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RESEARCH ARTICLE

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Mesozooplankton distribution, metabolism and grazing in an anticyclonic slope water oceanic eddy (SWODDY) in the Bay of Biscay

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Abstract Mesozooplankton distribution, metabolism and feeding were investigated in the slope water oceanic anticyclonic eddy (SWODDY) AE6 during the cruise Gigovi-0898, which was conducted in August 1998 in the Bay of Biscay. According to the distribution of isotherms at 200 m depth, the sampling area was divided into three zones: SWODDY centre (C), edge (E) and outside the SWODDY (O). Multivariate analysis identified four different zooplankton assemblages. Such separation was closely related to the structure of the SWODDY, with each grouping associated to a particular zone of this mesoscale structure. Thus, two of the groups were located at the SWODDY centre and outside (groups C and O, respectively), whereas the two remaining station groupings (T_{WE} and T_{NS}) were situated at the SWODDY margin. The assemblages C and O differed clearly from each other in their taxonomic composition. In contrast, T_{WE} and T_{NS} were separated because of the differences observed in numerical abundance rather than by a different composition. Some taxa were found exclusively outside the SWODDY, while others were confined to the centre, suggesting a large degree of isolation of the SWODDY with respect to the surrounding waters. Phytoplankton and mesozooplankton biomass followed a similar pattern, with highest values in the SWODDY centre, although the differences between zones were significant only for phytoplankton. The highest grazing impact for both phytoplankton standing stock (3.4%) and primary production (12.7%) was observed outside the SWODDY. Ammonium released by mesozooplankton accounted for between 25.3% (outside the SWODDY) and 44.4% (SWODDY centre) of total phytoplankton nitrogen demands. The percentage of total phosphorus required to be fulfilled by phosphate excretion ranged from 14.0% at the edge to 17.5% outside. Mesozooplankton underwent intense vertical migrations, especially at the SWODDY edge. The role of the mesozooplankton in the biological pump releasing metabolic end-products below 200 m at night time is proposed as one of the main sources of downward export of biogenic material in these systems.

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Introduction

Anticyclonic eddies are recurrent mesoscale structures in the Bay of Biscay circulation (Pingree and Le Cann 1992a, 1992b; van Aken 2002). They are shed from the slope current that flows along the Iberian slope (Pingree and Le Cann 1992b), and hence are named SWODDIES (slope water oceanic eddies). A large number of authors have reported the importance of eddies in enhancing primary productivity in oceanic waters, both on the basis of direct observations (e.g. Perissinotto and Duncombe Rae 1990; Falkowski et al. 1991; Froneman et al. 1999) as well as modelling (Oschlies and Garçon 1998; Garçon et al. 2001; Kawamiya and Kishi 2002). A different ecosystem structure and functioning is therefore expected in oceanic eddies compared to the surrounding waters.

The programme GIGOVI was designed to obtain a comprehensive view of the SWODDIES, considering both physical and biological aspects as well as their relationships. Within the framework of this programme a detailed study was carried out over one of these SWODDIES (AE6), which had previously been traced through satellite imagery (Sánchez and Gil 2004). The SWODDIES in the Bay of Biscay are well described from a physical point of view (see Pingree and Le Cann 1992a, 1992b). Briefly, they characteristically have a

diameter of ~100 km, an eddy core of mixed water that retains slope water properties, a domed thermocline in the eddy centre and a lifetime of ca. 1 year. Nevertheless, information on their biological properties remains scarce (Rodríguez et al. 2003; Fernández et al. 2004). Given that anticyclonic eddies seem to have a strong impact on ecosystems (Savenkoff et al. 1993; Garçon et al. 2001), the main aim of this study was to investigate the mesozooplankton impact on biogeochemical cycles and food web structure in AE6. Mesozooplankton is expected to play a major role in the functioning of SWODDIES, through their relevance to key processes such as nutrient regeneration (Lehman 1980) and vertical export (Longhurst and Harrison 1989), but empirical evidence is rather limited.

Mesozooplankton distribution and diversity may be influenced by the presence of mesoscale eddies (Pinca and Dallot 1995; Beaugrand and Ibañez 2002). Furthermore, zooplankton diversity in our study area seems to be primarily regulated by physical factors (Beaugrand et al. 2001; Beaugrand and Ibañez 2002). Eddies can transport zooplanktonic assemblages inside (Pakhomov and Perissinotto 1997; Ginzburg et al. 2002). This fact, along with the strong relationship between copepod species assemblages and currents (Beaugrand et al. 2002) and the large degree of isolation between the inner and the outer sides of the SWODDIES in the Bay of Biscay (Pingree and Le Cann 1992a), led us to speculate on the possible differences in zooplanktonic composition inside AE6 versus the adjacent waters. Besides inside and outside the eddy, the transition zone between them was also considered, given the peculiar characteristics that this peripheral area might have as regards zooplankton distribution (Piontkovski et al. 1995; Froneman and Perissinotto 1996).

Previous studies suggest that the role of mesozooplankton on biogeochemical cycles within anticyclonic eddies is determined by their spatial distribution (Pinca and Dallot 1995; Pakhomov and Perissinotto 1997). In the present study we investigated mesozooplankton distribution along with its grazing impact, metabolic rates and its influence on nutrient regeneration and on the biological pump. Different zooplankton assemblages were found at the SWODDY centre, edge and outside, so this spatial classification was used to investigate whether the changes observed in the zooplankton composition affect the functioning of the ecosystem.

