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Vertical biogenic particle flux in a western Galician ria (NW Iberian Peninsula)

Manuel Varela[1,*], Ricardo Prego[2], Yolanda Pazos[3]

[1]Instituto Español de Oceanografía, Muelle de Ànimas, s/n., 15001 A Coruña, Spain
[2]Marine Biogeochemistry Research Group, Institute of Marine Research (CSIC), 36208 Vigo, Spain
[3]Centro de Control da Calidade do Medio Mariño, Peirao de Vilaxoan, 36611 Villagarcia de Arousa, Spain

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ABSTRACT: Fluxes of particulate pelagic material were measured in the Pontevedra Ría (northwest Spain) using sediment traps moored at the base of the photic zone, deployed for 24 h periods from February to June 1998. Measurements of water column hydrography, chlorophyll, primary production and phytoplankton were taken. Samples were divided into low, moderate and high productivity periods, according to phytoplankton biomass. The vertical flux of carbon ranged from 530 to 1780 mg C m^{-2} d^{-1}. Minimum values were recorded during high productivity periods, and were related to offshore advection of surface water. The daily export of carbon accounted for 75% of primary production. The contribution of phytoplankton to the sedimented carbon ranged from 18 to 66%, and the fraction corresponding to living phytoplankton from 5 to 25%. The dominance of phytoplanktonic over phytobenthic species, and the low C:N ratio, indicated a pelagic origin and a rapid sinking of the particles. Diatoms were predominant; however, microflagellates accounted for ca. 20% and dinoflagellates for 13% of the total biomass, suggesting the rapid formation of aggregates, increasing the sinking speed of individual cells. A decrease in sedimentation was observed from the inner to the outer ria, and from low to higher productivity periods. However, no differences were found among stations and periods. The flux of particulate carbon was similar in intensity throughout the ria in all periods. Sedimentation is influenced by hydrography, showing a negative relationship with water flux. Balance between advection and retention processes in the ria play an important role in the coupling between biomass stock in water and deposition of material in traps.

KEY WORDS: Particle flux · Carbon · Chlorophyll · Phytoplankton · Galicia · Pontevedra Ría

INTRODUCTION

The export of biogenic material from the euphotic zone to the sea bottom is a key mechanism in the regulation of biogeochemical cycling of essential elements linking pelagic and benthic systems. It is also a process that serves to eliminate the carbon accumulated in the upper layer of the oceans. (Knauer et al. 1984, Asper et al. 1992, Olesen & Lundsgaard 1995, Bode et al. 1998). Despite their comparatively limited spatial extent, biogeochemical fluxes in coastal and shelf areas are of great importance. These areas account for more than 50% of the primary production of the world's oceans and ca. 80% of the particle flux to the sea floor (Berger et al. 1989).

In areas of marked seasonality, the pulses of primary productivity tend to sediment to the sea floor. This is what occurs in temperate areas (Smetacek 1980, Bender et al. 1992) like Galicia, where the main productivity and vertical flux take place in conjunction with spring and upwelling blooms. The composition and structure of pelagic communities, together with various hydrographic and biological processes, affect the magnitude of vertical flux and, consequently, the quality and quantity of settling material (Fernández et al. 1995, Bode et al. 1998, Anadón et al. 2002). These different situations have a direct impact on the transport of organic material and, sometimes, the process results in a clear uncoupling between pelagic production and vertical flux to the bottom (Bode et al. 1998, Olli et al. 2001).

*Email: manuel.varela@co.ieo.es

The upwelling system off northwest Spain is characterized by episodic enrichment of nutrients into the coastal zone and associated high rates of primary productivity (Bode et al. 1994, Tenore et al. 1995). In the 4 western Galician rias, (Rías Baixas), upwelling events are common from April to October, with a stronger intensity during summer (McClain et al. 1986, Blanton et al. 1987, Tilstone et al. 1994). This phenomenon is commonly attributed to the action of the northerly winds on the shelf, which produce, by Coriolis effect, an Ekman transport of offshore surface water, which is then replaced by deeper, colder, and nutrient-rich water (Wooster et al. 1976). These events result in cycles of high production that allow for intensive aquaculture activity in the rias and support important pelagic fisheries (Blanton et al. 1987, Tenore et al. 1995).

Large amounts of organic material accumulate in the shallow continental shelf, especially opposite the western rias (López-Jamar et al. 1992). These deposits have been associated with organic matter exported from the rias (Fraga 1976, Tenore et al. 1982, 1995, Varela et al. 1991, Varela 1992) and have been modeled by Prego (1993) and Alvarez-Salgado et al. (1996). However, studies have only recently been conducted in the areas off the rias, based on sediment cores (Dias et al. 2002, Jouanneau et al. 2002) and sediment traps (Olli et al. 2001).

Of the Galician rias, the western rias have been targeted as the subject of numerous studies aimed at understanding nutrient cycles (see overview by Fraga 1996, Prego & Bao 1997, Prego et al. 1999), phytoplankton species composition and biomass (Margalef et al. 1955, Vives & López-Benito 1957, Campos & Mariño 1982, 1984, Figueiras & Niell 1987, Figueiras & Pazos 1991a), as well as the distribution of diatoms on surface sediments (Bao et al. 1997). However, studies directed at measuring the vertical flux of organic matter have not been conducted. Cabanas et al. (1980) and Tenore et al. (1982) reported data on sedimentation rates as a part of a more general study related to the influence of mussel rafts on the bottom communities in the Ría Arosa. Nevertheless, these data shed light on the influence of mussel deposition rather than on the flux of original pelagic materials under natural conditions.

Our study was an attempt to characterize vertical particle and carbon flux in one of the rias, using sediment traps deployed for short periods of time at 3 stations in the Pontevedra Ría between February and June 1998. This is the first study to be done on the relationship between the composition and biomass of phytoplankton and export to sediment, covering the main oceanographic periods described in the area. The chief objective of this work was to estimate the magnitude of vertical transport and the biological composition of the settled material, and its relation to the hydrography of the ria, the structure of the plankton community and the processes occurring in the pelagic system.

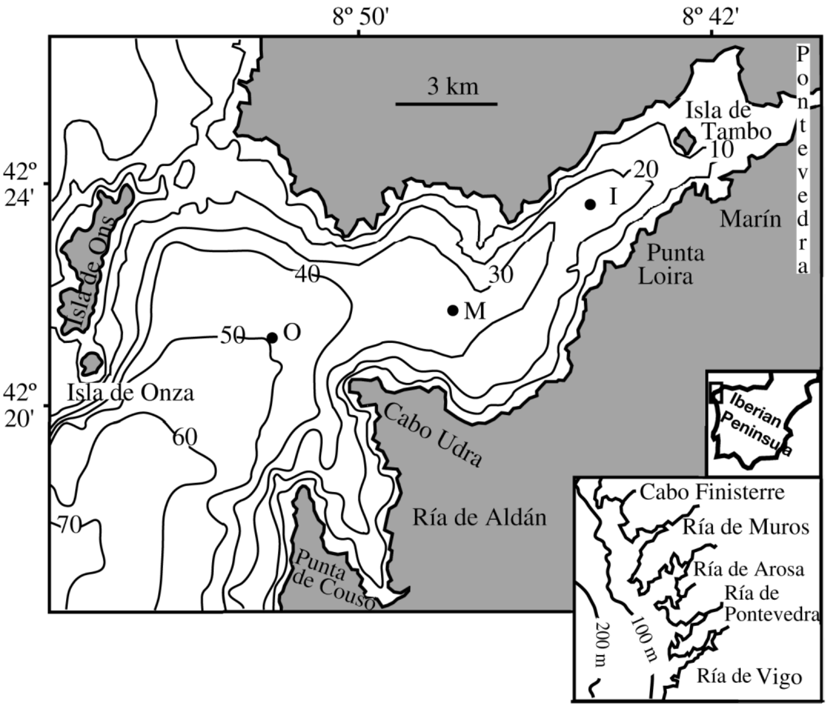

Fig. 1. Pontevedra Ría. Black circles indicate the 3 stations (O: outer; M: middle; I: inner) where sediment traps were moored and water column sampling carried out. Contour lines show depth (m)

