JOURNAL OF PLANKTON RESEARCH | VOLUME 23 | NUMBER 7 | PAGES 671–691 | 2001

Mesozooplankton distribution and copepod grazing in the Subtropical Atlantic near the Azores: Influence of mesoscale structures

I. HUSKIN, R. ANADÓN, G. MEDINA[1], R. N. HEAD[1] AND R. P. HARRIS[1]

UNIVERSITY OF OVIEDO, DEPTO B.O.S. C/CATEDRÁTICO RODRIGO URÍA, S/N 33071 OVIEDO, SPAIN AND [1]PLYMOUTH MARINE LABORATORY, PROSPECT PLACE, THE HOE, PLYMOUTH PL1 3DH, UK

Mesozooplankton distribution and copepod grazing were investigated in the Subtropical Atlantic Ocean near the Azores during the AZORES I (August) and II (April–May) cruises. Mesozooplankton biomass and abundance remained low throughout the region, but significant increases were found related to the presence of the Azores Front. The Azores Front also exhibited maximum values of copepod community ingestion, reaching 250 mg C m^{-2} ingested daily. This increase in ingestion was related to increases in copepod abundance, but not in copepod gut contents. No relationship was found between gut contents, or ingestion, and phytoplankton biomass or production. Daily cycles were found in copepod gut contents, being higher during the night, but not in copepod abundance. Multidimensional scaling analysis revealed differences in copepod taxonomic composition between both sides of the front. During spring, daily copepod ingestion represents an average of 6% of the integrated chlorophyll (Chl) a concentration and 22% of the primary production. These percentages increase to 15% of Chl and 61% of production if we only consider large (>2 μm) phytoplankton. No clear influence of the cyclonic eddy LETICIA was found in mesozooplankton biomass or grazing. A significant effect of the Great Meteor Tablemount was found in copepod abundance and grazing, with higher values located west of the mount.

INTRODUCTION

Zooplankton grazing, which controls phytoplankton populations (Banse, 1994) and mediates vertical carbon flux through faecal pellet sinking (Noji, 1991), has been widely studied in the last decades, as an important part of the so-called biological pump. However, most of these investigations have been carried out in coastal and productive areas [e.g. (Morales *et al.*, 1991; Pakhomov and Perissinotto, 1997; Gowen *et al.*, 1999)], while the vast oligotrophic areas of the open ocean have been much less explored (Dam *et al.*, 1995; Zhang *et al.*, 1995), especially in the Atlantic Ocean. This is an important lack of information considering that these oligotrophic regions contribute up to 80% of the global ocean production and 70% of the total export production (Karl *et al.*, 1996). These areas are usually characterized by low levels of biological productivity, but the presence of hydrodynamic features such as fronts (Le Fèvre, 1986), eddies (Falkowski *et al.*, 1991) or topographic features like seamounts (Boehlert and Genin, 1987) has been suggested to sustain enhanced levels of plankton biomass and production.

The European Union CANIGO project (Canary Islands Azores Gibraltar Observations) was developed to study the most relevant oceanographic features and associated biological processes in the area from the Canary Islands to the Azores, between 20 and 40°N. The most remarkable hydrographic feature in this region is the Azores Current (AC), which transports water eastwards and southwards from 35°N 40°W (Klein and Siedler, 1989) as an extension of the Gulf Stream, and the associated Azores Front (AF) lying between 35 and 36°N and separating Western Atlantic Water (warmer and saltier) to the south from Eastern Atlantic Water (cold and fresher) to the north. Owing to the large spatial extension of this frontal area (18–35°W), any linked biological effect [such as those reported by Fernández and Pingree (Fernández

© Oxford University Press 2001

and Pingree, 1996) or González *et al.* (González *et al.*, 2001)] becomes quantitatively important within the context of the North Atlantic Subtropical gyre, especially considering that this area has been proposed as an important source of mesoscale eddies (Gould, 1985), whose effect in enhancing biological activity has been fully reported (The Ring Group, 1981; Angel and Fasham, 1983).

The main objective of this paper is to provide an overall description of mesozooplankton distribution and copepod grazing in an oligotrophic environment during two different seasons characterized by maximum thermal stratification (midsummer) or maximum vertical homogeneity (early spring). We also examine the influence of three different mesoscale features (the AF, a cyclonic eddy and the Great Meteor Tablemount) on those parameters.

METHOD

A total of 36 and 35 zooplankton stations, respectively, were sampled during August 1998 (AZORES I) and May 1999 (AZORES II) in the CANIGO area onboard B.I.O. 'Hespérides' (Figure 1). During AZORES I, sampling was located in three quasimeridional sections, transverse to the AC. The easternmost transect (TA1), also sampled in AZORES II (TA2), was coincident with the track of Atlantic Meridional Transect (AMT) cruises in this region. Twice a year (spring and autumn), and within the AMT programme, the British Antarctic Survey (BAS) vessel RRS 'James Clark Ross' covers the transect Grimsby (UK)–Falkland Islands in her passage to and from Antarctica, providing an opportunity to develop a programme for investigating biological processes in the Atlantic Ocean over broad spatial scales (Robins and Aiken, 1996). We have included data from AMT4 and AMT5 cruises in our study to obtain a better description of seasonal variation in the area. Intensive sampling across the AC was carried out in the westernmost transect (TC1) from AZORES I (Figure 1).

During AZORES II, sampling was located in three main transects (Figure 1). Besides the previously mentioned TA2, two different mesoscale structures were sampled during this cruise: the cyclonic eddy named LETICIA (TC2) and the Great Meteor Tablemount (GMT, TD2).

Temperature and salinity profiles were obtained at every station, using a Neil Brown Mark III CTD attached to a rosette equipped with 12 l Niskin bottles. Water samples were collected with Niskin bottles at 5–7 depths on each station. Chlorophyll (Chl) *a* concentration was determined with a SAFAS flx spectrofluorometer calibrated with a pure Chl *a* extract obtained by HPLC, after extraction with 90% acetone overnight at 4°C. No reliable Chl *a* data are available from AZORES I, so only data from AZORES II are reported. Primary production was measured by ^{14}C incubation. Water samples were inoculated with 555 kBq $NaH^{14}CO_3$, incubated for 6.5–7.5 h, filtered onto polycarbonate filters, exposed for 12 h to concentrated HCl fumes to remove inorganic ^{14}C, and counted in a Beckman liquid scintillation counter after addition of 3.5 ml of scintillation cocktail. Primary production was only measured in AZORES II, at seven stations from TA2 (1, 2, 4, 6, 8, 10 and 11), three stations from TC2 (18, 20 and 23) and three stations from TD2 (31, 32 and 34).

At each zooplankton station, two double WP-2 (57 cm diameter and 200 μm mesh) net casts were deployed to 200 m. Tow speed was 1 m s^{-1}. One net was used for grazing experiments and the other for biomass and taxonomic composition. Three (AZORES I) and two (AZORES II) 24 h stations (Figure 1) were used in order to study daily cycles in copepod abundance and ingestion. At these stations, sampling was carried out every ~4 h, for a final number of 4–6 samples at each location. The ship's position was maintained by following a drifting sediment trap.

Mesozooplankton biomass and composition

After the tow, the net was gently rinsed, cod end contents poured into a 10 l bucket filled with 0.2-μm-filtered surface sea water and screened through 1000, 500 and 200 μm meshes to divide them into 200–500, 500–1000 and >1000 μm size fractions. For biomass measurements, each size fraction obtained from the first cod end was filtered onto 47-mm-diameter GF-F pre-combusted filters, maintained at 60°C for 48 h and placed in boxes containing silica gel for further determination of C content (Perkin-Elmer 2400 CNH analyser).

The sample from the second cod end was preserved with borax-buffered formalin (4%) for subsequent taxonomic analysis. Zooplankton were determined to the level of species or genus in the case of copepods in 23 samples from AZORES I. Thirteen of these samples correspond to the three 24 h stations located at TA1, while the other 10 samples correspond to stations located in TC1. At the rest of the stations, samples were determined to the level of main taxonomic groups.

To compare communities from different locations, multi-dimensional scaling (MDS) analysis was carried out with copepod species abundance, using the Bray–Curtis index to create the similarity matrix. Analysis of similarity between groups obtained in MDS and identification of main species in determining observed grouping were performed with ANOSIM and SIMPER modules of the PRIMER software package.

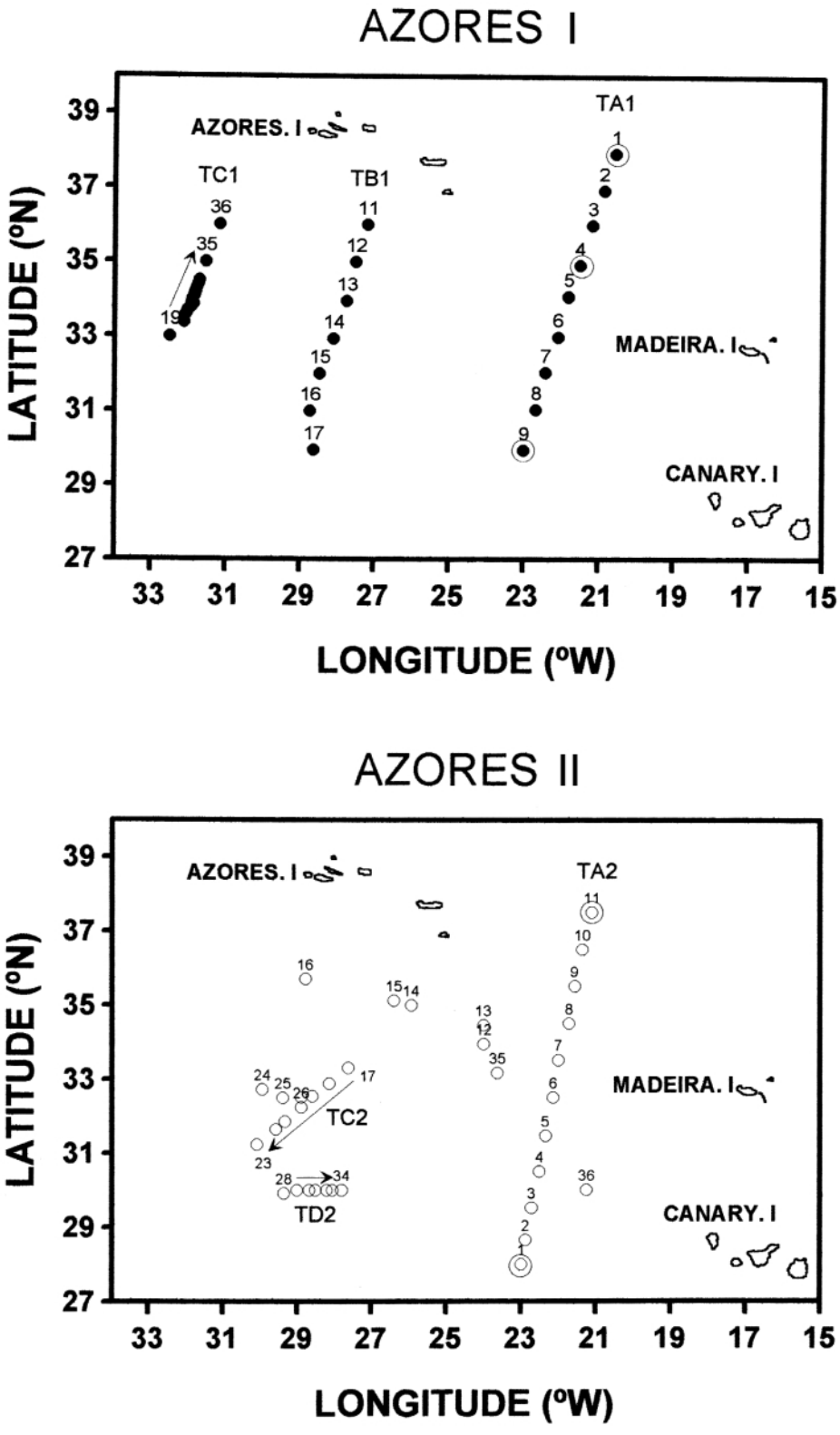

Fig. 1. Position and number of stations and transects sampled during AZORES cruises (24 h stations circled).

