Pergamon

0967-0645(96)00002-1

Deep-Sea Research II, Vol. 43, No. 2-3, pp. 539-568, 1996
Copyright © 1996 Elsevier Science Ltd
Printed in Great Britain. All rights reserved
0967-0645/96 $15.00 + 0.00

Seasonal and interannual variability in primary production and particle flux at Station ALOHA

D. M. KARL,* J. R. CHRISTIAN,* J. E. DORE,* D. V. HEBEL,* R. M. LETELIER,* L. M. TUPAS* and C. D. WINN*

(*Received* 28 *March* 1995; *in revised form* 12 *October* 1995; *accepted* 12 *December* 1995)

Abstract—A 5-year time-series study of primary production and euphotic-zone particle export in the subtropical North Pacific Ocean near Hawaii (Sta. ALOHA, 22°45'N, 158°W) with measurements collected at approximately monthly intervals has revealed significant variability in both ecosystem processes. Depth-integrated (0–200 m) primary production averaged 463 mg C m^{-2} day^{-1} (s = 156, n = 54) or 14.1 mol C m^{-2} $year^{-1}$. This mean value is greater than estimates for the North Pacific Ocean gyre made prior to 1984, but conforms to data obtained since the advent of trace metal-clean techniques. Daily rates of primary productivity at Sta. ALOHA exhibited interannual variability including a nearly 3-year sustained increase during the period 1990–1992 that coincided with a prolonged El Niño–Southern Oscillation (ENSO) event. Export production, defined as the particulate carbon (PC) flux measured at the 150 m reference depth, also varied considerably during the initial 5 years of the ongoing field experiment. The PC flux averaged 29 mg C m^{-2} day^{-1} (s = 11, n = 43) or 0.88 mol C m^{-2} $year^{-1}$. A 5-fold variation between the minimum and maximum fluxes, measured in any given year, was observed. During the first 3 years of this program (1989–1991), a pattern was resolved that included two major export events per annum one centered in late winter and the other in late summer. After 1991, export production exhibited a systematic decrease with time during the prolonged ENSO event. When expressed as a percentage of the contemporaneous primary production, PC export ranged from 2 to 16.9%, with a 5-year mean of 6.7% (s = 3.3, n = 40). Contrary to existing empirical models, contemporaneous primary production and PC flux were poorly correlated, and during the ENSO period they exhibited a significant inverse correlation. This unexpected decoupling of particle production and flux has numerous implications for oceanic biogeochemical cycles and for the response of the ocean to environmental perturbations. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

The large and dynamic oceanic reservoir of carbon, approximately 4×10^{19} g distributed unequally among dissolved and particulate constituents with various redox states, plays an important role in global biogeochemical cycles. The two largest pools are dissolved inorganic carbon (DIC = $[H_2CO_3]$ + $[HCO_3^-]$ + $[CO_3^{2-}]$) and the less oxidized pool of mostly uncharacterized dissolved organic carbon (DOC). A chemical disequilibrium between DIC and organic matter is produced and maintained by numerous biological processes. The reversible, usually biologically-mediated interconversions between dissolved and particulate carbon pools in the sea collectively define the oceanic carbon cycle.

Primary conversion of oxidized DIC to reduced organic matter (dissolved and particulate

*Department of Oceanography, School of Ocean and Earth Science and Technology, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822, U.S.A.

pools) is generally restricted to the euphotic zone of the world ocean through the process of photosynthesis. The supply of reduced carbon and energy required to support subeuphotic zone metabolic processes is ultimately derived from the upper ocean and is transported down by advection and diffusion of dissolved organic matter (Toggweiler, 1989), gravitational settling of particulate matter (McCave, 1975) and by the vertical migrations of pelagic animals (Longhurst and Harrison, 1989) and phytoplankton (Villareal *et al.*, 1993). Each of these individual processes, collectively termed the "biological pump" (Volk and Hoffert, 1985), is controlled by a distinct set of environmental factors and, therefore, the relative contribution of each process may be expected to vary with changes in habitat or with water depth for a given habitat. Longhurst (1991) has recently defined three components of the biological pump, each representing a separate set of ecological processes. The rotary pump circulates materials through the microbial food web, the Archimedian pump defines the gravitational flux of fecal pellets and aggregated materials and the reciprocating pump represents the daily bi-directional migration of animals in response to light. For open ocean ecosystems, the relative contributions of these processes are poorly known. Although the Archimedian pump is generally assumed to dominate total euphotic zone export (Martin *et al.*, 1987; Knauer *et al.*, 1990; Karl *et al.*, 1992), the role of yet another component, the diffusion pump, may also be important (Toggweiler, 1989; Carlson *et al.*, 1994). The rates at which the individual components of the biological pump operate are under the control of both physical (light, temperature, turbulence) and biological (species composition, growth rate, food web structure) processes.

Each year, the biological pump removes an estimated 7 GT C (1 GT = 10^{15} g) from the surface waters of the world ocean, a value that is equivalent to ~15% of the annual global ocean primary production (Martin *et al.*, 1987). Microbial transformation of sinking particles in the thermocline (Taylor *et al.*, 1986; Karl *et al.*, 1988) that gives rise to increased C:N and C:P ratios with depth can potentially drive a net atmosphere–ocean flux of CO_2 in the subtropical Pacific (cf. Winn *et al.*, 1994). Episodic flux "events" carry to the deep sea large amounts of "fresh" organic matter with near-Redfield (Redfield *et al.*, 1963) elemental ratios. These events may represent the bulk of the flux reaching depths greater than 1000 m (Anderson and Sarmiento, 1994), making processes within the main thermocline also dependent upon the biological pump. In the North Pacific gyre, isopycnal surfaces below about 500 m ($\sigma_\Theta > 26.7$) do not intersect the sea surface, so carbon remineralized in the lower thermocline may be isolated from atmosphere–ocean exchange on timescales of decades to centuries.

The role of the ocean as a net sink in the global carbon cycle is dependent largely upon the balance between the export flux of planktonic primary production (Eppley and Peterson, 1979; Williams and von Bodungen, 1989) and the rate of dissolved inorganic resupply by upward eddy-diffusion processes. When particulate export is expressed as a percentage of contemporaneous primary production, this value is termed the export ratio (Baines *et al.*, 1994). Results from broad-scale, cross-ecosystem analyses suggest that the export ratio (generally measured/reported only as the Archimedian component of total export) in oceanic habitats is a positive, non-linear function of total integrated primary production (Suess, 1980; Pace *et al.*, 1987; Martin *et al.*, 1987; Wassman, 1990), with values ranging from less than 10% in oligotrophic waters to greater than 50% in productive coastal regions. It should be emphasized, however, that the field data from which the existing export production models were derived are extremely limited and that open ocean habitats, in particular, are underrepresented (Baines *et al.*, 1994). Because most global ocean primary

and export production occurs in oceanic habitats (Martin *et al.*, 1987), it is important to understand the mechanisms that control the biological pump so that we can make accurate and meaningful predictions of the response of the oceanic carbon cycle to global environmental change.

As part of the interdisciplinary Hawaii Ocean Time-series (HOT) research program (Karl and Lukas, 1996) we have made direct measurements of the rates of primary production and particle flux on approximately monthly intervals for a period of 5 years at Sta. ALOHA (22°45'N, 158°W). This extensive data base provides an opportunity to investigate the relationships between these two central ecosystem processes, and to test predictions of the existing models.

MATERIALS AND METHODS

Sampling location and cruise chronology

All field experiments were conducted at Sta. ALOHA (22°45'N, 158°W), the U.S. WOCE/JGOFS oligotrophic Pacific Ocean site (Karl and Lukas, 1996). The data presented in this paper were collected on 50 cruises between October 1988 and November 1993, on approximately monthly intervals (Table 1). During each 5-day cruise, except where noted, a single, approximately 12 h, primary production experiment and a single, approximately 72 h, sediment trap experiment were performed. Numerous complementary hydrographical, chemical and biological measurements were obtained (Karl and Lukas, 1996). The rationale for site selection is presented elsewhere (Karl and Winn, 1991; Karl and Lukas, 1996).

Primary production experiments

Rates of primary production were estimated using water samples collected before dawn and incubated either on deck in a simulated *in situ* light- and temperature-controlled incubator (Lohrenz *et al.*, 1992b) or *in situ* attached to a free-drifting, radio-tracked spar buoy (Table 1). During 9 out of 10 cruises over a period of approximately 9 months, we performed both types of incubation. A detailed comparison of these results is presented elsewhere in this volume (Letelier *et al.*, 1996). All field data, without regard to method, are included in subsequent calculations, except for SIS on H-2 which we determined to have been compromised. For cruises where both *in situ* and deck incubations were performed, the mean production estimate was used. The sampling and incubation procedures followed the recommendations of Fitzwater *et al.* (1982) to minimize metal contamination, including the use of acid-rinsed Go-Flo^R bottles (General Oceanics Inc., Miami, FL), Kevlar^R cable, a plastic sheave, Teflon^R messengers and a stainless steel bottom weight. A dedicated hydrowinch was used in a further effort to control contamination.

Water samples were collected from eight depths (5, 25, 45, 75, 100, 125, 150 and 175 m) and were subsampled directly into 500 ml acid-washed/distilled, deionized water rinsed polycarbonate bottles. Generally six separate bottles were prepared from each depth, three for incubation in the light and three for incubation in the dark. Each bottle was inoculated with $H^{14}CO_3^-$ to yield a final radioactivity of approximately 50–100 μCi l^{-1}. Total radioactivity was measured for each sample bottle by removing a subsample for liquid scintillation counting. In this procedure, β-phenylethylamine was used as an inorganic

Table 1. *Chronology of HOT Program cruise and experiment dates, durations and other selected information*

	Primary Productivity Experiments				Sediment Trap Experiments		
Cruise	Date	Duration (h)	Deck/*In situ* (D/IS)	PAR* (mol quanta m^{-2} day^{-1})	Dates	(h)	Drift Vector†
1	31 October 1988	12	D	34.4	Traps lost	—	—
2	2 December 1988	12	D	32.6	1–4 December 1988	71	2.4/135°
3	8 January 1989	12	D	41.7 (+ +)	7–10 January 1989	70	3.1/180°
4	26 February 1989	12	D	44.5 (+)	27–28 February 1989	32	7.1/270°
5	27 March 1989	11.5	D	41.9	26–29 March 1989	72	2.0/225°
6	18 May 1989	12	D	47.6	17–20 May 1989	72	4.7/225°
7	24 June 1989	12.5	D	52.6	23–26 June 1989	72	3.5/135°
8	29 July 1989	12/12	D/IS	—‡	28–31 July 1989	72	4.2/180°
9	24 August 1989	12	D	53.4 (+)	23–26 August 1989	72	4.4/135°
10	22 September 1989	12.8/12.8	D/IS	54.6 (+)	22–25 September 1989	72	8.5/135°
11	18 October 1989	13.4/12.4	D/IS	—	17–20 October 1989	72	10.5/135°
12	27 November 1989	12.4/12.4	D/IS	—	Not deployed	—	—
13	5 January 1990	11.9/13.4	D/IS	27.7	4–7 January 1990	73	15.9/135°
14	15 February 1990	11.7/12	D/IS	20.7 (−)	14–17 February 1990	72	6.3/90°
15	18 March 1990	13.7	IS	48.8	18–21 March 1990	72	7.4/90°
15	19 March 1990	12.8/13.5	D/IS	46.9			
15	20 March 1990	13.4	IS	44.5			
16	13 April 1990	12.8/12.8	D/IS	48.5	12–14 April 1990	60	12.4/135°
17	9 May 1990	13.7/13.7	D/IS	55.4	8–11 May 1990	71	2.3/135°
18	13 June 1990	14	IS	—	12–14 December 1990	64	3.2/315°
19	25 July 1990	13.2	IS	—	24–27 July 1990	67	5.9/90°
20	Not deployed		—	44.3 (−)	14–16 September 1990	63	1.5/135°
22	18 December 1990	13.8	IS	17.9 (−)	17–19 June 1990	65	1.1/225°
23	3 February 1991	12	IS	37.8	2–5 February 1991	79	7.4/315°
24	Not deployed		—	44.7	6–8 March 1991	60	3.5/45°

