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Size-fractionated mesozooplankton biomass, metabolism and grazing along a 50°N–30°S transect of the Atlantic Ocean

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Size-fractionated mesozooplankton grazing and metabolism were investigated along the wide latitudinal range (50°N–30°S) covered during the Atlantic Meridional Transect (AMT) 11 cruise. Five different oceanic provinces were traversed in this cruise: North Atlantic Drift (NADR), North Atlantic Subtropical Gyral (NAST), Canary Coastal (CNRY), Eastern Tropical Atlantic (ETRA), and South Atlantic Gyral (SATL). CNRY and ETRA were affected by the upwelling Mauritanian and equatorial respectively and primary production in these provinces was higher than in the oligotrophic subtropical gyres (NAST and SATL). Both mesozooplankton and phytoplankton biomass were highest around the equator. The amount of chlorophyll a ingested daily by copepods was noticeably higher in mesotrophic than in oligotrophic provinces as shown by the spatial distribution of gut content values and the high abundances of copepods recorded at the equator. Grazing impact along the transect ranged from 0.2 to 5.6% of the phytoplankton standing stock and from 1.6 to 14.5% of primary production. If only phytoplankton >2 μm are considered, the ranges are 1.0–19.4% (stock) and 3.4–44.7% (primary production). Grazing impact upon both phytoplankton biomass and primary production followed a spatial distribution similar to that of chlorophyll a ingestion, with higher values in upwelling zones than in the gyres. Weight-specific rates of respiration and NH_4^+ and PO_4^{3-} excretion showed large variability both along the transect and within provinces, but did not differ between provinces. Therefore, zooplankton assemblages inhabiting the different provinces visited in the AMT 11 seem to be adapted to the prevailing thermal conditions. Given the substantial proportion of nitrogen and phosphorus that are supplied to primary producers through the excretory activity of mesozooplankton (the percentage of nitrogen and phosphorus requirements of phytoplankton accounted for by mesozooplankton excretion was >30% in all the provinces) it follows that they may play a crucial role as nutrient regenerators, especially in the oligotrophic gyres where regenerated production dominates.

INTRODUCTION

Mesozooplankton play a key role in marine ecosystems given their capacity to control phytoplankton populations (Banse, 1994), to regenerate nutrients (Ketchum, 1962), and to export downward biogenic matter (Longhurst and Harrison, 1989; Legendre and Rivkin, 2002). Traditionally most of the investigations on mesozooplankton have been centred in coastal areas, despite levels of primary production in the open ocean being 2.5–4 times that of the coastal provinces (Longhurst *et al.*, 1995). There are also many studies concerning zooplankton in the open ocean, but they are mostly focused on its distribution [see for example Finenko *et al.* (Finenko *et al.*, 2003) and references therein]. Zooplankton processes such as grazing and metabolism in the open ocean waters have received growing attention in recent years, particularly in the Pacific Ocean within the JGOFS Equatorial Pacific study [e.g. (Dam *et al.*, 1995; Zhang *et al.*, 1995; Le Borgne and

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Rodier, 1997; Roman and Gauzens, 1997; Zhang and Dam, 1997; Roman *et al.*, 2002; Le Borgne and Landry, 2003)]. In contrast, studies on mesozooplankton grazing and metabolism in the Atlantic Ocean until the start of the Atlantic Meridional Transect (AMT) programme (Aiken and Bale, 2000) are practically restricted to those investigations carried out by Le Borgne [e.g. (Le Borgne 1977, 1981, 1982a, b)] in the 1970s and 1980s in the Gulf of Guinea. For both the Pacific and the Atlantic Ocean, information on mesozooplankton metabolism and grazing in the subtropical oligotrophic gyres remains rather limited (Welschmeyer and Lorenzen, 1985; Harrison *et al.*, 2001; Huskin *et al.*, 2001; Woodd-Walker *et al.*, 2002), and the role of mesozooplankton on biogeochemical fluxes in tropical and subtropical areas is still poorly studied, especially in the Atlantic Ocean.

The AMT cruises traverse several oceanic provinces characterized by particular physical and biological properties (Longhurst, 1998), and thus provide an excellent opportunity to investigate the mesozooplankton on a variety of ecological domains. However, from the large number of papers derived from previous AMT cruises, only a few are devoted to mesozooplankton. Studies concerning mesozooplankton in the AMT programme are focused on its size structure (Gallienne and Robins, 1998), distribution (Woodd-Walker, 2001; Woodd-Walker *et al.*, 2002), and grazing (Huskin *et al.*, 2001). The main objective of our study is to gain some knowledge about the role of mesozooplankton on biogeochemical cycles and on the food web functioning in the different ecological domains of the Atlantic Ocean located between 50°N and 30°S (i.e. northern and southern oligotrophic subtropical gyres, upwelling areas, and northern temperate waters). To achieve this, we analysed during the AMT 11 cruise the latitudinal changes in mesozooplankton size structure, grazing impact in different productive regimes, and variations in metabolic rates of mesozooplankton exposed to the wide range of temperatures prevailing between 50°N and 30°S. We also investigated whether the grazing impact and the regeneration of nutrients by mesozooplankton are as important to phytoplankton under oligotrophic conditions as it has been suggested [e.g. (Banse, 1995)]. In AMT 11 only two stations were sampled in the northern temperate province, so most of our results will be discussed on the basis of the differences between oligotrophic subtropical and mesotrophic equatorial areas.

To our knowledge, the results presented here are the first reporting the latitudinal variations of mesozooplankton grazing and metabolism on a quasi-synoptic basis in such a large range (~50°N–30°S). Furthermore, they will contribute to fill the gap in knowledge concerning the lack of information on mesozooplankton in oligotrophic subtropical provinces.