Copepod grazing

Copepod grazing was estimated using the gut fluorescence technique (Mackas and Bohrer, 1976). The content of the net (not rinsed) was immediately screened into the same three size fractions as for biomass and abundance. Subsamples from each size fraction were filtered onto shark skin filters, stored in Petri dishes and immediately frozen at –70°C in the dark for further gut content analysis.

For gut evacuation experiments, animals from each size fraction were placed in a cool box containing filtered (0.2 μm) surface sea water from the same station, and kept in darkness at surface water temperature. The copepods were subsampled every 5 min during 30 min, filtered onto shark skin filters and frozen as above.

Twenty-five copepods for the large, 50 for the medium and 75 for the small fraction were picked from the filters using jeweller's forceps under a microscope with dim light. No attention was paid to copepod species or development stage. One to three replicates were collected from each fraction. The copepods were placed in 20 ml glass vials with 5 ml of acetone (90%) and extracted for 24 h at 4°C in the dark. The fluorescence of the sample was measured using a Turner fluorometer before and after acidification, and expressed as nanograms of Chl *a* equivalents. Owing to the wide range of pigment destruction reported in the literature (0–100%), we have chosen not to apply any conversion factor and consider our estimates to be conservative values.

Gut evacuation data were fitted to an exponential decay model (Dagg and Wyman, 1983):

$$G_t = G_0 \times e^{-kt}$$

where G_0 is the initial gut content, G_t is the gut content at time t and k is the instantaneous gut evacuation constant rate. Individual ingestion rates for each size fraction were obtained by multiplying the initial gut content by the gut evacuation rate. Community ingestion rates were calculated by multiplying individual rates by copepod abundance, and were compared with integrated Chl *a* standing stock and primary production to estimate grazing impact. A C:Chl index of 60 was used.

RESULTS

Hydrography

Position of the AF

The vertical distribution of temperature, salinity, Chl *a* concentration and primary production across the AF is shown in Figure 2. The position of the AF can be identified by the outcropping of isotherms and isohalines observed at different locations along transects TA1, TA2 and TC1. During AZORES I, uplifting of isolines is located at 34°N in TC1 and at two locations in TA1: ~36°N and 32–33°N. Pérez, F. (unpublished) proposed both locations as two branches of a meandering front. AF features are detected below 50 m. Surface temperature ranges between 23.1 and 23.8°C, and between 26.1 and 26.4°C at TA1 and TC1, respectively, while surface salinity varies from 36.18 to 37.18 and from 36.42 to 36.67. During AZORES II (TA2), we can also observe two elevations of isolines: at 31–32°N and 36°N. González *et al.* (González *et al.*, 2001) located the AF at 36°N, while the outcropping of isolines at 31–32°N possibly reflects the signature of another mesoscale feature (not identified) linked to the AC. Surface temperature and salinity increase southwards from 17.34 to 19.79°C and from 36.43 to 36.99, respectively.

Chlorophyll *a* and production data are only available from AZORES II. The maximum integrated Chl *a* concentration along TA2 was found at 32.5°N, reaching 20 mg m^{-2}, while maximum production (~200 mg C m^{-2} day^{-1}) was located at 32.5 and 36.5°N.

Eddy and GMT

A cyclonic eddy named LETICIA is clearly identified by the elevation of isotherms and isohalines detectable below 50 m, between 32 and 33°N at transect TC2 (Figure 3). At 200 m depth, water at the core of the eddy (32.35°N) is colder and fresher than that outside the eddy. The integrated Chl *a* concentration along the transect ranged between 10 and 19 mg m^{-2} with maximum values at two stations inside the eddy. Primary production ranged between 182 and 208 mg C m^{-2} day^{-1}. A full description of LETICIA hydrography is reported in González *et al.* (González *et al.*, 2001) and Mouriño, B. (unpublished).

The presence of the Great Meteor Seamount (located at 30°N 28.5°W) is reflected by oscillations of isotherms and isohalines at 28.3°W in transect TD2. No clear influence of the mount was found in integrated Chl *a* concentration. Only production data from stations located east of the mount are available, with a maximum value of 250 mg C m^{-2} day^{-1} just over the mount.

Mesozooplankton taxonomic composition

A total of 26 main groups and 130 copepod taxa were identified. Copepods were the most abundant group in all the samples, representing 91.3 ± 3% and 88.7 ± 4.4% of total mesozooplankton abundance on AZORES I and AZORES II, respectively. During AZORES I, copepod abundance was dominated by small calanoid copepodites, *Clausocalanus* spp., *Oncaea* spp., *Corycaeus* spp. and *Oithona helgolandica*, accounting for 60% of total abundance.

Three main groups of AZORES I samples were identified by MDS analysis ($P < 0.01$, stress = 0.07)

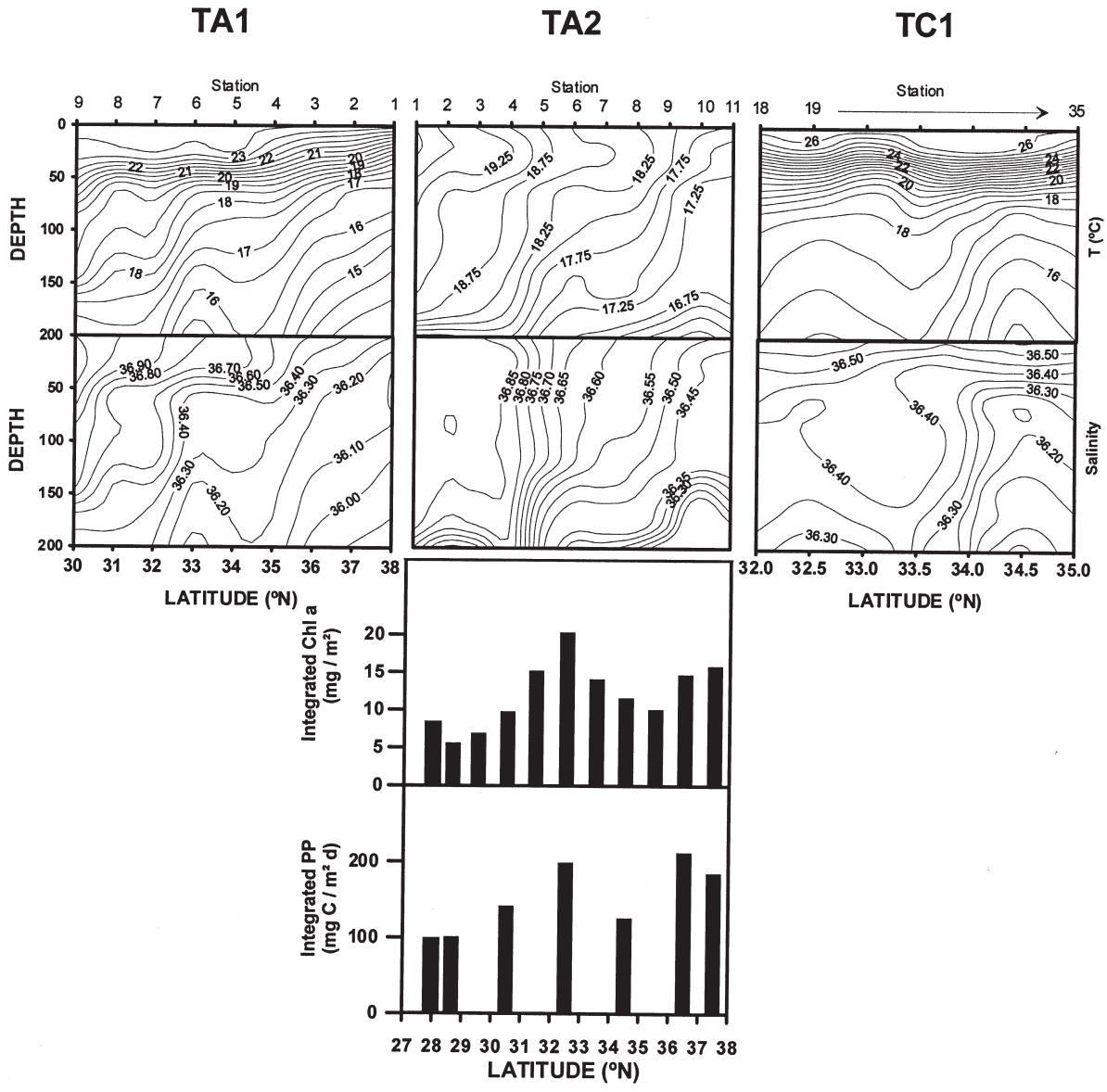

Fig. 2. Vertical profiles of temperature and salinity in transects TA1, TA2 and TC1. Integrated Chl concentration and primary production in transect TA2.

(Figure 4). The first group is composed of all the samples from the TA1 northernmost station (Station 1), the second group is composed of samples from the TA1 southernmost station (Station 9) and the third group is composed of samples obtained close to the AF (Stations 4, 21, 24, 26, 28, 30, 32 and 34). Station 31 was not included in any of the groups.

Table I show the most important copepod taxa in determining the grouping obtained in MDS analysis, as well as their average abundance in each group and the contribution to the observed dissimilarity between groups. A higher abundance for most of the taxa (except *Clausocalanus* spp., *Ctenocalanus vanus* and *Pleuromamma* spp.) in the southern station separates it from the northern one (Table I). In the same way, stations located away from the AF present a lower abundance of animals than those close to the front, except for *O. helgolandica*, *Paracalanus parvus* and *Calanus* spp., which reached maximum abundance in the southern station.

Daily cycles

Daily variation in size-fractionated copepod gut contents and abundance in the 24 h stations is shown in Figures 5 and 6. Station 4 from AZORES I has not been included

