Journal of Oceanography, Vol. 55, pp. 471 to 482. 1999

Large-Scale and Mesoscale Distribution of Plankton Biomass and Metabolic Activity in the Northeastern Central Atlantic

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(Received 5 May 1998; in revised form 26 January 1999; accepted 27 January 1999)

Plankton biomass and indices of metabolism and growth [electron transport system (ETS), glutamate dehydrogenase (GDH) and aspartate transcarbamylase (ATC) activities] were studied over a 2,800 km east-west section of the tropical North Atlantic Ocean (21°N) in <200, 200–500 and >500 μm size classes. On the large-scale, zooplankton (>200 μm) enzymatic activities increased westward in the study section, where large cyanobacteria chains (*Trichodesmium spp.*) were observed. Parallel to it, an increase in medium calanoids (1–2 mm length) was observed towards the western part of the transect, whereas small calanoids (<1 mm) were dominant throughout the boundary area of the subtropical gyre. Microplankton ETS and mesoplankton ETS and ATC activities seemed to match the wave length of low frequency waves. Our results suggest that such waves are related to the observed enhancement of metabolic activity of micro- and mesoplankton. The large-scale and mesoscale variability observed give evidence of the inadequacy of assuming a steady-state picture of the euphotic zone of tropical and subtropical waters.

Keywords:
· Plankton,
· biomass,
· metabolism,
· northeast Central Atlantic.

1. Introduction

Subtropical gyres are considered to be among the most stable areas of the ocean. The thermal and saline structures of the water column do not undergo drastic seasonal changes. Generally, low variations are observed in the values of both chlorophyll and zooplankton biomass. In contrast, high fluctuations are found in temperate and equatorial areas, where seasonality and large-scale divergences cause variations in the thermal structure (e.g., Voituriez and Herbland, 1977; Kaiser and Postel, 1979). The relationship between the productivity of a system and the vertical structure of the water column has been widely studied during the last decades. Extensive work has been carried out related to the presence of subsurface chlorophyll maxima (see Longhurst and Harrison, 1989), the importance of new and regenerated production (Platt *et al.*, 1992), the role of zooplankton in controlling the vertical structure of phytoplankton populations (Roman *et al.*, 1986) and zooplankton vertical migrations as a mediating process in the vertical transport of organic and inorganic material in the ocean (Longhurst *et al.*, 1990). However, most of these studies were done in single locations and the results extrapolated to large regions of the ocean (see Longhurst and Harrison, 1989 for review).

Recent work on the effect of mesoscale and large-scale physical variability on phytoplankton in subtropical waters, has shown that these areas are not as homogeneous as believed. Venrick (1990) suggested that long period waves (e.g., Rossby waves) were probably responsible of the mesoscale variability of phytoplankton in the Central Pacific. However, this author stated that the agreement between spatial scales of chlorophyll and dynamic topography could result from vertical displacement of the chlorophyll profile without a change in absolute concentration, or alternatively, the redistribution of chlorophyll in the water column, or the effect of phytoplankton growth. Patterns of biological variability in relation to these mesoscale physical instabilities in tropical and subtropical areas still remain relatively unknown.

Here we report the results of a transect of 2,800 km, perpendicular to the African coast at 21°N (Fig. 1) which was sampled every 60 nautical miles in order to study the variability of both micro- and mesoplankton biomass and metabolic activity distributions caused by large-scale and mesoscale physical processes. Measurements of stock pa-

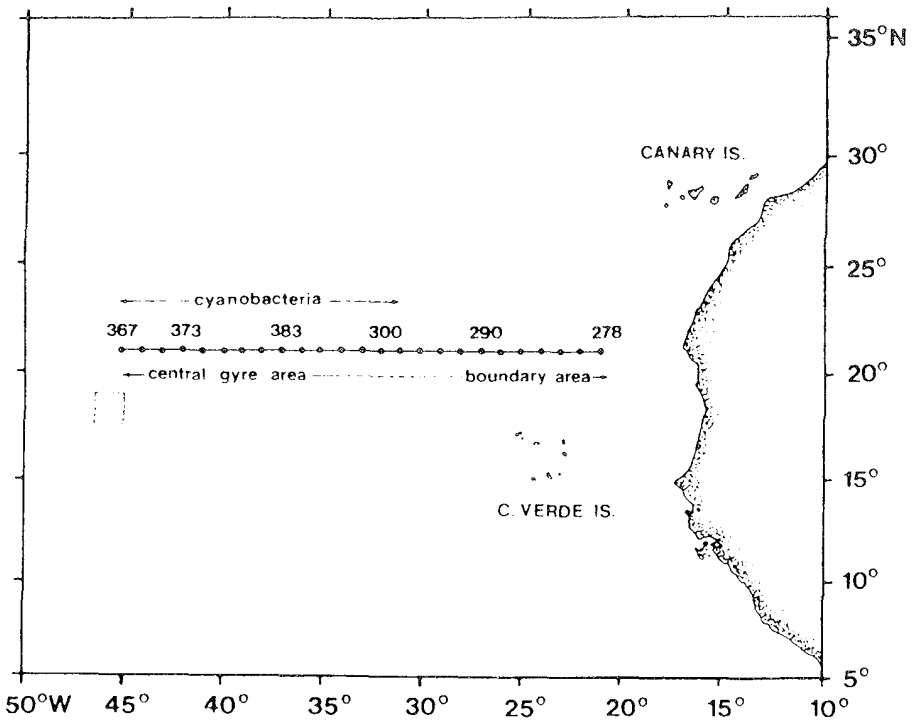

Fig. 1. Location of oceanographic sampling stations in the north Central Atlantic. The research cruise was conducted in September 1989 and biological sampling was carried out every 60 miles. Indicated boundary and central gyre conditions are based on temperature and salinity data. Presence of cyanobacteria chains is also indicated, as observed from plankton net catches. The squared area south of station 367 correspond to the area where stations 318, 346 and 362 of Table 1 were sampled.

