Nitrogen, Phosphorus, Silica, and Carbon in Moreton Bay, Queensland, Australia: Differential Limitation of Phytoplankton Biomass and Production

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ABSTRACT: Subtropical estuaries have received comparatively little attention in the study of nutrient loading and subsequent nutrient processing relative to temperate estuaries. Australian estuaries are particularly susceptible to increased nutrient loading and eutrophication, as 75% of the population resides within 200 km of the coastline. We assessed the factors potentially limiting both biomass and production in one Australian estuary, Moreton Bay, through stoichiometric comparisons of nitrogen (N), phosphorus (P), silicon (Si), and carbon (C) concentrations, particulate compositions, and rates of uptake. Samples were collected over 3 seasons in 1997–1998 at stations located throughout the bay system, including one riverine end-member site. Concentrations of all dissolved nutrients, as well as particulate nutrients and chlorophyll, declined 10-fold to 100-fold from the impacted western embayments to the eastern, more oceanic-influenced regions of the bay during all seasons. For all seasons and all regions, both the dissolved nutrients and particulate biomass yielded N : P ratios <6 and N : Si ratios <1. Both relationships suggest strong limitation of biomass by N throughout the bay. Limitation of rates of nutrient uptake and productivity were more complex. Low C : N and C : P uptake ratios at the riverine site suggested light limitation at all seasons, low N : P ratios suggested some degree of N limitation and high N : Si uptake ratios in austral winter suggested Si limitation of uptake during that season only. No evidence of P limitation of biomass or productivity was evident.

Introduction

Nutrient enrichment of coastal and estuarine waters is a global concern. Estuaries are heavily affected by nutrient loading from application of fertilizers in agricultural and residential areas, sewage loadings, and groundwater and atmospheric inputs, with a tendency for high retention of nutrients once delivered to these systems (Boynton et al. 1982; Nixon et al. 1986; Kemp and Boynton 1992; Smil 2001). An understanding of the factors that may be limiting primary production and the time and space scales over which such limitation may be occurring is important for effective management of nutrient delivery to these systems.

Subtropical estuaries have received comparatively little attention in the study of nutrient loading and subsequent nutrient processing relative to temperate estuaries. In some cases, these estuaries have not become eutrophied to the same extent as many temperate estuaries. Australian estuaries tend to be oligotrophic (Jeffrey et al. 1990), and strong gradients in phytoplankton processes can develop between river-influenced coastal embayments and the more oceanic-influenced regions (Heil et al. 1998; Jones et al. 1998; Harris 2001). Australian estuaries are susceptible to increased nutrient loading and eutrophication, as 75% of the population resides within 200 km of the coastline. In contrast to many temperate systems, nutrient delivery to Australian, as well as many other, subtropical estuaries is highly pulsed corresponding to the wet season of the year (Findlayson and McMahon 1988; McComb and Davis 1993; Young et al. 1996). Such nutrient inputs to Australian coastal regions can equal annual point source inputs (Heil et al. 1998; Moss 1998). The goal of this study was to determine the relationships between nutrient loading and the processing of these nutrients within the water column of Moreton Bay, a subtropical estuary in northeastern Australia.

In the past decade the issue of coastal eutrophication has received considerable attention from scientists, managers, and law makers. In particular, the question of whether systems are limited by nitrogen (N) or phosphorus (P) has become of primary importance in this debate. This debate is

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being carried on from the coast of Australia to the Florida Shelf and the Gulf of Mexico, the Chesapeake Bay, the Baltic Sea, the plume of the Yangtze River, and elsewhere. This study applies a stoichiometric approach to assessing nutrient limitation. We extend the traditional comparison of ambient nutrient ratios to include a comparison of the inputs, particulate composition, and uptake rates of N, P, silicon (Si), and carbon (C). For this study area we also extend the work of O'Donohue and Dennison (1997) and O'Donohue et al. (2000), which focused on a more limited suite of nutrients and processes. We use the current results to highlight the complexities of interpretation of nutrient limitation. Through the multiple ratio approach we show that nutrients may be limiting phytoplankton processes (production, nutrient uptake) and biomass differently. We further demonstrate that assumptions and extrapolations to system-wide nutrient limitation may be fraught with difficulty. This study was conducted as part of the Moreton Bay and Brisbane River Wastewater Management Study; other aspects of this program focused on nutrient cycling processes within other members of the biota and the sediment (Dennison and Abal 1999).

Fig. 1. Sampling locations for the Moreton Bay estuary and riverine system.

STUDY AREA

Moreton Bay, located on the southeast coast of Queensland, Australia, is a shallow (mean depth of 8 m), well mixed estuarine system that receives inflow from two dominant river systems (Fig. 1). The Brisbane River, with a catchment of 13,556 km², and the Logan River, with a catchment of 3,650 km² (O'Donohue and Dennison 1997), deliver the runoff of the city of Brisbane and surrounding suburban shires, as well as nearby rural areas (Moss 1998). A third river, the Caboolture, drains a smaller catchment area, 510 km², which contains both agricultural and rural areas (O'Donohue et al. 2000). Western Moreton Bay is characterized by high nutrient and chlorophyll *a* (chl *a*) concentrations and is considered eutrophic, while the eastern Bay is characterized by low inorganic nutrient and chl *a* concentrations (Dennison and Abal 1999). Eastern Moreton Bay is bordered by large sand barrier islands, Moreton and Stradbroke Islands, which restrict water exchange between Moreton Bay and the eastern Coral Sea and developed areas along the coast south of the Bay. Strong lateral gradients persist in Moreton Bay. Eastern Moreton Bay is characterized by residence times on the order of days to weeks, oceanic salinities, and relatively clear water. Western Moreton Bay is characterized by residence times on the order of weeks to months, variable salinities ranging
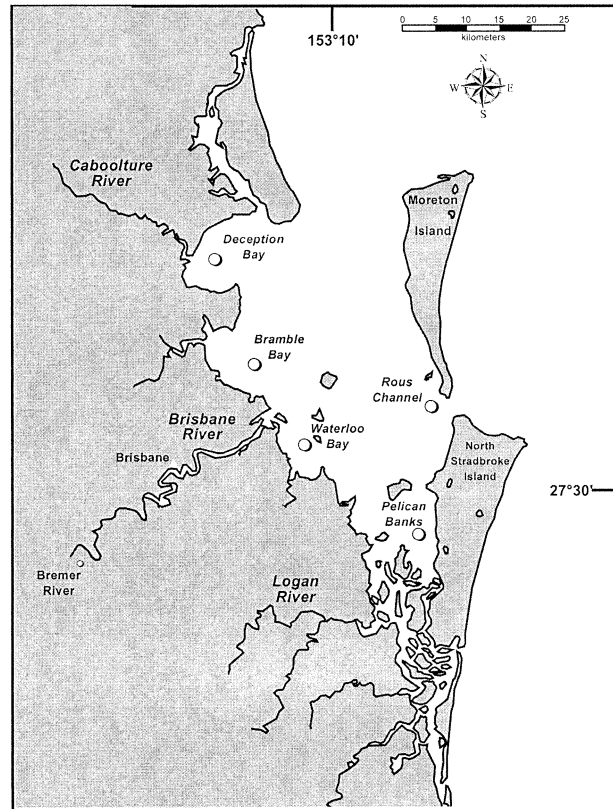
from oceanic to fresh, and turbid water (Dennison and Abal 1999).

