

# Vertical particle flux in outer shelf waters of the southern Bay of Biscay in summer 1993

Particle flux  
Carbon  
Nitrogen  
Shelf waters  
Bay of Biscay

Flux de particules  
Carbone  
Azote  
Eau du plateau  
Golfe de Gascogne

Emilio FERNÁNDEZ <sup>a</sup>, Emilio MARAÑÓN <sup>b</sup>, Jesús CABAL <sup>b</sup>,  
Florentina ALVAREZ <sup>b</sup> and Ricardo ANADÓN <sup>b</sup>.

<sup>a</sup> Departamento de Recursos Naturais e Medio Ambiente, Universidade de Vigo,  
Campus Lagoas-Marcosende, E-36200 Vigo, Spain.

<sup>b</sup> Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo,  
E-33005 Oviedo, Spain.

Received 02/08/94, in revised form 20/04/95, accepted 27/04/95.

## ABSTRACT

Export of particulate matter out of the euphotic zone was measured in the southern Bay of Biscay in summer 1993 using shallow (50 m) sediment traps deployed for a short period in outer shelf waters. The sedimented material consisted of intact and degraded faecal pellets, diatom frustules, coccolithophorid cells, detached coccoliths and zooplankton remains. Measured vertical fluxes were 173-236 mg C m<sup>-2</sup> day<sup>-1</sup>, 18-20 mg N m<sup>-2</sup> day<sup>-1</sup> and 3.8-4.5 mg C m<sup>-2</sup> day<sup>-1</sup>, respectively for particulate organic carbon (POC), particulate organic nitrogen (PON) and particulate inorganic carbon (PIC). The downward flux of POC represented 24-37 % of the estimated primary production. Export of PIC accounted for only 2 % of the total carbon flux. A large proportion (50-70 %) of the material retained in the traps originated from phytoplankton. The contribution of 'living' phytoplankton to organic carbon fluxing out of the fertile zone was, however, less than 10 %.

## RÉSUMÉ

Sédimentation des particules sur la marge continentale au sud du golfe de Gascogne, été 1993.

Le flux de matière particulaire sortant de la zone euphotique a été mesuré en été dans le sud du golfe de Gascogne, deux pièges à sédiments ont été déployés sur le bord externe du plateau continental à 50 m de profondeur. L'examen au microscope du matériel sédimenté révèle la présence de bols fécaux intacts et dégradés, de frustules de diatomées, de cellules de Coccolithophorides et de restes de carapaces de zooplancton. Les flux verticaux mesurés sont de 173-236 mg C m<sup>-2</sup> jour<sup>-1</sup>, 18-20 mg N m<sup>-2</sup> jour<sup>-1</sup> et 3,8-4,5 mg C m<sup>-2</sup> jour<sup>-1</sup>, pour le carbone organique particulaire (POC), l'azote organique particulaire (PON) et le carbone inorganique particulaire (PIC), respectivement. Le flux de carbone organique particulaire vers le fond représente 24 à 37 % de la production primaire. L'exportation de PIC représente seulement 2 % du flux de carbone total. Une grande proportion (50-70 %) du matériel retenu dans le piège trouve son origine dans le phytoplancton. La contribution du phytoplancton « vif » au carbone organique au dehors de la zone fertile est inférieure à 10 %.

## INTRODUCTION

The export of biogenic material from the euphotic zone is an essential process for the regulation of the biogeochemical cycling of elements. Coastal environments, together with subpolar regions, constitute areas of special significance in this context as they account for more than 50 % of the global primary production and about 80 % of the particle flux to the sea floor (Berger *et al.*, 1987). Biogeochemical fluxes occurring at continental margins have been suggested as being of similar magnitude to those typical of open oceanic waters, despite their comparatively reduced extension (Walsh, 1991). There is a great deal of controversy, however, as to whether a significant proportion of the large amounts of particulate matter being synthesized in shelf regions is eventually oxidized within the pelagic food web (Rowe *et al.*, 1986; Falkowski *et al.*, 1988) or alternatively exported to the continental slope and sequestered in deep sediments (Walsh *et al.*, 1981; Malone *et al.*, 1983).

Information on rates of export production in the oceans is still scarce (Bender *et al.*, 1992). Such paucity of data led us to present in this paper the results from two short-term, shallow, sediment traps deployed in outer shelf waters of the southern Bay of Biscay in summer 1993, together with a description of the water column characteristics. To our knowledge, these are the first data on vertical particle fluxes reported so far for this oceanographic region.