rameters such as plant pigment concentrations could not be used to detect biological consequences of physical instabilities because of the uncertainties mentioned by Venrick (*op. cit.*) as well as the effect of grazing on a day-night basis (Le Bouteiller and Herbland, 1982). Moreover, very low values of chlorophyll and primary production are commonly observed in those areas (e.g., Gieskes and Kraay, 1986; Venrick, 1990). The lack of a phytoplankton-specific productivity method and the effect of grazing hinder the observation of the physical instability effects on the autotrophic communities of warm waters. The rates of processes related to the transfer of energy between the different trophic levels is high in warm oceanic waters, and the energy flow must be rapidly channeled to the so-called microbial loop and zooplankton. Therefore, indices of metabolism and growth can lead to the ultimate result of an increase in phytoplankton specific production. Enzymatic methods were used as indices to study the variability in plankton metabolism and growth. The electron transport system (ETS), glutamate dehydrogenase (GDH) and aspartate transcarbamylase (ATC) activities were used respectively as indices of respiration (Packard, 1969, 1971; King and Packard, 1975; Owens and King, 1975 and others), ammonium excretion (Bidigare and King, 1981; Bidigare *et al.*, 1982; King, 1984; King *et al.*, 1987) and growth (Bergeron and Buestel, 1979; Alayse-Danet, 1980; Bergeron, 1982) or moulting (Hernández-León *et al.*, 1995). Other approaches would not be useful in this case because classical procedures could not produce enough data to get a sufficient resolution in space. Nowadays, there is some agreement that this methodology produces rather good estimations when the enzyme is not limited by intracellular substrates (Hernández-León and Gómez, 1996; Packard *et al.*, 1996; Hernández-León and Torres, 1997). A clear underestimation of metabolic activity is achieved when the cell is substrate limited. Therefore, our estimations should be considered as a lower limit on metabolic activity.

2. Material and Methods

The transect was carried out on board the R/V "A.v. Humboldt" during August–September, 1989 (Fig. 1). Stations 278 to 308 were sampled from August 30th to September 5th and stations 367 to 383 from September 14th to 17th. Measurements of temperature and salinity were made by means of a CTD probe mounted in a rosette with Niskin-type bottles (3 L) from which samples for salinity, nutrients and primary production were obtained. Nutrients (nitrate, phosphate and silicate) were analysed using the procedures described in Strickland and Parsons (1972), although only phosphate concentrations are shown in the figures.

Community production and respiration were measured by the oxygen method. Water samples were prefiltered through a 200 μm mesh, poured into acid-cleaned plastic carboys and mixed well before using for productivity experiments. Problems related to the formation of air bubbles inside the bottles restricted the sampling to the mixed layer. Six to eight clear and dark acid-cleaned borosilicate bottles (c.a. 125 ml) were incubated for 8 to 12 hours from dawn to dusk. We used on-deck incubators cooled with surface water, screened to simulate the "in situ" light conditions. Dissolved oxygen was measured with the Winkler technique following the recomendations of Carrit and Carpenter (1966), Bryan *et al.* (1976) and Grasshoff *et al.* (1983). The final end point of the titration process was controlled by means of an automated precise oxygen titration system similar to that described by Williams and Jenkinson (1982). Corrections for "in situ" temperature and salinity at the time of fixing the samples were taken into consideration. The precision achieved in the replicates was in the order of CV < 0.1%. Only experiments where differences between the initial dark and clear bottles were statistically significant at the 95% confidence limits were considered. ^{14}C-uptake determinations were obtained after incubating two clear and one dark 125 ml bottles, at saturating light levels, in an artificial-light incubator for three hours. At the end of the experiment, samples were filtered, dried, fumed over concentrated HCl and stored for later analysis in the laboratory.

For microplankton ETS activity determinations, about five liters of seawater were sampled with acid-cleaned Niskin bottles (5 L) at standard depths ranging from surface to 100 m. Only samples for the determination of respiration/ETS (R/ETS) ratio in microplankton were obtained from the rosette sampler. Filtration was done immediately onto glass fiber filters (Whatman GF/F), after prefiltering the samples through 200 μm. The plankton-coated filters were then immediately frozen in liquid nitrogen until assayed in the laboratory. ETS activity was measured using the procedure of Kenner and Ahmed (1975). Samples were incubated at 18°C, but all the activities were corrected to "in situ" temperature using the Arrhenius equation and an activation energy of 15 kcal·mol^{-1} (Packard *et al.*, 1975).

Zooplankton were caught by means of a WP-2 double net (UNESCO, 1968), equipped with a 200 μm mesh size net in the 0–25, 25–75 and 75–200 m layers. Seawater volume filtered was measured with a previously-calibrated TSK-like flowmeter in one of the two nets. Biomass was determined as protein content (Lowry *et al.*, 1951) using bovine serum albumine (BSA) as the standard. Samples were fractionated on board for the 200–500 μm and >500 μm size classes. N_2 fixating cyanobacteria were found in the plankton net catches over long distances in our transect (Fig. 1). We were unable to quantify the biomass and production of these organisms, mainly due to methodological problems. We opted to avoid these organisms from our micro- and mesoplankton samples. These large cyanobacteria chains could interfere with our measurements of biomass and metabolic indices, hindering the response of plankton to the presence of such organisms. Therefore, care was taken in order to clean the samples as much as possible from *Trichodesmium spp.* in the fractionation process. Samples

