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Seasonal and interannual variations in photosynthetic carbon assimilation at Station ALOHA

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Abstract—Autotrophic carbon assimilation measurements using a trace metal-free ^{14}C technique were performed at near monthly intervals between 1988 and 1992 in the North Pacific subtropical gyre (U.S. JGOFS–WOCE Sta. ALOHA; 22°45′N, 158°00′W). Integrated photosynthetic values ranged from 127 to 1055 mg C m^{-2} day^{-1} while the average carbon assimilation number (P^B), defined as carbon assimilation rate per unit chlorophyll *a* (chl *a*), varied between 1.6 and 12 g C (g chl *a*)$^{-1}$ h^{-1} in the 0–45 m depth range. Consistently low P^B values (< 5 g C (g chl *a*)$^{-1}$ h^{-1}, averaged in the upper 45 m of the water column) were observed during the first 2 years of this study but increased to > 5 g C (g chl *a*)$^{-1}$ h^{-1} during 1991–1992. This rise in P^B was not associated with an increase in chl *a*. Furthermore, it occurred during a period of increased water column stability. Reduction in ATP and (NO_3^- + NO_2^-) concentrations in the upper euphotic zone suggests that nutrient injections due to mixing events were minor or absent after January 1991.

Two non-exclusive hypotheses are presented to explain the rise of P^B in the absence of an enhancement of inorganic nutrient fluxes from below the euphotic zone: (i) high P^B values observed during 1991–1992 are indicative of phytoplankton growth being balanced as a result of a decrease in the variability of nutrient injection due to a reduction in the frequency of mixing events, and (ii) the rise of P^B during 1991–1992 is caused by an ecosystem shift from nitrogen to phosphorus limitation. The stability of the water column during 1991–1992 may have increased the availability of reduced nitrogen relative to phosphorus due to the enhancement of nitrogen fixation. Because these hypotheses do not require an increase in algal biomass or elemental fluxes across the base of the euphotic zone to explain an increase in autotrophic carbon assimilation, they imply that nutrient dynamics within the euphotic zone of the North Pacific subtropical gyre need to be understood in order to interpret changes in P^B and predict carbon fluxes. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

Nutrient limitation on photoautotrophic processes in the marine environment remains a matter of debate (Smith, 1984; Howarth, 1988; Falkowski *et al.*, 1992). Based on studies carried out in oligotrophic oceans, it is not clear whether nutrient availability limits the growth rate of autotrophs (Thomas, 1970; Falkowski *et al.*, 1991), the carrying capacity of the system (Martin, 1991), or both. Historically, the water column light-saturated photosynthetic rates normalized to chlorophyll *a* (P_S^B), a specific case of P^B (photosynthetic rate per unit chlorophyll *a*) and also known as assimilation number (Geider and Osborne, 1992), has been correlated with the nutritional status and growth

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rates of phytoplankton in the euphotic zone of oceanic regions (McAllister *et al.*, 1964; Gundersen *et al.*, 1976; Platt *et al.*, 1992). Curl and Small (1965) suggested that, while P_S^B values lower than 3 g C (g chl *a*)$^{-1}$ h^{-1} are found in nutrient depleted waters, values higher than 5 g C (g chl *a*)$^{-1}$ h^{-1} occur only in nutrient-sufficient environments. Based on these relationships, the low P_S^B values typically observed in surface waters of the North Pacific subtropical gyre ($P_S^B < 5$ g C (g chl *a*)$^{-1}$ h^{-1}) have been interpreted as evidence of low phytoplankton growth rates resulting from nutrient limitation (Thomas, 1970; Eppley *et al.*, 1973; Gilmartin and Revelante, 1974; Gundersen *et al.*, 1976; Sharp *et al.*, 1980; Hayward *et al.*, 1983; Bienfang *et al.*, 1984). However, more recent P_S^B estimates obtained during and after the Plankton Rate Processes in Oligotrophic Oceans (PRPOOS) program have yielded P_S^B values as high as 10 g C (g chl *a*)$^{-1}$ h^{-1} for the North Pacific subtropical gyre, suggesting high phytoplankton growth rates and negligible nutrient stress (Laws *et al.*, 1987; Marra and Heinemann, 1987).

At present, the historical low autotrophic carbon assimilation rates (50–200 mg C m^{-2} day^{-1}) observed in central gyres (Steeman Nielsen and Jensen, 1957; Eppley, 1981) and the derived low phytoplankton growth rates (0.2 day^{-1}) and P_S^B values (Eppley *et al.*, 1973; Sharp *et al.*, 1980) are considered to be in error as a result of improper sample handling. With the advent of trace metal-clean techniques (Fitzwater *et al.*, 1982) and the identification and avoidance of materials containing trace metals toxic to phytoplankton, such as black neoprene (Williams and Robertson, 1989), the risk of poisoning phytoplankton has been reduced. The recently observed high P_S^B combined with evidence that pre-trace-metal clean sampling procedures had inhibitory effects on phytoplankton assemblages (Fitzwater *et al.*, 1982; Williams and Robertson, 1989) suggests that the historical view on algal growth rates in the North Pacific subtropical gyre may be in error.

A closer look at both historical and recent P_S^B values reported for the North Pacific central gyre indicate a large variability even within a single study. Eppley *et al.* (1973) found values ranging from 4 to 8 g C (g chl *a*)$^{-1}$ h^{-1} in November 1971. Gundersen *et al.* (1976) measured consistently low values during their study ($\leq$2 g C (g chl *a*)$^{-1}$ h^{-1}), but they also mentioned the unpublished results of A. Cattell and D. Gordon in the same region with values ranging from 0.7 to 20.0 g C (g chl *a*)$^{-1}$ h^{-1}. More recent results presented by DiTullio and Laws (1991) encompass values ranging from 6.6 to 13.9 g C (g chl *a*)$^{-1}$ h^{-1}. To date, this short term variability in P_S^B has been associated with nutrient injection into the euphotic zone as a result of deep mixing events (McGowan and Hayward, 1978; Marra *et al.*, 1990) or atmospheric dust events (Young *et al.*, 1991). However, Bienfang and Szyper (1981) suggested that changes in P_S^B could also be the result of changes in nutrient regeneration rates within the euphotic zone. Because carbon assimilation per unit biomass (P^B) represents a rate per unit of photosynthetic pigment (chl *a*), and the nutrient flux in the euphotic zone of the North Pacific subtropical gyre is controlled principally through the rate of recycling, changes in the assimilation number may reflect variations in the turnover time of the limiting nutrient. These variations could be attributed to changes in the ecosystem structure or in the nature of the limiting nutrient (i.e. nitrogen versus phosphorus, Smith *et al.*, 1986).

As part of the United States-Joint Global Ocean Flux Study (U.S.-JGOFS) and the World Ocean Circulation Experiment (U.S.-WOCE) programs, Hawaii Ocean Time-series (HOT) scientists have been characterizing the physics, biology and chemistry of the open ocean water column at Sta. ALOHA (Karl and Winn, 1991; Karl and Lukas, 1996). In the present paper, we summarize results from periodic measurements of autotrophic carbon

assimilation and chl *a* conducted at Sta. ALOHA between 1988 and 1992. We analyze the variability in phytoplankton assimilation number (P_S^B), particulate carbon (PC), inorganic nutrients, adenosine 5'-triphosphate (ATP) and physical properties of the euphotic zone in an attempt to elucidate the mechanisms controlling P_S^B temporal variability in the North Pacific subtropical gyre.

METHODS

Measurements of carbon assimilation in the euphotic zone of Sta. ALOHA (22°45'N; 158°00'W) were performed at approximately monthly intervals between October 1988 and December 1992 using the radiocarbon (^{14}C) method. Sample collection and manipulation followed the trace metal-clean recommendations of Fitzwater *et al.* (1982). Although the protocol underwent minor modifications over time, it followed the general description outlined below.

Water samples were collected at 8 depths (5, 25, 45, 75, 100, 125, 150, 175 m) 3–4 h before dawn with 10-l Teflon®-coated Go-Flo bottles (General Oceanics). After collection, subsamples were withdrawn under dim light into incubation bottles (500 ml polycarbonate), inoculated with $NaH^{14}CO_3$ (final activity $\sim$0.05–0.1 μCi ml^{-1}) and placed in the dark until minutes before sunrise when the timed incubation began.

