



Biomass and productivity in Monterey Bay, California: contribution of the large phytoplankton

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Abstract

The contribution of large phytoplankton to the standing stock and productivity of the eastern-boundary ecosystem of Monterey Bay, California, was evaluated during 1992 and 1993, using size fractionation. Eight cruises sampled the variability of the bay both spatially (within the upwelling plume and offshore) and temporally (during upwelling and non-upwelling seasons, El Niño and non-El Niño years). The larger cell sized ($> 5 \mu\text{m}$) autotrophs contributed significantly to chlorophyll, particulate nitrogen, and new and primary productivity in most cruises. This was especially noticeable above a threshold nutrient concentration of 10–12 μM nitrate. Pooling the entire dataset, there were good linear relationships between biomass and productivity parameters measured using GF/F and 5 μm filters. The contribution of the $> 5 \mu\text{m}$ size fraction was greatest at higher biomass concentrations and productivity rates, supporting the idea that to reach maximal values, large cells are required. There were linear trends with Chl : PON ratio of close to 1, and $^{14}\text{C} : ^{15}\text{NO}_3$ uptake ratio of about 10 in both total and $> 5 \mu\text{m}$ size fractions. These large cells are major contributors to carbon and nitrogen productivity in Monterey Bay. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

Biological production is important to global carbon and nitrogen cycles, particularly in eastern-boundary upwelling systems where the flux of new nutrients from depth to the euphotic zone results in enhanced primary production. The quality of

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new and primary production and the composition and size structure of the autotrophic assemblage are major determinants of the quantity of productivity that occurs. In waters supplied with high-nutrient concentrations, phytoplankton biomass (and associated productivity) may be dominated by large cell-sized net plankton (e.g. $> 5 \mu\text{m}$, Brink et al., 1995; Probyn, 1985). These eutrophic areas support relatively large phytoplankton standing stocks (e.g. Malone, 1980; Goldman, 1988) that can develop as a consequence of the addition of the larger size class (Raimbault et al., 1988; Chisholm, 1992). The larger ($> 5 \mu\text{m}$) phytoplankton thrive under conditions of high nutrients (Varela et al., 1991; Tamigneaux et al., 1995). They include chain-forming and colonial diatoms (5–30 μm diameter) (Estrada and Blasco, 1985; Hutchings et al., 1995) described by Smetacek (1998) as the workhorses running the pelagic ecosystem. Malone (1980) was one of the first to propose that these net plankton use primarily new nitrogen (*sensu* Dugdale and Goering, 1967) and that the smaller size classes (pico- and nanoplankton) use mainly regenerated nitrogen such as ammonium (e.g. Glibert et al., 1982; Nalewajko and Garside, 1983; Probyn, 1985; Koike et al., 1986). There is growing evidence for this concept in coastal upwelling studies where net phytoplankton blooms develop in response to upwelled nutrient inputs (e.g., Pitcher, 1988; Chavez et al., 1991; Probyn, 1992).

Monterey Bay, CA (herein, “MB”, Fig. 1) is a deep embayment in central California located at the edge of the California Current, on the eastern boundary of the North Pacific gyre (for review, see Breaker and Broenkow, 1994). It provides an ideal site to examine the contribution of large cell-sized autotrophs to biomass and new and total production. Upwelling supplies nutrients that support high levels of productivity (e.g. Kudela and Dugdale, 1996; Pennington and Chavez, 2000). Net plankton samples going back to 1954 (Abbott and Albee, 1967; Bolin and Abbott, 1963; Malone, 1971; Garrison, 1976, 1979; Schrader, 1981 etc.) show diatom dominance of the phytoplankton assemblage. More recent studies (e.g. Kudela et al., 1997; Buck et al., 1992; Chavez, 1995, 1996) that have included sampling cells smaller than net plankton (i.e. *Synechococcus* and red fluorescing picoplankton) also report high diatom abundances during upwelling conditions ($313 \mu\text{g C l}^{-1}$ for diatoms versus $0.35 \mu\text{g C l}^{-1}$ for picoplankton, Chavez, 1996). Malone (1971) linked the increases in net plankton ($> 20 \mu\text{m}$, ~ diatoms) in MB with increases in ambient NO_3 concentrations during upwelling.

Seasonal upwelling (March–September) in MB has been well documented (e.g. Skogsberg, 1936; Abbott and Albee, 1967; Garrison, 1976; Garrison, 1979; Schrader, 1981). A persistent upwelling center (Fig. 1) has been identified at Point Año Nuevo to the north of MB, near Davenport (Tracy, 1990; Schwing et al., 1990; Graham et al., 1992; Rosenfeld et al., 1994; Lenarz et al., 1995; White and Dugdale, 1997), from which bifurcating plumes of cool, saline, nutrient-rich surface water are advected offshore and equatorward into the bay. Following the upwelling season is the “oceanic” season characterized by warm sea-surface temperatures and increased stratification, and the winter “Davidson” season when water in MB is well mixed and the Davidson Current flows northward over the shelf (Hickey, 1979). During the oceanic and Davidson seasons the smaller autotrophs might be expected to dominate the lower concentrations of biomass (Chavez, 1996) and rates of productivity in the bay.

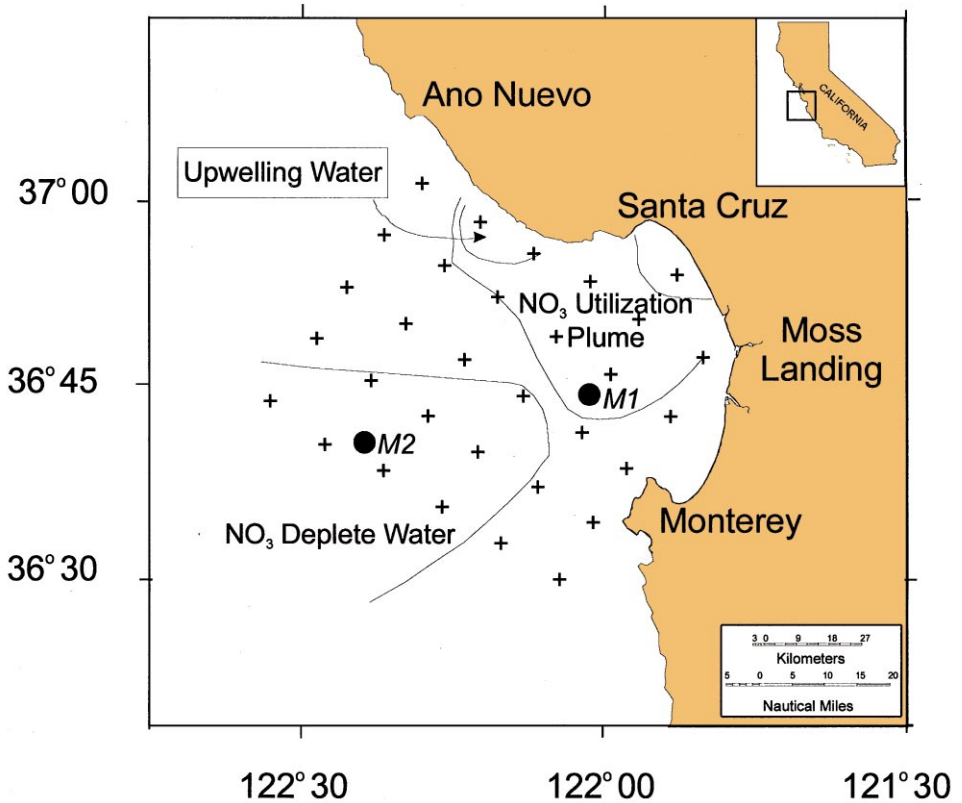


Fig. 1. Map of the study site of Monterey Bay, CA, showing the upwelling center and plume and the MBARI moorings, M1 and M2.

