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Copepod communities along an Atlantic Meridional Transect: Abundance, size structure, and grazing rates

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ABSTRACT

Large-scale variability in copepod abundance, size structure, and ingestion rates on phytoplankton was investigated during the cruise Atlantic Meridional Transect-13. The main aim of the study was to assess the relative importance of small copepods and copepod nauplii in different regions (Temperate N and S, Oligotrophic N and S, Equatorial and Mauritanian upwelling). Samples were fractionated into four size fractions (<200, 200–500, 500–1000, and >1000 μm). The only factor that significantly affected copepod biomass was chlorophyll concentration, which explained 71% of the variation. The gut fluorescence technique was used to estimate ingestion rates and experiments were performed to obtain naupliar gut evacuation rates. We found a similar relationship between nauplii gut evacuation rates and temperature as that described by Dam and Peterson [1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. Journal of Experimental Marine Biology and Ecology 123, 1–14] for larger copepods. Chlorophyll ingested daily by copepods was higher in regions affected by Mauritanian and Equatorial upwellings and the South Subtropical Convergence. Copepods were found to be major grazers of phytoplankton. Grazing impact upon primary production was more important for upwelling areas, with values higher than 100% of primary production at some stations. Even in oligotrophic gyres, where the relative importance of protists increases, copepods exert substantial feeding impact on their autotrophic prey. In oligotrophic gyres, small copepods and nauplii were relatively more abundant, and accounted for a higher amount of total chlorophyll ingestion than larger ones. Thus, studies with 200 μm mesh nets in oligotrophic areas are seriously underestimating nauplii and copepod abundance and grazing impact on phytoplankton.

1. Introduction

Since 1995, the Atlantic Meridional Transect (AMT) programme has coordinated spatially extensive investigations with the purpose of improving our knowledge of basin-scale biogeochemical processes, ecosystem dynamics, and food webs across the Atlantic Ocean (Aiken et al., 2000). A goal of the programme has been to characterize metazooplankton community abundance, size structure, and physiological rates (Gallienne et al., 1996; Gallienne and Robins, 1998; Huskin et al., 2001; Woodd-Walker, 2001; Woodd-Walker et al., 2001; Isla et al., 2004; San Martin et al., 2006a, b).

Among the various animal taxa included in the metazooplankton copepods are the most numerous group (Longhurst, 1985); thus, information about their biology and physiology is key to understanding the different functions of metazooplankton in marine ecosystems (Ikeda et al., 2001).

Previous investigations on copepods during AMT cruises have focused on larger taxa by using the standardised sampling methods for mesozooplankton.

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Recently, several studies (reviews by Gallienne and Robins, 2001; Turner, 2004) have demonstrated that the use of the common WP-2 (200 μm mesh) net is not appropriate to sample copepods, as the abundance and sometimes the biomass of small copepods not retained by this net can vastly exceed those of larger ones. This mesh selection problem has led to under-representation of early juvenile stages (nauplii of almost all copepod species are not retained by this net) and also copepodites and adults of ubiquitous genera with small species such as *Oithona* (Paffenhöfer, 1993), presently thought to be one of the most abundant group of copepods in the world (Gallienne and Robins, 2001). As a result of this methodological problem, the feeding ecology of small copepods is less well known than that of copepodites and adults of larger species (Turner, 2004), and in the case of nauplii, available data are even more scarce (López et al., 2007a, b). Nevertheless, current knowledge of this group suggests that they could play an important role in marine ecosystems: (1) different species of nauplii have been shown to feed upon bacterioplankton (Turner and Tester, 1992; Roff et al., 1995); thus, they could act as a trophic link between "classical" and microbial food webs by using resources not available for other copepod stages (Roff et al. 1995), (2) they produce small fecal pellets with low sinking rates enabling remineralisation by microbes in the epipelagic (Turner, 2002), (3) they are the major prey of larval stages of commercially important fish species (Last, 1980; Incze et al., 1996; González-Quirós and Anadón, 2001; Munuera, 2006; Munuera and González-Quirós, 2006), so the size structure of nauplii populations can be expected to influence larval fish survival and subsequent recruitment (Lucic et al., 2003), and (4) they have weight-specific ingestion rates higher than adults (Lonsdale et al., 1996; López et al., 2007c) and sometimes surpass adults in biomass (Turner, 2004). Roman and Gauzens (1997) found in the equatorial Pacific that the fraction of copepods <200 μm ingested a similar amount of phytoplankton than larger copepods during some periods of the year. All these aspects indicate that the importance of this group in zooplankton-mediated fluxes must be too important to keep ignoring them in carbon budgets.

Our knowledge of copepod nauplii feeding habits includes an outline of their potential prey, coming from experiments with cultures in the laboratory. They feed not only on the picoplankton size fraction, but also on the size range of adult copepod prey (see review in López et al., 2007a, b). However, quantitative information is sparse, and we have no idea of their feeding impact on most of the naturally occurring planktonic communities. This kind of information cannot be inferred from experiments with cultures, and field data are scarce and focused mostly on high latitudes and coastal areas (Tackx et al., 1990; White and Roman, 1992; Uitto, 1996; Hansen et al., 2000; Turner et al., 2001; Irigoien et al., 2003; López et al., 2007c). To the best of our knowledge, studies on the abundance and feeding rates of all sizes and stages of copepods have not been attempted previously in oceanic regions crossed by AMT cruises.

The present study reports data on the large-scale latitudinal variability of the abundance, size structure, and ingestion rates of phytoplankton of copepod populations in the Atlantic Ocean, with our main objective to elucidate the importance of small copepods and nauplii in these ecosystems.

2. Methods

Sampling was conducted on board the *RRS "James Clark Ross"* on passage between Great Britain and the Falkland Islands (14 September–10 October 2003) as part of the AMT programme (Fig. 1).

Temperature and fluorescence profiles were obtained from CTD casts made with a Sea-Bird 911*plus* equipped with a 0363 Chelsea MkIII Aquatracka Fluorometer. The CTD fluorometer was calibrated against chlorophyll *a* (chl-*a*) concentration extracted from water samples and determined by fluorometric analysis.

Water samples from different depths were collected for phytoplankton carbon fixation (details in Poulton et al., 2006). Unfortunately, data on primary production are not available for stations 1, 2, 3, 5, 11, 14, and 24. For regions Temperate N and Temperate S, we do not consider the average data representative as it comes from only one station.

Vertical net samples were taken from 200 m to the surface with a triple WP-2 net (53 μm mesh), equipped

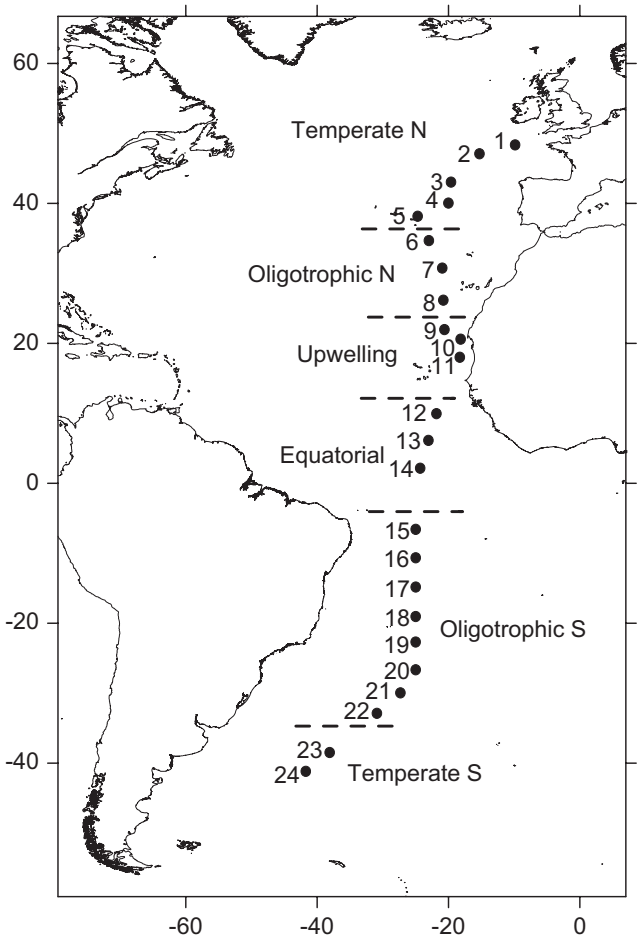

Fig. 1. Location of stations sampled during AMT-13.

with filtering cod ends, during night stations (between 00:30 and 4:30 h local time). Two tows were performed at low speed (0.5 m s^{-1}). One cod end from the first tow was devoted to metazooplankton composition, abundance, and size structure, and another one to copepod gut fluorescence analysis. The second tow was performed every other day for nauplii gut evacuation experiments. The nets were rinsed to concentrate all the organisms in the cod ends devoted to abundance and size structure analysis, but not for gut fluorescence analysis or gut evacuation experiments. Flow meters were not used and the volume filtered through the net was calculated as the volume contained in a cylinder with length equal to the sampling depth and radius equal to the net mouth. Although net clogging could lead to errors in abundance calculations when flow meters are not used, clogging was not observed during the cruise. In addition, the net was designed to avoid clogging problems following recommendations in Sameoto et al. (2000), with an $R = 10.5$ ($R = \alpha \times \beta/A$, where α is total area of net mesh forming the net, β is net porosity, and A is area of the mouth opening of the net).