MATERIALS AND METHODS

Study area. The Pontevedra Ría, which belongs to the Rías Baixas group, is located in the northwest of the Iberian Peninsula. With a surface area of 141 km^2, a mean depth of 31 m and a volume of 3.5 km^3, the Pontevedra Ría is the second largest estuary of the Rías Baixas. This ria is oriented in a SW–NE direction, converging with the Lérez River in its innermost part, and flowing out towards the islands of Onza and Ons in the outer part of the estuary. The Lérez River (57 km in length), provides the main freshwater input. Like the rest of the Rías Baixas, the Pontevedra Ría is V-shaped, becoming progressively wider from the head to the mouth. It has 3 well-defined zones (Fig. 1): the inner zone, mainly estuarine, from the mouth of the river to Tambo Islet or Punta Loira, depending on the river flow; the middle zone extending up to Cape Udra; and the outer zone, bounded by Ons Island, which is subject to oceanic influence for most of the year. The Pontevedra Ría behaves like an estuary with positive residual circulation that is enhanced in summer by coastal upwelling (Fraga 1981, Prego & Bao 1997). According to Prego et al. (2001), there is an annual cycle of different water masses in front of the estuary. The most important masses are present from April to September and pertain to ENACW (Eastern North Atlantic Central Water; Fiuza et al. 1998), and the water is transported by the poleward current (Frouin et al. 1990) on the Iberian continental margin during winter.

The hydrodynamics of the Pontevedra Ría are driven mostly by inputs from rivers and continental runoff, of the water masses on the adjacent shelf, and the wind regime (de Castro et al. 2000, Prego et al. 2000, Gómez-Gesteira et al. 2001). The monthly average discharge of the Lérez River fluctuates between 2 and 80 m^3 s^{-1} This discharge is high from December to March, with a maximum in February and a minimum in September. Nevertheless, in 1998 the annual river discharge was 30.3 m^3 s^{-1}, with an exceptionally low river discharge (17.8 m^3 s^{-1}) during February.

Water column sampling and sample processing. Water column observations were carried out at 3 stations (O, M and I: outer, middle and inner ria) (Fig. 1). Samples were taken twice at month, from February to June 1998. Vertical profiles of temperature, salinity and photosynthetic active radiation (PAR) were obtained with a Seabird-19 and Seabird-25 CTD probe at each station. Descriptive and complementary aspects of the physical and chemical oceanography in the area can be found in recent publications on hydrography (Prego et al. 2001), hydrodynamics (de Castro et al. 2000, Gómez-Gesteira et al. 2001, Ruiz-Villareal et al. 2002) and biogeochemical cycling (Dale & Prego 2002).

Bottle (General Oceanic, 1.7 l) casts were made to obtain water samples for chlorophyll *a* (chl *a*) and phaeopigments, phytoplankton counts and primary production measurements at depths of 100, 50, 25, 10 and 1% of PAR received at the surface. Chl *a* and phaeopigment (hereafter referred to as 'phaeo') concentrations were measured by fluorimetry, using acetone extracts after filtration through Whatman GF/F filters (UNESCO 1994). Primary production was estimated by the C-14 method, using 2 h on-board incubations in simulated *in situ* conditions as described in Bode et al. (1994). After incubation, samples were filtered through Whatman GF/F filters. Daily primary production rates were calculated by multiplying hourly rates by the total number of hours during the day, based on data from by the Centro Meteorológico Zonal of A Coruña for the surrounding area. Flux of water (including upwelling and river input) was quantified with a non-steady-state water and salt budget (Dale & Prego 2000).

Samples for microscopic examination were preserved in Lugol's solution and kept cool and dark until they were ready to be examined under a Nikon Eclipse TE 300 inverted microscope following the technique described by Utermöhl (1958). A magnification of 40 and 100× was used for large cells, 250× for intermediate ones and 400 and 1000× for flagellates. When organisms were too small (3 µm to 10–15 µm) to be classified at the genus level, they were categorized as dinoflagellates or flagellates. The nomenclature for species followed that of Tomas (1997). Cell volumes were calculated separately for each group by the geometric shape of the cells, and cell carbon was estimated with the equations proposed by Strathmann (1967) and Smetacek (1975). The recommendations outlined by Working Group 9 of the Baltic Marine Biologists were adhered to in performing these calculations (Anonymous 1979). Results are expressed as cells m^{-2}.

Sediment traps and sample processing. A Multitrap collector system was deployed 5 m above the bottom at each station and anchored to the sea-bottom (48, 37 and 25 m depth for Stns O, M and I respectively) for a 24 h period, after sampling the water column. The trap system was described in Knauer et al. (1979) following the JGOFS protocols (UNESCO 1994) and consisted of 4 individual multiptrap baffled cylinders of 6 cm diameter and 60 cm length. Each cylinder was placed at the end of a PVC cross, and the entire system was designed following suggestions made by Gardner (1980a,b) with respect to aspect ratio, axial geometry of collectors, baffles and mooring configuration, to ensure thus the trap was efficient in collecting material for most environmental situations. The design is also adequate for advection conditions prevailing in the ria. The tidal currents during the study varied from 3 to 10 cm s^{-1} (de Castroet al. 2000) and are in the range reported by Gardner (1980b) for good trap efficiency. Prior to each deployment, the cylinders were filled with a solution of filtered seawater to which 35 g of NaCl was added per liter of solution. This solution prevented the exchange of material with the surrounding water. Since the traps were deployed for a very short period, degradation of the sedimented material was expected to be minimal (Nelson et al. 1987), so no preservatives were added to the collection tubes.

On recovery, the material collected in the tubes was transferred to 5 l polycarbonate bottles, and aliquots were filtered through Whatman GF/F filters to deter-

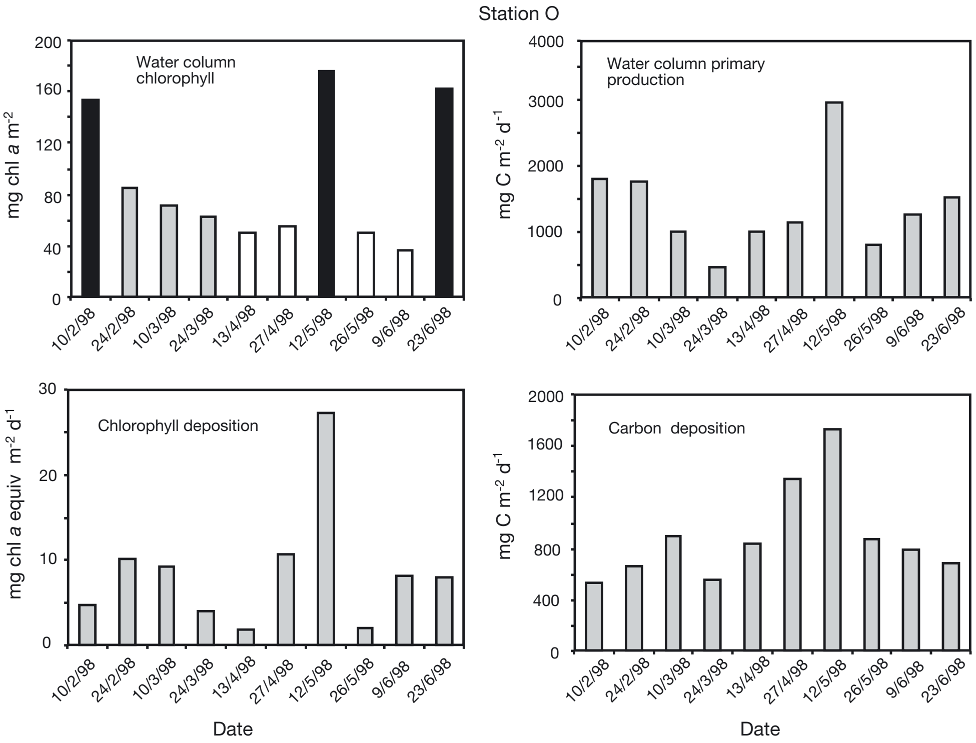

Fig. 2. Water column chlorophyll, primary production, and trap chlorophyll and carbon for Stn O (outer ria) during the period of study. White bars: date of low productivity; gray bars: medium productivity; black bars: high productivity. Dates given as d/mo/yr

mine total carbon and nitrogen, using a FlashEA 11-12 Termoquesth CNH analyzer. Carbonate was not removed from the filters, but the contribution of carbonate to total sedimented carbon probably represented ca. 2% of total carbon flux to the sea bottom (Fernández et al. 1995, Palanques et al. 2002). Chl *a* and phaeopigments, were determined as described above for the water column. Phytoplankton derived carbon was calculated as described in Bode et al. (1998). First, chlorophyll-equivalent concentrations (hereafter referred to as chl *a* equiv) were computed as: chl *a* equiv = chl *a* + 1.51 phaeo, where 1.51 is the ratio of the molecular weights of chl *a* and phaeo. Carbon from living, non-degraded phytoplankton was estimated as the product of chl *a* and (50 g C g chl a^{-1}.) Similarly, total phytoplankton carbon (living + degraded) was estimated using chl *a* equiv and the above conversion.