During 1992 and 1993 we collected seasonal data of biomass and productivity in Monterey Bay during eight one-week cruises. These cruises were part of a larger investigation of the physiological response of phytoplankton to upwelling that showed increased rates of NO₃ uptake and carbon fixation as upwelled water aged (Kudela and Dugdale, 1996; Kudela et al., 1997). White and Dugdale (1997) reported spatial maxima of NO₃ and Si(OH)₄ uptake rates that co-occurred with the NO₃ and Si(OH)₄ concentration maxima; near the coast during weak upwelling or relaxation, and offshore during strong upwelling. Wilkerson and Dugdale (1998) described the interannual variability in NO₃ uptake due to the 1992 El Niño. The size-fractionated biomass and productivity data reported in the present paper were collected to understand the biogeochemical functioning of the large and small phytoplankton in the MB upwelling system.

2. Methods

2.1. General

Sampling was conducted aboard the R/V *Point Sur* and R/V *New Horizon* in MB (Figs. 1 and 2) during one-week cruises made in 1992 and 1993 (designated SU 92 and SU 93, Table 1). Stations were sampled throughout the bay (Fig. 2), and each cruise typically sampled at the upwelling center and downstream in the upwelling plume, sometimes sampling at the original Hopkins Marine Station H-3 location, just north-east of the MBARI mooring M1 (Fig. 1). The combined station coverage sampled the high spatial variability of Monterey Bay representing a continuum between upwelling and full nutrient utilization (Fig. 2). Near-surface maps (5 m depth) made during these cruises are described elsewhere (e.g. White and Dugdale, 1997; Wilkerson and Dugdale, 1998; Pennington and Chavez, 2000). Seawater was collected using acid-cleaned 10-L PVC Niskin bottles equipped with Teflon-coated springs and fittings and silicone tubing mounted on an instrumented rosette sampler. Surface data (0 or 1 m depth) are described here since this was the only sampling depth at which size-fractionated chlorophyll and ^{14}C uptake were obtained, although water was sampled vertically to the bottom of the euphotic zone for other parameters. Inorganic nutrient concentrations, particulate biomass concentrations (chlorophyll *a* and particulate nitrogen, PON), carbon fixation, and nutrient uptake rates were determined at all stations.

2.2. Nutrient analyses

Samples for NO_3 and $\text{Si}(\text{OH})_4$ analysis were frozen in acid-washed 30-ml polypropylene bottles until analysis using a Technicon AutoAnalyzer II according to the procedures of Whitledge et al. (1981). Combined NO_3 and NO_2 concentrations are reported as NO_3 . Ammonium concentrations were measured on shipboard within 24 h of collection using a spectrophotometer equipped with a 10-cm cuvette according to Solorzano (1969).

2.3. Biomass analyses

Water samples (100–280 ml) were filtered and assayed for either PON concentration according to Wilkerson and Dugdale (1992) using a Europa Scientific Roboprep-Tracermass mass spectrometer system, or chlorophyll *a* using the fluorometric technique (Holm-Hansen et al., 1965), with a 24–30 h extraction in 90% acetone at -20°C (Venrick and Hayward, 1984). Chlorophyll *a* was calculated from data obtained using a Turner Designs model 10-005 R fluorometer calibrated (Parsons et al., 1984) with commercially available chlorophyll *a* (Sigma Chemical Co.).

2.4. ^{15}N uptake

Surface water was dispensed into 280-ml polycarbonate bottles and maintained under low light until inoculation with ^{15}N isotope (45 min at most). Trace additions

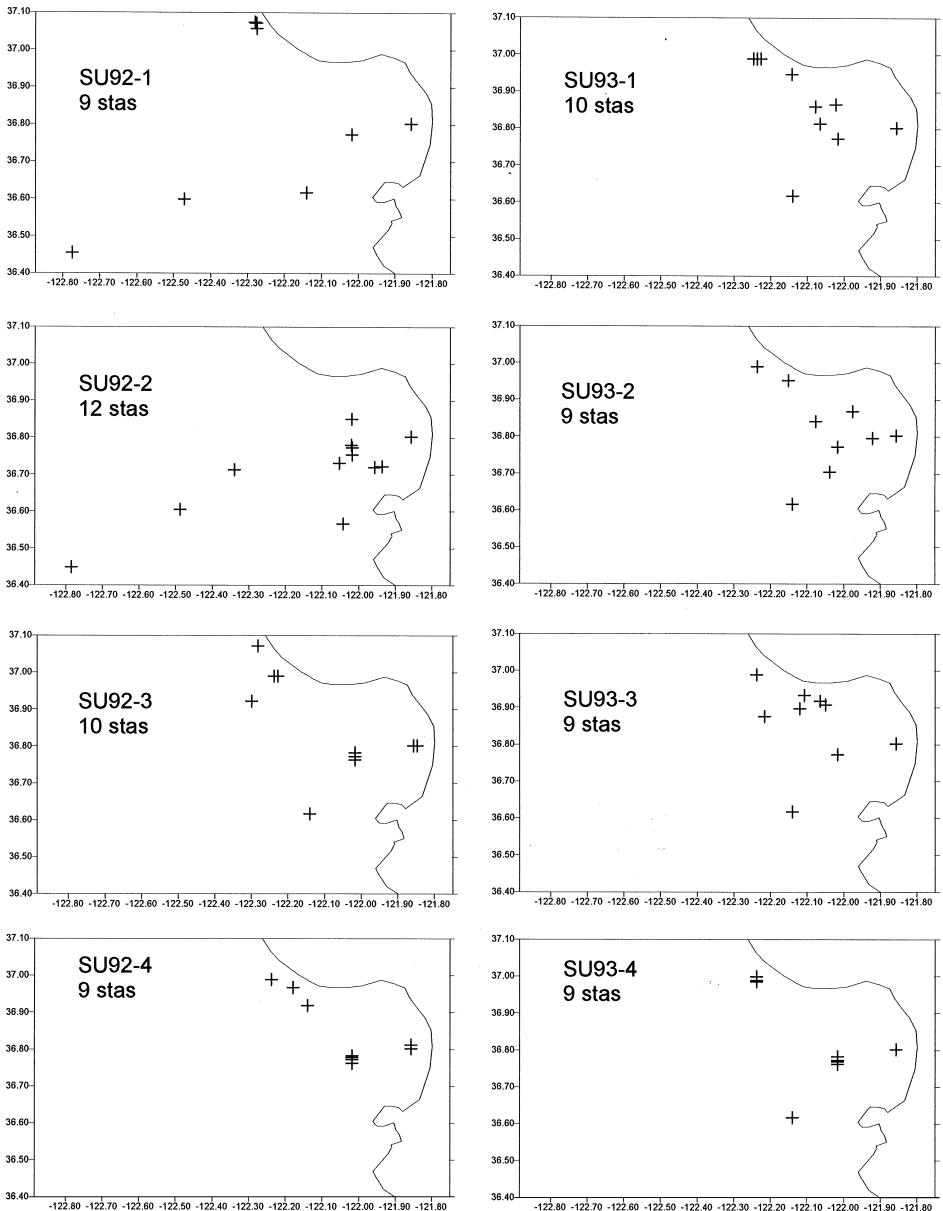


Fig. 2. Station locations for SU 92 and SU 93 cruises sampled during the study.

