

In the other 90%: phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef Lagoon

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Abstract

Our view of how water quality effects ecosystems of the Great Barrier Reef (GBR) is largely framed by observed or expected responses of large benthic organisms (corals, algae, seagrasses) to enhanced levels of dissolved nutrients, sediments and other pollutants in reef waters. In the case of nutrients, however, benthic organisms and communities are largely responding to materials which have cycled through and been transformed by pelagic communities dominated by micro-algae (phytoplankton), protozoa, flagellates and bacteria. Because GBR waters are characterised by high ambient light intensities and water temperatures, inputs of nutrients from both internal and external sources are rapidly taken up and converted to organic matter in inter-reefal waters. Phytoplankton growth, pelagic grazing and remineralisation rates are very rapid. Dominant phytoplankton species in GBR waters have in situ growth rates which range from ~1 to several doublings per day. To a first approximation, phytoplankton communities and their constituent nutrient content turn over on a daily basis. Relative abundances of dissolved nutrient species strongly indicate N limitation of new biomass formation. Direct (¹⁵N) and indirect (¹⁴C) estimates of N demand by phytoplankton indicate dissolved inorganic N pools have turnover times on the order of hours to days. Turnover times for inorganic phosphorus in the water column range from hours to weeks. Because of the rapid assimilation of nutrients by plankton communities, biological responses in benthic communities to changed water quality are more likely driven (at several ecological levels) by organic matter derived from pelagic primary production than by dissolved nutrient stocks alone.

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Keywords: Great Barrier Reef; Water quality; Nutrients; Phytoplankton; Productivity

1. Introduction

The Great Barrier Reef (GBR) of Australia is the largest contiguous coral reef ecosystem in the world and one of the most biodiverse. At a time when many coral reef ecosystems have been degraded by direct or indirect human disturbances (Wilkinson, 2002), the high ecological quality of the GBR is due to the relatively small human population within the region, the physical remoteness of much of the reef from direct human impacts, and in recent decades, to pro-active and effective

management at a regional (ecosystem) scale. Most coral reefs within the broader GBR province are located within the Great Barrier Reef World Heritage Area (GBRWHA) and the co-located Great Barrier Reef Marine Park (GBRMP). The GBR, however, is not immune from human pressures. The GBRMP is managed for multiple uses and lies adjacent to a large (422,000 km²) catchment in which a range of agricultural and industrial activities take place. Among other things, terrestrial runoff of sediment and nutrients (chiefly N and P) to the GBRWHA has increased 2- to 4-fold over the last century (Furnas, 2003; Brodie et al., 2004). A variety of evidence shows that gradients of reef and community structure, biodiversity and ecological function in

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nearshore coral reef systems are associated with environmental gradients of influence by terrestrial runoff (Fabricius and De'ath, 2004; Fabricius, 2004). The extent and degree of runoff-related effects on the GBR as a whole is controversial (Larcombe and Wolfe, 1999; Wolanski and Duke, 2002), but reefs in a number of nearshore areas (e.g. Van Woessik et al., 1999; Fabricius and De'ath, 2004) exhibit changes consistent with eutrophication or runoff-affected disturbance (e.g. Smith et al., 1981; Fabricius, 2004).

The approximately 3200 identified coral reefs within the GBR World Heritage Area (Fig. 1) are distributed throughout a broad continental shelf ecosystem (shelf area ca. 224,000 km²) in which reefs (area ca. 20,000 km²) comprise less than 10% of shelf area (Lewis, 2001). Most (90%) of the continental shelf is a complex lagoonal habitat, isolated to varying degree from the adjoining oceanic waters of the Coral Sea by a porous matrix of shelfbreak reefs. Physical and biological processes within these shelf waters, and in underlying sediments (Alongi and McKinnon, 2004), are the most important determinant of the state of water quality directly affecting reefs and other benthic habitats of the GBRWHA.

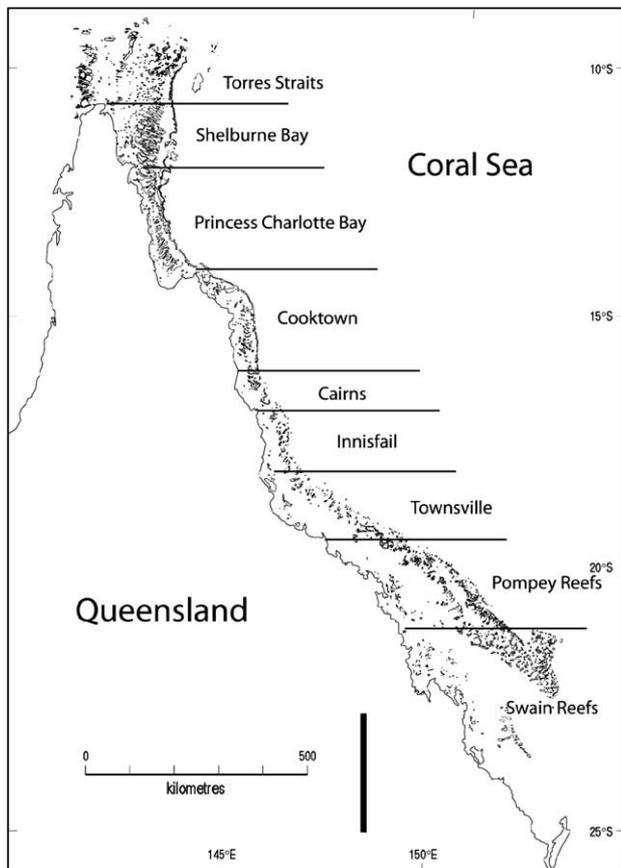


Fig. 1. The Great Barrier Reef of Australia and latitudinal zones used for aggregation of nutrient statistics. The vertical bar shows the width of the coastal zone (≤ 15 km from the coastline).

