

Mesozooplankton metabolism and feeding in the NW Iberian upwelling

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Received 30 January 2004; accepted 20 April 2004

Abstract

Mesozooplankton size-fractionated biomass, feeding, and metabolic rates were investigated during a cruise conducted off NW Spain in August 1998. Based on different hydrographic conditions observed throughout the study area (upwelling events nearshore and stratified waters offshore), the sampling area was divided into coastal and oceanic zones. Both phytoplankton and mesozooplankton biomass were higher in the coastal upwelling than in the offshore zone. Size structure analysis shows that the small fraction (200–500 μm) of mesozooplankton was more important than the larger fractions (500–1000 μm and >1000 μm) in the open ocean in terms of both biomass and grazing activity. The relationship between copepod ingestion rate and the concentration of chlorophyll *a* >5 μm resembled a type II functional response. Saturation occurred at the coastal stations, where copepod gut contents were highest. The grazing impact on both phytoplankton biomass and primary production seemed to be higher offshore (5.7 and 12.9%, respectively) than in upwelled waters (5.2 and 5.2%), although the differences were not statistically significant. Phytoplankton ingestion was enough to fulfil the basal metabolism of mesozooplankton in the upwelling area (102.1% of the minimum carbon requirements met) but not in the offshore (45.9%). Feeding activity and metabolic measurements on mesozooplankton point to a herbivorous food web in the coastal upwelling zone and a multivorous food web in the stratified open oceanic waters. The amount of metabolic end products released by mesozooplankton was higher in the coastal zone, but mesozooplankton played a more important role as nutrient regenerators in the multivorous food web (30.3 and 21.7% of the nitrogen and phosphorus phytoplankton demand accounted for ammonium and phosphate excretion, respectively) than in the herbivorous one (3.8% for ammonium and 2.6% for phosphate).

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Keywords: mesozooplankton; respiration; ammonium and phosphate excretion; grazing; upwelling; NW Spain

1. Introduction

The dominance of northerly winds from March to October in the NW of the Iberian Peninsula favours the upwelling of Eastern North Atlantic Central Water off the Galician coast (Tenore et al., 1995; Álvarez-Salgado et al., 2002). The nutrient-rich upwelled water enhances phytoplankton growth (Varela et al., 2003), so that the highest values of primary production and chlorophyll *a* (Chl*a*) concentration in the area throughout the year are detected under upwelling conditions (Tilstone et al.,

2003). The comparison between these highly productive coastal systems and the adjacent open ocean waters has received a growing attention in recent years in order to understand the biogeochemical cycles in the ocean margins (e.g. Wollast and Chou, 2001). In this regard the multidisciplinary Ocean Margin EXchange II (OMEX II) project, in which framework this study was developed, has focused on the understanding of the carbon cycle in the Iberian margin. Given the highly productive situation found in the coastal upwelling system accompanied with filaments that transport organic matter off-shelf (Álvarez-Salgado et al., 2001), this area is particularly interesting to understanding the role of productive coastal waters on biogeochemical fluxes.

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Biological studies in the NW Iberian upwelling system have been focused mostly on phytoplankton (e.g. Castro et al., 1997; Teira et al., 2001), whereas the scarce information available on zooplankton mainly concerns their distribution (Valdés et al., 1990; Tenore et al., 1995). Within the OMEX programme, a number of studies were devoted to zooplankton feeding (Batten et al., 2001; Fileman and Burkill, 2001; Halvorsen et al., 2001) and faecal pellets production (Riser et al., 2001) helping, at least partially, to fill this gap. Nevertheless, to our knowledge, information on the metabolic properties of zooplankton off NW Spain still remains rather limited.

The aim of this study was to estimate the metabolic rates and grazing impact of mesozooplankton in the NW Iberian upwelling system in a broader spatial scale than was attempted by the above mentioned authors, comparing coastal upwelling and offshore stratified waters. The implications of the results on metabolic rates (i.e., the potential contribution of the metabolic end products released to the nutrient requirements of primary producers) are discussed. The combination of mesozooplankton distribution, size structure, feeding, and metabolism will contribute to knowledge of the structure and functioning of the food webs, which play a key role in determining material fluxes within the food chain (Legendre and Rassoulzadegan, 1996). In addition, the results are compared with those obtained by other authors in the same area and date in an upwelling filament (Batten et al., 2001; Fileman and Burkill, 2001; Halvorsen et al., 2001).

2. Materials and methods

2.1. The study area and environmental variables

Data were collected during the cruise OMEX-0898 (1–11 August 1998, on board R/V Professor Shtokman) off the coast of Galicia, in the NW of the Iberian margin. Stations were distributed along three onshore–offshore transects (Fig. 1). Samples for mesozooplankton biomass, abundance and gut contents were collected at all the stations, whereas incubations to estimate metabolic and gut evacuation rates were performed only at the stations classed as ‘biological’. Biological stations were sampled during the day and at night, whereas for the remaining stations the samples were taken only during daytime hours. Diurnal and nocturnal values of mesozooplankton biomass, abundance and copepod gut contents in the biological stations were averaged. Continuous profiles of temperature were recorded at each station using a Neil Brown MARK-III CTD probe attached to a rosette equipped with 24 Niskin bottles. The methodology employed to determine both size-fractionated Chl *a* (fluorometric measurement) and

primary production (NaH ¹⁴CO₃ method) can be found in Teira et al. (2001).