Materials and methods

Sampling area

The cruise Gigovi-0898 was carried out in the Bay of Biscay from 12 to 31 August 1998 on board R.V. ''Professor Shtokman''. The sampling area (Fig. 1) was established after a satellite image obtained on 6 August recorded SWODDY AE6 centred at ~45.5°N; 6°W. Prior to this, the evolution of AE6 through the Bay of Biscay had been followed by satellite imagery since being

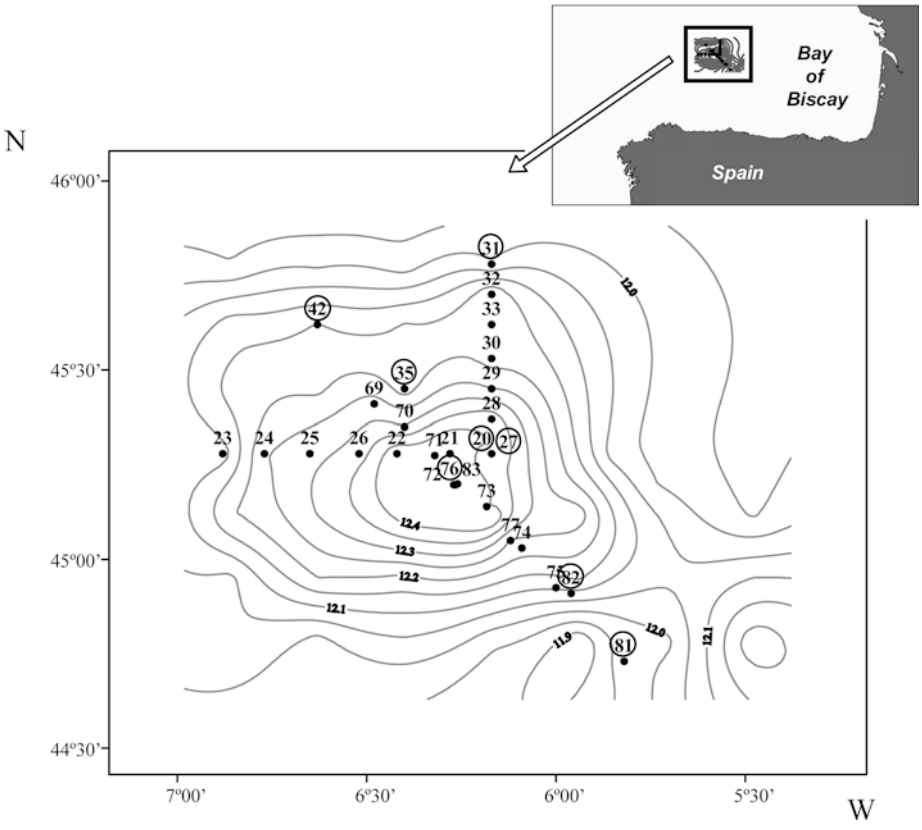

Fig. 1 Map of the study area with the stations sampled during Gigovi-0898. The positions of the stations from which mesozooplankton samples were taken are illustrated in detail in the enlarged area. The biological stations are *encircled*. Isolines represent temperature (°C) at 200 m depth. This parameter was also used to delimit the extension of the slope water oceanic anticyclonic eddy (SWODDY)

first detected on 20 May 1998. A total of 83 stations were sampled. Stns 1–20 were sampled to identify precisely the position of the SWODDY, and mesozooplankton sampling started immediately after the SWODDY was located. CTD deployments were performed at each station to describe the thermohaline structure. Both a Neil Brown MARK-III CTD and/or a Seabird SBE25 CTD were used alternatively. An intercalibration did not reveal any difference between their output measurements. Three regions were considered within the area surveyed: eddy centre (C), eddy edge (E), which coincides with the area of higher geostrophic velocity (Sánchez and Gil 2004), and outside the eddy (O). This division was made according to the spatial distribution of isotherms at 200 m depth, which were used to delimit the extension of the SWODDY as well.

Zooplankton collection

A total number of 28 stations were sampled to estimate abundance and biomass of mesozooplankton, as well as copepod gut contents. In addition, gut evacuation and metabolic rates were measured at eight stations labelled as "biological" (Fig. 1). These biological stations were sampled during both daytime and night time. Samples for taxonomic composition were collected at 13 stations located along the perpendicular transects W–E (stns 20–26) and N–S (stns 27–32), which converged at the eddy centre (Fig. 1). Given that most of the stations were located within the transition zone between the eddy centre and the outside two additional samples were analysed, one at the eddy centre (stn 76) and the other one clearly outside the eddy (stn 81).

Mesozooplankton was collected with a modified triple WP-2 net, each ring measuring 40 cm in diameter, supplied with 200-μm mesh, and equipped with filtering cod-ends. Hauls were made vertically from 200 m to the surface at ca. 0.5 m s^{-1}. Samples used for biomass and abundance measurements were obtained with tows where the nets were rinsed to concentrate all the organisms in the cod-ends. This procedure, however, was avoided when collecting mesozooplankton for either measurements of gut contents or for deck incubations. Cod-end contents were always sieved sequentially through meshes of 1000, 500 and 200 μm, to separate the large, medium and small mesozooplankton fractions.

Samples for abundance and taxonomic determination were preserved in 4% borax-buffered formalin–seawater solution in 250-ml polyethylene jars until counting and determination in the laboratory under a Leica MZ8 stereomicroscope. Taxonomic identification was made to species level for most of the taxa (Table 1). Depending on the concentration of animals in each jar, the samples were examined entirely or sub-sampled into aliquots by a Stempel pipette. Samples for taxonomic identification were the same as those for abundance determinations, which had previously been size fractionated on deck to divide the mesozooplankton into large, medium and small fractions. Both gross data and calculations presented here, however, refer to total abundance, i.e. the sum of the three size classes for each station. Abundance data for the different stations were standardised to individuals per square metre. Biomass samples were filtered onto pre-weighed Whatman GF/A filters and then stored at −20°C. Prior to dry weight estimation, the filters were dried at 60°C for ~24 h. Finally, carbon and nitrogen content analyses were performed with a Perkin Elmer 2400 elemental analyser.

Feeding

The ingestion rate of copepods was estimated using the gut pigment method (Mackas and Bohrer 1976). Copepods were gathered on sharkskin filters immediately after size fractionation and stored at −20°C in complete darkness until laboratory analysis. Three sub-replicates were taken for gut fluorescence measurements, each consisting of 75, 30–50 and 5–15 individuals for the small, medium and large fractions, respectively. Gut pigments were extracted in 6 ml of 90% acetone overnight 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 chlorophyll *a* (chl *a*) destruction were applied. For gut evacuation experiments, size fractionated mesozooplankton was transferred to a cool box filled with 0.2-μm-filtered surface seawater. Sub-samples were taken at consecutive time intervals (0, 2, 5, 8, 10, 15, 20, 30 and 40 min) and processed as described above for the gut pigment measurements. The amount of chl *a* grazed daily by copepods was estimated by multiplying their numerical abundance by the corresponding ingestion rate. Grazing impact was assessed both on the total phytoplankton and on the >2 μm phytoplankton fraction. The phytoplankton carbon ingested was estimated by applying a C to chl *a* ratio of 50 (Båmstedt et al. 2000). Size fractionated chl *a* concentration and primary production were measured as described in Teira et al. (2001).

