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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 changes in subarctic primary productivity

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Abstract

An extended time series of particle fluxes at 3800 m was recorded using automated sediment traps moored at Ocean Station Papa (OSP, 50° N, 145° W) in the northeast Pacific Ocean for more than a decade (1982–1993). Time-series observations at 200 and 1000 m, and short-term measurements using surface-tethered free-drifting sediment traps also were made intermittently. We present data for fluxes of total mass (dry weight), particulate organic carbon (POC), particulate organic nitrogen (PON), biogenic Si (BSi), and particulate inorganic carbon (PIC) in calcium carbonate. Mean monthly fluxes at 3800 m showed distinct seasonality with an annual minimum during winter months (December–March), and maximum during summer and fall (April–November). Fluxes of total mass, POC, PIC and BSi showed 4-, 10-, 7- and 5-fold increases between extreme months, respectively. Mean monthly fluxes of PIC often showed two plateaus, one in May–August dominated by < 63 µm particles and one in October–November, which was mainly > 63 µm particles. Dominant components of the mass flux throughout the

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year were CaCO₃ and opal in equal amounts. The mean annual fluxes at 3800 m were 32 ± 9 g dry weight g m⁻² yr⁻¹, 1.1 ± 0.5 g POC m⁻² yr⁻¹, 0.15 ± 0.07 g PON m⁻² yr⁻¹, 5.9 ± 2.0 g BSi m⁻² yr⁻¹ and 1.7 ± 0.6 g PIC m⁻² yr⁻¹. These biogenic fluxes clearly decreased with depth, and increased during "warm" years (1983 and 1987) of the El Niño, Southern Oscillation cycle (ENSO). Enhancement of annual mass flux rates to 3800 m was 49% in 1983 and 36% in 1987 above the decadal average, and was especially rich in biogenic Si. Biological events allowed estimates of sinking rates of detritus that range from 175 to 300 m d⁻¹, and demonstrate that, during periods of high productivity, particles sink quickly to deep ocean with less loss of organic components. Average POC flux into the deep ocean approximated the "canonical" 1% of the surface primary production. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

Ocean Station Papa (OSP) at 50°N 145°W in the northeastern subarctic Pacific Ocean has been an oceanographic time-series station since 1956 and since then, subject to sustained monitoring of physical, chemical and biological parameters (Whitney and Freeland, 1999). Concentrations of macronutrients and chlorophyll a, and rates of primary productivity (e.g. Wong et al., 1995, 1998) have been monitored as indicators of biological production. In the late 1970s, substantial improvements in the automation and mooring of sediment traps enabled the collection of sedimenting material over extended periods. These traps have now become a reliable tool with which to monitor changes in the biogeochemistry of the ocean, although data from extended periods are only now becoming known. The subarctic northeast Pacific is of particular interest as one of several "high nutrient-low chlorophyll" (HNLC) open ocean areas in which chlorophyll *a* concentration is relatively low and constant year round, and where nitrate is never depleted. However, primary productivity (Parsons and Lalli, 1988; Wong et al., 1995) and zooplankton biomass (Parsons and Lalli, 1988) do show more "typical" seasonal variations, suggesting that the downward flux of biogenic materials also might vary seasonally.

In the open subarctic Pacific Ocean, the weathership program terminated in 1981 and research cruises are now relatively infrequent. Therefore, moored sediment traps are one of the few available tools with which to monitor fluxes of carbon and other materials continuously. Variations in vertical transport of biogenic materials on the scale of decades could be important indicators of shifts in primary production and thus potential ocean-climate CO_2 interactions. Globally, there are very few sites of long time series for deep-water particle flux studies (Lampitt and Antia, 1997), an example being the Sargasso Sea site which commenced in 1978 (Deuser and Ross, 1980). In recent years, the Joint Global Ocean Flux Study (JGOFS) has initiated sediment trap stations off Bermuda (Michaels and Knap, 1996) and at the ALOHA Station near Hawaii (Karl et al., 1996).

This paper reports the first substantial time series (1982–1993) of particle fluxes in the NE subarctic Pacific, and is one of few such extended data sets in HNLC waters that can correlate primary production to export production (Miller et al., 1991; Boyd et al., 1998).

2. Methods

2.1. Sampling location and depths

The time-series station of moored sequential sediment traps was initiated in September 1982 at OSP (50°N 145°W), , as a joint program between the Institute of Ocean Sciences (IOS, within the Canadian Department of Fisheries and Oceans) and Woods Hole Oceanographic Institution. Traps were deployed at 200, 1000 and 3800 m depth on a Mooring line. Since 1986, the time series has been operated by the Centre for Ocean Climate Chemistry at IOS. The program has expanded to include sediment trap moorings at several stations between OSP and the British Columbia coast. In recent years the flux studies at OSP have been undertaken in close collaboration with the Department of Earth and Ocean Sciences at the University of British Columbia as a part of the Canadian Joint Global Ocean Flux Study (CJGOFS).

2.2. Moored sequential sediment traps

The types of automated sequential sediment traps used in these studies and the chronology of deployments are summarized in Table 1. Deployment periods varied between 6 and 12 months, depending on availability of ship time. For the period 1982–1989, PARFLUX Mark 5 traps (Honjo and Doherty, 1988) were used, which permitted a series of 12 consecutive 16-day collection periods. Polyethylene collecting bottles were filled with seawater supplemented with 1 g NaN₃ as a preservative, and 5 g l⁻¹ NaCl in order to increase the density of the supernatant liquid and so minimize diffusive loss of material. Sodium azide is thought to inhibit decomposition of organics less than formaldehyde (Knap et al., 1996), but since this program began before much of the current studies on effectiveness of preservatives, and because it is important to retain consistent protocols in time-series measurements, the choice of preservatives was not altered.

The trap deployed at 1000 m is within the oxygen minimum at OSP, and the 3800 m deployment was positioned 500 m above the sea floor (4240 m depth) in order to avoid the effects of the nepheloid layer. After recovery of the traps, samples were removed from the carousel, capped, and kept at 4° C until they could be processed. Storage periods after recovery were kept short, typically less than 3 months.

2.3. Surface-tethered free-drifting sediment traps

Downward fluxes of biogenic material in the upper 1000 m also were collected intermittently during research cruises to OSP. These measurements were made over periods of much shorter duration (2–5 days) using a free-drifting trap array (Wong, 1989) suspended from a string of floatation buoys (Benthos) equipped with a radio beacon (NOVATEC) and satellite transmitter (ARGOS). The array consisted of a series of nine pairs of cylindrical bongo-type traps (PVC, 12.5 cm diameter \times 45 cm height, 5.5 l volume), attached at 100-m intervals on Kevlar line which was weighted at the bottom. The traps had baffle-grids at the top of each cylinder and in a bottom

