the coastal and oceanic zones and higher ratios in the poleward current. Although small, these differences might be indicative of the occurrence of different zooplankton assemblages. Variations in zooplankton C:N ratios between different hydrographic regimes were also reported by Youssara and Gaudy (2001) in the Mediterranean Sea. They attributed this variation to the different composition of the zooplankton communities that are transported passively to the sampling area by the Atlantic Current. The poleward current might have a similar effect in our study area. Information concerning the taxonomic composition of the zooplankton community in the area associated with the saline current is limited. Valdés *et al.* (1990) reported on the main zooplankton taxa found during two cruises conducted in June and September 1994 off NW Spain, but upwelling conditions prevailed during both months. Also, all the stations they sampled were located within the zone that we considered as coastal in our study. Bode *et al.* (1998) analysed mesozooplankton samples collected on a monthly basis between 1990 and 1995 at two stations (one close to the coast and one over the shelf) located slightly eastward of transect 76−82 of the cruise Gigovi-1099. According to their results, gelatinous zooplankton becomes more important, in terms of abundance, in October, but only at the outer station. This station does not seem to be far enough from the coast to be located inside the poleward current, but it could be affected by the saline front, where Huskin *et al.* (2003) found the maximum abundance of salps during Gigovi-1099. Only samples from biological stations were analysed to determine the taxonomic composition of zooplankton during Omex-1099. Cluster analysis and non-metric multidimensional scaling (Blanco *et al.*, in prep.) showed a separation between the coastal stations and those affected by the poleward current. The only data available on the zooplankton taxonomic composition during the Gigovi-1099 cruise are for salps, as reported in Huskin *et al.* (2003). Total abundance and biomass of salps were highest in frontal areas, but high values were also found inside the poleward
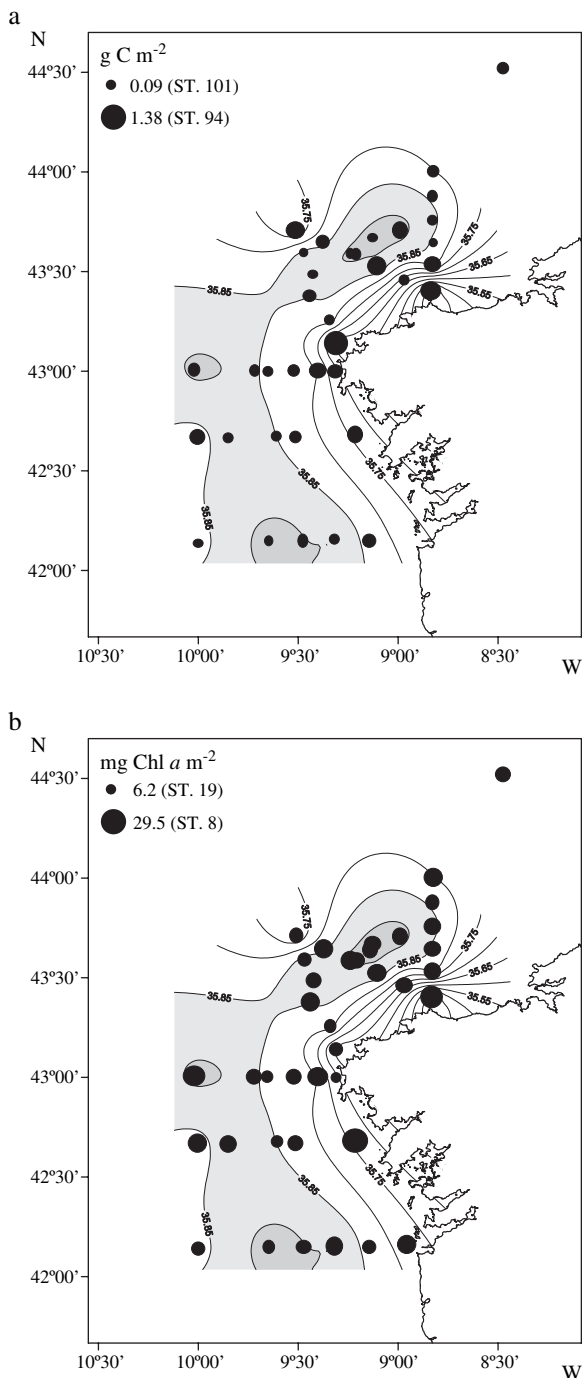
Figure 6. Mesozooplankton (a) and phytoplankton (b) biomass at each station. Legends indicate the minimum and maximum values and, in parentheses, the stations where these values were measured. Isolines represent salinity at 100-m depth; the grey areas are the zones considered as the poleward current.

current. By contrast, salps were hardly detected at coastal stations, and their importance in oceanic zones decreased compared to that in poleward current waters.