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 with 0.2-μm-filtered seawater, where they were kept for about 2 h to acclimate. Randomly selected crustaceans were then introduced into 1-l glass bottles filled with 0.2-μm-filtered seawater. The numbers of individuals incubated per litre (mean ± SD), averaged over all biological stations, were 165 ± 129, 37 ± 22 and 17 ± 9 for the small, medium and large fractions, respectively. Gelatinous zooplankton was excluded because of the high mortality rates observed in previous incubations. Three control

Table 1 List of taxa identified in Gigovi-0898

Appendicularia	Chaetognatha	*Gaidius*sp.
Appendicularians	*Saggita* spp. juv.	*Heterorhabdus norvegicus*
	Saggita friderici	*Heterorhabdus papilliger*
Amphipoda	*Saggita lyra*	*Heterorhabdus spinifrons*
Parathemisto gaudichaudii	*Saggita serratodentata*	*Ischnocalanus tenius*
Phronima sedentaria	*Saggita tasmanica*	*Lucicutia*sp. juv.
	Saggita zetesios	*Mecynocera clausi*
Euphausiacea		*Mesocalanus tenuicornis*
Euphausiacea larvae	Polychaeta	*Metridia lucens*
Euphausiacea krohni	*Tomopteris helgolandica*	*Microcalanus pygmaeus*
Nematobrachion boopis		*Microsetella norvegica*
Nematobrachion megalops	Bivalvia	*Microsetella rosea*
Nyctiphanes sp.	Bivalve veliger	*Mimocalanus cultrifer*
Stylocheiron longicorne		*Nannocalanus minor*
Thysanoessa longipes	Gastropoda	*Neocalanus gracilis*
	Gastropod veliger	*Oithona helgolandica*
Foraminifera		*Oithona plumifera*
Globigerinidae	Copepoda	*Oithona*spp. juv.
	Acartia clausi	*Oncaea conifera*
Hydroidomedusa	*Acrocalanus* sp.	*Oncaea media*
Trachymedusae	*Aetideidae* juv.	*Oncaea mediterranea*
	Aetideus armatus	*Oncaea minuta*
Siphonophora	*Anomalocera patersoni*	*Paracalanus aculeatus*
Siphonophorae Calycophorae	*Calanoides carinatus*	*Paracalanus parvus*
Siphonophorae Physonectae	*Calanus helgolandicus*	*Paracalanus*spp. juv.
	Calanus sp.	*Paraeucheta*spp. juv.
Scyphozoa	*Calocalanus contractus*	*Paraeucheta gracilis*
Sciphomedusae	*Calocalanus pavo*	*Paraeucheta norvegica*
	Calocalanus sp.	*Paraeucheta tonsa*
Ostracoda	*Calocalanus styliremis*	*Pleuromamma abdominalis*
Conchoecia subarcuata	*Candacia armata*	*Pleuromamma gracilis*
Conchoecilla daphnoides	*Centropages chierchieae*	*Pleuromamma robusta*
Conchoecissa imbricata	*Centropages hamatus*	*Pleuromamma*spp. juv.
Discoconchoecia elegans	*Centropages* spp.	*Pleuromamma xiphias*
Halocypria globosa	*Centropages typicus*	*Pseudocalanus elongatus*
Metaconchoecia rotundata	*Clausocalanus arcuicornis*	*Rhincalanus*sp. juv.
Mikroconchoecia acuticosta	*Clausocalanus jobei*	*Scaphocalanus echinatus*
Mikroconchoecia curta	*Clausocalanus lividus*	*Scaphocalanus*sp.
Mikroconchoecia sp. juv.	*Clausocalanus pergens*	*Scolecithricella dentata*
Orthoconchecia haddoni	*Corycaeus lautus*	*Scolecithricella minor*
	Corycaeus sp. juv.	*Scolecithricella ovata*
Fishes	*Ctenocalanus vanus*	*Scolecithricella*spp. juv.
Belone sp. larvae	*Euchaeta acuta*	*Scolecithricella vittata*
Myctophidae larvae	*Euchaeta hebes*	*Spinocalanus*sp.
Fish eggs	*Euchaeta media*	*Temora longicornis*
	Euchirella bitumida	*Temora stylifera*
Pteropoda	*Eucherilla curticauda*	*Undeuchaeta major*
Cymbulia peroni	*Eucherilla maxima*	*Undeuchaeta plumosa*
Euclio pyramidata	*Gaetanus minor*	*Undeuchaeta*spp. juv.
Limacina inflata	*Gaidius brevispinus*	*Vettoria granulosa*

bottles without animals and three experimental replicates for each size fraction were incubated for 20–24 h under dim-light conditions. Within the incubator, bottles were immersed in a continuous flow of seawater taken directly from the surface. At the end of the incubation, two sub-samples for oxygen and another two for ammonium and phosphate were taken by siphoning out water through a 200-μm mesh in order to retain the organisms in the bottles. Dissolved oxygen concentrations were measured on board with a 721 NET Titrino according to the Winkler titration method. Samples for the determination of ammonium and phosphate were frozen at −20°C for subsequent analysis in the laboratory according to Grasshoff et al. (1983) and using a Technicon AAII autoanalyser. After sub-sampling, the animals incubated were recovered on Whatman GF/A filters and frozen until their analysis for carbon and nitrogen content, as mentioned for the biomass samples.

Respired oxygen was converted to carbon assuming a respiratory quotient of 0.97 (Omori and Ikeda 1984). The flux of carbon respired and ammonium and phosphate excreted to the mesopelagic zone was estimated as in Zhang and Dam (1997), by applying the equation:

$$F = B \times M \times T \quad (1)$$

where B is the diel-migrating mesozooplankton calculated as the difference in biomass (mg C m^{-2}) between day and night samples in the top 200 m, M is the hourly metabolic rate and T is the number of hours of darkness

per day (10 h in this case) during which migrating mesozooplankton stay below the euphotic zone.