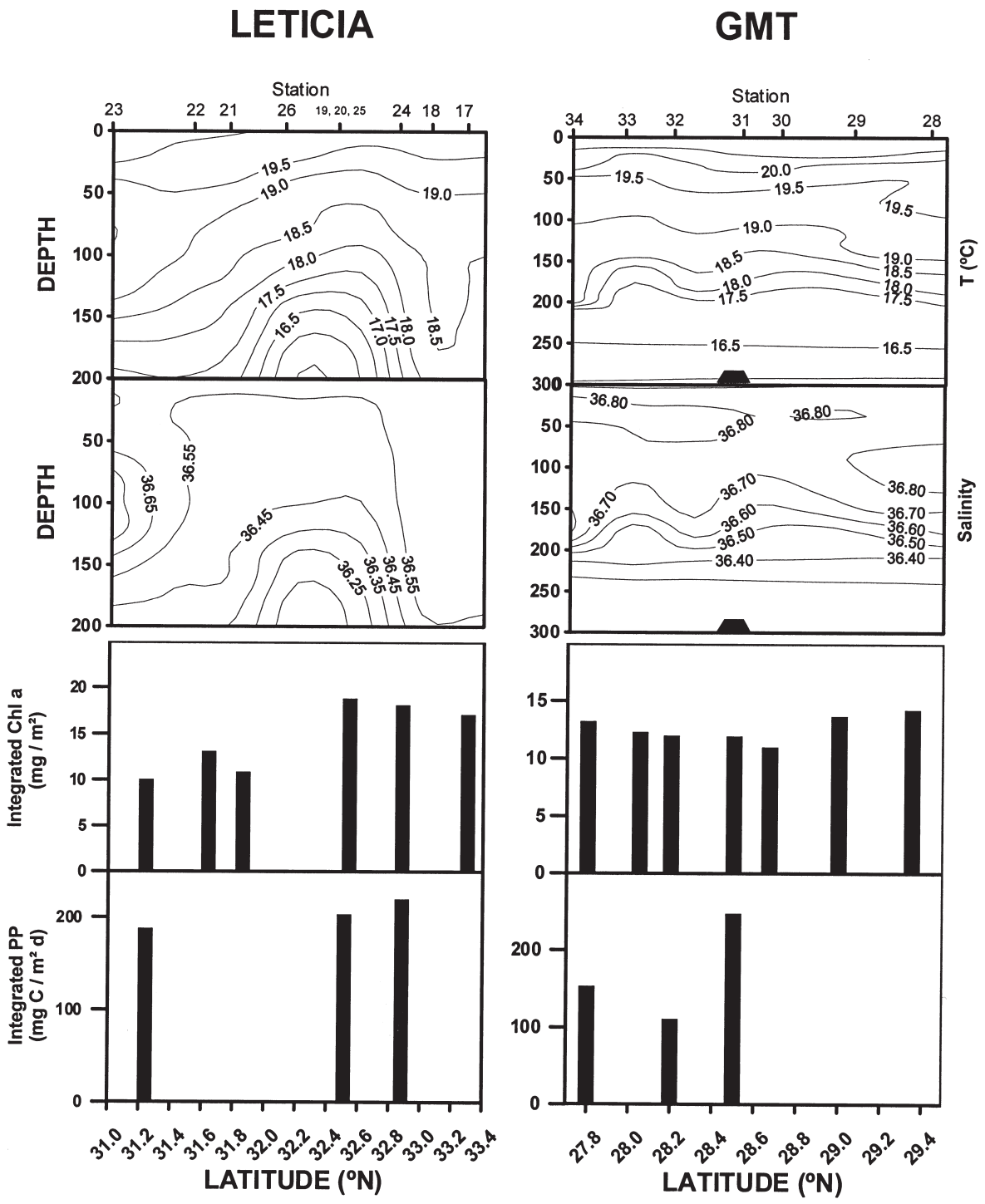

Fig. 3. Vertical profiles of temperature and salinity, integrated Chl concentration and primary production in transects TC2 (LETICIA) and TD2 (GMT).

due to the low number of samples (three) obtained. We have considered as day stations those sampled between 7.30 a.m. and 20.00 p.m., coinciding with observed sunrise and sunset during both cruises. Copepod gut contents presented a clear daily pattern at all the stations and for all the size fractions, with peaks of maximum contents during night and pooled (all stations from both cruises) night values higher than daytime ones (ANOVA,

Table I: Most important copepod taxa in determining the grouping obtained in MDS analysis, average abundance in each group and contribution (%) of each taxon to the observed dissimilarity between groups

	Abundance (no. m^{-2})					Abundance (no. m^{-2})					Abundance (no.$^{-2}$)			
	North	South	%	%Cum		Front	North	%	%Cum		Front	South	%	%Cum
Oithona helgolandica	1137	4240	14.28	14.28	Small calanoid copepodites	9035	4458	12.81	12.81	Small calanoid copepodites	9035	5006	13.09	13.09
Corycaeus spp	958	3175	10.46	24.74	*Clausocalanus* spp.	7159	2278	11.58	24.39	*Clausocalanus* spp.	7159	2082	13.09	26.17
Paracalanus parvus	48	1596	7.59	32.33	*Corycaeus* spp.	4774	958	9.7	34.09	*Oncaea* spp.	5787	2633	8.51	34.68
Calanus spp.	236	1556	6.29	38.62	*Oncaea* spp.	5787	1843	9.45	43.55	*Corycaeus* spp.	4774	3175	6.27	40.95
Small calanoid copepodites	4458	5006	5.71	44.33	*Oithona helgolandica*	3528	1137	6.11	49.66	*Oithona helgolandica*	3528	4240	5.94	46.88
Oncaea spp.	1843	2633	5.33	49.66	*Mecynocera clausi*	2087	57	4.74	54.4	*Ctenocalanus vanus*	2296	545	4.58	51.46
Lucicutia spp.	10	1103	4.98	54.64	*Calanus minor*	1836	57	4.69	59.09	*Calanus minor*	1836	342	4.23	55.7
Clausocalanus spp.	2278	2082	4.11	58.75	*Calocalanus stylirremis*	1844	172	3.96	63.04	*Ichniocalanus* spp.	1736	258	3.79	59.48
Ctenocalanus vanus	1292	545	4.06	62.81	*Ichniocalanus* spp.	1736	6	3.78	66.82	*Calocalanus stylirremis*	1844	930	3.61	63.09
Pleuromamma spp.	974	559	3.7	66.51	*Ctenocalanus vanus*	2296	1292	3.52	70.34	*Mecynocera clausi*	2087	800	3.57	66.67
Mecynocera clausi	57	800	3.53	70.03	*Calanus* spp.	1381	236	2.71	73.05	*Paracalanus parvus*	721	1596	3.47	70.13
Calocalanus stylirremis	172	930	3.44	73.47	*Lucicutia* spp.	1130	10	2.7	75.76	*Pleuromamma* spp.	1416	559	2.82	72.95
Haloptilus longicornis	5	637	2.86	76.33						*Calanus* spp.	1381	1556	2.72	75.67

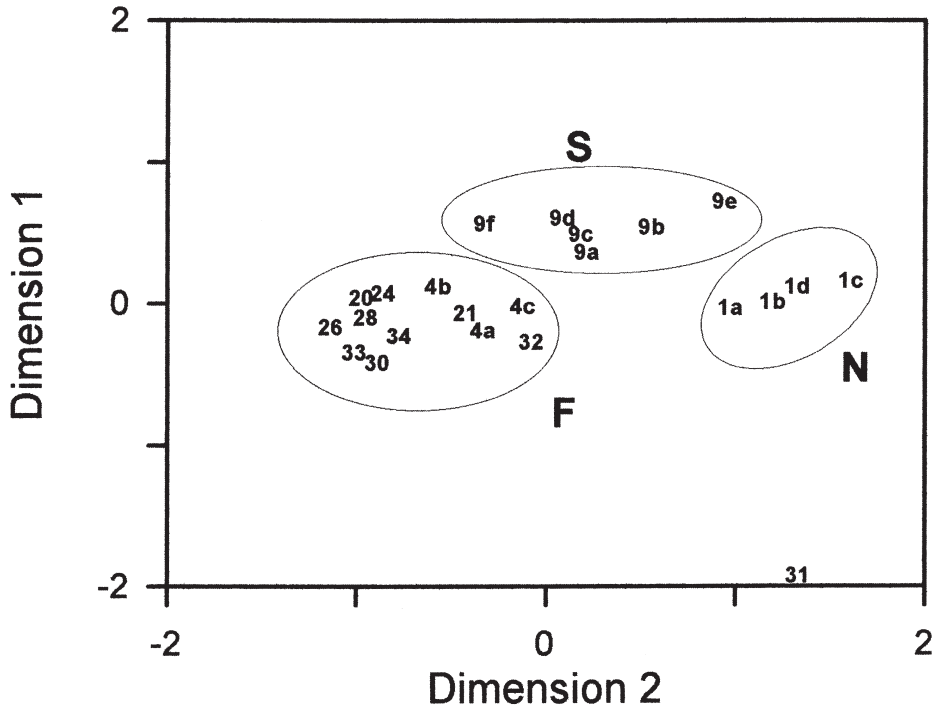

Fig. 4. MDS ordination of the 23 taxonomic samples obtained during AZORES I, based on copepod abundance and Bray–Curtis similarities (stress = 0.07). Labels correspond to the station number. a–f correspond to the different samples obtained at the 24 h stations. Groups are statistically different at $P < 0.01$. F, frontal samples; N, north of the front; S, south of the front.

$P < 0.05$) in all size fractions. Average values for day stations were 0.15, 0.34 and 2.44 ng Chl *a* equivalents per copepod in the small, medium and large size fractions, while in night stations they were 0.21, 0.6 and 4.64 ng Chl *a* equivalents per copepod. On the other hand, copepod abundance does not show any clear pattern of variation, with maximum values located at both night and daytime, and no significant day–night differences in any size fraction.

Gut evacuation rates

A final number of 13 and 15 gut evacuation curves were obtained in AZORES I and AZORES II, respectively (Table II). Gut evacuation rates were not influenced by body size, time of day, latitude or season. No significant differences in the slopes of the curves were observed on either cruise (test of parallelism, $P > 0.1$), averaging 0.029 ± 0.011 (AZORES I) and 0.032 ± 0.008 min^{-1} (AZORES II). These average values were used for further calculations of copepod ingestion rates in each cruise.

Mesozooplankton distribution and grazing across the AF

The latitudinal distribution of abundance and feeding across the AF is shown in Figures 7–9. In order to correct the effect of daily cycles, day and night stations were considered independently. TA1 (Figure 7) presents higher mesozooplankton biomass at 33°N (Station 6) and 36°N (Station 3), coinciding with the position of the front (data on the large fraction are not available at Station 3), and similar increases (but only at Station 3) are also observed in copepod abundance and gut contents, although in the large size fraction gut contents were higher north of the front. The copepod community ingestion rate reaches its maximum value (~80 mg C m^{-2} day^{-1}) at 36°N (Station 3), while remaining <20 mg C m^{-2} day^{-1} along the rest of the transect. No apparent influence of AF (Stations 26–29) on either biomass or abundance is observed in the small-scale sampling performed along TC1 (Figure 8). However, copepod gut contents (especially in the large fraction) in this transect were higher than in TA1, which translates into higher ingestion rates: ~50 mg C m^{-2} day^{-1}.

During the AZORES II cruise (transect TA2; Figure 9), the AF was sampled at night (Station 9), showing significant increases in biomass, copepod abundance and ingestion, which reached 275 mg C m^{-2} day^{-1} at this location (~35.5°N). Copepod gut contents and ingestion were not related to Chl *a* concentration or primary production on any of the cruises.

