Journal of Marine Research, 60, 327–346, 2002

Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off northwest Africa

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ABSTRACT

Zooplankton biomass and indices of grazing (gut fluorescence), respiration (electron transfer system activity, ETS) and growth (aspartate transcarbamylase, ATC) were studied in relation to an upwelling filament off northwest Africa during August 1993. The filament extended 150 km offshore into the oligotrophic waters. It was generated by a trapped, quasi-permanent cyclonic eddy located between the Canary Islands and the African shelf. High biomass, specific gut fluorescence and electron transfer system activity in zooplankton were observed along the filament structure. In contrast, low values of biomass, gut fluorescence, ETS and ATC specific activities were found in the center of the trapped cyclonic eddy. Assuming a 50% of pigment destruction, the calculated grazing impact of zooplankton on primary production varied between 16 and 97%, a high range compared to other oceanic systems. Ingestion, estimated from indices of metabolism and growth, accounted for 47–296% of the primary production (assuming an herbivorous feeding). Mesozooplankton transported offshore into the oligotrophic area fulfilled their metabolic demands with nonpigmented food as observed from the increase of omnivory from the coastal waters to the open ocean. The progressive decay of grazing and metabolic indices along the filament suggests that advection, rather than local enrichment processes, is mostly responsible for the high biomass values in this physical structure.

1. Introduction

Upwelling filaments of colder and fresher water flowing to the open ocean in coastal upwelling areas are important features in the transport of organic matter to the adjacent warm and oligotrophic waters. These structures may influence the composition of biological communities of open ocean waters. In addition, they could have important consequences in the modification of the trophic relationships, and therefore in the energy fluxes, of planktonic organisms in oceanic areas.

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The development of upwelling filaments are related to (1) "squirts" or one-way jets transporting coastally upwelled waters into the ocean, (2) the presence of mesoscale eddies which draw recently upwelled water away from the coast, or (3) because of meandering of the upwelling front which entrains coastally upwelled waters nearshore and creates filaments of cold water (Ramp *et al.,* 1991; Strub *et al.,* 1991). Location of the filament is often, but not always, related to a topographic feature such as a cape. Filaments have been described in the upwelling areas off southwestern Africa (Lutjeharms and Stockton, 1987), California (Brink and Cowles, 1991), Portugal (Haynes *et al.,* 1993) and northwest Africa (Navarro-Pérez and Barton, 1998). Although filaments were recognized in remote sensing images of sea-surface temperature and in field sampling more than twenty years ago (Traganza *et al.,* 1980), their physical and biological functioning are still poorly understood. An important advance in the knowledge of such features took place under the so-called Coastal Transition Zone program off the upwelling area of the California Current (Brink and Cowles, 1991). In this program, Strub *et al.* (1991) found that the filament core originated upstream in the inshore area, something which was partially confirmed by the results of Mackas *et al.* (1991) working on zooplankton species composition. Because of this, there is interest in quantifying the level of productivity in these structures to determine if plankton biomass is simply advected offshore by the filament, or if in addition growth is stimulated inside the core of cold water. Chavez *et al.* (1991) found higher nutrient and chlorophyll levels in the bounds of the filament, and Smith and Lane (1991) showed increased egg production of the copepod *Eucalanus californicus* in the same filament. It was suggested that both advective and *in situ* processes (local upwelling) took place in those filaments.

Off the northwest African upwelling area the presence of filaments has been observed by remote sensing studies of sea-surface temperature as well as ocean color (Van Camp *et al.,* 1991; Hernández-Guerra *et al.,* 1993; Arístegui *et al.,* 1997; Barton *et al.,* 1998). *In situ* measurements made by Arístegui *et al.* (1997) showed evidence of water masses of northwest African upwelling origin close to the east of Gran Canaria Island during two cruises (March and October, 1991). Barton *et al.* (1998) and Navarro-Pérez and Barton (1998) have described the structure and development of these repeatedly observed filaments during August 1993. Remote sensing images show that the filaments in this area are normally found between Cape Juby and Bojador (Fig. 1). Those structures could give rise to a slight enrichment of the open ocean, which could then be considered mesotrophic in the frame of the so-called boundary area, characterized by a high physical and biological mesoscale variability.

We studied the filament described by Navarro-Pérez and Barton (1998) during the August 1993 experiment in the coastal upwelling off northwest Africa between Cape Juby and Cape Bojador. Our objective was to better understand the influence of such a physical structure on the biomass distribution, feeding and metabolic activity of the zooplanktonic community. Gut fluorescence and gut evacuation rates were used as indices of grazing (Mackas and Bohrer, 1976) while enzyme activities were measured as indices of respira-