## MATERIAL AND METHODS

The observations were carried out in July 1993 in an outer shelf station (43°42' N, 6°09' W; 145 m depth) located at the mouth of the Avilés Canyon (1.5 nautical miles from the shelf-break) in the Central Cantabrian Sea (Southern Bay of Biscay).

A Multitrap sediment collector system was deployed at 50 m depth on 12 and 14 July for two periods of 48 and 77 h, respectively. The Multitrap system, comprising four transparent plexiglass collection cylinders as described in Knauer *et al.* (1979), was anchored to the sea floor. Prior to deployment, each tube was filled with 0.2 µm filtered seawater to which sodium chloride (5 mg ml<sup>-1</sup>) was added to increase its density, thus preventing significant exchange of material with the ambient seawater. No preservatives were added to the collection tubes. Since the traps were deployed for a very short period, degradation of the sedimented material should have been minimal (see *e.g.* Nelson *et al.*, 1987).

On recovery, the material collected in the tubes was immediately transferred to 2-litre polycarbonate bottles and refrigerated (*ca.* 4 °C) until further processing 3–4 h later. Once in the laboratory ashore, large 'swimmers' were removed with forceps when present, the bottles were gently shaken and 2 subsamples drawn from each. These were filtered on to pre-combusted Whatman GF/F filters for the determination of total particulate carbon and nitrogen, particulate calcium, chlorophyll *a* and phaeopigments. A

small amount of material was also taken for examination with a scanning electron microscope. Total particulate carbon (TPC) and particulate organic nitrogen (PON) were analysed with a Carlo-Erba 1500 series 2 CHN analyser without treatment to remove carbonates. Particulate inorganic carbon (PIC) was estimated from the measured calcium content, assuming that all of the particulate calcium was present as calcium carbonate. Calcium concentration was determined by flame atomic absorption spectrometry as described in Fernández *et al.* (1992). Particulate organic carbon (POC) was considered as the difference between TPC and PIC. Chlorophyll *a* and phaeopigments were determined fluorometrically (Yentsch and Menzel, 1963).

Vertical profiles of temperature, salinity and oxygen were obtained with a Seabird-25 CTD probe on each deployment (12 and 14 July) and recovery (14 and 17 July) of the traps. Water samples were also collected from six different depths with 30-l Van Dohrn bottles. Mesozooplankton carbon and nitrogen biomass was measured by filtering the contents of the sampling bottles through a 200 µm mesh size at sea. The material collected was carefully transferred to pre-combusted Whatman GF/C filters by rinsing the mesh with filtered seawater (0.2 µm Poretics polycarbonate filter). Samples for the determination of TPC, PON, PIC, chlorophyll *a* and phaeopigments were drawn from the filtrates and analyzed as described above.

## RESULTS AND DISCUSSION

The physical structure of the water column at the time of sediment trap deployment and recovery did not show a large temporal variability (Fig. 1). An upper mixed layer, approximately 20–30 m in depth, characterized by relatively warm and low salinity water, was present throughout the sampling period. Below this depth, temperature decreased moderately and salinity remained constant or decreased slightly down to 100 m. Surface temperature was around 18 (± 0.4) °C during the three sampling dates whilst upper layer salinity ranged from 35.58 psu on 12 and 14 July to 35.46 psu on 17 July. The depth of the euphotic zone (1 % isolume) varied from 49 m on 12 and 17 July to 57 m on 14 July. The depth where the sediment trap was deployed was thus representative of the base of the productive layer but outside the influence of resuspension. Upper layer currents in the region have been reported to be highly variable in both speed and direction, with maximum velocities reaching 20–25 cm s<sup>-1</sup> (Pingree and Le Cann, 1990). Consequently, particle flux measurements reported in this paper could be to some extent underestimated.

Dissolved oxygen showed maximum values at the base of the upper mixed layer (Fig. 1), with concentrations increasing towards the end of the sampling period. The vertical distribution of chlorophyll *a* showed a trend similar to that of dissolved oxygen. Typical chlorophyll *a* values recorded at the subsurface maximum were about 1–1.7 mg m<sup>-3</sup>, on 12 and 17 July. Pigment concentrations were much lower on 14 July, when maximum values did not exceed 0.4 mg m<sup>-3</sup>.