Phytoplankton identification and cell counting were performed in samples preserved with Lugol's solution. Organisms were identified and counted as described for water column phytoplankton counts.

RESULTS

Water column conditions

Variations in surface water salinity were closely related to river discharge, whereas bottom waters presented oceanic characteristics over the whole year. Currents were controlled by tide, river discharge and wind in the inner ria (de Castro et al. 2000, Prego et al. 2001). The water column was mixed in winter and stratified in summer, with phytoplankton blooms occurring in the transition period between mixing and stratification. A peculiar characteristic in Galicia is the existence of upwelling events from spring to autumn, especially important during summer, which interrupt the stratification or raise the thermocline, injecting nutrients and allowing summer phytoplankton blooms (Campos & González 1975, Campos & Mariño 1984, Estrada 1984, Mariño et al. 1985, Figueiras & Niell 1987, Figueiras & Pazos 1991b, Varela 1992, Casas et al. 1997, Prego & Varela 1998, Varela et al. 2001).

Considering hydrography and phytoplankton biomass, the different sampling dates were divided into 3 categories: high, moderate and low productivity periods (Figs. 2 to 4, Table 1). The high productivity periods included spring as well as upwelling blooms. The low production periods coincided, in general, with stratification in the water column, and the rest of the periods were considered to be of moderate productivity. ANOVA for water column chl *a* showed significant differences ($p < 0.01$) among these 3 periods.

During high productivity periods, integrated values of water chl *a* of ca. 150 mg m^{-2} were observed in all stations (Table 1, Figs. 2 to 4). These concentrations dropped down to 40 mg m^{-2} in low productivity periods. Primary production reached values of over 2 g C m^{-2} d^{-1} during high productivity periods, similar to

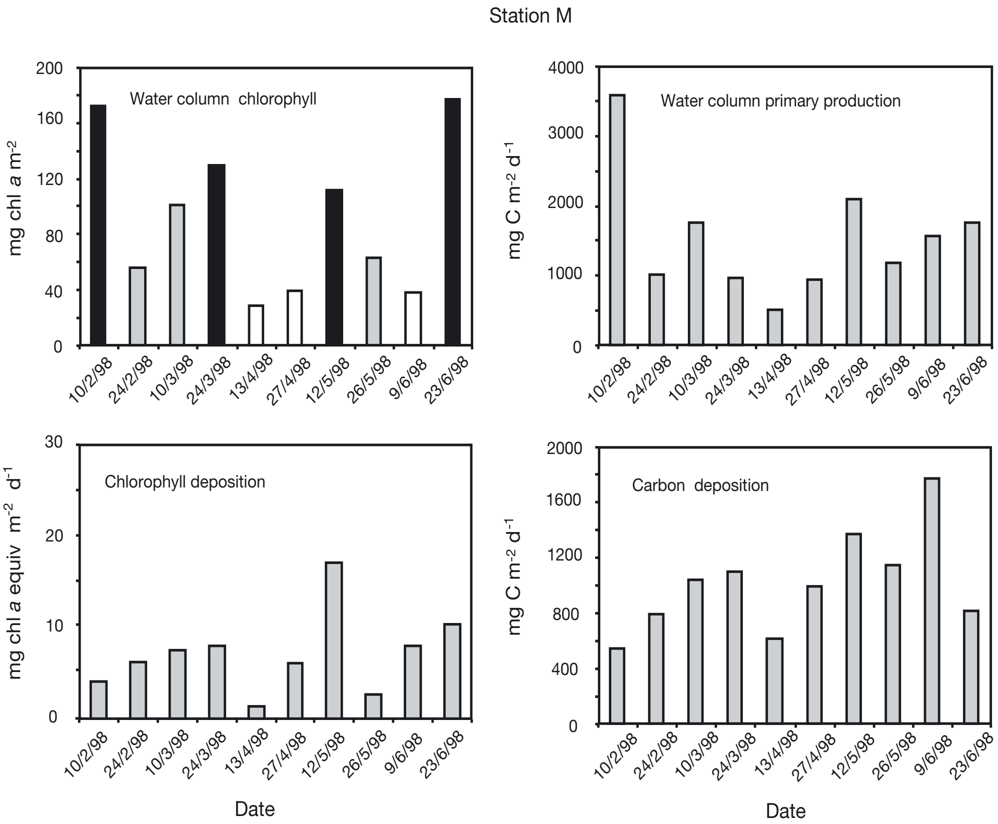

Fig. 3. Water column chlorophyll, primary production, and trap chlorophyll and carbon for Stn M (middle ria) during the period of study. Bars as in Fig. 2. Dates given as d/mo/yr

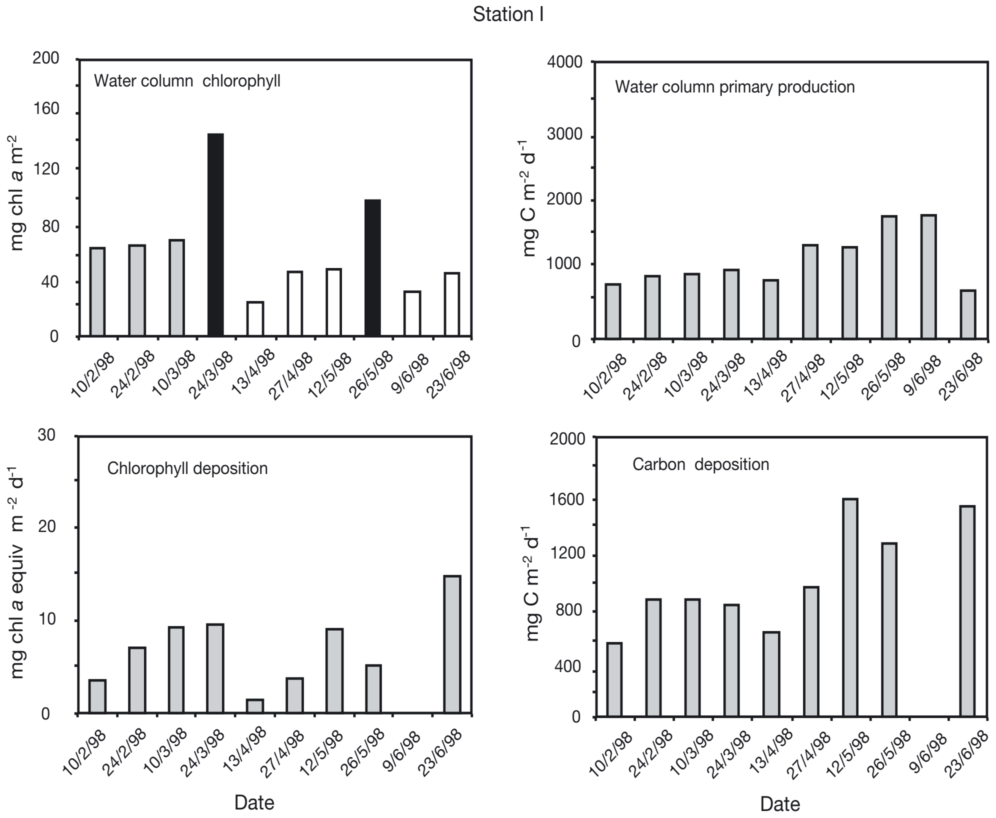

Fig. 4. Water column chlorophyll, primary production, and trap chlorophyll and carbon for Stn I (inner ria) during the period of study. Bars as in Fig. 2. Dates given as d/mo/yr

