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# Denitrification, N-fixation and nitrogen and phosphorus fluxes in different benthic habitats and their contribution to the nitrogen and phosphorus budgets of a shallow oligotrophic sub-tropical coastal system (southern Moreton Bay, Australia)

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**Abstract** Denitrification, N-fixation, and dissolved inorganic and organic fluxes of nitrogen (N) and phosphorus (P) were measured in each of the major benthic habitat types of a shallow oligotrophic sub-tropical coastal system, and N and P budgets were constructed to quantify the importance of each habitat to N and P cycling in the whole ecosystem. The productivity/respiration (p/r) ratio (trophic status) of the habitats was an important control on the rates, direction (uptake, efflux) and composition (dissolved inorganic N (DIN), dissolved organic N (DON), $N_2$) of N fluxes across the sediment–water interface, with an efflux below $p/r = 1.5$ and an uptake above $p/r = 1.5$. The Zostera Seagrass Community was the most important habitat for N loss via net $N_2$ effluxes (denitrification; 48%). Denitrification rates in seagrass were higher than those previously measured in temperate regions, most likely due to greater availability of $NH_4^+$ for coupled nitrification–denitrification. Yabby Shoals (sub-tidal shoals inhabited by burrowing shrimp, *Trypaea australiensis*) accounted for the second largest loss of N via denitrification, the largest recycling of DIN and dissolved inorganic P (DIP; statistically significant only during the dark in summer) across the sediment–water interface and the second largest uptake of DON (statistically significant only in summer). This study highlighted that shallow subtropical coastal systems have a complex mosaic of benthic habitats and that some less 'iconic' habitats (i.e. non-seagrass) also make an important functional contribution that controls the flow of N and P through the whole ecosystem.

**Keywords** Benthic microalgae (BMA) · Budgets · Denitrification · Dissolved organic nitrogen (DON) · Habitats · Mangroves · Seagrass

## Introduction

The land–sea interface, where large quantities of organic matter and nutrients derived from the land, ocean and atmosphere are processed, is one of the most biogeochemically active areas of the earth's biosphere. Much of our understanding of the cycling

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of nitrogen (N) and phosphorus (P) at the land–sea interface comes from studies in deep temperate coastal systems (e.g. Fisher et al. 1988; de Jonge et al. 1994; Kemp et al. 2005). Less is known about how N and P are cycled in shallow coastal systems, particularly in tropical and sub-tropical climates (Eyre and Balls 1999). The metabolism of coastal systems is central to the cycling of N and P, with autotrophs consuming nutrients and producing organic matter and heterotrophs remineralising organic matter (respiration) and releasing nutrients. In shallow coastal systems light can reach much of the seafloor and, as such, the majority of this primary production and respiration occurs in the benthos (McGlathery et al. 2007).

Shallow coastal systems typically have a complex mosaic of benthic habitats coupled to pelagic habitats (Ziegler and Benner 1999; Eyre et al. submitted). It is the sum of the net rates of production and respiration in each of the benthic habitats that mostly controls how N and P will be cycled. Net heterotrophic communities tend to release N and P to the water column, and $N_2$ to the atmosphere, with the rate of release determined by factors such as organic matter quantity and quality, temperature, and biological and physical advective flow (Cowan and Boynton 1996; Kristensen and Hansen 1999). In contrast, net autotrophic communities tend to remove dissolved inorganic N (DIN) and P (DIP) (Rizzo et al. 1992; Sundback et al. 2000) and dissolved organic N (DON) from the water column (Linares 2005; Vonk et al. 2008) but can also be a source of DON (Eyre and Ferguson 2002; Ferguson et al. 2003; Eyre et al. 2008) and enhance $N_2$ efflux (An and Joye 2001). In addition, oxygen production by net autotrophic communities can modify heterotrophic processes by modifying the sediment redox status (Risgaard-Petersen et al. 1994) and through competition for limited resources (Risgaard-Petersen 2003). As such, the productivity/respiration (p/r) ratio (metabolism) of the benthic communities is a good indicator of the rates, direction (uptake, efflux) and composition of benthic fluxes in shallow coastal systems (Eyre and Ferguson 2002, 2005; Engelsen et al. 2008).

Previous studies of benthic N and P cycling in shallow coastal systems have tended to focus on single habitat types such as seagrass (Welsh et al. 2000), subtidal shoals (Dollar et al. 1991), intertidal shoals (Feuillet-Girard et al. 1997), shoals with macrofauna (Pelegri and Blackburn 1995) and permeable sands (Cook et al. 2006). Studies of benthic N and P cycling in shallow coastal systems that include a spatial component mostly compare similar habitats (e.g. muds) along a gradient of interest (e.g. salinity, eutrophication; e.g. Boynton and Kemp 1985; Sundback et al. 2004; Ferguson et al. 2007) or channels and shoals (e.g. Murrell et al. 2009). Some studies in shallow temperate coastal systems have compared habitats such as muddy sediments and seagrass communities or macroalgae and seagrass communities but these tend to be limited to one aspect of N or P cycling such as benthic fluxes or denitrification (Asmus 1986; Rysgaard et al. 1996; Risgaard-Petersen and Ottosen 2000). The lack of a detailed spatial component in many of these studies is also due to the fact that they were done in disturbed systems (mesotrophic, eutrophic), which lack the complex mosaic of benthic habitats that are found in oligotrophic coastal systems. To our knowledge the trophic status (p/r), and denitrification, N-fixation and inorganic and organic N and P fluxes in all major benthic habitats within one oligotrophic coastal system have never been compared, and the importance of each of these habitats to N and P flow within the whole ecosystem has never been estimated. This study aimed to measure denitrification, N-fixation, and dissolved inorganic and organic fluxes of N and P in each of the major habitat types of a shallow oligotrophic sub-tropical coastal system and develop first-order N and P budgets to estimate the importance of each habitat to N and P cycling in the whole ecosystem. It was expected that the trophic status of a benthic habitat (from Eyre et al. submitted) would be an important control on the rates, direction (uptake, efflux) and composition of benthic N and P fluxes and that some of the less ‘iconic’ habitats (i.e. non-seagrass) would make an important functional contribution to the flow of N and P through the whole ecosystem.

## Study area

The study area covers a representative section of open water and mangroves (37.8 $km^2$) in Southern Moreton Bay on the east coast of Australia (Fig. 1). South Stradbroke Island, a barrier island system, provides protection to the study area from the open

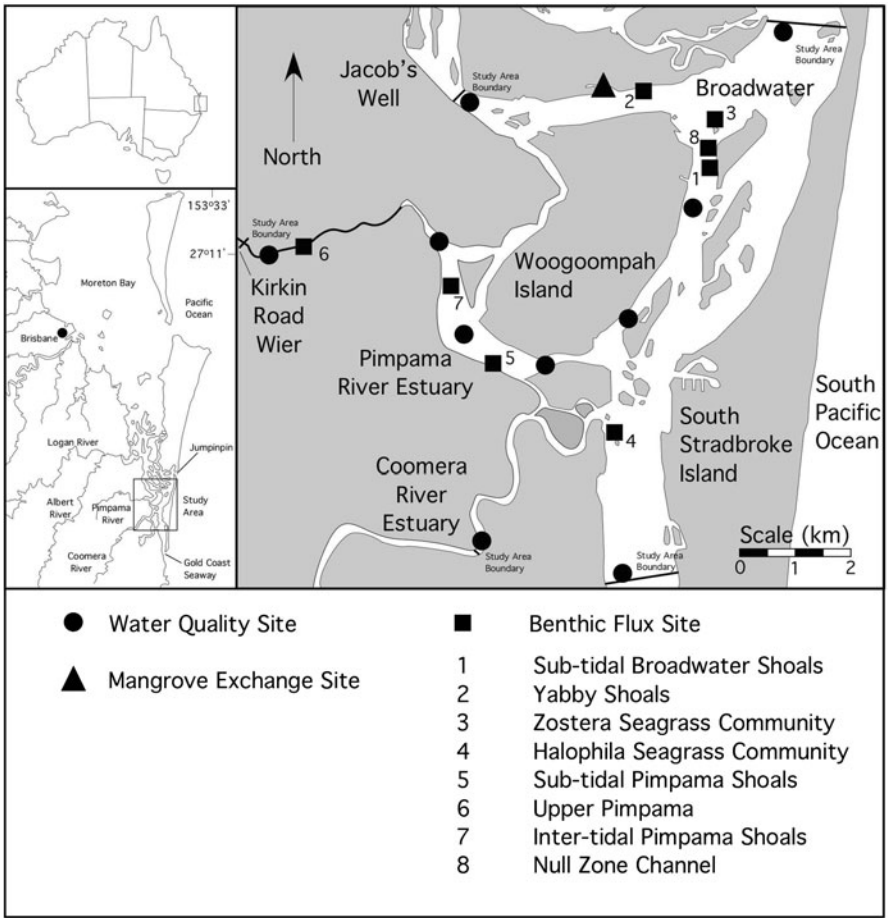


**Fig. 1** Location and boundary of the study area. The water quality and core/chamber sites are also shown

ocean allowing a complex mosaic of islands, shoals and channels to develop. The study area is called the Broadwater, except for the Pimpama River Estuary, and has nine major benthic habitats that cover 96.6% of the study area: Mangroves and the eight open water benthic habitats: Sub-tidal Broadwater Shoals, Yabby Shoals, Zostera Seagrass Community, Sub-tidal Pimpama Shoals, Upper Pimpama Shoals, Upper Pimpama, Inter-tidal Pimpama Shoals and Null Channel (see Table 1, Eyre et al. submitted). Maps and detailed descriptions of each benthic habitat can be found in Eyre et al. (submitted). The Pimpama River Estuary is classified as a tide-dominated delta (Harris and Heap 2003) and the Broadwater is classified as a barrier lagoon type of wave-dominated estuary (Roy et al. 2001; Harris and Heap 2003). The southern section of the Broadwater is well flushed with oceanic water through the Gold Coast Seaway and the northern section of the Broadwater is well flushed with oceanic water through Jumpinpin. Overall the study area is shallow with the open water area averaging just 1.74 m deep at mid-tide, but there are some deep channels (up to 9 m) in places.

