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The seasonal cycle in sinking particle fluxes off Vancouver Island, British Columbia

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Abstract

We have made year-long observations of sinking particle fluxes with sequential sediment traps moored at a depth of 200 m at three sites proceeding offshore from Vancouver Island, Canada in water depths of 500-2500 m. Total particle flux and biogenic silica decreased offshore as expected in an eastern boundary current regime. No obvious gradient was observed in POC, and CaCO₃ was proportionally greater offshore. Even there POC dominated over particulate inorganic carbon (as $CaCO_3$) indicating a net removal of CO_2 from surface water by biological activity. Common to all three sites, we observed an annual cycle in total particle flux, with highest fluxes during spring/summer, reflecting the higher primary production during these seasons. In spite of changes in total fluxes, the ratios between organic C, CaCO3 and biogenic silica of the sedimented material did not change over the annual cycle. Atomic C_{organic}/N_{total} ratios were highest in the summer and lowest in the winter, possibly reflecting an increase in the relative contribution of lithogenic particles during winter. The isotopic composition of sinking particulate nitrogen ($\delta^{15}N_{total}$) tended to be lighter during periods of higher fluxes, most likely reflecting variation in relative nutrient utilization and length of the food chain. The $\delta^{13}C_{\text{organic}}$ composition of sinking particles varied among sites, probably reflecting differences in planktonic species composition; contributions of terrestrial organic matter appear unlikely. Currents at 50 m depth were higher and more variable at the inshore site, and temperature and salinity were also more variable, consistent with the tendency for dominance of diatoms (silica shells) in more energetic environments. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Particle settling provides an important mechanism for transporting material from the upper ocean to deep water. Surface production is the most important source of particles in the open ocean, the sinking flux of organic carbon being a nonlinear increasing function of the rate of primary productivity in surface waters (Suess, 1980; Betzer et al., 1984; Berger et al., 1989). Sedimentation is much greater in areas where primary production is high, such as in upwelling areas and temperate regions subject to spring blooms (Smetacek et al., 1978; Honjo, 1996). Because continental shelf and upper slope areas have much higher nutrient fluxes to the upper layer and higher primary production rates compared with those in the open ocean, they are expected to contribute significantly to the global export of carbon and nitrogen from the sea surface. In the open ocean, sinking particles can transport organic carbon from the surface ocean to below the depth of winter mixing, thereby sequestering the carbon for periods up to the time scale for deep oceanic turnover (10^2-10^4 yr) . On continental margins, the fate of particulate matter and the associated sequestering of carbon dioxide from the atmosphere are unclear. It has been suggested that a significant fraction of the organic matter produced on continental shelves is exported laterally to the central ocean basins or to continental slope sediments (Walsh et al., 1981). For example, Pilskaln et al. (1996) found that the export of organic material below the euphotic zone relative to daily primary production in the coastal upwelling system of Monterey Bay was lower during the high productive season compared with the less productive months. This led them to suggest that offshore transport of biogenic particles was important. Similarly, McClain et al. (1990) showed that there is significant advection of phytoplankton biomass from the coastal upwelling regime of northwest Africa to the open ocean. In contrast, Mackas and Yelland (1999) estimate that cross-shore exchange of nutrients and plankton biomass off the Vancouver Island continental margin is only a small fraction (< 10%) of estimated shelf phytoplankton production. In the Mid Atlantic Bight, Biscaye et al. (1994) showed that most of the phytoplankton production was being consumed and recycled on the shelf by bacteria and other organisms, and only a small proportion (< 5%) was transported offshore.

Due to the biological control of particle sedimentation, sediment trap studies in several regions show significant seasonality in particle fluxes, with higher values during the spring/summer season (Honjo and Manganini, 1993; Fischer et al., 1996; Wong et al., 1999). Also, the composition of settling particles usually varies during the year, particularly the content of biogenic silica and calcium carbonate, reflecting the seasonal ecological succession of plankton organisms. Time-series observations in several oceanic regions (Honjo, 1996), as well as in coastal upwelling regions (Fischer et al., 1996; Pilskaln et al., 1996), often reveal a massive flux of biogenic silica from diatom frustules in the spring, whereas CaCO₃, mostly produced by coccolithophore and foraminifera blooms, occurs in the autumn. A seasonal signal also is found in the isotopic composition (δ^{13} C and δ^{15} N) of sinking particles, reflecting changes in nutrient availability and plankton composition (Wada et al., 1987; Voss et al., 1996). Changes in biota have important impacts on the ocean carbon cycle since they can affect the atmosphere-CO₂ balance by changing the magnitude of the biological pump

and/or the carbonate system (Tsunogai and Noriki, 1991; Archer and Maier-Reimer, 1994; Robertson et al., 1994). Variations in sinking particulate fluxes estimated from moored time-series sediment traps can be related to variations in surface-water condition, enabling us to detect and identify possible causes for periodically or episodically occurring sedimentation events that might not be observed in short-term studies.

The main objectives of this study were to determine the seasonal cycle in sinking particle fluxes, and to compare these cycles at three cross-shore sites over the continental shelf and slope of western Vancouver Island, as part of the Canadian JGOFS program. The continental shelf of Vancouver Island lies within the broad transition zone separating the California Current and Alaska Current eastern boundary current systems, and is highly productive at both the phytoplankton and top-predator trophic levels (Denman et al., 1981; Freeland and Denman, 1982; Robinson et al., 1993; Mackas, 1995). Oceanographic conditions in this region are dominated by seasonal variability of the regional winds and currents (Freeland et al., 1984; Thomson et al., 1989). There is a marked summer upwelling season with prevailing winds from the north that normally extends from May to September, and an equally pronounced winter downwelling season extending from November to February (Thomson and Ware, 1996). The two primary seasons are separated by the spring transition, which normally occurs in February, and by the autumn transition, beginning in mid-October. A previous sediment trap study in this region during the spring and summer (Peña et al., 1996) demonstrated the dominance of biogenic silica to the total particle fluxes. The study also revealed significant spatial variability and high-frequency fluctuations in fluxes and isotopic composition of sinking particles associated with upwelling events. In the present study, we extend these measurements to the annual cycle and investigate onshore-offshore gradients in sinking particles.

2. Methods

Sinking particles were collected by conical Oregon State University Tracer 15 sequencing sediment traps (area 0.49 m^2 , 14 sample cup capacity) moored at three sites offshore from Vancouver Island (Fig. 1) in water depths ranging from 500 to 2500 m. Our inshore site (G) was located about 120 km north of the coastal endmember of line P transect (station P4), the main focus of the JGOFS-Canada programme. The traps were positioned at 200 m depth at each site, well below the euphotic zone. Current meters were attached to each of the moorings at 50 m depth to obtain information on changes in surface layer flow. Sampling intervals varied between 8 and 19 days, permitting higher sampling resolution during periods of anticipated higher particle fluxes (e.g. spring blooms). The overall duration of the experiment was 386 days. The moorings were deployed twice, August 1994 and April 1995, and recovered in September 1995. A complete time-series of sinking particles was obtained only at site O (49°07'N, 127°45'W). At sites G (49°39'N, 127°38'W) and S (48°47'N, 127°59'W), samples were obtained for 65 and 96% of the total time period, respectively.

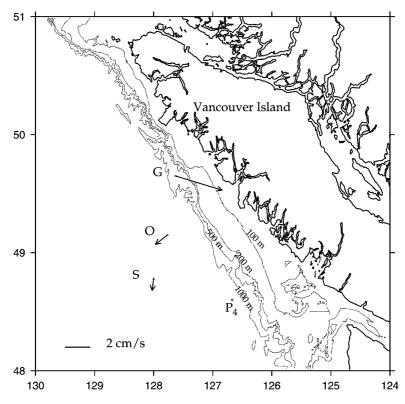


Fig. 1. Location of sediment trap mooring sites and mean current velocity at a nominal depth of 50 m. Site P4, discussed in other papers in this volume is also shown for reference.

