Deep-Sea Research, Vol. 36, No. 1, pp. 103-120, 1989.
Printed in Great Britain.

0198-0149/89 $3.00 + 0.00
© 1989 Pergamon Press plc.

Autotrophic production and elemental fluxes at 26°N, 155°W in the North Pacific subtropical gyre

EDWARD A. LAWS,* GIACOMO R. DITULLIO,*† PETER R. BETZER,‡ DAVID M. KARL* and KENDAL L. CARDER‡

(*Received* 19 *April* 1988; *in revised form* 10 *July* 1988; *accepted* 27 *July* 1988)

Abstract—Autotrophic carbon and nitrogen assimilation rates and the fluxes of particulate carbon (PC) and particulate nitrogen (PN) into sediment traps positioned near the base of the euphotic zone were measured at 26°N, 155°W in the North Pacific subtropical gyre. Carbon assimilation uncorrected and corrected for grazing and algal respiration losses averaged 484 ± 81 and 692 ± 115 mg C $m^{-2}d^{-1}$, respectively. Carbon:nitrogen assimilation ratios were always higher than the Redfield ratio and averaged 7.1 ± 0.6 g C g^{-1}N. Absolute growth rates were estimated to be 69 ± 10% of nutrient-saturated values.

A comparison of conical and cylindrical sediment traps indicated that the conical traps underestimated PN and PC fluxes by factors of 30 and 40, respectively. This undertrapping probably occurred in part because the effective trapping area of the conical traps is significantly less than the mouth area of the trap for slowly sinking particles. However, several lines of evidence suggest that the major cause of the discrepancy was the breakup of marine snow aggregates that encountered the sloping sides of the conical traps. The *f* ratios calculated from PN fluxes into the cylindrical traps varied by about a factor of three and averaged 19 ± 10%. Part of the temporal variability in the *f* ratio appeared to be due to the fact that particulate material accumulated in the euphotic zone during storm events and subsequently appeared as a large flux of PN as the storm dissipated. The PC:PN ratio of the material that sedimented at the base of the euphotic zone (9.2 ± 1.1 g C g^{-1}N) was consistently higher than the corresponding autotrophic assimilation rate ratio. Because of this fact net community production exceeded new production in terms of carbon by about 30%. The latter was calculated by multiplying the downward flux of PN by the autotrophic carbon:nitrogen assimilation rate ratio.

INTRODUCTION

IN 1967, Dugdale and Goering introduced the terms "regenerated production" and "new production" into the phytoplankton ecology literature. They defined regenerated production as primary production associated with recycled nitrogen in the form of ammonium or dissolved organic N, and new production as primary production associated with newly incorporated nitrogen such as nitrate or N_2. As long as there is no long-term monotonic trend in the areal concentration of fixed N in the euphotic zone, the rate of new production must be balanced by the flux of fixed N out of the euphotic zone. This flux is believed to occur primarily in the form of sinking organic matter, although some export undoubtedly occurs as a result of grazing by vertical migrators as well (MANN, 1984).

* University of Hawaii Oceanography Department, 1000 Pope Road, Honolulu, HI 96822, U.S.A.
† Present address: Biological Laboratories, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, U.S.A.
‡ Marine Science Department, University of South Florida, St. Petersburg, FL 33701, U.S.A.

Knowledge of the magnitude of this flux and of its relationship to areal primary production rates is crucial to understanding the mechanisms by which food is provided to mesopelagic and deep-sea animal communities. Calculations often have indicated that primary production rates are too low and particle fluxes too small to provide the amount of food needed by mesopelagic and deep-sea organisms (MANN, 1984; SMITH, 1987). The implication is that for some reason the production and/or flux numbers have been systematically underestimated, or that conceptual models of biomass and energy transformations in the ocean need to be revised (ISAACS, 1972, 1973). Knowledge of primary production rates and vertical particle fluxes in the ocean also are needed to estimate the ability of the ocean to act as a sink for increasing concentrations of atmospheric CO_2 and various atmospheric pollutants (SCOR, 1987; WALSH *et al.*, 1985).

In recent years there has been much controversy regarding the magnitude of both particle fluxes and areal primary production rates, particularly in the open ocean (KNAUER *et al.*, 1979; SHULENBERGER and REID, 1981; PLATT and HARRISON, 1985). For example, recent primary production estimates at 28°N, 155°W in the North Pacific subtropical gyre have yielded daily production rates of about 0.4 g C $m^{-2}d^{-1}$ (LAWS *et al.*, 1987; MARRA and HEINEMANN, 1987), a figure about twice the mean of historical productivity numbers for that location (HAYWARD *et al.*, 1983). The historical productivity estimates were obtained using conventional ^{14}C techniques, while the more recent estimate of 0.4 g C $m^{-2}d^{-1}$ was obtained using clean techniques (FITZWATER *et al.*, 1982) and large incubation bottles (GIESKES *et al.*, 1979) to minimize artifacts caused by trace metal contamination and bottle confinement, respectively. Particle fluxes have been estimated from both moored and free-floating sediment traps, but there is disagreement concerning the optimal geometry of such traps (GARDNER, 1980a,b; DYMOND *et al.*, 1981; BUTMAN, 1986), duration of employment (BYRNE *et al.*, 1984), and method of sample analysis. Studies in flumes have shown that in the presence of currents a moored trap collects particles through a process of fluid exchange rather than through settling of the particles into the trap (GARDNER, 1980a). In order to circumvent this problem, STARESINIC *et al.* (1982) advocated the use of free-drifting sediment traps. They reasoned that, "sediment traps used properly in the free-drifting mode should correspond to the moored situation in which there is no horizontal current" (STARESINIC *et al.*, 1982, p. 274). In deployments lasting more than about a week, a preservative such as 5% buffered formalin is usually added to the collection cup of sediment traps to prevent both decomposition of the sedimented organic matter and microbial growth on the inside of the collectors (KNAUER *et al.*, 1979). Studies by KNAUER *et al.* (1984) show no significant difference in results obtained from unpreserved and preserved traps during 6-day deployments off Point Sur, California, but particulate carbon and nitrogen fluxes were about 50% higher in 0.12 M formalin-preserved traps vs controls (no preservatives) during 20.6 day deployments off Manzanillo, Mexico. However, preservatives do nothing to slow the rate of strictly chemical processes. Because of the rapid dissolution kinetics of pteropod frustules, BYRNE *et al.* (1984, p. 325) have noted that, "Long duration sediment trap deployments in undersaturated seawater will lead to large underestimates of aragonite fluxes." Furthermore, strictly physical processes can convert fragile organic matter such as marine snow into much smaller particles, some of which may pass through standard filters. Thus it may be necessary to assay the concentrations of both dissolved and particulate constituents in collection cups if an accurate estimate of the fluxes of organic matter are to be obtained. The conclusion seems to be that the

proper design of sediment trap experiments depends both on the type of particles to be trapped and on the physical and chemical characteristics of the water at the study site.

An alternative to the use of sediment traps is to estimate new production from the uptake of nitrate within the euphotic zone and to assume an approximate balance between areal nitrate uptake rates and the flux of particulate nitrogen (PN) from the euphotic zone (EPPLEY and PETERSON, 1979). Nitrate uptake rates have usually been estimated using $^{15}NO_3^-$ as a tracer, but throughout much of the euphotic zone in the open ocean ambient nitrate concentrations are so low (~10–50 nM) that addition of ^{15}N in concentrations (~50 nM) sufficient for subsequent isotope ratio measurements significantly increases the NO_3^- concentrations in the water and may therefore alter uptake rates (GLIBERT and GOLDMAN, 1981). Furthermore, prior to the development of GARSIDE's (1982) chemiluminescent technique for NO_3^- analysis, concentrations of nitrate in the upper euphotic zone of the open ocean bordered on the limit of detection and therefore could not be estimated with much accuracy (EPPLEY *et al.*, 1977).

