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Particle flux in the Subtropical Atlantic near the Azores: influence of mesozooplankton

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The amount and composition of sinking material were studied at two depths (200 m and base of the photic layer) in the Subtropical Atlantic Ocean near the Azores during the AZORES I (August 1998) and II (April–May 1999) cruises. Particulate carbon and nitrogen fluxes collected in sediment traps decreased with depth, and presented maximum values near the Azores Front. However, this frontal system represents an increase of only 4.5% in the overall regional exportation during summer. Sedimentation rates outside the front were higher during spring. Particulate organic carbon exported at 200 m always represented <1.5% of water column (photic zone) standing stock. Mesozooplankton faecal pellets contributed significantly to carbon flux. On average, carbon in the form of faeces represented 31% (spring) and 65% (summer) of total carbon collected at 200 m. Composition of the copepod community seems to be related to the pattern of faecal pellet sedimentation, with omnivorous copepods (Oithona and Oncaea) being more abundant at stations where faecal flux decreased with depth. Phytoplankton sedimented at 200 m were dominated by diatoms and dinoflagellates. Phytoplankton exported at 200 m represented <0.5% of water column (photic zone) standing stock.

INTRODUCTION

One of the main subjects discussed by oceanographers in the last few decades is the potential importance of the ocean in sequestering atmospheric CO_2, mitigating the progressive increase in human emissions of this climate change-related gas (Falkowski *et al.*, 1998). The sedimentation of organic matter through the so-called biological pump (Longhurst, 1991) is an important component of the ocean carbon cycle. This mechanism links surface primary production with deeper waters, transferring particulate carbon to the deep ocean. One of the major pathways for this transport to sediments is the sinking of a great variety of particles (organic aggregates, zooplankton faecal pellets and remains, ungrazed phytoplankton, etc.). The study of the quantity and composition of this material using sediment traps, either free-floating or bottom-moored, is essential for a better understanding of the carbon cycle (Berger *et al.*, 1989) and has received increased attention [see references in (Asper, 1996) or in (Moran *et al.*, 2003)].

Carbon flux is strongly affected by the structure and dynamics of planktonic communities, ultimately controlled by hydrography (Legendre and Le Fèvre, 1989). The ecosystems dominated by large phytoplankton and mesozooplankton grazing would favour sedimentation, while those dominated by small phytoplankton, grazed by microzooplankton, would result in the recycling of matter in the upper layers of the ocean (Wassmann, 1998). According to this, productive regions of the ocean should have higher carbon export rates than unproductive ones (Legendre and Rassoulzadegan, 1996). Subtropical gyres, characterized by an oligotrophic regime dominated by small phytoplankton, have been traditionally considered as the most unproductive regions of the ocean (Blackburn, 1981). However, estimating the rates of carbon export in these regions is essential to quantify the magnitude of the global ocean flux (Benitez-Nelson *et al.*, 2001; Patsch *et al.*, 2002), because their large extent [covering close to 40% of the earth's surface (Karl, 1999)] means that they could contribute up to 70% of total export production (Karl *et al.*, 1996).

In spite of their importance, sedimentation processes in these areas have been much less studied [but see (Benitez-Nelson *et al.*, 2001) and references therein] than in

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productive regions, such as continental shelves [(McCave *et al.*, 2001) and references therein], or upwelling areas [e.g. (Head *et al.*, 1996; Bory *et al.*, 2001)]. The European Union CANIGO (Canary Islands Azores Gibraltar Observations) project was developed to study the most important oceanographic features in the area from the Canary Islands to the Strait of Gibraltar. Within this project, the AZORES cruises were focused on the study of carbon flux under oligotrophic conditions, and its relationship to the main hydrological structures in the area. In this context, the main objective of this paper was to study the amount and composition of sinking material in the North Atlantic Subtropical Gyre, and its relationship with the biological properties of the surface layer during periods of maximum thermal stratification (midsummer) and maximum vertical homogeneity (early spring)

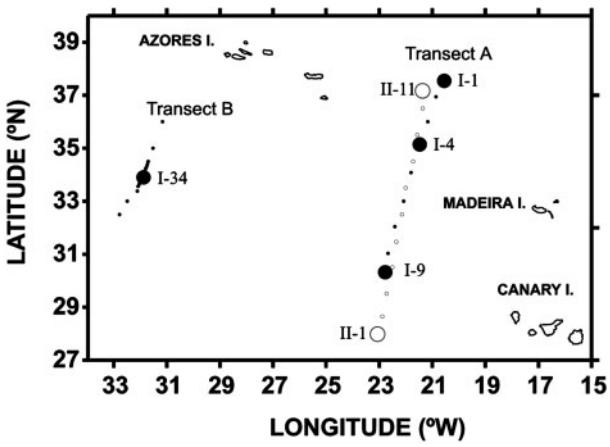

Fig. 1. Position of stations sampled during AZORES cruises (black dots, AZORES I; white dots, AZORES II). Small symbols, CTD casts; large symbols, sedimentation trap deployment.

METHOD

Study area

The Azores Current (AC) is the dominant hydrographic feature in the region, flowing eastwards and southwards from 35°N, 40°W as an extension of the Gulf Stream (Klein and Siedler, 1989). The area is characterized by a significant mesoscale activity, confirmed by the importance of eddies in the biological activity of the region (González *et al.*, 2001; Huskin *et al.*, 2001). However, the main mesoscale structure influencing the functioning of the area (Fernández and Pingree, 1996; González *et al.*, 2001; Huskin *et al.*, 2001) is probably the Azores Front. This frontal structure extends from 18 to 35°W at ~35°N, separating Western Atlantic Water (warmer and saltier) to the south from Eastern Atlantic Water (cold and fresher) to the north (Gould, 1985). A total of four and two sediment traps, respectively, were deployed during August 1998 (AZORES I cruise) and April–May 1999 (AZORES II cruise) on board *B.I.O. 'Hesperides'*. Sampling sites (Figure 1) were selected in order to represent the different water masses separated by the AC. Accordingly, stations were located at both ends of a CTD (Neil Brown Mark III) transect transverse to the AC (AZORES I and II), and at two locations inside the current (only on AZORES I).