Statistical analysis

Prior to any analysis, abundance was $\log(x+1)$ transformed to weight the contributions of rare and extremely highly abundant species. Cluster analysis (q-type) was performed based on a Bray–Curtis similarity index and complete linkage classification of transformed data. The stations were then ordinated using non-metric multidimensional scaling (MDS). The BIOENV procedure was applied to examine the relationship between the mesozooplankton pattern and some environmental variables. The similarity matrix of abundance was compared with the similarity matrix of environmental variables, which was based on normalised Euclidean distance. The environmental variables used were mean temperature in the upper 200 m, surface temperature, temperature at 200 m depth, mixed layer depth and the depth of the 11.5°C isotherm. The last variable was used by Pingree and Le Cann (1992a) to delimit the extension of a SWODDY in the Bay of Biscay. Margalef's species' richness index (d) was estimated as follows:

$$d = (S-1)/\log N \qquad (2)$$

where N is the total number of individuals in the sample. This index corrects the effect of sample size on the number of taxa (S). Cluster, MDS, BIOENV and Margalef's index analyses were performed using the software package PRIMER (Plymouth Routines In Multivariate Ecological Research). Differences between provinces in copepod gut contents, grazing impact and in the variables presented in Table 3 were tested with ANOVAs. Post hoc comparisons were made by Newman–Keuls' tests.

Results

Thermohaline structure

The spatial distribution of isotherms at 200 m depth (Fig. 1) delimited the extension of AE6. Temperature at this depth ranged from 12.0°C outside the eddy to >12.4°C at the centre. Deepening of isotherms below ca. 100 m indicated the presence of warmer waters at the eddy centre than in the surrounding waters (Fig. 2). A higher salinity was also observed in this body of water (Fernández et al. 2004). In the upper layer, by contrast, the doming of the seasonal pycnocline led to cooler waters at the eddy centre than outside.

Mesozooplankton distribution

Cluster analysis identified four different groups of stations at a similarity level of ~48% (Fig. 3a). Such grouping reflected the position of the stations in relation to the SWODDY. Thus, the four stations that comprised group C were located in the SWODDY centre, group O included stations that lay outside the SWODDY, and the groupings T_{WE} and T_{NS} included stations located along the W–E and N–S transects, respectively, that ran from the eddy centre. Two-dimensional ordination of the stations by MDS also separated the same groups (Fig. 3b). Among the different environmental variables considered in the BIOENV analysis, the best fit of the matrix of abundance was observed with temperature at 200 m depth, although with a low value (Spearman rank correlation coefficient, $\rho = 0.39$). This was the variable we used to delimit the extension of the SWODDY (see Fig. 1). The next variable that best explained the mesozooplankton distribution patterns was

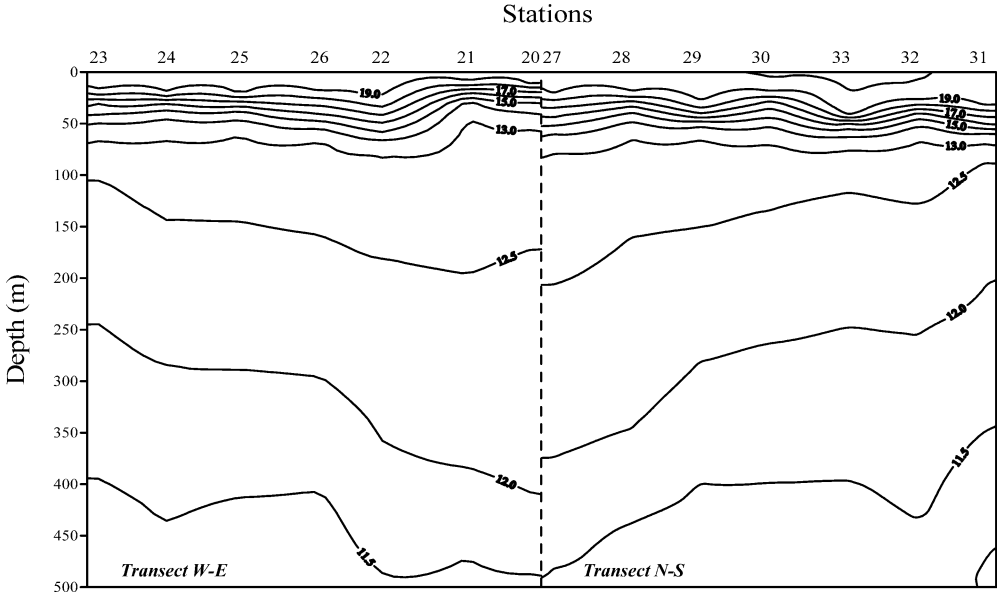

Fig. 2 Vertical section of temperature (°C) along the W–E and N–S transects. A core of warmer water is observed inside the SWODDY, as shown by the deepening of the 12.0°C isotherm towards this area, whereas surface waters are cooler at the SWODDY centre than in the surrounding zones