Because of the physical processes influencing water flows and sediment dispersal on the continental shelf (e.g. Brinkman et al., 2001; King and Wolanski, 1992; Larcombe et al., 1995; King et al., 2002), most direct effects of land runoff (Devlin et al., 2001) are focused within a narrow (10–20 km) nearshore zone (ca. 15% of shelf area and 4% of shelf water volume), where water depths are generally less than 20 m (Furnas, 2003). The nearshore zone contains approximately 700 coral reefs which can be highly productive and biodiverse (Veron, 1995). These nearshore reefs have always been influenced by runoff of freshwater, sediment and nutrients from the adjoining land. In contrast, reef and benthic habitats away from the coast, or distant from the river sources of runoff are only influenced by the nutrients and suspended materials in runoff after they have been physically diluted or cycled through pelagic and benthic biological communities. The warm, well-lit shelf waters of the GBR support diverse (Ferran, 1936; Revelante et al., 1982) and highly productive (Furnas and Mitchell, 1989; McKinnon, 1996) pelagic communities. We show here that the pelagic communities of the GBR lagoon rapidly assimilate, produce, transform and metabolise nutrients and organic matter. These recycled and transformed nutrients, and the organic matter produced with them are what most directly influences coral reefs and other benthic communities of the GBR and largely determine the effective state of water quality in the lagoon.

2. Data sources and methods

Portions (often significant) of the data sets used here-in have previously been published or summarised (Table 1). Significant new additions to the base data sets have been amalgamated and the details will be published elsewhere.

3. Regional variations in nutrients, chlorophyll and suspended sediment

Because of the size and structural diversity of the GBR, the pronounced seasonality of nutrient inputs from a variety of sources (Furnas and Mitchell, 1996b; Furnas, 2003) and the complex circulation of water within the GBR lagoon (e.g. Brinkman et al., 2001; King et al., 2002), nutrients (or their availability), suspended sediment loads, phytoplankton biomass and other factors influencing water quality are not distributed evenly throughout the GBR lagoon; nor do they vary in predictable cycles at particular locations. On average, more than 100,000 tonnes of N and 13,000 tonnes of P enter GBR waters each year from marine, terrestrial and atmospheric sources (Furnas, 2003). These inputs vary over an order of magnitude depending upon inter-an-

Table 1
Methods and published data sources used herein

Data type	Method references	Published data summaries or sources	Comments
Geographical data		Lewis (2001), Furnas (2003)	Including sources therein
Dissolved nutrients, plant pigments, suspended solids	Furnas and Mitchell (1987, 1997), Furnas et al. (1995)	Furnas (1991b), Furnas and Mitchell (1997)	From post-1980 sampling by AIMS oceanographers. Analysis based on depth-weighted average concentrations for shelf stations (depth < 80 m)
Primary production	Furnas and Mitchell (1987, 1989, 1999)	Furnas and Mitchell (1989)	
Phytoplankton growth rates	Furnas (1991a) and Crosbie (1999)	Furnas (1991a), Crosbie (1999) and Crosbie and Furnas (2002)	
Nitrogen uptake (^{15}N)	Furnas and Mitchell (1999)	Furnas, unpublished	
Benthic nutrient mineralisation	Alongi (1989); in preparation	Alongi (1989) and Lourey et al. (2001)	
Nutrient inputs in river runoff, rainfall and sewage		Furnas (2003)	

nual variations in rainfall over the GBR and its catchment, the distribution of rainfall between catchments (Furnas, 2003), and the number and magnitude of upwelling events (Furnas and Mitchell, 1996b).

Fig. 2 summarizes the regional and seasonal patterns of “normal” (median) water column concentrations of dissolved inorganic nitrogen (DIN), phosphate (PO_4^{3-}), phytoplankton biomass (as chlorophyll) and suspended solids in GBR waters. The latitudinal zones are identified in Fig. 1. Numbers of sampling stations within particular season-latitude-cross shelf combinations range from nil to several hundred. The median concentrations shown are derived from depth-weighted mean water column concentrations at individual sampling sites in GBR shelf waters (depth < 80 m). In most cases, shelf waters are well mixed vertically, so depth-weighted means are a good indicator of concentrations through the water column. Sampling stations where the water column and nutrient concentrations were known to have been affected by a significant disturbance (river plume, cyclonic resuspension, upwelling) have been excluded.

Important spatial factors that influence water quality are distance from the coast (exposure to terrestrial runoff and shelfbreak upwelling), water depth (influence of wind-driven sediment resuspension) and placement or density of reefs (barriers to north–south transport and lateral exchange of water with the Coral Sea). Seasonal variations in nutrient and chlorophyll concentrations, especially near the coast, are influenced by the seasonality of river runoff and to a lesser extent, the south-easterly trade winds. Virtually all of the annual freshwater runoff occurs during the summer wet season (December–April; Lough, 2001; Furnas, 2003). Wind-driven sediment resuspension in coastal waters occurs episodically through the year (Larcombe et al., 1995), but most persistently during the dry season (May–November). To

illustrate these broad patterns in water quality, we have divided the GBR into nearshore (<15 km from the coast) and offshore (>15 km from the coast) zones in the nine latitudinal sections that reflect historical sampling effort, the geographical structure of the coast and the density of the reef matrix, which influences north–south water movements or lateral exchanges with the Coral Sea.

Concentrations of the two most important and readily assimilated forms of nitrogen (NH_4^+ or NO_3^-) in both inter-reefal and coastal waters of the GBR are typically on the order of $0.05 \mu\text{M}$, and usually only exceed $0.1 \mu\text{M}$ for short-periods of time. Total dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$) concentrations are usually on the order of $0.1 \mu\text{mol N L}^{-1}$ (Fig. 2A). Exceptions occur when nearshore waters are affected by river flood plumes (Devlin et al., 2001), during sediment resuspension events caused by strong winds (Walker, 1981; Ullman and Sandstrom, 1987; Chongprasith, 1992), and at the shelfbreak during upwelling events (Furnas and Mitchell, 1996b). Median DIN concentrations are low and relatively similar, irrespective of latitude, cross-shelf location and season in the northern ($9\text{--}17^\circ\text{S}$) and far southern ($21\text{--}24^\circ\text{S}$) GBR. Higher median water column DIN concentrations are observed in the central GBR ($17\text{--}20^\circ\text{S}$), particularly on the outer shelf where intrusive upwelling and mixing occurs episodically during the summer wet season along the shelfbreak. Sediment resuspension events in coastal waters are generally short-lived (lasting one to several days), but occur many times throughout the year. River plumes (near the coast) and upwelling events (at the shelfbreak) usually only occur a few times per year, predominantly during the summer wet season, and last for periods ranging from days to several weeks.