The present study, undertaken as a part of the ADIOS (Asian Dust Input to the Oceanic System) project, was intended to provide estimates of new production and the ratio of new production to total production (*f* ratio) in terms of both carbon and nitrogen at a location (26°N, 155°W) in the southern portion of the North Pacific subtropical gyre. The studies were conducted during March–April 1986 (ADIOS I), September–October 1986 (ADIOS II), and March–April 1987 (ADIOS III), in order to permit an interseasonal comparison of results. The ADIOS I cruise was of sufficient duration to allow a meaningful study of shorter term temporal variability in production and particle flux as well. The experimental design was specifically intended to examine the conclusions of PLATT and HARRISON (1985, p. 56) that, "The distributions of biological properties in the ocean are highly variable in . . . time" and that, "A given oceanic province can be expected . . . to manifest a range of characteristics from apparent extreme oligotrophy to eutrophy." The study also provided a revealing comparison of the efficiency of two types of free-drifting sediment traps in collecting sinking organic matter.

MATERIALS AND METHODS

All sampling was done at approximately 26°N, 155°W (Fig. 1) from the R.V. *Moana Wave*. The primary productivity studies were performed using the sampling and incubation techniques described by LAWS *et al.* (1987) with the exception of the light quality in the on-deck incubators. Rather than by neutral density filters, light was attenuated in the incubators with a combination of neutral density filters and blue and blue-violet Rohm and Haas plexiglass filters (nos. 2069 and 2424, respectively) in order to simulate submarine light quality. The incubators had simulated visible light transmission levels of 100, 35, 18, 3.5, 1.0 and 0.1% of subsurface (0.5 m) photon fluxes. To determine the depths corresponding to these light intensities, photon flux densities in the water column were measured at local noon on the day after the ship arrived on station using a spherical quantum sensor (LiCor model 193SB) which was attached to a frame mounted to the top of a Seabird conductivity–temperature–depth (CTD) system. The CTD system was used to locate depths accurately and to provide essential hydrographic data. On-deck photon fluxes were monitored simultaneously with a LiCor model 190SB cosine-corrected quantum sensor. Outputs from both sensors were integrated for 1 min and submarine photon fluxes calculated as a fraction of surface photon fluxes by a LiCor model 1000

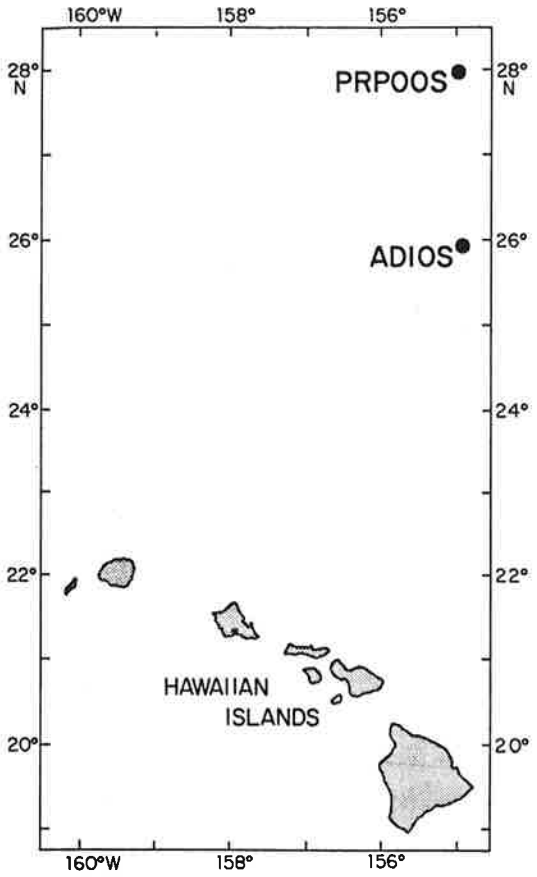


Fig. 1. Location of the ADIOS and PRPOOS sampling stations.

Data Logger. Continuously flowing surface seawater was used to maintain the temperature in the incubators. Temperature differences between the surface and 150 m (the greatest depth sampled) averaged 1.3, 7.2 and 3.5°C durig ADIOS I, II and III, respectively.

Hydrocasts were started at approximately 0400, and incubations in 4.4 l polycarbonate bottles were begun just before sunrise with the addition of 1 ml of $NaH^{14}CO_3$ solution (sp. act. 15–25 Ci mol^{-1}, 500 mCi l^{-1}). All incubations lasted 24 h, and all samples for ^{14}C activity were taken in triplicate except as noted. Total inorganic ^{14}C activity in the bottles was measured by the addition of 0.5 ml of water to 0.2 ml of a 1:1 solution of phenethylamine:methanol. Total particulate ^{14}C activity was measured by filtering 100 ml sample aliquots onto Whatman GF/F glass fiber filters. The filters were stored in scintillation vials containing 1 ml of 10% HCl to drive off residual inorganic ^{14}C (LEAN and BURNISON, 1979; GOLDMAN and DENNETT, 1985). A time zero blank was subtracted from all productivity samples in accord with the recommendation of MORRIS *et al.* (1971). Dark bottles were not used as corrections for non-photosynthetic processes because non-photosynthetic ^{14}C uptake may occur at very different rates in the light and dark (HECKY and FEE, 1981). The rate of incorporation of ^{14}C into protein was estimated from duplicate 750 ml samples analysed according to the procedures outlined in DITULLIO and LAWS (1986). Autotrophic nitrogen assimilation was estimated by dividing the protein carbon assimilation rate by 2.8 g C $g^{-1}N$ (DITULLIO and LAWS, 1986). Inorganic carbon concentrations were determined by titration (STRICKLAND and PARSONS, 1972). Radioacti-

vity measurements were made by liquid scintillation counting using ACS (Amersham) as the fluor on a Searle Analytic Delta 300 liquid scintillation counter. Quench corrections were made using the external standard ratio. Activities were converted to uptake rates using equations in STRICKLAND and PARSONS (1972).

Chlorophyll *a* (Chl *a*) concentrations were estimated by filtering 2 liters of water from Go-Flo water sampling bottles onto GF/F filters at the start of the incubations. These samples were not replicated. On a few occasions the water was taken directly from the incubation bottles, in which cases only 1 liter was filtered. The filters were placed in cryogenic tubes and the tubes flushed with N_2 prior to storage in liquid N_2. In the laboratory filters were homogenized in 90% acetone and allowed to extract overnight under N_2 at –4°C. The extracts were clarified by centrifugation and concentrated with C18 Sep-Pak cartridges (Waters Assoc.) before analysis on a Varian 5000 high performance liquid chromatograph (HPLC) connected to a Varian 4270 integrator. Chl *a* was eluted isocratically with 100% methanol at a flow rate of 1.5 ml min^{-1} on a 15 × 0.4 cm (3 μm) Spherisorb ODS II column (Alltech) and quantified using a Kratos 970 spectrofluorometer. The system was calibrated with pure Chl *a* supplied by Sigma Chemical. The concentrations of the Chl *a* standards were measured on a Varian DMS 100 spectrophotometer.

Downward fluxes of particulate carbon (PC) and particulate nitrogen (PN) were measured in two different types of free-floating sediment traps deployed at depths of 30, 120 and 200 m. The first type of trap was a conical trap previously described by BETZER *et al.* (1984). The trap has a mouth area of 0.66 m^2, a height of 1.88 m, and a collection cup area of 5.07 cm^2. The ratio of mouth area to collection cup area is 1296. The mouth of the trap contains a baffle consisting of 60 tubes with an inside diameter of 10 cm. The inner tubes are 29 cm long and the outer tubes 18 cm long. The collection cup (Teflon) and its contents can be isolated by a double ball valve seal that is activated by an electronic release. The conical traps were always deployed in an open configuration, and except as noted, collected material for 24 h, at which time the Teflon collection cup was sealed shut. The collection cup contained no preservatives. After retrieval of the traps, the contents of the collection cup were passed through either a 64 μm (ADIOS I) or 500 μm (ADIOS II and III) screen, and the entire screened sample or an aliquot thereof was filtered onto a previously combusted (450°C, 24 h) GF/F filter for PC and PN analysis. The filters were stored frozen (–20°C) until just prior to analysis on a Hewlett-Packard model 185B CHN analyser. Due to electronics problems, the only conical trap samples collected during ADIOS III came from a depth of 200 m.