Two different incubation methods were used during this study. On deck, simulated *in situ* (SIS) incubations were performed between October 1988 and May 1990 using a NORDA/USM system that reproduced both *in situ* photosynthetically available radiation (PAR) and temperature (Lohrenz *et al.*, 1992). *In situ* (IS) incubations using a free-floating productivity array began in July 1989 and overlapped the SIS incubations for eight cruises. For each depth three samples were incubated in the light and three in the dark from dawn to dusk (L12 and D12, respectively). When performing the SIS incubations, a second set of bottles was incubated for 24 h (LD24) to assess the magnitude of the nighttime respiration. Initial procedural blanks (t = 0 h) were obtained by filtering a sample from each depth just after dawn. The 24 h dark uptake (D24) from the *in situ* experiments was calculated by extrapolating the hourly rate obtained during the 12 h incubation period (D12) to 24 h.

At the end of the incubation period (*ca* 12 or 24 h) 200 μl were withdrawn from each incubation bottle and placed into a liquid scintillation vial containing 800 μl β-phenylethylamine (Sigma Chemical Co.) to measure the total ^{14}C activity added to each sample. Dissolved inorganic carbon specific activity ($^{14}C/^{12}C$; mCi mmol^{-1}) was calculated based on direct measurements of total inorganic carbon by CO_2 coulometry (Winn *et al.*, 1994) at each depth. Particulate matter from 100–500 ml subsamples was collected onto 25 mm glass fiber filters (Whatman, GF/F) and the filters were placed into liquid scintillation vials and stored for 2–3 days at -20°C. Upon arrival at our shore-based laboratories, the samples were acidified by adding 1 ml of 2 M HCl to each filter and vented for 24 h prior to the addition of scintillation cocktail. All samples were analyzed in a TRI-CARB 4640 liquid scintillation counter (Packard Instruments Co.) using Aquasol II (Dupont Corp.) as the scintillation cocktail. Because of a significant increase (5–35%) of the total ^{14}C activity measured in samples with filters immersed in the scintillation cocktail over the first 15–20 days, the samples were recounted after one month and these final dpm were used in all productivity calculations.

Triplicate 150 ml subsamples from each Go-Flo bottle also were collected for the fluorometric determination of chl *a*. The particulate matter was concentrated onto a 25 mm

GF/F filter and pigments were extracted in 100% cold acetone. All samples were stored at −20°C in the dark for 7 days before measuring the concentration of chl *a* in a Turner model 111 fluorometer (Strickland and Parsons, 1972). A model II linear regression analysis between chl *a* concentrations obtained with the described extraction method versus those obtained after sonication of replicate samples indicated that both methods have the same extraction efficiency for the phytoplankton assemblage of Sta. ALOHA (at a confidence interval of 95%).

Water samples collected from separate hydrocasts were used for the measurements of particulate carbon (PC) and adenosine 5′-triphosphate (ATP) concentrations. Four to 10 l of water, prescreened through a 202 μm Nitex mesh were filtered by positive pressure onto combusted (500°C, 3 h) 25 mm GF/F filters for PC analyses. The PC retained on the filter was quantified using a Perkin-Elmer model 2400 CHN analyzer. For ATP measurements, triplicate 1–2 l samples, also pre-screened through a 202 μm mesh, were concentrated by vacuum filtration onto 47 mm GF/F filters and immediately extracted in 5 ml of boiling TRIS buffer (0.02 M, pH = 7.4). These extracts were stored frozen for subsequent laboratory analysis of ATP using the firefly bioluminescence method with peak height detection (Karl and Holm-Hansen, 1978).

For the measurement of nutrient concentrations in the water column, approximately 100 ml subsamples were drawn into acid-washed 125 ml polyethylene bottles from water collected at predetermined depths. The polyethylene bottles were rinsed three times before collecting the final sample and all samples for phosphorus and nitrogen determinations were stored at −20°C until the date of analysis. Nitrate plus nitrite ($NO_3^- + NO_2^-$) and soluble reactive phosphorus (SRP) concentrations were measured by standard autoanalytical methods (Technicon Industrial Systems, 1977). Because the autoanalyzer lacks the sensitivity necessary to measure nanomolar quantities of ($NO_3^- + NO_2^-$) replicate samples were analyzed using a chemiluminiscence method (Dore and Karl, 1996 after Garside, 1982).

The underwater extinction coefficient of PAR and the *in situ* primary production light levels were estimated by measuring PAR simultaneously on deck, with a cosine collector, and on a continuous depth profile, by lowering a Profiling Natural Fluorometer (PNF-300; Biospherical Instruments Inc.) down to approximately 150 m. A Licor® model LI-192S collector was used to log surface PAR during the incubation period. Vertical distributions of other environmental parameters were assessed at 3 h intervals during a 36 h period with a SeaBird CTD equipped with an internal pressure sensor and external temperature, conductivity, dissolved oxygen and fluorescence sensors. To convert pressure into depth values a constant conversion factor of 1.024 db per meter was assumed. The maximum error in the upper 200 m when using this constant factor was less than 2%.

RESULTS

The average depth of the euphotic zone at Sta. ALOHA, calculated as the depth at which inorganic carbon assimilation in the light is not significantly different from carbon assimilation in the dark ($P \leqslant 0.05$, $n = 38$), was 173 m (±7 m) or 0.05% (±0.01%) surface PAR. The mixed-layer depth, defined here as the shallowest depth at which the density gradient equals or becomes greater than 5 g m^{-4}, and calculated based on the average density profile of all CTD casts performed at Sta. ALOHA during a given cruise, varied between <5 m and 114 m ($\bar{x} = 35$ m, $s = 23$, $n = 40$). Based on the analysis of

variance of mixed-layer depths, the variation within cruises accounted for 24% of the total variance observed between 1989 and 1992, while the variation between cruises accounted for the remaining 76% (s = 11.8 m, df = 536, and s = 21.3 m, df = 536, respectively).

A subsurface fluorescence maximum, identified as the deep chlorophyll maximum layer (DCML), was present at depths greater than 75 m on all cruises. The depth of this subsurface fluorescence maximum displayed an annual oscillation probably related to the seasonal cycle of solar irradiation (Fig. 1; Letelier *et al.*, 1993). Depth-integrated values of chl *a* (0–200 m), calculated from the primary production bottle cast samples, varied between 14.5 mg m^{-2} in January 1989 and 38.3 mg m^{-2} in June 1990 ($\bar{x}$ = 23.0, s = 5.7, n = 36; Fig. 1). Although large integrated values were found during 1989 and 1990, corresponding to increases of chl *a* at 100 m depth, annual mean concentrations were found to be significantly different only when comparing 1989 with 1991 and 1992 (t-test, $P \leqslant 0.05$; Table 1).

There was no evidence of a seasonal cycle in the euphotic zone (0–200 m) integrated assimilation of carbon estimated from *in situ* (IS) and simulated *in situ* (SIS) incubations even though photosynthesis and carbon assimilation rate per unit chl *a* (P^B) appeared to follow the solar cycle at water column depths greater than 100 m (Fig. 2 and Fig. 3, Table 2). The integrated euphotic zone carbon assimilation estimated from *in situ* and on-deck L12 incubations ranged from 217 to 1055 mg C m^{-2} day^{-1} ($\bar{x}$ = 462, s = 167, n = 46; Fig. 2). Although there was no correlation between 0–25 m chl *a* and euphotic zone integrated production (Fig. 4), on average 30% of the carbon assimilation took place in the first 25 m of

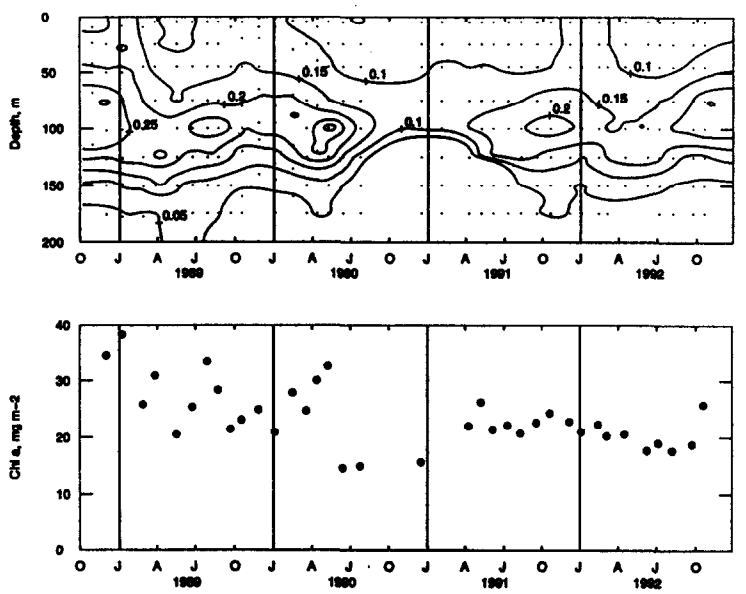


Fig. 1. Temporal distribution of chlorophyll *a* (chl *a*) measured by fluorometry at Sta. ALOHA for the period October 1988–December 1992. Top: contour plot displaying temporal and depth distributions. Dashed lines depict the seasonal trend in position of the deep chlorophyll maximum layer (DCML) between spring and fall. Bottom: euphotic zone (0–200 m) depth-integrated values of chl *a*.