Concentrations of dissolved organic nitrogen ($\text{DON} \approx 4\text{--}6 \mu\text{mol L}^{-1}$) and particulate nitrogen

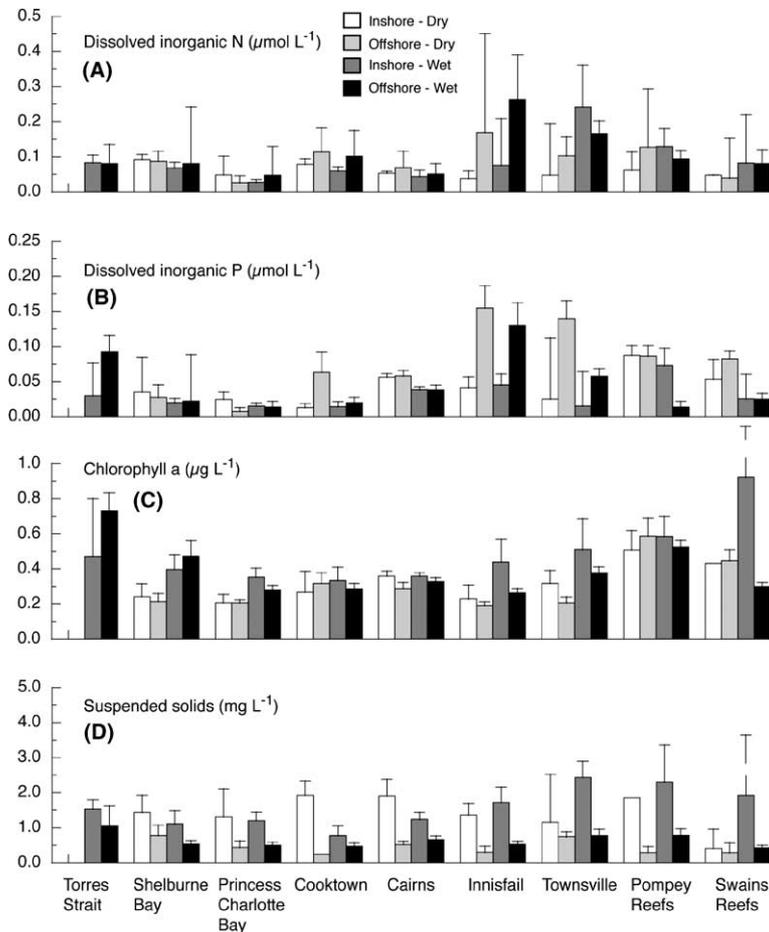


Fig. 2. Seasonal, latitudinal and cross-shelf variation in median concentrations of A: dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$), B: inorganic phosphorus (PO_4^{3-}), C: chlorophyll *a* and D: suspended particulate matter ($>0.45\mu\text{m}$) in GBR waters for the latitudinal and cross-shelf zones identified in Fig. 1. Error bars indicate the 95% confidence interval for the mean concentration. Dry season = April–September, wet season = October–March.

($\text{PN} \approx 1\mu\text{molL}^{-1}$) (e.g. Furnas and Mitchell, 1997) are consistently higher than those of the dissolved inorganic forms readily taken up by phytoplankton and bacteria. The chemical composition of DON and PN are not well characterised. Concentrations of easily bio-accessible DON species (e.g. amino acids) are normally very low in GBR waters (ca. $0.01\mu\text{molNL}^{-1}$; Ayukai et al., 1995). The PN is largely in the form of detritus (non-living particulate organic matter). Higher molecular weight forms of DON and PN can only be assimilated by phytoplankton and benthic algae following consumption and mineralisation by grazers, detritivores or bacteria.

Concentrations of dissolved inorganic phosphorus (PO_4^{3-} ; Fig. 2B) are of similar order to DIN, ranging between 0.05 and $0.2\mu\text{M}$ among regional–seasonal–cross shelf zonal combinations. The spatial pattern of normal water column phosphate concentrations generally follows that of DIN. Concentrations of dissolved organic and particulate forms of P (DOP, PP) are similar to those of dissolved inorganic P.

Silicate concentrations (not shown) exhibit a persistent cross-shelf gradient in GBR waters, with higher concentrations near the coast, reflecting the terrestrial source of this nutrient in runoff and its active (re-)mineralisation in shallow coastal sediments (e.g. Alongi, 1989). Median concentrations of Si within the latitudinal zones range from 0.5 to $9\mu\text{M}$ near the coast (average of median values $\approx 4\mu\text{M}$) to 0.4 – $3.2\mu\text{M}$ offshore (average of median values $\approx 2\mu\text{M}$). Silicate is a required nutrient for diatoms, which characteristically form blooms following nutrient input events (Marshall, 1933; Revelante and Gilmartin, 1982; Furnas, 1989). Importantly though, silicate is not required by the very small ($<2\mu\text{m}$) pelagic cyanobacteria (*Synechococcus*, *Prochlorococcus*) which usually dominate phytoplankton biomass and primary production in GBR waters (Furnas and Mitchell, 1987, 1989). As a result, there is almost always sufficient silicate present to support active growth of resident diatom populations.

Median concentrations of chlorophyll, the primary index of phytoplankton biomass, vary over a 4-fold

range (ca. 0.2–0.8 $\mu\text{g L}^{-1}$) within the defined seasonal-latitude-cross shelf zones (Fig. 2C). The highest chlorophyll levels occur in the far-northern and southern GBR, particularly during the summer wet season. In the northern and central GBR (12–17°S), median chlorophyll concentrations are lower and exhibit relatively little seasonal or spatial variability in the absence of obvious disturbance. Higher concentration (typically $> 0.5 \mu\text{g L}^{-1}$) are routinely measured in both near-shore and offshore waters between 18.5°S and 22°S (Pompey Reefs sector) where the shelf is the widest ($>150 \text{ km}$).

Like silicate, median suspended sediment concentrations (Fig. 2D) show a clear cross-shelf gradient, with higher concentrations in nearshore waters, regardless of latitude or season. This clearly reflects the greater influence of wind- and wave-forced sediment resuspension in shallow coastal waters.