The second type of sediment trap employed in these studies was the cylindrical trap described by KNAUER *et al.* (1979). These traps were deployed in an array of 12 individual polycarbonate cylinders mounted on a polyvinyl-chloride frame. The mouth of each trap contains a baffle consisting of 14 small tubes with a length of 7.6 cm and inside diameter of 1.27 cm. The cylinders have a collection area of 39 cm^2 and a height of 62 cm. The cylinders contained no preservatives, bud did contain a high-density NaCl solution to prevent flushing during recovery and a 335 μm pre-screen to exclude swimmers (KARL *et al.*, 1988). During ADIOS I the cylinders were closed during their descent to depth with the use of plastic sheeting secured by a rubberband and soluble link as described by KNAUER *et al.* (1979). However, during ADIOS II and III the cylinders were deployed in an open configuration. The cylindrical trap arrays were deployed from 3 to 12 days, and were retrieved in an open configuration. Upon retrieval triplicate aliquots from one of

the cylindrical traps were filtered separately onto precombusted GF/F filters and analysed for PC and PN as previously described.

RESULTS

The results of the primary production studies are shown in Fig. 2 and Table 1. Production results from ADIOS III are not included because sediment trap data from the base of the euphotic zone were not obtained for comparison purposes. Production:biomass ratios (P:B) less than 95 g C g^{-1}Chl *a* d^{-1} were significantly correlated with subsurface photon fluxes ($r = 0.735$, $P < 0.01$), but the correlation was improved ($r = 0.874$)

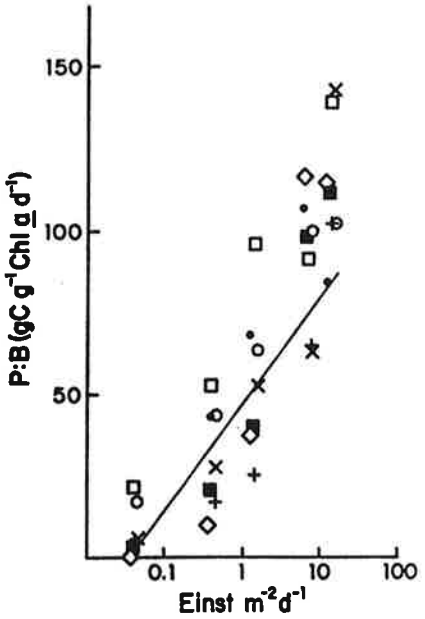


Fig. 2. P:B ratios as a function of irradiance during ADIOS I and II cruises. Results at 100% surface irradiance have not been included. Dots, open circles, X's, open squares, +'s, closed squares and diamonds correspond to results from 25 March, 29 March, 1 April, 4 April, 6 April, 11 October and 14 October, respectively.

Table 1. *Autotrophic carbon and nitrogen assimilation rates integrated to the* 0.1% *light level, the ratio of integral* C *to integral* N *assimilation, and integral average Chl* a *concentrations above the* 0.1% *light level during ADIOS* I *and* II. *The integrations were performed using the trapezoid rule* (HORNBECK, 1975)

Date incubation begun (1986)	C Assimilation (mg C $m^{-2}d^{-1}$)	N Assimilation (mg N $m^{-2}d^{-1}$)	C:N (g:g)	Chl *a* (mg m^{-3})
25 Mar.	372	62.6	5.9	0.057
29 Mar.	426	58.7	7.3	0.047
1 Apr.	449	61.0	7.4	0.068
4 Apr.	591	80.7	7.3	0.055
6 Apr.	513	67.4	7.6	0.143
14 Apr.	605*	84.9*	–	0.089
11 Oct.	454	67.6	6.7	0.068
14 Oct.	461	60.0	7.7	0.084

* On this date rough weather resulted in damage to the incubators, and only sunrise–noon production numbers were salvaged. Photoperiod production was estimated to be twice the sunrise–noon value, and dark loss to equal 24% of photoperiod production (see text). N assimilation was equated to C assimilation divided by the mean C:N assimilation ratio (7.1 ± 0.6) from the other seven dates.

if the photon fluxes were log transformed (Fig. 2). The fact that a logarithmic transformation tends to linearize such data has been noted by others (FALKOWSKI and OWENS, 1980; TERRY *et al.*, 1983) and reflects the curvilinear nature of the underlying relationship. If the regression line in Fig. 2 is extrapolated to a P:B of zero, the associated photon flux is 0.037 E $m^{-2}d^{-1}$. This figure may be compared to the average surface photon flux of 43 ± 4 and 36 ± 4 E $m^{-2}d^{-1}$ during the March–April and October sampling, respectively. Thus the compensation depth appeared to be at approximately the 0.1% light level. For P:B ratios greater than 95 g C g^{-1}Chl *a* d^{-1} there was an insignificant correlation ($r = 0.51$, $P > 0.05$) between P:B ratios and subsurface photon fluxes, a fact presumably reflecting the importance of nutrient limitation rather than light intensity in controlling P:B ratios at higher light levels (see following discussion). P:B ratios in bottles incubated in full sunlight were lower than the P:B ratios in bottles incubated at 35% surface irradiance in five of the seven 24 h incubations, a result consistent with the often-observed phenomenon of inhibition of phytoplankton production by full sunlight (JOKIEL and YORK, 1984).

Because the analysis in Fig. 2 indicated that the compensation depth occurred at about the 0.1% light level, we estimated areal carbon and nitrogen assimilation rates by integrating our calculated carbon and nitrogen uptake rates from the surface to the 0.1% light level (Table 1). The average depth of the 0.1% light level was 148 ± 7 m. Had the integrations been extended to only the 1% light level (average depth 99 ± 4 m), the areal carbon assimilation rates would have been reduced by 19 ± 7%.

Because of day-to-day variations in particle fluxes, the differences in time of deployment between the cylindrical and conical sediment traps would be expected to produce some differences in measured fluxes. However, examination of the results from the conical traps between 29 March and 12 April 1986 shows that at depths of 30 and 120 m these day-to-day variations amounted to no more than about 30% (Table 2). If the cylindrical and conical traps were operating with equal efficiency, one might therefore expect the calculated fluxes from the two types of traps to agree to within ±30%. However, if the average daily fluxes into the cylindrical traps are compared to the daily fluxes into the conical traps measured during the time interval when the cylindrical traps were deployed, the discrepancy is much larger than 30%. Using the fluxes into the cylindrical traps as the standards for comparison, the trapping efficiencies (±95% confidence intervals) of the conical traps averaged over all three deployment depths from 29 March to 12 April 1986 are only 3.3 ± 1.0% and 2.5 ± 0.9% for PN and PC fluxes, respectively. The difference in trapping efficiency of PC and PN is significant at $P < 0.01$ by a paired *t*-test.