Table 1. *Temporal variability of mean annual chlorophyll* a *concentration (chl* a*), and carbon assimilation rates (L*12 *and D*24*) integrated over the upper* 200 *m of the water column at Sta. ALOHA (values in parentheses are standard deviations)*

Parameter	Year			
	1989	1990	1991	1992
Chl *a* (mg m^{-2})	27.4	22.8	21.4	20.1
	(6.0)	(7.5)	(3.3)	(2.7)
L12 (12 h light) (mg C m^{-2} day^{-1})	447	383	529	540
	(73)	(91)	(118)	(103)
D24 (24 h dark) (mg C m^{-2} day^{-1})	66	46	29	29
	(21)	(14)	(5)	(8)

the water column (Figs 4 and 5) and only 10% of the production was found below 100 m (Fig. 5). In contrast, less than 10% of the 0–200 m depth integrated chl *a* was found in the upper 25 m (Fig. 5). Euphotic zone depth-integrated dark assimilation (0–200 m), extrapolated to 24 h, varied from 20 to 140 mg C m^{-2} day^{-1} ($\bar{x}$ = 49, s = 36, n = 45) and was relatively constant with depth (Fig. 5).

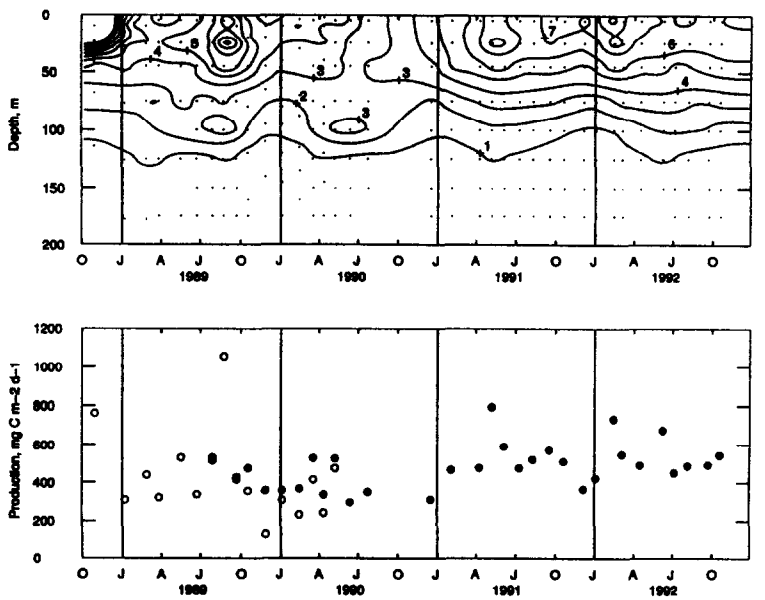


Fig. 2. Temporal distribution of autotrophic carbon assimilation (L12) at Sta. ALOHA for the period October 1988–December 1992. Top: contour plot displaying temporal and depth distributions of carbon assimilation in units of mg C m^{-3} day^{-1}. Bottom: euphotic zone (0–200 m) depth-integrated values of carbon assimilation. Open circles represent simulated *in situ* incubation (SIS) and closed circles represent *in situ* (SI) incubations.

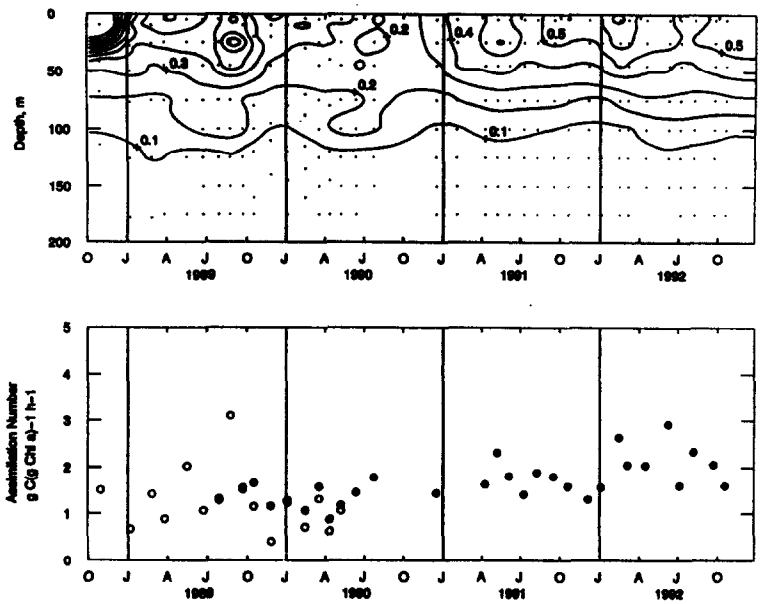


Fig. 3. Temporal distribution of inorganic carbon assimilation per unit chl *a* (P^B) at Sta. ALOHA for the period October 1988–December 1992. Top: contour plot showing temporal and depth distributions in units of g C (g chl *a*)$^{-1}$ h^{-1}. Bottom: water column photosynthetic carbon assimilation per unit chl *a* calculated as the euphotic zone (0–200 m) depth-integrated inorganic carbon assimilation rate divided by chl *a* integrated over the same depth interval. Open circles represent simulated *in situ* (SIS) incubations and closed circles represent *in situ* incubations.

Table 2. Seasonal variability of mean surface irradiance, integrated carbon assimilation rates and carbon assimilation efficiency (P^B) from below 100 m depth at Sta. ALOHA (values in parentheses represent standard deviations)

Variable	Season			
	Autumn*	Winter†	Spring‡	Summer§
Surface irradiance (mol quanta m^{-2} day^{-1})	38 (12)	39 (10)	51 (3)	52 (3)
L12 (12 h light) (mg C m^{-2} day^{-1})	28 (16)	38 (27)	75 (26)	50 (13)
D24 (24 h dark) (mg C m^{-2} day^{-1})	12 (5)	12 (7)	14 (10)	10 (5)
P^B (g C(g chl *a*)$^{-1}$ h^{-1})	0.24	0.26	0.37	0.30

*Data collected between 21 September and 20 December.
†Data collected between 21 December and 20 March.
‡Data collected between 21 March and 20 June.

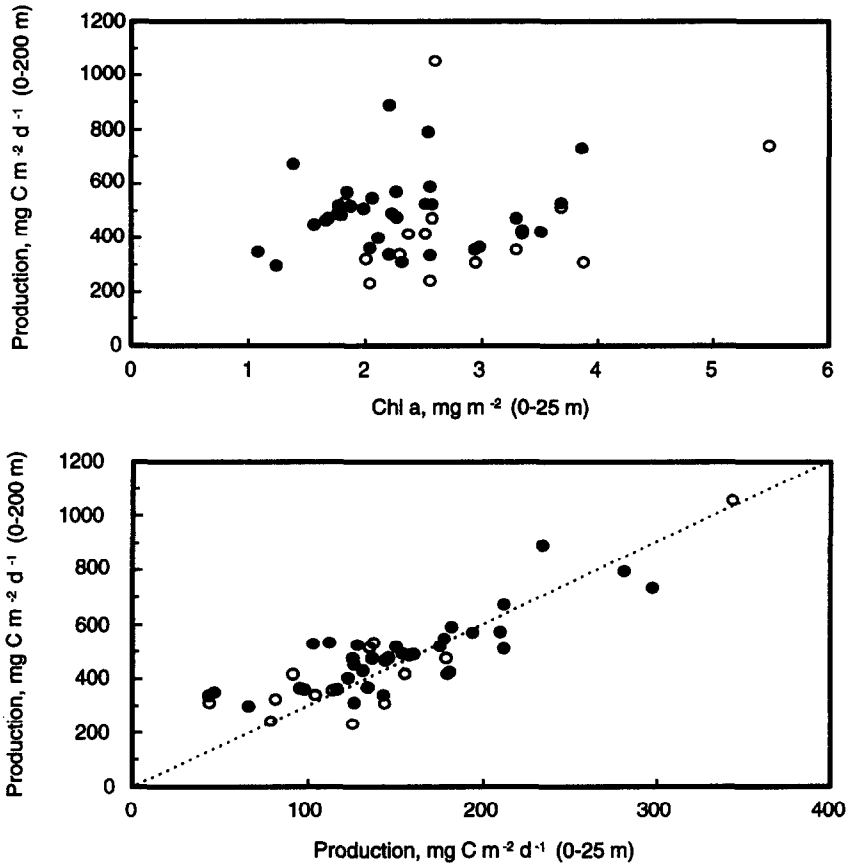


Fig. 4. Top: euphotic zone (0–200 m) depth-integrated inorganic carbon assimilation versus 0–25 m upper water column depth-integrated chlorophyll *a*; and bottom: euphotic zone (0–200 m) depth-integrated inorganic carbon assimilation versus 0–25 m upper water column depth-integrated inorganic carbon assimilation. Open circles represent simulated *in situ* (SIS) incubations and closed circles represent *in situ* (IS) incubations.