Materials and Methods

SAMPLING

This study encompassed three periods of sample collection and experimentation: austral spring, September 18–28, 1997 (referred to as September); austral summer, January 27-February 7, 1998 (referred to as February); and austral winter, July 26–31, 1998 (referred to as July). Sample sites (Fig. 1) were selected based on spatial distribution and, in some cases, on established monitoring stations for productivity measurements (O'Donohue and Dennison 1997; O'Donohue et al. 2000). A riverine station was located in the Bremer River, a tributary of the Brisbane River, three western bay stations were located in the three major bays (Deception, Bramble, and Waterloo) and two eastern bay stations (Pelican Banks and Rous Channel) were located closer to the eastern islands. The riverine site represents the end member of nutrient source inputs. It should be noted that some other studies (e.g., O'Donohue et al. 2000) have used the Logan riverine inputs for nutrient source comparison. For

the purposes of data analyses and interpretation, data from the three western bays were averaged into a western bay data average and stations within the eastern bay were averaged within an eastern bay data average.

Stations were sampled at a rate of one per day during each sampling period to allow sufficient processing time for all the simultaneous parameters investigated. Sampling times were approximately 0700 h and 2100–2200 h. Water temperature and salinity were measured on site with a Horiba Model DU Water Quality Checker. Water samples for all nutrient analyses were collected in multiple acid-rinsed, 20-l black polycarbonate drums. These were lowered off the stern of the boat, rinsed twice with ambient seawater, and filled 10–15 cm below the water surface. All drums were stored in the shade and returned to the laboratory within 1–2 h of sampling, except those from Bremer River, which required longer transit time. Concurrent with the collection of water samples, samples were taken for analysis of phytoplankton composition.

NUTRIENT AND BIOMASS CONCENTRATIONS

Upon collection and return to the laboratory, samples were processed as rapidly as possible. Triplicate water samples were filtered through Whatman GF/F filters and immediately frozen for spectrophotometric determination of chl a concentration (Parsons et al. 1984). Filtrate from chl a processing was retained for the analysis of ammonium (NH_4^+), dissolved oxides of N (NO_3^- and NO_2^-), and filterable reactive P (PO_4^{3-}). These analyses were conducted by the Queensland Government Chemistry Laboratory according to the methods of Clesceri et al. (1989) based on the standards methods of Parsons et al. (1984). Concentrations of urea were determined according to the urease method (Parsons et al. 1984). Concentrations of silicate ($Si(OH)_4$) were also determined according to Parsons et al. (1984) on water samples filtered through 0.45-μm Millipore filters. Additional nutrient measurements were made for the determination of total dissolved N, through high temperature combustion (Antek Instruments; Bronk et al. 2000), and total dissolved P (Lambert and Oviatt 1986). The latter results will be reported elsewhere.

Although the focus of this paper is on inorganic nutrient inputs, the organic form of N urea is also included in this data analysis. This was done in order to provide the most accurate available data on total N availability and rates of total N uptake. As urea can represent a significant fraction of total N uptake in some estuaries and coastal waters (e.g., Glibert et al. 1995, 2005; Kudela and Cochlan 2000),

only examining the inorganic N forms would lead to biases (e.g., Dodds 2003).

Concentrations of particulate N (PN) and particulate C (PC) were determined on triplicate samples filtered through precombusted (2 h, 450°C) Whatman GF/F filters, using a Control Equipment CHN analyzer. Concentrations of particulate phosphate (PP) and particulate silicate (PSi) were analyzed according to the method of Solárzano and Sharp (1980) and Paasche (1980), respectively.

PRODUCTIVITY AND NUTRIENT UPTAKE RATES

Nitrogen Uptake

Rates of N uptake were measured using stable isotope techniques (Glibert and Capone 1993). Experiments were initiated by the addition of ^{15}N substrates (NH_4^+, NO_3^-, urea) to whole water samples at concentrations that represented roughly 10% of ambient values. All experimental treatments were run in triplicate. Incubations were conducted in polycarbonate bottles under ambient light and temperature conditions in incubators that received natural light conditions and that were maintained within 1–2°C of ambient water temperature for approximately 0.5–1 h. Samples were subsequently gently filtered onto precombusted GF/F filters, dried, and analyzed using mass spectrometry. A Nuclide 3″ 60° Sector mass spectrometer was used for these analyses. Rates of uptake were calculated according to Glibert and Capone (1993) and extrapolated to daily rates using day and night values.

Phosphorus Uptake

Rates of PO_4^{3-} uptake were measured within 2–3 h of collection on samples from selected sites according to the method of Lean and Nalewajko (1979). Carrier free $^{32}PO_4^{3-}$ was added to each sample in duplicate, acid-cleaned plastic bottles, at trace levels. The specific activity of the stock solution was measured in triplicate prior to each uptake measurement. Samples were incubated between 20 and 60 min under artificial light, which was provided by four Eye Lighting Industries Type HL-500 spotlights. Incubations times were established prior to uptake measurements by adding $^{32}PO_4^{3-}$ to a station water sample and subsampling every 3 min for 24 min. Time zero and formalin-treated (final concentration 5%) samples, incubated for the duration of the experiment, served as controls to correct for abiotic uptake of $^{32}PO_4^{3-}$ (Rivkin and Swift 1982; Herbland 1984). Abiotic adsorption was never more than 15% of total uptake rates, but the greatest adsorption due to non-living particles was always present in western bay samples. At the end of the incubations, samples were filtered onto 0.22-μm filters and immediately placed in 5-ml

scintillation vials with 5 ml of Beckman Redi Safe scintillation fluid. Radioactivity of samples was measured with a Packard Tricarb 1600 Scintillation Counter.