Table III shows the average values of selected

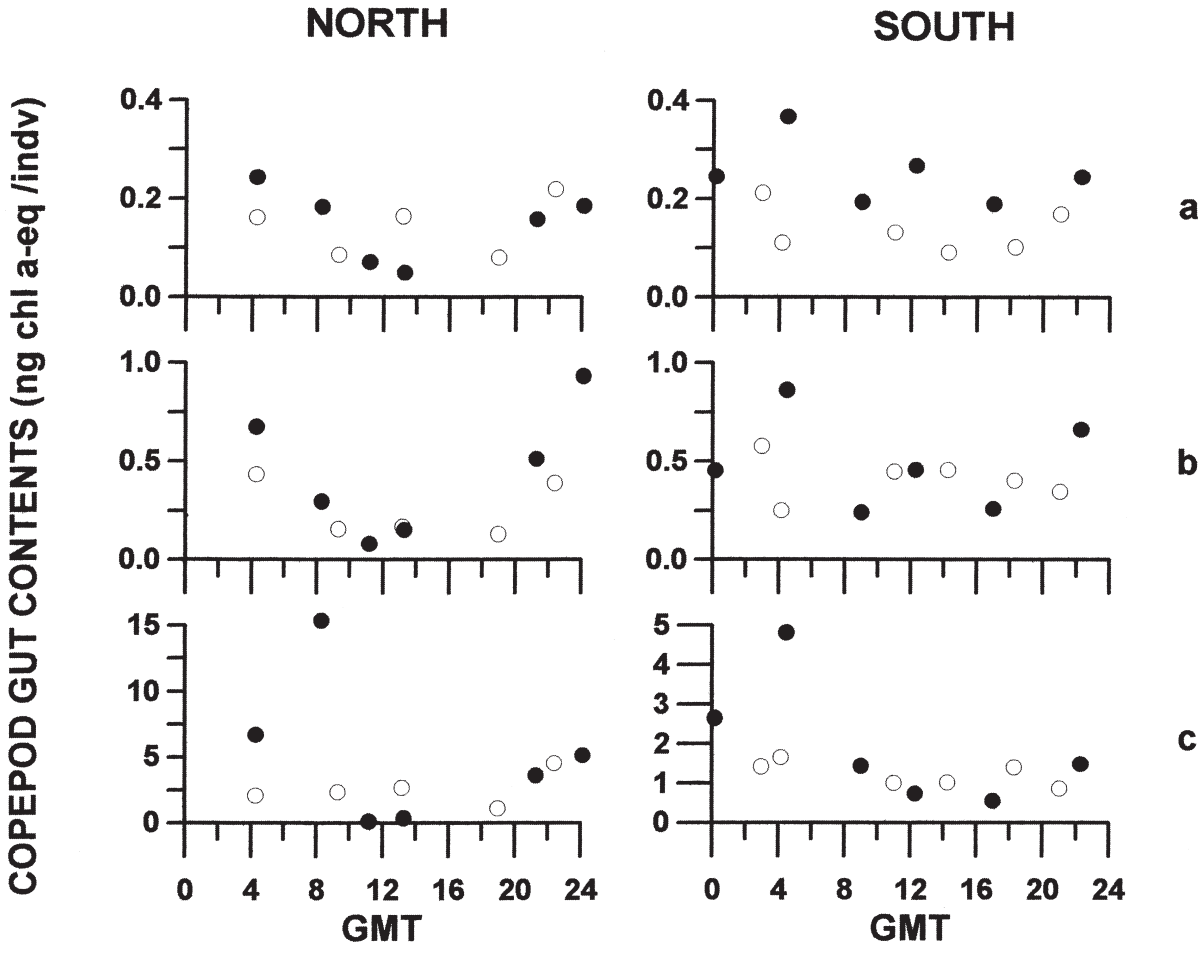

Fig. 5. Daily variation in size-fractionated (a, small; b, medium; c, large) copepod gut contents in northernmost and southernmost stations of transect A in AZORES I (●) (north, station 1; south, station 9) and AZORES II (○) (north, station 11; south, station 1).

parameters for stations located within and outside the front during AZORES I. All parameters studied showed higher values at the frontal stations. Differences were significant (ANOVA, $P < 0.05$) for mesozooplankton biomass and copepod abundance in the small, medium and total size fractions, and for ingestion in the small and total fractions.

During AZORES II (TA2), observed ingestion rates translate into low percentages of total Chl *a* standing stock ingested daily by copepods. Percentages ingested are in general <10%, except at the AF (Station 9), where it reaches 45%. Grazing impact increases if we only consider large phytoplankton (>2 μm). No fractionated Chl *a* is available at the frontal station, but in the rest of the transect copepod ingestion represents between 5 and 40% of the Chl *a* in this size fraction. Copepods ingest daily between 17 and 38% of total primary production in this transect, increasing up to 28–153% of large phytoplankton production.

Influence of the cyclonic eddy LETICIA

There was no influence of the eddy on the distribution and grazing of copepods compared to the adjacent stations (Figure 10). If we compare the eddy with all the stations located outside the eddy and not influenced by other mesoscale structures (Table III), mesozooplankton biomass, copepod abundance and total copepod ingestion seem to be higher outside the eddy, but differences are not significant (ANOVA, $P > 0.05$). Daily copepod ingestion inside the eddy represents 2.6–5.48% of total Chl *a* standing stock and 8–19% of primary production, increasing to 9–18 and 19–52% of large cell Chl *a* and production, respectively.

Influence of GMT

Figure 11 shows a general tendency of increasing biomass, copepod abundance, gut contents and ingestion from east to west of the GMT (TD2) (except the high

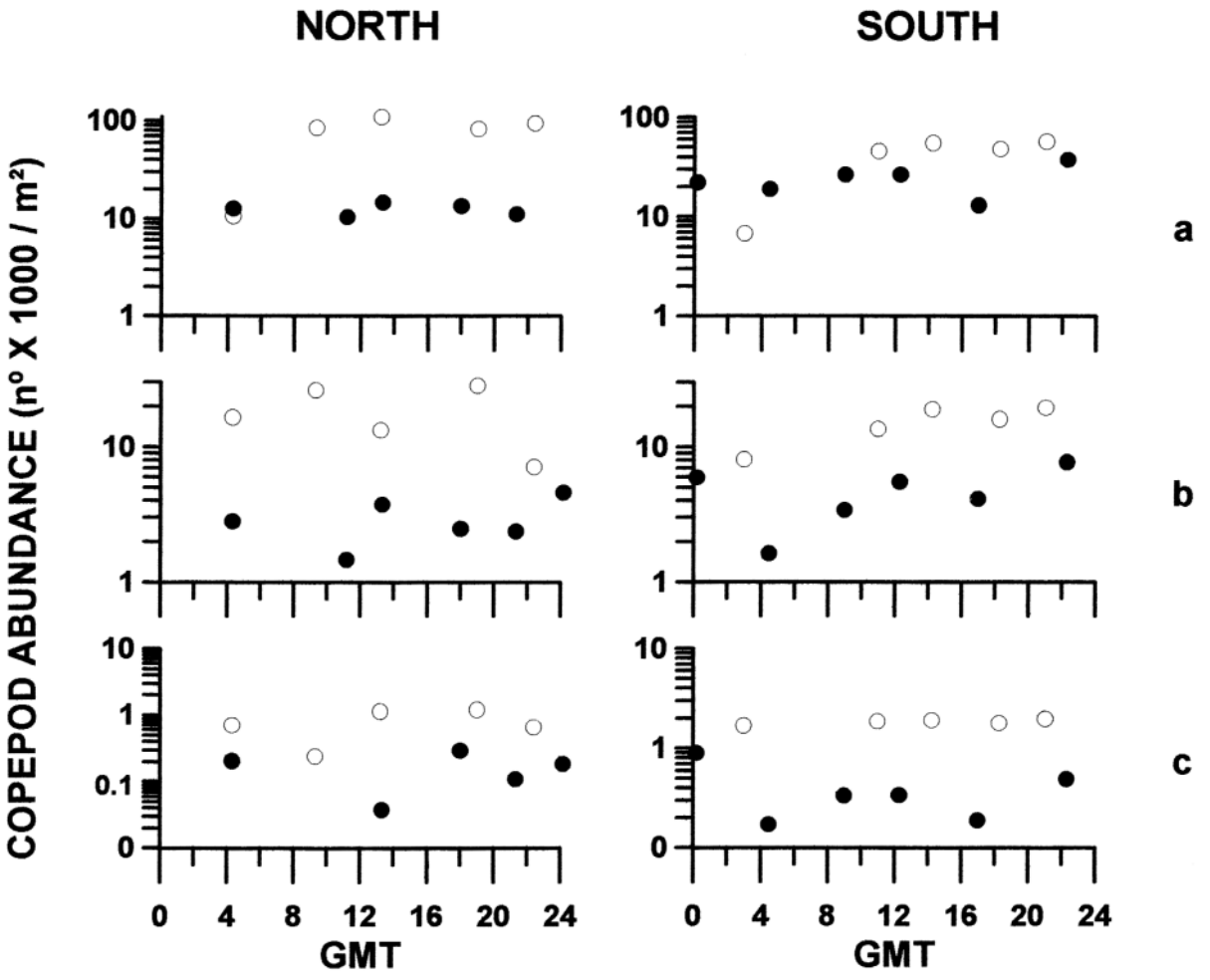

Fig. 6. Daily variation in size-fractionated (a, small; b, medium; c, large) copepod abundance in northernmost and southernmost stations of transect A in AZORES I (●) (north, station 1; south, station 9) and AZORES II (○) (north, station 11; south, station 1).

values of gut contents found at the easternmost station) with no remarkable features above the seamount (located at 28.5°W). In general, higher average values were found on the west side (Table III), presenting significant (ANOVA, $P < 0.05$) differences in large biomass, abundance in all sizes, gut contents in the small fraction, and community ingestion in the small, medium and total size fraction. Ingestion along TD2 translates into 2.8–9.6% of Chl *a* standing stock and 8–23% of primary production. Percentages increase to 8–10.5% of Chl *a* and 24–50% of production by large phytoplankton cells.

Seasonal variation along transect A

Mesozooplankton distribution and grazing at different seasons (Table IV) were compared using data from transect A on four different cruises: AZORES II (April 1999), AMT4 (May 1997), AZORES I (August 1998) and AMT5 (September 1997). Because of the time limitations of the AMT cruises, with no night sampling, only day samples from AZORES cruises were considered. Higher mesozooplankton biomass and copepod abundance in all the size fractions were found on AZORES II, but no difference was found in gut contents. Community ingestion rates also showed higher values on AZORES II for the large, medium and total fractions, while no differences between cruises were found in the small fraction.

DISCUSSION

The gut fluorescence technique has been the most popular and widely used procedure to estimate *in situ* zooplankton grazing rates in the last decades. However, its accuracy is open to discussion because of its assumption

Table II: Latitudinal variation in size-fractionated gut evacuation rates (k in min^{-1}) obtained in AZORES cruises, statistical adjustment to exponential model (P), number of data in each curve (n) and experimental temperature (T)

	Azores I							Azores II					
Latitude (°N)	Size	r^2	*n*	*P*	*k*	*T*	Latitude (°N)	Size	r^2	*n*	*P*	*k*	*T*
31	s	0.72	18	0.0004	0.037	24	28.6	m	0.52	10	0.012	0.044	19.5
31	m	0.55	14	0.0051	0.024	24	28.6	s	0.43	15	0.008	0.024	19.5
30	s	0.47	17	0.002	0.037	24.2	30.5	m	0.73	14	0	0.029	19.3
30	m	0.31	14	0.07	0.018	24.2	30.5	s	0.66	15	0	0.043	19.3
30	l	0.29	14	0.05	0.028	24.2	30	m	0.47	13	0.02	0.037	20
36	l	0.57	8	0.08	0.053	25	30	s	0.25	19	0.034	0.013	20
33	s	0.59	17	0.00029	0.027	26.4	31.25	m	0.69	15	0	0.026	20.5
33	m	0.72	10	0.015	0.032	26.4	31.25	s	0.73	16	0	0.037	25.0
32	s	0.15	21	0.08	0.009	26.3	32.5	m	0.54	13	0.015	0.03	19.6
32	m	0.32	14	0.042	0.024	26.3	32.5	s	0.43	15	0.011	0.025	1.6
35	s	0.24	18	0.005	0.026	25.9	30	s	0.57	17	0	0.042	20
36	l	0.89	10	0.004	0.044	25.6	37.5	m	0.25	20	0.021	0.03	17.4
36	m	0.31	16	0.023	0.02	25.6	37.5	s	0.56	21	0	0.038	17.4
							33.3	s	0.51	19	0.001	0.031	19.6
							37.5	l	0.7	11	0.001	0.043	17.4
Parallelism test				*P* = 0.406							*P* = 0.39		

s, small; m, medium; l, large.

