The contribution of denitrification and burial to the nitrogen budgets of three geomorphically distinct Australian estuaries: Importance of seagrass habitats

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The contribution of denitrification and burial to the nitrogen budgets of three geomorphically distinct Australian estuaries: importance of seagrass habitats

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Abstract

Nitrogen (N) loss from different benthic habitats via net denitrification and burial was quantified, and first-order N budgets were constructed, for three geomorphically distinct shallow warm temperate South-East Australian barrier estuaries. Seagrass communities were the most important benthic habitats for N loss via net denitrification due to a combination of their area and high denitrification rates. Similarly, the largest N loss via burial occurred in the seagrass communities in the Hastings River Estuary and Wallis Lake, but in contrast, the largest annual loss of N via burial in the Camden Haven occurred in the subtidal muds due to their large area. N inputs to the river-dominated Hasting River Estuary were dominated by diffuse sources from the catchment. Budget deficits in Camden Haven and Wallis Lake suggest that the largest input of N may have been from the ocean, although missing N-fixation and/or groundwater cannot be excluded. Export to the ocean was the largest loss of N in the Hasting River Estuary followed by net denitrification and then burial. Net denitrification was the largest loss of N in the Camden Haven and Wallis Lake followed by burial. As the systems mature (evolve) the burial of N per m², the loss of N via denitrification per m² and the % of the total N load that is removed as fish per m², all decrease. Overall N loss via denitrification for a given residence time may be higher in shallow and oligotrophic coastal systems with extensive seagrass habitats than deeper temperate systems.

Introduction

Planetary-scale changes in the nitrogen (N) cycle have the potential to erode Earth-system functioning (Rockström et al. 2009). Anthropogenic rates of N₂ fixation,
mostly due to fertiliser production for food crops, production of leguminous crops and
burning of fossil fuel, now exceed natural (pre-industrial) rates (Gruber and Galloway
2008). Much of this anthropogenic N is transported to estuaries and coastal waters where
it stimulates the production of excess organic matter (eutrophication; Nixon et al. 1996).
However, the link between N loading and excess organic matter production in coastal
systems is complex with many modulating controls (Cloern 2001). Most importantly, to
understand and manage eutrophication in coastal waters we must know the sources
(loads) and sinks of N.
Ecosystem scale budgets are a useful tool for constraining our knowledge about
the sources and sinks of N in coastal systems (Nixon 1987; Eyre 1995). As such, there are
many published N budgets for coastal systems, but few have directly measured rates of
denitrification (e.g., Yoon and Benner 1992; Tuominen et al. 1998; Eyre and Mckee
2002) or N burial (Eyre 1995) and even fewer have directly measured rates of
denitrification and burial (Boynton et al. 1995; Deutsch et al. 2010), despite these two
pathways being important internal sinks for N. Further, these N coastal budgets that
include both measured rates of denitrification and burial are all in deep, nutrient enriched
west European and eastern United States systems. In these studies, denitrification and
burial measurements are typically only undertaken at muddy subtidal sites, although a
recent Patuxent River Estuary budget on the east coast of the United States also included
measurements in tidal marshes (Boynton et al. 2008).
Shallow and relatively pristine coastal systems have a complex mosaic of benthic
habitats, each contributing differently to N loss via denitrification. For example,
denitrification rates are typically higher in seagrass habitats than adjacent bare muds and
sands, reflecting the higher rates of benthic respiration (Eyre et al. 2011; Smyth et al. 2012; Eyre et al. 2013a). Ecosystem N loss via burial has never been compared in different benthic habitats of shallow coastal systems, but it is expected that N burial rates would also be higher in vegetated habitats such as seagrasses due to their high carbon burial rates (Mcleod et al. 2011). The area is also an important control on the amount of N loss via denitrification and burial in a given benthic habitat, which in-turn is controlled by the geomorphology of the system. For example, as a bar-built, wave-dominated estuary or barrier lagoon estuary infills/evolves over time (matures), the relative area of various benthic habitats changes from those associated with central mud basin to habitats linked to the marine tidal delta and riverine channel. Gradual infilling of immature barrier estuaries results in a loss of large productive subtidal mud shoals leaving mangrove/saltmarsh habitats landward with channel and remnant subtidal shoals instream (Roy et al. 2001; Harris and Heap 2003). This evolution is evident in the three systems in this study with the proportional coverage of subtidal mud shoals/depositional mud basins and stable Zostera seagrass communities decreasing with lagoon maturity i.e. Wallis Lake > Camden Haven > Hastings (Eyre and Maher 2010). Concurrently Marine Sand Channel and Fluvial Sands and Gravel increase with maturity (Wallis Lake < Camden Haven < Hastings).