Mesozooplankton size-structure varied across the study area. The contribution of the large size fraction to total biomass decreased gradually from the coast to the offshore region. This pattern is similar to that observed previously for phytoplankton in the area by Álvarez-Salgado *et al.* (2003), who reported a higher importance of large phytoplankton cells in coastal areas than in the poleward current. The correlation between phytoplankton and zooplankton size-structures is a phenomenon widely observed in pelagic ecosystems (e.g. Stelfox *et al.*, 1999; Clark *et al.*, 2001), and suggests a "bottom-up" control over the zooplankton community. The total amount of Chl *a* ingested by copepods, as well as their grazing impact on the phytoplankton standing stock, was lower in the poleward current than in coastal and oceanic zones. Coastal values were slightly higher than oceanic ones. This distribution is determined by the spatial variation of copepod abundance, rather than by changes in copepod gut contents. The relative importance of the three size classes of copepods to phytoplankton ingestion also differs between the poleward current and the other two zones. The contribution of the small size fraction to total Chl *a* ingested accounted for approximately 50% of the total in coastal and oceanic waters, whereas this percentage rose to ca. 70% in the poleward current (Figure 5b). The taxonomic composition of phytoplankton for the two cruises is not available, but previous studies have shown a higher importance of small phytoplankton cells in the poleward current compared to the surrounding coastal and oceanic waters (Fernández *et al.*, 1991, 1993; Álvarez-Salgado *et al.*, 2003). Accordingly, given that the size of particles fed on seems to vary with the size of copepods (Mauchline, 1998), it is conceivable that the observed pattern of copepod size class contribution to total Chl *a* ingestion may be linked to the phytoplankton size-structure observed within each zone. Despite the differences between zones, herbivory by copepods exerted a weak impact on phytoplankton standing stock throughout the study area. It could be argued that our figures are underestimated because no parallel experiments were performed to assess Chl *a* destruction during the digestive process. Reported values on Chl *a* destruction during digestion show a great deal of variability (see review in Båmstedt *et al.*, 2000). Dam and Peterson (1988) proposed an average percentage of Chl *a* destruction of 33%, and this figure has been applied by several authors when direct estimates are not available (e.g. Pakhomov *et al.*, 1997; Calbet, 2001). The application of this correction factor to our results did not alter our conclusions, namely that the grazing impact was too low to control phytoplankton biomass. However, adding the phytoplankton ingested by salps during the Gigovi-1099 cruise (Table 2 in Huskin *et al.*, 2003) to copepod ingestion at the same stations, the percentage of Chl *a* removed daily increased significantly (Table 1). This increase was particularly important in the poleward current,

where values of Chl *a* ingested were lowest for copepods and highest for salps. The grazing impact of copepods was higher on primary production than on phytoplankton biomass. The highest percentage was obtained offshore (12.4%), at Station 89, i.e. the only oceanic station where primary production was measured. At all stations, the phytoplankton carbon ingested was not enough to meet the minimum requirements of mesozooplankton to maintain their basal metabolism. So they must have complemented their diet with other food sources, such as microzooplankton or detritus. In support of this hypothesis are the O : N ratios obtained from the three zones, which indicate a protein-oriented metabolism, typical of situations where an omnivorous diet is used.

Given the absence of differences between zones in mesozooplankton metabolic rates, the pattern of metabolic end-products released into the medium in each zone would depend mainly on mesozooplankton biomass. Consequently, total carbon respired as well as NH_4 and PO_4 excreted were similar in the nearshore and offshore zones, and clearly higher here than in the poleward current zone. The contribution of mesozooplankton excretion to phytoplankton requirements followed the same spatial distribution. Such a contribution is relatively important, especially in the case of phosphorus. Nevertheless, mesozooplankton undergoes diel vertical migrations (DVM), releasing nutrients below the euphotic zone where they are not available to primary producers. During this study, the percentages of the total NH_4 excreted daily that were produced below 200 m at night were 31.9, 31.4, and 4.6 in the nearshore, the poleward current, and the open ocean, respectively. In the case of PO_4 excretion, these percentages were 33.6, 18.5, and 3.0. The importance of vertical migration therefore seems to be less in oceanic waters than in the other two zones. This difference is explained by the mesozooplankton size-structure of each zone, specifically by a decrease in the contribution of the largest fraction to the total biomass of the oceanic zone. In his review of DVM of zooplankton in the North Atlantic, Hays (1996) found a strong correlation between mean body size and the magnitude of DVM. Mesozooplankton excretion and respiration below the photic zone via DVM play an important role in the downward export of organic matter (Longhurst and Harrison, 1989), especially in coastal areas (Morales, 1999). In our study, active fluxes of carbon, nitrogen, and phosphorus as a result of the metabolic activity of mesozooplankton were lowest in oceanic waters, in accordance with the observed spatial variations in DVM. In contrast, the values measured in coastal areas are among the highest published to date (Longhurst *et al.*, 1990; Dam *et al.*, 1995; Le Borgne and Rodier, 1997; Zhang and Dam, 1997; Morales, 1999; Steinberg *et al.*, 2000; Al-Mutairi and Landry, 2001; Roman *et al.*, 2002). Taking into account that mesozooplankton may also excrete dissolved organic carbon (DOC) and nitrogen (DON) below the euphotic zone when they migrate to depth at night (Le Borgne and Rodier, 1997; Steinberg *et al.*, 2000), our estimates of active flux and their

significance with respect to the biological pump should be interpreted as conservative.

Overall, under the conditions analysed in this study, a "bottom-up" control of mesozooplankton distribution is suggested. Given that the response of zooplankton to shifts in phytoplankton communities seems to be ultimately controlled by hydrodynamics (Legendre and Rassoulzadegan, 1996), the mesozooplankton contribution to biogeochemical cycles and its importance within the food web off NW Spain during autumn would be largely determined by the poleward current.

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