Deep-Sea Research, Vol. 39, No. 9, pp. 1535–1552, 1992.
Printed in Great Britain.

0198–0149/92 $5.00 + 0.00
© 1992 Pergamon Press Ltd

Nitrogen dynamics at the VERTEX time-series site

WILLIAM G. HARRISON,* LESLIE R. HARRIS,* DAVID M. KARL,†
GEORGE A. KNAUER‡ and DONALD G. REDALJE‡

(*Received* 5 *July* 1991; *in revised form* 27 *November* 1991; *accepted* 6 *December* 1991)

Abstract—Euphotic zone concentrations and fluxes of nitrate, ammonium, particulate and dissolved organic nitrogen were measured over an 18 month period at the VERTEX time-series site in the oligotrophic northeast Pacific (33°N, 139°W). Variations in all N-forms were significant but not clearly linked to the temporal hydrographic cycle. Inorganic-N uptake (nitrate + ammonium) from ^{15}N tracer experiments generally paralleled primary productivity variations, peaking in summer; ammonium accounted for most of the uptake (~90%) and temporal variability. Comparisons of ^{15}N results with estimates of autotrophic N-uptake from ^{14}C incorporation into protein suggest that as much as 40% of the annual inorganic-N uptake was due to microheterotrophs; peak heterotrophic N-uptake occurred in summer when heterotrophic biomass was at its maximum. Nitrate uptake (new production) was less variable than ammonium uptake and annually equivalent to particulate nitrogen export from sediment traps. Dissolved organic-N (DON) represented the largest and most variable N-pool, accounting for 80–90% of the total nitrogen in the euphotic zone. Vertical DON gradients, however, were small and temporally invariant, implying little contribution to the biogenic nitrogen export from the euphotic zone.

INTRODUCTION

A BASIC understanding of the major biogeochemical cycles in the ocean is fundamental to current international research initiatives aimed at elucidating the role of the oceans in the global carbon cycle and climate change (SCOR, 1990). Marine phytoplankton, through their photosynthetic activity, constitute the major biological sink for oceanic CO_2. Most of the carbon fixed by primary productivity, however, is respired near the sea surface, with only a small fraction of the biogenic matter transported to the ocean interior, in the form of particles (EPPLEY and PETERSON, 1979; KNAUER *et al.*, 1979); it is this "export" production that is most relevant to the CO_2 problem (PLATT *et al.*, 1989). With respect to climate change, there is general consensus that ocean productivity will not respond *directly* to CO_2 increase but will be controlled by second-order processes such as ocean mixing which, among other things, regulates the supply of nutrients essential for photosynthesis (LONGHURST, in press). Indeed, in most ocean regions, the exportable fraction of production is

*Biological Oceanography Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Box 1006, Dartmouth, NS, Canada B2Y 4A2.

†School of Ocean and Earth Sciences and Technology, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822, U.S.A.

‡University of Southern Mississippi Center for Marine Science, John C. Stennis Space Center, SSC, MS 39529, U.S.A.

thought to be balanced by the upward transport of NO_3^- that fuels the so-called "new" primary production (DUGDALE and GOERING, 1967), i.e. export production = new production. More recent studies have suggested that dissolved organic matter may also be a significant contributor to the biogenic export flux (SUZUKI *et al.*, 1985; TOGGWEILER, 1989; LEGENDRE and GOSSELIN, 1989; SARMIENTO *et al.*, 1990).

It is clear therefore that an understanding of the dynamics of the nitrogen cycle, particularly on the annual time scale (PLATT and HARRISON, 1985; PLATT *et al.*, 1989), is a critical consideration for ongoing and future climate-related ocean research. Although much has been learned about nitrogen cycling in the past two decades (e.g. CARPENTER and CAPONE, 1983; BLACKBURN and SORENSEN, 1988), the open oceans, in particular, have been grossly undersampled in space and time. With this in mind, the Vertical Transport and Exchange (VERTEX) program had as one of its objectives a detailed temporal description of the production and export of biogenic matter from the euphotic zone in the oceanic Pacific (33°N, 139°W). KNAUER *et al.* (1990) have recently described particulate organic carbon and nitrogen export fluxes at the VERTEX time-series site. Here, we expand the analysis to include a description of the temporal dynamics of dissolved inorganic and organic nitrogen in the euphotic zone.

METHODS AND MATERIALS

Studies were conducted at the VERTEX time-series site (33°N, 139°W) from October 1986 to May 1988 (Table 1). Over this 18 month period, the study site was visited on seven occasions (~90 day interval) and occupied for approximately 1 week for retrieval/redeployment of sediment traps and to carry out various short term flux measurements (KNAUER *et al.*, 1990).

Sampling

Samples for water chemistry, microbial biomass and flux measurements were collected from pre-dawn Niskin bottle casts. Niskin bottles were acid-cleaned prior to use and equipped with silicone rubber tubing for bottle closure. During sampling, the Niskin

Table 1. *Inorganic and organic-*N *concentrations at the VERTEX time-series site; integration over upper* 150 m (mmol m^{-2}), H/L = *ratio of high/low value*

Cruise	Dates	NO_3^-	NH_4^+	PON	DON
Sea-1	24 Oct.–8 Nov. 86	91.5	17.9	36.3	671.3
Sea-2	18–31 Jan. 87	34.2	13.8	39.5	755.5
Sea-3	1–15 May 87	24.3	15.4	13.5	586.1
Sea-4	6–19 July 87	49.3	1.6	50.5	665.4
Sea-5	19–30 Oct. 87	34.2	5.1	29.7	715.1
Sea-6	27 Jan.–12 Feb. 88	70.9	7.8	35.6	672.9
Sea-7	1–18 May 88	5.9	4.2	38.2	620.6
	Mean	44.3	9.4	34.8	669.6
	S.D.	29.0	6.3	11.3	56.1
	H/L	15.5	11.2	3.7	1.3

bottles were attached to Kevlar hydroline. All incubation procedures followed those outlined by FITZWATER *et al.* (1982) to minimize metal contamination.

Hydrography and water chemistry

Temperature–salinity profiles were generated using the Moss Landing Marine Laboratories CTD/rosette multichannel profiling instrument (BROENKOW *et al.*, 1988). Samples for nutrient analysis were drawn from the Niskin bottle casts (~20 depths over the upper 400 m). Nitrate (NO_3^-) was determined using automated methods (ATLAS *et al.*, 1971) and ammonium (NH_4^+) determined manually by the method of SOLORZANO (1969). In most cases, NO_3^- analyses were performed aboard ship on freshly collected samples; all NH_4^+ analyses were done on fresh, filtered (GF/F glass fiber) samples. Total dissolved nitrogen (TDN) was estimated by measuring NO_3^-, NO_2^- and NH_4^+ in previously filtered and frozen samples following a 24 h ultraviolet photo-oxidation treatment (ARMSTRONG *et al.*, 1966). Dissolved organic nitrogen (DON) was calculated by difference between $[NO_3^- + NO_2^- + NH_4^+]$ before and after photo-oxidation. Comparisons of the DON estimated by ultraviolet photo-oxidation with a non-catalytic high-temperature (1100°C) combustion method indicated no significant differences for samples collected at the VERTEX study area (WALSH *et al.*, 1989). Particulate organic nitrogen (PON) was determined by high temperature combustion using a Carlo-Erba NA 1500 nitrogen/carbon analyser (KNAUER *et al.*, 1990). Detection limits for NO_3^-, NH_4^+, DON and PON were 0.05, 0.03, 0.05 and 0.1 mmol m^{-3} with coefficients of variation of replicate analyses averaging 5, 20, 5 and 10%, respectively (see also KARL *et al.*, 1990).