Water column measurements

Water samples were collected with Niskin bottles at 5–7 depths at each station. Samples for determination of particulate organic carbon (POC) were filtered (500 mL) onto precombusted 24 mm GF/F filters, stored at −30°C, acidified with sulphurous acid to remove inorganic carbonates, dried at 50°C for 48 h and analysed with a Carlo Erba NA 1500 elemental analyser.

Chlorophyll *a* (Chl *a*) concentration was determined with a SAFAS FLX spectrofluorometer calibrated with a pure Chl *a* extract obtained by HPLC, after extraction with 90% acetone overnight at 4°C. As no reliable Chl *a* data are available from AZORES I, we used the initial Chl *a* concentration from microzooplankton grazing experiments performed during that cruise [see (Quevedo and Anadón, 2001) for details]. Primary production was measured by ^{14}C incubation, and only during AZORES II. Water samples (70 mL) were inoculated with 555 kBq $NaH^{14}CO_3$, incubated for 6.5–7.5 h, filtered onto polycarbonate filters, exposed for 12 h to concentrated HCl fumes to remove inorganic ^{14}C, and counted in a Beckman liquid scintillation counter after addition of 3.5 mL scintillation cocktail. Phytoplankton cells were counted and identified under an inverted microscope from separate samples preserved with Lugol's solution and buffered formaldehyde. Phytoplankton cell counts were converted to carbon biomass as described in Holligan *et al.* (Holligan *et al.*, 1984).

Mesozooplankton were sampled by means of vertical double WP-2 (57 cm diameter and 200 μm mesh) net casts, deployed to 200 m at 1 m s^{-1}. One net was used for grazing experiments and the other for biomass and taxonomic composition. For biomass measurements, the sample from one cod end was filtered onto 47 mm diameter GF-F precombusted filters, maintained for 48 h at 60°C and placed in boxes containing silica gel for further determination of carbon content (Perkin-Elmer 2400 CNH analyser). The sample from the second cod end was preserved with borax-buffered formaldehyde (4%) for subsequent taxonomic analysis. Extra nets were deployed to estimate copepod grazing by analysis

of gut fluorescence (Mackas and Bohrer, 1976). The contents of the net were filtered onto Sharkskin® filters, stored in Petri dishes and immediately frozen at −70°C in the dark for further gut content analysis [see (Huskin *et al.*, 2001) for details]. Due to the wide range of pigment destruction reported in the literature (0–100%), we have chosen not to apply any conversion factor and consider our estimates to be conservative values.

Sediment traps

The trap array was similar to the design by Knauer *et al.* (Knauer *et al.*, 1979), containing two sediment traps moored at the base of the euphotic layer (100–130 m, depending on the station) and at 200 m, respectively. Each trap consisted of eight cylindrical baffled collectors (60 mm diameter, 640 mm long) filled with filtered (Whatman GF/F) seawater supplemented with NaCl (5 g L^{-1}) to avoid turbulence losses. No poison or preservatives were used, so some grazing and bacterial decomposition might have taken place. However, the short duration of deployment (~24 h) is not likely to produce a significant decrease in collected material.

Trapped material was gently mixed and subsampled for the different analyses immediately after recovering. Swimmers were not removed from the collectors. Subsamples intended for particulate carbon and nitrogen analysis (900 mL, $n = 4$ for each sampling depth) were filtered onto GF/F precombusted filters and measured in a Perkin Elmer 2400 elemental analyser, using acetanilide as standard. Carbonate was not removed. Particulate inorganic carbon (PIC) content was calculated from total Ca concentration as $CaCO_3$ in 400 mL subsamples ($n = 4$) filtered through 0.2 μm polycarbonate filters. The filters were treated with ultrapure nitric acid, and the dissolved fraction was spiked using scandium as internal standard. Calcium concentration was determined with a double focusing inductively coupled plasma mass spectrometer (Finigan MAT-ELEMENT). POC was estimated as Particulate Carbon – PIC.

Samples for the determination of phytoplankton composition (200 mL, $n = 3$) were filtered and processed as above, but samples were only preserved in Lugol's solution (no formaldehyde). Taxonomic composition of sedimented material was only analysed in deeper traps, but faecal pellets were counted and measured in both shallow and deep traps. The lengths and widths of collected faecal pellets were measured using an image-analysis system. Practically all pellets looked like cylinders with rounded ends, typical of copepods, so their carbon content was obtained by multiplying pellet volume by 0.042 mg C mm^{-3} (González *et al.*, 1994) as in Fortier *et al.* (Fortier *et al.*, 2002).

Subsamples of 200 mL were filtered onto Poretics polycarbonate filters (0.2 μm) and observed with a Philips XL30 scanning electron microscope (SEM). Microbial production was estimated as the rate of ^3H leucine assimilation in 25 mL subsamples ($n = 2$), following the method described by Smith and Azam (Smith and Azam, 1992), and using a conversion factor of 3.1 kg C mol^{-1} leu (Simon and Azam, 1989).

Following Hargrave and Taguchi (Hargrave and Taguchi, 1978), all results were expressed as sedimentation rates (mg m^{-2} day^{-1}) or as daily loss rates (% of suspended stock) using integrated (in the photic layer) water column measurements as suspended stock values. ANOVA was used to test differences in fluxes, C/N ratios and faecal pellet volumes between sampling depths, using pooled data from the same depth and cruise. Variables were log-transformed when necessary to homogenize variances (see Results).

RESULTS

Hydrography

During AZORES I, two branches of a meandering front (Pérez *et al.*, unpublished) are identified (Figure 2) by the outcropping of isotherms and isohalines observed at 35°N [station (St) I-4] and 32–33°N in Transect A, and at 34°N (St I-34) in Transect B. During AZORES II, the front is located at 36°N, while the elevation of isolines observed at 31–32°N (Figure 2) reflects the signature of another unidentified mesoscale feature (González *et al.*, 2001). As suggested by Gould (Gould, 1985), the position of the front is also marked by the 16°C isotherm at 200 m, separating water masses with differences of 1.5°C and 0.2 salinity on spatial scales <100 km.

