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Carbon, nitrogen, and phosphorus budgets for a shallow subtropical coastal embayment (Moreton Bay, Australia)

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Abstract

Average annual carbon, nitrogen, and phosphorus budgets were constructed for Moreton Bay. Primary production was the dominant source of carbon (by two orders of magnitude), N fixation was the dominant source of nitrogen, and point sources were the dominant source of phosphorus to the bay. About 41% of the nitrogen and 70% of the phosphorus entering Moreton Bay was exported to the ocean, and about 56% of the nitrogen was lost to denitrification. The high percentage loss of phosphorus to the ocean was directly related to the short residence time of the bay (46 d), which was consistent with other shallow coastal ecosystems. In contrast, the percentage loss of nitrogen to the ocean was low compared to other coastal systems due to the high percentage loss through denitrification associated with autotrophic sediments in the bay that enhance denitrification. Because most denitrification studies have been carried out using only dark incubations, the importance of denitrification to the nitrogen budgets of coastal systems in general may be underestimated. Carbon loss from Moreton Bay was dominated (by two orders of magnitude) by atmospheric exchange of CO_2 associated with benthic and pelagic respiration. The distinct difference between Moreton Bay (subtropical) and temperate systems was the dominance of biological (microbial: N fixation and denitrification) over physical inputs and losses of nitrogen. High N fixation in turn fuels a positive annual mean net ecosystem metabolism (NEM) of 21 g C m^{-2} yr^{-1} and suggests that primary production in the bay is phosphorus limited at the whole ecosystem scale.

The metabolism of temperate coastal ecosystems is closely linked to the magnitude of terrestrially derived nutrient (C, N, P) loads (Nixon et al. 1986; Borum 1996; Kemp et al. 1997). However, it remains difficult to predict the impact of increased nutrient loading on different coastal ecosystems, particularly tropical systems, because of confounding physical and biogeochemical factors (Pennock et al. 1994; Eyre and Balls 1999; Cloern 2001) and the influence of other nutrient sources and sinks such as the atmosphere and adjacent ocean (Smith 1984; Paerl et al. 1994; Eyre and France 1997; Smith and Hollibaugh 1997). Construction of nutrient budgets is a way of constraining these compounding factors, which then allows an evaluation of the pathways of nutrient flow and the fate and effect of nutrient loads on the metabolism of coastal ecosystems. Nutrient budgets also provide a means of quantitatively comparing different coastal systems.

There are many published nutrient budgets for temperate shallow coastal ecosystems (e.g., Boynton et al. 1995; Nixon et al. 1995; Kemp et al. 1997; Smith and Hollibaugh 1997). However, whole ecosystem scale nutrient mass balance studies in tropical and subtropical coastal systems are rare (e.g., Smith 1984; Eyre 1995; Eyre et al. 1999; McKee et al. 2000*a*), and these previous studies were restricted to only physical boundary fluxes of nitrogen and phosphorus and internal biological fluxes were only inferred. There have been no complete (i.e., physical boundary and internal biological fluxes) carbon, nitrogen, and phosphorus budgets constructed for large subtropical shallow coastal ecosystems.

The overall aim of this paper is to establish a quantitative inventory of the carbon, nitrogen, and phosphorus inputs, exports, and standing stocks and the cycling between major compartments in Moreton Bay. This will give an insight into the way nutrient inputs are modified as they move from the land into coastal waters and how these, in conjunction with internal biological fluxes, effect the system metabolism. The subtropical Moreton Bay Study Area will then be compared with other shallow coastal systems to enhance the understanding of nutrient behavior and to place the findings in a regional and global context.

Study area

Moreton Bay is a semienclosed embayment located adjacent to the city of Brisbane in southeast Queensland (Fig. 1). The bay, with a surface area of approximately 1,845 km^2, a depth of up to 29 m (average = 6.25 m), and a volume of approximately 11.1 km^3, is separated from the Pacific Ocean by Moreton Island and North Stradbroke Island. Moreton Bay exchanges water with the ocean via a 16-km wide opening to the north, Pumicestone Passage (0.5 km) in the northwest, and two minor openings to the east and south: south passage (3.5 km), and Jumpinpin (1 km). The bay receives terrestrial runoff from four river catchments (Logan, Brisbane, Pine, and Caboolture), which have a combined area of 19,255 km^2. The region receives a summer-dominated rainfall associated with tropical depressions that move on to the catchment from the north. Moreton Bay receives an annual average rainfall of 1,177 mm (Brisbane International Airport Sta. 40223; n = 49 yr) and a mean evaporation that is greater than the mean rainfall (Epan = 1,961 mm; n = 12 yr). Ap-

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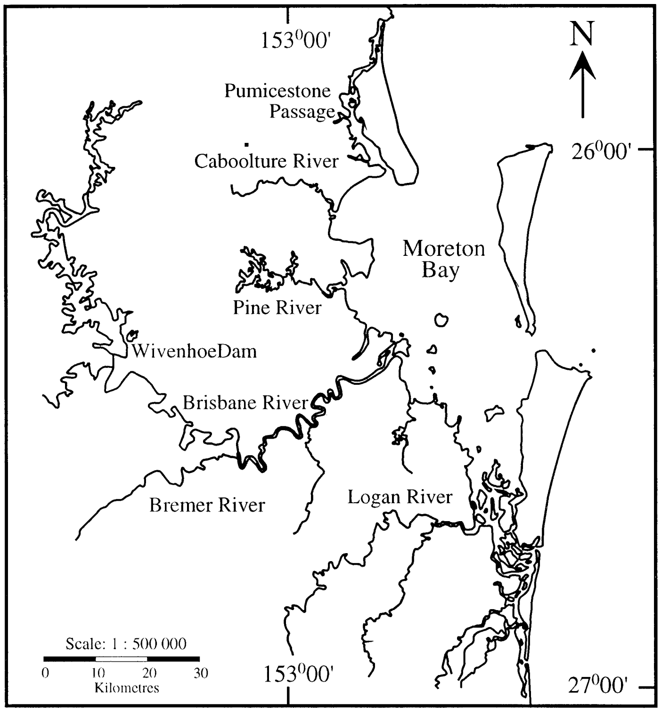

Fig. 1. The Moreton Bay region of southeast Queensland, Australia.

proximately 28% of the catchment remains undisturbed, and the catchment has approximately two million people.

Methods

The budget modeling assumes steady state; therefore, the sum of inputs, outputs, and storage of each element (C, N, P) within the defined system should equal zero ± error. The model includes five major inputs for carbon, nitrogen, and phosphorus: point source, diffuse source, urban runoff, groundwater, and atmospheric deposition. A sixth input, primary production, was considered for carbon, and nitrogen fixation was also considered for nitrogen (Fig. 2). Outputs of carbon, nitrogen, and phosphorus include burial, fisheries harvest, exchange through Pumicestone Passage, dredging, and ocean exchange. A nitrogen loss through denitrification and a carbon loss through CO_2 exchange with the atmosphere were also considered (Fig. 2). Standing stocks include dissolved and particulate nutrients in the water column, solid phase sediment nutrients, pore-water nutrients, and floral biomass (mangroves, sea grasses, macroalgae, benthic microalgae, and phytoplankton) (Fig. 2). Three nutrient recycling pathways were considered: biological uptake (mangroves, sea grasses, macroalgae, benthic microalgae, and phytoplankton), benthic fluxes, and phytoplankton sedimentation (Fig. 2).