Microbial biomass and productivities

Total microbial biomass was estimated from the adenosine triphosphate (ATP) content of the particulates (HOLM-HANSEN and KARL, 1978). Autotrophic (phytoplankton) biomass was derived using the ^{14}C labeled chlorophyll *a* technique (REDALJE and LAWS, 1981; REDALJE, 1983). Heterotrophic biomass was calculated by difference.

Primary productivity was determined using the ^{14}C-method (STRICKLAND and PARSONS, 1972; FITZWATER *et al.*, 1982). Samples were collected prior to sunrise from eight depths between the surface and ~1% light level and incubated *in situ* in trace metal clean 4 l polycarbonate bottles for 24 h. Recovered samples were filtered through GF/F glass fiber filters and the filters processed as described in KNAUER *et al.* (1990). Autotrophic N-uptake was determined in subsamples by measuring the incorporation of ^{14}C into protein (DITULLIO and LAWS, 1983).

Nitrate and ammonium productivities were determined by the ^{15}N stable isotope tracer method first described by DUGDALE and GOERING (1967). Samples for the ^{15}N and ^{14}C tracer experiments were drawn from the same Niskin bottles; sampling and incubation protocols were identical. ^{15}N isotope (99 atom %) was added at "trace" concentrations of 0.05 and 0.03 mmol m^{-3} for NO_3^- and NH_4^+, respectively, our operational detection limits for NO_3^- and NH_4^+ concentrations. After incubation, samples were filtered through precombusted GF/F filters, oven dried and analysed onshore for nitrogen isotope ratios by emission spectrometry (FIEDLER and PROKSCH, 1975). Long incubations (24 h) introduce errors from a variety of sources in ^{15}N experiments, resulting in apparent non-linearity of isotope uptake, particularly when ambient nutrient concentrations are low (e.g. HARRI-

SON, 1983). Experiments designed specifically to evaluate isotope uptake linearity were carried out on a number of the VERTEX cruises. Results showed that $^{15}NO_3^-$ uptake rates were essentially constant (i.e. uptake was linear) over the 24 h incubation period. However, $^{15}NH_4^+$ uptake decreased with time; uptake rates were underestimated by a factor of 2.5 after 24 h based on comparisons with short-term (<6 h) incubations (KNAUER *et al.*, 1990; see also SAHLSTEN, 1987). This factor was subsequently used to correct all 24 h NH_4^+ uptake rates.

RESULTS

Hydrography, inorganic and organic-N

The expected temporal development and erosion of a shallow mixed layer were evident in CTD profiles (Fig. 1). Mixed layer depths (>0.02°C m^{-1}) varied from 30 m in summer to 130 m in winter and were consistently shallower than the euphotic depth (depth of zero primary production; D. REDALJE, in preparation) which averaged ~140 m (Fig. 2).

Temporal changes in NO_3^- and NH_4^+ concentrations were less clear (Fig. 3). NO_3^- concentrations were always at or below the conventional analytical detection limit (0.05 mmol m^{-3}) in the upper 50–100 m. Values below 100 m peaked (>1 mmol m^{-3}) during wintertime; however, mixing was not sufficient to increase residual concentrations in the upper water column. NH_4^+ concentrations were marginally greater (~0.06 mmol m^{-3}) than detection limits and exhibited no recurrent temporal pattern. However, maximum concentrations were observed in the upper 50 m in the summer of 1987 (Cruise Sea-4, Table 1) and the following winter of 1988 (Cruise Sea-6); elevated concentrations also were observed below 100 m during the Sea-4 cruise.

Conspicuous maxima in PON concentrations near surface and below 100 m were observed during the summer Sea-4 cruise, similar to NH_4^+ concentrations (Fig. 4). A near-surface peak also was noted during the previous winter (Sea-2). DON concentrations

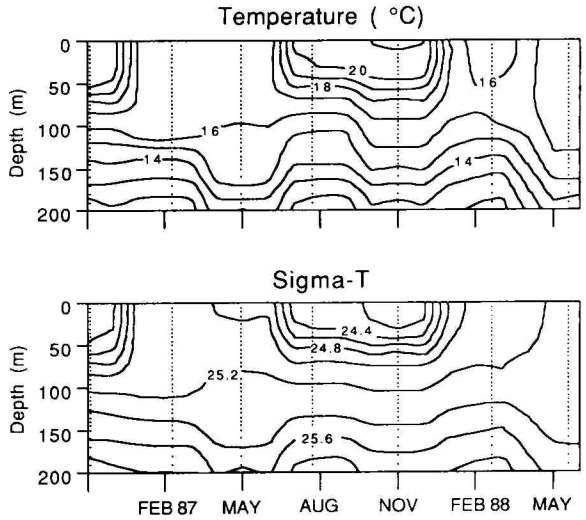


Fig. 1. Temporal variations in temperature (°C) and density (σ_t) in the upper 150 m at the VERTEX time-series site (33°N, 139°W). Dots are sampling depths.

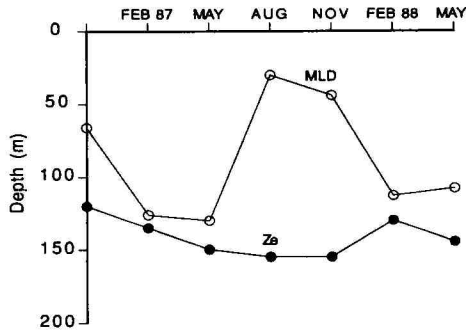


Fig. 2. Temporal variations in mixed layer depth (MLD) and euphotic depth (Ze) at the VERTEX time-series site. MLD derived from CTD or XBT profiles using a temperature change of $>0.02°C\ m^{-1}$ as the criterion. Ze determined by extrapolation of primary productivity profiles to depth of zero production (D. REDALJE, in preparation).

also peaked during the Sea-2 cruise but differed from PON distribution in that elevated concentrations were not observed during the summer (Sea-4). However, a clear surface maximum was seen during the following fall cruise (Sea-5). Lowest PON and DON concentrations were observed during the spring 1987 cruise (Sea-3).

The temporal amplitude in total-N (sum of inorganic and organic-N pools) was small and influenced predominantly by DON, accounting for 80–90% of the total (Table 1). There was no clear co-variance, either direct or inverse, among the nitrogen pools although elevated surface DON in the fall of 1987 did follow the summer PON maximum (Fig. 4). Among the various N-pools, temporal concentration changes were greatest for DON, followed by NO_3^-, PON and NH_4^+.