Water column measurements

Depth-integrated values of POC, Chl *a* concentration, primary production, mesozooplankton biomass and copepod community carbon ingestion are shown in Table I. Higher POC values were found during AZORES II (~7500 mg C m^{-2}), averaging 5150 mg C m^{-2} during AZORES I. However, Chl *a* concentration presented the opposite pattern, averaging 20.75 mg m^{-2} on AZORES I and 12.2 mg m^{-2} on AZORES II. Primary production was only estimated on the AZORES II cruise, being 100 and 184 mg C m^{-2} day^{-1} at St II-1 and II-11, respectively. Both mesozooplankton biomass and copepod ingestion were higher during AZORES II. During AZORES I, higher mesozooplankton biomass was found near the AF (St I-4 and I-34), while the influence of the front on copepod ingestion was only noticeable at station

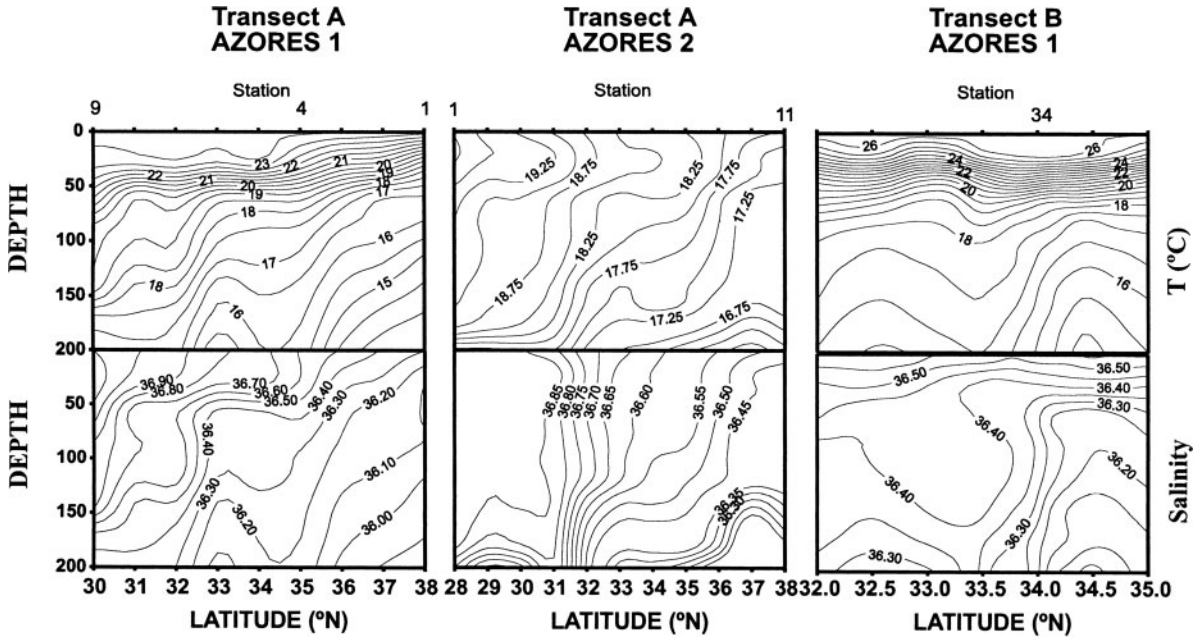

Fig. 2. Vertical distribution of temperature and salinity along the main transects sampled during AZORES cruises.

Table I: Depth integrated values of selected variables at stations sampled during AZORES cruises

Station	POC (mg C m^{-2})	Chl *a* (mg Chl *a* m^{-2})	Carbon fixation (mg C m^{-2} day^{-1})	Mesozooplankton	
				Carbon biomass (mg C m^{-2})	Carbon ingestion (mg C m^{-2} day^{-1})
I-1	6188	19		159	9
I-4	4681	22		226	32
I-9	4630	21		192	23
I-34		21		305	22
II-1	7515	8.5	100	796	39
II-11	7410	15.8	184	1031	46

POC, Chl *a* and carbon fixation values were integrated in the photic layer (100–130 m) while mesozooplankton biomass and ingestion were integrated in the upper 200 m.

I-4. A total of 130 copepod taxa were identified on AZORES cruises, but only 25 (the more abundant) are presented here (Table II). Copepod populations were dominated by small calanoid copepodites, *Clausocalanus* spp., *Oncaea* spp., *Corycaeus* spp. and *Oithona helgolandica*, accounting for 67% of total copepod abundance.

The phytoplankton community was dominated (in carbon biomass) by picoplankton and flagellates (Table III), which accounted for 50% and 40% of total phytoplankton carbon, respectively. The sum of diatoms, dinoflagellates, coccolithophorids and ciliates constituted <10% of phytoplankton stocks [see (Head *et al.*, 2002) for a detailed description].

Sedimented material

During AZORES I, both carbon and nitrogen showed similar sedimentation patterns (Figure 3). Maximum fluxes of both elements were found at the frontal station (I-4) located on Transect A. Sedimentation rates outside the AF were higher during AZORES II, especially at the northernmost location. On average, 83% of total carbon sedimented was in organic form. Only at three locations

Table II: Main copepod species during AZORES cruises and contribution (%) of each one to total copepod abundance