The region receives most of its average annual rainfall of 1,094 mm (Gold Coast Seaway) in summer. The Pimpama with a catchment of 130 km$^2$ is the only river that discharges directly into the study area, however, during large floods the northern section of the study area can be briefly influenced by freshwater from the Logan River and the southern section can be briefly influenced by freshwater from the Coomera River. Dry season algal biomass (chlorophyll-a) concentrations are typically $<2$ µg l$^{-1}$ (Eyre et al. submitted) and DIN concentrations are typically around 1.0 µmol l$^{-1}$ (see "Results"). Following floods, diffuse loads of DIN from the catchment can stimulate algal growth in the Coomera

**Table 1** Water column nitrogen and phosphorus concentrations in the Southern Moreton Bay study area

| | Pimpama/Coomera summer (n = 36) | | Pimpama/Coomera winter (n = 24) | | Pimpama/Coomera post-flood (n = 18) | | Broadwater summer (n = 24) | | Broadwater winter (n = 16) | | Broadwater post-flood (n = 12) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean ± SE | Range | Mean ± SE | Range | Mean ± SE | Range | Mean ± SE | Range | Mean ± SE | Range | Mean ± SD | Range |
| PN (μmol $l^{-1}$) | 7.5 ± 1.2 | 0.4–35.5 | 6.4 ± 1.9 | 0.4–35.3 | 8.8 ± 1.6 | 0.4–23 | 5.7 ± 1.7 | 0.4–40.2 | 5.5 ± 1.4 | 0.4–17.8 | 6.9 ± 1.4 | 0.8–15.7 |
| DON (μmol $l^{-1}$) | 15.4 ± 1.3 | 3.1–37.5 | 17.7 ± 1.4 | 1.5–35.1 | 27.4 ± 2.6 | 16–54.7 | 14.7 ± 6.6 | 2.2–31.8 | 16.6 ± 3 | 11.8–23.3 | 7.5 ± 1.2 | 0.4–1.6 |
| $NH_4$ (μmol $l^{-1}$) | 0.9 ± 0.2 | 0.2–8.0 | 1.3 ± 0.4 | 0.2–9.4 | 3.6 ± 1.0 | 0.6–10.6 | 0.8 ± 0.1 | 0.1–1.6 | 0.6 ± 0.1 | 0.1–1.0 | 2.1 ± 0.7 | 0.6–7.4 |
| $NO_x$ (μmol $l^{-1}$) | 0.5 ± 0.1 | 0.1–1.2 | 0.6 ± 0.1 | 0.1–3.1 | 5 ± 1.9 | 0.1–28.2 | 0.4 ± 0.0 | 0.1–0.9 | 0.3 ± 0.1 | 0.1–0.8 | 2.3 ± 1.1 | 0.1–11.1 |
| PP (μmol $l^{-1}$) | 0.4 ± 0.0 | 0.2–1.2 | 0.3 ± 0.0 | 0.2–0.6 | 0.9 ± 0.3 | 0.4–1.6 | 0.4 ± 0.0 | 0.2–0.9 | 0.3 ± 0.0 | 0.2–0.7 | 0.7 ± 0.1 | 0.4–1.3 |
| DOP (μmol $l^{-1}$) | 0.5 ± 0.1 | 0–1.5 | 0.6 ± 0.0 | 0.2–1.0 | 0.9 ± 0.0 | 0.5–1.3 | 0.5 ± 0.1 | 0–1.4 | 0.6 ± 0.1 | 0.2–1.2 | 1 ± 0.0 | 0.8–1.2 |
| $PO_4$ (μmol $l^{-1}$) | 0.3 ± 0.0 | 0–0.9 | 0.3 ± 0.0 | 0.1–0.5 | 0.3 ± 0.0 | 0.1–0.9 | 0.4 ± 0.1 | 0.1–1 | 0.3 ± 0.0 | 0.1–0.5 | 0.3 ± 0.0 | 0–0.5 |
| DIN: $PO_4$ | 7.6 ± 2.2 | 0.7–71.3 | 10.9 ± 5.3 | 1.4–127.9 | 20.9 ± 5.3 | 3–69.6 | 4.3 ± 0.7 | 0.9–16.2 | 3.9 ± 0.5 | 1.4–8.4 | 17.3 ± 6.0 | 2.4–65.5 |

Winter is the average of samples collected in May, June, July and August at 10 sites, summer is the average of samples collected in September, October, November, December, January and April at 10 sites, and post-flood is the average of samples collected twice in February and in March, in 2003 and 2004

and upper Pimpama river estuaries with recorded chlorophyll-*a* concentrations up to 57.2 and 33.1 μg $l^{-1}$ respectively (Eyre et al. submitted).

## Methods

### Water quality

Nutrient sampling was undertaken at 10 sites across the study area at approximately monthly intervals from July 2003 to June 2004, and three additional sampling runs were also undertaken immediately following a February 2004 flood (Fig. 1). All sampling was completed, as close as possible, on a similar tide phase by starting mid-flood tide and completing sample runs within about 2–3 h. An acid washed and sample rinsed bottle was used to collect mid-channel surface samples (top 20 cm) (being careful not to collect the surface scum). Samples for dissolved nutrients were filtered immediately through 0.45 μm cellulose acetate membrane filters into a milli-Q pre-soaked and sample-rinsed polyethylene vials. An unfiltered sample was also collected in a milli-Q pre-soaked and sample-rinsed polycarbonate vial. All nutrient samples were kept cold on ice and frozen within 2–3 h. Vertical profiles of temperature, salinity and dissolved oxygen were taken at 1 metre intervals at each sampling location using a Hydrolab Quanta multi-probe. Secchi disk depth was also measured at each site. The physico-chemical data is presented in Eyre et al. (submitted). Analytical details including methods, errors and detection limits can be found in Eyre (2000).

### Biogeochemical process measurements

Benthic fluxes of $NH_4^+$, $NO_x^-$, DON, DIP, DOP, net $N_2$ effluxes (denitrification) and N-fixation (summer only) were measured in triplicate in summer (December) and winter (July) in all eight of the open water benthic habitats (i.e. not mangroves). Benthic chambers were used in the Yabby Shoals and *Zostera capricorni* Seagrass Communities, as the important structural elements of these habitats could not be captured in cores. Undisturbed cores were used in the other benthic habitats. Previous studies have shown that in shallow water coastal systems cores and chambers give comparable nutrient flux data (Asmus et al. 1998). Details of the core and chamber incubations are given in Eyre et al. (submitted). Briefly, triplicate sediment cores (approximately 20 cm long) including overlying water (approximately 2.3 l) were collected from the six benthic habitats in 50 cm long, 90 mm I.D. clear acrylic pipes using a hand operated surface corer. The incubations were done ex-situ at the study site under natural shaded light conditions. The incubation commenced at sunset following a 24 h equilibration period. The first sample was taken approximately 2 h after closing the stirred cores with a Plexiglas lid to allow the partial pressure and concentration of $O_2$ to drop below 100% saturation. This was particularly important for $N_2$:Ar (denitrification) measurements in cores from highly productive sites where bubble formation at the sediment surface occurred during the light period. Dissolved oxygen concentrations ($\pm$0.01 mg $l^{-1}$) and pH ($\pm$0.001 pH units) were measured electro-chemically, and alkalinity, nutrient and $N_2$ samples were collected at 0, 3, 10/12 h during the dark cycle and 0 (i.e. dawn), 2, 4 and 12/14 h during the light cycle. Nutrient and alkalinity samples were withdrawn with a plastic syringe and 0.45 µm filtered water was transferred to two 10 ml milli-Q soaked and sample-rinsed polyethylene vials for total and dissolved inorganic nutrient and alkalinity analysis. As a sample was withdrawn, an equal amount was replaced from a gravity-fed reservoir of site water. To minimise the introduction of bubbles, $N_2$ samples were collected in triplicate by allowing water to flow, driven by the reservoir head, directly into 7 ml gas-tight glass-stoppered glass vials filled to overflowing. The replacement water was withdrawn from a sealed collapsible reservoir bag, also equilibrated at in situ light (±5.0%) and temperature (±1°C) conditions, to maintain constant Ar concentrations. All nutrient samples were immediately frozen at −20°C, except alkalinity samples which were refrigerated at 4°C. $N_2$ samples were poisoned with 20 µl of 5% $HgCl_2$ and stored submerged at ambient temperature. Details of nutrient and $N_2$:Ar analytical methods are given in Eyre and Ferguson (2005). The $O_2$, alkalinity and $TCO_2$ (alkalinity and pH) data is presented in Eyre et al. (submitted). A 30 g solid phase sample from the upper 20 mm of sediment was also taken and stored frozen for sediment nitrogen and phosphorus (summer only) analysis (analytical methods detailed in Eyre et al. (2008)).

$N_2$ fixation was determined using an acetylene reduction assay (Capone 1993). Following the benthic flux incubations the same cores, and triplicate additional cores from the Zostera Seagrass Community and Yabby Shoals, were uncapped and equilibrated in 100 l tanks for 24 h. The cores were then recapped and 20% of the water was removed and replaced with acetylene saturated site water. Cores were then sealed with a Plexiglas lids. Five samples were drawn from each core during the 24 h incubation at 0, 3, 10/12 h during the dark cycle and 0 (i.e. dawn), 2, 4 and 12/14 h during the light cycle. All samples were transferred to 10 ml Vacutainers containing 20 µl of $ZnCl_2$, sealed and stored in the dark at ambient temperatures until analysis (4 days later). Details of the analytical methods are given in Eyre et al. (2008).

Benthic chamber incubations were done over four consecutive days during high tide using triplicate transparent acrylic benthic flux chambers (290 × 290 × 200 mm deep—approximate volume 16.8 l; see Webb and Eyre (2004b) for details). Light (day) and dark (night) incubations were done for representative populations of marine yabbies (*Trypaea australiensis)* (80–100 $m^{-2}$) over the first 2 days and in the Zostera Seagrass Community during the last 2 days. Four samples were withdrawn from the chambers over a 210 min incubation period. The first 60 ml drawn from the remote sample tubes of each chamber (60 ml = volume of sample tubes plus 20% extra for tube flushing) was discarded. A 150 ml sample vessel with probe ports was then filled from each chamber and dissolved oxygen (YSI 5000 BOD probe, $\pm$0.01 mg $l^{-1}$), pH and temperature (Denver AP25 pH probe, ±0.001) were recorded. Nutrient and $N_2$:Ar samples were collected, preserved and analysed as detailed above. Data for $O_2$, alkalinity and $TCO_2$ (alkalinity and pH) data is presented in Eyre et al. (submitted). At the end of the chamber incubations cores were collected from within the chambers and sampled for sediment nitrogen and phosphorus as detailed above.

Fluxes across the sediment–water interface were calculated by linear regression of the concentration data, corrected for the addition of replacement water, as a function of incubation time, core water volume and surface area. Dark flux rates were calculated using concentration data from the night-time part of the incubation and light flux rates were calculated using concentration data from the day-time part of the incubation.

### N and P exchange between mangroves and open water

Mangrove pneumatophores and roots make it difficult to use cores and benthic chambers to undertake benthic process measurements. As such, to quantify the role of mangroves in the N and P budgets of the open water section of the study area, the exchange of N and P between the mangroves and open water was measured. A mangrove creek with a well-defined catchment area was chosen where most of the water flowed in and out through the creek mouth with little exchange with adjacent creeks (personal observation). A sample transect was surveyed at the creek mouth and six subsections demarcated for sampling. A datum pole was established to record tidal height. Hourly sampling over 24 h was undertaken on neap and spring tides in winter and summer. At each sample time, tidal height was recorded and flow was measured at 40% of the total depth in each of the transect subsections using a propeller flow meter. Physico-chemical properties (temperature, pH, dissolved oxygen, conductivity and turbidity) were measured midstream using a Hydrolab Quanta. Nutrient samples were collected from 15 cm below the surface midstream of each section and preserved, stored and analysed as detailed above.

