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The protistan microzooplankton community in the oligotrophic north-eastern Atlantic: large- and mesoscale patterns

MARIO QUEVEDO[1,*], LETICIA VIESCA, RICARDO ANADÓN AND EMILIO FERNÁNDEZ[2]

DEPARTAMENTO BIOLOGÍA DE ORGANISMOS Y SISTEMAS, ECOLOGÍA, UNIVERSIDAD DE OVIEDO, CATEDRÁTICO R. URÍA S/N, E-33071 OVIEDO, ASTURIAS AND [2]DEPARTAMENTO ECOLOGÍA Y BIOLOGÍA ANIMAL, FACULTAD DE CIENCIAS, UNIVERSIDAD DE VIGO, CAMPUS LAGOAS-MARCOSENDE, E-36200 VIGO, SPAIN

[1]PRESENT ADDRESS: DEPARTMENT OF LIMNOLOGY, EVOLUTIONARY BIOLOGY CENTRE, UPPSALA UNIVERSITY, NORBYVÄGEN 20, S-752 36 UPPSALA, SWEDEN

*CORRESPONDING AUTHOR: Mario.Quevedo@ebc.uu.se

We surveyed the oligotrophic waters of the north-eastern Atlantic subtropical gyre to investigate the biomass, abundance, composition and variability of the protistan microzooplankton community. Aloricate ciliates and gymnodinoid dinoflagellates dominated the community, which did not show broad seasonal variations. Large mixotrophic ciliates, with a high carbon content per cell, accounted for a substantial amount of the variability of the standing stock. We found average values of microzooplankton biomass and abundance of 1.1 mg C m^{-3} and 3.7 × 10^3 cells l^{-1}, respectively, which are among the lowest measured in marine systems, 5- to 10-fold lower than in the neighbouring waters of the North Atlantic Drift. The mesoscale structures surveyed, a cyclonic eddy and the hydrographical structures over a submarine mount, significantly enhanced microzooplankton biomass and sustained the presence of cells with a carbon content higher than in neighbouring waters. Microzooplankton followed complex patterns of distribution that did not correspond to the variability of primary production or of chlorophyll a.

INTRODUCTION

The biogenic carbon pool and its partitioning among trophic compartments, the abundance of organisms, or the composition and size-structure of the food chain, are highly relevant characteristics in understanding the functioning of the pelagic ecosystem (Hansen *et al.*, 1994; Thingstad, 1998). Recently, several studies have revolved around the productivity and carbon balance of the producer–decomposer compartments in highly oligotrophic oceanic waters, dealing with the existence of a carbon deficit over large areas of the ocean (del Giorgio *et al.*, 1997; Duarte *et al.*, 2001). Such focal attention, with special emphasis on the north-east Atlantic Ocean, yielded a substantial body of knowledge regarding the composition, biomass and metabolism of primary producers and bacteria in the subtropical gyres (Li and Harrison, 2001; Marañón *et al.*, 2001; González *et al.*, 2002).

On the other hand, this wealth of studies on the planktonic community in oligotrophic waters is strongly biased towards the smallest cells; much less effort has been devoted to the upper compartments of the trophic pathways, i.e. protistan grazers and predators. These organisms are a key link in the marine food web (Stoecker and McDowell-Capuzzo, 1990; Sherr and Sherr, 1994), contributing to the modulation of phytoplankton populations via nutrient recycling, dissolved organic carbon release and size-selective grazing, particularly in the photic layer of stratified waters without allochthonous inputs (Fenchel, 1988; Nagata, 2000). Among the organisms constituting the assemblage of marine protist grazers, ciliates and heterotrophic dinoflagellates are the major groups in the 20–200 μm size-range, formally named microzooplankton, and also constitute an important fraction of the nanoplankton size-range (Sherr *et al.*, 1986). Despite their potential importance in oligotrophic

waters, they have received less attention than in more productive waters, perhaps because they frequently require time-consuming procedures and do not fit synoptically with the logistics planned to cover the phytoplankton and hydrographic features.

The subtropical gyre of the north-eastern Atlantic is an extremely resource-poor environment (Louanchi and Najjar, 2001) where the proportion of heterotrophic carbon might exceed 50% of the total biogenic carbon, resulting in an inverted trophic pyramid (Buck *et al.*, 1996) and intense coupling between phytoplankton and protist grazers (Quevedo and Anadón, 2001). The area is rich in hydrographic mesoscale processes (Garçon *et al.*, 2001) that might influence food-web structure, favouring nutrient pulses (Falkowski *et al.*, 1998), and controlling the size structure of phytoplankton (Rodríguez *et al.*, 2001). Hence, this region was perceived as pertinent to gaining knowledge on several issues regarding open-ocean microzooplankton, i.e. its composition, contribution to the biogenic carbon pool, and variability along seasonal or spatial scales, which are reported herein while keeping the ecogeographical significance of the data and the methodological implications in focus.

METHOD

Area of study

This study is focused on the subtropical gyre of the north-eastern Atlantic Ocean (Figure 1), a stratified, nutrient-depleted region. This is bounded to the north and north-west by the Subtropical Front and its associated Azores Current and eddy field, which form a continuous link with the south-eastern branch of the Gulf Stream, centred at ~34–35°N (Klein and Siedler, 1989; Mouriño *et al.*, 2002). The southern and eastern boundaries are delimited by the weakly defined Subtropical Convergence (25–30ºN) and the equatorward Canary Current, respectively (Longhurst, 1998).

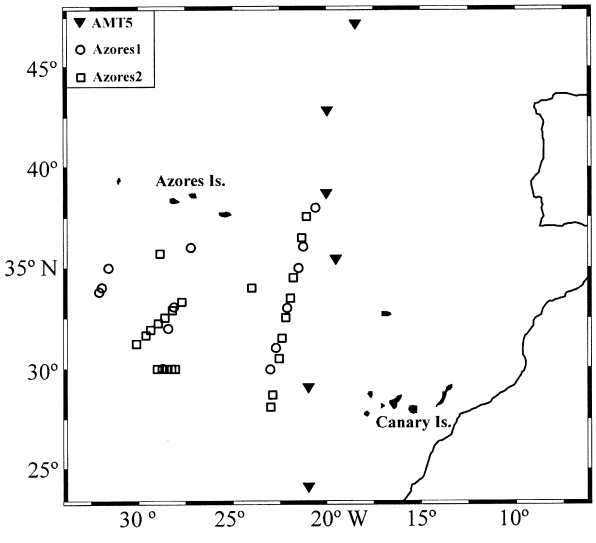

Fig. 1. Area of study and position of stations. ▼ = stations sampled in cruise AMT5, early autumn 1997; ○ = stations sampled in cruise Azores 1, summer 1998; □ = stations sampled in cruise Azores 2, spring 1999.