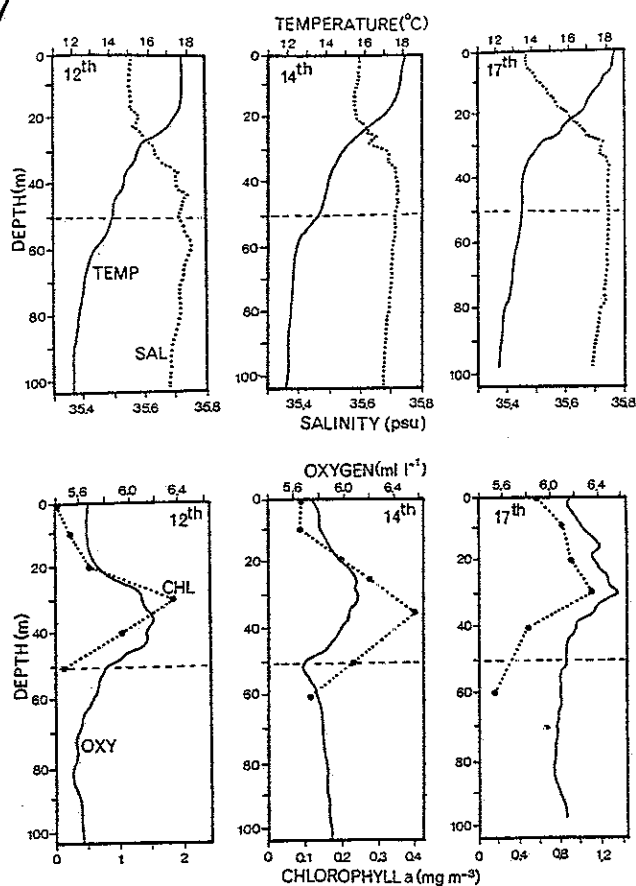


Figure 1

Vertical distribution of temperature (TEMP), salinity (SAL), dissolved oxygen (OXY) and chlorophyll *a* (CHL) corresponding to dates of trap deployment (trap 1, 12 July; trap 2, 14 July) and recovery (trap 1, 14 July; trap 2, 17 July). Upper panel: temperature ( $^{\circ}\text{C}$ ; "solid line"), salinity (psu; "dotted line"). Lower panel: dissolved oxygen ( $\text{ml l}^{-1}$ ; "solid line"), chlorophyll *a* ( $\text{mg m}^{-3}$ ; "dotted line"). The horizontal dashed line indicates the depth of trap deployment. Note differences in the scale for chlorophyll *a*.

Integrated values (0-50 m) of the standing stocks of particulate carbon and zooplankton are shown in Table 1. Chlorophyll *a* values were about  $37 \text{ mg m}^{-2}$  on the first and last

Table 1

Integrated values (in  $\text{mg m}^{-2}$  of chlorophyll *a* (Chl *a*); phaeopigments (Phaeo); Chlorophyll *a* equivalents (Chl equiv.); particulate organic carbon (POC); particulate organic nitrogen (PON); POC/PON molar ratio; particulate organic carbon (PIC); mesozooplankton (> 200  $\mu\text{m}$ ) carbon (Zooplank. C); and mesozooplankton nitrogen (Zooplank. N) in the upper water column (0-50 m) corresponding to the three visits to the sediment trap deployment station.

	12 July	14 July	17 July
Chl <i>a</i>	37.3	11.6	37.2
Phaeo	13.7	5.5	14.8
Chl <i>a</i> equiv.*	57.9	19.9	59.9
POC	6317	2345	2979
PON	995	367	6.9
POC/PON	7.4	7.4	6.9
PIC	496	184	180
Zooplank. C	669	-	549
Zooplank. N	135	-	102

\*Chl *a* equiv. = Chl *a* + 1.51 x Phaeo (the factor 1.51 is the ratio of molar weights).

sampling dates, but considerably lower on 14 July. The concentration of phaeopigments and, consequently, that of chlorophyll *a*-equivalents followed the same pattern. By contrast, POC, PON and PIC levels were 2-3 times higher at the time of trap 1 deployment (12 July) than on the subsequent dates. The contribution of PIC to TPC varied between 5.7 % and 7.3 %. The molar POC:PON ratios were slightly higher than the Redfield ratio (*ca.* 6.6 by atoms). Mesozooplankton carbon biomass represented between 10 % (12 July) and 17 % (17 July) of the TPC measured in the seston.