25	10 April 1991	13.3	IS	47.0	Not deployed	—	—
26	8 May 1991	13.1	IS	51.5	7–10 May 1991	72	9.0/45°
27	5 June 1991	15.3	IS	54.7	4–9 June 1991	120	6.9/225°
28	10 July 1991	15.2	IS	55.7	9–12 July 1991	73	4.8/225°
29	10 August 1991	13.3	IS	52.1	9–12 August 1991	72	4.6/90°
30	18 September 1991	14	IS	48.5	17–20 September 1991	73	8.6/225°
31	21 October 1991	13.2	IS	40.4	20–23 October 1991	75	5.2/45°
32	7 December 1991	12.3	IS	32.6	5–8 December 1991	73	0.7/90°
33	5 January 1992	12.9	IS	37.0	4–7 January 1992	70	0.4/90°
34	15 February 1992	12.5	IS	39.0	13–16 February 1992	74	2.0/135°
35	6 March 1992	13.2	IS	55.0 (+ +)	4–7 March 1992	76	7.1/315°
36	17 April 1992	11.7	IS	57.0	16–19 April 1992	72	1.8/90°
37	9 June 1992	13.1	IS	51.0 (−)	6–10 June 1992	94	4.7/225°
38	6 July 1992	14.8	IS	56.0	4–7 July 1992	74	4.4/225°
39	7 August 1992	11.8	IS	—	4–7 August 1992	75	5.4/135°
40	23 September 1992	12.7	IS	50.6	21–24 September 1992	81	8.1/225°
41	20 October 1992	12.1	IS	46.4 (+)	18–21 October 1992	79	8.0/225°
44	20 January 1993	12.3	IS	35.8 (+)	19–22 January 1993	71	6.2/225°
45	17 February 1993	13.8	IS	41.9	16–19 February 1993	75	7.8/45°
46	14 April 1993	11.8	IS	57.3 (+)	13–16 April 1993	84	7.7/135°
47	20 May 1993	13.7	IS	58.2 (+)	19–22 May 1993	75	2.2/315°
49	11 September 1993	13.7	IS	51.1	10–16 September 1993	154	3.7/270°
50	29 October 1993	11.8	IS	34.5	28–31 October 1993	80	5.8/180°

On selected cruises, as indicated, one of the experiments was not performed and on HOT cruises 21, 42, 43 and 48 neither of the experiments was performed due to research vessel limitations.

*Daily PAR (400–700 m) determined from shipboard measurements using a Licor model LI-192SA quantum sensor; where noted, the (+) and (−) indicate that integrated light flux on that particular day was greater than (+) or less than (−) 1 standard deviation of the 5-year mean value measured at Sta. ALOHA for the month in which that particular incubation experiment was performed. The (+ +) notation indicates that the measured light flux was greater than 2 standard deviations from the monthly mean value.

†The average drift speed (nmi day^{-1}) and true direction during the approximately 3-day sediment trap experiment.

‡No light data collected on this cruise.

carbon trapping agent and Aquasol-II was used as the scintillation cocktail. The ^{14}C activities of the samples were counted using a Packard model no. 4640 liquid scintillation counter, and sample quench was determined using the spectral index of external standard (SIE) estimation. Total DIC was measured using CO_2 coulometry (Winn *et al.*, 1994) for calculation of the DIC specific radioactivity ($^{14}C/^{12}C$; mCi mol^{-1}). This value was used for subsequent estimation of primary production.

Following either on-deck or *in situ* incubation, subsamples (100–500 ml) were filtered onto 25 mm glass fiber filters (Whatman GF/F) and each filter was placed directly into a glass vial for subsequent measurement of ^{14}C incorporation into particulate matter. The sample vials were stored for 2–3 days at −20°C until processed at our shore-based laboratories. The samples were thawed and acidified by direct addition of HCl (1 ml, 2 M) to each vial and vented for 24 h prior to the addition of 10 ml of Aquasol-II in preparation for liquid scintillation counting.

Primary production, reported in this paper, is expressed as the mean carbon assimilation rates in the light-incubated samples. These values do not include ^{14}C-DOC that may have been produced during the incubation period and are not corrected for daytime or nighttime respiration, grazing losses or dark ^{14}C uptake. The total euphotic zone primary production values (mg C m^{-2} day^{-1}) were calculated using the trapezoid rule (Hornbeck, 1975) and were routinely integrated to 200 m to include net incorporation occasionally detected at the deepest reference depth (175 m). For these calculations light assimilation was assumed to be zero at 200 m.

Measurements of solar radiative flux at the sea surface were made using a Licor quantum sensor and data logger (models LI-192SA and LI-1000, respectively) on most HOT cruises. The sensor was positioned approximately 4 m above the deck to minimize the influence of shadows from the ship's superstructure. The quantum sensor was a cosine collector and measured photosynthetically available radiation (PAR; 400–700 nm). Irradiance was averaged over 10 min intervals and logged throughout each day.

Sediment trap experiments

A free-drifting sediment trap array of the Multitrap design (Knauer *et al.*, 1979) was used to collect sinking particulate matter. The array consisted of 12 individual polycarbonate collector tubes fitted with baffles and attached to a PVC crossframe positioned at each of three reference depths (150, 300 and 500 m). The shallowest depth was selected to correspond to the estimated base of the euphotic zone. After several years of measurement, we have determined this depth to be 173 ± 7 m based on comparisons of ^{14}C-HCO_3^- uptake in the light to ^{14}C-HCO_3^- uptake in the dark (Letelier *et al.*, 1996). Because less than 2% of total euphotic zone primary production at Sta. ALOHA occurs in the 150–200 m depth stratum, we are confident that the sediment trap fluxes we measured at 150 m are representative of euphotic zone exports. The sediment trap array was deployed routinely within 6 nautical miles of Sta. ALOHA. During each experiment, the array was tracked using the Argos satellite system. This provided a direct measure of the drift vectors, which varied considerably (Table 1). A VHF radiotransmitter and a strobelight, both encased in the spar buoy, assisted in recovery operations.

Prior to deployment, all collector tubes were acid-washed and rinsed thoroughly with distilled, deionized water. The tubes were then filled with a high density seawater brine solution to prevent loss of preservative during deployment and loss of sample materials

during recovery (Knauer *et al.*, 1979). The trap solution used in our program consisted of a sodium chloride-amended seawater solution (50 g NaCl l^{-1} surface seawater) containing a final concentration of 1% formalin. The solution was filtered through a cartridge filter (0.5 μm) prior to use. Subsamples of this trap solution from each cruise were processed as time-zero blanks.

Immediately following recovery of the traps, the baffles were removed and the collector tubes capped. Care was taken not to homogenize the high density brine with the overlying seawater that on deployment typically displaced the brine to a level beneath the collar that joined the baffle to the tube. The position of this interface was marked, and the overlying low-density seawater was removed by vacuum aspiration to a level 5 cm above the mark. At this point the traps were either processed further or stored for a brief period of time (up to 1–2 days), depending upon weather conditions and other cruise priorities. The contents of each trap were then decanted through a 335 μm Nitex screen to remove larger zooplankton. The screen was retained for subsequent microscopic analysis, and the filtrate was processed for total particulate mass, carbon (PC), nitrogen (PN) and phosphorus (PP), as described below.

From the 12 collector tubes deployed at each depth, six were used for the determination of PC and PN, three for PP and three for total mass measurements. From HOT-2 to HOT-7, the contents of all 12 traps at a common reference depth were combined, homogenized and subsampled for the individual analyses. Since HOT-8 (July 1989), the individual tubes have been processed separately to gain additional information on replicate collector variability. For PC/PN analyses, trap particulate matter was collected onto combusted (450°C, 4 h) 25 mm diameter glass fiber filters (Whatman GF/F), using a pressure filtration system (6–8 psi of nitrogen gas). Filters were placed onto combusted foil and stored frozen (−20°C) in plastic Petri dishes. All samples were dried at 60°C prior to analysis. A Perkin-Elmer model 2400 CN analyzer was used for all measurements with acetanilide (C_8H_9NO) as the primary standard.

Particulate materials for PP analyses were collected onto combusted, HCl-washed GF/F filters using pressure filtration as above. The samples were stored frozen in combusted, acid-rinsed glass test tubes prior to analysis. PP was determined by a high temperature ashing procedure (475–500°C, 3 h), which converts organic P to inorganic P. The samples were then extracted in 10 ml of 0.5 M HCl (90°C, 90 min) and centrifuged (2800 × g, 30 min). A 5 ml portion of the supernatant was removed for analysis of soluble reactive phosphorus (SRP) by the molybdate blue spectrophotometric procedure (Strickland and Parsons, 1972).

Particulate materials for total mass determinations were collected from triplicate 250 ml subsamples from each of three separate collector tubes. The solution was filtered onto tared 25 mm diameter Nuclepore filters (0.2 μm), which were then rinsed three times each with 5 ml of an approximately isotonic (1 M) solution of ammonium formate to remove sea salts. Tared filters were prepared by first rinsing each filter with distilled water, followed by drying at 55°C, cooling to room temperature in a dessicator and weighing to constant weight (i.e. repeat drying, cooling and weighing steps until a relative standard deviation of $< 0.015\%$ is achieved). All measurements were made on a Cahn electrobalance capable of a 0.1 μg resolution. The rinsed samples were enclosed in aluminum foil and placed into a plastic Petri dish and dried at 55°C for at least 8 h until a constant weight was achieved. Blanks were prepared by processing subsamples of the time-zero trap solutions. Following the completion of the total mass analyses, the dried Nuclepore filters were archived.

Beginning with HOT-27, all GF/F filters were examined microscopically to quantify and

remove recognizable organisms (i.e. swimmers) that may have passed through the 335 μm screens. Swimmers were pooled and their C and N contents measured independently. For cruises HOT-44 through HOT-50, a similar independent analysis was made for swimmer-contributed PP and mass. The >335 μm fraction is archived but, to date, has not been routinely characterized.

To determine "total" fluxes it is necessary to analyze both the particulate and soluble portions of the sediment trap collections because preserved sinking organic matter can leach significant amounts of materials into the trap solutions (Knauer *et al.*, 1984a; Karl *et al.*, 1988). The presence of swimmers further exacerbates the problem (Lee *et al.*, 1988; Karl and Knauer, 1989; Peterson and Dam, 1990). The solute phases of our sediment trap solutions were not measured routinely for leached materials, so the particle flux data presented herein should be considered to be the lower bound of the actual *in situ* flux. The standard procedures that we adopted for sediment trap processing in the HOT program were an analytical compromise among various existing methodologies (Knauer and Asper, 1989).

In addition to these free drifting sediment trap experiments, we also deployed an array of bottom-moored, PARFLUX type (MK 7-21; 0.5 m^2 opening) sequencing sediment traps (Honjo and Doherty, 1988) for 1 year beginning 6 June 1992. Individual traps were deployed at 800, 1500, 2800 and 4000 m. Each of the 21 individual cups collected particulate materials for a period of 17.4 days. After the mooring was recovered, the samples were water-sieved through a 1 mm Nitex mesh before quantitative splitting into four aliquots using a rotating splitter device (Honjo, 1980). Subsamples were processed for PC and PN analyses, as described above.

RESULTS

Primary production of organic matter

During the 5-year period of field observation, primary production ranged from a minimum of 127 mg C m^{-2} day^{-1} for the on-deck incubation during HOT-12 (November 1989) to a maximum of 1055 mg C m^{-2} day^{-1} for the on-deck incubation during HOT-9 (August 1989), a variation of nearly an order of magnitude (Figs 1 and 2). The HOT-9 cruise coincided with a large bloom of *Trichodesmium* spp. near Sta. ALOHA (Karl *et al.*, 1992). Euphotic zone depth-integrated dark ^{14}C uptake averaged 6.20% (s = 5.13) of the corresponding light uptake values. Dark respiration rates, estimated from paired comparisons of 12-h (dawn to dusk) and 24-h (dawn to dawn) incubations performed on HOT cruises 1–17, averaged 15.3% (s = 13.5).