The nutrient budget boundaries were Moreton and Stradbroke Islands to the east and the mainland of southeast Queensland to the west (Fig. 1). There are four open sea boundaries defined by the cotidal line from Cape Moreton to the northern end of Bribie Island, Pumicestone Passage, South Passage, and Jumpinpin. The terrestrial riverine boundaries were defined as the tidal limits of the four largest river estuaries (Logan, Brisbane, Caboolture, and Pine). In order to develop a closed budget, all the inputs to and all the outputs from the Moreton Bay study area must be measured independently over the same period of time. The nutrient budget was developed for the hydrological year (the period between minimum events in consecutive calendar years) that most closely corresponds with the period over which most of the data were collected (1997/1998). Some data were measured during a single season. Where possible these have been extrapolated for an entire year by considering seasonal patterns found by other similar studies in Australia or from other parts of the world. Where data have been collected or estimated for a number of hydrological regimes (i.e., flood, average, dry), average year fluxes were adopted for the budget construction.

Owing to the lack of information about the different nutrient species, only total nitrogen, total phosphorus, and total carbon were considered. Mass (tonnes = 10^3 kg) was used throughout all calculations. All terms were rounded to 1 tonne, even though the accuracy this suggests is much greater than can be justified by the methods used. This was to avoid progressive accumulation of rounding errors and to avoid loss of some of the smaller fluxes, which were less than the rounding errors of the larger fluxes. Instead of a detailed quantitative error analysis, which is not particularly useful for this type of budgeting procedure, we relied on the ‘‘convergence of multiple estimates’’ approach (Kemp et al. 1997) to evaluate errors associated with the budget.

Over the period from 1997 to 1998, a number of studies quantified the different nutrient flux components of the bay and its catchments that together describe most of the sources and sinks of nutrients that impact the Moreton Bay system (Dennison and Abal 1999). Most of these studies were undertaken as part of the Moreton Bay Study: A Scientific basis for the Healthy Waterways Campaign, which was to provide scientific data, interpretation, and rationale for developing a water strategy for the region (Dennison and Abal 1999). Some additional studies were also undertaken in 2000 and 2001, and some previously published data have been used. The following sections describe briefly the methods used to quantify each of the nutrient flux components.

Nitrogen and phosphorus point-source loads, below the sampling point for diffuse loads, were calculated using chemical and flow data (Pillsworth 1997). In the absence of analytical data, the nutrient loads were based on the treatment technology and typical nitrogen and phosphorus concentrations for the given technology. Nutrient loadings from minor point sources were estimated using available flow and analytical data. In the absence of information, a ‘‘best estimate’’ was made given industry experience.

A relatively simple rainfall-runoff and pollutant export model (AQUALM-XP) was used to estimate diffuse catchment loads (McAlister and Walden 1999). In addition, a field sampling program was undertaken in 1996 in the Logan, Brisbane, Bremer, and Caboolture Rivers (Fig. 1) with the objective of quantifying nutrient loads entering Moreton Bay. Samples were collected routinely (approximately one per month) and on a flow-weighted basis during floods (maximum two samples per day). Samples were analyzed for total

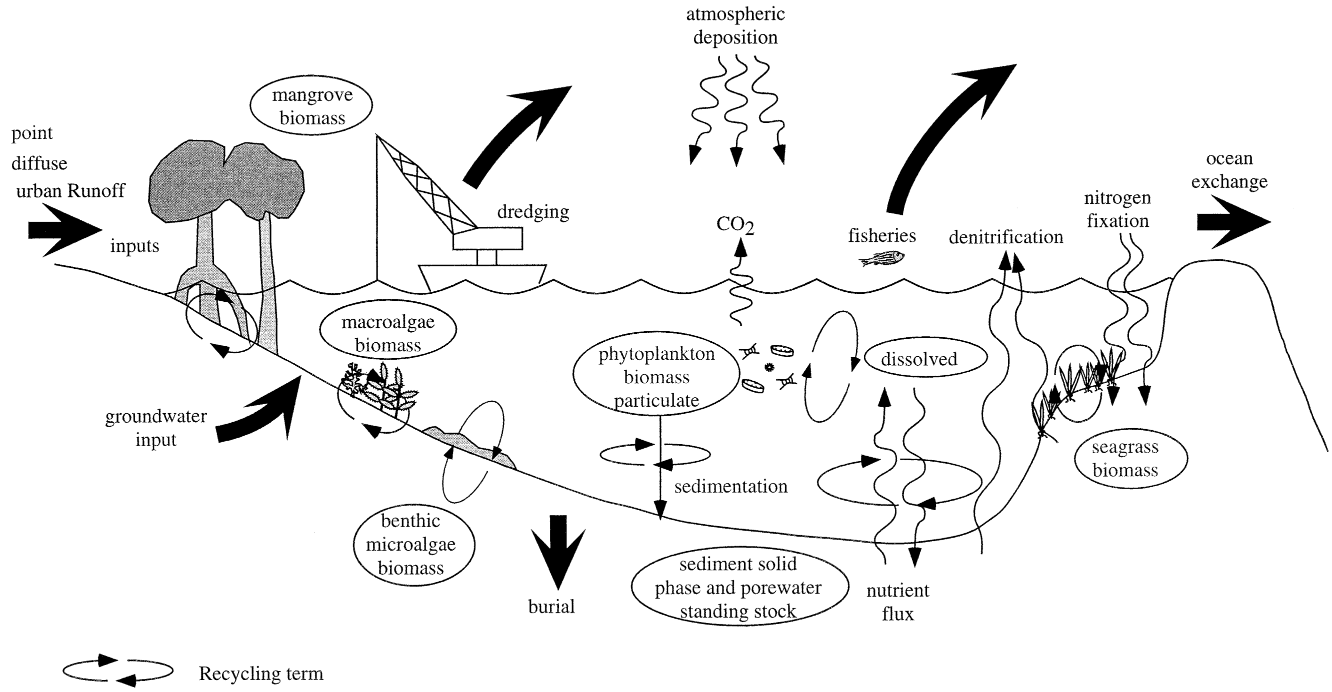

Fig. 2. Conceptual model of the Moreton Bay C, N, and P budget showing nutrient sources, storages, recycling pathways, and losses.

nitrogen and phosphorus using standard methods. Daily discharge data for the Logan (Stas. 145102B and 145014A), Bremer (Sta. 143007), Brisbane (Sta. 143001), and Caboolture (Sta. 145001) rivers were obtained from the Queensland Department of Natural Resources and increased by an area coefficient for the area not gauged (excluding urban areas below the sampling location). Flow-weighted data were combined with discharge using linear interpolation between samples (Kronvang and Bruhn 1996). Loads calculated for the Bremer and Brisbane were added to give a total loading on the Brisbane River estuary and are hereafter referred to as a loading for the Brisbane River catchment.

Because 1996 was a flood year an additional field sampling program of the Logan and Albert Rivers was undertaken during 1997 and 1998 to quantify nutrient loads entering Moreton Bay during an average year. Samples were collected approximately every 2 weeks from the Albert and Logan Rivers just above the estuarine bay line. Samples were analyzed for total nitrogen and phosphorus as above. Daily discharge data for the Logan (Sta. 145014A) and Albert (Sta. 145102B) rivers were obtained from the Queensland Department of Natural Resources and increased by an area coefficient for the area not gauged (excluding urban areas below the sampling location). A regression between load and discharge was developed and applied to the daily discharge data to calculate an annual load for the period August 1997 to August 1998 (Kronvang and Bruhn 1996).