(at approximately 10% of ambient concentrations of NO_3 or NH_4) of either K^{15}NO_3 or $^{15}\text{NH}_4\text{Cl}$ (99 at% ^{15}N , Cambridge Isotope Laboratories) were made and bottles placed in transparent Plexiglas tubes in on-deck Plexiglas incubators, cooled by flowing surface seawater for 6 h around local noon. Following incubation, all samples

Table 1

Cruise dates and upwelling conditions for size fractionation cruises to Monterey Bay, CA

Cruise	Date	Research Vessel	Conditions
1993 Cruises (SU 92)			
SU 92-1	27 March–2 April	Point Sur	El Niño, non upwelling,
SU 92-2	3 May–3 June	New Horizon	El Niño, weak upwelling
SU 92-3	24–30 September	Point Sur	Moderate upwelling
SU 92-4	17–23 November	Point Sur	Davidson, weak upwelling
1993 Cruises (SU 93)			
SU 93-1	23–29 March	Point Sur	Moderate upwelling
SU 93-2	7–13 May	Point Sur	Strong upwelling
SU 93-3	11–16 September	Point Sur	Strong upwelling
SU 93-4	10–15 November	Point Sur	Davidson, non upwelling

were collected by filtration (pressure differential, 150 mm Hg). Frozen filters were transported to the laboratory and then dried ($<60^{\circ}\text{C}$ for >24 h) and analyzed for ^{15}N enrichment with a Europa Scientific Roboprep-Tracermass mass spectrometer system (Wilkerson and Dugdale, 1992). The transport rate ρ was calculated according to Dugdale and Wilkerson (1986). Hourly rates were converted to daily rates by multiplying by 12 for NO_3 uptake and 18 for NH_4 uptake.

2.5. ^{14}C fixation

Surface water samples (280 ml) were inoculated with $\sim 10 \mu\text{Ci}$ of ^{14}C as $\text{Na}_2^{14}\text{CO}_3$ and incubated for 24 h under running seawater on deck in transparent Plexiglas tubes. After incubation, excess ^{14}C was filtered. The filters were fumed overnight in 0.5 ml 0.5 N HCl to remove unbound label, 10 ml CytoScint ES scintillation cocktail added, and the disintegrations counted in a Beckman LS-3801 counter. Prior to filtration, 1 ml from each of 2 incubation bottles was added to 20 ml scintillation cocktail; counts of these samples estimated activity of the ^{14}C originally added to the samples. Instead of dark bottle controls, some samples were filtered before incubation to assay non-photosynthetically retained ^{14}C . Counts were converted to $\mu\text{g-at C l}^{-1} \text{d}^{-1}$ as in Parsons et al. (1984).

2.6. Size fractionation

Biomass or productivity determination for the entire assemblage were made on precombusted 25-mm Whatman GF/F glass fiber filters. The greater than $5 \mu\text{m}$ fraction was sampled using either 25-mm $5\text{-}\mu\text{m}$ polycarbonate membrane filters (Poretics) for chlorophyll a and ^{14}C fixation measurements, or 25-mm $5\text{-}\mu\text{m}$ silver filters (Poretics) for PON and ^{15}N uptake since polycarbonate membranes cannot be used in the combustion procedure of the mass spectrometry analysis. To evaluate the

contribution of the $>5\text{-}\mu\text{m}$ cells to the total assemblage, the $5\text{-}\mu\text{m}$ fraction values were calculated as percentage of the total assemblage values. In some situations this value was more than 100%. In these circumstances we checked the sample procedures and have chosen to report percentages up to 130% allowing for this to be within methodological error. Interestingly, this feature mainly occurred in percentages involving rates, particularly ^{14}C uptake measurements.

3. Results

3.1. Mean values for all cruises

Surface data from all stations sampled (Fig. 2) for size fractionation were averaged for biomass (Table 2) and rate measurements (Table 3) for each cruise (i.e. for the whole bay) and for all eight cruises. The summed data show the wide range of conditions that can occur in MB, from the lowest NO_3 concentration of 0 or undetectable in SU 92-1, March 1992 (influenced by El Niño) to a maximum value of $24.8\ \mu\text{M}$ measured in SU 93-2, May 1993 (non El Niño) when upwelling was occurring. $\text{Si}(\text{OH})_4$ showed the same wide range of concentrations, with a minimum surface value of $0.65\ \mu\text{M}$ and maximum value of $33\ \mu\text{M}$ in May 1993. The overall mean NO_3 concentration was $5.5 \pm 6.5\ \mu\text{M}$ and for $\text{Si}(\text{OH})_4$ was $9.5 \pm 7.67\ \mu\text{M}$. PON concentrations ranged from a minimum of $0.07\ \mu\text{g-at N l}^{-1}$ ($>5\ \mu\text{m}$ fraction) during SU 92-1, March 1992-El Niño cruise to a maximum of $8\ \mu\text{g-at N l}^{-1}$ (total assemblage) measured during SU 93-2, May cruise that had strong upwelling. Mean PON concentrations for all data collected with GF/F filters was $2.69 \pm 1.62\ \mu\text{g-at N l}^{-1}$. The substantial contribution of the larger sized phytoplankton to biomass was evident from size-fractionated PON and chlorophyll *a* data. The mean for all PON samples collected on $5\text{-}\mu\text{m}$ filters was $1.82 \pm 1.58\ \mu\text{g-at N l}^{-1}$, and the average percent due to PON in the larger size fractions was 62%. Chlorophyll *a* concentrations showed the same trend as PON, with an average of 50% of the total assemblage chlorophyll *a* (mean of $2.16 \pm 1.88\ \mu\text{g l}^{-1}$) contributed from chlorophyll *a* in the $>5\ \mu\text{m}$ fraction (mean of $1.16 \pm 1.23\ \mu\text{g l}^{-1}$). The range of chlorophyll *a* concentrations throughout the bay was great, with a minimum of $0.15\ \mu\text{g l}^{-1}$ for the total assemblage and $0.07\ \mu\text{g l}^{-1}$ for the $>5\text{-}\mu\text{m}$ fraction and maximum values of 9.6 and $6.09\ \mu\text{g l}^{-1}$ for the two fractions, respectively.

Rate measurements were also very variable with large ranges (Table 3). Nitrate uptake, $\rho^{15}\text{NO}_3$ for the GF/F samples ranged from 0.02 to $2.91\ \mu\text{g-at N l}^{-1}\text{d}^{-1}$, and for the $>5\text{-}\mu\text{m}$ fraction, from 0.02 to $2.67\ \mu\text{g-at N l}^{-1}\text{d}^{-1}$. The range for carbon fixation, $\rho^{14}\text{C}$ was greater, 0.16 to $22.68\ \mu\text{g-at C l}^{-1}\text{h}^{-1}$, with the highest fixation rate ($28.63\ \mu\text{g-at C l}^{-1}\text{h}^{-1}$) measured in a $>5\text{-}\mu\text{m}$ fraction sample. Substantial contribution was made by the $>5\text{-}\mu\text{m}$ fraction to both nitrate uptake and ^{14}C fixation rates of the total assemblage (Table 3). Mean $\rho^{15}\text{NO}_3$ of the entire assemblage was $0.54 \pm 0.67\ \mu\text{g-at N l}^{-1}\text{d}^{-1}$, with a contribution by the larger algae of 68%. Similarly, 56% of the total assemblage carbon uptake ($6.32 \pm 5.44\ \mu\text{g-at C d}^{-1}$), was by the $>5\text{-}\mu\text{m}$ fraction ($4.12 \pm 4.93\ \mu\text{g-at C l}^{-1}\text{d}^{-1}$).