Scanning microscopic examination of the material retained in the traps revealed the presence of frustules of several diatom species (*Chaetoceros decipiens*, *Bacteriastrium hyalinum*, *Thalassiosira sp.*, unidentified pennate diatoms, etc.), coccolithophorids (*Emiliania huxleyi*, *Gephyrocapsa oceanica*), detached coccoliths and thecate dinoflagellates. However, a large proportion of the material observed was composed of amorphous material, intact and degraded copepod faecal pellets and zooplankton remains (Fig. 2).

Export production of particulate carbon, nitrogen and pigments out of the euphotic zone was higher in trap 1 than in trap 2 (Tab. 2). This difference was consistent with that of the concentrations of particulate carbon in the water column between sampling dates (Tab. 1). The downward fluxes of POC and PON (Tab. 2) are comparable to previous observations from shallow sediment-trap studies in productive on-shelf environments. In this connection, the flux of POC measured at 50 m in the coastal eutrophic VERTEX stations V5c ( $35^{\circ}50' \text{ N}$ ,  $122^{\circ}30' \text{ W}$ ) and V1 ( $35^{\circ}70' \text{ N}$ ,  $124^{\circ}00' \text{ W}$ ) were  $333$  and  $212 \text{ mg C m}^{-2} \text{ day}^{-1}$  in August-September (Knauer *et al.*, 1984). Falkowski *et al.* (1988) reported downward carbon fluxes of  $54$ - $140 \text{ mg C m}^{-2} \text{ d}^{-1}$  during spring at  $145 \text{ m}$  in the SEEP shelf-break region of the Northwest Atlantic ( $40^{\circ} \text{ N}$ ,  $72^{\circ} \text{ W}$ ). Similar rates ( $160$ - $185 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) were also obtained during the spring bloom in the North Sea (Davies and Payne, 1984) and in the shelf waters of the Indian Ocean in spring-summer (Pollehne *et al.*, 1993). It is interesting to note for comparison that carbon export from the euphotic layer (50 m) in coastal upwelling systems ( $432 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; Knauer *et al.*, 1979) or during an oceanic spring diatom bloom in the North Atlantic at  $47^{\circ} \text{ N}$ ,  $20^{\circ} \text{ W}$  (*ca.*  $305 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Bender *et al.*, 1992) was higher than the values reported in this study.

At integrated chlorophyll *a* levels similar to those in the present study, rates of primary production in the shelf

Table 2

Downward flux of pigments and particulate carbon at 50 m ( $\text{mg m}^{-2} \text{ d}^{-1}$ ) corresponding to the periods 12-14 July (trap 1) and 14-17 July (trap 2). Values in parentheses represent standard errors ( $n = 4$ ).

	TRAP 1	TRAP 2
Chl <i>a</i>	$0.50 (\pm 0.06)$	$0.29 (\pm 0.09)$
Phaeo	$2.04 (\pm 0.37)$	$1.10 (\pm 0.23)$
Chl <i>a</i> equiv *	$3.58 (\pm 0.57)$	$1.95 (\pm 0.37)$
POC	$236.0 (\pm 21.6)$	$172.8 (\pm 23.1)$
PON	$19.7 (\pm 2.6)$	$18.4 (\pm 1.8)$
PIC	$4.5 (\pm 0.3)$	$3.8 (\pm 0.6)$

