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Basin-scale latitudinal patterns of copepod grazing in the Atlantic Ocean

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Size-fractionated copepod abundance and ingestion rates were investigated along a 50°S–50°N latitudinal transect, during the Atlantic Meridional Transect (AMT) 4, 5 and 6 cruises (boreal spring–autumn 1997, boreal spring–summer 1998). Copepod abundance was higher at high latitudes in spring, near northwest Africa, in the equatorial and Benguela upwelling systems, and in the Subtropical Convergence, and lower in oligotrophic gyres. Gut contents were not related to phytoplankton biomass or production. Gut evacuation rate averaged 0.03 min^{-1}, and was not related to latitude or body size. Conservative estimates of copepod community total ingestion rates ranged between 3.4 and 173 mg C m^{-2} day^{-1} for AMT4, 1.6–252 mg C m^{-2} day^{-1} in AMT5 and 10–160 mg C m^{-2} day^{-1} in AMT6. Maximum values were always in the upwelling regions, the subtropical convergence and high latitudes in the Northern Hemisphere during boreal spring. Calculated ingestion rates translate into average daily minimal consumption values of 2.07%, 1.89% and 2.6% of total chlorophyll stock, or 8.02%, 14.5% and 12.9% of total primary production ingested daily on AMT4, 5 and 6 respectively. Grazing impact increases considerably if we consider ingestion of phytoplankton larger than 2 μm, especially under the influence of the Equatorial and North African upwellings, where copepod ingestion represents up to 30% of the biomass and >100% of production by large cells.

INTRODUCTION

Research on the activity of the so-called biological pump, at a range of temporal and spatial scales, has been the focus of recent international programmes, for example the Joint Global Ocean Flux Study (JGOFS). Although these programmes address global problems, replicated studies at quasi-synoptic, global scales are logistically complicated and therefore infrequent. In close agreement with this trend, grazing studies of herbivorous zooplankton, which control phytoplankton populations (Banse, 1994) and mediate vertical carbon fluxes through sinking of their faecal pellets (Noji, 1991) are non-existent on an ocean basin scale. Our present knowledge is strongly biased toward oversampled boreal regions of the world's oceans near developed countries or polar oceans (Morales *et al.*, 1991; Painting *et al.*, 1993; Pakomov and Perissinotto, 1997; Gowen *et al.*, 1999). Vast areas of the equatorial and tropical oceans are essentially unstudied [but see (Arinardi *et al.*, 1990; Zhang *et al.*, 1995; Dam *et al.*, 1995)], even though they contribute up to 80% of the global ocean production and 70% of the total export production (Karl *et al.*, 1996).

Twice a year as part of the Atlantic Meridional Transect programme (AMT), the British Antarctic Survey vessel R.R.S. 'James Clark Ross' covers the transect UK–Falkland Islands on her passage to and from Antarctica (with exceptional deviations from this route, e.g. Cape Town–UK), providing an excellent platform from which to investigate biological processes in the Atlantic Ocean over broad spatial scales (Robins and Aiken, 1996). We have taken advantage of this opportunity to study for the first time the magnitude of copepod grazing on a global scale, allowing comparison of vast areas of the ocean of contrasting productivity and function. To achieve this goal, we adopted the gut pigment technique (Mackas and Bohrer, 1976) as a means of making minimum estimates of zooplankton grazing activity. In this paper we describe the results of copepod grazing measurements conducted during three AMT transects, within the context of the major biogeochemical provinces as described previously (Longhurst *et al.*, 1995).

Our analysis points to the quantitative importance of copepod grazing in some of the largest and least studied areas of the global ocean.

MATERIALS AND METHODS

A total number of 28, 27 and 29 zooplankton stations respectively were sampled during April–May 1997 (AMT4), September–October 1997 (AMT5) and May–June 1998 (AMT6) onboard R.R.S. 'James Clark Ross' (Figure 1). All stations on AMT4 and AMT5 were sampled between 10:00 and 11:00 h local time, while on AMT6 sampling was carried out between 08:00 and 09:00 h local time.

Phytoplankton biomass and production

Water samples were collected with Niskin Bottles at five to seven depths on each station. Chlorophyll *a* (Chl *a*) concentration was determined fluorometrically with a 10 AU Turner Designs Fluorometer after 24 h of extraction in 90% acetone at –20°C. The non-acidification technique (Welschmeyer and Naughton, 1994) was used. Primary production was measured by ^{14}C incubation with a range of 10 irradiances (from 97% to 1% of incident irradiance). Water samples (in 70 ml polycarbonate bottles) were inoculated with 10 μCi $NaH^{14}CO_3$, 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 scintillation cocktail. Quenching was corrected with the channel ratio method. Chlorophyll concentration and production rates were expressed as integrated values in the photic layer, estimated from the vertical PAR distribution. Daily production rates were obtained by multiplying hourly rates by the number of daylight hours at each station.