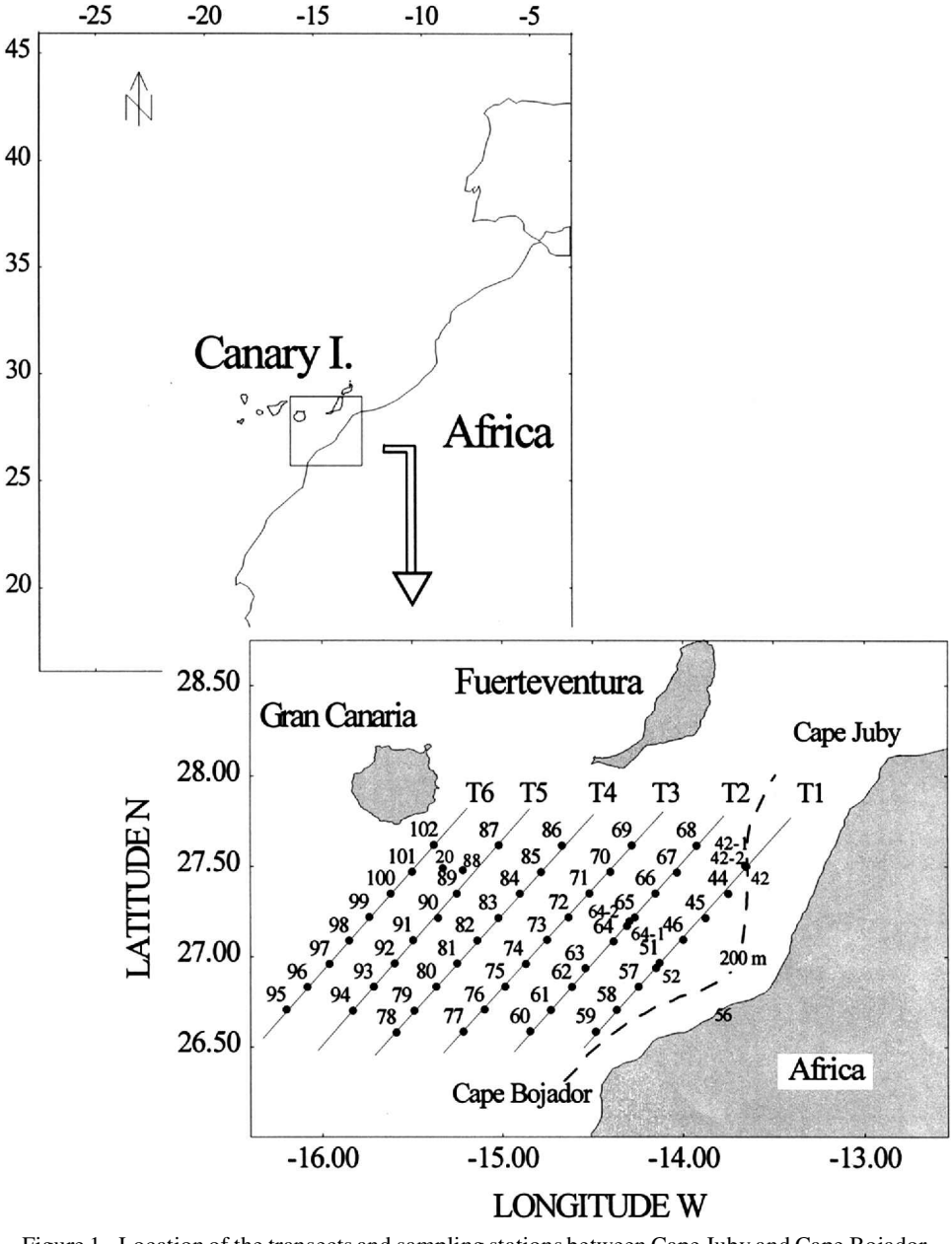

Figure 1. Location of the transects and sampling stations between Cape Juby and Cape Bojador.

tion (electron transfer system, ETS; Packard, 1971; King and Packard, 1975; Owens and King, 1975 and others) and growth (aspartate transcarbamylase, ATC; Bergeron and Buestel, 1979; Alayse-Danet, 1980; Bergeron, 1982). ETS activity is commonly used in

biological oceanography to assess plankton metabolism, and ATC activity controls the first specific step to *de novo* synthesis of pyrimidine bases, which are used in the cell to build RNA and DNA. The factors affecting the relationships between growth and ATC activity, and respiration and ETS activity in zooplankton have been studied by Hernández-León *et al.* (1995) and Hernández-León and Gómez (1996), respectively. The obtained metabolic rates allowed the estimation of zooplankton ingestion (pigmented plus nonpigmented food) assuming a constant efficiency of assimilation. These bioindices were used because they respond to changing food conditions (Hernández-León and Gómez, 1996) and can be measured rapidly. They facilitate the mapping of potential respiration and growth over a short time interval. This type of mapping procedure is required to resolve the importance of the different components of the energy budget of the zooplanktonic community at the mesoscale level. No other methodology facilitates the acquisition of the large data sets necessary to map the dynamics of mesoscale biological features. A review of enzymatic indices and their usefulness is given by Ikeda *et al.* (2000). Here we present the results of the distribution, feeding and metabolic activity of zooplankton in relation to a filament from an area of persistent generation of filaments in order to evaluate the fate of the zooplankton biomass advected offshore into the oceanic waters.

2. Material and methods

Samples were obtained between 5 and 26 August, 1993 onboard the R.V. *Hespérides* covering a filament observed between Cape Juby and Cape Bojador by AVHRR (Advanced Very High Resolution Radiometer) images of sea-surface temperature. Profiles of temperature, salinity and fluorescence as well as zooplankton net hauls were made in a grid of stations forming six transects at about 30 km separation and parallel to the coast (Fig. 1). Vertical profiles were made by means of a rosette-CTD ("SeaBird" 911 plus). Phytoplankton chlorophyll was derived from depth profiles of *in-situ* fluorescence, calibrated with samples collected at 6 to 8 depths within the upper 100 m of the water column. For this, 500 ml samples were filtered through Whatman GF/F fiberglass filters and extracted overnight in 10 ml of 90% acetone at 4°C in dark. Fluorescence before and after acidification was measured with a Turner Designs bench fluorometer (Holm-Hansen *et al.,* 1965) calibrated with pure chlorophyll *a* (Sigma Chemical Corp.). Primary production was measured as described in Basterretxea and Aristegui (2000). Samples for P-I (photosynthesis-irradiance) experiments were taken in every transect (Fig. 1) around local noon at two depths corresponding to the mixed layer (ML) and to the chlorophyll maximum (CM). Chlorophyll-specific photosynthetic parameters α, P_m and β were fitted to standardized production values by nonlinear regression fitting of the expression of Platt *et al.* (1980). Daily depth-integrated production rates (0–100 m) were estimated using measured light attenuation coefficients, surface P-I parameters and chlorophyll data for each station. Daily light variation was calculated assuming a sinusoidal variation of the measured mid-day surface irradiance.

Zooplankton hauls were made at each station from 200 m depth to the surface, using a

double WP-2 net (UNESCO, 1968) equipped with a 200 μm mesh. A WP-2 net with a 100 μm mesh was tried but its use was rejected because large amounts of phytoplankton were obtained in the catch in areas affected by upwelled waters. Samples from one of the nets were immediately size fractionated in 200–500, 500–1000 and >1000 μm ranges and frozen in liquid nitrogen (−196°C) until later analysis in the laboratory. Care was taken to wash out the phytoplanktonic cells from the smallest size fraction by streaming water over the mesh. Because the sampling grid was covered during a relatively short period and day and night samples needed to be pooled, a day/night ratio was calculated in every size fraction of biomass and activities to convert night values to a day situation. This is an artifact needed when the research vessel is sampling continuously during day and night. We have to assume an unavoidable balance between the synoptical sampling used in mesoscale studies and the effect of the diel variability. This correction was important and highly significant in the biomass values of the large size fraction where the day/night ratio was 0.44 due to the diel vertical migration of the interzonal fauna.

Gut evacuation rates were measured in freshly collected animals of 200–500 μm which were transferred to 1-liter plastic containers containing filtered sea water. The incubation was maintained at constant temperature (19°C) and subsampled at 0, 5, 10, 15, 30, 45, 60 and 120 minutes. Samples were immediately frozen in liquid nitrogen and later placed in 10 ml of 90% acetone and stored for 24 hours at −20°C. Gut evacuation rate (min^{-1}) was estimated by fitting the pigment values per individual versus time to a negative exponential curve.

In the laboratory, field samples were homogenized in a teflon pestle at 0–4°C and subsamples were taken for protein analysis, gut fluorescence and enzyme activity measurements. Biomass of each size fraction was determined as protein content using the method of Lowry *et al.* (1951) or the method of Peterson (1983) for samples with very low protein content and using bovine serum albumine (BSA) as standards.