METHOD

Study area and phytoplankton

The AMT 11 cruise was conducted from 12 September to 10 October 2000, covering a wide latitudinal range (~50°N–30°S). A total number of 21 stations were sampled along the transect (Fig. 1). Vertical profiles of temperature were measured with a Seabird 911 + CTD. Size-fractionated chlorophyll *a* (Chl *a*) concentration and primary production were measured as described in Fernández *et al.* (Fernández *et al.*, 2003). Briefly, 250 mL water samples for Chl *a* determination were collected from 5–6 depths with Niskin bottles and then filtered sequentially through 20, 2 and 0.2 μm pore polycarbonate filters. After extraction with 90% acetone at 4°C overnight, the Chl *a* fluorescence was determined with a 10 SU Turner Designs fluorometer. As for primary production, three clear and one black 70 mL polypropylene bottles were filled with seawater taken from the same depths as the Chl *a* samples. After inoculating with $NaH^{14}CO_3$, the bottles were incubated for 24 h, and then were filtered through 20, 2 and 0.2 μm

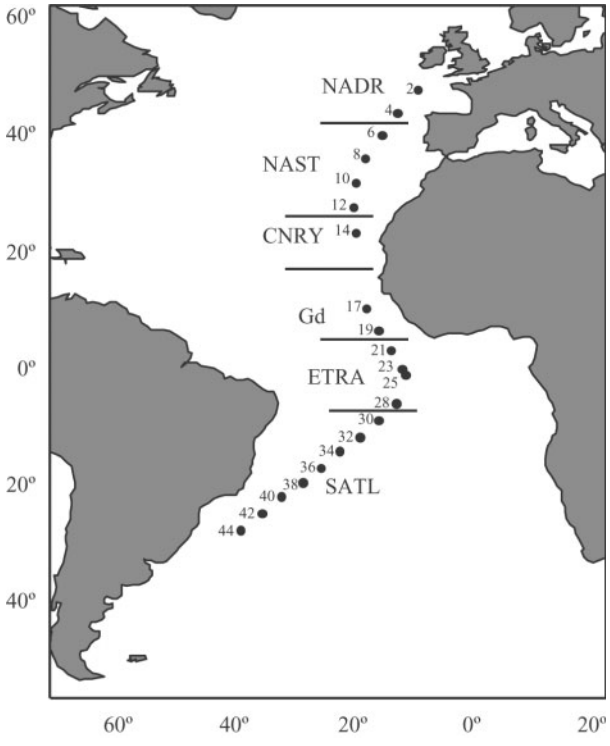

Fig. 1. AMT 11 cruise track showing the location of the 21 stations sampled and the approximate boundaries of the five oceanic provinces traversed: North Atlantic Drift (NADR), North Atlantic Subtropical Gyral (NAST), Canary Coastal (CNRY), Eastern Tropical Atlantic (ETRA), and South Atlantic Gyral (SATL). Gd indicates the location of the Guinea dome, a transition zone between CNRY and ETRA.

pore polycarbonate filters. Radioactivity of the samples was measured on a Beckman LS6000 SC counter.

Zooplankton collection

Mesozooplankton samples were collected between 04:00 and 06:00 h (local time) using a 60 cm diameter WP-2 triple net, supplied with 200 μm mesh size, and equipped with filtering cod-ends. Hauls were made vertically from 200 m to surface at ~0.5 m s^{-1}. The nets were rinsed to concentrate all the organisms in the cod-ends for biomass and abundance samples but not for gut content measurements or for deck incubations. Only one haul could be carried out at stations 2, 4 and 12, so samples for abundance and gut contents were not taken there. Cod-end contents were always sieved sequentially through meshes of 1000, 500 and 200 μm to separate the mesozooplankton into large, medium and small fractions. The same samples were used to estimate abundance and for taxonomic composition. Samples were preserved in 4% borax-buffered formalin–seawater solution in 250 mL polyethylene jars until counting and determination in the laboratory under a dissecting stereomicroscope. Depending on the concentration of animals in each jar, the samples were examined entirely or sub-sampled into aliquots by a Stempel pipette. Biomass samples were filtered onto pre-weighted Whatman GF/A glass fibre filters and then stored at −20°C. The filters were dried at 60°C for ~24 h before weighing. Carbon and nitrogen content analyses were performed with a Perkin Elmer 2400 Elemental Analyser using acetanilide as the standard.

Feeding

The ingestion rate of copepods was estimated using the gut pigment method (Mackas and Bohrer, 1976). To determine the content of Chl *a* in the gut, copepods were gathered on sharkskin filters immediately after size fractionation and stored at −20°C in complete darkness until laboratory analysis. The numbers of individuals picked up for gut fluorescence measurements were 75–100, 50 and 15–25 for the small, medium and large fractions, respectively. Four sub-replicates were taken in each case except for the large fraction at stations 6 and 34, where the number of sub-replicates was two and three respectively because of low availability of individuals. Gut pigments were extracted overnight in 6 mL of 90% acetone at 4°C in darkness, and fluorescence was measured with a Turner Designs 10–005R fluorometer before and after acidification with 1 N HCl. No corrections for Chl *a* destruction were applied. The gut evacuation rates (k) were calculated following the equation of Dam and Peterson (Dam and Peterson, 1988):

$$k = 0.012 + 0.001 \times \text{Temp } (^{\circ}\text{C})$$

The daily ingestion rate (I) was estimated as the product of copepod gut content (GC) and the gut evacuation rate:

$$\text{I} = \text{GC} \times k$$

Given that stations were sampled during night-time, I values probably represent maximum daily ingestion rates (Båmstedt *et al.*, 2000). Finally, the amount of Chl *a* grazed daily by copepods was estimated by multiplying their numerical abundance with the corresponding ingestion rate. Grazing impact was assessed both on total phytoplankton and on the >2 μm phytoplankton fraction. The phytoplankton carbon ingested was calculated by applying a C to Chl *a* ratio of 61, which is the average value calculated by Marañón *et al.* (Marañón *et al.*, 2001) for the AMT 1, 2 and 3. To estimate the percentage of the minimum carbon requirements of the mesozooplankton that were met by phytoplankton ingestion, assimilation efficiency was assumed to be 70% (Conover, 1966).