Copepod abundance and composition

At each daily station, two double WP-2 (57 cm diameter and 200 μm mesh) net casts were deployed to 200 m, except in the shallow coastal waters off England and the Falkland Islands, where the net was deployed to 50 m, and

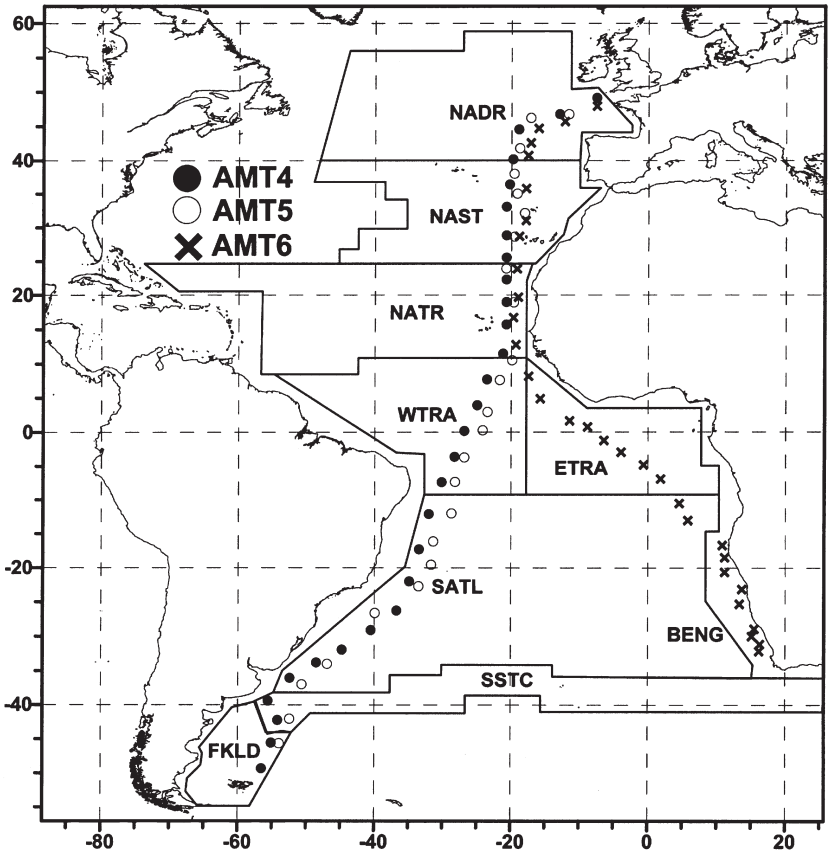

Fig. 1. Locations of stations sampled during AMT4, AMT5 and AMT6 cruises. Biogeochemical provinces: NADR, North Atlantic Drift; NAST, North Atlantic Subtropical Gyral; NATR, North Atlantic Tropical Gyral; WTRA, Western Tropical Atlantic; ETRA, Eastern Tropical Atlantic; SATL, South Atlantic Gyral; SSTC, South Subtropical Convergence; FKLD, Southwest Atlantic Shelves; BENG, Benguela Current Coastal.

the southern stations in AMT6 (24–33°S), where sampling depth was 100 m. Towing speed was 1 m s^{-1}. Copepods collected from one net were used for gut content analysis and evacuation experiments, while copepods from the other net were analysed for abundance determination and taxonomic identification. After the tow, the net was gently rinsed, the cod-end contents were poured into a bucket filled with 0.2 μm filtered surface sea water and subsampled using a Folsom splitter. Half of the sample was preserved with borax-buffered formalin (4%) for subsequent counts of copepod abundance. Before microscopic analysis, samples were screened through 1000, 500 and 200 μm meshes to divide them into 200–500 (small), 500-1000 (medium) and >1000 μm (large) size fractions. Copepod abundance was expressed as integrated values in the upper 200 m.

Copepod grazing

Copepod grazing was estimated using the gut fluorescence technique (Mackas and Bohrer, 1976). The content of the first net (not rinsed) was immediately screened into the same three size fractions considered for abundance. The sieving procedure took less than 3 min after recovery of the net. Subsamples from each size fraction were filtered onto sharkskin filters, stored in Petri dishes and immediately frozen at –70°C for further gut content analysis.

Gut evacuation experiments were only performed during AMT4 and AMT5. Animals from each size fraction were introduced into a cool box containing filtered (0.2 μm) surface sea water from the same station, and kept in darkness. The copepods were subsampled every 5 min for half an hour, filtered onto sharkskin filters and frozen as above. Extra subsamples at 45 and 60 min were taken when copepods were abundant.

Twenty-five copepods for the large, 50 for the medium and 75 for the small fractions were picked from the filter 24 h after collection, using jeweller 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 ng Chl *a* equivalents.

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 rate.

Individual ingestion rates for each size-fraction were obtained by multiplying the initial gut content by the gut evacuation rate. The average value of gut evacuation rates obtained for the AMT4 and AMT5 cruises (0.0303 min^{-1}) was applied for AMT6. 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 applied. This index comes from comparison between Chl values and phytoplankton carbon contents (estimated from taxonomic composition) obtained on previous AMT cruises (Marañon *et al.*, 2000).