During HOT-15 (March 1990) three IS primary production incubations were performed according to standard procedures on three consecutive days. The variability of euphotic zone integrated carbon assimilation over this period was 9.2% ($\bar{x}$ = 488 mg C m^{-2} day^{-1}, s = 45, n = 3) and the variability of the averaged P^B in the upper 45 m depth of the water column was below 3% ($\bar{x}$ = 3.55 g C (g chl *a*)$^{-1}$ h^{-1}, s = 0.08, n = 3).

On all eight cruises in which SIS and IS incubations were performed simultaneously, the IS incubations yielded higher euphotic-zone depth integrated carbon assimilation in the L12 treatments. The differences ranged from 2% to > 50% ($\bar{x}$ = 23, s = 19) and appear to have been caused by an underestimation of carbon assimilation in the SIS incubation for samples collected at and below 45 m depth (Fig. 6). Because this underestimation was not seen for dark carbon assimilation treatments (Fig. 6) it is probable this difference is due to anomalies in the light field of the SIS incubators rather than poor control of the incubation temperatures. For this reason we have restricted our subsequent analyses to IS results when comparing seasonal or interannual trends.

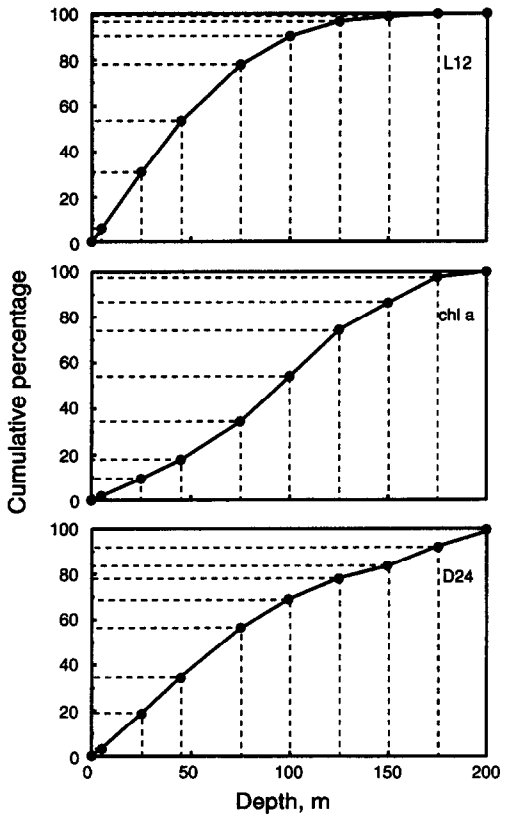


Fig. 5. Cumulative percentage of depth-integrated parameters relative to the full euphotic zone (0–200 m) depth-integrated value based on 30 *in situ* field experiments. Top: light inorganic carbon assimilation (L12); middle: chl *a*; bottom: dark inorganic carbon assimilation. The dark 24 h values were extrapolated from hourly values measured during dawn to dusk incubations.

The depth distribution of photosynthetic carbon assimilation (L12) presents two distinct patterns (Fig. 7). During the first 2 years of this study (1989–1990), an increase of total C assimilation at 100 m with respect to carbon assimilated at 75 m depth was observed in half of the IS incubations. This local maximum was absent from all IS incubations during the 1991–1992 observation period. On the other hand, even though the vertical distribution of photosynthetic carbon assimilation in the upper 75 m followed a similar trend between 1989–1990 and 1991–1992, observations during the second period displayed a significant increase in productivity (t-test; $P < 0.05$). When normalizing the carbon assimilation profiles (Fig. 7(B)) to the chl *a* depth distribution for each period (Fig. 7(A)), the difference in average production between the profiles disappears below 75 m but remains significant (t-test; $P \leqslant 0.05$) in the upper 45 m of the water column.

Although discrete water depth P^B versus irradiance (P^B vs I) experiments were not performed as part of the HOT program measurements, it is still possible to reconstruct a general P^B vs I relationship for the entire water column to compare general trends in the euphotic zone over both periods (Fig. 8). For the 1989–1990 data set the average surface photosynthesis per unit chl *a* measured at 5 m depth ($\bar{x} = 4.5$ g C (g chl *a*)$^{-1}$ h^{-1}, $s = 0.8$,

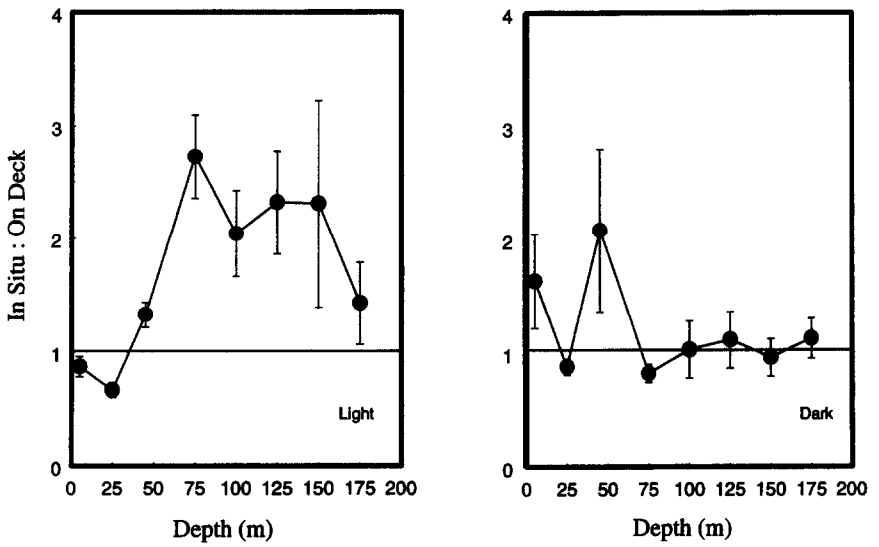


Fig. 6. Depth-dependent ratio between inorganic carbon assimilation values from *in situ* (IS) and simulated *in situ* (SIS) incubations obtained during simultaneous incubations. Left: light incubations. Right: dark incubations.

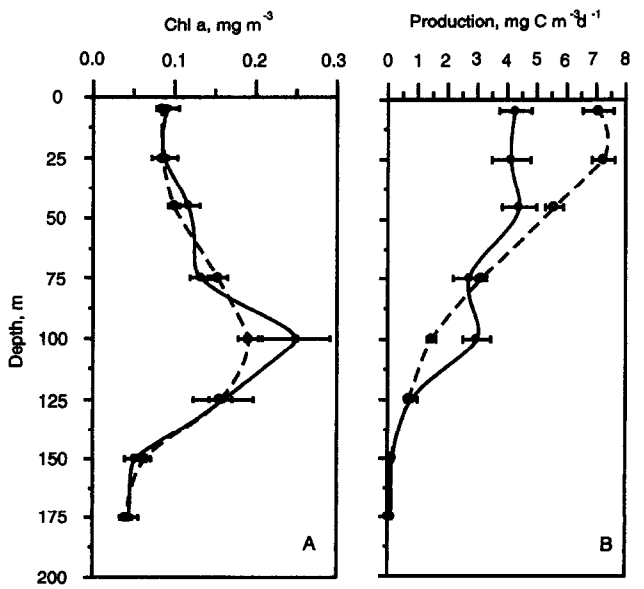


Fig. 7. Vertical distributions of (A) chlorophyll *a* and (B) photosynthetic carbon assimilation measured at Sta. ALOHA for the period October 1988–December 1992. Closed circles and solid lines represent average values for samples collected through January 1991. Open circles and dashed lines represent average values for samples collected after January 1991. Error bars indicate ± 1 standard error.