We conducted three cruises in the region: Azores 1 in August 1998 and Azores 2 in April 1999 on board RV 'Hespérides' (hereafter the summer and spring cruises, respectively), and a portion of cruise AMT5 (Atlantic Meridional Transect project) on board RV 'James Clark Ross' in September 1997 (hereafter early autumn cruise). The whole area of study comprised stations located in three different ecogeographical provinces: North Atlantic Drift (NADR), North Atlantic Subtropical Gyre (NAST) and Eastern (Canary) Coastal (CNRY) provinces (Longhurst, 1998).

A transect roughly coincident with the 20°W meridian was conducted during the three cruises to assess latitudinal and seasonal variability in the subtropical region. This transect will be referred to as '20ºW' throughout the study. The spring cruise specifically targeted two mesoscale features, a cyclonic eddy named Leticia and the hydrographic structures over the Great Meteor Tablemount (GMT), to investigate their effect on the biological fields. These features are described in detail elsewhere (González *et al.*, 2001; Mouriño *et al.*, 2001, 2002).

Sample collection and processing

We collected water samples for microzooplankton analyses directly from 5 l Niskin bottles mounted onto a CTD/rosette. A silicone tube was directed to the bottom of double-capped plastic vials to avoid air contact as much as possible. Samples were fixed in pre-added, acidic Lugol's solution (3–5% final concentration), and stored at 5°C in the dark until analysis. Since the concentration of Lugol's fixative decreases with time in plastic vials, we added the equivalent of 2% final concentration three times: first at the arrival of the samples from the sea, and then at 3 and 6 months after the samples' arrival. We assumed saturation of the plastic vials afterwards. During the early autumn cruise, four to six 500 ml samples were collected per station from the daily main CTD, with three sampling depths fixed *a priori*: surface, deep chlorophyll maximum (DCM) and a sample beyond DCM. During the spring and summer cruises, four to six samples were collected depending on the number of available sampling depths above DCM. A total of 161 samples was processed in this study.

We determined the sample volume to be processed

according to the presumed amount of cells at the sampling site, estimated from chlorophyll *a* (Chl *a*) concentration. Consequently, for most samples the whole volume (500 ml) was processed. Preceding analyses, the whole samples were settled in sealed 500 or 250 ml test tubes for at least 6 days. The upper 450 (200) ml were gently siphoned with silicone tubing and discarded, and the rest of the volume was allowed to settle for a minimum of 20 h in 25 mm Utermöhl chambers. The samples were analysed under a phase-contrast Olympus IMT-2 inverted microscope, at magnifications of 150×, 400×, or 600×. To account for cell losses during the sedimentation process, a correction factor was obtained from the average number of cells remaining in the discarded portions of five samples, resulting in a correction of 1.3× for small dinoflagellates and no correction for small ciliates and larger microzooplankton. To count the cells, in most cases we enumerated the whole settling chamber for cells >20 μm, and two transverse transects covering the whole diameter of the chamber for cells <20 μm at 150× magnification. This procedure was switched to half the chamber and one transect for the most populated samples. Counts for dinoflagellates <20 μm were cross-validated with a transect at 400× magnification.

To estimate microzooplankton biomass, the linear dimensions of cells were measured with an image-analysis system attached to the inverted microscope, and converted to volumes assuming geometric shapes (Hillebrand *et al.*, 1999). We measured a minimum of 25 cells from common genera or morphotypes, and each cell from rare ones. Carbon content of cells was estimated from volume using the following carbon to volume conversions: pg C $cell^{-1} = 0.76 \times (\mu m^3)^{0.819}$ for dinoflagellates, and pg C $cell^{-1} = 0.22 \times (\mu m^3)^{0.939}$ for the rest of the protists (Menden-Deuer and Lessard, 2000).

Biomass and abundance of microzooplankton in each sample resulted from the pooled biomass and cell numbers of each group. The values obtained at the different sampling depths in the water column were subsequently integrated through the photic layer to the depth of 1% of surface irradiance, via trapezoidal integration. Photic zone depth ranged from 80 to 120 m, 100 to 140 m and 100 to 135 m in the early autumn, spring and summer cruises, respectively.

Despite the growing evidence for photosynthetic dinoflagellates performing phagotrophy or extracellular digestion, we considered only genera well documented as phagotrophic or mixotrophic (Lessard and Swift, 1986; Gaines and Elbrächter, 1987; Jeong, 1999). We also took into account our own observations through epifluorescence microscopy in the area of study, which showed that 57% of the small gymnodinoids and 63% of the much less abundant thecate dinoflagellates <20 μm lacked chloroplasts (Quevedo and Anadón, 2001).

Data analysis

Most microzooplankton community variables in this study showed log–normal distributions. Therefore, to achieve normality and homoscedasticity, data were $\log_{10}(X + 1)$ transformed, with the exception of ratio variables, which were $\sqrt{X}$ transformed. Kolmogorov–Smirnov and Levene tests were used to assess normality and homoscedasticity of the transformed variables.

The seasonal, spatial and water column variability of microzooplankton was tested with a hierarchical analysis of variance (ANOVA), considering the data gathered along 20ºW transect of the spring and summer cruises. We entered total microzooplankton biomass (MzB, mg C m^{-3}) and total microzooplankton abundance (MzA, cells l^{-1}) in the analyses. The number of samples per station in the data set ranged from four to six. Hence, to achieve the required balance in the number of cases for the analysis, we excluded one depth at random from the analysis in stations with six sampled depths. In stations with four sampled depths, an extra depth was calculated as the average value of the real samples in the target station (Zar, 1999). Additionally, a one-way ANOVA was performed including the stations of the early autumn cruise pertaining to the subtropical region. To assess if the difference between the 20ºW transect and the mesoscale features in the spring cruise was significant, we performed a hierarchical ANOVA for MzB and MzA, and a one-way ANOVA plus a Tukey post-hoc test for the photic layer integrated microzooplankton biomass (MzBI).