Metabolism

Mesozooplankton respiration and excretion rates were measured by on deck incubations. Animals collected for incubation were size-fractionated in a cool box filled with surface seawater and transferred at once to 3 L jars filled with 0.2 μm filtered seawater, where they were kept for ~2 h for acclimation. Mixed crustaceans swimming actively were introduced with a pipette, avoiding exposure of the animals to air, in 1 L glass bottles filled with 0.2 μm filtered seawater. Gelatinous zooplankton were not selected due to the high mortality rates observed in previous trials. The numbers of individuals incubated per litre, averaged over all stations, were 162 ± 98 (mean ± SD), 56 ± 36 and 10 ± 4 for the fractions small, medium and large respectively. Three control bottles without animals and three experimental replicates for each size fraction were incubated for 18–20 h in a bath at the temperature recorded for the deep Chl *a* maximum (±0.1°C) and under dim light conditions. At the end of the incubation, two subsamples for oxygen and another two for NH_4^+ and PO_4^{3-} were taken by siphoning out water through a 200 μm mesh. Dissolved O_2 concentrations were measured on board with the Winkler titration method using a Metrohm 716 DMS Titrino. Respired oxygen was calculated as the difference of control minus experimental O_2 concentration, and was converted to carbon to estimate the minimum carbon requirements (basal metabolism) of mesozooplankton, assuming a respiratory quotient of 0.97 (Omori and Ikeda, 1984). Oxygen saturation at the end of the incubations was >85% in all cases. Samples for NH_4^+ and PO_4^{3-} determination were frozen at −20°C for later

analysis in the laboratory according to Grasshoff *et al.* (Grasshoff *et al.*, 1983) and using a Technicon AAII autoanalyzer. After subsampling, the animals incubated were collected on Whatman GF/A filters and frozen until their analysis for carbon and nitrogen content, as mentioned for the biomass samples. The percentages of N and P required by phytoplankton were estimated from primary production rates and by applying standard Redfield ratios, i.e. C:N:P = 106:16:1.

RESULTS

Thermal structure and phytoplankton distribution

The vertical distribution of temperature (Fig. 2) and the productive regime (Fig. 3) reflect the differences between the five provinces traversed in AMT 11: North Atlantic Drift (NADR), North Atlantic Subtropical Gyral (NAST), Canary Coastal (CNRY), Eastern Tropical Atlantic (ETRA), and South Atlantic Gyral (SATL) (Longhurst, 1998). The more productive situations were found in ETRA, coinciding with the equatorial upwelling, and in the only station sampled in CNRY, which seems to be affected by the Mauritanian coastal upwelling. The Guinea dome (Gd) appears as a transition zone between CNRY and ETRA, and differed from these two provinces by a deepening of the isotherms and lower primary production values. Phytoplankton biomass was also higher in the equatorial zone than in the oligotrophic gyres, although the differences were not as marked as for primary production (Fig. 3), and a similar pattern was observed for the contribution of large cells (>2 μm) to total phytoplankton (Fig. 3).

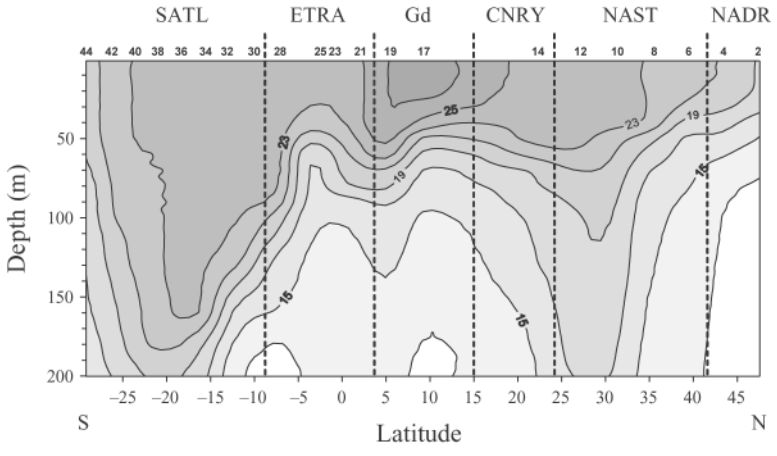

Fig. 2. Spatial distribution of temperature (°C) along the AMT 11 transect. Station numbers are indicated above the top axis. Vertical dashed lines separate the different oceanic provinces.

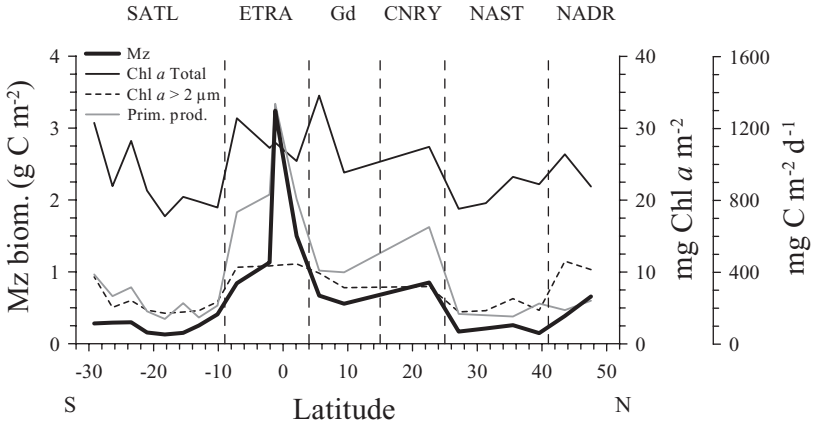

Fig. 3. Latitudinal variation in mesozooplankton (Mz) biomass (in g C m^{-2}) integrated over the upper 200 m, and phytoplankton biomass (in mg Chl *a* m^{-2}) and primary production (in mg C m^{-2} day^{-1}) integrated over the euphotic zone along the AMT 11 transect.

Mesozooplankton biomass and distribution

The highest mesozooplankton biomass was found in ETRA, particularly around the equator (3.24 g C m^{-2} at station 23), and the lowest in the two oligotrophic gyres [0.20 ± 0.05 (SD) and 0.25 ± 0.10 g C m^{-2} in NAST and SATL respectively], where variability was also low. Mesozooplankton and phytoplankton biomass and primary production followed a similar pattern along the transect (Fig. 3). Mesozooplankton biomass fitted to primary production better than to phytoplankton biomass (Figs 3 and 4). The matching between mesozooplankton and phytoplankton biomass was better when only the fraction of phytoplankton >2 μm was considered (Fig. 3). This observation was supported by regression analysis, which showed a higher coefficient of determination for total than for >2 μm phytoplankton (Figs 4A and B). The ratio of total phytoplankton to mesozooplankton biomass (P:Z) in carbon units m^{-2} was much lower in the mesotrophic provinces than in the oligotrophic gyres, inversely to the pattern observed for large phytoplankton (Fig. 5). The coefficient of correlation between the P:Z ratio and the percentage of Chl *a* > 2 μm was −0.76 (n = 21; P < 0.001).