2.1. Metazooplankton abundance and copepod size structure

Samples were screened through 1000, 500, 200, and 30 μm meshes and fixed with 4% buffered formalin. In the laboratory, abundance of the major taxa of metazooplankton was determined under a stereomicroscope. Depending on the concentration of animals, each sample was examined entirely or sub-sampled into aliquots.

To elucidate the size structure of copepod populations at the different stations, at least 60 nauplii and/or 60 copepods from every size fraction were photographed under the stereomicroscope, and image analysis software was used to measure body length. In the >500 μm fraction, nauplii appeared only occasionally, and in the 200–500 μm fraction they were usually scarce. Thus, in some cases a lower number of individuals was measured; the same applied for copepods belonging to the >1000 μm fraction. Individual dry weight was estimated, after corrections for shrinkage due to fixation with formalin (White and Roman, 1992), by using the following relationships:

$$\text{Log dry weight}\,(\mu g) = 2.1034\ \log\ \text{nauplii total length}\,(\mu m) - 5.2105$$

$$\text{Log dry weight}\,(\mu g) = 2.6757\ \log\ \text{copepod prosome length}\,(\mu m) - 6.7625$$

These length–weight relationships were calculated by López et al. (2007c) with data of Klein Breteler et al. (1982) for different species, with the purpose of using them for a natural copepod assemblage. We assume a constant relationship between copepod body weight and body length although it is known that this can vary by copepod species, and be affected by temperature, and food availability (e.g. Rey et al., 2001). Copepods and nauplii were grouped in logarithmic size classes, following a series of w, $2w$, and $4w$, where w is individual body weight (Sheldon et al., 1972).

The statistical analysis methodology of unbalanced ANOVA was employed to detect differences between regions in copepod and nauplii abundance and average body weight. However, results must be cautiously interpreted, as the ANOVA method is characterised by low power of the test when the design is unbalanced.

Copepod and nauplii biomass, average body weight, and the ratio "number of nauplii/number of copepods" were related by multiple regressions to temperature, chlorophyll concentration, integrated primary production, and latitude. The vertical distribution of copepods was not studied during the cruise, thus other water column parameters were used in the regression analysis: average temperature in the first 200 m (T), average temperature in the first 50 m (T_{50}), integrated chlorophyll (Chl), chlorophyll in the deep chlorophyll maximum (DCM) (Chl_{max}), and chlorophyll in the upper mixed layer (Chl_{ML}).

2.2. Grazing rates

The cod end content was screened through 1000, 500, 200, and 30 μm meshes. Samples were poured onto mesh filters, frozen at −70 °C, and kept frozen until analysis.

Copepod gut fluorescence was measured following Mackas and Bohrer (1976). Nauplii and copepods were randomly sorted from the samples. For each station, 4 groups of 20 nauplii and 4 groups of 20 copepods from the 30–200 μm fraction, 3 groups of 60 copepods from the 200–500 μm fraction, 3 groups of 50 copepods from the 500–1000 μm fraction, and 3 groups of 20 copepods from the >1000 μm fraction were analysed. In some cases there were not enough individuals in the samples and it was necessary to reduce the number of replicates. Samples from the 30–200 μm fraction were extracted in 120 μl of 90% acetone for 24 h at 4 °C and measured with a Turner Designs 700 fluorometer with a minicell adapter kit, following the protocol described in López et al. (2007a, b) for small metazoans. Samples from the other fractions were extracted in 5 ml of 90% acetone for 24 h at 4 °C and measured with a Turner Designs 10 fluorometer. A correction for chl-*a* destruction was not applied as the extent of chlorophyll degradation to non-fluorescent compounds in copepod guts is still unclear (discussed in López et al., 2007a, b).

Ingestion rates were calculated with the formula:

$$I = k \times G,$$

where k is the gut clearance coefficient and G is gut content (expressed as ng chl-*a* eq. ind^{-1}).

Gut evacuation experiments were performed to calculate k for nauplii. Immediately upon net retrieval, the contents of the cod ends were transferred to a container filled with 0.45 μm filtered seawater at surface temperature. While being poured into the container, the contents were filtered through a 200 μm mesh to remove mesozooplankton. Nauplii were taken from the container at different times (0, 2, 4, 8, 10, 15, 20, 25, and 30 min),

poured onto mesh filters, and frozen immediately at −70 °C. Gut pigment contents were measured for 4 groups of 20 nauplii from each time point. The following equation was used to estimate k:

$$G_t = G_0 \times \exp(-k \times t),$$

assuming that a constant percentage of the gut content is evacuated per unit time (Baars and Oosterhuis, 1984; Kiørboe et al., 1985; Christoffersen and Jespersen, 1986). In the equation, G_0 and G_t are the gut contents at times 0 and t.

Gut evacuation experiments were not carried out with copepods. The empirical relationship with temperature (T) proposed by Dam and Peterson (1988) was used to calculate theoretical k for copepods:

$$k = 0.0117 + 0.0018 \times T.$$

The effect of T, T_{50}, Chl, Chl_{max}, and Chl_{ML} on individual ingestion rates was analysed by multiple regression.

Chl-*a* ingestion was transformed to C units, to estimate grazing impact on primary production, by applying different C/Chl ratios for each station and depth. C/Chl ratios were calculated using the relationships between C and chl-*a* for the surface and deep chlorophyll maximum obtained by Marañón et al. (2000) during previous AMT cruises. These ratios were applied to obtain maximum (surface) and minimum (deep chlorophyll maximum) copepod and nauplii potential grazing impact on primary production. The characteristics of the water column at Stations 22 and 23 were quite homogeneous, so only the equation for the surface layer was applied.

Average specific ingestion rates for each fraction of copepods were calculated by dividing grazing rates by average individual body weight.

2.3. Ecological domains

To compare stations over such a wide spatial scale, stations were grouped according to the ecological domains defined by Marañón et al. (2001) for the AMT transect. These domains take into account the vertical structure of the water column and the distribution and concentration of nutrients and chl-*a*. The stations sampled at higher latitudes correspond to the 'Temperate' ecological domain, with the thermocline weaker or absent, nitrate detectable throughout the water column, and surface chl-*a* concentration always $>0.2\,\mathrm{mg\,m^{-3}}$ (35–50°N, 35–50°S). Stations from the region 'Temperate S' were sampled during austral spring; they were affected by the South Subtropical Convergence and contained the highest integrated chlorophyll concentration (Fig. 2). Station 24 from the Temperate S domain also showed the highest primary production on the transect (Poulton et al., 2006). The 'Oligotrophic' regions are defined as those with a well-developed thermocline located at a depth greater than 50 m, an upper mixed layer where nitrate is undetectable (i.e. $<0.05\,\mu M$), and chl-*a* concentration $<0.2\,\mathrm{mg\,m^{-3}}$ (23–35°N, 5–35°S). The 'Equatorial' region is characterized by an uplifted thermocline and shallower deep chlorophyll maximum than the subtropical central gyres (5°S–10°N). Finally, the 'Upwelling' region is affected by the Mauritanian coastal upwelling, the upper mixed layer extends only for 30–40 m, and the chl-*a* maximum is located in subsurface waters at ca. 50 m depth, where nitrate concentrations are $>1\,\mu M$ (10–23°N).