Microbial biomass and productivities

Temporal variations in autotrophic and heterotrophic biomass were similar during the first three cruises (Sea-1 to Sea-3: October 1986–May 1987). However, heterotrophic

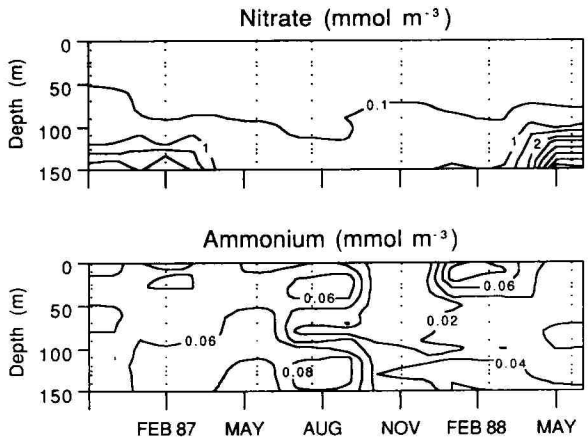


Fig. 3. Temporal variations in nitrate (NO_3^-) and ammonium (NH_4^+) concentrations (mmol m^{-3}) in the upper 150 m at the VERTEX time-series site.

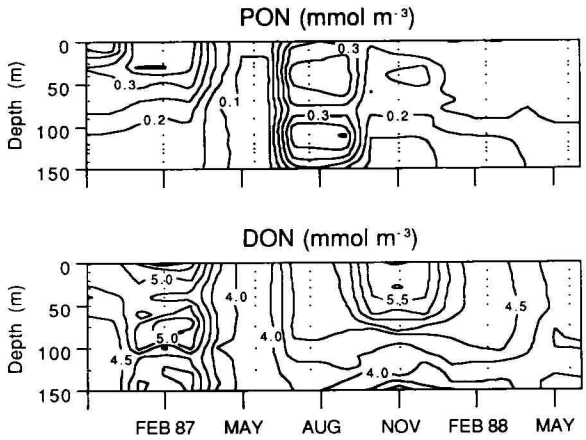


Fig. 4. Temporal variations in particulate organic nitrogen (PON) and dissolved organic nitrogen (DON) concentrations (mmol m^{-3}) in the upper 150 m at the VERTEX time-series site.

biomass far exceeded autotrophic biomass during the following summer and fall (Sea-4 and 5), particularly during the summer cruise (Table 2; see also KNAUER *et al.*, 1990). Only during the winter 1987 cruise (Sea-6) did autotrophic biomass exceed heterotrophic biomass.

Temporal patterns in primary productivity and autotrophic N-uptake were similar with highest rates observed during the 1987 summer cruise, Sea-4 (Fig. 5). Patterns of NO_3^- and NH_4^+ uptake showed some similarities to primary productivity and autotrophic N-uptake, particularly with regard to the maximum during the Sea-4 summer cruise (Fig. 6). They differed, however, in that elevated NO_3^- and NH_4^+ uptake rates were observed during the winter 1987 cruise (Sea-2). Also, significant NO_3^- and NH_4^+ uptake occurred deeper within the water column than primary productivity and autotrophic N-uptake, particularly in the case of NH_4^+ uptake during the Sea-4 summer cruise. The near-surface and deep peaks in NH_4^+ uptake were similar to the patterns seen in NH_4^+ and PON concentrations during this cruise; there was no corresponding NO_3^- uptake peak below 100 m. NO_3^- uptake showed less temporal variation than did NH_4^+ uptake (Table 2). *f*-ratios [NO_3^- uptake/(NO_3^- + NH_4^+) uptake] showed no clear temporal pattern, but ratios increased with depth on all cruises, with values generally <0.1 in the mixed layer and >0.4 below the nitracline (Fig. 6). Autotrophic N-uptake was comparable to the summed NO_3^- + NH_4^+ uptake in three of the five cruises where comparisons were made (Table 2). At the remaining two stations, NO_3^- + NH_4^+ uptake significantly exceeded autotrophic N-uptake. One of these, the summer cruise (Sea-4), also exhibited the highest heterotrophic biomass (see above).

DISCUSSION

The temporal cycle: NO_3^- *and* NH_4^+ *uptake and primary productivity*

Seasonal primary production studies in the open ocean are few (e.g. MENZEL and RYTHER, 1960, 1961; BIENFANG *et al.*, 1984), but recent investigations of carbon and nitrogen export fluxes have renewed interest in seasonal cycles (e.g. ALTABET, 1989;

Table 2. Microbial biomass and productivities at the VERTEX time-series site. Autotrophic and heterotrophic biomass = gC m^{-2}; *primary productivity* = mgC m^{-2} day^{-1}; *autotrophic*-N, NO_3^- *and* NH_4^+ *uptake* = mmol m^{-2} day^{-1}. *Annual* = mol m^{-2} y^{-1}

(1) Cruise	(2) Total microbial biomass*	(3) Autotrophic biomass	(4) Heterotrophic biomass	(5) Primary productivity	(6) NO_3^- uptake	(7) NH_4^+ uptake	(8) $NO_3^- + NH_4^+$ uptake	(9) Autotrophic N-uptake	(10) *f*-ratio (6)/(8)	(11) NO_3^-/Auto (6)/(9)
Sea-1	1.43	0.71	0.72	272	0.55	3.67	4.21	4.39	0.13	0.13
Sea-2	1.07	0.50	0.57	222	0.75	8.40	9.15	n.d.	0.08	n.d.
Sea-3	1.34	0.64	0.70	219	0.23	2.66	2.89	2.47	0.08	0.09
Sea-4	1.94	0.43	1.51	555	0.79	13.10	13.88	6.40	0.06	0.12
Sea-5	1.57	0.53	1.04	385	0.55	2.74	3.29	4.04	0.17	0.14
Sea-6	0.90	0.63	0.27	264	0.70	5.33	6.03	3.33	0.12	0.21
Sea-7	1.49	0.58	0.91	417	n.d.	n.d.	n.d.	4.76	n.d.	n.d.
Mean	1.39	0.57	0.82	333	0.59	5.98	6.58	4.23	0.11	0.14
S.D.	0.34	0.10	0.39	124	0.21	4.09	4.25	1.34	0.04	0.04
H/L	2.2	1.7	0.5	2.5	3.5	4.9	4.8	2.6	2.1	2.3
Annual				10.1	0.22	2.23	2.45	1.47	0.09	0.15

*Biomass = ATP × 250 (KARL, 1980); *f*-ratio = [NO_3^- uptake/($NO_3^- + NH_4^+$) uptake]; *H/L* = ratio of high/low value, n.d. = no data.

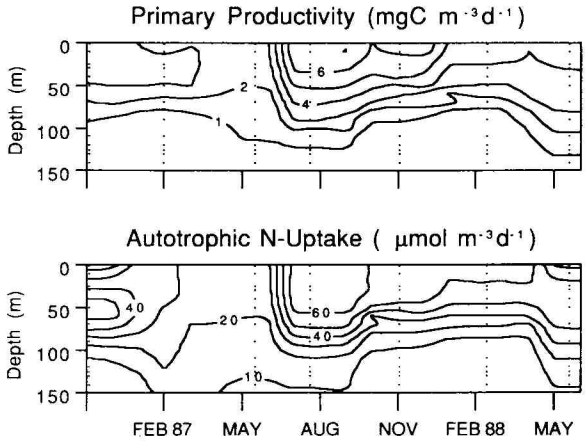


Fig. 5. Temporal variations in primary productivity (mgC m^{-3} day^{-1}) and autotrophic N-uptake rates (μmol m^{-3} day^{-1}) in the upper 150 m at the VERTEX time-series site.