Biogeochemical provinces

To compare stations over such a wide spatial scale, stations were grouped according to the concept of biogeochemical provinces proposed by Longhurst *et al.* (Longhurst *et al.*, 1995) which is based on global-scale productivity as inferred from remotely sensed ocean colour. Nine different biogeochemical provinces were sampled during the AMT cruises (Figure 1): North Atlantic Drift (NADR), North Atlantic Subtropical Gyre (NAST), North Atlantic Tropical Gyre (NATR), Eastern Tropical Atlantic (ETRA), Western Tropical Atlantic (WTRA), South Atlantic Gyre (SATL), South Subtropical Convergence (SSTC), Southwest Atlantic Shelves (FKLD) and Benguela Current Coastal (BENG) A full hydrographic description for all the transects is available in (Aiken *et al.*, 2000). The main hydrographic features are the presence of a major thermal front coinciding with the convergence of the cold Falklands current and the warm Brazil current, affecting the SSTC region, and the influence of upwelling of nutrient-rich water in the NATR, WTRA and BENG provinces.

RESULTS

AMT4

AMT4 coincided with the boreal spring, characterized by high phytoplankton biomass in temperate waters north of 40°N (Figure 2a). Unfortunately, primary production is not available at these stations. Phytoplankton biomass and production (Figure 2a,b) were also high in the Subtropical Convergence, and in the region under the influence of the Equatorial and North African upwelling system (5°S–20°N) and low in both Northern and Southern oligotrophic gyres. Picoplankton (<2 μm) accounted for more than 70% of the biomass along most of the transect, except for high latitudes where large cells were dominant. All three copepod size fractions (Figure 2 c) were more abundant at high latitudes in the Northern Hemisphere,

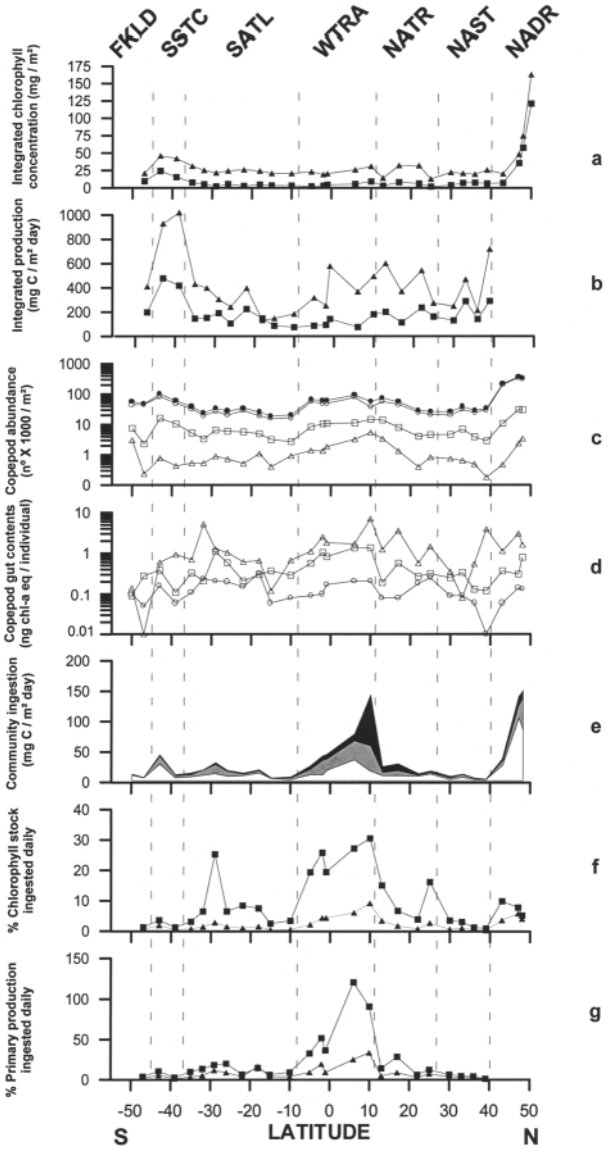

Fig. 2. Latitudinal variation in integrated chlorophyll concentration (**a**), integrated primary production (**b**), copepod abundance (**c**), copepod gut contents (**d**), total community ingestion rate (**e**), grazing impact on phytoplankyton biomass (**f**) and production (**g**) during AMT4. KEY: (**a**), (**b**), (**f**) and (**g**) (▲) total phytoplankton; (■) phytoplankton >2 μm. (**c**) and (**d**) (●) total; (△) >1000 μm; (□) 500–1000 μm; (○) 200–500 μm**.** (**e**) solid shading, >1000 μm; grey shading, 500–1000 μm; unshaded area, 200–500 μm.

the upwelling areas and the Subtropical Convergence, and less abundant in the oligotrophic gyres, following a similar pattern to that of the phytoplankton.

Latitudinal variations in copepod gut contents (Figure 2d) were not as clear. Gut contents were higher in upwelling areas and at some stations at the northern end of the transect, but also at several stations located in the oligotrophic gyres, and no increase was found in the Subtropical convergence. There was no relationship between gut contents in any of the fractions and integrated biomass or production of phytoplankton. (Spearman correlation coefficient $P>0.1$). Regression analysis did not show significant differences for gut evacuation rates ($P>0.1$) in the slopes of the 15 curves obtained (Table I). The average k value used for calculations of copepod individual ingestion rates was 0.0302 (± 0.01) min^{-1}.