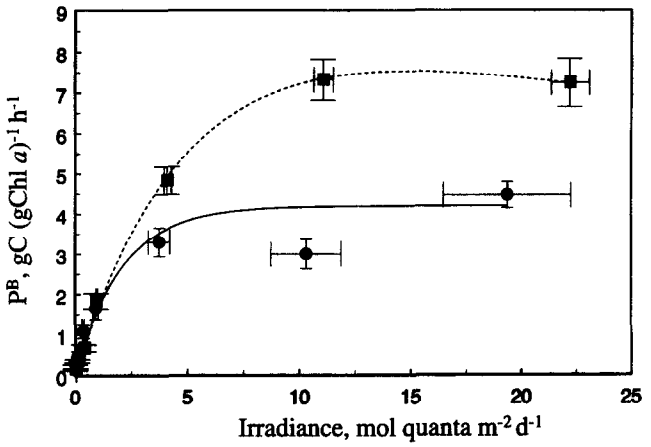


Fig. 8. Phytoplankton photosynthetic rate per unit chl a (P^B) versus irradiance for samples collected at Sta. ALOHA. Closed circles indicate samples collected prior to 1 January 1991. Closed squares represent values collected after 1 January 1991. Error bars indicate ± 1 standard error. Light levels correspond to 5, 25, 45, 75, 100, 125, 150, and 175 m depths. Lines correspond to the curve models generated by using parameters presented in Table 3.

$n = 7$) was not significantly different from the value found at 45 m ($\bar{x} = 3.3$ g C (g chl a)$^{-1}$ h^{-1}, $s = 0.9$, $n = 7$; $P \leqslant 0.05$). This was not the case for the second period (1991–1992) when surface values found at 5 and 25 m exceeded 7 g C (g chl a)$^{-1}$ h^{-1}.

To compare further both periods we described the P^B vs I curves by fitting an exponential model including photoinhibiting light levels as proposed by Platt *et al.* (1980):

$$P^B = P_M^B[1 - \exp(-\alpha I_z/P_M^B)]\exp(-\beta I_z/P_M^B)$$

where P^B is the production normalized to chl a, I_z is the irradiance at depth z, P_M^B is the potential maximum P^B in the absence of photoinhibition, α is the initial slope of the curve, and β characterizes the negative slope at photoinhibiting light levels. The parameters describing this function (Table 3) were obtained by least-squares estimation using the Levenberg–Marquardt algorithm (Marquardt, 1963).

Although both curves have a similar initial slope ($\alpha = 0.045$ and 0.043 g C (g chl a)$^{-1}$ h^{-1}

Table 3. Temporal variability of the mixed layer depth and estimated productivity versus irradiance parameters at Sta. ALOHA

Parameter	1989–1990	1991–1992
Depth fluctuation of mixed-layer between cruises ($\lvert m_{i+1} - m_i \rvert$)	34* (30)	16 (17)
α (g C (g chl a)$^{-1}$ h^{-1}) (μmol quanta m^{-2} s^{-1})$^{-1}$	0.045	0.043
β (g C (g chl a)$^{-1}$ h^{-1}) (μmol quanta m^{-2} s^{-1})$^{-1}$	0	0.003
P_M^B (g C (g chl a)$^{-1}$ h^{-1})	4.2	9.5
I_k (μmol quanta m^{-2} s^{-1})	92	219
Depth of I_k (m)	47	29

*Mean and, in parentheses, one standard deviation of the mean.

(μmol quanta m^{-2} s^{-1})$^{-1}$ for 1989–1990 and 1990–1991, respectively) they differ in the maximum potential rate of assimilation P_S^B and in the photoinhibition term β (Table 3).

Independently measured values that also display a strong shift between 1990 and 1991 are: (i) the mean 0–200 m integrated dark assimilation (Fig. 9, Table 1), and (ii) the 0–45 m integrated ATP concentration (Table 4). Both parameters display a consistent decrease between 1990 and 1991. Furthermore, the integrated dark assimilation becomes less variable over time.

DISCUSSION

Although there still exists some uncertainty over the precise meaning of phytoplankton carbon assimilation estimated by ^{14}C uptake experiments, our light incubation results (L12) can be interpreted as a lower bound on gross primary production (Williams, 1993). Furthermore, because the same experimental procedure was used for a majority of this study, the observed temporal changes in plankton processes are believed to be a manifestation of variability in the planktonic community.

Euphotic zone depth-integrated photosynthetic carbon assimilation rates estimated during the first four years of this study are consistently greater than 200 mg C m^{-2} day^{-1}. These results, when compared to the historical range of 50–200 mg C m^{-2} day^{-1} for estimates of phytoplankton carbon assimilation rates in the North Pacific subtropical gyre (Eppley *et al.*, 1973; Gundersen *et al.*, 1976; McGowan and Hayward, 1978; Bienfang and Szyper, 1981; Eppley, 1981; Hayward *et al.*, 1983), support the hypothesis that low carbon assimilation values of early reports are the result of sample contamination (Fitzwater *et al.*, 1982; Williams and Robertson, 1989). However, the large range of values obtained during our time-series study precludes the assumption that the old productivity estimates of the North Pacific gyre are in error. Because we made no attempts to duplicate the pre-1982 "contaminated" methods, we cannot be certain that the historical production estimates are in error.

During the PRPOOS study, P_S^B values approached 10 g C (g chl *a*)$^{-1}$ h^{-1} (Laws *et al.*, 1984, 1987). These values are within the range of light-saturated photosynthetic rate

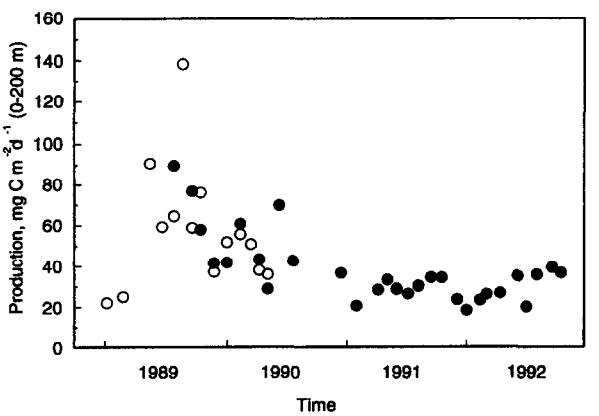


Fig. 9. Temporal variability of euphotic zone (0–200 m) depth-integrated 24 h dark inorganic carbon uptake. Open circles represent the results of simulated *in situ* (SIS) incubations and closed circles represent *in situ* (IS) incubation results.

Table 4. Temporal variability of mean annual chlorophyll a (chl a), adenosine 5'-triphosphate (ATP), particulate carbon (PC), light and dark carbon assimilation rates (L12 and D24), carbon assimilation per unit chl a (P^B), and phytoplankton growth rate (μ) in the upper 45 m of the euphotic zone at Sta. ALOHA

Parameter	Year			
	1989	1990	1991	1992
Chl *a* (mg m^{-2})	5.5 (1.7)*	4.3 (1.4)	3.8 (0.7)	4.2 (1.6)
ATP (mg m^{-2})	1.5 (0.4)	1.4 (0.2)	1.1 (0.2)	1.1 (0.2)
PC (g m^{-2})	1.2 (0.4)	1.1 (0.1)	1.2 (0.2)	1.2 (0.2)
L12† (mg C m^{-2} day^{-1})	209 (27)	155 (55)	303 (71)	312 (62)
D24‡ (mg C m^{-2} day^{-1})	26 (8)	16 (6)	10 (2)	11 (4)
P^B (g C (g chl *a*)$^{-1}$ h^{-1})	3.0(0.2)	3.2 (0.8)	6.7 (1.6)	6.8 (1.5)
μ§ (day^{-1})	0.32	0.30	0.49	0.53

*Mean and, in parentheses, 1 standard deviation from the mean.

†Twelve hour daylight incubation.

‡Twenty-four hour dark incubation, extrapolated from hourly rates measured during dawn to dusk incubations.

§Phytoplankton growth rate based on biomass conversion factors calculated for Sta. ALOHA (Campbell *et al.*, 1994).

observed during 1991–1992 (Fig. 10). Nevertheless P_S^B values observed in surface waters during the first 2 years of our study are closer to the pre-PRPOOS study range of values. Therefore, it is conceivable that the historical variations observed in carbon assimilation and P_S^B in the North Pacific subtropical gyre are the result of temporal habitat variability on a decadal scale (Venrick *et al.*, 1987; Polovina *et al.*, 1994; Latif and Barnett, 1994; Trenberth and Hurrell, 1995) rather than an artifact derived from improper methodology.