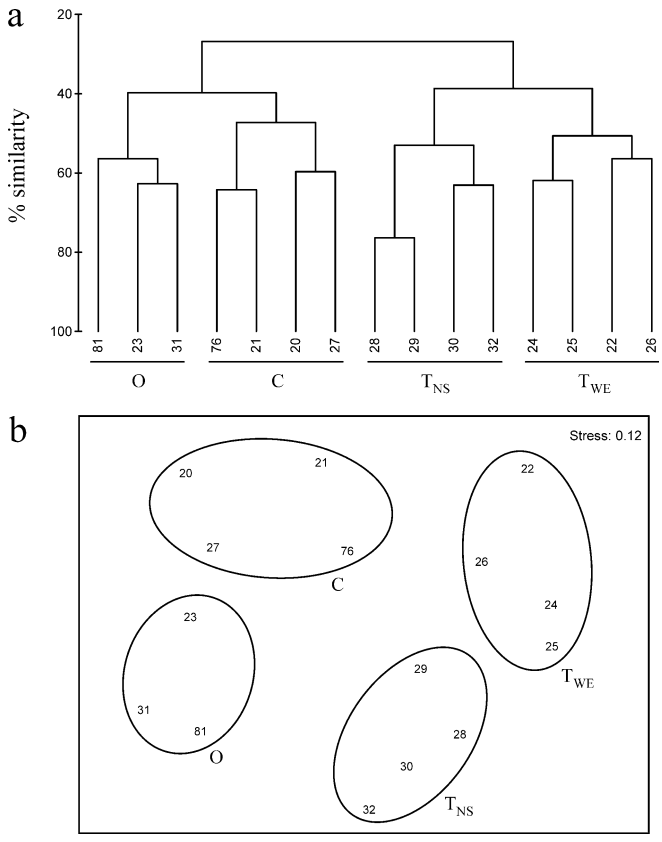

Fig. 3 Results of cluster (**a**) and multidimensional scaling (**b**) analyses of mesozooplankton community structure based on the Bray–Curtis similarity index. Four station groups are identified, each of them associated to a different region of AE6 (*C* stations situated at the SWODDY centre; *O* outside the SWODDY; T_{WE} stations at the SWODDY edge and located along the W–E transect; T_{NS} stations at the SWODDY edge and located along the N–S transect)

the depth of the 11.5°C isotherm ($\rho = 0.34$). For each of the remaining variables, ρ was < 0.2. The two groups representative of the SWODDY edge (T_{WE} and T_{NS}) were separated due to differences in abundance rather than in composition. Mean ($\pm$SE) values of abundance in the two transects, expressed as number of individuals ($\times 10^3$) per square metre, were 12.3 ± 2.0 in T_{WE} and 209.5 ± 66.9 in T_{NS}.

Zooplankton composition was largely dominated by copepods in the SWODDY centre, edge and outside, with *Clausocalanus pergens* and *Oithona helgolandica* always being the most abundant taxa (Table 2). Eight taxa were found exclusively outside the SWODDY, and eight others were restricted to its centre (Table 2). The taxa that occurred solely at the SWODDY centre are typical of coastal areas, the occurrence of the meroplanktonic bivalve and gastropod veliger being especially striking in a place so remote from the coast. None of the taxa identified in this study were found exclusively at the transition zone.

Both phytoplankton and mesozooplankton biomass followed a similar pattern, with highest values in the SWODDY centre (Table 3), although the differences between zones were significant only for phytoplankton. The relationship between phyto- and mesozooplankton is also evidenced by their distribution along the two perpendicular transects that converge at the SWODDY centre, with a peak at the central stations (Fig. 4). Conversely to phytoplankton biomass, the highest values of primary production were found outside the SWODDY (Table 3). Size structure of mesozooplankton does not seem to be influenced by the hydrographic features of AE6. The contribution of large mesozooplankton to total biomass did not differ between zones (Table 3). In terms of abundance, mesozooplankton was mostly comprised by copepods. Their contribution to total abundance ranged from 86.6% (stn 21) to 97.3% (stn 20). The Margalef's index of species' richness was significantly higher at the centre and outside the SWODDY than at the SWODDY edge (Table 3).

Table 2 Main groups and major contributors to total abundance in each zone, and list of taxa exclusive to each zone (species detected at only one station were not considered) (*Ot.* the most abundant taxa of planktonic organisms other than copepods)

Zone	Main groups	Major contributors	Exclusive taxa
Centre	Copepoda (93.1%) Chaetognatha (1.9%) Appendicularia (1.7%) Ostracoda (0.7%) Euphausiacea (0.4%)	*Clausocalanus pergens*(25.9%), *Oithona helgolandica* (17.1%),*Clausocalanus arcuicornis* (8.4%), *Oithona plumifera*(8.0%), *Paracalanus parvus* (3.8%) (Ot.) Appendicularians (3.1%),*Sagitta tasmanica* (1.0%), *Sagitta friderici*(0.6%)	*Artica clausi*,*Aetideidae* juv., bivalve veliger, gastropod veliger,*Sagitta frederici*, *Temora longicornis*,*Temora stylifera*, *Undeuchaeta major*
Edge	Copepoda (94.6%) Appendicularia (1.8%) Chaetognatha (1.2%) Ostracoda (0.6%) Euphausiacea (0.2%)	*Oithona helgolandica*(40.3%) *Clausocalanus pergens*(17.0%) *Pleuromamma*spp. juv. (7.4%), *Ctenocalanus vanus* (5.0%),*Oithona plumifera* (4.1%) (Ot.) Appendicularians (3.5%),*Salpa fusiformis* (1.8%), *Sagitta tasmanica*(1.7%)	
Outside	Copepoda (92.8%) Appendicularia (3.8%) Chaetognatha (0.7%) Euphausiacea (0.7%) Ostracoda (0.5%)	*Clausocalanus pergens*(27.0%), *Oithona helgolandica* (15.1%),*Clausocalanus arcuicornis* (7.6%), *Paracalanus*spp. juv. (5.9%), *Ctenocalanus vanus* (5.1%) (Ot.) Appendicularians (4.3%), Euphausiacea larvae (0.7%), *Sagitta tasmanica* (0.4%)	*Cymbulia peroni*,*Euclio pyramidata*, *Heterorhabdus norvegicus*, Myctophidae larvae, *Oncaea conifera*,*Paraeucheta tonsa*, *Parathemisto gaudichaudii*,*Sagitta serratodentata*

Table 3 Mean (±SD) values of several structural characteristics of mesozooplankton and phytoplankton in the three zones considered in AE6, and results of the ANOVAs and post hoc Newman–Keuls' tests performed to test for differences between zones (*n.s.* not significant)

Variable	Centre (C)	Edge (E)	Outside (O)	*F*	*P*	Post hoc
Biomass (g dry wt m^{-2})	1.6 ± 0.7	1.3 ± 0.5	1.3 ± 0.4	1.21	n.s.	
Percent biomass > 1000 μm	53.4 ± 20.1	54.4 ± 15.1	43.5 ± 10.8	1.18	n.s.	
d (Margalef's index)	4.1 ± 1.1	2.6 ± 0.5	4.4 ± 0.4	10.1	< 0.01	C, O > E
Chl *a* (mg m^{-2})	23.3 ± 4.7	18.1 ± 3.5	18.4 ± 3.5	4.9	< 0.05	C > E, O
Primary production (mg C $m^{-2}day^{-1}$)	345.6 ± 65.6	331.3 ± 9.0	438.1 ± 165.0	1.1	n.s.	