Following the same pattern described for phytoplankton and copepod abundance, community ingestion rates (Figure 2e) present maximum values of 175 mg C m^{-2} day^{-1} above 40°N and in the upwelling area (specially around 10°N), and to a lower extent (50 mg C m^{-2} day^{-1}) in the Subtropical Convergence. In the oligotrophic areas copepod ingestion was always lower than 30 mg C m^{-2} day^{-1}. However, as previously noted for gut contents, no correlation was found between ingestion rates and phytoplankton biomass or production ($P>0.1$). On average, medium and large animals accounted for 45% of total ingestion, although in upwelling areas this contribution increased to up to 88%. Ingestion of phytoplankton translates into low grazing impact on phytoplankton biomass and production (Figure 2f,g). Average values of 2% of chlorophyll standing stock and 8% primary production were ingested by copepods daily. As an exception to this trend, in upwelling areas ingestion represents up to 9% and 33% of chlorophyll and production respectively, and these values increased considerably to 30% of phytoplankton biomass and >100% of primary production if we only consider the phytoplankton size potentially available to copepods (>2 μm).

AMT5

During AMT5 the area comprised by the oligotrophic gyres and upwelling systems presents no significant differences from AMT4 in terms of phytoplankton biomass, production, copepod abundance, gut contents and community ingestion (Figure 3a–e). The most remarkable difference is the high primary production estimated at the equator. On the other hand, the high latitude areas showed changes related to spring season in the austral hemisphere, with high values of integrated chlorophyll and production (Figure 3a,b) in the south of the transect, especially in the Subtropical Convergence. Copepod abundance (Figure 3c) follows the same pattern, but increases in abundance were only related to the Sub-tropical Convergence and not to the southernmost station at the Falklands coastal region. Maximum values of copepod gut contents (Figure 3d) are also located in the Subtropical Convergence, except in the small size fraction, which increase significantly at the northernmost station. Gut contents in the medium and large fractions were corre-

Table I: Latitudinal variation in gut evacuation rate (k min^{-1}), and experimental temperature (T) in AMT4 and AMT5 cruises

AMT4					AMT5				
Latitude	Size fraction	r^2	k	T	Latitude	Size fraction	r^2	k	T
47°N	m	0.32	0.026	18.3	47°N	s	0.3	0.012	17.4
43°N	m	0.6	0.030	23.3	47°N	m	0.69	0.025	17.4
35°N	s	0.58	0.027	23.3	42°N	s	0.61	0.025	19.1
17°N	m	0.39	0.054	27.1	38°N	m	0.29	0.034	22.1
17°N	s	0.3	0.032	27.1	15°N	l	0.58	0.034	25.2
10°N	l	0.53	0.029	27.3	7°N	s	0.43	0.03	28.6
10°N	m	0.78	0.020	28	2°N	s	0.69	0.048	27.6
6°N	s	0.46	0.030	27.7	0°N	s	0.31	0.026	26.1
0°S	m	0.61	0.019	28.2	4°S	m	0.5	0.026	25.5
2°S	s	0.26	0.034	25.3	8°S	s	0.37	0.028	26.2
5°S	l	0.39	0.040	23.5	16°S	s	0.52	0.02	25.4
26°S	s	0.36	0.012	18.8	31°S	s	0.35	0.038	19
29°S	s	0.54	0.023	13.4	35°S	s	0.46	0.05	18.7
49°S	s	0.42	0.032		38°S	l	0.5	0.03	14.3
52°S	m	0.62	0.041						
Test of parallelism			$P = 0.529$				$P = 0.197$		

Copepod size fraction: l, large; m, medium; s, small.

lated with integrated chlorophyll ($P < 0.05$), but the correlation was not significant when stations with levels above 55 mg Chl m^{-2} were excluded. As in AMT5, there was no difference (regression analysis, $P > 0.1$) in the slopes of the 14 gut evacuation curves, averaging 0.0304 ± 0.0101 min^{-1} (Table I). No difference was found between slopes of curves from AMT4 and AMT5. As a consequence of the high copepod abundance and gut contents in the Subtropical Convergence, this area presented the highest community ingestion rate along the whole transect (Figure 3e), with values around 250 mg C m^{-2} day^{-1} (75% accounted for by medium and large animals). Grazing impact (Figure 3f,g) in this region reaches 10% and 50% of phytoplankton biomass and production respectively, and increases to 20% of biomass and almost 100% of production of large (>2 μm) phytoplankton. However, the maximum grazing impact along the transect was again located in the upwelling areas, where copepod ingestion represents up to 8% and 75% of biomass and production, or 30% and 325% of larger cells.

AMT6

AMT6 (Figure 4) presents a picture very similar to AMT4 in the latitudinal range between 18°S and 50°N, corresponding again to boreal spring. The most remarkable differences are the higher phytoplankton biomass and production values related to the North African upwelling (Figure 4a,b) and the absence of the extremely high copepod abundance (Figure 4c) in the northernmost stations found in AMT4. Gut contents were not related to integrated chlorophyll or production.