	I-1	I-4	I-9	I-34	II-1	II-11
Calanus minor	0.69	8.75	1.39	1.87	10.11	0.61
Calanus spp.	1.38	3.89	5.81	0.06	6.16	6.55
Mecynocera clausi	0.32	3.71	2.9	2.8	0.87	0.55
Paracalanus parvus	–	0.73	8.56	1.35	2.32	2.41
Calocalanus pavo	0.16	1.41	1.01	0.9	–	1.07
Calocalanus stylirremis	–	3.64	1.15	1.8	3.48	2.89
Clausocalanus spp.	13.38	12.43	8.02	15.39	25.03	7.96
Ctenocalanus vanus	11.39	2.97	2.52	3.18	1.45	3.89
Ichniocalanus spp.	0.15	0.36	1.15	4.75	–	–
Small calanoid copepodites	23.33	16.98	20.99	13.79	20.30	25.43
Euchaeta spp.	4.1	1.16	1.69	0.03	7.81	0.51
Pleuromamma spp.	3.74	0.99	0.61	2.44	0.61	2.59
Lucicutia flavicornis	0.11	0.16	0.46	1.53	0.31	0.07
Lucicutia spp.	0.05	2.05	2.09	1.93	2.11	1.66
Heterorhabdus spp.	1.93	0.36	1.23	–	–	0.11
Haloptilus longicornis	0.11	0.71	1.23	0.03	–	–
Acartia clausi	0.64	1.88	0.81	1.41	–	–
Acartia danae	–	0.16	–	2.66	0.07	0.48
Acartia spp.	–	0.73	1.53	0.45	–	–
Oithona helgolandica	5.94	7.09	14.44	6.43	7.64	7.22
Oithona plumifera	2.03	1.25	0.58	0.45	0.29	0.04
Oithona nana	0.54	–	0.38	2.28	0.58	0.96
Oncaea spp.	17.50	8.76	7.07	17.10	0.89	24.18
Corycaeus spp.	7.53	18.03	8.99	14.91	1.22	4.43

Table III: Taxonomic composition of the phytoplankton community (plus ciliates) during AZORES cruises

Station	Diatoms	Dinoflagellates	Heterotrotrophic dinoflagellates	Flagellates	Coccolithophorids	Picoplankton	Ciliates
I-1	19 (1.3)	12 (0.8)	42 (3)	286 (20.9)	48 (3.5)	948 (69.3)	12 (0.8)
I-4	3 (0.3)	4.6 (0.4)	81.3 (8.8)	405 (43.9)	42.5 (4.6)	339 (36.7)	46.6 (5)
I-9	2.4 (0.4)	2 (0.3)	19.1 (3.7)	249 (48.4)	20.3 (3.9)	213 (41.4)	8.3 (1.6)
II-1	72 (4.7)	1.3 (0.08)	40.3 (2.6)	575 (37.8)	27.1 (1.7)	789 (51.8)	15.9 (1)
II-11	10.9 (0.9)	4 (0.3)	29.7 (2.7)	492 (44.9)	4.82 (0.4)	541 (49.4)	11.4 (1)

Biomass in mg C m^{-2}. Values integrated in the photic layer. Contribution (in %) of each group to total biomass in brackets.

did inorganic carbon contribute >25% to total carbon collected: St I-1 (37%), St I-34 (31%) and St II-1 (43%), all of them at 200 m depth. Observed differences in PIC sedimented at both sampling depths were not statistically significant (ANOVA, AZORES I: $P = 0.31$, AZORES II: $P = 0.5$). POC exported at 200 m always represented <1.5% of water column standing stock (Table IV). During AZORES II, organic carbon collected at 200 m represented 20% (St II-1) and 24% (St II-11) of integrated primary production.

Total carbon and nitrogen fluxes collected in traps decreased with depth (Figure 3) (ANOVA, AZORES I: $P = 0.014$, AZORES II: $P = 0.0004$; in both cruises variables were log-transformed to homogenize variances).

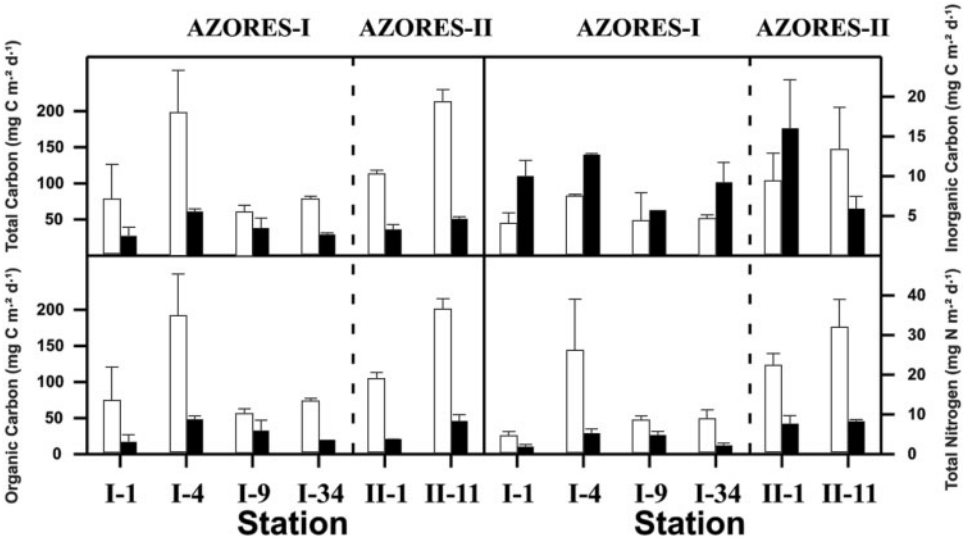

Fig. 3. Average fluxes (+SE) of particulate carbon and nitrogen. White bar, fluxes at the base of the photic layer; black bar, fluxes at 200 m.

Table IV: Losses (%) of suspended standing stocks and primary production at 200 m during AZORES cruises

Station	POC	PP	Phytoplankton stocks				
			Dia	Din	Fla	Tin	Cil
I-1	0.44	–	0.09	0.19	0.08	0.35	2.6
I-4	1.3	–	0.06	0.03	<0.01	0.23	0.05
I-9	0.82	–	<0.01	<0.01	<0.01	<0.01	<0.01
I-34	–	–					
II-1	0.48	20	0.06	0.4	0.24	5.1	0.48
II-11	0.69	24	<0.01	0.2	<0.01	0.21	0.31

Dia, diatoms; Din, dinoflagellates; Tin, tintinids; Fla, flagellates; Cil, ciliates.