Deployment	Sampling period		Trap	Number	Exposure	Comments
	Start y/m/d	Finish y/m/d	type	of rotations	(days)	
200 m						
Papa 15	89/5/8	89/9/29	Mark 5	12	12	
Papa 17	90/5/21	90/11/11	Mark 7	12	15	
Papa 20	92/4/10	92/9/7	Mark 7	21	17	Lost mooring
Papa 22	93/5/24	94/5/16	Mark 7	21	17	C
1000 m						
Papa 2	83/3/27	83/10/5	Mark 5	12	16	
Papa 6	84/11/20	85/5/4	Mark 5	6	12	Sample 6 for 105 days
Papa 7	85/5/10	85/10/25	Mark 5	12	14	
Papa 8	85/11/13	86/4/23	Mark 5	12	14.5	
Papa 15	89/5/8	89/9/29	Mark 5	12	12	
Papa 17	90/5/21	90/11/11	Mark 6	12	15	
Papa 20	92/4/10	92/9/7	Baker	10	15	Lost mooring
Papa 22	93/5/24	94/5/16	Mark 7	21	17	0
3800 m						
Papa 1	82/9/23	83/3/18	Mark 5	12	15	
Papa 2	83/3/27	85/10/5	Mark 5	12	16	
Papa 3	83/10/14	84/4/23	Mark 5	12	16	Failed timer
Papa 4	84/5/2	84/8/24	Mark 5	12	14	
Papa 5	84/8/28	84/11/12	Mark 5	12	-	Failed timer
Papa 6	84/11/20	85/4/13	Mark 5	12	12	
Papa 7	85/5/10	85/10/25	Mark 5	12	14	
Papa 8	85/11/13	86/4/23	Mark 5	12	14.5	Failed after 7
Papa 9	86/5/25	86/8/31	Mark 5	12	14	Missing last 6 bottles
Papa 10	86/10/19	87/4/4	Mark 5	12	15	e
Papa 11	87/4/7	87/9/22	Mark 5	12	14	
Papa 12	87/10/2	88/5/6	Mark 5	12	18	
Papa 13	88/5/10	88/11/24	Mark 5	12	16.5	Plug? (9, 10, 11, 12 empty)
Papa 14	88/12/11	89/5/4	Mark 5	12	12	
Papa 15	89/5/8	89/9/29	Mark 5	12	12	
Papa 16	89/10/13	90/5/2	Mark 6	12	16.5	
Papa 17	90/5/21	90/11/11	Mark 6	12	15	
Papa 18	91/3/5	91/10/7	Mark 7	11	_	Lost mooring
Papa 19	91/10/23	92/4/15	Mark 7	13	13.5	Failed timer
Papa 20	92/4/10	92/9/7	Mark 7	21	15	Lost mooring
Papa 21	92/9/26	93/5/10	Mark 7	21	14	c
Papa 22	93/5/24	94/5/16	Mark 7	21	17	

Table 1	
List of deployments of sediment traps moored at 200, 10	000 and 3800 m at OSP for 1982-1993

Mark 5: collecting area = 1.1 m^2 ; minimum hole size = 59 mm.

Mark 6: collecting area = 0.5 m^2 ; minimum hole size = 30 mm.

Mark 7: collecting area = 0.5 m^2 ; minimum hole size = 28 mm.

Baker: see Baker and Milburn (1983).

cup of 11 volume that was supplemented with 1 g l^{-1} NaN₃ and 5 g l^{-1} NaCl. Rhodamine B dye was routinely added to the sample cups to provide a visible check for sample and preservative loss, since loss of material occurred occasionally when traps were being recovered during high winds. Prior to deployment, traps were rinsed with 5% HCl, then with milliQ water. After recovery, the contents of each PVC cylinder was passed through 0.5- or 1.0-mm Nitex netting to remove zooplankton swimmers (visible detrital material was not removed) and then filtered onto precombusted (1 h at 450°C) 24- or 47-mm silver filters of 0.8-µm pore size. Particulate forms of inorganic C, organic C and N were measured as described below for sequential trap samples.

2.4. Laboratory treatment of sequential trap samples and analysis

In the shore laboratory, samples were wet-sieved through 1-mm and 63-µm mesh screens, and split into aliquots using an Erez-Honjo precision rotary splitter (Honjo, 1978) or a Folsom plankton splitter. After 1986, the procedure was changed so that samples were not size-fractionated (except for sieving to remove swimmers), so that only total flux was recorded. Particulate samples were split into $\frac{1}{4}$, $\frac{1}{16}$ or $\frac{1}{64}$ aliquots for analysis, distribution or archiving. Between 1982 and 1986, samples were sieved for each of the size fractions > 1 mm, 63–1000 µm and < 63 µm, and these data were summed to provide total flux estimates.

Aliquots were filtered onto preweighed 47-mm polycarbonate (0.8 or $1.0 \,\mu$ m, Nuclepore or Poretics) or precombusted (450°C for 1 h) and preweighed silver (0.8 μ m, Poretics) filters, rinsed lightly with deionized water, then dried at 50–60°C for 24 h. Filters were then reweighed to provide total mass (dry weight) flux measurements.

 $CaCO_3$ was determined as the difference between this first weighing and a second weighing following a process of decalcification with 4% HCl for 20 min, rinsing with distilled water and drying. Either the whole or a portion of the decalcified filter was analyzed for POC and PON by combustion at 980°C using a Perkin-Elmer 240 or a CEC 440 Elemental Analyzer. Seawater samples, typically 5-l volume, were also filtered onto silver filters (0.8 μ m, 47 mm Poretics) and combusted for POC and PON measurements.

Biogenic Si was converted to reactive dissolved silicate by the soda hydrolysis technique of Hurd (1972) and modified by DeMaster (1981) as follows. About 5–50 mg of dried material was placed in a 50-ml polypropylene centrifuge tube containing 50 ml of 0.1 N Na₂CO₃ solution at pH 11.2, and digested in a water bath at 85°C for 2 h. The mixture was centrifuged (2000 rpm, 5 min), and 1 ml of the supernatant liquid was diluted to 25 ml with distilled water. The final solution was analyzed for reactive silicate using a Technicon AutoAnalyzer (Barwell-Clarke and Whitney, 1996). A blank correction with unused filters was found to be < 1% (< 5% for pre-1986 measurements) of typical sample signals. Data were expressed as weight of Si, although opal (SiO₂ · 0.4H₂O (Mortlock and Froelich, 1989)) constitutes a much higher portion (2.4 times greater) of the total mass flux.

2.5. Swimmers in trap samples

Migrating zooplankton are a persistent problem in sediment trap samples. In the vicinity of OSP, zooplankton can migrate to a depth of 700 m (Goldblatt et al., 1999) influencing trap samples to that depth. In 1000 and 3800 m, only rare events (pteropod swarms) introduced swimmers into samples, and these were generally easy to separate because there was less organic C to produce mucous clumping of material. However at 200 m, there were frequently several hundred zooplankton (mainly copepods, amphipods and pteropods) in a sample. This biomass overpowered the preservative solution, which resulted in some decomposition of these migrators (an obvious rotting smell was often present) and suspected contamination of samples with released lipids and body fragments. The high C : N ratios (up to 22) measured in 200 m samples in 1993 arose from this problem. After careful reanalysis of several samples, it is evident that high C : N is a result of lipid contamination rather than incomplete dissolution of $CaCO_3$.

Swimmers and trap particles were sporadically viewed under various microscopes. Identifiable organisms were divided into dominant groups that included zooplankton such as copepods, amphipods, foraminifera, radiolarians and pteropods, and phytoplankton such as diatoms and their frustule fragments.

3. Results

Measurements made during the period 1982–1993 for the moored sediment traps at OSP are summarized in Fig. 1. Particle fluxes are shown at 200, 1000 and 3800 m for (a) mass in dry weight, (b) particulate organic carbon (POC), (c) particulate organic nitrogen (PON), (d) particulate inorganic carbon (PIC), commonly referred to as calcium carbonate-carbon, and (e) particulate biogenic Si (BSi). When results of biogenic analyses are summed (CaCO₃, opal, organic C and N), recoveries are $86 \pm 12\%$ for 200-m trap samples (n = 53), $94 \pm 10\%$ for 1000-m samples (n = 104) and $95 \pm 8\%$ for 3800-m samples (n = 200). The balance of the material will be biogenic elements that were not analyzed (H, O, S, P, etc) and a small amount of lithogenic material. The improved recovery with depth likely arises from the diminished influence of organic C, thus less unaccounted for material will be present.