The hypothesis of this study is that the distribution of different benthic habitats in a coastal system, which in-turn is controlled by the geomorphology, will be an important control on N loss via denitrification and burial. This was tested by estimating the N loss from different benthic habitats via denitrification and burial and constructing first-order N budgets for three geomorphically distinct shallow warm temperate South-East Australian
barrier estuaries. The N budgets are based predominantly on directly measured N flows measured seasonally over one year, and measured N burial rates averaged over 21 to 105 years (age of core) and fisheries harvest averaged over 20 years (1984 - 2004). The three estuaries were selected as they are close geographically (within 100 km), vary in freshwater inputs, span a range of river to marine dominated systems, vary in seagrass coverage (from approximately 6 to 38%) and represent the dominant geomorphic types of barrier estuaries on the Australian southeast coast.

Methods

Study site

The three study estuaries are described in detail in Eyre and Maher (2010) and Maher and Eyre (2011) and some characteristics are summarised in Table 1. Briefly, the South-East Australian estuaries have a relatively small catchment population (24 000 - 48 000; (Maher and Eyre 2011) with only low to moderate modification of the catchment for agricultural uses (for full description of estuarine stressors see Eyre and Maher 2010). The estuaries reflect different evolutionary stages of infilling or maturity (Roy et al. 2001), similar to the the successional development or ontogeny of inland aquatic ecosystems largely associated with sedimentation (Wetzel 2001). Wallis Lake is an immature stage estuary with a large central mud basin and the largest area of open water. Camden Haven is an intermediate stage estuary with a more restricted shallower central basin and open water area. The mature stage Hastings River Estuary is a riverdominated system characterized by river channels with a highly restricted/absent central mud basin and only a small area of open water. These different stages of maturity are also reflected...
in the water residence time, catchment area and freshwater inflow (Table 1), the
distribution of benthic habitats in each system (Table 2)(also see maps in Eyre and Maher
2010) and ecosystem scale carbon cycling (Maher and Eyre 2010; Maher and Eyre 2012).
Up to 12 benthic habitats were identified in each of the three estuaries using a
combination of underwater video, diving transects, and remote sensing techniques. The
main factors used to delineate benthic habitats were their depth (subtidal, intertidal),
sediment grain size (mud dominant, sand dominant), geomorphology (channels,
depositional basins, shoals) and dominant autotrophs (macroalgae, seagrass (*Halophila
ovalis*, *Zostera capricorni*, *Posidonia australis* and *Ruppia megacarpa*). The *Halophila*
community in Hasting River Estuary was heavily degraded (ephemeral) with little plant
biomass and could be classified as either a seagrass or subtidal habitat.

**Nitrogen budget framework**

The budgeting framework of Eyre and McKee (2002) and Eyre et al. (2011) was used to assess the importance of denitrification and burial in each of the open water benthic habitats to each of the three whole ecosystems and to approximate N budgets for the estuaries. The focus of the budgets is on N loss via denitrification and burial in different benthic habitats. The other N budget terms were calculated to put the N burial and denitrification losses in context of the whole system and to identify and major missing inputs or losses. Steady state was assumed in the budgeting and therefore the sum of inputs and outputs within the study area should equal zero ± error (storage was assumed not to change of the time scale of the budgeting). The N budget includes three major inputs: diffuse, point-source and atmospheric deposition. Outputs of N include net
denitrification, burial and fisheries harvest. Missing N, or excess N, was assigned to
ocean exchange and determined as the difference between in the inputs and outputs, and
includes all the errors in the other terms. There was insufficient data to independently
calculate ocean exchange,

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

Annual N budgets were developed (July 2006 to June 2007) for the three study
areas as described for carbon in Maher and Eyre (2012). The N budgets were calculated
for the water column and therefore N burial represents a loss from the system. Mass
(tonnes = $10^3$ kg) rounded to 0.1 tonne (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 two 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 x area) using the following formula (modified from (Eyre
1995):

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

Where errors for a given term were unknown, or not well quantified, a
conservative 100% error was assigned. This was done to illustrate the possible effect of
large errors in these terms on the overall outcomes of the N budget. Secondly, a
sensitivity analysis was done where each of the terms in the budget (e.g. overall N burial) were adjusted up or down by their estimated error determine if the overall conclusions derived from the budget changed (Eyre et al., 2011).