During AZORES I, carbon losses between sampling depths averaged 58%, ranging from 36% (St I-9) to 69% (St I-4). Nitrogen losses varied between 44% (St I-9) and 79% (St I-4), averaging 64%. During AZORES II, carbon and nitrogen losses were ~70% at both sampling sites. Average PC:PN ratios (Figure 4) seemed to be higher in deeper traps during AZORES I, while similar ratios were found at both sampling depths on AZORES II. However, differences in C:N ratio between sampling depths were never statistically significant (ANOVA, AZORES I: $P = 0.27$, AZORES II: $P = 0.34$).

The rates of heterotrophic prokaryotic activity in the material collected during AZORES II (Table V) indicate that <10% of sedimented carbon was degraded daily, with the exception of St II-11 at 200 m where degradation reached 23%.

Faecal carbon fluxes (Table VI) collected at the base of the photic layer averaged 26 ± 13 mg C m^{-2} day^{-1} during AZORES I, with higher values located at both frontal stations. Carbon in the form of faecal pellets represented, on average, 30% of total sedimented carbon. During AZORES II, faecal carbon fluxes at this depth were 2 and 11 mg C m^{-2} day^{-1} south and north of the front, respectively, representing 1.8 and 5% of sedimented carbon. The amount of carbon exported in the form of faeces decreased with depth at St I-1, and I-34, while it increased at the rest of the stations. Faecal carbon fluxes (Table VI) measured at 200 m averaged 16.2 ± 11.2 mg C m^{-2} day^{-1} during AZORES I (31% of sedimented carbon). During AZORES II, carbon fluxes at 200 m in both stations were ~28 mg C m^{-2} day^{-1}, representing 77 and 54% of sedimented carbon

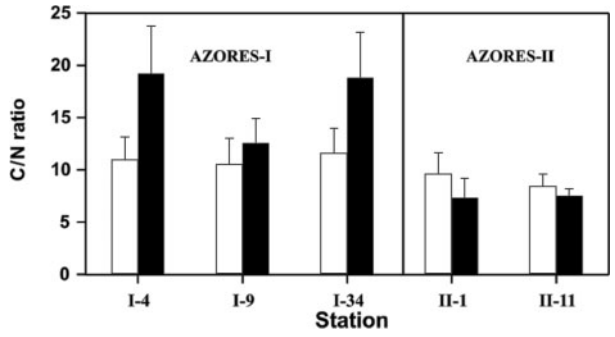

Fig. 4. Average C:N (mole) ratios (+SE) of sedimented material. White bar, base of the photic layer; black bar, 200 m.

Table V: Bacterial activity in traps during the AZORES II cruise and its equivalent as a percentage of the sedimented carbon

Station	Depth	Bacterial activity ($\mu g\ C\ L^{-1}\ day^{-1}$)	% sedimented carbon
II-1	100	17	9.1
II-1	200	0.32	0.31
II-11	100	12.1	3.51
II-11	200	26.2	23.1

south and north of the front, respectively. Although average individual pellet volume (Table VI) seems to be higher in deeper traps (except St II-1), differences were never significant (ANOVA, AZORES I: $P = 0.53$, AZORES II: $P = 0.94$; in both cruises variables were log-transformed to homogenize variances).

Phytoplankton sedimented at 200 m was dominated (in carbon biomass) by diatoms and dinoflagellates at all stations (Figure 5, Table VII). Diatoms constituted, on average, 50% of collected phytoplankton, ranging from 3% (St I-4) to 95% (St I-9). Heterotrophic dinoflagellates were the main component of sedimented phytoplankton at St I-4 and I-34, accounting for 45 and 65% of total carbon respectively, while autotrophic dinoflagellates presented maximum contribution at St II-1 (34%). Flagellates showed little contribution to plankton flux (<3%), while ciliates constituted, on average, 11% of sedimented plankton. Phytoplankton exported at 200 m always represented <1% of water column standing stock (Table IV), except for diatoms at St II-11 (6%) and dinoflagellates at St I-4 (2.5%) and St II-1 (13%). SEM analysis of sedimented material (Figure 6) revealed the presence of large amounts of coccolithophorids and aggregates of coccoliths in the traps, undetectable in Lugol-preserved samples.

DISCUSSION

Quantification of vertical particle flux is still a major objective of ocean science. Although the use of different kinds of sediment traps has provided valuable information in the past [see references in (Asper, 1996)], their accuracy is still open to discussion. An extensive body of literature has tried to evaluate the efficiency of trap collecting, most of the studies focusing on hydrodynamic effects, activity of swimmers and degradation of particles between collection and recovery of the trap (Buesseler,

Table VI: Faecal carbon fluxes at both sampling depths during AZORES cruises, average (SE) individual pellet volume at each location and percentage of sedimented carbon represented by faecal pellets

Station	Depth (m)	Pellet sedimentation ($n\ m^{-2}\ day^{-1}$)	Individual pellet volume ($mm^3 \pm SE$)	Total pellet carbon ($mg\ m^{-2}\ day^{-1}$)	% sedimented PC
I-1	120	935 211	$1.5 \times 10^{-4} \pm 2.7 \times 10^{-5}$	6	7.6
I-1	200	148 533	$2 \times 10^{-4} \pm 5 \times 10^{-5}$	1.26	4.6
I-4	120	764 780	$6.8 \times 10^{-4} \pm 4.7 \times 10^{-4}$	22	11.1
I-4	200	829 714	$1.4 \times 10^{-3} \pm 1.1 \times 10^{-3}$	49.2	80
I-9	130	182 659	$1.4 \times 10^{-3} \pm 7.5 \times 10^{-4}$	11.4	19
I-9	200	62 372	$4.3 \times 10^{-3} \pm 4.1 \times 10^{-3}$	11.28	29
I-34	100	1 397 631	$1.1 \times 10^{-3} \pm 1.2 \times 10^{-3}$	64.5	82
I-34	200	72 100	$1 \times 10^{-3} \pm 4.9 \times 10^{-4}$	3.14	10
II-1	100	55 491	$8.8 \times 10^{-4} \pm 2.1 \times 10^{-4}$	2	1.8
II-1	200	1 082 069	$6.1 \times 10^{-4} \pm 2.8 \times 10^{-4}$	27.95	77
II-11	100	641 642	$3.9 \times 10^{-4} \pm 5.6 \times 10^{-5}$	10.7	5
II-11	200	1 361 063	$4.8 \times 10^{-4} \pm 3.4 \times 10^{-4}$	27.78	54