When growing with access to sufficient light and nutrients (generally regardless of concentration), natural phytoplankton communities often approach an average chemical composition characterised by a C:N:P ratio (by atoms) close to 106:16:1, the ‘Redfield ratio’ (Redfield et al., 1963; e.g. Goldman, 1980), though this is influenced by community and environmental factors (Klausmeier et al., 2004). Diatoms, an important group within the phytoplankton, also require silicon at an N:Si ratio (by atoms) of approximately 1:1 (Brzezinsky, 1985). To sustain growth with a balanced chemical composition, phytoplankton communities must take up nutrients at close to the Redfield ratio. Physiologically, uptake capacity is usually not a constraint. Phytoplankton, particularly when nutrient depleted, can take up N, P and other nutrients at rates considerably in excess of their maximum potential growth rate to take advantage of intermittent sources of nutrients at higher concentrations (e.g. McCarthy and Goldman, 1979). Average DIN: PO_4^{3-} ratios (overall mean 1.6) in both coastal and offshore waters of the GBR are considerably lower than the Redfield ratio, indicating that increases in phytoplankton biomass are usually strongly constrained by nitrogen availability. Continued growth of phytoplankton can only be sustained through ongoing recycling and mineralisation of organic nitrogen and phosphorus in biomass, detritus, and dissolved organic forms (DON, DOP). Phytoplankton biomass can only increase if new bio-available nitrogen is added to reef waters, for example, through upwelling, N-fixation or river runoff. DIN:Si ratios in GBR waters are almost always less than 1:1, the ratio normally found in diatoms (Brzezinsky, 1985). However, because the dominant picoplanktonic cyanobacteria do not require Si, it is unlikely that silicate strongly limits phytoplankton community growth in the GBR. Dissolved inorganic nutrients (e.g. N, P, Si) only accumulate or persist at readily measurable levels ($>0.1 \mu\text{M}$) in situations where local inputs

or remineralisation temporarily exceeds local demand (e.g. in river plumes or freshly upwelled water), or more frequently, where the stocks and inputs of a particular nutrient are excess of that required to sustained growth at a balanced chemical composition which is constrained by the availability of other nutrients.

Natural phytoplankton populations have the capacity to take up virtually all bio-available nutrients from the water column if they are needed to support growth. As a result, ambient concentrations may be a poor guide to nutrient availability and usage. Where ambient nutrient concentrations are low and remain within relatively restricted ranges (e.g. $<0.1 \mu\text{M}$) due to active uptake by phytoplankton and bacteria, indices of phytoplankton biomass or fresh detritus such as chlorophyll *a* or protein are better guides to the quantities of available and cycling nutrients. Rapidly growing phytoplankton with access to sufficient light and nutrients (regardless of ambient concentration) typically have nitrogen: chlorophyll (N:Chl *a*) ratios of 0.5–1 $\mu\text{mol N}$ per μg chlorophyll (7–14 $\mu\text{g N}$ per μg chlorophyll; e.g. Goldman, 1980; Laws et al., 1983). Regionally averaged DIN:Chl ratios in the GBR lagoon vary between 0.1 and 0.9 $\mu\text{mol}:\mu\text{g}$ (median ~ 0.3). The low DIN:Chl ratio (<1) in lagoon waters indicates that in the absence of additional, usually external nitrogen inputs, there is insufficient ambient DIN for more than one doubling of phytoplankton biomass.

4. Phytoplankton growth

Despite the low concentration of readily bio-available N and P in GBR lagoon waters, direct measurements of phytoplankton in situ growth in the central and southern GBR lagoon (Furnas, 1991a,b; Crosbie, 1999; Crosbie and Furnas, 2002) show that resident populations are actively growing, often at high relative (μ/μ_{max} : Goldman, 1980) growth rates (Fig. 3). Continual growth under nominally nutrient-limited conditions can only be sustained by inputs of additional nutrients from external sources (“new” nutrients), or by rapid consumption and recycling of the nutrients in plankton biomass, detritus and dissolved organic matter (DON, DOP) by benthic animals, zooplankton and bacteria.

Individual species or groups of phytoplankton in GBR waters exhibit inherent differences in growth potential. A number of common small to medium-sized diatom species (typified here by *Leptocylindrus danicus*; Fig. 3A and *Cylindrotheca* spp.; Fig. 3B) are capable of growth rates on the order of 2–4 population (and biomass) doublings day^{-1} if there are sufficient available nutrients. Dinoflagellate species have a lower growth potential (maximum ca. 1 doubling day^{-1}). Populations of the very small ($<2 \mu\text{m}$) photosynthetic cyanobacteria (*Synechococcus*, *Prochlorococcus*) which dominate phytoplankton

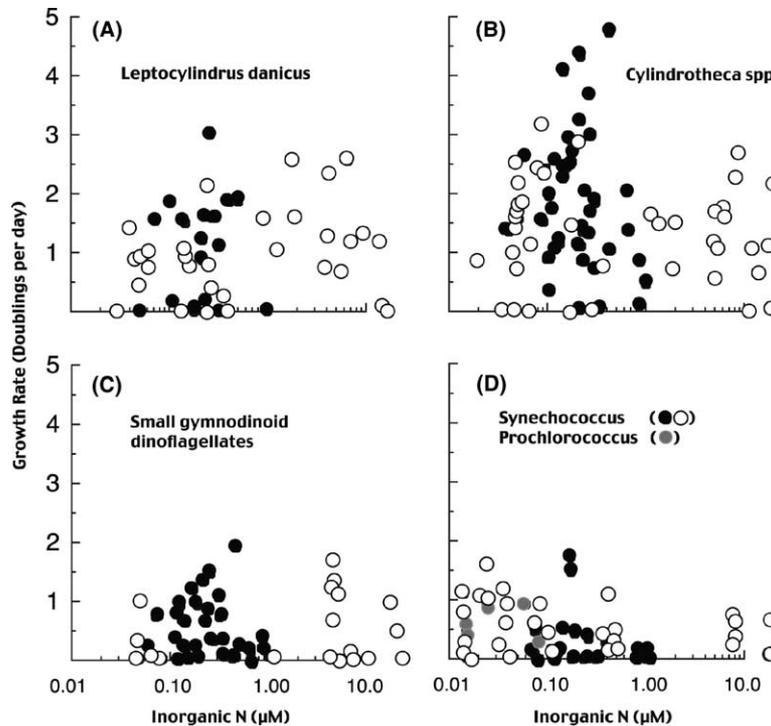


Fig. 3. Measured in situ growth rates of two common diatom taxa (A: *Leptocylindrus danicus*, B: *Cylandrotheca* spp.), C: small gymnodinoid dinoflagellates and D: pelagic coccoid cyanobacteria (*Synechococcus*, *Prochlorococcus*) in GBR shelf waters of the central and southern GBR (17°–20°S) in relation to average ambient concentrations of DIN at the experimental sites during the incubations.

biomass in GBR waters have maximum growth rates of 3 and 2 population doublings day⁻¹, respectively. In most cases, however, their growth is linked to the diel light cycle and populations of these cyanobacteria usually only divide once day⁻¹.