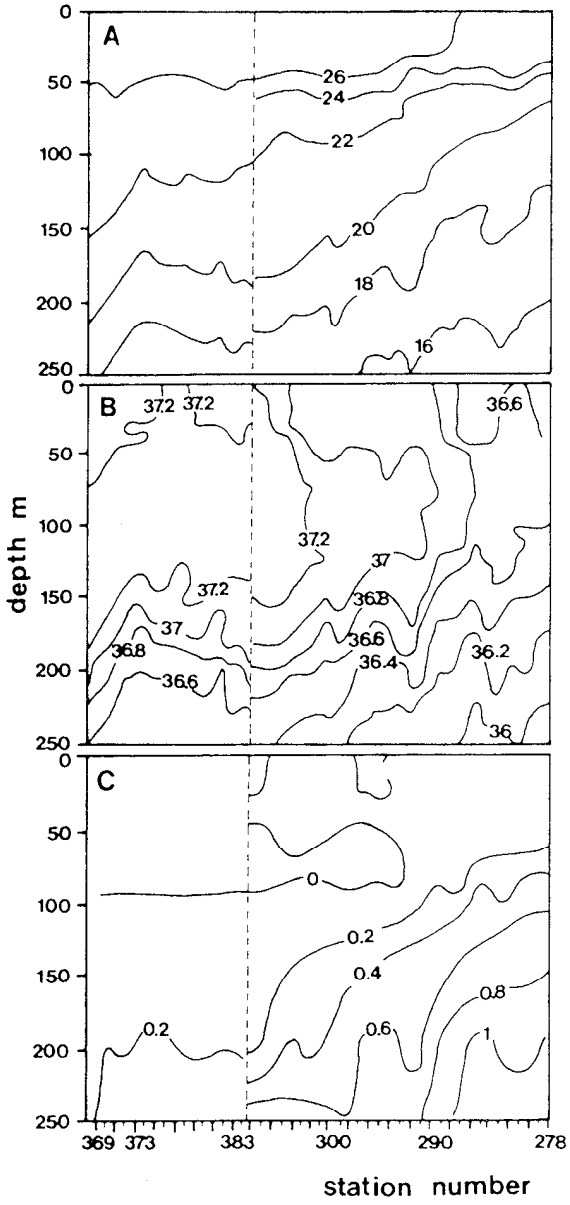

Fig. 2. Temperature (°C), salinity (PSU) and phosphate (μmol dm^{-3}) profiles. The vertical line in the profiles represents a break of 12 days between the two sampling periods of the transect (see text). Observe the differences in temperature, salinity and phosphate between the east and west sides of the section. Changes in salinity and phosphate distribution were used to distinguish between boundary and central gyre conditions.

of the >500 μm size fraction were easily cleaned of cyanobacteria while a slightly higher water pressure was applied to the 200–500 μm samples until those organisms visually disappeared. Samples were preserved in liquid nitrogen until analysis in the laboratory. Electron transport system (ETS), glutamate dehydrogenase (GDH) and aspartate transcarbamylase (ATC) activities were also measured from the same samples we used for the protein content determination. We utilized the procedures given by Kenner and Ahmed (1975) for the determination of ETS activity. Details of the assay are provided in Hernández-León (1988) and Hernández-León and Gómez (1996). GDH activity was measured by the method proposed by Bidigare *et al.* (1982) with the difference that total volume in the cuvette of the spectrophotometer was 3.0 ml (Hernández-León and Torres, 1997). ATC activity was measured using the procedure given by Bergeron and Alayse-Danet (1981). Details of the procedure are given in Hernández-León *et al.* (1995).

The zooplankton taxonomic composition was determined to the species level by binocular microscope analysis, although only data grouped by sizes are presented for the purposes of the paper.

3. Results

3.1 Large-scale distribution

3.1.1 Hydrological structure

Sampling took place (August–September) when the surface waters are warmer in relation to the annual cycle and the north Trade Winds are still blowing with persistence. An apparently stable thermal structure was observed in the upper 100 m, with a seasonal thermocline at 50–75 m depth. Temperature and salinity increased in the surface layer from east to west whereas phosphate concentration declined slightly (Fig. 2). Surface layer thickness increased to the west while the lowest salinity values was observed in the eastern part of the transect. These indicated two areas representative of boundary and central gyre conditions. Nutrient values increased not only in the eastern part but also with depth due to the presence of South Atlantic Central Water.

3.1.2 Microplankton

Gross production ranged from 0.01 to 0.05 μmol $O_2 \cdot l^{-1} \cdot h^{-1}$. These values were of the same magnitude as those obtained by the ^{14}C method at the same depths and

Table 1. Gross production, community respiration, net community production and ^{14}C uptake measurements in microplankton (<200 μm). All rates are expressed as $\mu moles \cdot dm^{-3} \cdot h^{-1}$. Sampling depths are given in meters. PQ is the apparent photosynthetic quotient ($O_2/^{14}C$) and R/ETS is the respiration/electron transport system activity ratio. "n.d." stand for no data available.

Station	Depth	Gross prod.	Resp.	Net prod.	PP (^{14}C)	PQ	R/ETS
290	25	0.02	0.11	–0.09	0.03	0.7	0.82
300	40	0.01	0.16	–0.15	n.d.	—	1.22
383	1	0.01	0.12	–0.11	n.d.	—	1.24
310	25	0.02	0.24	–0.22	0.02	1.0	n.d.
318	25	0.03	0.18	–0.15	0.02	1.5	n.d.
346	25	0.02	0.14	–0.12	0.02	1.0	1.29
362	25	0.05	0.28	–0.23	0.05	1.0	n.d.
Average		0.03	0.16	–0.13	0.03	1.04	1.14
(±SD)		(0.02)	(0.08)	(0.08)	(0.01)	(0.29)	(0.22)