Table 2
Surface nutrient and fractionated biomass data for SU cruises to Monterey Bay (mean \pm SD, *n*)

Cruise Date	NO ₃ (μM)	Si(OH) ₄ (μM)	PON GF/F (μg-at l ⁻¹)	PON >5 μm (μg-at l ⁻¹)	PON % >5 μm	Chl GF/F (μg l ⁻¹)	Chl >5 μm (μg l ⁻¹)	Chl % >5 μm
All 8 cruises	5.52 \pm 6.47 <i>n</i> = 76	9.50 \pm 7.67 <i>n</i> = 74	2.69 \pm 1.62 <i>n</i> = 41	1.82 \pm 1.58 <i>n</i> = 35	61.7 \pm 30.9 <i>n</i> = 34	2.16 \pm 1.88 <i>n</i> = 71	1.16 \pm 1.23 <i>n</i> = 71	50.4 \pm 19.8 <i>n</i> = 71
Minimum	0	0.65	1.04	0.07	5.8	0.15	0.07	6.2
Maximum	24.81	33.04	7.95	7.21	107.8	9.589	6.09	95.2
SU 92-1 Mar 92	0.34 \pm 0.37 <i>n</i> = 9	4.59 \pm 1.20 <i>n</i> = 8	1.96 \pm 1.17 <i>n</i> = 3	0.57 \pm 0.77 <i>n</i> = 3	35.9 \pm 51.5 <i>n</i> = 3	0.73 \pm 0.51 <i>n</i> = 7	0.42 \pm 0.36 <i>n</i> = 7	53.5 \pm 19.7 <i>n</i> = 7
SU 92-2 May 92	2.69 \pm 2.08 <i>n</i> = 12	9.55 \pm 3.10 <i>n</i> = 12	2.74 \pm 1.80 <i>n</i> = 5	1.88 \pm 2.17 <i>n</i> = 5	55.6 \pm 34.5 <i>n</i> = 5	2.89 \pm 2.55 <i>n</i> = 12	1.28 \pm 1.51 <i>n</i> = 12	37.3 \pm 21.0 <i>n</i> = 12
SU 92-3 Sept 92	5.02 \pm 3.31 <i>n</i> = 10	6.37 \pm 2.86 <i>n</i> = 10	2.78 \pm 0.93 <i>n</i> = 5	1.63 \pm 0.62 <i>n</i> = 6	58.0 \pm 26.0 <i>n</i> = 5	2.58 \pm 0.82 <i>n</i> = 9	1.07 \pm 0.48 <i>n</i> = 9	42.0 \pm 14.0 <i>n</i> = 9
SU 92-4 Nov 92	0.76 \pm 0.66 <i>n</i> = 8	2.68 \pm 0.77 <i>n</i> = 8	2.47 \pm 0.80 <i>n</i> = 6	0.83 \pm 0.47 <i>n</i> = 4	40.7 \pm 29.9 <i>n</i> = 4	1.24 \pm 0.86 <i>n</i> = 8	0.8 \pm 0.795 <i>n</i> = 8	59.6 \pm 28.0 <i>n</i> = 8
SU 93-1 Mar 93	6.51 \pm 5.91 <i>n</i> = 10	11.16 \pm 5.47 <i>n</i> = 10	2.63 \pm 1.14 <i>n</i> = 6	2.42 \pm 1.09 <i>n</i> = 3	65.7 \pm 16.2 <i>n</i> = 3	1.95 \pm 1.18 <i>n</i> = 10	1.01 \pm 0.61 <i>n</i> = 10	52.7 \pm 8.1 <i>n</i> = 10
SU 93-2 May 93	18.29 \pm 5.95 <i>n</i> = 9	27.85 \pm 3.87 <i>n</i> = 8	4.67 \pm 3.00 <i>n</i> = 5	3.79 \pm 2.37 <i>n</i> = 5	85.6 \pm 14.9 <i>n</i> = 5	4.34 \pm 2.66 <i>n</i> = 9	2.89 \pm 1.87 <i>n</i> = 9	67.9 \pm 19.9 <i>n</i> = 9
SU 93-3 Sept 93	8.41 \pm 5.09 <i>n</i> = 9	9.45 \pm 4.09 <i>n</i> = 9	2.86 \pm 1.40 <i>n</i> = 5	1.99 \pm 0.98 <i>n</i> = 5	77.8 \pm 32.2 <i>n</i> = 5	1.74 \pm 1.17 <i>n</i> = 7	0.89 \pm 0.79 <i>n</i> = 7	48.8 \pm 17.9 <i>n</i> = 7
SU 93-4 Nov 93	2.53 \pm 1.80 <i>n</i> = 9	5.21 \pm 2.39 <i>n</i> = 9	1.42 \pm 0.36 <i>n</i> = 6	0.83 \pm 0.19 <i>n</i> = 4	61.3 \pm 27.9 <i>n</i> = 4	1.07 \pm 0.69 <i>n</i> = 9	0.55 \pm 0.49 <i>n</i> = 9	46.8 \pm 12.5 <i>n</i> = 9

Table 3

Fractionated surface nitrate uptake and carbon fixation data for SU cruises to Monterey Bay (mean \pm SD, *n*)

Cruise Date	$\rho^{15}\text{NO}_3$ GF/F ($\mu\text{g-at N l}^{-1} \text{d}^{-1}$)	$\rho^{15}\text{NO}_3 > 5 \mu\text{m}$ ($\mu\text{g-at N l}^{-1} \text{d}^{-1}$)	$\rho^{15}\text{NO}_3 \%$ $> 5 \mu\text{m}$	$\rho^{14}\text{C}$ GF/F ($\mu\text{g-at C l}^{-1} \text{d}^{-1}$)	$\rho^{14}\text{C} > 5 \mu\text{m}$ ($\mu\text{g-at C l}^{-1} \text{d}^{-1}$)	$\rho^{14}\text{C}\%$ $> 5 \mu\text{m}$
All 8 cruises	0.54 ± 0.67 <i>n</i> = 41	0.47 ± 0.67 <i>n</i> = 34	67.7 ± 31.1 <i>n</i> = 33	6.32 ± 5.44 <i>n</i> = 63	4.12 ± 4.93 <i>n</i> = 62	55.6 ± 33.0 <i>n</i> = 62
Minimum	0.02	0.02	8.5	0.16	0.06	3.0
Maximum	2.91	2.67	128.8	22.68	28.63	129.5
SU 92-1 Mar 92	0.16 ± 0.08 <i>n</i> = 3	0.11 ± 0.07 <i>n</i> = 3	70.1 ± 40.3 <i>n</i> = 3	4.88 ± 5.76 <i>n</i> = 6	0.98 ± 1.52 <i>n</i> = 7	8.36 ± 2.0 <i>n</i> = 6
SU 92-2 May 92	0.64 ± 0.82 <i>n</i> = 5	0.45 ± 0.90 <i>n</i> = 5	54.3 ± 38.6 <i>n</i> = 5	8.20 ± 8.23 <i>n</i> = 10	6.3 ± 6.54 <i>n</i> = 8	57.3 ± 38.7 <i>n</i> = 8
SU 92-3 Sept 92	0.63 ± 0.34 <i>n</i> = 5	0.65 ± 0.41 <i>n</i> = 6	81.2 ± 47.4 <i>n</i> = 5	7.79 ± 4.15 <i>n</i> = 7	4.70 ± 3.20 <i>n</i> = 7	50.1 ± 35.3 <i>n</i> = 8
SU 92-4 Nov 92	0.15 ± 0.16 <i>n</i> = 6	0.11 ± 0.12 <i>n</i> = 4	74.2 ± 15.8 <i>n</i> = 4	3.36 ± 1.93 <i>n</i> = 7	2.72 ± 1.99 <i>n</i> = 7	75.3 ± 28.9 <i>n</i> = 7
SU 93-1 Mar 93	0.41 ± 0.17 <i>n</i> = 6	0.34 ± 0.14 <i>n</i> = 3	63.1 ± 16.7 <i>n</i> = 3	5.20 ± 3.95 <i>n</i> = 10	2.37 ± 2.01 <i>n</i> = 10	46.7 ± 16.7 <i>n</i> = 10
SU 93-2 May 93	1.74 ± 1.07 <i>n</i> = 5	1.6 ± 1.03 <i>n</i> = 4	86.3 ± 8.5 <i>n</i> = 4	11.39 ± 7.28 <i>n</i> = 7	10.86 ± 8.92 <i>n</i> = 7	95.3 ± 32.0 <i>n</i> = 7
SU 93-3 Sept 93	0.4 ± 0.29 <i>n</i> = 5	0.25 ± 0.19 <i>n</i> = 5	67.6 ± 37.1 <i>n</i> = 5	6.48 ± 3.05 <i>n</i> = 7	3.82 ± 2.55 <i>n</i> = 7	54.2 ± 18.1 <i>n</i> = 7
SU 93-4 Nov 93	0.18 ± 0.11 <i>n</i> = 6	0.09 ± 0.04 <i>n</i> = 4	44.0 ± 4.5 <i>n</i> = 4	3.52 ± 2.07 <i>n</i> = 9	2.12 ± 1.65 <i>n</i> = 9	55.4 ± 19.9 <i>n</i> = 9