Table 1. Integrated values (±SE) of variables for water column and mean daily flux rates and mean molar C:N ratio (± SE) of settling particles for each station and productivity periods. O: outer station, M: middle station, I: inner station. Equiv: equivalent; Phaeo: phaeopigment; PP: primary production; C-chl *a*:C: percentage of carbon flux attributed to living phytoplankton; C-chl *a* equiv:C: percentage of total phytoplankton in the carbon flux; biovol: biovolume; POC: particulate organic carbon; PON: particulate organic nitrogen; sed: sediment

Water column

Station	Productivity	Chl *a* (mg m^{-2})	Chl *a* equiv (mg m^{-2})	Phaeo (mg m^{-2})	PP (mg m^{-2} d^{-1})	Phaeo: chl *a*	C-chl *a* (mg m^{-2})	C biovol (mg m^{-2})
O	High	164 ± 6	228 ± 30	42 ± 16	2201 ± 461	0.26	8200 ± 236	9724 ± 1258
	Moderate	74 ± 6	94 ± 8	13 ± 1	1139 ± 396	0.17	3700 ± 291	2869 ± 989
	Low	48 ± 4	77 ± 5	19 ± 4	1114 ± 102	0.40	2400 ± 152	1768 ± 627
M	High	148 ± 15	221 ± 30	48 ± 15	2107 ± 547	0.32	7400 ± 420	8802 ± 2510
	Moderate	79 ± 22	98 ± 22	12 ± 0	1407 ± 371	0.15	3950 ± 890	3811 ± 1021
	Low	43 ± 7	68 ± 12	17 ± 4	1069 ± 222	0.40	2150 ± 400	2213 ± 650
I	High	122 ± 23	161 ± 27	26 ± 3	1368 ± 358	0.21	6100 ± 989	7448 ± 1985
	Moderate	67 ± 2	84 ± 4	11 ± 3	864 ± 41	0.16	3350 ± 95	5359 ± 963
	Low	40 ± 4	65 ± 9	16 ± 3	1181 ± 184	0.40	2000 ± 265	5393 ± 1022

Sediment trap

Station	Productivity	Chl *a* (mg m^{-2} d^{-1})	Chl *a* equiv (mg m^{-2} d^{-1})	Phaeo (mg m^{-2} d^{-1})	C ± SE (mg m^{-2} d^{-1})	N ± SE (mg m^{-2} d^{-1})	C-chl *a* (mg m^{-2} d^{-1})	C-chl *a* equiv (mg m^{-2} d^{-1})
O	High	5 ± 3	13 ± 7	5 ± 3	984 ± 375	171 ± 99	250 ± 138	650 ± 348
	Moderate	1 ± 0.2	8 ± 2	4 ± 1	710 ± 100	107 ± 6	50 ± 12	400 ± 88
	Low	1 ± 0.4	6 ± 2	3 ± 1	962 ± 127	129 ± 25	50 ± 8	285 ± 83
M	High	5 ± 2	10 ± 2	3 ± 0.5	964 ± 176	182 ± 75	250 ± 100	500 ± 148
	Moderate	2 ± 0.1	7 ± 0	3 ± 0.5	923 ± 125	129 ± 8	100 ± 15	350 ± 45
	Low	1 ± 0.2	5 ± 2	2 ± 0.9	1139 ± 240	154 ± 21	50 ± 11	250 ± 48
I	High	3 ± 1.6	8 ± 2	3 ± 0.6	1127 ± 239	153 ± 31	150 ± 110	400 ± 108
	Moderate	3 ± 0.9	7 ± 1	3 ± 0.7	817 ± 113	107 ± 23	150 ± 48	350 ± 52
	Low	5 ± 2	7 ± 2	2 ± 0.5	1237 ± 201	234 ± 54	250 ± 90	350 ± 102

Station	Productivity	C-chl *a*:C (%)	C-chl *a* equiv:C (%)	C:PP (%)	POC/PON (by atoms)	Chl *a* sed: chl *a* water (%)	Chl *a* equiv trap: chl *a* equiv water (%)	Phaeo: chl *a*
O	High	25 ± 8	66 ± 25	45 ± 17	8 ± 2	3 ± 1.4	5 ± 2	1.00
	Moderate	7 ± 1	49 ± 7	62 ± 9	7 ± 1	2 ± 0.2	8 ± 2	4.00
	Low	5 ± 0.5	26 ± 3	86 ± 11	8 ± 0.5	2 ± 0.7	7 ± 3	3.00
M	High	26 ± 3	52 ± 9	46 ± 8	7 ± 1.5	4 ± 2	5 ± 2	0.60
	Moderate	11 ± 1	38 ± 5	66 ± 9	8.1 ± 0.6	3 ± 1	7 ± 1	1.50
	Low	4 ± 1	18 ± 4	107 ± 21	8.1 ± 0.9	3 ± 0.6	7 ± 4	2.00
I	High	14 ± 3	35 ± 7	82 ± 17	8.1 ± 0.2	2 ± 0.8	5 ± 1	1.00
	Moderate	18 ± 3	43 ± 10	95 ± 13	9.1 ± 1	4 ± 1.2	9 ± 2	1.00
	Low	20 ± 3	28 ± 5	105 ± 16	5.8 ± 0.5	10 ± 5	12 ± 4	0.40

Station	Productivity	C biovol (mg m^{-2} d^{-1})	C biovol:C (%)	C biovol trap: C biovol water (%)
O	High	129 ± 68	13 ± 3	1.4 ± 1
	Moderate	70 ± 59	9 ± 2	2.4 ± 0.5
	Low	32 ± 13	3 ± 0.5	1.8 ± 1
M	High	106 ± 77	9 ± 1	1.3 ± 0.5
	Moderate	97 ± 51	8 ± 2	2.5 ± 0.8
	Low	34 ± 11	2 ± 0.2	1.6 ± 1
I	High	59 ± 37	5 ± 1	0.9 ± 0.2
	Moderate	185 ± 110	18 ± 5	3.5 ± 2.1
	Low	232 ± 157	15 ± 6	4.3 ± 1.5

those reported in the middle area of the Vigo Ría (Prego 1993). Values of around 1 g C m^{-2} d^{-1} occurred during moderate to low periods. In general, the lowest values were observed in the innermost ria (Stn I). Differences among periods were less important for production than for chlorophyll.

Diatoms dominated the microphytoplankton (>20 µm) community in all stations and periods (Table 2). Several species of *Chaetoceros* (especially *C. socialis* and *C. curvisetus*), *Leptocylindrus danicus*, *Pseudo-nitzschia* spp. and *Skeletonema costatum* were the most representative components

Table 2. Water column phytoplankton biomass (mg C m^{-2}, calculated from cell biovolume), of main phytoplankton species and groups. O: outer station, M: middle station, I: inner station

Phytoplankton group	Station O Productivity period			Station M Productivity period			Station I Productivity period		
	High	Moderate	Low	High	Moderate	Low	High	Moderate	Low
Dinoflagellates									
Amphidinium flagellans	11	3	2	9	2	3	4	2	7
Dinophysis acuminata	104	5	<1	49	3	3	3	<1	19
Heterocapsa niei	12	1	5	6	<1	6	2	2	9
Protoperidinium bipes	181	9	3	72	1	11	7	2	9
Scrippssiella trochoidea	129	62	25	88	35	20	13	45	42
Total dinoflagellate biomass	477	284	98	300	303	84	105	343	211
Diatomaceae									
Asterionellopsis glacialis	33	5	3	56	9	2	22	3	43
Chaetoceros auxospores	518	34	1	471	197	0	83	1348	32
Chaetoceros curvisetus	290	39	4	74	91	5	31	68	36
Chaetoceros debilis	9	<1	<1	12	<1	<1	<1	2	6
Chaetoceros decipiens	21	<1	2	16	7	1	20	<1	9
Chaetoceros didymus	103	35	9	39	29	6	10	97	21
Chaetoceros gracilis	<1	<1	1	<1	<1	83	<1	<1	1
Chaetoceros lorenzianus	87	1	<1	37	7	5	11	13	6
Chaetoceros socialis	1	65	1	2	64	<1	2	57	1
Chaetoceros spp.	2002	745	69	1602	1238	91	2668	904	649
Dactyliosolen fragilissimus	25	7	7	21	5	9	9	<1	22
Detonula pumila	557	200	<1	330	410	<1	2	566	<1
Eucampia zodiacus	<1	<1	<1	1	<1	1	32	<1	1
Guinardia delicatula	652	16	8	361	11	9	22	11	101
Guinardia striata	55	21	4	147	8	5	754	5	20
Lauderia annulata	53	128	3	61	33	2	109	41	3
Leptocylindrus danicus	920	67	101	748	79	150	124	119	848
Leptocylindrus minimus	2	2	<1	1	3	1	<1	<1	2
Melosira islandica	21	3	8	52	0	7	4	5	43
Nitzschia longissima	38	3	10	20	4	10	12	13	23
Paralia sulcata	<1	<1	2	<1	<1	2	2	<1	4
Pseudonitzschia delicatissima	27	1	2	36	<1	2	2	<1	62
Pseudonitzschia spp.	49	313	7	255	143	9	379	104	83
Rhizosolenia imbricata	104	8	6	69	4	11	59	6	74
Rhizosolenia setigera	50	9	7	116	22	4	65	12	102
Skeletonema costatum	87	1	2	124	<1	2	1	6	112
Thalassionema nitzschioides	25	21	28	31	30	34	18	48	26
Thalassiosira anguste F-lineata	157	<1	<1	464	<1	<1	2	1	73
Thalassiosira rotula	97	<1	<1	81	<1	2	8	119	8
Total diatom biomass	7819	2080	368	6598	3020	620	5545	4290	3481
Flagellates (including Cryptophyceae)	1425	505	1302	1182	488	1508	1796	726	1701
Total phytoplankton biomass	9724	2869	1768	8082	3811	2213	7448	5359	5393