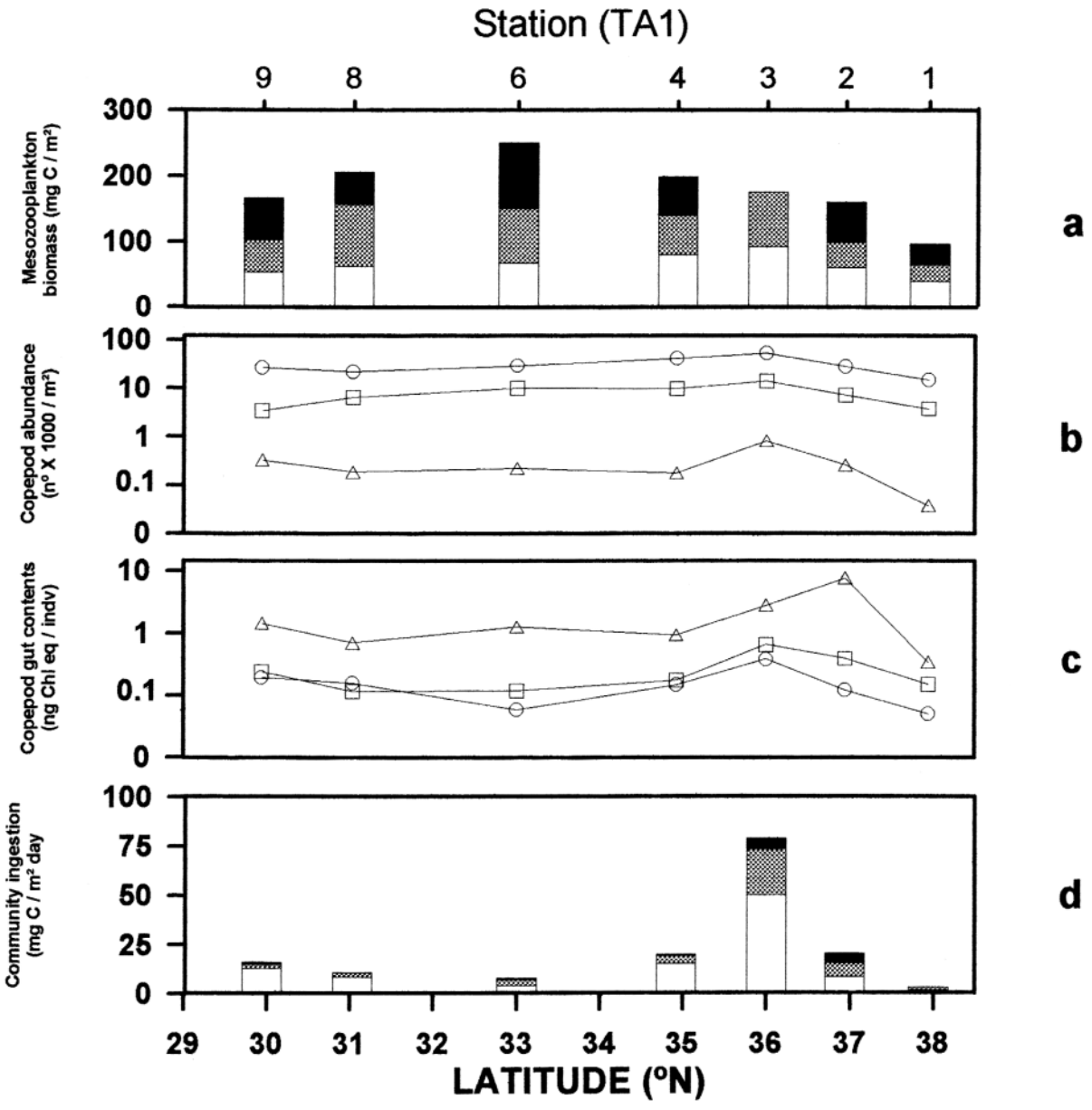

Fig. 7. Latitudinal variation of mesozooplankton biomass (**a**), copepod abundance (**b**), copepod gut contents (**c**) and copepod community ingestion rate (**d**) along transect A1. (a) and (d): (white) 200–500 μm; (hatched) 500-1000 μm; (black) >1000 μm. (b) and (c): (○) 200–500 μm; (□) 500-1000 μm; (△) >1000 μm.

that the Chl molecule does not degrade to undetectable products within the copepod gut (Penry and Frost, 1991; Head and Harris, 1996; McLeroy-Etheridge and McManus, 1999). Dam and Peterson (Dam and Peterson, 1988) proposed an average destruction value of 33%, which has been applied by several authors when direct estimates are not available (Morales *et al.*, 1991; Dam *et al.*, 1993; Peterson and Dam, 1996), and would lead to an underestimation by a factor of 1.4, which would not affect our general conclusions. It has also been suggested (Penry and Frost, 1991) that pigment destruction is low (<20%) at low food concentrations, such as those we found in all our study area. In spite of this limitation, the method certainly provides a minimum estimate of grazing rates and presents clear advantages over alternative incubation methods, minimizing potential sources of stress due to experimental handling and manipulation of animals (Head and Harris, 1996). For the above reasons,

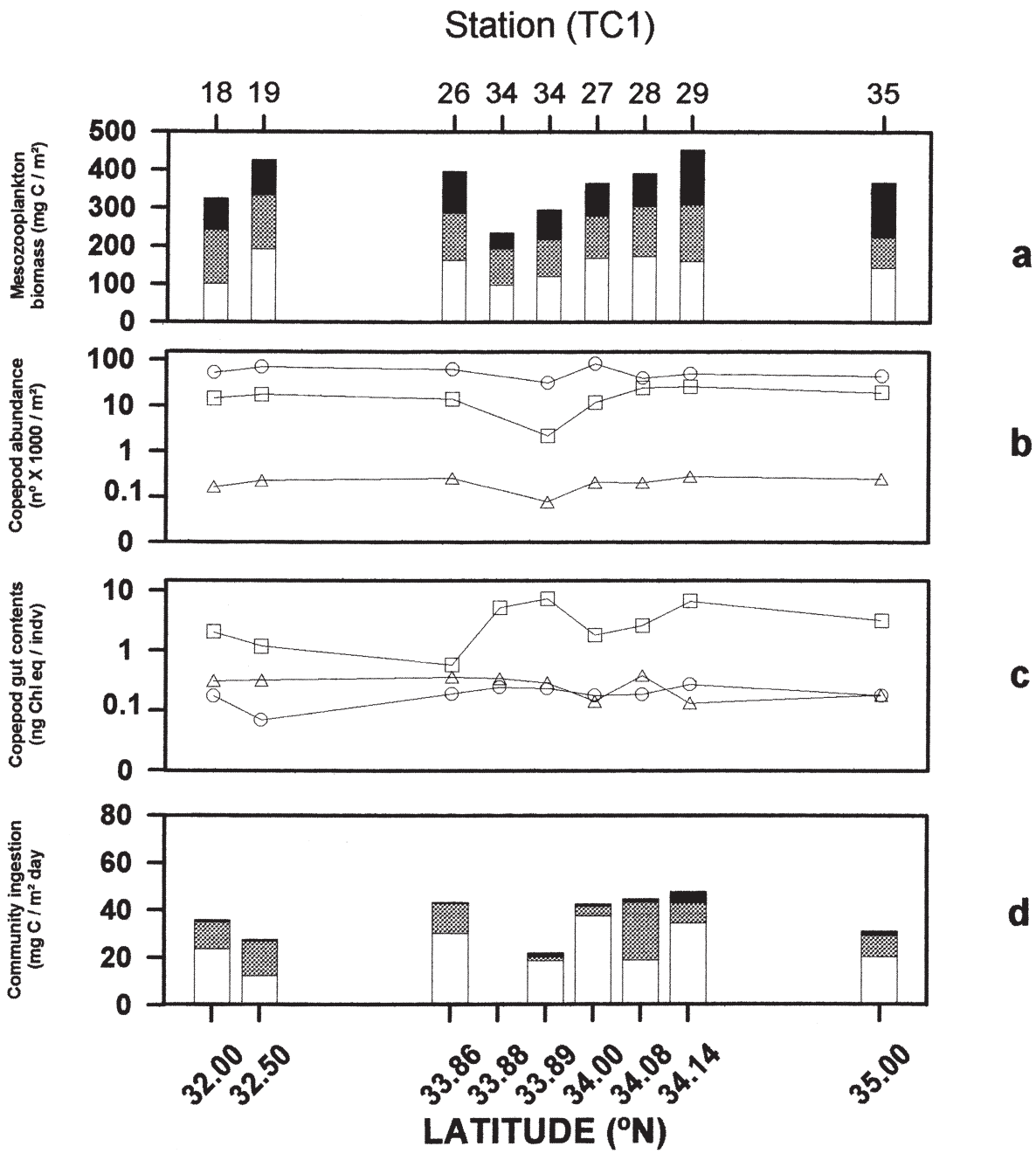

Fig. 8. Latitudinal variation of mesozooplankton biomass (**a**), copepod abundance (**b**), copepod gut contents (**c**) and copepod community ingestion rate (**d**) along transect C1. Key as in Figure 7.

the ingestion data presented must be considered to be minimal estimates of grazing impact.

Subtropical gyres are the least productive regions of the oceans (Blackburn, 1981), considered as biological deserts characterized by an oligotrophic regime where production is nutrient limited and zooplankton biomass remains low throughout the year. We report low mesozooplankton biomass (especially in summer) for the oligotrophic area of the North Atlantic Subtropical gyre, in the range found by several authors for oligotrophic regions at different locations [in the Equatorial Pacific (Zhang *et al.*, 1995) and in the Banda Sea (Arinardi *et al.*, 1990)] including the Atlantic Ocean (Lenz *et al.*, 1993; Head *et al.*, 1999). One of the most remarkable characteristics of these open-ocean

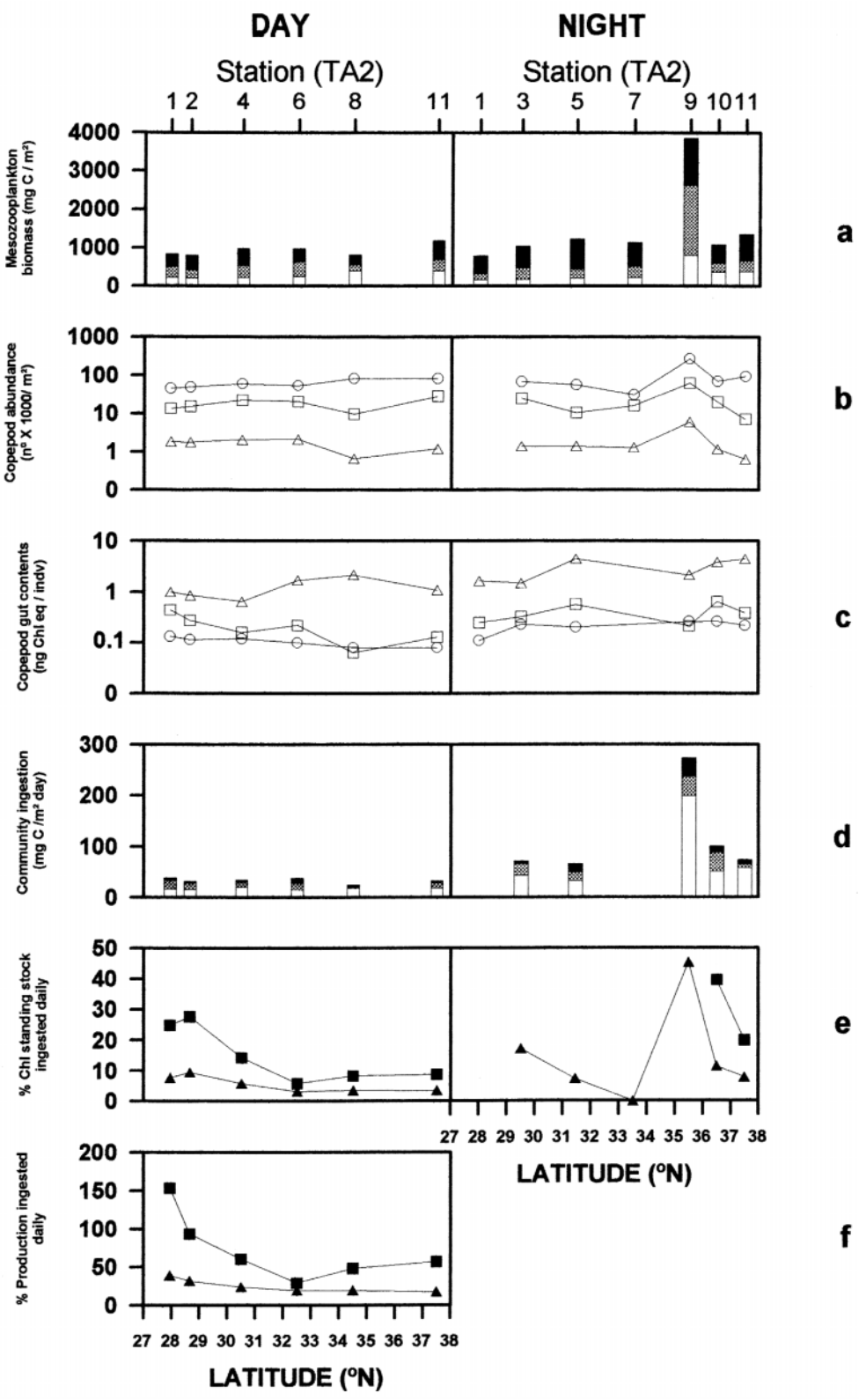

Fig. 9. Latitudinal variation of mesozooplankton biomass (**a**), copepod abundance (**b**), copepod gut contents (**c**), copepod community ingestion rate (**d**) and grazing impact (**e** and **f**) along transect A2. (a) and (d): (white) 200–500 μm; (hatched) 500–1000 μm; (black) >1000 μm. (b) and (c): (○) 200–500 μm; (□) 500–1000 μm; (△) >1000 μm. (e) and (f): (▲) total; (■) >2 μm.