From these data, mole ratios of particles were calculated for (a) POC : PON, (b) POC : PIC, (c) POC : BSi and (d) PIC : BSi from traps moored at 200, 1000 and 3800 m at OSP for 1982–1993 (Fig. 2). Abnormally high POC : PON ratios found in the 200-m trap samples in 1993 are believed to arise from the large number of swimmers that were caught. These organisms (mainly pteropods, copepods and amphipods) likely lost lipids during their storage in situ, which artificially enriched the organic C content of the samples. Particulate materials were oily and smelled fishy.

All data were averaged to provide seasonal fluxes of each biogenic component at the three sampled depths (Fig. 3). Yearly fluxes (Table 2) were summed when a full year was sampled, or interpolated for years with enough sampling to provide a reasonable estimate. The only year for which a flux was estimated in which there was less

than 8 months of sampling, was 1993 at 1000 m. In this year, the 5 months that were sampled covered most of the high flux period (May-September). Interpolations assumed that missing fluxes were averages of adjacent samples, or were estimated from long-term averages (winter only). The annual mass flux at 3800 m depth for



Fig. 1. Particle fluxes of (a) mass in dry weight, (b) POC, (c) PON, (d) PIC and (e) BSi into sediment traps moored at 200, 1000 and 3800 m for the period 1982–1993 at OSP.



Fig. 1 Continued.

1982–1993 averaged to $32 \pm 9 \text{ gm}^{-2} \text{ yr}^{-1}$. Large interannual variations were observed, with a factor of 2 between lows of 19 and 22 g m⁻² yr⁻¹ in 1984 and 1993, and highs of 48 and 44 g m⁻² yr⁻¹ in 1983 and 1987. The total mass fluxes at 200 and 1000 m were 60 \pm 21 and 52 \pm 16 g m⁻² yr⁻¹, respectively. Similar changes in fluxes are noted for major biogenic fractions (Table 2).

Molar ratios of the average monthly fluxes were computed as for the time-series data (Fig. 4). High POC values at 200 m (see Table 2) in 1990 and 1993 yield anomalous POC : PON, POC : PIC and POC : BSi ratios because monthly ratios are based on only 3 years of data.

Collections by free-floating traps arrays, deployed at 50–1000 m, were made intermittently. All data from 1987 to 1993 (Fig. 5) have been averaged for particle fluxes of (a) mass in dry weight, (b) POC, (c) PON and (d) PIC, expressed in mg m⁻² d⁻¹. These data provide details on changes in freshly trapped particles as they sink out of the surface layer.

The agreement between fluxes obtained by surface-tethered free-drifting trap arrays and moored sediment traps is variable (Fig. 6). POC and PON fluxes at 200 m were more variable and higher by a factor of as much as 5 in 1989, but there was much better agreement for the high 1990 fluxes. Free-drifting traps can only be deployed in mild weather, so their collections may be biased towards periods of higher productivity during periods of calm. The fluxes at 1000 m were comparable within a factor of 2. Mass flux and CaCO₃ fluxes are in better agreement (within a factor of 2) for collections by free-floating and moored traps, since CaCO₃ is not as readily



Fig. 2. Interannual changes in the molar ratios of (a) POC : PON, (b) POC : PIC, (c) POC : BSi and (d) PIC : BSi in particles collected by sediment traps moored at 200, 1000 and 3800 m at OSP between 1982 and 1993.



Fig. 3. Monthly averaged fluxes (mg m⁻² d⁻¹) into sediment traps moored at 200, 1000 and 3800 m at OSP between 1982 and 1993 for (a) mass in dry weight, (b) POC, (c) PON, (d) PIC and (e) BSi.



Fig. 3. Continued.

remineralized as the biogenic elements of carbon and nitrogen. This suggests that more work is needed on the decomposition of POC and PON within traps in order to improve our understanding of the biological pump, and more in situ storage studies are required to further evaluate decay of organic components.

4. Discussion

4.1. The average annual cycle

Away from the influence of terrigenous inputs, the vertical detritus flux mediated by ocean biology is the most important transfer process in the open ocean of the subarctic Pacific. The biological pump in the upper ocean, as the mechanism of pelagic consumption and production of biologically active elements, transfers these biogenic compounds from the surface into deeper waters (Bishop, 1989; Longhurst, 1995). Subarctic circulation, dominated by an estuarine pattern of fresher surface waters over saline deep waters, has a strong pycnocline that typically limits diapycnal vertical exchange between the surface and deeper layers (Matear and Wong, 1997). Thus, the biological pump controls the profile gradients of these biogenic elements

Year	Months sampled	Total flux	POC $(g m^{-2} yr^{-1})$	PIC $(g m^{-2} yr^{-1})$	$PON (g m^{-2} yr^{-1})$	BSi $(g m^{-2} yr^{-1})$
200 m						
1989	8	45.2	3.36	2.42	0.40	7.27
1990 ^a	11	75.6	6.75	4.86	0.79	8.32
1993 ^a	8	58.9	9.77	3.43	0.78	5.20
Avg. ^a		59.9	6.63	3.57	0.66	6.93
S.D.		12.4	2.62	1.00	0.18	1.30
1000 m						
1983	8	78.5	4.82	3.20	0.69	15.7
1984	2	-	-	-	_	-
1985	12	53.3	2.95	2.49	0.34	9.23
1986	4	-	-	-	-	_
1989	8	44.9	1.65	2.21	0.23	8.71
1990	11	47.1	1.74	3.20	0.26	6.35
1993	5	35	2.4	1.8	0.27	5.0
Avg.		51.7	2.71	2.59	0.36	9.00
S.D.		16.4	1.29	0.61	0.19	4.12
3800 m						
1982	4	-	-	-	-	-
1983	12	48.2	2.46	2.23	0.35	8.80
1984	10	19.2	0.83	1.09	0.12	2.92
1985	12	30.4	0.82	1.72	0.12	5.18
1986	8	34.2	1.04	2.06	0.12	5.62
1987	12	44.1	1.10	2.71	0.14	7.88
1988	10	30.4	0.93	1.00	0.13	7.74
1989	12	30.7	0.83	1.45	0.12	6.94
1990	11	32.4	0.85	2.09	0.12	4.45
1991	0	-	-	-	_	-
1992	4	-	_	_	_	_
1993	11	22.1	1.29	1.25	0.16	3.76
Avg.		32.4	1.13	1.73	0.15	5.92
S.D.		9.2	0.52	0.58	0.07	2.03

Table 2Annual fluxes of biogenic materials to 200, 1000 and 3800 m at OSP from 1982 to 1993

^aSwimmers contaminated 200 m trap samples in 1990 and 1993.

through the vertical detritus flux. Fluxes of all biogenic materials show distinct seasonality related to surface water biology, despite this being an HNLC oceanic area.

The pattern of annual particle fluxes to 3800 m at OSP shows a winter minimum in total mass flux of 38 mg m⁻² d⁻¹ in February and summer maxima of 150 mg

Fig. 4. Monthly averaged molar ratios of (a) POC: PON, (b) POC: PIC (c) POC: BSi and (d) PIC: BSi in particles collected by sediment traps moored at 200, 1000 and 3800 m at OSP between 1982 and 1993.