2.2. Mesozooplankton collection

Samples to determine mesozooplankton abundance and biomass were collected by means of vertical hauls from 200 m (or near the bottom, where the depth was less than 200 m) to surface. A 40 cm diameter WP2 triple net, with 200 μm mesh size and filtering cod-ends was used. The net was towed at approx. 0.5 m s⁻¹. All the samples were fractionated into three size classes using 1000, 500 and 200 μm sieves. Samples for abundance were fixed in 4% formalin, and those for biomass calculation were filtered onto pre-weighed Whatman GF/A glass-fiber filters and then frozen until dry-weight determination ashore. Filters were dried at 60 °C for about 24 h before weighting. Finally, carbon and nitrogen content analyses were performed using a Perkin Elmer 2400 Elemental Analyser.

2.3. Grazing

Feeding of copepods was estimated by the gut pigment method (Mackas and Bohrer, 1976). Cod-end contents were fractionated in three size classes as for biomass and abundance. Immediately after fractionation, animals were placed on sharkskin filters and stored at –20 °C in complete darkness until laboratory analysis. The number of individuals picked up for gut fluorescence measurements was 75, 30–50, and 5–15 for the fractions small, medium and large, respectively. Three subreplicates were taken in each case. Gut pigments were extracted in 6 ml of 90% acetone overnight at 4 °C in darkness, and fluorescence was measured using a Turner Designs 10-005R fluorometer before and after acidification with 1 N HCl. No corrections for Chl *a* destruction were applied. Gut evacuation rates were calculated from experiments carried out during nighttime at the biological stations. The mesozooplankton were fractionated and placed in 0.2 μm filtered surface seawater shortly afterwards. Subsamples were taken at consecutive time intervals (0, 3, 5, 8, 10, 15, 20, 30, and 40 min) and processed as described for gut pigment measurement. Copepod grazing impact was estimated by multiplying their abundance by individual ingestion rates. Phytoplankton ingested was converted to carbon units by applying a C:Chl *a* ratio of 50 (Båmstedt et al., 2000). Ingestion rates were plotted against phytoplankton >5 μm to estimate the functional response of copepods, which was fitted to the Michaelis–Menten model:

$$IR = \frac{I_{\max}FC}{K_m + FC}$$

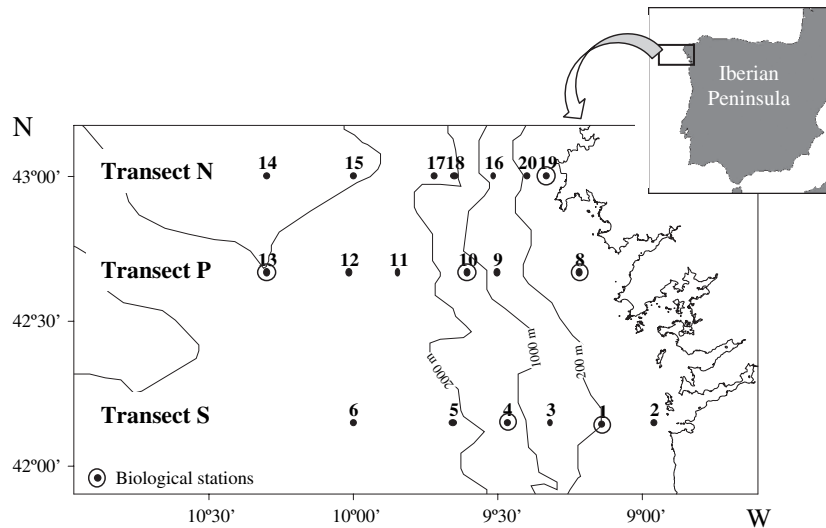


Fig. 1. Study area showing the stations sampled during OMEX-0898. The locations of the biological stations are indicated by encircled dots.

This equation describes a type II hyperbolic relationship between copepod ingestion rates (IR) and food concentration (FC).

2.4. Metabolism

Animals collected for respiration and excretion incubations were size-fractionated into a cool box filled with surface seawater and transferred at once, without being exposed to air, into 3 L jars filled with 0.2 μm filtered seawater, where they were kept for about 2 h for acclimation. Mixed crustaceans were introduced in 1 L glass bottles filled with 0.2 μm filtered seawater and incubated for 20–24 h at the surface temperature. Three control bottles without animals and three replicates for each size fraction were incubated. 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 replicate subsamples for oxygen and two subsamples for ammonia and phosphate were taken from each bottle. Subsampling was done by siphoning through a 200 μm mesh, while retaining the organisms in the bottles. The dissolved oxygen concentration was determined on board by the Winkler titration method using a 721 NET Titrino. The samples for determination of ammonia and phosphate were frozen at $-20\text{ }^{\circ}\text{C}$ for their subsequent analysis at the laboratory according to Grasshoff et al. (1983) using an autoanalyzer Technicon AAI. After subsampling, the experimental animals were recovered on Whatman GF/A filters and frozen until analysis of C and N content, as described for biomass samples. The carbon requirements of the zooplankton for basal metabolism were estimated from respiration rates assuming a respiratory quotient of 0.97 (Omori and Ikeda, 1984). The amounts of N and P required by primary producers were estimated from

primary production rates given in Teira et al. (2001) and by applying standard Redfield ratios, i.e. C:N:P = 106:16:1.