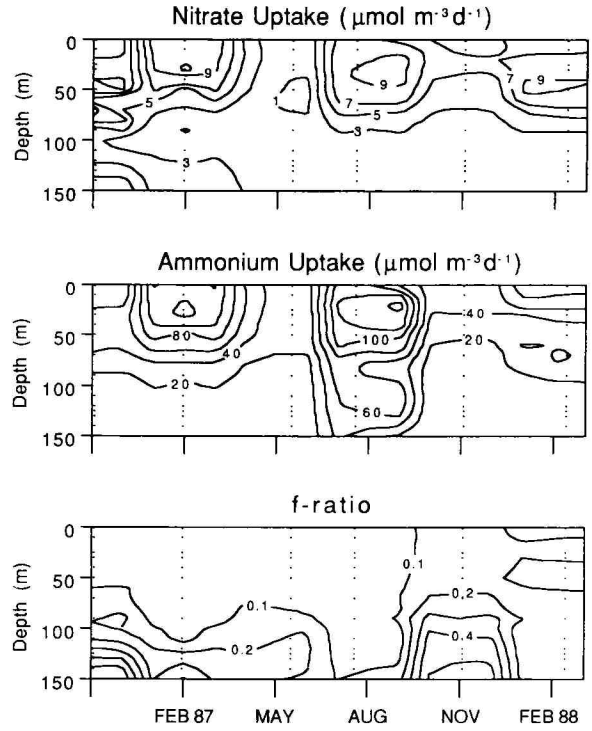


Fig. 6. Temporal variations in NO_3^- and NH_4^- uptake rates (μmol m^{-3} day^{-1}) and the *f*-ratio [NO_3^- uptake/(NO_3^- + NH_4^+) uptake] in the upper 150 m at the VERTEX time-series site.

KNAUER *et al.*, 1990; LOHRENZ *et al.*, 1992; CHISWELL *et al.*, 1990). Much less work has been done on temporal nutrient dynamics (EPPLEY *et al.*, 1973, 1977; HAYWARD, 1987), and the few studies reported have suffered from very limited temporal coverage. Ecosystem models (FASHAM *et al.*, 1990) have been useful in "filling in the gaps" but must be experimentally validated.

The conceptual model for the open ocean production cycle is based on the regulation of primary productivity by the supply of nitrogen to the euphotic zone (DUGDALE and GOERING, 1967). Nitrogen is made available principally by two mechanisms, one biological and one physical. Reduced N-forms (e.g. NH_4^+) are provided *in situ* from biological sources as waste products of plankton metabolism and support the so-called "regenerated" primary production. Oxidized-N forms (e.g NO_3^-), provided most often by physical mechanisms such as vertical mixing, support the so-called "new" production. New production has been equated with the fraction of primary production *in excess* of community metabolic demands and is approximately equivalent, under steady state conditions, to the biogenic matter exported from the euphotic zone (DUGDALE and GOERING, 1967; EPPLEY and PETERSON, 1979). Moreover, the absolute primary productivity is thought to be positively correlated with the fractional new production the "f-ratio", i.e. high primary production regions are characterized by a higher relative proportion of new production and therefore a higher proportion of exported primary production (EPPLEY and PETERSON, 1979). By inference, the more productive regions are those characterized by greater temporal variability due in large part to their physical dynamics. More intense mixing and greater availability of new nitrogen in the North Atlantic, for example, may explain higher and more variable production levels there than in the Pacific (EPPLEY, 1981).

Because of the paucity of data, primary productivity and related variables often are perceived to be low and temporally uniform in the open ocean. At the VERTEX time-series site, however, primary productivity, microbial biomass and nitrogen concentrations and uptake rates in the euphotic zone varied substantially (2–15×) over the 18 month study period (Tables 1 and 2; see also KNAUER *et al.*, 1990). In many respects, temporal variations were comparable to or exceeded those observed in other studies of the subtropical Pacific (EPPLEY *et al.*, 1977; HAYWARD *et al.*, 1983; BIENFANG *et al.*, 1984; HAYWARD and MCGOWAN, 1985; LAWS *et al.*, 1989) and the subtropical Atlantic (MENZEL and RYTHER, 1960, 1961; LOHRENZ *et al.*, 1992).

Maximum primary productivities in the oligotrophic subtropical gyres typically occur in the winter/spring periods when nutrient resupply is greatest, driven principally by winter convective (MENZEL and RYTHER, 1960, 1961; LOHRENZ *et al.*, 1992) or wind-induced (BIENFANG *et al.*, 1984) mixing. In more permanently stratified oceans also, variations in primary productivity have been clearly linked to nitrate supply (HERBLAND and VOITURIEZ, 1979; KING, 1986). In contrast, highest primary productivities at the VERTEX site occurred in summer, out of phase with the winter nutrient maximum conditions. EPPLEY *et al.* (1977) and HAYWARD (1987) noted a similar pattern in the central North Pacific Gyre. Total inorganic-N uptake at the VERTEX site also peaked in summer, but this was largely due to variations in NH_4^+ uptake. New production (NO_3^- uptake) was relatively constant, 0.59 ± 0.21 mmol m^{-2} day^{-1} (Table 2), with fractional new production (*f*-ratio) highest in the lower euphotic zone (Fig. 6). This vertical pattern of *f*-ratio is consistent with the classical two-layer system (DUGDALE and GOERING, 1967; BIENFANG *et al.*, 1984; KNAUER *et al.*, 1984; COALE and BRULAND, 1987; SMALL *et al.*, 1987). Primary productivity was not

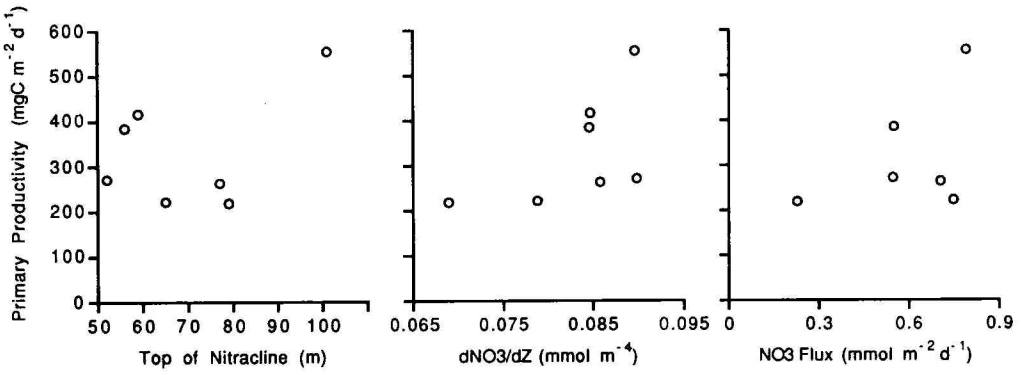


Fig. 7. Relationships between primary productivity (mgC m^{-2} day^{-1}) and nitracline depth (m), NO_3^- gradient (mmol m^{-4}) and NO_3^- flux (mmol m^{-2} day^{-1}) at the VERTEX time-series site.