Primary production during this study varied in excess of 8-fold (from 127 mg C m^{-2} day^{-1} in November 1989 to 1055 mg C m^{-2} day^{-1} in August 1989) demonstrating that photosynthetic carbon assimilation (L12) is highly variable in these waters. Annual mean carbon assimilation also varies significantly ranging from 140 g C m^{-2} $year^{-1}$ in 1990 to 200 g C m^{-2} $year^{-1}$ in 1992, an interannual difference of greater than 40%. Because carbon fixation through photosynthesis is the main source of energy for the water column and benthic communities, this interannual variation may cause significant fluctuations in nutrient dynamics, carbon export, and mesopelagic and benthic processes.

Changes in the mean photosynthetic carbon assimilation depth profiles, observed when comparing *in situ* incubations performed during 1989–1990 with those performed during the 1991–1992 period (Fig. 7(B)), appear to be caused by two different processes. The difference in the local maximum found at 100 m depth (Fig. 7(B)) converges when normalized to chl *a* (Fig. 7(A)). P^B values estimated for samples collected at and below 75 m depth are not significantly different between both periods (*t*-test; $P \leqslant 0.1$). The similarity in P^B values below 75 m is also perceived when comparing the initial P^B versus I slope (α) calculated for both periods (Fig. 8, Table 3). This observation is consistent with a primary control by total phytoplankton biomass (i.e. chl *a*) near the DCML. As proposed in Letelier *et al.* (1993), an increase of chl *a* at the DCML appears to be correlated with an increase in phytoplankton

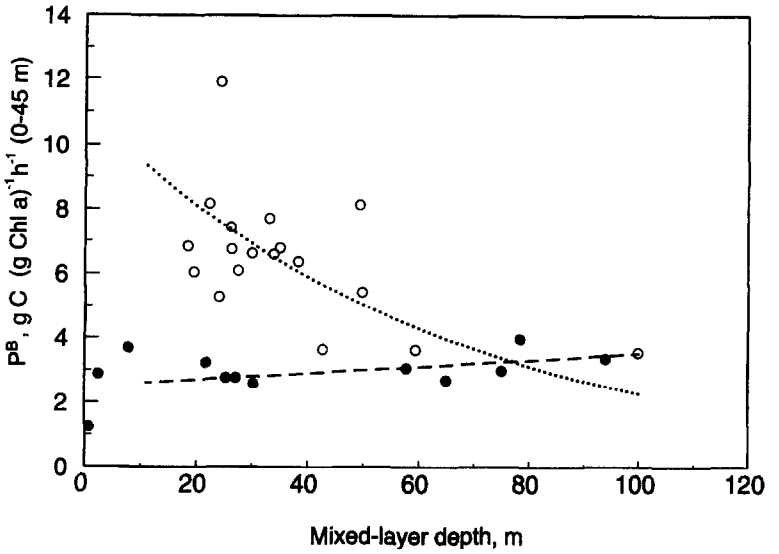


Fig. 10. Upper water column (0–45 m) photosynthetic carbon assimilation per unit chl *a* versus the cruise average mixed-layer depth. Closed circles represent values observed prior to 1 January 1991 and open circles represent samples collected after 1 January 1991. The curve fitting for the open circles data (dotted line) and the closed circles data (dashed lines) were obtained using a model II linear regression after converting the carbon assimilation efficiency to natural logarithmic values. The equations describing the regressions are: $y = 11.12e^{(-0.015x)}$, $n = 18$, $r = 0.63$, $P < 0.05$, and $y = 2.55e^{(+0.004x)}$, $n = 12$, $r = 0.42$, $P \leqslant 0.1$, respectively.

carbon biomass near the DCML. Biomass changes at the DCML could result from mixing events bringing nutrients into shallow waters or from an increase in the frequency of upward vertical displacements of the DCML with respect to isopycnals. The result in both cases would be an increase of nutrient availability within the depth region at which the DCML is located. Because instantaneous carbon assimilation is a function of phytoplankton biomass and specific growth rate, an increase in nutrient availability at a given isolume above the DCML would result in a higher carbon assimilation due to a transient increase in phytoplankton biomass. However, for an increase in algal growth rate to translate into an increase in algal biomass, a lag time between the increase in primary and secondary production must be invoked (Letelier *et al.*, 1993).

Vertical displacements of the DCML at Sta. ALOHA may be considered relative to isobaths or isopycnals. On short timescales (h) the depth displacements of the DCML follow the vertical oscillations of isopycnals (see Letelier *et al.*, 1993). Taylor *et al.* (1986) and Banse (1987) proposed that a decrease in irradiance reaching the DCML during periods of extensive cloud cover translates into an input of nutrients above the DCML as a result of a reduction in the steady-state rate of nutrient uptake. Vertical displacements of isopycnals at the base of the euphotic zone are also considered a potential mechanism for nutrient injection through the breaking of internal waves (McGowan and Hayward, 1978) or through their effect on the phytoplankton compensation depth (Lande and Yentsch, 1988). Based on the observed dynamics of isopycnals located at the base of the euphotic zone at Sta. ALOHA we have modeled the photon flux reaching an isopycnal surface located on average at 100 m depth but displaced vertically by an internal wave with near-inertial period

of 31 h and amplitude of 18 m. The daily integrated irradiance obtained through this analysis varies by a factor of three (Fig. 11). This variation rises to a factor of six if the effect due to cloud cover is included in the model and suggests high variability in photosynthetic rates, and probably nutrient uptake, in the lower layers of the DCML.

On longer timescales (weeks to months), the repeated stochastic displacement of the isopycnal depth at the base of the euphotic zone, after removing the near-inertial oscillation component of the vertical movement, results in the migration of the DCML across isopycnals (Letelier *et al.*, 1993), exposing the DCML to sporadic increases in nutrient concentrations. The physical data collected during the first 2 years in the euphotic zone of Sta. ALOHA indicate large and frequent stochastic vertical displacements of isopycnals at the base of the euphotic zone during 1989 and part of 1990 (Letelier *et al.*, 1993). The frequency of these vertical displacements decreases during 1990 and isopycnal depths between 100 and 200 m display a stronger seasonal cycle thereafter. The frequent vertical displacement of isopycnals during the first period of this study may have had the effect of increasing nutrient flux into the lower layers of the euphotic zone through the breaking of internal waves (McGowan and Hayward, 1978) or through the passive migration of the phytoplankton across isopycnals.

A second difference between 1989–1990 and 1991–1992 is found in the upper two optical depths of the water column (0–45 m). Although chl *a* concentrations do not vary significantly when comparing these two periods, P_S^B increases on average by 40% after 1990 (*t*-test; $P \leqslant 0.05$). The depth of the photosynthesis saturation light level (I_k), calculated from Fig. 8, is located at 45 m during the first 2 years, but shoals to 29 m during 1991–1992 (Table 3). These observations suggest that the changes in P_S^B are the result of phytoplankton

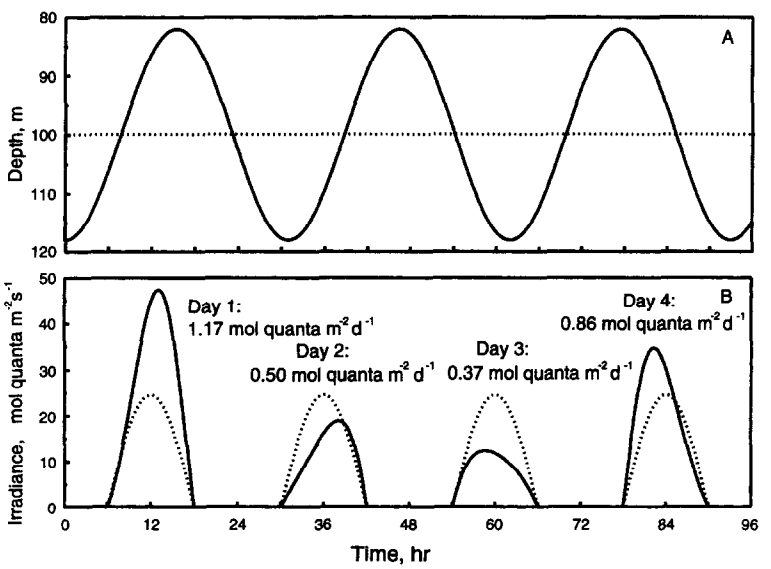


Fig. 11. Effect of near-inertial period internal waves on the light flux at the deep chlorophyll maximum layer (DCML). (A) Oscillation of the DCML depth (solid line) assuming an amplitude of 18 m and a near-inertial period of 31 h. (B) Calculated irradiance at the DCML (solid line) and at 100 m reference depth (dotted line).

photoadaptation due to the shoaling of the mixed-layer depth. However, a further analysis of the relationship between P^B in the upper 45 m and depth of the mixed-layer suggests that low values observed before 1991 are independent of the mixed-layer light regime during the first 2 years (Fig. 10).