While growth rates of individual species vary from day to day, measured in situ growth rates of common diatoms and dinoflagellates fall within envelopes that indicate that GBR lagoon populations can maintain high relative growth rates down to ambient DIN concentrations on the order of 0.02–0.05 µM. These concentrations are similar to the minimum levels detectable by normal chemical analytical methods. Growth rates of larger eukaryotic phytoplankton (e.g. diatoms, dinoflagellates) appear to exhibit nutrient limitation at the lower end of DIN levels in GBR waters (<0.05 µM). The small pelagic prokaryotes, *Synechococcus* and *Prochlorococcus* which dominate phytoplankton biomass are even more efficient at using nutrients, exhibiting a capacity for near-maximal growth down to available DIN levels of 0.02 µM, or less. Instantaneous growth rates of these populations do not appear to be limited by ambient inorganic N and P concentrations in GBR waters. Importantly, however, even slight or ephemeral increases in DIN concentrations to levels on the order of 0.1 µM, as would occur during a sediment resuspension event, in a dispersed river plume or during and after upwelling, are sufficient to support maximal or near-maximal growth of most important phytoplankton spe-

cies or groups for at least short periods of time. This capacity for rapid growth at low ambient nutrient concentrations means that bloom formation can begin immediately (<1 day) after disturbance events. Bloom initiation appears to be dependent upon the level of underwater light, which is influenced by water column depth and turbidity (Furnas, 1989).

Grazing has a significant effect upon the magnitude and dynamics of phytoplankton responses to nutrient inputs and nutrient availability. Grazers are important agents in recycling organic nutrients back to inorganic forms accessible to phytoplankton. Heterotrophic micro- and nanoflagellates, the principal grazers on picoplankters (bacteria, cyanobacteria) have potential growth rates (1–3 doublings day⁻¹; e.g. Sherr et al., 1984; Verity, 1985; Geider and Leadbeater, 1988) of similar magnitude to those of their prey. As a result, blooms of small cyanobacteria with growth rates on the order of 1 doubling day⁻¹ almost immediately come under grazing control and large populations of these groups do not develop. In contrast, generation times of small copepods, the principal grazers on small to mid-sized diatoms are on the order of one week (McKinnon, 1996), giving the faster-growing diatoms ample time to develop bloom populations until growth is constrained by nutrient availability. The absence of blooms of these fast-growing diatom species during un-disturbed conditions indicates that their rapid growth rates are matched by equally high grazing mortality.

5. Nitrogen uptake and turnover in GBR waters

Ongoing rapid phytoplankton growth requires sustained nutrient uptake to support that growth. Direct measurements of NH_4^+ and NO_3^- uptake from GBR lagoon waters using ^{15}N tracer methods show active uptake throughout the water column. Measured NH_4^+ uptake rates usually range between 0.01 and $0.1 \mu\text{mol NL}^{-1}\text{hr}^{-1}$ (Fig. 4(A)). Nitrate uptake rates are generally slower, ranging between 0.0002 and $0.1 \mu\text{mol NL}^{-1}\text{hr}^{-1}$ (Fig. 4(C)). While the absolute uptake rates are not large, they are very often sufficient to fully deplete the low ambient water column stocks of NH_4^+ and NO_3^- within hours in the absence of concurrent remineralisation (Figs. 4(B) and 4(D)). Depletion times, the time required for the ambient nutrient stock to be fully taken up at the measured uptake rate, provide an index of the rate of nutrient turnover in the water column. On a number of occasions, calculated nitrate depletion times were on the order of days to weeks, suggesting phytoplankton preferences for the more easily assimilated ammonium. The estimates of uptake rates and depletion times shown are conservative as they do not incorporate concurrent ammonium mineralisation (e.g. Harrison and Harris, 1986) or nitrification rates (Chongprasith, 1992). Over time scales of one to several days, in situ N and P mineralisation rates are balanced with uptake rates (e.g. Harrison et al., 1984), so ambient concentrations of nutrients remain relatively constant.

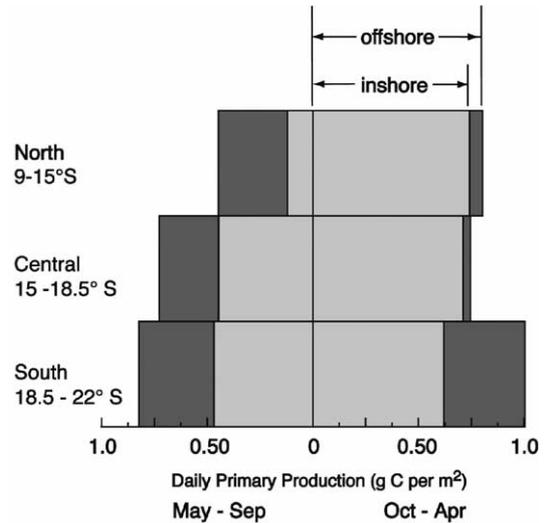


Fig. 5. Average areal primary production rates in the north, central and southern GBR lagoon at nearshore (≤ 15 km from the coast) and offshore locations (> 15 km from the coast) during the winter-dry (left) and summer-wet (right) seasons.

6. Primary production and estimates of nutrient demand

Fig. 5 presents a summary of water column primary production rates ($\text{g C m}^{-2}\text{day}^{-2}$) measured in GBR lagoon waters between 1983 and the present ($n = 150$ measurements). The number of latitudinal zones has been reduced because of the smaller number of production