With regard to size structure, the contribution of the large fractions of both phytoplankton (>2 μm) and mesozooplankton (>1000 μm) to total biomass seems to increase towards the equatorial upwelling (Fig. 6). Nevertheless, the relative importance of the large mesozooplankton showed much more variability along the transect than the large phytoplankton. Despite this variability, the average percentages of total mesozooplankton biomass accounted for the large fraction were similar in the two oligotrophic gyres [42.7 ± 7.1 (SD) % in NAST and 46.5 ± 9.5% in SATL]. This percentage rose up to 59.3 ± 10.1% in ETRA, close to the value obtained in the CNRY station (63.2%).

In terms of abundance, mesozooplankton composition was mostly comprised of copepods. Their contribution to total abundance ranged from 82.7% (station 38, in SATL) to 97.7% (station 6, NADR). This contribution did not vary between provinces, and presented an average value for the whole transect of 90.2 ± 3.6 (SD) %. Total abundance of copepods along the transect resembled the distribution of mesozooplankton biomass, with highest values in ETRA (Fig. 7A). Copepod abundance showed, however, greater variability than biomass in the oligotrophic gyres, and also increased at the southern end of the transect more markedly than biomass. Such increase was also observed for phytoplankton biomass and production, and was probably due to the influence of the Brazil Coastal Current.

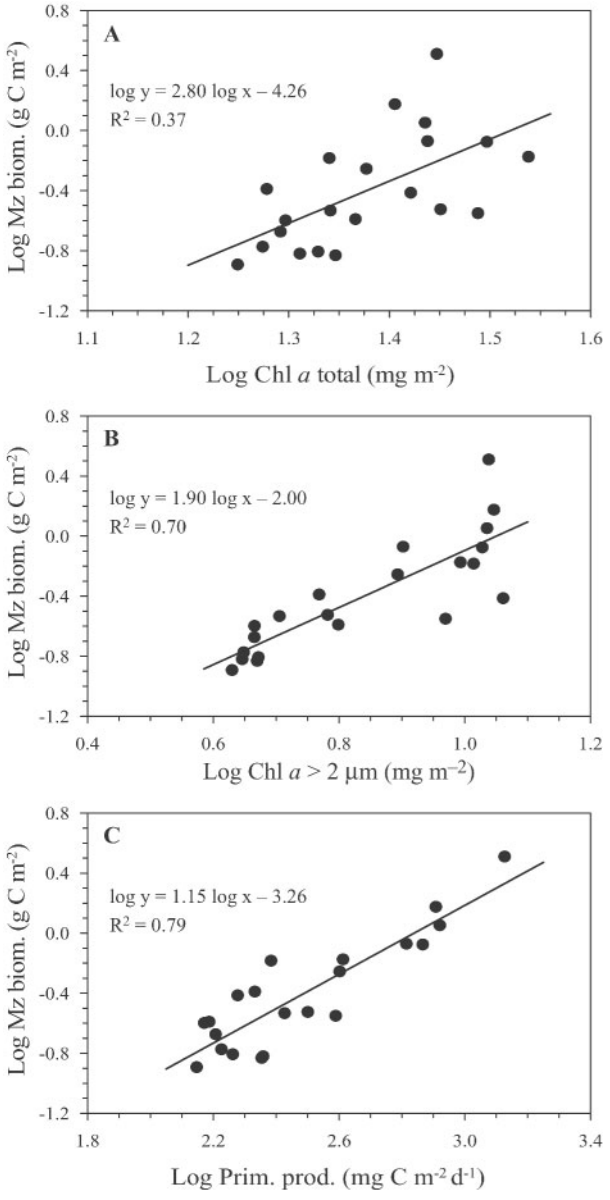

Fig. 4. Relationships of mesozooplankton (Mz) biomass with total (**A**) and >2 μm (**B**) phytoplankton biomass, and with primary production (**C**).

Feeding

The highest copepod gut contents values were obtained in the CNRY station for the fractions medium and large, and in the station 19 (in Gd) for small copepods (Fig. 7B). Despite the differences in Chl *a* concentration, copepod gut contents in ETRA did not differ from those measured in the subtropical gyres. Nevertheless, given the high abundances of copepods recorded at the equator the amount of Chl *a* ingested daily by copepods was clearly higher in

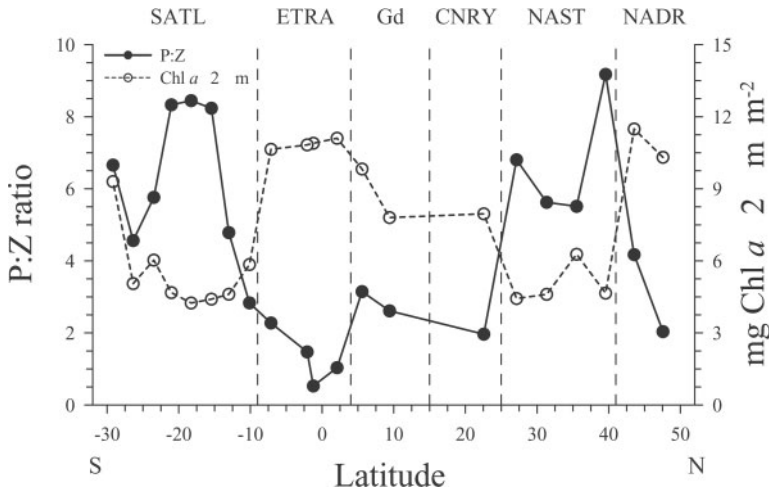

Fig. 5. Latitudinal variation in phytoplankton to mesozooplankton biomass ratio (P:Z) and integrated Chl *a* >2 μm.