Fig. 5. Changes with depth of particle fluxes into surface-tethered free-drifting sediment traps over the depth range 50–1000 m. Particle fluxes are averaged for short-duration deployments in 1987, 1988 and 1993 at OSP for (a) mass in dry weight, (b) POC, (c) PON, (d) PIC.

 $m^{-2} d^{-1}$ in May/June and in August (Fig. 3). Fluxes in OSP waters are dominated by biological processes, with little influence from terrigenous or aeolean inputs. This contrasts with records for the North Atlantic near the Canary Islands, where Saharan dust inputs produce a winter-spring maximum (Neuer et al., 1997). Fluxes to 3800 m at OSP increase rapidly from February to reach a level transport rate between May and September. Mass flux in subarctic Pacific waters is greater than in the North Atlantic and Equatorial Pacific, about equal to that of the Sea of Okhotsk, and less than that observed in the Bering Sea (Honjo et al., 1995). However, biogenic materials are a smaller fraction of particles in the Bering and Okhotsk Seas, areas where terrestrial inputs are probable owing to the proximity of land. The average mass flux at OSP is 52 g m⁻² yr⁻¹ at 1000 m and 32 g m⁻² yr⁻¹ at 3800 m, whereas at 48°N in the Atlantic vertical transport averages $26 \text{ g m}^{-2} \text{ yr}^{-1}$ at 2 km, and from a series of stations across the equatorial Pacific at depths of 2200-4400 m, average fluxes are $28.5 \text{ g m}^{-2} \text{ yr}^{-1}$ (range of 7.8–34.8 g m⁻² yr⁻¹ (Honjo et al., 1995)). In the Bering Sea, high fluxes of 52.4 g m⁻² yr⁻¹ were measured at 3137 m, and about 10–15% of this appears to be non-biogenic compared to less than 5% at OSP. The maximum POC flux, based on monthly averages over 1982-1993, occurs in August at $0.27 \text{ g C m}^{-2} \text{ month}^{-1}$ and the minimum in February at $0.026 \text{ g C m}^{-2} \text{ month}^{-1}$.



Fig. 6. Particle fluxes over the period 1989–1990 measured at 200, 1000 and 3800 m using moored traps, and fluxes derived from surface-tethered free-drifting traps at 200 and 1000 m. Data collected from moored traps (—) represent mean flux over a 2-week sequential collection. Data collected by free-drifting traps are given as measurements collected by each of the dual collectors (•) over short-term (3–5 days) deployments.

meaning a 10-fold change through the annual cycle. Low flux occurred during the four winter months of December–March with a total of 0.1 g C m⁻² over this period, and the peak productive period lasted from April to October with a total flux of 0.83 g C m⁻², which accounted for 78% of the annual flux into the deep ocean.

At 200 m, a distinct spring pulse is observed in all parameters. Of the material that sinks into the deep ocean, PIC appears at subsequent depths most rapidly, arriving at 3800 m in June (Fig. 3d). Opal shows some bimodality at depth, with peak fluxes in May at all depths, July at 1000 m and August at 3800 m (Fig. 3e). POC and PON (Fig. 3b and c) show a large peak at 200 m in May, but do not show peaks in deep ocean until late summer. Bishop et al. (1999) have found that POC accumulates in the water column through spring and summer to a depth greater than 500 m. It appears, therefore, that spring production is not being transferred efficiently to the deep ocean; rather, a substantial portion of this material is being left in the water column following the intense spring grazing period (Goldblatt et al., 1999). The mean annual POC fluxes arriving at 200, 1000 and 3800 m were 6.6 ± 2.6 , 2.7 ± 1.3 and 1.1 ± 0.5 g C m⁻² yr⁻¹, respectively; the mean PON flux equaled 0.66 ± 0.18 , 0.36 ± 0.19 and 0.15 ± 0.07 g N m⁻² yr⁻¹, respectively (Table 2).

The flux of biogenic Si is closely correlated with sinking POC. The annual BSi fluxes arriving at 200, 1000 and 3800 m were 6.9 ± 1.3 , 8.7 ± 3.6 and 5.9 ± 2.0 g Si m⁻² yr⁻¹. The BSi maximum and minimum fluxes were 0.90 and 0.17 g Si m⁻² month⁻¹ in August and February, respectively. The winter months (December-March) accounted for 1 g Si m⁻² or 15% of the annual budget, and the productive spring-summer period (May-October) accounted for 4.7 g Si m⁻² or 72%, consistent with other biogenic fluxes. On an annual basis, opal is the fraction of the particulate material that is most efficiently transferred to depth, 78% of the 1000 m flux reaching 3800 m compared with 69% of PIC and only 40% of POC.

Along with opal, CaCO₃ flux is a major component of the total mass flux of sedimented material at OSP, arising mainly from coccolithophores, pteropods and for a minifera. The annual PIC fluxes at 200, 1000 and 3800 m were 3.6 ± 1.0 , 2.6 ± 0.6 and 1.7 ± 0.6 g C m⁻² yr⁻¹, respectively. The high flux at 200 m was due largely to a major episodic flux of foraminifera in 1990. The sedimentation of PIC was more uniform throughout the year with spring to early fall producing 62% of the annual flux to 3800 m, or about 1.3 g C m⁻², and the winter 12% or 0.25 g C m⁻². Peak sedimentation occurs in June at $0.29 \text{ g C m}^{-2} \text{ month}^{-1}$, about seven times higher than the February low at 0.04 g C m⁻². A secondary peak occurred in November of 1982, 1985 and 1987, which increased the decadal average for that month to that of September and October. The annual PIC flux at OSP is as large as that in the deep North Atlantic at the 4000 m level at 34°N and 48°N (about 1.6 and 1.9 g C m⁻² yr⁻¹, respectively; Honjo and Manganini, 1993). The PIC production and fluxes were similar in both temperate oceans, although the net accumulation in the ocean bottom was different for the two oceans because of post-deposition dissolution (Archer, 1996). In contrast with the North Atlantic and Equatorial Pacific, where CaCO₃ is the largest component (Honjo et al., 1995), the flux at OSP has equal amounts of CaCO₃ and opal (44% each at 3800 m). Opal is by far the major component of settling particles in the Bering and Okhotsk Seas (Honjo et al., 1995) which, like the NE subarctic Pacific, are areas rich in dissolved silicate.

The mass flux, averaging $32 \text{ g m}^{-2} \text{ yr}^{-1}$ at 3800 m at OSP, was about 40% higher than the global average at 2000 m (Lampitt and Antia, 1997). Both the POC and PIC

fluxes at 3800 m for OSP are about the same as the global average values at 2000 m, but the BSi flux is 3.5 times higher in subarctic waters.

4.2. 1982–1993 time-series measurements

Episodic fluxes occur in time-series measurements as short-duration events with fluxes substantially higher than that expected from the normal seasonal trends, and are caused mainly by the increase in biological activity in the upper ocean due to higher levels of diatom or coccolithophore growth, or elevated grazing by salps, copepods, pteropods or foraminifera. This definition differs from that of Honjo and Manganini (1993), who referred to a "particle bloom episode" that lasted over a hundred days in the North Atlantic. In subarctic events, which are identified by high mass fluxes, calcareous population explosions and diatom blooms do not necessarily occur at the same time. Major episodic events were identified in October 1982, late July–August 1983, May 1984, May–June 1986, August–September 1988, June–July 1990 and May–June 1993, two events in April–May and November 1985 and in April and June–July 1989, and four unusual events in April, June, August and November 1987 (Fig. 1). For POC, PON, PIC and BSi, the episodic events all occurred in the same periods as the mass flux, suggesting that biological events in surface waters were the main cause of the episodicity.