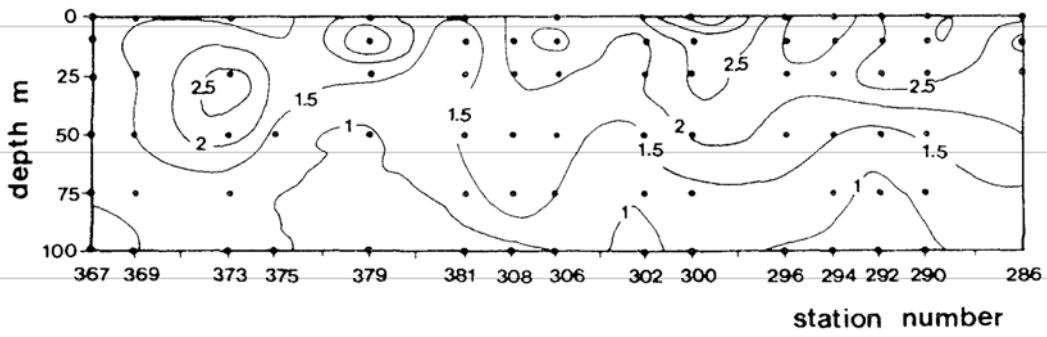

Fig. 3. Microplankton ETS activity profiles (in μl $O_2 \cdot dm^{-3} \cdot h^{-1}$) showing the enhanced activity in the upper 50 m.

stations (Table 1). Respiration rates varied from 0.11 to 0.28 μmol $O_2 \cdot l^{-1} \cdot h^{-1}$. Net production was always negative indicating that oxygen consumption of microplankton was higher than its production at those depths. ETS activity showed higher values in the upper 50 m layer (Fig. 3), the R/ETS ratio varying between 0.82 and 1.28 (Table 1).

3.1.3 Mesozooplankton

In order to suppress daily variability, biomass values were converted according to the night/day (N/D) ratios obtained for both size fractions (Table 2). Using a significance test according to the Student distribution, we observed no significant differences in the N/D ratio of zooplankton ETS activities for the two size classes studied at the different depth levels. This agreed with the ETS activity results obtained for the same ratio in the Canary Island waters (Hernández-León, 1991). No differences were also observed for GDH activities, except for the >500 μm size class in the upper 25 m ($p < 0.01$). Significant differences were observed, however, between day and night ATC activity values in the upper 25 m ($p < 0.05$) and in the average value for the 200–500 μm fraction ($p < 0.05$). Therefore, these values were converted according to the N/D ratio.

Average values of biomass were always higher in the upper layer (0–25 m) in both size fractions (Table 2). Biomass by night was higher in the large size fraction, while it decreased in the 200–500 μm size class. ETS and GDH activities did not show any difference between day and night. However, ATC activity showed an increase during night in the surface layer (Table 2). Biomass and ATC activity data were recalculated using the N/D ratios of Table 2 in order to suppress the daily variability (Fig. 4). The integrated biomass down to a depth of 200 m reflected the pattern of transition between the eastern boundary and central gyre area by a reduction towards the west in the amount of biomass in both size classes (Fig. 4C). A minimum was observed in the 0–25 m layer for the larger size fraction in the central part of the transect, with a slight westward increase in biomass (Fig. 4B). Calanoid copepods were grouped into three different size classes. The abundance of small calanoids (<1 mm) diminished from east to west in the surface layer (Fig. 5A). This feature was observed from the surface to a depth of 75 m, but not for the 75–200 m layer. Large calanoids (>2 mm) were present in very low densities showing no defined patterns in their distribution along the transect. Cyclopoid abundance gradually increased westward at the surface layer, as expected from observed boundary and central gyre conditions (not shown).

Average values of specific ETS activity in the 200–500

Table 2. Average values (±SD) and night to day (N/D) ratios of protein biomass ($mg \cdot m^{-3}$), specific activities of ETS ($\mu l\ O_2 \cdot mg\ prot^{-1} \cdot h^{-1}$), GDH ($\mu mol\ NH_4 \cdot mg\ prot^{-1} \cdot h^{-1}$) and ATC (nmol carbamyl-aspartate·mg $prot^{-1} \cdot min^{-1}$) for the two size fractions.

Depth (m)	200–500 μm			>500 μm		
	Day	Night	N/D	Day	Night	N/D
Biomass						
0–25	1.38 ± 1.21	1.20 ± 0.68	0.87	1.20 ± 0.56	2.43 ± 0.49	2.03
25–75	0.78 ± 1.01	0.62 ± 0.24	0.79	0.72 ± 0.31	1.44 ± 0.52	2.00
75–200	0.23 ± 0.10	0.14 ± 0.10	0.61	0.48 ± 0.25	0.64 ± 0.25	1.33
Average	0.80 ± 1.01	0.65 ± 0.60	0.81	0.80 ± 0.49	1.50 ± 0.86	1.88
Specific ETS						
0–25	79.86 ± 28.47	81.71 ± 18.35	1.02	64.47 ± 47.87	59.44 ± 17.42	0.92
25–75	57.56 ± 27.88	61.45 ± 34.16	1.07	49.81 ± 21.71	55.86 ± 20.17	1.12
75–200	45.22 ± 39.53	48.93 ± 21.27	1.08	32.16 ± 14.42	30.17 ± 7.49	0.94
Average	60.98 ± 34.78	64.03 ± 28.03	1.05	48.82 ± 33.29	48.67 ± 20.37	1.00
Specific GDH						
0–25	1.17 ± 0.82	0.83 ± 0.45	0.71	0.47 ± 0.23	0.94 ± 0.33	2.00
25–75	1.04 ± 0.50	1.25 ± 0.57	1.20	1.51 ± 0.99	1.25 ± 0.28	0.83
75–200	1.18 ± 0.40	1.54 ± 1.03	1.31	1.03 ± 0.35	1.06 ± 0.39	1.03
Average	1.13 ± 0.58	1.19 ± 0.74	1.05	1.00 ± 0.77	1.06 ± 0.34	1.06
Specific ATC						
0–25	0.63 ± 0.86	3.19 ± 3.02	5.06	1.03 ± 1.54	2.60 ± 2.06	2.52
25–75	0.76 ± 1.51	1.33 ± 1.28	1.75	1.11 ± 1.21	0.66 ± 0.63	0.59
75–200	1.74 ± 1.13	2.10 ± 1.51	1.21	1.22 ± 1.10	1.29 ± 1.23	1.06
Average	1.00 ± 1.26	2.13 ± 2.04	2.13	1.12 ± 1.29	1.40 ± 1.55	1.25