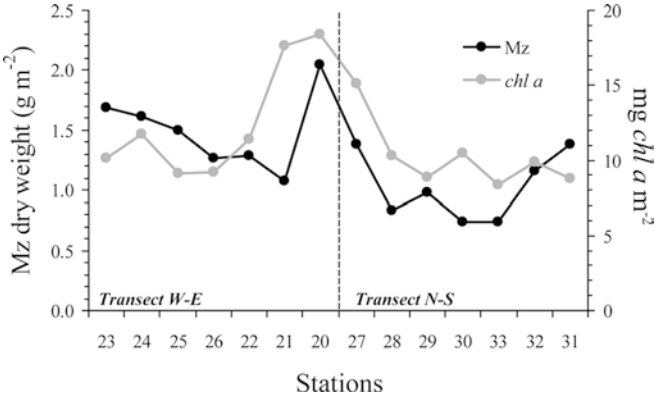

Fig. 4 Depth-integrated biomass of mesozooplankton (*Mz*) and phytoplankton (*chl a*) along the W–E and N–S transects

Feeding

Average gut contents for large copepods seemed to decrease from the SWODDY centre to the outside (Table 4), but gut contents did not vary significantly between zones for any of the three size classes (ANOVA tests, $P > 0.05$ for each fraction). The highest grazing impact on phytoplankton biomass and primary production was recorded outside the SWODDY for both total and > 2 μm phytoplankton (Table 5), although the differences were not significant (ANOVA tests, $P > 0.05$ in all cases). Ingested phytoplankton carbon was only a fraction of the carbon required by mesozooplankton to maintain their basal metabolism: 8.2% of minimum carbon demands was met at the centre, 9.4% at the eddy edge and 13.2% outside. These estimates were obtained after applying an assimilation efficiency of 70% (Conover 1966).

Table 4 Mean (±SD) values of copepod gut pigment contents at the SWODDY centre, at its edge and outside. Small, medium and large represent the three size classes in which mesozooplankton was fractionated (see "Materials and methods")

Size class	Chl *a* equiv. (ng $ind.^{-1}$)		
	Centre	Edge	Outside
Small	0.06 ± 0.05	0.08 ± 0.05	0.08 ± 0.05
Medium	0.23 ± 0.14	0.22 ± 0.07	0.24 ± 0.10
Large	2.31 ± 1.85	1.88 ± 1.04	1.11 ± 0.54

Table 5 Mean (±SD) values of percentage of total and > 2 μm phytoplankton biomass and production grazed daily by copepods

Zone	Percent chl *a*		Percent primary production	
	Total	> 2 μm	Total	> 2 μm
Centre	1.2 ± 1.2	2.3 ± 2.3	4.6 ± 2.6	7.1 ± 4.7
Edge	1.1 ± 0.6	2.6 ± 1.6	3.9 ± 0.3	8.2 ± 1.1
Outside	3.4 ± 2.9	7.7 ± 6.3	12.7 ± 10.3	23.7 ± 13.4

Metabolism

The lowest respiration and ammonium excretion rates were generally observed outside the SWODDY, whereas phosphate excretion rates were similar in the three regions (Table 6). As a consequence of the metabolic rate pattern and mesozooplankton abundance, the total amount of carbon respired and ammonium released showed a decreasing trend from the eddy centre to its outside (Table 7). By contrast, the highest value of total phosphate excretion was recorded outside.

The contribution of mesozooplankton to the biological pump through diel vertical migrations appeared to be driven mainly by the largest fraction, which accounted for the largest proportions of carbon respired (64.4%), ammonium excreted (59.5%) and phosphate excreted (56.2%) below 200 m during night. Vertical migration was more conspicuous at the eddy edge, where Sánchez and Gil (2004) measured the highest geostrophic velocities. Nevertheless, the total amount of metabolic end-products released into the mesopelagic zone by migrant mesozooplankton did not show marked differences between regions (Table 7).

The excretory activity of mesozooplankton accounted for a large proportion of the nitrogen and phosphorus requirements of phytoplankton. These were estimated by applying standard Redfield ratios, i.e. C:N:P = 106:16:1. Ammonium released by mesozooplankton accounted for 44.4% of total phytoplankton nitrogen demands at the SWODDY centre, 39.7% at the edge and 25.3% outside the eddy. The percentage of total phosphorus required fulfilled by phosphate excretion was 16.2% at the centre, 14.0% at the edge and 17.5% outside.

Table 6 Mean (±SD) values of metabolic rates of small, medium and large mesozooplankton at the swoddy centre (*C*), at its edge (*E*) and outside (*O*)

Size class	O_2 (μmol μmol^{-1} C day^{-1})			NH_4 (μmol μmol^{-1} C day^{-1})			PO_4 (μmol μmol^{-1} C day^{-1})		
	C	E	O	C	E	O	C	E	O
Small	0.41 ± 0.20	0.39	0.19 ± 0.01	0.100 ± 0.039	0.083 ± 0.005	0.059 ± 0.022	0.0026 ± 0.0016	0.0031 ± 0.0038	0.0030 ± 0.0013
Medium	0.26 ± 0.06	0.37	0.21 ± 0.02	0.053 ± 0.005	0.062 ± 0.001	0.054 ± 0.011	0.0016	0.0014 ± 0.0017	0.0019 ± 0.0011
Large	0.18 ± 0.04	0.16 ± 0.08	0.18 ± 0.04	0.055	0.057 ± 0.027	0.038 ± 0.024	0.0015	0.0009 ± 0.0006	0.0014 ± 0.0003

Table 7 Summary of carbon respired and ammonium and phosphate excreted daily by the mesozooplankton in the three regions of the study area (*Resp. C flux*,*Excr. NH4flux* and *Excr. PO4flux* the amounts of these products released below 200 m during the night time by diel vertical migrators, representing the active flux driven by mesozooplankton within the biological pump)