Although both the scope of the study and the fixative method prevent high taxonomic resolution being obtained, we summarized the community into eight groups to assess the patterns of association among major microzooplankton groups in the study area. The resulting groups were: choreotrich and oligotrich ciliates (hereafter COC) <20 μm, COC >20 μm, large mixotrophic ciliates, tintinnids, other ciliates, gymnodinoid dinoflagellates <20 μm, gymnodinoid dinoflagellates >20 μm, and large thecate dinoflagellates. On this basis, we conducted non-metric multi-dimensional scaling (NMDS) analyses (Legendre and Legendre, 1998) for the abundance of the different groups. We used the Bray–Curtis coefficient to build the similarity matrix from untransformed, standardized abundance data (Clarke, 1993). This coefficient was used because differences between abundant species and between rare species contribute to it equally. Preliminary analyses showed that including non-oligotrich ciliates distorted the results because of the large number of zero values in the matrix. Therefore, non-oligotrich ciliates were excluded from these analyses. NMDS

analyses were performed with PRIMER (Plymouth Marine Laboratory, UK) software package.

RESULTS

The microzooplanktonic and environmental variables in the area of study, though in a context of overall oligotrophy, showed great variability, ranging between one and two orders of magnitude (Table I). The average vertical variability, estimated as the average coefficient of variation of microzooplanktonic variables in the water column, remained almost constant irrespective of the scale considered. Vertical variability of MzB averaged 45% for the whole area of study, 47% for transect 20°W in Azores cruises, 40% along cyclonic eddy Leticia and 54% along the GMT transect. The equivalent values for MzA were 55, 61, 41 and 54%, respectively.

Overall trends in abundance and biomass

Figure 2 depicts the trends in temperature, Chl *a* concentration, MzB and MzA along the three latitudinal transects conducted in the region of study in the vicinity of the 20°W parallel, in early autumn 1997, summer 1998 and spring 1999. The subtropical north-eastern Atlantic is perceived as a rather homogeneous area in the abundance and biomass along the early autumn transect because of the sampling scale of the survey (Figure 2a), but the more detailed sampling during the spring and summer cruises showed the complex, patchy distribution of microzooplankton in the area (Figure 2b and c). Abundance and biomass along the 20°W transect during the spring and summer cruises rendered very similar values, and microzooplankton minima might be perceived in both transects at ~35°N. Shallower microzooplankton maxima at the southern part of the transects were perceivable in both cruises. However, the higher abundance values registered in early autumn (see below) should be noted. The overall results of MzA and MzB in the subtropical north-eastern Atlantic are presented in Table I.

Seasonality

Azores cruises were planned to cover the period of high stratification in summer, and a period of deeper mixed layering in spring. The mixed layer depth, based on the criterion of a temperature change from the ocean surface of 0.5°C (Monterey and Levitus, 1997), averaged 50 ± 42 m on the spring cruise and 25 ± 8 m on the summer cruise. This seasonality in water-column properties is reflected in the specific results for each Azores cruise, which showed slightly increased microzooplankton values for the spring cruise. MzB and MzA in spring were ca 1.4-fold greater than in summer, and almost the same proportion holds for integrated values. However, sampling strategy in the spring cruise specifically targeted mesoscale features, presumed to enrich the water column. Thus, the 20°W transect in both cruises is used as a control. No significant differences between cruises were found in MzA and MzB along the 20°W transects in spring and summer through a nested ANOVA. However, a significant variability was observed among stations. Moreover, a great amount of the variance was explained by vertical variability (Table II). Conversely, a one-way ANOVA including three stations from the early autumn cruise revealed some variability among seasons in microzooplanktonic fields along the 20°W transect. This analysis showed significant differences both in MzA ($F_{2,71} = 24.6$; $P < 0.001$) and MzB ($F_{2,71} = 14.2$; $P < 0.001$), which were higher in early autumn. Indeed, these

Table I: Overall values of microzooplankton in the subtropical north-eastern Atlantic: mean ± standard deviation, median, maximum and minimum values

	n	Mean ± SD	Median	Maximum	Minimum
MzB (mg C m^{-3})	150	1.1±0.8	0.9	4.2	0.1
MzA (cell $l^{-1} \times 10^3$)	150	3.7±3.5	2.6	23	0.2
MzBI (mg C m^{-2})	39	136±70	115	289	39
MzAI (cell $m^{-2} \times 10^8$)	39	4.7±3.3	3.4	14	0.9
Chl (mg m^{-3})	134	0.15±0.16	0.09	1.10	0.01
PP (mg C m^{-3} h^{-1})	122	0.10±0.08	0.08	0.32	0.01
IChl (mg m^{-2})	33	18.9±12.5	16.5	62.1	3.8
IPP (mg C m^{-2} h^{-1})	25	15.8±13.7	10.7	52.8	1.3

MzB, MzA = volumetric microzooplankton biomass and abundance; MzBI, MzAI = photic layer integrated microzooplankton biomass and abundance; Chl = volumetric chlorophyll *a* concentration; PP = volumetric primary production rate; IChl, IPP = photic layer integrated chlorophyll *a* concentration and rate of primary production. The average depth of the photic layer was 115 m.