Based on our analysis of the primary productivity data, downward fluxes from the euphotic zone would be estimated best from traps deployed at a depth of about 150 m. Traps were deployed at this depth only during the ADIOS II cruise (October 1986). However, because the 1% light level was found at a depth of 99 ± 4 m and because production between 1 and 0.1% light levels accounted for only 19 ± 7% of areal production, it seems reasonable to assume that over 90% of areal production occurred in the water column above the traps deployed at 120 m. We therefore have estimated flux:assimilation ratios by calculating the ratio of PC and PN fallout into these traps to the areal production rates of carbon and nitrogen, respectively. Except as noted, flux:assimilation ratios were calculated using only the fluxes into the cylindrical traps, and for this purpose the areal production rates in Table 1 were averaged over the

Table 2. Results of sediment trap studies. Fluxes are mg $m^{-2}d^{-1}$

Trap type	Duration of deployment	Depth of deployment	C flux	N flux	C:N ($g\ g^{-1}$)
Cylinder	24–31 Mar. 1986	30	69.8	8.1	8.6
		120	50.5	5.1	9.9
		200	54.3	5.7	9.5
Cone	29–30 Mar. 1986	120	1.93	0.245	7.9
Cylinder	31 Mar.–12 Apr. 1986	30	79.6	8.8	9.1
		120	63.6	7.9	8.0
		200	44.3	4.0	11.0
Cone	31 Mar.–1 Apr. 1986	30	1.88	0.366	5.1
		120	2.55	0.317	8.0
	2–3 Apr. 1986	30	1.61	0.230	3.5
		120	2.23	0.261	8.5
	3–4 Apr. 1986	200	0.65	0.100	6.5
	10–11 Apr. 1986	30	2.42	0.373	6.5
	11–12 Apr. 1986	120	2.04	0.282	7.3
		200	0.13	0.039	3.3
Cylinder	14–17 Apr. 1986	30	174	15.9	10.9
		120	231	23.6	9.8
		200	108	8.7	12.4
Cone	16–17 Apr. 1986	30	1.97	0.305	6.5
		120	1.59	0.251	6.3
	11–12 Oct. 1986	160	2.76	0.288	9.6
	15–16 Oct. 1986	150	5.24	0.743	7.1
Cylinder	4–11 Apr. 1987	200	36.6	6.81	5.4
Cone	8–11 Apr. 1987	200	0.71	0.17	4.1

Table 3. Ratios of PC *and* PN *flux into sediment traps near the base of the euphotic zone to areal primary production rates during ADIOS* I *and* II

Time interval (1986)	PC flux/C assimilation	PN flux/N assimilation
24–31 Mar.	0.15	0.10
31 Mar.–12 Apr.	0.12	0.12
14–17 Apr.	0.38	0.28
11–12 Oct.	0.24	0.13
14–15 Oct.	0.40	0.32
Means	0.26 ± 0.13	0.19 ± 0.10

duration of trap deployment using the trapezoid rule (HORNBECK, 1975) to calculate the temporal average. In the case of the ADIOS II cruise, trap data were available from only the conical traps. In order to provide a consistent comparison, the ADIOS II results were scaled by assuming a trapping efficiency of 3.3 and 2.5% for PN and PC fluxes, respectively, based on the inter-trap comparisons during ADIOS I. The calculated flux:assimilation ratios are shown in Table 3.

DISCUSSION

Primary production and nutrient limitation

The primary production rates reported in Table 1 are all higher than the average of 315 ± 25 g C $m^{-2}d^{-1}$ reported by LAWS *et al.* (1987) from 24 h incubations at 28°N, 155°W during August and September of 1985, as a part of the PRPOOS expedition. The

difference between the two data sets is significant at $P < 0.02$ by a Wilcoxon two-sample test. The principal methodological difference in the two studies was the effort to simulate submarine light quality in the ADIOS work with the use of blue and blue-violet filters in the on-deck incubators. Whether this effort to simulate submarine light quality significantly enhanced our production results is unknown, because we did not perform parallel experiments using only neutral density filters. Data reported by HAYWARD *et al.* (1983) show no significant difference at this longitude between productivities at 26° and 28°N (Wilcoxon, $P > 0.20$), but their data do show considerable temporal variability, with productivities at 28°N varying by almost a factor of three. Thus we cannot rule out temporal variability as the principal cause of the difference between the ADIOS results and those of LAWS *et al.* (1987). Both studies yielded productivities that were considerably higher than average values for the period 1968–1980 reported by HAYWARD *et al.* (1983) at 28°N, 155°W. The latter studies sampled the water column to only the 1% light level and involved incubations of only 5–8 h. Multiplying their hourly rates by 12 to give photoperiod values and assuming a night-time loss of 24% of particulate ^{14}C activity (see below) give estimated daily production rates of 155 with a range of 81–258 mg C $m^{-2}d^{-1}$. Corresponding results integrated to the 1% light level are 273 ± 33 and 392 ± 59 mg C $m^{-2}d^{-1}$ from the PRPOOS and ADIOS cruises, respectively. Thus the more recent results are about twice the mean of the 1968–1980 data. We suspect that this difference in large part reflects the use of clean sampling techniques and large incubation bottles in the PRPOOS and ADIOS studies (FITZWATER *et al.*, 1982; GIESKES *et al.*, 1979).

The extent to which the phytoplankton populations studied during the ADIOS cruises were nutrient limited may be inferred from an examination of the calculated C:N assimilation rate ratios (Table 1). These ratios showed no correlation with incubation light intensity and were virtually the same at 100 and 0.1% surface light (7.0 ± 0.5 and 7.2 ± 1.5 g C $g^{-1}N$, respectively). The ratios were consistently higher than the Redfield ratio of 5.7 g C $g^{-1}N$, a fact which implies some degree of nutrient limitation of growth (GOLDMAN, 1980). DITULLIO and LAWS (1986) have shown that these C:N ratios are negatively correlated with the relative growth rates of nitrogen-limited marine phytoplankton, and that the C:N ratios vary from about 18.7 to 5.7 g C $g^{-1}N$ as the relative growth rate varies from 0 to 1. Relative growth rate is defined as the ratio of the absolute growth rate to the nutrient-saturated growth rate (GOLDMAN, 1980). The mean C:N ratio of 7.1 ± 0.6 g C $g^{-1}N$ estimated during the ADIOS cruises translates into a relative growth rate of 0.69 ± 0.10. This figure is somewhat lower than the relative growth rates of 0.85–0.90 estimated during the PRPOOS cruise to 28°N, 155°W (LAWS *et al.*, 1987), and would seem to imply a moderate but certainly not severe degree of nutrient limitation.

A significant decline in particulate ^{14}C activity occurred in our incubation bottles during the night, calculated areal production rates after 24 h (467 ± 69 mg C $m^{-2}d^{-1}$) being on average 24% lower than 12 h values (618 ± 93 mg C $m^{-2}d^{-1}$) in the seven cases where 24 h incubations were completed. This loss in activity presumably reflects the combined effects of grazing and phytoplankton respiration. Assuming an additional 8% loss due to grazing during the photoperiod (LAWS *et al.*, 1987), gross production for all eight experiments is estimated to be 692 ± 115 mg C $m^{-2}d^{-1}$.

Sediment trap results

Perhaps the most noteworthy aspect of the sediment trap results was the large discrepancy in PC and PN fluxes estimated from the cylindrical and conical sediment

traps. Unfortunately a comparison of sediment traps was not part of the original research plan. Had such a comparison been anticipated, differences in trap design other than size and shape and in the method and duration of deployment would have been eliminated. However, for reasons explained in the following paragraphs, we feel the 30–40 fold differences in calculated PN and PC fluxes reflect primarily differences in trap shape and size and not, for example, whether the traps were deployed in an open or closed configuration.