3.2. Differences between cruises

Comparing mean values from individual cruises (Tables 2 and 3) shows the temporal variability in the bay with a general trend for greater phytoplankton standing stocks to accompany higher surface nutrients as occurred during upwelling in the March, May and September cruises. The lowest nutrient and biomass concentrations were measured during the November cruises (Davidson season), except for low values in March 1992 resulting from the tail-end of the 1991/1992 El Niño. The same trend occurred for $^{15}\text{NO}_3$ uptake and ^{14}C fixation (Table 3), with lower values in March and November and higher values in May and September when there was upwelling. The cruise with the highest mean values for both rate processes and biomass concentrations was SU 93-2 May 1993, non El Niño, when there was strong upwelling and the contribution by the $> 5 \mu\text{m}$ fraction to the entire assemblage was 86% for $^{15}\text{NO}_3$ uptake and 95% for ^{14}C fixation.

3.3. Pooled fractionated PON and chlorophyll *a* data

Pooling all data from the eight cruises, there was a linear relationship (slope = 0.8, $r^2 = 0.75$, $n = 34$) between PON in the large cell size fraction ($> 5 \mu\text{m}$) and the total PON captured by GF/F filters, (Fig. 3a). Much of the particulate biomass in MB was made up of large cells, especially when higher total PON concentrations were encountered. The same trend was shown by chlorophyll (Fig. 3b) but with a slightly smaller proportion of chlorophyll in the $> 5\text{-}\mu\text{m}$ class (slope = 0.6, $r^2 = 0.85$, $n = 71$) compared to PON (Fig. 3a).

3.4. Pooled fractionated $^{15}\text{NO}_3$, $^{15}\text{NH}_4$ uptake and ^{14}C fixation

Using the same approach to pool the data for rate processes the high relative contribution of the large cell sizes was clear (Fig. 4). The linear slope of $^{15}\rho\text{NO}_3$ of the $> 5\text{-}\mu\text{m}$ fraction versus the entire population (Fig. 4a) was 0.9 ($r^2 = 0.89$, $n = 33$). NH_4 was taken up by both size fractions, but the contribution by the $> 5\text{-}\mu\text{m}$ cells to the total assemblage uptake was not as great as that for NO_3 uptake. The slope of $\rho^{15}\text{NH}_4$ by $> 5\text{-}\mu\text{m}$ cells versus $\rho^{15}\text{NH}_4$ measured on GF/F filters was 0.65 ($r^2 = 0.91$, $n = 26$) although this relationship was driven by one high point (Fig. 4b). Using the slopes of Fig. 4a and b, mean f -ratios were calculated; $f = 0.57$ for $> 5\text{-}\mu\text{m}$ cells and 0.25 for the $< 5\text{-}\mu\text{m}$ cells. The $\rho^{14}\text{C}$ values showed the same linear relationship as NO_3 uptake, with a slightly smaller slope (slope = 0.8, $r^2 = 0.72$, $n = 61$) between fixation by the $> 5\text{-}\mu\text{m}$ cells versus the total assemblage (Fig. 4c).

3.5. Chlorophyll *a* versus PON

The slope of total chlorophyll *a* versus total PON (Fig. 5a) was nearly 1 – i.e. $1 \mu\text{g l}^{-1}$ Chl *a*: $1 \mu\text{g-at l}^{-1}$ PON (slope = 0.97, $r^2 = 0.8$, $n = 38$). The slope for the $> 5\text{-}\mu\text{m}$ fraction (Fig. 5b) was slightly less (slope = 0.8, $r^2 = 0.8$, $n = 32$).

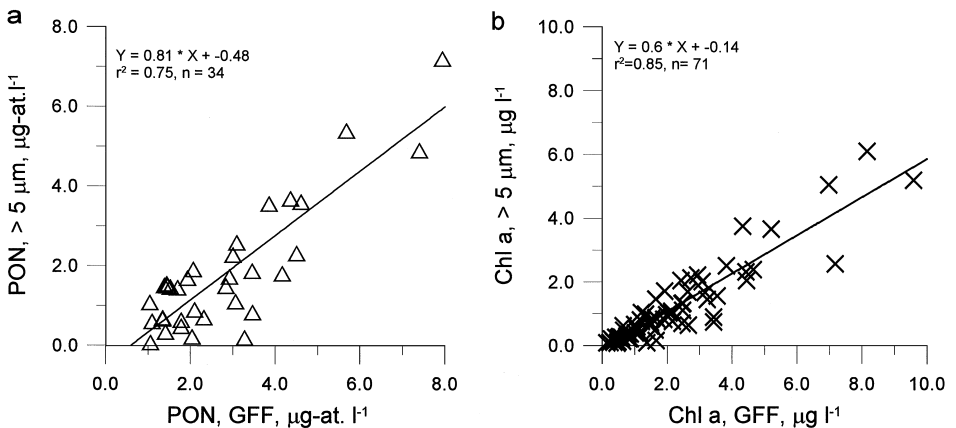


Fig. 3. Surface fractionated biomass from all 8 cruises $> 5 \mu\text{m}$ samples versus total assemblage GF/F samples: (a) PON ($\mu\text{g-at N l}^{-1}$); (b) chlorophyll *a* ($\mu\text{g l}^{-1}$).