The observed variation in primary production covers nearly the entire range of historical measurements reported for the subtropical North Pacific Ocean (see Table 1 in Karl and Lukas, 1996) despite using a standardized, modern ^{14}C-based method. Based on variance among triplicate light bottle uptake measurements, we estimate the precision of our integrated primary production experiment to be on the order of 10%; the accuracy, however, is not known. On a single cruise (HOT-15, March 1990), we made three independent *in situ* primary production measurements on consecutive days (18–20 March 1990) to evaluate the reproducibility of such field experiments at our site. The results of this experiment ($\bar{x}$ = 488 mg C m^{-2} day^{-1}, s = 45, n = 3) support the above-referenced precision estimate. Furthermore, this comparison assumes that the rate of primary production did not change over this 3-day period, so it is probably an upper bound on *in*

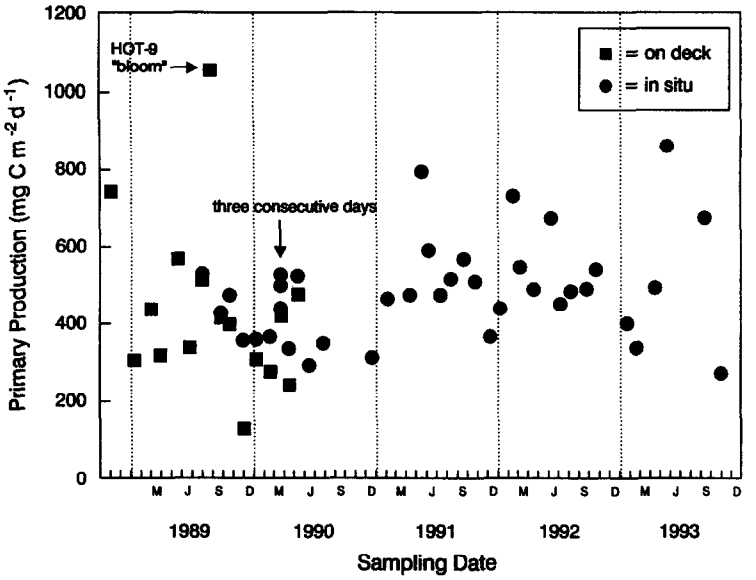


Fig. 1. Temporal variability in primary production estimates for Sta. ALOHA based on on-deck and *in situ* incubation field experiments. Each data point represents the euphotic zone (0–200 m) depth-integrated value for primary production based on trace metal-clean ^{14}C–HCO_3 uptake at eight depths, as described in the Materials and Methods section. During the HOT-15 cruise, primary production was measured on three consecutive days.

situ primary productivity measurement precision. The accuracy of our estimates is neither known nor easily determined.

The mean and standard deviation of the entire primary production data set is 463 (s = 156, n = 54), and the median value is 465 mg C m^{-2} day^{-1}. On average, 90% of the total euphotic zone (0–200 m) primary production occurred in the upper 100 m (Fig. 2), despite chronic nutrient depletion (NO_3^- $\leq$15 nM). Based on the average daily estimate, annual primary production at Sta. ALOHA during our observation period is 169 g C m^{-2}, or 14.1 mol C m^{-2} $year^{-1}$.

We resolved both seasonal and interannual variations in primary production (Fig. 2). For example, in the lower portion of the euphotic zone (100–200 m), we observed a regular oscillation with winter minima and late spring maxima (Fig. 2). The double-peak in 1989 appears to be an anomalous feature in this emergent data base and may be, in part, related to the *Trichodesmium* bloom (HOT-9) mentioned previously. The recurrent pattern of increasing primary production in spring is probably controlled by light availability, which had a minimum monthly average of 26.7 mol quanta m^{-2} day^{-1} in December and a maximum monthly average of 52.4 mol quanta m^{-2} day^{-1} in May (also see Table 1). Production in the upper euphotic zone (0–100 m) was poorly correlated with contemporaneous production in the lower euphotic zone (100–200 m) at Sta. ALOHA (r^2 = 0.12, n = 43), and did not reveal any consistent seasonal patterns (also see Winn *et al.*, 1995).

We observed significant interannual variations in total euphotic-zone primary production, a result that is largely attributable to changes in rates of primary production in the upper (0–100 m) euphotic zone (Fig. 2). The most dramatic interannual variations in

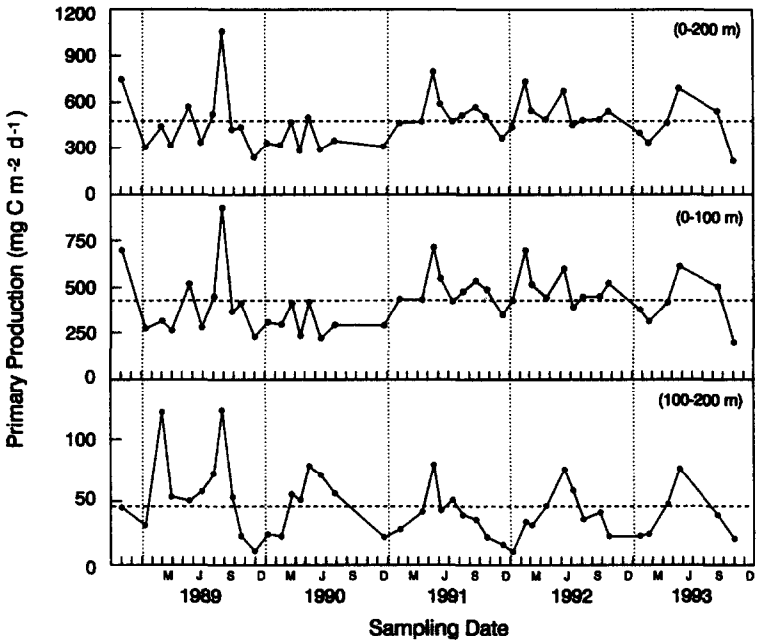


Fig. 2. Depth-integrated primary production measured at Sta. ALOHA. (Top) Total euphotic zone (0–200 m) depth-integrated production rates; (center) upper euphotic zone (0–100 m) depth-integrated production rates; (bottom) lower euphotic zone (100–200 m) depth-integrated production rates. For cruises where more than one primary production measurement was made (see Table 1) the mean values are displayed. The broken horizontal line in each panel is the 5-year mean value for that data set.

primary production include: (i) the sustained, average or lower than average rates from September 1989 to April 1991 with the exception of one cruise and (ii) the sustained higher than average rates measured from May 1991 to October 1992 with the exception of three cruises. Both of these interannual productivity features appear to be restricted to the upper 100 m of the water column (Fig. 2). Increased surface ocean primary production during the period 1991–1992 is believed to be a consequence of the prolonged El Niño–Southern Oscillation (ENSO) event, resulting in other significant subtropical North Pacific Ocean ecosystem changes including an increase in phytoplankton assimilation efficiency (primary production per unit chlorophyll) and a shift from a N-limited to a P-limited habitat attributed to the activities of N_2-fixing cyanobacteria (Karl *et al.*, 1995; Letelier and Karl, in press; Letelier *et al.*, 1996).

Particulate matter fluxes

As expected, the measured downward fluxes of PC, PN and PP were greatest at the 150 m reference depth, and decreased systematically with increasing depth (Fig. 3). PC, PN and PP fluxes at the 150 m reference depth averaged 29.0 mg C m^{-2} day^{-1} (s = 11.0, n = 43), 4.3 mg N m^{-2} day^{-1} (s = 1.7, n = 43) and 0.44 mg P m^{-2} day^{-1} (s = 0.23, n = 43). From the mean estimates presented, an annual PC export of 10.6 g C m^{-2} (0.88 mol C m^{-2} $year^{-1}$) is derived.

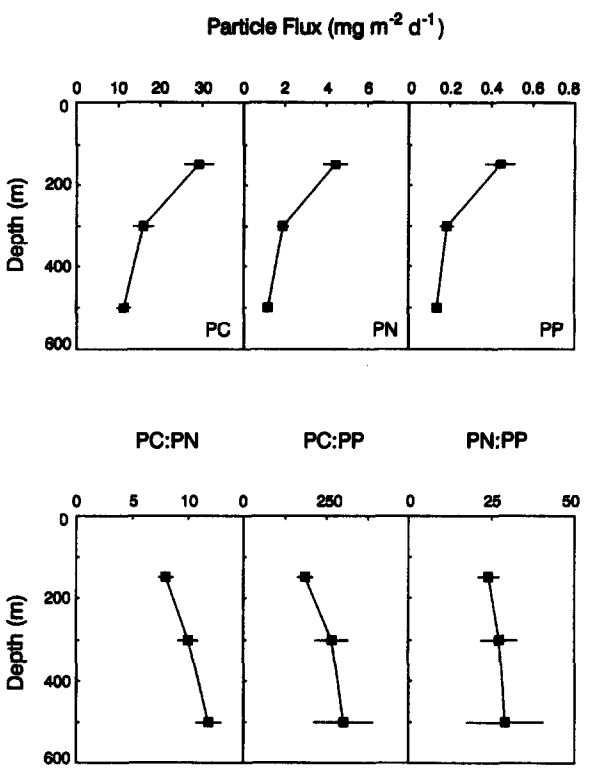


Fig. 3. (Top) Particulate carbon (PC), nitrogen (PN) and phosphorus (PP) fluxes versus water depth at Sta. ALOHA determined using free drifting sediment traps. The data shown are the 5-year mean values (n = 43) with their respective 95% confidence intervals. (Bottom) Elemental compositional ratios (by atoms) for sinking particulate matter collected at Sta. ALOHA. Shown are the 5-year mean values (n = 43) with their respective 95% confidence intervals.

Our results indicate that particulate matter contamination from swimmers passing the 335 μm Nitex screen used in the processing of our sediment trap samples is minimal (Fig. 4). For the 19 cruises where swimmer contamination was determined, fluxes for samples with swimmers removed averaged 88.0% (s = 8.4), 93.2% (s = 9.5) and 97.2% (s = 5.8) of the uncorrected values for the 150, 300 and 500 m reference depths, respectively. Because the removal of preserved zooplankton also, inadvertently, removes associated particulate materials that should be included in the flux estimation, we consider these determinations to be maximum corrections for the data presented. When presented as a combined data set, the PC, PN and PP fluxes of particulate matter conform to the *a priori* expectations of previous oceanic flux models for both the export magnitudes and depth-dependent attrition of the sinking particles (Martin *et al.*, 1987; Knauer *et al.*, 1990; Fig. 3 and Fig. 5, and Table 2). This provides both a confirmation of the smaller historical data set and a demonstration of the internal consistency and reproducibility of these complicated field measurements.

Although changes in the magnitude of the total sinking flux of particulate matter with depth appear to be predictable in open ocean habitats, the bulk elemental composition is more variable both with depth and time (Fig. 3). At the base of the euphotic zone (i.e. 150 m

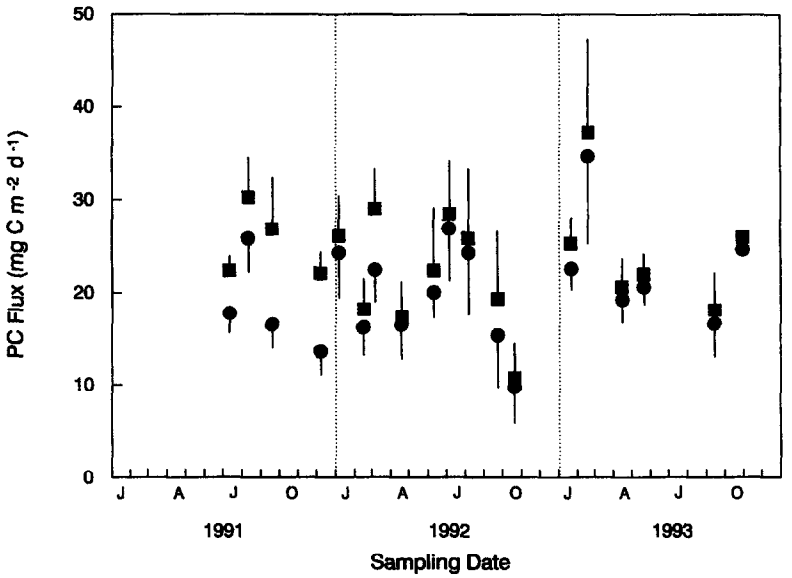


Fig. 4. Particulate carbon (PC) fluxes at the 150 m reference level for HOT-28 (July 1991) to HOT-50 (October 1993) with and without post-screening (335 μm Nitex) removal of swimmers by direct microscopy. Data shown are the mean and one standard deviation estimates: (■) with small zooplankton included, (●) with all zooplankton removed. Overall, the samples with zooplankton removed averaged 88.0% (s = 8.4, n = 19).

reference level), the "average particle" has an elemental composition of approximately C_{187}:N_{24}:P_1 compared to Redfield *et al.* (1963) stoichiometry of C_{106}:N_{16}:P_1. This average ratio increases to C_{303}:N_{29}:P_1 at the 500 m reference level (Fig. 3), indicating a preferential release of P during descent.