**Diffuse and point-source loads**

Diffuse catchment total nitrogen (TN) loads were estimated by integrating flow-weighted concentrations and river discharge (Eyre and Pont 2003). TN samples were collected in the main river as close as possible to the most downstream gauging station above the tidal limit. Samples were filtered immediately through 0.45 µm cellulose acetate membrane filters into sample-rinsed polyethylene vials and analysed as detailed in Eyre and Ferguson (2005). A total of 12 samples in the Hastings, 24 samples in the Camden Haven and 19 samples in Wallis Lake were collected over a range of river flows from July 2006 to June 2007. A linear regression of TN concentration versus river flow (Hastings $r^2 = 0.61$, p<0.01; Camden Haven $r^2 = 0.75$, p<0.001; Wallis Lake $r^2 = 0.65$, p<0.001) was applied to daily river flows to estimate TN concentrations for each non-sampled day in each system. Gauged river flows were scaled to the whole catchment by linear interpolation. Scaled daily river flows were multiplied by daily TN concentrations and integrated over the study period to estimate annual diffuse TN catchment loads in each estuary. Because it is unknown how well linear interpolation captures N loads the ungauged areas of the catchment a 100% error was assigned.

Treated wastewater is discharged into the Hastings River and Camden Haven estuaries. Data on effluent discharge was multiplied by effluent TN concentrations to obtain the effluent TN loads (supplied by Port Macquarie Hastings Council). There are no
other major point sources of nitrogen into these estuaries. A measurement error of 4% was assigned to TN concentrations and an error of 10% was assigned to the discharge volume.

**Atmospheric deposition**

Rainfall TN concentrations for the Richmond River catchment (McKee et al. 2001), mean annual rainfall for each of the three estuaries and the open water surface area of each system was used to estimate atmospheric deposition loads. The rainfall concentration data were from coastal sites in northern NSW, 350 km north of the study area, 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. 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 error. A 100% error was therefore assigned to atmospheric TN loads.

**Net denitrification**

Benthic dark and light N\textsubscript{2} effluxes were measured using benthic chamber and core incubations in up to 12 benthic habitats in each of the estuaries (Eyre et al. 2013a). N\textsubscript{2} efflux measurements were undertaken in summer, spring, winter and autumn. Both dark and light net N\textsubscript{2} effluxes were measured in all seasons for all estuaries, and in all habitats in all estuaries, but not all habitats in all seasons in all estuaries. Dark N\textsubscript{2} effluxes in each of the 12 benthic habitats were strongly correlated to sediment oxygen demand.
(respiration) \( r^2 = 0.440 \) to 0.889; average \( r^2 = 0.743 \); (Eyre et al. 2013a) and sediment oxygen demand was measured in all benthic habitats, in all seasons, and in all estuaries (Maher and Eyre 2011). As such, the relationship between N\(_2\) efflux and sediment oxygen demand was applied to measured sediment oxygen demand to estimate the dark N\(_2\) efflux in each habitat, in each season, in each estuary. N\(_2\) effluxes were reduced in the light and this was proportional to the net benthic productivity of each habitat \( (r^2 = 0.849) \); (Eyre et al. 2013a). Net benthic productivity measured in all habitats, in all seasons, and in all estuaries (Maher and Eyre 2011) was used to estimate the light N\(_2\) effluxes. Dark and light N\(_2\) effluxes were scaled to annual fluxes by multiplying the hourly rate, by the number of day, or night, hours for each season, by the surface area of the habitat, and by the numbers of days of each season. Because N\(_2\) effluxes were measured they include both canonical denitrification and anammox. N\(_2\) effluxes reflect the balance between N-fixation and denitrification and as such, are a measure of net denitrification. The terms N\(_2\) efflux and net denitrification are used interchangeably. The standard error of the triplicate N\(_2\) flux measurements in each habitat was adopted as the error for the rate measurements and a 10% measurement error was assigned to the area estimates.

