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Photosynthetic response of subtropical phytoplankton populations to deep water nutrient enrichment

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Running head: Phytoplankton response to deep water nutrients

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ABSTRACT

This work describes the response of naturally occurring subtropical phytoplankton to deep water nutrient enrichment. Focusing on vertical and temporal variations, the effects on photosynthetic rates and P/B ratios (mg C·mg chlorophyll $\underline{a}^{-1}\cdot h^{-1}$) were examined over the entire photic zone in six sets of trials.

The net difference in depth-integrated carbon fixation rates between enriched and reference profiles ranged from 1.23 to 5.47 mg $C\cdot m^{-2}\cdot h^{-1}$ and represents increases of 9.3 - 149% over natural levels. The degree of biostimulation was depth-dependent and related to the availability of light. The greatest stimulations occurred in the upper, light-saturated layer, the lower boundary (about 40 m) of which is defined by the half-saturation constant ($K_L \cong 168$ μEinsteins$\cdot m^{-2}\cdot s^{-1}$) for light, calculated empirically from this study. Below depths defined by K_L values, there appeared little evidence of stimulation effect, despite low ambient nutrient levels and P/B ratios indicative of strong nutrient limitation. These findings on the degree and vertical extent of deep water biostimulation potential in natural populations have implications to the effects of OTEC systems on the surrounding environment.

INTRODUCTION

In subtropical regions, a warm, relatively deep mixed layer is underlain by a strong thermocline which extends from about 70 to 300 m. The absence of pronounced seasonal climatic variation gives permanence to this thermal stratification, which isolates the nutrient-depleted surface waters from the waters of high nutrient concentration below. This isolation accounts, in part, for the oligotrophic character of the ecosystem in the mixed layer. Within such systems the availability of inorganic nutrients, principally nitrogen and phosphorus, controls phytoplankton standing stocks and production (8,9,17,24,25,26,28,29). Within the photic zone, the availability of light also controls the photosynthetic capability of phytoplankton; and with increasing depth, the relative availability of light and nutrients creates a transition from a surface, nutrient-limited layer to a deeper, light-limited layer.

The pronounced temperature differential between the warm surface layer in these regions and the cold, deep waters provides the potential to generate electricity by ocean thermal energy conversion (OTEC). This is accomplished by the alternate evaporation of liquid ammonia via contact, through heat exchangers, with warm surface water, and condensation by contact with cold, deep (about 600 m) water. This process will result in the introduction of large quantitites of nutrient-rich deep water into the nutrient-poor surface layer of these subtropical systems. Deep water redistribution occurs naturally in the upwelling regions along some continental coasts, and the resultant biostimulation and increased

productivity support fisheries. The OTEC situation differs somewhat from natural upwelling, being a point source of rapid deep-water injection into biological communities adapted to the characteristics of subtropical surface waters. Natural upwellings are diffuse, and much slower (23). Despite these differences, the introduction of deep water to the surface is likely to cause some stimulation of phytoplankton productivity in the affected areas.

The effects of this nutrient introduction to the photic zone must be examined in the context of the transition from nutrient-limitation to light-limitation of phytoplankton activity. The rates and magnitude of biostimulation response by subtropical populations are largely undetermined (23). Assessment of this response is complicated by the downstream dilution kinetics between the surface and deep waters; the possibility of time lags in the biostimulation response, or "water conditioning" (1,2,3); and the unknown preconditioning history of the phytoplankton populations sampled for trials.

This study examined the response of naturally occurring subtropical phytoplankton to deep water enrichment. In these enrichment experiments, the effects on photosynthetic carbon-fixation rates and production-to-biomass (P/B) ratios were investigated over the entire photic zone (about 150 m). The responses of enriched populations were compared against untreated reference samples in seven sets of trials on five separate cruises. The trials focused primarily on temporal and vertical variations in biostimulation effects. These studies were performed within the context of extensive survey efforts (5,16) describing the physico-

chemical, nutrient and phytoplankton characteristics of the subject locales.