of this group. Dinoflagellates were comparatively less important, even during low productivity periods, and their abundances were 1 order of magnitude lower than those of diatoms. *Heterocapsa niei*, *Protoperidinium bipes*, *Scripssiella trochoidea* and *Dinophysis acuminata* were the main species. Numerically, microflagellates are the most abundant component of phytoplankton, comprising between 16 and 20% of total phytoplankton biomass. However, these proportions increased during low productivity seasons, when the percentage of flagellate biomass versus total phytoplankton biomass reached values of nearly 75%.

Sediment traps

Pigment concentrations in trap-collected material were consistently low when compared to pigments present in the water column, at all stations (Table 1, Figs. 2 to 4). The mean values of chl *a* recovered in traps accounted for only 4% of the chl *a* in the water column. This percentage increased to 7% when the 'total' chl *a* estimated from chl *a* equivalents was considered. The contribution of phytoplankton material to the sinking matter estimated by the chlorophyll equivalents was higher during high productivity periods at Stns O and M. At Stn I, however, values were similar for all periods. Fluxes of carbon and nitrogen were not found to be related to production or biomass of the water column, and, in general, slightly higher sedimentation rates were observed during low productivity periods, even though ANOVA did not show any significant differences among productivity periods.

The phytoplankton-derived carbon (living + dead) constituted a considerable fraction of the sinking carbon, especially at times of high chlorophyll concentration in the water column (Table 1). On average, 40% of the carbon flux measured in all periods for all stations could be linked to phytoplankton remains. Higher contributions were observed at Stn O during high productivity periods, with percentages of nearly 70% of the C-derived phytoplankton, as compared to total C recovered in the traps. The lowest contribution was observed at Stn M at times when productivity was low, with values of roughly 20%. Living phytoplankton carbon represented ca. 14% of total carbon flux, with maximum values of around 25% at Stns O and M during high productivity, and 5% during low productivity periods. In contrast, Stn I showed similar values for all periods, ranging from 15 to 20% of total carbon flux to sediment. However, as in the case of production periods ANOVA did not show any significant differences among stations.

The C:N ratio was usually between 7 and 8, with an average value of 7.6, close to the Redfield ratio, and similar to the value reported for phytoplankton in the Vigo Ría (C:N of 7.4, Rios & Fraga 1987), indicating that this material was mainly comprised of fresh planktonic material that had recently sedimented (Table 1). The phaeo:chl *a* ratio was low, around 1.6, during all the periods of study, confirming that the phytoplankton material collected in the traps was only partially degraded.

Flagellates were consistently the dominant group by numbers in the traps. For the rest of phytoplankters, diatoms were, by far, the dominant group, as in the water column. Some phytoplankton species appeared in the traps with a higher frequency than expected based on their abundances in the water column. As an example, several species of *Chaetoceros* were well represented in the water, with percentages of over 50% of total diatoms + dinoflagellates. However, *Chaetoceros* species accounted for only 2% of total phytoplankton in the traps. *Pseudonitzschia* spp. represented 13% in water column, but only 2% in traps. On the other hand, *Leptocylindrus danicus*, which represented over 10% of phytoplankton abundance in the water, was not found in the trap-collected material. This would suggest an extremely low sedimentation rate or a remineralization during the sedimentation processes, causing a dissolution of the weak silica wall of this species. The opposite occurred with *Thalassionema nitzschioides* and *Guinardia delicatula*, which were found in greater abundance in the sediment collected material. A stronger silification of these species, especially *Thalassionema* (Bao et al. 1997), would explain the predominance in traps versus water.

Cell volumes were used as a measurement independent of chlorophyll to estimate the importance of phytoplankton carbon settled to the bottom (Table 3). The mean value of C-chl *a* reaching the bottom over the period of study was 144 mg m^{-2} d^{-1} while C-biovol was 87 mg m^{-2} d^{-1} This mismatch may be explained by the presence of diatoms in faecal pellets in the traps. The abundance of faecal pellets in the traps was not estimated, but microscopic examination showed that copepod pellets were especially plentiful in March and May, coinciding with the maximum abundance of copepods in the water column (Bode et al. 1998). Great amounts of unidentified diatom frustula were observed in the pellets, but the precise counting of this material was not possible. Therefore, total phytoplankton estimated from cell volumes in traps is probably underestimated. This would explain the mismatch observed between the percentage of sedimented carbon estimated from chl *a* (14%) and the value calculated from phytoplankton biovolumes (9%), with respect to total sedimented carbon.

DISCUSSION

Sedimentation rates: spatial and temporal variations

The rates of sedimented organic matter in the Pontevedra Ría ranged from 530 to 1780 mg C m^{-2} d^{-1}. These values are high when compared to other studies carried out in different areas of the world's oceans (Table 4).

Primary production of the water column measured during this study ranged between 865 and 2200 mg C m^{-2} d^{-1} (Table 1). The export of POC from the photic layer represented ca. 75% of the primary production (range 45 to 107%). These values are higher than those reported by Falkowski et al. (1988; 25 to 50%), Davies & Payne (1984) and Fernández et al. (1995; 24 to 37%) or Knauer et al. (1984; 29%), and are well beyond the overall range (25 to 30%) postulated by Berger et al. (1989) for coastal regions on an annual scale. However, the values found in Pontevedra (Table 4) are in agreement with those reported by Bode et al. (1998) for the adjacent A Coruña shelf for low and moderate productivity periods (68 to 120%), even though their data are lower than ours for higher productivity periods by 4 to 9%.

Phytoplankton-derived carbon represented, on average, 40% of carbon recovered in the traps, and ranged from 18 to 66%. This value is higher than those

Table 3. Sediment trap mean daily flux of biomass (mg C m^{-2} d^{-1}, calculated from cell biovolume), for the main phytoplankton species and groups. O: outer station, M: middle station, I: inner station