The sediment trap cups were deployed filled with filtered seawater (Millipore GS 0.22 µm membrane filter, Whatman 934AH glass fiber prefilter) to which was added $2 \text{ g } l^{-1}$ of mercuric chloride (HgCl) as a poison and $5 \text{ g } l^{-1}$ of NaCl to create a density gradient with ambient seawater. Upon retrieval, the sample cups were stored at $4^{\circ}C$ until they were processed in the laboratory. All sediment traps collected large numbers of zooplankton, which presumably arrived in the cups by active swimming not passive sinking. To remove the zooplankton, samples were passed through a 1 mm screen and then the remaining swimmers were removed manually under a dissecting microscope. Half of the remaining sediment trap material was freezedried, weighed and ground to a fine powder for determination of total dry weight flux (TDW), particulate organic carbon (POC), particulate nitrogen (PN), biogenic silica (SiO₂), calcium carbonate (CaCO₃), and stable isotopic composition ($\delta^{13}C_{\text{organic}}$ and $\delta^{15}N_{total}$). Lithogenic particle fluxes were obtained by subtracting the weight of biogenic particles (i.e. POC, CaCO₃ and biogenic silica) from TDW. Subsamples were analyzed for Hg content to correct the data for apparent precipitation of HgCl used to preserve the samples.

Total carbon and nitrogen were determined by combustion/gas chromatography with a Carlo Erba CHN analyzer. Carbonate carbon was determined by acid evolution of CO₂ and quantification with a UIC coulometer. Organic carbon was determined by subtracting carbonate carbon from total carbon. The precision of the analyses was $\pm 3\%$ for organic C, carbonate C and nitrogen. Biogenic silica was determined following the method and equations of Mortlock and Froelich (1989), which consisted of extracting amorphous silica from a sediment sample with 2 M Na₂CO₃ and then measuring the dissolved silicon concentration in the extract by molybdate-blue spectrophotometry. The precision of the analyses was $\pm 4\%$. The isotopic composition of organic C and total N were determined on decarbonated (10% HCl) subsamples with a VG PRISM isotope ratio mass spectrometer, with a Carlo Erba CHN fitted in-line as a gas preparation device. The isotopic data are reported in the conventional δ -notation with respect to the PBD standard for C, and air nitrogen for N, with precision of ± 0.2 and $\pm 0.3\%$, respectively.

Time-series of temperature, salinity and horizontal currents were obtained with Aanderaa RCM4 current meters located at a nominal depth of 50 m. Residual (de-tided) daily-mean values were calculated by low-pass filtering the 30-min data with a squared Butterworth filter with a cutoff frequency of (1/40) h⁻¹ and then selecting the mid-day value. The current velocity was then defined in terms of its cross-shore (U) and alongshore (V) components, with U positive onshore and V positive at an angle of 40° counterclockwise from north parallel to the local coastline. Mean values of temperature, salinity and velocity for the sediment trap sampling intervals were obtained using the residual time series. To estimate ambient currents experienced by the traps, we also calculated the root-mean squared (rms) current speeds for the times of the sediment trap sampling intervals using the unfiltered data.

Profiles of temperature, salinity, macronutrients, particulate organic carbon (POC), and particulate nitrogen (PN) were obtained from CTD/Rosette casts at the times of sediment trap servicing (August 1994, April and September 1995). Water samples of 20 ml were taken for the analysis of nutrients (nitrate, phosphate and silica), frozen immediately in an alcohol bath at -40° C and stored until analysis. In the laboratory, a Technicon II autoanalyzer and standard techniques were used for their analyses (Strickland and Parsons, 1972). Samples for POC and PN were obtained by filtering seawater (500 ml–2 l) through combusted (500°C, 4 h), Micro filtration systems GF75 glass fiber filters. The filters were then stored at -20° C, dried at 60°C, and placed in a desiccator with silica gel. The decarbonated samples were then analyzed with a Carlo Erba CHN analyzer, standardized with acetanilide for both carbon and nitrogen.

3. Results

3.1. Temperature, salinity, and nutrients

Vertical profiles of temperature, salinity and nutrients (Fig. 2) in August, 1994 and September, 1995 showed a warm ($> 15^{\circ}$ C), low salinity (< 32 psu) surface mixed

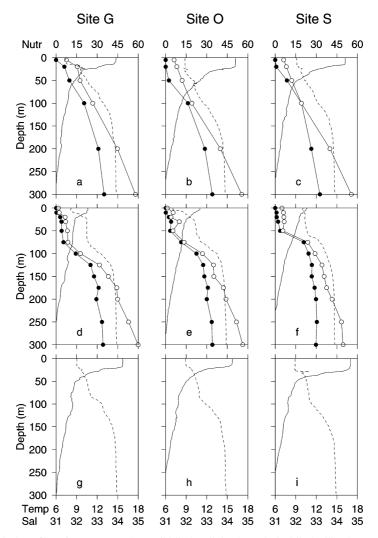


Fig. 2. Vertical profiles of temperature (°C; solid line), salinity (psu; dashed line), silica (μ M; open circles) and nitrate (μ M; filled circles) in August 1994 (a–c), April 1995 (d–f) and September 1995 (g, h and i) at sites G, O and S.

layer and a pronounced thermocline at about 20–30 m. In April, temperatures were lower ($< 11^{\circ}$ C) at all sites and seasonal thermoclines were shallower (< 10 m) and weaker. Temperatures decreased below the thermocline with a similar pattern in all profiles. At times of sampling, nitrate concentrations were low ($< 0.2 \,\mu$ M) in the first 20 m but silica was more abundant. Surface silica reached values of 6 μ M in August, but decreased to 1.5 μ M at sites G and O in April, signifying intense silica drawdown during spring. In contrast, surface silica remained high ($\sim 4.9 \,\mu$ M) at site S.

3.2. Suspended particles

Profiles of suspended POC concentration at the end of summer were similar at each site (Fig. 3) and showed a decrease in POC from 50 to 180 mg C m⁻³ in the upper 50 m to about 30 mg C m⁻³ below. The concentration of suspended PN showed a similar vertical distribution to that of POC with higher values in the upper layer, decreasing with depth. C/N atomic ratios were, on average, around 5.9–8 for suspended particulate matter (close to the Redfield ratio of 6.7) and relatively uniform with depth.

3.3. Current meter records

Low-pass filtered time-series of temperature, salinity and current velocity at 50 m depth are shown in Fig. 4. Temperatures in autumn were generally higher than those in spring/summer. The lowest temperatures (average 8.7° C and range $7.2-10.3^{\circ}$ C) and highest salinities (average 32.9 psu and range 31.9-33.9 psu) occurred at the inshore site G during the summer, presumably as a result of upwelling. Temperatures were generally higher at site O (average 9.0° C, range $7.9-10.9^{\circ}$ C) and S (average 9.2° C,

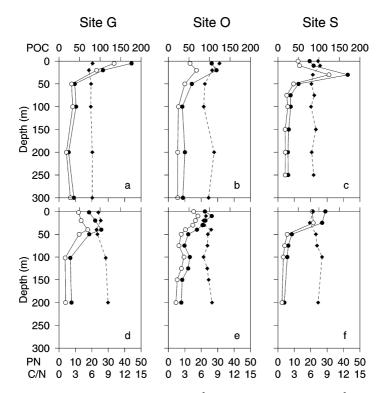


Fig. 3. Vertical profiles of suspended POC (mg C m⁻³; filled circles), PN (mg N m⁻³; open circles) and atomic C/N ratios (triangles) in August 1994 (a–c) and September 1995 (d–f) at sites G, O and S.