### Statistical analysis

For water quality and fluxes, two-way analyses of variance (ANOVAs) were run in SPSS (version 17.0) to test differences between sites (Broadwater, Pimpama) and season (summer, winter, post-flood). Two-way analyses of variance (ANOVAs) were also run for the dark, light and net fluxes to test differences among the eight sites and between seasons (summer, winter) and for interacting effects of site and season. The significance level (alpha) was specified as 0.05. In some cases variances in the compared groups were heterogeneous (Levene's test). Homogeneity of variances in the data set could not be improved using log transformations due to the presence of negative values. However, ANOVAs are robust to violations of the assumption of homogeneous variances, provided that sample sizes are similar (Zar 1999), as was the case for most of the tests undertaken. The significance level was defined as 0.01 when Levene's tests were violated to further reduce the chance of a type I error (falsely identifying a significant difference). Where there was an interaction, with the effect of season therefore dependent on site, one-way ANOVAs were used to further investigate the component parts of the interaction. That is, the effect of site was investigated separately for summer and winter, and the effect of season was investigated separately for each site. Where significant differences were found using two-way and one-way ANOVAs, post-hoc Tukey tests were used to determine which sites or seasons had similar or different water quality or fluxes.

### Nitrogen (N) and phosphorus (P) budgets

The budgeting framework of Eyre and McKee (2002) was used to illustrate the functional importance of each of the open water benthic habitats and mangroves to the whole ecosystem and to approximate N and P budgets for the whole study area. Steady state was assumed in the budgeting and therefore the sum of inputs, outputs and storage of each element (N, P) within the study area should equal zero ± error. The N and P budgets includes four major inputs: diffuse (Pimpama River), lateral (Logan and Coomera River during flooding), atmospheric deposition, and mangrove exchange. A fifth input, N-fixation, was also considered for N. Outputs of N and P include burial, fisheries harvest, and mangrove exchange. N loss through denitrification was also considered. Broadwater Exchange was determined as the difference between the inputs and outputs. Standing stocks include dissolved and particulate nutrients in the water column, solid phase sediment nutrients and floral biomass (mangroves, seagrasses, benthic microalgae and phytoplankton). Two nutrient recycling pathways were considered: biological uptake (mangroves, seagrasses, benthic microalgae and phytoplankton) and benthic fluxes.

### *Spatial and temporal boundaries, units of mass, significant figures and errors*

An annual nutrient budget was developed (July 2003 to June 2004) for the study area shown in Fig. 1. Mass (tonnes (t) = $10^3$ kg) rounded to 0.1 t (100 kg) was used for all terms throughout all calculations. Although 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. The robustness of the budgets were assessed in three ways. Firstly, errors were assigned to each of the budget terms that were the product of two terms (e.g. benthic $N_2$ loss = benthic $N_2$ efflux rate × area) using the following formula (modified from Eyre (1995)):

$$\text{Budget Term Error} = \left((\text{mean}_1 \times \text{error}_2)^2 + (\text{mean}_2 \times \text{error}_1)^2 + (\text{error}_1 \times \text{error}_2)\right)^{0.5}$$

Errors are given for each individual data set. Secondly, a sensitivity analysis was done where each of the terms in the budget (e.g. overall N and P burial rates) were adjusted up and down by their estimated errors to determine if the overall conclusions derived from the budget changed. Thirdly, some of the budget terms were verified by independent measures using a "convergence of multiple estimates" approach (Kemp et al. 1997; Eyre and McKee 2002).

### *Diffuse, lateral catchment and atmospheric loads*

A rainfall-runoff and pollutant export model (Expert Management Support System; EMSS) was used to estimate diffuse catchment loads (SKM 2006). The EMSS model predicts daily runoff, and daily loads of total nitrogen (TN) and total phosphorus (TP) from the main Pimpama River catchment above the Kirkin Road weir and from five smaller sub-catchments that discharge into the study area below the weir.

Catchment loads from the Logan and Coomera rivers (lateral loads) were delivered to the study area during a late February 2004 flood and were estimated by calculating the volume of freshwater delivered to the study area and multiplying this freshwater volume by the flood concentration of TN and TP. The volume of freshwater delivered from the Logan and Coomera rivers was estimated by calculating the volume of freshwater in the study area using salinity data (i.e. salinity depression) collected 1 day post-flood after accounting for rainfall and freshwater from the Pimpama. Based on observations of the sediment plumes it appeared that the Logan River influenced the Jacobs Well arm of the Broadwater and the Coomera River influenced the remainder of the study area. TN and TP concentrations measured at the Coomera River boundary of the study area, after correcting for salinity, were used for the Coomera flood concentration (SKM 2006). Flood concentrations measured in 1996 (Eyre and McKee 2002) were used for the Logan. Errors associated with the diffuse N and P loads are difficult to quantify and so a 100% error was assigned.

Rainfall concentration data (McKee et al. 2001), mean annual rainfall for the study area (Gold Coast Seaway = 1,094 mm) and the total surface area of the study area (37.8 $km^2$) was used to estimate atmospheric deposition loads. The rainfall concentration data were from coastal sites in northern NSW, 200 km south of the study site, and therefore represent similar conditions to the study area (i.e. clean air sourced from the Pacific Ocean). Dry fall data were not available. As such, the ratio of total N (wet + dry) to wet N deposition for the South Pacific Ocean (1.2; Paerl 1995) was applied; the same ratio was assumed to apply for P. Because the concentration data were derived from coastal northern NSW, it is unknown how applicable the data are to the study area, making it difficult to quantify the atmospheric N and P load errors. A 100% error was therefore assigned to atmospheric carbon loads.

### *Denitrification, N-fixation and net $N_2$ loss*

Gross N inputs via N-fixation were estimated by multiplying the average of the estimated winter and measured summer N-fixation rates by the area of each habitat. Winter N-fixation rates were estimated as 50% of summer rates based on the difference between winter and summer N-fixation rates measured in Moreton Bay (O'Donohue et al. 1991). Because the N-fixation technique most likely did not capture N-fixation associated with seagrass rhizosphere, the rates are probably underestimated (see "Results"). As such, to better illustrate the role of N-fixation in the N budget, measured rates for *Halophila ovalis* and *H. spinulosa* and *Zostera capricorni* in eastern Moreton Bay (just north of the study area; Dennison and Abal 1999) were used for these habitats. Gross N losses via denitrification were estimated by adding measured net $N_2$ flux to winter and summer N-fixation rates in each habitat and then multiplying the total by the area of each habitat. The N loss via denitrification and N inputs via N-fixation do not affect the balance of the overall N budget because when denitrification is taken away from N-fixation you are left with the measured net $N_2$ efflux. The N-fixation and denitrification terms were included to simply illustrate the potential of these two pathways for N flow. The net loss of N from the study area via $N_2$ gas flux was estimated by multiplying the average of measured winter and summer net $N_2$ fluxes by the area of each habitat. It is this measured net flux of $N_2$ that determines the balance of the N budget. The standard deviation of the triplicate $N_2$ flux measurements in each habitat was adopted as the error for the rate measurements. Errors associated with N-fixation (and denitrification—the sum of net $N_2$ flux and N-fixation) are difficult to quantify because literature values were used for the seagrass habitats. As such, a 100% error was assigned to N-fixation in the seagrass habitats.

### *Nutrient burial, mangrove exchange, fisheries harvest and Broadwater exchange*

World-average burial rates for mangrove and seagrass communities and non-vegetated estuarine sediments (Duarte et al. 2005) were multiplied by the areal extent of these habitats to estimate carbon burial for the whole study area (see Eyre et al. submitted). N and P burial was estimated by applying the measured sediment C:N and C:P ratios (see Fig. 2) to the carbon burial rates. Because literature values were used, it is unknown how applicable the burial rates are to the current study. This makes it difficult to quantify N and P burial errors. A 100% error was therefore assigned to N and P burial.

N and P exchange between the mangroves and open water was calculated by integrating flow and concentration data over the complete neap and spring tides in summer and winter. These fluxes were then scaled up to annual rates for the whole study area

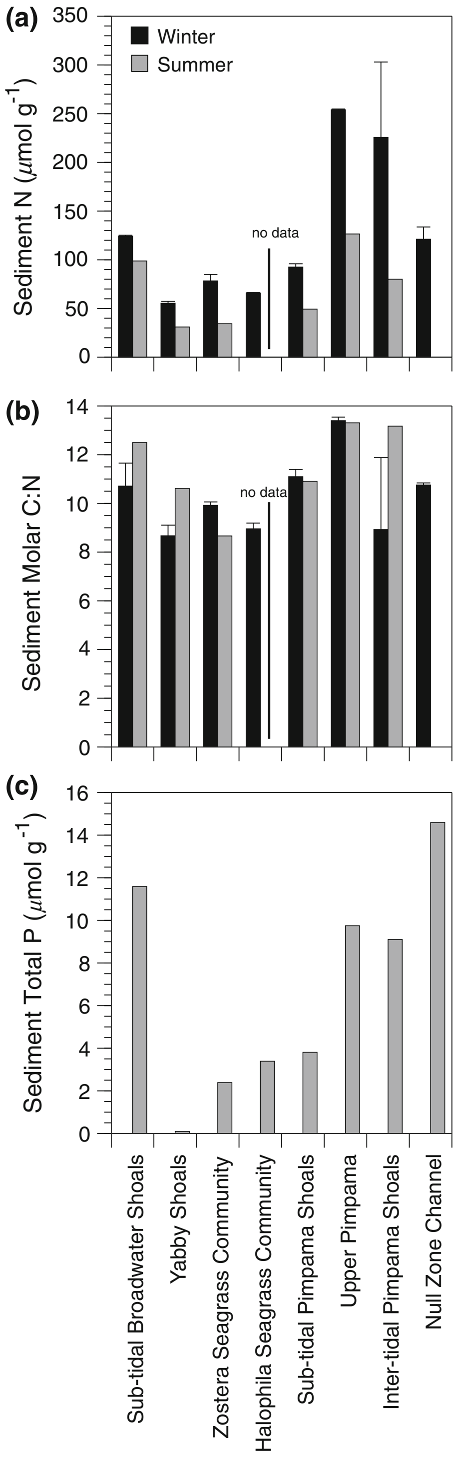


**Fig. 2** Sediment **a** nitrogen concentrations, **b** carbon:nitrogen ratios and **c** phosphorus concentrations (mean ± SE) in the eight major benthic habitats in the Southern Moreton Bay study area (winter n = 3; summer n = 1)

using the measured fluxes and a calibrated and verified hydrodynamic (MIKE 21) and ecological (ECOlab) model (Szylkarski et al. 2005; SKM 2006) that quantified water movement into, and out of, the mangroves over an annual cycle.