Silica Uptake

Rates of $Si(OH)_4$ uptake were measured by the depletion of reactive $Si(OH)_4$ from the samples with the appropriate chemical blanks (Werner 1977). Water samples were transferred to duplicate, acid-rinsed, plastic bottles and were either amended by the addition of 15 µmol l^{-1} $Si(OH)_4$ or formalin (final concentration 5%) or left unamended as a control for measurement of potential $Si(OH)_4$ regeneration during the incubation period. The concentration of the added $Si(OH)_4$, 15 µmol l^{-1}, was determined in preliminary experiments (data not shown) as optimal to measure uptake over the concentration range present in Moreton Bay. Samples were incubated for 2–3 h as described for N uptake measurements, then each sample was filtered through a 0.45-µm Millipore filter, and the filtrate was immediately frozen. Concentrations of $Si(OH)_4$ were subsequently determined according to Parsons et al. (1984). Samples with salinity <25 were allowed to equilibrate in a 4°C refrigerator for 2 wk prior to measurement. Uptake rates were determined by concentration differences over time after correction for any abiotic uptake or regeneration of $Si(OH)_4$ in samples during the incubation.

Primary and Bacterial Productivity

Primary productivity was measured by the incorporation of ^{14}C-bicarbonate (Parsons et al. 1984; O'Donohue and Dennison 1997). Replicate whole water samples (100 ml) from each site were dispensed into clean plastic bottles, to which aqueous $H^{14}CO_3$ (final concentration of 4 µCi) was added. Samples were incubated for up to 4 h under similar conditions as for N uptake then filtered onto 0.45-µm Nuclepore filters to terminate the incubations (O'Donohue and Dennison 1997). Filters were placed into 5-ml scintillation vials and two drops of 5N HCl were added. Beckman Ready Safe scintillation fluid (4 ml) was added to each vial and radioactivity as disintegrations per minute of radioactivity of samples was measured on a Scintillation Counter (Packard Tricarb 1600). Total CO_2 concentrations in the samples were determined from carbonate alkalinity (Parsons et al. 1984).

Bacterial productivity was measured by the incorporation of the radiolabeled precursor of DNA, ^{3}H-thymidine (Fuhrman and Azam 1982). Triplicate 30-ml samples were dispensed into acid-washed polycarbonate flasks. Control samples, with additions of 1% formalin, were used to correct for abiotic uptake of label. ^{3}H-thymidine was added to a final concentration of 5 nmol l^{-1}, and samples were incubated for 0.25–0.5 h under similar conditions as for N uptake. Subsamples (10 ml) were pipetted from each sample into polycarbonate test-tubes, which were then placed on ice for 1 min. Additions of 10 ml ice-cold 10% trichloractetic acid (TCA) were added and maintained on ice for 5 min. Samples were then filtered through 0.22-µm Poretics filter under gentle vacuum. Filters were rinsed 5 times with 1 ml 5% TCA, then with 90% ethanol. Radioactivity of filters was determined as described for primary productivity measurements. Bacterial productivity was calculated as pmol thymidine l^{-1} h^{-1} and µg C l^{-1} h^{-1} based on equations in Fuhrman and Azam (1982). Daily, molar rates were then calculated.

Results

Dissolved Nutrient Concentrations

Nutrient concentrations at the riverine end-member station were high for all inorganic nutrients and for all seasons measured; concentrations of dissolved inorganic N + urea exceeded 100 µmol l^{-1}, while those of PO_4^{3-} exceeded 30 µM, and $Si(OH)_4$ exceeded 80 µmol l^{-1} (Fig. 2). Concentrations rapidly declined from the riverine source to the western embayments and the eastern, more oceanic-influenced regions of the Bay during all surveys. Decreases on the order of 10-fold to 100-fold were noted for each nutrient from the riverine source to the western bays.

Nitrogenous nutrient availability changed with region and season in terms of the relative proportion of the dominant N form. At the riverine end-member site virtually all of the N was in the form of NO_3^- (Fig. 2). At the other sites, NO_3^- contributed from a low of 6% in the eastern region in July to 36% in the western region in September and February. The proportion that NH_4^+ contributed to N availability was highest in July, representing 78% in both the western and eastern regions. The contribution of urea to N availability increased from the western to the eastern region, representing a maximum of contribution of 55% in the eastern region in September.

Particulate Nutrients and Phytoplankton Biomass

Particulate nutrient concentrations also declined from the riverine sites to the eastern bay sites (Fig. 3). Spatial gradients were reduced compared with the dissolved nutrients, and there were greater differences between seasons and between nutrients. Concentrations of PN exceeded 50 µmol l^{-1} at the riverine site in September, but were on the order of
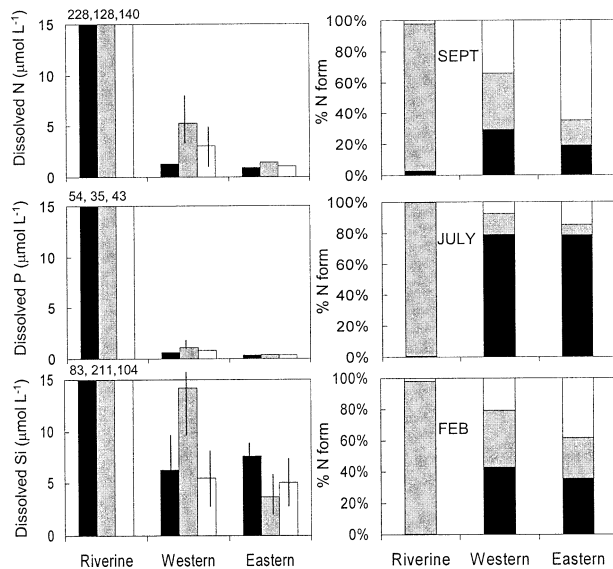
Fig. 2. Mean ambient nutrient concentrations ($\mu mol\ l^{-1}$) for the three major dissolved nutrients: nitrogen, phosphate, and $Si(OH)_4$ for the regions of Moreton Bay. Black bars represent data for September, gray bars are for February, and clear bars are for July. Values given at the top of bars indicate actual value when the scale was exceeded. Error bars represent standard deviations of the means of the stations within each region. Where error bars are not given, they are too small to be displayed on the graph. Panels to the right indicate the fraction (as percent of the sum of the three measured nitrogen substrates) of dissolved nitrogen as NH_4^+ (black), NO_3^- (gray), and urea (clear) for the three sampling periods.

Fig. 3. Mean ambient particulate nutrient concentrations ($\mu mol\ l^{-1}$) for the major particulate nutrients (nitrogen, phosphorus, biogenic silica, and carbon), chl a ($\mu g\ l^{-1}$), and PN : Chl a ($\mu mol\ l^{-1}$: $\mu g\ l^{-1}$) for the regions of Moreton Bay. Black bars represent data from September, gray bars from February, and clear bars from July. Values given at the top of bars indicate actual value when the scale was exceeded. Error bars represent standard deviations of the means of the stations within each region. Where error bars are not given, they are too small to be displayed on the graph.