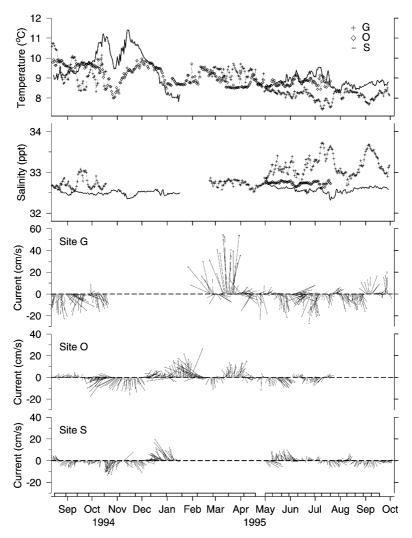


Fig. 4. Time-series of temperature, salinity and current velocities from current meters at 50 m nominal depth at sites G, O and S. Positive U(V) values represent currents directed inshore (northwest); negative values represent flow offshore (southeast). Sediment trap sampling periods are shown along the bottom axis. There are gaps in the records at all sites due to instrument malfunction. At site G, there is a 125-day record gap between 18 October and 21 February, at site S there is a 103-day gap between 17 January and 1 May, and at site O the current meter stopped working on 20 July, 72 days before recovery.

range 7.8–11.6°C) and salinities lower (average 32.7 and 32.5 psu, respectively). The mean (record-average) surface current (50 m) was strongest at site G (mean speed 15.6 cm s⁻¹) and somewhat weaker at sites O and S (mean speeds of 11.6 and 12.3 cm s⁻¹, respectively). At all sites, the along-shore current component was predominantly negative (to the southeast) during the sampling period. The strongest

southeast current components were observed during the summer/autumn period, reaching peak speeds of -30 cm s^{-1} . During winter (December-April), the currents were mainly towards the northwest, reaching peak speeds of 60 cm s^{-1} at site G. At sites G and S, the mean alongshore currents (mean $V = -2.41 \text{ cm s}^{-1}$ at site G, and -0.69 cm s^{-1} at S) were generally stronger than the mean cross-shore currents (mean $U = 1.92 \text{ cm s}^{-1}$ at site G and -0.44 cm s^{-1} at S). However, at site O, the mean cross-shore current ($U = -1.25 \text{ cm s}^{-1}$) was stronger than the mean along-shore component ($V = -0.12 \text{ cm s}^{-1}$), indicating a marked offshore flow.

3.4. Sinking fluxes of particles

The highest total particle fluxes (TDW) during the deployment period (Fig. 5) were obtained at site G located nearest to the continental shelf (mean of 427 mg m⁻² d⁻¹) and the lowest fluxes were found at site S (mean of 123 mg m⁻² d⁻¹) located farthest offshore. Particle fluxes at 200 m and mean current speeds at 50 m were not significantly correlated at any site during the sediment trap sampling intervals. There were two periods of increased fluxes during the year at each site: at the end of spring/early summer and during autumn. The autumn increase in sinking particle was less marked at site S. The main peak in total particle flux occurred in May at site G and O, but it was a month later (beginning of July) at the most offshore mooring, site S.

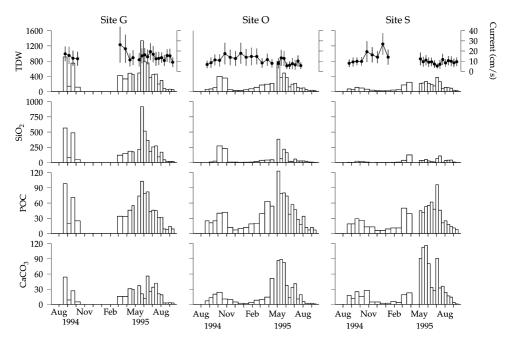


Fig. 5. Annual cycles of total particulate matter (TDW), biogenic silica (SiO₂), particulate organic carbon (POC), and calcium carbonate (CaCO₃) fluxes in mg m⁻² d⁻¹, and mean and standard deviation of current speeds for each sampling interval at sites G, O and S.

Although total mass fluxes in the traps decreased with distance from the coast, POC fluxes were similar among sites (range 6.2–123 mg m⁻² d⁻¹ over the year) and were highly correlated with TDW fluxes throughout the time-series (Table 1, Fig. 5). Biogenic silica fluxes also followed the same trend as TDW, decreasing in the offshore direction, ranging from 17 to 919 mg m⁻² d⁻¹ at site G, from 1 to 384 mg m⁻² d⁻¹ at site O, and from 1 to 125 mg m⁻² d⁻¹ at site S (Fig. 5). On the other hand, CaCO₃ fluxes tended to increase with distance from shore, ranging from 3 to 56 mg m⁻² d⁻¹ at site S (Fig. 5). Biogenic silica fluxes displayed a strong positive correlation with TDW fluxes that decreased offshore; CaCO₃ fluxes displayed a positive correlation with TDW that increased offshore (Table 1). Together these data indicate a trend of increasing dominance from biogenic silica to CaCO₃ in the offshore direction.

Fluxes of biogenic particles (i.e. POC, $CaCO_3$ and biogenic silica) were usually higher than but followed a similar seasonal trend as lithogenic particle fluxes (i.e. TDW – biogenic particles) with peaks occurring in spring/early summer and in autumn (Fig. 6). However, lithogenic fluxes decreased less during November to April

Table 1

Correlation matrix of sediment trap constituents from 200 m, and speed and temperature for the same sampling periods from current meters at 50 m

	TDW	POC	SiO_2	CaCO ₃	$\delta^{13}C$	$\delta^{15} N$
(a) Site G						
POC	0.95	1.00				
SiO ₂	0.97	0.90	1.00			
CaCO ₃	0.59	0.71	0.48	1.00		
$\delta^{13}C$	0.53	0.48	0.64	0.21	1.00	
$\delta^{15}N$	-0.51	-0.51	-0.41	-0.51	-0.04	1.00
Speed	0.15	0.08	0.08	0.01	-0.08	-0.18
Temperature	0.05	0.06	-0.03	0.03	-0.27	0.12
(b) Site O						
POC	0.91	1.00				
SiO ₂	0.93	0.72	1.00			
CaCO ₃	0.81	0.86	0.59	1.00		
$\delta^{13}C$	0.14	-0.19	0.41	-0.21	1.00	
$\delta^{15}N$	-0.63	-0.67	-0.50	-0.64	0.24	1.00
Speed	-0.14	-0.31	-0.03	-0.21	0.64	0.47
Temperature	-0.44	- 0.53	-0.30	-0.42	0.17	0.58
(c) Site S						
POC	0.94	1.00				
SiO ₂	0.78	0.60	1.00			
CaCO ₃	0.84	0.74	0.49	1.00		
δ ¹³ C	-0.69	-0.76	-0.39	-0.56	1.00	
$\delta^{15}N$	-0.77	-0.73	-0.65	-0.62	0.76	1.00
Speed	-0.49	-0.51	-0.43	-0.27	0.66	0.61
Temperature	-0.16	-0.09	-0.21	-0.19	0.44	0.45

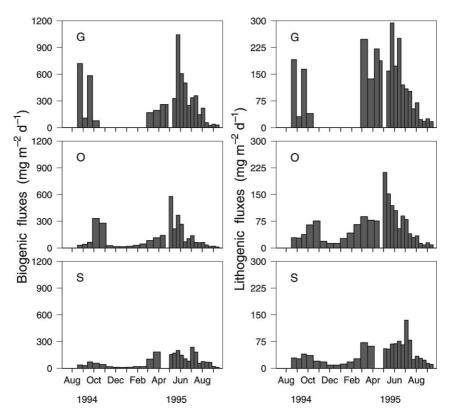


Fig. 6. Fluxes of biogenic particles (calculated as POC, $CaCO_3$ and biogenic silica) and lithogenic particles (calculated as TDW-biogenic particles) into the sediment trap in mg m⁻² d⁻¹ during the sampling period.

than biogenic fluxes. Thus, lithogenic particles were relatively more abundant during the winter period (Fig. 7). Biogenic particles contributed 41–79% (mean = 68%) of the TDW at site G, 41–78% (mean = 61%) at site O, and 43–76% (mean = 62%) at site S. Biogenic silica dominated the sinking fluxes of biogenic particles (mean = 50% of TDW) at site G, followed by POC (mean = 13%) and CaCO₃ (mean = 6%). At site O, biogenic silica (mean = 26%) and POC (mean = 25%) made similar average contributions. The biogenic silica fraction displays the widest range of values (2–69% of TDW) at this site, its contribution being largest in October and May when the peak fluxes of total particles were also high. At site S, POC was the main contributor to sinking particles (mean = 26%) and both biogenic silica and CaCO₃ contributed 18% to the TDW, on average.