This approach divides the transect in a way quite similar to the biogeochemical provinces defined by Longhurst (1998), with the main differences in the regions NAST (North Atlantic Subtropical Gyre) and NATR (North Atlantic Tropical Gyre) (Fig. 2). The northern part of NAST is traversed by the Azores Current and the water column is higher in chlorophyll concentration and colder than the part close to NATR. Thus, we think the division of Marañón et al. (2001), which puts together the oligotrophic parts of both NAST and NATR, is more useful in our study.

3. Results

3.1. Metazooplankton abundance and copepod size structure

Copepods were the most numerous group in the four size fractions of zooplankton (Appendices A–D), with the exception of Station 10 from the Mauritanian coastal upwelling where pteropods surpassed copepods in the $>1000\,\mu m$ fraction. In that fraction, chaetognaths also made a substantial contribution, and were especially important in the regions Oligotrophic N, upwelling, and Equatorial. Copepods represented on average 65% of total metazooplankton in the $>1000\,\mu m$ fraction, 87% in the 500–1000 μm fraction, 96% in the 200–500 μm fraction, and more than 99% in the 30–200 μm fraction (the only other metazoans in the 30–200 μm fraction were pteropods, which appeared at some stations but were not quantified). Nauplii represented on average 65% of total copepod abundance, but only 15% of total biomass.

Average values for copepod abundance and size spectra, chlorophyll concentration and primary production for each region are presented in Fig. 3. Copepod abundance differed significantly between regions (unbalanced ANOVA; $F_{5,18} = 2.966$, $p = 0.04$). There was a significant difference in the average size of nauplii between regions ($F_{5,18} = 6.049$, $p = 0.002$), but not in the average size of copepods ($p = 0.226$) (unbalanced ANOVA). The relationship between total copepod biomass (including nauplii) for each station and: (1) temperature, (2) chlorophyll concentration, (3) primary production, and (4) latitude, was analysed by linear multiple regression (stepwise method). The same analysis was performed for copepods and nauplii average size. T and primary production were found to be correlated with Chl (T-Chl: corrected $r^2 = 0.46$; PP-Chl: corrected $r^2 = 0.56$). In the regression analysis, among all the options for chlorophyll (Chl, Chl_{max}, and Chl_{ML}) and temperature variables (T, T_{50}) the best fits were obtained for T and Chl. Significant effects were only detected in the multiple regression analysis for Chl in copepod biomass (corrected $r^2 = 0.717$, $F_{1,22} = 59.17$, $p < 0.001$), copepod average size (corrected

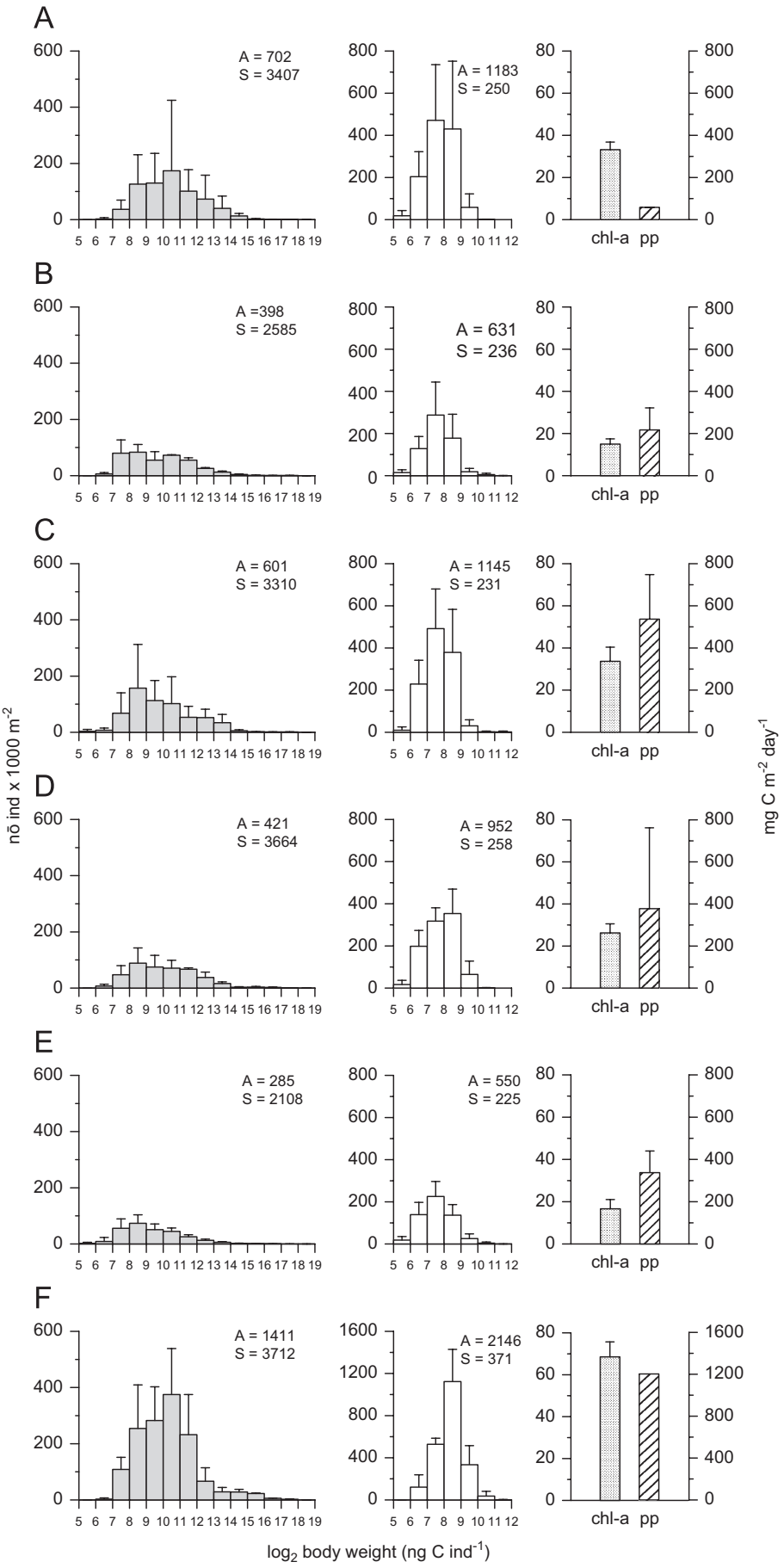

Table 1
Multiple regression analyses for the ratio "number of nauplii/number of copepods" and integrated chl-*a* concentration in the water column, integrated primary production, copepod abundance and mesozooplankton abundance

Independent variables	Corrected r^2	F	p	β	p
Chlorophyll concentration	0.121	$F_{2,21} = 2.584$	0.099	0.417	0.165
Copepod abundance				−0.652	0.035
Chlorophyll concentration	0.129	$F_{2,21} = 2.710$	0.09	0.323	0.223
Mesozooplankton abundance				−0.593	0.032
Primary production	0.126	$F_{2,14} = 2.152$	0.153	0.630	0.059
Copepod abundance				−0.467	0.149
Primary production	0.222	$F_{2,14} = 3.285$	0.068	0.827	0.023
Mesozooplankton abundance				−0.678	0.056

Table 2
Results for significant regressions for the gut evacuation experiments

Region	Station	T	k	r	p
Temperate N	1	13.9	0.032	0.75	<0.001
Temperate N	3	14.9	0.025	0.66	<0.001
Temperate N	5	18.1	0.035	0.81	<0.001
Upwelling	9	19.8	0.031	0.52	<0.01
Upwelling	11	20.5	0.034	0.75	<0.001
Equatorial	13	20.9	0.043	0.61	<0.001
Oligotrophic S	15	18.6	0.043	0.62	<0.005
Oligotrophic S	17	21.0	0.044	0.76	<0.001
Oligotrophic S	19	19.8	0.034	0.37	<0.05
Oligotrophic S	21	17.4	0.041	0.5	<0.01

T (°C) is water temperature at which experiments were performed, and k (min^{-1}) is gut clearance coefficient.