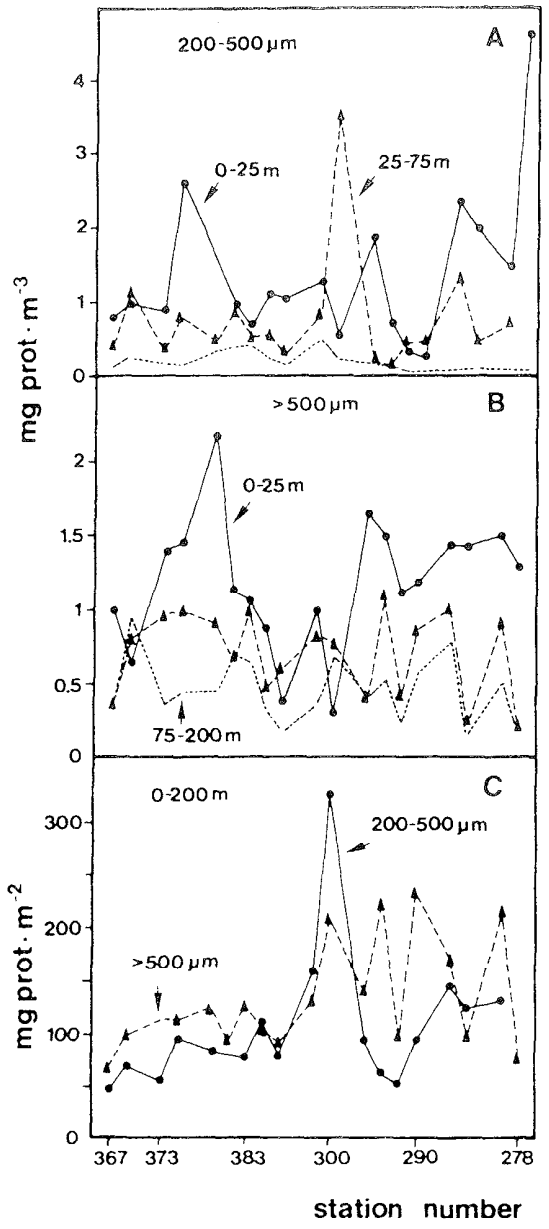

Fig. 4. Zooplankton biomass as protein in size fractionated samples for the (A) 200–500, (B) >500 µm size classes and (C) total biomass integrated in 0–200 m.

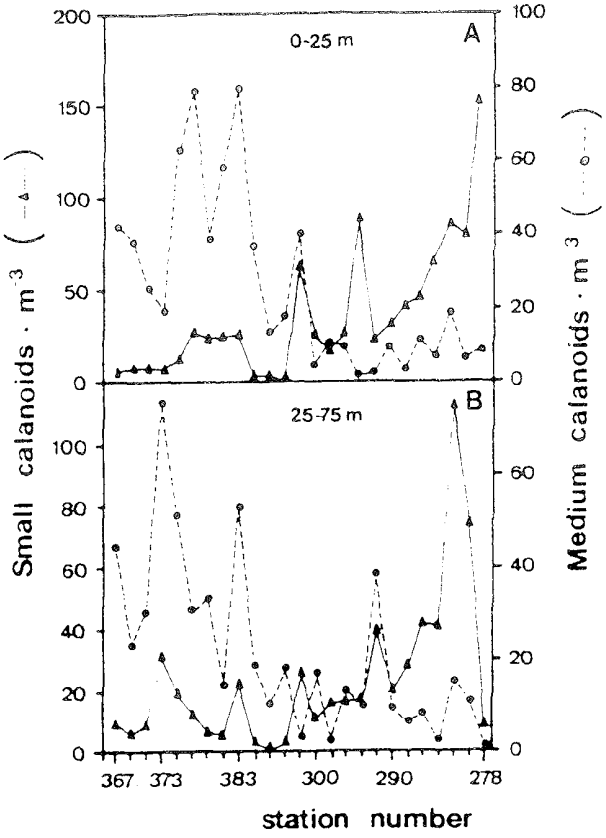

Fig. 5. Copepod density (A) at the surface (0–25 m) and (B) at the seasonal thermocline (25–75 m) layers. The two sizes considered were <1 mm (solid line) and 1–2 mm (dashed line), representing small and medium size calanoid copepods. The increase in medium size calanoids was not observed at the deeper layer (75–200 m).

and >500 µm fractions, as well as GDH and ATC activities in 200–500 µm, showed an increasing trend westward from the middle of the section (Fig. 6). This trend coincided with the increases in the number of medium size calanoids and the presence of *Trichodesmium spp.*

Respiration and ammonia excretion rates were calculated from ETS and GDH activities using the respiration/ETS (0.34) and ammonia/GDH (0.77) ratios experimentally obtained during the cruise (Table 3). Respiration rates by day represented 5.9% of primary production while by night this percentage increased to 8.9. This 50% increase by night was due to the large size fraction which showed nightly values of more than 100% higher. The ammonia excretion rate was 3.4% of primary production by day while by night it was 6.9%. Once again the increase in biomass by night due to vertical migration produced the important increase in community metabolic rates.