Nitrogen and phosphorus loads associated with runoff from urban areas below the sampling locations for diffuse loads were calculated using urban areas and areal loading rates (N = 6.0 kg ha^{-1} yr^{-1}; P = 0.8 kg ha^{-1} yr^{-1}; Young et al. 1996). The urban loads were added to the measured non–point-source loads. Atmospheric deposition loads were estimated using rainfall concentration data for coastal northern New South Wales 200 km south of the study area (McKee et al. 2001), mean annual rainfall for Moreton Bay (Brisbane Airport = 1,177 mm), and the surface area of Moreton Bay (1,845 km^2). The northern New South Wales rainfall concentration data are from coastal sites and therefore represent similar conditions to Moreton Bay (i.e., clean air sourced from the Pacific Ocean). No dry fall data were available. As such, the wet fall loads were multiplied by 1.2, which is the ratio of total nitrogen deposition (wet + dry) to wet nitrogen deposition for the South Pacific Ocean (Paerl 1995); the same ratio was assumed to apply for phosphorus. Groundwater nutrient loads to Moreton Bay were estimated by (a) the determination of volume of groundwater discharged and (b) the assignment of concentrations of the selected pollutants to groundwater (Cox et al. 1999). Groundwater discharges were calculated for a 2-km wide strip around the bay and estuaries by first dividing the strip into many segments and then considering geological materials/aquifer type, field permeability, likely depth of the water table, hydraulic gradient, and saturated thickness for each segment and then applying Darcy's Law of groundwater flow. Nutrient concentrations were assigned to each discharge based on land use, rainfall, and aquifer type. Nitrate concentrations ranged between 0.1 and 20 mg L^{-1}; phosphate concentrations ranged between 0 and 0.26 mg L^{-1}.

Phytoplankton productivity was measured by size fractionated C^{14} (Dennison et al. 1999*b*; Greenwood et al. 1999). Total carbon production for Moreton Bay by phytoplankton was estimated by adding individual carbon productions for Bramble Bay, Deception Bay, Waterloo Bay, and the remaining parts of Moreton Bay. The September 1997 and February 1998 measured C^{14} productivities for each area were averaged, and productivity of mg C m^{-3} h^{-1} was converted to t C yr^{-1} by multiplying by 3 m (photic depth) $\times$ 12 h $\times$ 365 d $\times$ area (m) $\times$ 1 $\times$ 10^{-9} t. Total carbon production for Moreton Bay by mangroves, sea grasses, macroalgae, and benthic microalage was estimated by multiplying the measured productivity of each flora group by their areal extent (Dennison et al. 1999*b*). Coral productivity is not included in the nutrient budget since it is smaller than the error term of the other components of the budgets.

Surface sediments were collected from 91 sites in Moreton Bay and Brisbane River during three field excursions (July 1997, September 1997, and February 1998) using a variety of methods (box cores, grab samples, and diver collected scoop samples) (Heggie et al. 1999). Solid phase and pore-water nitrogen and phosphorus pool sizes contained within the top 2 cm and the top 11 cm for each zone were quantified. Nutrient burial was estimated by multiplying the average annual suspended sediment load to Moreton Bay (Eyre et al. 1998) by the average organic carbon, nitrogen, and phosphorus concentration of the external delta sediments (Heggie et al. 1999). This assumes that all the suspended sediment that enters Moreton Bay is retained within the external delta, which is reasonable considering that the average annual load of 92,801 t is also similar to the annual quantity of sediment needed over the last 6,500 yr to build the external delta (Eyre et al. 1998). The similarity between the external load of sediment and sediment needed for the external delta also suggests that there is little accumulation of biological sediment (i.e., from primary productivity). Burial of inorganic carbon ($CaCO_3$) was estimated by multiplying the average ratio between organic and inorganic carbon (1 : 1.7 in Moreton Bay sediments; Eyre and Ferguson 2001) by the amount of organic carbon buried.

During February (midsummer) 1998, benthic chambers were deployed covering both day and night at 10 locations within Moreton Bay and two locations in Brisbane River (Heggie et al. 1999). Individual TCO_2 dissolved inorganic carbon (DIC) fluxes were extrapolated over the bay. Pelagic respiration was estimated by applying respiration rates of 16% (diatoms) and 35% (dinoflagellates) (Langdon 1993; Greenwood et al. 1999) to the phytoplankton primary production (carbon fixation) in the bay. The percentage respiration used was proportioned according to the percentage of diatoms or dioflagellates in each part of the bay.

Sediment denitrification rates were measured directly using N_2 : Ar ratios analyzed on a modified membrane inlet mass spectrometer with oxygen removal (Eyre et al. in press). Undisturbed sediment cores were collected in triplicate from eight sites in the western and central sections of Moreton Bay in July 2000 (winter) and March 2001 (summer) (Eyre and Ferguson 2001). The cores were incubated over a full 24 h light/dark cycle, and the average net N_2 fluxes were extrapolated over the surface area of Moreton Bay (1,845.5 km^2). Sediment N_2 fluxes measured using N_2 : Ar fluxes are the net result of denitrification minus N fixation. Small nitrogen inputs through sediment N fixation have been accounted for in the direct flux N_2 measurements in the western and central bays because N_2 : Ar fluxes are the net result of denitrification minus N fixation. However, the highest N-fixation rates in the world have been recorded in extensive sea grass beds in eastern Moreton Bay (Perry 1998; Dennison and Abal 1999). Nitrogen inputs associated with N fixation in sea grass beds were estimated by multiplying N-fixation rates by the area of sea grass (181 km^2) (Dennison and Abal 1999).

The lower Brisbane River estuary is maintained at a depth of between 9 and 13 m for navigation. During normal years, between 0.7 and 1.83 $\times$ 10^6 m^3 (Eyre et al. 1998) or 280,000 to 732,000 t (0.4 tm^{-3}) of sediment is dredged for maintenance of the port. This sediment is used for reclamation and therefore removed from the Moreton Bay system. The sediment removal was combined with the average sediment concentration in the estuary (Heggie et al. 1999) to estimate nutrient removal associated with dredging. Nitrogen and phosphorus exchange between Moreton Bay (Deception Bay) and Pumicestone Passage has been directly measured (Eyre and France 1997). Water samples and velocity measurements were collected over a range of tidal and flow conditions in a cross-section transect at the southern end of Pumicestone Passage. The products of discharge and concentration were integrated for complete tidal cycles and extrapolated to give annual load estimates. The average water column TC : TP ratio of the bay (39.1 : 1 mass; Table 3) was used to calculate carbon exchange.

The commercial catch of fish from Moreton Bay was obtained from the QFISH database (Queensland Fish Management Authority) and includes all catches within the east coast trawl industry and all catches within the line, net, and pot industries. No estimates were available for the recreational catch, and it was therefore assumed equal to the commercial catch (Pollock and Williams 1983). Dry weight was assumed to be 20% of the wet catch, and the carbon, nitrogen, and phosphorus content of the dry catch was assumed to be 50%, 15%, and 0.62% respectively (Boynton et al. 1995; Nixon et al. 1995).

When all the nutrient inputs and outputs were added, the ocean exchange of phosphorus and nitrogen was calculated by difference; $+ve$ = an input and $-ve$ = an export. This term also includes the sum of the errors associated with the other components of the budget. Because the errors associated with carbon productivity and respiration are so large (*see* Smith and Hollibaugh 1997), it is not possible to calculate ocean exchange by difference. As such, ocean exchange was estimated by assuming that carbon is flushed to the ocean in proportion to phosphorus based on the average TC : TP ratio in the bay (39.1 mass; Table 3; *see Discussion*).

Total and dissolved inorganic water column nitrogen and phosphorus standing stocks were estimated by applying the average concentration from contour maps generated from water column nutrient data collected during baseline sampling in 1997 (Dennison et al. 1999*a*). These concentrations were combined with the corresponding volume of Moreton Bay. Moreton Bay volumes were obtained from bathymetric maps (Queensland Transport). Particulate carbon, nitrogen, and phosphorus water column standing stocks for Moreton Bay were calculated by averaging the day and night September 1997, February 1998, and July 1998 particulate concentrations for each part of the bay (Greenwood et al. 1999) and multiplying by the volume of each part of the bay. No dissolved organic carbon (DOC) concentration data were

Table 1. Non–point source catchment loads (t yr^{-1}) impacting Moreton Bay.