The downward fluxes of PC, PN and PP at Sta. ALOHA displayed both seasonal and interannual variations in particle export from the euphotic zone (Fig. 6, Table 3). For example, during the first three years of the program (1989–1991) we detected two major export pulses per year, one centered in late winter and the other in late summer. This variation can best be seen by calculating the standard score, or "Z" score, given by $Z = (Y - \bar{x})/s$ where $\bar{x}$ is the mean of all Y values and s the standard deviation (e.g. $Z = [X - 29]/11$; Triola, 1989). During the period 1989–1991, we observed a recurrent pattern of high and low particle fluxes that appears to disintegrate in late 1991 (Fig. 7).

For the PC flux data set presented, there is a 5-fold variation between the minimum and maximum fluxes observed in any given year (Fig. 6 top, and Table 3). The interannual variability in export fluxes of PC, PN and PP is also quite large (Fig. 6). Again taking PC flux as an example, the 1992 annual export was only 61% of the export measured during 1989 (Fig. 6 top, and Table 3) and, in general, there was a decreasing trend in the magnitude of particle export over the entire 5-year observation period (Figs 6 and 7), despite increased rates of primary production. With a single exception in February 1993, PC fluxes during the period Sept. 1991 to Oct. 1993 were consistently below the 5-year mean value (Fig. 7). The observed temporal variations in the export PN and PP were coherent with those presented

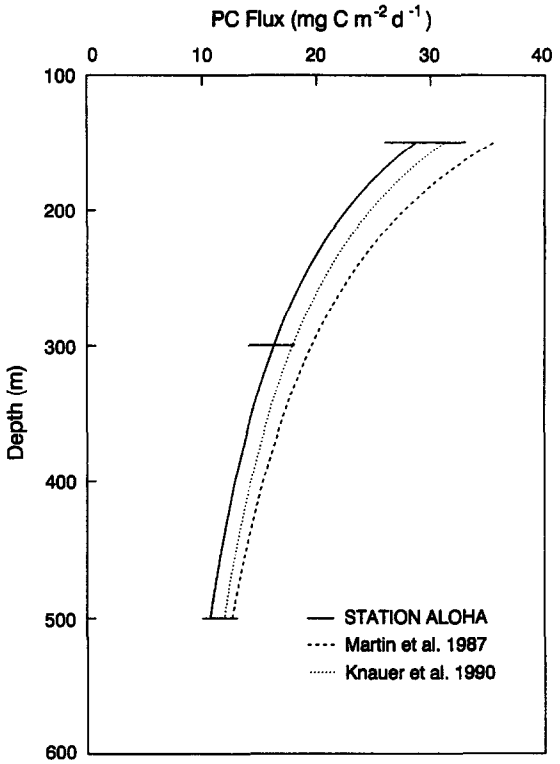


Fig. 5. Best fit values for particulate carbon (PC) flux measured at several North Pacific Ocean stations. The data were fit to a normalized power function of the form, $F_Z = F_{150}(Z/150)^b$ where Z is water depth and F and F_{150} are carbon fluxes at depth Z m and 150 m, respectively (also see Table 2).

Table 2. Summary of log-transformed normalized power functions of the form: PC-FLUX(Z) = PC-FLUX$_{(150\ m)}$ · (Z/150)^b, where Z is water depth in m, *for upper ocean particulate carbon flux data obtained during three independent North Pacific open ocean studies*

Study	Location	PC Flux at 150 m (mg C m^{-2} day^{-1})	b	Reference
VERTEX	OOC*	35.5	−0.858	Martin *et al.* (1987)
VERTEX† time-series	33°N, 139°W	31.2	−0.800	Knauer *et al.* (1990)
HOT‡	ALOHA (22°45′N, 158°W)	28.7	−0.818	This study

*OOC is the "open ocean composite" derived from data obtained at six separate stations in the North Pacific Ocean (35°N, 128°W; 33°N, 139°W; 28°N, 155°W; 18°N, 108°W; 16°N, 108°W; 14°N, 130°W).

†Based on mean values from six separate sediment trap deployments over an 18-month period.

‡Based on mean values for the entire 5-year data set at Sta. ALOHA that is comprised of 43 separate pooled cruise mean estimates at each of three reference depths (see Fig. 4) derived from more than 500 individual carbon determinations.

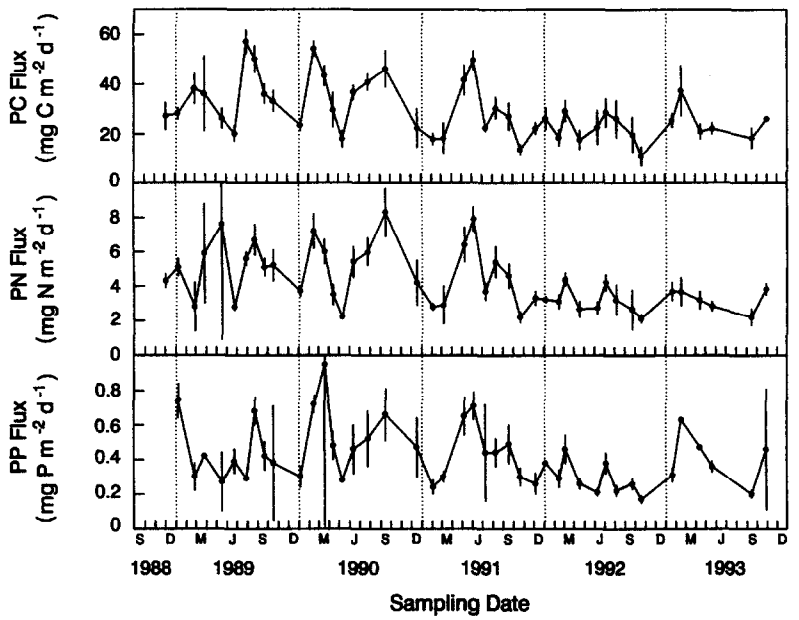


Fig. 6. Temporal variability in (top) particulate carbon (PC) flux, (center) particulate nitrogen (PN) flux and (bottom) particulate phosphorus (PP) flux, measured from free drifting sediment traps positioned at 150 m. Data shown are mean values ± 1 standard deviation of the mean for 3–6 replicate determinations.

here for PC, including both the seasonal patterns and dramatic interannual variations (Fig. 6 center and bottom, Table 3).

Deep-sea particle fluxes

The above-referenced pattern of two major export pulses per year was confirmed for the period June 1992–June 1993 using an array of sequencing, bottom-moored sediment traps deployed at Sta. ALOHA (Fig. 8). The larger of the two PC flux events occurred in summer (13 July 1992–16 August 1992) and averaged approximately 4–6 mg C m^{-2} day^{-1} at the 4000 m reference depth. The temporal coherence of the main export event between 800 and 4000 m (Fig. 8) suggests that this sinking material had a relatively rapid sinking rate (> 200–300 m day^{-1}) and exhibited only minimal attrition of mass during descent. A more detailed account of these patterns and their implications to deep-sea benthic ecology will be presented elsewhere.

Coupling between primary production and particle flux

When expressed as a percentage of total euphotic-zone primary production measured during the same cruise (Fig. 9), carbon export ranged from a minimum of 2% on HOT-41 (October 1992) to a maximum of 16.9% on HOT-14 (February 1990), with a 5-year mean of 6.7% (s = 3.3, n = 40). If compared only to contemporaneous primary production measured in the lower portion of the euphotic zone (100–200 m), to test the two-layer

Table 3. Fluxes of PC, PN, PP and total mass, all in mg m^{-2} day^{-1}, measured at the 150 m reference depth at Sta. ALOHA during the 5-year period of observation. Also shown are data for total euphotic zone depth-integrated primary production in mg C m^{-2} day^{-1}

Observation Period	PC flux Mean ± SD (range)	PN flux Mean ± SD (range)	PP flux Mean ± SD (range)	Mass flux Mean ± SD (range)	Primary Production Mean ± SD (range)
1989	36 ±12 (20–57) $n = 9$	5.2 ±1.6 (2.8–7.6) $n = 9$	0.43 ±0.17 (0.27–0.68) $n = 9$	78 ±20 (59–105) $n = 4$	490 ±230 (307–1055) $n = 9$
1990	35 ±12 (18–54) $n = 9$	5.2 ±1.9 (2.2–8.3) $n = 9$	0.54 ±0.21 (0.28–0.95) $n = 9$	72 ±29 (29–103) $n = 9$	359 ±81 (288–499) $n = 8$
1991	27 ±12 (13–50) $n = 9$	4.4 ±1.9 (2.2–7.9) $n = 9$	0.42 ±0.17 (0.24–0.71) $n = 9$	64 ±29 (28–125) $n = 9$	535 ±125 (366–793) $n = 8$
1992	22 ±6 (11–29) $n = 9$	3.1 ±0.7 (2.1–4.4) $n = 9$	0.29 ±0.10 (0.17–0.46) $n = 9$	58 ±18 (27–84) $n = 9$	539 ±101 (439–732) $n = 9$
1993	25 ±7 (18–37) $n = 6$	3.2 ±0.6 (2.2–3.8) $n = 6$	0.41 ±0.15 (0.20–0.63) $n = 6$	62 ±31 (32–103) $n = 6$	442 ±164 (219–689) $n = 6$

euphotic zone model (Small *et al.*, 1987), carbon export ranged from a minimum of 22.5% on HOT-17 to a maximum of 252% on HOT-33, with a 5-year mean of 78.4% ($s = 51.0$, $n = 40$). Contrary to empirical model predictions extrapolated from other marine ecosystems (Eppley and Peterson, 1979; Baines *et al.*, 1994) particle export at Sta. ALOHA is poorly correlated with primary production (Fig. 9). This observation is consistent with previous investigations conducted in oligotrophic ocean environments (Knauer *et al.*, 1990; Lohrenz *et al.*, 1992a).

DISCUSSION

Temporal variability in primary production

The concept of new production, first introduced by Dugdale and Goering (1967) and subsequently expanded by Eppley and Peterson (1979), has provided a conceptual framework for studies linking primary production and particle export. If biological steady-state conditions are assumed, or if primary and new production measurements are compared over sufficiently long time periods (months to years), then new production in a given ecosystem is equivalent to the amount of primary production that is available for export, a value that is quantitatively balanced by the resupply of production-rate limiting nutrients (Eppley and Peterson, 1979; Eppley *et al.*, 1982; Eppley, 1989; Knauer *et al.*, 1990). However, the export of particulate carbon also can be decoupled from the "expected" rate

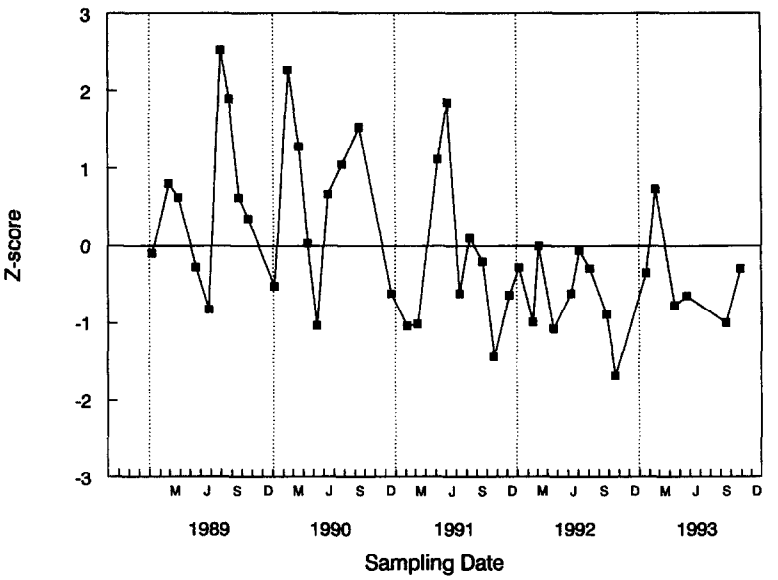


Fig. 7. Standard scores (Z-scores) for the export of particulate carbon (PC) from the euphotic zone at Sta. ALOHA, relative to the 5-year mean and standard deviation of 29 ± 11 mg C m^{-2} day^{-1}. See text for derivation of Z-score.

extrapolated from the re-supply of the limiting nutrients (Michaels *et al.*, 1994b), expecially if there are deviations from Redfield stoichiometry (Sambrotto *et al.*, 1993).

