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# Sinking particle fluxes from the euphotic zone over the continental slope of an eastern boundary current region

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#### ABSTRACT

We analyze data from sediment traps and current meters moored at two locations 100 km apart over the Vancouver Island continental slope during the spring and summer of 1990. Time-series of sinking particle fluxes, major biogenic components (biogenic silica, calcium carbonate, and particulate organic carbon and nitrogen), and stable isotopic composition ( $\delta^{13}C_{organic}$  and  $\delta^{15}N_{total}$ ) were determined on samples obtained with sequential sediment traps moored at 200-250 m depth. Associated water property data were obtained from CTD/Rosette profiles taken during trap service periods and from current meters positioned in the surface layer and near the sediment trap. These data indicate that the two locations (a southern site J and a northern site NJ) were hydrographically distinct during the investigation. At site J, we found evidence for frequent upwelling events and more variability in the upper layer water properties. The main difference in the sinking fluxes of particles between the two sites was the occurrence of a one-week event at the end of May at J that contributed about one third of the total particle flux during the sampling period. Otherwise, the total flux collected during the study and the flux of major biogenic particles were similar at both sites. Silica shells dominated the flux of particles, particularly during the spring and early summer period. At both sites, particulate organic carbon rather than calcium carbonate was the main contributor to particulate carbon fluxes. The  $\delta^{13}C_{\text{organic}}$  showed marked variations during the sampling period at both sites likely due to variations in the growth rate of phytoplankton and in species composition. In comparison, variations in nitrate availability appear to dominate the changes in  $\delta^{15}N_{total}$ .

#### 1. Introduction

The export of particulate organic carbon and calcium carbonate shells from the euphotic zone is an important process in the oceanic carbon cycle. To date, most of the information on sinking particles in the ocean has been obtained with sediment traps. Several studies have shown a strong correlation between primary production and the fluxes of particulate organic carbon and nitrogen beneath the euphotic zone (Suess, 1980; Betzer *et al.*, 1984; Pace *et al.*, 1987). This biological control of particle sedimentation results in a marked seasonality in both the composition and magnitude of the fluxes. Over time scales longer than a year, the production of phytoplankton resulting from nitrogen supplied from outside the euphotic zone (i.e. new production) is considered to be quantitatively equivalent to the

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organic matter that can be exported out of the euphotic zone without the production system running down (Eppley and Peterson, 1979). The export of organic matter occurs as sinking particles and as dissolved organic matter transported away from the euphotic zone by currents and turbulent diffusion. It has been estimated (Bienfang and Ziemann, 1992) that, despite the lower areal extent, coastal regions support about 64% of the global new production (and thus the export of organic matter) while offshore regions contribute only 36%. Thus, continental margins could play an important role globally in the transport flux of carbon from the surface ocean where it is in contact with the atmosphere.

Of the organic particles produced over continental margins, some are decomposed by bacteria and other organisms in the water column, some sink and are deposited in shelf sediments, and some are advected into deeper waters. It has been suggested (Walsh *et al.*, 1981) that a significant proportion of the organic matter produced on continental shelves is exported to continental slope sediments. However, results from the SEEP (Shelf Edge Exchange Processes)-II program (Biscaye *et al.*, 1994) on the eastern US continental shelf, have recently shown that most of the biogenic particulate matter was remineralized over the shelf and only a small proportion (<5%) was exported to the adjacent slope, primarily due to weak seaward mean currents (generally <2 cm s<sup>-1</sup>). In contrast, in eastern boundary current regions, the upwelling that provides the nutrients for the high photosynthetic production of carbon could also be responsible for transporting much of the production (i.e. phytoplankton) seaward via the wind-induced surface Ekman transport and by localized offshore-flowing surface currents (i.e. "upwelling filaments") before it can sink or be utilized by zooplankton on the continental shelf.

The currents off the west coast of Vancouver Island have a pronounced seasonal cycle (Freeland et al., 1984; Thomson et al., 1989; Hickey et al., 1991). In winter, the predominant circulation consists of wind-driven poleward flow over the slope and outer shelf and buoyancy-driven poleward flow over the inner shelf. In summer, the wind-driven flow reverses direction in response to the changing winds while the prevailing current over the inner shelf continues to flow poleward in response to buoyancy output from Juan de Fuca Strait. The spring transition to the summer flow regime begins around early February to early March and the fall transition to the winter flow regime from mid September to mid November when the prevailing winds return to the southeast direction. As in other eastern boundary current regions (Brink and Cowles, 1991), there is considerable spatial and temporal variability in the flow field seaward of Vancouver Island. For example, satellite thermal images taken during the summer months often show cool bands of surface water that have formed as a result of upwelling filaments that can extend up to 100 km offshore (Freeland and Denman, 1982; Ikeda and Emery, 1984; Fang and Hsieh, 1993; Brown et al., 1993). It has been suggested (Ikeda and Emery, 1984; Staples, 1993) that cold water bands along the shelf break off Vancouver Island during the upwelling season are likely the result of shelf break upwelling, although it is also possible that the water was advected from regions farther north. Also, observations of Coastal Zone Color Scanner (CZCS) images in this region during the summer (Thomson and Gower, 1985) have revealed the presence of eddies and current filaments which usually have relatively high concentrations of chlorophyll (Abbott and Zion, 1987; Cochlan *et al.*, 1991).

The main objectives of this study were: (i) to characterize the time variability in the amount and composition of the biogenic fluxes of materials sinking out of the euphotic zone over the continental slope in an eastern boundary current region during the spring/ summer season; and (ii) to compare the sinking flux of particles and related hydrographic environment in an area of persistent upwelling filaments with the same measurements from an area where upwelling filaments rarely occur. To that end, we report on the magnitude and composition of sinking particle fluxes collected with time-series sediment traps at two sites over the continental slope off Vancouver Island. Trap data are complemented with current meter observations taken in the surface layer and just below the sediment traps, and with water column observations obtained during the mooring deployments for the spring/summer season of 1990.

#### 2. Methods

Two sequential sediment traps were moored for two consecutive periods between April 26 and September 30, 1990 in the shelf break waters off Vancouver Island (Fig. 1). There was a three-day gap (18-20 of July) in the sampling between the first and second deployment. One sediment trap mooring was located under the path frequently followed by filaments (site J; 49° 39' N and 127° 38' W) and the other about 100 km to the north (site NJ; 50° 17' N and 128° 22' W), where satellite imagery indicated that upwelling filaments were rare (Thomson and Gower, 1985). The sediment trap at site J was located (based on the pressure transducer in a deep current meter) at a depth of 197 and 195 m, and at site NJ at a depth of 245 and 204 m, during the first and second deployments respectively. These depths are well below the euphotic zone and between the near-surface southward-flowing shelf edge current and the deeper northward-flowing California Undercurrent. The bottom depths at the sites are 577 and 754 m, respectively. Each mooring consisted of a cone-shaped sediment trap (Honjo Mark V; Honjo and Doherty, 1988) with 12 time-series cup collectors and a collection area covered by baffles of 1.14 m<sup>2</sup> at the depths given above, and a current meter (Aanderaa RCM4) 5 m below the sediment trap. A shallow current meter was located at a depth of 27 and 36 m on the J mooring and at 75 and 45 m on the NJ mooring during the first and second deployments, respectively. Profiles of temperature and salinity, in situ fluorescence and macronutrients were obtained from CTD/Rosette casts (Fig. 1) at the time of sediment trap servicing (April, July and October).