3.2. Nauplii gut evacuation rates

Ten out of 12 gut evacuation experiments yielded significant fits for the exponential decrease model (Table 2). No relation between initial gut chl-*a* content and gut clearance coefficients was found. A significant linear regression was obtained between gut clearance coefficients and water temperature (Fig. 4), although it explained only 30% of the variability, suggesting that other factors influence evacuation rates. Differences among regions were observed in the relationship with temperature: while stations from Temperate N and upwelling usually had lower gut clearance coefficients than expected from the regression model, those from Equatorial and Oligotrophic S were higher than expected, suggesting that differences in the taxonomic composition could be responsible for a significant amount of variability. Unfortunately, we have no data to test this hypothesis.

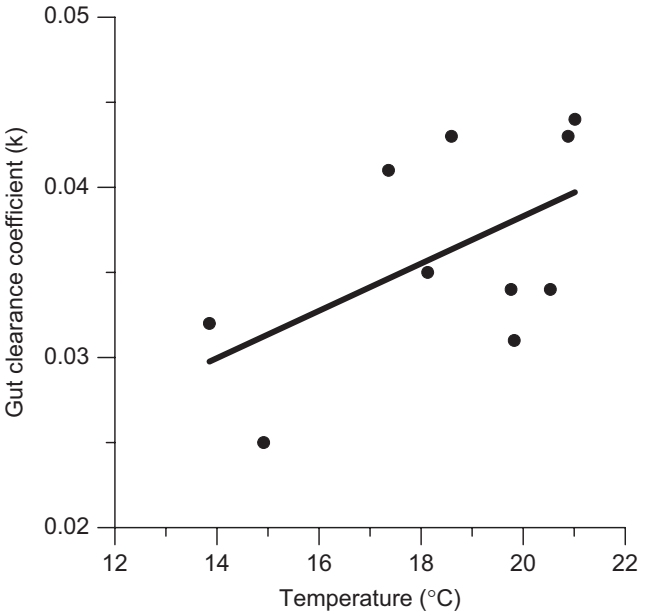

Fig. 4. Nauplii gut clearance coefficients as a function of water temperature. A linear regression is fitted to data ($k = 0.0014 \times T + 0.0105$, $r^2 = 0.299$, $p = 0.05$).

3.3. Nauplii and copepod grazing rates

Copepod ingestion of phytoplankton was significantly different between regions (unbalanced ANOVA, $F_{5,17} = 6.091$, $p = 0.002$) and the same applied for nauplii assemblages (unbalanced ANOVA, $F_{5,17} = 3.310$, $p = 0.029$) (Fig. 5). The impact on primary production was obtained for different C:chl-*a* ratios (Table 3). The smallest fraction of copepods (<200 μm) and nauplii accounted for a higher proportion of total community ingestion in oligotrophic regions (34% in Oligotrophic N and 38% in Oligotrophic S), while the largest

Fig. 3. Average copepod (grey boxes) and nauplii (white boxes) abundance for the different size classes, and average chl-*a* and primary production (mean and standard deviation) in the different ecological domains. *A* is average abundance in the region (no ind × 1000 m^{-2}) and *S* is average size (ng C ind^{-1}). (A) Temperate N, (B) Oligotrophic N, (C) upwelling, (D) Equatorial, (E) Oligotrophic S, and (F) Temperate S. Only one measurement was available for primary production in Temperate N and Temperate S.

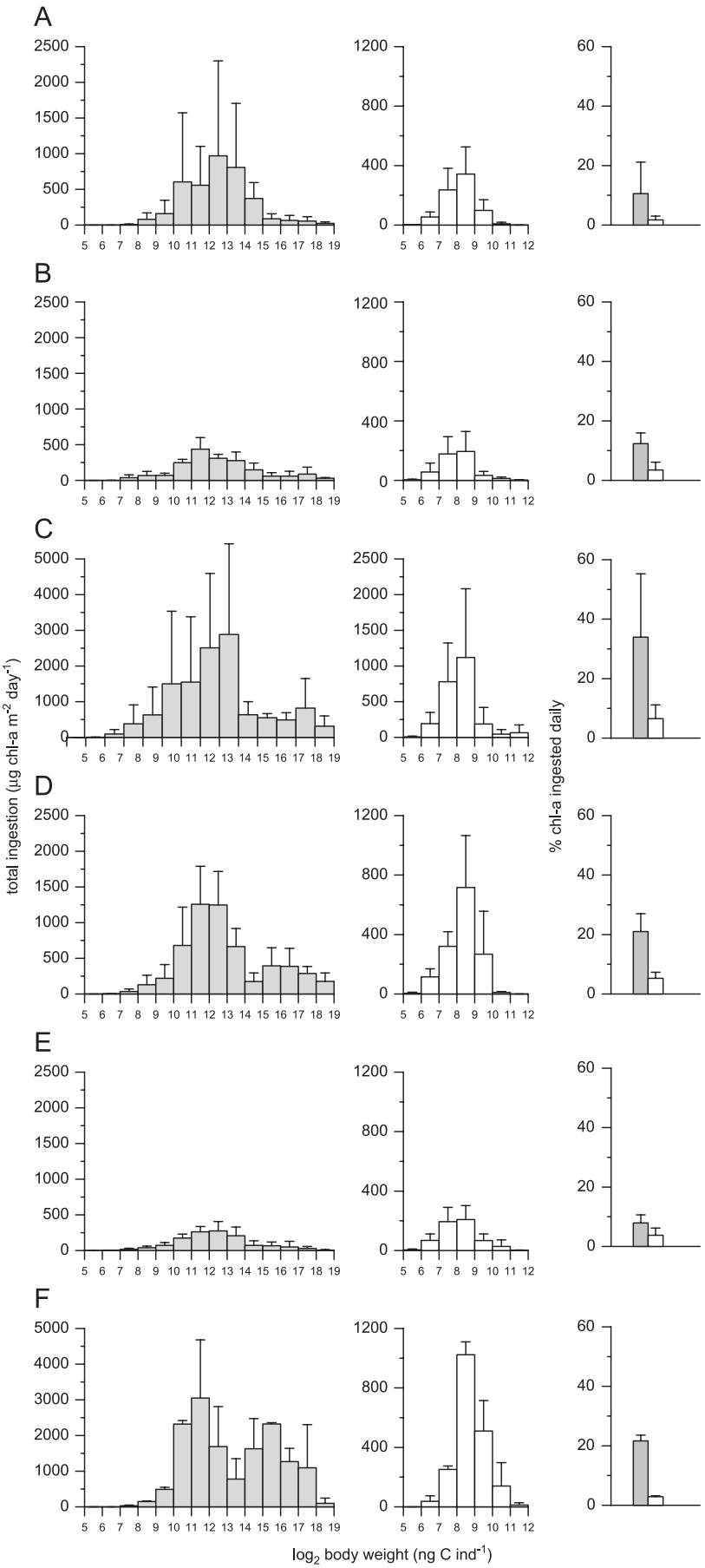

Fig. 5. Average copepod (grey boxes) and nauplii (white boxes) total ingestion on phytoplankton in the different size classes, and average grazing impact on chl-*a* (mean and standard deviation), for the different ecological domains. (A) Temperate N, (B) Oligotrophic N, (C) upwelling, (D) Equatorial, (E) Oligotrophic S, and (F) Temperate S.

Table 3
Copepods and nauplii grazing impact on primary production

Region	Station	C:chl 1	C:chl 2	% cop 1	% cop 2	% nau 1	% nau 2	% cop+nau
Temperate N	4	159	30	212	39	81	15	54–292
Oligotrophic N	6	184	46	460	116	100	25	141–560
Oligotrophic N	7	167	68	112	46	52	21	67–164
Oligotrophic N	8	183	58	82	26	9	3	28–90
Upwelling	9	106	29	186	51	16	4	55–201
Upwelling	10	58	28	51	26	17	8	34–68
Equatorial	12	76	33	98	43	27	12	54–125
Equatorial	13	133	39	455	132	102	30	162–557
Oligotrophic S	15	154	37	70	17	12	3	20–82
Oligotrophic S	16	136	41	30	9	9	3	12–39
Oligotrophic S	17	234	44	134	25	40	8	33–175
Oligotrophic S	18	184	43	71	17	25	6	22–96
Oligotrophic S	19	182	45	58	14	33	8	22–91
Oligotrophic S	20	121	64	35	19	35	19	37–70
Oligotrophic S	21	167	65	58	22	50	19	42–108
Oligotrophic S	22	59		34		15		48
Temperate S	23	41		44		6		50

C:chl-*a* ratios were calculated with the relationships between C and chl-*a* obtained by Marañón et al. (2000) during previous AMT cruises for surface (1) and deep chlorophyll maximum (2). These ratios were applied to obtain maximum (1) and minimum (2) copepods and nauplii potential grazing impact on primary production.