Two lines of evidence indicate that the cylindrical trap fluxes are reasonable and that the conical trap fluxes are unrealistically low. First, flux:assimilation ratios calculated from the cylindrical trap data (Table 3) are comparable to the ratios reported by other investigators (KNAUER and MARTIN, 1981) and to f ratios calculated using nitrate uptake (EPPLEY and PETERSON, 1979; PLATT and HARRISON, 1985) as measures of new production. The flux:assimilation ratios would have been 30–40 times smaller if the conical trap fluxes had been used in the calculations. Second, SMITH's (1987) estimated sediment oxygen consumption rates in the central North Pacific at a depth of 5900 m are equivalent to 1.6 ± 0.8 mg C $m^{-2}d^{-1}$ assuming a respiratory quotient of 0.85. This figure is 67% of the mean conical trap PC flux (2.4 ± 1.3 mg C $m^{-2}d^{-1}$) at 120–160 m. Particle fluxes generally decrease with depth below the euphotic zone, and can be expected to decrease by about a factor of 20 between 150 and 600 m (SUESS, 1980; BETZER *et al.*, 1984). If particulate fluxes in fact decline by about a factor of 20 between the base of the euphotic zone and 5900 m, the implication of this comparison is that the deep-sea benthos acquires most of its organic carbon from some source other than the downward flux of small particulate organic carbon, or else the conical trap flux estimates are too low by at least a factor of 13. However, the cylindrical trap PC fluxes, which were about 40 times greater than the conical trap PC fluxes, imply that the PC flux at 5900 m would be $(40)(2.4 \pm 1.3)/20 = 4.8 \pm 2.6$ mg C $m^{-2}d^{-1}$, which is three times SMITH's (1987) estimated sediment oxygen consumption rate in terms of carbon. Since the organic carbon provided to the benthos must support both the growth and respiratory requirements of the sediment community as well as benthopelagic animals and plankton, the cylindrical trap results seem reasonable and consistent with SMITH's (1987) observations. Why then are the conical trap results so much lower?

Causes of the discrepancy

One possible explanation for the discrepancy between the conical and cylindrical trap results is that the effective collection surface area for PC and PN in the conical traps was much less than the trap mouth area of 0.66 m^2. In order to examine this hypothesis quantitatively, we calculate using the diagram in Fig. 3, the flux of particles reaching the collection cup as a function of time. We assume the radius of the collection cup to be r_0 and the radius of the trap mouth to be R. The sides of the cone make an angle A with the vertical, and all particles are assumed to fall through the water at a speed S. We now calculate, using Fig. 3, the initial loci of all particles which reach the collection cup in time T. For particles initially less than a horizontal distance r_0 from the center of the cone, these loci are a vertical distance TS above the cup. However, particles initially above the cone but at a distance r greater than r_0 from the center will fall freely only until they reach the side of the cone. We assume that these particles do not stick to the side of the cone and that frictional forces associated with the side walls are negligible. As the particles move down the side of the cone they must travel a total distance $Z/\cos A$ in

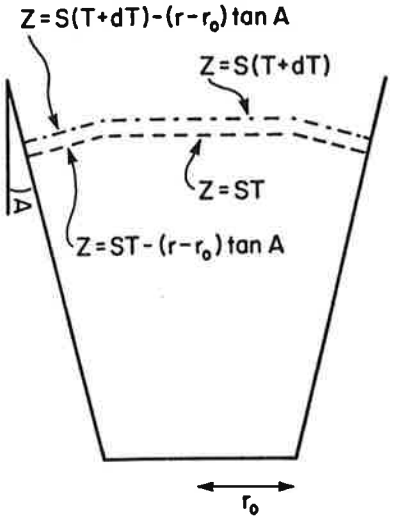


Fig. 3. Cross section of conical trap indicating loci of particles which reach the bottom of the trap in time T (dashed line) and time $T + dT$ (dash–dot line).

order to move a vertical distance Z. Furthermore, the component of gravity parallel to the sides of the cone will equal cos A times the vertical component of gravity. Hence the speed of the particles as they move along the surface of the cone will equal S cos A.

Given this model one can show that the loci of initial positions of particles that reach the collection cup in time T lies a distance ST above the cup for $0 \leqslant r \leqslant r_0$ and a vertical distance $ST - (r - r_0)$ tan A above the plane of the cup for $r_0 \leqslant r \leqslant r_0 + ST$ sin A cos A. These loci are indicated in Fig. 3. One can then show that to first order in dT the volume dV enclosed by the loci of particles that reach the collection cup between time T and $T + dT$ is

$$dV = \pi S\, dt\, (r_0 + SV \sin A \cos A)^2. \tag{1}$$

If the initial concentration of sinking particles was uniform and equal to Q per unit volume and if the flux of particles is normalized to the area of the cone mouth (πR^2) then the instantaneous flux calculated at time T will be

$$F = Q dV/(\pi R^2 dT) = QS(r_0 + ST \sin A \cos A)^2/R^2. \tag{2}$$

Equation (2) applies as long as $r_0 + ST \sin A \cos A \leqslant R$ or in other words when $T \leqslant (R - r_0)/(S \sin A \cos A)$. For larger values of T the instantaneous flux of particles into the collecting cup (normalized to the mouth area of the cone) equals the flux of particles through the mouth of the cone, and $F = QS$.

Since sediment traps collect particles over a finite period of time, it is necessary to integrate equation (2) over time to obtain an average flux which can be compared to experimental results. For $T \leqslant (R - r_0)/(S \sin A \cos A)$ the average flux F_{av} normalized to the cone mouth area is

$$F_{av} = QS[(r_0 + ST \sin A \cos A)^3 - r_0^3]/(3\, ST\, R^2 \sin A \cos A). \tag{3}$$

Dividing equation (3) by QS (i.e. the true flux) to obtain an apparent average trapping efficiency E gives

$$E = [(r_0 + ST \sin A \cos A)^3 - r_0^3]/(3\, ST\, R^2 \sin A \cos A). \tag{4}$$

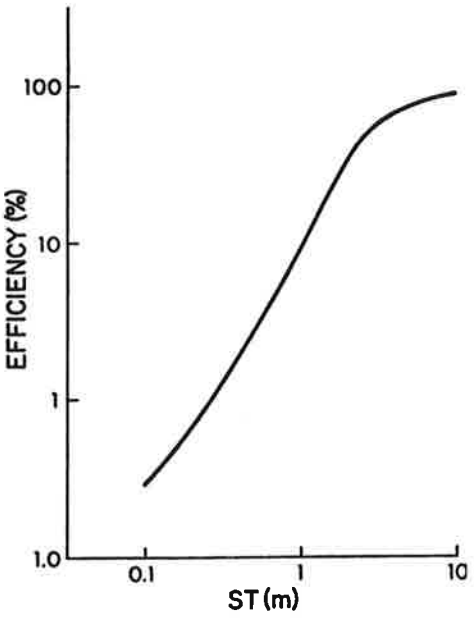


Fig. 4. Efficiency of the conical traps as a function of ST calculated using equations (4) and (5).

The analogous equation for the case when $T \geq (R - r_0)/(S \sin A \cos A)$ is

$$E = 1 - [R - r_0 - (R^3 - r_0^3)/(3\,R^2)]/(ST \sin A \cos A). \quad (5)$$

Note that in the limit as T approaches 0, equation (4) equals $(r_0/R)^2$ while in the limit as T approaches infinity, equation (5) equals 1.

In Fig. 4 we have plotted equations (4) and (5) for the values of R, r_0, and A which describe our conical traps. The equations predict a trapping efficiency of 2.5–3.3% for $T = 1$ day if the settling rate of the particles is 0.47–0.55 m d^{-1}. This correspondence is only approximate, since all particles reaching the traps undoubtedly do not sink at the same rate. Nevertheless, the model does provide an estimate of the mean particle sinking rate which would be required to explain the discrepancy between the conical and cylindrical trap results. Is there any evidence to support a mean sinking rate of about 0.5 m d^{-1}?