3.2 Mesoscale distribution

3.2.1 Hydrological structure

Hagen (1992), in a preliminary analysis of our transect, found a wave-like zonal pattern which was consistent with the westward dispersion of Rossby waves radiating from the coastal region. In a more detailed study of the same transect, Hagen (in prep.) found an average zonal wave length of 727 km. The residuals of the thickness of the layer between the 15 and 18°C isotherms in dbars (Fig. 7A) analysed by Hagen (1992; in prep.) indicate potential energy anomalies in this

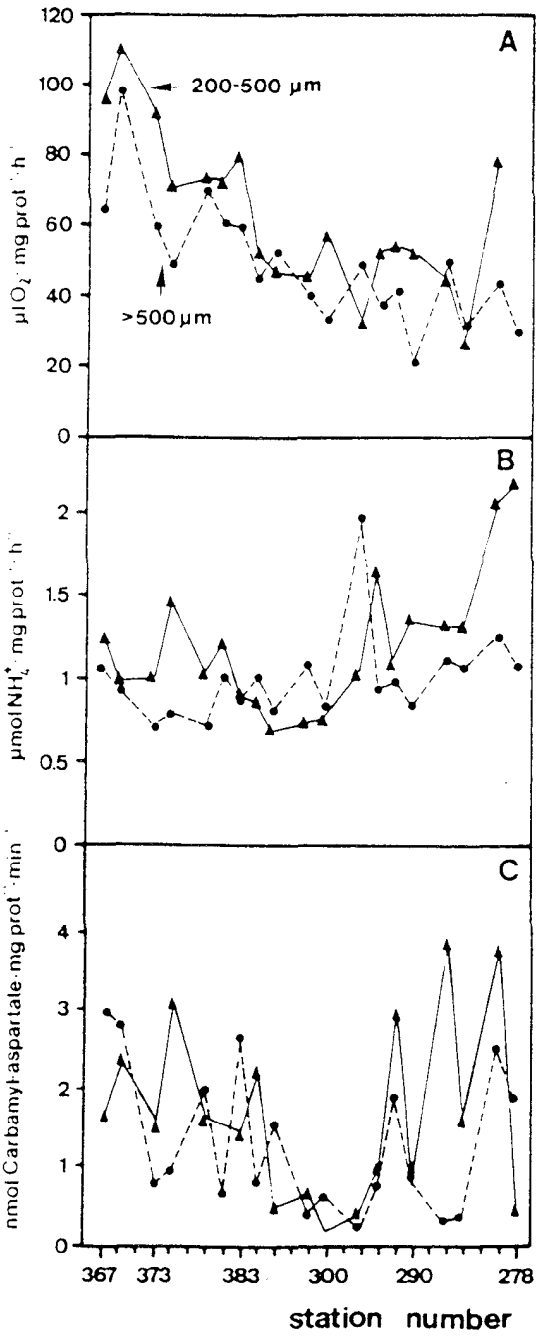

Fig. 6. Average specific ETS, GDH and ATC activities (A, B and C respectively) for the 200–500 µm (solid line) and >500 µm (dashed line) size classes. ATC activity has been corrected for differences between day and night values (see text).

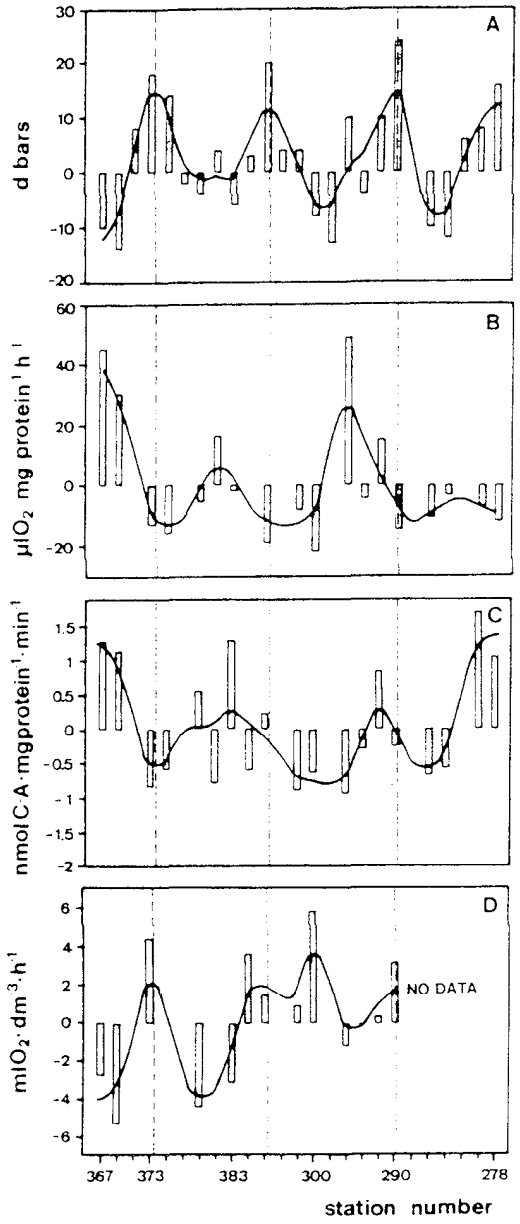

Fig. 7. Comparison of the deviations of (A) the distance between the 15 and 18°C isothermes (from Hagen, 1992) after substracting the large-scale zonal gradient, (B) mesoplankton specific ETS activity in the >500 µm at the seasonal thermocline level, (C) average specific ATC activity in mesoplankton >500 µm and (D) ETS activity (on a unit-volume basis) in microplankton at the seasonal thermocline level. Samples were taken at depths of 25, 50 and 75 m. Cyanobacteria chains were excluded because samples were drained using a 200 µm mesh net. ETS activity in (D) has been calculated after substracting the increasing eastward trend in activity. ATC activity in (C) has been corrected for differences between day and night values. The superimposed line in A, B, C and D is the smoothed representation of data (histograms). C–A in (C) stand for carbamyl-aspartate. Note that ETS activity in micro- and mesoplankton presents clear peaks in the central gyre area.

intermediate layer. That excludes processes such as wind mixing and convection, which are surface-driven. The variations in the distance between isotherms reflect the presence of a Rossby wave-like phenomenon (Hagen, 1992). The zonal wave length was found to be determined in the range between 620–830 km.