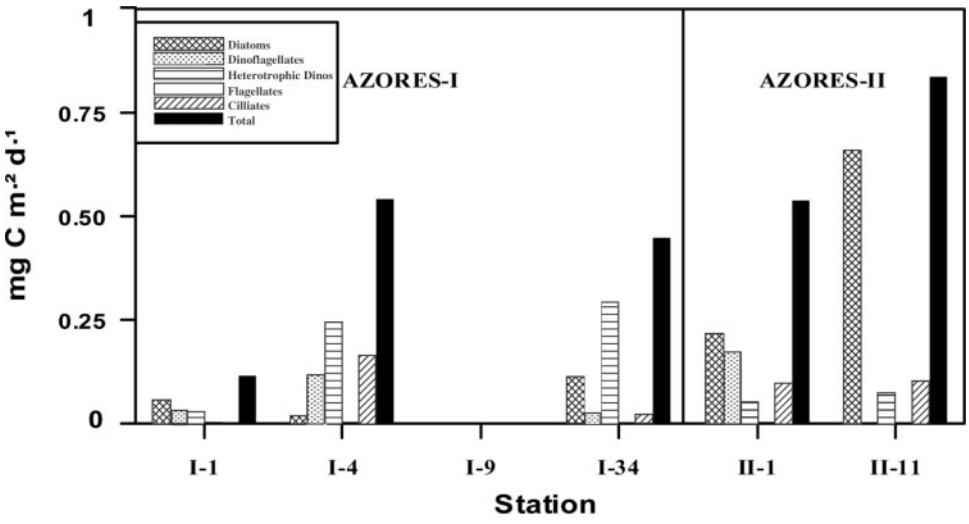

Fig. 5. Taxonomic composition of material collected in deeper (200 m) sediment traps.

1991; Boyd and Newton, 1997) [See references in (Buesseler *et al.*, 2000)]. We cannot account for hydrodynamic biases in our traps. Although the use of drifting arrays decreases the flow relative to the trap, it does not eliminate it entirely (Bacon, 1996) and several studies [e.g. (Buesseler, 1991)] have pointed to severe hydrodynamic biases in the use of near-surface drifting traps. We did not remove swimmers in our study, but visual observation did not reveal the presence of mesoplanktonic organisms in the collectors, as expected in an oligotrophic area characterized by low abundance of animals in the water column. However, we must also take into account the possible effect of cryptic swimmers, undetectable without microscopic analysis, whose contribution to collected material could be important (Michaels *et al.*, 1990). Finally, degradation of collected material by bacterial activity is probably not an important factor in our traps, due to the short duration of deployment and the low bacterial activity measured inside them. The only instance where this process could be important is Station II-11 at 200 m depth, where fluxes could be underestimated by a factor of 1.3. We have not calculated bacterial activity in the traps during AZORES I, but bacterial activity in the water column was lower than on AZORES II (González *et al.*, 2001). Despite such potential shortcomings, sediment traps are a powerful instrument to provide basic flux measurements. However, we cannot rule out some degree of underestimation in our calculated fluxes, so results must be interpreted with caution.

The oligotrophic subtropical gyres have been traditionally thought to be marine deserts where phytoplankton production is nutrient limited and contribution to carbon sequestration is minimal. However, this concept has changed in the last decade (Doney, 1997), and these vast areas must be considered when discussing carbon fluxes to the deep ocean (Benitez-Nelson *et al.*, 2001). We report low export fluxes for the oligotrophic area of the North Atlantic Subtropical Gyre, always representing a minor fraction of suspended standing stocks. Comparison with published values for similar oceanic areas is difficult, mainly due to the different depths and duration of deployments as well as differences in trap design. However, applying the Martin *et al.* (Martin *et al.*, 1987) equation, which parameterizes the depth decline of fluxes, we obtain carbon sedimentation rates in the range found by other authors in tropical and subtropical regions of both the Atlantic and Pacific Oceans. We present particulate carbon fluxes at 200 m ranging between 27 and 61 mg C m^{-2} day^{-1}, while Lohrenz *et al.* (Lohrenz *et al.*, 1992), Karl *et al.* (Karl *et al.*, 1996), Neuer *et al.* (Neuer *et al.*, 1997), Bory *et al.* (Bory *et al.*, 2001) and Conte *et al.* (Conte *et al.*, 2001) reported standardized fluxes at 200 m between 7 and 36 mg C m^{-2} day^{-1} for subtropical areas of the Atlantic Ocean. Published fluxes in the Pacific Ocean [e.g. (Martin *et al.*, 1987; Knauer *et al.*, 1990; Karl *et al.*, 1996; Christian *et al.*, 1997; Benitez-Nelson *et al.*, 2001)] are slightly higher, varying between 18 and 73 mg C m^{-2} day^{-1}. These values are low when compared with those of more productive areas [e.g. (Landry *et al.*, 1994; Head *et al.*, 1996; Roy *et al.*, 2000)], but the large extent of subtropical gyres increases their role in the oceans' global transport mediated by the biological pump (Karl *et al.*, 1996).