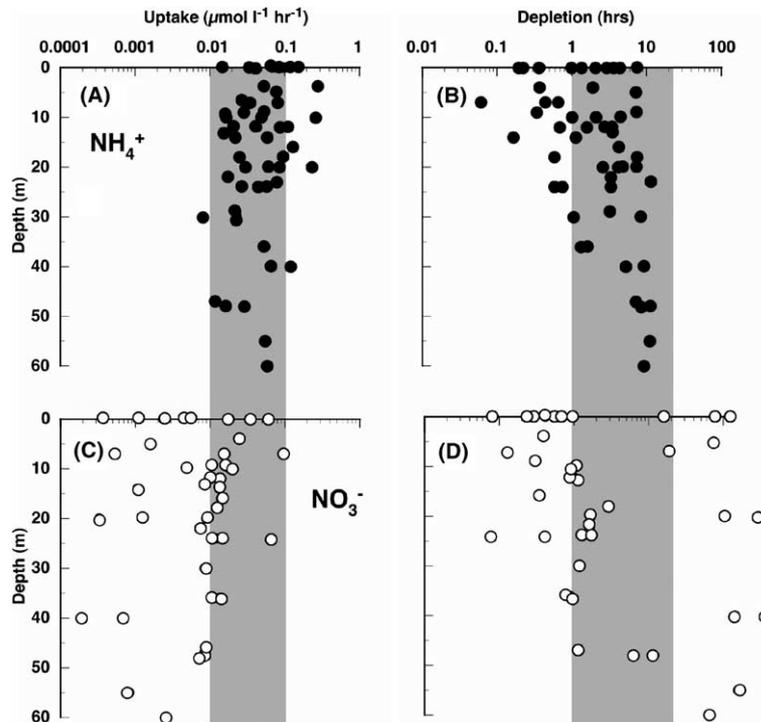


Fig. 4. Measured uptake rates of ammonium (A) and nitrate (C) by phytoplankton at eight sites in the central GBR lagoon, and estimated times for complete uptake (depletion times) of ambient stocks of ammonium (B) and nitrate (D) at the measured uptake rates.

experiments. Latitudinal, seasonal and cross-shelf differences in average daily production rates are readily apparent. Regardless of season or location, daily production on the mid- to outer-shelf is usually higher than in coastal waters (<15 km from the coast) because of the greater penetration of light in clearer offshore waters and the greater depth of the water column in which production occurs. Average areal production rates in all parts of the GBR are higher during the summer wet season (October–April). Differences between areal production rates in nearshore and offshore waters are greatest during the winter dry season at all latitudes (May–September).

Daily primary production rates measured at individual production stations within the latitudinal and cross-shelf zones vary from approximately $0.1 \text{ gCm}^{-2} \text{ day}^{-1}$ (tonnes $\text{km}^{-2} \text{ day}^{-1}$) in far northern inshore waters (dry season) to $1.5 \text{ gCm}^{-2} \text{ day}^{-1}$ at offshore sites (wet season) in the Pompey Reef complex (21°S). This southern offshore area is characterised by intense, tidal mixing through a dense reef matrix and relatively higher levels of phytoplankton biomass (shown by chlorophyll: Fig. 2C). The nutrients to support this higher biomass and production overwhelmingly come from oceanic sources as the Pompey Reefs are more than 100 km offshore. The largest seasonal variation in production occurs in the northern GBR, presumably due to the large seasonal (monsoonal) changes in rainfall and terrestrial runoff. Over all regions and seasons, the average shelf primary production rate is close to $0.68 \text{ gCm}^{-2} \text{ day}^{-1}$ ($250 \text{ gCm}^{-2} \text{ year}^{-1}$), or $1.57 \mu\text{molCL}^{-1} \text{ day}^{-1}$ for the average depth of the GBR shelf (36 m).

The production of phytoplankton biomass from newly fixed carbon requires the uptake and assimilation of nutrients (N, P, Si, trace metals). Primary production rates can therefore be used to make upper bound estimates of the nutrient demand necessary to support that biomass production. The average daily primary production rate of $1.57 \mu\text{molCL}^{-1} \text{ day}^{-1}$ would require the daily assimilation of $0.24 \mu\text{molNL}^{-1}$ and $0.015 \mu\text{molPL}^{-1}$ to produce phytoplankton biomass with a Redfield C:N:P composition. If we assume that GBR phytoplankton have a composition similar to the Redfield ratio, the nutrient demand associated with primary production can also be used to calculate the time in which ambient nutrient stocks would be exhausted (depletion times). Fig. 6 shows distributions of estimated depletion times for water column stocks of DIN and PO_4^{3-} at sites throughout the GBR where primary production experiments were carried out. The primary production based estimates of DIN depletion times are of similar order to those estimated directly from ^{15}N uptake rates. In half of the cases, the inferred nitrogen demand would exhaust available DIN stocks in 8 h or less. Only 38 of 150 calculated DIN depletion times exceeded 24 h. Phosphorus depletion times were considerably longer than nitrogen depletion times, exceeding 24 h in 122 of 150 experiments. The much longer phosphorus depletion times further indicate that P is rarely a limiting nutrient for phytoplankton growth in GBR waters. Likewise, estimates of daily silicate demand based on primary production rates and phytoplankton composition ratios are far below ambient stocks at most stations.

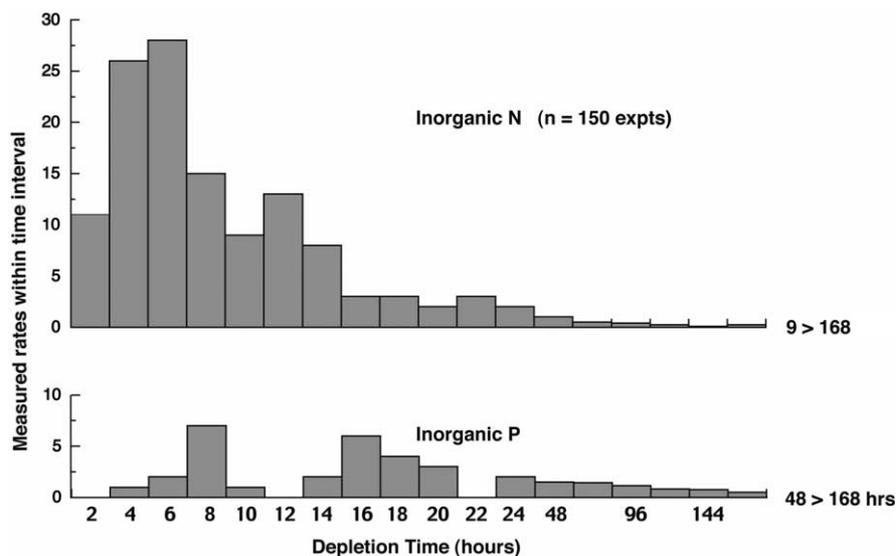


Fig. 6. Estimated depletion times for water column stocks of DIN (top) and phosphate (bottom) at primary production stations in the GBR lagoon based upon daily primary production rates ($\text{gCm}^{-2} \text{ day}^{-1}$) and Redfield composition ratios (C:N:P = 106:16:1 by atoms).