Cruise average mixed-layer depths at Sta. ALOHA are more frequently found below 60 m and present higher variability during the first 2 years of this study (Fig. 10). Also, the fluctuation of the average mixed-layer depth between cruises (calculated as the absolute difference between consecutive cruises) decreases significantly during the 1991–1992 observation period (Table 3; Karl *et al.*, 1995).

The average mixed-layer depth for any given cruise is calculated from the data collected in CTD casts performed over a 2–3 day period. Because the variance of the pooled mixed-layer depths sampled is largely due to the variance between cruises (76%) rather than that within cruises (24%, based on 40 cruises and 576 CTD casts), the variability in the depth of the mixed-layer does not appear to be dominated by short timescale (h–days) fluctuations. Hence, the temporal trends of mixed-layer depth observed when using the cruise average value are probably not aliased by our sampling design. Furthermore, the concentrations of $(NO_3^- + NO_2^-)$ in the upper euphotic zone consistently decrease between 1991 and 1992 (Fig. 12). The stabilization of the mixed-layer depth and the temporal decrease in $(NO_3^- + NO_2^-)$ concentrations during 1991 and 1992 argue in favor of a decline in the input of nutrients from the nutricline as a result of physical processes. However, soluble reactive phosphorus concentrations averaged over the upper 45 m do not decrease with

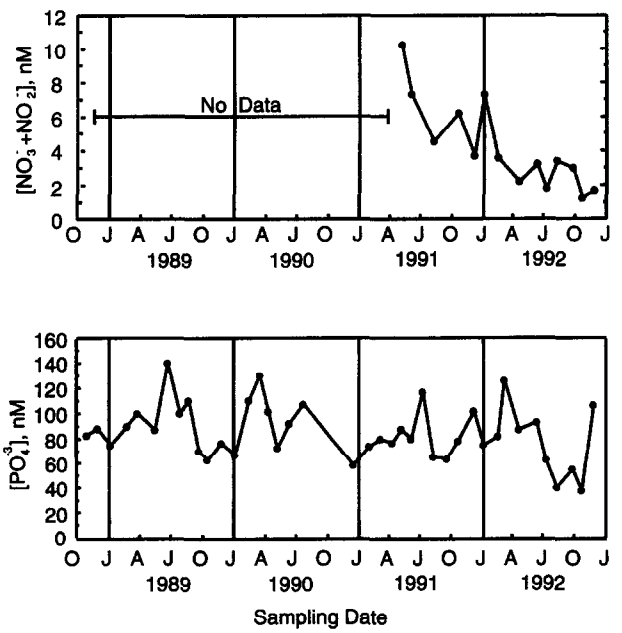


Fig. 12. Temporal variability of the average concentration of nutrients in the upper portion of the water column (0–45 m) at Sta. ALOHA. Top: low level $[NO_3^- + NO_2^-]$ measured by chemiluminescence. Bottom: soluble reactive phosphorus concentrations measured by standard colorimetric analyses.

(NO_3^- + NO_2^-) concentrations (Fig. 12) suggesting an uncoupling in sources, sinks or recycling rates between both nutrients.

High productivity events in subtropical oligotrophic gyres generally have been attributed to inputs of nutrients into the euphotic zone resulting from mixing events that penetrate the top of the nutricline (Platt and Harrison, 1985; DiTullio and Laws, 1991). For this reason the observed increases in autotrophic carbon assimilation and assimilation number during a period of stabilization of the mixed-layer depth may appear counterintuitive. We propose two non-exclusive hypotheses to explain the pattern observed at Sta. ALOHA.

Variability of nutrient input and phytoplankton growth rates

Our present understanding of algal photosynthesis and growth in the ocean is mainly derived from laboratory batch and nutrient-limited continuous culture experiments. Cullen *et al.* (1992) suggest that results from the study of nutrient stress using these two distinct laboratory culture methods are not interchangeable. Because in batch cultures the rate of supply of nutrients is nil, the proliferation of microalgae depletes a limiting nutrient resulting in unbalanced growth (*sensu* Cohen and Barner, 1954). Balanced growth, as defined by Campbell (1957), occurs when all cellular constituents increase by the same factor during a given time interval. When a nutrient becomes depleted, cellular components dependent upon the limiting nutrient start to decrease in concentration relative to other cellular constituents. Under these conditions photosynthetic carbon assimilation per unit volume may be high due to a large standing crop even though both the relative growth rate of phytoplankton (μ/μ_{max}) and P_S^B decrease as a result of nutritional stress (Glover, 1980; Welschmeyer and Lorenzen, 1981).

In a nutrient-limited continuous culture the rate of supply of the limiting nutrient is always positive. The ratio between the cellular constituents that require the limiting nutrient and storage products that do not require this nutrient vary as a function of growth rate (Bannister and Laws, 1980). Hence, the ratios between cellular elements may be used as an index of nutrient limitation. However, the measurement of these relations in nature also is affected by the presence of non-algal sources (McCarthy, 1980).

Under nutrient-limited continuous culture conditions the crop of phytoplankton increases until production equals the rate of supply of the limiting nutrient and balanced growth is achieved. The growth rate (μ) is also balanced by changes in the cellular content of C:chl *a* (Bannister and Laws, 1980) and results presented by Eppley and Renger (1974), Hertzig and Falkowski (1989), and Sakshaug *et al.* (1989) suggest that P_S^B may remain high and independent of relative growth rate (Cullen, 1990). However, reports from other nutrient-limited continuous culture experiments appear to contradict the above results by showing a strong correlation between P_S^B and μ/μ_{max} (Thomas and Dodson, 1972; Osborne and Gieder, 1986; Chalup and Laws, 1990) suggesting interspecific variations.

Based on the observation that P_S^B can remain high in nutrient-limited continuous cultures even when the relative growth rate is low as a result of severe nutrient limitation, Cullen *et al.* (1992) concluded that the assimilation number is an unreliable predictor of nutrient stress. Nevertheless, if we define the carrying capacity of a given system as "the rate of supply of some limiting form of nutrient or energy divided by the per individual requirement for maintenance" (Jumars, 1993), our present knowledge of phytoplankton physiology suggests that the assimilation number decreases as a reflection of the nutrient stress and unbalanced growth when the phytoplankton standing crop surpasses the carrying capacity

of the environment (i.e. nutrient depletion in a batch culture). High P_S^B probably is found only when the phytoplankton concentration does not exceed the carrying capacity of the system.

Phytoplankton growth in nature approaches the batch culture analogue only when remineralization of the limiting nutrient is minor or absent. However, in the euphotic zone of oligotrophic gyres most (> 80–90%) of the autotrophic production is supported by recycled nutrients (Eppley and Peterson, 1979; Karl *et al.*, 1995). Under these conditions, a more realistic growth model would be that obtained from nutrient-limited continuous cultures. For stratified conditions with a stable mixed-layer, the variability in the input rate of nutrients into the upper euphotic zone would be dependent primarily on eddy-diffusive processes. If these conditions are maintained, the phytoplankton standing crop will vary to levels where net growth rate equals the rate of regeneration plus the "new" input rate of the limiting nutrient. Under this scenario we should expect to observe a decrease in the production exported from the euphotic zone.

Nevertheless, unbalanced growth is possible if, for example, the recycling or resupply rates of the major nutrients are uncoupled with respect to each other or if there are temporal variations in the input of nutrients into the euphotic zone. Therefore, the conceptual description of P_S^B as it relates to phytoplankton in the North Pacific subtropical gyre may not be rigorously described by either batch or nutrient-limited continuous cultures. Observed temporal changes in P_S^B may reflect changes in the variability rather than in the absolute magnitude of nutrient input rates. In other words, while ecosystems with different carrying capacities may have the same assimilation number, fluctuations in the carrying capacity within a given ecosystem will probably induce changes in P_S^B.

Based on the above analysis we postulate that a decrease in the variability of nutrient fluxes into the upper euphotic zone may explain why, during 1991–1992, P_S^B was high and varied with the depth of the mixed-layer, even though nutrient supply as a consequence of deep mixing events may have decreased. However, the variability in nutrient fluxes during the first 2 year period does not explain the constancy of low P_S^B values observed, unless the probability of sampling a mixing event and the period of enhanced nutrient availability is small compared to that of sampling a phytoplankton community under nutrient stress.