We noticed an important decrease in sedimented PC and PN with depth, as previously found by many other authors [e.g. (Lohrenz *et al.*, 1992; Honjo, 1996; Jackson and Burd, 2002) and references therein]. On average,

Table VII: Main phytoplankton species sedimented at 200 m and contribution (in %) of each species to total phytoplankton carbon collected

Station	I-1	I-4	I-9	I-34	II-1	II-11
Diatoms						
Bacteriastrum spp.	2.5	–	–	–	–	–
Centric	–	2.3	–	–	1.6	–
Cerataulina spp.	–	–	–	–	4.3	–
Chaetoceros spp.	–	–	–	–	–	4.2
Coscinodiscus spp.	14.3	–	94.1	–	5.6	14.1
Guinardia flaccida	–	–	–	–	60.1	15.2
Hemiaulus spp.	–	–	–	–	–	2.4
Meuniera membranacea	–	–	–	–	4.5	–
Navicula spp.	–	1.8	–	–	–	–
Nitzschia spp.	13.9	–	–	0.9	–	1.7
Pennate	4.2	1.8	–	–	–	–
Pleurosigma spp.	12.9	–	–	–	–	–
Proboscia alata	–	–	–	24.5	–	–
Rhizosolenia fragilissima	–	–	–	–	–	22.5
Rhizosolenia hebetata	–	–	–	–	–	17.9
Rhizosolenia imbricata	4.3	–	–	–	–	–
Rhizosolenia sp.	–	–	–	–	–	5.6
Rhizosolenia stolterfothii	–	–	–	–	–	5.6
Dinoflagellates						
Ceratium arietinum	–	–	–	5.5	–	–
Ceratium hexacanthum	9.1	–	–	–	–	–
Cladopyxis spp.	12.9	16.4	–	–	–	–
Gonyaulax spp.	–	7.4	–	–	–	–
Prorocentrum sp. (15 μm)	–	2.1	–	–	–	–
Torodinium spp.	–	–	–	–	4.5	–
Heterotrophic dinoflagellates						
Gymnodinium spp.	1.4	1.8	–	–	–	1.7
Gyrodinium spp.	17.1	43.4	–	43.2	–	–
Histioneis hyalina	–	9.6	–	–	–	–
Oxytoxum spp.	–	–	–	–	–	1.4
Protoperidinium spp.	–	–	–	24.1	–	–
Flagellates						
Dictyocha fibula	1.7	–	–	–	–	–
Ciliates						
Tintinnid spp.	5.1	13.1	5.6	1.7	12.7	1.7

Only species accounting for >1% of phytoplankton sedimented carbon are represented.

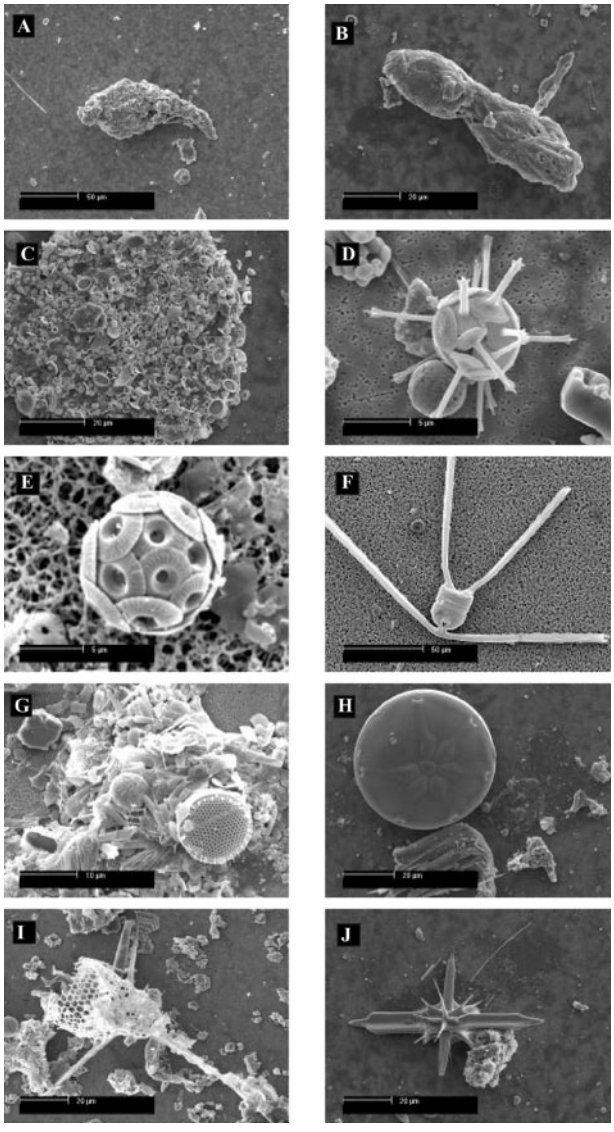

Fig. 6. SEM images of material collected in sediment traps. (**A** and **B**) Faecal pellets, (**C**) coccolithophorid remains, (**D**) *Rhabdosphaera claviger* (coccolithophorid), (**E**) *Emiliania huxleyi* (coccolithophorid), (**F**) *Chaetoceros peruvianus* (diatom), (**G**) frustule of centric diatom, (**H**) *Asteronphalus* sp. (diatom), (**I** and **J**) radiolarians.

65% of POM collected at the base of the photic layer is reingested or solubilized before leaving the upper 200 m. The high C:N ratios of collected particles reflect transformation of primary produced matter. No differences were found between PIC sedimented at both sampling depths. In most sedimentation studies [e.g. (Miquel *et al.*, 1994; Neuer *et al.*, 1997)] $CaCO_3$ flux remains basically unaltered with depth, because coccoliths and carbonate skeletons are not as easily degraded as particulate organic matter during their descent (Honjo, 1996). Although we cannot assess the importance of coccolithophorids in phytoplankton fluxes due to the preservative solution used (Lugo's solution), SEM analysis of sedimented material revealed the existence of a great number of coccoliths. As suggested by Neuer *et al.* (Neuer

et al., 1997), coccolithophorids could be important for export flux in the Subtropical Atlantic.

The role of zooplankton feeding and egestion in the functioning of the biological pump has been well documented in the past [e.g. (Noji, 1991) and references therein]. The contribution of mesozooplankton faecal carbon to export production seems to be highly variable depending on region or season (Miquel *et al.*, 1994; Carroll *et al.*, 1998), increasing with the degree of oligotrophy of the system. Roman *et al.* (Roman *et al.*, 1995) found that 87% of the carbon flux at 150 m in the oligotrophic Sargasso Sea was due to mesozooplankton faecal pellets, while Dam *et al.* (Dam *et al.*, 1995) suggests that up to 100% of the sinking POC in the equatorial Pacific Ocean comes from that source. Our results also point to an important mesozooplankton-mediated pathway for carbon export in the NAESG compared with direct phytoplankton sinking. On average, faecal carbon accounted for 40% of PC sedimented at 200 m, reaching maximum values up to 80%.