Table III: Average values (SD in parentheses) of mesozooplankton biomass, copepod abundance, copepod gut contents, total community ingestion rate and grazing impact in the different mesoscale structures sampled on the AZORES cruises

		AF			Eddy		GMT		
		Inside		Outside	Inside	Outside	West		East
Biomass	200–500 µm	130 (41)	>**	77 (43)	172 (51)	189 (85)	244 (97)		181 (53)
(mg C m^{-2})	500–1000 µm	109 (23)	>*	72 (40)	128 (53)	212 (90)	269 (130)		165 (58)
	>1000 µm	92 (31)		71 (27)	248 (89)	374 (210)	404 (100)	>*	198 (95)
	Total	341 (81)	>**	221 (95)	549 (141)	836 (302)	918 (318)		545 (158)
Copepod	200–500 µm	48 (18)	>*	30 (16)	40 (20)	52 (28)	82 (13)	>**	36 (12)
abundance	500–1000 µm	14 (7)	>*	8 (5)	4,3 (2)	9 (7)	6.28 (1.3)	>*	4 (0.9)
(no. × 1000 m^{-2})	>1000 µm	0.29 (0.22)		0.22 (0.09)	0.3 (0.3)	0.8 (0.6)	0.69 (0.32)	>**	0.4 (0.18)
	Total	62 (21)	>*	41 (20)	45 (20)	62 (29)	89 (14)	>**	41 (12)
Gut content	200–500 µm	0.21 (0.09)		0.15 (0.05)	0.2 (0.09)	0.19 (0.05)	0.22 (0.06)	>*	0.13 (0.02)
(ng Chl-eq $ind.^{-1}$)	500–1000 µm	0.30 (0.16)		0.29 (0.16)	0.6 (0.3)	0.63 (0.39)	1 (0.25)		0.8 (0.44)
	>1000 µm	3.52 (2.4)		2.73 (3.8)	5 (5.9)	2.8 (1.6)	2.82 (0.55)		2.65 (2.25)
Total ingestion	200–500 µm	25.6 (15)	>**	11 (6.4)	23 (7)	31 (20)	49 (11)	>**	12.8 (2.78)
(mg C m^{-2} day^{-1})	500–1000 µm	10.72 (8.5)		6.6 (5)	7.2 (3.8)	12 (7.1)	18 (8.5)		8.36 (3.05)
	>1000 µm	2.1 (1.9)		1.21 (1.36)	2.26 (1.24)	4.4 (2.2)	5.25 (2.25)	>*	2.6 (1.27)
	Total	38.5 (21)	>*	21 (9.7)	32 (5)	48.7 (21)	72 (11)	>***	23 (2–3)
% Chl *a* ingested daily	Total				3.42 (1.85)	6.44 (4.6)	9.3 (0.3)		3.2 (0.32)
% Production ingested daily	Total				20 (2.71)	27.8 (15.4)			15 (7.6)

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

oligotrophic regions is the absence of seasonality in phytoplankton biomass (Venrick, 1990). Zooplankton grazing (as well as alternative explanations such as iron limitation) has been suggested as one of the main reasons for this steady state (Cullen *et al.*, 1992), although, due to the size structure of phytoplankton, microzooplankton are considered to be more important than copepods in this control of phytoplankton populations (Jackson, 1980). The low community ingestion rates reported in this study support this view when considering total phytoplankton biomass, with copepods ingesting (on average) <6% of total Chl *a* standing stock daily, but also point to an important copepod control of large (>2 µm) cell production, ingesting 61% of primary production in this size fraction and reaching extremely high values >100% at several locations.

In spite of this apparent coupling between copepod ingestion and large phytoplankton production, there was no relationship between gut contents and phytoplankton biomass or production in any size fraction. This points to a great importance of non-phytoplankton components of the diet in determining copepod feeding, as suggested by Stoecker and Capuzzo for oligotrophic seasons or environments dominated by phytoplankton <5 µm (Stoecker and Capuzzo, 1990). In this sense, Woods and Barkmann proposed a conceptual model for the oligotrophic area off the Azores where a phytoplankton diet leads the copepod population to extinction, only avoided if alternative sources of food are included (Woods and Barkmann, 1995).

Within these oligotrophic regimes, the presence of mesoscale features such as fronts, eddies and seamounts represents important inputs of nutrients to the photic layer, leading to increases in biological production, favouring export production and the prevalence of short food webs (Legendre and Le Fèvre, 1989). The AF extends from 18 to 35°W at ~35°N as a permanent, subsurface structure, which during the AZORES cruises separated water masses with differences of 1.5°C and 0.2 p.s.u. on spatial scales <100 km. Although its physical structure has

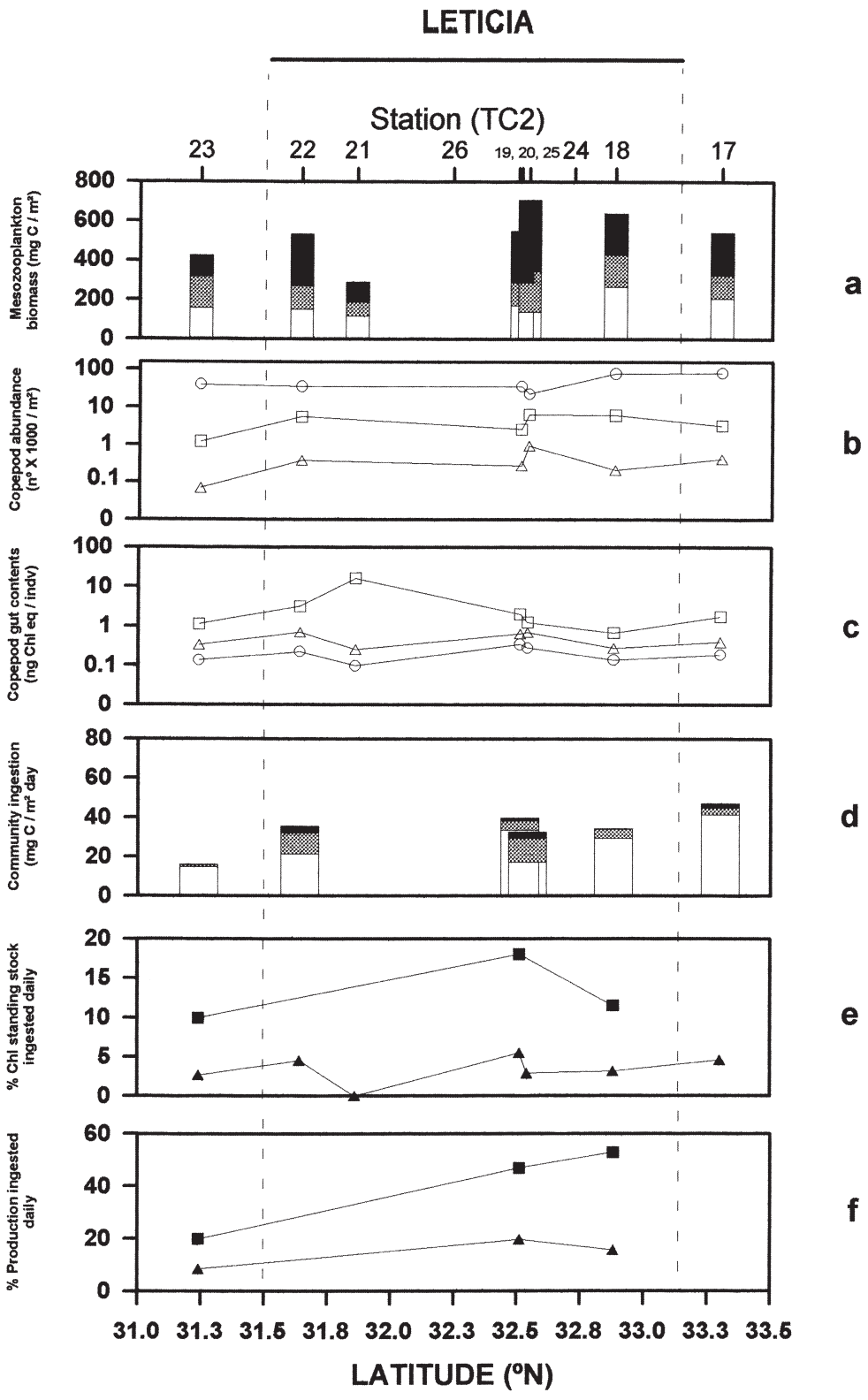

Fig. 10. Latitudinal variation of mesozooplankton biomass (**a**), copepod abundance (**b**), copepod gut contents (**c**), copepod community ingestion rate (**d**) and grazing impact (**e** and **f**) along transect C2 (LETICIA). Key as in Figure 9.