Fecal pellets have been estimated to sink at rates of roughly 15–170 m d^{-1} (TURNER, 1977; BIENFANG, 1980a), rates which are far too high to account for the observed discrepancy between the conical and cylindrical trap results (Fig. 4). However, based on microscopic examination of material that sedimented into the cylindrical traps during ADIOS I, TAYLOR (1989) estimated that recognizable fecal material accounted for an average of only 0.6% of the measured PC fluxes. Most of the material that accumulated in the traps appeared to be marine snow aggregates, although intact cells of phytoplankton and protozoans also were evident (TAYLOR, in review). BIENFANG's (1980b) field studies in oligotrophic waters off Hawaii have shown that phytoplankton cells sink at rates of 0.34–1.65 m d^{-1}, with smaller cells (3–20 μm) sinking at consistently lower rates (0.6 ± 0.26 m d^{-1}) than larger cells (20–102 μm, 1.4 ± 0.4 m d^{-1}). Since 40–70% of the Chl *a* at the station we sampled passed through a 1 μm filter (DITULLIO, 1987), it is quite possible that the flux of intact phytoplankton cells into our traps was associated with a mean sinking rate less than 0.5 m d^{-1}. ASPER (1987) calculated the

sinking rates of marine snow aggregates on the assumption that all aggregates in a given size range sank at the same rate. On the basis of this assumption, he estimated mean sinking rates of about 1 m d^{-1} for 4–5 mm aggregates, but smaller aggregates (1–2.5 and 2.5–4 mm) were estimated to sink much more rapidly (36 and 26 m d^{-1}, respectively). The implication of these studies is that an estimated mean particle sinking rate of about 0.5 m d^{-1} would be reasonable if most of the sedimenting material consisted of small (<20 μm) phytoplankton cells and large (>4 mm) marine snow aggregates.

However, two other pieces of information suggest that a mean particle sinking rate of about 0.5 m d^{-1} does not explain the discrepancy between the cylindrical and conical trap results. First, if all sinking particles sink with approximately the same rate, then the flux F of particles can be approximated by the product QS, and hence $Q = F/S$. The fluxes of PN and PC measured at depths between 30 and 120 m with the cylindrical traps were 11.6 ± 6.9 mg N $m^{-2}d^{-1}$ and 111 ± 73 mg C $m^{-2}d^{-1}$, respectively. If we assume $S = 0.5$ m d^{-1}, the associated concentration of sinking particles would be 23 ± 14 mg N m^{-3} and 222 ± 146 mg C m^{-3}. For comparison, PN and PC concentrations measured as a part of this study during ADIOS I and II averaged 5.1 ± 0.8 mg N m^{-3} and 35 ± 3 mg C m^{-3}, respectively, in the upper 150 m of the water column. Similar concentrations have been reported from the subtropical North Pacific by Eppley *et al.* (1973) and Sharp *et al.* (1980). Eppley *et al.* (1983, p. 313) have noted that, "Arguments related to particle size and sinking rate suggest that water bottles and sediment traps sample different material." In particular, because particle concentrations are expected to be negatively correlated with particle sinking speeds, and because the concentration of sinking particles cannot exceed the concentration of all particles (sinking and suspended), one would expect particle concentrations estimated from water sampling bottles to exceed Q. Hence the fact that the value of Q calculated assuming a sinking rate of 0.5 m d^{-1} exceeds the concentrations measured with water bottles by a factor of 5–6 seems highly improbable. The implication of this calculation is that the mean particle sinking rate is at least 5–6 times the assumed value of 0.5 m d^{-1}. Such sinking rates (i.e. 2.5–3.0 m d^{-1}) are well within the range of values (1–36 m d^{-1}) reported by Asper (1987) for marine snow aggregates, but according to our model (Fig. 4) would lead to at most a two-fold underestimation of particle fluxes with our conical traps.

The second piece of evidence that argues against a sinking rate of 0.5 m d^{-1} is the inter-trap comparison experiment conducted during April 1987. In this case the conical trap collected material for a total of 3 days. If equations (4) and (5) account for most of the discrepancy between the conical and cylindrical trap results, then lengthening the deployment time of the conical traps from 1 to 3 days should have reduced the discrepancy. However, the calculated PC and PN fluxes were only 1.9 and 2.5%, respectively, of the corresponding fluxes into the cylindrical traps that were deployed at the same depth during an overlapping interval of time (Table 2). Our model (Fig. 4) predicts an efficiency of 1.9–2.5% for $T = 3$ days only if $S = 0.13$–0.16 m d^{-1}. If the cylindrical trap fluxes (Table 2) are assumed to be correct, the implied PN and PC concentrations ($= F/S$) would be 43 mg N m^{-3} and 282 mg C m^{-3}, respectively, values which are about eight times the concentrations we measured. We conclude that while equations (4) and (5) may account for as much as a factor of two in the 30–40 fold discrepancy between the cylindrical and conical trap results, some other mechanism must account for most of the difference.

Marine snow

We feel that the most likely explanation is that organic aggregates that encounter the sides of the cone either stick to the sides or are physically destroyed as they move down the sides. Although we cannot rule out sticking as a possible explanation, the fact that the sides of the cone made only a 13.3° angle with the vertical and that care was taken to make the sides of the cone as smooth as possible would both tend to minimize sticking. In this context it is noteworthy that a total of seven experiments conducted by SOUTAR *et al.* (1977) with these same conical traps 10–40 m off the bottom in the Santa Barbara, San Pedro, and Soledad Basins yielded sedimentation rates which were 83 ± 49% (mean ± 95% confidence interval) of surface sedimentation rates determined by lead-210 chronology. However, sediment observed accumulating in those traps during the rainy season was, "made up of clay flocculates with abundant silt particles", and "in May 1969 in both the Santa Barbara Basin and the Soledad Basin almost the entire fallout was made up of faecal pellets" (SOUTAR *et al.*, 1977, p. 139). Thus these traps may work well as long as most of the sinking particles consist of material other than marine snow. However, marine snow aggregates are extremely fragile (SILVER *et al.*, 1978; TRENT *et al.*, 1978) and could easily disintegrate if required to roll or slide a distance of a meter or more down the side of a conical trap. Although the small particles into which such aggregates might disintegrate could conceivably fall into the collection cup, such aggregate fragments might sink much more slowly than the original intact aggregate or in some cases be small enough to pass through GF/F filters. With respect to this latter point, KARL (unpublished data) has noted that even in cylindrical traps there is an increase during deployment in dissolved organic nitrogen and dissolved organic carbon concentrations which may reflect the breakdown of organic aggregates through physical processes. In the case of the cylindrical traps a correction for this breakdown could be made by monitoring the concentrations of both particulate and dissolved organics in the trap. A similar correction would be impossible in the case of the conical traps, since the conical portion is flushed with overlying seawater during retrieval.

The significant discrepancy between the apparent efficiency of the conical trap in collecting PC (2.5%) and PN (3.3%) can also be explained if it is assumed that most of the missing material consisted of marine snow. The C:N ratio of the material collected in the conical traps at depths of 120–160 m was 7.8 ± 1.1 g C g^{-1}N. With a little algebra it is straightforward to show using this C:N ratio and the foregoing trapping efficiencies that the C:N ratio of the missing particles equaled 10.4 g C g^{-1}N. This figure may be compared to the C:N ratios for marine snow aggregates of 11.3 ± 1.6 and 9.4 ± 1.0 in the Gulf of California and Santa Barbara Channel, respectively (ALLDREDGE, 1979). The overall implication is that most of the material collected by the cylindrical traps was marine snow, and that the failure of this marine snow to find its way into the collection cup of the conical traps largely accounts for the discrepancy in the trapping efficiencies of the two systems.