METHODS

The nutrient enrichment experiments were performed at sea between October 1979 and October 1980 using natural, heterogeneous phytoplankton populations. The seven experiments, designated NE-1 to NE-7, were performed in August 1979 (NE-1), October 1979 (NE-2 and -3), December 1979 (NE-4), May 1980 (NE-5 and -6), and August 1980 (NE-7). Trials NE-1 through -4 took place off Ke-ahole Point, Hawaii (19° 55' N, 156°, 10' W); trials NE-5 through -7 took place off Kahe Point, Oahu (two closely spaced stations at approximately 21° 21' N, 158° 14' W). Water samples were collected from nine target depths (2, 10, 30, 50, 70, 90, 110, 130 and 150 m) using 10-liter Niskin samplers. Subsamples were prescreened through 202-μm mesh Nitex to remove larger zooplankton.

For each depth in the photic zone, two sets of subsamples were prepared--one to assess the reference (i.e., unenriched) level of carbon fixation, and the other enriched with deep water for the NE trials; the percent deep water additions ranged from 3.3 to 16.3%. The deep water used in these trials was collected within 6 h prior to the injection and stored in clean plastic bottles in a refrigerator. This water, taken from depths near 600 m, was characterized by temperatures of 4-6°C, salinities between 34.3 and 34.5°/$_{oo}$, and approximate concentrations of nitrate, phosphate, and silicate of 40, 3, and 60-90 μM, respectively.

Carbon fixation rates were determined by ^{14}C-uptake methodology (19) as described by Strickland and Parsons (21). Triplicate samples were taken for both the reference and the NE trials at each depth. Samples were placed in glass BOD bottles andinjected with about 40 µCi $NaH^{14}CO_3$ in basic (ph = 9) salt (5%) solution. The deepwater additions were made by withdrawing a known volume of water from the sample bottles with an automatic volumetric pipette, then injecting the same volume of deep water into the bottle. Reference and enrichment trials for NE-1 through -4 involved in situ incubations; reference and enrichment trials for NE-5 through -7 used on-deck incubation in an apparatus designed to simulate both the light intensity (quantum flux) and spectral distribution at the subject depths (4). All samples were prepared and set to incubate shortly before dawn to avoid exposure of samples from the lower photic zone to surface light intensities (9,11,20). Incubations took place from dawn to late afternoon, incubation periods ranged from 10.0 to 11.5 h. Upon completion, DCMU was injected as described in (5), and samples were immediately filtered through Gelman GN-6 filters (0.45-µm pore size. Filters were place into vials containing 0.5 ml of 10% HCl to drive off residual ^{14}C in solution (14) and later counted on a Searle Delta 300 liquid scintillation counter, calibrated to convert cpm to dpm. Standardization of the total ^{14}C activity used was performed for each cruise by a series of five serial dilutions; aliquots of each dilution were added to vials containing phenethylamine (12) and subsequently admixed with cocktail. Linear regression analysis of dpm versus dilution factor was performed to give the working activity used; correlation coefficients from these regressions were typically r = 0.99.

Samples for chlorophyll a analysis were taken from the same Niskin bottles as samples for ^{14}C experiments, and were used to calculate P/B ratios (mg C·mg chlorophyll $a^{-1}.h^{-1}$). Chlorophyll a (chl a) was determined fluorometrically, according to the procedures for extracted samples (21). Typically coefficients of variation ($100 \cdot SD/\bar{x}$) for the analysis of chlorophyll a were about 10%.

Scalar (nondirectional) irradiance was measured to give both incident levels and vertical profiles using Model QSR 250 (integrating) and QSP (profiling) quantum scalar irradiance meters (Biospherical Instruments, Inc.). Light measurements for calibrations of the on-deck incubator were made with a QSL100 laboratory meter; all three units are designed to be sensitive to photosynthetically active radiation in the 400-700 nm region.

RESULTS

Vertical profiles of carbon fixation rates for the reference and NE trials 1-6 are given in Fig. 1. During these incubations, total (i.e., time-integrated) irradiance ranged from 9.4 to 26.2 x 10^{20} quanta·cm^{-2} for incubation periods of about 11 h. The amount of nitrate and phosphate added in the various trials was calculated based upon deepwater nutrient concentrations and the volume of additions; the resultant nitrate additions ranged from 1.20 to 5.94 µM, and the phosphate additions ranged from 0.09 to 0.45 µM (Table 1). The vertical distribution of the carbon fixation in the reference samples (Fig. 1) shows considerable temporal variation in the carbon fixation rates of these natural assemblages; this variability is addressed in detail in Bienfang and Szyper (5). The lower extreme of