Author	Catchment	Carbon	Nitrogen	Phosphorus
Average year				
Modeled (McAlister and Walden 1999)	Logan		550	79
	Brisbane		1,100	160
	Caboolture		100	15
	Other		650	86
	Total		2,400	340
Measured 1997/1998	Logan	571	131	31
1996 (Flood Year)				
Modeled (McAlister and Walden 1999)	Logan		1,400	140
	Brisbane		4,500	620
	Caboolture		190	29
	Other		1,610	181
	Total		7,700	970
Measured 1996	Logan	8,702	832	207
	Brisbane	24,864	2,374	382
	Caboolture	3,898	348	24
	Total	37,464	3,554	613

available for the Moreton Bay water column. As such, the standing stock of DOC was obtained by scaling the standing stock of dissolved organic nitrogen (DON) by the average ocean end member DOC : DON ratio (8.2 : 1 mass) for subtropical East Australian estuaries (Jenitta Gay pers. comm.; Eyre 2000).

Phytoplankton carbon biomass for Moreton Bay was calculated by averaging the day and night September 1997, February 1998, and July 1998 Strathman and Eppley estimates of phytoplankton carbon concentrations for each part of the bay (Greenwood et al. 1999) and multiplying by 3 m (photic depth) $\times$ the area of each part of the bay. The Redfield ratio was applied to the phytoplankton carbon biomass to obtain estimates of the nitrogen and phosphorus phytoplankton biomass. Carbon, nitrogen, and phosphorus biomass for Moreton Bay contributed by mangroves, sea grasses, macroalgae, and benthic microalage were estimated by multiplying the measured biomass of each flora group by their areal extent (Dennison et al. 1999*b*). Coral biomass is not included in the nutrient budget since it is smaller than the error term of the other biomass components of the budgets.

Three major nutrient recycling terms were considered in the Moreton Bay nutrient budget (1) benthic fluxes, (2) biological nitrogen and phosphorus uptake, and (3) phytoplankton sedimentation. None of these terms result in a net input, loss, or storage but represent recycling within the system. Nutrient fluxes were measured using benthic chambers (Heggie et al. 1999) at 10 sites in Moreton Bay and the Brisbane River in February 1998 (summer). Individual fluxes were extrapolated over the entire bay. Nitrogen and phosphorus uptake by phytoplankton was calculated by two methods. First, the Redfield C : N : P ratio (106 : 16 : 1) was applied to pelagic primary productivity (i.e., carbon). Second, the ^{15}N and ^{32}P uptake data were extrapolated baywide. The day and night September 1997 and February 1998 measured ^{15}N (100% ammonium) and ^{32}P uptakes for each area were averaged, and the uptakes of μM N h^{-1} (Greenwood et al. 1999) were converted to tonnes N and P yr^{-1} by multiplying by 14 or 31 (mol. wt.) $\times$ 1000 (l) $\times$ 3 m (photic depth) $\times$ 24 h $\times$ 365 d $\times$ area (m) $\times 1 \times 10^{-9}$(t). Nitrogen and phosphorus uptake by mangroves, sea grasses, macroalgae, and benthic microalgae was estimated by applying an appropriate C : N : P ratio to primary productivity estimates (i.e., carbon; Dennison et al. 1999*b*). However, Dennison et al. (1999*b*) applied the molar C : N : P Redfield ratio (106 : 16 : 1) to nitrogen and phosphorus uptake weights for benthic microalage and not a weight ratio, as such their original estimates have been corrected. Phytoplankton sedimentation was assumed equal to phytoplankton production minus respiration and grazing (Greenwood et al. 1999).

Results

There are 28 major sewage treatment plants and seven major industrial wastewater treatment plants that discharge an average of 3,383 t of nitrogen and 1,182 t of phosphorus to the study area each year. These estimates are similar to previous estimates of 2,985 t of nitrogen and 993 t of phosphorus (SKM Economics 1995), which gives some confidence in the values. Point-source carbon loads of 4,330 t were estimated using a wastewater carbon : nitrogen loading ratio of 1.28 (Nixon et al. 1995).

Modeling of catchment exports suggests that on average 2,400 t of nitrogen and 340 t of phosphorus were delivered to the study area from non–point sources each year (Table 1). These estimates are based on very simple modeling with little calibration and no verification of the total loads. A comparison of modeled loads and measured loads for 1996 (Table 1) indicates that for a flood year (i.e., 1996) modeling overestimated nitrogen loads by a factor of 2.2 and overestimated phosphorus loads by a factor of 1.6. Nitrogen and phosphorus loads in the Logan catchment were also measured during 1997/1998. The total annual gauged flow in the Logan catchment during 1997/1998 was 78.5×10^6 m^3, which is very similar to the gauged flow during 1995 (90×10^6 m^3), which was the average modeled year. A comparison

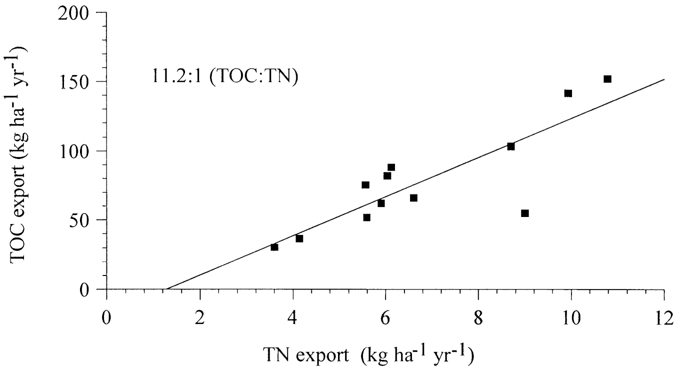

Fig. 3. Carbon export as a function of total nitrogen export constructed from data from temperate and tropical catchments around the world. (Naiman and Sibert 1978; Meyer et al. 1981; Meybeck et al. 1988; Wafar et al. 1989; Howarth et al. 1991; McDowell and Asbury 1994; Nelson et al. 1996; Hope 1997).

of modeled loads for the average year and measured loads for 1997/1998 (also an average year) in the Logan catchment (Table 1) indicates modeling overestimated nitrogen loads by a factor of 4.2 and overestimated phosphorus loads by a factor of 2.6.

The land use/export model (AQUALM-XP) used (McAlister and Walden 1999) is based on relationships that may not be applicable to Australian conditions, and, as such, this type of model commonly gives poor estimates of catchment loads (Wasson et al. 1996; Letcher et al. 1999). The overestimation of loads by the model is most likely the result of poor characterization of in-catchment processes such as floodplain storage and in-stream assimilation, which would have the effect of decreasing the load exported out of a catchment. Consistent with this is the better agreement between modeled and measured loads in small subcatchments such as Enoggera, and the better agreement during the flood year than the average year (McAlister and Walden 1999). In-catchment processes are likely to be less important in smaller catchments (i.e., Enoggera), where there is a short transport path between the source and catchment outlet, and in-stream assimilation is likely to be less important during flood years due to shorter residence times. Because average year measured loads were not available for the whole catchment and the model appears to overestimate the diffuse loads, the average year modeled loads were scaled by a factor of 4.2 for nitrogen and a factor of 2.6 for phosphorus, which gives an annual diffuse load of 571 t nitrogen and 131 t of phosphorus. A review of the relationships between carbon export and export of total nitrogen from catchments around the world (Fig. 3) shows there is a good relationships between export of nitrogen and total organic carbon (TOC). The relationship gives a ratio of 11.2 : 1 TOC : TN. Using the TOC : TN ratio of 11.2 : 1 and the average annual nitrogen loading of 571 t results in a diffuse carbon loading of 6,395 t to the study area.