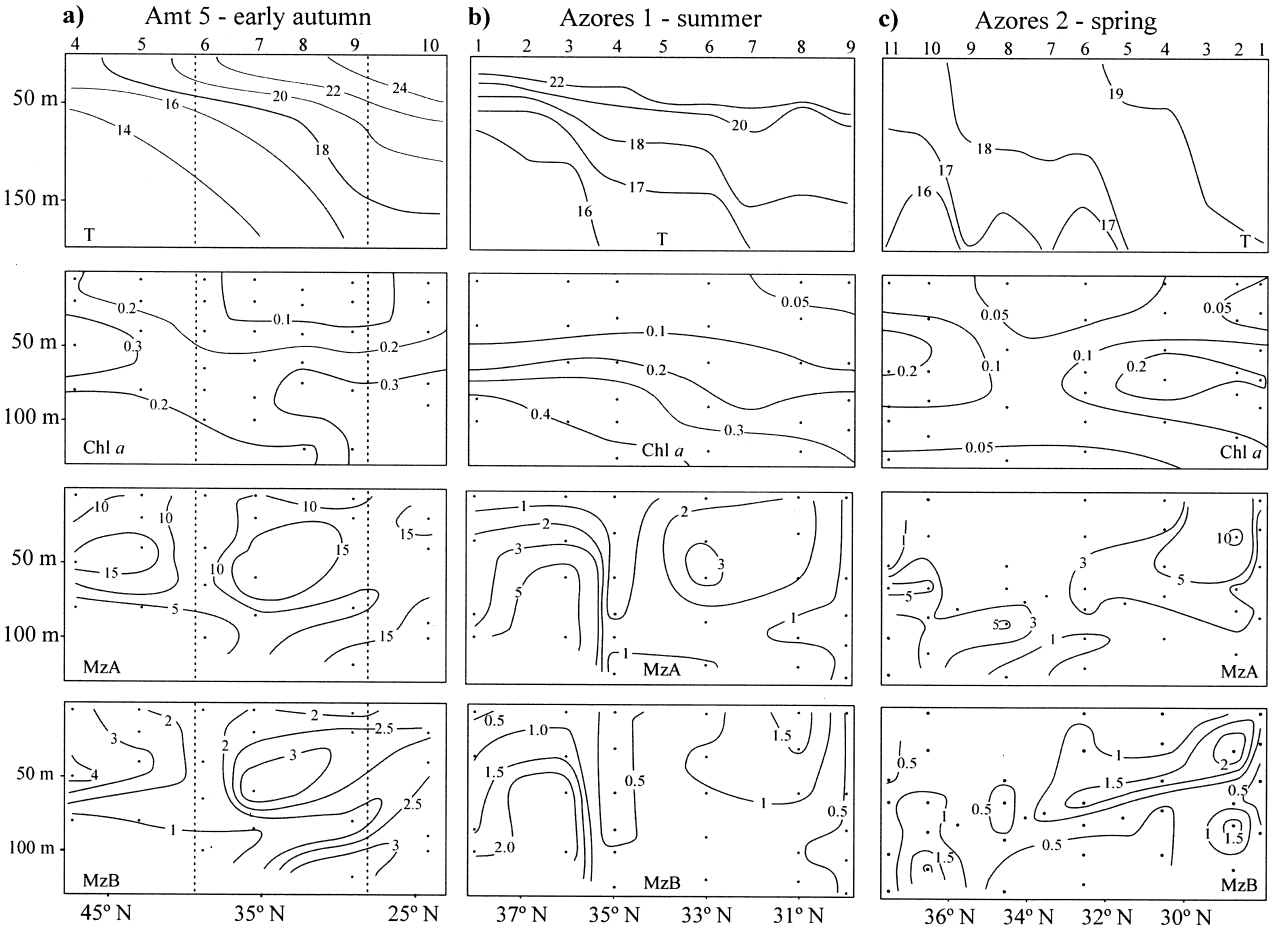

Fig. 2. Contour plots of temperature (T; °C), chlorophyll *a* concentration (Chl *a*; mg m^{-3}), microzooplankton abundance (MzA; cells ml^{-1}) and biomass (MzB; mg C m^{-3}). (**a**) Early autumn transect, (**b**, **c**) the 20°W transect in spring and summer cruises. Dashed lines in plot (a) delineate the approximate latitudinal range shared with the Azores cruises. Temperature contours for spring and summer cruises result from CTD profiles.

differences are explained by the increased abundance ($F_{2,71}$ = 26.7; $P < 0.001$) and biomass ($F_{2,71}$ = 34.8; $P < 0.001$) of heterotrophic dinoflagellates (hereafter HD) in the early autumn, reflected in HD clearly dominating microzooplankton biomass in contrast to the more equilibrated spring and summer values.

Mesoscale features

A major aim of the spring cruise was to analyse the effect of mesoscale instabilities on the oligotrophic system of the subtropical north-eastern Atlantic. We found an increase in microzooplankton biomass along these instabilities, particularly noticeable in the integrated biomass values (Figure 3). A biomass maximum was apparent at the centre of Leticia (station 19), coinciding with dome-shaped isotherms and a shallower, bigger subsurface Chl *a* maximum (Figure 4). The abundance maximum in Leticia was more diffuse. The distribution of MzA and MzB along the GMT transect was quite patchy, with a maximum located at the surface of the easternmost station, and no emerging relationship with temperature or Chl *a* (data not shown). Despite the great vertical variability, we found statistically significant differences (Table III) in MzB between the three transects sampled in the cruise: the cyclonic eddy Leticia, the GMT and the 20°W transect. Average MzB was higher in Leticia than in the GMT and in the 20°W transect: 1.6, 1.2 and 0.7 mg C m^{-3}, respectively. The comparison conducted with the integrated microzooplankton biomass rendered similar results, both mesoscale transects showing greater biomass values than the 20°W transect ($F_{2,16}$ = 9.7; P = 0.002). Tukey test rendered P values of 0.001 and 0.048 for the comparison with *Leticia* and GMT, respectively. The differences between transects in spring accounted for 21% of the biomass variability in the cruise, while vertical variability among samples accounted for 66% of the variance (Table III).

Table II: Nested ANOVA for total microzooplankton biomass (MzB) and abundance (MzA) in transect 20°W of spring and summer cruises

MzB	df	MS	*F*	*P*	% Var
Cruise	1	0.002	0.05	0.83	0
Station (cruise)	10	0.045	4.66	<0.00	42
Depth [station (cruise)]	48	0.009			58
MzA					
Cruise	1	0.385	1.70	0.22	0
Station (cruise)	10	0.226	2.48	0.02	23
Depth [station (cruise)]	48	0.090			77

% Var: percentage of variance explained by each factor.

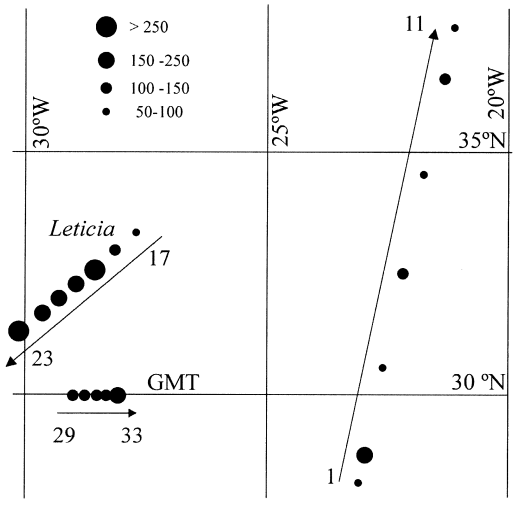

Fig. 3. Photic layer-integrated microzooplankton biomass (mg C m^{-2}) along transects through cyclonic eddy *Leticia*, *GMT* and 20°W during the spring cruise. Numbers identify the initial and final stations of each transect.