natural productivity was encountered in connection with the NE-4 trial. Carbon fixation at most depths was barely detectable; depth-integrated primary production was only 0.72 mg $C \cdot m^{-2} \cdot h^{-1}$; and the enriched samples showed no appreciable stimulation. We are aware of no experimental or analytical artifact which might have produced this result. The observation of negligible photosynthetic activity on this occasion represents an extreme case of natural variability, and this condition was not alleviated by the short-term availability of deep water inorganic substrates. We present the profile data (Figs. 1 and 2) only to report this instance of extremely low photoautotrophic activity. Because of the uncertainty in defining a well established baseline condition for this case, we do not include it in the subsequent discussion of biostimulation results. In the remaining sets, depth-integrated production values (Table 1) show a range of 2.47 to 17.21 mg $C \cdot m^{-2} \cdot h^{-1}$, a sevenfold variation in natural productivity rates. Also presented in the table is information describing the percentage stimulation, surface irradiance levels, and enrichment details for each trial.

The enriched samples showed carbon fixation rates slightly higher than reference values (Fig. 1); often the standard deviations about the means of reference and enriched samples overlap. Depth-integrated carbon fixation rates (Table 1) for the five enrichment experiments were in all cases higher than those of the reference samples, and showed values ranging from 2.87 to 18.81 mg $C \cdot m^{-2} \cdot h^{-1}$. The mean integrated carbon fixation for the five enriched profiles is significantly greater ($P < 0.05$, t-test) than the mean for the five reference samples. The net difference between enriched and reference profiles ranged from 1.23 to 5.47 mg $C \cdot m^{-2} \cdot h^{-1}$ and on a percentage basis represents stimulations of primary production

ranging from 9.3 to 149%. Correlation analyses showed that no single parameter (e.g., percent deepwater addition, incident irradiance levels, or reference levels of carbon fixation rates) accounted for a significant part of the stimulation effect.

Vertical profiles of P/B ratios (mg C·mg chl $\underline{a}^{-1}\cdot h^{-1}$) for the reference (o) and enriched (Δ) samples from the six trials are shown in Fig. 2. The reference P/B ratios ranged from 0.11 to 8.35 mg C·mg chl $\underline{a}^{-1}\cdot h^{-1}$); nearly all were less than 3.0 and indicative of strong nutrient limitation (7,9,13,15,25,27). The decline of P/B values with depth reflects the diminishing light availability for photosynthesis. As was ture in the carbon fixation profiles, enriched samples (Δ) generally showed higher P/B values than the reference samples (Fig. 2). The increases in P/B values in enriched samples were generally greatest within the upper 80 m.

The P/B ratios for samples constituting the reference profiles (o) followed a hyperbolic relation to prevailing light levels (Fig. 3). The plots in Fig. 3 show that the estimated maximum P/B varied considerably among these trials, but the calculated half-saturation constant (K_L) was remarkably consistent (Table 2). The depth at which the K_L occurred varied, dependent on the incident irradiance. The K_L parameter is taken here as a functional term marking the transition between tne nutrient-limited and light-limited layers. Figure 3 also shows that the P/B values for the enriched samples (Δ) exceeded the reference values primarily at higher light levels, i.e. light levels greater than the calculated K_L values. This indicates that the biostimulation effects of

deep water nutrient enrichment were dependent on the availability of light above a minimum level (K_L), and this light level (K_L) is considerably higher than that level which defines the floor of the photic zone. The average half-saturation constant from the various reference trials (Table 2) was $3.86 \pm 1.19 \times 10^{20}$ quanta$\cdot$cm^{-2} for incubation periods averaging 11 h; this represents an average irradiance level of 162 μEinsteins$\cdot$m$^{-2}\cdot$s^{-1}.