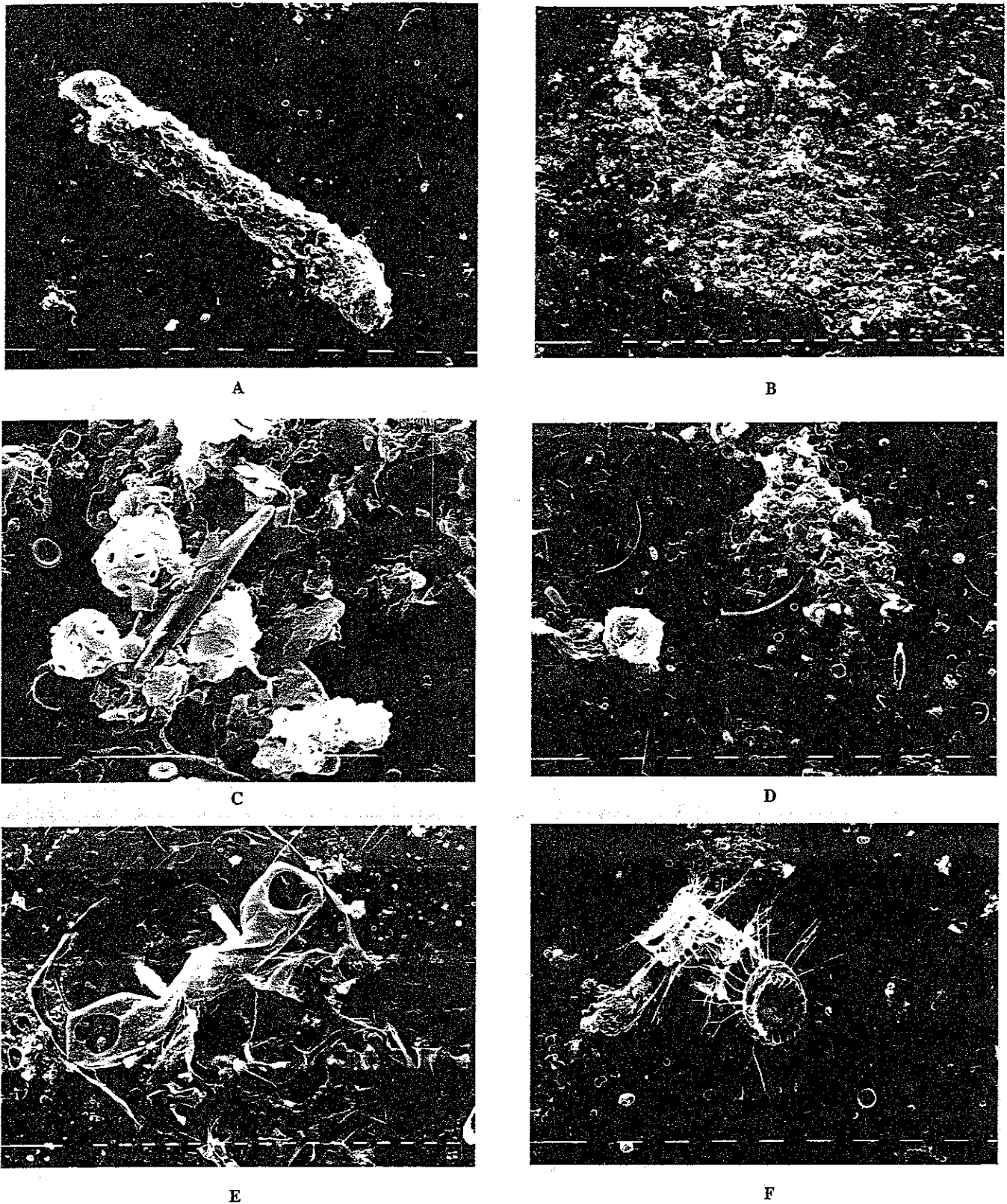


Figure 2

Scanning electron micrographs of the particulate material collected in the traps. A) intact copepod faecal pellet (trap 1); B) amorphous material (trap 2); C) cells of the coccolithophorid *Gephyrocapsa oceanica* and detached coccoliths of *Emiliana huxleyi* (trap 1); D) degraded copepod faecal pellet (trap 1); E) copepod remains (trap 2); and F) unidentified material and frustule of *Bacteriastrium hyalium* (trap 2). Bars in the microphotographs represent 10 µm.

waters of the southern Bay of Biscay in summer typically range between 630 and 735 mg C m<sup>-2</sup> d<sup>-1</sup> (Fernández and Bode, 1991). Taking these rates as representative of the sampling period, the export of POC out of the euphotic

layer represents 24-37 % of the primary production. These values are in close agreement with previous estimates in shelf and shelf-break environments such as those reported by Falkowski *et al.* (1988), 25-50 %, Davies and Payne

Table 3

Characteristics of trap-caught particulate matter corresponding to the periods 12-14 July (trap 1) and 14-17 July (trap 2). Values in parenthesis represent standard errors ( $n = 4$ ).