Because there is no commercial fishing within the study area, only recreational fish harvest was estimated. The areal recreational catch for Moreton Bay (Eyre and McKee 2002) was multiplied by the water surface area of the study area to estimate fish catch. Dry weight was assumed to be 20% of the wet catch and the carbon, N and P content of the dry catch was assumed to be 50, 15 and 0.62% respectively (Eyre and McKee 2002). Errors associated with fisheries harvest are difficult to quantify because values from Moreton Bay were used. As such a 100% error was assigned to fisheries harvest.

When all the inputs and outputs were added, the Broadwater exchange (including the northern and southern Broadwater, Coomera River and Jacobs Well boundaries) of N and P was calculated by difference; surplus = an export and deficit = an input. This term also includes the sum of the errors associated with the other components of the budget.

### *Standing stocks and recycling*

Water column N and P standing stocks were estimated by multiplying the average total concentration from each of the 10 sampling sites (12 × monthly samples) by the corresponding volume of the study area. Solid phase N and P pool sizes in the study area were estimated by multiplying the average of measured winter and summer sediment solid phase concentrations in each habitat by the area of each habitat by 2 cm. An arbitrary depth of 2 cm was chosen as this was the sediment layer sampled for N and P concentrations and this material is probably still biogeochemically active within the system (i.e. not deeply buried). N and P biomass contributed by mangrove, seagrasses and benthic microalgae (BMA) were estimated by multiplying the measured biomass of each flora group (from Eyre et al. submitted) by their areal extent by an appropriate N and P content (see Eyre and McKee 2002).

Two nutrient recycling pathways were considered (1) biological uptake (seagrasses, benthic microalgae and phytoplankton) and (2) benthic fluxes. These terms do not result in a net input, loss or storage, but represent recycling within the system. Benthic nutrient fluxes were estimated by multiplying the average of measured net winter and summer fluxes in each habitat by its area. N and P uptake by the floral groups was estimated by applying a C:N:P ratio of 106:16:1 to phytoplankton and benthic microalgae, and a ratio of 480:30:1 to seagrasses (Eyre and McKee 2002).

## Results

### Water quality

During summer and winter total nitrogen concentrations consisted of mostly Dissolved Organic Nitrogen (DON) and Particulate Nitrogen (PN). $NH_4$ and $NO_x$ concentrations were mostly below 1.0 μmol $l^{-1}$ (Table 1). Dissolved Organic Phosphorus (DOP) was the largest fraction of Total Phosphorus (TP) with similar fractions of $PO_4$ and Particulate Phosphorus (PP). There was no significant difference ($p > 0.05$) between summer and winter or between the Broadwater and Pimpama/Coomera River Estuary in summer and winter for any of the nitrogen or phosphorus fractions. Following the late February flood event there was a significant increase in DON, $NH_4$, $NO_x$, PP and DOP concentrations across the study area. In particular, $NO_x$ and $NH_4$ concentrations increased dramatically due to diffuse runoff from the catchment. The highest Dissolved Inorganic Nitrogen ($NO_x + NH_4$) concentration (38.8 μmol $l^{-1}$) was recorded in the Coomera River Estuary. DIN:$PO_4$ ratios during summer and winter were below 'Redfield' in both the Broadwater and Pimpama/Coomera River Estuary but increased to above 'Redfield' across the study area post-flood due to the larger increase in the diffuse load of nitrogen than phosphorus.

### Sediment nitrogen (N) and phosphorus (P)

Sediment N concentrations showed a similar pattern to sediment carbon (Eyre et al. submitted) with the highest winter sediment N concentrations in the upper Pimpama (254.1 μmol $g^{-1}$), followed by the Inter-tidal Pimpama Shoals (225.7 μmol $g^{-1}$), Null Zone Channel (121.1 μmol $g^{-1}$), Subtidal Broadwater Shoals (124.3 μmol $g^{-1}$), Sub-tidal Pimpama

(92.5 μmol $g^{-1}$), *Zostera* Seagrass Community (78.3 μmol $g^{-1}$), *Halophila* Seagrass Community (65.8 μmol $g^{-1}$) and finally the Yabby Shoals (55.4 μmol $g^{-1}$; Fig. 2). There was a significant difference between seasons depending on site (2-way interaction: F = 3.932; $p = 0.030$; df = 7,9) with significantly lower concentrations during summer at all sites except the Zostera Seagrass Community, Upper Pimpama and Null Zone Channel. Sediment C:N ratios ranged between ~9 and 12 (Fig. 2). C:N ratios showed no significant difference between seasons in any habitats. Sediment total P concentrations were only measured in summer and showed a much larger variation across the study area compared to sediment N. The highest sediment total P concentrations were in the Null Zone Channel (14.6 μmol $g^{-1}$) where fine sediment accumulates and the lowest concentrations in the Yabby Shoals (0.1 μmol $g^{-1}$; Fig. 2).

## Benthic nitrogen fluxes

Effluxes of ammonium ($NH_4^+$) in the dark during winter were largely confined to the Upper Pimpama, Yabby Shoals and Zostera Seagrass Community (Fig. 3). The other benthic habitats showed negligible $NH_4^+$ fluxes or a small uptake during winter that were not significantly different from zero. There was an overall significant increase in dark $NH_4^+$ fluxes across the study area from winter to summer (F = 18.270; $p < 0.001$; df = 1,25). There was a significant difference between light and dark fluxes, depending on season (2-way interaction: F = 4.710; $p = 0.035$; df = 1,50) with a reduction in $NH_4^+$ effluxes or a conversion to an uptake at most sites during the light in summer and no significant change in winter. The exception to this was at the Yabby Shoals where there was an enhanced $NH_4^+$ efflux during the light in winter.

Oxidised N (nitrate + nitrite = $NO_x$) fluxes in the dark were dominated by an uptake during winter, with a small uptake (< 5 μmol $m^{-2}$ $h^{-1}$) in five of the Southern Moreton Bay habitats, and a significantly larger ($p < 0.001$) uptake (10–20 μmol $m^{-2}$ $h^{-1}$) in the Sub-tidal Broadwater Shoals, Halophila Seagrass Community and Null Zone Channel (Fig. 3). The Yabby Shoals showed a small $NO_x$ efflux in winter. There was a significant difference between light and dark fluxes depending on season (2-way interaction: F = 4.238; $p = 0.045$; df = 1,48) with a reduction in the uptake of $NO_x$ or a conversion to an efflux at most sites during the light in winter and no significant change in summer. During summer there were larger effluxes (5–15 μmol $m^{-2}$ $h^{-1}$) in the Sub-tidal Broadwater Shoals, Null Zone Channel and Yabby Shoals in both light and dark, and small fluxes undistinguishable from zero in the other habitats.

Dissolved organic nitrogen (DON) fluxes comprised the major fraction of N fluxes at all sites during the dark in both seasons (Fig. 3). However, the large variability between replicates made it difficult to distinguish fluxes in some habitats from zero. During winter there was a significant uptake of DON in the Inter- and Sub-tidal Pimpama Shoals and Halophila Seagrass Community, a smaller uptake in the Null Zone Channel and an efflux in the Sub-tidal Broadwater, Zostera Seagrass Community and Upper Pimpama. There was a significant difference in DON fluxes between seasons (F = 5.124; $p = 0.028$; df = 1,50). During summer there were significant effluxes of DON in the dark in the Sub-tidal Broadwater Shoals, Upper Pimpama and Null Zone Channel and a significant uptake in the Halophila Seagrass Community. There was a general reversal in DON fluxes from dark to light during winter, with a switch to a significant light uptake at the Sub-tidal Broadwater Shoals, and Zostera Seagrass Community and a switch to effluxes at the Sub-Tidal Pimpama, and Null Zone Channel. During summer there was a significant efflux of DON in the light from the Zostera Seagrass Community, Sub-tidal Pimpama Shoals, and Null Zone Channel and a large significant uptake in the Yabby Shoals and Halophila Seagrass Community.

## Dinitrogen gas ($N_2$) fluxes and N-fixation

During winter, dark dinitrogen gas ($N_2$) effluxes were very high in the Zostera Seagrass Community habitat (412 μmol $N_2$ $m^{-2}$ $h^{-1}$), exceeding other habitats by a factor of 4 (Fig. 3). High and similar $N_2$ effluxes (77–109 μmol $m^{-2}$ $h^{-1}$) occurred in the Sub-tidal Broadwater, Halophila Seagrass Community, Upper Pimpama and Null Zone Channel. There was a significant difference in $N_2$ fluxes between seasons depending on site (2-way interaction: F = 10.669; $p < 0.001$; df = 5,19), with smaller dark and light $N_2$