Phytoplankton group	Station O Productivity period			Station M Productivity period			Station I Productivity period		
	High	Moderate	Low	High	Moderate	Low	High	Moderate	Low
Dinoflagellates									
Cachonina niei	<1	<1	<1	<1	<1	<1	<1	<1	<1
Dinoflagellate spp.	2	3	4	6	3	3	3	6	6
Dinophysis acuminata	<1	<1	<1	<1	<1	<1	<1	<1	3
Protoperidinium bipes	2	<1	<1	1	<1	<1	<1	<1	<1
Scrippsiella trochoidea	<1	<1	<1	<1	<1	<1	<1	<1	<1
Total dinoflagellate biomass	8	6	7	14	14	7	5	18	39
Diatomaceae									
Asterionellopsis glacialis	<1	<1	<1	1	<1	<1	<1	<1	3
Chaetoceros auxospores	63	49	2	52	59	<1	24	117	49
Chaetoceros curvisetus	<1	<1	<1	<1	<1	<1	<1	<1	<1
Chaetoceros debilis	<1	<1	<1	<1	<1	<1	<1	<1	<1
Chaetoceros decipiens	<1	<1	<1	<1	<1	<1	<1	<1	<1
Chaetoceros didymus	<1	<1	<1	<1	<1	<1	<1	<1	2
Chaetoceros gracilis	<1	<1	<1	<1	<1	<1	<1	<1	<1
Chaetoceros lorenzianus	<1	<1	<1	<1	<1	<1	<1	<1	<1
Chaetoceros socialis	<1	<1	<1	1	<1	<1	<1	<1	2
Chaetoceros spp.	<1	<1	<1	<1	<1	<1	<1	<1	1
Dactyliosolen fragilissimus	<1	<1	<1	<1	<1	<1	<1	<1	1
Detonula pumila	2	2	<1	2	3	<1	1	4	<1
Eucampia zodiacus	<1	<1	<1	<1	<1	<1	<1	<1	1
Guinardia delicatula	8	1	<1	7	<1	<1	<1	<1	72
Guinardia striata	2	<1	<1	3	<1	<1	1	<1	1
Leptocylindrus danicus	<1	<1	<1	<1	<1	<1	<1	<1	<1
Leptocylindrus minimus	<1	<1	<1	<1	<1	<1	<1	<1	<1
Nitzschia longissima	3	<1	<1	2	<1	<1	<1	1	2
Paralia sulcata	<1	<1	<1	<1	<1	<1	<1	<1	<1
Pseudonoitschia spp.	<1	<1	<1	1	1	<1	1	1	2
Rhizosolenia imbricata	<1	<1	<1	<1	<1	<1	<1	<1	<1
Rhizosolenia setigera	2	<1	<1	2	1	<1	<1	<1	7
Skeletonema costatum	1	<1	<1	1	<1	<1	<1	<1	<1
Thalassionema nitzschioides	2	1	1	1	2	2	1	3	4
Thalassiosira anguste F-lineata	<1	<1	<1	<1	<1	<1	<1	<1	<1
Thalassiosira rotula	2	<1	1	1	<1	1	1	2	<1
Total diatom biomass	96	56	9	81	70	6	36	136	167
Flagellate (including Cryptophyceae)	10	7	13	9	8	17	16	14	23
Total phytoplankton biomass (mg C m^{-2} d^{-1})	129	70	32	106	97	34	59	185	232

Table 4. Comparison of sedimentation rates of organic carbon in rias and other oceanic regions

Area	Sedimentation (mg C m^{-2} d^{-1})	Source
Ría Pontevedra, NW Iberian Peninsula	530–1780	Present study
Ría de Arosa, NW Iberian Peninsula	200–2400	Tenore et al. (1982)
A Coruña shelf, NW Iberian Peninsula	323–1203	Bode et al. (1998)
Cantabrian Sea	173–236	Fernández et al. (1995)
Kattegat	up to 700	Olesen & Lundsgaard (1995)
North Atlantic	305	Bender et al. (1992)
Northeast Pacific	432	Knauer et al. (1979)
North Pacific, Vertex stations	212–333	Knauer et al. (1984)
Antarctic Peninsula, Bransfield Strait	97–1404	Bodungen et al. (1986)
Ría Vigo	540–760[a]	Prego (1993)
Antarctic Peninsula, Gerlache Strait	115–800	Anadón et al. (2002)

[a] Calculated from carbon budget

reported by Bode et al. (1998; 30%) on the shelf off A Coruña and lower than values measured in the Cantabrian Sea by Fernández et al. (1995; 50 to 70%). In those studies, the fraction of living phytoplankton was lower than 10%. However, in the case of the Pontevedra Ría, it was around 14%, and during periods of high productivity, living phytoplankton accounted for over 25% of total exported carbon to sediments.

Even though a slight gradient in the sedimentation of particulate carbon was found, with increasing values towards the inner part of the ria (Table 1), ANOVA tests did not show any significant differences in terms of the stations. The inner area exhibited a relatively higher sedimentation rate, probably related to riverine influence, which is expected to be higher in the innermost ria. In general, the ria does not show any important spatial variation, and the flux of particulate material to the bottom is similar in the whole area.

As for the case of spatial variations, ANOVA tests did not reveal significant differences among the productivity periods studied. Lower sedimentation rates of particulate carbon were observed in seasons of moderate productivity (Table 1). Increasing values were measured in periods of lower productivity, except at the outer station, but, in general, all sedimentation rates were quite constant during all periods. The reason for this balanced sedimentation in all the productivity periods may be partially related to hydrography.

Hydrodynamic conditions favoring high productivity in the water column (as the upwelling) also enhanced advection and consequent transport of particulate material away from the ria. On the contrary, low productivity periods (mainly stratification) were associated with reduced water dynamics, which favor the flux of material to the bottom.

Composition of sinking material

Most of the material collected in the traps was essentially pelagic in origin. Microscopic examination revealed that the abundance of recognizable benthic diatoms in the traps was very low, compared to water column samples. Fresh and degraded phytoplankton and copepod faecal pellets made up most of the material observed. The C:N molar ratio (Table 1) seen in the material collected by traps was similar to the Redfield ratio, which also suggested a pelagic origin. This ratio was lower when compared to values observed in the material collected by traps in the Cantabrian Sea (C:N ratio ~11; Fernández et al. 1995) and the shelf off A Coruña (C:N ratio 7.4 to 8.9; Bode et al. 1998). However, those traps were moored at deeper levels (from 10 to 20 m) than in the Pontevedra Ría and the particulate matter had more time to be remineralized. On the other hand, the more oligotrophic open seas, as compared to rias, showed a higher rate of remineralization. Also, the higher abundance of diatoms in the rias favors a faster sedimentation and the material has less chance to be remineralized.

Higher C:N values have also been reported by Cabanas et al. (1980) and Tenore et al. (1982) in material collected under mussel rafts (C:N ratio ranging from 8 to 15). According to Olesen & Lundsgaard (1995), allochthonous material usually has a C:N ratio greater than 9 (Lancelot & Billen 1985). Additional evidence was found concerning the pelagic origin of the material collected in the Pontevedra Ría. The phaeo:chl *a* ratio in the sediment trap material was low (1.6), but higher than the value recorded in the water column (0.3). This value is lower than what was found by Fernández et al. (1995; 3.9) and Bode et al. 1998; 4.4) for trap collected material in nearby coastal areas. This is probably related to mooring the traps in shallower waters (20 to 40 m) and a relatively homogeneous ria sedimentation pattern. Results from the 3 trap stations (Table 1) did not show any major spatial differences.

Some resuspension of sedimented material should be expected during upwelling periods when the deep waters flowing on the bottom from the shelf rise up near the coast. Temperature profiles (Prego et al. 2001) and associated chl *a* in the water manifested the presence of upwelling events on 23 June. These samples showed high values of C in the traps in the 3 stations, but this is related to the increasing phytoplankton biomass in the water column and not to resuspension, as suggested by the low C:N ratio. On the other hand, the values of litogenic silica in the water column were very low during all periods of study (R. Prego unpubl. data), indicating again that resuspension does not have an important contribution to collected material in the traps. The upward velocities of upwelling in the near Ría de Vigo (Prego & Fraga 1992) confirm this assumption, since they ranged between 0.0003 and 0.0078, about 3 orders of magnitude lower than tidal currents. The percentage of chl *a* collected in the traps, compared to that of water column, during the June upwelling was very low, between 3 and 4% for Stns O and M, and these values were among the lowest recorded during the period of study. This may be a consequence of horizontal advection as suggested by Bode et al. (1998) for the near A Coruña shelf. A special case is that of Stn I, where the chl *a* in the traps accounted for 22% of the chl *a* in the water column. The upwelling in this station caused a subsurface chlorophyll maximum at 15 to 20 m, with values of ca. 10 mg chl *a* m^{-3} just 5 m above the trap mooring. The rest of chlorophyll in the water column was very low, probably due to strong surface advection favored by the river proximity. When integrated by squared meter, because of the lower depth at Stn I, it resulted in a lower integrated chl *a* as compared to other stations. However, the subsurface maximum sedimented very fast, as the amount of sedimented chl *a* recovered in the traps was similar to that of other stations, as were the values of C:N and phaeo:chl *a* ratios.