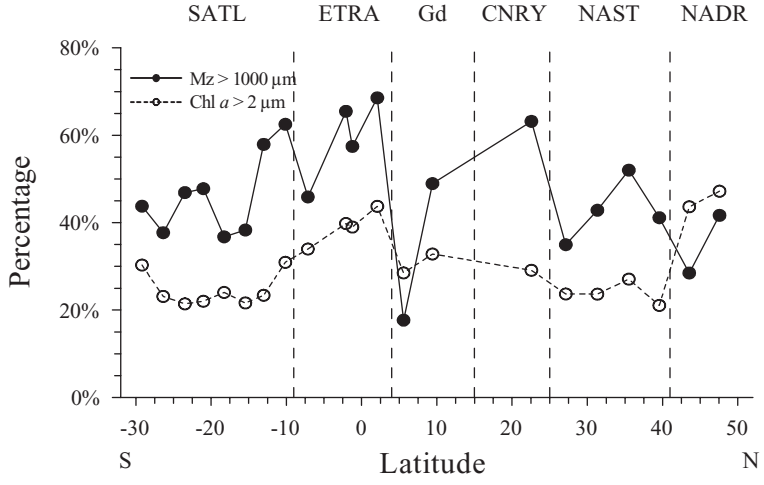

Fig. 6. Contribution of the large fractions of phytoplankton (>2 μm) and mesozooplankton (>1000 μm) to total biomass.

ETRA than in the gyres (Fig. 7C). Total Chl *a* ingested daily was positively correlated with mean Chl *a* concentration in the photic layer ($R^2 = 0.64$; $P < 0.001$).

Grazing impact upon both phytoplankton biomass and primary production was highest in CNRY, and there were no marked differences between ETRA and the gyres (Fig. 8). The percentage of phytoplankton standing stock grazed daily by copepods ranged from 0.3 to 6.1%. Grazing impact upon phytoplankton >2 μm ranged from 1.1 to 21.0%. As for primary production, the grazing impact varied from 1.8 to 15.7% of total production and from 3.4 to 48.4% of the production due to phytoplankton >2 μm. In all instances maximum and minimum values of grazing impact were observed at stations 14 (CNRY) and 38 (SATL), respectively. The average percentages for the different provinces are presented in Table I. Phytoplankton ingestion was not enough to maintain the basal metabolism of mesozooplankton except at station 14 (CNRY). Herbivory accounted for 104.5% of the minimum metabolic requirements of mesozooplankton at the CNRY station, where phytoplankton ingestion by copepods was highest. For the rest of the stations, this percentage did not exceed 60%.

Metabolism

Weight-specific rates of mesozooplankton respiration and NH_4^+ and PO_4^{3-} excretion showed a great variability both along the transect and within provinces (Fig. 9). In general these rates decreased from the small to the large size fraction, in accordance with the allometric relationship

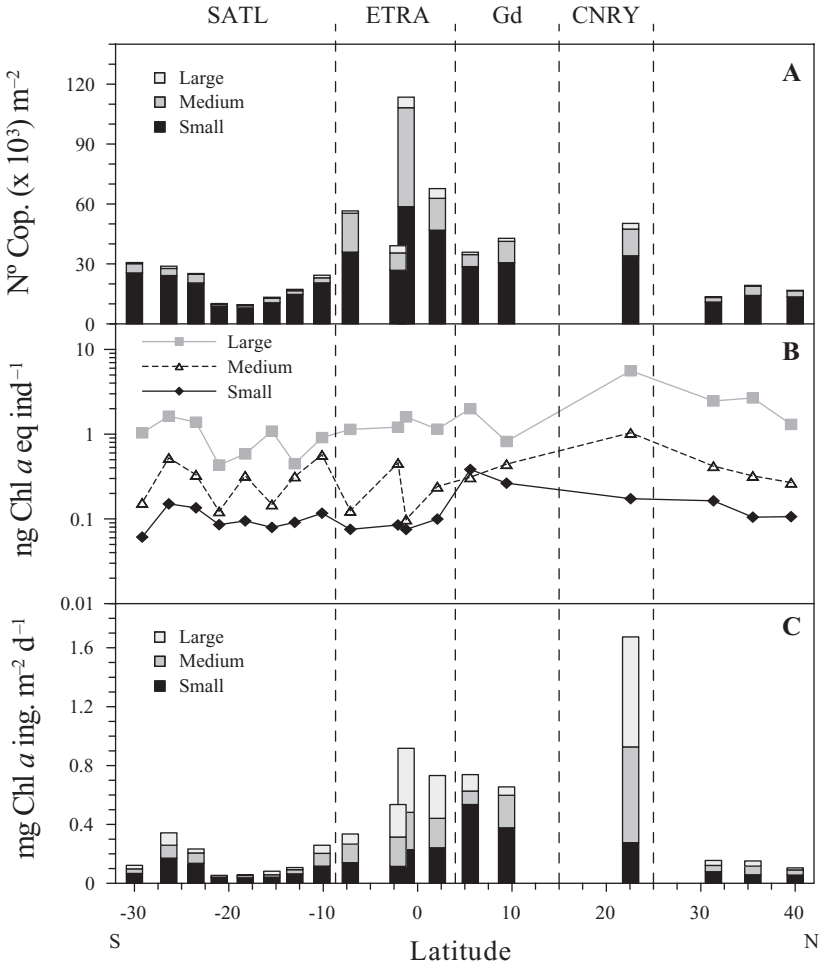

Fig. 7. Abundance (**A**), gut pigment contents (**B**), and total amount of Chl *a* ingested (**C**) by the three size classes of copepods along the transect.

between metabolic rate and body size. As observed for gut contents, the metabolic rates did not follow a clear pattern for any of the three size fractions incubated. The total amount of metabolic end-products released to the medium by mesozooplankton followed the same pattern along the transect as biomass, with highest values at the equatorial stations.

The NH_4^+ excreted by mesozooplankton provided a considerable proportion of the estimated nitrogen requirements of primary producers [120.5 ± 38.9 (SD) % in NADR, 47.1 ± 38.4% in NAST, 30.9% in CNRY, 35.9 ± 14.8% in Gd, 41.7 ± 13.8% in ETRA and 33.6 ± 12.3% in SATL]. The elevated mean percentage estimated for NAST (northern gyre) as compared with SATL (southern gyre) was due to the very high value of station 8 (89.7%), whereas percentages in the other two stations in NAST were similar to those in SATL (Fig. 10). The percentages of phosphorus requirement of phytoplankton met through mesozooplankton PO_4^{3-} excretion were 75.7 ± 17.2% (NADR), 54.3 ± 30.4% (NAST), 46.3% (CNRY), 83.0 ± 60.8% (Gd), 60.3 ± 17.8% (ETRA) and 35.2 ± 16.3% (SATL). The latitudinal variation in the contribution of PO_4^{3-} excretion to phytoplankton requirements was similar to that observed for NH_4^+ excretion. With the exception of station 8, the percentages in NAST were similar to those in SATL (Fig. 10).