During this cruise, sampling was carried out in the Benguela upwelling system, where high values of phytoplankton biomass (Figure 4a), production (Figure 4b) and copepod abundance (Figure 4c) were found at all the stations. Copepod gut contents (Figure 4d) in this area presented the higher values on the transect for the small fraction, but the pattern, as for previous cruises is not clear, with some stations in all the size fractions showing values similar or even lower than in the oligotrophic gyres. This region presents copepod community ingestion rates of 150 mg C m^{-2} day^{-1} (Figure 4e), even higher than the North African and equatorial upwellings (90 mg C m^{-2} day^{-1}), but the high phytoplankton biomass and production found in this area means that the grazing impact is lower (5% biomass and 40% production, or 8% and 45% of >2 μm cells, Figure 4f,g) than in the equatorial upwelling, where copepods ingest up to 10% and 60% of

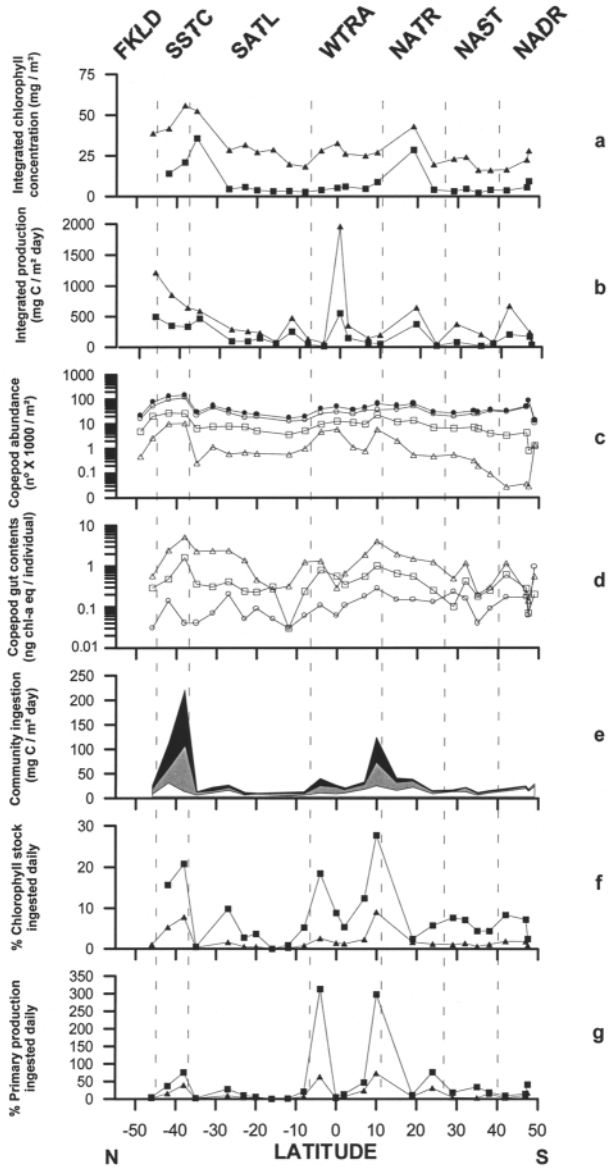

Fig. 3. Latitudinal variation in integrated chlorophyll concentration (**a**), integrated primary production (**b**), copepod abundance (**c**), copepod gut contents (**d**), total community ingestion rate (**e**), grazing impact on phytoplankyton biomass (**f**) and production (**g**) during AMT5. KEY: (**a**), (**b**), (**f**) and (**g**) (▲) total phytoplankton; (■) phytoplankton >2 μm. (**c**) and (**d**) (●) total; (△) >1000 μm; (□) 500–1000 μm; (○) 200–500 μm**.** (**e**) solid shading, >1000 μm; grey shading, 500–1000 μm; unshaded area, 200–500 μm.

biomass and production, or 30% and 160% considering the large phytoplankton.

Biogeochemical provinces

Average ingestion rates and grazing impact for each biogeochemical province are given in Table II. In order to determine differences in ingestion between provinces, stations from the three cruises have been grouped in two categories: stations from oligotrophic provinces (NAST and SATL) and stations from provinces with nutrient enrichment, at least in some period of the year (SSTC, FKLD, NADR, NATR, WTRA and BENG). ANOVA analysis (P <0.0001) revealed significant differences between both groups, with higher ingestion in the second group. Seasonal differences were only found in the NADR region, with higher ingestion rates (P = 0.02) during spring (AMT4).

DISCUSSION

The nature of the AMT cruises places significant limitations on the application of the gut fluorescence technique: with no opportunity for night-time sampling, daily cycles in gut pigment fluorescence cannot be determined, and there is no information on diel vertical migration. The latter is particularly likely to show latitudinal differences over the range of environments studied on the AMT. Although the gut fluorescence technique is open to discussion because of its assumption that the chlorophyll molecule does not degrade to undetectable products within the copepod gut (Penry and Frost, 1991; Head and Harris, 1996; McLeroy-Etheridge and McManus, 1999), it certainly provides a minimum estimate of grazing rates and is logistically convenient given the typical time limitations of such a broad-scale survey. We consider that the technique presents clear advantages over alternative incubation methods, that it best represents *in situ* ingestion, and minimizes potential sources of stress due to experimental handling and manipulation of animals (Head and Harris, 1996). For the above reasons the data presented must be considered to be minimal estimates of grazing impact.