Unusual episodic events have occurred where pteropods have appeared alive in large quantities at 3800 m. In November 1986, swarms of the pteropod *Clio* sp. were caught, and in October and November 1987, even larger swarms of over 400 large *Clio* sp. per cup were found. Another pteropod, *Limacina* sp., also was found in numbers of over 100 per cup in December 1988 and July–September 1989. A similar persistent *Clio* sp. event was found in 1993, but in only the 200-m trap. These aragonite flux events, although not included in the analytical scheme because they were removed as swimmers, could become another significant mechanism in transferring biogenic elements to the deep ocean.

PIC fluxes to 3800 m tended to be elevated in May–June of the year (7 of 9 years showed spring peaks). Additional peak fluxes were also observed in late summer or fall (1983, 1985, 1987, 1990). Where size-fractionated data were available, the tendency was for the majority of the PIC to be in $< 63 \mu m$ particles in spring, and for the larger size fractions to dominate in late summer and fall. November fluxes in 1985 and 1987 were due distinctly to larger particles, typically foraminifera. Thus if coccolithophores are an important component of this material, they must be so in spring. Recent counts of phytoplankton from OSP confirm that the coccolithophore *Emiliana huxleyi* was very abundant in June 1998 (Jennifer Putland, pers. comm.)

Episodic changes and increased fluxes occurred in the Sargasso Sea (Deuser, 1986; Berger et al., 1989) for 1981 (significantly), 1982 and 1983. A three-year sustained increase in fluxes occurred between 1990 and 1992 at Station ALOHA in the subtropical Central Pacific, and was associated with ENSO events. However, the correlation between primary production and particle fluxes was poor (Karl et al., 1996). Strong coherence between production and particle flux was not found in the Bermuda time-series station in the subtropical Atlantic (Michaels and Knap, 1996). The records of OSP in the subarctic Pacific perhaps indicate a better coupling between primary production, particle fluxes and ENSO events, possibly due to a stronger ocean-atmosphere interaction on subarctic processes.

Since 200 m trap collections have been sporadic, and are subject to contamination from swimmers, little can be conclusively drawn from this data record. Perhaps the most striking feature at this depth is the large PIC flux of 75 mg C m⁻² d⁻¹ in May 1990. This event resulted in increased PIC fluxes to 1000 and 3800 m within one sampling period of 14.5 days. Similar PIC peak fluxes were seen in June 1989 and 1993 (Fig. 1d) at depth.

Longer observations at 1000 m show the highest flux in summer 1983, an event coincident with the strong El Niño of that year. This anomalous transport to the deep ocean was rich in POC, PON and BSi but not PIC, which suggests this was a period of unusual diatom growth. Although measurements in the mixed layer at OSP were sporadic in the early 1980s, Wong et al. (1998) show that El Niño periods produce higher nitrate uptake, more solar radiation, and shallower mixed layers. If, under such conditions, high primary production of 600–900 mg C m⁻² d⁻¹ could be sustained (Wong et al., 1995), then 6–9% of the production from August 1983 would have to reach 1000 m depth. This is much higher than the average of 2% that reaches 1000 m on an annual basis, and suggests that a more efficient transport of organic material occurred. Iseki (1981) found that salps can contribute substantially to particle transport in the NE Pacific and that the fast sinking rate of their fecal pellets results in less loss to particles between 200 and 900 m than observed in the OSP time series.

ENSO enhancement was prominent at 3800 m with a dominant peak in 1983 and higher than average fluxes in 1987. Annual mass fluxes showed 49 and 36% increases in 1983 and 1987, respectively (Table 2). These years showed especially high fluxes of POC (2.3-fold increase in 1983; none in 1987) and BSi (1.5-fold increase in 1983, 1.3-fold increase in 1987), which again suggests that diatom production was much higher during these years. PIC fluxes were enhanced by 29% in 1983 and 57% in 1987.

High sedimentation events, when 200-, 1000- and 3800-m traps were operating in concert, were used to estimate sinking rates of particles and comparative remineralization of various biogenic components. The sinking speed between 1000 and 3800 m was one sampling period (12-16 d) for four identifiable events, indicating that particles were sinking at rates of at least $175-250 \text{ m d}^{-1}$. Sedimentation between 200 and 3800 m also took only one sampling period in 1989 and 1990, which increased sinking rate estimates to $250-300 \text{ m d}^{-1}$. During three of those events in which the start and end of anomalous flux episodes could be resolved, 64-80% of the 1000-m flux reached 3800 m. Particles were enriched in PIC with increasing depth, POC and PON either changed little (1983) or declined in concentration (by 30% in 1985 and 15% in 1990), and biogenic Si was always less abundant, comprising 5-9% less of the particulate material at 3800 m. Thus through either remineralization or fragmentation of particles, Si, C and N tended to be lost during the sedimentation of a biological event, whereas carbonates were more efficiently transported to the deep ocean. This result is not observed over the annual cycle, where BSi is most efficiently transported to depth. The intense 1983 event lasted the shortest time, and most efficiently

transported biogenic materials to deep ocean. The more prolonged the event (1985 > 1990 > 1983), the greater the loss of the labile components of the particles (1985 > 1990 > 1983) for POC and PON).

4.3. Elemental ratios in particle flux

4.3.1. POC: PON

The elemental ratios for POC: PON in all sediment traps are consistently higher than the Redfield ratio of 6.6 for phytoplankton. The ratios in particle fluxes reflect both the conditions of algal growth in the upper ocean and the relative remineralization rates of C and N while passing through zooplankton guts or being consumed by bacteria while sinking through the water column. Phytoplankton POC : PON ratios can vary between 3 (vigorous growth with excess nitrate) and 15 (inhibited growth due to nitrate depletion) in extreme conditions (Antia et al., 1963). POC : PON ratios of marine phytoplankton are variable (Antia et al., 1963) and in culture appear to increase irrespective of the limiting nutrient (e.g. Perry, 1976), even when this limiting nutrient is CO₂ (Burkhardt and Riebesell, 1997). However, given that neither nitrogen nor CO_2 is limiting at OSP, it is unlikely that these factors have a role in the variability of POC: PON ratios. It has been suggested that availability of iron (Fe) may limit growth of phytoplankton at OSP (e.g. Martin and Fitzwater, 1988; Boyd et al., 1996), but to date there is no evidence that Fe limitation has a significant impact on POC: PON ratios of cultured or natural marine phytoplankton (e.g. Greene et al., 1991; van Leeuwe et al., 1997). Measurements from the euphotic zone in 1987 and 1996 (from 45 samples collected on six occasions) show that POC : PON of suspended matter at OSP is rather stable throughout the year, varying from 6.8 in winter to 6.4 in spring and summer. The stable ratio is reflected in the small change in POC from winter (~ 50 µg C l^{-1}) to summer (~ 70–90 µg C l^{-1}).