	TRAP 1	TRAP 2
POC/PON	12.2 ( $\pm 0.5$ )	9.5 ( $\pm 1.2$ )
PIC/POC	0.019 ( $\pm 0.002$ )	0.021 ( $\pm 0.002$ )
POC/Chl <i>a</i> -C equiv *	68.8 ( $\pm 6.5$ )	93.7 ( $\pm 10.3$ )
% POC flux ('living' Chl <i>a</i> -C)**	10.8 ( $\pm 1.7$ )	8.5 ( $\pm 2.6$ )
% POC flux (Chl <i>a</i> -C equiv)***	74.6 ( $\pm 6.6$ )	55.5 ( $\pm 6.6$ )
PIC	4.5 ( $\pm 0.3$ )	3.8 ( $\pm 0.6$ )

\* Chl *a* C equi. = Chl *a* + 1.51 x Phaeo (the factor 1.51 is the ratio of molar weights). A C/Chl *a* ratio of 50 was assumed.

\*\* Percentage of organic carbon flux represented by 'living' phytoplankton carbon, assuming a C/Chl *a* ratio of 50.

\*\*\* Percentage of organic carbon represented by phytoplankton-derived material calculated from Chl *a* equivalents.

(1984), 25-35 %, or Knauer *et al.* (1984), 29 %, and lie within the overall range (25-30 %) postulated by Berger *et al.* (1989) for coastal regions on an annual scale. These percentages are also similar to the f-ratio found by Eppley and Peterson (1979) for inshore waters.

The POC/PON ratio of the sedimented material varied from 9.5 to 12.2 (Tab. 3). These figures lie within the range reported for shallow sediment traps from different geographical regions (*e.g.* Biscaye *et al.*, 1988; Nelson *et al.*, 1988; Falkowski *et al.*, 1988; Wassman *et al.*, 1994). The higher POC/PON ratio in trap-caught material compared to that of seston particulates is the result of a more rapid remineralization of nitrogen relative to carbon, as the latter is usually found in complex macromolecules which are relatively refractory.

Not only the net downward flux of organic carbon, but also the ratio of organic to inorganic carbon in the sedimented material is an important biogeochemical variable, due to its implications for the partial pressure of CO<sub>2</sub> in surface waters (Berger and Keir, 1984). The export of PIC was very low, representing, on average, some 2 % of the total carbon flux (Tab. 3). Comparison of this result with others is difficult given the high sensitivity of the PIC/POC ratio to depth variations caused by different regeneration rates of PIC and POC. It can be seen, how-

ever, that the contribution of PIC to TPC in the seston of the upper water column is 3-4 times higher than that measured in the material collected in the sediment trap (see Tab. 1 and 3). This mismatch is likely to be the result of the dissolution of calcium carbonate during digestion by grazers (see *e.g.* Harris, 1994). This hypothesis is supported by the relatively high biomass of mesozooplankton in the euphotic layer (Tab. 1) and also by the large amount of fecal pellet material in the sedimented material (Fig. 2). If this suggestion is correct, it follows that some 75 % of the PIC ingested by grazers would be returned to sea water as CO<sub>2</sub> during the feeding process. Moreover, comparatively reduced vertical flux of PIC derived from selective feeding of zooplankton upon non-calcareous materials cannot be completely ruled out.

The vertical fluxes of intact ('living') chlorophyll *a* represented only 1 - 2.5 % of the bulk of photosynthetic pigment present in the upper 50 m (Tab. 1 and 2). This contribution rises significantly when 'total' chlorophyll *a*, estimated from chlorophyll *a* equivalents, is considered. In this case, between 5 % and 10 % of the total chlorophyll *a* is removed daily from the fertile zone. An estimation of the contribution of phytoplankton-derived carbon to the total POC flux was attempted by assuming a carbon to chlorophyll ratio of 50 (Eppley *et al.*, 1977). A significant proportion of the organic carbon caught in the traps, between 50 % and 75 %, originated from phytoplankton in the surface waters (Tab. 3). 'Living' phytoplankton, however, represented only 8-10 % of the organic carbon exported to deeper layers. The observed contribution of phytoplankton to total carbon flux is close to the values reported in other regions (*eg.* Nelson *et al.*, 1987; Falkowski *et al.*, 1988) but is considerably higher than those found in summer conditions in high latitudes (Wassman *et al.*, 1994).