Table 4
Copepod size-fractionated abundance, biomass and ingestion on phytoplankton in the different regions (average value ± S.D. (percentage of total copepods))

	Temp N	Oligo N	Upwel	Equat	Oligo S	Temp S
Abundance (ind × 1000 m^{-2})						
nauplii	1183 ± 710 (63)	631 ± 272 (61)	1145 ± 535 (66)	952 ± 319 (69)	549 ± 170 (66)	2146 ± 476 (60)
cop <200	308 ± 171 (16)	248 ± 102 (24)	305 ± 213 (17)	227 ± 125 (16)	194 ± 65 (23)	663 ± 334 (18)
cop 200–500	352 ± 510 (19)	130 ± 24 (13)	242 ± 226 (14)	162 ± 41 (12)	81 ± 21 (10)	645 ± 257 (18)
cop 500–1000	36.4 ± 36.3 (1.9)	15.5 ± 5.6 (1.5)	43.3 ± 53.8 (2.5)	24.8 ± 9.3 (1.8)	9.8 ± 7.2 (1.2)	80.1 ± 37.8 (2.2)
cop >1000	4.7 ± 4.5 (0.25)	2.7 ± 1.9 (0.26)	10.5 ± 5.3 (0.60)	6.4 ± 2.9 (0.46)	1.6 ± 1.0 (0.19)	22.4 ± 12.4 (0.62)
Biomass (mg C m^{-2})						
nauplii	299 ± 201 (12)	144 ± 51 (12)	274 ± 149 (14)	251 ± 113 (15)	125 ± 44 (18)	809 ± 299 (14)
cop <200	262 ± 166 (11)	148 ± 47 (13)	185 ± 126 (9)	148 ± 58 (9)	98 ± 26 (14)	401 ± 236 (7)
cop 200–500	1025 ± 1240 (42)	402 ± 39 (35)	591 ± 323 (29)	438 ± 167 (25)	204 ± 41 (30)	1380 ± 747 (24)
cop 500–1000	533 ± 496 (22)	200 ± 69 (17)	415 ± 436 (21)	313 ± 152 (18)	127 ± 96 (19)	1642 ± 923 (28)
cop >1000	313 ± 161 (13)	260 ± 159 (22)	540 ± 268 (27)	578 ± 240 (33)	119 ± 77 (17)	1581 ± 684 (27))
Ingestion (mg chl-*a* m^{-2})						
nauplii	0.73 ± 0.37 (16)	0.48 ± 0.32 (21)	2.4 ± 2.1 (16)	1.4 ± 0.78 (20)	0.57 ± 0.27 (31)	1.9 ± 0.4 (12)
cop <200	0.3 ± 0.2 (6.6)	0.3 ± 0.25 (13)	0.78 ± 0.82 (5.3)	0.43 ± 0.38 (6.2)	0.12 ± 0.06 (6.7)	0.47 ± 0.2 (2.8)
cop 200–500	2.6 ± 3.6 (58)	1.1 ± 0.33 (46)	6.4 ± 6.4 (43)	3.1 ± 1.2 (44)	0.78 ± 0.22 (43)	7.1 ± 2.7 (42)
cop 500–1000	0.58 ± 0.47 (13)	0.26 ± 0.13 (12)	2.6 ± 2.7 (17)	1.0 ± 0.72 (14)	0.25 ± 0.17 (13)	3.9 ± 3.2 (23)
cop >1000	0.28 ± 0.37 (6.2)	0.2 ± 0.17 (8.4)	2.63 ± 1 (18)	1.1 ± 0.45 (15)	0.11 ± 0.1 (6)	3.5 ± 3.3 (20)

one (>1000 μm) was more important in upwelling, Equatorial, and Temperate S (18%, 15%, and 20% of total ingestion, respectively) (Table 4). Individual ingestion rates for the different stages and sizes of copepods also were highly variable between stations (Table 5), and specific ingestion rates were generally negatively correlated with body weight, but this relationship differed between regions (Table 5 and Fig. 6). Differences in individual ingestion rates were not explained by variations in T, T_{50}, Chl, Chl_{max}, and Chl_{ML}, as multiple regression showed no significant effect for any of the variables with the exception of copepods belonging to the size fraction <200 μm. In this case, the most significant fit was obtained when Chl_{max} and T were introduced as variables (corrected $r^2 = 0.376$, $F_{2,20} = 7.638$, $p = 0.003$). Ingestion rates for the other size fractions also showed a positive relationship with Chl_{max}, although the fits were not significant. Nauplii and copepod ingestion rates translated into a grazing of 0.9–11.2% and 2.8–58.5% of phytoplankton stock, respectively (Fig. 5).

Table 5
Average individual chl-*a* ingestion (ng chl-*a* ind^{-1} d^{-1}, mean ± S.D.), body weight (ng C) and specific ingestion (μg C μg^{-1} ind C d^{-1}) for each station

Station	Nauplii			Copepods <200 μm			Copepods 200–500 μm			Copepods 500–1000 μm			Copepods >1000 μm		
	Ingestion	C weight	Sp. ingestion	Ingestion	C weight	Sp. ingestion	Ingestion	C weight	Sp. ingestion	Ingestion	C weight	Sp. ingestion	Ingestion	C weight	Sp. ingestion
1	1.47±0.45	228	0.24–0.28	1.65±0.44	793	0.08–0.09	4.24	3582	0.04–0.05	11.4	14742	0.03–0.04	78.4	36363	0.08–0.10
3	0.51±0.15	292	0.05–0.19	1.01±0.27	652	0.05–0.17	6.49±1.51	2640	0.07–0.27	11.6±4.68	14108	0.02–0.09	20.5±11.7	64372	0.01–0.03
4	0.56±0.23	236	0.07–0.38	0.63±0.09	606	0.03–0.16	7.52±0.34	5863	0.04–0.20	16.4±7.19	17710	0.03–0.15	27.6±8.00	212234	0.004–0.02
5	0.72±0.10	217	0.09–0.32	1.31±0.16	1428	0.03–0.09	11.8±0.95	3826	0.08–0.30	23.2±1.55	13111	0.05–0.17	61.1±32.9	116854	0.01–0.05
6	0.57±0.05	213	0.12–0.50	0.89±0.33	604	0.07–0.27	12.7	3894	0.15–0.60	20.3	13128	0.07–0.28	85.2	93945	0.04–0.17
7	1.22±0.24	192	0.43–1.06	1.78±0.09	538	0.23–0.55	8.33	3921	0.14–0.35	19.7±7.46	14685	0.09–0.22	108	146452	0.05–0.12
8	0.35±0.09	274	0.07–0.24	0.45±0.12	719	0.04–0.12	7.64±2.55	3067	0.14–0.46	12.1	11467	0.06–0.19	38.2	82373	0.03–0.08
9	1.09±0.20	208	0.15–0.56	1.86±0.47	505	0.11–0.39	29.7±1.76	4597	0.19–0.69	63.9±16.0	15216	0.12–0.45	175±60.3	27396	0.19–0.68
10	1.46±0.36	235	0.18–0.36	1.57±0.54	726	0.06–0.12	25.5±6.54	4504	0.16–0.33	106±36.7	11336	0.27–0.54	487±39.8	104773	0.13–0.27
11	2.54±0.44	215	0.30–0.58	3.13±0.69	590	0.13–0.26	33.9±11.8	2200	0.39–0.76	53.9±6.56	8689	0.16–0.31	193±74.6	42041	0.12–0.23
12	1.73±0.40	284	0.20–0.46	2.37±0.92	517	0.15–0.35	31.3±3.99	2686	0.38–0.88	74.2±18.6	13612	0.18–0.41	226±156	91148	0.08–0.19
13	1.09±0.14	235	0.18–0.62	1.35±0.25	1020	0.05–0.18	21.2	2829	0.29–1.00	33.8	9652	0.14–0.47	131	96804	0.05–0.18
14	1.29±0.25	220	0.22–0.51	1.49±0.19	578	0.10–0.22	16.3	3809	0.16–0.37	19.9	13203	0.06–0.13	145	86995	0.06–0.14
15	0.84±0.08	207	0.15–0.62	0.45±0.06	541	0.03–0.13	13.1±2.85	3672	0.13–0.55	34.9±17.9	20291	0.06–0.26	93.1±1.02	73508	0.05–0.19
16	0.87±0.05	201	0.18–0.59	0.55±0.15	738	0.03–0.10	22.8	3920	0.24–0.79	19.3	15979	0.05–0.16	92.1	123348	0.03–0.10
17	1.07±0.14	186	0.25–1.34	0.71±0.22	719	0.04–0.23	16.8±6.40	3400	0.22–1.16	20.8±8.55	10528	0.09–0.46	59.7±10.3	51279	0.05–0.27
18	0.98±0.06	191	0.22–0.94	0.62±0.11	574	0.05–0.20	14.8±10.8	3075	0.21–0.89	37.2±8.6	14230	0.11–0.48	35.9±16.3	62200	0.02–0.11
19	0.78±0.03	294	0.12–0.49	0.40±0.15	487	0.04–0.15	7.39±2.34	2795	0.12–0.49	15.2±1.99	10996	0.06–0.25	69.6±36.2	79654	0.04–0.16
20	1.40±0.22	197	0.46–0.86	0.73±0.06	289	0.16–0.31	8.33	2552	0.21–0.39	34.4	12705	0.17–0.33	46.9±6.23	74847	0.04–0.08
21	0.98±0.29	225	0.28–0.73	0.48±0.15	463	0.07–0.17	7.90±1.88	2658	0.19–0.49	15.6±3.20	15500	0.06–0.17	65.1±27.3	168625	0.02–0.06
22	0.82±0.07	222	0.22	0.96±0.31	445	0.13	9.44±1.02	2764	0.20	27.8±7.46	3060	0.53	54.1±11.4	14383	0.22
23	0.85±0.11	302	0.11	0.77±0.22	550	0.06	12.1±4.58	1981	0.25	30.4±8.12	18516	0.07	184±59.6	66179	0.11
24	0.86±0.18	391	0.10	0.67±0.22	631	0.05	11.8±0.84	2502	0.22	57.9±11.6	21488	0.12	84.8±31.7	80658	0.05