During the first 5 years of field investigation at Sta. ALOHA, we documented an unexpectedly high level of variability in the rate of euphotic-zone primary production. Although the full range of our data spans nearly all previous measurements reported for the oligotrophic North Pacific gyre (see Table 1 in Karl and Lukas, 1996), it is important to emphasize that the annual primary production either extrapolated from the mean daily rate of primary production at Sta. ALOHA or calculated as the time-integrated rate exceeds recently reported estimates by at least a factor of three (Berger, 1989). These revised estimates of oligotrophic North Pacific gyre productivity, if applied to the world ocean gyres as a whole, yield significantly greater global productivity rates and an increased potential for carbon export (Table 4). It is also interesting to note that the average rate of primary production at our "oligotrophic" site (170 g C m^{-2} $year^{-1}$) is only 2–3-fold lower than rates measured in the "productive" California coastal waters using similar trace metal-clean techniques (Martin *et al.*, 1987). Although the subtropical gyre is characterized by low biomass and low concentrations of inorganic nutrients, the past perception of low sustained rates of primary production may be in need of revision.

While the mean rates of primary production are, on average, higher than those measured prior to the advent of the "clean" technique (Fitzwater *et al.*, 1982), we are not suggesting that all primary production estimates made prior to that time are invalid. First, the range of primary production estimates in our own data set includes several values $\leq$350 mg C m^{-2} day^{-1} (Figs 1 and 2) that are closer in magnitude to the values measured mostly in the 1970s (Eppley *et al.*, 1973, 1985; Hayward, 1987). It is possible that these decade-scale differences may be due to habitat changes, rather than to methodological shortcomings of the previous

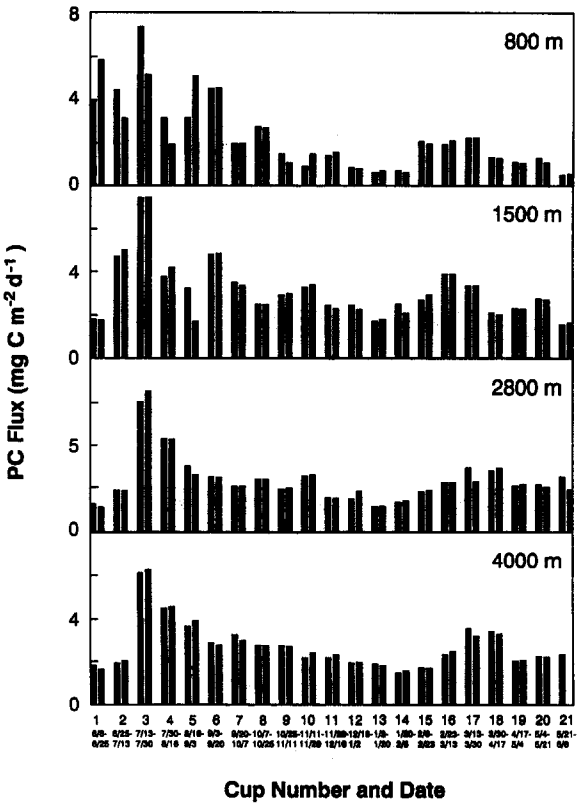


Fig. 8. Continuous record of particulate carbon (PC) flux (mg C m^{-2} day^{-1}) measured at four separate reference depths (as shown) at Station ALOHA for the period 6 June 1992–8 June 1993. The data presented are the duplicate determinations of PC made for samples collected in each cup (nos 1–21), in chronological order. The collection dates are shown beneath each cup number; each period was 17.4 days.

investigations. Climate analyses provide evidence for a substantial change in the North Pacific Ocean during the period 1977–1988 ultimately resulting in increased productivity at several trophic levels (Trenberth and Hurrell, 1994; Polovina *et al.*, 1994).

On much shorter timescales (< 1 year), we have documented considerable variability in biological rates and processes. If we assume that this shorter-term variability in rates of primary production is caused by changes in nutrient and light availability, we can begin to explore some of the underlying causes of the observed changes in primary production at Sta. ALOHA. Although poorly resolved by the HOT program data set at the present time, waters of the subtropical gyre appear to be subjected to episodic mixing and stirring events that supply nutrients to the euphotic zone at rates that overwhelm the calculated steady-state eddy diffusive flux. To date, we have observed four major "events", three during February (Fig. 10) when the total 0–100 m integrated NO_3^- concentration was greatly elevated above the long-term mean inventory. The physical mechanism(s) responsible for these episodic nutrient injections is not well understood. These mixing events coincide with both a shoaling of the nitracline depth, and a decrease in the nitrate concentration gradient

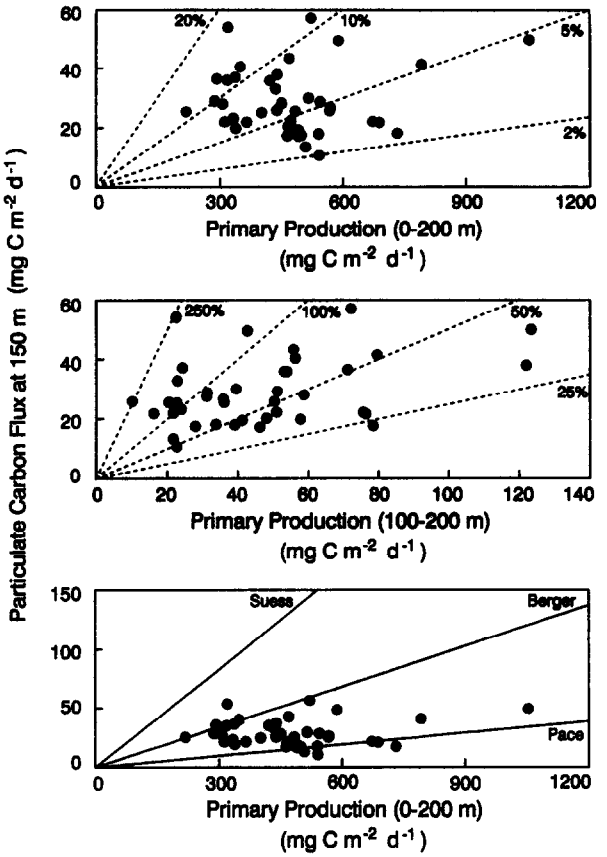


Fig. 9. Plots of particulate carbon (PC) flux measured at the 150 m reference level versus primary production at Sta. ALOHA for the complete 5-year data set. (Top) Total euphotic zone (0–200 m) depth integrated primary production, (center) lower euphotic zone (100–200 m) depth integrated primary production and (bottom) Sta. ALOHA data in relation to extrapolations predicted by empirical models developed by Suess (1980), Pace *et al.* (1987) and Berger *et al.* (1987) (see also Table 6). The dashed lines shown in the upper two graphs represent lines of constant export ratio, from 2–20% for top graph and from 25–250% for the center graph. During the period October 1988–December 1993, contemporaneous primary and export production are not significantly correlated at Sta. ALOHA ($r = 0.090$, $P > 0.5$).

with depth and are all consistent with the hypothesized "bottom-up" mixing mechanism described previously for breaking internal waves (McGowan and Hayward, 1978). Due to a general erosion of the pycnocline in winter as a result of surface ocean cooling (Bingham and Lukas, 1996) and generally deeper mixed-layers (Karl *et al.*, 1995), the vertical transport of nutrients may be accelerated. During a recent HOT cruise (HOT-52; February 1994) we observed relatively rapid (< 1 day) changes in the depth profiles of potential density that are also consistent with the above-mentioned physical model (Fig. 11, top). Continuous measurements of flash fluorescence, which revealed a disruption of chl *a* stratification on casts 3–7, are further evidence of contemporaneous mixing at depths of 50–150 m (Fig. 11, bottom). Nitrate concentrations of 53 nM at 85 m and 155 nM at 111 m measured for

Table 4. Revised estimates of total global ocean primary productivity and export production based on results from the BATS and HOT time-series programs

Province*	Percentage of Ocean	Area* (10^{12} m^2)	Average Primary Production (g C m^{-2} year^{-1})	Global Primary Production (GT C year^{-1})†	Average Export Production (g C m^{-2} year^{-1})	Global Export Production (GT C year^{-1})
Open ocean	90	326	169	55	10.6	3.5
Coastal zone	9.9	36	250	9.0	42	1.5
Upwelling area	0.1	0.36	420	0.15	85	0.03
Total		362		66		5.0

*From Ryther (1969).
†1 GT = 10^{15} g.

discrete water samples obtained on cast 19 also provided direct evidence of nutrient entrainment into the euphotic zone. Other physical processes, including double diffusion (Hamilton *et al.*, 1989) and non-linear interactions between mesoscale eddies and wind-driven Ekman processes (Klein and Hua, 1988; Lee *et al.*, 1994), are also likely to be important in the subtropical North Pacific.

Particulate matter export

Upper water column particle flux estimates at Sta. ALOHA yielded results similar to other recent experiments in the northeast Pacific Ocean using similar sediment trap collection protocols (Figs 3 and 5). The 5-year data set collected at Sta. ALOHA, supports both the concept and quantitative validity of the "open ocean composite" flux profile (Martin *et al.*, 1987). Furthermore, particle flux data collected at our sister JGOFS time-series station near Bermuda also conform to a similar particle export versus depth model

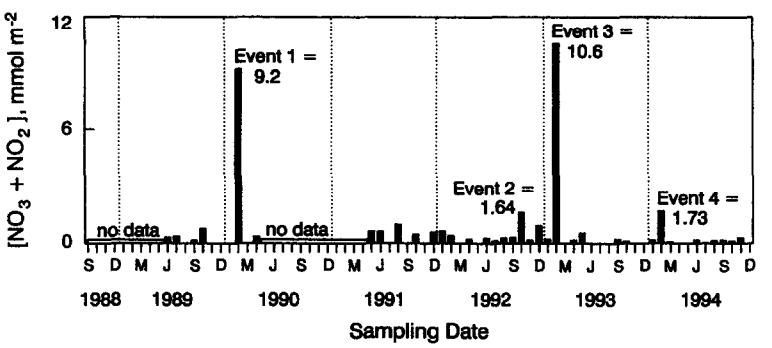


Fig. 10. Temporal variability in the depth-integrated inventories of nitrate ($NO_3^- + NO_2^-$) concentrations (mmol m^{-2}) measured at Sta. ALOHA. The four "events" shown are believed to be manifestations of mixing/stirring processes. With the exclusion of these four events, the mean and standard deviation values for the upper water column (0–100 m) inventories are 0.36 and 0.25 (mmol m^{-2}), respectively (n = 32).

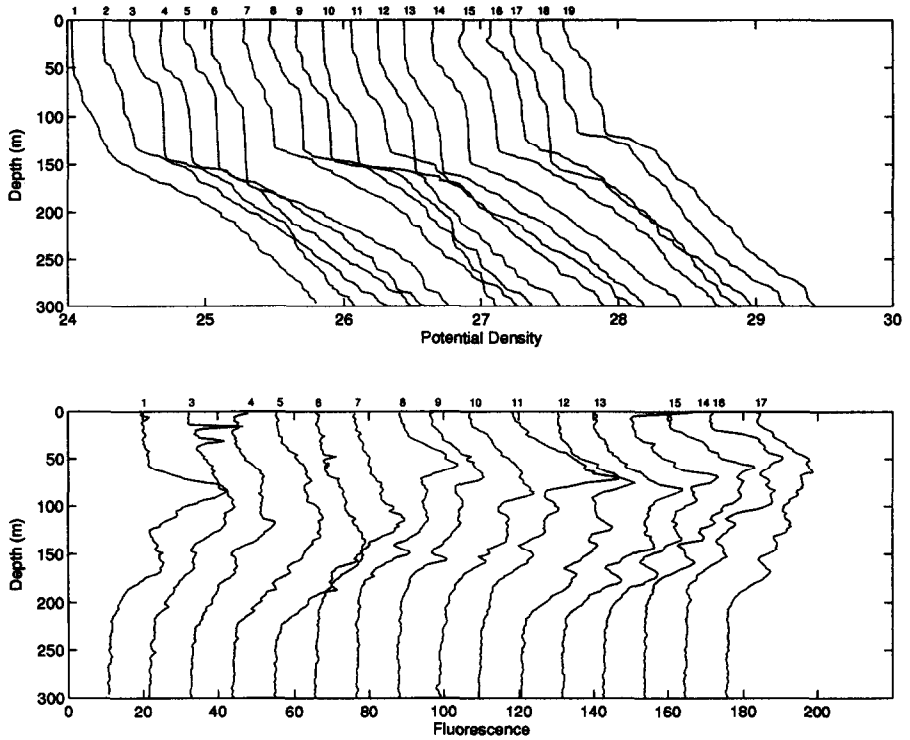


Fig. 11. Stack plots showing the depth distributions of (top) potential density anomaly (kg m^{-3}) and (bottom) flash fluorescence (arbitrary units) for the water column at Sta. ALOHA during HOT-52 (February 1994). The scale offsets are 0.2 kg m^{-3} for potential density and 10 units for flash fluorescence. Cast No. 1 began at 20:00 h (GMT) on 16 February 1994 and each consecutive cast was obtained approximately 3 h later.