DISCUSSION

Biomass and distribution

Mesozooplankton biomass between 50°N and 30°S was highest in the vicinity of the equator, coinciding with the maximum productivity along the transect, and lowest in the oligotrophic gyres. The inverse relationship between mesozooplankton biomass and the depth of the thermocline

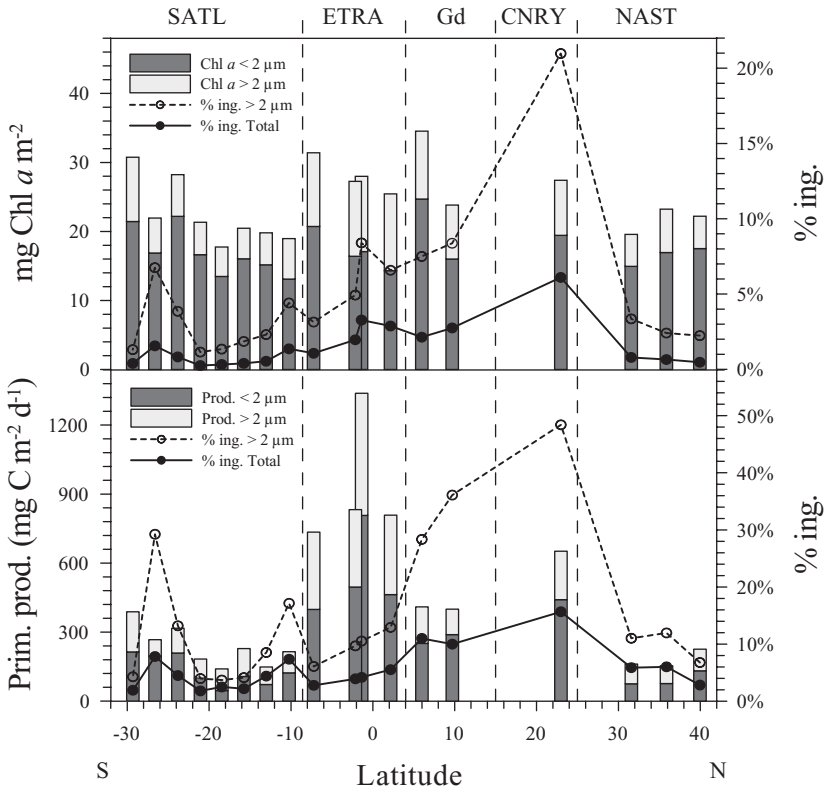

Fig. 8. Grazing impact upon both total and >2 µm phytoplankton standing stock and primary production.

Table I: Mean ± SD values of copepods grazing impact upon total and >2 µm phytoplankton standing stock (% Chl a ingested) and production (% Pp ingested)

Province	% Chl *a* ing.		% Pp ing.	
	>2 µm	Total	>2 µm	Total
NAST	2.7 ± 0.6 (4.0 ± 0.9)	0.6 ± 0.2 (1.0 ± 0.2)	9.9 ± 2.8 (14.9 ± 4.1)	4.9 ± 1.8 (7.4 ± 2.7)
CNRY	21.0 (31.5)	6.1 (9.2)	48.4 (72.6)	15.7 (23.5)
Gd	7.9 ± 0.6 (11.9 ± 0.9)	2.4 ± 0.4 (3.7 ± 0.6)	32.2 ± .5.5 (48.3 ± 8.2)	10.5 ± 0.7 (15.7 ± 1.1)
ETRA	5.8 ± 2.2 (8.6 ± 3.4)	2.3 ± 1.0 (3.4 ± 1.5)	9.8 ± .2.1 (14.7 ± 4.3)	4.1 ± 1.1 (6.2 ± 1.7)
SATL	2.9 ± 2.0 (4.3 ± 3.0)	0.7 ± 0.5 (1.0 ± 0.7)	10.5 ± 9.1 (15.8 ± 13.6)	4.1 ± 2.4 (6.1 ± 3.6)

In brackets, values corrected by applying a factor of 33% of Chl *a* destruction (see text for more details).

found by Le Borgne (Le Borgne, 1981) in the Gulf of Guinea seems to be thus valid for the latitudinal range covered in AMT 11 (Figs 2 and 3). Mesozooplankton distribution along the transect was similar to that of phytoplankton, especially to that of the fraction >2 µm. The latitudinal trend of mesozooplankton biomass and its concordance with phytoplankton are in agreement with the pattern presented by Finenko *et al.* (Finenko *et al.*, 2003) in their review of a large dataset of phytoplankton and mesozooplankton biomass between 40°N and 40°S in the Atlantic Ocean, as well as with observations from previous AMT cruises (Woodd-Walker *et al.*, 2001). As for size structure it seems that the large fraction is more important in the equatorial than in the oligotrophic provinces, which would be in accordance with the general pattern described by Piontkovski *et al.* (Piontkovski *et al.*, 2003) and with the size structure distribution observed in AMT 2 by Gallienne and Robins (Gallienne and Robins, 1998). On