Knowledge of trophic relationships in the ocean at broad spatial and temporal scales is of great importance if prediction of the magnitude of carbon flux to the deep ocean is to be attempted based on global chlorophyll concentration or productivity inferred from remotely sensed measurements. If it is possible to establish a clear relationship between these measurements and mesozooplankton carbon ingestion, this would provide a means for possibly estimating the amount of carbon susceptible to being exported via zooplankton-mediated processes on a global scale. The absence of seasonal and latitudinal variation in copepod gut evacuation rates reported in this study could facilitate such calculations, providing an average value over a very extensive spatial scale. Though the lack of information on diel behaviour is a significant limitation. With this in mind, our results contrast with those reported previously (Dam and Peterson, 1988; Irigoien, 1998), which suggest a strong influence of temperature on gut evacuation rates, but are supported by the

Table II: Average values (standard error in brackets) of total copepod community ingestion rates (mg C m^{-2} day^{-1}) and grazing impact in the different biogeochemical provinces sampled in AMT4, AMT5 and AMT6 cruises

Province	Cruise	Copepod community ingestion rates	Ingested daily Total Chl	Chl >2 μm	Total PP	PP >2 μm
NADR	AMT4	95 (43)	0.2	0,90	0.47	1.16
	AMT5	20 (3)	1.5 (0.3)	6 (1.5)	9.8 (3.6)	21 (8.6)
	AMT6	12.8	0.9	1.9	2.25	3.8
NAST	AMT4	9 (2)	0.7 (0.1)	2.6 (0.7)	3 (0.2)	5 (0.7)
	AMT5	12 (3)	1 (0.15)	5.9 (0.9)	6.6 (3)	23 (4.4)
	AMT6	10.12	0.8	3	4.65	8.5
NATR	AMT4	24 (4)	2.1 (0.5)	10.5 (3)	6 (1.3)	15.2 (4.7)
	AMT5	32 (9)	1.4 (0.17)	4 (1.3)	18.4 (10)	43.3 (26.6)
	AMT6	39(11)	2 (0.4)	3.4 (0.8)	6 (2.2)	11 (5)
ETRA	AMT6	49(14)	4.3 (2)	12.1 (5.1)	22 (13)	56 (33)
WTRA	AMT4	77 (24)	5.2 (1.7)	24.4 (2.2)	19 (4.7)	66 (17)
	AMT5	44 (19)	3 (1.3)	13 (3.5)	28.7 (12.8)	116 (60)
SATL	AMT4	17 (3)	1.2 (0.25)	7.8 (2.6)	7 (1.68)	12.2 (1.8)
	AMT5	21 (3)	0.6 (0.15)	3.8 (1.2)	4 (1.1)	11 (3.8)
	AMT6	34	6.25	6.25	8.1	15
SSTC	AMT4	30 (19)	1.15 (0.7)	2.4 (1.15)	3.25 (2.13)	6.6 (3.9)
	AMT5	189 (62)	6.5 (1.25)	18.25 (2.5)	27 (12.1)	56 (19.3)
FKLD	AMT4	10 (3)	0.6	1.3	1.8	3.7
	AMT5	22.4	0.99	1.84	1.8	4.5
BENG	AMT6	80(30)	3.25 (1.45)	3.25 (1.45)	15.2 (8.1)	19.3 (9.5)

results of Zhang *et al.* (Zhang *et al.*, 1995). This author, and others such as Dagg (Dagg, 1985), suggest that low chlorophyll concentrations in the field result in decreased evacuation rates. In fact, proposed empirical models (Dam and Peterson, 1988) are not applicable when food is limiting and that is exactly the case for AMT cruises, where chlorophyll concentration is lower than 1 μg l^{-1} at the Deep Chlorophyll Maximum at most stations, mainly (70–90%) in the form of phytoplankton groups which are either not available to copepods because of their small size, or are of poor nutritional value for copepods, such as cyanobacteria and small flagellates (Marañon *et al.*, 2000). We must also consider that our measurements are obtained from a mixture of animals, which could hide effects in particular copepod species or development stages.

In our study, copepod gut contents, and consequently the estimates of conservative ingestion rates, were not related to phytoplankton biomass or production. This lack of relationship has been reported previously (Boyd *et al.*, 1980; Dam *et al.*, 1995; Zhang *et al.*, 1995), and could be due to delay in zooplankton responses to changes in phytoplankton biomass, sampling of non-feeding copepods below the photic layer, preferential grazing in phytoplankton patches or feeding on non-algal diets. Predation on protozoa is expected to be especially important in seasons or environments dominated by cells <5 μm (Stoecker and Capuzzo, 1990) but also in productive regions (Boyd *et al.*, 1980; Arinardi *et al.*, 1990; Painting *et al.*, 1993). Omnivory must be responsible for most of the copepod ingestion in our study, especially in oligotrophic areas where phytoplankton ingestion does not satisfy maintenance-carbon demands (Zhang *et al.*, 1995). Roman and Gauzens (Roman and Gauzens, 1997) suggest that total carbon ingested by copepods is two to six times higher than that obtained considering only chlorophyll alone. This makes any estimation of carbon flux based only in herbivory unrealistic.