clearly related to any of the conventional indices of nitrate availability (nitracline depth, NO_3^- gradient, NO_3^- flux; Fig. 7), although *f*-ratios did increase with productivity (EPPLEY and PETERSON, 1979) except for one cruise, the summer (Sea-4) cruise (Fig. 8). It is also noteworthy that these *f*-ratios are considerably lower for comparable productivities than predicted from the Eppley and Peterson relationship, due in part to the higher productivities using "clean" techniques (FITZWATER *et al.*, 1982; LAWS *et al.*, 1984, 1989). HAYWARD (1987) similarly failed to detect any relationship between primary productivity and nitrate distribution in his thorough investigation of the nutrient sources fuelling primary productivity in the North Pacific Gyre. Moreover, his calculations suggested that NO_3^- supply based on classical Fickian diffusion was insufficient to meet primary productivity requirements. Sources of new nitrogen originating from episodic or mesoscale processes were offered as an explanation for this discrepancy but direct evidence was lacking. Significant new nitrogen sources arising from isopycnic and episodic diapycnic processes also have been suggested for the subtropical Atlantic (JENKINS, 1988; MARTIN *et al.*, 1987; BIGG *et al.*, 1989; SARMIENTO *et al.*, 1990; see also HAMILTON *et al.*, 1989).

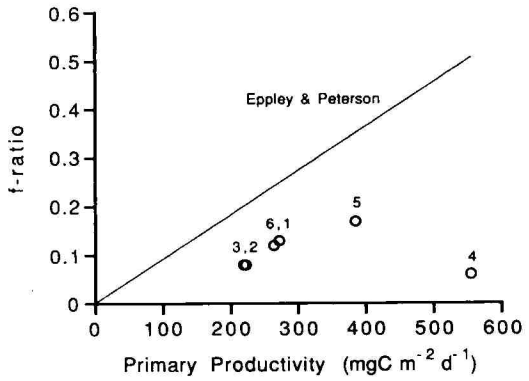


Fig. 8. Relationship between *f*-ratio [NO_3^- uptake/(NO_3^- + NH_4^+) uptake] and primary productivity (mgC m^{-2} day^{-1}) at the VERTEX time-series site. Solid line is the EPPLEY and PETERSON (1979) relationship, numbers over data points are cruises (i.e. Sea-1 to Sea-7).

The absence of a link between NO_3^- availability and the high primary productivity during the summer (Sea-4) cruise at the VERTEX site was unexpected. Although NO_3^- gradients and new production rates were highest then (relative to values observed during the other cruises), fractional new production (*f*-ratio) and euphotic zone NO_3^- concentrations were lowest and nitracline depth was the deepest observed during the 18 month study (Figs 3, 6 and 7). In addition, there was no suggestion of enhanced mixing associated with the Sea-4 productivity peak; estimated eddy diffusivities were relatively invariant during the 18 month study ($0.82 \pm 0.26\ 10^{-4}\ m^2\ s^{-1}$; Table 3) and at the low end of the range expected for oceanic waters (DENMAN and GARGETT, 1983; KING and DEVOL, 1979; EPPLEY *et al.*, 1979; LEWIS *et al.*, 1986; HAYWARD, 1987; JENKINS, 1988). Coincident also with the high primary productivity during Sea-4 were the highest heterotrophic biomass and heterotrophic N-uptake rates (see below). Current concepts require an external nutrient input to explain the elevated productivity during the summer cruise. Regenerated production can be simulated by an increase in new production (EPPLEY *et al.*, 1979), therefore it is plausible that some undetected "event" occurred in the intervening time between the Sea-3 spring and Sea-4 summer cruises, supplying an external source of new nitrogen to the euphotic zone that fuelled the primary productivity increase and, in turn, stimulated microbial growth and regenerated production, resulting in the elevated levels observed during the Sea-4 cruise. Evidence for a large scale advective perturbation, however, was lacking based on similarities of the hydrography of the time-series stations with long-term patterns for the region (D. REDALJE, in preparation; BATHEN, 1972). Unfortunately, the critical long term (~90 day) sediment trap deployment (KNAUER *et al.*, 1990) between cruises Sea-3 and Sea-4 that could have provided evidence for an intervening source of new (export) production was lost. The underlying cause for the anomalous summer peak in primary productivity, therefore, remains unresolved. It is clear, nonetheless, that more highly resolved temporal sampling will be essential to detect and evaluate properly these shorter term/episodic events (HAYWARD, 1987; JENKINS, 1988; BIGG *et al.*, 1989). This is now underway, for example, at the Joint Global Ocean Flux Study (JGOFS) time-series sites in Hawaii and Bermuda.

Particulate organic nitrogen

KNAUER *et al.* (1990) have discussed the temporal particle flux at the VERTEX time series site based on sediment traps. Trap PON fluxes varied temporally, but highest fractional export (trap flux/primary productivity) occurred in winter/spring when primary productivity was lowest. This unexpected (EPPLEY *et al.*, 1979; PLATT and HARRISON, 1985) inverse relationship between fractional PON flux (and *f*-ratios) and primary productivity also has been observed in the subtropical North Atlantic (LOHRENZ *et al.*, 1992). The latter authors have suggested that the apparent inverse relationship could result from a mismatch between sampling and process-interaction time scales, a point well illustrated in ecosystem models (FASHAM *et al.*, 1990). The temporal forcing underlying the observed PON fluxes at the VERTEX site was not evident; neither suspended PON concentrations nor NO_3^- fluxes were correlated with PON fluxes (Fig. 9) as has been observed in the North Atlantic (ALTABET, 1989).

Annual PON fluxes and fractional export at the VERTEX site were in line with earlier estimates for the oligotrophic North Pacific (MARTIN *et al.*, 1987) but generally lower than estimates for the subtropical Atlantic (PLATT and HARRISON, 1985; ALTABET, 1989;

Table 3. Nitrate, PON and DON vertical gradients (mmol m^{-4}) *and fluxes* (mmol m^{-2} day^{-1}). *Vertical eddy diffusivities* (Kz) = 10^{-4} m^2 s^{-1}. *Negative values represent decreasing concentrations with depth or downward flux. Numbers in parentheses are computational depth ranges*

(1) Cruise	(2) dNO_3/dZ (125–400 m)	(3) NO_3 flux	(4) Kz	(5) dPON/dZ (0–150 m)	(6) dDON/dZ (0–400 m)	(7) PON_s flux	(8) PON_t flux	(9) DON flux	(10) DON/NO_3 flux (9)/(3)
Sea-1	0.0898	0.547	0.71	−0.00019	−0.0050	−0.001		−0.030	0.06
							−0.493		
Sea-2	0.0788	0.747	1.10	−0.00158	−0.0059	−0.015		−0.056	0.07
							−0.386		
Sea-3	0.0689	0.227	0.38	−0.00026	−0.0043	−0.001		−0.014	0.06
							—		
Sea-4	0.0896	0.788	1.02	−0.00029	−0.0042	−0.003		−0.037	0.05
							−0.300		
Sea-5	0.0846	0.550	0.75	−0.00101	−0.0042	−0.007		−0.027	0.05
							−0.320		
Sea-6	0.0858	0.704	0.95	−0.00046	−0.0037	−0.004		−0.030	0.04
							−0.636		
Sea-7	0.0847	—	—	−0.00022	−0.0025	—		—	—
Mean	0.0832	0.594	0.82	−0.00057	−0.0043	−0.005	−0.427	−0.033	0.06
S.D.	0.0073	0.206	0.26	0.00053	0.0011	0.005	0.139	0.014	0.01

Kz = NO_3 flux/(dNO_3/dz), PON_s = suspended PON, PON_t = trap-derived PON.