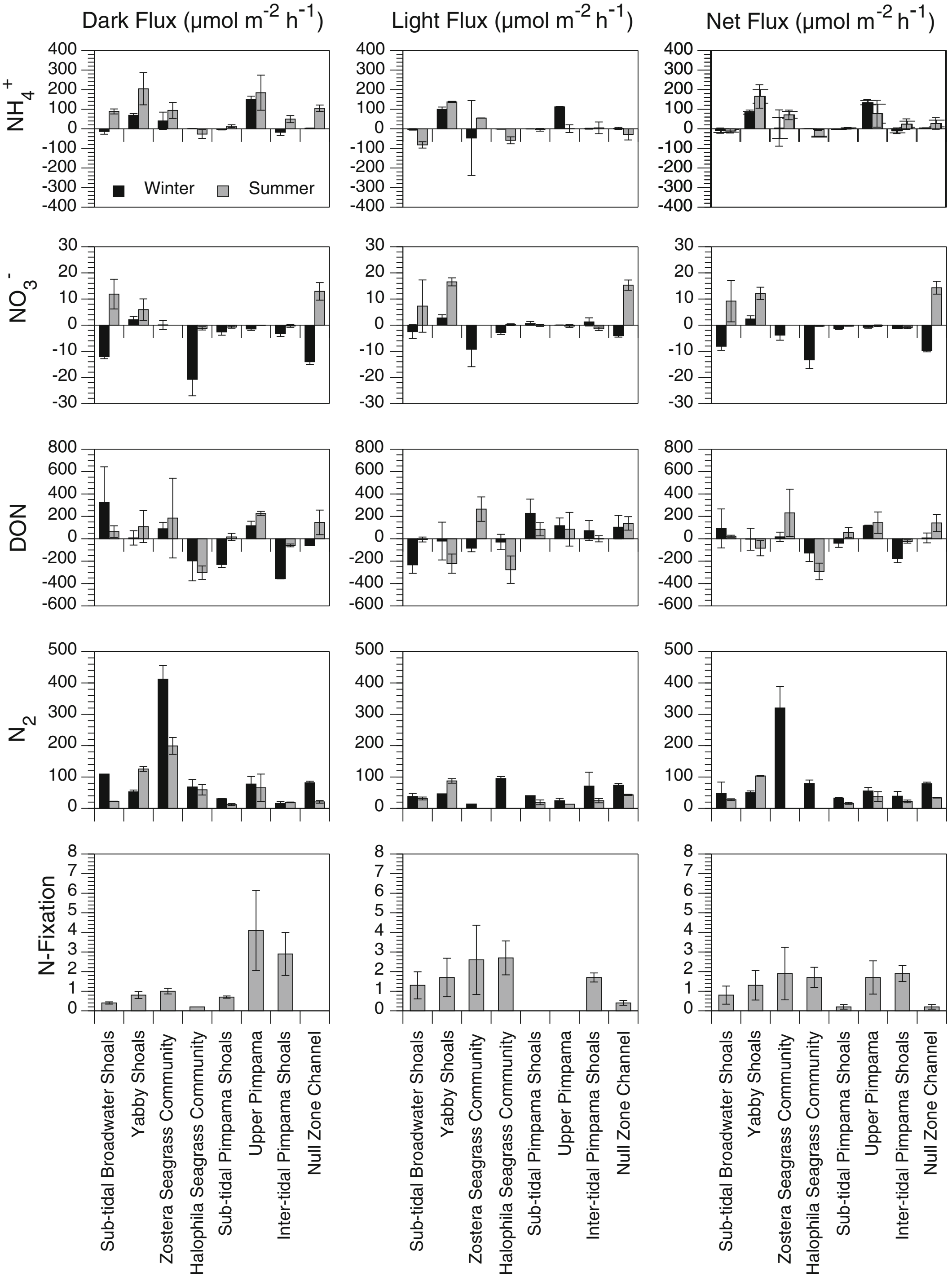


**Fig. 3** Benthic fluxes of N in the eight major benthic habitats in the Southern Moreton Bay study area (mean ± SE; n = 3)

fluxes during summer in all habitats except Yabby Shoals where there was a large increase. Similar to winter, the highest dark $N_2$ effluxes in summer were in the Zostera Seagrass Community. There was a significant difference between light and dark $N_2$ fluxes, but this was dependent on site (2-way interaction: F = 30.328; $p < 0.001$; df = 7,33). During winter, light $N_2$ efflux increased (relative to dark fluxes) at Inter-tidal Pimpama Shoals, Halophila Seagrass Community and Yabby Shoals, but decreased at the other habitats. During summer, there was little difference between light and dark rates of $N_2$ efflux at all habitats except Sub-tidal Pimpama Shoals where light $N_2$ effluxes were much lower than the dark rates. Summer light $N_2$ effluxes could not be measured in the Halophila and Zostera Seagrass communities due to minor bubble formation from the high rates of benthic production (see Eyre et al. submitted). As such, for budgeting it was assumed that the net fluxes equalled the dark fluxes.

N-fixation rates measured by acetylene reduction were low compared to the other N fluxes across all the habitats (Fig. 3). The Upper Pimpama and Inter-tidal Pimpama Shoals had the highest dark N-fixation rates. Rates were very low rates in the other habitats. The reverse was the case in the light, with low N-fixation rates in the Upper Pimpama and Inter-tidal Pimpama Shoals and higher rates in most of the other habitats. The highest N-fixation rates in the light occurred in the Zostera and Halophila seagrass communities, however these rates were very low compared to other measured rates (e.g. O'Donohue et al. 1991) as they are only surface rates and do not include the seagrass rhizosphere. The net N-fixation rates were low and similar in most of the habitats.

## Benthic phosphorus fluxes

Dark and light DIP and DOP fluxes in winter and summer were mostly small with only a few sites having rates significantly different from zero (Fig. 4). There was no significant difference between dark and light DIP and DOP fluxes and no significant difference between seasons. In winter the Sub-tidal Pimpama Shoals and Upper Pimpama had a dark uptake, and the Yabby Shoals had a light uptake, of DIP that was significantly different from zero. In summer the Yabby Shoals, Inter-tidal Pimpama and Null Zone Channel had dark effluxes, and the Zostera Seagrass Community had light effluxes, of DIP that were significantly different from zero. In winter the Inter-tidal Pimpama had a dark efflux, the Yabby Shoals and Upper Pimpama had light effluxes, and the Halophila Seagrass Community a light uptake, of DOP that were significantly different from zero (Fig. 4). None of the DOP fluxes were significantly different from zero in summer.

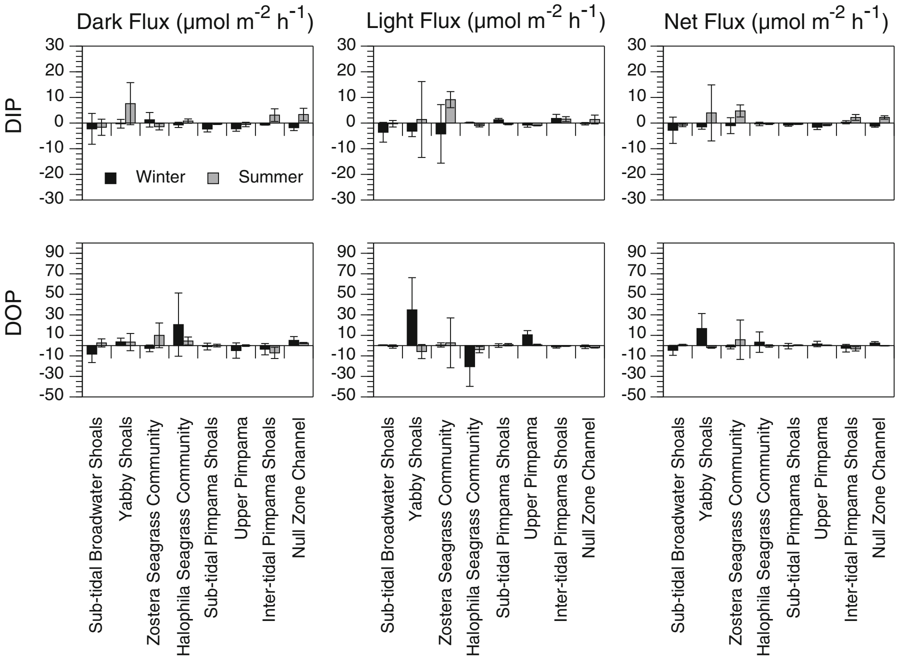
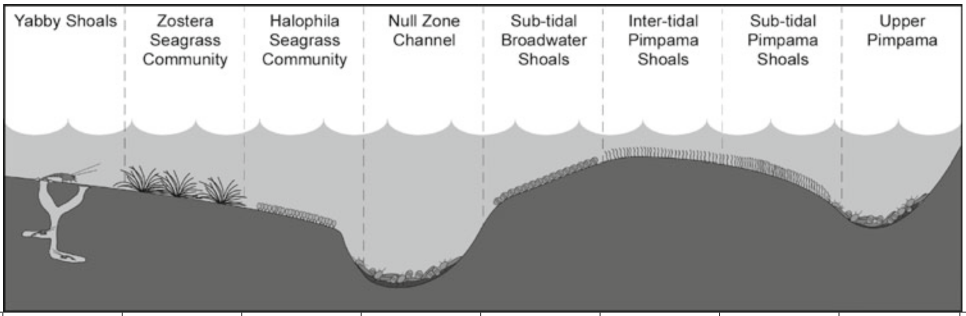


**Fig. 4** Benthic fluxes of P in the eight major benthic habitats in the Southern Moreton Bay study area (mean ± SE; n = 3)

## System wide annual estimates of benthic nitrogen and phosphorus fluxes

The largest gross loss of N via denitrification in the study area occurred in the Zostera and Halophila Seagrass communities (Fig. 5). A large proportion of the total gross N loss via denitrification also occurred in the Yabby Shoals and Sub-tidal Broadwater Shoals. N-fixation was only significant in the seagrass habitats. Caution needs to be applied to the denitrification and N-fixation loads for the seagrass habitats as the rates used in the calculations are based on literature values (see "Methods"). However, the net $N_2$ loss was directly measured and hence well-constrained giving confidence to the overall N budget (i.e. any error introduced by using the N-fixation literature values are removed in the budgeting). The largest net loss of $N_2$ occurred in the Zostera Seagrass Community. There was also a large net $N_2$ loss from the Yabby Shoals and Sub-tidal Broadwater Shoals. The Yabby Shoals were the only significant source of DIN to the water column via sediment–water efflux. The Zostera Seagrass Community (significant only in summer) and Sub-tidal Broadwater Shoals (significant only in the dark) were both large sources of DON to the water column and the Halophila Seagrass Community and Yabby Shoals (significant only for light fluxes in summer) were both large sinks of DON. The largest amount of N was recycled through the benthic microalgae (see Fig. 5) reflecting its large areal extent and high rates of production (Eyre et al. submitted).

The Yabby Shoals were the only significant source of DIP (only significant during the dark in summer) and DOP (only significant during the light in winter) to the water column via sediment–water efflux (Fig. 5). In contrast, the Sub-tidal Broadwater Shoals had a significant uptake of both DIP (only significant during the light in winter) and DOP (only significant