Table 3. Average values (±SD) of respiration and ammonia excretion calculated from ETS and GDH activities and using the respiration /ETS (0.34) and ammonia/GDH (0.77) ratios obtained experimentaly during the cruise. Percentages of respiration and of the contribution of regenerated nitrogen by mesozooplankton in relation to primary production (oxygen method) are also given. An average value of 30 nmol $O_2 \cdot dm^{-3} \cdot h^{-1}$ and O/C and N/C ratios of 2.66 and 0.16 were used. %PP stand for the percentage of primary production respired or regenerated by mesozooplankton.

	ETS $\mu l\ O_2 \cdot m^{-3} \cdot h^{-1}$	Respiration nmol $O_2 \cdot dm^{-3} \cdot h^{-1}$	%PP	GDH $\mu mol\ NH_4 \cdot dm^{-3} \cdot h^{-1}$	Excretion nmol $NH_4 \cdot dm^{-3} \cdot h^{-1}$	%PP
200–500 μm						
Day	63.18 ± 37.48	0.96 ± 0.57	3.2	0.85 ± 0.55	65.95 ± 42.62	1.83
Night	65.37 ± 29.39	0.99 ± 0.45	3.3	0.84 ± 0.52	65.41 ± 40.38	1.81
>500 μm						
Day	54.09 ± 40.51	0.82 ± 0.61	2.7	0.76 ± 0.35	58.59 ± 26.74	1.62
Night	110.99 ± 36.19	1.68 ± 0.55	5.6	2.38 ± 0.82	184.14 ± 63.47	5.10

3.2.2 Micro- and mesoplankton

Zooplankton biomass showed a high variability in the two size classes studied as well as at the different depth levels (Fig. 4). The very low values observed did not allow us to recognize any pattern of distribution at the mesoscale. However, specific ETS activity in the >500 μm size class at the thermocline level showed a succession of mesoscale peaks (Fig. 7B). This plot was obtained by substracting the westward increase in activity. This trend was also found in the 200–500 μm fraction within the central gyre area (not shown). Additionally, this effect was also observed in the average specific ATC activity in the >500 μm size fraction (Fig. 7C). Microplankton ETS activity at the seasonal thermocline level (Fig. 7D) showed an inverse pattern to the one observed for zooplankton ETS and ATC activities. Since microplankton ETS activity is given in a unit-volume basis, which is highly related to biomass, it is suggested that zooplankton might control the microplankton community (<200 μm).

4. Discussion

Our results show that microplankton respiration clearly exceed gross primary production. These results agree with Duarte and Agustí (1998) conclusions that unproductive aquatic ecosystems support a disproportionately higher rate respiration than that of productive ecosystems, tending to be heterotrophic and acting as a carbon dioxide source. In our case, microplankton respiration rates were even slightly higher than those reported by other authors for oligotrophic waters (e.g., Williams, 1984). A simple explanation for these differences may account for the fact that, during most of our sampling, the surface waters were dominated by colonies of *Trichodesmium spp.* (see material and methods) which are known to exhibit, jointly with the associated bacteria, high respiration rates (Kana, 1992; Carpenter *et al.*, 1993). Respiration/ETS ratios were also higher than those obtained in experiments with phytoplankton cultures (0.15 in Kenner and Ahmed, 1975) or in natural samples were phytoplankton predominated (about 0.3 in Packard and Williams, 1981). However, they agree with rates reported for active growing populations of bacteria (Christensen and Packard, 1979), or from natural communities in other oligotrophic areas like the Mediterranean Sea or the Canary Island waters (Arístegui and Montero, 1995).

Zooplankton activity increased in the western part of the zonal section. The magnitude of metabolic processes was as high or higher in the central subtropical gyre than in the boundary area of the ocean. Figure 6 shows increased activity westward of the transect, where *Trichodesmium spp.* were observed. The contamination of the small size fraction (200–500 μm) with cyanobacteria could be a possible cause of the increased activity westward. Although we visually tested the samples, cells could remain in the 200 μm filters after the washing procedure. However, this possibility is unlikely as the fact that both size fractions displayed the same pattern of activity along the transect (Fig. 6A). Therefore, it is suggested that the presence of cyanobacteria could promote an increased zooplankton activity in the central gyre area, as well as the increase in medium-sized calanoid copepods (Fig. 5). In this respect, small calanoids were expected to be found mostly in central gyre conditions, due to the presumably predominance of small phytoplankton cells in oligotrophic waters. However, medium size copepods were more abundant westward. The relationship between the increase in zooplankton activity and the presence of *Trichodesmium spp.* is unknown, although it has been observed that some mesozooplanktonic organisms feed directly on *Trichodesmium spp.* (Carpenter, 1983), or on associated organisms. However, we were unable to measure biomass and production of the cyanobacteria chains. Therefore, it was not possible to assess the contribution of this new production on the increase of zooplankton metabolism in the central gyre area. The coupling between both processes remains unknown although one possibility to

explain those increases in activity and the presence of medium sized calanoids would be related to the growth increment of other organisms associated with *Trichodesmium* such as protista.

Our observations at the mesoscale level suggest that the presence of a low frequency phenomena could influence the biomass and metabolism of planktonic organisms. Baroclinic Rossby waves have been observed to play a major role in the mesoscale variation of thermocline displacement and sea level height in the central north Pacific (see Van Woert and Price, 1993, and references therein). These waves are of long wavelength and low period and are generated due to temporal variations in the wind stress curl (White and Saur, 1981) and sea level height (White and Saur, 1983) along the eastern boundary (Van Woert and Price, 1993). Recent models suggest that these waves are expected to be produced annually in the central north Atlantic (Hermann and Krauss, 1989). Hagen (1992) observed a zonal wave pattern related to a Rossby wave-like phenomena which could be forced in the east with wave-lengths between 620 and 830 km. Using a zonally-averaged value for the internal Rossby radius of 48 km from the belt placed between 20° and 40°W and 20° and 25°N (Emery *et al.*, 1984) together with the range of zonal wave lengths estimated, we obtained a period range which includes a semiannual cycle. If we accept the notion that our observations result from a resonant oceanic response, then we may speculate about semiannual forcing. We know from the literature that in our area under consideration the half-year period is also a very energy rich cycle due to the meridional displacement of the northeast Trade Winds.