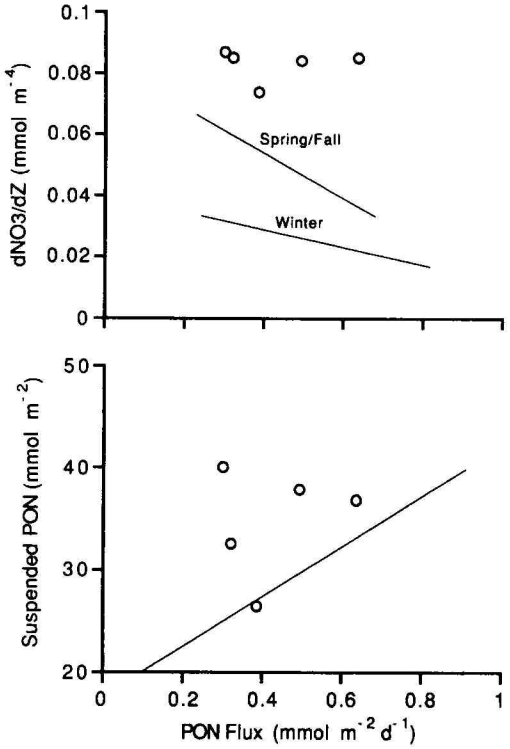


Fig. 9. Relationships between PON flux (mmol m^{-2} day^{-1}) and NO_3^- gradient (mmol m^{-4}) and suspended PON concentration (mmol m^{-2}), NO_3^- gradient and PON concentrations are averages of adjacent cruises. Solid lines are relationships derived from studies in the subtropical Atlantic (ALTABET, 1989).

LOHRENZ *et al.*, 1992). Vertical flux of suspended PON was an insignificant fraction of the trap-derived PON flux at the VERTEX site (Table 3) in contrast to results obtained from the subtropical Atlantic where 40% of the annual particulate flux was attributed to suspended PON losses (ALTABET, 1989). Annual *f*-ratios based on conventional measurements of NO_3^- and NH_4^+ uptake compared well with ratios from trap flux/primary productivity (KNAUER *et al.*, 1990; see also MURRAY *et al.*, 1989).

Dissolved organic nitrogen

Dissolved organic-N represented the largest and temporally most variable (in absolute terms) nitrogen pool in the euphotic zone at the VERTEX time-series site. No temporal pattern was evident, although elevated surface DON concentrations occurred in the fall, following high PON, primary productivity and nitrogen uptake rates in summer (Fig. 4). Whether the observed variations in DON represented local biological processes or were a consequence of advective processes is difficult to evaluate. Hydrographic analysis, as mentioned earlier, provided no evidence that large-scale advection strongly influenced the temporal patterns observed during our 18 month study. Furthermore, the observation that DON changes decreased in amplitude with depth (Fig. 10) is easiest explained by local

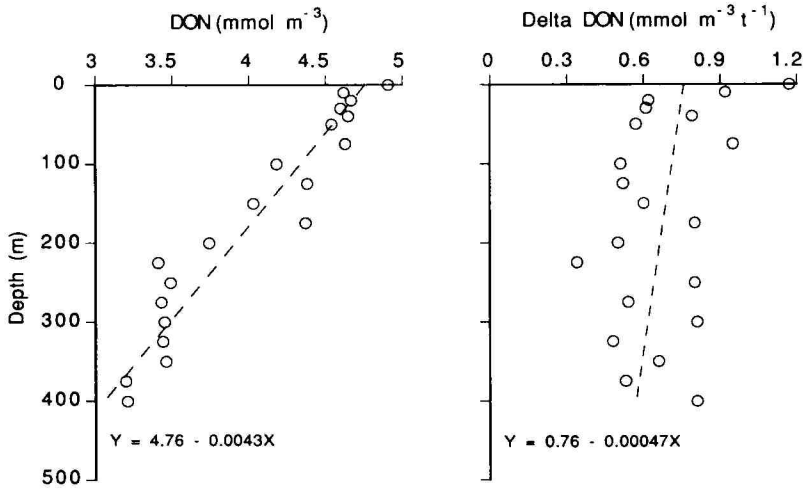


Fig. 10. Depth profiles of DON concentrations (mmol m^{-3}) and DON concentration changes between crusies (δ DON: mmol m^{-3} t^{-1}) at the VERTEX time-series site. Data are mean values for all cruises.

biological processes. The largest observed variation in DON concentrations between cruises (2.12 mmol m^{-2} day^{-1}) translated to a turnover rate (~0.003 day^{-1}) which is consistent with other workers' estimates of biologically-mediated DON turnover in oceanic waters (JACKSON and WILLIAMS, 1985).

Despite large temporal changes in DON concentrations, vertical gradients were small and relatively invariant. Vertical DON fluxes (downward) averaged 0.033 (±0.014) mmol m^{-2} day^{-1} over the 18 month study, represented only 6% (±1%) of the annual NO_3^- flux (upward) and accounted for little of the total nitrogen export flux (Table 3). This result further supports the suggestion made by KNAUER *et al.* (1990) in their analysis of temporal PON fluxes that the activity of the heterotrophic communities acted to effectively conserve products of autotrophic production within the euphotic zone, i.e. the large temporal variations in primary productivity were not translated into comparable variations in export flux. SMITH *et al.* (1986) found correspondingly low DON fluxes (compared to NO_3^- fluxes) in the North Pacific Gyre. These low values are clearly insufficient to balance the vertical material fluxes envisaged in present day ocean biogeochemical models (e.g. TOGGWEILER, 1989). If, however, the substantially higher DON concentrations reported by SUZUKI *et al.* (1985), ~40 instead of the ~4 mmol m^{-3} we report, are more representative, then estimated DON fluxes become significant, approaching 60% of the NO_3^- and PON flux. The importance of resolving the current discrepancies in estimates of dissolved organic matter in the surface ocean is obvious.

Autotrophy versus heterotrophy

Results from this study support earlier findings in coastal (WHEELER and KIRCHMAN, 1986) and oceanic waters (EPPLEY *et al.*, 1977; LAWS *et al.*, 1985; see also LAWS, 1991) that a significant portion of the uptake of inorganic-N may be mediated by microheterotrophs.