An aliquot of the homogenate made for the analysis of protein was placed in a test tube with 10 ml of 90% acetone and stored at −20°C (24 hours) for gut pigment analysis. Fluorescence of the samples was measured before and after acidification in a Turner Design fluorometer, previously calibrated with pure chlorophyll (Yentsch and Menzel, 1963). Pigments were calculated with the equations given by Strickland and Parsons (1972) slightly modified to

$$\text{Chlorophyll} = k \cdot (F_o - F_a) \cdot \text{mg}^{-1}\ \text{protein}$$

$$\text{Pheopigments} = k \cdot (R \cdot F_a - F_o) \cdot \text{mg}^{-1}\ \text{protein}$$

where k is the instrument calibration constant, F_o and F_a are the fluorescence readings before and after acidification and R is the acidification coefficient. Gut pigment concentration in this study refers to the addition of chlorophyll and pheopigments.

Electron transfer system activity was measured according to Kenner and Ahmed (1975) with the modifications introduced by Gómez *et al.* (1996) for zooplankton samples. Details of the procedure are also given in Hernández-León and Gómez (1996). ETS activity was

recalculated to *in situ* temperature using the Arrhenius equation and an activation energy of 15 Kcal · mol^{-1} (Packard *et al.,* 1975). Aspartate transcarbamylase activity was assayed following the procedure given by Bergeron and Alayse-Danet (1981). Minor modifications were the duration of incubation (15, 30 and 60 minutes), the use of different ion exchange resin (Dowex-50W from Sigma) and the scintillation liquid for counting (High-Safe III from Pharmacia). Enzymatic activities and gut fluorescence were normalized to the amount of protein to indicate areas of increased metabolism and feeding in relation to the filament.

There is some agreement that the enzymatic methodology produces rather good estimations when the enzyme is not limited by intracellular substrates (Hernández-León and Gómez, 1996; Packard *et al.,* 1996a,b; Hernández-León and Torres, 1997; Roy and Packard, 1998; Roy *et al.,* 1999). When the cell is substrate-limited in nature, enzyme activities are higher than physiological rates because of the addition of substrates in the assay, showing low physiological/enzyme ratios. Thus, our estimations for the waters around the Canary Islands using a respiration/ETS ratio of 0.5 (Hernández-León *et al.,* 1995; Hernández-León and Gómez, 1996), should be considered as conservative estimates of metabolic activity, because this ratio tends to underestimate physiological rates when the substrates are not limited *in vivo.*

3. Results

a. Hydrography and chlorophyll distribution

The hydrographic features of the filament under study were recently described in detail by Barton *et al.* (1998), Navarro-Pérez and Barton (1998), Rodríguez *et al.* (1999) and Basterretxea and Arístegui (2000). Briefly, the upwelling filament in this area is a quasi-permanent structure related to an apparently permanent cyclonic eddy located between the eastern islands of the Canary archipelago and the African shelf edge. The filament is less than 20 km wide and <200 m in depth, and transports chlorophyll (Navarro-Pérez and Barton, 1998) and fish larvae offshore (Rodríguez *et al.,* 1999). While salinity at 25 m depth showed rather homogeneous values (Fig. 2b), temperature and salinity at 25 and 50 m depth, respectively, showed the signature of the filament (Fig. 2a,d). Temperature at 50 m depth described the oval-shaped and cold-core (<17.5°C) cyclonic eddy, trapped between the islands and the African shelf. The structure of this eddy was evident down to 350 m depth (not shown). Note that the coastal jet of the filament (tongue of cooler water in Fig. 2a) is located on the northern side of the 18°C isotherm (Fig. 2c) which delineated the cyclonic eddy. Chlorophyll distribution also showed high values near the African shelf extending offshore in the filament area but with a sharp decrease to typical oceanic values between transects 2 and 3 (Fig. 2e). The lowest values were found in the center of the cyclonic eddy. Correlation analysis between chlorophyll *a* and temperature and salinity at 25 and 50 m depth showed significant ($p < 0.05$) relationships (Table 2).