In the aforementioned experiments, the incubation of samples enriched with deep water was begun immediately. To examine for effects of lag in stimulation, a seventh trial was conducted to assess the responses of phytoplankton samples injected with nutrients, but held for 24 hours before determination of carbon fixation rates. Stimulation effects in such samples were compared with the results of a zero lag-time experiment (similar to NE-1 through -6) performed on the day samples were taken. Only the 10 and 70 m depths were sampled for this trial. On neither day of the experiment did enriched samples show significantly different rates from the reference samples. On the second day, carbon fixation rates in both reference and enriched samples from the two depths were considerably higher than the on the first day (Table 3). Isolation of the lag phenomenon is further complicated because the two days differed markedly in incident irradiance levels (cloudy and sunny days, respectively). Because the comparisons fail to reveal a striking increase in stimulation effect after 24 hours of pre-incubation, it is likely that the previous six 1-day trials did not seriously underestimate the stimulation response because of lag effects.

DISCUSSION

Deep water nutrient enrichments were observed to produce immediate biostimulation of phytoplankton activity in this subtropical environment. The degree of this response was dependent on the light availability with depth and probably the preconditioning history of the populations sampled. Throughout the photic zone, the enhancement of primary energy fixation brought about by the deep water additions ranged from 1.23 to 5.47 mg $C \cdot m^{-2} \cdot h^{-1}$ and represents increases of 9.3 to 149% over natural levels.

Within the upper, light-saturated layer the short-term increases in carbon fixation represent alleviation of the strongly nutrient-limited conditions indicated by the low P/B ratios (Fig. 2). It is likely that all the additional nutrients supplied were not exhausted over the 11-h incubations; this together with the inherent response capabilities of these populations to deep water nutrients may have influenced the degree of biostimulation observed within the experimental framework. At depths where the ambient irradiance was below the half-saturation level (K_L) for the reference trials, the P/B ratios of enriched samples show little or no difference from those of the reference samples.

The lack of biostimulation in the deepest samples (< 100 m) is related to the fact that ambient nutrient concentrations in the water column begin to increase as depths of 90 m are exceeded, making the small experimental additions superfluous. The elevated nutrient levels in this deeper layer reflect nutrient supply rates in excess of phyto-

plankton requirements, which are restricted primarily by the light availability. There is a range of depths, however, in which the ambient nutrients are low, and yet deep water nutrient enrichments did not stimulate photosynthesis. The depths are below those of the K_L light levels (Table 2), yet well above the depths where ambient nutrients begin to increase.

Thus there appears to be a transition zone in the water column, with its upper limit ranging between 24 and 61 m depth, and its lower limit around 90 m. In this zone, the low ambient nutrient levels indicate that phytoplankton uptake is occurring in parallel with the rates of nutrient supply. Considered together wtih the low P/B ratios, the low ambient nutrient concentrations suggest that photosynthesis in this layer is limited (i.e., constrained), at least in part, by nutrient availability. The lack of response to deep water nutrient additions suggests that light availability also influences the photosynthetic activity in this zone. The reduced photic field in this region may well have influenced the rate of response to the added nutrients and thus the ability to observe stimulated photosynthetic activity within the time frame of these experiments. If, indeed, the reduced light regime in this region delays the inception of stimulated photosynthesis, the net response to deep water nutrient additions would be extended in both time and space. The dynamics of this situation are not generally appreciated in modelling efforts, but must be addressed for the total photoautotrophic response to be accurately evaluated. It is abundantly clear that a much improved understanding of the phytoplankton dynamics in this region is essential for assessment of the vertical extent of the biostimulation effect, and thus the total photic zone response.

The average half-saturation intensity (162 Einsteins$\cdot m^{-2} \cdot s^{-1}$) was obtained from experiments performed with water samples from five cruises to three different stations in oligotrophic waters off the Hawaiian islands. Light measurements were made with instruments capable of sensing scalar (spherical-field) irradiance, which is most appropriate for studies of suspended phytoplankton (10,30). Our estimate is higher than those obtained by Bienfang and Gundersen (4), and apparently higher than values that can be calculated from the energy flux data given by Platt and Jassby (18). These studies differe from the present work in thatlight measurements were made with instruments (e.g., cosine collectors) sensitive to only a portion of the spherical light field, in other aspects of experimental design, and in some cases the type of environment sampled.