Based on comparisons of NO_3^- + NH_4^+ uptake and autotrophic N-uptake (Table 2), only 60% (1.47/2.45 mol m^{-2} y^{-1}) of the annual inorganic-N productivity was attributable to autotrophs. The maximum heterotrophic N-uptake coincided with highest heterotrophic microbial biomass during the summer cruise (Sea-4). Moreover, close similarities in biomass and NH_4^+ uptake in particular, suggested that NH_4^+ was a more important N-source than NO_3^- for the heterotrophs (e.g. WHEELER and KIRCHMAN, 1986). Microheterotroph biomass equalled or exceeded autotroph biomass in all except one cruise (Table 2), an observation not uncommon in oceanic waters (e.g. LAWS *et al.*, 1984; FUHRMAN *et al.*, 1989). The implications of these findings reinforce concerns previously expressed regarding the interpretation of new production and *f*-ratios using conventional assumptions of autotroph dominance (WHEELER and KIRCHMAN, 1986; HARRISON *et al.*, 1987; LAWS, 1991). For example, basing *f*-ratio computations on autotrophic N-uptake rather than total (NO_3 + NH_4) uptake resulted in a significantly higher fractional new production estimate at the VERTEX site (0.15 vs 0.09; Table 2). These findings clearly illustrate the importance of differentiating the relative roles of heterotrophs and autotrophs in nitrogen cycling studies in the upper ocean.

SUMMARY

In some respects, results from the VERTEX time-series study did not conform to the conventional model of new and regenerated production (DUGDALE and GOERING, 1967; EPPLEY and PETERSON, 1979). (1) The hypothesized positive co-variance between new production, *f*-ratio and total production was not evident in our study. Our lowest *f*-ratios (and fractional PON fluxes), in fact, were associated with highest observed primary productivities. Among the possible explanations considered, inadequate matching of sampling and physical forcing time scales seemed the most plausible. Oceanographic properties compared on time scales shorter than the annual one are likely to deviate substantially from the assumed steady state condition, even in the relatively stable oligotrophic open ocean (PLATT and HARRISON, 1985). (2) Our *f*-ratios were significantly lower than expected (EPPLEY and PETERSON, 1979) based on observed productivity levels. This could be attributed to improvements in primary productivity measurements through the use of "clean" techniques; contemporary values are significantly higher than the historical ones at comparable *f*-ratios. Also, our ^{15}N-derived *f*-ratios are likely lower than historical values because of corrections to regenerated production to account for non-linearity in NH_4^+ uptake (see Methods and Materials). (3) The conventional new and regeneration model has not adequately addressed the role of microheterotrophs in inorganic-N dynamics. From our VERTEX work and that of others, it is clear that microheterotrophs can account for a significant fraction of the nitrogen productivity in the euphotic zone, particularly with regard to regenerated production, and that *f*-ratios can be in error if this is not taken into account.

In other respects, the new and regenerated production model provides a good representation of the oceanic euphotic zone. (1) The perceived two-layer system (DUGDALE and GOERING, 1967) was clearly evident in the VERTEX time-series study. Temporal depth profiles of *f*-ratios revealed that much of the new production occurred in the lower euphotic zone as others have shown or suggested. (2) Annual estimates of new production based on $^{15}NO_3^-$ uptake compared well with estimates from PON flux, revealing among other things that the appropriate comparison time scale is, indeed, the annual one (PLATT

and HARRISON, 1985). Interestingly, DON flux represented a relatively insignificant component of the nitrogen balance in the surface ocean. This observation is clearly at odds with current views that dissolved organic matter may play a very important role in the export of biogenic matter to the ocean interior and underscores the need for further study.

Acknowledgements—We thank M. Tuel, C. Hunter and G. Tien for their help with the field work and laboratory analyses. We also thank the captains and crews of the R.V. *Wecoma*, R.V. *Point Sur* and R.V. *Thompson* for their able assistance. This research was supported by the Canadian Federal Department of Fisheries & Oceans (W.G.H.) and grants from the U.S. National Science Foundation of Marine Chemistry (OCE-8600458 to G.A.K. and D.G.R.; OCE-8600462 to D.M.K.).

REFERENCES

ALTABET M. A. (1989) Particulate new nitrogen fluxes in the Sargasso Sea. *Journal of Geophysical Research*, **94**, 12,771–12,779.

ARMSTRONG F. A. J., P. M. WILLIAMS and J. D. H. STRICKLAND (1966) Photo-oxidation of organic matter in seawater by ultraviolet radiation; analytical and other considerations. *Nature*, **211**, 481–483.

ATLAS E. L., L. I. GORDON, S. W. AHGER and P. K. PARK (1971) A practical manual for the use of the Technicon Autoanalyzer in seawater nutrient analysis: revised. Technical Report 215, Reference 71-22, Oregon State University, College of Oceanography, 48 pp.

BATHEN K. H. (1972) On the seasonal changes in depth of the mixed layer in the north Pacific Ocean. *Journal of Geophysical Research*, **77**, 7138–7150.

BIENFANG P. K., J. P. SZYPER, M. Y. OKAMOTO and E. K. NODA (1984) Temporal and spatial variability of phytoplankton in a subtropical ecosystem. *Limnology and Oceanography*, **29**, 527–539.

BIGG G. R., T. D. JICKELLS, A. H. KNAP and R. SHERRIFF-DOW (1989) The significance of short term wind induced mixing events for 'new' primary production in sub-tropical gyres. *Oceanologica Acta*, **12**, 437–442.

BLACKBURN T. H. and J. SORENSEN (1988) *Nitrogen cycling in coastal marine environments*. John Wiley & Sons, Chichester, 451 pp.

BROENKOW W. W., M. A. YARBROUGH and M. A. YUEN (1988) Oceanographic results from the VERTEX seasonal experiments. Moss Landing Laboratories Technical Publication 88-1, Moss Landing, CA, 67 pp.

CARPENTER E. J. and D. G. CAPONE (1983) *Nitrogen in the marine environment*. Academic Press, New York, 900 pp.

CHISWELL S., E. FIRING, D. KARL, R. LUKAS and C. WINN (1990) Hawaii Ocean Time-series Data Report H-1, U.S. Joint Global Ocean Flux Study Report.

COALE K. H and K. W. BRULAND (1987) Oceanic stratified euphotic zone as elucidated by ^{234}Th:^{238}U disequilibria. *Limnology and Oceanography*, **32**, 189–200.

DENMAN K. L. and A. E. GARGETT (1983) Time and space scales of vertical mixing and advection of phyloplankton in the upper ocean. *Limnology and Oceanography*, **28**, 801–815.

DITULLIO G. and E. A. LAWS (1983) Estimates of phytoplankton N uptake based on $^{14}CO_2$ incorporation into protein. *Limnology and Oceanography*, **28**, 177–185.

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. (1981) Autotrophic production of particulate matter. In: *Analysis of marine ecosystems*, A. R. LONGHURST, editor, Academic Press, London, pp. 343–361.

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., 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**, 11–120.

EPPLEY R. W., E. H. RENGER and W. G. HARRISON (1979) Nitrate and phytoplankton production in southern California coastal waters. *Limnology and Oceanography*, **24**, 483–494.

FASHAM M. J. R., H. W. DUCKLOW and S. M. MCKELVIE (1990) A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research*, **48**, 591–639.

FIEDLER R. and G. PROKSCH (1975) The determination of nitrogen-15 by emission and mass spectrometry in biochemical analysis: a review. *Analytica Chimica Acta*, **78**, 1–62.

FITZWATER S. E., G. A. KNAUER and J. H. MARTIN (1982) Metal contamination and its effects on primary production measurements. *Limnology and Oceanography*, **27**, 544–551.

FUHRMAN J. A., T. D. SLEETER, C. A. CARLSON and L. M. PROCTOR (1989) Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. *Marine Ecology Progress Series*, **57**, 207–217.