| Processes | Yabby Shoals | Zostera Seagrass Community | Halophila Seagrass Community | Null Zone Channel | Sub-tidal Broadwater Shoals | Inter-tidal Pimpama Shoals | Sub-tidal Pimpama Shoals | Upper Pimpama | Total |
|---|---|---|---|---|---|---|---|---|---|
| Denitrification ($t\ N\ yr^{-1}$) | 103.0 ± 6.8 | 318.4 ±143.5 | 176.5 ± 150.3 | 5.5 ± 0.4 | 61.2 ± 31.2 | 4.5 ± 1.5 | 9.0 ±1.0 | 10.3 ± 3.0 | 688.4 ± 337.7 |
| N-fixation ($t\ N\ yr^{-1}$) | 1.3 ± <0.1 | 114.6 ± 114.6 | 147.6 ±147.6 | <0.1 ± <0.1 | 1.0 ± <0.1 | <0.1 ± <0.1 | 0.1 ± <0.1 | <0.1 ± <0.1 | 264.6 ± 264.6 |
| Net $N_2$ Flux ($t\ N\ yr^{-1}$) | 101.7 ± 6.8 | 203.8 ± 28.9 | 28.9 ± 2.7 | 5.5 ± 0.4 | 60.2 ± 31.2 | 4.5 ± 1.5 | 9.0 ± 1.0 | 10.3 ± 3.0 | 423.8 ±75.6 |
| DIN Flux ($t\ N\ yr^{-1}$) | 86.7±15.1 | 14.0±14.3 | -5.6± 0.6 | 0.8 ± 0.5 | -7.6±9.4 | 0.4 ± 1.0 | -0.2 ± 0.2 | 11.6 ± 3.3 | 100.1 ± 44.7 |
| DON Flux ($t\ N\ yr^{-1}$) | -29.2 ±54.9 | 48.7 ± 49.9 | -43.7 ± 15.7 | 3.6 ±3.0 | 45.8 ± 73.0 | -7.4 ±1.9 | 1.5 ±7.4 | 14.4 ±5.6 | 33.7 ± 211.5 |
| N-Recycling ($t\ N\ yr^{-1}$) | 135.6 ± 162.1 | 1013.2 ± 157.3 | 412.8 ± 89.5 | 24.0 ± 2.5 | 584.0 ± 91.7 | 76.8 ± 10.4 | 250.7 ± 27.0 | 21.1 ± 17.2 | 2909.0 ± 557.9 |
| DIP Flux ($t\ P\ yr^{-1}$) | 1.8 ± 8.7 | 1.6 ± 2.4 | -0.1 ± 0.3 | 0.1 ± 0.1 | -3.2 ±5.0 | 0.2 ± 0.2 | -0.3 ±0.1 | -0.3 ± 0.2 | -0.2 ± 27.6 |
| DOP Flux ($t\ P\ yr^{-1}$) | 10.8 ± 11.2 | 1.9 ± 9.2 | 0.7 ± 2.6 | 0.1 ± 0.1 | -3.6 ± 5.0 | -0.5 ± 0.5 | 0.0 ± 0.6 | 0.2 ± 0.4 | 9.7 ± 29.5 |
| P-Recycling ($t\ P\ yr^{-1}$) | 8.5 ± 10.1 | 62.0 ± 9.8 | 25.3 ± 5.6 | 1.5 ± 0.2 | 36.5 ± 5.7 | 4.8 ± 0.7 | 15.7 ± 1.7 | 1.3 ± 1.1 | 168.6 ± 34.9 |
| Area ($km^2$) | 5.4 ± 0.3 | 3.2 ± 0.2 | 1.7 ± 0.1 | 0.4 ± <0.1 | 6.5 ± 0.3 | 0.6 ± ≤0.1 | 1.5 ± 0.1 | 0.9 ± ≤0.1 | 20.2 ± 1.0 |

**Fig. 5** System wide annual estimates of denitrification, N-fixation, net $N_2$ effluxes, DIN fluxes, DON fluxes, N recycling, DIP, DOP fluxes and P recycling in the eight major open water benthic habitats in the Southern Moreton Bay study area

during the dark in winter). Most of the other habitats had DIP and DOP fluxes indistinguishable from zero. Similar to N, the largest amount of P was recycled through the benthic microalgae.

### Nitrogen and phosphorus budgets for the study area

N inputs to the study area were dominated by exchange with the Broadwater (see "Discussion") and N-fixation (Table 2). The Broadwater was also the largest input of P to the study area. Atmospheric deposition was the smallest input of N (1%) and P (1.1%). N outputs were dominated by denitrification and burial and P outputs were dominated by burial. Only a small amount of N was imported to, and only a small amount of P was exported from, the mangroves. Most of the N and P was stored in the mangroves and top 2 cm of sediments with very little stored in the seagrass, water column, BMA or phytoplankton (Table 2).

## Discussion

### Influence of benthic trophic status on nitrogen and phosphorus cycling

There was a high degree of spatial and temporal variability in the magnitude, direction and forms of benthic N and P fluxes in the shallow, oligotrophic southern Moreton Bay. Much of the variability in benthic N fluxes can be explained by the benthic oxygen productivity/respiration (p/r) ratio (Eyre et al. submitted). In contrast, benthic p/r was unrelated to benthic P fluxes. The total net flux of N ($TN = DIN + DON + N_2$) from the sediments to the water column in winter and summer was negatively related

**Table 2** Nitrogen and phosphorus budgets for the Southern Moreton Bay study area

| | Nitrogen | Phosphorus |
|---|---|---|
| Inputs (t year$^{-1}$) | | |
| Diffuse | 47.7 ± 47.7 | 5.4 ± 5.4 |
| Atmosphere | 16.5 ± 16.5 | 0.9 ± 0.9 |
| Lateral | 6.1 ± 6.1 | 0.6 ± 0.6 |
| N-fixation | 264.6 ± 264.4 | |
| Mangrove exchange | 22.5 ± 22.5 | |
| Net Broadwater exchange | 734.1 | 94.4 |
| Outputs (t year$^{-1}$) | | |
| Denitrification | 688.4 ± 337.7 | |
| Burial | 402.3 ± 402.3 | 100.6 ± 100.6 |
| Fisheries | 0.8 ± 0.8 | <0.1 ± <0.1 |
| Mangrove exchange | | 0.7 ± 0.7 |
| Standing stocks (t) | | |
| Water column (includes phytoplankton) | 11.3 ± 1.8 | 1.5 ± 0.3 |
| Sediment (top 2 cm) | 1001.4 ± 78.1 | 114.0 ± 5.7 |
| Mangrove biomass | 6207.4 ± 6207.4 | 203.2 ± 203.2 |
| Phytoplankton biomass | 0.4 ± <0.1 | <0.1 ± <0.1 |
| Benthic microalgae biomass | 2.1 ± 0.6 | 0.1 ± <0.1 |
| Seagrass biomass | 7.0 ± 7.0 | 0.2 ± 0.2 |
| Recycling (t year$^{-1}$) | | |
| Benthic fluxes | 133.8 ± 256.2 | 9.5 ± 57.1 |
| Mangrove | 390.8 ± 390.8 | 13.0 ± 13.0 |
| Phytoplankton | 187.1 ± 45.7 | 11.7 ± 2.9 |
| Benthic microalgae | 279.9 ± 141.4 | 18.6 ± 8.8 |
| Seagrasses | 171.1 ± 99.9 | 5.7 ± 6.2 |

to benthic p/r ($r^2 = 0.56$; $p < 0.05$; n = 16) with an efflux below p/r = 1.5 and an uptake above p/r = 1.5. This relationship improves greatly when the Zostera Seagrass Communities are removed ($r^2 = 0.84$, $p < 0.001$, n = 14; Fig. 6a) as they have a high net TN efflux for a given p/r due mostly to very high $N_2$ effluxes (see later discussion). Despite the strong relationship between benthic p/r and benthic TN fluxes, the influence of benthic p/r on benthic fluxes was different for each of the different N forms.

Net DIN fluxes as a function of p/r were best explained by a log relationship ($r^2 = 0.75$; $p < 0.001$; n = 16) due to the rapid increase in net DIN release (mostly $NH_4^+$) when sediments became net heterotrophic (p/r < 1), a small uptake when p/r = 1.0 to 2.0 and a larger uptake when the sediment was strongly net autotrophic (p/r = 2.8; Fig. 6b). Similar net DIN ($NH_4^+$) versus p/r relationships have also been found in other warm temperate and subtropical coastal systems (Eyre and Ferguson 2002, 2005, but the switch between net DIN release and uptake occurred at a lower p/r (0.4–0.6)). Engelsen et al. (2008) also found a similar relationship between net oxygen fluxes and DIN and $NH_4$ fluxes in a cold temperate coastal system and in their study the switch between release and uptake also occurred above a net oxygen flux of zero (p/r = 1). Theoretically DIN should be released when the benthic p/r < 1, consumed when p/r > 1, and reduced close to zero when p/r = 1 (Ferguson et al. 2004a). However, the p/r at which the switch between uptake and release of DIN occurs can decrease due allochthonous inputs of carbon from phytodetritus and terrestrial sources (Ferguson et al. 2004a; Eyre and Ferguson 2005). Because the switch between benthic release and uptake of DIN in Southern Moreton Bay occurs at around p/r = 1 this suggests that most of the organic matter being respired was produced in situ (i.e. benthic microalgae, epiphytes, seagrass). However, this is not entirely consistent with the carbon budget which suggests about 30% of the carbon load is phytodetritus both from within and from outside the study area (Eyre et al. submitted).

Benthic net DON fluxes were weakly negatively correlated with benthic p/r ($r^2 = 0.43$; not significant; n = 16). However, the strength of the benthic net DON versus p/r relationship improved significantly when the Yabby Shoals, which had low net DON

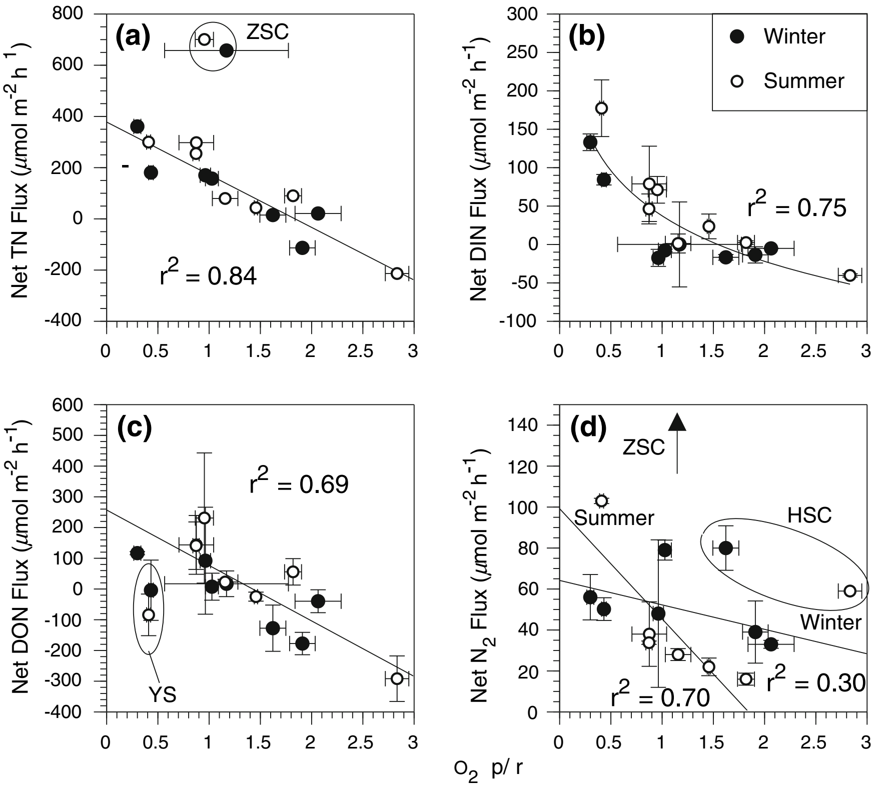


**Fig. 6** Apparent control of benthic gross productivity/respiration (p/r) (from Eyre et al. submitted) in the eight major open water benthic habitats in the Southern Moreton Bay study area on the rates, direction (uptake, efflux) and composition of benthic N and P fluxes **a** benthic p/r as a function of net TN (DIN + DON + $N_2$) flux, **b** benthic p/r as a function of net DIN flux, **c** benthic p/r as a function of net DON flux, and **d** benthic p/r as a function of net $N_2$ flux. *ZS* Zostera Seagrass Community, *HSC* Halophila Seagrass Community, *YS* Yabby Shoals

effluxes for a given p/r (see later discussion), were excluded ($r^2 = 0.69$; $p < 0.01$; n = 14; Fig. 6c). Net DON and net DIN fluxes were significantly related ($r^2 = 0.63$; $p < 0.05$; n = 14; Yabby Shoals excluded) and hence showed a similar pattern with large effluxes below p/r = 1, little flux between p/r = 1 and 1.5 and a large uptake above p/r = 1.5. Similar net DON versus p/r relationships have also been found in other coastal systems (Eyre and Ferguson 2005), but, similar to DIN, the switch between net DON release and uptake occurred at a lower p/r (0.4–0.6). The large DON releases when the sediments were net heterotrophic, and the strong correlation with DIN fluxes, is consistent with decomposition of organic matter. Because effluxes of DON exceeded those of DIN it appears that fresh autochthonous organic matter was being hydrolysed at the sediment surface (Blackburn et al. 1996; Eyre and Ferguson 2002). The efflux of DON (and associated DOC) from the Zostera Seagrass Community probably also reflects decomposition of fresh organic material trapped in the seagrass canopy (Barron et al. 2004). In addition some of the DON effluxes may reflect grazing of benthic microalgae (Eyre and Ferguson 2002).