Relationship between the phytoplankton structure in seawater and sedimentation

In general, our results suggest an uncoupling between production and biomass in the water column and sinking of particulate organic material. The percentage of chl *a* equiv sinking to the sediment versus chl *a* equiv in the water column is ca. 5% during the most productive periods, while during lower productivity periods this value may increase to 12%. The short time-period of deployment used in this study may account for this uncoupling. Longer periods of time, on a monthly or annual scale, would probably result in a better coupling (Berger et al. 1989, Asper et al. 1992). As pointed out by Bode et al. (1998), the traps deployed for short periods (<3 d) reflect past productive events and the activity of phytoplankton during the time of deployment may be different. The initial stages of blooms when cells and particles have less of a chance to sink will result in lower sedimentation rates as compared to low productivity stages or final bloom development, when production is low and sedimentation high. Our results appear to confirm this assumption, since higher rates were recorded during low productivity periods in the water column. In addition, the presence of some species, such as *Nitzschia longissima*, *Guinardia delicatula* or *Thalassionema nitzschioides*, which were clearly more prevalent in the traps than in the water column, may be an indication of previous blooms dominated by these species. Also, the decreasing estuarine circulation during low productivity periods enhances particle settling. Special cases are the spores of *Chaetoceros*. In the water column, spores accounted for less than 5% of total phytoplankton abundance (excluding microflagellates). However, in the trap-collected material, the spores are more ubiquitous, accounting for 65% of the total phytoplankton abundance collected in traps. The percentage of auxospores observed in the traps represented ca. 30% of auxospores present in the water, on average, for all periods and stations. Unlike the auxospores, the phytoplankton collected in traps accounted for only 1.5% of the amount present in the water column, indicating that sporulation processes occur, particularly in the traps, as a survival mechanism to adapt to adverse conditions (Smetacek 1985).

Phytoplankton cells of different groups accumulate at different rates in the traps, as can be seen in Table 5 where the ratio of their dominance in the trap/water column is shown. Diatoms displayed the same ratio value (ca. 1) in all stations. However the ratios for microflagellates (0.6) and dinoflagellates (3.4) offer very interesting and relevant information about the differential accumulation for both groups. First, the vertical flux of phytoplankton species to bottom does not involve only diatoms, even though they form the bulk of phytoplankton material settling to traps. Second, microflagellates and dinoflagellates are well represented in trap-collected matter, but in different proportions when compared to water column communities, indicating that the mechanisms of sedimentation are different for both groups. The contribution of microflagellate biomass to phytoplankton sedimented to sea floor is higher than expected, because they are not expected to sediment at all or sediment at extremely low rates due to their small size and motility. We found that microflagellate biomass in the traps accounted, on average, for 19% of total phytoplankton biomass, a high value compared to their dominance in water column communities, which was ca. 30%. On the other hand, there was a high relative contribution of dinoflagellate biomass to trap material. The contribution of this group in the water column was lower (5% of total biomass) than that of microflagellates, but the contribution of both groups to trap-collected matter (ca. 15%) was similar.

All the information we have obtained emphasizes that sedimentation cannot be seen as a passive process of inactive material. Particles, while sinking, form aggregates (Smetacek 1985, Bode et al. 1998). This also could be observed by microscopical examination

Table 5. Ratio of sediment trap:water column biomass percentages for different phytoplankton groups. O: outer station, M: middle station, I: inner station. H: high , M: moderate, L: low productivity periods

	Station O			Station M			Station I		
	H	M	L	H	M	L	H	M	L
Dinoflagellates	1.26	0.87	3.95	3.56	1.82	5.42	6.01	3.65	4.30
Diatoms	0.93	1.10	1.35	0.94	0.91	0.63	0.82	0.92	1.12
Microflagellates	0.53	0.57	0.55	0.58	0.64	0.73	1.12	0.56	0.31

of trapped material in Pontevedra Ría, where these aggregates consisted mainly of diatoms and different kinds of pelagic matter that entangle or are colonized by microflagellates. As material sinks, biological processes occur. Bode et al. (1998) found high numbers of bacteria in the water inside the traps in the near shelf of A Coruña, suggesting an important bacterial activity. The decomposition of the aggregates releases nutrients that are used by flagellates. This process of entangling or direct colonization can explain the high presence of microflagellates in the sedimented material.

The relative high contribution of dinoflagellates could also be the result of a similar mechanism, but other factors may be involved. As aggregates sink, bacterial activity also releases high amounts of dissolved organic matter (DOM). In the nearby Ría of Ferrol, Varela et al. (in press) found maximum bacterial abundance and dissolved organic carbon (DOC) release in the depth of subsurface chlorophyll maxima where the aggregates have more chance to be formed. On the other hand, attached bacteria are more active and showed, especially under warmer conditions, higher cellular volume (Iriberri et al. 1987). All this suggests a release of large amounts of DOC around the aggregates. Most of dinoflagellates are known to be myxotrophics and can utilize DOM as a source of nutrients. This ability would imply the existence of active searching of aggregates. Due their larger size, as compared to microflagellates, the colonization of aggregates by dinoflagellates would be faster, and could explain the higher proportion of this group as compared to flagellates in traps (Table 5). Vertical migration of dinoflagellates through the water column towards the aphotic zone during the night to assimilate nutrients, and later upward movement during daytime to photosynthesize, is well documented (Cullen 1985, Vilariño et al. 1995, Figueroa et al. 1998). However, many dinoflagellates are myxotrophs and they would remain close to aggregates at all times, using the DOC released by bacterial activity. Thus, its diel migration to photosynthesize is not strictly necessary, depending on the DOC available in the aggregates more than other factors, such as the spectral light ratios as suggested by Figueroa et al. (1995) in Vigo Ría.

With respect to diatoms (Table 3), *Chaetoceros* auxospores are, by far, the main contributors to phytoplankton trapped material. The important relative contribution of the auxospores in the traps as compared to the water column indicates that most vegetative cells of *Chaetoceros* develop resting spores during sedimentation. This suggestion is confirmed by studies on the distribution of planktonic diatoms in surface sediments along the rias and Galician shelf. (Bao et al. 1997).

As mentioned above, we found abundant faecal pellets in traps. According to Csanady (1986), an increase of 1 order of magnitude in the diameter of a particle would increase the sinking speed by ca. 2 orders of magnitude. Copepod pellets are one of the main vehicles of particle aggregation and transfer from the water column to the sea bottom. In the Pontevedra Ría, the numerous diatoms observed to be constituents of faecal pellets confirm this mechanism used to export pelagic matter to the sediment. These diatoms, which are formed into pellets and cannot be counted accurately, might be able to explain the differences observed between C:chl *a* (144 mg C m^{-2} d^{-1}) and C:biovolume (87 mg C m^{-2} d^{-1}) ratios. Based on the equations of Csanady (1986), we can estimate that a faecal pellet measuring 200 µm in diameter would attain an average speed of ca. 100 m d^{-1}, while a particle 20 µm in diameter would sink only ca. 1 m d^{-1}. This rapid sedimentation of the pellets, would lead to their being abundant in traps, implying that most of the large pellets observed under the microscope were produced at the time the traps were deployed.