Changes in ratios of the biogenic elements result from their susceptibility to remineralization, with the order of increasing resistance: PON, POC, BSi and PIC (Honjo and Manganini, 1993). Thus, the POC: PON ratio in the settling particles should increase with depth according to conventional wisdom! The expected change in the POC: PON ratio, using Eqs. (1) and (2) in Pace et al. (1987) is from 8.2 at 200 m to 9.7 at 1000 m and 11.2 at 3800 m. POC: PON ratios in the upper ocean (50-1000 m) based on the average of all data of POC and PON collected by free-drifting traps are shown in Fig. 7, which also displays the values calculated from the equations in Pace et al. (1987). The POC: PON ratios of ~ 8 in the upper 100 m for the newly formed detritus exported from the surface mixed layer were higher than that for suspended particles, which averaged 6.5 + 0.3 in 1987 and 1996. The ratios increased with depth, in good agreement with estimates of Pace et al. (1987) in the upper 500 m, but it appears that an additional fractionation of C and N happens before sedimentation, probably due to grazing by zooplankton (Thibault and Roy, 1999). In the deeper waters at 600-1000 m, at about the depth of the oxygen minimum, POC: PON ratios increase by between 2 and 3. This depth to which zooplankton migrate (Goldblatt et al., 1999), is also where an incursion of the California countercurrent was found by examining lead isotopic ratios (Flegal et al., 1986).



Fig. 7. POC: PON molar ratio, averaged from 1987 to 1993 in particles collected by surface-tethered free-drifting sediment traps at depths of 50–1000 m at OSP. The POC: PON ratios derived using the equations of Pace et al. (1987) are also shown by the solid line.

POC: PON ratios from the moored traps (Fig. 2a) averaged about 8.5 at both 1000 and 3800 m, although the 1000-m ratios showed a much higher variability. For example, in 1982–1983, the ratios were ~ 8 , reflecting higher productivity and higher transfer rate of particles from upper to deep ocean (i.e. less time for remineralization). The trend of increasing POC: PON ratio with depth seen in particles collected from short-term deployments of drifting traps (Fig. 7) disagrees with observations from moored sediment traps (Fig. 4a). These contradictory results call for an urgent need to study the decomposition of materials in situ in the traps.

4.3.2. POC: PIC and PIC: BSi

The rain ratio of POC : PIC determines whether the biological pump is removing or adding CO₂ in the upper ocean as a result of photosynthesis and calcification. When carbon fixation by phytoplankton is incorporated at a POC : PIC ratio of 0.7, there is no net decrease in pCO₂ concentrations in seawater (Crawford and Purdie, 1997). It is not clear how to interpret ratios in detrital rain, but higher values will indicate preferential carbon fixation as POC rather than PIC, thus will favor the biological pump as a mechanism for drawing atmospheric CO₂ into the ocean. The ratio in the 200 m trap shows marked interannual and episodic variability (Fig. 2). The ratio varied from 0.2 (early June 1989) to 7.3 (late October 1989), and averaged ~ 2. A few high values in 1993 (Fig. 2b) are discounted as arising from contamination by swimmers who were so abundant that they overwhelmed the sample preservative. At 1000 m, the ratio varied between < 0.1 in May–September 1989 and July–November 1990 to about 4.6 in August of 1983. At 3800 m, maxima were observed in the late summers of 1983, 1984, 1986 and 1988, and October–November 1993. The minimum level of < 0.1 (November–April 1990) reflected a period of high PIC and low POC fluxes.

Interannually, the rain ratio at 3800 m varied between 0.4 (1990) and 1.1 (1983), and averaged 0.6 (calculated from Table 2). This ratio was in the same range as the terminal ratio of 0.54 (48°N, 21°W) and 0.57 (34°N, 21°W) in the North Atlantic (Honjo and Manganini, 1993), and 0.5 in the abyssal layers in the equatorial Atlantic and Pacific Oceans (Honjo et al., 1982). In the review by Tsunogai and Noriki (1991), the ratio at 4000 m depth in the eastern North Pacific is 1.15, a factor of 2 smaller than the global median value. However, this ratio was based on a small data set that was collected in two periods of relatively high POC flux. The POC flux in the eastern North Pacific is about the same as the global median average (Tsunogai and Noriki, 1991), and the large PIC flux, especially in 1987 and 1990, clearly contributed to the smaller ratio.

The PIC : BSi ratio reflects the switching of biological activity between diatoms and coccolithophores or foraminifera. Particles that have a high ratio are the product of the latter populations and were observed at 0.8 in the spring and fall of 1983. During the maximum flux to 3800 m in 1983, however, opal comprised 60% of sinking particles and the PIC : BSi ratio decreased to 0.3. The average annual cycle (Fig. 4) shows that this is a typical pattern, and coincides with the strong utilization of dissolved Si in surface waters in summer (Wong and Matear, 1999). A second minor peak occurred in November, and as mentioned previously, is linked to carbonate transport of > 63 μ m particles. It is noteworthy that the highest annual PIC : BSi ratios occurred during the El Niño years 1983 and 1987. May–June PIC : BSi peaks occured in non-El Niño years (1984, 1985, 1986, and 1990).

5. Primary production and vertical particle fluxes

One of the major objectives of the sediment trap program was to assess how the vertical fluxes at various depths reflect primary production in the upper ocean. The corollary is how far the assumption of a steady state between production and vertical flux holds. Recent measurements of primary production at OSP using clean techniques and in situ incubations give higher annual production rates in the subarctic Pacific Ocean than reported previously, with non-clean techniques (Wong et al., 1995). Estimates of primary production thus have been revised to give 140 g C m⁻² yr⁻¹ (Wong et al., 1995), which agree with that obtained by seasonal nitrate change of 133 g C m⁻² yr⁻¹ (Wong et al., 1998). Longhurst et al. (1995) assigned 199 g C m⁻² y⁻¹ to the Alaskan gyre of subarctic waters, and McClain et al. (1996) obtained 189 g C m⁻² yr⁻¹ using a modelling approach. These values are somewhat high compared to the historical value of only 60 g C m⁻² yr⁻¹ (McAllister et al., 1972) and are thought to be influenced by the use of non-clean techniques.

The empirical equations describing the relationships between primary production and the detritus flux rates are summarized in Bishop (1989), Lampitt and Antia (1997) and Honda et al. (1997). The decadal average of the POC flux into the deep ocean at 3800 m is $1.26 \text{ g C m}^{-2} \text{ yr}^{-1}$ and primary production by ¹⁴C uptake is 140 g C m⁻² yr⁻¹ (Wong et al., 1995). These estimates give a ratio of export to primary production on an annual basis at OSP of 0.9% for $J_{3800 \text{ m}}$, the flux to 3800 m. This is very close to the canonical value of about 1% of the primary production exported to the deep ocean, as expected from the formulation of Eppley and Peterson (1979) and summarized in Berger et al. (1989). The relative lack of variability of POC flux over the decadal time scale, except during episodic events, implies that primary production and export production in the upper ocean are in equilibrium. Under such conditions, the biological pump is not removing anthropogenic CO₂ from the upper ocean into deep water storage.

6. Non-steady state and net carbon removal

The ocean is traditionally regarded as in steady state for balance between production and decomposition, and despite very large gross fluxes for these two processes, the net change in carbon is thought to be insignificant on an annual basis. A nonsteady change will occur if there is an imbalance between the two processes. For example, an episodic supply of nutrients from wind events, runoff from land, atmospheric input, or horizontal advection may produce a burst of production, which leads to a "leakage" of detritus flux resulting from a disequilibrium in the ecosystem in the upper ocean, e.g., phytoplankton abundance not in equilibrium with zooplankton grazing. During elevated primary production, loss through sedimentation increases (Lampitt and Antia, 1997) until a plateau is reached.