The sediment trap sample cups were deployed filled with filtered seawater (Millipore GS 0.22  $\mu$ m membrane filter and Whatman 934AH glass fiber prefilter) to which 5 g L<sup>-1</sup> of NaCl was added to increase salinity and 1 g L<sup>-1</sup> sodium azide (NaN<sub>3</sub>) as a poison/ preservative. Upon recovery of the traps, the sample cups were removed from the trap body and stored at 4°C until they could be examined. A total of 23 sediment trap samples were collected from site NJ and 24 samples from site J over the 155 day period (Table 1), each representing a 6–7 day collection period, except for one sample at NJ where the duration



Figure 1. Location of sampling sites. Circles represent CTD/Rosette station and asterisks the location of the sediment trap mooring.

was 14 days. All sediment traps collected large numbers of zooplankton which were not passively sinking particles. In the laboratory, samples were screened with a 1 mm sieve to remove large zooplankton and then the remaining swimmers were hand-picked under a dissecting microscope. After removal of swimmers, half of the sediment trap material was freeze-dried and subsampled for analysis of total mass flux, particulate organic carbon (POC), particulate total nitrogen (PON), calcium carbonate (CaCO<sub>3</sub>), and stable isotopic composition ( $\delta^{13}C_{organic}$  and  $\delta^{15}N_{total}$ ). The remainder was subsampled for biogenic silica and other analyses not reported here.

To obtain total mass fluxes, samples were filtered onto preweighted 0.8 µm Nucleopore polycarbonate filters, dried at 60°C and weighed. Total carbon and nitrogen were determined by combustion/gas chromatography using a Carlo Erba CHN analyzer. Carbonate carbon was separately determined by acid evolution of  $CO_2$  and quantification using a UIC coulometer. Organic carbon was obtained by difference. The precision of the analyses was  $\pm 3\%$  for organic C, carbonate C and nitrogen. Biogenic silica was determined by a simplification of DeMaster's (1981) technique which consisted of dissolution in hot 1% Na<sub>2</sub>CO<sub>3</sub> and analysis by Technicon autoanalyzer (Technicon industrial method No 186Table 1. Dates and duration of the sediment trap samples at J and NJ sites obtained in the two deployments. All collection periods were the same for both sites except for samples 1–8 and 1–9 that were combined in the sediment trap at NJ site.

|                       | Sampling dates |              | Interval |
|-----------------------|----------------|--------------|----------|
| Sample Cup            | Open           | Closed       | (days)   |
| 1-1                   | 26-Apr1990     | 2-May-1990   | 6        |
| 1-2                   | 2-May-1990     | 9-May-1990   | 7        |
| 1-3                   | 9-May-1990     | 16-May-1990  | 7        |
| 1-4                   | 16-May-1990    | 23-May-1990  | 7        |
| 1-5                   | 23-May-1990    | 30-May-1990  | 7        |
| 1-6                   | 30-May-1990    | 6-June-1990  | 7        |
| 1-7                   | 6-June-1990    | 13-June-1990 | 7        |
| 1-8                   | 13-June-1990   | 20-June-1990 | 7        |
| 1-9                   | 20-June-1990   | 27-June-1990 | 7        |
| 1-10                  | 27-June-1990   | 4-July-1990  | 7        |
| 1-11                  | 4-July-1990    | 11-July-1990 | 7        |
| 1-12                  | 11-July-1990   | 20-July-1990 | 7        |
| 2-1                   | 20-July-1990   | 26-July-1990 | 6        |
| 2-2                   | 26-July-1990   | 1-Aug1990    | 6        |
| 2-3                   | 1-Aug1990      | 7-Aug1990    | 6        |
| 2-4                   | 7-Aug1990      | 13-Aug1990   | 6        |
| 2-5                   | 13-Aug1990     | 19-Aug1990   | 6        |
| 2-6                   | 19-Aug1990     | 25-Aug1990   | 6        |
| 2-7                   | 25-Aug1990     | 31-Aug1990   | 6        |
| 2-8                   | 31-Aug1990     | 6-Sept1990   | 6        |
| 2-9                   | 6-Sept1990     | 12-Sept1990  | 6        |
| 2-10                  | 12-Sept1990    | 18-Sept1990  | 6        |
| 2-11                  | 18-Sept1990    | 24-Sept1990  | 6        |
| 2-12                  | 24-Sept1990    | 30-Sept1990  | 6        |
| Total Sampling Period |                |              | 155      |

72W). The isotopic composition of organic carbon was determined on decarbonated (10% HCl) subsamples using 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 ‰ notation with respect to the PDB standard. Precision was  $\pm 0.2\%$ .  $\delta^{15}N_{total}$  values were determined on separate subsamples by Dumas combustion (Minagawa *et al.*, 1984) followed by cryogenic separation of the N<sub>2</sub> gas and mass spectrometry. The results are reported relative to air and with a precision of  $\pm 0.3\%$ .

Daily values of temperature, salinity, and current velocity were obtained from the current meter records by first low-pass filtering the 30 min data with a squared Butterworth filter with a cutoff frequency of (1/40) h<sup>-1</sup> and then picking out the mid-day value. The current velocity was then defined in terms of its cross-shore (*U*) and longshore (*V*) velocity components, with *U* positive onshore and *V* positive at an angle of 40° counterclockwise from north parallel to the local coastline. A time-dependent current velocity index

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(Thomson and Ware, 1996) of coastal ocean variability,  $I_v \equiv \alpha |V_s \partial V/\partial z| \partial V/\partial z$ , was derived from the vertical shear between the observed longshore currents,  $\partial V/\partial z \approx \Delta V/\Delta z$ , measured by the upper and lower current meters. The variable z is depth, t is time, and  $\alpha$  $(= -1/[(f^2 + \delta^2)\sigma_v])$  is a normalization factor constructed from the Coriolis parameter, f, a frictional parameter,  $\delta$ , and the standard deviation,  $\sigma_v$ , of the upper current velocity,  $V_s$ . Derived from the thermal wind relation for the longshore flow, the index is positive during upwelling-favorable flow conditions and negative during downwelling-favorable conditions.

Water samples of 20 ml for the analysis of nutrients (nitrate, phosphate and silicate) were taken at several depths at each station and frozen immediately in an alcohol bath at  $-40^{\circ}$ C and stored until analysis. In the laboratory, a Technicon II autoanalyzer and standard techniques were used for analyses of these samples (Strickland and Parsons, 1972).

#### 3. Results

a. Hydrography, nutrients and chlorophyll. Cross-shelf sections of temperature, salinity and nitrate (Fig. 2) through the NJ and J sites during July 1990 show marked horizontal gradients in water properties. As one would expect for upwelling conditions, temperatures decrease while salinity and nitrate concentrations increase in the onshore direction. At the time of the survey, slightly lower temperatures and higher salinities, nutrients and phytoplankton biomass were found at J than at NJ. Low temperature (<11°C) and high nitrate (>10  $\mu$ M) contours intersected the surface waters farther offshore at J than at NJ (at about 48 and 20 km from shore, respectively). The distribution of silicate and phosphate (not shown) followed a pattern similar to that of nitrate with significant abundances along both transects and higher concentrations inshore. Chlorophyll fluorescence values along both transects were higher towards the surface with peak values at roughly 12 and 18 km inshore of the trap location at NJ and J, respectively.