The atmosphere contributed 1,692 t of nitrogen and 114 t of phosphorus to the bay. Groundwater loads of <1 t carbon, 120 t nitrogen, and 2 t phosphorus only represent a small component of the nutrient budget. The average net N_2 flux for sediments in the western and central regions of Moreton Bay was 36 μmol N m^{-2} h^{-1}, which gives an annual loss of 8,152 t of nitrogen. The average middle range of N-fixation rates in the sea grass beds of the eastern bay was 252 μmol N m^{-2} h^{-1}, which would result in an annual input of 5,156 t of nitrogen, and the average upper range of N-fixation rates was 410 μmol N m^{-2} h^{-1}, which would result in an annual input of 9,117 t nitrogen. The high N-fixation rates are associated with very low interstitial nitrogen concentrations (O'Donohue et al. 1991; Perry 1998) and grazing by dugongs. Dugong grazing increases the availability of organic matter and provides aeration for bacterial metabolism (Dennison and Abal 1999). The upper value was used because it provided a reasonable balance to the budget. Further, the upper value was also used because this pathway of nitrogen input was most likely underestimated due to other observed, but not quantified, sources of N fixation in the bay, such as Lyngbya *majuscula* and Trichodesmium *erythraeum.* N-fixation rates from 40 to 13,333 μmol N m^{-3} h^{-1} have been recorded for Trichodesmium *erythraeum* in Moreton Bay, but there is no information available on its spatial and temporal distribution (Greenwood et al. 1999).

Table 2. Primary production (carbon fixation; t) in Moreton Bay.

Primary producer	Carbon
Mangroves	59,000
Sea grasses	36,000
Macroalgae	20,000
Benthic microalgae	85,000
Phytoplankton	301,000
Total	501,000

Primary production by mangroves, sea grasses, macroalgae, and phytoplankton was measured both spatially and temporally, which gives some confidence in the values (Table 2; Dennison et al. 1999*b*). In contrast, benthic microalgae productivity was only measured once at two sites, which gives a very high baywide carbon production of 560,000 t (Dennison et al. 1999*b*). Using the total biomass of benthic microalgae in Moreton Bay (300 t), which has been well quantified, and benthic productivity rates from Port Phillip Bay (Harris et al. 1996) suggests that the biomass of benthic microalgae in Moreton Bay should fix about 85,000 t of carbon per year. It could be argued that benthic microalage in Moreton Bay may be more productive than in Port Phillip Bay because of increased light associated with the lower latitude. However, previous studies have shown that there is no apparent gradient in benthic microalgae productivity with latitude (MacIntyre et al. 1996). Further, in contrast to latitude, biomass (chlorophyll) appears to be a reasonable scalar of benthic microalgae productivity (MacIntyre et al. 1996). As such, a value of 85,000 t for benthic microalgae production has been used in the budget.

There are four major nutrient standing stocks in Moreton Bay: (1) solid phase sediment nutrients, (2) porewater nutrients, (3) biomass nutrients, and (4) water column nutrients. When estimating standing stocks of nutrients in bottom sediments, the depth of sediment used is a large determinant of the total stock. Data are available for two depth ranges in

Table 3. Biomass and water column nutrient standing stocks (t) in Moreton Bay.

Standing stock	Carbon	Nitrogen	Phosphorus
Biomass nutrients			
Mangroves	2,300,000	33,000	2,200
Sea grasses	11,000	320	50
Macroalgae	800	50	10
Benthic microalgae	1,800	300	20
Phytoplankton	1,993	301	19
Total	2,315,593	33,971	2,299
Water column nutrients			
Dissolved inorganic	—	78	120
Dissolved organic	3,059	373	16
Particulate	3,667	326	36
Total	6,726	777	172

the bottom sediments of Moreton Bay: 0 to 2 cm and 0 to 11 cm. The 0- to 2-cm depth range is readily exchangeable with the water column and may have elevated concentrations due to recent deposition. In contrast, the 0- to 11-cm depth range should give a better estimate of average nutrient burial over a longer time period, although this will depend to some degree on the depth of and degree of bioturbation. Very little seasonal variability was seen in the 0- to 11-cm solid phase and pore-water nutrient pool sizes. An average of the 0- to 11-cm September and February solid phase nutrient pool sizes was adopted, which gives 116,872 t carbon, 66,081 t nitrogen, and 38,870 t phosphorus for the nutrient budget. The solid phase sediment pools were a substantial store of nitrogen and phosphorus, which represents about five times the annual input of nitrogen and about 24 times the annual input of phosphorus. In contrast, using an average of the 0- to 11-cm September and February pool sizes shows that the pore waters were a much smaller storage of carbon (690 t), nitrogen (92 t), and phosphorus (25 t) than the solid phase.

Mangroves were the largest store of carbon in Moreton Bay, containing about 20 times the carbon stored in the sediments (Table 3). A substantial amount of carbon was also stored in the sea grass beds. The largest biomass nitrogen store was the mangroves, but this was only half that contained in the sediments. The sediments were also a much larger store of phosphorus than the biomass. Similar amounts of carbon, nitrogen, and phosphorus were stored in the macroalgal, benthic microalgal, and phytoplankton biomass as contained in the water column (Table 3). However, phytoplankton are also particulate carbon and, as such, were also included as part of the water column particulate standing stocks (Table 3).

With the exception of the DIC flux, which represents a net carbon loss from the system, the nutrient fluxes across the sediment–water interface represent nutrient recycling within Moreton Bay and not an input, output, or storage. Benthic nitrogen (5,841 t) and phosphorus (2,885 t) fluxes are much smaller recycling terms than the turnover by phytoplankton and benthic microalgae but similar in magnitude to the combined catchment and atmospheric inputs (Table 4). Nitrogen and phosphorus uptakes estimated from ^{15}N and ^{32}P experiments give nitrogen and phosphorus uptake rates of about three and two times, respectively, the uptakes estimated from Redfield ratios. The Redfield estimated phytoplankton uptakes were used in the budget since the same approach was used for estimating the nitrogen and phosphorus uptakes for the other flora components of the budget (Table 4).

Table 4. Biological nutrient recycling (t) in Moreton Bay.

Recycling term	Nitrogen	Phosphorus
Mangroves	2,300	200
Sea grasses	1,500	200
Macroalgae	1,200	160
Benthic microalgae	15,000	2,100
Phytoplankton (Redfield)	53,000	7,300
Total	73,000	9,960
Phytoplankton (^{15}N and ^{32}P)	144,300	15,015

Nitrogen inputs to Moreton Bay were dominated by N fixation (Table 5), which contrasts with temperate systems where N fixation is considered insignificant (e.g., Boynton et al. 1995; Nixon et al. 1995). A similar conclusion was reached if either the low or high values of N fixation were used. However, the input of nitrogen through N fixation may be even higher because other sources of N fixation in the bay, such as Lyngbya *majuscula* and Trichodesmium *erythraeu,* were not included. Point-source inputs were the largest source of phosphorus and second largest source of nitrogen, which also contrasts with temperate systems where diffuse loads typically make up a larger proportion of the loads (e.g., Boynton et al. 1995; Nixon et al. 1995, 1996).

Table 5. Nutrient budget for Moreton Bay (t yr^{-1}).

Budget components	Carbon	Nitrogen	Phosphorus
Standing stocks			
Sediment (solid phase)	116,872	68,081	38,870
Sediment (pore water)	—	92	25
Water column (total)	3,667	777	172
Biomass	2,313,766	33,695	2,282
Inputs			
Point sources	4,330	3,383	1,182
Non–point sources	6,395	571	131
Atmosphere	5,223	1,692	95
Groundwater	1	120	2
Primary production	501,000	—	—
N fixation	—	9,177	—
Total	516,949	14,883	1,429
Outputs			
Denitrification	—	−8,152	—
Pelagic respiration	−63,187	—	—
Benthic respiration	−465,632	—	—
Dredging	−2,560	−187	−309
Burial	−1,291	−31	−36
Fisheries harvest	−488	−147	−6
Pumicestone passage	−2,776	−160	−71
Ocean exchange	−48,171	−6,206	−1,007
Recycling			
Benthic fluxes	—	5,841	2,885
Biological uptake	—	73,000	9,960
Phytoplankton Sedimentation	121,944	21,469	2,974

This reflects the episodic nature of subtropical systems with only small diffuse loads delivered during average years (i.e., this budget) and much larger diffuse loads delivered during flood years (Table 1; McKee et al. 2000*a,b*). Atmospheric deposition was the next largest input of nitrogen, with groundwater loads making up the remainder of the nitrogen inputs. Atmospheric nitrogen loads were about 11% of the total nitrogen inputs, which is low compared to many temperate systems (Paerl 1995). Most of the remaining phosphorus inputs were equally distributed between non–point-source loads and atmospheric deposition. In contrast, carbon inputs to Moreton Bay were clearly dominated (by two orders of magnitude) by primary production (carbon fixation). The dominance of biological over physical inputs of carbon was also seen in temperate Narragansett and Chesapeake Bays (Nixon et al. 1995; Kemp et al. 1997). The remaining sources (point sources, non–point sources, atmospheric deposition) contributed a similar, but much smaller, amount of carbon.