7. Discussion

In low-nutrient ecosystems such as the Great Barrier Reef lagoon, where warm water temperatures and abundant light energy support high rates of primary production by phytoplankton, rapid nutrient metabolism and rapid microbial (bacteria, micro-algae, protists) growth, the state of water quality is less determined by static concentrations of suspended sediments, nutrients or pollutants in reef waters than by local or regional levels of sediment, nutrient or pollutant delivery to affected communities, nutrient uptake and (re-)cycling by phyto- and bacterioplankton and organic matter production by plankton communities. While nearshore reefs are annually or episodically inundated by resuspended sediment (Larcombe et al., 1995) or floodwaters with elevated concentrations of suspended material and nutrients derived from terrestrial sources (Devlin et al., 2001), only a small fraction of this water and its nutrient and sediment burden comes into direct physical contact with reefs or other benthic communities, allowing benthic plants or corals to take up nutrient materials and pollutants or respond to sedimentation. The overwhelming bulk of nutrients and other pollutant materials remain well outside of the benthic boundary layer of reefs or seagrass beds, flowing past, around or over coastal benthic communities and into the open waters of the GBR lagoon where the nutrients are dispersed and particulate materials sediment onto the inter-reefal benthos. The nutrients in this water are primarily consumed by phytoplankton and cycled to other forms by pelagic heterotrophs.

The observed rapid growth and productivity of phytoplankton and the accompanying high levels of nutrient demand in GBR lagoon waters to support this indicate that most bio-available nutrients delivered through N-fixation, terrestrial runoff, rainfall and upwelling are quickly taken up to support plankton biomass and organic matter production. This rapid uptake keeps stocks of dissolved inorganic nutrients within a relatively narrow range of low concentrations. Most of the nutrients which influence coral reefs or benthic communities in the GBR lagoon do so once they have been taken up and cycled (once or many times) through pelagic food webs. A similar pathway has been noted in other eutrophied coral reef systems (e.g. Kaneohe Bay, Hawaii; Smith et al., 1981; Laws and Redalje, 1982). These nutrients support the production of organic matter, largely by the plankton (e.g. Laws and Redalje, 1982), and to a lesser (though locally important) extent in benthic communities (e.g. Wild et al., 2004). It is likely that ecosystem responses to the organic matter (soluble and particulate; e.g. Anthony, 2000; Fabricius and Domisse, 2000) produced with new and recycled nutrients (Laws and Redalje, 1982; Bruno et al., 2003; Fabricius and Wolanski, 2000; Wild et al., 2004) are

greater than the effect of the nutrients themselves (Fabricius, 2004).

Direct measurements of phytoplankton primary production and growth rates in GBR waters show a very productive and rapidly growing plankton community. All of the dominant phytoplankton species or groups in GBR waters have potential population growth rates exceeding one doubling day^{-1} . Community production/biomass ratios (median = $52.5 \text{ g C g chl}^{-1} \text{ day}^{-1}$) are indicative of community biomass growth rates on the order of 0.5–2 carbon doublings day^{-1} for phytoplankton with C:chl *a* ratios (50–60 $\mu\text{g}:\mu\text{g}$) typical of healthy phytoplankton communities (e.g. Goldman, 1980). Phytoplankton biomass in GBR waters normally remains low and relatively constant because biomass production is held in check by low levels of nutrient availability (low-water column DIN and PO_4^{3-} concentrations, sub-Redfield DIN: PO_4^{3-} ratios) and equally rapid consumption by grazers (Calbet and Landry, 2004; McKinnon and Furnas, in preparation).

Many of the important phytoplankton species and groups in GBR waters are capable of near-maximal growth rates at concentrations only slightly greater (ca. $0.1 \mu\text{M}$ for DIN and PO_4^{3-}) than the very low nutrient concentrations which typify GBR waters (Fig. 2). Instantaneous growth rates of the dominant *Synechococcus* and *Prochlorococcus* populations, in particular, do not appear to be materially limited at ambient DIN concentrations, even at the very lowest concentrations measured (ca. $0.02 \mu\text{M}$). At a community doubling rate of 1 day^{-1} , ungrazed phytoplankton supplied with sufficient nutrients will increase their biomass by an order of magnitude in 3–4 days. Fast growing diatoms such as *Pseudonitzschia*, *Chaetoceros* and *Leptocylindrus* spp. can make order of magnitude increases in biomass within 1–2 days. Changes in phytoplankton biomass (as chlorophyll) and of individual species or groups of this order have been observed (Furnas, 1989) over large areas of the central GBR (18°S) following tropical cyclone Winifred (1986) which caused a massive sediment resuspension and nutrient release event (Chongprasith, 1992) or in dispersing river plumes (Devlin et al., 2001). The phytoplankton populations which initiate and form such blooms are always present and growing (Marshall, 1933; Revelante et al., 1982; Furnas, 1991a,b; Crosbie and Furnas, 2002). Bloom initiation only requires sufficient light to support active growth throughout the water column (for example, following sedimentation of the fine material in a flood plume or resuspended coastal sediment) and adequate mixing of resident phytoplankton into waters containing nutrients (both to bring phytoplankton into contact with the nutrients, or in the case of freshwater runoff, to raise salinities to a degree where growth is not limited). Once started, bloom size and formation rate are constrained by the quantity of available

nutrients and responses of grazer populations. Despite the high growth potential of resident phytoplankters, the general absence of bloom formation in GBR water indicates that nutrient limitation and grazing processes keep resident phytoplankton populations at low biomass levels.

As with growth and primary production, both direct (^{15}N) and indirect (^{14}C -based) estimates of N and P demand indicate rapid turnover of water column nutrient stocks. Ammonium pools typically turn over within one day, and in many cases, within hours. The longer nitrate turnover times likely reflect phytoplankton and bacterial preferences for the more readily assimilated ammonium. The still-longer phosphate turnover times are due to relatively higher ambient concentrations (vis a vis Redfield ratios) and rapid remineralisation. The measured nitrogen uptake rates based on ^{15}N are likely reasonable estimates of N demand as unmeasured isotope dilution (Harrison and Harris, 1986) balances short-term uptake enhancement caused by saturating isotope substrate concentrations ($0.1\ \mu\text{M}$). The ^{14}C -based estimates of nutrient demand are likely to be closer to the upper bounds of demand as all production is assumed to utilize N and P at Redfield ratios. In situations where there are not enough nutrients available to support balanced growth of biomass with a near-Redfield composition (C:N:P \sim 106:16:1), the extra carbon produced by photosynthesis is likely excreted to the environment as dissolved organic carbon or more complex organic polymers (e.g. coral mucus, e.g. Wild et al., 2004) or stored by algal cells as carbohydrates.