Profiles of temperature, salinity, and nutrients for the times of the ship survey periods in April, July and October are shown in Figure 3. At times of sampling, nutrients were always detectable at both sites, with concentrations lower in the mixed layer than below. At the time of mooring deployment in April, the upper layer was thoroughly mixed down to about 30 m at NJ. The concentration of nitrate was >3  $\mu$ M in the surface layer at NJ and >2  $\mu$ M at J. In July, when warmer temperatures and a sharper seasonal thermocline were present, especially at NJ, the mixed layer was shallower (about 20 m), and nutrients were lower (<1  $\mu$ M of nitrate) at NJ but considerably higher (>10  $\mu$ M nitrate) at site J. In October (more than two weeks after the last sediment trap sampling cup closed), the surface mixed layer at both sites had deepened to about 50 m and nutrient concentrations were high (>10  $\mu$ M nitrate).

*b. Current meter records.* Low-pass filtered time-series of temperature, salinity and horizontal currents from the shallow (27–75 m) and deep current meters (200–250 m) are shown in Figure 4. At site J, there is a 22-day gap in the current of the shallow current meter



Chl Chl 100 20 40 30 10 0 -10 30 20 0 10 -10 Distance (km) Distance (km)

Figure 2. Cross-shelf sections of temperature (°C), salinity (psu), nitrate ( $\mu$ M) and chlorophyll fluorescence (mg m<sup>-3</sup>) passing through the NJ and J sites during July 1990. The arrows indicate the location of the sediment trap mooring and horizontal distance is shown relative to the shelf edge (200 m isobath). Note the expanded vertical scale for the chlorophyll section.

record between June 26 and July 17 due to an instrument malfunction. The shallower current meters were moored near the coincident thermocline and halocline (Fig. 3) whose depths change as a result of passing internal waves and lateral advection. Variations in the depth of these surfaces are responsible for the abrupt peaks and troughs in the temperature



Figure 3. Vertical profiles of temperature (solid line), salinity (dashed line), nitrate (diamond), phosphate (circle) and silicate (triangle) obtained in: (a) April 26, (b) April 28, (c) July 20, (d) July 18, (e) October 18, and (f) October 15 at sites NJ and J. Units as in Figure 2.

and salinity records. Temperatures from the shallow current meters were warmer (average 10°C) and more variable (range 7.9–13.5°C) at J than at NJ (average 8°C, range 6.7–9.9°C). At NJ, salinities were higher than at J particularly during the first deployment when the current meter was at a greater depth than during the second deployment (75

versus 45 m). At J, fluctuations in salinity followed a similar pattern to those of temperature but of opposite sense (temperature decreases and salinity increases with depth in the North Pacific). Mean salinities at J were higher during the second deployment (32.4 psu) than during the first deployment (31.8 psu) due to the greater depth of the current meter during the second deployment (36 versus 27 m). The data from the deep current meters at both sites had similar, near constant temperatures (6–7°C) and salinities (34.1 psu) during the sampling period.

For the period of sediment trap measurements, the current records show a strong flow near the surface (mean unfiltered speed =  $16 \text{ cm s}^{-1}$  at NJ and  $22 \text{ cm s}^{-1}$  at J) and somewhat weaker flow at the deep current meter (mean unfiltered speed = 9.8 cm s<sup>-1</sup> at NJ and 9.2 cm s<sup>-1</sup> at J). At J, surface currents were predominantly to the southeast (mean V = -12.5 cm s<sup>-1</sup>) for all but a small fraction of the total time series, reaching peak speeds in excess of 40 cm s<sup>-1</sup> during May and the end of July. In comparison, surface currents at NJ were highly variable with net surface transport to the northwest (mean  $V = 3.8 \text{ cm s}^{-1}$ ) interrupted by intermittent reversals in flow direction over periods of days to weeks. At the two sites, the longshore currents were generally stronger than the cross-shore currents. The small mean cross-shore speeds (0.6 cm s<sup>-1</sup> at J and 2.1 cm s<sup>-1</sup> at NJ) indicate a net onshore flow throughout the sampling period but are sensitive to the orientation of axes. The magnitudes of episodic seaward flow events were larger at J than at NJ, reaching values greater than 20 cm s<sup>-1</sup>. At the nominal 200 m depth, the along-shore current component was generally to the northwest (on average 4.1 cm s<sup>-1</sup> at NJ and 3.8 cm s<sup>-1</sup> at J), so that the deep currents were in the same direction as those near the surface layer at NJ but in the opposite direction to the surface currents at J. The current velocity index  $(I_y)$  shows little upwelling activity at NJ: only on four occasions during the sampling period were values greater than 100 obtained. In contrast, site J seems to be subjected to upwelling events during much of the summer with the most intense event  $(I_v > 400)$  at the end of July. During the first deployment, an upwelling event that lasted about 20 days was observed in May. During the second deployment, the  $I_{v}$  indicates upwelling activity during most of the period, except for the first week of August and after the 15 of September.

c. Sediment trap fluxes. Particle fluxes to the sediment traps were substantial and highly variable (Fig. 5). Total dry weight (TDW) flux ranged from 36 to 805 mg m<sup>-2</sup> d<sup>-1</sup> at NJ and from 15 to 2150 mg m<sup>-2</sup> d<sup>-1</sup> at J. Both sediment traps received higher fluxes of material during the spring (until the second week of June). At J, an episode of particularly high particle flux was observed in late May. This one-week spring pulse contributed 36% of the TDW collected. Although the sampling interval was longer at the NJ trap during this period (16–30 of May), the flux of 764 mg m<sup>-2</sup> d<sup>-1</sup> during this peak was lower than the average flux of 1455 mg m<sup>-2</sup> d<sup>-1</sup> recorded at J over the same period. In comparison, the integrated TDW flux over the full deployment period (155 days) was roughly equal at both sites (39.9 g m<sup>-2</sup> at J and 43.3 g m<sup>-2</sup> at NJ). Similarly, biogenic silica fluxes integrated for the



Figure 4. Daily variations in temperature, salinity, current data and  $I_v$  index from the shallow (located at a depth of 75 and 45 m at NJ and at 27 and 36 m at site J, during the first and second deployments respectively) and deep (located at a depth of 251 and 210 m at NJ and at 203 and 201 m at site J, during the first and second deployments respectively) current meters at sites (a) NJ and (b) J. Positive U(V) values represent currents directed inshore (northwest); negative values represents flow offshore (southeast). Sediment trap sampling periods are shown along the bottom axis.

two sites, ranging from 3 to 385 mg m<sup>-2</sup> d<sup>-1</sup> at NJ and from 3 to 1155 mg m<sup>-2</sup> d<sup>-1</sup> at J. The sinking fluxes of TDW (for each sampling interval) were highly correlated with biogenic silica fluxes, indicating that plankton biomass in the upper layer was dominated by diatoms with significant skeletal structures. In contrast to the similarities in the TDW and biogenic



silicate fluxes at both sites, the total flux of POC was ~25% lower at J than at NJ over the same period. The POC fluxes ranged from 6 to 65 mg m<sup>-2</sup> d<sup>-1</sup> at NJ and from 3 to 152 mg m<sup>-2</sup> d<sup>-1</sup> at J. The overall trend in the temporal pattern was the same as for TDW. CaCO<sub>3</sub> fluxes ranged from 4 to 77 mg m<sup>-2</sup> d<sup>-1</sup> and 2 to 99 mg m<sup>-2</sup> d<sup>-1</sup> at NJ and J, respectively. In contrast to POC, PON and biogenic silica fluxes which closely follow the TDW flux, CaCO<sub>3</sub> fluxes were higher at the end of the summer rather than during the spring.