Although it is impossible to obtain accurate quantitative estimates of copepod-mediated flux without knowledge of processes such as omnivory, assimilation rates, pellet degradation, or sinking velocity, the present study provides a comparative basis to locate regions of the Atlantic

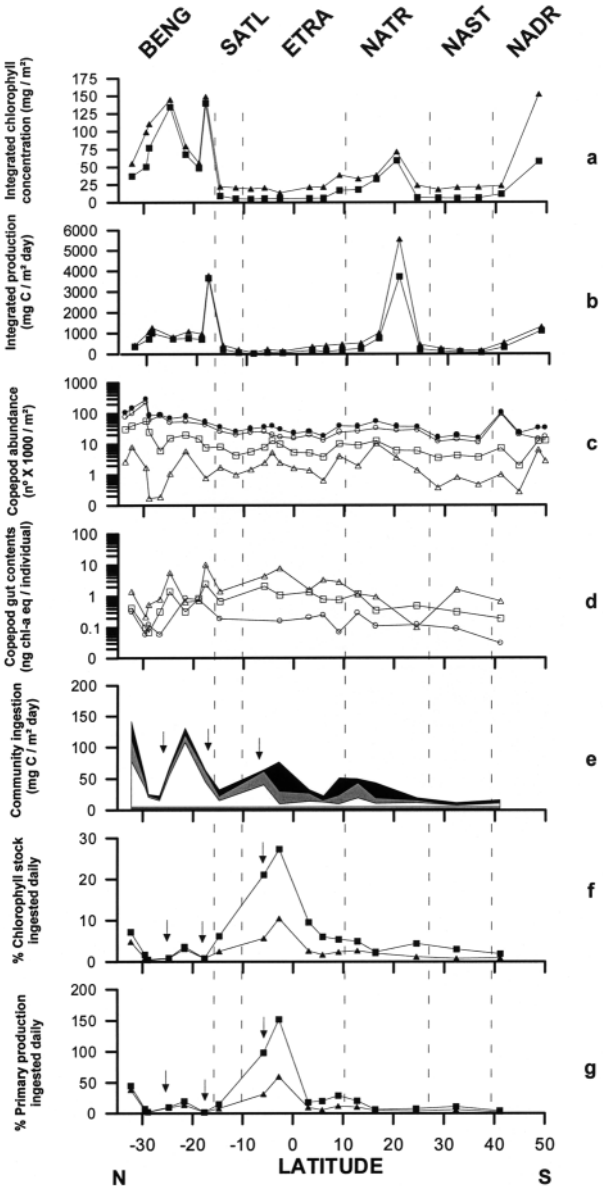

Fig. 4. Latitudinal variation in integrated chlorophyll concentration (**a**), integrated primary production (**b**), copepod abundance (**c**), copepod gut contents (**d**), total community ingestion rate (**e**), grazing impact on phytoplankyton biomass (**f**) and production (**g**) during AMT6. KEY: (**a**), (**b**), (**f**) and (**g**) (▲) total phytoplankton; (■) phytoplankton >2 μm. (**c**) and (**d**) (●) total; (△) >1000 μm; (□) 500–1000 μm; (○) 200–500 μm**.** (**e**) solid shading, >1000 μm; grey shading, 500–1000 μm; unshaded area, 200–500 μm. (↓) 200–500 μm fraction not available.

Ocean where this flux is potentially important. In general, it has been proposed that productive regions present higher carbon export rates than unproductive ones, but mesozooplankton contribution to flux varies considerably between oceanic areas, being higher in oligotrophic regions [reaching up to 100% of total flux, (Dam *et al.*, 1995)] where sinking rates of individual cells and small microzooplankton pellets are minimal (Gowing and Silver, 1985).

In spite of its qualitative importance, low carbon ingestion reported in the present study, enhanced by the low contribution of large animals (producers of larger pellets), confirms the suggested low quantitative importance of flux under oligotrophic conditions. Copepod ingestion in both oligotrophic gyres was always lower than 30 mg C m^{-2} day^{-1} with a minimum of 1.6 mg C, and in the range found in the oligotrophic Pacific Ocean [11.6–98 mg C m^{-2} day^{-1}; by (Zhang *et al.*, 1995)] or Head *et al.* (Head *et al.*, 1999) for the North East Atlantic at 37°N (0.4–5.3 mg C m^{-2} day^{-1}).