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.

HARRISON W. G. (1983) Use of isotopes. In: *Nitrogen in the marine environment*, E. CARPENTER and D. CAPONE, editors, Academic Press, New York, pp. 763–807.

HARRISON W. G., T. PLATT and M. R. LEWIS (1987) f-Ratio and its relationship to ambient nitrate concentration in coastal waters. *Journal of Plankton Research*, **9**, 235–248.

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

HAYWARD T. L. and J. A. MCGOWAN (1985) Spatial patterns of chlorophyll, primary production, macrozooplankton biomass, and physical structure in the central North Pacific Ocean. *Journal of Plankton Research*, **7**, 147–167.

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.

HERBLAND A. and B. VOITURIEZ (1979) Hydrological structure analysis for estimating the primary production in the Atlantic Ocean. *Journal of Marine Research*, **37**, 87–101.

HOLM-HANSEN O. and D. M. KARL (1978) Biomass and adenylate energy charge determination in microbial cell extracts and environmental samples. *Methods in Enzymology*, **57**, 832–835.

JACKSON G. A. and P. M. WILLIAMS (1985) Importance of dissolved organic nitrogen and phosphorus to biological nutrient cycling. *Deep-Sea Research*, **32**, 223–235.

JENKINS W. J. (1988) Nitrate flux into the euphotic zone near Bermuda. *Nature*, **331**, 521–523.

KARL D. M. (1980) Cellular nucleotide measurements and applications in microbial ecology. *Microbiological Reviews*, **44**, 739–796.

KARL D. M., C. D. WINN, D. V. W. HEBEL, R. LETELIER, S. M. CHISWELL, T. W. WALSH and D. F. BIRD (1990) Hawaii Ocean Time-Series Program. Field and laboratory protocols. University of Hawaii.

KING F. D. (1986) The dependence of primary production in the mixed layer of the eastern tropical Pacific on the vertical transport of nitrate. *Deep-Sea Research*, **33**, 733–754.

KING F. D. and A. H. DEVOL (1979) Estimates of vertical eddy diffusion through the thermocline from phytoplankton nitrate uptake rates in the mixed layer of the eastern tropical Pacific. *Limnology and Oceanography*, **24**, 645–651.

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

KNAUER G. A., J. H. MARTIN and D. M. KARL (1984) The flux of particulate organic matter out of the euphotic zone. In: *Global Ocean Flux Studies. Proceedings of a workshop*, Woods Hole, National Academic Press.

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.

LAWS E. A. (1991) Photosynthetic quotients, new production and net community production in the open ocean. *Deep-Sea Research*, **38**, 143–167.

LAWS E. A., D. G. REDALJE, L. W. HAAS, P. K. BIENFANG, R. W. EPPLEY, W. G. HARRISON, D. M. KARL and J. MARRA (1984) High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. *Limnology and Oceanography*, **29**, 1161–1169.

LAWS E. A., W. G. HARRISON and G. R. DITULLIO (1985) A comparison of nitrogen assimilation rates based on ^{15}N uptake and autotrophic protein synthesis. *Deep-Sea Research*, **32**, 85–95.

LAWS E. A., G. R. DITULLIO, P. R. BETZER, D. M. KARL and K. L. CARDER (1989) Autotrophic production and elemental fluxes at 26°N, 155°W in the North Pacific subtropical gyre. *Deep-Sea Research*, **36**, 103–120.

LEGENDRE L. and M. GOSSELIN (1989) New production and export of organic matter to the deep ocean: consequences of some recent discoveries. *Limnology and Oceanography*, **34**, 1374–1380.

LEWIS M. R., W. G. HARRISON, N. S. OAKEY, D. HERBERT and T. PLATT (1986) Vertical nitrate fluxes in the oligotrophic ocean. *Science*, **234**, 870–873.

LOHRENZ S. E., G. A. KNAUER, V. L. ASPER, M. TUEL, A. F. MICHAELS and A. H. KNAP (1992) Seasonal variability in primary production and particle flux in the northwestern Sargasso Sea: U.S. JGOFS Bermuda Atlantic time series Study. *Deep-Sea Research*, **39**, 1373–1391.

LONGHURST A. R. (in press) Role of the marine biosphere in the global carbon cycle. *Limnology and Oceanography*.

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.

MENZEL D. W. and J. H. RYTHER (1960) The annual cycle of primary production of the Sargasso Sea off Bermuda. *Deep-Sea Research*, **6**, 351–367.

MENZEL D. W. and J. H. RYTHER (1961) Annual variations in primary production of the Sargasso Sea off Bermuda. *Deep-Sea Research*, **7**, 282–288.

MURRAY J. W., J. N. DOWNS, S. STROM, C.-L. WEI and H. W. JANNASCH (1989) Nutrient assimilation, export production and ^{234}Th scavenging in the eastern equatorial Pacific. *Deep-Sea Research*, **36**, 1471–1489.

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

PLATT T., W. G. HARRISON, M. R. LEWIS, W. K. W. LI, S. SATHYENDRANATH, R. E. SMITH and A. VEZINA (1989) Biological production of the oceans: the case for a consensus. *Marine Ecology Progress Series*, **52**, 77–88.

REDALJE D. G. (1983) Phytoplankton carbon biomass and specific growth rates determined with the labeled chlorophyll *a* technique. *Marine Ecology Progress Series*, **11**, 217–225.

REDALJE D. G. and E. A. LAWS (1981) A new method for estimating phytoplankton growth rates and carbon biomass. *Marine Biology*, **62**, 73–79.

SAHLSTEN E. (1987) Nitrogenous nutrition in the euphotic zone of the Central North Pacific Gyre. *Marine Biology*, **96**, 433–439.

SARMIENTO J. L., G. THIELE, R. M. KEY and W. S. MOORE (1990) Oxygen and nitrate new production and remineralization in the north Atlantic subtropical gyre. *Journal of Geophysical Research*, **95**, 18,303–18,315.

SCOR (1990) Joint Global Ocean Flux Study (JGOFS). Science Plan. JGOFS Report No. 5, 61 pp.

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.

SMITH S. V., W. J. KIMMERER and T. W. WALSH (1986) Vertical flux and biogeochemical turnover regulate nutrient limitation of net organic production in the North Pacific Gyre. *Limnology and Oceanography*, **31**, 161–167.

SOLORZANO L. (1969) Determination of ammonia in natural waters by the phenolhypochlorite method. *Limnology and Oceanography*, **14**, 799–801.

STRICKLAND J. D. H. and T. R. PARSONS (1972) *A practical handbook of seawater analysis*. Bull. 167, Fisheries Research Board of Canada, 310 pp.

SUZUKI Y., Y. SUGIMURA and T. ITOH (1985) A catalytic oxidation method for the determination of total nitrogen dissolved in seawater. *Marine Chemistry*, **16**, 83–97.

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 & Sons, Chichester, pp. 65–83.

WALSH T. W. (1989) Total dissolved nitrogen in seawater: a new high-temperature combustion method and a comparison with photo-oxidation. *Marine Chemistry*, **26**, 295–311.

WHEELER P. A. and D. L. KIRCHMAN (1986) Utilization of inorganic and organic nitrogen by bacteria in marine systems. *Limnology and Oceanography*, **31**, 998–1009.