The fluxes of major biogenic particles (i.e. POC, CaCO<sub>3</sub>, and biogenic silica) contributed 53–76% (mean = 64%) of the TDW at NJ and 55–91% (mean = 68%) at J (Fig. 6). On average, biogenic silica was the largest component of settling particles during the study



Figure 5. Time-series plots of: total mass of particulate matter (TDW), biogenic silicate (SiO<sub>2</sub>), particulate organic carbon (POC), and calcium carbonate (CaCO<sub>3</sub>) fluxes at both trap sites from 26 April to 30 September. The average flux in mg m<sup>-2</sup> day<sup>-1</sup> of each component during the sampling period is given between brackets.

period (39% at NJ and 37% at J) followed by POC (14% at NJ and 16% at J) and  $CaCO_3$  (13% at both sites). However, there were significant differences among samples contributing to the different components. For example, the biogenic silica contribution to the total flux varied from 11 to 56% at NJ and from 15 to 66% at J. At both sites, biogenic silica generally dominated the fluxes of biogenic particles until July. Afterwards, the proportion of POC and CaCO<sub>3</sub> increased.



Figure 6. Temporal variability in the relative contribution of the major biogenic components of the sediment trap sample.

*d. Composition ratios.* The mean organic C/total N atomic ratios from the trap samples were similar (9.7 and 9.8) at both sites, and were slightly higher than those found in Ocean Station Papa (~8.9 at 250 m; Wong and Whitney, personal communication). The C/N ratios ranged from 7.5 to 12.6 at NJ and from 7.7 to 12 at J (Fig. 7). These values suggest that the material falling into the traps were dominantly of marine rather than terrigenous origin (C/N ratio of ~16; Venkatesan, 1988). At both sites, the atomic C<sub>organic</sub>/C<sub>carbonate</sub> ratios were highly variable (range 3 to 29) during the sampling period and were on average



Figure 7. Changes in the atomic ratio between biogenic elements (Si, N, organic and inorganic carbon) during the sampling period. C<sub>organic</sub> indicates organic carbon, C<sub>carbonate</sub> indicates carbon in calcium carbonate.



Figure 8. Time-series of stable isotopic composition (δ<sup>13</sup>C<sub>organic</sub> and δ<sup>15</sup>N<sub>total</sub>) of the sediment trap material and particulate organic carbon and nitrogen fluxes for samples collected at sites NJ and J.

slightly lower at NJ (11  $\pm$  5.4) than at J (12.8  $\pm$  7.1). The value of this ratio indicates that at 200 m depth organic carbon is much more important in the vertical transport of particulate carbon than inorganic carbon (i.e. calcium carbonate).

The Si<sub>biogenic</sub>/C<sub>organic</sub> atomic ratios varied between 0.1 and 2.1, and were usually higher than the typical ratios of marine diatoms (0.13; Brzezinski, 1985). In particular, the Si<sub>biogenic</sub>/C<sub>organic</sub> ratio of the material collected in May during the spring peak at J was significantly higher (16 times) than that of diatoms indicating that most of the flux was due to diatom frustules rather than to intact cells. In the few occasions where Si<sub>biogenic</sub>/C<sub>organic</sub> approaches the values of intact cells, the Si<sub>biogenic</sub>/C<sub>carbonate</sub> ratio was lower than the average indicating an increase in the relative contribution of calcareous organisms. The Si<sub>biogenic</sub>/C<sub>carbonate</sub> ratios were high and variable at both sites before August when diatom frustules dominated the flux, becoming lower afterwards. Only during August at NJ did we find samples with Si<sub>biogenic</sub>/C<sub>carbonate</sub> <1.

e. Isotopic composition. Time series of the variations in  $\delta^{13}C_{\text{organic}}$  and  $\delta^{15}N_{\text{total}}$  in the trap samples, together with the flux values for organic carbon and nitrogen are shown in Figure 8. Apart from  $\delta^{13}C_{\text{organic}}$  at NJ, the isotope variations are not clearly related to the flux variations. Moreover, the mean values of  $\delta^{13}C_{\text{organic}}$  (-21.7 and -21.9) and  $\delta^{15}N_{\text{total}}$  (9.2 and 9.3) are similar at the two sites.

The  $\delta^{13}C_{\text{organic}}$  values range from -19.7 to -24.1% at NJ and from -18 to -24.7% at J over the six-month sampling period. These ranges encompass a large part of the variation

of marine planktonic and suspended sediment values reported in the literature (Degens *et al.*, 1968b; Rau *et al.*, 1982; Fry and Sherr, 1984; Wada *et al.*, 1987; Fry, 1988; Fry and Wainwright, 1991; Rau *et al.*, 1991; Sackett, 1991). At J,  $\delta^{13}C_{\text{organic}}$  increased slightly (became heavier) prior to, and reached a maximum at, the spring flux maximum, decreasing markedly thereafter. This change was followed by a steady increase during the period of declining POC fluxes until August, after which there was another decrease to a minimum in mid-August. Finally, the  $\delta^{13}C_{\text{organic}}$  values increased to the highest values at the end of September. At NJ, there were no clear trends in  $\delta^{13}C_{\text{organic}}$  while the carbon fluxes varied between fairly narrow limits. Some of the maxima in  $\delta^{13}C_{\text{organic}}$  values do, however, coincide with maxima in POC fluxes.

The  $\delta^{15}N_{total}$  values range from 7.6 to 12.8% at NJ and from 7.2 to 10.5% at J. Once again, these values are similar to literature values for plankton samples from coastal sites (Mullin *et al.*, 1984; Altabet and Deuser, 1985; Altabet and McCarthy, 1985, 1986; Libes and Deuser, 1988; Wada and Hattori, 1991; Montoya *et al.*, 1992; Montoya, 1994), but are markedly heavier than those reported for open ocean observations (Saino and Kattori, 1980; Mullin *et al.*, 1984; Altabet and McCarthy, 1986; Wada *et al.*, 1987; Altabet, 1988; Altabet *et al.*, 1991; Wada and Hattori, 1991; François and Altabet, 1992; Saino, 1992). At J,  $\delta^{15}N_{total}$  decreased to a minimum during the spring flux maximum (around the end of May), and then increased abruptly by 3% thereafter. The values then remained at a high level for the remaining three months, with slight minima during two minor PON flux maxima.  $\delta^{15}N_{total}$  varied to a greater extent at NJ, with minima once again generally coinciding with PON flux maxima. Examination of the major variations in both isotope ratios suggests that  $\delta^{13}C_{organic}$  changes to heavier values and  $\delta^{15}N_{total}$  changes to lighter values during major flux events.

#### 4. Discussion

The intended purpose of this study was to describe and compare the fluxes of particles during the spring and summer months at two sites seaward of Vancouver Island. One site (J) was located under the path of a recurring upwelling filament (Denman *et al.*, 1989; Brown *et al.*, 1993) and the other (NJ) was located where upwelling jets are rare. We did not observe a definitive upwelling filament from our shipboard sampling during April, July and October, nor was there evidence for a filament in the current meter records. We did, however, observe significant differences in water property conditions between the two sites during the study. At J, current measurements provided evidence of upwelling over much of the study period and, in particular, during the summer. Previously, satellite sea-surface temperature observations in the region near J (Ikeda and Emery, 1984; Staples, 1993; Brown *et al.*, 1993) have shown the presence of a cold water tongue extending southwest from Brooks Peninsula during the summer, and in two years, drifters deployed in the cool waters moved offshore for several days (Denman *et al.*, 1989). These studies suggested that the cold water was advected by southward flow from the cooler northern region, but could also be the expression of local upwelling at the shelf break. At NJ, cold water was also

present, but current measurements indicate little upwelling activity at this site. Comparable low temperature water, which seems to have originated from the northern tip of Vancouver Island, has been observed in satellite sea-surface temperature images of this region (Ikeda and Emery, 1984).