25 $\mu mol\ l^{-1}$ or less at this site during the other months of measurements. Concentrations at the western and eastern sites were <10 $\mu mol\ l^{-1}$ during all seasons. Concentrations of PP ranged from 3.42 (±3.40) to 51.16 $\mu mol\ l^{-1}$, but were significantly higher during the month of July at all sites relative to the other periods of sampling. At the riverine site, concentrations were <20 $\mu mol\ l^{-1}$ in September and February, but exceeded 50 $\mu mol\ l^{-1}$ in July. Likewise, at the western and eastern sites, concentrations in July were more than twice the concentrations previously measured. Patterns in PSi paralleled those of PP, with two exceptions. Concentrations were highest at all sites in July, and these values were several-fold higher than those measured at other times of the year. Concentrations were also high in September at the riverine site.

Concentrations of PC varied from 23.58 (± 3.49) to 196 $\mu g\ l^{-1}$. Concentrations were highest in February and July at the riverine site, up to 196 $\mu g\ l^{-1}$, and were lowest in July at the western and eastern bay sites (Fig. 3).

Concentrations of chl a also showed a sharp gradient from riverine to western bay to eastern bay sites (Fig. 3). At the riverine site, values ranged from
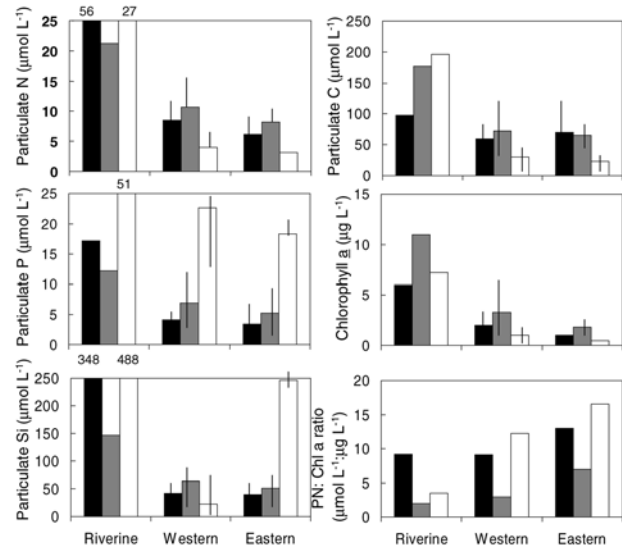
6.2 to 11.3 $\mu g\ l^{-1}$, but only 0.2–1.13 $\mu g\ l^{-1}$ in the east and 0.5–3.3 $\mu g\ L^{-1}$ in the west. Concentrations were approximately 2-fold higher in all three regions in February compared to September.

The ratio of PN : chl a ($\mu mol\ l^{-1}$: $\mu g\ l^{-1}$) is a useful indicator of the fraction of the PN that is composed of autotrophic plankton. Normally, a ratio of 1:1 is taken to be representative of biomass that is composed of healthy phytoplankton (McCarthy and Nevins 1986). With the exception of the riverine site in February, all PN : chl a ratios exceeded 1:1. Ratios of PN : chl a > 8 were observed for the river in September and for the western and eastern sites in September and July (Fig. 3).

RATES OF NUTRIENT UPTAKE

The patterns in the rates of nutrient uptake were quite different between the substrates measured (Fig. 4). For N, uptake rates ranged from 1.35 (±0.71) to 73.15 $\mu mol\ l^{-1}\ d^{-1}$ and were higher at the riverine site than the western or eastern bay sites during September and February. During July, the rates for all three regions were very low. The dominant form of N taken up shifted from the riverine end-member station to the western and eastern bay sites, and from sampling period to sampling period. The dominant fraction of N taken up at the riverine site was NO_3^-, representing 48–
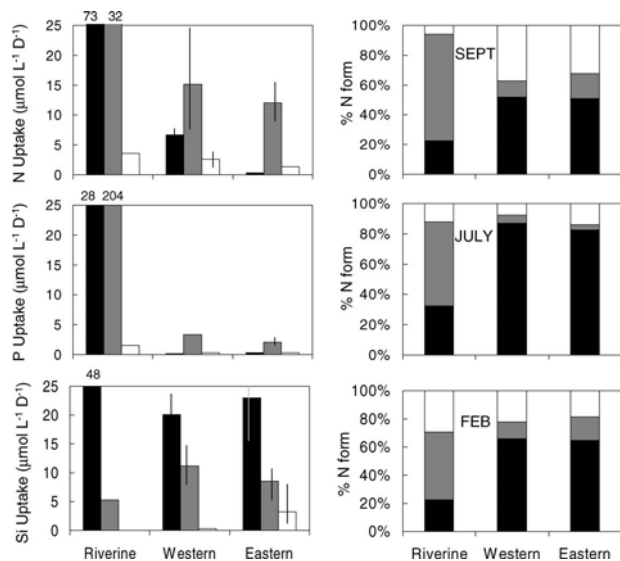
Fig. 4. Mean rates of uptake (μmol l^{-1} d^{-1}) for nitrogen, phosphate, and Si(OH)$_4$ for the regions of Moreton Bay. Black bars represent data from September, gray bars from February, and clear bars from July. Values given at the top of bars indicate actual value when the scale was exceeded. Error bars represent standard deviations of the means of the stations within each region. Where error bars are not given, they are too small to be displayed on the graph. The right panels show the fraction (as percent of the sum of the three measured nitrogen substrates) of nitrogen uptake as NH$_4^+$ (black), NO$_3^-$ (gray), and urea (clear) for the three sampling periods.

71% of total N uptake, while NH$_4^+$ uptake ranged from 23% to 32% and urea uptake ranged from 6% to 29%. Uptake of N was dominated by NH$_4^+$ at both the western and eastern bay sites, although it was proportionally greatest during the July sampling, when it averaged above 80%. Urea uptake was proportionally greatest during September, when it represented more than 30% of total N uptake. There were no significant differences in the proportional use of each N substrate between western and eastern bay sites for any of the sampling periods. Applying the relative preference index to these data (e.g., McCarthy et al. 1977), NH$_4^+$ and urea were found to be always used preferentially at the riverine site. Preferential uptake of NH$_4^+$ was also observed at the other sites in the spring and summer, while urea was used preferentially at the other sites during the winter sampling.

For PO$_4^{3-}$ uptake, the highest rates were found at the riverine site, but only for September and February (Fig. 4). Rates of uptake of PO$_4^{3-}$ measured in February (204 μmol l^{-1} d^{-1}) were roughly an order of magnitude higher than those measured in September (28.61 μmol l^{-1} d^{-1}), which, in turn, were about an order of magnitude higher than in July (1.49 μmol l^{-1} d^{-1}) in the river region. Although controls were run to correct for

chemical adsorption of PO$_4^{3-}$ onto particulates, it is possible that at the riverine station there was additional chemical adsorption of PO$_4^{3-}$ that exceeded that accounted for in the controls. Uptake rates of PO$_4^{3-}$ for the eastern and western stations ranged from 0.17 to 3.36 μmol l^{-1} d^{-1}.