In general, the fluxes of sinking particles underwent a seasonal cycle (Fig. 8) at all sites, with higher fluxes of material during the spring upwelling months and lower fluxes of biogenic particles during the winter months. At sites G and O, in addition to the spring peak there was a second peak in particle fluxes in the autumn. The relative contributions of individual biogenic components to the TDW fluxes, however, did not

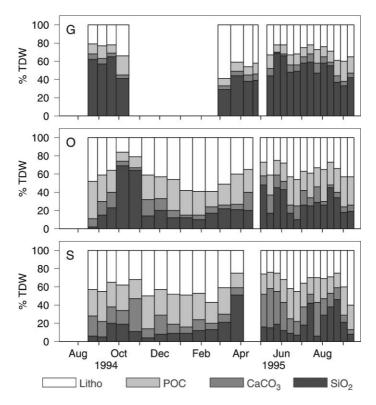


Fig. 7. Relative contribution of the major biogenic components and lithogenic material to the sediment trap samples.

change significantly with season, although there was considerable short term variability (Fig. 7).

3.5. Atomic ratios of biogenic components

Differences in atomic ratios of the particle constituents were observed among sites (Table 2). In particular, the Si/C_{organic} and Si/C_{carbonate} ratios were several times higher at the inshore site G, probably indicating an increase in the relative contribution of diatom frustules at this site. At all sites, the C_{organic}/C_{carbonate} ratios were high (range 4–66) during the sampling period indicating that POC rather than CaCO₃ was the main contributor to particulate C fluxes. Although the ratios of organic C, CaCO₃ and biogenic silica were highly variable at each site, a clear seasonal pattern was not evident. Similarly, the C/N ratios of sinking particles (Fig. 9) show a marked temporal variability coherent over all sites with minimum values of about 6 (lower than the Redfield ratio of 6.7) during the winter and more variable and higher values of about 9 during the spring/summer season.

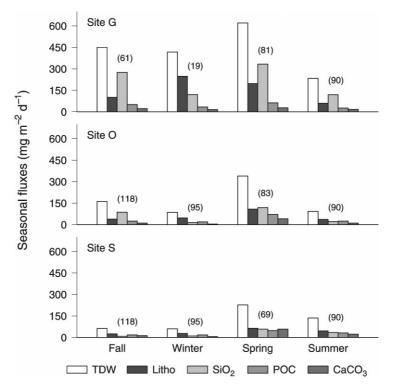


Fig. 8. Mean seasonal fluxes of biogenic and lithogenic particles at the trap sites. The number of days sampled in each season is shown in parentheses.

3.6. Isotopic composition of sinking particles

 $\delta^{15}N_{total}$ values ranged from 7 to 12% during the annual cycle. The variations in $\delta^{15}N_{total}$ were similar at all sites (Fig. 10) and were inversely related to variations in the flux of organic particles (Table 1); that is, $\delta^{15}N_{total}$ values were lowest, especially at sites O and S, during the summer flux maxima and highest during the winter months. Although annual variations were similar among sites, actual $\delta^{15}N_{total}$ values of sinking particles were higher (i.e. isotopically heavier) at sites O and S (mean = 8.84 and 8.54%, respectively), than at site G (mean = 7.33%) during spring/summer.

The $\delta^{13}C_{\text{organic}}$ of sinking particles (Fig. 11) showed more high-frequency variability than $\delta^{15}N_{\text{total}}$ and a different temporal trend among sites. At site G, $\delta^{13}C_{\text{organic}}$ increased in the spring and autumn when the fluxes of POC were higher, whereas at site O, $\delta^{13}C_{\text{organic}}$ increased in autumn when the POC flux increased but decreased during the main bloom in spring. At site S, $\delta^{13}C_{\text{organic}}$ was inversely correlated with POC fluxes over the year (Table 1). In general, $\delta^{13}C_{\text{organic}}$ was higher at site G (mean = $-21.2 \pm 1.2\%$) than at sites O and S (mean = $-23.3 \pm 0.4\%$) and $-23.4 \pm 0.5\%$, respectively) during spring/summer, the reverse of the $\delta^{15}N_{\text{total}}$ data. Table 2

Seasonal changes in the atomic ratios between biogenic components. Mean values were calculated over number of days in each season. Range and standard deviation (SD) were calculated between samples

Season	$C_{\text{organic}}/C_{\text{carbonate}}$			$\rm Si/C_{organic}$			$\rm Si/C_{carbonate}$		
	G	0	S	G	0	S	G	0	S
Autumn									
Mean	26	21	15	0.88	0.48	0.08	19	12	1
S.D.	11	11	8	0.4	0.5	0.005	7	16	0.7
Range	(15-40)	(12-39)	(5–29)	(0.4–1.4)	(0.0–1.4)	(0.0-0.2)	(17-30)	(0.4–42)	(0.5–2.3)
Winter									
Mean	18	44	28	0.71	0.13	0.1	13	5	2
S.D.		17	8		0.06	0.04		2	1
Range		(22–69)	(20–41)		(0.1–0.2)	(0.1–0.2)		(3-8)	(1.3-3.9)
Spring									
Mean	23	22	10	0.98	0.28	0.27	27	5	4
S.D.	17	13	7	0.4	0.2	0.2	31	3	4
Range	(12–56)	(9–43)	(4–18)	(0.6–1.8)	(0.1–0.6)	(0.1–0.2)	(10-74)	(1-9)	(0.6–11)
Summer									
Mean	18	34	19	0.77	0.20	0.24	12	7	3
S.D.	8	20	16	0.3	0.1	0.2	4	7	2
Range	(9–34)	(10-66)	(6–55)	(0.3–1.2)	(0.1–0.3)	(0.0-0.6)	(7–23)	(1–23)	(0.3–7)
Mean	22	30	18	0.8	0.2	0.2	19	8	2

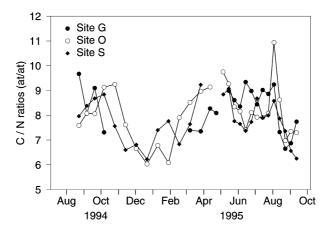


Fig. 9. Atomic ratios of particulate organic carbon (POC) and particulate nitrogen (PN).

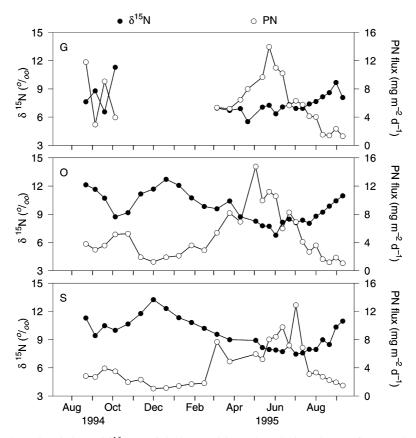


Fig. 10. Annual variations of $\delta^{15}N_{total}$ of sinking particles and particulate nitrogen fluxes at sites G, O and S.