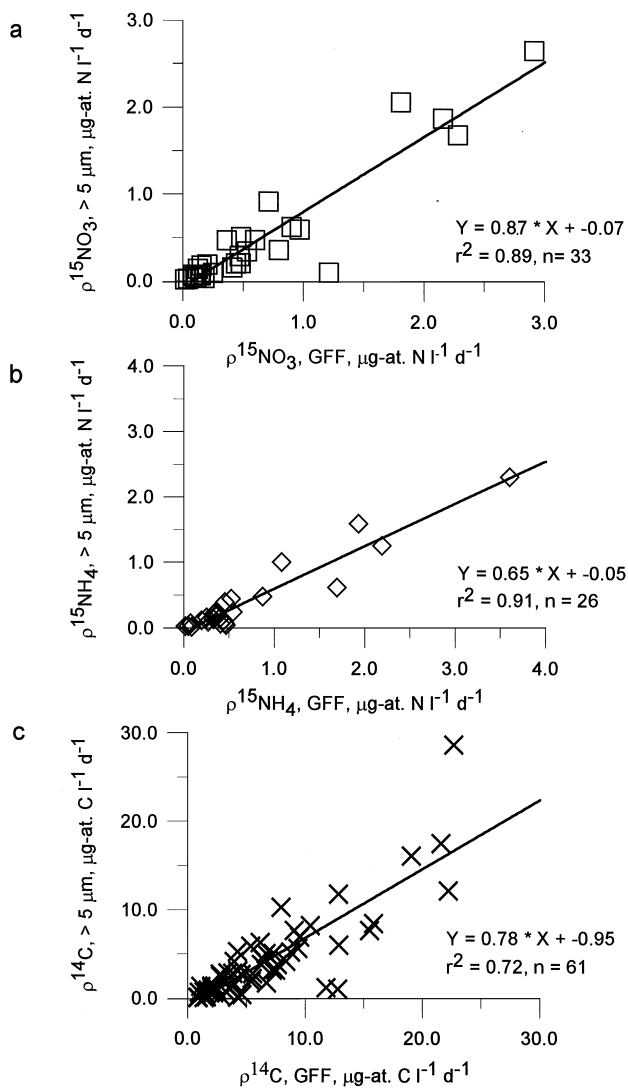


Fig. 4. Surface fractionated productivity from all 8 cruises $> 5 \mu\text{m}$ samples versus total assemblage GF/F samples: (a) $\rho^{15}\text{NO}_3$ ($\mu\text{g-at N l}^{-1} \text{d}^{-1}$); (b) $\rho^{15}\text{NH}_4$ ($\mu\text{g-at N l}^{-1} \text{d}^{-1}$); (c) $\rho^{14}\text{C}$ ($\mu\text{g-at C l}^{-1} \text{d}^{-1}$).

3.6. ^{14}C uptake versus $^{15}\text{NO}_3$ uptake

When $\rho^{14}\text{C}$ was plotted against $\rho^{15}\text{NO}_3$ for all surface samples at which both were measured, there was a good linear relationship between the two parameters, both for the total assemblage (Fig. 6a) and the larger cell-sized fraction (Fig. 6b) of the population. The slopes were slightly greater than Redfield, being 9.6:1 for the total

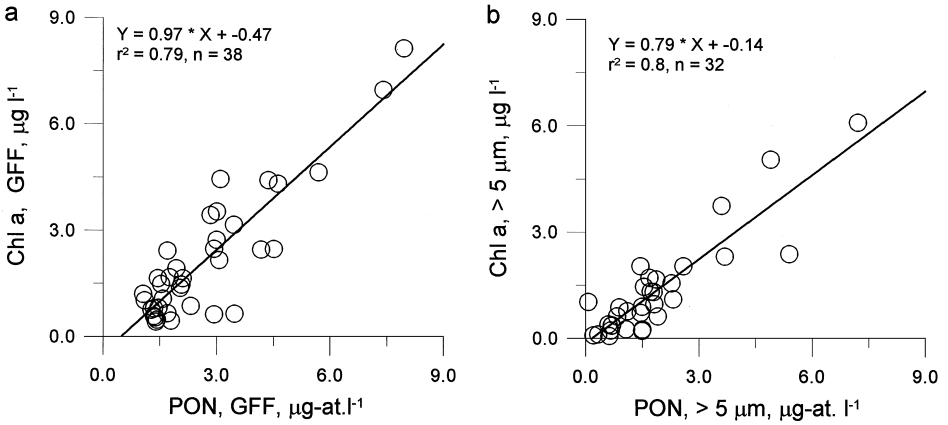


Fig. 5. Chlorophyll a ($\mu\text{g l}^{-1}$) versus PON ($\mu\text{g-at N l}^{-1}$) for all 8 cruises: (a) for the total assemblage sampled on GF/F filters and (b) for samples collected using 5 μm filters.

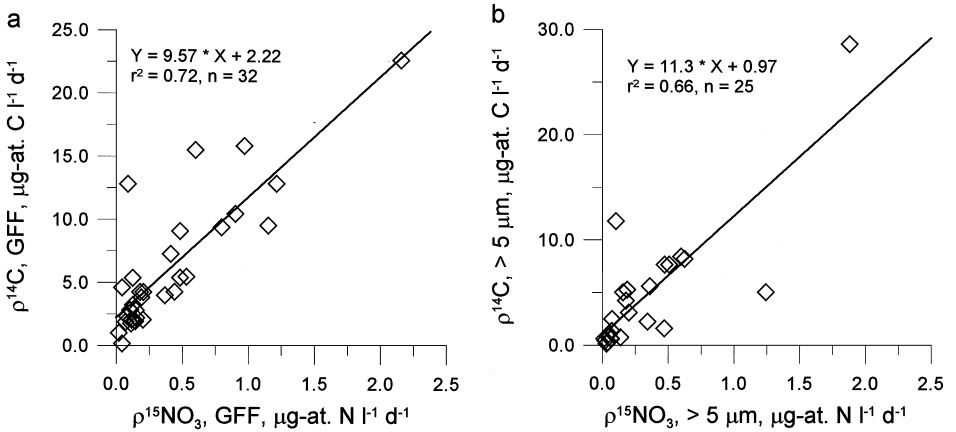


Fig. 6. $\rho^{14}\text{C}$ uptake ($\mu\text{g-at C l}^{-1} \text{d}^{-1}$) versus $\rho^{15}\text{NO}_3$ ($\mu\text{g-at N l}^{-1} \text{d}^{-1}$) for all 8 cruises: (a) for the total assemblage sampled on GF/F filters and (b) for samples collected using 5 μm filters.

$\rho^{14}\text{C}$ versus $\rho^{15}\text{NO}_3$ ($r^2 = 0.72$, $n = 32$) and 11.3 for the $>5\text{-}\mu\text{m}$ fraction ($r^2 = 0.66$, $n = 25$). This departure from 6.5 is not unexpected since ^{14}C uptake will include productivity based upon NH_4 as well as that on NO_3 .

4. Discussion

These data show that the larger cell-sized ($>5\ \mu\text{m}$) phytoplankton dominate the biomass and productivity in Monterey Bay, California. On average, the contribution

Table 4
Regressions of $> 5 \mu\text{m}$ fraction versus the total phytoplankton assemblage

	% Contribution	r^2	n	Relationship ^a
<i>Biomass Parameters</i>				
Particulate Nitrogen	81	0.75	34	$y = 0.81 x - 0.48$
Chlorophyll a	60	0.85	71	$y = 0.60 x - 0.14$
<i>Rate Parameters</i>				
$\rho^{15}\text{NO}_3$	87	0.89	33	$y = 0.87 x - 0.07$
$\rho^{15}\text{NH}_4$	65	0.91	26	$y = 0.65 x - 0.05$
$\rho^{14}\text{C}$	78	0.72	61	$y = 0.78 x - 0.95$

^a $y = > 5 \mu\text{m}$ size, $x =$ total assemblage.

by the $> 5\text{-}\mu\text{m}$ component to the total biomass parameters ranged from 60% for chlorophyll to 81% for PON, and for rate processes from 65% for NH_4 uptake and 78% for carbon assimilation to 87% for NO_3 uptake (Table 4). Although these are surface data, size-fractionated PON and $^{15}\text{NO}_3$ uptake measurements made throughout the euphotic zone showed the same pattern of contribution by the $> 5\text{-}\mu\text{m}$ size fraction (unpublished data). The MB region rarely displays a sub-surface-chlorophyll maximum, and populations within the surface-chlorophyll maximum (that account for the majority of the biomass), tend to have the same dominant species at all depth levels.