3. Results

3.1. Thermohaline structure

Two different hydrographic situations were detected in the study area: upwelling conditions close to the coast and stratified waters offshore (Fig. 2). These conditions led to an increasing gradient in surface temperature from coastal to oceanic waters. According to the temperature profiles the study area was divided into two zones. Stations 1, 2, 8, 16, 19 and 20 were designated coastal upwelling stations, the rest were oceanic. The thermohaline structure during the OMEX-0898 cruise is detailed in Teira et al. (2001).

3.2. Mesozooplankton distribution

Mesozooplankton biomass was significantly higher ($t_{14} = 3.14$; $p < 0.01$) at coastal (0.74 ± 0.16 (SE) g C m^{-2}) than at oceanic areas (0.36 ± 0.05 g C m^{-2}). The pattern of spatial distribution of mesozooplankton biomass was similar to that of phytoplankton biomass (Fig. 3a and b), with highest values in the coastal stations. Thus, mesozooplankton and phytoplankton biomass were positively correlated ($R^2 = 0.56$; $p < 0.01$; $n = 11$). By contrast, the highest abundance of copepods was measured offshore (Fig. 3c), which is attributable to the greater importance of the small fraction in this area (Fig. 4a). Mesozooplankton composition was largely dominated by copepods (Fig. 4a). Their relative importance was lower nearshore (73.4% of total abundance) than offshore (93.4%), mainly due to the abundance of

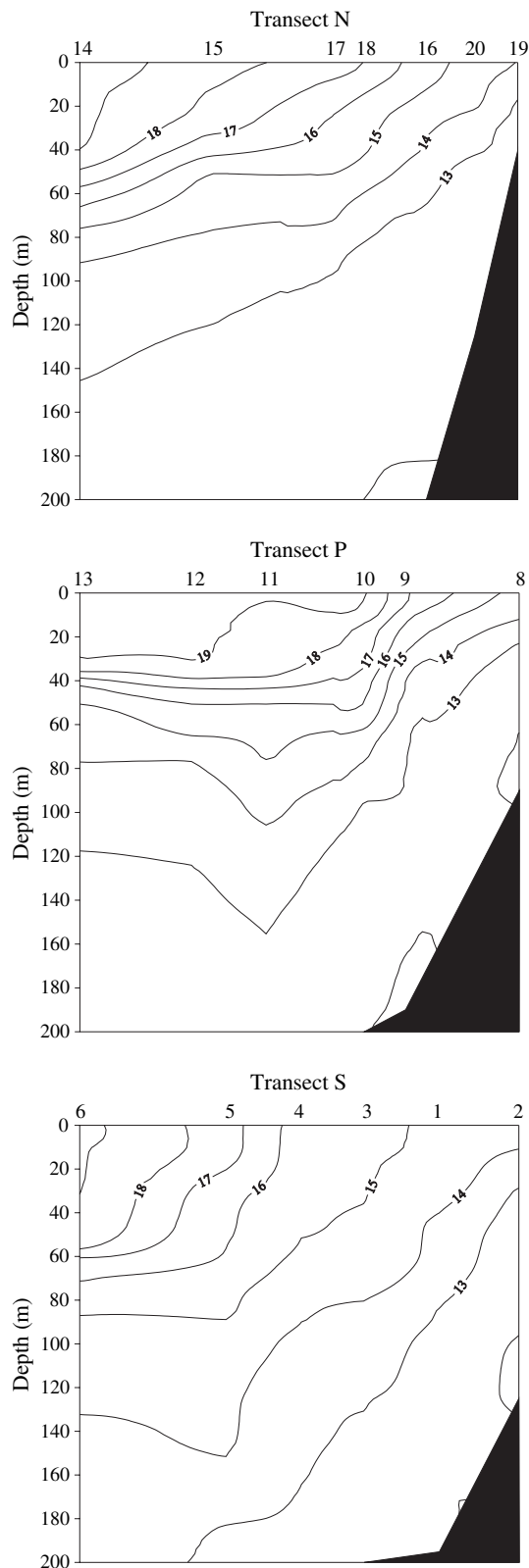


Fig. 2. Vertical distribution of temperature (°C) along the three transects. The numbers above the top axes indicate the position of the stations.