#### Acknowledgements

We are grateful to R. González-Quirós, A. Bode and the crew of RV *José Rioja* for their advice and help at sea. This study was funded by the Spanish C.I.C.Y.T. under contract No. AMB 92-0834

#### REFERENCES

- Bender M., H. Ducklow, J. Kiddon, J. Marra and J. Martin (1992). The carbon balance during the 1989 spring bloom in the North Atlantic Ocean, 47° N, 20° W. *Deep-Sea Res.* **39**, 1707-1725.
- Berger W.H., K. Fisher, C. Lai, G. Wu (1987). Ocean productivity and organic carbon flux. I. Overview and maps of primary production and export production. University of California, San Diego, SIO reference 87-30.
- Berger W.H., R.S. Keir (1984). Glacial-Holocene changes in atmospheric CO<sub>2</sub> and the deep-sea record. In: *Climate Processes and Climate Sensitivity*, J.E. Hansen and T. Takahashi eds. *Geophys. Monog.* **29**, 337-351. Washington D.C., American Geophysical Union.
- Berger W.H., V.S. Smetacek, G. Wefer (1989). Ocean productivity and paleoproductivity - An overview. In: *Productivity of the Ocean: Present and Past*. W.H. Berger, V.S. Smetacek, G. Wefer eds. John Wiley and Sons Limited. p. 1-34.
- Biscaye P.E., R.F. Anderson, B.L. Deck (1988). Fluxes of particles and constituents to the eastern United States continental slope and rise: SEEP-I. *Deep-Sea Res.* **8**, 855-904.

- Payne J.M., R. Payne (1984). Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. *Mar. Biol.* **78**, 315-324.
- Eppley R.W., W.H. Harrison, S.W. Chisholm, E. Steward (1977). Particulate organic matter in surface waters of southern California and its relationship to phytoplankton. *J. Mar. Res.* **35**, 671-696.
- Eppley R.W., B.J. Peterson (1979). Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* **282**, 677-680.
- Falkowski P.G., C.N. Flagg, G.T. Rowe, S.L. Smith, T.E. Whitledge, C.D. Wirik (1988). The fate of a spring bloom: export or oxidation? *Contin. Shelf Res.* **8**, 457-484.
- Fernández E., A. Bode (1991). Seasonal patterns of primary production in the Central Cantabrian Sea (Bay of Biscay). *Sci. Mar.* **55**, 4, 629-636.
- Fernández E., P. Boyd, P.M. Holligan, D.S. Harbour (1993). Production of organic and inorganic carbon within a large-scale coccolithophore bloom in the northeast Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **97**, 271-285.
- Harris R.P. (1994). Zooplankton grazing on the coccolithophore *Emiliania huxleyi* and its role in inorganic carbon flux. *Mar. Biol.* **119**, 431-439.
- Knauer G.A., J.H. Martin, K.W. Bruland (1979). Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the northeast Pacific. *Deep-Sea Res.* **26**, 97-108.
- Knauer G.A., J.H. Martin, D.M. Karl (1984). The flux of organic material out of the euphotic zone. In: *Global Ocean Flux Studies. Proceedings of a Workshop*. Woods Hole, National Academy Press, 136-150.
- Malone T.C., T.S. Hopkins, P.G. Falkowski, T.E. Whitledge (1983). Production and transport of phytoplankton biomass over the continental shelf of the New York Bight. *Contin. Shelf Res.* **1**, 305-337.
- Nelson J.R., J.R. Beers, R.W. Eppley, G.A. Jackson, J.J. McCarthy, A. Soutar (1987). A particle flux study in the Santa Monica-San Pedro Basin off Los Angeles: Particle flux, primary production, and transmissometer survey. *Contin. Shelf Res.* **7**, 307-328.
- Pingree R.D., B. Le Cann (1990). Structure, strength and seasonality of the slope currents in the Bay of Biscay region. *J. mar. biol. Ass. U.K.* **70**, 857-885.
- Pollehne F., B. Zeitzschel, R. Peinert (1993). Short-term sedimentation patterns in the northern Indian Ocean. *Deep-Sea Res.* **40**, 821-831.
- Rowe G.T., S. Smith, P. Falkowski, T. Whitledge, R. Theroux, W. Phoel, H. Ducklow (1986). Do continental shelves export organic matter? *Nature* **324**, 559-561.
- Walsh J.J. (1991). Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. *Nature* **350**, 53-55.
- Walsh J.J., G.T. Rowe, R.L. Iverson, C.P. McRoy (1981). Biological export of shelf carbon is a sink of the global CO<sub>2</sub> cycle. *Nature* **291**, 196-201.
- Wassman P., R. Martínez, M. Vernet (1994). Respiration and biochemical composition of sedimenting organic matter during summer in the Barents Sea. *Contin. Shelf Res.* **14**, 79-90.
- Yentsch, C.S., D.W. Menzel (1963). A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Res.* **10**, 221-231.