Nitrogen outputs were dominated by denitrification and ocean exchange, with most of the remaining nitrogen lost, in smaller, but about similar, amounts, through dredging, fishery harvest, and Pumicestone Passage. Burial only accounted for a small amount of nitrogen loss. Phosphorus outputs were dominated by ocean exchange. Most of the remaining phosphorus was removed through dredging, with a small amount also buried and exported through Pumicestone Passage. Fishery harvest only accounted for a small amount of phosphorus loss. In contrast, carbon loss from Moreton Bay was dominated (by two orders of magnitude) by atmospheric exchange of DIC (CO_2) associated with benthic and pelagic respiration. Benthic respiration was significantly higher than pelagic respiration, which reflects the shallow water column ($<$6 m) in Moreton Bay. Ocean exchange was the next largest loss of carbon. Most of the remaining carbon was removed, in similar proportions, through Pumicestone Passage and dredging. Burial and fisheries harvest only accounted for a small amount of carbon loss.

Discussion

Budgeting of phosphorus is more straightforward than that of nitrogen and carbon because it has no gaseous pathways. As such, the phosphorus budget provides a useful check on the overall conceptual framework of the Moreton Bay budget (Table 5). Moreton Bay receives, on average, about 1,429 t of phosphorus per year. Dividing this load by the bay volume of 1.11×10^{10} m^3 suggests that total phosphorus concentrations in the water column would be about 4.0 μM if the bay has a flushing time of about 1 yr. However, average total phosphorus concentrations in the water column are about 0.5 μM. If phosphorus cycling (concentrations) in Moreton Bay was dominated by ocean exchange, a water column concentration of 0.5 μM suggests that the bay flushes about every 46 d, which is very similar to the average flushing times of 44 d calculated by the receiving water quality model constructed for the bay (Dennison and Abal 1999). Using an annual loading of 1,429 t and a flushing time of 46 d suggests that 1,243 t of phosphorus are flushed to the ocean each year. This is similar to the ocean exchange of phosphorus calculated by the input–output budget (1007 t; Table 5) and well within the error associated with the budget estimate. Moreton Bay would need an additional phosphorus loading of 236 t yr^{-1} (1,243 t minus 1007 t) to balance the budget. The similarity in magnitude of the ocean exchange term calculated by two independent approaches gives some confidence in the phosphorus budget.

Moreton Bay receives, on average, an excess (total nitrogen load minus denitrification loss) of about 6,731 t of nitrogen per year. Dividing this load by the bay volume and assuming that the bay flushes every 46 d suggests that total nitrogen concentrations in the water column should be about 4.9 μM. This is similar to average bay concentration of about 5.0 μM, which suggests that ocean flushing is also important for nitrogen cycling (concentrations) in Moreton Bay. Using an annual loading of 6,731 t and a flushing time of 46 d suggests that 5,883 t of nitrogen are flushed to the ocean each year. A similar calculation can be made by assuming that nitrogen is flushed to the ocean in proportion to phosphorus based on the average TN : TP ratio in the bay. Using the average TN : TP ratio (4.5; Table 3) gives an ocean export of 5,544 t of nitrogen, which is similar to the previous estimate. The average of these two estimates of ocean export (5,714 t) is very similar to the ocean exchange term calculated by the input–output approach (6,206 t; Table 5). The similarity in magnitude of the ocean exchange term calculated by three independent approaches also gives some confidence in the nitrogen budget.

Changing land use patterns in the Moreton Bay catchment and an associated increase in the loading of point and non-point nutrients is the major cause of water quality problems in the bay. This is of particular concern because urban growth in southeast Queensland is expected to be one of the four or five fastest in the developed world. Cole et al. (1993) and Caraco (1995) summarized data from a number of river systems around the world and established a good relationship between human population density and nitrate and phosphate concentrations in the rivers. Comparison of the Moreton Bay catchment with other systems from around the world shows that for a given population density the Moreton Bay catchment has lower nitrate concentrations and higher phosphate concentrations (Fig. 4). With the exception of the Murray Darling, the other Australian systems also have lower nitrate concentrations and higher phosphate concentrations at a given population density than the rest of the world. The lower nitrate concentrations are most likely due to less intensive land use practices in Australian systems, including the Moreton Bay catchment. In contrast, many of the overseas countries, particularly the European countries, have been removing phosphorus from the sewage effluent for some time, which may account for the higher phosphate concentrations in the Australian systems. Despite the lower nitrate concentrations for the Australian systems, the important point illustrated by Fig. 4 is that with a fast-growing catchment population, exports of nutrients will also increase and may accelerate water quality problems in Moreton Bay.

Nixon et al. (1996) established a linear relationship between the fractional net transport of nitrogen and phosphorus

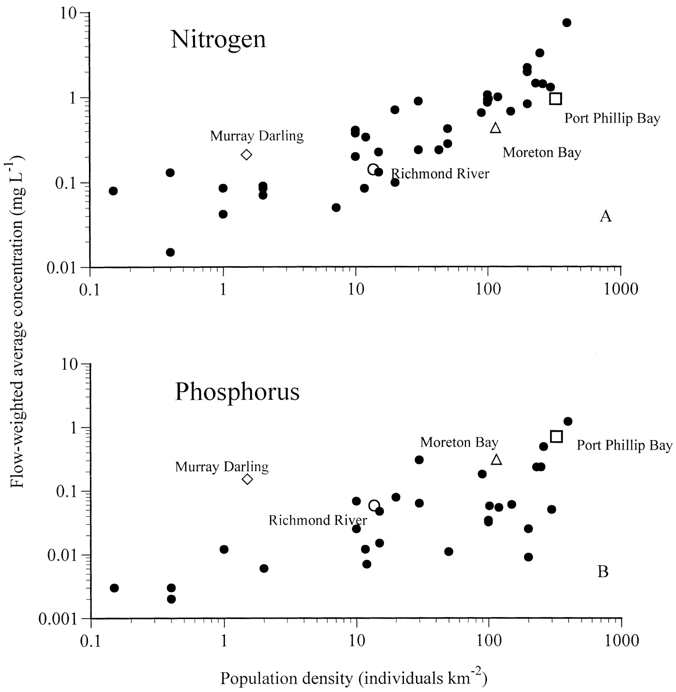

Fig. 4. Flow-weighted average (A) nitrogen and (B) phosphorus concentrations as a function of population density for a number of catchments from around the world and Australian catchments, including Moreton Bay. World data, Cole et al. 1993 and Caraco 1995; Richmond River, McKee et al. 2000*b;* Port Phillip Bay, Harris et al. 1996; South Pine, Cosser 1989.