The lower regions of the transition zone are a critical area in the understanding of oceanic phytoplankton dynamics. Despite the demonstrated indications of light limitation at these depths, the plant cells appear to use the low light levels quite efficiently, attaining more than 60% of the theoretical maximum quantum yield in carbon fixation (22) in chlorophyll maximum layers of subtropical waters southeast of Hawaii. A maximum in absolute carbon fixation rate was found at 70 m by Bienfang and Gundersen (4) at an oceanic station off Oahu. While there is little or no indication of photosynthetic maxima in our present data (Figs. 1 and 2), the mean (±SD) depth of the chlorophyll maximum layer off Ke-ahole Point, Hawaii, was 85 ± 9 m (5), which corresponds approximately to the bottom of the transition zone under discussion here. Ambient nutrient concentrations were always low at these chlorophyll maxima, indicating active metabolism by the phytoplankton.

It should be noted that, for the five nutrient enrichment experiments showing positive stimulation of depth-integrated carbon fixation, there was no significant correlation of the relative stimulation effect with time-integrated irradiance during the incubation period. This is in contrast to the controlling influence of light within each individual experiment, as discussed above. For any given experimental date, the phytoplankton community at a site has a common history of recent preconditioning to environmental conditions, and so this community reacts in a regular way to manipulation of variables (e.g., nutrient enrichment). Since, however, the environmental conditions affecting plant response can vary with time, the preconditioned state of the phytoplankton is both unknown and variable among experiments. An important indicator of nutrient experience in plants is the internal nitrogen concentration (6), which is difficult to assess for natural phytoplankton because they exist in a mixture with unknown proportions of detrital particles. This means that phytoplankton response to enrichment is difficult to predict in our present state of knowledge, and that there are remaining questions and subtle interactions among environmental parameters (5) to be addressed.

The mixture of surface and deep waters discharged by OTEC power generating facilities will spread from the site at depths having water densities similar to its own. These depths will usually be clearly in the transition zone of light- to nutrient-limitation for phytoplankton. In regions where the discharge mixes with oceanic water, and dilutes the deep-water nutrients to concentrations equal to or less than those used in our experiments, little immediate biostimulation can be expected.

Until a future date when OTEC plants and their discharges become very large, the areas encompassed by concentrations of deep water greater than those used in this work will be very small, because coastal currents around the Hawaiian islands attain speeds in excess of one meter per second, and because deep water is diluted considerably with surface water during the discharge process. When the generating facilities become large, the areas occupied by plumes of a given discharge concentration will be larger, and phytoplankton will reside in such concentrations for longer periods of time. Considerable growth stimulation response have been observed in enrichment experiments incubated for periods of days to weeks, and assessed in terms of final plant yield (23).

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Table 1. Effects of deep-water nutrient enrichment on depth-integrated carbon fixation estimates, with associated environmental and experimental data.

Experiment No.	Productivity: Enriched (NE) (mg C·m^{-2}·h^{-1})	Productivity: Reference (REF) (mg C·m^{-2}·h^{-1})	Stimulation Effect (NE - REF) (mg C·m^{-2}·h^{-1})	Relative Stimulation Effect 100(NE-REF)/REF (%)	Surface Irradiance at incubation (10^{20} quanta.cm^{-2})	Enrichment Injection: Volume Replaced (%)	Enrichment Injection: NO_3^- Added (μM)	Enrichment Injection: $PO_4^{\equiv}$ Added (μM)
1	6.15	2.47	3.68	149	26.2	8.2	3.05	0.24
2	12.76	11.54	1.22	10.6	11.4	3.3	1.20	0.09
3	18.81	17.21	1.60	9.3	11.4	16.3	5.94	0.45
5	13.70	8.23	5.47	66.5	9.4	6.8	1.78	0.15
6	4.87	3.64	1.23	33.8	10.0	6.8	2.28	0.18

Table 2. Half-saturation constants (K_L) in terms of total irradiance during the incubation period, for the reference (non-enriched) carbon fixation profiles. The mean (±SD) K_L value from these trials was 3.86 ± 1.19 x 10^{20} quanta·m^{-2}; the mean (±SD) depth at which these values occurred was 40 ± 13 m.

Experiment No.	Total irradiance at 1-2 m depth during incubation (10^{20} quanta.cm^{-2})	K_L (10^{20} quanta·cm^{-2})	Depth of K_L (m)
1	26.2	3.78	61
2	11.4	3.56	37
3	11.4	3.56	37
5	9.4	2.62	40
6	10.0	5.47	24

Table 3. Deep-water enrichment effects on carbon fixation rates in freshly-collected natural phytoplankton samples and in samples held for one day before measurement (experiment NE-7). Enrichments replaced 11% of the original sample water.