Composition and distribution

The microzooplankton community was clearly dominated by COC (families Strombidiidae and Strobilidiidae) and gymnodinoid dinoflagellates. The most common ciliate genera were the widespread *Strombidium* spp. and *Strobilidium* spp., present in every sample and averaging 0.2×10^3 cells l^{-1} and 0.30 mg C m^{-3}. Maximum COC abundance, 2.1×10^3 cells l^{-1}, was found under the influence of eddy Leticia in station 18 of the spring cruise (Figure 4), not coincident with the COC biomass maximum that appeared in the adjacent station 19, at 1.4 mg C m^{-3}. The mixotrophic oligotrich ciliates *Tontonia* spp. and *Laboea strobila* were also common and showed 44 and 30% occurrence, the latter somewhat restricted to upper layers with an average depth of 36 m. Mixotrophic ciliates, at 0.01×10^3 cells l^{-1} and 0.05 mg C m^{-3}, averaged low values (but see Discussion). Aloricate COC <20 μm averaged 0.4×10^3 cells l^{-1} and 0.05 mg C m^{-3} in the subtropical region. Tintinnids, up to 25 hyaline genera without including those found only as empty loricas, showed a 97% occurrence, though very low abundance values averaging 0.03×10^3 cells l^{-1} and 0.04 mg C m^{-3}. The commonest genera of tintinnids were *Acanthostomella*, *Dadayiella* and *Salpingella*, with 59, 23 and 15% occurrences, respectively. Predatory haptorid ciliates like *Didinium* were very uncommon in this study, with a 4% ocurrence and averaging 9 cells l^{-1}.

The naked dinoflagellates *Gymnodinium* spp. and *Gyrodinium* spp. were present in every sample, ranging widely from 7 μm (the smallest gymnodinoid recorded) to ~100 μm (*Gyrodinium spirale*). Other common genera were the naked *Cochlodinium* and *Torodinium* (20–60 μm). The cosmopolitan genus *Protoperidinium*, although not abundant, was also rather common with a 45% occurrence. The pooled abundance of the most common gymnodinoid dinoflagellates >20 μm, i.e. *Gymnodinium*, *Gyrodinium*, *Cochlodinium* and *Torodinium*, averaged 0.3×10^3 cells l^{-1} and 0.24 mg C m^{-3}, with maxima values of 1.8×10^3 cells l^{-1} and 1.1 mg C m^{-3}. HD <20 μm ranged from 0.05×10^3 to 21×10^3 cells l^{-1} and from 0.01 to 2.8 mg C m^{-3}, averaging 2.9×10^3 cells l^{-1} and 0.4 mg C m^{-3}.

The maximum value of microzooplankton abundance, 23×10^3 cells l^{-1}, was found in early autumn at 35.27°N, 19.31°W, driven by peak abundance of HD <20 μm. In contrast, peak values of biomass were registered under the influence of mesoscale physical features sampled in the spring cruise: 3.9 and 4.2 mg C m^{-3} at stations 19 and

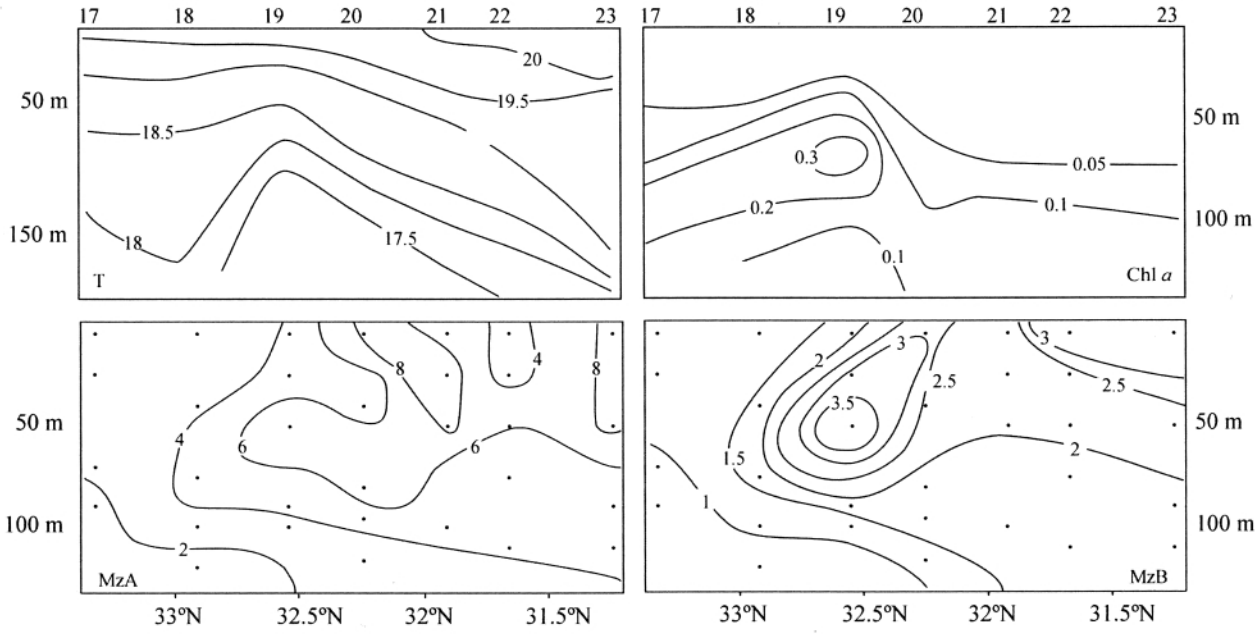

Fig. 4. Contour plots of temperature (T; °C), chlorophyll *a* concentration (Chl *a*; mg m^{-3}), microzooplankton abundance (MzA; cells ml^{-1}) and biomass (MzB; mg C m^{-3}) along the mesoscale eddy Leticia in the spring cruise. Temperature and Chl *a* contours result from CTD profiles.

Table III: Nested ANOVA for total microzooplankton biomass (MzB) in spring

MzB	df	MS	*F*	*P*	% Var
Transect	2	0.148	4.505	0.035	21
Station (transect)	12	0.033	1.862	0.066	13
Sample [station (transect)]	45	0.018			66

%Var: percentage of variance explained by each factor.

33, respectively, i.e. under the influence of eddy Leticia and the GMT. *Leticia* held the highest biomass values for COC >20 μm and large mixotrophic ciliates, whilst the maxima biomass values of gymnodinoids >20 and large thecate dinoflagellates appeared over the GMT.

The relative contribution of HD and COC (Table IV) reflects that HD clearly outnumbered COC. HD <20 μm, mainly composed of small *Gymnodinum* spp. and *Gyrodinium* spp., were the most common cells throughout the study. The overall, average biomass and abundance ratios between HD and COC were 2.4 and 8.1, respectively. These values were higher because of the distinctly high abundance of small dinoflagellates in the early autumn cruise. In addition, HD appeared as the dominant grazers in the microzooplankton because their potential, relative ingestion rate, estimated from cell carbon content and the compilation of I_{max} values included in Hansen *et al.* (Hansen *et al.*, 1997), was 2.7-fold bigger than that of COCs. The HD:COC abundance ratio showed a slightly positive relationship with primary production ($r = 0.47$, $P < 0.0001$).