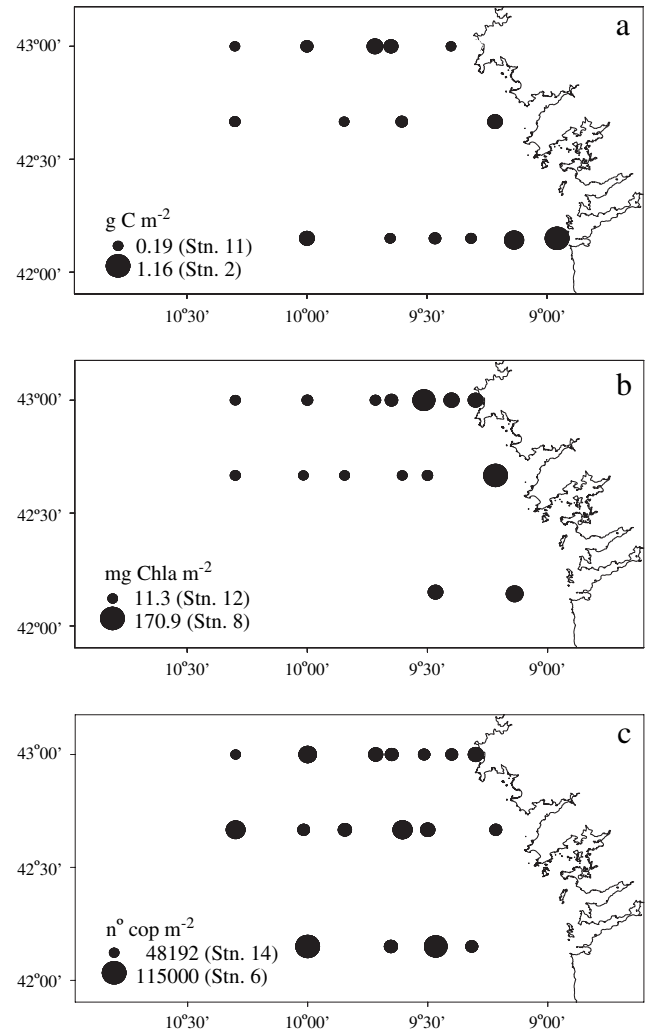


Fig. 3. Mesozooplankton (a) and phytoplankton (b) biomass, and abundance of copepods (c) at each station. Legends indicate the minimum and maximum values and, in brackets, the stations where these values were measured.

gelatinous zooplankton at coastal stations on the northern transect. The bulk of the copepod community was comprised of calanoids (Table 1). Other holoplanktonic organisms represented a small portion of the total abundance (Fig. 4a). After copepods, appendicularians were the most abundant group (Table 1). In terms of biomass, mesozooplankton size structure resembled the distribution of copepod abundance. The contribution of the small fraction to total biomass (Fig. 4b) was significantly higher offshore than in coastal upwelling ($t_{14} = -3.85$; $p < 0.01$).

3.3. Grazing

For all three size fractions, copepod gut contents averaged over coastal stations, where the phytoplankton available as food ($\text{mg Chla} > 5 \mu\text{m m}^{-2}$) was more

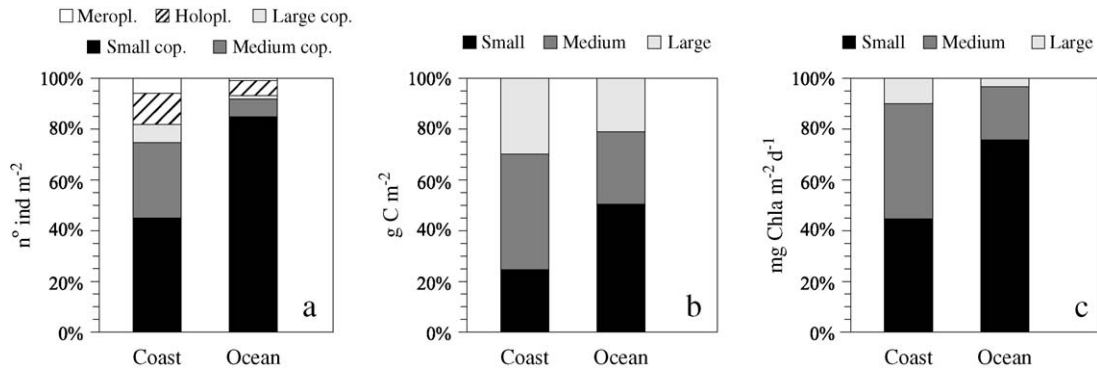


Fig. 4. (a) Percentages of abundance of the three size classes of copepods (large, medium and small), and remaining holoplanktonic (Holopl.) and meroplanktonic (Meropl.) organisms. (b) Frequency of mesozooplankton biomass due to each fraction. (c) Relative contribution of each fraction of copepods to phytoplankton ingestion.

abundant, were higher than values averaged over oceanic stations (Table 2). In addition, during upwelling events the phytoplankton composition was dominated by large cells (Teira et al., 2001), which presumably enhanced herbivory of copepods. There were no diel differences in copepod gut contents (*t*-test for paired samples, $t_6 = 2.01$; $p > 0.05$). Gut evacuation rate constants, averaged over all experiments, were highest for the large size class (0.0272, 0.0274 and 0.0407 min^{-1} for small, medium, and large fractions, respectively), although the differences between fractions were not statistically significant (test of parallelism, $F_{2,88} = 2.31$; $p > 0.1$). The functional responses of the three size classes of copepods exhibited saturation at the high levels of Chla found in coastal stations (Fig. 5). According to the Michaelis–Menten fitted curves, the amount of Chla $> 5 \mu\text{m}$ explained 48.5, 80.1, and 72.1% of the variance on ingestion rates for the small, medium, and large size classes, respectively. The theoretical maximum ingestion rate (I_{max}) increased with size, from 2.35 ± 0.71 (SE) $\text{ng Chla ind}^{-1} \text{h}^{-1}$ estimated for the

small fraction to $6.31 \pm 0.51 \text{ ng Chla ind}^{-1} \text{h}^{-1}$ for the largest one. By contrast, the half saturation constant (K_m) seemed to be independent of body size, as was mentioned by Hansen et al. (1997).