Depth (m)	Freshly collected		Δ (%)	Held one day		Δ (%)
	Reference	Enriched		Reference	Enriched	
	(mg $C \cdot m^{-3} \cdot h^{-1}$)			(mg $C \cdot m^{-3} \cdot h^{-1}$)		
10	0.017 ±0.007	0.022 ±0.010	+29	0.058 ±0.023	0.065 ±0.011	+12
70	0.045 ±0.018	0.035 ±0.004	-22	0.068 ±0.023	0.078 ±0.010	+15

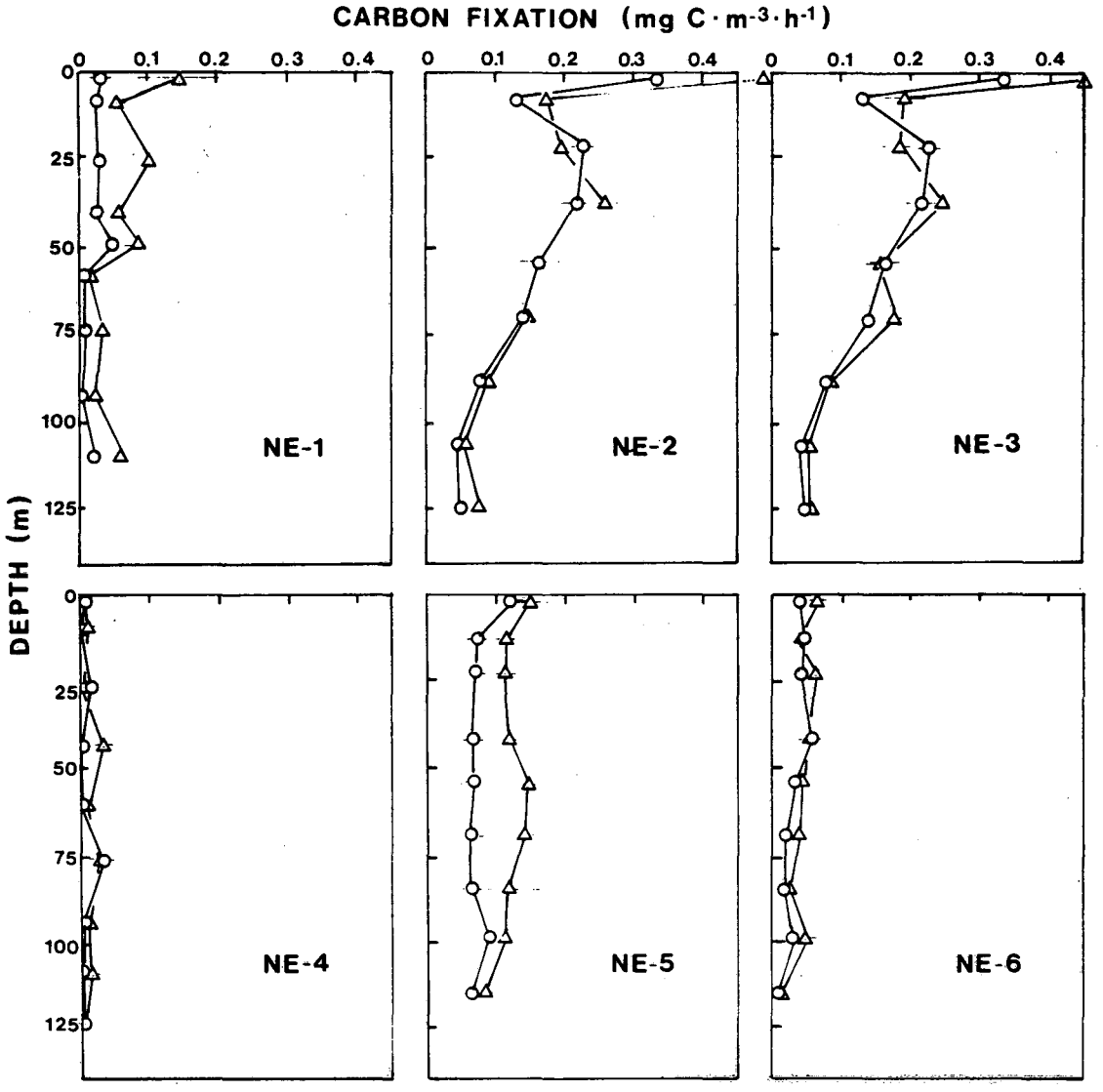

Fig. 1 Vertical profiles of carbon fixation rates for nutrient enrichment trials NE-1 through -6. Enriched samples (Δ); reference (unenriched) samples (o).