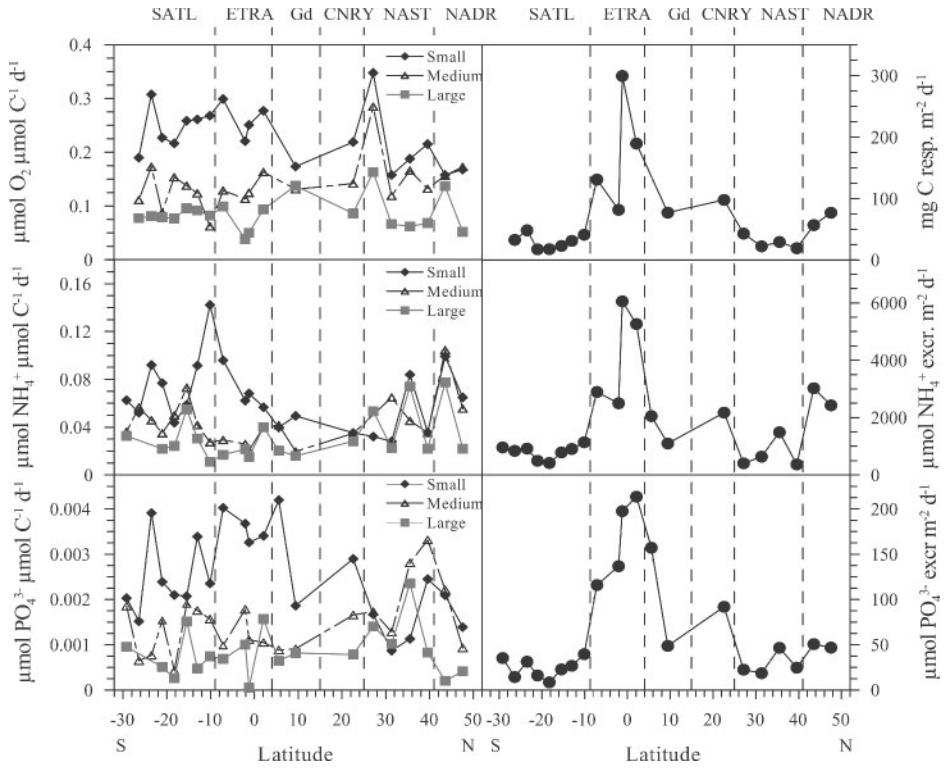

Fig. 9. Weight-specific respiration, NH_4^+ excretion and PO_4^{3-} excretion rates of the three size classes of mesozooplankton (**left**) and total amount of C respired and NH_4^+ and PO_4^{3-} excreted (**right**).

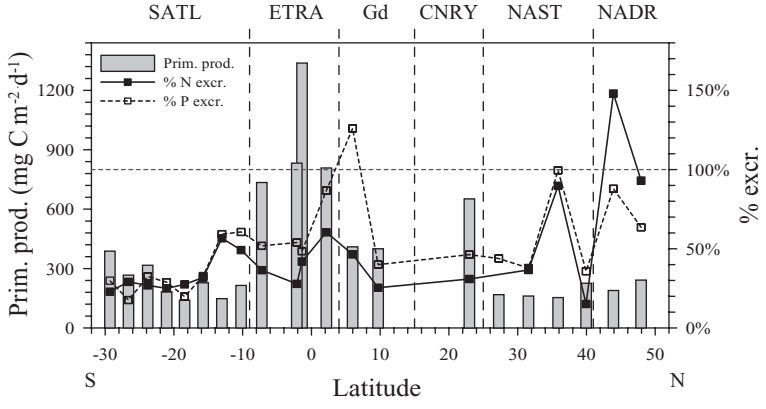

Fig. 10. Percentage of the nitrogen and phosphorus demands of phytoplankton accounted for mesozooplankton NH_4^+ (% N excr.) and PO_4^{3-} (% P excr.) excretion.

the other hand, Woodd-Walker (Woodd-Walker, 2001) pointed out that mesozooplankton assemblages from the two subtropical gyres were very similar, and different from those in the equatorial province.

P:Z ratio was higher in the oligotrophic gyres than in the mesotrophic provinces, similar to the pattern reported by Finenko *et al.* (Finenko *et al.*, 2003) and Piontkovski *et al.* (Piontkovski *et al.*, 2003). These authors suggested that such distribution could be due to a higher contribution of large phytoplankton in the equatorial province, which would be more effectively consumed by mesozooplankton. Supporting this, P:Z ratio was found to be negatively correlated with the percentage of phytoplankton >2 µm. Also, mesozooplankton distribution seemed to match phytoplankton >2 µm better than total phytoplankton biomass. In addition, considering Chl *a* destruction that is associated to

gut pigment measurements, Huskin *et al.* (Huskin *et al.*, 2001) suggested that copepod gut contents were more likely to be underestimated in the equatorial stations than in the gyres.

The comparison of phytoplankton and mesozooplankton distribution observed in the Equatorial Atlantic during AMT 11 with that described in the Equatorial Pacific by the JGOFS EqPac study [e.g. (Murray *et al.*, 1994; Dam *et al.*, 1995; Zhang *et al.*, 1995; Roman and Gauzens, 1997; Zhang and Dam, 1997; Roman *et al.*, 2002)] presents some differences between the two oceans. Phytoplankton biomass and primary production values around the equator are similar, but mesozooplankton biomass and the relative importance of the large fractions of phytoplankton and mesozooplankton are higher in the Atlantic than in the Equatorial Pacific. Mesozooplankton biomass in the equatorial area in AMT 11 is within the range reported for ETRA by Longhurst (Longhurst, 1998), so our values should not be considered exceptionally high and support higher biomass in the Equatorial Atlantic as a common feature. On the other hand, mesozooplankton biomass in the Pacific Central gyre (Karl, 1999; Al-Mutairi and Landry, 2001; Landry *et al.*, 2001) coincides with the values found in NAST in AMT 11, so the differences between oceans seem to be restricted to the equatorial area.

Feeding

The values of phytoplankton carbon ingested in the equatorial zone during AMT 11 were within the range reported for the same province by Huskin *et al.* (Huskin *et al.*, 2001) on AMT 4, 5 and 6, with the only exception of the CNRY station where the value was higher (102.1 mg C grazed m^{-2} day^{-1}). Nevertheless, for the rest of the provinces our measurements of copepod community ingestion were lower than on AMT 4, 5 and 6. The spatial distribution of copepod community ingestion in AMT 11 showed highest values in the upwelling stations and low and quite constant values in the subtropical gyres. This pattern agrees with that found by Huskin *et al.* (Huskin *et al.*, 2001) in AMT 4 and 5, but not in AMT 6, which had a different cruise track and where the stations sampled below ~15°S corresponded to the highly productive Benguela upwelling system instead of the southern oligotrophic gyre. Grazing impact upon both Chl *a* and primary production was also higher under upwelling conditions than in the gyres, again coinciding with the pattern observed in AMT 4 and 5 (Huskin *et al.*, 2001). The ingestion of phytoplankton by copepods represents an important impact on the primary production of large phytoplankton, especially in CNRY and Gd (Table I). It should be noted that the SATL stations visited in AMT 4, 5 and 6 were located at the peripheral area of this province (Huskin, 2001), so our results represent the first data of copepod ingestion in the core of this oligotrophic subtropical gyre.