With these provisos, a comparison (Fig. 7) between estimates of N and P demand by phytoplankton in near-

shore waters based upon average daily primary production clearly shows that under most circumstances, daily water column nutrient demand far outstrips daily inputs from benthic mineralisation in coastal sediments (Alongi, 1989; Alongi and McKinnon, 2004; Lourey et al., 2001) and time-averaged daily inputs from river runoff, shelfbreak upwelling and urban sewage discharges (Furnas, 2003). The considerable disparity between water column demand and external inputs illustrates the primary role of water column remineralisation processes in sustaining phytoplankton growth and production in the GBR lagoon under “normal”, undisturbed conditions. The annual N and P inputs from land-based sources and upwelling have been averaged to a daily rate. In reality, these inputs are seasonal and event-focused (Furnas, 2003; Furnas and Mitchell, 1996a,b). For short-periods, therefore, external inputs may be much closer to, or even exceed phytoplankton nutrient demand (e.g. Devlin et al., 2001). As these nutrients are dispersed, phytoplankton rapidly take up the nutrients and converting them to biomass or other forms of organic matter (DOC, DON, DOP, detritus). This organic matter can be transported over large distances and is ultimately transformed into forms (e.g. marine snow) that may be deposited on benthic communities, such as coral reefs, and influence their structure, productivity (Anthony, 2000) and health (e.g. Fabricius and Wolanski, 2000).

Because of the rapid uptake, production and turnover of nutrients and organic matter (living and dead) in GBR waters, what substances or properties make useful measures of water quality? The observed rapid nutrient uptake and turnover rates mean that concentration measurements, by themselves, are a relatively insensitive

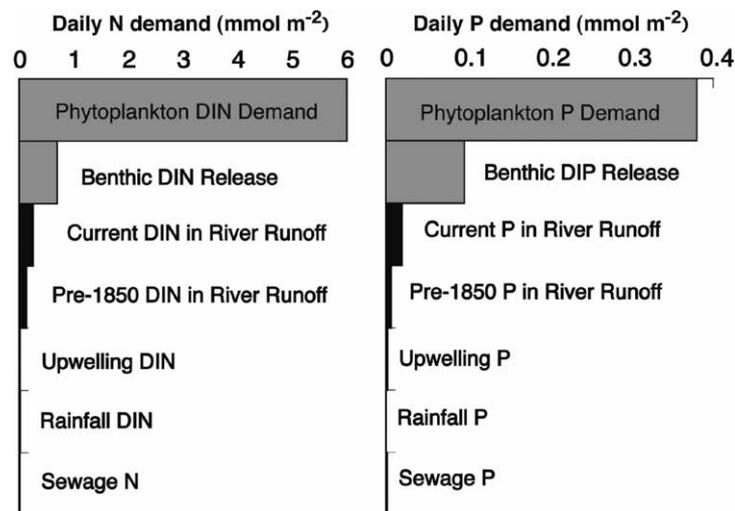


Fig. 7. Average daily demands for DIN (left) and phosphate (right) by phytoplankton in the nearshore zone ($\leq 15\text{ km}$ from the coast) as estimated from primary production rates and Redfield C:N:P ratios in relation to average daily inputs of DIN and phosphate from benthic mineralisation, river runoff, rainfall and shelfbreak upwelling.

measure of nutrient availability and effects on the ecosystem. High nutrient concentrations exist only fleetingly, until they are dispersed by mixing or consumed by uptake, while the only slightly higher concentrations which occur more frequently due to processes such as sediment resuspension do not appear to cause significant physiological or ecological effects in corals or macro-algae (Fabricius, 2004). Likewise, because photosynthetic carbon production is so widespread, its magnitude largely influenced by the abundant light in tropical waters and consumption funneled through so many ecosystem pathways, measures of water column organic carbon are also not a sensitive indicator of water quality. Concentrations of these materials are important context variables when combined with robust measures or estimates of nutrient and carbon input, consumption and turnover rates as they indicate the flows of materials and energy which support or disrupt reef and other benthic communities (e.g. Anthony, 2000; Fabricius and Dommissie, 2000).

The challenge of water quality monitoring is therefore to develop, apply and interpret measures of materials (e.g. nutrients, pollutants) or other properties that influence or usefully reflect the structure, productivity and health of reefs and other communities within the GBR. The available evidence clearly indicates that concentrations of easily measured inorganic nutrients are insensitive indicators of water quality status as their abundance is strongly influenced by plankton demand and transformation processes. Indices of plankton biomass (e.g. chlorophyll) or materials which have longer natural cycling times (for example, dissolved and particulate nutrients in detrital forms) are likely to be better measures of change in water quality status as they reflect nutrient availability, nutrient storage in biomass and the production of organic materials used by higher trophic levels, and may accumulate to a greater extent due to slower mineralisation rates. While measures of ecosystem rate processes are attractive as monitoring indices, their usefulness is constrained by high variability linked to natural environmental variability, and to physiological or methodological artefacts associated with rate process measurements. An effective water quality monitoring program should involve both measurements of ambient concentrations of key materials (e.g. nutrients, organic matter or key indicator species) to establish current status and temporal changes in ecosystem conditions and coupled measurements of key biological processes to define ecosystem responses to a changing environment. Although nutrient concentrations are usually very low in GBR waters due to strong natural biological demand and rapid recycling, even small but persistent increases must be regarded as strong indicators of significant ecosystem change as they are now in excess of previously tightly coupled levels of input, demand and cycling.

8. Management implications

- Nutrients added to shallow tropical coastal and shelf waters, such as the GBR lagoon, are very rapidly converted to plankton biomass and derived organic matter (excreted DOM, marine snow, detritus) following uptake by phytoplankton. Benthic organisms and ecosystems are most likely responding to this organic matter rather than the dissolved nutrients.
- Dissolved nutrient concentrations, by themselves, are not sensitive indicators of water quality because of rapid uptake and transformation by plankton populations. Monitoring programs should include a broader range of variables, including forms of organic matter consumed by or influencing larger organisms.
- Because of the very high demand for nutrients by plankton which normally keeps ambient concentrations at very low levels, even small but persistent changes in nutrients may be a strong indicator of significant changes in nutrient loading and the likelihood of ecosystem change. Monitoring programs need to be sustained over sufficient periods (probably > 10 years) and have sampling designs capable of detecting such small changes in concentration.

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