Satellite sea surface temperature data over eight summers (1984–1991) were analyzed by Fang and Hsieh (1993) to study the variability in long-term temperature patterns off the west coast of Vancouver Island and the seasonal and interannual variability in coastal upwelling. They found that the mean summer upwelling pattern of cold surface water, which is similar to the mean summer temperature field, was strongest during 1990, the year of our study. Moreover, they estimated a coolness index which indicated that in the summer of 1990 coastal waters were colder than in the previous three summers (although not the coolest of the 8 years). Their observations suggest that during summer 1990, coastal upwelling was stronger than normal, although Mackas (1995) found the Bakun upwelling index (Bakun, 1973) at 48N, 125W during April to October 1990 to be lower than the 1979–91 average.

a. Comparison of particle fluxes at NJ and J sites. Overall, there were no clear differences in the average fluxes of all major biogenic components at the two sites during the sampling period. As a consequence, our expectation that more biogenic particles would sediment out of a site under a recurring offshore-flowing upwelling filament than at a site where upwelling filaments seldom occur, was not confirmed for the sampling period. On the contrary, a 25% higher flux of particulate organic carbon was found at the northern NJ site. Quantitative field studies of particle fluxes are difficult because sediment traps of any type are subjected to hydrodynamic biases in trap collection particularly under conditions of varying current speed (see review in US GOFS Report No. 10, 1989). Baker et al. (1988) have found that in the field the trapping efficiency of moored sediment traps decreases with current speed greater than  $\sim 12$  cm s<sup>-1</sup>. Although our traps are of a different design than the one used in that study, during our deployments, the current speed (before filtering) at the deep current meter (5 m below the traps) at site NJ was <12 cm s<sup>-1</sup> 68% of the time and  $<18 \text{ cm s}^{-1} 86\%$  of the time, and at site J was  $<12 \text{ cm s}^{-1} 73\%$  of the time and <18 cm s<sup>-1</sup> 92% of the time. Such low speeds suggest that trapping efficiency was not a major problem, but could have decreased during perhaps  $\frac{1}{4}$  of the time.

The major difference between the two sites was the greater number of particles (mostly biogenic silica) collected in a one-week sample in spring at J which contributed about one third of the total particles collected during the study period. Prior to the pulse of particles, current meter records indicate that there was a persistent upwelling event lasting about 20 days. This suggests that the peak in particle flux at J was due to the response of diatoms to widespread (regional) nutrient enrichment after the upwelling event. However, there is also indication of other upwelling events during the study period which were not associated with increases in the flux of material. For example, the most intense upwelling event at J seems to have occurred at the end of July, yet the flux of particles was lower than the

average flux for the entire series. At this time, chlorophyll and nutrient concentrations in the surface layer were relatively high (>10  $\mu$ M nitrate), not significantly different from those found in August 1986 at the same location by Cochlan *et al.* (1991). If the upwelling (and subsequent bloom) had been of limited areal extent, the strong advective currents (order 40 cm s<sup>-1</sup>) at the upper current meter could have transported any bloom out of the region before significant particle sinking occurred.

Although upwelling did not always result in an increase in the particulate material settling into the sediment traps, a response in the isotopic composition of the samples collected during and immediately after the upwelling events was found. This was particularly marked at J, where  $\delta^{13}C_{\text{organic}}$  increased slightly to a maximum during the flux maximum and then decreased rapidly immediately thereafter. The change in  $\delta^{15}N_{\text{total}}$  was in the opposite sense; it decreased to a minimum during the flux maximum and then increased immediately thereafter, and the values appeared to remain at a higher level for the rest of the sampling period.

The variability of the stable isotope signals reflects the dynamic nature of the coastal regime in which the traps were moored. During upwelling events, surface water temperatures would be expected to fall and nutrient levels would rise, as observed during the late spring and summer months off Vancouver Island (Parsons et al., 1966; Parsons and LeBrasseur, 1968; Anderson et al., 1969, 1977; Freeland and Denman, 1982). These two effects would work to decrease the  $\delta^{13}C_{\text{organic}}$  values via the increase in pCO<sub>2</sub> due to the temperature decrease (Rau et al., 1989) and via the supply of regenerated CO<sub>2</sub> from deeper water, and also to increase the values through an increase in growth rate because of the increase in nutrient levels (Degens et al., 1968a; François et al., 1993; Hinga et al., 1994; Laws et al., 1995; Nakatsuka et al., 1992). In addition, since the spring/summer blooms would be dominated by diatom productivity (Sambrotto and Lorenzen, 1987), as reflected in the increase of the Sibiogenic/Corganic ratio in the trap samples during this time-period, the settling particulate matter would be enriched in  $\delta^{13}$ C (Fry and Wainwright, 1991). In the present case, the growth rate and species composition effects appear to have been dominant during the upwelling event, whereas conditions changed markedly after the event. The large decrease in  $\delta^{13}C_{\text{organic}}$  during this time period may reflect the maintenance of a relatively high  $pCO_2$  in the surface waters because of the low temperatures and nutrient levels following the diatom bloom, together with a change in the phytoplankton assemblage to relatively <sup>13</sup>C-deficient species, for example flagellates. Thus, during the upwelling event, there was less discrimination against the heavy carbon isotope when the phytoplankton were growing rapidly. The rise in  $\delta^{13}C_{\text{organic}}$  from mid-June to early August at this site would then reflect the warming of the surface waters and outgassing of  $CO_2$ . Two other decreases in  $\delta^{13}C_{\text{organic}}$  later in the summer probably record smaller upwelling/ productivity events, although only the first of these isotope minima correspond to flux maxima.

The  $\delta^{15}N_{total}$  value of planktonic and particulate organic matter depends on the isotopic composition of the source nitrogenous nutrient and the isotopic fractionation during

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nutrient assimilation. Recent work has suggested that  $\delta^{15}N_{\text{plankton}}$  is generally inversely related to the surface concentration of nitrate (reviewed by Altabet and François, 1994; Montoya, 1994). In addition,  $\delta^{15}N_{\text{plankton}}$  can record the influence of subsurface denitrification, which has a large isotope effect (Wada and Hattori, 1991) in low oxygen waters if some of the residual, isotopically heavy nitrate is supplied to the photic zone. Isotopically heavy organic  $\delta^{15}N$  values in the eastern tropical Pacific (Libes and Deuser, 1988; Liu and Kaplan, 1989; Ganeshram *et al.*, 1995) most likely reflect this effect, and the  $\delta^{15}N$ enrichment of plankton off central California described by Mullin *et al.* (1984) may also be influenced by the delivery of residual nitrate from the California Undercurrent that flows from south to north along this margin. The nitrogen isotopes are also fractionated substantially during food-chain transfer, wherein the heavy isotope is enriched by roughly  $3\%_{c}$  at each trophic step (Minagawa and Wada, 1984). Thus, particulate organic matter originating from a shorter food chain will have lower  $\delta^{15}N$  values than that produced by a longer or more complex food web.

On average, the  $\delta^{15}N_{total}$  values observed at both sites in this study are heavier than those found in open ocean plankton and suspended particulate organic matter. They are also similar to the values reported off Peru by Libes and Deuser (1988) and also in zooplankton samples collected off central California by Mullin *et al.* (1984). The pattern of change of the values off Vancouver Island, lower values occurring during flux maxima and higher values occurring during periods of low fluxes, probably reflects increased nutrient availability during bloom events and a concomitant decrease in nitrate utilization by biological activity relative to physical supply. The increase in  $\delta^{15}N_{total}$  after the flux maximum then reflects the increase in relative nutrient utilization (a larger "drawdown") and the heavy isotope enrichment of the residual nitrate in the surface waters after the removal of the light isotope in settling particulate matter. These effects are also seen in the J site during the three smaller increases in flux after the large spring pulse. At the NJ site, there is also a rough correspondence between the sporadic flux increases and lower  $\delta^{15}N_{total}$ values, most likely reflecting the same processes.