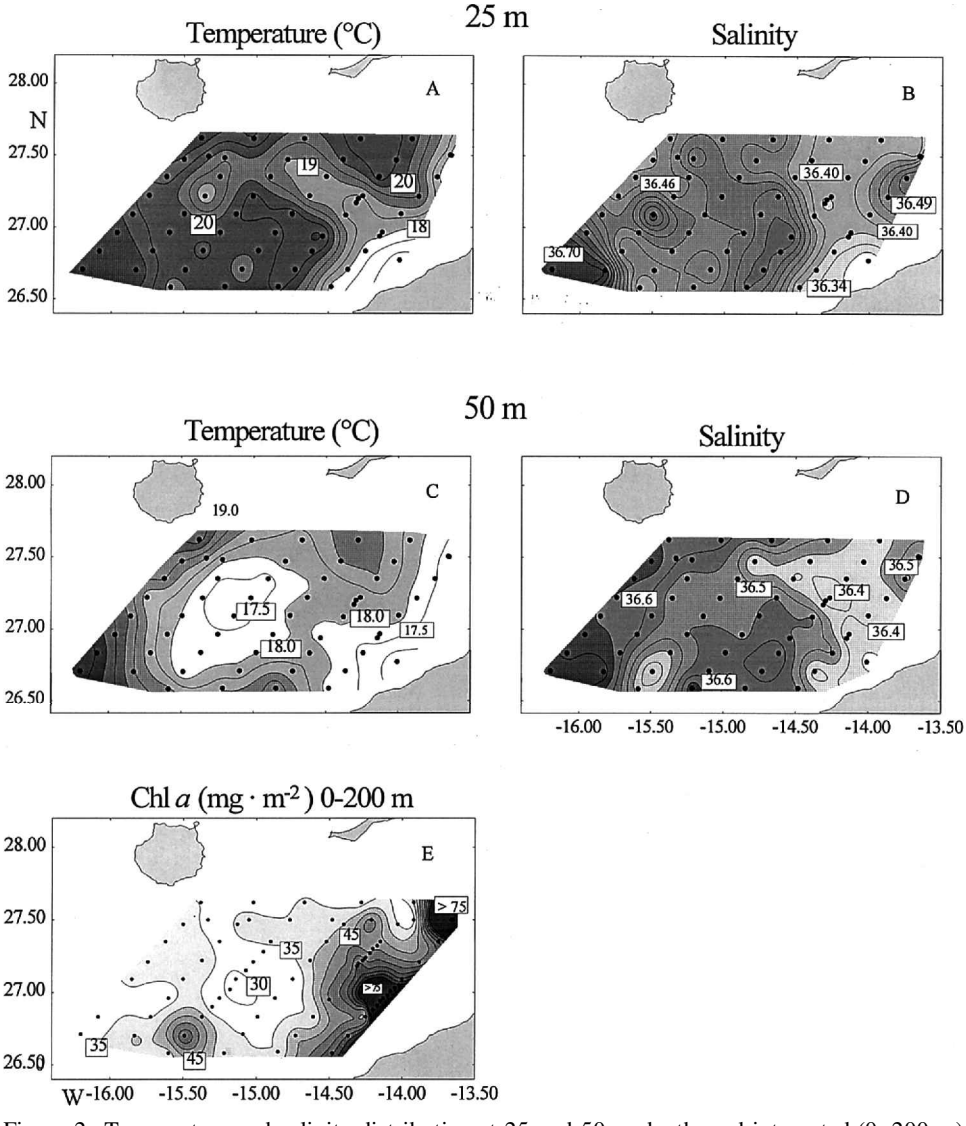

Figure 2. Temperature and salinity distribution at 25 and 50 m depth, and integrated (0–200 m) chlorophyll.

b. Zooplankton biomass

Size fractionated biomass showed the highest values in the large size fraction which represented about 68% of total biomass (Table 1), the 200–500 and 500–1000 μm being 13 and 19%, respectively. A preliminary study of samples showed that zooplankton composition was dominated by middle-size and large copepods. Their abundance decreased toward the ocean as well as other groups such as apendicularians, cladocerans,

Table 1. Mean (±SD) values of biomass, specific gut fluorescence (ng pigments · mg^{-1} protein), ETS (μlO_2 · mg^{-1} protein · h^{-1}) and ATC (nmol carbamyl aspartate · mg^{-1} protein · min^{-1}) activities in the different size classes sampled. Data from the two lower size fractions were pooled to obtain the 200–1000 μm size class. The percentage of each size fraction to the total value and the number of samples (in parentheses) are also given.

Size fraction	Biomass	%	Gut Fluorescence	%	ETS	%	ATC	%
200–500 μm	69.0 ± 48.3 (52)	13.0	66.0 ± 113.3 (43)	41.5	28.5 ± 21.1 (43)	37.5	6.4 ± 4.7 (44)	32.2
500–1000 μm	95.3 ± 79.3 (54)	18.7	36.8 ± 52.0 (45)	24.2	25.2 ± 13.1 (48)	37.0	5.6 ± 4.3 (50)	32.2
>1000 μm	361.3 ± 501.6 (52)	68.3	55.9 ± 74.2 (42)	34.3	18.1 ± 13.4 (46)	25.5	6.8 ± 4.5 (46)	35.6
200–1000 μm	162.3 ± 116.5 (50)	31.7	50.2 ± 68.6 (48)	65.7	26.1 ± 15.0 (51)	74.5	5.9 ± 2.9 (55)	64.4
Total or mean	536.0 ± 535.8 (47)	100	50.9 ± 61.0 (49)	100	22.6 ± 11.9 (55)	100	6.0 ± 2.9 (59)	100

chaetognaths and gelatinous zooplankton. Differences between the average biomass values of all size fractions were statistically significant (ANOVA, $p < 0.05$). Biomass distribution showed higher values along the filament structure turning anticlockwise following the cyclonic eddy structure (Fig. 3), most clearly in the large size fraction. Lower values were related to the center of the eddy while the largest biomass was found near the African shelf, as expected, and around the edge of the cyclonic eddy. Near the shelf (transect 1), zooplankton biomass and chlorophyll did not coincide, showing opposed distribution

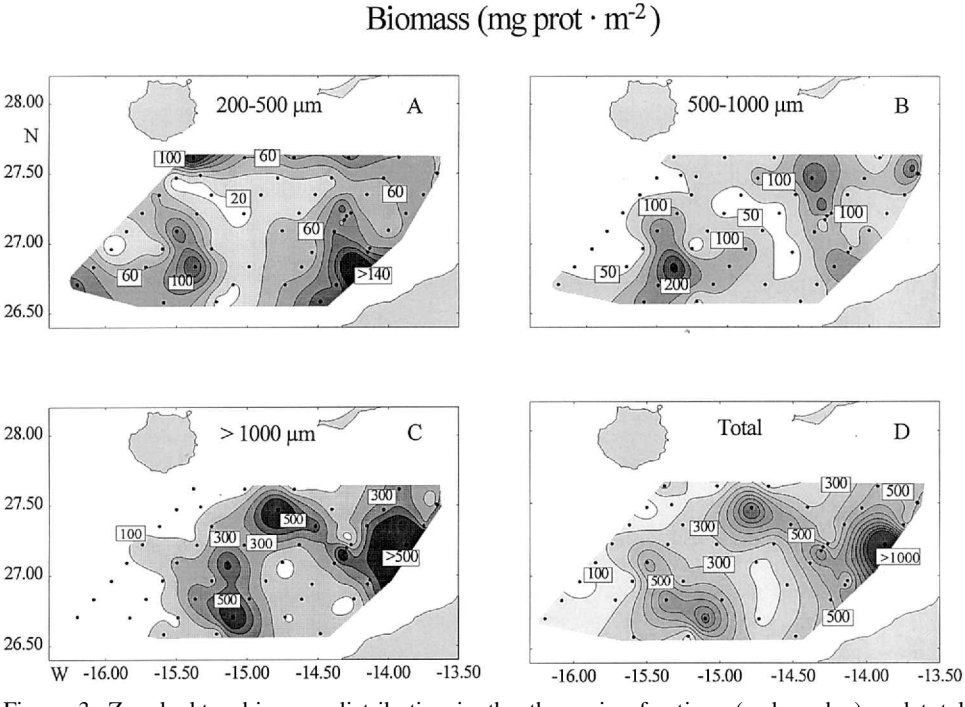

Figure 3. Zooplankton biomass distribution in the three size fractions (a, b and c) and total zooplankton biomass (d) in mg protein · m^{-2}.

Table 2. Correlation coefficients (r) between zooplankton biomass, specific gut fluorescence, electron transfer system (ETS) and aspartate transcarbamylase (ATC) specific activities, and temperature and salinity at 25 and 50 m depth. Significant correlations at $p < 0.05$ are marked with double asterisks (**). Observe the positive relationship in ATC activity.