To obtain specific ingestion, the C:chl-*a* ratios presented in Table 4 were employed.

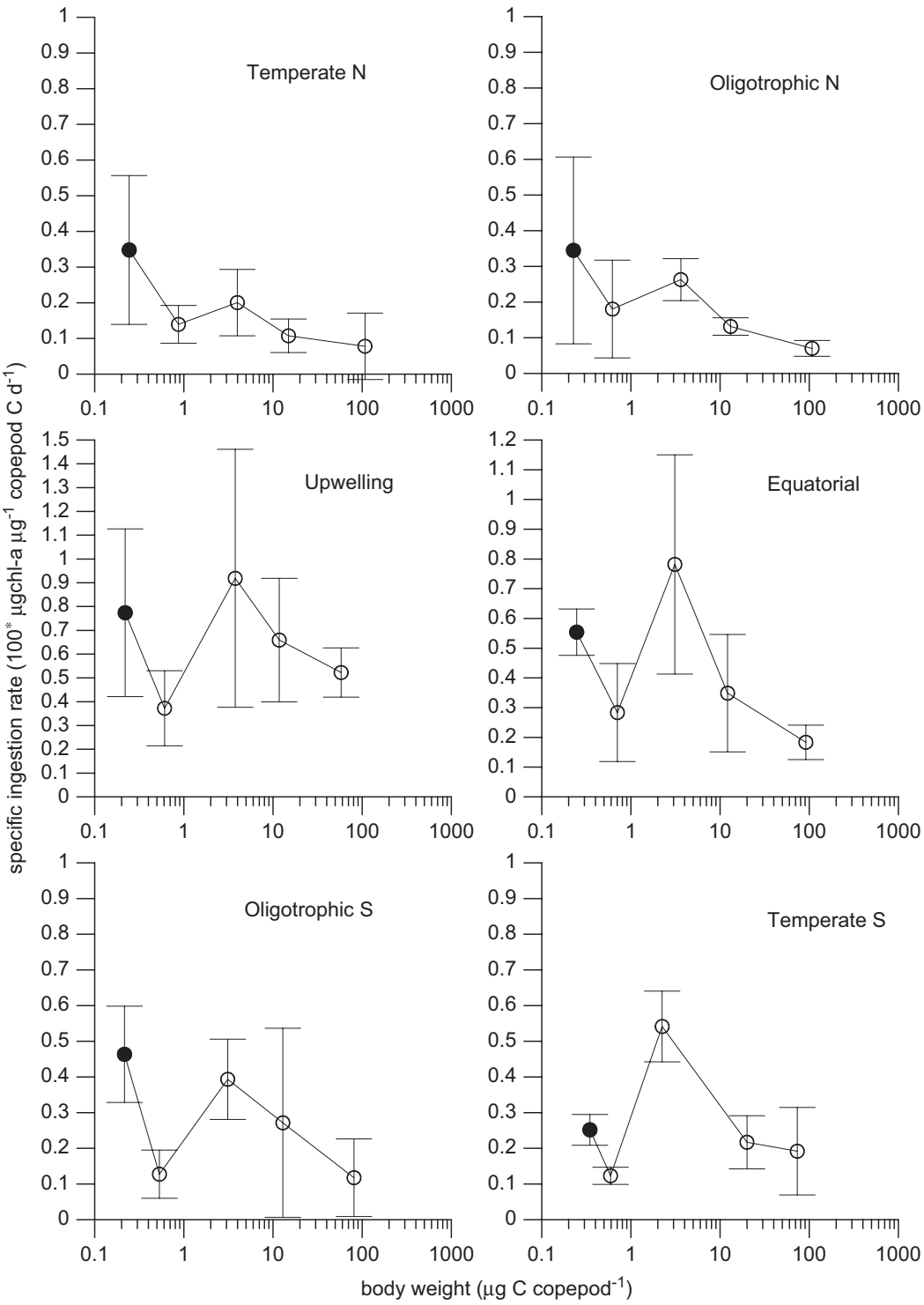

Fig. 6. Specific ingestion rates for all the stages and size fractions of copepods (expressed as the amount of chl-*a* ingested per unit of body C, mean ± S.D. for each region). Filled circles stand for nauplii and open circles for copepods.

4. Discussion

4.1. Copepod abundance and biomass

Copepod abundance varied by a factor of 10 among stations, reflecting the fact that samples came from regions representing different physical and biological characteristics, which affected zooplankton populations.

Nauplii densities oscillated within the same range as reported in other studies in different meso- to oligotrophic regions (Roff et al., 1995; Calbet et al., 2001; Pedersen et al., 2005; López et al., 2007c), but were more

than an order of magnitude lower than densities reported from highly productive systems, such as the northern Adriatic Sea (Lucic et al., 2003) or the Inland Sea of Japan (Uye et al., 1996). In the present study and most of the previously cited, nauplii abundances might have been underestimated as 53 μm mesh nets could have permitted the passage of nauplii of small copepods (López et al., 2007c). Copepod densities reported here were similar to those described for previous AMT cruises for the 500–1000 μm and >1000 μm fractions (Huskin et al., 2001, Isla et al., 2004), but much higher for the 200–500 μm fraction. This difference in the small fraction can be explained by different efficiencies in the filtering process, as we performed net hauls with a 53 μm mesh net and fractionated later, while these authors used a 200 μm mesh net. Because most copepods belonged to the smallest fractions, this difference translates into an average abundance of total copepods >200 μm in this study that is approximately 5 times higher than in previous studies. If we also take into account copepods from the <200 μm fraction, this would translate into approximately 10 times higher densities in the present study. Similar results were obtained by Paffenhöfer and Mazzocchi (2003) in the JGOFS station near Bermuda. They found that the abundance of total copepods retained with a 200 μm mesh net was about one order of magnitude less than that retained with a 63 μm mesh net.