The variability of COC and HD showed quite similar results: the biomass variability was identical for the subtropical region (CV = 78%). This covariance is reflected in a significant positive correlation for the whole area of study between the biomass of COC and HD ($r = 0.67$, $P < 0.001$). On the other hand, the abundance of COC was less variable than that of HD (61% versus 86%).

The ordination analyses (NMDS) performed to map the inter-relationship among major groups of microzooplankton showed that large mixotrophic ciliates were the organisms of the community that varied most, either considering the whole study area or analysing mesoscale features alone (Figure 5a and b). The stress values, which reflect the lack of fit between the similarity matrix and

Table IV: Relative contribution of HD and COC: ratios of abundance, biomass and estimated ingestion, in the summer and spring cruises

	n	B_r		A_r		EI_r	
		Total	<20 μm	Total	<20 μm	Total	<20 μm
Early autumn	12	13 ± 24	8 ± 13	20 ± 18	30 ± 24	14 ± 23	34 ± 30
Spring	89	1.6 ± 1.2	5.6 ± 4.5	4.4 ± 2.8	7.1 ± 4.8	1.9 ± 1.3	5.7 ± 4.3
Summer	49	1.3 ± 0.8	4.4 ± 4.0	2.8 ± 1.9	4.7 ± 4.2	1.5 ± 0.9	4.1 ± 3.9

B_r = biomass ratio; A_r = abundance ratio; EI_r = ratio of estimated maximum ingestion (I_{max}). The potential, relative ingestion rate of each group was estimated from the cell body carbon according to the allometric function: $\log_{10} I_{max} = 0.84 \log_{10}$ Cell Carbon – 0.29 ($n = 21$, $R^2 = 0.76$, $F = 61.3$, $P < 0.001$). This equation was obtained from the compilation of ingestion data of dinoflagellates and ciliates in Hansen *et al.* (Hansen *et al.*, 1997).

the ordination in two dimensions, were very low in both cases.

DISCUSSION

Herein we have described the variability patterns of the microzooplankton community of an open-ocean, data-deficient oligotrophic region. We showed that, not surprisingly, the oligotrophic north-eastern Atlantic might be regarded as a diluted environment in terms of microzooplankton biomass. However, despite the overall 'blue-water' conditions perceivable in the subtropical gyre, a particularly homogeneous distribution of protistan biomass in the region should not be expected.

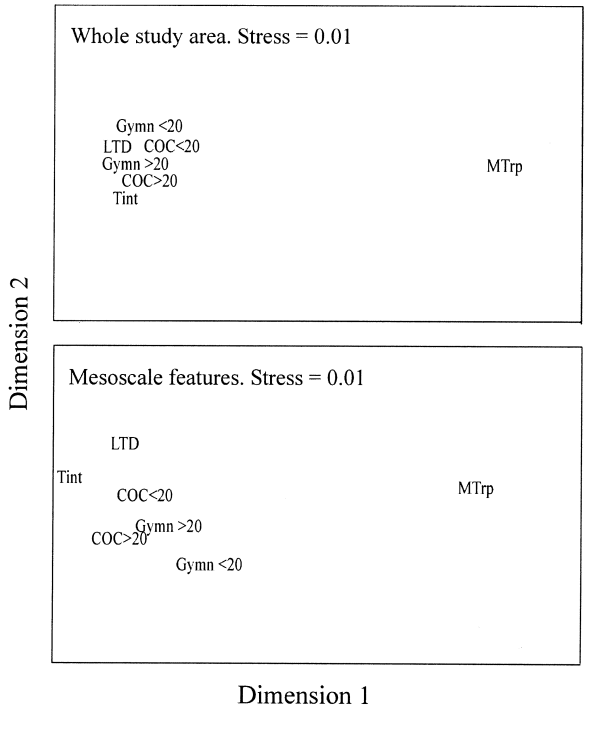

Fig. 5. Non-metric multi-dimensional scaling (NMDS) ordinations for the abundance of the different microzooplankton groups. (top) Subtropical region, all samples clumped together; (bottom) mesoscale features. COC = choreotrich–oligotrich ciliates; MTrp = large mixotrophic ciliates (*Laboea*, *Tontonia*); Tint = tintinnids; Gymn = gymnodinoid dinoflagellates; LTD = large thecate dinoflagellates.

Abundance, biomass and composition

We found widespread dominance of naked ciliates (choreotrichs and oligotrichs) and gymnodinoid dinoflagellates, the major groups of micro-sized phagotrophic protists in marine systems. Despite such dominance, the abundance and biomass values of COC and HD are among the lowest in marine environments (Table V), and are consistent with the overall low biomass of the system. Specifically, the average values of abundance and biomass of HD, and their relationship to ciliate biomass, were very similar to the values reported for the western part of the subtropical gyre, the Sargasso Sea (Lessard, 1991). Conversely, the abundance values for COC and HD were almost an order of magnitude lower than in the neighbouring waters at 47°N (Verity *et al.*, 1993a; Sleigh *et al.*, 1996), and the ones in our own study from stations AMT5-4 and AMT5-5, which were located within the North Atlantic Drift region. The complete community of protist grazers would be fully accounted for by including the heterotrophic nanoflagellates (HNF), combining epifluorescence with common optical microscopic techniques. We found an average value of HNF abundance of 41 cells ml^{-1} in 50 samples from the summer cruise (Quevedo and Anadón, 2001), a quite low value as compared to other marine systems (Fenchel, 1982; Capriulo, 1990), consistent with COC and HD abundances.

We found an overall covariance between ciliates and dinoflagellates, suggesting an underlying equilibrium