Rates of Si(OH)$_4$ uptake showed the least variability from bay region to bay region compared with the rates of uptake of the other nutrients, with values ranging from 0.00 to 48.24 μmol l^{-1} d^{-1} (Fig. 4). The highest measured rate was in the river in September (48.24 μmol l^{-1} d^{-1}), and rates measured at the other sites remained roughly half those in the river. During February, the highest uptake rate for Si(OH)$_4$ was observed in the western bay (11.20 $\pm$ 6.00 μmol l^{-1} d^{-1}), and for July, the highest rate was noted in the eastern bay (3.23 $\pm$ 4.58 μmol l^{-1} d^{-1}), with virtually nondetectable rates of Si(OH)$_4$ uptake at the riverine site at this time.

RATES OF PRIMARY AND BACTERIAL PRODUCTIVITY

Rates of C uptake were highest at all times measured in the western bays relative to both the riverine and eastern bay sites (Fig. 5). For C uptake, the rates were highest during the month of February in the western and eastern regions, with little seasonal difference observed at the riverine site.

Bacterial productivity was highest at the riverine site except in February when the western and riverine sites had similar rates (Fig. 5). The riverine site had significantly greater activity in September (16.4 μmol C l^{-1} d^{-1}) than any other sampling time or site. Eastern bay sites routinely had the lowest bacterial productivity.

The comparison of primary to bacterial productivity demonstrates the gradients in autotrophic and heterotrophic production (Fig. 5). Ratios of primary to bacterial production at the riverine site were consistently low and were <1.0 for September, demonstrating the overwhelming contribution of bacterial production to total production in this region. The ratio of primary to bacterial production increased sharply in the western and eastern bays for all seasons.

Discussion

The concept of limiting nutrients in a eutrophic system is now recognized to be very complex (e.g., Nixon 1995; Cloern 2001). The ecosystem response to nutrient enrichment, or eutrophication, is a continual process rather than a static condition or a trophic state (Cloern 2001; Smayda 2005). Eutrophication includes the complex suite of processes that affect system-level responses, not just
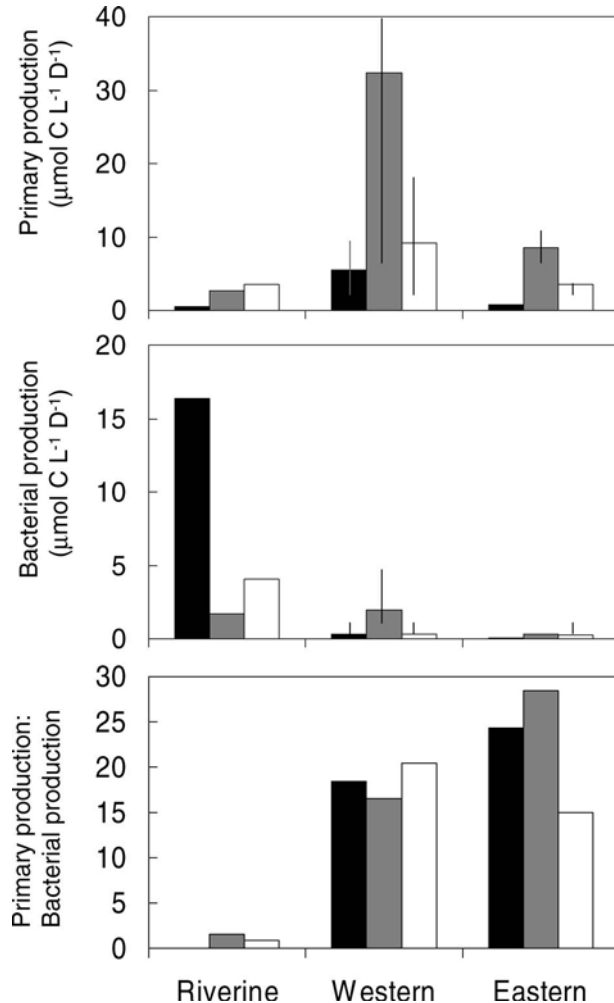
Fig. 5.   Mean rates of carbon uptake (μmol C l^{-1} d^{-1}), bacterial production, and the ratio of primary to bacterial productivity (μmol C l^{-1} d^{-1} : μmol C l^{-1} d^{-1}) for the three regions (riverine and western and eastern bay sites). Black bars represent data from September sampling period, gray bars from the February sampling period, and clear bars from the July period. Error bars represent standard deviations of the means of the stations within each region.

phytoplankton production (Cloern 2001). Changes in community composition of the phytoplankton, such as the development of harmful algal blooms, development of hypoxia and anoxia, and other habitat disturbances alter trophic interactions and biogeochemical processes. Although no longer viewed as an isolated factor in ecosystem responses, nutrients remain the center of focus for science and management of many coastal waters. It is of critical importance that approaches for assessing nutrient limitation be applied appropriately. The results of this paper highlight several factors that are not frequently considered when assessing nutrient limitation: differential limitation of growth and

biomass, and the difficulties in extrapolation from individual ecosystem components to limitation at the system-wide level.

Nutrient limitation of nutrient uptake and primary productivity in Moreton Bay is also complex, as is true for most estuarine systems. In this analysis we used comparisons of ratios of N, P, Si, and C uptake determined simultaneously, in comparison with the ratios of the same elements in the ambient nutrient pool and in the algal biomass. This approach extends the typical application of nutrient ratios, in which the ratios of nutrients in the ambient pool only are compared (e.g., Dodds 2003). Use of ambient nutrients alone may lead to biases in nutrient status for a number of reasons, including the fact that not all forms, especially organic forms, of nutrients are often considered and different nutrient forms may be used preferentially. We included urea in the suite of nutrient forms in the N ratios, as it is increasingly recognized to not only be significant in some coastal waters (e.g., Glibert et al. 2006), but often preferred by many phytoplankton. Although rates of uptake of dissolved organic substrates, other than urea, were not measured here, it is probably reasonable to assume that organic C or N substrates did contribute to the nutrition of some of these organisms. Many flagellates, including dinoflagellates are capable of mixotrophy and osmotrophy (Berg et al. 1997; Stoecker et al. 1997; Lewitus et al. 1999; Glibert et al. 2001). The extent to which organic substrates may have helped alleviate N or light limitation is unknown and is certainly an important question for future study.