In contrast, in productive areas carbon ingestion is higher, as is the contribution of large-medium animals. In all upwelling regions, where the amount of exportable material may be 10–100 times higher than in other marine ecosystems (Barber and Smith, 1981), up to 150 mg C m^{-2} were ingested daily. These values are in the range proposed by Peterson *et al.* (Peterson *et al.*, 1990) in the Benguela region (although integrated over 20 m) but lower than those reported for upwellings in the Banda Sea (Arinardi *et al.*, 1990). Northern temperate waters present values of 174 mg C m^{-2} day^{-1} in spring, similar to those reported by Morales *et al.* (Morales *et al.*, 1993) at 50° North (141 mg C m^{-2} day^{-1}), while ingestion is much lower in autumn (around 20 mg C m^{-2} day^{-1}) and in the range (6.1–65 mg C m^{-2} day^{-1}) found previously (Dam *et al.*, 1993; and Barquero *et al.* (1998) at similar latitudes. Maximum ingestion on all the transects was found in the Subtropical Convergence during spring (250 mg C m^{-2} day^{-1}), in the range proposed for the STC area off South Africa [28–257 mg C, (Pakhomov and Perissinotto, 1997)] but higher than near New Zealand [1–40 mg C, (Bradford-Grieve *et al.*, 1998)]. Increases in biological activity in the STC point to an important sink of atmospheric CO_2, although some authors (Pakhomov *et al.*, 1994) have suggested this area (near South Africa), and all the southern Ocean (Huntley *et al.*, 1991) is characterized by an inefficient biological pump due to high macroplankton/micronekton biomass which leads to an increase in top predators and CO_2 respiratory losses to the atmosphere.

The role of zooplankton in controlling phytoplankton populations has been widely reported in the literature. Zooplankton grazing is supposed to be one of the main reasons for the steady state in phytoplankton biomass typically found in the oligotrophic ocean (Cullen *et al.*, 1992; Banse, 1995). Phytoplankton size structure in these areas, points to a low importance of copepods compared with microzooplankton, but this is the first study (Table III) which supports that view in the extensive oligotrophic

gyres of the Atlantic Ocean, where less than 3% of total chlorophyll standing stock and less than 10% of total primary production is ingested daily by copepods. However, although it seems clear that the main grazer of the dominant small phytoplankton should be microzooplankton, copepod grazing could represent an important control mechanism of large phytoplankton ingesting 30% of its primary production at several locations in these areas. We are aware of the inaccuracy of a 2 μm limit to distinguish phytoplankton suitable for copepods but the preferable 5 μm limit (Nival and Nival, 1976) is not available for AMT cruises.

In temperate waters grazing impact is similar or even lower than in oligotrophic areas due to uncoupling between phytoplankton and zooplankton. However, we also found high grazing impact of copepods in large cell production at higher latitudes in the Northern Hemisphere (reaching 40% of its production) and the Subtropical Convergence during spring. At this location, copepods ingest 20% and ~100% of large cell biomass and production, in the range reported by Pakhomov and Perissinotto (Pakhomov and Perissinotto, 1997) (13% and 90% of biomass and production). The importance of copepod grazing was more evident in the areas influenced by upwelling. These are very dynamic regions where high phytoplankton growth rates usually mean that zooplankton do not exert grazing control. However, zooplankton grazing could also represent very high impact on phytoplankton biomass and production, especially at late stages of the upwelling (Painting *et al.*, 1993). We report extremely high percentages (>100%) of phytoplankton biomass and production (especially large cells) grazed daily by copepods, although in the Benguela upwelling zone the very high chlorophyll and primary production make the grazing impact lower.

The main source of error associated with the methodology employed is the destruction of pigment in the copepod guts. Published data report a high variability in degree of destruction, ranging between 0 and 100% of ingested chlorophyll. Goericke *et al.* (Goericke *et al.*, 2000) suggest that this variability could be due to recovery of fluorescence by degradation products under certain conditions. In this sense, if extracts are in contact with oxygen for a certain time (as in our case) and not analysed shortly after extraction, underestimation will be lower. Dam and Peterson (Dam and Peterson, 1988) proposed an average value of 33%, which has been applied by several authors when direct estimates are not available (Dam *et al.*, 1993; Peterson and Dam, 1996; Morales *et al.*, 1991), and would lead to an underestimation by a factor of 1.4, which does not represent significant changes in our general conclusions. However, extent of destruction seems to vary depending on environmental conditions, and the factors involved are still not clear. It has been suggested (Penry and Frost, 1991) that pigment destruction is low (<20%) at low food levels, such as those found in the oligotrophic gyres. Recent results (McLeroy-Etheridge and McManus, 1999) seem to contradict this fact, with higher destruction at low food concentrations, but the same authors proposed the short acclimation period of animals to experimental conditions as an explanation to their results. According to this, possible underestimation of our ingestion rates will be low in the oligotrophic gyres, while higher destruction in productive areas would increase the suggested importance of copepod grazing in these regions.

Table III: Literature values of copepod ingestion rates, grazing impact on phytoplankton standing stock and primary production in the biogeochemical provinces sampled on the AMT cruises

Ingestion rate (mg C m^{-2} day^{-1})	Chl *a* standing stock	Primary production	Province	Source
40–65	0.2	<3%	NADR	Barquero *et al.*, 1998
6.1–50		2.7%	NADR	Dam *et al.*, 1993
9.18–32	<1%	<2%	NADR	Morales *et al.*, 1991
5.6–141		<10%	NADR	Morales *et al.*, 1993
57–91	1.5–2.1%		NADR	Head *et al.*, 1999
121–221	5–20		BENG	Peterson *et al.*, 1990
	5–38%		BENG	Painting *et al.*, 1993
	<25 %		BENG	Verheye *et al.*, 1992
0.4–5.3	2.6–8.9 %		NAST	Head *et al.*, 1999

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