We might expect isotopically heavy nitrate below the photic zone if waters affected by denitrification in the northeastern tropical Pacific were transported from central California, where Liu and Kaplan (1989) found  $\delta^{15}NO_3^-$  values of 11.6% at 350 m depth, via the California Undercurrent that flows northwards along the shelf edge off Vancouver Island throughout the annual cycle (Freeland and Denman, 1982). This current occurs at depths of 100–200 m (Mackas *et al.*, 1987), especially during the months of June–October (Freeland and Denman, 1982; Mackas *et al.*, 1987). However, the isotopic composition of dissolved nitrate at a single station off southern Vancouver Island (48°39'N, 126°40'W) in May, 1993 was 11% at the surface layer and 5% at 400 m depth (Wu *et al.*, 1996), illustrating only the effect of preferential phytoplanktonic removal of the light isotope at the sea surface and the concomitant enrichment of the residual nitrate pool.

The effects of changes in the structure of the food web off Vancouver Island during this study cannot be determined from these data, since the changes in  $\delta^{15}N_{total}$  respond closely

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to the composition and abundance of nitrate. That is to say, the increase in  $\delta^{15}N_{total}$  after the large flux maximum at the J site due to the development of a longer food chain is confounded by the decrease in nutrient availability after the spring bloom which would cause a concomitant increase in the  $\delta^{15}N$  of the settling organic matter.

b. Carbon fluxes and remineralization. Phytoplankton organisms, such as coccolithophores, can produce calcium carbonate plates (i.e. calcification) and thus be involved in the production of both organic and inorganic particulate carbon. While the production of organic matter acts as a sink for atmospheric carbon dioxide, calcification has the net effect of generating dissolved carbon dioxide while still reducing the total inorganic carbon concentration (e.g. Broecker and Peng, 1982; Robertson et al., 1994). It has been pointed out by Tsunogai and Noriki (1991) among others that attention should be given not only to absolute amounts of carbonate and organic carbon produced and decayed, but also to their relative ratios, since marine biological activity has no net effect on the atmospheric  $CO_2$ if the ratio of preserved carbonate carbon to organic carbon is unity. Offshore from Vancouver Island, we have found that, at 200 m depth, the organic carbon flux was significantly larger than the carbonate carbon flux, indicating a net biological sink of carbon in this region. The  $C_{\text{organic}}/C_{\text{carbonate}}$  ratios we observed (mean = 11.9; range = 3-29) were higher than those previously reported in the eastern North Pacific and were similar to those of the Antarctic Ocean (Noriki and Tsunogai, 1986; Tsunogai and Noriki, 1991).

Fluxes of sinking particles are generally found to decrease with depth due to *in situ* degradation of sinking organic matter (e.g. Martin *et al.*, 1987) by bacteria or to transfer to the dissolved organic matter pool. To determine the magnitude of these processes, it is desirable to compare the sinking fluxes of POC with the carbon fixed in the surface layer by primary productivity. Usually, the primary production rate during the sediment trap sampling interval is obtained by integrating daily measurements of primary productivity in the euphotic zone overlying the traps. However, in regions where surface currents are strong, such as offshore Vancouver Island, some of the particles collected by sediment traps could be produced in surface waters far from the mooring location. Instead, we can back-estimate the production of POC leaving the euphotic zone by multiplying typical elemental ratios of Si<sub>biogenic</sub>/C<sub>organic</sub> (0.13; Brzezinski, 1985) and C<sub>organic</sub>/C<sub>carbonate</sub> (1.0; Robertson *et al.*, 1994) of phytoplankton by the fluxes in mmol m<sup>-2</sup> d<sup>-1</sup> of SiO<sub>2</sub> and CaCO<sub>3</sub> into the sediment trap, such that,

POC production (mg-C m<sup>-2</sup> d<sup>-1</sup>) = 
$$\left( \text{SiO}_2 \text{flux} / \frac{\text{Si}_{\text{biogenic}}}{\text{C}_{\text{organic}}} + \text{CaCO}_3 \text{flux} * \frac{\text{C}_{\text{organic}}}{\text{C}_{\text{carbonate}}} \right) * 12$$

This procedure assumes that only the phytoplankton with shells (mostly diatoms and coccolithophores) contribute to the production of organic matter, and that dissolution of biogenic silica and  $CaCO_3$  shells is negligible in the water column above the sediment trap. Recently, Nelson *et al.* (1995) have estimated that globally at least 50% of the silica



Figure 9. Time-series of estimated primary production (solid circles) and the ratio (in %) of POC flux into the sediment trap to estimated primary production (open circles), at the sites NJ and J.

produced by diatoms dissolves in the upper ocean, but in coastal upwelling regions biogenic silica dissolution is less important (~10%). Because of these assumptions, the values of primary production estimated in this way are minimum values. Using this approach, we obtained a primary production of 33.1 g-C m<sup>-2</sup> at NJ and 32.9 g-C m<sup>-2</sup> at J site during the study period (155 days). In comparison, using a C/N ratio of 6.6 (Redfield *et al.*, 1963), we estimate that the rate of nitrogen removal necessary to sustain the above primary production was 413 mmol-N m<sup>-2</sup> at NJ and 410 mmol-N m<sup>-2</sup> at J. This is not an unreasonable number given the high availability of nitrate in the euphotic zone (i.e. 10 mmol-NO<sub>3</sub><sup>-</sup> m<sup>-3</sup> × 30 m = 300 mmol-N m<sup>-2</sup>) even without considering replenishment from upwelling, vertical mixing or longshore advection.

Based on measurements of the flux of sinking particles at different depths in the open ocean, an empirical organic carbon *in situ* regeneration relation was obtained by Martin *et* 

al. (1987) linking vertical flux with depth. From this function, only about 20% of the total carbon exported from a 30 m thick euphotic zone reaches 200 m depth. This value is close to our mean estimate of 35% (especially since we are underestimating POC production), although estimates were highly variability (range of 9 to 130% at NJ and 6 to 127% at site J) at both sites (Fig. 9). Also, we did not find a relationship between the estimated POC production and the proportion of POC recycled above the sediment traps. In contrast to previous studies (Suess, 1980; Betzer et al., 1984), the organic carbon content of the sinking particles at both sites was not relatively higher when the particle flux was high. For example, the ratio of POC flux versus POC production was 8% during the peak of particle flux at site J whereas it was 32% on average during the sampling period. Thus, the suggestion that recycling of carbon is less efficient at times of high productivity was not supported by the data presented here. On the other hand, the high Coreanic/Ccarbonate ratios observed at these sites suggest that eastern boundary current regions are especially efficient at removing organic carbon and hence diminishing the surface pCO<sub>2</sub> concentrations. However, more quantitative estimates of carbon fluxes in eastern boundary current regions will require better knowledge of both onshore-offshore and vertical gradients of the sinking fluxes. We are currently analyzing more recent observations from a study designed to address these deficiencies.