	Temperature 25 m	Salinity 25 m	Temperature 50 m	Salinity 50 m
Chlorophyll *a*	−0.478**	−0.264	−0.242	−0.439**
Zooplankton biomass	−0.391**	−0.298	−0.412**	−0.475**
Gut fluorescence	−0.415**	−0.329**	−0.202	−0.272
ETS activity	−0.468**	−0.398**	−0.187	−0.388**
ATC activity	0.323**	0.256	0.235	0.461**

patterns. A localized biomass maximum was also observed in the return flow in the southern part of the eddy, coinciding with the anomalously low salinity found in the same area (Fig. 2) and also with a relative maximum in chlorophyll. Correlation analysis between the biomass of zooplankton and temperature at 25 and 50 m, and salinity at 50 m depth (Table 2), clearly showed that biomass were associated with the filament structure.

c. Indices of feeding, metabolism and growth

Specific gut fluorescence and ATC activity showed no significant differences (ANOVA, $p > 0.05$) between the size classes while ETS activity showed significantly lower values (ANOVA, $p < 0.05$) in the large size fraction (Table 1). Specific gut fluorescence and ETS activity also showed higher values in the upwelling filament jet in all the size fractions, decreasing dramatically around the third transect (Fig. 4 and 5). Gut fluorescence and ETS activity were significantly correlated ($p < 0.05$) with temperature and salinity at 25 m depth (Table 2). Specific ATC activity, however, showed increased activity related to the west side of the cold water filament jet. It showed a belt of increased activity at the bound of the filament (Fig. 6d). We also observed a significant positive correlation (Table 2) with temperature at 25 m and salinity at 50 m depth.

The decrease of gut pigment content in the evacuation rate experiments was exponential and the gut was emptied almost completely in 30–40 minutes. The results of 22 experiments performed in the area to measure gut evacuation rates showed a high variability with a mean ($\pm$ standard deviation) of $0.056 \pm 0.036\ \text{min}^{-1}$ for a gut fluorescence ranging from 0.05 to 2.04 ng of pigments per individual. However, gut pigment content (gpc) and gut evacuation rates (ger) showed a positive correlation ($\text{ger} = 0.025 + 0.036 \cdot \text{gpc}$, $r = 0.732$, $p < 0.05$).

d. Horizontal exchange

Although the upwelling filament under study was driven by the topographically trapped cyclonic eddy, we have averaged the values of the six transects sampled in order to study

the gradients in biomass and indices of feeding, metabolism and growth from the upwelling area into the oligotrophic waters.

Average values of chlorophyll sharply declined from transect 1 to 2 (Fig. 7a) and remained low from transect 3 to 6 as would be typical of oceanic (oligotrophic) waters. Primary production (see methods), however, still showed high values in transect 2 and 3, but then declined to low and constant values from the fourth to sixth transects. No values were obtained in transect 1. However, primary production measured at a single station on the shelf gives a value of 5326 mgC $m^{-2} d^{-1}$ indicating that the figure in transect 1 could be assumed to be higher than in transect 2 and typical of upwelling areas (around 1 gC $m^{-2} d^{-1}$ or more).

Zooplankton biomass showed the highest average value in transect 1 as expected, but remained relatively high until transect 4 (Fig. 7b) as the effect of the previously observed relationship between the filament structure and zooplankton biomass (Fig. 3). Biomass in transects 5 and 6 (at the edge of the filament structure) was significantly lower (ANOVA, $p < 0.05$). Gut fluorescence and the activity of the ETS (Fig. 7c,d) showed, however, a smooth decline toward the ocean with significant differences between transects 1 to 3 and 4 to 6 (ANOVA, $p < 0.05$). In contrast, the activity of aspartate transcarbamylase showed a smooth increase toward the ocean (Fig. 7e) with significant differences only between transects 1 and 5 (ANOVA, $p < 0.05$).

4. Discussion

Our results show that upwelling filaments can transport organic matter to the open ocean as observed by Jones *et al.* (1991) and Strub *et al.* (1991) for phytoplankton, Mackas *et al.* (1991) for zooplankton and Rodríguez *et al.* (1999) for icthyoplankton. We have observed a close relationship between zooplankton biomass and the physical structure responsible for the formation of the upwelling filament. Moreover, our results also indicate that indices of feeding, metabolism and growth also follow the physical signature. They showed higher values in the filament structure while low values were related to the center of the trapped cyclonic eddy (Figs. 4 to 6). This is in agreement with previous observations by Smith and Lane (1991) who observed increased egg production of the copepod *Eucalanus californicus* in a filament structure in the California Current system. However, the question of whether the increased activity in the filaments is due to advective or *in situ* processes (local enrichment) remains. In this sense, Basterretxea and Arístegui (2000) observed in transect 2 (station 65) a change from the upwelling zone to the filament. This was observed on the basis of the T-S diagram, the sharp decrease in chlorophyll from transect 1 to 3 (see also Fig. 7), the higher contribution of diatoms to total chlorophyll in transect 1 and the maximum of the specific primary production at limiting light intensities (α). Thus, although chlorophyll decreased sharply from transect 1 to 2, primary production remained high after transect 2 (Fig. 7). It is in this area and out to transect 4 where we observed the highest zooplankton biomass. It then decreased 2–3 fold in transects 5 and 6, at the edge of the filament structure.

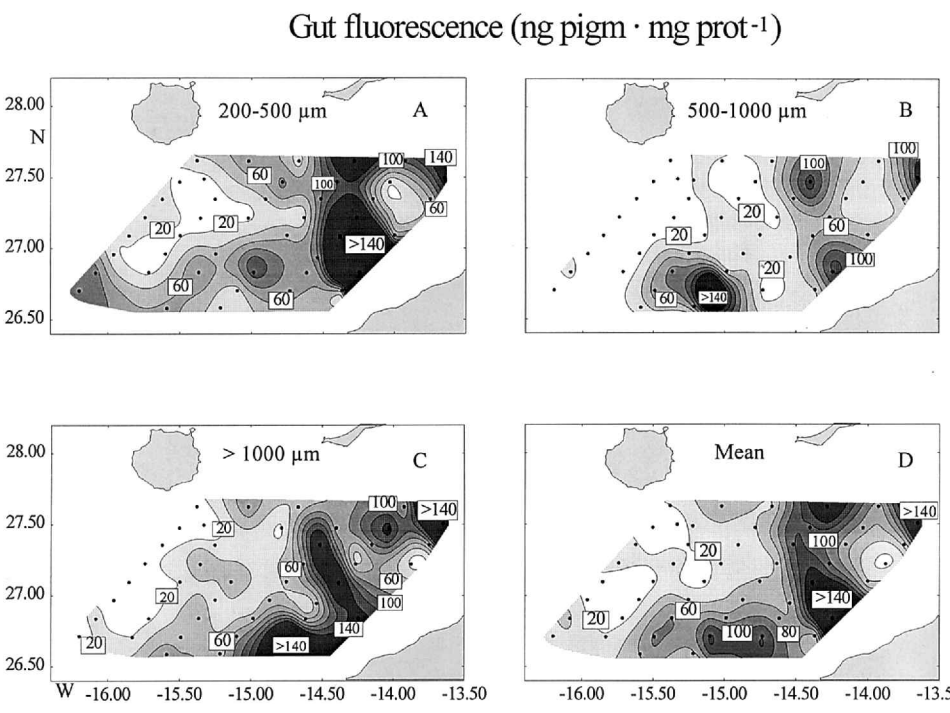

Figure 4. Specific gut fluorescence (ng pigments · mg^{-1} protein) distribution in the three size fractions and the average of all size classes. Observe the higher gut contents coinciding with the filament structure.