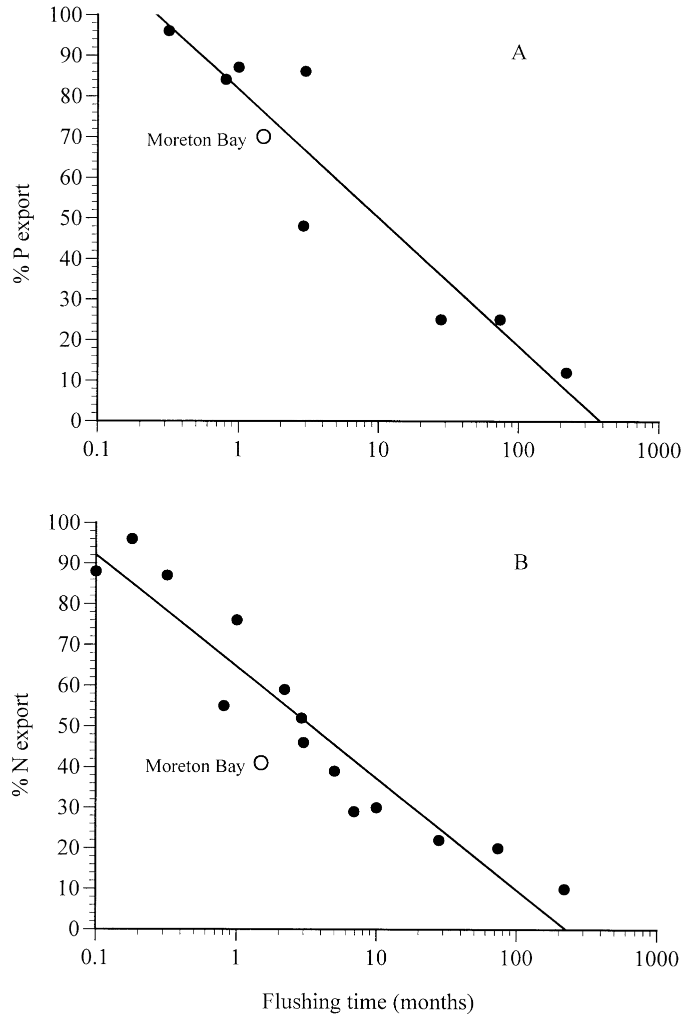

Fig. 5. Percentage of the total input of (A) phosphorus and (B) nitrogen that is exported as a function of flushing time for a number of shallow coastal ecosystems from around the world and Moreton Bay (modified from Nixon et al. 1996).

from the land to the coastal ocean and the log mean residence time for a number of shallow temperate coastal ecosystems from around the world. Using a residence time of 46 d, the Nixon et al. (1996) relationship suggests that Moreton Bay should export about 70% of its total nitrogen load and 73% of its total phosphorus load (Fig. 5A,B). The budget estimate of 70% of the phosphorus exported, if the missing phosphorus is included (Table 5), is very similar to the Nixon et al. (1996) relationship, but the nitrogen export of 41% is much lower. This suggests that a similar set of physical and biogeochemical processes is responsible for the transport, transformation, and retention phosphorus in the subtropical Moreton Bay, but that the behavior of nitrogen is different. The distinct difference in nitrogen cycling in the subtropical Moreton Bay compared to temperate systems (Boynton et al. 1995; Nixon et al. 1995, 1996) was the dominance of biological (microbiological denitrification and N fixation) over physical inputs and losses of nitrogen. N fixation and denitrification were also inferred to dominate nitrogen fluxes in the subtropical Shark Bay (Smith 1984).

Nixon et al. (1996) and Nowicki et al. (1997) established relationships between the percentage of the nitrogen load removed through denitrification and the residence time for a number of estuaries from around the world. Using a residence time of 46 d, the combined Nixon et al. (1996) and Nowicki et al. (1997) data sets suggest that Moreton Bay should only denitrify about 26% of its total nitrogen load (Fig. 6) compared to 56% of the total nitrogen load to Moreton Bay, which was denitrified (Table 5). Denitrification rates in Moreton Bay at several sites were stimulated during the light (Eyre and Ferguson 2001), most likely associated with increased oxygen penetration from benthic production, which would enhance coupled nitrification–denitrification (Risgaard-Petersen et al. 1994), and/or an increase in the supply of labile carbon. Interestingly, Port Phillip Bay, Australia (Harris et al. 1996); Galveston Bay, Texas (An and Joye 2001); and the River Colne Estuary, England (Dong et al. 2000), where denitrification rates were also measured in the dark and light, all fall above the residence time–denitrification relationship (Fig. 6), which suggests that the loss of nitrogen through denitrification is enhanced in systems with autotrophic sediments. Because most denitrification studies have been carried out using only dark incubations, the importance of denitrification to the nitrogen budgets of coastal systems may in general be underestimated (i.e., Fig. 6).

Phytoplankton production in shallow coastal ecosystems typically shows a good relationship to nitrogen loading (Nixon et al. 1995; Borum 1996). Moreton Bay receives an excess average annual loading (total nitrogen load minus de-

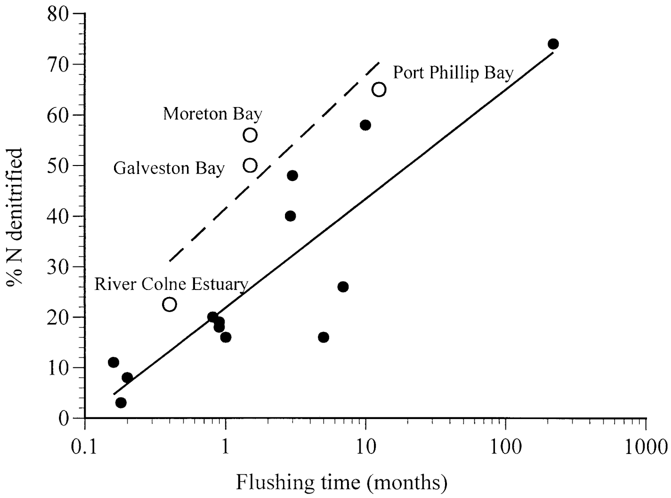

Fig. 6. The fraction of the total nitrogen input that is denitrified as a function of flushing time. The full line is a regression through data from a number of shallow coastal ecosystems from around the world where only dark denitrification rates were determined (after Nixon et al. 1996 and Nowicki et al. 1997). The broken line is a regression through data from a number of systems from around the world where denitrification rates were determined in the light and dark; Moreton Bay, this study; Galveston Bay, An and Joye (2001); Port Phillip Bay, Harris et al. (1996); River Colne Estuary, Dong et al. (2000), D. Nedwell (pers. comm.).

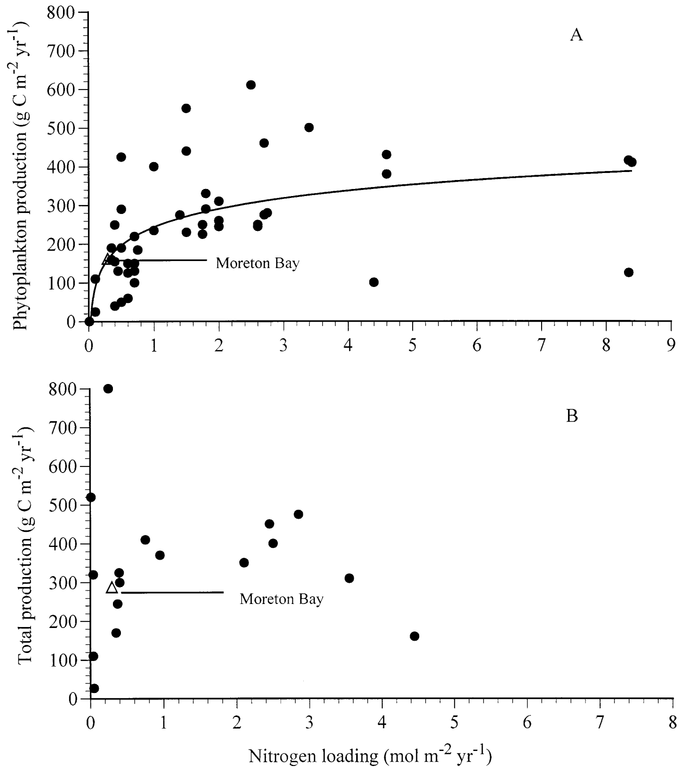

Fig. 7. Annual (A) phytoplankton and (B) total production as a function of nitrogen loading for a number of shallow coastal ecosystem from around the world and Moreton Bay (modified from Borum 1996).