Nauplii abundance is expected to be related to chlorophyll concentration in the water, as high availability of food increases egg production; however, cannibalism (Ohman and Hirche, 2001) or predation by other groups (e.g. chaetognaths) can control nauplii when mesozooplankton are abundant. The lack of significant differences among regions in the ratio "number of nauplii/number of copepods", and the negative (non-significant) relationship between this ratio and copepod and metazooplankton abundance, suggest that one of these factors could be affecting copepod recruitment in the most productive systems. Other variables, such as temperature and quality of available food (López et al., 2007c), could also influence copepod reproduction.

Surprisingly, the only factor significantly affecting copepod biomass was chlorophyll concentration, which explained 71% of the variation. Previous studies during AMT cruises found a weaker relationship with chlorophyll: Isla et al. (2004) found $r^2 = 0.37$ between mesozooplankton biomass and total chlorophyll ($r^2 = 0.7$ for >2 μm chlorophyll), and Woodd-Walker et al. (2001) found that latitude, temperature, density, chlorophyll, total incident radiation, and diel time (sampling hour in a continuous survey), acting together, accounted for 55% of the variation in their regression model. Isla et al. (2004) sampled with a 200 μm net, and Woodd-Walker et al. (2001) used only data from >250 μm-equivalent spherical diameter particles. Therefore, the lower r^2 in their regression models could be due to biased sampling. In our study, 83% of total copepods and nauplii belonged to the <200 μm fraction (a 200 μm mesh net would have retained an even a lower percentage, for reason noted above), translating into 26% of total biomass, but showing important differences among stations (<200 μm biomass ranged between 47% at Station 22 in Oligotrophic S, and 9% at Station 1 in Temperate N).

Temperate and Oligotrophic regions showed characteristic size spectra, with large copepods dominating in Temperate areas and small in Oligotrophic (although in our statistical analyses differences between regions were significant only for nauplii average size, not for copepods). Phytoplankton size spectra follow the same pattern as zooplankton in these regions. Marañón et al. (2000) found during previous AMT cruises that the abundance of photosynthetic plankton in the subtropical gyres exhibited little temporal variability. In most cases, cyanobacteria (*Synechococcus* spp. and *Prochlorococcus* spp.) and small (<5 μm in diameter) flagellates were the dominant groups, accounting for 70–90% of the total photosynthetic C biomass. In contrast, there is no common pattern in upwelling areas. The Equatorial upwelling region is characterized by an increase in phytoplankton abundance and productivity, but the phytoplankton shows the typical size structure found in the less productive regions of the oligotrophic gyres (Marañón et al., 2000, 2001; Pérez et al., 2005). The seasonal upwelling in the eastern equatorial Atlantic seems not to affect the size distribution of primary producers (Herbland et al., 1987), thus phytoplankton assemblages in the equatorial domain are dominated by picophytoplankton. To the contrary, the Mauritanian upwelling region contains a phytoplankton community more similar to that of the Temperate S region, with high abundance of diatoms, coccolithophores and cryptophytes (Barlow et al., 2002; Tarran et al., 2006). In spite of this, differences were not observed between copepod size spectra in either of the two upwelling areas. In upwelling and Equatorial regions copepod average body weights are similar, and larger than in oligotrophic gyres. Therefore, planktonic communities from the Equatorial region do not show the typical pattern, as a phytoplankton community dominated by small cells sustains a trophic web with large copepods dominating the metazooplankton.

4.2. Grazing rates

The gut fluorescence technique has some potential sources of error resulting from: (1) calculation of gut evacuation rate, (2) pigment degradation in copepod guts, and (3) diel feeding periodicities. The design of this study did not allow the evaluation of feeding periodicities, so extrapolation of feeding rates obtained to daily rates are influenced by this source of error. We have performed experiments to estimate gut evacuation rate for nauplii, as the only previous values in the literature were those obtained by López et al. (2007a, b) in laboratory conditions. In both cases, experimental gut clearance coefficients did not differ substantially from those predicted by the Dam and Peterson (1988) relationship with temperature for adult

copepods. In addition, a relationship between gut evacuation rates and temperature was also found, suggesting that nauplii behave in the same way as adult copepods.

Another possible source of error is the C:chl-*a* ratio employed. Recent studies have pointed out the depth variability found in C:chl-*a* ratios along the AMT transect (Pérez et al., 2006, and references therein). Depth variability was unavoidable in this study as we were working with 200 m integrated samples, so we decided to present results as a range instead of as a single value, using regressions by Marañón et al. (2000) to obtain C:chl-*a* ratios for surface and deep chlorophyll maximum.

Weight-specific ingestion rates of copepods usually decrease with increasing stage and weight (Paffenhöfer, 1971). Individual ingestion rates of nauplii in this study are only minimal estimates, as we included all stages of nauplii in the analysis, and the first developmental stages of most genera of copepods do not feed (Mauchline, 1998). This may be why individual ingestion rates observed in the 200–500 μm fraction of copepods were in some cases higher than those of nauplii. Also, although some previous studies have concluded that nauplii have weight-specific ingestion rates 3–4 times higher than copepods (Paffenhöfer, 1971; White and Roman, 1992; Lonsdale et al., 1996), other authors have found an increase of specific ingestion from the first stages of nauplii to the copepodite stages (Fernández, 1979; Klein Breteler et al., 1990). Paffenhöfer (1984), in multialgal experiments simulating conditions of summer upwelling, found that *Paracalanus* sp. weight-specific ingestion rates increased from stage N IV to stage CIII and then decreased in adult females. On the contrary, when only one algal species was offered as food, nauplii weight-specific ingestion rates were higher than in copepodites. These results suggest that the stage composition in the nauplii and copepod assemblages as well as the characteristics of the available food have an important influence on weight-specific ingestion rates observed in the field.

Furthermore, in regions where picoplankton dominated phytoplankton communities (75–80% of total phytoplankton in oligotrophic gyres, Marañón et al., 2001), nauplii and copepod specific ingestion rates were within the same range, and sometimes higher, than in temperate regions. Phytoplankton assemblages from temperate regions have larger cells (Barlow et al., 2002; Tarran et al., 2006), more suitable for copepods to ingest (Nival and Nival, 1976; Bartram, 1980; Mullin, 1980; Berggreen et al., 1988). We suggest that in these regions dominated by picoplankton copepods were acclimatised or adapted to feed on small cells, although morphological and/or behavioural experiments would be necessary to test this hypothesis. A similar hypothesis was proposed by Poulet (1978), who performed feeding experiments with five species of copepods and natural seawater from the Bedford Basin. He observed a shift in copepod feeding from one size range to another, showing a high feeding efficiency on particles <5 μm when the size spectra was dominated by this size range, as if copepods were able to adapt to changes in concentration peaks.

Maximum impact of copepod grazing on primary production was in areas affected by equatorial upwelling and in the Mauritanian region, similar to the pattern presented by Huskin et al. (2001) and Isla et al. (2004). Mesozooplankton response to short upwelling events is an increase in grazing rates (Franks, 2001), and this strategy by its own is not usually enough to control phytoplankton growth. To the contrary, in these quasi-permanent upwelling regions, chlorophyll concentration remains high during most of the year, so copepods are able to increase their numbers, in spite of their long generation times, and exert a more efficient control on primary production. Even so, we would not expect that copepods in the upwelling centre to exert such efficient control on primary production because of the episodic oscillations in upwelling intensity. However, the cruise traversed an area only marginally affected by Mauritanian upwelling, where nutrients are expected to be exhausted, causing a decrease in primary production; in these conditions, losses due to grazing can overtake phytoplankton growth rates (Estrada and Blasco, 1985).

Previous studies (Marañón et al., 2000; Calbet, 2001; San Martin et al., 2006a) have suggested a strong coupling between phytoplankton and zooplankton via grazing in oligotrophic areas. This coupling is favoured by the practical absence of seasonal changes, a typical characteristic of these ecosystems. We found an average impact on primary production that ranges 28–164% in Oligotrophic N (without taking into account the surprisingly high values obtained for Station 6) and 12–175% in Oligotrophic S. This contrasts with conclusions from previous studies that attributed the control of primary production in these regions only to protists (Quevedo and Anadón, 2001), with copepods ingesting daily less than 10% of primary production (Huskin et al., 2001; Isla et al., 2004). Peterson (1980) and Carignan et al. (2000) pointed out that the use of ^{14}C methodology could lead to an underestimation of primary production, especially in oligotrophic waters. Therefore, this is a potential error in all these studies. Our study shows that copepods also play an important role as consumers in oligotrophic regions, a role that has been previously underestimated because of scarcity of studies in these areas and failures to account for small copepods and nauplii.