This filament is a rather shallow structure flowing over the typical stratified subtropical waters (Navarro-Pérez and Barton, 1998). No evidence of mixing was found and the only feature that needs elucidation is the convergence zone at the northern edge of the filament structure. This feature would promote the accumulation of plankton and therefore the presence of food organisms in the filament. However, offshore transport in the filament was in excess of 1 Sv (Navarro-Pérez and Barton, 1998) which is a considerable flow injected into the open ocean waters. Rodríguez *et al.* (1999) also showed that neritic fish larvae (mainly *Sardina pilchardus*) were associated with this filament structure while oceanic larvae were strongly excluded. Therefore, we suggest that advection and biological transport from the very rich upwelled waters to oceanic ones must be a major function of these filaments in view of their richness in biomass and biological activity. In fact, the decrease in gut fluorescence and ETS activity was not as sharp as chlorophyll and primary production and perhaps this is the consequence of a rapid consumption on phytoplankton biomass and on primary production which remained high in transects 2 and 3 (Fig. 7). Zooplankton has much longer generation times than phytoplankton and can remain longer in the water column.

In order to assess whether zooplankton is controlling primary production, we calculated zooplankton grazing from gut fluorescence and the gut evacuation rates obtained. We

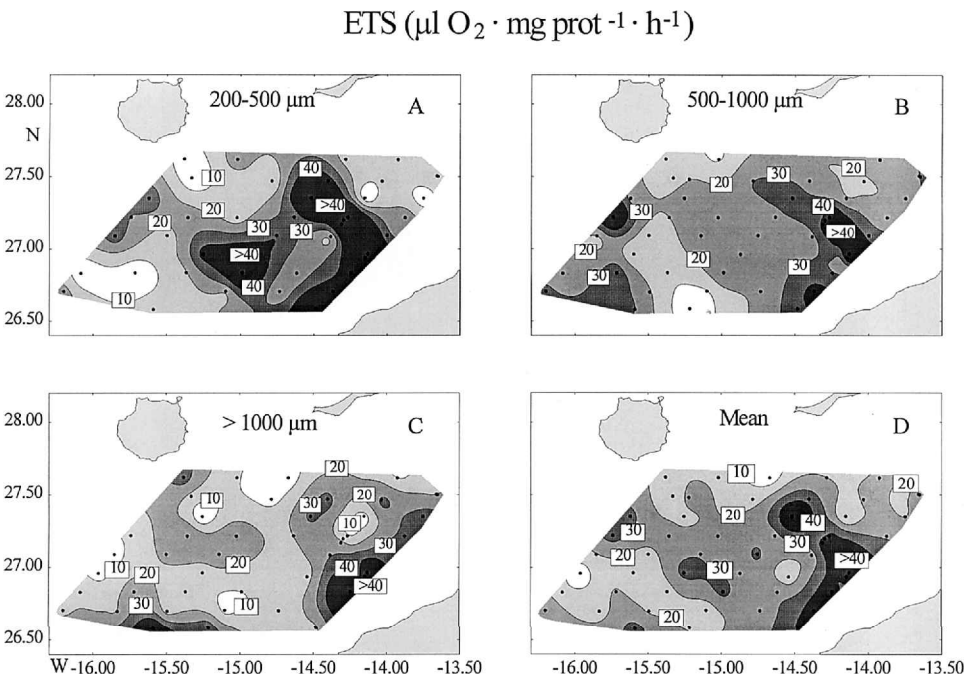

Figure 5. Specific electron transfer system activity ($\mu lO_2 \cdot mg^{-1}$ protein $\cdot h^{-1}$) in the three size fractions (a, b and c) and the average of all size classes. Higher activities were observed related to the filament structure.

found that gut evacuation rates covariated with gut fullness assessed from the gut fluorescence. However, we have observed that food changed from pigment to nonpigment-based diet along the transects (Fig. 7f, see below). The intense spatial gradient of gut fullness is correct for pigmented food but not for total food (pigmented plus nonpigmented). Therefore, our gut fullness based on the gut fluorescence should not be used to calculate evacuation rates. Then, we use the average value obtained (0.056 min^{-1}), which will also account for the diel feeding variability. The obtained value was in good agreement with the values reviewed by Irigoien (1998) for the range of temperature experienced during the cruise. In order to estimate the grazing rates, we also used the obtained average value of gut evacuation rates for the three size fractions studied. Barquero *et al.* (1998) and Bautista and Harris (1992) observed slight differences between the gut evacuation rates of different size fractions, although their values were variable within each size fraction and the evacuation curves might be somewhat biased in their initial slopes. However, Morales *et al.* (1990, 1991, 1993) and Wang *et al.* (1998) found a high variability in this parameter and showed that it is not clearly related to the different size fractions and body size, even after correction for temperature effects and possible artifacts in the analysis. The no-clear differences between the size fractions and the rather good relationship obtained in the