The large net uptake of DON was driven by a combination of a dark uptake of DON in the Sub-tidal Pimpama Shoals, Inter-tidal Pimpama Shoals and Null Zone Channel in winter and Inter-tidal Pimpama Shoals in summer and a light uptake of DON in the Halophila Seagrass Community in summer and winter. An uptake of DON in the dark has also been found in the sediments of other shallow sub-tropical coastal systems (Eyre and Ferguson 2005; Ferguson et al. 2007), temperate coastal systems (Tyler and McGlathery 2003), mangroves (amino acids; Stanley et al. 1987) and coral reefs (Eyre et al. 2008), and were attributed to assimilation by heterotrophic bacteria. Recent $^{15}$N-labelling experiments in the sub-tropical Brunswick Estuary demonstrated that the sediment microbial community uses both urea and amino acids (labile DON) as a source of N (Veuger et al. 2007). The light uptake of DON in the Halophila Seagrass Communities could be due to either direct uptake by the seagrass (McRoy and Goering 1974; Bird et al. 1998; Vonk et al. 2008) and/or benthic microalgae (Linares 2005; Eyre et al. 2008), or a combination of these. Uptake of DON (and associated DOC) in the ephemeral Halophila Seagrass Community and an efflux in the stable Zostera Seagrass Community is also consistent with the findings of Barron et al. (2004) that DOC fluxes changes from uptake to efflux as seagrass communities age. Net DON fluxes were significantly correlated with gross benthic productivity but uptake only occurred above about 4,000 µmol $O_2$ $m^{-2}$ $h^{-1}$. Net DON uptake was also correlated to gross primary production in the Baltic Sea, but uptake occurred above about 1,000 µmol $O_2$ $m^{-2}$ $h^{-1}$ (Sundback et al. 2006). This work has further highlighted the importance of DON as a N source for both heterotrophic and autotrophic benthic communities in oligotrophic tropical coastal systems that have low concentrations of DIN.

Benthic net $N_2$ fluxes were weakly negatively correlated with benthic p/r ($r^2 = 0.36$; not significant; n = 12) if the seagrass communities, which had very high net $N_2$ effluxes (see later discussion), are excluded. The weaker relationship between benthic p/r and net $N_2$ fluxes compared to DIN and DON reflects the competing controlling factors on denitrification and N-fixation (Eyre and Ferguson 2005). Firstly, there is a distinct seasonality in the net $N_2$ fluxes with a different relationship with benthic p/r in summer and winter (same trend, different slope; Fig. 6d). The increase in net $N_2$ effluxes as the benthic p/r decreases in summer is mostly driven by the strong control of benthic respiration on dark $N_2$ effluxes ($r^2 = 0.91$; $p < 0.001$; n = 8; Fig. 7a). Increasing benthic respiration would increase the supply of $NH_4^+$ for coupled nitrification–denitrification. Consistent with most of the $N_2$ efflux being associated with coupled nitrification–denitrification was the low $NO_x$ uptake (Fig. 3) and the dark oxygen consumption rates exceeding $TCO_2$ efflux rates (Eyre et al. submitted). However, this difference can only account for about 60% of the denitrification rate. Assuming Redfield type material (i.e. phytodetritus) is the primary source of organic material being decomposed, about 25% of the released nitrogen is denitrified in summer (see Fig. 7a). However, the denitrification efficiency (amount of $N_2$ released as a proportion of the DIN + $N_2$ release) decreased with decreasing p/r due to a more rapid increase in the DIN efflux (see Fig. 6b) most likely associated with a loss of sediment biocomplexity (Eyre and Ferguson 2009). In contrast to summer, dark $N_2$ effluxes in winter were unrelated to benthic respiration

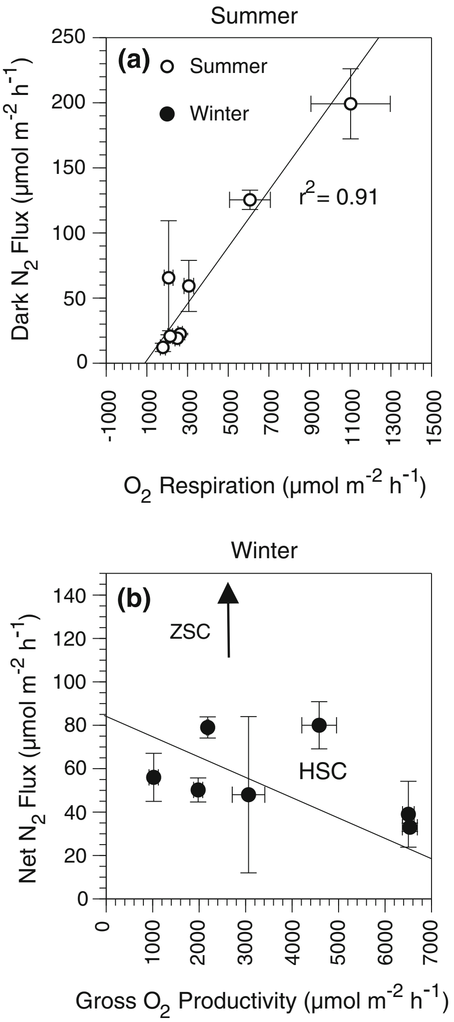


**Fig. 7** Apparent controls on net $N_2$ fluxes in the eight major open water benthic habitats in the Southern Moreton Bay study area **a** summer net $N_2$ as a function of respiration (dark $O_2$ fluxes), **b** winter net $N_2$ fluxes as a function of gross $O_2$ productivity (from Eyre et al. submitted). *ZS* Zostera Seagrass Community, *HSC* Halophila Seagrass Community

($r^2$ = 0.29; not significant; n = 7) but net $N_2$ effluxes were negatively related to benthic production ($r^2$ = 0.51; not significant; n = 6; seagrass communities excluded; Fig. 7b). This suggests that in winter the absence of a good supply of $NH_4^+$ from respiration results in the benthic producers decreasing denitrification through competition for N resources (Risgaard-Petersen 2003). It is unknown what is driving the high winter denitrification rates in the seagrass communities. However, because of the low respiration rates, 72% of the $NH_4^+$ released during organic matter decomposition in the Halophila Seagrass community and over 100% in the Zostera Seagrass Community would have to be nitrified and then denitrified to account for the dark $N_2$ efflux observed (assuming Redfield stoichiometry). Alternatively, the large uptake of DON in the Halophila Seagrass Community is sufficient to account for the dark $N_2$ efflux.

## Seagrass habitats

The Zostera Seagrass Community was the most important habitat for N loss via net $N_2$ effluxes (denitrification; 48%) due to the combination of high $N_2$ effluxes and large areal extent. The high denitrification rate in the sub-tropical Southern Moreton Bay seagrass communities contrasts with temperate seagrass communities where very low denitrification rates have been measured (Rysgaard et al. 1996; Risgaard-Petersen et al. 1998; Risgaard-Petersen and Ottosen 2000; Welsh et al. 2000). In Southern Moreton Bay, the high denitrification rates in summer are clearly driven by high rates of respiration (see Fig. 7a) and associated coupled nitrification–denitrification. However, this does not explain the difference in denitrification rates between tropical and temperate systems, as temperate systems with low denitrification rates can have respiration rates as high as or higher than southern Moreton Bay (Risgaard-Petersen et al. 1998; Risgaard-Petersen and Ottosen 2000). It may be the fraction of $NH_4^+$ released during organic matter decomposition and available for coupled nitrification–denitrification, rather than the rates of organic matter decomposition, that is important for the differences in denitrification. Coupled nitrification–denitrification in the rhizosphere of temperate seagrass communities is typically suppressed due to competition for N resources between nitrifying bacteria and seagrass and benthic microalgae (Rysgaard et al. 1996; Risgaard-Petersen et al. 1998; Risgaard-Petersen and Ottosen 2000; Welsh et al. 2000). Consistent with more freely available N are the higher porewater $NH_4^+$ concentrations found in the sediments of tropical seagrass communities compared to temperate seagrass communities (Touchette and Burkholder 2000) and the Zostera Seagrass Communities in Southern Moreton Bay being the largest source of DON (significant only in summer). The lack of competition between plants and bacteria in tropical seagrass communities may be driven by P-limitation associated with carbonate sediments (Short et al. 1990) and higher rates of N-fixation (O'Donohue et al. 1991). We are not entirely satisfied with this explanation as it is at odds with the oligotrophic environment in which seagrass typically grow, where N resources are scarce (Eyre and Ferguson 2005).

### Non-seagrass benthic habitats

The most important outcome of this study is that it highlighted that in shallow subtropical coastal systems less 'iconic' habitats also make an important functional contribution to the N and P budgets for the whole ecosystem. For example, the Yabby Shoals accounted for the second largest loss of N via net $N_2$ effluxes (denitrification) and the largest recycling of DIN and DIP (significant only during the dark in summer) across the sediment–water interface and the second largest uptake of DON (significant only in summer; Fig. 5). Dissolved inorganic nutrients regenerated in the Yabby Shoals would be an important source of N and P for the net autotrophic habitats in the study area (Eyre et al. submitted) with strong connectivity facilitated by large tidal flows (SKM 2006). However, large lateral inputs of N and P across the study area boundaries were still required to balance the budget (see later discussion). Much of the stimulated denitrification and N recycling in burrowing shrimp burrows has previously been linked to the increased supply of ammonia from animal excretion, organic matter accumulation and enhanced microbial activity and biomass (Howe et al. 2004; Webb and Eyre 2004a). However, this study has suggested that they may also take up DON, which may contribute to the enhanced effluxes of DIN and $N_2$. The associated dissolved organic carbon (DOC) uptake may be an additional energy source of benthic metabolism. The Zostera Seagrass Community was the largest source of DON (and associated DOC) suggesting strong connectivity between these two habitats; similar to the benthic-pelagic coupling via DOC between seagrass and heterotrophic bacterioplankton in the water column (Ziegler and Benner 1999). To our knowledge no other studies have looked at the cycling of DON, and no studies have looked at the cycling of DOC, in *T. australiensis* burrows or the burrows of any burrowing shrimp. In addition, permeable sandy sediments can also have significant rates of organic matter mineralisation, denitrification and N efflux in the absence of *T. australiensis* (Cook et al. 2006, 2007; Eyre et al. 2008). Although our chambers were designed to capture the passive flow through *T. australiensis* burrows (Webb and Eyre 2004b), it is unknown if they reproduce in situ advective flows through the permeable sands and therefore if they captured the total denitrification rates of the permeable sands.