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Appendix A

Abundance (no ind m^{-2}) of the different taxonomic groups in the fraction $>1000\,\mu m$

Fraction	Station	cop	naup	chae	app	clad	siph	polyl	decal	ostr	pter	doli	fishl	amph	jelly	salp
>1000 μm	1	10375	–	454	70	–	175	105	35	–	–	–	–	–	279	–
	2	1886	–	175	–	–	–	17	87	35	–	–	–	–	–	–
	3	8750	–	629	70	–	17	–	17	–	17	–	–	192	–	–
	4	961	–	–	–	–	35	–	–	–	192	–	–	17	–	–
	5	1869	–	105	87	17	175	–	35	17	35	–	–	–	–	–
	6	4611	–	1118	140	–	175	87	611	157	17	17	105	70	35	–
	7	838	–	611	–	–	70	70	367	70	–	–	35	17	70	–
	8	2829	–	1729	70	–	279	52	384	105	–	122	70	122	122	–
	9	8715	–	873	1659	–	349	192	367	157	87	–	52	17	–	–
	10	6689	–	262	611	–	52	–	227	87	18269	–	–	87	35	–
	11	16732	–	3004	70	–	70	35	699	–	1467	70	70	–	–	140
	12	5292	–	1100	454	–	17	35	332	70	–	17	52	52	17	–
	13	4174	–	1712	175	–	227	87	210	87	17	–	35	87	70	–
	14	9746	–	2515	1048	–	594	245	1816	140	–	245	70	70	35	–
	15	3947	–	838	349	–	314	–	978	384	35	–	105	175	175	–
	16	1135	–	227	70	–	140	17	245	–	–	–	–	17	17	–
	17	1834	–	314	–	–	70	35	175	17	17	35	70	35	17	–
	18	978	–	489	–	–	297	17	192	70	17	–	–	–	52	–
	19	1607	–	332	17	–	35	–	227	–	–	–	70	70	–	–
	20	1956	–	314	17	–	175	–	140	52	–	35	–	–	17	–
	21	576	–	437	–	–	157	17	157	17	35	–	–	17	–	–
	22	1013	–	472	52	–	70	279	157	52	–	–	–	35	52	–
	23	31294	–	679	–	–	170	–	962	1754	679	–	–	–	–	–
	24	13610	–	410	–	–	28	14	523	325	42	–	–	–	–	–

cop—copepods, naup—nauplii, chae—chaetognaths, app—appendicularians, clad—cladocerans, siph—siphonophors, polyl—polychaeta larvae, decal—decapod larvae, ostr—ostracods, pter—pteropodos, doli—doliolids, fishl—fish larvae, amph—amphipods, jelly—jellyfishes, and salp—salps.

Appendix B

Abundance (no ind m^{-2}) of the different taxonomic groups in the fraction 500–1000 μm

Fraction	Station	cop	naup	chae	app	clad	siph	polyl	decal	ostr	pter	doli	fishl	amph	jelly	salp
500–1000 μm	1	26234	–	70	314	–	–	175	210	175	–	–	–	–	35	–
	2	15649	–	–	70	–	–	–	35	210	–	–	–	–	–	–
	3	99119	–	349	349	87	–	–	–	–	–	–	–	262	–	–
	4	8052	–	17	52	35	–	17	–	35	122	–	–	–	–	–
	5	33395	–	140	2585	279	140	210	–	279	489	–	–	–	–	–
	6	21169	70	629	1677	210	279	419	210	1048	–	70	–	–	–	–
	7	9956	–	559	35	–	175	70	524	384	–	140	70	35	–	–
	8	15370	–	594	559	35	35	140	70	454	–	140	70	–	–	–
	9	14043	–	349	3563	–	–	140	559	210	–	140	210	–	–	–
	10	10480	–	–	2061	–	35	35	–	140	–	–	35	–	–	–
	11	105354	489	2236	6078	–	–	419	1188	908	559	629	349	–	–	279
	12	24871	–	70	1607	–	–	140	–	978	–	70	140	–	–	–
	13	15649	–	245	978	–	35	140	210	140	–	–	–	35	–	–
	14	34146	–	349	3668	–	349	87	611	437	–	–	–	87	–	–
	15	13623	–	70	1537	–	–	–	768	559	–	–	70	–	–	–
	16	5205	–	70	210	–	–	35	–	35	–	35	–	–	70	–
	17	10410	–	35	105	–	140	35	140	140	–	–	–	–	–	–
	18	5013	–	105	140	–	87	70	52	279	17	17	35	–	–	–
	19	7650	–	35	70	–	–	–	–	349	–	–	35	–	–	–
	20	7196	35	105	454	–	–	–	35	594	35	–	–	–	–	–
	21	7493	–	332	821	–	140	175	105	437	52	–	17	52	17	–
	22	6043	–	245	838	–	175	175	105	245	–	70	–	35	–	–
	23	53364	–	170	57	–	113	113	1754	2094	57	–	–	–	–	–
	24	106840	–	453	113	–	–	226	5489	14996	509	–	–	–	–	–

Abbreviations as in Table 1.

Appendix C

Abundance (no ind m^{-2}) of the different taxonomic groups in the fraction 200–500 μm

Fraction	Station	cop	naup	chae	app	clad	siph	polyl	decal	ostr	pter	doli	fishl	amph	jelly	salp
200–500 μm	1	126904	35001	–	104	–	–	768	–	419	–	–	–	–	–	–
	2	155653	25779	–	419	70	–	70	–	1327	–	–	–	–	–	–
	3	1259408	243609	–	3842	349	–	–	–	699	349	–	–	–	–	–
	4	61583	4192	175	419	279	–	140	–	35	1153	–	–	–	–	–
	5	159216	55191	–	3982	279	70	629	–	699	838	–	–	–	–	–
	6	124983	21448	140	2515	629	–	489	210	4052	698	70	–	–	–	–
	7	112757	22076	419	1187	1188	210	140	–	2585	628	–	70	–	–	–
	8	155164	37865	419	3353	768	349	70	–	2725	1257	–	–	70	–	–
	9	155443	23264	279	12400	140	140	559	140	699	611	–	–	–	–	–
	10	73006	16417	70	1118	–	–	–	70	1048	6916	–	–	–	–	–
	11	497559	160962	–	13273	–	–	140	140	1956	33114	–	–	–	–	–
	12	166481	64622	140	2445	70	–	210	–	1677	279	140	17	–	–	–
	13	118975	35350	70	3563	–	–	140	70	1956	489	–	–	140	–	–
	14	200644	93894	–	7125	–	–	140	210	2026	2864	–	70	140	–	–
	15	72997	8217	70	2166	70	–	–	838	978	210	–	–	–	–	–
	16	50126	4541	–	140	–	–	–	–	419	768	–	–	–	–	–
	17	81110	23543	–	279	–	–	70	–	768	–	–	–	–	–	–
	18	72272	16103	175	943	35	35	35	35	1886	245	–	–	–	–	–
	19	85790	35245	–	70	–	–	–	–	1118	–	–	–	–	–	–
	20	84603	28154	–	489	–	–	140	–	1258	350	–	–	–	–	–
	21	96410	34791	70	8802	–	70	140	–	1677	140	–	–	–	–	–
	22	107098	31647	–	6008	–	–	–	279	978	–	–	–	–	–	–
	23	463577	177237	–	453	–	–	–	453	7922	8714	–	–	–	–	–
	24	827143	164108	–	–	–	–	354	707	10375	943	–	–	–	–	–

Abbreviations as in Table 1.

Appendix D

Abundance (no ind m^{-2}) of the different taxonomic groups in the fraction <200 μm

Fraction	Station	cop	naup
<200 μm	1	40171	305648
	2	360490	1637573
	3	512789	1706736
	4	296566	525365
	5	332545	1379781
	6	296216	904018
	7	318921	559248
	8	131341	350010
	9	150903	514885
	10	215176	1331576
	11	549118	1388863
	12	371667	1250535
	13	167670	676267
	14	143567	736349
	15	97109	329750
	16	118766	389832
	17	186882	477858
	18	189327	403804
	19	187930	503009
	20	273162	718883
	21	275956	769184
	22	227751	624569
	23	426677	1632012
	24	899757	2318996

Abbreviations as in Table 1.

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