Table V: Overview of microzooplankton values in oceanic, low productivity waters

Region	Abundance (cells ml^{-1})	Biomass (mg C m^{-3})	Source
Heterotrophic dinoflagellates			
NE Atlantic, 47–49ºN, spring	2–410	0.1–18.3	Verity *et al.*, 1993b
Equatorial Pacific, Feb.–April	24	1.3	Verity *et al.*, 1996
Subtropical NE Atlantic, spring	0.1–11.6	0.1–2.5	This study
Ciliates			
NE Atlantic, 47ºN, spring	1.1–17.2	–	Verity *et al.*, 1993a
Equatorial Pacific, Feb.–April	0.1	0.1	Verity *et al.*, 1996
Subtropical NE Atlantic, summer	0.2–1.8	0.1–1.0	This study
Subtropical NE Atlantic, spring	0.1–2.1	0.1–2.0	This study
> 20 µm protist			
Sargasso Sea, NW Atlantic, summer	1.1–20.8	0.2–1.7	Caron *et al.*, 1995
Sargasso Sea, NW Atlantic, spring	2.8–27.2	0.2–2.9	Caron *et al.*, 1995
Arabian Sea, intermonsoon	–	0.7–5.9	Stelfox *et al.*, 1999
Arabian Sea, SW monsoon	–	0.4–7–6	Stelfox *et al.*, 1999
Subtropical NE Atlantic, summer	0.2–1.4	0.2–1.6	This study
Subtropical NE Atlantic, spring	0.1–2.2	0.1–2.8	This study
Microzooplankton*			
Arabian Sea, intermonsoon	2.7–18.4	0.4–12.5	Stelfox *et al.*, 1999
Arabian Sea, SW monsoon	2.1–17.6	0.7–6.5	Stelfox *et al.*, 1999
Subtropical NE Atlantic, 37ºN, summer	2.4	1±0.4	Stelfox-Widdicombe *et al.*, 2000
NE Atlantic, 47ºN, spring	~3.3	1.7–4.7	Sleigh *et al.*, 1996
Subtropical NE Atlantic, summer	0.4–11.6	0.2–2.3	This study
Subtropical NE Atlantic, spring	0.2–12.4	0.1–4.2	This study

Only methodologically comparable data were included.
* including ciliates and dinoflagellates <20 µm; ~, value obtained from a figure.

between these two major groups of micro-sized pelagic protists, consistent with theories depicting competition as the major interaction influencing community patterns in low-productivity systems (Bohannan and Lenski, 2000). Jeong (Jeong, 1999) proposed that the ability of HD to maintain higher abundances than ciliates, despite lower growth and ingestion rates, relies on their ability to use a wider range of prey through their diverse feeding mechanisms, and this could be the case in the oligotrophic north-eastern Atlantic. However, another potential contributing factor could be the ability of HD to prey on heterotrophs, including ciliates, reviewed by Jeong (Jeong, 1999). Indeed, understanding the regulation of the interaction between COC and HD in oligotrophic systems with reduced seasonality could be an interesting topic for future surveys in the oligotrophic ocean.

The results of ordination analyses on the co-occurrence of taxa showed that the dominant groups seemed to covary through the study area, and that large mixotrophic ciliates accounted for most of the variability among samples. These ciliates, showing average carbon and volume contents of 6 ng C cell^{-1} and 50×10^3 µm^3 cell^{-1}, would require increased productivity in the system to thrive. This might help to explain their variability, and the highest abundances of *L. strobila*, 0.2×10^3 and 0.06×10^3 cells l^{-1} (~10 and 4 times the mean abundance, respectively) that were found in stations 22 and 23 during the spring cruise, inside the cyclonic eddy Leticia. These values represent increases in the microzooplankton carbon biomass in the region of 1.1 and 0.9 mg C m^{-3}, respectively, a 2-fold increment with respect to the average MzB calculated for the region, 1.1 mg C m^{-3}. High abundance values of 0.08×10^3 cells l^{-1} of *L. strobila* were also recorded in stations along AMT5 and AMT6 cruises located to the south of the study area (M. Quevedo, unpublished data), under the influence of the north-west African upwelling and with higher relative abundance of nanoplankton and diatoms (Marañón

et al., 2001). Therefore, according to our results, the occurrence of large protists in oligotrophic environments might be favoured by nutrient input events, as total nutrient content represents a measure of the carrying capacity of the system (Thingstad, 1998). This result also points to the need for screening a large volume of sea water to assess properly the biomass and composition of microzooplankton in oligotrophic, oceanic systems. The opposite approach, i.e. using typical 50–100 ml samples intended for phytoplankton taxonomy, will avoid detecting these large cells and therefore substantially underestimate their biomass and diversity.

We did not specifically target metazoan microzooplankton in this study because it would require specific sampling techniques including the screening of larger water volumes. Nevertheless, copepod nauplii were the only kind of metazoan encountered in our samples, with 83% occurrence. The average cephalothorax width of these nauplii, the most relevant measure in relation to the efficiency of plankton nets, was 50 μm [± 15 (SD)]. In addition to their high occurrence, which certainly would have increased with larger water volumes (along with statistical consistency of the data), copepod nauplii showed abundances up to 0.08×10^3 individuals l^{-1}, with average abundance of 0.02×10^3 individuals l^{-1}. This is a fairly high value for oligotrophic oceanic waters (Roff *et al.*, 1995), and implies 0.45 mg C m^{-3} according to the average carapace length, i.e. 41% of the average MzB in the region.

Regional characteristics

The values of MzB and MzA in the oligotrophic north-eastern Atlantic were very low, as can be perceived in Table V, and in the compilation by Sherr *et al.* (Sherr *et al.*, 1997). Indeed, overall microzooplankton community values were 5- to 10-fold lower than those reported for the adjacent oceanic waters in the NADR province at 47°N, 20°W (Sleigh *et al.*, 1996). The same paper reports a similar dominance of biomass by dinoflagellates, with HD:COC biomass ratio between 1.9 and 3.4.

We found microzooplankton minima at ~35°N during both the spring and summer cruises. The minima neared the point where the 16°C isotherm intersects the 200 m depth, a proxy for the location of the Subtropical (Azores) Front (Gould, 1985; Fernández and Pingree, 1996). The Azores Front affects several properties of the planktonic community: increased net community production (González *et al.*, 2001) and higher mesozooplankton biomass and copepod ingestion (Huskin *et al.*, 2001) were reported for the same spring and summer cruises included in this study.

The seasonal variability in the microzooplankton community of the subtropical region of the north-eastern Atlantic was rather subtle. The comparison between spring and summer rendered no significant variability in terms of abundance, biomass and dominance of the latter by HD. However, an analysis including the stations of the early autumn cruise located within the subtropical region showed that seasonality might occur in the area, with a notable lift in dominance of biomass by HD. Indeed, the seasonality in the north-eastern Atlantic subtropical area occurs among phytoplankton variables (Longhurst *et al.*, 1995).

Heterogeneity of microzooplankton fields

The variability of microzooplankton fields has been recorded along temporal scales (Strom *et al.*, 1993; Vaqué *et al.*, 1997), but rarely along spatial and vertical scales. We encountered substantial heterogeneity in microzooplankton abundance and biomass, far beyond the heterogeneity in the temperature or Chl *a* fields (Figures 2 and 4). The water column heterogeneity explained a substantial amount of microzooplankton variance, accounting for most of the variance between spring and summer (Table II), and for 66% of the variance of MzB in spring (Table III). This variability arose from samples that are on average 27 m away from each other. Such a distance among samples is situated in the boundary between patches and local communities (Azovsky, 2000), thus the high degree of variability might be a consistent feature of the system. The sampling locations contributed significantly to the spatial heterogeneity of microzooplankton along the 20°W transect in spring and summer (Table II). The deviations from the mean integrated biomass along each particular transect might help to visualize the spatial heterogeneity (Piontkovski *et al.*, 1997) at different length scales. These resulted in a range of biomass variability of 195, 241 and 165 mg C m^{-2} along transects 20°W (1130 km), Leticia (325 km) and GMT (92 km), respectively, suggesting regularities that are perceived when different scales are considered (Azovsky, 2000).