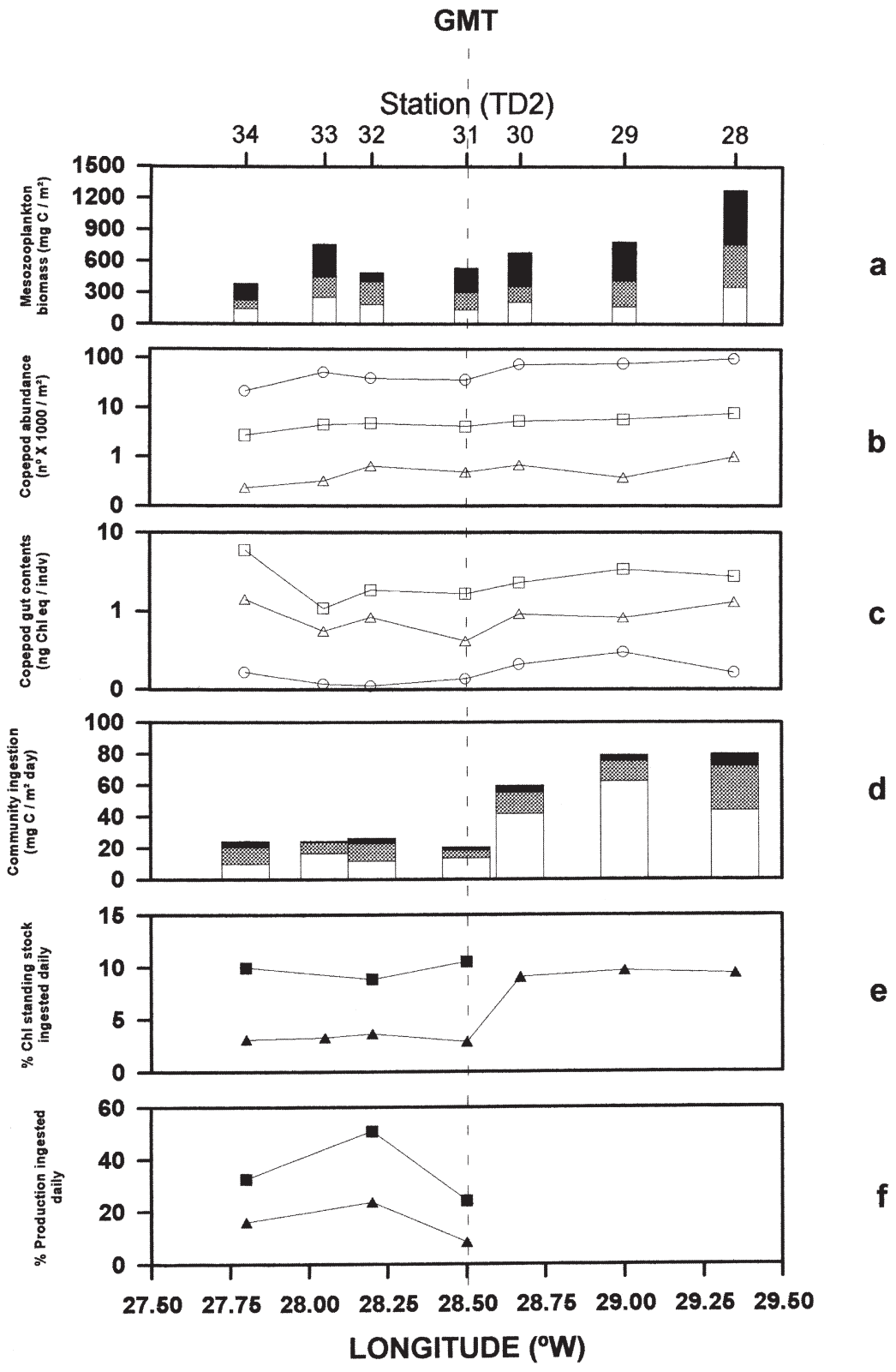

Fig. 11. Latitudinal variation of mesozooplankton biomass (**a**), copepod abundance (**b**), copepod gut contents (**c**), copepod community ingestion rate (**d**) and grazing impact (**e** and **f**) along transect D2 (GMT). Key as in Figure 9.

Table IV: Seasonal average values (SD in parentheses) of mesozooplankton biomass, copepod abundance, copepod gut contents and total community ingestion rate in the CANIGO area (20–40°N)

		AZORES II (April)		AMT4 (May)		AZORES I (August)		AMT5 (September)
Biomass	200–500 µm	277 (77)	>***	96 (19)	=	64 (17)	=	75 (41)
(mg C m^{-2})	500–1000 µm	253 (83)	>***	64 (15)	=	61 (25)	=	48 (14)
	>1000 µm	359 (78)	>***	120 (69)	>***	61 (22)	>***	32 (18)
	Total	890 (118)	>***	280 (78)	>***	179 (51)	=	156 (72)
Copepod abundance	200–500 µm	64 (15)	>***	25 (4)	=	30.7 (12.7)	=	30 (12)
(no. × 1000 m^{-2})	500–1000 µm	18.4 (5.7)	>***	4.4 (1.3)	=	7.8 (3.8)	=	7.3 (3.5)
	>1000 µm	1.4 (0.7)	>***	0.5 (0.2)	=	0.3 (0.24)	=	0.3 (0.2)
	Total	84 (17)	>***	30 (4.5)	=	38.8 (16)	=	37.8 (15.8)
Gut content	200–500 µm	0.13 (0.06)		0.11 (0.09)		0.16 (0.11)		0.13 (0.07)
(ng Chl-eq $ind.^{-1}$)	500–1000 µm	0.28 (0.2)		0.24 (0.09)		0.26 (0.2)		0.27 (0.17)
	>1000 µm	1.8 (1.12)		1.16 (1.43)		2.16 (2.54)		0.74 (0.58)
Total ingestion	200–500 µm	22 (12)		7.45 (5.24)		14.5 (16.4)		10 (7)
(mg C m^{-2} day^{-1})	500–1000 µm	14 (10)	>*	3.19 (2.01)	=	6.11 (7.72)	=	6.5 (7.8)
	>1000 µm	5.8 (4)	>*	1.26 (1.19)	=	1.92 (2.39)	=	0.9 (0.9)
	Total	42 (25)	>*	12 (6.8)	=	22 (25)	=	18 (15)

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

been widely studied in the last decades (Käse and Siedler, 1982; Gould, 1985; Tokmakian and Challenor, 1993), few biological studies are available (Fasham *et al.*, 1985; Angel, 1989; Fernández and Pingree, 1996), especially concerning mesozooplankton. In general, all kinds of fronts are supposed to present associated increases in biological production (Le Fèvre, 1986), although the mechanism (physical accumulation or enhancement of physiological activity) is still not clear (Franks, 1992). In the case of the AF, these biological increases are not always found: Fernández and Pingree (Fernández and Pingree, 1996) reported higher Chl concentration and primary production at the front, but Fasham *et al.* (Fasham *et al.*, 1985) and Angel (Angel, 1989) did not find such a pattern.

Our results point to an important effect of the AF for mesozooplankton in transect A (but not in transect C) from both AZORES I and II cruises, with frontal stations showing biomass, abundance and ingestion values 1.5–4 times higher than surrounding areas. However, no increases were found in copepod gut contents, so the observed enhanced community ingestion is mainly due to the higher copepod abundance.

The AF, although broad and persistent, is relatively weakly defined when compared with other frontal systems, and the few zooplankton studies carried out within it [(Angel, 1985) and references therein] reported no taxonomic differences in macrozooplankton communities from both sides of the front. According to this, the main differences in composition yielded by our MDS analysis are again due to numerical abundance, higher at the front, while specific composition is less important in separating locations (the same group of main species was found in all samples).

Copepod carbon ingestion provides a preliminary estimate of the magnitude of the vertical carbon fluxes mediated by zooplankton, mainly by sinking faecal pellets. Although no quantitative estimations can be inferred from our dataset, they point to a significant importance of this frontal system in regional carbon budgets, as suggested by Fernández and Pingree (Fernández and Pingree, 1996). Considering the spatial and temporal persistence of the front, our results suggest that between 10% (AZORES I) and 25% (AZORES II) of total phytoplankton carbon ingested by copepods in all the CANIGO region is supported by <5.5% of the area. For these calculations, we have assumed an area of 4.2×10^{12} m^2 for the CANIGO region and 0.22×10^{12} m^2 for the AF (González *et al.*, 2001). We must consider that phytoplankton carbon probably represents a minor part of total carbon ingested (and exported), due to the importance of non-algal food in the copepod diet. According to this, Roman and Gauzens suggested that total carbon ingested by copepods is 2–6 times higher than that obtained from phytoplankton (Roman and Gauzens, 1997).

Physical processes associated with eddies in the open ocean are suggested to modify the magnitude of biological processes inside them (Angel and Fasham, 1983), increasing primary production by a factor of 3.5 (Falkowski *et al.*, 1991), or representing 40% of regional new production in subtropical and medium latitudes (Oschlies and Garçon, 1998). The AC area has been proposed as an important source of mesoscale eddies (Gould, 1985) and Pingree and Sinha located a 'STORM corridor' at the southern part of the Subtropical front, between 32 and 34°N, where about two cyclonic westwards-displacing eddies are formed each year (Pingree and Sinha, 1998). Although the physical structure of these eddies has been fully described (Pingree *et al.*, 1996), no biological studies are available. The influence of eddies on zooplankton community structure at other locations has been reported for both anticyclonic (Roman *et al.*, 1985; Bradford and Chapman, 1988; Young, 1989; Pinca and Dallot, 1995) and cyclonic ones (The Ring Group, 1981; Yamamoto and Nishizawa, 1986; Beckmann *et al.*, 1987; Lobel and Robinson, 1988; Harris *et al.*, 1997). In general, cyclonic eddies present 1.3–1.8 higher zooplankton biomass than surrounding waters (The Ring Group, 1981), but there are many exceptions to this trend [see the references in (Beckmann *et al.*, 1987)]. In particular, the eddy LETICIA averaged lower mesozooplankton biomass than surrounding areas, and very similar to those reported by Harris *et al.* (Harris *et al.*, 1997) for a cyclonic eddy in the North Atlantic. Anyway, differences inside–outside the eddy were never significant, due to the high variability between samples, so must be considered carefully. The Ring Group proposed a possible explanation for these differences, considering the age of the eddy and the vertical distribution of animals (The Ring Group, 1981). In old cyclonic eddies (LETICIA is ~1 year old; Mouriño, B., unpublished), water in the upper layers is warmed and zooplankton migrate downward to reach temperatures similar to their waters of origin. This translates into lower abundance in the upper 200 m, although deep integrated densities are higher inside the eddy. The absence of temperature data in the eddy when it was formed and the lack of mesozooplankton biomass from depths >200 m make it impossible to confirm this theory. Death of animals confined in old eddies is an alternative explanation proposed by The Ring Group (The Ring Group, 1981).

To our knowledge, the only grazing estimates reported for cyclonic eddies are those of Harris *et al.* in an eddy located in the vicinity of 61°N 20°W (Harris *et al.*, 1997). In that study, C ingestion reaches maximum values of 15 mg C m^{-2} day^{-1}, representing <5% of daily primary production. Average ingestion inside the eddy LETICIA doubled these values (although lower than outside the eddy) and also translates into low grazing impact on Chl *a* standing stock (<5%) and primary production (<25%). With our results, and considering that 4–5 eddies can be located at any time in the STORM corridor, this mesoscale structure does not imply a significant effect on global ingestion within the study area. However, we must consider that the results obtained in the eddy LETICIA may not be directly comparable with eddies at a different development stage.

Effects of seamounts on biological processes have been described on many occasions [see the review in (Boehlert and Genin, 1987)], but evidence concerning mesozooplankton features over mounts is conflicting. Fedosova (Fedosova, 1974) reported 2- to 8-fold increases in zooplankton abundance over mounts, while Genin *et al.* (Genin *et al.*, 1994) detected gaps of zooplankton above them, and a reduction in zooplankton biomass over other submarine elevations has been reported by several authors [see the references in (Genin *et al.*, 1994)]. We found significant increases in zooplankton biomass (1.6-fold) and ingestion (3.1-fold) to the east of the GMT, although not properly above it. Owing to the sampling design (only one transect crossing the mount), it is impossible to determine the direction of the current, so no explanation (i.e. downstream effects) for the observed plankton distributions can be demonstrated.

Although the number of seamounts [>300 (Longhurst, 1998)] located in the CANIGO region points to significant global effect of these structures, high variability in temporal persistence of their effects probably diminishes their real importance. Consequences of physical anomalies detected at mounts are first observed in phytoplankton, and will only have a zooplankton response if these are maintained for a few weeks (Genin and Boehlert, 1985). As an example of this variability, the same authors reported zooplankton increases above Minami–Kasuga seamount, but further cruises, only a few days later, did not find the same pattern.

In conclusion, although the oligotrophic CANIGO region is characterized by low mesozooplankton stocks, conservative grazing rates reported suggest an important effect in controlling large phytoplankton production in the area. Mesoscale structures influence mesozooplankton distribution and ingestion in the region, although more detailed temporal studies would be required to determine the real influence of eddies and seamounts. Mesoscale features could represent locations of significant sedimentation through mesozooplankton grazing, mainly due to increases in numerical abundance but not in individual ingestion rates. Our results suggest that these kind of hydrodynamic singularities, often not detectable in broad-scale cruises due to limited spatial extension, must be considered in global calculations of carbon budgets.