Although the results presented here indicate that particle flux estimates derived from conical sediment trap studies severely underestimate true fluxes when much of the sinking material consists of marine snow, it must be stressed that the length of conical trap deployment was 3 days in one case and 1 day in all other cases. If interactions between the sides of the traps and sedimenting particles in effect merely slow the downward movement of the particles, then over time the concentration of particulate matter in the conical section of the trap will increase, and eventually the flux of particles

into the collection cup will equal the flux into the mouth of the trap. How long this process takes will depend on the extent to which the descent of particles is slowed by interactions with the sides of the trap. Our results do not rule out the possibility that conical traps deployed for much longer time periods may give much better flux estimates. Relevant to this point is the fact that during the 1979 sediment trap intercomparison experiment in the Panama Basin, conical traps with a mouth area of 0.25 m^2 deployed at a depth of 2288 m for 123 days gave PC and PN fluxes that were within 10% of the corresponding fluxes obtained from cylindrical traps with a mouth area of 39 cm^2 deployed at a depth of 2167 m for 112 days (ANDERSON and BACON, 1981).

Temporal variability and f *ratios*

A few final comments concern the magnitude and temporal variability of the calculated flux:assimilation ratios (Table 3). First, a paired *t*-test revealed that PC flux:C assimilation ratios were significantly higher than PN flux:N assimilation ratios ($P < 0.05$). The difference in mean ratios equaled 0.07 ± 0.04. In other words, the C:N ratio of the material collected in the cylindrical sediment traps at 120 m was consistently higher (9.2 ± 1.1 g g^{-1}) than the estimated phytoplankton C:N assimilation ratios (7.1 ± 0.6 g g^{-1}). The difference is significant at $P = 0.02$ by Wilcoxon's two-sample test. The implication is that a higher percentage of the carbon than nitrogen assimilated by phytoplankton sinks out of the euphotic zone. If sinking of PN is the only significant mechanism by which fixed N is removed from the euphotic zone and if rates are averaged over a sufficient period of time, then the downward flux of PN should equal new production in terms of nitrogen as defined by DUGDALE and GOERING (1967). However, if the phytoplankton C:N assimilation ratio differs from the C:N ratio of the sedimenting material, then the sinking flux of PC cannot be equated to new production in terms of carbon. In this study the mean C:N ratios differed by almost 30%. Although it is reasonable to equate the fallout of PC from the euphotic zone to net community production if rates are averaged over a sufficient time, this rate will equal new production in terms of carbon only if the C:N ratio of the PC equals the C:N assimilation ratio of the phytoplankton. In cases where these ratios differ, new production in terms of carbon must be estimated by multiplying the C:N areal assimilation rate ratios (Table 1) by the flux of PN into the sediment traps near the base of the euphotic zone. Furthermore, if *f* ratios are calculated based on sediment trap results, the calculation must be based on PN rather than PC fluxes.

The *f* ratios (= PN flux:N assimilation) calculated in this study varied by over a factor of three, and the coefficient of variation (53%) is almost identical to that of PLATT and HARRISON's (1985) data (48%). In the latter study the *f* ratios were calculated from monthly averages of new and total production. Our ratios on the other hand were calculated from rates integrated over at most 12 days. Although one might expect calculated *f* ratios to stabilize as the integration process is extended over longer time periods, no such tendency is apparent in the comparison of our *f* ratios with those of PLATT and HARRISON (1985). In our case the cause of the temporal variability seems apparent. A storm associated with high winds passed through the study area during 4–14 April 1986. Average wind speeds during a total of 16 days immediately preceding and following the storm were 12 ± 4 kn, but during the period of the storm winds averaged 19 ± 4 kn. Areal carbon and nitrogen assimilation rates were about 33% higher during the storm than preceding the storm. However, the fluxes of PC and PN into the

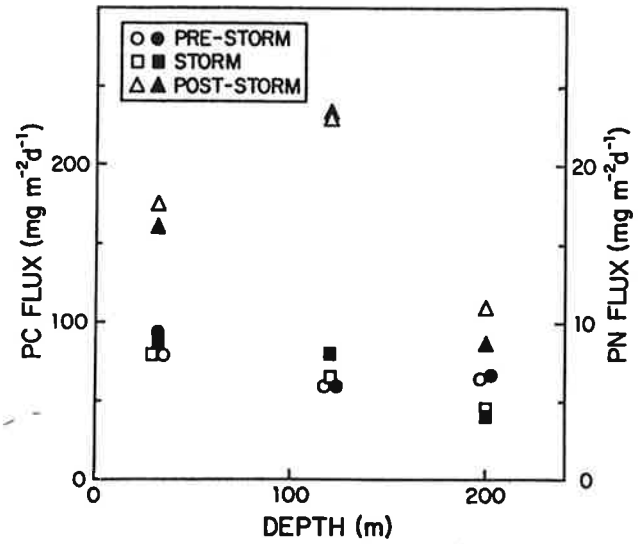


Fig. 5. Fluxes of PC (open symbols) and PN (closed symbols) during ADIOS I.

cylindrical sediment traps showed no consistent difference between storm and pre-storm conditions, and in general declined with depth (Fig. 5). In the 3 days following the storm however, PC and PN fluxes increased by a factor of two or more, with the greatest fluxes appearing at 120 m (Fig. 5). The implication is that much of the additional PC and PN production stimulated by the storm did not begin to appear as sedimenting particles until after the storm, presumably because storm-induced turbulence effectively retained particles within the mixed layer. It is also possible that significant amounts of additional PC and PN were created from dissolved organics within the mixed layer as a result of the turbulence associated with the storm. The roughly 2.5-fold increase in flux:assimilation ratios apparent after the storm (Table 3) therefore most likely reflects the fallout of organic matter which accumulated in the mixed layer during the storm. In this context it is noteworthy that a storm event also immediately preceded the October 1986 sampling, and for similar reasons may have been responsible for the high flux:assimilation ratios calculated for 14–15 October. Obviously, in other than strictly steady-state systems, sediment trap fluxes may show little correlation with concurrently measured primary production rates if both rates are averaged over sufficiently short time intervals. The residence time of particles in the mixed layer, as well as the frequency and magnitude of environmental perturbations, will both be important in determining over what time interval rates must be averaged before a temporal sequence of calculated f ratios stabilizes, or whether in fact it is even meaningful to speak of an f ratio for a particular region of the ocean. In this context it is noteworthy that EPPLEY *et al.*'s (1983) calculated residence times of particulate organic carbon in the Southern California Bight vary from 3 to 100 days. A similar range of particle residence times may explain why PLATT and HARRISON's (1985) calculated f ratios vary as much or more than ours, even though their averaging was performed over time intervals more than twice as long as ours.

Acknowledgements—We thank B. Tilbrook, D. Jones, and Dr V. Asper for their assistance in the field work, and Dr R. Feeley for making available his inorganic carbon concentrations. The thoughtful comments of two anonymous reviewers are gratefully acknowledged. This research was supported by National Science Foundation Biological Oceanography Program grants OCE85–13594 to E. Laws and OCE86–00462 to D. Karl, and by Chemical Oceanography Program grant OCE85–02474 to P. Betzer. Hawaii Institute of Marine Biology Contribution No. 762 and Hawaii Institute of Geophysics Contribution No. 2031.

REFERENCES

ALLDREDGE A. L. (1979) The chemical composition of macroscopic aggregates in two neretic seas. *Limnology and Oceanography*, **24**, 855–866.

ANDERSON R. F. and M. P. BACON (1981) Sediment trap intercomparison experiment. Woods Hole Oceanographic Institution Technical Memorandum No. 1–81, 120 pp. (Unpublished document.)

ASPER V. L. (1987) Measuring the flux and sinking speed of marine snow aggregates. *Deep-Sea Research*, **34**, 1–17.

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.

BIENFANG P. K. (1980a) Herbivore diet affects fecal pellet settling. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1352–1357.

BIENFANG P. K. (1980b) Phytoplankton sinking rates in oligotrophic waters off Hawaii, USA. *Marine Biology*, **61**, 69–77.

BUTMAN C. A. (1986) Sediment trap biases in turbulent flows: results from a laboratory flume study. *Journal of Marine Research*, **44**, 645–693.