NUTRIENT LIMITATION OF BIOMASS AND UPTAKE PROCESSES

In attempting to understand the effects of nutrient availability on an ecosystem, it is important to make the distinction between effects on total biomass and effects on nutrient assimilation processes or production rates. As initially developed conceptually by Caperon et al. (1971), and applied more recently to the Chesapeake Bay ecosystem (Malone et al. 1996), nutrient enrichment responses can be viewed in a manner analogous to saturating response curves. Responses to nutrient perturbations may fall in the maximum response or the minimum response region of the curve. The maximum physiological response region of the relationship is the initial slope of the saturation curve, not the region in which maximum biomass has been attained. Under maximum response mode, the responses are rapid, usually driven by physiological adaptations, but may not necessarily result in significant biomass changes. Analogously, the minimum physiological response region is that

in which maximum biomass is reached. In the minimal response mode, incremental increases in nutrient availability do not result in significant changes in responses as nutrient uptake or productivity may be operating at maximal levels, but increases in biomass may result on a slower time scale. Different nutrients (or other abiotic factors) may limit biomass and production.

Jassby et al. (2002) argue that in systems for which phytoplankton are the primary factor regulating light attenuation, changes in biomass will be compensated for by changes in photic depth, leading to larger changes in biomass than productivity. Extreme examples of differences in limitation of biomass and productivity can be found in Hudson River estuary, where grazing pressure on phytoplankton has increased due to the invasion of the zebra mussel (*Dreissena polymorpha*) which has been the controlling factor of biomass for more than a decade, but the estuary has, in fact, exhibited enhanced primary production (Caraco et al. 1997; Howarth et al. 2000). Narragansett Bay has also witnessed an increase in primary production from increased sewage loading, but a long-term decrease in phytoplankton biomass due to changes in the zooplankton community, as well as temperature changes (Li and Smayda 1998). Stoichiometric relationships between nutrients in dissolved and particulate form, and the ratio in which they are consumed, are also useful in determining which may be limiting and whether they limit biomass or production. With this conceptual framework in mind, we aim to differentiate the factors that are limiting to plankton biomass and to primary or bacterial productivity in the three distinct regions of Moreton Bay.

LIMITATION OF BIOMASS

In order to determine limitation of biomass, the ratios of dissolved nutrients were compared to the ratios of the particulate biomass. Under conditions in which nutrients are supplied in proportion to that which is typically required to support biomass, the ratio of N : P is 16:1 (Redfield et al. 1963), and the ratio of N : Si is 1:1 when the phytoplankton biomass is diatom dominated (Redfield et al. 1963; Conley et al. 1993).

For all seasons and all regions, both the dissolved nutrients and the particulate biomass yielded N : P ratios <6, and for the particulate nutrients, this ratio in some cases was <1 (Fig. 6). The extremely low N : P ratios of particulate biomass are strongly indicative of N limitation. A similar analysis for the ratios of N : Si further supports the notion that N is the nutrient limiting biomass in Moreton Bay. The ratios of N : Si for the dissolved nutrient pool were <1 for 7 of the 9 analysis periods. Only in the
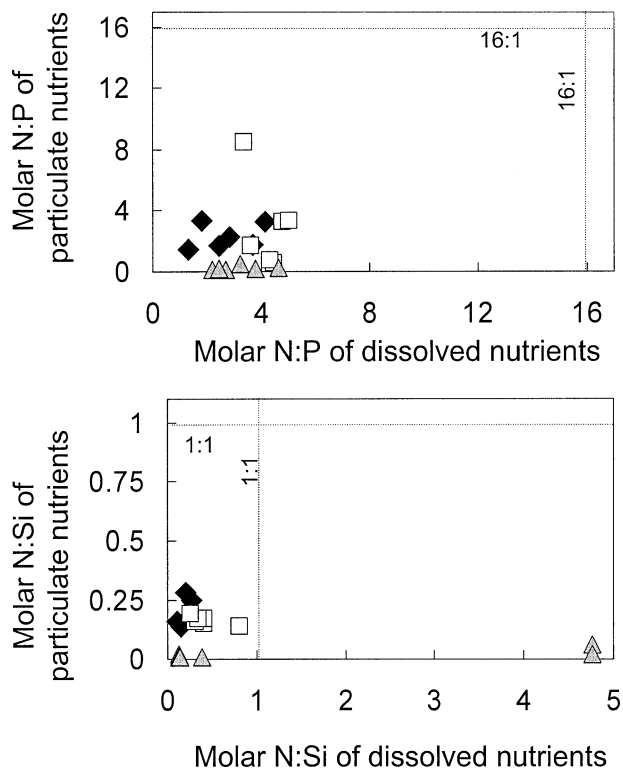

Fig. 6. The relationship between the molar ratio of the dissolved nutrient pool and the molar ratio of the particulate material for N : P and N : Si. The dashed lines indicate the Redfield stoichiometric proportions. ◆ = September; ● = February, and △ = July.

riverine region in July was this ratio >1.0, suggesting that during this limited time $Si(OH)_4$ was potentially limiting. The ratio of N : Si for all the regions and seasons studied was <0.25 indicating strong limitation by N relative to $Si(OH)_4$ for biomass.

The suggestion of N limitation of total biomass in these data are consistent with previous reported findings on the stimulation of chl *a* synthesis in several-day bioassay experiments with Moreton Bay phytoplankton communities (O'Donohue and Dennison 1997; Jones et al. 1998; O'Donohue et al. 1998). Related bioassay experiments conducted on seagrasses (Udy and Dennison 1997) and macroalgae (Jones et al. 1996) also have demonstrated a consistent, strong response to N addition.

Although plankton biomass within Moreton Bay as a whole must be considered limited by N, there are sites within the system that are experiencing an excess of N inputs. Bramble Bay is the most degraded embayment within the Moreton Bay system (Dennison and Abal 1999), and the western sites had consistently elevated concentrations of all the dissolved nutrients measured during the course of this study (Fig. 2). Bramble Bay once had

extensive seagrass beds (Abal et al. 1998; Dennison and Abal 1999), but no seagrass in this region can now be documented (Dennison and Abal 1999), suggesting that water quality degradation has been occurring. Direct inputs of sewage have been previously traced into Bramble Bay using ^{15}N isotopic signatures (Dennison and Abal 1999; Costanzo et al. 2001). As a result of these nutrient inputs, the highest chl a biomass and PN composition were found in Bramble Bay, and to a lesser extent, Waterloo Bay. The effect of these nutrient inputs appears to now be localized within these western Moreton Bay embayments.

LIMITATION OF PRODUCTIVITY AND NUTRIENT UPTAKE

The stoichiometry of nutrient and C uptake has also been shown to be useful in determining potential limitation of productivity and nutrient uptake (Glibert et al. 1995; Metzler et al. 1997). Here we compare the ratios of uptake for all substrates for each region.