4. Discussion

For the most part, reliable measurements of vertical particle fluxes with sediment traps have been made in deep waters. Similar measurements in the upper ocean have been less successful, mostly due to uncertainties associated with the collection efficiency of sediment traps (see review in US GOFS, 1989). For example, Baker et al. (1988) found that in the field the trapping efficiency of moored sediment traps decreases with current speeds greater than ~ 12 cm s⁻¹. In contrast, Gardner et al. (1997) recently concluded that at current speeds from 1 to 22 cm s⁻¹ vertical fluxes measured with moored, cylindrical traps should exhibit little effect from horizontal currents. Although we did not measure current speeds at the sediment trap depth (200 m), previous determinations of current speeds at 200 m at site G during the spring/summer months of 1990 were < 12 cm s⁻¹ for 73% of the time (Peña et al., 1996). In 1990, the ratio of mean current speeds at site G at depths of 200 m and

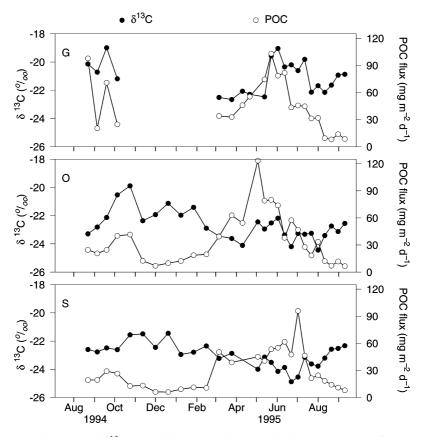


Fig. 11. Annual variations of $\delta^{13}C_{\text{organic}}$ of sinking particles and particulate organic carbon fluxes at sites G, O and S.

 ~ 35 m was 0.42, suggesting a mean current speed during the present deployment at 200 m at site G of order 6–7 cm s⁻¹. Equally important, our current measurements revealed no significant correlation between particle fluxes at 200 m depth and current speeds at 50 m depth at any site (see Fig. 5). Since the magnitude of the combined tidal and residual currents generally decreased with depth off the west coast of Vancouver Island (e.g. Thomson and Ware, 1996; Foreman and Thomson, 1997), the current observations at 50 m represent an upper bound to those at the trap depths (200 m). Thus, even though high current might influence trapping efficiency of moored sediment traps, current speeds at 200 m depth at our sites appear to have been sufficiently low for most of the deployment period that they were not a major problem in this study.

Another factor influencing trapping efficiency is the density gradients created by brine solutions. For cylindrical traps, Gardner and Zhang (1997) found a decrease in trapping efficiency by nearly 50% at low current speed (5 cm s⁻¹) when a trap is filled

with a brine solution of 5 psu similar to the one used here. Although we are not aware of studies of the effect of brine solutions on conical sediment traps, our particle collection might underestimate particle fluxes.

In the coastal upwelling region off Cape Blanc, northwest Africa, Fischer et al. (1996) observed significant interannual variability in particle fluxes and sea-surface temperature. Interannual variability in sinking particle fluxes has also been observed in the coastal upwelling system of Monterey Bay, California during El Niño conditions (Pilskaln et al., 1996). Off Vancouver Island, coastal upwelling is largely wind-driven and interannual variability in the strength of upwelling has been documented (Fang and Hsieh, 1993; Thomson and Ware, 1996). Intensified winds should lead to enrichment in surface nutrients and, as a consequence, to enhanced production and sinking fluxes of particles. During the spring/summer of 1995, the Bakun upwelling index (Bakun et al., 1974) at 48°N, 125°W suggests that coastal upwelling was lower than the 1979–1995 average (Mackas and Yelland, 1999). Also, the upwelling index of Thomson and Ware (1996) indicated that upwelling was well below the average in 1995. Thus, our particle flux estimates may be lower than the long-term annual average for the region.

4.1. Comparison among the sites

The main differences in the sinking fluxes of particles among the three trap sites were the decrease in total and biogenic silica fluxes and the increase in CaCO₃ fluxes with distance from shore. No obvious onshore-offshore gradient was found in POC fluxes. In contrast to CaCO₃ particles that are well preserved in the upper ocean (Honjo, 1996), biogenic silica dissolves (Nelson and Goering, 1977) as a function of temperature (Hurd, 1983). The difference in biogenic silica among sites is unlikely the result of increased dissolution of biogenic silica with distance from shore since temperature differences among sites were far too small to have the observed effect on biogenic silica. The observed temperature difference ($< 1^{\circ}$ C) could produce a maximum increase of only 10% of silica solubility (Hurd, 1983), not nearly enough to account for the observed differences. Thus, we infer that a change in the particleproducing species assemblages in the surface water is the most likely cause. Satellite observations of the region offshore from Vancouver Island have revealed the presence of coccolith blooms in summer (Gower, personal communication). Nutrient concentrations were similar at all sites in August and April, suggesting that differences in nutrient availability, particularly silica, were not responsible for the decrease in the fluxes of biogenic silica at the most offshore site. The higher fluxes and inferred dominance of diatoms at site G located nearest to the continental shelf are likely due to higher variability in the environment as detected by the current meters, temperature and salinity signatures associated with seasonal shelf-edge current reversals and wind-driven upwelling (Semina, 1972; Malone, 1980; Smetacek, 1985). Generally, planktonic ecosystems in environments that are dominated by highly variable physical forcing also lose a larger proportion of primary production as sinking particles than in more stable environments (Lampitt and Antia, 1997). Therefore, the resultant vertical flux to the sediments is not only a function of nutrient availability and total

primary production, but also of the type of phytoplankton and grazers present in the system (e.g. Bienfang and Ziemann, 1992).

POC fluxes ranged from 6.2 to $123 \text{ mg C m}^{-2} \text{ d}^{-1}$ in this study and were not significantly different from those obtained in other studies at mid-water (150–500 m) depths. For example, in the upwelling region of Monterey Bay, POC fluxes at 450 m depth ranged from 10 to $120 \text{ mg C m}^{-2} \text{ d}^{-1}$ and at 100 m a mean flux of 236 mg C m⁻² d⁻¹ was estimated (Pilskaln et al., 1996). Previous studies offshore Vancouver Island reported POC fluxes from 1.8 to 58 mg C m⁻² d⁻¹ at 500 m (Wu et al., 1999a) and from 3 to $152 \text{ mg C m}^{-2} \text{ d}^{-1}$ at 200 m depth during spring/summer at site G (Peña et al., 1996). In the subarctic north Pacific, the mean annual POC flux at 200 m was 22 mg C m⁻² d⁻¹ (Wong et al., 1999). At the BATS time-series site near Bermuda, particle fluxes at 150 m reached 56 mg C m⁻² d⁻¹ in February (Michaels et al., 1994). A comparison of POC fluxes at site G with primary production measurements at station P4 (Boyd and Harrison, 1999) estimates particle fluxes to be 16 and 10% of integrated primary production in winter and spring, respectively.

Although the average CaCO₃ fluxes were highest at the most offshore site, it was three times lower than the mean annual flux of CaCO₃ at 200 m at station P (Wong et al., 1999). The C_{organic}/C_{carbonate} ratio was always > 1 in our study, indicating that POC rather than CaCO₃ was the main contributor to particulate C fluxes. Phytoplankton organisms such as coccolithophores can produce CaCO₃ plates (i.e. calcification) and thus be involved in the production of both organic and inorganic particulate matter. Because the production of a mole of CaCO₃ produces a mole of CO₂, knowledge of the ratio between organic carbon and inorganic carbon flux is critical for understanding the net effectiveness of the biological pump in an area as a sink of atmospheric CO₂ (Tsunogai and Noriki, 1991). Over the continental shelf and slope off Vancouver Island, the sinking flux of POC was significantly higher than that of particulate inorganic C as CaCO₃ at all times during the year, indicating that sinking biogenic particles efficiently remove carbon dioxide from the surface waters. To determine the net exchange of CO₂ with the atmosphere would require time series of surface pCO_2 determinations.