This pelagic ecosystem apparently fits the type 1 category of Legendre and Le Fèvre (1991), with primary production dominated by large cells, resulting in phytoplankton standing stocks being dominated by large cells (Tremblay and Legendre, 1994). The large phytoplankton in MB are most likely diatoms. Although taxonomic analyses are not available for all these cruises (SU92 and SU93), epifluorescence slides for the analysis of phytoplankton taxonomic groups were prepared and the phytoplankton enumerated as described by Chavez et al. (1991) from cruises (R/V *Point Lobos* time series cruises) every two to three weeks in MB during 1992–93, including one or two samples from the SU cruises. During 1992 centric diatoms accounted for about 30% of the total phytoplankton biomass and 50% of the $> 5\text{-}\mu\text{m}$ fraction. The remainder of the $> 5\text{-}\mu\text{m}$ fraction was composed of pennate diatoms, dinoflagellates and naked flagellates. Colonies of *Phaeocystis* were rarely if ever present. Occasionally during 1992, and at some of the SU stations, dinoflagellates dominated. During 1993, presumably in response to increased nutrient flux, the proportion of centric diatoms increased to 50% of the total phytoplankton biomass and 70% of the $> 5\text{-}\mu\text{m}$ fraction. The increases in $> 5\text{-}\mu\text{m}$ chlorophyll and PON during 1993 when compared to 1992 reflect this shift in species composition. While most of the flagellates are greater than $5\text{-}\mu\text{m}$ in all dimensions some are likely to pass through a $5\text{-}\mu\text{m}$ filter. On average the $< 5\text{-}\mu\text{m}$ fraction (*Synechococcus* and eukaryotic picoplankton) account for on the order of 30% of the biomass sampled in the time-series cruises. Early in 1992 there were higher proportions of *Synechococcus* sp., and later that year there were higher proportions of eukaryotic picoplankton.

The stations sampled in this study (Fig. 2) are representative of various stages of upwelling in MB, and our data compare well with other upwelling and eutrophic areas in which size fractionation studies have been carried out. For example, in the upwelling region of the northwestern Indian Ocean Owens et al. (1993) reported percentages for carbon and nitrogen assimilation of 90% by the $>5\text{-}\mu\text{m}$ fraction. Comparisons with other data sets are more difficult as different boundaries (often 10 or $20\text{-}\mu\text{m}$) have been used to delineate “large” cells. However, large cells (in the $10\text{--}212\text{-}\mu\text{m}$ fraction) contributed 65% to the total N assimilation in the Benguela upwelling shelf region (Probyn, 1985). The mean contribution of $>20\text{-}\mu\text{m}$ cells was 60% for PON and 66% for integrated N assimilation (Owens et al., 1991, calculated from Table 1) for the Scotia Sea where mixed-layer NO_3 concentrations ranged from $15\text{--}34\ \mu\text{M}$.

Our size fractionation data for MB support the scenario described by Raimbault et al. (1988) and Chisholm (1992), whereby to obtain high standing stocks or productivity rates, large cell-sized constituents are required. When percent biomass due to cells $>5\ \mu\text{m}$ are plotted against total biomass (Fig. 7 a and b), there are no data in the bottom right quadrant, i.e. smaller cells rarely show a significant contribution to the biomass at the higher values of either total PON or chlorophyll. The larger cells dominate at biomass concentrations above about $3\ \mu\text{g-at N l}^{-1}$ for PON or $4\ \mu\text{g l}^{-1}$ chlorophyll, and above these concentrations there are no values of % PON or chlorophyll $>5\ \mu\text{m}$ less than 50% (Fig. 7 a and b). Below these concentrations both large and small cells contribute. Chavez et al. (1991) observed virtually the same pattern for chlorophyll in the coastal transition zone off northern California, with cells $>5\ \mu\text{m}$ dominating at chlorophyll concentrations greater than $4\ \mu\text{g l}^{-1}$. He reported that the correlation between chlorophyll and abundance of diatoms was higher than any other taxonomic group. In MB our rate data (Fig. 8a and b) also show small cells to contribute to total uptake or fixation only at lower overall rates. Below about

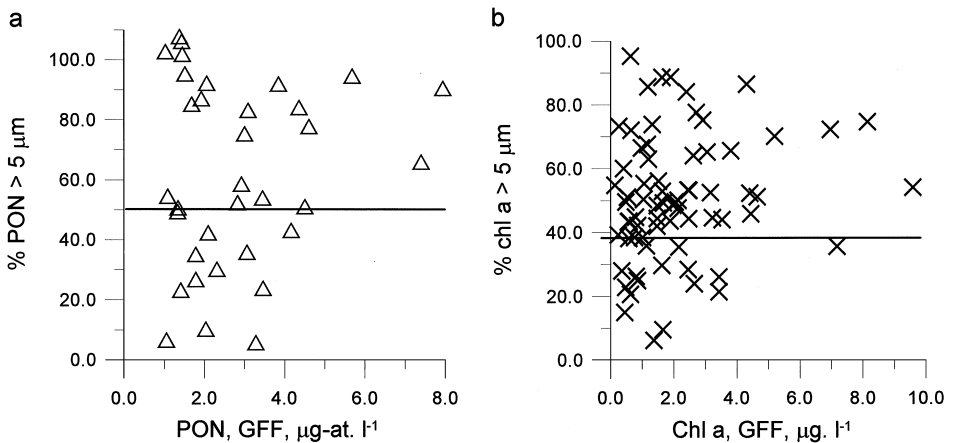


Fig. 7. Percent biomass in the $>5\ \mu\text{m}$ fraction versus total assemblage (GF/F data): (a) PON; (b) chlorophyll *a*.

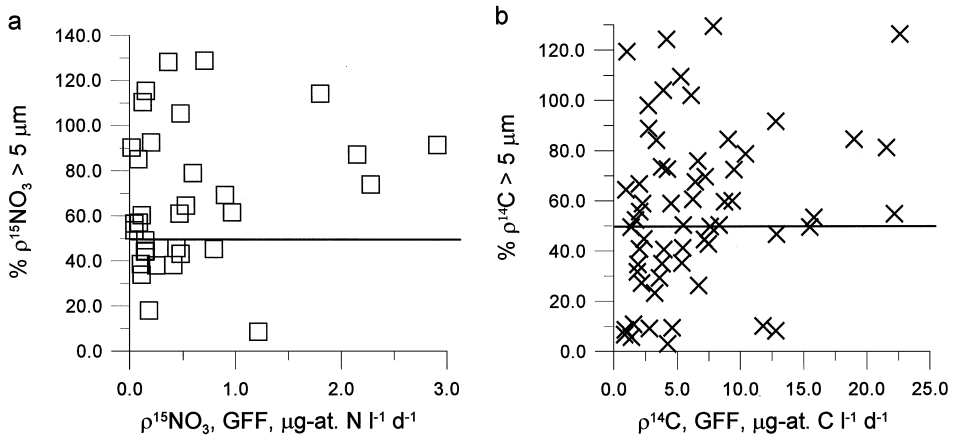


Fig. 8. Percent uptake rate in the $> 5 \mu\text{m}$ fraction versus total assemblage (GF/F data): (a) $\rho^{15}\text{NO}_3$; (b) $\rho^{14}\text{C}$.