**Burial**

Sediment cores (\( \sim 25\)-cm in length) were retrieved from 10 benthic habitats across the three estuaries utilizing a peat corer. An aliquot of sediment was taken from each 4cm interval for gravimetric analyses of wet weight and dry weight. Dry weight was obtained by freeze drying for three days. The dry bulk density was calculated as aliquot dry mass divided by initial wet volume. Sediment accumulation rates were determined using
excess $^{210}$Pb ($^{210}$Pb$_{ex}$), a radionuclide with a half-life of 22.3 years and well suited to the timescale of interest here (≤ 100 years). Measurements and calculations were conducted as described by (Sanders et al. 2010). Briefly, sediments at each interval were sealed in 70 ml petri-dishes for at least three weeks to establish secular equilibrium between $^{226}$Ra and its daughter products $^{214}$Pb and $^{214}$Bi. Gamma-ray measurements were conducted by using a semi-planar intrinsic germanium high purity coaxial detector with 40% efficiency, housed in a lead shield, coupled to a multichannel analyzer. Lead-210 activity was determined by the direct measurement of 46.5 KeV gamma peak, while $^{226}$Ra activity was calculated averaging its daughters’ peaks $^{214}$Pb and $^{214}$Bi (295.2 KeV) (351.9 KeV) (609.3 KeV) (Moore 1984). The excess $^{210}$Pb ($^{210}$Pb$_{ex}$) activity was estimated by subtracting the $^{226}$Ra from the total $^{210}$Pb activity. Samples were counted for at least 86000 s in identical geometrical cylinders. Self-absorption corrections were calculated following Cutshall et al. (1982).

The sediment accumulation rates were obtained through the Constant Initial Concentration (CIC) dating method (Appleby and Oldfield 1992) as $^{210}$Pb$_{ex}$ was fitted via the least square procedure and the slope of the log-linear curve was used to calculate sediment accumulation rates and multiplied by specific interval density to determine downcore mass accumulation rates. Depth averaged N burial rates were calculated based on mass accumulation rates, dry bulk densities (g cm$^{-3}$) and total N concentration of each interval. N concentration and stable isotopes were analyzed using an elemental analyzer (Flash EA) coupled to a Thermo Delta V+ IRMS (Oakes et al. 2010). Sediment N samples were standardised against working standards, which in turn were calibrated against the international standard IAEA-N-1.
An additional three carbon (C) burial rates, one from the sub-tidal muds in the Hastings River Estuary and Camden Haven and one from the Depositional Mud Basin in Wallis Lake, were obtained from Maher and Eyre (2012). Mass accumulation rates were measured over a similar depth to this study (26 cm) (Maher and Eyre 2012), but only surface N concentration data from Eyre et al. (2013a) were available to calculate surface N burial rates. All N burial rates were scaled to annual fluxes by multiplying by the surface area of the habitat. N burial rates in all seagrass habitats were sampled except the Zostera community in the Hasting River Estuary. For this habitat the average of the N burial rates for the Zostera communities in the Wallis Lake and Camden Haven were used. The average of the N burial rates in the non-seagrass habitats in each system was applied to the un-sampled non-seagrass habitat in the respective system. Because burial rate measurements were not replicated in each individual habitat, and because burial rates were not measured in all habitats, a 100% error was applied.

**Fisheries harvest**

Commercial fisheries harvest data was obtained from the New South Wales Department of Primary Industries for each of the three systems for the years 1984 - 2004 (including oyster aquaculture production). Fisheries export from each of the three systems was estimated using the average commercial fisheries catch and assuming that the recreational catch is equal to the commercial catch (excluding oysters) (Maher and Eyre 2012). Wet weight of total catch was converted to g N dry weight by assuming that dry weight was 20% of wet weight and 15% of dry weight was N (Eyre and Mckee 2002). A 100% error was assigned to fisheries harvest.
Results

Net denitrification

The largest total annual loss of N via net denitrification occurred in the Zostera communities in all three estuaries (Table 2). Although the Zostera communities dominated N loss via denitrification in all three estuaries, the benthic habitats that contributed to the next largest loss of N varied across the three systems (Table 2). In the Hasting River Estuary and Wallis Lake the Fluvial Muds and Sands contributed the second largest annual loss of N via net denitrification. Subtidal Muds contributed the second largest loss of N via net denitrification in the Camden Haven. The smallest contribution to the total annual loss of N via net denitrification occurred in the Intertidal Muds and Halophila communities in the Hastings River Estuary, in the Marine Channels in Camden Haven, and in the Intertidal Muds and Marine Channels in Wallis Lake (Table 2).