Significant differences among the three sites in the ratios of biogenic components of sinking particles suggest differences in species assemblage of the particle-producing community. At site G, Si : $C_{organic}$ was highest among the sites reflecting the dominance of biogenic silica fluxes. Lower Si : $C_{organic}$ ratios at sites O and S and higher proportions of POC could be due to an increase of small cell-sized phytoplankton, namely flagellates and picoplankton. Phytoplankton HPLC pigment analysis on line P transect (Thibault et al., 1999) also indicated that diatoms were more abundant at the inshore (station P4, Fig. 1) than offshore stations. Similarly, the $\delta^{13}C_{organic}$ of sinking particles was on average lighter at sites O and S (-23.3 and $-23.4\%_{oo}$, respectively) than at site G ($-21.2\%_{o}$) during spring/summer possibly reflecting differences in phytoplankton composition and/or growth rates (Bidigare et al., 1997). At site G, diatoms that have heavier $\delta^{13}C_{organic}$ than nanophytoplankton (Wu et al., 1999b) likely dominate the sinking fluxes of particles. In contrast, at sites O and S, POC and CaCO₃ fluxes were more important than biogenic silica fluxes. Terrestrial input

apparently does not significantly influence the $\delta^{13}C_{\text{organic}}$ of sinking particles in our study as observed off southern Vancouver Island (Wu et al., 1999a). Since terrestrial C₃ plants have isotopically lighter $\delta^{13}C$ of about -27% (Park and Epstein, 1960) compared with heavier values of marine particulate organic matter (-20 to 24%), one would expect lighter $\delta^{13}C_{\text{organic}}$ values closer to shore if there were a significant contribution from terrestrial organic matter. However, we observed the opposite trend in this study.

We found a slightly higher average δ^{15} N of sinking particles at sites O and S (8.84 and 8.54%, respectively), than at site G (7.33%). All these values are heavier than those found in open ocean particulate organic matter but similar to the 8.94% $\delta^{15}N$ values found by Wu et al. (1999a) at a site 120 km to the south of G. They are also similar to the values reported off Peru by Libes and Deuser (1988). The δ^{15} N value of planktonic and particulate organic matter depends on the isotope composition of the source nitrogenous nutrient as well as the isotopic fractionation during nutrient assimilation (Altabet and Deuser, 1985). The global average δ^{15} N value of nitrate in the open-ocean deep water is reported to be around 6% (Montoya, 1994), and is generally lower in the open ocean and higher in coastal upwelling areas (Liu and Kaplan, 1989). We might expect isotopically heavy nitrate off Vancouver Island if upwelled nutrients to the euphotic zone originate in the California Undercurrent (Freeland and Denman, 1982), which carries ¹⁵N-enriched water affected by denitrification from the eastern tropical North Pacific. However, off southern Vancouver Island the isotopic composition of dissolved nitrate at 400 m depth is 5% (Wu et al., 1999a), indicating that such a source of heavy nitrate does not affect this area. A possible explanation for the higher $\delta^{15}N$ of sinking particles at sites O and S, where diatoms are probably less abundant, is the occurrence of a longer or more complex food chain. Nitrogen isotopes are fractionated substantially during food-chain transfer, being enriched by roughly 3.5% each trophic step (Minagawa and Wada, 1984). Thus, particulate organic matter produced by a more complex food web will have a higher δ^{15} N than that produced by a simpler food web.

4.2. Seasonal cycle

We observed seasonal variability in the fluxes of all major biogenic components (Fig. 5), with the primary flux maxima occurring during the spring upwelling months and the minimal fluxes occurring in winter. At the sites located closest to the continental shelf (sites G and O), the flux maxima were in late May to early June, with secondary flux maxima in autumn. In comparison, the maximum particle flux occurred a month later farther offshore (site S), although a peak in CaCO₃ flux was observed at the end of May. At site G, a peak in the particle flux at the end of May was also observed during the spring/summer of 1990 (Peña et al., 1996). Particle fluxes over the shelf break, about 120 km south of site G, showed a peak flux in September and October (Wu et al., 1999a), somewhat later than at site G. In the subarctic Pacific, a flux maxima is generally found in August (Wong et al., 1999). Similarly, the biomass of zooplankton, which are the producer of large rapidly sinking fecal and detrital particles, is maximum in late spring-early summer on the continental shelf off

Vancouver Island and in middle to late summer over the continental shelf break and slope (Mackas, 1995). Along line P, POC fluxes were well correlated with pheopigment fluxes (representative of zooplankton feces) and represented 15–60% of the POC flux at station P4 (Thibault et al., 1999). Thus, the difference in the timing and magnitude of the particle flux maxima is likely due both to differences in physical oceanic conditions and to differences in the planktonic community.

In our samples, lithogenic (non-biogenic) material comprised about 35% of the sinking particulate matter over the study period, and was relatively more abundant in winter (Fig. 7). In Monterey Bay, Pilskaln et al. (1996) obtained a higher contribution of lithogenic matter (50-60% of sinking particles), which they attributed to high potential for periodic resuspension and lateral advection of fine sediments from the adjacent shelf and upper slope as well as river inflow. At our sites, the contribution of resuspension of bottom sediments to lithogenic particles was likely much less important than rainfall and river flow since the sediment traps were positioned at 300-2300 m above the sea floor. The west coast of Canada experiences high amounts of precipitation causing large fresh-water runoff that can carry lithogenic particles offshore, particularly in winter. In comparison, over 80% of the settling particles at an average site in the open Pacific Ocean consist of biogenic material (Noriki and Tsunogai, 1986) and over 90% at station P (Wong et al., 1999). Thus, in coastal regions the contribution of lithogenic particles is more important. The relative increase in clay and fine-grained rock-forming mineral particles during the winter could be responsible for the unexpected decrease in C/N ratios below Redfield values due to sedimentation of inorganic nitrogen present in these particles. Also, inputs of high amounts of relatively heavy mineral grains from riverine and aeolian particles may act as "ballast", increasing sinking rates and reducing organic matter degradation during particle transport (Ittekkot, 1993).

Despite the strong seasonal variability in the magnitude of particle fluxes and the isotopic composition of the settling particles, we did not observe a clear annual succession in inferred phytoplankton species composition. The high correlation between total particle fluxes and the fluxes of individual biogenic components during the year indicate a synchrony in fluxes. At site G, the relative contribution of biogenic silica was high all year, whereas at site O, the relative contribution of biogenic silica increased only during the autumn period of high fluxes, indicating dominance of diatoms during that event. In contrast, phytoplankton in Monterey Bay varies from diatom-dominated populations in the spring/summer upwelling months to picoplankton-dominated communities in the winter non-upwelling months (Pilskaln et al., 1996). A similar change in phytoplankton composition offshore from Vancouver Island was suggested by Wu et al. (1999a) based on the isotopic composition of sinking particles. Diatoms are considered to be the main primary producers in episodic open-ocean phytoplankton blooms (e.g. Smetacek, 1985; Goldman, 1988) and may dominate export production in the spring. If high upwelling and nutrients lead to dominance of diatoms, one would expect a negative correlation between $\delta^{13}C_{\text{organic}}$ and $\delta^{15}N_{\text{total}}$ of sinking particles, since $\delta^{13}C_{\text{organic}}$ of diatoms tends to be heavier than that of other phytoplankton (Fry and Wainright, 1991) and $\delta^{15}N_{\text{total}}$ decreases with nutrient abundance. This was not observed in the present study. At

sites G and O, no significant correlation was found between δ^{13} C and δ^{15} N, whereas at the offshore site S where silica was much less abundant, suggestive of weaker or no upwelling, the correlation was positive.