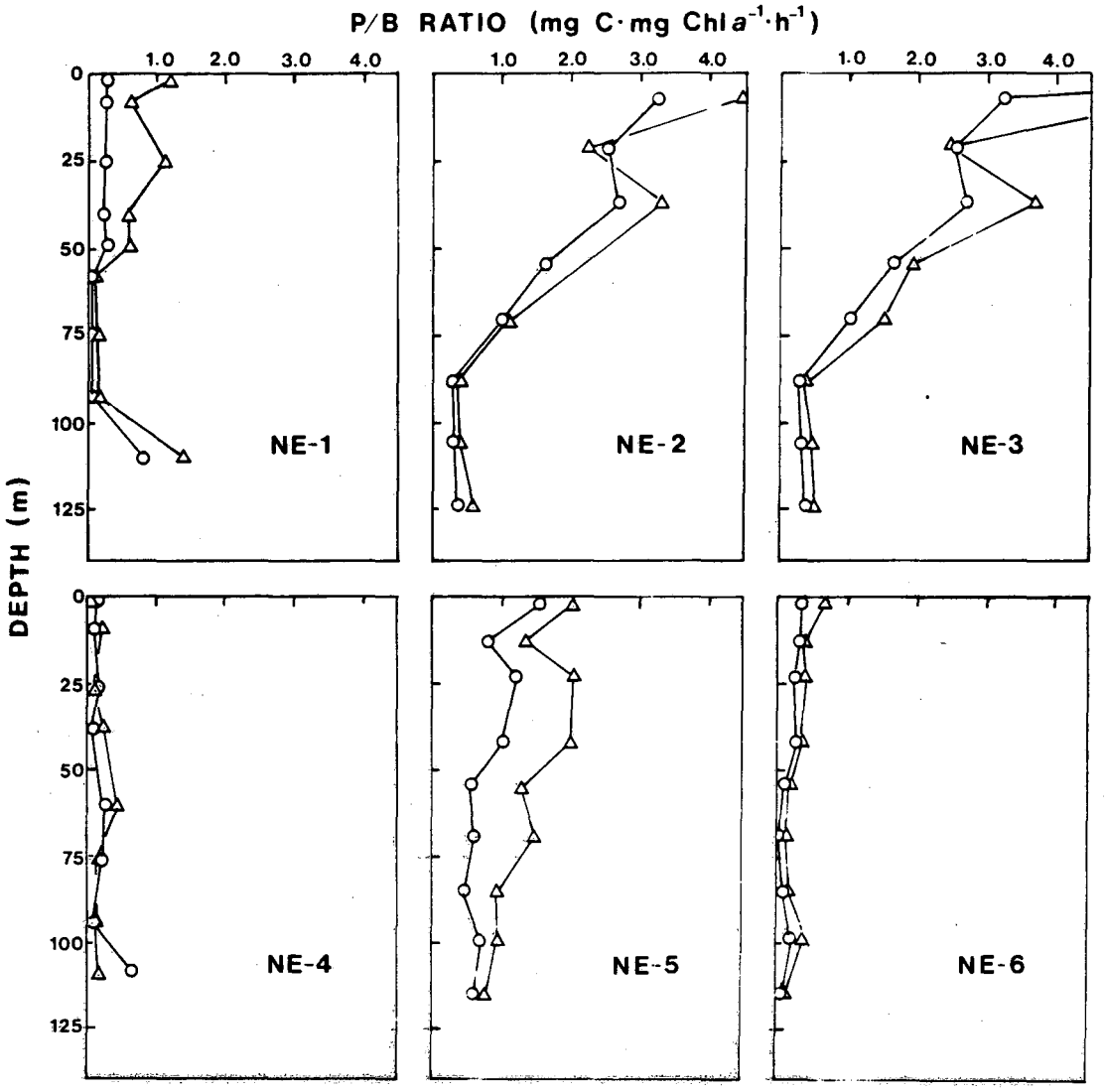

Fig. 2 Productivity-to-biomass ratios for nutrient enrichment trials NE-1 through -6. Enriched samples (Δ); reference (unenriched) samples (o).