The percentage of phytoplankton standing stock grazed daily by copepods ranged from 1.3% in station 8 to 11.1% at station 19. If we consider only the fraction of Chla $> 5 \mu\text{m}$ these percentages range from 1.7 (station 8) to 32.7% (station 10). The average grazing impact on the total and the $> 5 \mu\text{m}$ phytoplankton standing stock and on primary production was higher offshore than in the coastal upwelling zone (Table 3). Nevertheless, the differences were not statistically significant (*t*-tests, $p > 0.05$ in all cases). The contribution of the different size classes to total grazing revealed a higher relative importance of the small fraction offshore than in the upwelling zone (Fig. 4c), the difference being statistically significant ($t_{10} = -4.63$, $p < 0.001$).

3.4. Metabolism

Specific metabolic rates seemed to be higher offshore (Table 4), probably due to the higher temperature of incubation. The data from open ocean waters correspond to only one station, so the differences were not tested statistically. Phytoplankton carbon ingested by copepods exceeded their minimum requirements at coastal stations

Table 1
Major contributors to total abundance in coastal upwelling and offshore waters, and percentage of the main orders of copepods

	Major contributors	Copepods (%)		
		Calanoida	Cyclopoida	Others
Coast	<i>Acartia clausi</i> (12.7%)	74.5	15.0	10.5
	<i>Paracalanus parvus</i> (12.7%)			
	<i>Clausocalanus</i> spp. (11.6%)			
	<i>Oithona similis</i> (11.0%)			
	<i>Oncaea media</i> (6.7%)			
	<i>Calanoides carinatus</i> (6.1%)			
	(H) Appendicularia (3.1%)			
Ocean	<i>Clausocalanus</i> spp. (28.7%)	82.6	15.5	1.9
	<i>Paracalanus parvus</i> (17.7%)			
	<i>Acartia clausi</i> (17.1%)			
	<i>Oithona similis</i> (13.7%)			
	(H) Appendicularia (4.5%)			

(H) indicates the most abundant taxa of holoplanktonic organisms other than copepods.

Table 2
Copepod gut contents for the size fractions small (200–500 μm), medium (500–1000 μm), and large ($> 1000 \mu\text{m}$), and results of the *t*-tests performed to compare values for coastal and oceanic areas

Size fraction	$\text{ng Chla eq ind}^{-1}$		<i>t</i> -value	<i>p</i>
	Coast	Ocean		
Small	0.98 ± 0.39	0.25 ± 0.07	2.8	< 0.05
Medium	1.92 ± 0.32	0.53 ± 0.07	6.2	< 0.001
Large	2.78 ± 0.26	1.37 ± 0.14	5.3	< 0.001

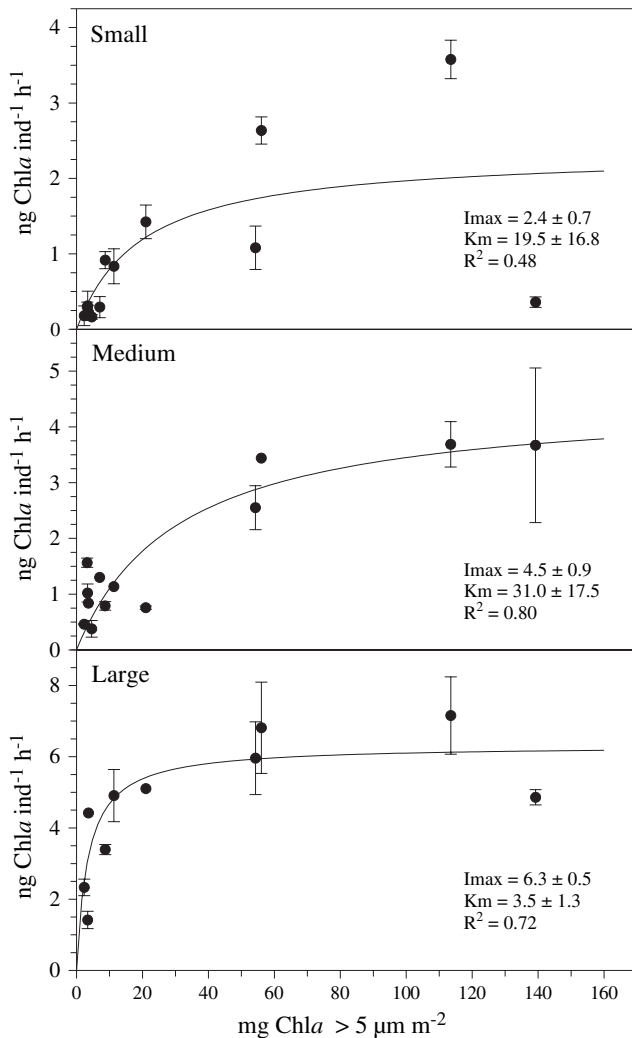


Fig. 5. Relationship between copepods ingestion rate (ng Chla ind⁻¹ h⁻¹) and the amount of Chla > 5 μm in the water column. These functional responses were fitted to a Michaelis–Menten model. The high values of Chla at which saturation is reached for the three size classes correspond to the coastal stations. Error bars indicate SE. Parameter estimates (±SE) for the Michaelis–Menten equations are shown for each fraction.