Hydrographical effects on sedimentation flux

The uncoupling between the water column phytoplankton biomass and biomass recovered in the traps is caused by various factors, some of the most important of which are the differential sedimentation rates for the different phytoplankton species, and hydrography. Estuarine circulation tends to export upper mixed layer pelagic material offshore. There is a significant relationship between chl *a* in the water and chl *a* in the trap (Fig. 5a). However the chl *a* in the water column explained only 30% of variance in chl *a* collected in traps. The hydrography of the Pontevedra Ría is complex (Prego et al. 2000, 2001, Dale & Prego 2002, Ruiz-Villareal et al. 2002) with different variables acting on different spatial and temporal scales. To simplify the system, the flux of water advected out of the ria (including upwelling and river flux) was chosen to summarize the influence of hydrography on the biological and sedimentary processes. The relationship between flux and chl *a* in the trap (Fig. 5b) was significant, and accounted for ca. 45% of the variance. However, the flux also affects the chl *a* in the water ($r^2 = 0.27$, Fig. 6a). In the latter case it is possible to take into account the variance that was not explained by the model chl *a* water/flux (residuals) and construct a new multiple regression model. This new model has a certain predictable value:

$$\text{chl } a \text{ trap} = 1.1 - (1.02 \times \log \text{water flux}) - (0.51 \times \log \text{residuals}), \ (r^2 = 0.54;\ p < 0.0001),$$

which explains around 55% of the variance. In this model, 2 factors affecting the export of chlorophyll to

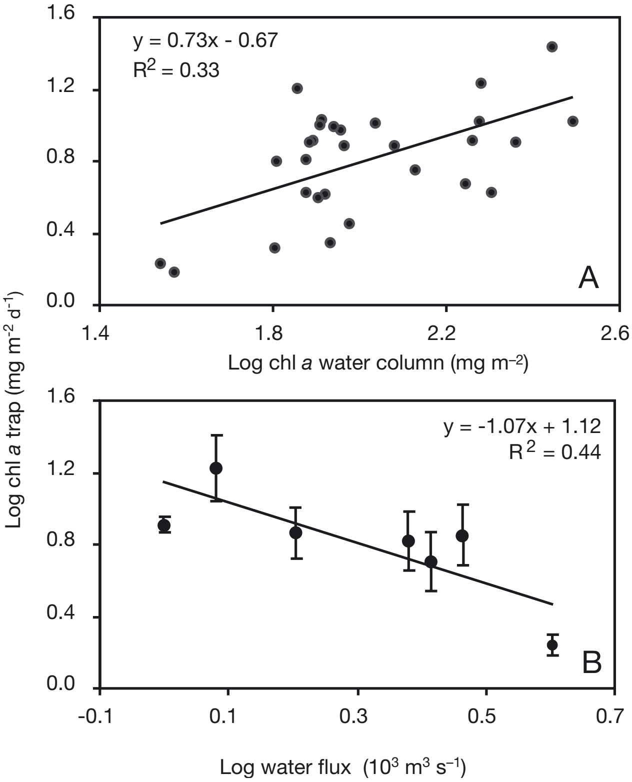

Fig. 5. (A) Log-log plot of water column vs sediment trap chlorophyll. (B) Log-log plot of water flux vs trap chlorophyll. Both relationships are significant ($p < 0.01$). For clarity, mean ± SDs are plotted. However, line fitting was made considering all original data

the sediment are considered. The first is the water flux itself, having a more immediate effect on the sedimentation process as higher fluxes favor advection and consequent lower sedimentation rates. The second factor, the residuals, comprises all variables, apart from the flux, influencing chlorophyll development in the water column, and then the amount of material able to sediment. The second factor acts with some delay since chlorophyll is a conservative variable, with inertia to change, reflecting, to some extent, the history of the ecosystem, and is the result not only of present, but also of past, hydrographic events.

There appeared to be a water flux threshold of ca. 1.4×10^{-3} m^3 s^{-1}. Up to this value, biological processes were enhanced (Figs. 5B & 6), as moderate water fluxes favor water column mixing and related nutrient availability. However, higher fluxes cause a significant decrease in the value of the variables studied by enhancement of advection processes. In any case, the flux would seem to have less of an effect on the variation of chl *a* in the water column as compared to chl *a* exported to the bottom. The slopes of the regression lines (Figs. 5B & 6A) indicate that the decrease in chl *a* in the water was half as much as the chl *a* in the trap as flux increases. This was probably related to the composition of the phytoplankton community. Higher fluxes favor the development of microflagellate populations. The contribution of microflagellates to the total phytoplankton biomass (mg C m^{-2}) in the water column was ca. 40 % during periods of higher flux, dropping down to 20 % when the flux was low. The highest contribution, 74 %, was observed on 13 April 1998, when the maximum flux was measured (4×10^3 m^{-3} s^{-1}). This relative increase in microflagellates in the water column during periods of high flux would also account for the lower sedimentation of the phytoplankton in these periods, since microflagellates have less of a chance to settle to the bottom.

One exception to the uncoupling between pelagic phytoplankton biomass and sinking of to traps was found on May 12 at Stns O and M. This was related to special hydrographic conditions on that date. Prior to sampling, conditions were favorable to upwelling, resulting in increasing phytoplankton biomass. However, this situation changed, and on May 12 downwelling conditions existed in the ria, resulting in a retention of water (Gómez-Gesteira et al. in press), and consequent accumulation of pelagic material, favoring the sinking of particles to sediment (Figs. 2 to 4). This downwelling situation coincides with lower fluxes of water measured during time of study (Dale & Prego

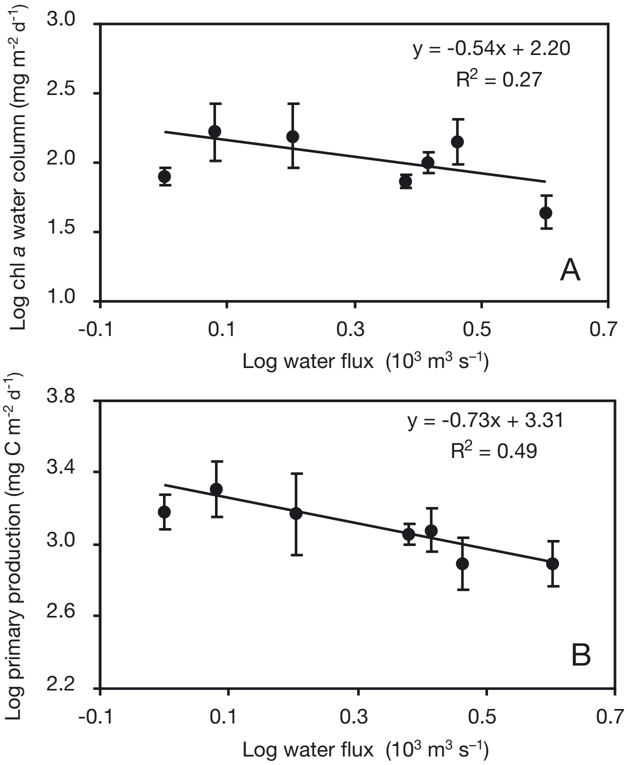

Fig. 6. (A) Log-log plot of water flux vs chlorophyll in water column, and (B) primary production. In both cases, the relationship was significant ($p < 0.01$). Line fitting as in Fig. 5B

2002). The balance between advection (upwelling and river discharge) and retention processes (downwelling) is a key mechanism to control the coupling between pelagic biomass and vertical flux to bottom.

CONCLUSIONS

This is the first study carried out in a Galician ria relating the composition and biomass of phytoplankton to particulate matter deposition to the sediment. This study, even though it was carried out for a period of 5 mo, presents adequate spatial and temporal coverage to describe sedimentation processes related to the main oceanographic periods described in the area.

The Pontevedra Ría is characterized by the export of large quantities of carbon, nitrogen and biogenic materials, ca. 1 g C m^{-2} d^{-1}. The phytoplankton-derived carbon accounted for 40% of the total carbon exported to the sediments, and the contribution of living phytoplankton was ca. 14% of the exported carbon. Only 4% of intact chl *a* stock in the water column sank daily to sediment. This contribution increased to 7% when the total chl *a* estimated from chlorophyll equivalents was considered. Most of the particles collected in traps appeared to be of pelagic origin, mainly because of low C:N ratios, a dominance of phytoplankton over phytobenthic species, and the large amount of faecal pellets. Moreover, the low phaeo:chl *a* ratio indicates that the degradation processes in the sinking material are not important as a consequence of rapid sedimentation.

The measured contribution of phytoplankton to the carbon exported to sediments is an intermediate value, as compared to those reported for near-shelf areas. A clear uncoupling between water column production and export to sediment clearly exists, with higher values of sedimentation during the lower production periods in the water column. The percentage of phytoplankton biomass exported to the sea bottom was lower during high production periods.

Microflagellates and dinoflagellates accounted for a high proportion of total phytoplankton biomass collected in the traps. This high contribution can only be explained by the formation of aggregates that entangle, or are actively colonized by, organisms.

Even though a slight decrease in sedimented C was observed from the inner to the outer ria, no significant differences were found among stations and periods, and the sediment processes had the same intensity throughout the whole ria during the period of study.

Hydrographic conditions, especially flux of water and balance between advection and retention processes, have been identified as key mechanisms for the coupling between pelagic material availability and settling of this material to traps.

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