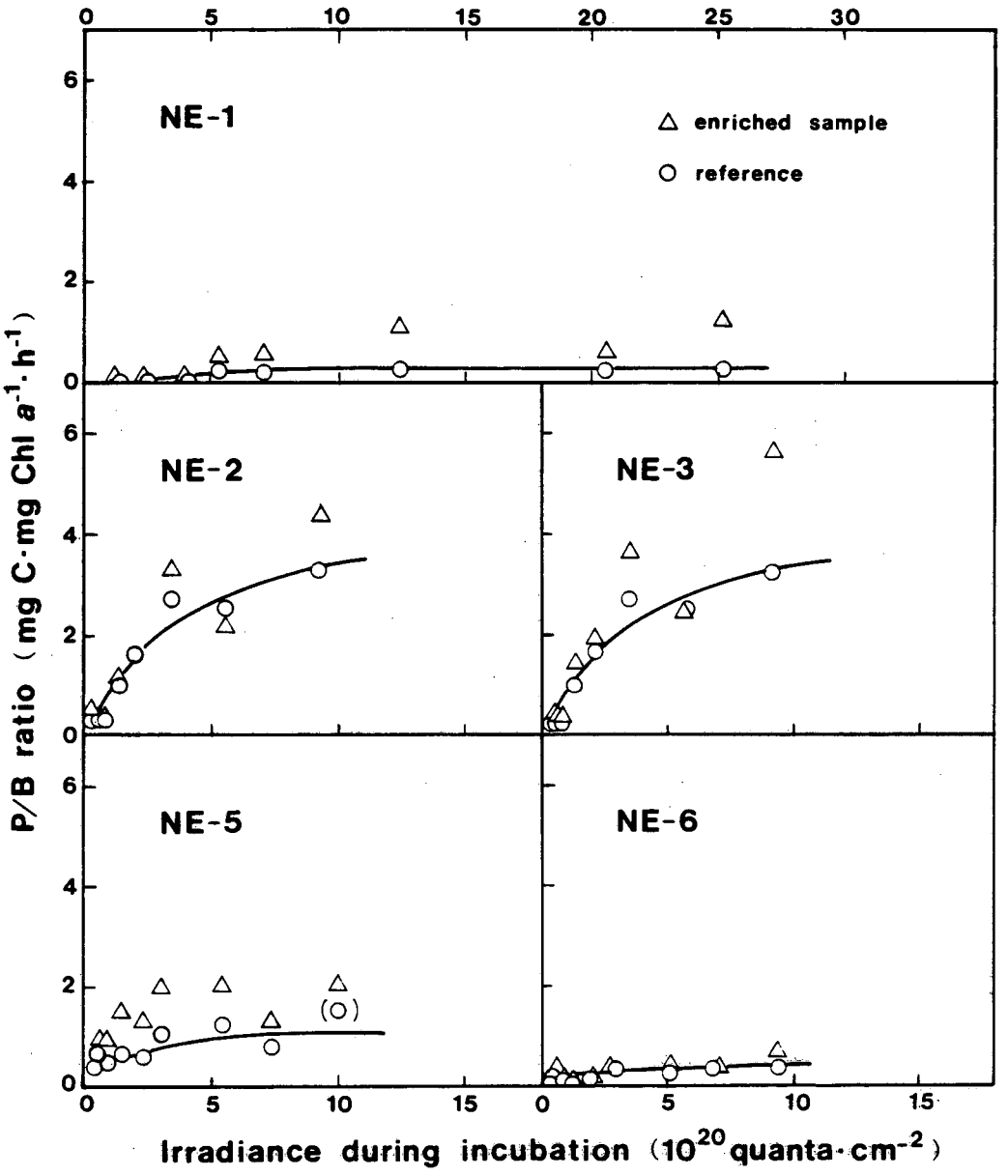

Fig. 3 Effects of irradiance during incubation on P/B ratio for nutrient enrichment trials NE-1 through -6.

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