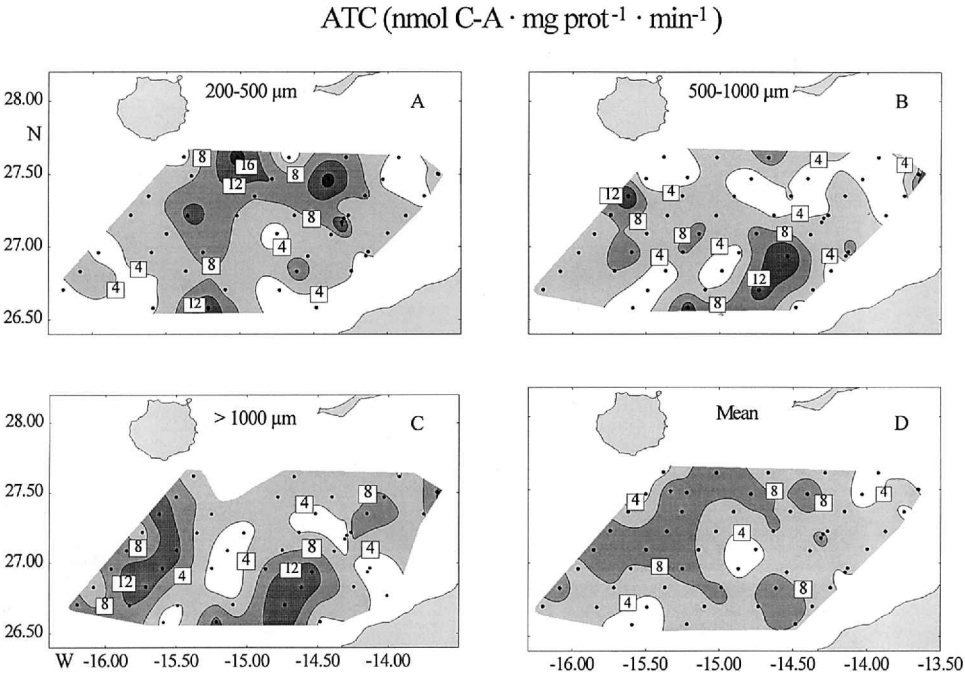

Figure 6. Specific aspartate transcarbamylase (nmol carbamyl aspartate · mg^{-1} protein · min^{-1}) activity in the three size fractions (a, b and c) and the average of all size classes. Observe the higher activities around the trapped cyclonic eddy (see text).

present work with the gut content, suggests that the gut evacuation rate is dependent of temperature (Christoffersen and Jespersen, 1986; Dam and Peterson, 1988; Irigoien, 1998) and feeding conditions (gut fullness), which in fact, is highly variable during the diel cycle (e.g., Christoffersen and Jespersen, 1986; Barquero *et al.,* 1998). Those characteristics would support the use of the above mentioned average value of the gut evacuation rates obtained for the mesoscale assessment of grazing where day and night samples from a rather highly variable environment need to be pooled. The method of gut fluorescence also suffers from the uncertainty of the pigment degradation in the gut (Conover *et al.,* 1986). Pigment destruction rate in zooplankton guts is not constant and, therefore, difficult to evaluate (see McLeroy-Etheridge and McManus, 1999). Peterson and Dam (1996) studied the egg production rates and pigment ingestion rates of *Temora longicornis* suggesting, however, that the gut pigment method underestimates pigment ingestion by no more than a factor of two. Thus, with the restrictions of using gut fluorescence and gut evacuation rates and assuming a pigment destruction of 50% (Peterson and Dam, 1996), the calculated grazing impact on primary production using a carbon/pigment ratio of 50 ranged from 16 to 97% in transects 2 to 6 (Table 3). Only assuming a 90% rate of pigment destruction (Tirelli and Mayzaud, 1998), mesozooplankton will be able to control primary production

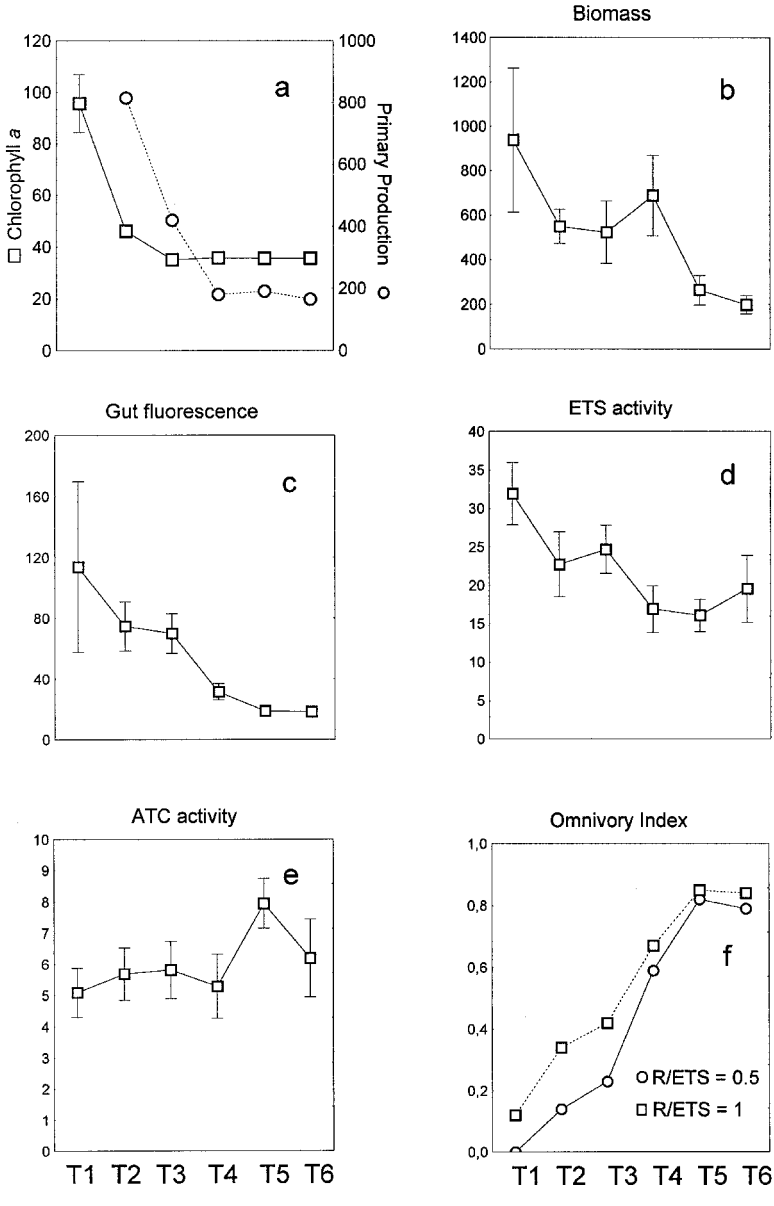

Figure 7. Average values (±SE) for each of the six sections of (a) chlorophyll ($\mu g \cdot l^{-1}$) and primary production ($mgC \cdot m^{-2} \cdot d^{-1}$), (b) zooplankton biomass (mg protein $\cdot m^{-2}$), (c) specific gut fluorescence (ng pigments $\cdot mg^{-1}$ protein), (d) specific ETS activity ($\mu lO_2 \cdot mg^{-1}$ protein $\cdot h^{-1}$), (e) specific ATC activity (nmol carbamyl aspartate $\cdot mg^{-1}$ protein $\cdot min^{-1}$), and (f) the index of omnivory (see text). The transect number is arrayed on the x-axis. Section 1 is close to the African coast; section 6 is the farthest offshore (Fig. 1). Observe the sharp decrease in chlorophyll followed by primary production and zooplankton biomass. While gut fluorescence and ETS activity decreased offshore, ATC activity remained constant and the calculated index of omnivory from Table 3 (ingestion-grazing/ingestion) sharply increased toward the ocean.

Table 3. Average values of grazing ingestion, respiration and production (in mgC m^{-2} d^{-1}) and percentage of grazing and ingestion (see text for calculation) in relation to primary production in the six transects sampled around the upwelling filament. Respiration has been calculated taking into account a respiration/ETS ratio of 0.5 and 1.0 (see text) while grazing was estimated assuming 50% of pigment destruction.