Even when the habitat is homogeneous, and the oligotrophic open ocean could be perceived as more homogeneous than less physically stable systems, populations become scattered over space in a heterogeneous, patchy distribution (Bascompte and Solé, 1998). In the case of the organisms considered here, their generation times, which are in the order of hours to days, allow consideration of fluctuations around an equilibrium as being responsible for such heterogeneity among sampling sites or through the water column. However, our results depict a certain degree of uncoupling with the variation of phytoplankton. Probably the most parsimonious explanation for the uncoupling is the fact that trophic cascades, implicit in the search for correlations among trophic

compartments, seldom occur at the community level (Persson, 1999). Nevertheless, it is tempting to speculate about predation by metazoans to explain some of the variability in microzooplankton, especially in a system where omnivory should be greater than in more productive regions (Roman and Gauzens, 1997). Indeed, we found that integrated mesozooplankton biomass explained 38% of the variance in microzooplankton biomass along spring and summer cruises (Figure 6), and that the copepod maximum and the microzooplankton minimum concurred in the frontal area. However, no causality can be derived from this and other factors should be considered as contributors to the formation of patchiness in oceanic waters, namely the splitting of large eddies into successively smaller ones (Piontkovski *et al.*, 1997). A more finely grained pattern for the aggregation of microzooplankton in comparison to phytoplankton, thus suggesting different aggregation mechanisms or increased resistance to turbulent diffusion, has been reported (Piontkovski *et al.*, 1997), and the subtropical north-eastern Atlantic is particularly rich in mesoscale eddy activity (Gould, 1985; Pingree *et al.*, 1999), a fact that adds feasibility to the latter explanation.

Effect of mesoscale features

We found that the mesoscale instabilities surveyed in the spring cruise had a significant effect, increasing the biomass of the microzooplankton community. This enhanced biomass was not paralleled by an equally distinct increase in abundance, and ordination analyses did not reveal clear differences in composition at the coarse taxonomic level of this study. Therefore, the increased biomass inside mesoscale features pivots on an increment in the carbon content per cell, which amounted to 350, 326 and 281 pg C cell^{-1} (weighted mean among groups) in Leticia, GMT and transect 20°W, respectively. In the case of the GMT, larger grazers might reflect changes in the size structure of the phytoplankton community, which have been reported in some of the several cruises over this seamount (Mouriño *et al.*, 2001). The cyclonic eddy Leticia had a scale of influence of >200 km in the east–west direction, and lasted ~400 days covering a longitudinal range of ~2° (Mouriño *et al.*, 2002). Hence, its effect on microzooplankton fields is substantial in the context of the oligotrophic, subtropical region. It is also conceivable that such effects are shared by similar or even more energetic eddies, which are common in the area and enhance biological productivity in most regions of the North Atlantic (Garçon *et al.*, 2001).

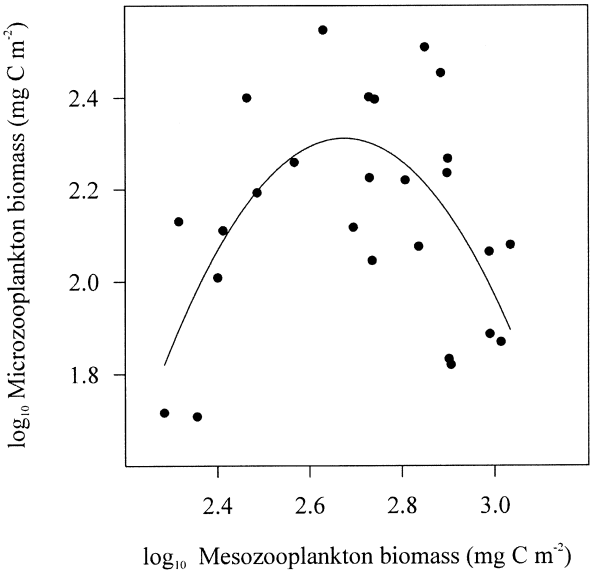

Fig. 6. Quadratic relationship between integrated micro- and mesozooplankton biomass in spring and summer cruises. Mesozooplankton biomass data can be found in Huskin *et al.* (Huskin *et al.*, 2001). Fit: $\log_{10} MzBI = 2.98 - 0.25\log_{10} MesoBI - 3.23\ (\log_{10} MesoBI - 2.71)^2$. Goodness of fit: $r^2 = 0.39$, $F = 7.34$, $P = 0.003$, $n = 26$.

Since enhanced biomass of grazers should follow an increase in resource stocks, simple reasoning allows a crude estimation of the magnitude of such an increase in terms of primary production: the differences between average microzooplankton biomass inside Leticia and the area outside mesoscale features was 0.9 mg C m^{-3}. Assuming a gross growth efficiency of microzooplankton of 40% (Caron and Goldmann, 1990), an increment of ca. 1.5 mg C m^{-3} in the phytoplankton standing stock would be required to sustain the above-mentioned microzooplankton biomass, a value that is highly consistent with the actual change in phytoplankton fields across *Leticia* (Mouriño *et al.*, 2002). Identical calculations would set the value of increase in phytoplankton carbon at ~1 mg C m^{-3} for the GMT. Of course, these values assume herbivory as the sole source of carbon for microzooplankton, which certainly is not the case, but also come from existing significant differences among transects. If the diluted nature of the system and the *P*-level obtained in the Tukey test ($P = 0.048$) are taken into account, it might be deduced that 1 mg C m^{-3} should be very close to the required increment in phytoplankton carbon for this change to be perceived in microzooplanktonic fields.

Conclusions

In the highly diluted environment of the subtropical north-eastern Atlantic Ocean, where Chl *a* concentration averages 0.1 mg m^{-3}, we found a constant dominance of HD and aloricate ciliates, and showed that mesoscale features had a significant enhancing effect over microzooplankton biomass through an increase in the size of

cells. The stocks of protistan microzooplankton, although reduced according to the oligotrophic nature of the system, showed great patchiness and complex patterns of distribution, which implies that direct scaling between the biomass of microzooplankton and that of phytoplankton should only be expected if the area of study comprises enough environmental variability, beyond that found in the oligotrophic gyre.

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