$8 \mu\text{g-at C l}^{-1} \text{d}^{-1}$ (Fig. 8b) there is contribution to uptake by small and large cells, whereas above these levels, more than half the uptake is by $> 5\text{-}\mu\text{m}$ cells. To obtain new production rates greater than $1.5 \mu\text{g-at l}^{-1} \text{d}^{-1}$, cells $> 5\text{-}\mu\text{m}$ are important (Fig. 8a). These patterns (e.g. Figs. 7 and 8) with no data in the lower-right quadrant are the result of transforming the statistical linear relationships between large and small phytoplankton, (e.g. Figs. 3 and 4) into hyperbolic plots, and illustrate well the important contribution by the large cells.

There may be a nutrient threshold related to the size distribution of MB phytoplankton. At surface nitrate concentrations below about $10\text{--}12 \mu\text{M}$, the percent contribution by the large cells to PON and chlorophyll was highly variable whereas above this concentration, the contribution by the large cells was always more than 50% (Fig. 9a and b). There is a similar trend for ρNO_3 and ρC (Fig. 10a and b); at the highest nitrate concentrations both rates were dominated by the $> 5\text{-}\mu\text{m}$ cells whereas at low nitrate concentrations there was highly variable percent contribution by the large cells. Dauchez et al. (1996a,b) reported the same type of threshold, with large cells dominating only when NO_3 was elevated (above $\sim 3.5 \mu\text{M}$) during the spring bloom in a non-upwelling region over the Scotian shelf. Tamigneaux et al. (1995) also found the $> 5\text{-}\mu\text{m}$ fraction dominated when nutrient conditions were non-limiting in near-shore Baie des Chaleurs, Canada.

The ratio of Chl : PON of 1 obtained here is typical of coastal upwelling communities (e.g. MacIsaac et al., 1985 for 15°S , Peru; Probyn, 1985 for Benguela upwelling; etc). The ratio of C : NO_3 uptake in upwelling regions is likely to be variable as carbon uptake, and NO_3 utilization rates will be stimulated at different times following upwelling, with only a short period when a state of “balanced growth” will be achieved and Redfield ratios approximated. MacIsaac et al. (1985) reported C : N uptake ratios of $10\text{--}12$ for the total assemblage in surface samples of the upwelling

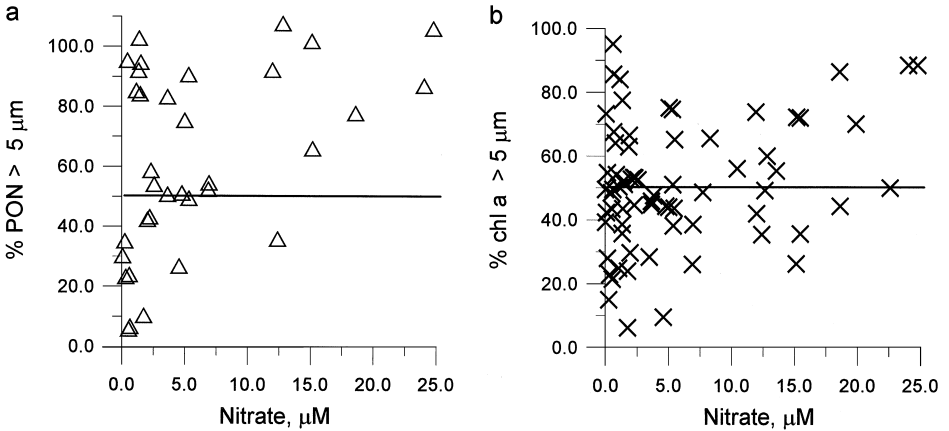


Fig. 9. Percent biomass in the $> 5 \mu\text{m}$ fraction versus surface nitrate concentration (μM): (a) PON; (b) chlorophyll *a*.

plume at 15°S . Kudela et al. (1997) measured C : N uptake ratios in MB near Redfield (~ 8 for surface values) for freshly upwelled water increasing to 15 for aged upwelled water and a maximum of about 22 in the frontal zone community. Our value of 10–11 by atoms for $\rho\text{C} : \rho\text{NO}_3$ for MB fits within these ranges well. The phytoplankton assemblage (including both large and small cells) is using other sources of nitrogen besides NO_3 to support carbon fixation.

As has been noted by others (e.g., Lenarz et al., 1995; Chavez, 1996; Pilskalns et al., 1996; Wilkerson and Dugdale, 1998), there were reduced nutrients, biomass and productivity in MB during the El Niño conditions in early 1992. Percent contribution to biomass and productivity by the $> 5\text{-}\mu\text{m}$ fraction also was reduced (Tables 2 and 3). These interannual differences in size-fractionated data are reflected in the species composition. The low-percent contribution by the larger cells (e.g. % PON $> 5 \mu\text{m} = 36\%$, Table 2), in March 1992 was due to an absence of diatoms; the phytoplankton were dominated by *Synechococcus* and red fluorescing picoplankton (Chavez, 1996). In contrast, during non-El Niño conditions of March 1990, analogous to our non-El Niño data from March 1993, Chavez (1996) describes high-productivity conditions associated with coastal upwelling and a bloom of centric diatoms.

The dominance of large phytoplankters may influence the amount of particle flux (or export) and trophic structure of a pelagic ecosystem (Probyn et al., 1990). With higher rates of productivity as occurs with greater dominance of the $> 5\text{-}\mu\text{m}$ fraction, export increases. Pilskalns et al. (1996) reported a high correlation between primary production and particulate organic carbon export in MB, and a high number of diatom valves in the sediment traps during the upwelling seasons. Size-fractionated biomass and production data were used to derive both potential export (Tremblay and Legendre, 1994) and by calculating *f*-ratios, the sinking flux of carbon (Tremblay et al., 1997), for use in models to estimate carbon export over wide time and space scales. The large phytoplankton cells should be considered as important components

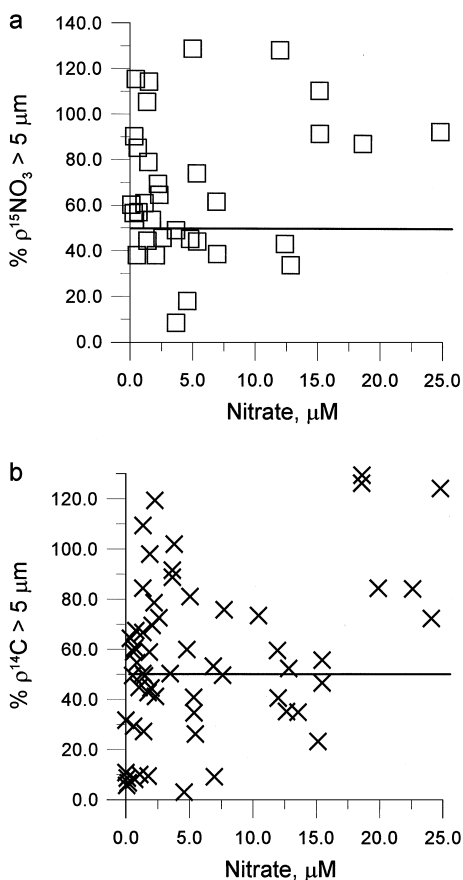


Fig. 10. Percent uptake rate in the > 5 μm fraction versus surface nitrate concentration (μM); (a) $\rho^{15}\text{NO}_3$; (b) $\rho^{14}\text{C}$.

in flux models of eastern-boundary and open ocean upwelling systems, e.g. Michaels and Silver (1988); Dugdale et al. (1995); Dugdale and Wilkerson (1998).

This study provides further evidence that carbon and nitrate assimilation by the larger autotrophs supports the high productivity of the MB coastal ecosystem. When considering the significant role that continental margins play in the global carbon budget (e.g. Walsh, 1991; Jahnke et al., 1990), the control that the larger cell-sized autotrophs could exert over carbon export and the biological pump in MB may be important also in the global productivity cycle.

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