Burial

In both the Hastings River Estuary and Wallis Lake the highest burial rates occurred in seagrass communities, although the seagrass species was different (Fig. 1; Table 2). The largest annual loss (burial) of N in Wallis Lakes occurred in the Zostera communities due to their large area combined with a moderate burial rate (Table 2). Of the measured burial rates the largest annual loss (burial) of N in Hasting River Estuary occurred in the Subtidal Muds/ degraded (ephemeral) Halophila community (Table 2). The highest, and similar, N burial rates in Camden Haven occurred in the Subtidal and
Intertidal Muds (Fig. 1). However, the largest annual loss (burial) of N in the Camden Haven occurred in the Subtidal Muds due to their larger area (Table 2).

Depth averaged Zostera community burial rates were similar in Wallis Lake (3.9 g m$^{-2}$ y$^{-1}$) and Camden Haven (2.7 g m$^{-2}$ y$^{-1}$) (Fig. 1). In contrast, burial rates in the Halophila community were highly variable across the three systems ranging from 1.3 to 8.0 g m$^{-2}$ y$^{-1}$, although the high end of the range reflects a high depositional subtidal area with a degraded Halophila community (little biomass). Similarly, burial rates in the Ruppia community were highly variable ranging from 1.8 g m$^{-2}$ y$^{-1}$ in Camden Haven to 8.2 g m$^{-2}$ y$^{-1}$ in Wallis Lake. Burial rates in the Intertidal Muds and Subtidal Muds were much higher in Camden Haven then the Hastings River Estuary.

A number of habitats showed some change in N burial rates over time, although they were not always consistent changes (Fig. 1a,b). The exceptions were Posidonia community in Wallis Lake that showed a rapid increase in N burial from 1997 to 2011. The Zostera community in Wallis Lake also showed an increase in N burial from 1975 to 1991. N burial in the Zostera community in Camden Haven also showed a small gradual increase from 1942 to 2006. It is unknown if these changes reflect changes in the N burial of the habitats, changes in the habitat type or bioturbation. Using the more recent burial rates, instead of average rates over the full depth of the core, made no change to the annual loss (burial) of N in Hasting River Estuary, and about a 10% increase to the annual loss (burial) of N in Camden Haven and Wallis Lake.

Budget
N inputs to the Hasting River Estuary were dominated by diffuse sources from the catchment (Table 3). A missing N source was the largest input to the Camden Haven and Wallis Lake. Diffuse sources of N were the second largest input of N to Camden Haven with similar loads of N delivered to Wallis Lake from rainfall and diffuse sources. Rainfall was the second largest input of N to the Hasting River Estuary and third largest input to Camden Haven with only minor amounts of N coming from wastewater.

Export to the ocean was the largest loss of N in the Hasting River Estuary followed by net denitrification and then burial. Net denitrification was the largest loss of N in the Camden Haven and Wallis Lake followed by burial (Table 3). N loss by fisheries was minor in all three systems.

Discussion

Role of different habitats in nitrogen loss

The seagrass communities were the most important habitats for N loss via net denitrification accounting for 70%, 62% and 27% of the total net denitrification N loss in the Wallis Lake, Camden Haven and Hastings River Estuary, respectively. This did not just reflect their area, as seagrasses only covered 36%, 38% and 8% of Wallis Lake, Camden Haven and Hastings River Estuary respectively, but also the high rates of net denitrification. The high rates of net denitrification are driven by high rates of respiration in the seagrass communities, which increases the supply of NH$_4$ from ammonification for coupled nitrification denitrification, increases the availability of electron donors for denitrification, and modifies the sediment redox conditions (Eyre et al. 2013a). Only two other studies (Southern Moreton Bay, Australia; Bogue Sound, USA) have measured
denitrification in a range of benthic habitats and scaled then up to the whole ecosystem, and both these found higher rates in seagrass habitats than adjacent bare muds and sands (Eyre et al. 2011; Smyth et al. 2012). Similar to the three systems in this study the largest loss of N via denitrification also occurred in the seagrass communities in Southern Moreton Bay (Eyre et al. 2011). In contrast, in Bogue Sound the largest loss of N via denitrification occurred in the subtidal flats due to the large extent of this habitat (64%) reflecting the geomorphology of the system (Smyth et al. 2012).