Picoplankton largely dominated phytoplankton communities in our study. These small cells have negligible settling velocities and are constrained by microzooplankton grazing (Quevedo and Anadón, 2001); thus they contribute little to vertical flux of organic matter. Within this context, diatoms and dinoflagellates accounted for 86% of direct phytoplankton flux. Diatoms are thought to have a high potential for passive sinking because of their size and silica frustule. Despite their low abundance in the region, diatoms could play an important role in the export of PC (Goldman, 1993; Scharek *et al.*, 1999b), but we found a low removal rate of POC by this phytoplankton group. On average, 1.5% of diatom standing stock sedimented at 200 m, similar to the low exportation (0.5% of standing stock) found by Scharek *et al.* (Scharek *et al.*, 1999a) at 165 m in the oligotrophic North Pacific Gyre.

The contribution of faecal pellets to sedimented carbon increased with depth in four out of six stations analysed due to an increase in the number of pellets collected in deeper traps. An increase in number of pellets in deeper traps has been previously found by other authors (Karl and Knauer, 1984; Carroll *et al.*, 1998) and it is probably due to vertical movements of animals within the upper water layers. On the other hand, the flux of pellets decreased with depth at St I-1, I-9 and I-34, as previously found for most sedimentation studies [e.g. (Roy *et al.*, 2000)]. The maximum faecal carbon flux at 200 m does not coincide with maximum mesozooplankton biomass or copepod ingestion (and presumably pellet production). This points to the importance of factors other than zooplankton standing stock in faecal pellet sinking. In fact, zooplankton mediation in carbon fluxes is not only due to faecal pellet production, but to pellet consumption and degradation as well, so an elevated faecal pellet production can be counteracted by processes such as coprophagy or coprorexy (Noji, 1991; Andreassen *et al.*, 1996; Carroll *et al.*, 1998).

Composition of zooplankton communities has been proposed largely to influence the fate of sinking particles [e.g. (Roy *et al.*, 2000)]. In this sense, several authors (Paffenhöfer, 1993; González and Smetacek, 1994; González *et al.*, 1994) suggest that copepods from the genera *Oithona* and *Oncaea* are more specialized for coprophagy than calanoids. González and Smetacek (González and Smetacek, 1994) proposed the use of a cyclopoid:calanoid ratio to evaluate the importance of faecal pellet retention in the surface layers. Ratios above 0.3 would translate into high reutilization of faeces in the upper water column. This could explain the observed decrease with depth in the number of faecal pellets collected at St I-1, I-9 and I-34, where the *Oithona* + *Oncaea* :calanoid ratios were 0.42, 0.36 and 0.47, respectively. On the other hand, this ratio remained lower than 0.3 at stations where faecal pellet flux increased with depth: 0.25 at St I-4 and 0.11 at St II-1. The only exception to this pattern was St II-11, where faecal pellet flux increased with depth in spite of a ratio of 0.59. The inclusion of the cyclopoid *Corycaeus*, also abundant at all stations, would increase the ratios to 0.51 (St I-1), 0.54 (St I-4), 0.49 (St I-9), 0.7 (St I-34), 0.12 (St II-1) and 0.65 (St II-11). The high ratio obtained at St I-4 contradicts the increase in faecal pellet flux at depth observed at that location. However, the few studies of *Corycaeus* feeding available in the literature suggest a carnivorous diet rather than an omnivorous/coprophagous one (Gophen and Harris, 1981; Brewer *et al.*, 1984; Turner *et al.*, 1984; Landry *et al.*, 1985). We must also consider that the short duration of the trap deployments may mask major trends in pellet recycling and sedimentation.

On average, faecal carbon collected in the traps represented 60% of carbon ingested by copepods, reflecting low assimilation efficiency. However, the gut fluorescence method only reflects phytoplankton consumption, while non-algal carbon should account for the majority of zooplankton requirements during AZORES cruises (Huskin, 2001). We also cannot discard a possible underestimation of ingestion rates due to pigment destruction within the guts of copepods [see review by (Bamstedt *et al.*, 2000)].

Oligotrophic regimes are largely influenced by mesoscale structures which lead to increases in biological activity and favour export production (Legendre and Le Févre, 1989). The Azores Front is the main hydrographic feature present in the region, and its physical structure and influence on the biology of the region have been widely studied in the past [e.g. (Fasham *et al.*, 1985;

Gould, 1985; Tokmakian and Challenor, 1993)]. Due to its extension and temporal persistence, this frontal system has been suggested to play a significant role in regional carbon budgets (Fernández and Pingree, 1996), but this is the first study to assess its influence in sedimentation processes. In our study, PC collected at 200 m on Transect A was 1.6–2.25 times higher than in surrounding areas, but not on Transect B, suggesting spatial differences in the influence of the front. Similar effects of frontal areas in particle fluxes have also been reported by Peinert and Miquel (Peinert and Miquel, 1994) in the Alboran Sea, although in their study the presence of the front increases the flux up to 100 times. Assuming a maximum area of 0.22×10^{12} m^2 for the Azores front and 4.2×10^{12} m^2 for the North Atlantic Eastern Subtropical Gyre (González *et al.*, 2001), the frontal system accounts for ~9% of carbon flux in the NAESG. This represents an increase of only 4.5%, suggesting a low impact of the Azores Front on the overall regional exportation during summer. Of course, this estimation must be considered with caution, because the spatial and temporal coverage of our study are restricted. Considering the large contribution of mesozooplankton faecal pellets to carbon fluxes, the influence of the Azores Front would probably increase in spring, when the frontal area supports 25% of total phytoplankton carbon ingested by copepods in the NAESG (Huskin *et al.*, 2001). In any case, further investigations should be carried out to evaluate properly the effect of this frontal system on the vertical flux of materials.

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