In the present work, the low frequency phenomena observed seemed to influence the hydrographic environment of micro- and mesoplankton along the extended zonal section. The peaks in zooplankton ETS activity at the level of the seasonal thermocline coincided with the reduction in distance between isotherms considered by Hagen (1992) (Fig. 7). This was also true for the index of growth. The processes involved in the increase in biological activity are thought to be quite complex. They could be related to the mesoscale eddy-like structures produced by the wave associated pressure instability and the lag normally observed in biological systems among the different trophic levels, as well as among the different responses of physiological rates (Checkley *et al.*, 1992) or enzymatic activities. In fact, we observed a slight mismatch of ETS and ATC peaks in relation to Rossby wave-like phenomena observed (Fig. 7). This uncoupling between the hydrological and biological data as well as the low number of stations at the mesoscale level meant that we could not attach any statistical significance to the apparent correlations. Moreover, Siedler and Finke (1993) measured temperature from an array of five moorings at 28°N to the west of the Canary archipelago. They found a superposition of two first-order baroclinic waves with annual and semi-annual periods and a baroclinic wave with a 90-day period. This complexity in the physical environment must produce difficult to explain variability in the associated biological measurements. Nevertheless, our observations suggest that Rossby wave-like phenomena and mesoscale associated eddies, could enhance and/or promote increased productivity in those areas due to positive vertical displacements in the wave crests. Eddy diffusivity at the crests of these subsurface waves may inject nutrients into the euphotic zone, or perhaps, the physical shallowing of nutrient-rich subsurface water enable motile phytoplankton to access nutrients. Whatever the mechanism is, they must be taken into account when time series studies in tropical or subtropical oceanic areas are undertaken. In trying to explain biological variability, such a pattern of biological instability can produce background noise in the data. This could produce serious problems when interpreting trends in time.

Diel variability showed an unexpected low N/D ratio in the 200–500 μm zooplankton fraction (Table 2). Differences between night and day hauls may be caused by methodological bias. Animals could more easily avoid the net during daylight hauls. However, if this were the case, the N/D ratio should be higher than unity. Another potential factor affecting this ratio might be the existence of an inverse migration, but the N/D ratio is lower than unity in the three layers sampled (Table 2). That is to say that these smaller organisms would have to migrate below 200 m from the upper most layers, which is something unexpected in these small organisms (200–500 μm). The important increase in biomass at night in the upper layers due to organisms >500 μm could produce an impact on the amount of prey animals in this size range. Our observation of an inverse relationship between the specific ETS in zooplankton and microplankton enzymatic activity (on a unit-volume basis) at the mesoscale (Fig. 7) also supports the previous observation about the control exerted by the large zooplankton on the smallest size fractions. There is evidence in the literature of such a diel impact on phytoplankton standing crop in equatorial waters. Le Bouteiller and Herbland (1982) found that the amount of chlorophyll *a* in the upper layers was always lower during the night. Lampitt *et al.* (1993) also found a strong diel variability of marine snow. They suggested that mid-water biota and their migratory behaviour were responsible for such a variability. In these warm environments, grazing and carnivorous activity could have important consequences on a daily basis as the >500 μm organisms could control the abundance of this small metazooplankton community (see also Hernández-León, 1998).

Daily impact of mesozooplankton on primary production could be assessed from our measurements of enzymatic activities. Hernández-León and Gómez (1996) found that values of R/ETS of 0.5 are rather conservative because of the influence of cell substrate limitation in the variability

of the R/ETS relationship. This is an inherent problem to enzymatic measurements as also stated by Packard *et al.* (1996) and Hernández-León and Torres (1997). Our experimentally obtained R/ETS ratio of 0.34 also seems conservative. Therefore, our metabolic calculations should be considered as a base line for the area considered.

A rough estimate of ingestion can be obtained by assuming that about two-thirds of the ingested food is assimilated, and one half of the assimilated food is metabolized and the other half is used for growth and reproduction. This estimate indicates that mesozooplankton potentially consume (assuming herbivorous feeding) 46% of primary production, ingestion being 33% higher by night than by day. This estimate agrees with the values calculated by Lenz *et al.* (1993) who found that potential grazing could account for half of the daily primary production in subtropical waters of the Atlantic Ocean. Therefore, mesozooplankton are processing an important amount of the energy which enter daily and then circulates into the pelagic ecosystem. This impact is even higher during the night because of the presence in the epipelagic zone of diel vertical migrators. This increase in ingestion at night could also explain, at least in part, the low N/D ratio of the small size fraction.

In summary, the main finding of this study is the inadequacy of assuming an steady-state picture in tropical and subtropical environments. The estimation of biological productivity in stations selected at random along the transect gave a low variability in the values of gross and net production (Table 1). However, our much finer sampling of plankton biomass and indices of metabolism detected important differences at the large-scale and mesoscale. Low frequency phenomena could be an important mechanism in thermocline variability (Van Woert and Price, 1993), and associated mesoscale eddies may enhance primary production in oligotrophic waters. Although further research is required in order to elucidate the importance of the large-scale and mesoscale variability observed, the changes in plankton activity associated with the long period waves and the presence of N_2 fixing organisms observed in the present work suggest that a better estimation in the biological calculation of new and export production of tropical and subtropical waters in relation to these features is needed.

Acknowledgements

The authors would like to thank two anonymous referees for their comments on the manuscript and constructive criticism. We are also grateful to C. Fraga for drawing the figures and to the crew and scientists of the R.V. "A.v. Humboldt". This work was partly supported by the "Comisión Interministerial de Ciencia y Tecnología" (CICYT PB88-0436) of the Spanish Government and the Autonomic Government of the Canary Islands (GAC 22/01.06.88).

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