(102.1% of the basal metabolic requirements met), whereas offshore this percentage was 45.9%. Assimilation efficiency was assumed to be 70% (Conover, 1966). The percentages of phytoplankton nutrient requirements

met through mesozooplankton excretion were low (3.8% and 2.6% for ammonium and phosphate, respectively) in coastal areas. These percentages rose considerably to 19.9% (ammonium) and 21.7% (phosphate) offshore. Furthermore, taking into account that ammonium excreted by the largest size class was not measured at oceanic stations, the percentage of nitrogen requirement in this zone has been underestimated. If the average N:P ratio excreted by small and medium mesozooplankton (mean ± SE: 23.4 ± 3.2) is applied to estimate the amount of ammonium released by the largest size class at oceanic stations, the percentage increases from 19.9% to 30.3%.

4. Discussion

Both phytoplankton and mesozooplankton biomass followed the same pattern of spatial distribution, and the two variables were positively correlated. The pattern in size structure was also similar, with a higher relative importance of the large fractions of phyto- (Teira et al., 2001) and zooplankton in upwelling areas. The mesozooplankton response to high phytoplankton biomass was apparent in their feeding activity. The functional response of the copepods showed the relationship between ingestion rate and Chla concentration in the water column fitted to a hyperbolic curve defined by the Michaelis–Menten equation. Saturation of ingestion rates was reached at coastal stations, where copepod gut contents and Chla levels were highest. By contrast, copepods would have been food limited offshore if phytoplankton had been their only food source.

The percentages of Chla and primary production removed daily by copepods are similar to those found by Barquero et al. (1998) and Bode et al. (2003) in the same area. Isla and Anadón (2004) measured a very similar grazing impact in both coastal and oceanic areas during autumn 1999, with values close to those observed offshore in OMEX-0898. The copepods grazing impact measured by Halvorsen et al. (2001) in an upwelling filament off NW Spain also measured in August of 1998 coincided with our values, especially with those measured offshore. Phytoplankton biomass and composition, primary production, and the contribution of the

Table 3

Percentages of phytoplankton total, phytoplankton > 5 μm, and primary production grazed daily by copepods

	Total phyt. (mg Chla m ⁻²)	% ing.	Phyt. > 5 μm (mg Chla m ⁻²)	% ing.	Prim. prod. (mg C m ⁻² d ⁻¹)	% ing.
Coast	116.6 ± 26.1	5.2 ± 2.1 (7.7 ± 3.1)	90.8 ± 21.2	6.7 ± 2.6 (10.0 ± 3.9)	4690 ± 798	5.2 ± 1.4 (7.8 ± 2.2)
Ocean	28.7 ± 7.9	5.7 ± 1.0 (8.6 ± 1.5)	15.2 ± 7.2	17.7 ± 3.5 (26.6 ± 5.3)	490 ± 14	12.9 ± 2.5 (19.4 ± 3.8)

In brackets: grazing impact estimated by assuming a 33% Chla destruction (see text). All the measurements are mean value ± SE.

Table 4

Respiration, ammonium excretion, and phosphate excretion rates (mean \pm SE) of the three size fractions of mesozooplankton, and O:N atomic ratios (n.d.: no data)

	$\mu\text{mol O}_2 \mu\text{mol C}^{-1} \text{d}^{-1}$			$\mu\text{mol NH}_4 \mu\text{mol C}^{-1} \text{d}^{-1}$			$\mu\text{mol PO}_4 \mu\text{mol C}^{-1} \text{d}^{-1}$			O:N
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	
Coast	0.41 \pm 0.21	0.33 \pm 0.10	0.19	0.052 \pm 0.025	0.046 \pm 0.016	0.046 \pm 0.025	0.0021 \pm 0.0002	0.0016 \pm 0.0004	0.0016 \pm 0.0002	12.9
Ocean	0.32	0.57	n.d.	0.086	0.044	n.d.	0.0038	0.0027	0.0025	16.7

small fraction of copepods to grazing were also similar in the upwelling filament and in the oceanic scenario described in the present study, and differed clearly from the coastal upwelling area. Tenore et al. (1995) reported percentages up to 100% of phytoplankton stock grazed daily by mesozooplankton off NW Spain, but this value was clearly overestimated due to the methodology applied in estimating mesozooplankton biomass (Bode et al., 1998). It could be argued that the present values are underestimates, because no parallel experiments were performed to assess Chl*a* destruction during the digestive process. Literature values concerning the extent to which Chl*a* is degraded to colourless products varies over a range from 0 to 100% (see Båmstedt et al., 2000). In their review, Dam and Peterson (1988) arrived at an average value of \sim 33% Chl*a* destruction. This value has been used by some authors to correct ingestion rates estimated by gut fluorescence (e.g. Pakhomov et al., 1997; Calbet, 2001). The application of such a correction would not alter the present results significantly (Table 3).