Given the temporal variations in primary production and the absence of temporal changes in Chl *a* found by Marañón *et al.* (Marañón *et al.*, 2000) in the oligotrophic gyres, they suggested that grazing would play an important role in controlling phytoplankton standing stock. Nevertheless, the low grazing impact measured in our study suggests that this control should mostly be exerted by microzooplankton, which would be in accordance with the findings of other authors in the Pacific gyres (Jackson, 1980; Welschmeyer and Lorenzen, 1985). Supporting this, the study carried out by Quevedo and Anadón (Quevedo and Anadón, 2001) in an oligotrophic area of the subtropical NE Atlantic showed that phytoplankton growth was controlled by protists grazing.

As stated above, our measurements of phytoplankton ingestion by copepods might be underestimated given that no parallel experiments were performed to assess Chl *a* destruction. Båmstedt *et al.* (Båmstedt *et al.*, 2000) highlighted the discrepancy found in the literature with regard to the extent of such destruction as well as to its relationship with environmental conditions. The average figure of 33% proposed by Dam and Peterson (Dam and Peterson, 1988) has been applied by several authors when direct estimates are not available [e.g. (Pakhomov *et al.*, 1997; Calbet, 2001)]. The application of this correction factor to our results does not alter our main conclusions. Corrected ingestion values are still too low to suggest a control of the phytoplankton populations by mesozooplankton (Table I), and the amount of phytoplankton ingested would exceed the minimum carbon requirements of mesozooplankton only at station 14 (156.7% of the requirements met). Furthermore, the latitudinal pattern of phytoplankton ingestion and grazing impact would not be altered if Chl *a* degradation were higher in the equator than in the gyres such as Huskin *et al.* (Huskin *et al.*, 2001) have suggested, albeit the differences between zones would be more pronounced. Ingestion rates could have been also underestimated because of the probable defecation losses during the time between the recovery of the net and the freezing of the samples and during the size fractionation processing. Nevertheless, we tried to minimize these losses by doing all the procedures as quickly as possible, and gently fractionating the samples to decrease the stress to copepods. On the other hand, it could be argued that copepod gut contents could have been to some extent overestimated since the samples were taken at night-time, when ingestion rates are expected to be highest (Båmstedt *et al.*, 2000).

Metabolism

Determinations of metabolic rate on live zooplankton can be affected by several factors (Ikeda *et al.*, 2000). In

our study the more critical factors were probably the overcrowding of animals in the incubation bottles and a possible decrease in oxygen concentration through the experiments. Nevertheless, both the concentration of animals and oxygen saturation in our incubations seem to be far from those values that can affect metabolic rates (Ikeda *et al.*, 2000). Another possible factor affecting metabolic rates could be the physiological state of the experimental animals, however ours were checked for active swimming at the end of the incubations.

Mesozooplankton respiration and excretion measurements in AMT 11 are, to our knowledge, the first approach to the latitudinal variations of these metabolic rates on a quasi-synoptic basis in such a large range (~50°N–30°S). Conversely to the latitudinal pattern of metabolic rates as a function of temperature described by Ikeda (Ikeda, 1985), our measurements of weight-specific respiration and excretion did not differ significantly between provinces despite the differences in incubation temperature (from 14°C in NADR to 24°C at the equator). Thus, the zooplankton assemblages inhabiting the provinces visited in the AMT cruises (Woodd-Walker, 2001) seem to be adapted to the prevailing thermal conditions. This adaptive response was also found by other authors [e.g. (Musayeva and Shushkina, 1978; Saborowski *et al.*, 2002)], who investigated the latitudinal variations in respiration rate of mesozooplankton incubated at local temperature. Ikeda (Ikeda, 1985) suggested that higher metabolic rates at low latitudes could be due to the negative relationship between body size and temperature. Nevertheless, size structure in AMT 11 pointed to a greater importance of the large size class in the equator. Moreover, size sorting of mesozooplankton into small, medium and large size classes might mitigate the effect of size on metabolic rates. Because of the absence of a pattern of latitudinal variations in respiration and excretion rates along the transect, the spatial distribution of total amount of metabolic end products released by mesozooplankton would be determined by their biomass. Total C respired and NH_4^+ and PO_4^{3-} excreted were thus highest in ETRA. Mesozooplankton respiration is ~1 order of magnitude lower than the values of microbial community respiration during AMT 11 reported by Serret *et al.* (Serret *et al.*, 2002). The incorporation of our values to the results of community respiration presented by these authors does not alter their conclusions about ecosystem functioning in the different provinces, i.e. net heterotrophy in NAST and autotrophy in upwelling provinces and in SATL. The amounts of NH_4^+ excreted in AMT 11 in the equatorial zone and in SATL were similar to those measured by Le Borgne *et al.* (Le Borgne *et al.*, 1983) in the same provinces. PO_4^{3-} values in ETRA were also similar in the two studies, but in SATL ours were lower.

Mesozooplankton excretion accounted for a substantial proportion of phytoplankton nutrient requirements throughout the transect. The percentages of phytoplankton demands that are potentially supported by mesozooplankton excretion in upwelling zones in AMT 11 lie within the wide range found in previous studies in upwelling areas off NW Africa (Smith and Whitledge, 1977, 1982; Head *et al.*, 1996) and in the equatorial Atlantic (Le Borgne, 1977). Information about the role of mesozooplankton as regenerators of nutrients in NAST (Harrison *et al.*, 2001) and SATL is scarce. The percentages of both nitrogen and phosphorus required by phytoplankton that are resupplied through the excretory activity of mesozooplankton are not significantly higher in the northern than in the southern gyre. These percentages showed a large variability along the transect. Given the differences in *f*-ratio values between zones [0.1 in NAST and 0.8 in CNRY (A. Bode, personal communication)], the nitrogen recycling efficiency (King, 1987) would be higher in the subtropical gyres (low *f*-ratio) than in upwelling zones. Therefore, the excretory activity of mesozooplankton might play an important role in decreasing the deficit of nitrogen suggested by Agustí *et al.* (Agustí *et al.*, 2001) for the subtropical N Atlantic.

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