Increases in fluxes of material above the average value were especially significant in 1983 (49%) and to a lesser extent in 1987 (36%). These episodic flux events may be the only periods when additional CO_2 is being converted by the biological pump into deep-ocean storage. The interannual changes as recorded in the time series give only an indication of the time when such events occur and suggest a lower limit of upper-ocean removal of about 1 g C m⁻² yr⁻¹. Because POC may be lost from traps in situ by decomposition, this should be regarded as the lower limit of the deep-sea flux. A disequilibrium removal of upper-ocean CO_2 of 25% above the baseline deep-sea flux is 0.25 g C m⁻² yr⁻¹, which equals 0.003 Gt C for the subarctic Pacific. This is, however, not the total net removal into the ocean below the mixed layer. The POC flux into the intermediate ocean at 1000 m is three times larger, and the interannual variability between years is 2- to 3-fold larger, thus the intermediate ocean may have received an order of magnitude greater carbon input than that observed at 3800 m.

The PIC flux to 3800 m is 1.7 ± 0.6 g C m⁻² yr⁻¹, about 50% larger than the POC flux. The PIC flux has smaller interannual variability and vertical change with depth, compared with the POC flux. The total carbon flux reaching the deep ocean, based on sediment trap data, is at 3 g C m⁻² yr⁻¹, about three times the POC flux value, thus raising the disequilibrium removal of carbon to the deep subarctic Pacific to

0.003–0.01 Gt C. Episodic events, such as those arising from elevated pteropod growth, could increase this value further. The uncertainty in the aragonite PIC flux is large, since aragonite is more soluble than calcite. During prolonged storage in sediment trap sampling cups, this fraction could be lost by dissolution.

The interannual variability of NO₃ seasonal uptake (Wong et al., 1998) is 30-70% higher during the 4 ENSO years in the period 1965-1990, i.e. 4 of 25 years × 50% increase on the average, which represents about 8% per year above the long-term average. The sediment trap variability is about the same in the 3800-m trap, but the 200- and 1000-m traps showed much larger variations interannually. If such large variations occur interannually, particle fluxes and the biological pump may be important mechanisms for removing excess CO₂ from the upper ocean into intermediate ocean, but not necessarily to the deep ocean and sea floor. Based on a single point at station ALOHA (22° 45'N, 150°W), Emerson et al. (1997) argued that the subtropical waters could contribute a sink of 5–6 Gt C yr⁻¹, as high as the present global oceanic organic carbon pump of 1.2 mol C m⁻² yr⁻¹ (Karl et al., 1996; Eppley and Peterson, 1979; Martin et al., 1987). The subpolar oceans (subarctic and subantarctic), with an area of $0.6 \times 10^{14} \text{ m}^2 (45^\circ - 60^\circ)$, could potentially yield 35 g C m⁻² yr⁻¹ based on OSP primary production of 140 g C m⁻² yr⁻¹ (Wong et al., 1995) and a mean annual f-ratio of about 0.25 (Varela and Harrison, 1999), or a global oceanic carbon pump of 2 Gt C yr^{-1} . The sediment traps at OSP did not sample the upper 200 m consistently, and this depth was also subjected to uncertainties due to swimmers. However, the summer export at 50 m and $J_{200 \text{ m}}$ of 8 g C m⁻² from drifting traps would give an export from the upper ocean of about $32 \text{ g C m}^{-2} \text{ yr}^{-1}$, close to the $35 \text{ g Cm}^{-2} \text{ yr}^{-1}$ from primary production and *f*-ratio. From the 3800-m data set at OSP, the average episodic change over the period is about 15% per decade or 1.5% per year. Thus, the net removal of carbon from the upper ocean is, at most, 0.03 Gt $C yr^{-1}$ in subpolar waters, and if at the same episodicity for the subtropical oceans, 0.05 Gt C yr⁻¹. The ocean organic carbon pump thus could remove about 0.1 Gt $C yr^{-1}$ of excess CO_2 in the upper ocean, an insignificant amount in the net oceanic uptake of fossil fuel CO_2 , which is about 2 Gt C yr⁻¹ (Quay et al., 1992). In Emerson et al. (1997), the increase in dissolved inorganic carbon (DIC) and decrease in δ^{13} C are about 1 μ mol kg⁻¹ and 0.02% yr⁻¹, respectively, about the magnitude expected of fossil-fuel CO₂ uptake by the upper ocean without net biological removal. The net carbon flux removal, if transfer into the intermediate ocean is also included, could be about 0.3–0.5 Gt C yr⁻¹ as the lower limit, bearing in mind the possible underestimation due to remineralization of carbon in the sediment traps under in situ conditions. However, more investigation on the episodic removal of \overline{CO}_2 is needed to confirm the upper limit of biological removal.

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References

- Antia, N.J., McAllister, C.D., Parsons, T.R., Stephens, K., Strickland, J.D.H., 1963. Further measurements of primary production using a large-volume plastic sphere. Limnology and Oceanography 8, 166–183.
- Archer, D., 1996. An atlas of the distribution of calcium carbonate in sediments of the deep sea. Global Biogeochemical Cycles 10, 159–174.
- Baker, E.T., Milburn, H.B., 1983. An instrument for the investigation of particle fluxes. Continental Shelf Research 1, 425–435.
- Barwell-Clarke, J., Whitney, F., 1996. Institute of Ocean Sciences nutrient methods and analyses. Canadian Technical Report of Hydrography and Ocean Sciences, Vol. 182, 43pp.
- 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, New York, pp. 1–34.
- Bishop, J.K.B., 1989. Regional extremes in particulate matter composition and flux: effects on the chemistry of the ocean interior. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), Productivity of the Ocean: Present and Past. Wiley, New York, pp. 117–137.
- Bishop, J.K., Calvert, S., Soon, M., 1999. Spatial and temporal variability of POC in the northeast subarctic Pacific. Deep-Sea Research II 46, 2699–2733.
- Boyd, P.W., Muggli, D.L., Varela, D.E., Goldblatt, R.H., Chretien, R., Orians, K.J., Harrison, P.J., 1996. In vitro iron enrichment experiments in the NE subarctic Pacific. Marine Ecology Progress Series 136, 179–193.
- Boyd, P.W., Wong, C.S., Merrill, J., Whitney, F., Snow, J., Harrison, P.J., Gower, J., 1998. Atmospheric iron supply and enhanced vertical carbon flux in the NE subarctic Pacific: is there a connection? Global Biogeochemical Cycles 12, 429–441.
- Burkhardt, S., Riebesell, U., 1997. CO₂ availability affects elemental composition (C : N : P) of the marine diatom Skeletonema costatum. Marine Ecology Progress Series 155, 67–76.
- Crawford, D.W., Purdie, D.A., 1997. Increase of pCO_2 during blooms of *Emiliania huxleyi*: theoretical considerations on the asymmetry between acquisition of HCO_3^- and respiration of free CO_2 . Limnology and Oceanography 42, 365–372.
- DeMaster, D.J., 1981. The supply and accumulation of silica in the marine environment. Geochimica et Cosmochima Acta 45, 1715–1732.
- Deuser, W.G., 1986. Seasonal and interannual variation in deep-water particle fluxes in the Sargasso Sea and their relation to surface hydrography. Deep-Sea Research 33, 225–246.
- Deuser, W.G., Ross, E.H., 1980. Seasonal change in the flux of organic carbon to the deep Sargasso Sea. Nature 283, 364–365.
- Emerson, S., Quay, P., Karl, D., Winn, C., Tupas, L., Landry, M., 1997. Experimental determination of the organic carbon flux from open-ocean surface waters. Nature 389, 951–954.
- Eppley, R.W., Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282, 677–680.