The mean N : P uptake ratios for all seasons studied showed a general increasing trend, from the riverine to the eastern bay regions, with values bracketing Redfield proportions in the western and eastern bays (Fig. 7). In spite of the exceptionally high concentrations of dissolved N in the delivery of the water from the Bremer River to Moreton Bay, the rates of uptake were indicative of limitation by N rather than P in the river. Even though the dissolved and particulate nutrients indicated strong N limitation based on their ratios of N : P, which were well below Redfield throughout much of the western and eastern Bay, the uptake of these nutrients reflected nearly balanced N and P nutrition.

The C : N uptake ratios for all seasons and all locations were below Redfield proportions, with the lowest values observed in the riverine region and in September (Fig. 7). These low overall ratios likely reflect several contributing factors. In the riverine region, where extremely low C : N uptake ratios were observed, the rates of C fixation were most likely limited by light. Many southeast Queensland rivers, including Brisbane and Logan, contain high sediment loads (Moss 1990). Influence of light limitation within the rivers is well described (Jones et al. 1998), but light limitation can also extend from the river mouths through the river plume regions in Moreton Bay (O'Donohue and Dennison 1997; Heil et al. 1998). With distance from the river mouth, there is a commensurate decrease in nutrient concentrations, reducing the effect of increased light availability.

C : N uptake ratios in the eastern region also were indicative of C limitation, particularly in February and September. Possible factors contributing to reduced C uptake in the east are photo-
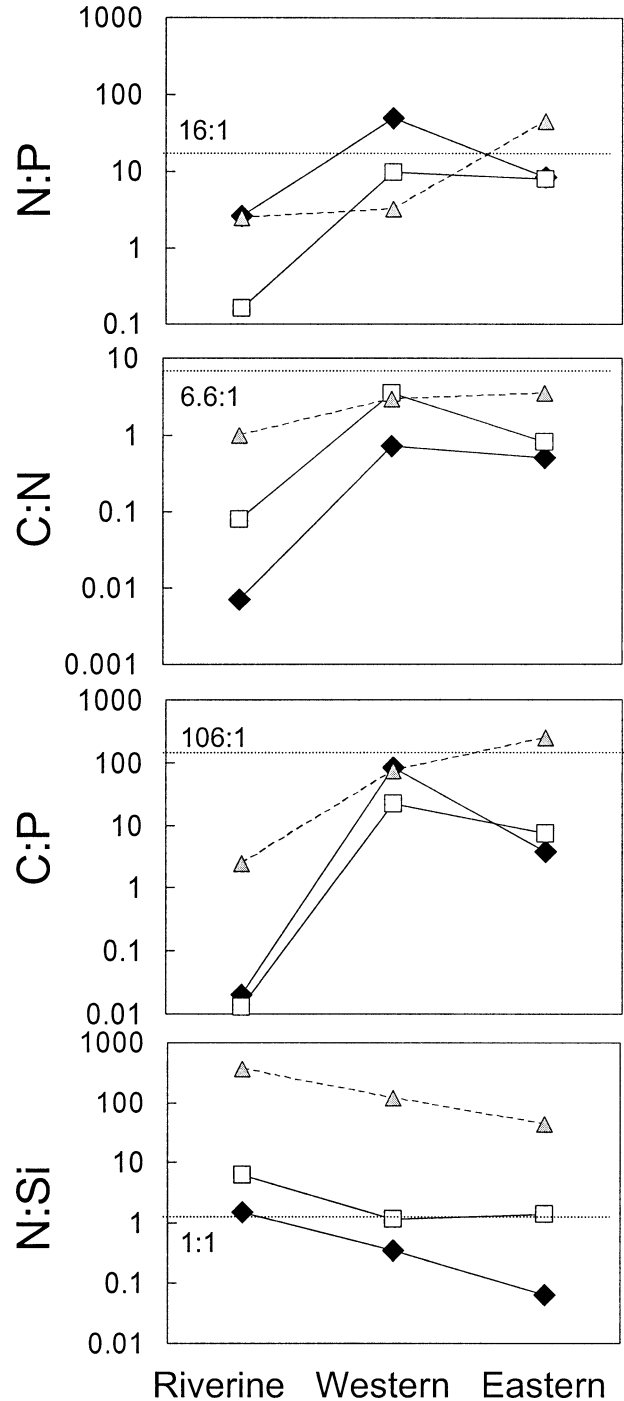

Fig. 7. The mean ratios of uptake of each of the nutrients and carbon, for each of the three regions (riverine and western and eastern bay sites) for the three periods of sampling. The dashed line in each panel represents the Redfield stoichiometric proportions. ◆ = September, ● = February, and △ = July.

inhibition and heterotrophic uptake of N. To explore the potential for photoinhibition at the eastern sites, we examined previously conducted light saturation curves for these sites and compara-

ble time periods (e.g., O'Donohue and Dennison 1997; data not shown). While photoinhibition occurred at some sites, this effect appeared to be insufficient to account for the depression in C uptake that would be required to yield these low C : N uptake ratios. Heterotophic uptake of N (but not C) is also a possibility. While bacterial productivity was low at the eastern sites, the PN : chl *a* ratio was elevated suggesting that nonchlorophyll containing biomass was dominant (Fig. 5). O'Donohue et al. (2000) also found depressed C : N uptake ratios in eastern Moreton Bay and suggested that a dynamic microbial food web and heterotrophic uptake of nutrients were likely.

The ratios of C : P uptake followed similar patterns as the uptake ratios of C : N, with indications of severe C limitation in the riverine regions, and in the eastern bay in February and September (Fig. 7). The potential for light limitation in the riverine regions, and photoinhibition or heterotrophic uptake of P in the eastern bay, remain the likely explanations for these observed patterns.

The ratios of N : Si uptake in all cases showed a downward trend from the riverine source waters to the eastern Bay (Fig. 7). During February, N : Si uptake rates were nearly balanced at values that ranged from 1.1 to 6.1. In September, balanced uptake was noted at the riverine site, but significant decreases in N : Si uptake were found in the western and eastern bay sites, indicating potential N limitation. An alternative possibility is the potential for luxury $Si(OH)_4$ uptake in September (e.g., Conway et al. 1976; Dugdale et al. 1981), and the highest uptake rates for $Si(OH)_4$ of all seasons was found in September. A contrasting relationship was noted in July when the uptake ratios of N : Si exceeded the proportion indicated by Redfield stoichiometry by as much as two orders of magnitude. For this period, $Si(OH)_4$ limitation is suggested, and this is underscored by the exceedingly low absolute $Si(OH)_4$ uptake rates that were measured.