Variable	Centre	Edge	Outside
Migrant biomass (g C m^{-2})	0.13	0.24	0.07
Total C resp. (mg m^{-2}day^{-1})	94.5	76.8	60.4
Resp. C flux (mg m^{-2}day^{-1})	28.8	20.4	7.1
Total NH_4 excr. (μmol m^{-2} day^{-1})	1930.1	1653.1	1380.5
Excr. NH_4 flux (μmol m^{-2} day^{-1})	414.9	563.6	132.7
Total PO_4 excr. (μmol m^{-2} day^{-1})	44.1	36.4	60.4
Excr. PO_4 (μmol m^{-2} day^{-1})	8.1	15.9	4.6

Discussion

Thermohaline structure and phytoplankton distribution

Thermohaline structure revealed that the centre of the SWODDY was clearly different from the surrounding areas during the period of the study. The eddy centre was characterised by the presence of a core of warmer and saltier water below 100 m, compared to the surrounding waters. By contrast, the doming of the seasonal pycnocline led to cooler surface waters at the SWODDY centre, which allowed its detection by satellite imagery. This thermohaline structure, with the isotherms deepening below 100 m and shoaling in the upper layer, was also observed by Pingree and Le Cann (1992a) in their description of SWODDY X91 in the Bay of Biscay.

Phytoplankton biomass was highest at the SWODDY centre and decreased gradually towards the outer region. Doming of the pycnocline and the internal waves observed across AE6 have been hypothesised as the cause of the higher phytoplankton biomass at its centre (Fernández et al. 2004). The decoupling between phytoplankton biomass and production could be explained by the fact that these SWODDIES retain the characteristics of their slope water origin (Pingree and Le Cann 1992a), isolated from the surrounding waters. So, distinct phytoplankton communities, with different properties, are expected inside and outside the eddy. In the case of AE6 this evidence is supported by the taxonomic composition, which shows marked quantitative and qualitative differences between phytoplankton assemblages inside and outside the SWODDY (Rodríguez et al. 2003).

Mesozooplankton distribution

Multivariate analysis performed on mesozooplankton composition identified four different eddy regions in our study area. Spatially, two of the groups were located at the SWODDY centre and outside (groups C and O, respectively). The two remaining station groupings, T_{WE}

and T_{NS}, were situated at the SWODDY margin. These two groupings were discriminated due to the difference in zooplankton abundance, but zooplankton composition and physical properties did not differ. Hence, the study area was divided into only three zones (SWODDY centre, edge and outside). In the same way, Rodríguez et al. (2003) also separated AE6 into centre, edge and external zones on the basis of phytoplankton composition.

T_{WE} and T_{NS} were clearly separated from each other by multivariate analysis, suggesting an asymmetry of mesozooplankton distribution within AE6. Sánchez and Gil (2004) likewise reported an asymmetric distribution of some physical variables in AE6. According to the findings of Rodríguez et al. (2003), this asymmetry would also be manifested by the phytoplankton distribution. They analysed two perpendicular transects, the so-called W–E and N–S transects in our study, and an additional oblique transect that crossed the eddy centre. Pigment distributions showed a large discrepancy between the perpendicular and the oblique transects (see Table 2 in Rodríguez et al. 2003). The influence of asymmetric anticyclonic eddies on zooplankton distribution has also been suggested for other latitudes (Hernández-León et al. 2001). On the other hand, peripheral areas of the eddies have been proposed as zones where there is a large spatial heterogeneity of zooplankton due to an enhancement of available potential energy (Piontkovski et al. 1995).

The taxa that were found exclusively in group C were characteristically from other environments. Bivalve and gastropod veliger are normally found near shore, because in their adult phase they occupy benthic habitats in shallow waters. The copepods *Acartia clausi* and *Temora longicornis* and the chaetognath *Sagitta friderici* are usually found in coastal waters. Finally, *Temora stylifera* and *Undeuchaeta major* are copepods rarely detected at this latitude, being typical of subtropical warm temperate waters instead. On the other hand, the taxa found exclusively outside the SWODDY generally have an oceanic distribution and are normally found in the Bay of Biscay. Among these taxa there were only three species of copepods (*Heterorhabdus norvegicus*, *Paraeuchaeta tonsa* and *Oncaea conifera*). It is noteworthy that the chaetognath *Sagitta serratodentata* was restricted to group O, whereas another species of the same genus (*S. friderici*) was detected only in group C. The value of chaetognaths as water-mass indicators is widely known (Postel et al. 1995). Given that the SWODDY edge was a transition area, the absence of species exclusive to this zone is not surprising.

Rodríguez et al. (2003) also found some phytoplanktonic taxa typical of coastal waters that were restricted to the SWODDY centre. In addition, they showed that the pigment composition of phytoplankton assemblages in the central region of the SWODDY was very similar to the pattern observed inside the poleward current off NW Spain. Both phytoplankton and zooplankton composition confirm the large level of isolation of the SWODDIES with respect to the surrounding waters and also that they originate from the poleward current and retain characteristics of their slope water origins, as was proposed by Pingree and Le Cann (1992a). Beaugrand et al. (2000) suggested that the transport of species native to subtropical or coastal waters by the SWODDIES would contribute to increased zooplanktonic diversity in the Bay of Biscay. In this sense, although the highest number of genera of copepods detected within a sample was 22 (stn 31), we identified 41 genera of copepods in this study, more than reported by Woodd-Walker et al. (2002) for this latitude.

Mesozooplankton biomass along the two perpendicular transects (N–S and W–E) resembled the distribution of phytoplankton biomass, with the highest values at the central stations of the SWODDY. Nevertheless, after pooling all the stations sampled, no significant differences in mesozooplankton biomass were obtained among the three regions considered, probably due to the high within-region variability. Enhancement of zooplankton accumulation has variously been reported at the centre (Roman et al. 1985; Cowles et al. 1987) or at the edge (Pakhomov and Perissinotto 1997; Hernández-León et al. 2001) of anticyclonic eddies.