nitrification loss) of 0.22 mol N m^{-2} and has an annual phytoplankton production of 163 g C m^{-2}, which is consistent with other shallow coastal ecosystems (Fig. 7A). To achieve this production, phytoplankton must rapidly turn over the nitrogen pool in the bay. The nitrogen standing stock of phytoplankton in Moreton Bay is about 301 t, which uptakes about 53,000 t N yr^{-1}, which gives an average phytoplankton growth rate of about 0.48 d^{-1}. These turnover times are very similar to Port Phillip Bay, where the nitrogen standing stock of phytoplankton is about 200 t and the annual uptake of nitrogen is about 40,000 t, which gives an average phytoplankton growth rate of about 0.55 d^{-1} (Harris et al. 1996). Assuming that the total allochthonous load of nitrogen (minus denitrification) is recycled, phytoplankton production in Moreton Bay alone would turn it over about 8.2 times before it was lost to the ocean.

In contrast to phytoplankton production, total primary production in shallow coastal ecosystems does not show as good a relationship to nitrogen loading (Borum 1996). This may be because benthic plant communities become shaded by phytoplankton under higher nitrogen loadings (Borum 1996). Moreton Bay has an average annual total production of 296 g C m^{-2}, which is consistent with other shallow coastal ecosystems (Fig. 7B). Total primary production turns over about 81,000 t N yr^{-1}, which would recycle the annual allochthonous load of nitrogen about 12.6 times before it was lost to the ocean. This suggests that about 92% of the total primary production was supported by recycled nitrogen. In contrast, nitrogen is only turned over five times in Chesapeake Bay (Kemp et al. 1997). The greater dependence on recycled nitrogen in Moreton Bay may reflect the high loss of nitrogen through denitrification and the large input of nitrogen through N fixation, which may not be readily assessable.

The fisheries yield in Moreton Bay is only a small percentage of the total carbon (<0.1%), nitrogen (1.0%), and phosphorus (0.4%) exports, and the yield per unit of primary production was also low compared with other shallow coastal systems. Alongi (1998) presented a relationship between fisheries yield (kg ha^{-1} yr^{-1}) and primary production (g C m^{-2} yr^{-1}) for a number of different coastal systems, which suggests Moreton Bay should have a fisheries yield of about 71 kg ha^{-1} yr^{-1} (using total production), which is much higher than the budget estimate of 26 kg ha^{-1} yr^{-1}. Using only phytoplankton production in Moreton Bay gives a fisheries yield of 30 kg ha^{-1} yr^{-1}, which is similar to the budget estimate and most likely reflects only phytoplankton-based estimates of productivity being used in the regression.

Net ecosystem metabolism (NEM) is equal to the production (p) of an ecosystem minus its respiration (r). When $p > r$, the system is said to be autotrophic and organic matter will be buried or exported, and when $p < r$, the system is said to be heterotrophic and its metabolism is supported by stored or imported organic matter (Kemp et al. 1997). Taking the physical inputs of carbon (15,948 t) away from the physical outputs of carbon (55,286 t) leaves a net export of 39,338 t of carbon, which is 8% of the total primary production. As such, Moreton Bay appears to be net autotrophic ($(p - r)/p = 1.08$), exporting more organic matter than it imports. Some studies have shown that ecosystems exposed

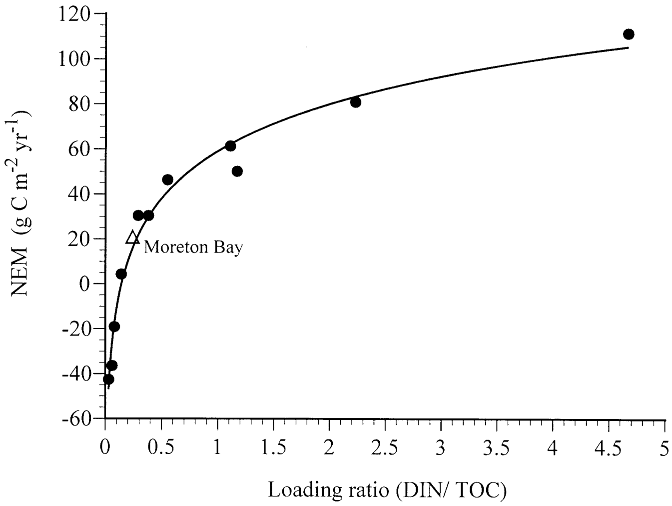

Fig. 8. Net ecosystem metabolism as a function of the DIN : TOC loading ratio for a number of shallow coastal ecosystems and Moreton Bay (modified from Kemp et al. 1997).

to increased nutrient enrichment tend toward net ecosystem autotrophy (Oviatt et al. 1986), and Kemp et al. (1997) suggest that the general global trend of eutrophication will lead to increasing values of NEM. However, other studies have shown that increased nutrient supply promotes ecosystem heterotrophy, while others have shown an overall balance between production and respiration in eutrophic estuaries (Valiela 1995).

Kemp et al. (1997) found a good relationship between NEM and the loading ratio of DIN/TOC for a number of shallow coastal ecosystems. Moreton Bay has an annual NEM of 21 g C m^{-2}. Assuming that 70% of the nitrogen loading (excluding N fixation) is DIN, which is reasonable considering the loading is dominated by point sources, the DIN : TOC loading ratio for Moreton Bay is about 0.24, which is a reasonable fit to the NEM-DIN/TOC relationship (Fig. 8). The positive NEM may be due to increased inputs of DIN and decreased loads of TOC. Inputs of DIN to Moreton Bay have increased over the last 30 yr due to increased wastewater discharges (McKee and Eyre in press). Over the same period, TOC inputs that are dominated by diffuse loads have probably decreased due to a decrease in freshwater discharge associated with the construction of Wivenhoe Dam and increased water extraction from the Brisbane River. Alternatively, the positive NEM may be associated with high N fixation, which provides nitrogen to support production as has been found in other tropical systems (Smith 1991; Smith et al. 1991). Consistent with a positive NEM being driven by N fixation were the low DIN : DIP molar ratios (2 : 1) in the water column of Moreton Bay (Dennison and Abal 1999). The DIN would have been insufficient to complement the DIP demand by primary production, and as such the nitrogen demand had to have been met by N fixation (Redfield 1958; Smith 1991). The nitrogen input through N fixation is not seen as an increase in the DIN : DIP ratio, most likely due to a rapid turnover of nitrogen as previously demonstrated. Low DIN : DIP ratios in systems with high N fixation have been previously recorded (Smith 1983, 1984). These arguments also suggest that primary production in Moreton Bay is phosphorus limited (Smith 1994).

Phosphorus limitation, however, appears to conflict with Figs. 7 and 8, which imply nitrogen limitation. Numerous small-scale nutrient addition experiments in Moreton Bay also suggest nitrogen limitation (Dennison and Abal 1999). These conflicts can be explained in terms of what the individual indicators of limitation reflect. Correlations between nitrogen inputs and primary production (i.e., Figs. 7 and 8) most likely suggest nutrient limitation in Moreton Bay but may not necessarily indicate nitrogen limitation because nitrogen, phosphorus, and silicate are often delivered together. This is consistent with other subtropical east Australian systems, which are also nutrient limited (Eyre 2000). Small-scale experimental manipulations exclude nitrogen recycling and N-fixation pathways and, as such, interpretation should be restricted to small temporal and spatial scales (days, litters) (Fisher et al. 1995). In contrast, nutrient budgets give insight to limitation at the whole ecosystem scale and over longer time frames.

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