The high rates of net denitrification in this study and the recent studies of (Ferguson et al. 2004; Eyre et al. 2011; Smyth et al. 2012) using the N₂: Ar technique (28 to 824 µmol m⁻² h⁻¹), contrast with earlier very low rates (<1 to 35 µmol m⁻² h⁻¹) of denitrification measured in seagrass communities using the isotope pairing technique (e.g. Risgaard-Petersen et al. 1998; Risgaard-Petersen and Ottosen 2000; Welsh et al. 2000- see review table in Murray et al. 2015). This suggests the differences may be methodological. One possibility is that the isotope pairing technique may underestimate denitrification in seagrass communities due to coupled nitrification-denitrification associated with O₂ release from the plant roots occurring deep within the sediment, thereby preventing uniform mixing of the added ¹⁵N (Welsh et al. 2001; Ferguson and Eyre 2007). Alternatively, the difference in denitrification rates may be due to different rates of biogeochemical processes, driven, in part, by different species and their proportional allocation of biomass to leaves, roots and rhizomes. For example, the fraction of the NH₄⁺ released during organic matter decomposition that is available for coupled nitrification-denitrification may vary between different species (Eyre et al. 2011) or low rates of coupled nitrification-denitrification might reflect irregular oxygen release
by the roots of some seagrass species (Frederiksen and Glud 2006). Diel variations in oxygen release and the transient nature of oxic microzones induced by growing roots may limit the growth potential of nitrifiers. While more regular oxygen release of some seagrass roots may drive higher rates of coupled nitrification-denitrification. Further work using both isotope pairing and N\textsubscript{2}/Ar techniques simultaneously in different seagrass communities is required to assess the apparent differences in the rates of denitrification measured by these methods.

N burial rates across the 3 estuaries (mean 4.1; range 1.3 to 8.2 g N m\textsuperscript{-2} y\textsuperscript{-1}) were at the lower end of the range for coastal systems (2.8 to 25.0 g N m\textsuperscript{-2} y\textsuperscript{-1}; (Boynton et al. 2008), which may reflect their oligotrophic status. Consistent with the typically high carbon burial rates in seagrasses (Mcleod et al. 2011), the highest N burial rates in Hasting River Estuary and Wallis Lake were in the seagrass communities (Figure 1). In contrast, the highest burial rate in Camden Haven was in the Subtidal Muds, which is consistent with a rapidly infilled depositional mud basin in this intermediate type system (Roy et al. 2001). Burial rates were measured in several of the same benthic habitats in different systems (Fig. 1). The Ruppia community, Halophila community, Subtidal muds and Intertidal muds all show a large variability in burial rates between systems. For example burial rates in the Halophila community, which were measured in all three systems, ranged from 1.3 to 8.0 g N m\textsuperscript{-2} y\textsuperscript{-1} and similarly, burial rates in the Ruppia community ranged from 1.8 to 8.2 g N m\textsuperscript{-2} y\textsuperscript{-1}. This suggests that it is the local conditions (depositional environment; benthic production etc.), rather than the habitat type, that dictates N (and likely C) burial rates and highlights the problem of extrapolating one, or few measurements across large spatial scales (e.g. Mcleod et al. 2011). However, burial
rates in the *Zostera* community were similar across systems (2.7 and 3.9 g N m$^{-2}$ y$^{-1}$) suggesting the community structure of some benthic habitats may influence burial rates. Similar to denitrification (Eyre et al. 2013a) loss of N via burial in the seagrass communities was correlated with respiration (exponential $r^2=0.74$; n=7; $p<0.05$) and net primary production ($r^2=0.69$; n=6; $p<0.05$; Fig. 2a,b). Net primary production reflects the autochthonous organic matter produced by the seagrass community and respiration also included any allochthonous organic matter trapped within the community. As such, the correlations are not surprising, with a greater supply of organic matter leading to higher N burial rates, but this has not been previously demonstrated empirically. N loss via denitrification as a function of N burial across the seagrass communities showed two trends with the *Halophila* and *Posidonia* communities and *Ruppia* community in Wallis Lake having higher N burial rates for a given rate of denitrification (or lower denitrification rate for a given burial rate) than the *Zostera* communities and *Ruppia* community in Camden Haven (Fig. 2c). This may reflect differences in the way the different canopy structures trap organic matter (Barrón et al. 2004) or the type and quality of organic matter trapped which regulates denitrification (Eyre et al. 2013a), below ground biomass, or other local depositional factors. Because the *Ruppia* community is in both relationships (Figure 2c) shows that the controlling factors are not just limited to the seagrass species. The correlation between net primary production ($r^2=0.26$; n=7; not significant) and respiration ($r^2=0.33$; n=7; not significant) and N burial in the non-seagrass habitats was weak and not significant, suggesting other controlling factors on N burial such as sediment accretion rates.
Influence of geomorphology on the nitrogen budgets