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#### REFERENCES

- Abbott, M. R. and P. M. Zion. 1987. Spatial and temporal variability of phytoplankton pigment off northern California during Coastal Ocean Dynamics Experiment I. J. Geophys. Res., 92, 1745–1755.
- Altabet, M. A. 1988. Variations in nitrogen isotopic composition between sinking and suspended particles: Implications for nitrogen cycling and particle transformation in the open ocean. Deep-Sea Res., 35, 535–554.
- Altabet, M. A. and W. G. Deuser. 1985. Seasonal variations in natural abundance of <sup>15</sup>N in particles sinking to the deep Sargasso Sea. Nature, 315, 218–219.
- Altabet, M. A., W. G. Deuser, S. Honjo and C. Steinen. 1991. Seasonal and depth-related changes in the source of sinking particles in the North Atlantic. Nature, *354*, 136–139.
- Altabet, M. A. and R. François. 1994. Sedimentary nitrogen isotopic ratio as a recorder for surface ocean nitrate utilization. Global Biogeochem. Cycles, 8, 103–116.
- Altabet, M. A. and J. J. McCarthy. 1985. Temporal and spatial variations in the natural abundance of <sup>15</sup>N in PON from a warm-core ring. Deep-Sea Res., *32*, 755–772.
- 1986. Vertical patterns in <sup>15</sup>N natural abundance in PON from the surface waters of warm-core rings. J. Mar. Res., 44, 185–201.

- Anderson, G. C., R. K. Lam, B. C. Booth and J. M. Glass. 1977. A description and numerical analysis of the factors affecting the processes of production in the Gulf of Alaska, University of Washington, Special Report No. 77 (M-77-40).
- Anderson, G. C., T. R. Parsons and K. Stephens. 1969. Nitrate distribution in the subarctic Northeast Pacific Ocean. Deep-Sea Res., 16, 329–334.
- Baker, E. T., H. B. Milburn and D. A. Tennant. 1988. Field assessment of sediment trap efficiency under varying flow conditions. J. Mar. Res., 46, 573–592.
- Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. Tech. Rep. NMFS SSRF-671, Natl. Oceanic and Atmos. Admin., Seattle, WA. 103 pp.
- Betzer, P. R., W. J. Showers, E. A. Laws, C. D. Winn, G. R. Di Tullio and P. M. Kroopnick. 1984. Primary productivity and particle fluxes on a transect of the equator at 153W in the Pacific Ocean. Deep-Sea Res., 31, 1–11.
- Bienfang, P. K. and D. A. Ziemann. 1992. The role of coastal high latitude ecosystems in global export production, *in* Primary Productivity and Biogeochemical Cycles in the Sea, P. G. Falkowski and A. D. Woodhead, eds., Plenum Press, NY, 285–297.
- Biscaye, P. E., C. N. Flagg and P. G. Falkowski. 1994. The shelf edge exchange processes experiment, SEEP-II: an introduction to hypotheses, results and conclusions. Deep-Sea Res., 41, 231–252.
- Brink, K. H. and T. J. Cowles. 1991. The coastal transition zone program. J. Geophys. Res., 96, 14,637–14,647.
- Broecker, W. S. and T.-H. Peng. 1982. Tracers in the Sea, Lamont-Doherty Geological Observatory, Columbia University, NY, 690 pp.
- Brown, R. M., K. L. Denman, G. A. Borstad and J. R. Parks. 1993. The use of satellite imagery to direct research ship sampling operations. Fish. Oceanogr., 2, 184–190.
- Brzezinski, M. A. 1985. The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. J. Phycol., 21, 347–357.
- Cochlan, W. P., P. J. Harrison and K. L. Denman. 1991. Diel periodicity of nitrogen uptake by marine phytoplankton in nitrate-rich environment. Limnol. Oceanogr., 36, 1689–1700.
- Degens, E. T., M. Behrendt, B. Gotthard and E. Reppmann. 1968a. Metabolic fractionation of carbon isotopes in marine plankton. II. Data on samples collected off the coast of Peru and Ecuador. Deep-Sea Res., 15, 11–20.
- Degens, E. T., R. R. L. Guillard, W. M. Sackett and J. A. Hellbust. 1968b. Metabolic fractionation of carbon isotopes in marine plankton. I. Temperature and respiration experiments. Deep-Sea Res., 15, 1–9.
- DeMaster, D. J. 1981. The supply and accumulation of silica in the marine environment. Geochim. Cosmochim Acta, 45, 1715–1732.
- Denman, K. L., H. J. Freeland and D. L. Mackas. 1989. Comparisons of time scales for biomass transfer up the marine food web and coastal transport processes, *in* Effects of Ocean Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment, R. J. Beamish and G. A. McFarlane, eds., Can. Spec. Publ. Fish. Aquat. Sci., 108, 255–264.
- Eppley, R. W. and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature, 282, 677–680.
- Fang, W. and W. W. Hsieh. 1993. Summer sea surface temperature variability off Vancouver Island from satellite data. J. Geophys. Res., 98, 14,391–14,400.
- François, R. and M. Altabet. 1992. Glacial to interglacial changes in surface nitrate utilization in the Indian sector of the Southern Ocean as recorded by sediment  $\delta^{15}$ N. Paleoceanogr., 7, 589–603.
- François, R., M. A. Altabet, R. Goericke, D. C. McCorkle, C. Brunet and A. Poisson. 1993. Changes in the δ<sup>13</sup>C of surface water particulate organic matter across the subtropical covergence in the SW Indian Ocean. Global Biogeochem. Cycles, 7, 627–644.

- Freeland, H. J., W. R. Crawford and R. E. Thomson. 1984. Currents along the Pacific coast of Canada. Atmosphere-Ocean, 22, 151–172.
- Freeland, H. J. and K. L. Denman. 1982. A topographically controlled upwelling center off southern Vancouver Island. J. Mar. Res., 40, 1069–1093.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N and S isotopic compositions. Limnol. Oceanogr., *33*, 1182–1190.
- Fry, B. and E. B. Sherr. 1984. <sup>13</sup>C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contr. Mar. Sci., 27, 15–47.
- Fry, B. and S. C. Wainwright. 1991. Diatom source of <sup>13</sup>C-rich carbon in marine food webs. Mar. Ecol. Prog. Ser., 76, 149–157.
- Ganeshram, R. S., T. F. Pedersen, S. E. Calvert and J. W. Murray. 1995. Large changes in oceanic nutrient inventories from glacial to interglacial periods. Nature, 376, 755–758.
- Hickey, B. M., R. E. Thomson, H. Yih and P. H. LeBlond. 1991. Velocity and temperature fluctuations in a buoyancy-driven current off Vancouver Island. J. Geophys. Res., 96, 10,507–10,538.
- Hinga, K. R., M. A. Arthur, M. E. Q. Pilson and D. Whitaker. 1994. Carbon isotope fractionation by marine phytoplankton in culture: The effects of CO<sub>2</sub> concentration, pH, temperature and species. Global Biogeochem. Cycles, 8, 91–102.
- Honjo, S. and K. W. Doherty. 1988. Large aperture time-series sediment traps: Design objectives, construction and applications. Deep-Sea Res., 35, 1415–1426.
- Ikeda, M. and W. J. Emery. 1984. A continental shelf upwelling event off Vancouver Island as revealed by satellite infrared imagery. J. Mar. Res., 42, 303–317.
- Laws, E. A., B. N. Popp, R. R. Bidigare, M. C. Kennicutt and S. A. Macko. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and [CO<sub>2</sub>]aq: Theoretical considerations and experimental results. Geochimica et Cosmochimica Acta, 59, 1131–1138.
- Libes, S. M. and W. G. Deuser. 1988. The isotope geochemistry of particulate nitrogen in the Peru upwelling area and the Gulf of Maine. Deep-Sea Res., *35*, 517–533.
- Liu, K.-K. and I. R. Kaplan. 1989. The eastern tropical Pacific as a source of <sup>15</sup>N-enriched nitrate in seawater off southern California. Limnol. Oceanogr., *34*, 820–830.
- Mackas, D. L. 1995. Interannual variability of the zooplankton community off southern Vancouver Island, *in* Climate Change and Northern Fish Populations, R. J. Beamish, ed., Can. Spec. Publ. Fish. Aquat. Sci., *121*, 603–615.
- Mackas, D. L., K. L. Denman and A. F. Bennett. 1987. Least squares multiple tracer analysis of water mass composition. J. Geophys. Res., 92, 2907–2918.
- Martin, J. H., G. A. Knauer, D. M. Karl and W. W. Broenkow. 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Res., 34, 267–285.
- Minagawa, M. and E. Wada. 1984. Stepwise enrichment of <sup>15</sup>N along food chains: Further evidence and the relationship between  $\delta^{15}$ N and animal age. Geochim. Cosmochim. Acta, 48, 1135–1140.
- Minagawa, M., D. A. Winter and I. R. Kaplan. 1984. Comparison of Kjeldahl and combustion methods for measurement of nitrogen isotope ratios in organic matter. Anal. Chem., 56, 1859–1861.
- Montoya, J. P. 1994. Nitrogen isotope fractionation in the modern ocean: Implications for the sedimentary record, *in* Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change, R. Zahn, M. Kaminski, L. D. Labeyrie and T. F. Pedersen, eds., Springer-Verlag, 259–279.
- Montoya, J. P., P. H. Wiebe and J. J. McCarthy. 1992. Natural abundance of <sup>15</sup>N in particulate nitrogen and zooplankton in the Gulf Stream region and warm-core ring 86A. Deep-Sea Res., *39* (Suppl. 1), S363–S392.