(Lohrenz *et al.*, 1992a), suggesting an inter-ocean basin coherence in the mechanisms of the regional Archimedian pump. Our revised estimates for open-ocean primary production and particulate export production of 169 g C m^{-2} $year^{-1}$ (14.1 mol C m^{-2} $year^{-1}$) and 10.6 g C m^{-2} $year^{-1}$ (0.88 mol C m^{-2} $year^{-1}$), respectively, emphasize the role of these vast, low nutrient regions. Greater than 80% of global ocean production and ~70% of export production is attributable to open-ocean habitats (Table 4).

Seasonal and interannual variability in particle export

Until now, we have focused attention on the mathematically-averaged, "mean ecosystem" export condition, which rarely exists at Sta. ALOHA. From the *Z*-score PC flux data analysis (Fig. 7), particle flux varies considerably about the 5-year mean value with both higher frequency (seasonal) and lower frequency (interannual) components.

There are several processes, both predictable and stochastic, that might contribute to temporal variations in particulate matter export from the euphotic zone. Increases in biogenic particle export from the euphotic zone must, ultimately, be coupled to processes controlling biogenic particle production, including nutrient and light availability. Potential

sources of nutrients are physical mixing or stirring events discussed previously or atmospheric deposition. The latter may be more important for controlling the availability of trace elements (e.g. Fe, Mo, Zn; Donaghay *et al.*, 1991) than macronutrients (e.g. N, P, Si). For North Pacific Ocean ecosystems at the latitude of Sta. ALOHA, atmospheric fluxes are seasonally-phased, with major depositional events in the spring (Donaghay *et al.*, 1991) and minimal to undetectable fluxes throughout the summer. Large interannual variations are also apparent (Donaghay *et al.*, 1991).

Although poorly resolved by our sampling frequency ($\sim$monthly), we believe that the waters of the subtropical gyre ecosystem are subjected to episodic mixing events of sufficient magnitude to inject nitrate into the euphotic zone at rates that overwhelm the calculated steady-state eddy diffusive flux. Three of the four major events observed to date (Fig. 10, top) occurred in late winter when mixed-layer depths were at their seasonal maximum (see Karl and Lukas, 1996). Although we have no information on the annual NO_3^- flux supported by these stochastic events, it is important to emphasize that a single instantaneous injection of the magnitude observed in February 1990 and February 1993 (i.e. $\sim$10 mmol NO_3^- m^{-2}) is sufficient to re-supply approximately 10% of the nitrogen to support export production for an entire year, assuming an *f*-ratio of 0.07. If there were several events each winter season, this could easily account for the increased PC, PN and PP export that is generally observed in the late winter season (Figs 7 and 8).

If we compare the depth distributions of NO_3^- and total production during one of these event periods (HOT-45) to the mean conditions at Sta. ALOHA (represented by HOT-26), it is apparent that nutrient injection could result in a coupled increase in new and export production (Table 5). If we apply an existing biogeochemical model relating the *f*-ratio (i.e. ratio of nitrate-based (new) production to total production) to ambient NO_3^- concentration (Platt and Harrison, 1985) to Sta. ALOHA conditions, we calculate that the "potential" export production during a typical mixing event exceeds that estimated under steady-state conditions by a factor of four (Table 5). Consequently, NO_3^--based production may be expected to exhibit considerable variability depending upon the mean position of the nitracline, the mixed layer depth and the euphotic zone NO_3^- concentration. We hypothesize that the late winter export pulses derive largely from these nutrient injection processes. This interpretation is consistent with data collected from the CLIMAX region (near 28°N, 155°W) which indicate the presence, in February, of deep-living phytoplankton species in near surface waters during >50% of the study period (Venrick, 1993). If stochastic events are a dominant source of nitrate to support export production, then our inability to balance the estimated nitrogen demands of the euphotic zone phytoplankton with the NO_3^- fluxes calculated from steady-state diffusion models (Hayward, 1987) should come as no surprise.

The late summer–early fall export peak, which was especially evident in 1989 and 1990 (Fig. 6, top and Figs 7–8), is more difficult to explain. During this period of the year, the water column is well stratified, average wind speeds are low and atmospheric storms and atmospheric depositional events are at their annual minima. Although the annual cycle of mean surface irradiance results in a systematic increase in carbon assimilation and assimilation efficiency (Letelier *et al.*, 1996), especially in the lower portion of the water column, which could lead to increased rates of new and export production (Fig. 2), this is probably not responsible for the fall export pulse for several reasons. First, the magnitude of the fall export pulse is highly variable from year to year whereas the radiance-induced increase in lower euphotic zone primary production is nearly identical (compare Figs 2 and

Table 5. Depth-dependent estimation of f*-ratio and potential export production based on measured nitrate concentrations and rates of primary production for "steady-state" (HOT-26) and "perturbed" (HOT-45) nutrient conditions*

HOT Cruise	Depth	$[NO_3^-]$ (nM)	*f*-ratio*	Total Production† (mg C m^{-3} day^{-1})	New Production‡ (mg C m^{-3} day^{-1})	Potential Export Production§ (mg C m^{-2} day^{-1})
26	25	2.2	0.012	10.69	0.13	3.3
	48	3.0	0.016	7.00	0.11	5.8
	81	1.8	0.010	3.80	0.04	7.1
	104	1.9	0.010	2.17	0.02	7.6
	113	3.0	0.016	1.97	0.03	7.9
	126	1.1	0.016	1.64	0.01	8.0
	132	1.2	0.007	1.31	0.01	8.1
	135	1.9	0.010	1.14	0.01	8.1
	141	18.5	0.095	0.80	0.08	8.6
	143	41.0	0.197	0.69	0.14	8.9
	152	98.9	0.398	0.28	0.11	9.9
	157	260	0.681	0.23	0.16	10.7
	162	278	0.698	0.19	0.13	11.4
	170	453	0.788	0.11	0.09	12.1
	179	677	0.821	0.05	0.04	12.5
45	5	2.4	0.013	6.39	0.08	0.4
	15	1.9	0.010	5.39	0.05	0.9
	24	2.3	0.013	4.46	0.06	1.4
	36	2.3	0.013	4.25	0.06	2.2
	45	5.5	0.030	4.16	0.13	3.3
	59	65.8	0.293	2.68	0.79	14.4
	74	172	0.563	0.47	0.27	18.5
	85	275	0.695	0.67	0.47	23.7
	95	429	0.781	0.87	0.68	30.5
	100	860	0.83	1.07	0.89	35.0
	110	1440	0.83	0.77	0.64	41.4
	125	1900	0.83	0.31	0.26	45.3
	144	2170	0.83	0.12	0.10	47.2
	152	2720	0.83	0.10	0.08	47.8
	175	3920	0.83	0.04	0.03	48.5

*Calculated according to Platt and Harrison (1985) as: $f = f_{max}(1 - e^{-(\alpha NO_3/f_{max})})$, where f_{max} = 0.83 (±0.08), α = 5.48 (±0.77) and NO_3^- (μM) is ambient nitrate concentration.

†Calculated from *in situ* ^{14}C primary production data obtained during the cruise with linear interpolation between the measured data points at 5, 25, 45, 75, 100, 125, 150 and 175 m to correspond to the precise depths where $[NO_3^-]$ was measured.

‡Based on total production and respective *f*-ratio.

§Depth integrated from surface to the reference depth indicated.

7; also see Karl *et al.*, 1995). During periods of extreme water column stratification, vertical migrations may become an important source of nutrients (Karl *et al.*, 1992; Villareal *et al.*, 1993) and the role of the reciprocating pump could be enhanced. Second, the increased production occurs prior to June, whereas the timing of the export peak varies considerably but generally occurs in late summer to early fall (Figs 6–8). Finally, the magnitude of the observed seasonal increase in lower euphotic zone primary production (i.e. ~20–30 mg C

m^{-2} day^{-1}) could not support the contemporaneous PC flux increases of 30–40 mg C m^{-2} day^{-1} (Fig. 6, top), even if the *f*-ratio were unity.

The late summer export pulses are well-resolved in at least 3 of the 5 years of field observations (Figs 6 and 7) as well as in the continuous particle flux records recently obtained from bottom-moored sequencing sediment traps deployed at Sta. ALOHA (Fig. 8). The fact that we apparently missed the 1992 summer export event with our short-term traps but clearly resolved it with the continuous bottom-moored collectors is a sobering example of the potential sampling bias in the HOT program data set.

Although evidence at this point is not extensive, we believe that this late summer export production is supported by nitrogen (N_2) fixation processes in the upper portion of the euphotic zone. Once thought to be insignificant in the marine N cycle, there is now a growing realization that cyanobacterial N_2 fixation is quantitatively important in the subtropical gyre of the North Pacific Ocean (Karl *et al.*, 1992, 1995; Letelier and Karl, in press). Both primary and secondary blooms of phytoplankton could be supported by N_2 as a source of new nitrogen. The timing of the late summer export pulse is consistent with the predictions of this hypothesis. Nevertheless, the rates and detailed mechanisms of the coupling between N_2 fixation and particle flux are sufficiently uncertain that closure of the N budget at Sta. ALOHA is not possible at the present time.

Decoupling of primary production and export processes

Carbon flux at the base of the euphotic zone ranged from 2 to 17% of the contemporaneous primary production, with an overall mean of 6.7% (Fig. 9, top). The mean export ratio is well within the range of values predicted to occur in oligotrophic oceanic habitats (Eppley and Peterson, 1979) and those previously observed (Knauer *et al.*, 1990; Lohrenz *et al.*, 1992a). However, the nearly order-of-magnitude range in the export ratio was unexpected. It is obvious that accurate assessments of export production using sediment traps rely upon selection of a meaningful reference depth below which regenerated nutrients are not available to sustain net primary production until transported back into the euphotic zone by diffusion or turbulent mixing (Knauer *et al.*, 1984b). The selection of 150 m as the reference level for Sta. ALOHA was made based on our best estimates of phytoplankton compensation depth. Although it is true that the values obtained for the export ratio are dependent upon total flux and, hence, reference depth (Figs 2 and 5), it is unlikely that the decoupling patterns observed at Sta. ALOHA between primary production and particle export are the result of using an inappropriate reference level for our comparisons.

Contrary to existing empirical models, carbon flux at Sta. ALOHA was not well predicted from measurements of primary production or chl *a* concentrations (Table 6 and Fig. 9, bottom). Selected model extrapolations (e.g. Suess, 1980; Betzer *et al.*, 1984; Berger *et al.*, 1987) overestimated carbon flux at the base of the euphotic zone by up to 350%, while for other models (e.g. Pace *et al.*, 1987) particulate carbon flux was underestimated by up to 50% (Table 6). The best fit was obtained using the relationship derived by Lohrenz *et al.* (1992a) for the BATS data set. It is possible that the large-scale cross-ecosystem, positive relationships that have been reported previously apply only over large trophic gradients, and that over narrower ranges the slope of the relationship may be different or even of opposite sign as is apparently the case for primary production and PC flux at Sta. ALOHA.