Transect	Grazing	Respiration (ETS = 0.5–1.0)	Production	Ingestion (ETS = 0.5–1.0)	(% of primary production) Grazing	Ingestion
1	860.9	187.0–374.0	270.0	692.4–975.7	—	—
2	330.9	77.9–155.8	176.8	385.9–503.9	40.6	47.3–61.8
3	294.7	80.5–161.0	172.1	382.7–504.6	70.3	91.3–120.4
4	174.8	72.5–145.0	206.1	422.1–532.0	97.1	234.5–295.6
5	30.1	19.9–39.8	89.2	165.4–195.5	15.7	86.6–102.4
6	38.8	32.1–64.3	92.4	188.6–237.3	23.5	114.3–143.8

in transects 1 to 4 but still not in transects 5 and 6. The impact of grazing on primary production was higher in the filament-affected transects (1 to 4, Table 3) than in the most oligotrophic area (transects 5 to 6). Our results are above the range normally given for oceanic warm waters of 1–12% (Dam *et al.,* 1995; Zhang *et al.,* 1993), and are also higher than the ones found in temperate waters (<10%, Morales *et al.,* 1991, 1993; Dam *et al.,* 1993; Barquero *et al.,* 1998). This grazing control on primary production in the filament may explain in part the fast offshore decay in primary production and the persistence of the zooplankters as far as transect 4. Nevertheless, nutrient depletion, microplankton grazing and sedimentation of large phytoplankton cells between coastal upwelled waters and offshore waters would also contribute to the sharp decline in the chlorophyll values.

Ingestion (pigmented plus nonpigmented food) was calculated in two ways: first, using a respiration/ETS ratio of 0.5 (Hernández-León and Gómez, 1996) and the growth/ATC ratio of 0.033 given by Hernández-León *et al.* (1995) and assuming that two-thirds of the ingested food is assimilated. Secondly, a respiration/ETS ratio of 1.0 was also used because of its increase associated with higher levels of chlorophyll (Hernández-León and Gómez, 1996). The respiration/ETS increase probably arises because the cells are not substrate limited when food is available (see also Hernández-León and Torres, 1997), as also suggested by the results of Packard *et al.* (1996a,b), Roy and Packard (1998) and Roy *et al.* (1999). The area under study showed relatively high values of phytoplankton biomass (Fig. 2) because of the influence of the filament structure. Therefore, the calculation of ingestion was also assessed in this way (R/ETS = 1). On the other hand, there is evidence of good relationships between ATC activity and growth rates in different organisms (Bergeron and Alayse-Danet, 1981; Bergeron, 1982). However, the same relationship in crustaceans is not always consistent (Alayse-Danet, 1980; Hernández-León *et al.,* 1995; Biegala and Harris, 1999; Biegala *et al.,* 1999). This is probably because ATC activity reflects the period of intensive cell multiplication (Koueta and Boucaud-Camou, 1992)

which in those organisms is related to the moulting process and not directly to structural growth, although both processes are in fact coupled in nature. Hernández-León *et al.* (1995) found that the ratio between growth and ATC suffers the same variability as the other physiological rate/enzyme activity ratios reported in the literature (e.g., respiration/ETS or glutamate dehydrogenase/ammonia excretion). Thus, based on enzymatic indices, ingestion was equivalent to 47–296% of the primary production (Table 3). Dam *et al.* (1995) found that the carbon flux through mesozooplankton in equatorial waters was equivalent to 23% of primary production. Hernández-León *et al.* (1999) also observed in tropical waters that ingestion, calculated from metabolic demands, accounted for 46% of primary production (also assuming herbivorous feeding). Then, our values in the transition zone, even in the conservative estimations, are higher than in other environments.

The ingestion rates obtained were higher than the grazing rates based on gut pigment content (transects 3 to 6), suggesting that mesozooplankton needed to include non-pigmented food, such as microzooplankton, to fulfill their physiological demands. This is clearly observed in the assessment of the importance of the nonpigmented food toward the ocean (Fig. 7f). As deduced from the index of omnivory (ingestion-grazing/ingestion, from Table 3), there is a decrease in the importance of pigmented food toward the open ocean, which shows the transition of this community from the eutrophic to the oligotrophic regime. In oceanic waters the observed values indicated that pigmented food was a low portion of the diet. This is coincident with the results of Dam *et al.* (1995) in equatorial waters which state that more than 80% of ingestion was not phytoplankton.

The index of growth (or cell multiplication) was rather high (see Hernández-León *et al.,* 1995) and constant throughout the area (Fig. 7), accounting for calculated average values of growth rates in the range 0.17–0.26 d^{-1}. Maximum values obtained from the equation of Huntley and Lopez (1992) for the average temperature at which organisms were captured showed values of 0.29 d^{-1}. This suggests that food was abundant enough to support mesozooplankton growth. So, the progressive decrease in zooplankton biomass along the transects (Fig. 3d) should be related to predation or dispersion rather than to a decrease in zooplankton metabolism and growth. It is not clear that dispersion would be the mechanism of biomass decrease because of the significant relationships between the hydrological structure and biomass and the high values at the end of the filament (St 76, 80, 91). Moreover, the average biomass by transects performed in this study would decrease the possible effect of dispersion. In this context, it has been recently suggested (Hernández-León, 1998; Hernández-León *et al.,* 2001; 2002) that diel vertical migrants of the deep scattering layers (DSL) can control epizooplankton in these waters. The sharp DSL's observed near the upwelling areas (see Boden and Kampa, 1967) would be the ultimate receivers of upwelling production, and therefore the ultimate living link (jointly with the microbial loop) in the transport of organic matter offshore in these transition zones between upwelling and the oligotrophic areas of the subtropical ocean.

Finally, three mechanisms are suggested to explain the high potential control of mesozooplankton on producers as well as their relatively high metabolic demands. First,

biomass is exported out from the proper upwelling area. The zooplanktonic organisms have longer generation times and can persist in the filament structure. Secondly, zooplankton and phytoplankton biomass and production are uncoupled because of the export mechanism. Third, the presence of nonpigmented food (microzooplankton) would allow mesozooplankton to maintain their metabolic demands in an environment of low primary productivity.

Acknowledgments. The authors would like to thank Dr. T. T. Packard and Dr. E. D. Barton and two anonymous reviewers for their comments and constructive criticism on the manuscript. This work was supported in part by the MAST programme of the European Commission through project 0031, and Spanish Ministry of Education project Mesopelagic (MAR97-1036). We are indebted to the crew of the R.V. *Hespérides* for technical assistance.

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Received: *25 April, 2000;* revised: *1 November, 2001.*