### Budget uncertainty and balance

The N and P budgets were constructed using a combination of measured benthic flux rates scaled up to the whole study area and literature values. We have done basic error analysis and tested the sensitivity of the budget to errors in the various terms. However, the error analysis does not account for spatial and temporal variability not captured by the limited replication (particularly temporal replication) of the benthic flux measurements and does not indicate how relevant literature values are to the study area. We erred on the side of caution with the literature values by assigning 100% errors to these terms but there are still obviously large uncertainties associated with the budgets. This is particularly the case for the Broadwater exchange term that includes the sum of the errors associated with all the other components of the budget. Despite these uncertainties we still considered it better to make some rough approximations to illustrate potential important fluxes and processes than not make the budget calculations at all. The budgets should be considered in this context. Some of the important uncertainties and their impacts on the budget are discussed below.

This study undertook a detailed assessment of the spatial variability in benthic N and P fluxes (i.e. triplicate measurements in eight benthic habitats that had been mapped in detail), but the rates were only measured in summer and winter. It was assumed that these summer and winter measurements were sufficient for scaling up to an annual N and P budget.

Averaging summer and winter benthic flux rates should give a reasonable estimate of average rates that can be scaled up to an annual budget because subtropical coastal systems do not have the distinct four seasons typical of temperate systems, and maximum benthic fluxes typically occur in summer, and minimum benthic fluxes typically occur in winter (Eyre and Ferguson 2005). To test this assumption the N data set from Eyre and Ferguson (2005) and an associated unpublished P data set (Eyre unpublished) were used to calculate benthic net $N_2$ (denitrification), $NH_4$ and $PO_4$ flux rates using (1) monthly data over 2 years and (2) just using the summer and winter rates. Annual benthic denitrification estimates by the two approaches only differed by 12% and annual benthic $NH_4$ fluxes only differed by 2%, which is less than the error associated with the individual measurements. In contrast, benthic $PO_4$ fluxes differed by 128% suggesting this internal recycling term could be in error by only using summer and winter rates. However, this would not influence the overall P budget.

The budget had a deficit of 734.1 ton of N and a deficit of 94.4 ton of P (Table 2). This deficit is mainly driven by the small catchment inputs of N and P and large loss via denitrification (net $N_2$ efflux) and burial. It is unlikely that catchment, lateral and atmospheric loads, and denitrification losses (net $N_2$ effluxes) are in error by that order of magnitude. Sensitivity analysis shows that the N and P deficits were most sensitive to the carbon (and associated N and P) burial rates, which were derived from the literature (Tables 3, 4). However, even adjusting burial rates from 0 to 200% of average rates showed that the same conclusion would be reached that an import of N would be required to balance the budget. An import of P would not be required to balance the budget if there was no burial, but this is highly

**Table 3** Sensitivity analysis on the nitrogen budget for the Southern Moreton Bay study area

| Nitrogen budget term adjusted | Net Broadwater exchange (t year$^{-1}$) | |
|---|---|---|
| | Error adjusted down | Error adjusted up |
| Diffuse | 781.9 | 686.5 |
| Atmosphere | 750.7 | 717.7 |
| Lateral | 740.3 | 728.1 |
| Mangrove exchange | 756.7 | 711.7 |
| Net $N_2$ efflux (denitrification minus N-fixation) | | |
| Sub-tidal Broadwater Shoals | 703.0 | 765.4 |
| Yabby Shoals | 727.4 | 741.0 |
| Zostera Seagrass Community | 705.3 | 763.1 |
| Halophila Seagrass Community | 731.5 | 736.9 |
| Sub-tidal Pimpama Shoals | 733.2 | 735.2 |
| Upper Pimpama | 731.2 | 737.2 |
| Inter-tidal Pimpama Shoals | 732.7 | 735.7 |
| Null Zone Channel | 733.7 | 734.7 |
| Net $N_2$ efflux whole study area | 613.8 | 854.4 |
| Burial | 336.1 | 1140.7 |
| Fisheries | 737.6 | 739.2 |

Each input and output term was adjusted up and down by its associated error to determine how these errors influenced the budget deficit/surplus (net Broadwater exchange)

**Table 4** Sensitivity analysis on the phosphorus budget for the Southern Moreton Bay study area

| Phosphorus budget term adjusted | Net Broadwater exchange (t year$^{-1}$) | |
|---|---|---|
| | Error adjusted down | Error adjusted up |
| Diffuse | 99.9 | 89.1 |
| Atmosphere | 95.4 | 93.6 |
| Lateral | 95.1 | 93.9 |
| Mangrove exchange | 93.8 | 95.2 |
| Burial | −6.1 | 195.1 |
| Fisheries | 94.4 | 94.6 |

Each input and output term was adjusted up and down by its associated error to determine how these errors influenced the budget deficit/surplus (net Broadwater exchange) unlikely in this low energy environment. It is unknown if having summer light $N_2$ flux rates in the seagrass communities would have increased or decreased the deficit; in winter $N_2$ effluxes increased from dark to light in the Halophila Seagrass Community and $N_2$ effluxes decreased from dark to light in the Zostera Seagrass Communities. The budget was less sensitive to changing denitrification rates than changing the burial rates. Even adjusting denitrification for the whole study area by its associated error showed that an import of N was required to balance the budget. Both burial rates and denitrification rates would have to be decreased to near zero, which is highly unlikely, for no N import to be required to balance the budget.

The budget deficits suggest that there may be an import of N and P to the study area across the Broadwater boundaries. This is also consistent with the carbon budget for the study area that also required an import across the Broadwater boundaries to balance (see Eyre et al. submitted). Phytoplankton is one possible source of the organic material (and associated N and P) imported into the study area (Eyre et al. submitted), which is consistent with the molar ratio of the carbon, N and P deficits which was similar to Redfield (73:18:1) considering the errors involved in the calculations. Based on the modelled gross Broadwater inputs of N and P to the study area via tidal flows (Szylkarski et al. 2005; SKM 2006), this N and P deficit could be accounted for if only about 10% of the N and about 11% of the P was retained in the study area, which seems reasonable.

## Budget comparisons

Inputs of nitrogen and phosphorus from the ocean were the largest fluxes in the nitrogen and phosphorus budget (Table 2). This contrasts with some large temperate systems where diffuse sources typically make up a larger proportion of the loads (e.g. Boynton et al. 1995; Nixon et al. 1995) but is similar to other temperate (Engqvist 1996; Mackas and Harrison 1997), subtropical (Eyre and France 1997), and tropical (Burford et al. 2008) coastal systems. Differences in the importance of ocean exchange to the N and P budgets is most likely due to the morphology of the coastal system with the ratio of catchment area: water volume an important driver of the relative importance of ocean input. For example, an input of N from the ocean during the dry season has also been seen in the sub-tropical Richmond and Brunswick estuaries just south of the study area (McKee et al. 2000; Ferguson et al. 2004b). However, the ratio of ocean to terrestrial input is much higher in southern Moreton Bay (N = 15:1; P = 18:1) than these other sub-tropical systems, which can be easily explained by the much smaller catchment inputs to southern Morton Bay compared to the Richmond and Brunswick estuaries.

Nitrogen loss via denitrification (net $N_2$ efflux) was the largest output term in the N budget (Table 2). Combining the modelled gross ocean input of 6,831 ton of N (SKM 2006) with the other N inputs (Table 2) gives a gross annual N input of 7,188 ton. About 10% of this gross annual load is denitrified (and >100% of the land and atmosphere load) which is very high for a coastal system with a residence time of around 1 day. Nixon et al. (1996) demonstrated that for 11 estuaries there was a relationship between the percentage of the total N input from the land and atmosphere that is denitrified and the system residence time. Based on this relationship and a residence time of 1 day virtually none of the N input to Southern Moreton Bay should have been denitrified. The high efficiency of N removal via denitrification in southern Moreton Bay most likely reflects the high denitrification rates in the seagrass beds, which accounted for 48% of the annual system denitrification. In addition, the overall shallowness of the system (average 1.7 m) would allow greater contact between N in the water column and the sediments where denitrification takes place than in deeper coastal systems. Similarly, in Ochlockonee Bay the percentage loss of land and atmosphere N via denitrification is high (10%; Seitzinger (1987) data recalculated in Nixon et al. (1996)) for a system with a residence time of only 3 days, which Seitzinger (1987) also suggested was due to its shallow water column allowing greater N turnover. The current study suggests that overall N loss via denitrification for a given residence may be higher in oligotrophic tropical coastal systems with extensive seagrass habitats than temperate systems. To our knowledge there are no other whole ecosystem budgets of tropical coastal systems that include denitrification rate measurements in seagrass beds.

## Further work

This study has highlighted a number of future research directions including:

(1) the importance of DON as an N source for both heterotrophic and autotrophic benthic communities in oligotrophic tropical coastal systems that have low concentrations of DIN. Further work on the composition of DON, which consists of many fractions (Bronk 2002), particularly the different fractions taken up and released by the different benthic communities, is required. Stable isotope tracing studies with $^{15}$N-labelled DON and other organic nitrogen compounds would be a useful approach for investigating use of DON by different benthic communities.

(2) the interactions of burrowing macrofauna and DON cycling. Further research on the interaction between flow through burrowing shrimp (yabby) burrows and flow through associated permeable sands, including the cycling of DON and DOC, is required.

(3) that oligotrophic subtropical coastal systems have a complex mosaic of autotrophic habitats that consume inorganic, and produce organic, nutrients and heterotrophic habitats that produce inorganic, and consume organic, nutrients. Further work on the connectivity between these different habitats, particularly Yabby Shoals and Zostera Seagrass Community via DON (and associated DOC), is required.

(4) that denitrification rates may be higher in subtropical and tropical seagrass beds than in temperate seagrass beds. Clearly further work is required, using similar methods, to better determine the factors controlling differences in denitrification rates between tropical and temperate coastal systems.

(5) that N loss via denitrification for a given residence time may be higher in oligotrophic tropical coastal systems with extensive seagrass habitats than temperate systems. Clearly more N budgeting studies are required in tropical systems that include denitrification measurements in seagrass beds (and all the other major habitats).

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