- Mullin, M. M., G. H. Rau and R. W. Eppley. 1984. Stable nitrogen isotopes in zooplankton: some geographic and temporal variations in the North Pacific. Limnol. Oceanogr., 29, 1267–1273.
- Nakatsuka, T., N. Handa, E. Wada and C. S. Wong. 1992. The dynamic changes in stable isotopic ratios of carbon and nitrogen in suspended and sedimented particulate organic matter during a phytoplankton bloom. J. Mar. Res., 50, 267–296.
- Nelson, D. M., P. Tréguer, M. A. Brzezinski, A. Leynaert and B. Quéguiner. 1995. Production and dissolution of biogenic silica in the ocean: Revised global estimates, comparison with regional data and relationship to biogenic sedimentation. Global Biogeochem. Cycles, 9, 359–372.
- Noriki, S. and S. Tsunogai. 1986. Particulate fluxes and major components of settling particles from sediment trap experiments in the Pacific Ocean. Deep-Sea Res., 33, 903–912.
- Pace, M. L., G. A. Knauer, D. M. Karl and J. H. Martin. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature, 325, 803–804.
- Parsons, T. R., L. F. Giovando and R. J. LeBrasseur. 1966. The advent of the spring bloom in the eastern subarctic Pacific Ocean. J. Fish. Res. Board Can., 23, 539-546.
- Parsons, T. R. and R. J. LeBrasseur. 1968. A discussion of some critical indices of primary and secondary production for large-scale ocean surveys. California Marine Resources Commission, CalCOFI, 12, 54–63.
- Rau, G. H., C. W. Sullivan and L. I. Gordon. 1991.  $\delta^{13}$ C and  $\delta^{15}$ N variations in Weddell Sea particulate organic matter. Mar. Chem., 35, 355–369.
- Rau, G. H., R. E. Sweeney and I. R. Kaplan. 1982. Plankton <sup>13</sup>C/<sup>12</sup>C ratio changes with latitude: differences between northern and southern ocean. Deep-Sea Res., 29, 1035–1039.
- Rau, G. H., T. Takahashi and D. J. Des Marais. 1989. Latitudinal variations in plankton  $\delta^{13}$ C: implications for CO<sub>2</sub> and productivity in past oceans. Nature, *341*, 516–518.
- Redfield, A. C., B. H. Ketchum and F. A. Richards. 1963. The influence of organisms on the composition of sea water, *in* The Sea, M. N. Hill, ed., 2, NY, 26–77.
- Robertson, J. E., C. Robinson, D. R. Turner, P. Holligan, A. J. Watson, P. Boyd, E. Fernandez and M. Finch. 1994. The impact of coccolithophore bloom on oceanic carbon uptake in the northeast Atlantic during summer 1991. Deep-Sea Res., 41, 297–314.
- Sackett, W. M. 1991. A history of the  $\delta^{13}$ C composition of oceanic plankton. Mar. Chem., 34, 153–156.
- Saino, T. 1992. <sup>15</sup>N and <sup>13</sup>C natural abundance in suspended particulate organic matter from a Kuroshio warm-core ring. Deep-Sea Res., 39 (Suppl. 1), S347–S362.
- Saino, T. and A. Kattori. 1980. <sup>15</sup>N natural abundance in oceanic suspended particulate matter. Nature, 283, 752–754.
- Sambrotto, R. N. and C. J. Lorenzen. 1987. Phytoplankton and primary production, in The Gulf of Alaska: Physical Environment and Biological Resources, D. W. Hood and S. T. Zimmerman, eds., Ocean Assessments Division, Alaska Office, NOAA, US Minerals Management Service, 249–282.
- Staples, G. 1993. Satellite AVHRR observations of the intensification of the shelf break Current during an upwelling event off Vancouver Island. M. Sc. thesis, University of British Columbia.
- Strickland, J. D. H. and T. R. Parsons. 1972. A practical handbook of sea water analysis. Can. Bull. Fish. Aquat. Sci., *167*, 311 pp.
- Suess, E. 1980. Particulate organic carbon flux in the ocean-surface productivity and oxygen utilization. Nature, 288, 260–263.
- Thomson, R. E. and J. F. R. Gower. 1985. A wind-induced mesoscale eddy over the Vancouver Island continental slope. J. Geophys. Res., *90*, 8981–8993.
- Thomson, R. E., B. M. Hickey and P. H. LeBlond. 1989. The Vancouver Island Coastal Current: Fisheries barrier and conduit, *in* Effects of Ocean Variability on Recruitment and an Evaluation of

Parameters used in Stock Assessment Models, R. Beamish and G. McFarlane, eds., Spec. Publ. Fish. Aquatic Sci., 108, 265-296.

- Thomson, R. E. and D. M. Ware. 1996. A current velocity index of ocean variability. J. Geophys. Res., 101, 14,297-14,310.
- Tsunogai, S. and S. Noriki. 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.
- U. S. GOFS Planning Office. 1989. Sediment trap technology and sampling. U. S. GOFS Planning Report Number 10, 94 pp.
- Venkatesan, M. I. 1988. Occurrence and possible sources of perylene in marine sediments-a review. Mar. Chem., 25, 1–27.
- Wada, E. and A. Hattori. 1991. Nitrogen in the Sea: Forms, Abundances, and Rate Processes, CRC Press, 208 pp.
- Wada, E., M. Terazaki, Y. Kabaya and T. Nemoto. 1987. <sup>15</sup>N and <sup>13</sup>C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Res., 34, 829-841.
- Walsh, J. J., G. T. Rowe, R. L. Iverson and C. P. McRoy. 1981. Biological export of shelf carbon is a sink of the global CO<sub>2</sub> cycle. Nature, 291, 196-201.
- Wu, J., S. E. Calvert and C. S. Wong. 1996. Nitrogen isotope variations in the subarctic northeast Pacific: relationships to nitrate utilization and trophic structure. Deep-Sea Res. (in press).