The apparent decoupling of primary production from export production observed both

Table 6. Accuracy of predicted particulate carbon (PC) fluxes for Sta. ALOHA based upon existing empirical models relating integrated primary production (P) or chlorophyll a *(chl* a*) concentrations to particulate carbon (PC) flux*

Model Equation*		Predicted PC Flux (mg C m^{-2} day^{-1})			Relative Per Cent Error† [(Predicted–Observed)/ Observed × 100%]			Reference
		150 m	300 m	500 m	150 m	300 m	500 m	
1	$J = P/0.024Z$	129	64	39	+349	+300	+255	Suess (1980)
2	$\log_{10}J = -0.388 - 0.628\log_{10}D + 1.41\log_{10}P$	67	43	31	+131	+169	+182	Betzer *et al.* (1984)
3	$J = 1.286P/Z^{0.734}$	15	9	6.2	−48	−44	−44	Pace *et al.* (1987)
4	$J = 20P/Z$	62	31	19	+114	+94	+72	Berger *et al.* (1987)
5	$J = 6.3P/Z^{0.8}$	53	30	20	+83	+88	+82	Berger *et al.* (1987)
6	$\log_e J = 0.88[\log_e(P)] - 2.21$	24	—	—	−17	—	—	Lohrenz *et al.* (1992a)
7	$\log_{10}J = 2.09 + (0.81 \cdot \log \text{chl } a)$	22	—	—	−24	—	—	Baines *et al.* (1994)

*Abbreviations: J = C flux at specified depth (Z, m); P = total euphotic zone primary production (mg C m^{-2} day^{-1}); chl a = average euphotic zone concentration (mg m^{-3}).

†Mean and standard deviations, where shown, for measured properties at Sta. ALOHA are: $P = 463 \pm 163$ ($n = 54$); $J_{150} = 29 \pm 11$ ($n = 43$); $J_{300} = 16 \pm 8$ ($n = 41$); $J_{500} = 11 \pm 5$ ($n = 40$); chl $a = 0.119$.

at Sta. ALOHA especially during the 1991–1992 ENSO event (Karl *et al.*, 1995; Fig. 12) and at the BATS time-series station in the North Atlantic Ocean (Lohrenz *et al.*, 1992a) was unexpected. Of course it may be illogical to expect these two generally consecutive processes (e.g. increases in primary production usually precede increases in export production) to be correlated on contemporaneous timescales, especially in temporally-variable habitats. However, even over fairly long periods of time (i.e. 3 years, Fig. 12) production and export appear to be decoupled.

Hypotheses for production–flux decoupling

Although it is conceivable that the time and space scales of variability for oligotrophic ocean ecosystems prevent mass balance closure using the sampling design and cruise frequency adopted by the HOT program (Karl and Lukas, 1996), we believe that more fundamental physical and biological processes are responsible for the trends that we have observed. The data recently obtained using continuous sequencing bottom-moored sediment traps deployed at Sta. ALOHA reveal flux patterns similar to the short-term, 3-day near-surface ocean experiments (Fig. 8). Because deep-moored traps integrate over larger space- and timescales (Siegel *et al.*, 1990) this argues for the coherence of the observed pattern over broad areas and argues against temporal sampling bias.

We present three hypotheses that focus on the apparent decoupling of production and particle flux processes: (i) the relative strengths of the individual biological pumps vary in proportion to primary production, with particle flux dominating when primary production is low and the dissolved pump dominating when primary production is high. This results in a more efficient retention of suspended particulate matter and, hence, longer residence times

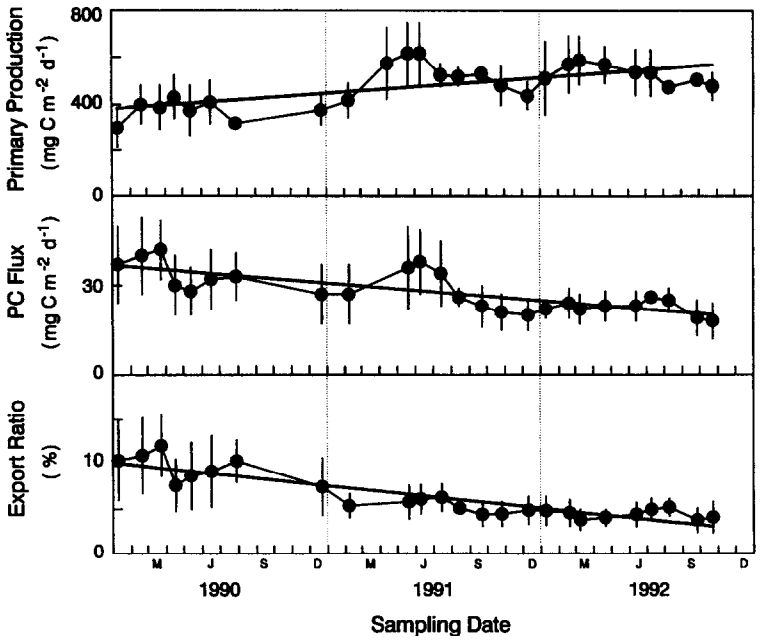


Fig. 12. Relationships between primary production, particulate carbon (PC) flux and export ratio (PC flux/Primary Production × 100%) for samples collected at Sta. ALOHA during the period 1990–1992. The data shown are the three-point running means for each parameter and ±1 standard deviation of the running mean estimate. The solid lines are the linear regressions for each data set. The regression equations for each of the three lines are: (top) $Y = 299.2 + 0.1823X$, $r = 0.655$; (center) $Y = 44.01 - 0.01619X$, $r = -0.770$; and (bottom) $Y = 13.30 - 0.006845X$, $r = -0.899$. In all cases X is time, in days, from 1 October 1988. All regression slopes are significantly different from zero at $\alpha = 0.001$ indicating that primary production and export are negatively correlated during this 3-year period of observation.

when primary production is high, and leads to a decoupling of production from particle flux; (ii) the downward flux of particulate carbon does not adequately represent the downward flux of biologically-available energy that ultimately controls ecosystem dynamics. However, to date, no quantitative measurements of total detrital energy flux have been possible (Karl and Knauer, 1984); and (iii) horizontal processes dominate the movements of carbon and energy in oligotrophic ocean habitats. Although this latter mechanism has recently been suggested to reconcile major carbon system imbalances at the Bermuda time-series site (Michaels *et al.*, 1994a), the generally rapid utilization of labile organic matter would suggest that transport of recently produced dissolved and particulate organic matter over long distances is unlikely in the open ocean. Any one, or a combination, of these processes could decouple primary and export production processes, and none of these hypotheses can be rejected at the present time.

The biological processes that we envision are occurring at Sta. ALOHA are inherently transient and stochastic. From studies conducted elsewhere in the world ocean, diatoms are known to be important in mediating particle export directly as aggregated, senescent cells or indirectly as a result of macrozooplankton grazing (Peinert *et al.*, 1989; Karl *et al.*, 1991); but they rarely dominate the standing stocks of phytoplankton cells. Mass sinking of

rhizosolenoid diatoms may be a common occurrence across diverse marine habitats (Sancetta *et al.*, 1991) and may even be part of their normal life cycle (Smetacek, 1985).

Goldman (1988, 1993) has previously described two independent production cycles based on the growth of small phytoplankton cells and sustained regeneration versus the growth of large cells (in particular, diatoms) that respond to mixing events. Legendre and Le Fevre (1989) have formalized this into a general "bifurcation" model. At Sta. ALOHA, we observed three independent euphotic zone conditions: (i) "steady-state" growth of picophytoplankton on regenerated nutrients, leading to low rates of new and export production but high total production, (ii) periods of rapid growth of larger phytoplankton cells, primarily in late winter (January–March) following periods of nutrient injection, leading to high rates of new and export production, and (iii) periods of rapid growth of N_2-fixing microorganisms, primarily in late summer (August–September) following periods of prolonged stratification, leading to high rates of new production but variable rates of export production. We emphasize that both strong and weak mixing can enhance new and export production, the former by import of NO_3^- and the latter by providing a habitat conducive for N_2-fixing organisms in surface waters (Karl *et al.*, 1992, 1995).

At Sta. ALOHA, the growth and activities of the N_2-fixing cyanobacterium *Trichodesmium* already have been shown to result in major ecosystem changes including increased primary and new production and a shift from N-limitation to P-limitation (Karl *et al.*, 1995; Letelier and Karl, in press). The decoupling of primary and export production at Sta. ALOHA (Fig. 12) also may be partly explained by variations in *Trichodesmium* abundance. During periods of elevated N_2-fixation, euphotic zone production and regeneration processes result in the accumulation of dissolved organic matter that is enriched in C and N relative to P (Karl *et al.*, 1995). For the period 1991–1992, primary production increased 40% relative to the 1989–1990 observation period, but PC flux decreased by 31% (Fig. 12; Karl *et al.*, 1995). The net accumulation of dissolved organic matter in the upper 50 m of the euphotic zone at Sta. ALOHA accounted for more than 50% of the particle flux "deficit", indicating a dramatic change in the relative efficiencies of the various components of the biological pump.

The more efficient and intensive particle regeneration processes observed during "N_2-fixation driven" time periods may be simply a manifestation of shift from N- to P-controlled new (and export) production. During periods when N_2 fixation dominates as the source of new nitrogen a decoupling between C (or N) production and C (or N) export is expected. The decoupling timescale will be determined largely by the combined rate of supply of P from beneath the euphotic zone or as atmospheric deposition. As fall approaches, a light level-induced phytoplankton cell senescence could result from a breakdown in density stratification and mean mixed-layer depth. Increased turbulence also might provide a physical mechanism for increased phytoplankton cell aggregation especially for particles with the characteristically high C:P ratios that have been observed at Sta. ALOHA during periods of increased rates of N_2-fixation (Karl *et al.*, 1992, 1995; Letelier and Karl, in press). Alternatively, changes in secondary production and grazing resulting from anticipated predator–prey oscillations (Vinogradov *et al.*, 1973) may be responsible for decoupling primary production and particle export. It is known, for example, that copepod grazing retards rather than accelerates particle export by locally recycling organic matter (Smetacek, 1985). In either case, these conditions could lead to an apparent negative correlation between rates of primary production and export, as observed at Sta. ALOHA during an extended 3-year period from 1990 to 1993 (Fig. 12). This model would explain

both the existence and interannual variability of the fall export pulse observed at Sta. ALOHA, as well as other ecosystem characteristics only partially summarized here.

Acknowledgements—The authors thank the HOT program personnel, especially T. Houlihan, U. Magaard, L. Fujieki, G. Tien, C. Carrillo, R. Lukas, E. Firing, S. Chiswell and J. Snyder for their numerous contributions to the success of this field-intensive study, and the Captains and Crew members of the nine different research vessels that were used during the first 5 years of our investigation. L. Lum and L. Fujieki were indispensible in the preparation of this paper. The HOT program was supported, in part, by National Science Foundation grants OCE-8717195 and OCE-9303094 (R. Lukas, P.I.), OCE-8800329 and OCE-90-16090 (D. Karl, P.I.), National Oceanic and Atmospheric Administration grant NA-90-RAH-00074 (C. Winn, P.I.) and by the State of Hawaii. SOEST Contribution 4061 and U.S. JGOFS Contribution 224.

REFERENCES

Anderson L. A. and J. L. Sarmiento (1994) Redfield ratios of remineralization determined by nutrient data analysis. *Global Biogeochemical Cycles*, **8**, 65–80.

Baines S. B., M. L. Pace and D. M. Karl (1994) Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans? *Limnology and Oceanography*, **39**, 213–226.

Berger W. H. (1989) Appendix: Global maps of ocean productivity. In: *Productivity of the Ocean: Present and Past*, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley and Sons Limited, New York, pp. 429–455.

Berger W. H., K. Fischer, C. Lai and G. Wu (1987) Ocean Productivity and Organic Carbon Flux. I. Overview and Maps of Primary Production and Export Production. Univ. California, San Diego, Sio Reference 87–30.

Betzer P. R., W. J. Showers, E. A. Laws, C. D. Winn, G. R. DiTullio and P. M. Kroopnick (1984) Primary productivity and particle fluxes on a transect of the equator at 153°W in the Pacific Ocean. *Deep-Sea Research*, **31**, 1–11.

Bingham F. M. and R. Lukas (1996) Seasonal cycles of temperature, salinity and dissolved oxygen observed in the Hawaii Ocean Time-series. *Deep-Sea Research II*, **43**, 199–213.

Carlson C. A., H. W. Ducklow and A. F. Michaels (1994) Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature*, **371**, 405–408.

Donaghay P. L., P. S. Liss, R. A. Duce, D. R. Kester, A. K. Hanson, T. Villareal, N. W. Tindale and D. J. Gifford (1991) The role of episodic atmospheric nutrient inputs in the chemical and biological dynamics of oceanic ecosystems. *Oceanography*, **4**, 62–70.

Dugdale R. C. and J. J. Goering (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography*, **12**, 196–206.

Eppley R. W. (1989) New production: History, methods, problems. In: *Productivity of the Ocean: Present and Past*, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley and Sons, New York, pp. 85–97.

Eppley R. W. and B. J. Peterson (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.