Weight-specific metabolic rates decreased from the small to the large size class, in agreement with the widely reported allometric relationship between metabolic rate and body size. Respiration and ammonium and phosphate excretion rates in OMEX-0898 were slightly higher than those measured in the same study area during autumn (Isla and Anadón, 2004). The O:N ratios yielded by the metabolic rates are below the theoretical value of 21 in both nearshore and offshore areas, suggesting a protein-oriented metabolism (Ikeda et al., 2000). These ratios (Table 4) were similar to those reported by Omori and Ikeda (1984) for mixed zooplankton in temperate seas. Phytoplankton carbon ingested by copepods met their minimum metabolic requirements only at coastal areas, where upwelling conditions enhanced phytoplankton concentration. The percentage measured (slightly higher than 100%) seems to be barely enough to support the active metabolism of copepods. Conservative estimations of phytoplankton carbon ingestion, however, suggest that the percentage of requirements being met might be higher than reported values. In open ocean waters copepods cannot maintain their metabolism by herbivory alone, so that they must complete the diet with other food sources. In this respect, during the CD114 cruise, which was conducted also off NW Spain in August 1998, Batten et al. (2001)

reported that mesozooplankton were feeding actively on microzooplankton, and Riser et al. (2001) suggested that faecal pellets and detritus could be an important part of the mesozooplankton diet. The shift from herbivory in coastal upwelled waters to omnivory offshore agrees well with the feeding rules described by Kleppel (1993) in his review about copepod diets in different food environments and with the observations made in CD114 by Halvorsen et al. (2001), who suggested that copepods ingested the different food categories in proportion to their abundance in the environment.

Ammonium and phosphate excreted by mesozooplankton accounted for a considerable proportion of nutrients required by primary producers offshore, but this was not true under upwelling conditions. The low contribution of mesozooplankton to phytoplankton nitrogen requirements seems to be a general feature in coastal upwelling systems, and our results are in the lower range of the literature values (Whitledge and Packard, 1971; Smith and Whitledge, 1977; Whitledge, 1978; Bode and Varela, 1994; Head et al., 1996; Bode et al., 2004). The amount of ammonium regenerated by mesozooplankton that we measured exceeds the values reported to date for the NW of Spain (Bode et al., 2004; Isla and Anadón, 2004; Barquero, pers. comm.). In addition, according to the microplanktonic regeneration measured in OMEX-0898 by Varela et al. (2003), the present results represent a higher contribution of mesozooplankton to total ammonium regeneration than those found by Barquero (pers. comm.) and Bode et al. (2004).

Phytoplankton–mesozooplankton coupling and its role in oceanic carbon, nitrogen and phosphorus cycling are summarised in Fig. 6. According to the trophic pathways classification proposed by Legendre and Rassoulzadegan (1996), the situation observed in coastal upwelling would correspond to a mostly herbivorous food web. A number of facts support it: the phytoplankton community was dominated by large cells (Teira et al., 2001); the ingestion rates of copepods were apparently saturated at the high levels of Chl*a* measured in this area; the metabolic requirements of mesozooplankton were fully met by the ingested phytoplankton carbon. Furthermore, in coastal upwellings there are very few steps in the carbon transfer from phytoplankton to mesozooplankton (Moloney et al., 1991), implying an almost negligible role for the microbial loop. By contrast, the open ocean stratified waters tend

to have more multivorous food webs, in agreement with some of the features we observed: the dominance of small phytoplankton and high rates of DOC production (Teira et al., 2001), the latter enhancing microbial activity; the greater importance of microzooplankton grazing (Fileman and Burkill, 2001); a shift towards omnivory in the mesozooplankton diet, inferred from the low percentage of carbon metabolic requirements met by phytoplankton ingestion and predation of copepods on microzooplankton observed by Batten et al. (2001); phytoplankton ingestion rates for copepods, which were not saturated. The sum of these

characteristics point to a more important role of the microbial loop in transferring carbon towards mesozooplankton compared to the situation described for coastal upwelling.

The contribution of mesozooplankton faecal pellets to total particulate organic carbon (POC) flux was higher nearshore, but it is still possible that most of the carbon passing through copepods is recycled in the euphotic zone for both herbivorous and multivorous food webs (Riser et al., 2001). Large microphages can play a significant role in transferring carbon to depth through their faecal pellets, which are not recycled in the