The $\delta^{15}N_{total}$ of sinking particles also shows a strong seasonal cycle at each site with a decrease in $\delta^{15}N_{total}$ values of about 5% from winter to spring/summer when upwelling events are frequent (Peña et al., 1996). In comparison, $\delta^{15}N$ of sedimenting particles decreases by $\sim 2\%$ during the summer bloom over La Perouse Bank (Wu et al., 1999a) and a decrease of 7% in the δ^{15} N was observed by Voss et al. (1996) in the northern North Atlantic from winter to spring. An inverse relationship between $\delta^{15}N$ and mass flux collected in traps observed previously (Altabet and Deuser, 1985; Voss et al., 1996) has been attributed to the effect of nitrate fractionation by phytoplankton during nutrient replete conditions (low relative nitrate utilization) and this leads to the formation of biomass with low $\delta^{15}N$. The increase in $\delta^{15}N_{total}$ in late summer and winter has been explained by surface water degradation processes, uptake of residual isotopically heavy nitrate, and heterotrophic activity (Libes and Deuser, 1988; Voss et al., 1996). The high winter $\delta^{15}N$ values also might due to a plankton community dominated by nanophytoplankton and microzooplankton during this season, and then a longer more complex food web with more recycling, leading to ¹⁵N-enrichment in the settling organic material originated by it as discussed previously.

5. Conclusions

We observed sinking particle fluxes for one year at 200 m at three sites located perpendicular to the continental margin. Our main conclusions are the following:

- (1) Total and biogenic silica fluxes decreased with distance from shore. No obvious gradient was observed in POC fluxes, whereas $CaCO_3$ fluxes were proportional greater offshore. Nonetheless, the ratios of $C_{organic}/C_{carbonate}$ were always higher than 1, indicating a net removal of CO_2 from surface water by biological activity.
- (2) Lithogenic particles contributed about 35% to the sinking flux of particles and were relatively more important in winter. The seasonal change in relative contribution of lithogenic particles could be responsible for the unexpected seasonal variation in C/N ratios (lower values in winter than summer).
- (3) The ratios of Si/C_{organic} and δ^{13} C_{organic} composition of sinking particles differ among sites, suggesting differences in species assemblage of the particle-producing community.
- (4) At all three sites, there was a seasonal cycle in particle fluxes with higher fluxes during the spring/summer, reflecting the higher primary production during these seasons. However, we did not observe a clear annual succession in sinking particle composition at any site.
- (5) The $\delta^{15}N_{total}$ of sinking particles was lower (lighter) during periods of high fluxes, most likely reflecting variations in relative nutrient utilization and length or complexity of the food chain.

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References

- Altabet, M.A., Deuser, W.G., 1985. Seasonal variations in natural abundance of ¹⁵N in particles sinking to the deep Sargasso Sea. Nature 315, 218–219.
- Archer, D., Maier-Reimer, E., 1994. Effect of deep-sea sedimentary calcite preservation on atmospheric CO₂ concentration. Nature 367, 260–263.
- Baker, E.T., Milburn, H.B., Tennant, D.A., 1988. Field assessment of sediment trap efficiency under varying flow conditions. Journal of Marine Research 46, 573–592.
- Bakun, A., McLain, D.R., Mayo, F.V., 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fishery Bulletin 72, 843–844.
- Berger, W.H., Smetacek, V.S., Wefer, G., 1989. Ocean productivity and paleoproductivity-An overview. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.) Productivity of the Ocean: Present and Past. Wiley, Chichester, pp. 1–34.
- Betzer, P.R., Showers, W.J., Laws, E.A., Winn, C.D., Di Tullio, G.R., Kroopnick, P.M., 1984. Primary productivity and particle fluxes on a transect of the equator at 153°W in the Pacific Ocean. Deep-Sea Research 31, 1–11.
- Bidigare, R.R., Fluegee, A., Freeman, K.H., Hanson, K.L., Hayes, J.M., Hollander, D., Jasper, J.P., King, L.L., Laws, E.A., Milder, J., Millero, F.J., Pancost, R., Popp, B.N., Steinberg, P.A., Wakeham, S.G., 1997. Consistent fractionation of ¹³C in nature and in the laboratory: growth-rate effects in some haptophyte algae. Global Biogeochemical Cycles 11, 279–292.
- Bienfang, P.K., Ziemann, D.A., 1992. The role of coastal high latitude ecosystem in global export production. In: Falkowski, P.G., Woodhead, A.D. (Eds.) Primary Productivity and Biogeochemical Cycles in the Sea. Plenum Press, New Yok, pp. 285–297.
- Biscaye, P.E., Flagg, C.N., Falkowski, P.G., 1994. The Shelf Edge Exchange Processes experiment, SEEP-II: an introduction to hypotheses, results and conclusions. Deep-Sea Research 41, 231–252.
- Boyd, P.W., Harrison, P.J., 1999. Phytoplankton dynamics in the NE subarctic Pacific. Deep-Sea Research II 46, 2405–2432.
- Denman, K.L., Mackas, D.L., Freeland, H.J., Austin, M.J., Hill, S.H., 1981. Persistent upwelling and mesoscale zones of high productivity off the west coast of Vancouver Island, Canada. In: Richards, F. (Ed.) Coastal upwelling. American Geophysical Union, Washington, DC, pp. 514–521.
- Fang, W., Hsieh, W.W., 1993. Summer sea surface temperature variability off Vancouver Island from satellite data. Journal of Geophysical Research 98, 14391–14400.
- Fischer, G., Donner, B., Ratmeyer, V., Davenport, R., Wefer, G., 1996. Distinct year-to-year particle flux variations off Cape Blanc during 1988–1991: relation to δ^{18} O-deduced sea-surface temperatures and trade winds. Journal of Marine Research 54, 73–98.
- Foreman, M.G.G., Thomson, R.E., 1997. Three-dimensional model simulations of tides and buoyancy currents along the west coast of Vancouver Island. Journal of Physical Oceanography 27, 1300–1325.
- Freeland, H.J., Denman, K.L., 1982. A topographically controlled upwelling center off southern Vancouver Island. Journal of Marine Research 40, 1069–1093.
- Freeland, H.J., Crawford, W.R., Thomson, R.E., 1984. Currents along the Pacific coast of Canada. Atmosphere-Ocean 22, 151-172.