ECOSYSTEM EXTRAPOLATION–SIGNIFICANCE OF ASSUMPTIONS

A recent paper of Eyre and McKee (2002), in which bay-wide budgets were estimated of all components of productivity, argues for P limitation of productivity in Moreton Bay. Their results were developed from the same multi-investigator program from which our results were collected, all designed toward developing an integrated water quality strategy for Moreton Bay. Eyre and McKee (2002) used our data (in preliminary form–Greenwood et al. 1999) as well as other published data (see below) in formulating their conclusions. On the one hand, there is tremendous value in

developing system-wide analyses of nutrient limitation, and few such analyses are available either in temperate or tropical systems. On the other hand, when management issues are so clearly tied to interpretations of nutrient limitation, there are subtleties that are commonly not reported or understood. As noted by Cloern (2001, p. 223), nutrient input is linked to a "complex suite of direct and indirect responses including linked changes in water transparency, distribution of vascular plants and biomass of macroalgae, sediment biogeochemistry and nutrient cycling, nutrient ratios and their regulation by phytoplankton community composition, frequency of toxic/harmful algal blooms, habitat quality for metazoans, reproduction/growth/survival of pelagic and benthic invertebrates, and subtle changes such as shifts in the seasonality of ecosystem functions." While it is tempting to speculate that the contrasting conclusion of our results and those of Eyre and McKee (2002) indicate fundamental differences in the functioning of the water and the benthos such that benthic processes overwhelm those of the water column, this is not the case. The comparison of our results with the analysis by Eyre and McKee (2002) for Moreton Bay underscores two important issues in extrapolating component ecosystem measurements to system-wide responses: various assumptions can have profound effects on system analyses, and differences in the scale of experiments and scale of interpretation can lead to large propagated errors. The specifics of how these issues apply to the interpretation of Eyre and McKee are provided below.

The goal of the Eyre and McKee (2002) paper was to model the inventories, inputs, exports, and cycling of C, N, and P in Moreton Bay. One of the significant conclusions of their analysis was that in order for P limitation to develop, significant rates of N_2 fixation were required. They extrapolated bay-wide rates of benthic N_2 fixation associated with seagrasses, using upper range values that were summertime measurements of the seagrass *Syringodium isoetifolium* in the oligotrophic eastern bay (Perry 1998). Their stated justification for using upper values was to provide a reasonable balance for the budget and to account for ephemeral inputs from other unquantified N_2-fixing cyanobacteria (*Trichodesmium erythraeum* and *Lyngbya majuscula*). The high rates they used do not extrapolate either seasonally or spatially. Significantly lower rates of N_2 fixation have been measured in winter in Moreton Bay (Roberts and Dennison 1998) and the most abundant seagrass species in Moreton Bay, *Zostera capricorni*, has much lower rates of N_2 fixation (Perry 1998). By using the measured N_2 fixation rates (average of aerobic and anaerobic) of *Z. capricorni*

and adding inputs from cyanobacteria (Greenwood et al. 1999), a more accurate annual N_2 fixation for bay-wide annual inputs is 3,800 t N yr^{-1}. This value is significantly less than the 9,177 t N yr^{-1} used by Eyre and McKee (2002), and does not even account for reduced rates in winter.

The conclusion of P limitation in the Eyre and McKee (2002) analysis also was based on phytoplankton N and P uptake rates calculated from a Redfield stoichiometric balance of C, N, and P. They justified use of these calculated values, rather than directly measured values (our preliminary data, which they also reported), on the basis of the application of consistent assumptions across all primary producers, despite the fact that they recognized a 2–3 fold discrepancy between estimated and actual rates (Table 4 in Eyre and McKee 2002). As shown here, phytoplankton N and P uptake rates calculated by Redfield stoichiometry underestimate measured uptake rates in Moreton Bay in all seasons and at all sites. Using measured N uptake rates instead of those estimated by stoichiometry, the N turnover by phytoplankton is much faster, indicative of N limitation.

The annual productivity estimates of all primary producers (benthic and pelagic microalgae, macroalgae, seagrasses, and mangroves) in Moreton Bay were based on spring and summer measurements only in the Eyre and McKee analysis. Strong seasonal responses due to variations in temperature and light have been documented for Moreton Bay phytoplankton C uptake (O'Donohue and Dennison 1997) as well as N, P, and Si uptake (O'Donohue et al. 2000; Fig. 5). Seasonality in processes is generally well recognized in most estuarine systems. In a subtropical system, where rainfall and consequently nutrient inputs are so strongly seasonally pulsed, the effect of seasonality can be even more significant (Heil et al. 1998; Moss 1998). In calculating system-wide annual nutrient budgets, rates measured in summer must be weighted accordingly.

While any one of these issues raised would cause a reevaluation of the Eyre and McKee (2002) model, taken together they constitute a revision of the overall conclusion-that is, Moreton Bay primary production is N, not P, limited. These issues underscore the importance of understanding model assumptions and the difficulties in extrapolating to system-wide nutrient limitation conclusions.

Synthesis

The regulation of biomass production, its composition, and the uptake of nutrients appeared to be regulated differently from each other and differently along the riverine-west-east gradient of the Moreton Bay system. Total biomass was N limited, as evidenced by the low N : P and N : Si particulate ratios. N was the primary determinant of total biomass measured as PN. Conflicting conclusions of system-wide limitation by P (Eyre and McKee 2002) were further shown to be biased by unrealistic assumptions.

Nutrient uptake was largely in stoichiometric proportion in the western bay, due to alleviation of light limitation, and sufficient nutrients were available to sustain near balanced growth. In the more nutrient deplete eastern bay regions, primary productivity, while substantially greater than bacterial productivity, may have been underestimated due to photoinhibition and C : N uptake ratios may have been depressed due to heterotrophic uptake of N and P.

Management Implications

Eutrophication is a major concern for water quality managers, and the identification of limiting nutrients for biomass production is of significance because it permits managers to concentrate resources and policy on the nutrient(s) that may have the greatest effect. Identification of the nutrient limiting biomass can lead to significant responses when reductions are undertaken. Excessive accumulations of chl *a* due to excess nutrient delivery have numerous deleterious effects on the ecosystem, which may be manifested differently in different systems depending on differing physical dynamics (e.g., temperature, water column depth, and flushing times) and other factors. Large chl *a* blooms are not yet a major concern in Moreton Bay, although localized areas, such as Bramble Bay, are experiencing greater effects of eutrophication, including species shifts leading to harmful species (Dennison et al. 1999).

The dominant forms of N available and taken up in Moreton Bay are NH_4^+ and urea, suggesting both sewage inputs and rapid regeneration and recycling of N. A major recommendation from the Moreton Bay Study was to reduce N inputs through upgraded sewage treatment, a recommendation that has been largely implemented (Abal et al. 2001). The result of these N reductions has been a measurable improvement in water quality (www.healthywaterways.org), lending credence to the practical application of N limitation at the system level.

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