Feeding

Mesozooplankton grazing pressure on both phytoplankton standing stock and primary production was highest outside the SWODDY. This was due to the higher copepod abundance found in this zone, since copepod gut contents did not change in the three zones. From the grazing impact measured, it follows that phytoplankton communities were not controlled by mesozooplankton in any of the three regions. However, the impact on the phytoplankton considered as available food (>2 μm) can be substantial, especially outside AE6. The pattern of grazing pressure may have some influence on the observed imbalance between chl *a* concentration and primary production. A similar imbalance was also observed by Froneman et al. (1999) in an anticyclonic eddy south of Africa, and they ascribed their results to different grazing impacts inside and outside the eddy. It is possible that the grazing effect is mainly mediated by microzooplankton, since they are the main consumers when phytoplanktonic communities are dominated by small algae (e.g. Murray et al. 1994; Sautour et al. 2000). Indeed, in the Southern Ocean warm core eddy mentioned above, Froneman and Perissinotto (1996) found a close relationship between microzooplankton abundance and small phytoplankton concentration, as well as a higher grazing impact of protozoans outside rather than inside the eddy. The phytoplankton size structure observed in AE6, with higher primary production outside, mainly driven by the small fraction (data not shown), may indicate that something similar could have happened in this study.

Unfortunately, neither microzooplankton grazing nor abundance were measured in Gigovi-0898.

Phytoplankton carbon ingested represents only a small proportion of the mesozooplankton carbon requirements, so they must complement their diet with alternative food sources. The limitation of herbivory towards fulfilling the basal metabolic demands of mesozooplankton and the inferred high predation rates on protozoans agree with previous studies developed under oligotrophic conditions (Bradford-Grieve et al. 1998; Calbet 2001).

Chl *a* degradation was not measured during this study, so it could be argued that copepod ingestion was underestimated. Despite the literature showing a large variability in the percentage of gut pigment degradation, a correction factor of ×1.5 is usually applied (e.g. Dam and Peterson 1988; Calbet 2001). The higher ingestion values obtained after applying such correction does not affect the bulk of our results. Grazing impact on phytoplankton is still of minor importance, accounting for 1.8%, 1.6% and 5.1% of total phytoplankton biomass grazed daily at the centre, the edge and outside the SWODDY, respectively. The corresponding percentages for primary production are 6.9%, 5.8% and 19.0%. Likewise, a recalculation of phytoplankton ingested is still far from satisfying mesozooplankton carbon requirements. The percentages of carbon demands that are met through these corrected grazing rates are 12.3% inside the SWODDY, 14.1% at its edge and 19.8% outside.

Metabolism

Mesozooplankton excretion accounted for a considerable proportion of the nutrients required by phytoplankton. Our estimations of nitrogen and phosphorus recycled by mesozooplankton are similar to those reported by other authors for pelagic waters and/or summer stratification conditions (Jawed 1973; Bidigare 1983; Alcaraz 1988). Given the low *f*-ratio measured for the three zones (always < 0.5, Fernández et al. 2004), ammonium appears to be the main source of nitrogen for primary production. So the high amounts of ammonium released by mesozooplankton play a major part in sustaining local primary production. When copepods exert strong predatory pressure on microzooplankton, as suggested here, ammonium release by protozoans is depressed (Hasegawa et al. 2000), and thus the role of mesozooplankton in nitrogen recycling would be even more important. In our estimates it was assumed that all ammonium and phosphorate excreted was available for phytoplankton uptake. However, some of the total excretion estimated takes place below the euphotic zone, and the percentage of nutrient supplied by mesozooplankton would hence be overestimated. In any case, if the proportion of ammonium and phosphate excreted below 200 m at night is subtracted from the total values, the amount of these two nutrients resupplied is still substantial, accounting for 34.9%, 26.1% and 22.6% of the total nitrogen required by phytoplankton at the SWODDY centre, edge and outside it, respectively. In the case of phosphorus requirements, the percentages are 11.5%, 7.9% and 16.2%.

Active fluxes

Sinking rates of picophytoplankton can be considered negligible (Michaels and Silver 1988; Pesant et al. 2000), whereas most copepod faecal pellets are decomposed or ingested within the euphotic layer (Turner 2002). Dominance of small phytoplankton is thus normally associated with high rates of organic carbon recycling in the upper layer and a reduced POC flux to the mesopelagic zone (Pesant et al. 2000; Sautour et al. 2000; Bory et al. 2001). The active flux mediated by vertical migrators is therefore expected to form a large proportion of total carbon export. The mean proportion of biomass that migrated below 200 m during night time was 0.30, which is within the range reported by Hays (1996) for this area. Substantial amounts of metabolic end-products were released below 200 m as a result of this marked vertical migration. Active migratory fluxes of both carbon respired and ammonium excreted are in the upper range reported for oceanic waters (Longhurst and Harrison 1988; Longhurst et al. 1990; Dam et al. 1995; Le Borgne and Rodier 1997; Zhang and Dam 1997; Al-Mutairi and Landry 2001). The respiratory carbon flux decreased gradually from inside to outside the SWODDY, whereas nitrogen and phosphorus fluxes were highest at its edge, where diel vertical migrations were more intense. Active flux patterns were mainly due to differences in vertical migrant biomass, but also to the metabolic rates of the largest fraction, since most of the mesozooplankton that undertook diel migrations were from this size class. Using data of gut passage time (GPT) measured in some vertical migrators, Schnetzer and Steinberg (2002) have suggested diel vertical migration as a mechanism transferring particulate organic carbon (POC) and nitrogen (PON) to the mesopelagic zone through egestion at depth of food previously ingested in surface waters. In our study we measured an average GPT of 32 min, appreciably lower that the values reported by Schnetzer and Steinberg (2002). Accordingly, active POC and PON fluxes would be clearly reduced in our case. Migrant mesozooplankton may also excrete dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) below the euphotic layer (Le Borgne and Rodier 1997; Steinberg et al. 2000), so our estimates of the role of mesozooplankton in the biological pump should be interpreted as conservative.

In summary, mesozooplankton relationships with phytoplankton, as well as its role within the biological pump, did not show marked differences between zones, probably due to the high within-region variability. Nevertheless, the role of mesozooplankton within the

biological pump was more important in the SWODDY, especially at its edge. Therefore, the proliferation of these mesoscale structures in the Bay of Biscay would enhance the downward fluxes of biogenic matter mediated by mesozooplankton.

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