- Fry, B., Wainwright, S.C., 1991. Diatom sources of ¹³C-rich carbon in marine food webs. Marine Ecology Progress Series 76, 149–157.
- Gardner, W.D., Zhang, Y., 1997. The effect of brine on the collection efficiency of cylindrical sediment trap. Journal of Marine Research 55, 1029–1048.
- Gardner, W.D., Biscaye, P.E., Richardson, M.J., 1997. A sediment trap experiment in the Vema Channel to evaluate the effect of horizontal particle fluxes on measured vertical fluxes. Journal of Marine Research 55, 995–1028.
- Goldman, J.C., 1988. Spatial and temporal discontinuities of biological processes in pelagic surface waters. In: Rothschild, B.J. (Ed.) Towards a Theory on Biological-Physical Interactions in the World Ocean. Kluwer Academic, Dordrecht, pp. 273–296.
- Honjo, S., 1996. Fluxes of particles to the interior of the open oceans. In: Ittekkot, V., Schäfer, P., Honjo, S., Depetris, P.J. (Eds.) Particle Fluxes in the Ocean. Wiley, Chichester, pp. 91–154.
- Honjo, S., Manganini, S.J., 1993. Annual biogenic particle fluxes to the interior of the North Atlantic Ocean; studied at 34°N 21°W and 48°N 21°W. Deep-Sea Research 40, 587–607.
- Hurd, D.C., 1983. Physical and chemical properties of siliceous skeletons. In: Aston, S.R. (Ed.) Silicon Geochemistry and Biogeochemistry. Academic Press, London, pp. 187–244.
- Ittekkot, V., 1993. The abiotically driven biological pump in the ocean and short-term fluctuations in atmospheric CO, contents. Global and Planetary Change 8, 17–25.
- Lampitt, R.S., Antia, A.N., 1997. Particle flux in deep seas: regional characteristics and temporal variability. Deep-Sea Research 44, 1377–1403.
- Libes, S.M., Deuser, W.G., 1988. The isotope geochemistry of particulate nitrogen in the Peru upwelling area and the Gulf of Maine. Deep-Sea Research 35, 517–533.
- Liu, K.-K., Kaplan, I.R., 1989. The eastern tropical Pacific as a source of ¹⁵N-enriched nitrate in seawater off southern California. Limnology and Oceanography 34, 820–830.
- Mackas, D.L., 1995. Interannual variability of the zooplankton community off southern Vancouver Island. In: Beamish, R.J. (Ed.) In Climate Change and Northern Fish Populations, Canadian Special Publication of Fisheries and Aquatic Science, Ottawa 121, 603–615.
- Mackas, D.L., Yelland, D.R., 1999. Horizontal flux of nutrients and plankton across and along the British Columbia continental margin. Deep-Sea Research II 46, 2941–2967.
- Malone, T.C., 1980. Algal size. In: Morris, I. (Ed.) The Physiological Ecology of Phytoplankton. Blackwell, Oxford, pp. 433–463.
- McClain, C.R., Esaias, W.E., Feldman, G.C., Elrod, J., Endres, D., 1990. Physical and biological processes in the North Atlantic during the first GARP global experiment. Journal of Geophysical Research 95, 18027–18048.
- Michaels, A.F., Knap, A.H., Dow, R.L., Gundersen, K., Johnson, R.J., Sorensen, J., Close, A., Knauer, G.A., Lohrenz, S.E., Asper, V.A., Tuel, M., Bidigare, R., 1994. Seasonal patterns of ocean biogeochemistry at the US JGOFS Bermuda Atlantic Time-series Study site. Deep-Sea Research 41, 1013–1038.
- Minagawa, M., Wada, E., 1984. Stepwise enrichment of ¹⁵N along food chains: further evidence and the relationship between δ¹⁵N and animal age. Geochimica et Cosmochimica Acta 48, 1135–1140.
- Montoya, J.P., 1994. Nitrogen isotope fractionation in the modern ocean: implications for the sedimentary record. In: Zahn, R., Kaminski, M., Labeyrie, L.D., Pedersen, T.F. (Eds.) Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change. Springer, Berlin, pp. 259–279.
- Mortlock, R.A., Froelich, P.N., 1989. A simple method for the rapid determination of biogenic opal in pelagic marine sediments. Deep-Sea Research 36, 1415–1426.
- Nelson, D.M., Goering, J.J., 1977. Near surface dissolution in the upwelling region off northwest Africa. Deep-Sea Research 24, 31–36.
- Noriki, S., Tsunogai, S., 1986. Particulate fluxes and major components of settling particles from sediment trap experiments in the Pacific Ocean. Deep-Sea Research 33, 903–912.
- Park, R., Epstein, S., 1960. Carbon isotope fractionation during photosynthesis. Geochimica et Cosmochimica Acta 21, 110-126.
- Peña, M.A., Denman, K.L., Forbes, J.R., Calvert, S.E., Thomson, R.E., 1996. Sinking particle fluxes from the euphotic zone over the continental slope of an eastern boundary current region. Journal of Marine Research 54, 1097–1122.

- Pilskaln, C., Paduan, J.B., Chavez, F.P., Anderson, R.Y., Berelson, W.M., 1996. Carbon export and regeneration in the coastal upwelling system of Monterey Bay, central California. Journal of Marine Research 54, 1149–1178.
- Robertson, J.E., Robinson, C., Turner, D.R., Holligan, P., Watson, A.J., Boyd, P., Fernandez, E., Finch, M., 1994. The impact of a coccolithophore bloom on oceanic carbon uptake in the northeast Atlantic during summer 1991. Deep-Sea Research 41, 297–314.
- Robinson, C.L.K., Ware, D.M., Parsons, T.R., 1993. Simulated annual plankton production in the northeastern Pacific coastal upwelling domain. Journal of Plankton Research 15, 161–183.
- Semina, H.J., 1972. The size of phytoplankton cells in the Pacific Ocean. International Revue Gesamten Hydrobiology 57, 177–205.
- Smetacek, V., von Bröckel, K., Zeitzschel, B., Zenk, W., 1978. Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Marine Biology 47, 211–226.
- Smetacek, V.S., 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology 84, 239–251.
- Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of sea water analysis. Canadian Bulletin of Fisheries and Aquatic Sciences 167, 311 pp.
- Suess, E., 1980. Particulate organic carbon flux in the ocean-surface productivity and oxygen utilization. Nature 288, 260–263.
- Thibault, D., Roy, S., Wong, C.S., 1999. The downward flux of biogenic material in the NE subarctic Pacific: importance of algal sinking and mesozooplankton herbivory. Deep-Sea Research II 46, 2669–2697.
- Thomson, R.E., Hickey, B.M., LeBlond, P.H., 1989. The Vancouver Island Coastal Current: fisheries barrier and Conduit. In: Beamish, R., McFarlane, G. (Eds.) Effects of Ocean Variability on Recruitment and an Evaluation of Parameters used in Stock Assessment Models. Special Publication of Fisheries and Aquatic Sciences, Ottawa, 108, 265–296.
- Thomson, R.E., Ware, D.M., 1996. A current velocity index of ocean variability. Journal of Geophysical Research 101, 14297–14310.
- Tsunogai, S., Noriki, S., 1991. Particulate fluxes of carbonate and organic carbon in the ocean. Is the marine biological activity working as a sink of the atmospheric carbon? Tellus 43, 256–266.
- US GOFS, 1989. Sediment trap technology and sampling. US GOFS Planning Report Number 10, 94 pp.
- Voss, M., Altabet, M.A., v. Bodungen, B., 1996. δ^{15} N in sedimenting particles as indicator of euphotic-zone precesses. Deep-Sea Research 43, 33–47.
- Wada, E., Terazaki, M., Kabaya, Y., Nemoto, T., 1987. ¹⁵N and ¹³C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Research 34, 829–841.
- Walsh, J.J., Rowe, G.T., Iverson, R.L., McRoy, C.P., 1981. Biological export of shelf carbon is a sink of the global CO, cycle. Nature 291, 196–201.
- Wong, C.S., Whitney, F.A., Crawford, D.W., Iseki, K., Matear, R.J., Johnson, W.K., Page, J.S., Timothy, D., 1999. Seasonal and interannual variability in particle fluxes of carbon, nitrogen and silicon from time series of sediment traps at Ocean Station P, 1982–1993: relationship to subarctic primary productivity. Deep-Sea Research II 46, 2735–2760.
- Wu, J., Calvert, S.E., Wong, C.S., 1999a. Carbon and nitrogen isotope ratios in sedimenting particulate organic matter at an upwelling site off Vancouver Island. Estuarine, Coastal and Shelf Science 48, 193–203.
- Wu, J., Calvert, S.E., Wong, C.S., Whitney, F.A., 1999b. Carbon and nitrogen isotopic composition of sedimenting particulate material at Station Papa in the subarctic northeast Pacific. Deep-Sea Research II 46, 2793–2832.