- Flegal, A.R., Itoh, K., Patterson, C.C., Wong, C.S., 1986. Vertical profile of lead isotopic composition in the north-east Pacific. Nature 321, 689–690.
- Goldblatt, R.H., Mackas, D.L., Lewis, A.G., 1999. Mesozooplankton community characteristics in the NE subarctic Pacific. Deep-Sea Research II 46, 2619–2644.
- Greene, R.M., Geider, R.J., Falkowski, P.G., 1991. Effect of iron limitation on photosynthesis in a marine diatom. Limnology and and Oceanography 36, 1772–1782.
- Honda, M.C., Kusakabe, M., Nakabayashi, S., Manganini, S.J., Honjo, S., 1997. Change in pCO₂ through biological activity in the marginal seas of the western North Pacific: the efficiency of the biological pump estimated by a sediment trap experiment. Journal of Oceanography 53, 645–662.
- Honjo, S., 1978. Sedimentation of materials in the Sargasso Sea at a 5,367 m deep station. Journal of Marine Research 36, 469–492.
- Honjo, S., Doherty, K.W., 1988. Large aperture time-series sediment traps; design objectives, construction and application. Deep-Sea Research 35, 133–149.
- Honjo, S., Manganini, S.J., Cole, J.J., 1982. Sedimentation of biogenic matter in the deep ocean. Deep-Sea Research 29, 609–625.
- Honjo, S., Dymond, J., Collier, R., Manganini, S.J., 1995. Export production of particles to the interior of the equatorial Pacific Ocean during the 1992 EqPac experiment. Deep-Sea Research 42, 831–870.
- 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., 1972. Factors affecting solution rate of biogenic opal in sea water. Earth and Planetary Science Letters 15, 411–417.
- Iseki, K., 1981. Particulate organic matter transport to the deep sea by salp fecal pellets. Marine Ecology Progress Series 5, 55–60.
- Karl, D.M., Christian, J.R., Dore, J.E., Hebel, D.V., Letelier, R.M., Tupas, L.M., Winn, C.D., 1996. Seasonal and interannual variability in primary production and particle flux at Station ALOHA. Deep-Sea Research 43, 539–568.
- Knap, A., Michaels, A., Close, A., Ducklow, H., Dickson, A. (Eds.), 1996. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurments. JGOFS Report Number 19, 170 pp. Reprint of the IOC Manuals and Guides No. 29, UNESCO 1994.
- Lampitt, R.S., Antia, A.N., 1997. Particle flux in deep sea: regional characteristics and temporal variability. Deep-Sea Research 44, 1377–1403.
- Longhurst, A.R., 1995. Seasonal cycles of pelagic production and consumption. Progress in Oceanography 36, 77–167.
- Longhurst, A.R., Sathyendranath, S., Platt, T., Caverhill, C., 1995. An estimate of global primary production in the ocean from satellite radiometer data. Journal of Plankton Research 17, 1245–1271.
- Martin, J.H., Fitzwater, S.E., 1988. Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. Nature 331, 341–343.
- Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Research 34, 267–285.
- Matear, R.J., Wong, C.S., 1997. Estimation of vertical mixing in the upper ocean at Station P from chlorfluorcarbons. Journal of Marine Research 55, 507–521.
- McAllister, C.D., et al., 1972. Estimates of the transfer of primary production to secondary production at Ocean Station P. In: Takenouti, A.Y. (Ed.), Biological Oceanography of the Northern North Pacific Ocean. Idemitsu Shoten, Tokyo, Japan, pp. 575–580.
- McClain, C.R., Arrigo, K., Tai, K.-S., Turk, D., 1996. Observations and simulations of physical and biological processes at ocean weather station P, 1951–1980. Journal of Geophysical Research 101 (C2), 3697–3713.
- Michaels, A.F., Knap, A.H., 1996. Overview of the U.S. JGOFS Bermuda Atlantic time-series study and the hydrostation S program. Deep-Sea Research 43, 157–198.
- Miller, C.B., Frost, B.W., Wheeler, P.A., Landry, M.R., Welschmeyer, N., Powell, T.M., 1991. Ecological dynamics in the subarctic Pacific, a possible iron-limiting ecosystem. Limnology and Oceanography 36, 1600–1615.

- Mortlock, R.A., Froelich, P.N., 1989. A simple method for the rapid determination of biogenic marine sediments. Deep-Sea Research 36, 1415–1426.
- Neuer, S., Raatmeyer, V., Davenport, R., Fischer, G., Wefer, G., 1997. Deep-sea particle flux in the Canary Island region: seasonal trends in relation to long-term satellite derived pigment data and lateral sources. Deep-Sea Research 44, 1451–1466.
- Pace, M.L., Knauer, G.A., Karl, D.M., Martin, J.M., 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature 325, 803–804.
- Parsons, T.R., Lalli, C.M., 1988. Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. Oceanography and Marine Biology Annual Reviews 26, 317–359.
- Perry, M.J., 1976. Phosphate utilization by an oceanic diatom in phosphorus-limited chemostat culture and in the oligotrophic waters of the central North Pacific. Limnology and Oceanography 21, 88–107.
- Quay, P.D., Tilbrook, B., Wong, C.S., 1992. Oceanic uptake of fossil fuel CO₂: carbon-13 evidence. Science 256, 74–79.
- Thibault, D., Roy, S., Wong, C.S., Bishop, J.K., 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.
- Tsunogai, S., Noriki, S., 1991. Particulate fluxes of carbonate and organic carbon in ocean. Is the marine biological activity working as a sink of the atmospheric carbon?. Tellus 43B, 256–266.
- van Leeuwe, M.A., Scharek, R., de Baar, H.J.W., de Jong, J.T.M., Goeyens, L., 1997. Iron enrichment experiments in the Southern Ocean: physiological responses of plankton communities. Deep-Sea Research II 44, 189–207.
- Varela, D.E., Harrison, P.J., 1999. Seasonal variability in the nitrogenous nutrition of phytoplankton in the northeastern subarctic Pacific Ocean. Deep-Sea Research II 46, 2505–2538.
- Whitney, F.A., Freeland, H.J., 1999. Variability in upper-ocean water properties in the NE Pacific Ocean. Deep-Sea Research II 46, 2351–2370.
- Wong, C.S., 1989. Recent advances in remote observational systems and their applications in the open ocean environment. Marine Mining 8, 83–90.
- Wong, C.S., Matear, R.J., 1999. Sporadic silicate limitation of phytoplankton productivity in the subarctic NE Pacific Deep-Sea Research II 46, 2539–2555.
- Wong, C.S., Matear, R.J., Whitney, F.A., Iseki, K., 1998. Enhancement of new production in the northeast subarctic Pacific Ocean during negative North Pacific index events. Limnology and Oceanography 43, 1418–1426.
- Wong, C.S., Whitney, F.A., Iseki, K., Page, J.S., Zeng, J., 1995. Analysis of trends in primary production and chlorophyll-a over two decades at Ocean Station P (50°N, 145°W) in the Subarctic northeast Pacific Ocean. In: Beamish, R.J. (Ed.), Climate Change and Northern Fish Populations. Canadian Special Publication Journal of Fisheries and Aquatic Science 121, pp. 107–117.