ACKNOWLEDGEMENTS

We wish to thank principal scientists Felix Pérez and Emilio Fernández for their support during AZORES I–II cruises. We are also grateful to Leticia Viesca for her help during work at sea and to Julio Arrontes for orienting the statistical analysis. The University of Vigo provided production and Chl data. Suggestions and comments of one anonymous reviewer greatly improved the first draft of this manuscript. This research was funded by the European Commission's Marine Science and Technology Programme (MAST III) under contract CANIGO (MAS3-CT96-0060). I. H. was funded by a fellowship from the University of Oviedo within the same project.

REFERENCES

Angel, M. V. (1989) Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean ecology. *Prog. Oceanogr.*, **22**, 1–46.

Angel, M. V. and Fasham, J. R. (1983) Eddies and biological processes. In Robinson, A. R. (ed.), *Eddies in Marine Science*. Springer-Verlag, New York, pp. 492–524.

Arinardi, O. H., Baars, M. A. and Oosterhuis, S. S. (1990) Grazing in tropical copepods measured by gut fluorescence, in relation to seasonal upwelling in the Banda Sea (Indonesia). *Neth. J. Sea Res.*, **25**, 545–560.

Banse, K. (1994) Grazing and zooplankton production as key controls of phytoplankton production in the ocean. *Oceanography*, **7**, 13–20.

Beckmann, W., Auras, A. and Hemleben, C. (1987) Cyclonic cold-core eddy in the eastern North Atlantic. III. Zooplankton. *Mar. Ecol. Prog. Ser.*, **30**, 165–173.

Blackburn, M. (1981) Low latitude gyral regions. In Longhurst, A. R. (ed.), *Analysis of Marine Ecosystems*. Academic Press, London, pp. 3–30.

Boehlert, G. W. and Genin, A. (1987) A review of the effects of seamounts on biological processes. In Keating, B. H., Fryer, P., Batiza, R. and Boehlert, G. W. (eds), *Seamounts, Islands and Atolls. Geophysical Monograph 43*. American Geophysical Union, pp. 319–334.

Bradford, J. M. and Chapman, B. R. (1988) Epipelagic zooplankton assemblages and a warm-core eddy off East Cape, New Zealand. *J. Plankton Res.*, **10**, 601–619.

Cullen, J. J., Lewis, M. R., Davis, C. O. and Barber, R. T. (1992) Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the Equatorial Pacific. *J. Geophys. Res.*, **97**, 639–654.

Dagg, M. J. and Wyman, K. D. (1983) Natural ingestion rates of the copepods *Neocalanus plumcrus* and *N. cristatus* calculated from gut contents. *Mar. Ecol. Prog. Ser.*, **13**, 37–46.

Dam, H. G., Zhang, X., Butler, M. and Roman, M. R. (1995) Mesozooplankton grazing and metabolism at the equator in the central Pacific: Implications for carbon and nitrogen fluxes. *Deep-Sea Res. II*, **42**, 735–756.

Dam, H. G. and Peterson, W. T. (1988) The effect of temperature on the gut clearance rate constant of planktonic copepods. *J. Exp. Mar. Biol. Ecol.*, **13**, 37–46.

Dam, H. G., Miller, C. A. and Jonasdottir, S. H. (1993) The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Res. II*, **40**, 197–212.

Falkowski, P. G., Ziemann, D., Kolber, Z. and Bienfang, P. (1991) Role of eddy pumping in enhancing primary production in the ocean. *Nature*, **352**, 55–58.

Fasham, M. J., Platt, T., Irwin, B. and Jones, K. (1985) Factors affecting the spatial pattern of the deep chlorophyll maximum in the region of the Azores Front. *Prog. Oceanogr.*, **14**, 129–165.

Fedosova, R. A. (1974) Distribution of some copepod species in the vicinity of the underwater Hawaiian Ridge. *Oceanology*, **14**, 724–727.

Fernández, E. and Pingree, R. D. (1996) Coupling between physical and biological fields in the North Atlantic subtropical front southeast of the Azores. *Deep-Sea Res. I*, **43**, 1369–1393.

Franks, P. J. S. (1992) Sink or swim: accumulation of biomass at fronts. *Mar. Ecol. Prog. Ser.*, **82**, 1–12.

Genin, A. and Boehlert, G. W. (1985) Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. *J. Mar. Res.*, **43**, 907–924.

Genin, A., Greene, C., Haury, L., Wibe, P., Gal, G., Kaartved, S., Meir, E., Fey, C. and Dawson, J. (1994) Zooplankton patch dynamics: daily gap formation over abrupt topography. *Deep-Sea Res. I*, **41**, 941–951.

González, N., Anadón, R., Mouriño, B., Fernández, E., Sinha, B., Escánez, J. and de Armas, D. (2001) The metabolic balance of the planktonic community in the N. Atlantic Subtropical Gyre: The role of mesoescale instabilities. *Limnol. Oceanogr.*, in press.

Gould, W. J. (1985) Physical oceanography of the Azores Front. *Prog. Oceanogr.*, **14**, 167–190.

Gowen, R. J., McCullough, G., Kleppel, G. S., Houchin, L. and Elliott, P. (1999) Are copepods important grazers of the spring phytoplankton bloom in the western Irish Sea? *J. Plankton Res.*, **21**, 465–483.

Harris, R. P., Boyd, P., Harbour, D. S., Head, R. N., Pingree, R. D. and Pomroy, A. J. (1997) Physical, chemical and biological features of a cyclonic eddy in the region of 61°10′N 19°50′W in the North Atlantic. *Deep-Sea Res. I*, **44**, 1815–1839.

Head, E. J. H. and Harris, L. R. (1996) Chlorophyll destruction by *Calanus* spp. grazing on phytoplankton: Kinetics, effects of ingestion rate and feeding history, and a mechanistic interpretation. *Mar. Ecol. Prog. Ser.*, **135**, 223–235.

Head, R. N., Harris, R. P., Bonnet, D. and Irigoien, X. (1999) A comparative study of size fractionated mesozooplankton biomass and grazing in the North East Atlantic. *J. Plankton Res.*, **21**, 2285–2308.

Jackson, G. A. (1980) Phytoplankton growth and zooplankton grazing in oligotrophic oceans. *Nature*, **284**, 439–441.

Karl, D. M., Christian, J. R., Dore, J. E., Hebel, D. V., Letelier, R. M., Tupas, L. M. and Winn, C. W. (1996) Seasonal and interannual variability in primary production and particulate flux at Station ALOHA. *Deep-Sea Res. II*, **43**, 359–568.

Käse, R. H. and Siedler, G. (1982) Meandering of the subtropical front south-east of the Azores. *Nature*, **300**, 245–246.

Klein, B. and Siedler, G. (1989) On the origin of the Azores Current. *J. Geophys. Res.*, **94**, 4905–4912.

Le Fèvre, J. (1986) Aspects of the biology of frontal systems. *Adv. Mar. Biol.*, **2**, 163–299.

Legendre, L and Le Fèvre, J. (1989) Hydrodynamical singularities as controls of recycled versus export production in oceans. In Berger, W. H.,

Smetaceck, V. S. and Wefer, G. (eds), *Productivity of the Ocean: Present and Past*. Wiley, Chichester, pp. 49–63.

Lenz, J., Morales, A. and Gunkel, J. (1993) Mesozooplankton standing stock during the North Atlantic spring bloom study in 1989 and its potential grazing presure on phytoplankton: a comparison between low, medium and high latitudes. *Deep-Sea Res.*, **40**, 559–572.

Lobel, P. S. and Robinson, A. (1988) Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. *J. Plankton Res.*, **10**, 1209–1223.

Longhurst, A. (1998) *Ecological Geography of the Sea*. Academic Press, San Diego.

Mackas, D. and Bohrer, R. (1976) Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. Exp. Mar. Biol. Ecol.*, **88**, 67–81.

McLeroy-Etheridge, S. L. and McManus, G. B. (1999) Food type and concentration affect chlorophyll and carotenoid destruction during copepod feeding. *Limnol. Oceanogr.*, **44**, 2005–2011.

Morales, C. E., Bedo, A., Harris, R. P. and Tranter, P. R. G. (1991) Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction. *J. Plankton Res.*, **13**, 455–472.

Noji, T. T. (1991) The influence of macrozooplankton on vertical particulate flux. *Sarsia*, **76**, 1–9.

Oschlies, A. and Garçon, V. (1998) Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature*, **394**, 266–269.

Pakhomov, E. A. and Perissinotto, R. (1997) Mesozooplankton community structure and grazing impact in the region of the subtropical convergence south of Africa. *J. Plankton Res.*, **19**, 675–691.

Penry, D. L. and Frost, B. W. (1991) Chlorophyll *a* degradation by *Calanus pacificus*: dependence on ingestion rate and digestive acclimation to food resources. *Limmnol. Oceanogr.*, **36**, 147–159.

Peterson, W. T. and Dam, H. G. (1996) Pigment ingestion rate and egg production rates of the calanoid copepod *Temora longicornis*: Implications for gut pigment loss and omnivorous feeding. *J. Plankton Res.*, **18**, 855–861.

Pinca, S. and Dallot, S. (1995) Meso- and macrozooplankton composition patterns related to hydrodynamic structures in the Ligurian Sea (Trophos-2 experiment, April–June 1986). *Mar. Ecol. Prog. Ser.*, **126**, 49–65.

Pingree, R. D. and Sinha, B. (1998) Dynamic topography (ERS-1/3 and Seatruth) of subtropical ring (STORM 0) in the STORM corridor (32–34°N, Eastern Basin, North Atlantic Ocean). *J. Mar. Biol. Assoc. UK*, **78**, 351–376.

Pingree, R. D., Sinha, B., New, A. L., Waddington, I., Head, R. H. and Nechvolodov, L. V. (1996) Will deep subtropical ring 'Storm Physalia' cross the Mid Atlantic Ridge and reach America? *J. Mar. Biol. Assoc. UK*, **76**, 553–567.

Robins, D. B. and Aiken, J. (1996) The Atlantic Meridional Transect: an oceanographic research programme to investigate physical, chemical, biological and optical variables of the Atlantic Ocean. *Underwater Technol.*, **21**, 8–14.

Roman, M. R. and Gauzens, A. L. (1997) Copepod grazing in the equatorial Pacific. *Limnol. Oceanogr.*, **42**, 623–634.

Roman, M., Gauzens, A. L. and Cowles, T. (1985) Temporal and spatial changes in epipelagic microzooplankton and mesozooplankton biomass in a warm-core Gulf Stream ring 82-B. *Deep-Sea Res. I*, **32**, 1007–1022.

Stoecker, D. K. and Capuzzo, J. (1990) Predation on Protozoa: its importance to zooplankton. *J. Plankton Res.*, **12**, 891–908.

The Ring Group (1981) Gulf Stream cold-core rings: their physics, chemistry, and biology. *Science*, **212**, 1091–1100.

Tokmakian, R. T. and Challenor, P. G. (1993) Observations in the Canary Basin and the Azores Frontal Region using Geosat data. *J. Geophys. Res.*, **98**, 4761–4773.

Venrick, G. L. (1990) Phytoplankton in an oligotrophic ocean: species structure and interannual variability. *Ecology*, **71**, 1547–1563.

Woods, J. D. and Barkmann, W. (1995) Modelling oligotrophic zooplankton production: seasonal oligotrophy off the Azores. *ICES J. Mar. Sci.*, **52**, 723–734.

Yamamoto, T. and Nishizawa, S. (1986) Small-scalle zooplankton aggregations at the front of a Kuroshio warm-core ring. *Deep-Sea Res. I*, **33**, 1729–1740.

Young, J. W. (1989) The distribution of hyperiid amphipods (Crustacea:Peracarida) in relation to warm-core eddy J in the Tasman Sea. *J. Plankton Res.*, **11**, 711–728.

Zhang, X., Dam, H. G., White, J. R. and Roman, M. R. (1995) Latitudinal variations in mesozooplankton grazing and metabolism in the central tropical Pacific during the U. S. JGOFS EqPac study. *Deep-Sea Res. II*, **42**, 695–714.

Received on November 5, 2000; accepted on February 26, 2001