From reported results on the evolution of nutrient concentration in the euphotic zone following a mixing event, the time required for nutrient concentrations in the upper euphotic zone to return to pre-mixing event levels does not appear to exceed 72 h (Eppley and Renger, 1988; Marra *et al.*, 1990; DiTullio and Laws, 1991). As a result, deep mixing events tend to be followed by periods of an increased biomass:nutrient ratio in the upper euphotic zone. Observations made by DiTullio and Laws (1991) suggest that, following a storm-induced deep mixing event, P_S^B values in the upper euphotic zone decreases below pre-storm values. Given the present HOT program sampling scheme, it is possible to have missed enhanced nutrient concentration events during a 2 year period, depending on the frequency of deep mixing events. However, unless we are able to assess the time it takes for the ecosystem to return to a steady state following a deep mixing event, it is not possible to explain fully the apparently constant low P_S^B observed during 1989–1990.

Enhancement of nitrogen fixation

Less well characterized than the effect of deep mixing events in the planktonic community, the increases in biomass of pelagic nitrogen fixing cyanobacteria after

extended periods of calm weather also result in the enhancement of primary production (Steven and Glombitza, 1972; Devassy *et al.*, 1978; Martinez *et al.*, 1983). The largest value in integrated carbon assimilation recorded at Sta. ALOHA over the first 4 years of the HOT program was measured in August 1989 after 2 weeks of calm weather. Although nitrogen-fixing cyanobacteria were not observed at the time when on-deck primary productivity incubations were performed, a large bloom of *Trichodesmium* spp. was conspicuous in the area during the following days (Karl *et al.*, 1992; Letelier and Karl, in press).

In a well-stratified water column, phytoplankton displaying buoyancy regulation mechanisms such as *Trichodesmium* spp. (Walsby, 1978) may play an important role by bringing nutrients up from below the euphotic zone (Fogg, 1982; Konopka, 1984; Karl *et al.*, 1992; Villareal *et al.*, 1993). If the scenario of a long-term stratified water column without input of nutrients from below the euphotic zone due to mixing events describes the situation observed in the euphotic zone of Sta. ALOHA during 1991–1992, and if the nutrient fluxes into the euphotic zone due to plankton vertical migration are on average lower than nutrient input due to mixing events, we should expect to see a decrease in biomass indicators in the upper 45 m depth. Chorophyll *a* is routinely used as an estimator of algal biomass. However, the variability in annual average chl *a* concentration observed in the upper 45 m of the water column between 1989 and 1992 (Table 4) may be, to some extent, the result of photo-adaptative processes driven by variations in the mixed-layer depth (also see Winn *et al.*, 1995).

Adenosine 5′-triphosphate (ATP) has been commonly used as an estimator of total microbial biomass in natural environments (Karl, 1980; Karl *et al.*, 1990; Karl and Lukas, 1996). However, the cellular C:ATP ratio can vary considerably, especially under phosphorus limitation (Karl, 1980), hence the interpretation of the reduction in ATP concentration in the upper 45 m depth during 1991 and 1992 with respect to 1989 and 1990 (Table 4) is not straightforward.

The only studies on temporal taxonomic changes at Sta. ALOHA during 1989–1992 were directed toward the phytoplankton assemblage. The analysis of algal pigment distribution by reverse-phase high performance liquid chromatography does not reveal a change in the phytoplankton community structure between 1990 and 1991 (Letelier *et al.*, 1993). Nevertheless, the mean abundance in the upper water column of the marine diazotroph *Trichodesmium* spp., quantified by microscopy, increased significantly during 1991–1992 (Letelier and Karl, in press) indicating that some degree of change in the composition of the pelagic ecosystem, not detectable through algal pigment analysis, may have taken place.

As suggested by Karl *et al.* (1995), phosphorus limitation in the euphotic zone also could explain the decrease in ATP concentration observed at Sta. ALOHA. The stability of the water column during 1991–1992 may have reduced the flux of nutrients from the nutricline and enhanced nitrogen fixation by diazotrophs, shifting the ecosystem toward phosphorus limitation. A decrease in the particulate carbon (PC) to particulate phosphorus (PP) and particulate nitrogen (PN) to PP ratios, consistent with the decrease in ATP, is observed during 1991 and 1992 (Karl *et al.*, 1995; Letelier and Karl, in press). Although, under this scenario, the reduction in ATP does not necessarily reflect a decrease in carbon biomass, it indicates a decrease in mixing events and the stabilization of nutrient fluxes.

An ecosystem shift between nitrogen and phosphorus limitation (Karl *et al.*, 1995) also could explain the increase in P_S^B. In 1986 Smith *et al.* (1986) suggested that the North Pacific subtropical gyre was nitrogen (N) limited due to the long turnover time of dissolved organic nitrogen relative to that of dissolved organic phosphorus in the euphotic zone. If an increase

in available reduced N, relative to phosphorus (P), took place in the euphotic zone during 1991–1992 as a result of increased nitrogen fixation by *Trichodesmium* spp. (Letelier and Karl, in press) and stratification, phosphorus may have become the limiting nutrient. Under this scenario it is possible to interpret the increase of P^B in the upper euphotic zone as a response to the shift in nutrient limitation and a concomitant increase in recycling rate of the limiting nutrient.

A decrease in biomass and an increase in recycling rates should be reflected by an increase in phytoplankton growth rates and a decrease in exported production. Although P_S^B increases during 1991–1992, a straightforward interpretation of P_S^B in terms of nutrient limitation and growth rate of oceanic planktonic assemblages is not possible because chl *a* is a poor surrogate for algal carbon biomass. Variations in P_S^B do not necessarily reflect changes in phytoplankton growth rates unless the phytoplankton cellular carbon-to-chl *a* ratio (C:chl *a*) remains constant. However, C:chl *a* can vary as a result of changes in nutrient status (Glover, 1980) or light regime (Kolber *et al.*, 1988; Nelson *et al.*, 1993). At this time, the best indication that phytoplankton growth rate increased during 1991–1992 comes from the observation that autotrophic carbon assimilation increased without a concomitant increase in ATP. However, as we stated above, cellular C:ATP ratios may vary depending in nutrient availability. Furthermore, the contribution of phytoplankton to the total microbial ATP also may vary. Campbell *et al.* (1994) used flow cytometry analyses to estimate the biovolume and carbon content of phytoplankton. Based on their results and our primary production measurements, we have estimated that phytoplankton growth rates increased by approximately 50% during 1991–1992 (Table 4).

The absolute magnitude of growth rates calculated based on biovolume conversion appear to be low when compared to growth rates based on C:chl *a* or C:ATP conversion factors. If we assume a constant annual mean C:chl *a* ratio for phytoplankton of 45:1 (w:w, Christian and Karl, 1994) over this 4 year period (1989–1992) the estimated growth rates using depth averaged 0–45 m carbon assimilation rate (L12) and chl *a* (Table 4) are 0.84, 0.80, 1.77, 1.66 day^{-1} for 1989, 1990, 1991, and 1992, respectively. Similar values of 0.79, 0.63, 1.57, and 1.62 day^{-1} for each consecutive year are obtained if we use a constant conversion factor of 250×0.7 (cellular ratio $\times$ fraction of living C contributed by phytoplankton; Karl, 1980 and Laws *et al.*, 1984) to calculate carbon phytoplankton based on ATP. Even though the assumption of the constancy in the C conversion factors is probably not valid, all three estimates indicate a significant increase in phytoplankton growth rates between 1989–1990 and 1991–1992. For this reason we suggest that, although the absolute magnitude of phytoplankton growth rate may be in error, the observed relative increase is real.

A decrease of 30% in the mean downward flux of PC measured at 150 m depth during 1991–1992, relative to fluxes observed during 1989–1990 (Karl *et al.*, 1996) suggests that exported production decreased significantly while autotrophic carbon assimilation increased. Hence, we must invoke an increase in microbial community respiration and/or production of dissolved organic matter in the euphotic zone to balance the carbon budget. While an increase in microbial respiration is consistent with our nutrient recycling hypothesis, the increase in DOM would suggest that carbon is exported by diffusion from the euphotic zone (Toggweiler, 1989). Regardless of the mechanism by which carbon is released from the particulate matter, a change in the community structure and the main carbon pathways must have occurred.

It is not possible at present to identify which of the two hypotheses describes best the

causes of an increase in P^B in the upper 45 m of the water column of Sta. ALOHA during 1991–1992. Both causes, the unbalanced versus balanced phytoplankton growth and the decrease in turnover time of a limiting nutrient due to a shift from nitrogen to phosphorus limitation, are consistent with the field data. They also are not mutually exclusive, and both are effects produced by a reduction in the frequency of deep mixing events.

In conclusion, our observations indicate that the North Pacific subtropical gyre experiences significant interannual variations in autotrophic carbon assimilation rates. These variations appear to result from changes in the stability of the upper water column and are not necessarily related to long term changes in chl *a* concentrations. Paradoxically, our analyses suggest that in the North Pacific subtropical gyre, periods of low new production occur during years with high autotrophic production.

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