BYRNE R. H., J. G. ACKER, P. R. BETZER, R. A. FEELY and M. CATES (1984) Water column dissolution of aragonite in the Pacific Ocean. *Nature*, **312**, 321–326.

DITULLIO G. R. (1987) Chemotaxonomic identification and physiological status of phytoplankton in the North Pacific subtropical gyre. Ph.D. dissertation, University of Hawaii.

DITULLIO G. R. and E. A. LAWS (1986) Diel periodicity of nitrogen and carbon assimilation in five species of marine phytoplankton: accuracy of methodology for predicting N-assimilation rates and N/C composition ratios. *Marine Ecology Progress Series*, **32**, 123–132.

DUGDALE and GOERING (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography*, **12**, 196–206.

DYMOND J., K. FISCHER, M. CLAUSON, R. COBLER, W. GARDNER, M. J. RICHARDSON, W. BERGER, A. SOUTAR and R. DUNBAR (1981) A sediment trap intercomparison study in the Santa Barbara Basin. *Earth and Planetary Letters*, **53**, 409–418.

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., J. H. SHARP, E. H. RENGER, M. J. PERRY and W. G. HARRISON (1977) Nitrogen assimilation by phytoplankton and other microorganisms in the surface waters of the central North Pacific Ocean. *Marine Biology*, **39**, 111–120.

EPPLEY R. W., E. H. RENGER and P. R. BETZER (1983) The residence time of particulate organic carbon in the surface layer of the ocean. *Deep-Sea Research*, **30**, 311–323.

FALKOWSKI P. G. and T. G. OWENS (1980) Light–shade adaptation. Two strategies in marine phytoplankton. *Plant Physiology*, **66**, 592–595.

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.

GARDNER W. D. (1980a) Sediment trap dynamics and calibration: a laboratory evaluation. *Deep-Sea Research*, **38**, 17–39.

GARDNER W. D. (1980b) Field assessment of sediment traps. *Journal of Marine Research*, **38**, 41–52.

GARSIDE C. (1982) A chemiluminescent technique for the determination of nanomolar concentrations of nitrate and nitrite in seawater. *Marine Chemistry*, **11**, 159–167.

GIESKES W. W. C., G. W. KRAAY and M. A. BAARS (1979) Current ^{14}C methods for measuring primary production: gross underestimates in oceanic waters. *Netherlands Journal of Sea Research*, **13**, 58–78.

GLIBERT P. M. and J. C. GOLDMAN (1981) Rapid ammonium uptake by marine phytoplankton. *Marine Biology Letters*, **2**, 25–31.

GOLDMAN J. C. (1980) Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology. In: *Primary productivity in the sea*, P. FALKOWSKI, editor, Plenum Press, New York, pp. 179–194.

GOLDMAN J. C. and M. R. DENNETT (1985) Susceptibility of some marine phytoplankton species to cell breakage during filtration and post-filtration. *Journal of Experimental Marine Biology and Ecology*, **86**, 47–58.

HAYWARD T. L., E. L. VENRICK and J. A. MCGOWAN (1983) Environmental heterogeneity and plankton community structure in the central North Pacific. *Journal of Marine Research*, **41**, 711–729.

HECKY R. E. and E. J. FEE (1981) Primary production and rates of algal growth in Lake Tanganyika. *Limnology and Oceanography*, **26**, 532–547.

HORNBECK R. W. (1975) *Numerical methods*. Quantum Publishers, New York, 465 pp.

ISAACS J. D. (1972) Unstructured marine food webs and "pollutant analogues". *Fishery Bulletin*, **70**, 1053–1059.

ISAACS J. D. (1973) Potential trophic biomasses and trace-substance concentrations in unstructured marine food webs. *Marine Biology*, **22**, 97–104.

JOKIEL P. L. and R. H. YORK (1984) Importance of ultraviolet radiation in photoinhibition of microalgal growth. *Limnology and Oceanography*, **29**, 192–199.

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.

KNAUER G. A. and J. H. MARTIN (1981) Primary production and carbon-nitrogen fluxes in the upper 1500 m of the northeast Pacific. *Limnology and Oceanography*, **26**, 181–186.

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 (1984) *In situ* effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. *Journal of Marine Research*, **42**, 445–462.

LAWS E. A., G. R. DITULLIO and D. G. REDALJE (1987) High phytoplankton growth and production rates in the North Pacific subtropical gyre. *Limnology and Oceanography*, **34**, 905–918.

LEAN D. R. S. and B. K. BURNISON (1979) An evaluation of errors in the ^{14}C method of primary production measurement. *Limnology and Oceanography*, **24**, 917–928.

MANN K. H. (1984) Fish production in open ocean ecosystems. In: *Flows of energy and materials in marine ecosystems*, M. J. R. FASHAM, editor, Plenum Press, New York, pp. 435–458.

MARRA J. and K. R. HEINMANN (1987) Primary production in the North Pacific central gyre: some new measurements based on ^{14}C. *Deep-Sea Research*, **34**, 1821–1829.

MORRIS I., C. M. YENTSCH and C. S. YENTSCH (1971) Relationship between light CO_2 fixation and dark CO_2 fixation by marine algae. *Limnology and Oceanography*, **16**, 854–858.

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

SCOR (1987) *The joint global ocean flux study*. Report of the international scientific planning and coordination meeting for global ocean flux studies, Scientific Committee on Oceanic Research, Paris, 42 pp.

SHARP J. H., M. J. PERRY, E. H. RENGER and R. W. EPPLEY (1980) Phytoplankton rate processes in the oligotrophic waters of the central North Pacific ocean. *Journal of Plankton Research*, **2**, 335–353.

SHULENBERGER E. and J. L. REID (1981) The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered. *Deep-Sea Research*, **28**, 901–919.

SILVER M. W., A. L. SHANKS and J. D. TRENT (1978) Marine snow: microplankton habitat and source of small-scale patchiness in pelagic populations. *Science*, **201**, 371–373.

SMITH K. L. Jr (1987) Food energy and demand: a discrepancy between particulate organic carbon flux and sediment community oxygen consumption in the deep ocean. *Limnology and Oceanography*, **32**, 201–220.

SOUTAR A., S. A. KLING, A. CRILL, E. DUFFRING and K. W. BRULAND (1977) Monitoring in the marine environment through sedimentation. *Nature*, **266**, 136–139.

STARESINIC N., K. V. BROCKEL, N. SMODLAKA and C. H. CLIFFORD (1982) A comparison of moored and free-drifting sediment traps of two different designs. *Journal of Marine Research*, **40**, 273–292.

STRICKLAND J. D. H. and T. R. PARSONS (1972) *A practical handbook of seawater analysis*, 2nd edn, *Bulletin of the Fisheries Research Board of Canada*, 167.

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

TERRY K. L., J. HIRATA and E. A. LAWS (1983) Light-limited growth of two strains of the marine diatom *Phaeodactylum tricornutum* Bohlin: chemical composition, carbon partitioning and the diel periodicity of physiological processes. *Journal of Experimental Marine Biology and Ecology*, **68**, 209–227.

TRENT J. D., A. L. SHANKS and M. W. SILVER (1978) *In situ* and laboratory measurements on macroscopic aggregates in Monterey Bay, California. *Limnology and Oceanography*, **23**, 626–635.

TURNER J. T. (1977) Sinking rates of fecal pellets from the marine copepod *Pontella meadii*. *Marine Biology*, **40**, 249–259.

WALSH J. J., E. T. PREMUZIC, J. S. GAFFNEY, G. T. ROWE, G. HARBOTTLE, E. V. SAYRE, R. W. STOENNER, W. L. BALSAM, P. R. BETZER and S. A. MACKO (1985) Organic storage of CO_2 on the continental slope off the mid-Atlantic bight, the southeastern Bering Sea, and the Peru coast. *Deep-Sea Research*, **32**, 853–883.