Eppley R. W., E. H. Renger, E. L. Venrick and M. M. Mullin (1973) A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. *Limnology and Oceanography*, **18**, 534–551.

Eppley R. W., E. H. Renger and P. R. Betzer (1982) The residence time of particulate organic carbon in the surface layer of the oceans. *Deep-Sea Research*, **29**, 311–323.

Eppley R. W., E. Stewart, M. R. Abbott and U. Heyman (1985) Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. *Journal of Plankton Research*, **7**, 57–70.

Fitzwater S. E., G. A. Knauer and J. H. Martin (1982) Metal contamination and its effect on primary production measurements. *Limnology and Oceanography*, **27**, 544–551.

Goldman J. C. (1988) Spatial and temporal discontinuities of biological processes in pelagic surface waters. In: *Toward a Theory on Biological–Physical Interactions in the World Ocean*, B. J. Rothschild, editor, Kluwer Academic, Dordrecht, pp. 273–296.

Goldman J. C. (1993) Potential role of large oceanic diatoms in new primary production. *Deep-Sea Research I*, **40**, 159–168.

Hamilton J. M., M. R. Lewis and B. R. Ruddick (1989) Vertical fluxes of nitrate associated with salt fingers in the world's oceans. *Journal of Geophysical Research*, **94**, 2137–2145.

Hayward T. L. (1987) The nutrient distribution and primary production in the central North Pacific. *Deep-Sea Research*, **34**, 1593–1627.

Honjo S. (1980) Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. *Journal of Marine Research*, **38**, 53–97.

Honjo S. and K. W. Doherty (1988) Large aperture time-series sediment traps; design objectives, construction and application. *Deep-Sea Research*, **35**, 133–149.

Hornbeck R. W. (1975) *Numerical Methods*. Quantum Publishers, New York, 465 pp.

Karl D. M. and G. A. Knauer (1984) Detritus–microbe interactions in the marine pelagic environment: Selected results from the VERTEX experiment. *Bulletin of Marine Science*, **35**, 550–565.

Karl D. M. and G. A. Knauer (1989) Swimmers: A recapitulation of the problem and a potential solution. *Oceanography*, **2**, 32–35.

Karl D. M. and C. D. Winn (1991) A sea of change: Monitoring the ocean's carbon cycle. *Environmental Science and Technology*, **25**, 1976–1981.

Karl D. M. and R. Lukas (1996) The Hawaii Ocean Time-series (HOT) program: Background, rationale and field implementation. *Deep-Sea Research II*, **43**, 129–156.

Karl D. M., G. A. Knauer and J. H. Martin (1988) Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. *Nature*, **332**, 438–441.

Karl D. M., B. D. Tilbrook and G. Tien (1991) Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antarctica. *Deep-Sea Research*, **38**, 1097–1126.

Karl D. M., R. Letelier, D. V. Hebel, D. F. Bird and C. D. Winn (1992) *Trichodesmium* blooms and new nitrogen in the North Pacific gyre. In: *Marine Pelagic Cyanobacteria: Trichodesmium and Other Diazotrophs*, E. J. Carpenter *et al.*, editors, Kluwer Academic, Dordrecht, pp. 219–237.

Karl D. M., R. Letelier, D. Hebel, L. Tupas, J. Dore, J. Christian and C. Winn (1995) Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. *Nature*, **373**, 230–234.

Klein P. and B. L. Hua (1988) Mesoscale heterogeneity of the wind-driven mixed layer: Influence of a quasigeostrophic flow. *Journal of Marine Research*, **46**, 495–525.

Knauer G. A. and V. Asper (1989) Sediment trap technology and sampling. U.S. GOFS Planning Report. 10, U.S. GOFS Planning Office, Woods Hole, Massachusetts, 94 pp.

Knauer G. A., J. H. Martin and K. W. Bruland (1979) Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the northeast Pacific. *Deep-Sea Research*, **26**, 97–108.

Knauer G. A., D. M. Karl, J. H. Martin and C. N. Hunter (1984a) *In situ* effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. *Journal of Marine Research*, **42**, 445–462.

Knauer G. A., J. H. Martin and D. M. Karl (1984b) The flux of particulate organic matter out of the euphotic zone. In: *Global Ocean Flux Study, Proceedings of a Workshop, September 10–14, 1982*, National Academic Press, Washington, D.C. pp. 136–150.

Knauer G. A., D. G. Redalje, W. G. Harrison and D. M. Karl (1990) New production at the VERTEX time-series site. *Deep-Sea Research*, **37**, 1121–1134.

Lee C., S. G. Wakeham and J. I. Hedges (1988) The measurement of oceanic particle flux — are "swimmers" a problem? *Oceanography*, **1**, 34–36.

Lee D.-K., P. P. Niiler, A. Warn-Varnas and S. Piacsek (1994) Wind-driven secondary circulation in ocean mesoscale. *Journal of Marine Research*, **52**, 371–396.

Legendre L. and J. Le Fevre (1989) Hydrodynamical singularities as controls of recycled versus export production in oceans. In: *Productivity of the ocean: Present and past*, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley and Sons Limited, New York, pp. 49–63.

Letelier R. M. and D. M. Karl (in press) The role of *Trichodesmium* spp. in the productivity of the subtropical North Pacific Ocean. *Marine Ecology Progress Series*.

Letelier R. M., J. E. Dore, C. D. Winn and D. M. Karl (1996) Seasonal and interannual variations in photosynthetic carbon assimilation at Station ALOHA. *Deep-Sea Research II*, **43**, 467–490.

Lohrenz S. E., G. A. Knauer, V. L. Asper, M. Tuel, A. F. Michaels and A. H. Knap (1992) Seasonal and interannual variability in primary production and particle flux in the northwestern Sargasso Sea: US. JGOFS Bermuda Atlantic Time-Series. *Deep-Sea Research*, **39**, 1373–1391.

Lohrenz S. E., D. A. Wiesenburg, C. R. Rein, R. A. Arnone, C. D. Taylor, G. A. Knauer and A. H. Knap (1992) A comparison of *in situ* and simulated *in situ* methods for estimating oceanic primary production. *Journal of Plankton Research*, **14**, 201–221.

Longhurst A. R. (1991) Role of the marine biosphere in the global carbon cycle. *Limnology and Oceanography*, **36**, 1507–1526.

Longhurst A. R. and W. G. Harrison (1989) The biological pump: Profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography*, **22**, 47–123.

Martin J. H., G. A. Knauer, D. M. Karl and W. W. Broenkow (1987) VERTEX: carbon cycling in the northeast Pacific. *Deep-Sea Research*, **34**, 267–285.

McCave I. N. (1975) Vertical flux of particles in the ocean. *Deep-Sea Research*, **22**, 491–502.

McGowan J. A. and T. L. Hayward (1978) Mixing and oceanic productivity. *Deep-Sea Research*, **25**, 771–793.

Michaels A. F., N. R. Bates, K. O. Buesseler, C. A. Carlson and A. H. Knap (1994) Carbon-cycle imbalances in the Sargasso Sea. *Nature*, **372**, 537–540.

Michaels A. F., A. H. Knap, R. L. Dow, K. Gundersen, R. J. Johnson, J. Sorensen, A. Close, G. A. Knauer, S. E. Lohrenz, V. A. Asper, M. Tuel and R. Bidigare (1994) Seasonal patterns of ocean biogeochemistry at the U.S. JGOFS Bermuda Atlantic Time-series Study site. *Deep-Sea Research*, **41**, 1013–1038.

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.

Peinert R., B. von Bodungen and V. S. Smetacek (1989) Food web structure and loss rate. In: *Productivity of the ocean: Present and past*, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley and Sons Limited, New York, pp. 35–48.

Peterson W. and H. G. Dam (1990) The influence of copepod "swimmers" on pigment fluxes in brine-filled vs. ambient seawater-filled sediment traps. *Limnology and Oceanography*, **35**, 448–455.

Platt T. and W. G. Harrison (1985) Biogenic fluxes of carbon and oxygen in the ocean. *Nature*, **318**, 55–58.

Polovina J. J., G. T. Mitchum, N. E. Graham, M. P. Craig, E. E. Demartini and E. N. Flint (1994) Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography*, **3**, 15–21.

Redfield A. C., B. H. Ketchum and F. A. Richards (1963) The influence of organisms on the composition of seawater. In: *The sea, ideas and observations on progress in the study of the seas, Vol. 2*, M. N. Hill, editor, Interscience, New York, pp. 26–77.

Ryther J. H. (1969) Photosynthesis and fish production in the sea. The production of organic matter and its conversion to higher forms of life vary throughout the world ocean. *Science*, **166**, 72–76.

Sambrotto R. N., G. Savidge, C. Robinson, P. Boyd, T. Takahashi, D. M. Karl, C. Langdon, D. Chipman, J. Marra and L. Codispoti (1993) Elevated consumption of carbon relative to nitrogen in the surface ocean. *Nature*, **363**, 248–250.

Sancetta C., T. Villareal and P. Falkowski (1991) Massive fluxes of rhizosolenid diatoms: A common occurrence? *Limnology and Oceanography*, **36**, 1452–1457.

Siegel D. A., T. C. Granata, A. F. Michaels and T. D. Dickey (1990) Eddy diffusion, particle sinking and the interpretation of sediment trap data. *Journal of Geophysical Research*, **95**, 5305–5312.

Small L. F., G. A. Knauer and M. D. Tuel (1987) The role of sinking fecal pellets in stratified euphotic zones. *Deep-Sea Research*, **34**, 1705–1712.

Smetacek V. S. (1985) The role of sinking in diatom life-history cycles: Ecological, evolutionary and geological significance. *Marine Biology*, **84**, 239–251.

Strickland J. D. H. and T. R. Parsons (1972) *A practical handbook of seawater analysis*. Fisheries Research Board of Canada, 167 pp.

Suess E. (1980) Particulate organic carbon flux in the oceans —surface productivity and oxygen utilization. *Nature*, **288**, 260–263.

Taylor G. T., D. M. Karl and M. L. Pace (1986) Impact of bacteria and zooflagellates on the composition of sinking particles: an *in situ* experiment. *Marine Ecology Progress Series*, **29**, 141–155.

Toggweiler J. R. (1989) Is the downward dissolved organic matter (DOM) flux important in carbon transport? In: *Productivity of the ocean: Present and past*, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley and Sons Limited, New York, pp. 65–83.

Trenberth K. E. and J. W. Hurrell (1994) Decadal atmosphere–ocean variations in the Pacific. *Climate Dynamics*, **9**, 303–319.

Triola M. (1989) *Elementary statistics*, 4th edn, Benjamin Cummings, 784 pp.

Venrick E. L. (1993) Phytoplankton seasonality in the central North Pacific: The endless summer reconsidered. *Limnology and Oceanography*, **38**, 1135–1149.

Villareal T. A., M. A. Altabet and K. Culver-Rymsza (1993) Nitrogen transport by migrating diatom mats in the North Pacific Ocean. *Nature*, **363**, 709–712.

Vinogradov M. E., V. F. Krapivin, V. V. Menshutkin, B. S. Fleyshman and E. A. Shuskina (1973) Mathematical model of the functions of the pelagical ecosystem in tropical regions (from the 50th voyage of the R.V. *Vityaz*). *Oceanology*, **13**, 704–717.

Volk T. and M. I. Hoffert (1985) Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO_2 changes. In: *The carbon cycle and atmospheric CO_2: Natural variations Archean to present*, E. T. Sundquist and W. S. Broecker, editors, American Geophysical Union, Washington, D.C., pp. 99–110.

Wassman P. (1990) Relationship between primary and export production in the boreal coastal zone of the North Atlantic. *Limnology and Oceanography*, **35**, 464–471.

Williams P. J. LeB. and B. von Bodungen (1989) Group report: Export productivity from the photic zone. In: *Productivity of the ocean: Present and past*, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley and Sons Limited, New York, pp. 99–115.

Winn C. D., L. Campbell, J. R. Christian, R. M. Letelier, D. V. Hebel, J. E. Dore, L. Fujieki and D. M. Karl (1995) Seasonal variability in the phytoplankton community of the North Pacific subtropical gyre. *Global Biogeochemical Cycles*, **9**, 605–620.

Winn C. D., F. T. Mackenzie, C. J. Carrillo, C. L. Sabine and D. M. Karl (1994) Air–sea carbon dioxide exchange in the North Pacific Subtropical Gyre: Implications for the global carbon budget. *Global Biogeochemical Cycles*, **8**, 157–163.