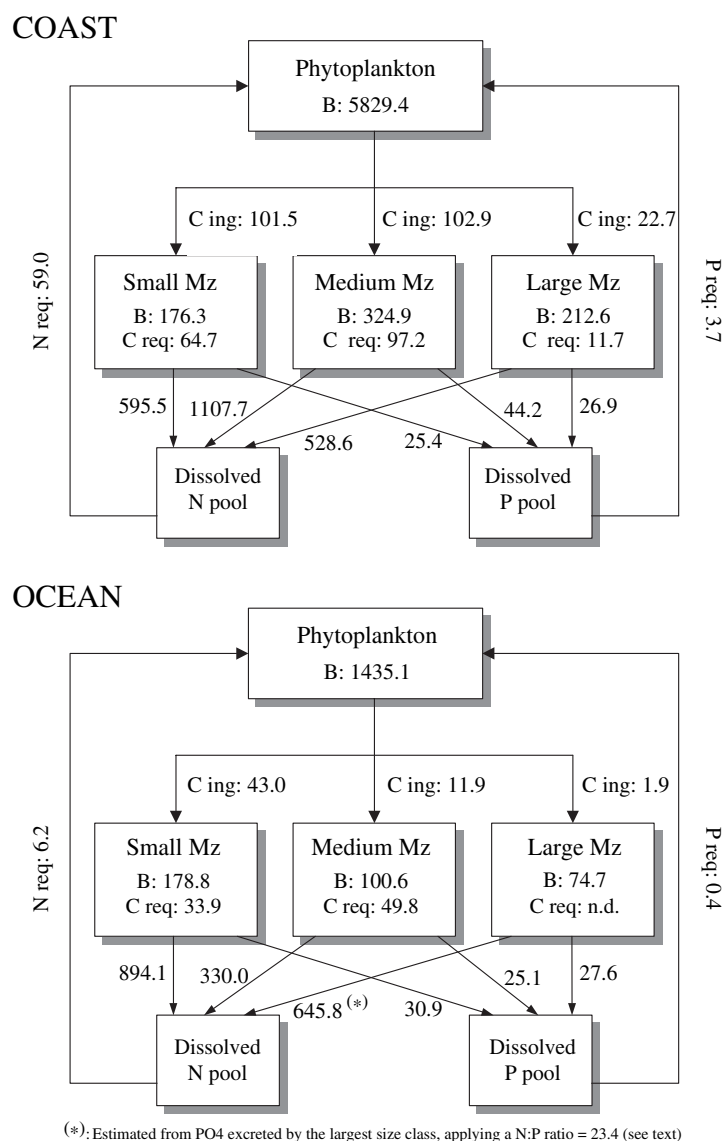


Fig. 6. Carbon, nitrogen, and phosphorus fluxes in coastal upwelling and in open ocean stratified waters mediated by mesozooplankton (Mz) small, medium, and large. B: biomass in carbon (mg C m^{-2}). C ing: phytoplankton carbon ingested by copepods ($\text{mg C m}^{-2} \text{d}^{-1}$). C req: carbon required ($\text{mg C m}^{-2} \text{d}^{-1}$) by mesozooplankton to maintain their basal metabolism. Arrows from mesozooplankton boxes to dissolved N and P pools represent, respectively, the amount of ammonium ($\mu\text{mol NH}_4 \text{m}^{-2} \text{d}^{-1}$) and phosphate ($\mu\text{mol PO}_4 \text{m}^{-2} \text{d}^{-1}$) excreted. N req and P req show the amount of nitrogen and phosphorus (in $\text{mmol m}^{-2} \text{d}^{-1}$), respectively, required by phytoplankton.

euphotic layer due to their fast sinking rates (Fortier et al., 1994). Appendicularians were the most abundant microphages in the present study, but their effect would have been minimal because of their low grazing impact (López-Urrutia, unpubl. data). It has been generally assumed that herbivorous pathways lead to a higher biogenic carbon export than multivorous pathways, but several studies comparing heterotrophic and autotrophic food webs have found no differences in POC fluxes between these two cases (e.g. Rivkin et al., 1996; Savenkoff et al., 2000). Thus, the relationship between the magnitude and pattern of biogenic carbon export and the trophic structure of the community does not seem to be as evident as thought, and interpretations concerning carbon fluxes derived from perceptions of trophic pathways must be taken with caution.

In summary, higher values of metabolic end products released by mesozooplankton were measured in the upwelling than the offshore area, and this was due to a higher biomass rather than to higher metabolic rates. In spite of this, the percentage of the N and P phytoplankton demand that was supplied by mesozooplankton through their excretory activity was substantially lower than in the offshore. From our results it follows that mesozooplankton organisms play a more important role as nutrient regenerators in multivorous than in herbivorous food webs. This conclusion is consistent with the dominance of regenerated production in open ocean and in stratified waters (Eppley and Peterson, 1979; Mengesha et al., 1999; Harrison et al., 2001), where multivorous food webs prevail. For highly productive coastal upwellings, as found in OMEX-0898 nearshore, primary production is probably predominantly new production (e.g. Moloney et al., 1991), fuelled by the input of nitrate from deeper waters. This predicted difference as to the main source of nitrogen used by phytoplankton is supported by the primary production measurements performed by Joint et al. (2001) in the course of a Lagrangian study carried out off NW Spain simultaneously with our OMEX-0898 cruise. They reported *f*-ratio values of up to 0.7 in upwelling areas and <0.1 offshore. The effect of zooplankton removing phytoplankton in offshore waters was not as important as their effect on nutrient recycling, although ca. 20% of the primary production was grazed daily in the open ocean if a 33% of Chl*a* destruction is assumed. The grazing impact of mesozooplankton was more important in the multivorous (offshore) than in the herbivorous (coastal) food web. It is noteworthy that in the offshore copepods grazing had a relatively large impact on phytoplankton >5 μm. Thus, mesozooplankton grazing would have favoured the dominance of small phytoplankton offshore because they grazed preferentially on the large phytoplankton.

Acknowledgements

We are grateful to the captain and crew of the R/V Professor Shtokman and to the participants of the cruise OMEX-0898, especially Principal Scientist A. Bode. E. Cabal and J. Álvarez Sostres made CN and nutrient analyses, respectively. E. Teira provided Chl*a* and primary production data. We appreciate the comments of M. Quevedo, J. L. Acuña, and two anonymous reviewers, which helped to improve the manuscript. This work was supported by the European Commission in the framework of its Marine Science and Technology Programme (OMEX-II-II project, contract N° MAS3-CT97-0076).

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