The degree of maturity, evolutionary stage or infilling of a coastal lagoons is an important determinant of the system trapping capacity (Harris and Heap 2003). For example, all of the N delivered to the immature coastal lagoons (Wallis Lake, Camden Haven) is trapped within the system (Table 3). In contrast, 61.1% of the total N input to the Hastings River Estuary is exported to the ocean, which is consistent with other mature infilled river dominated estuaries during non-flood years (McKee et al., 2000). During years with large floods the trapping capacity of N in mature river dominated estuaries is reduced to only a few percent (e.g. McKee et al. 2000).

As the system matures both the burial of N per m$^2$ (Wallis Lake 3.5 > Camden Haven 3.4 > Hastings 1.7 g N m$^{-2}$ y$^{-1}$), and loss of N via denitrification (Wallis Lake 6.6 > Camden Haven 5.5 > Hastings 4.7 g N m$^{-2}$ y$^{-1}$), decreases. This reflects a reduction in the relative proportion of habitats such as the Zostera community, which have high rates of denitrification and burial and replacement with habitats such Marine Sand Channel and Fluvial Sands and Gravel, which have lower rates of denitrification (burial rates were not measured in these habitats). There is also a decrease in the % of the total N load (including missing N) that is removed as fish as the system matures (Wallis Lake 0.57% > Camden Haven 0.36% > Hastings 0.31%).

Budget uncertainty and balance

N budgets for the three coastal systems were constructed using detailed field measurements. In particular, what separates these budgets form previous coastal N budgets were measurements of net denitrification and burial in a range of different
benthic habitats. We have undertaken a 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 even by the detailed field measurements.
This is particularly the case for the missing-N 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, and missing N terms, then not make the budget
calculations at all. The budgets should be considered in this context.

The Hasting River Estuary budget had an annual excess of 188.9 t of N, which
was most likely exported to the ocean (Fig. 3). This ocean export is 61.1% of the total N
input and is consistent with other mature infilled river dominated estuaries during non-
flood years (McKee et al. 2000). In contrast, Camden Haven and Wallis Lake both had
large annual deficits of 192.1 and 826.1 t N respectively (Fig. 3). This deficit is mainly
driven by the small catchment and subsequently small freshwater and associated diffuse
N inputs, and large losses via net denitrification and burial. It is unlikely that catchment
and atmospheric loads, and net denitrification and burial losses, are in error by that order
of magnitude. Sensitivity analysis shows that the N deficits were most sensitive to burial
(Table 4). However, even adjusting burial rates from 50% to 200% showed that the same
conclusion would be reached that an import of N would be required to balance the
budgets. Both burial and net denitrification losses would have to be decreased together to
near zero for no N import to be required to balance the budgets, which is highly unlikely.
This is in contrast to carbon which was exported from the system during the study (Maher
and Eyre, 2012), which may be due to shifts in the C:N ratio between diffuse
allochthonous inputs (high C:N related to terrestrial organic matter) and the lower C:N ratio of estuarine autochthonous organic material, leading to a N deficit relative to carbon.

The budget deficits in Camden Haven and Wallis Lake suggest that there may be an import of N from the ocean. East coast Australian estuaries in general are nutrient limited for much of the year, particularly during the dry season (Eyre 2000), and therefore would rapidly use any imported ocean N. A rough estimate of the total amount of N flux from the ocean can be estimated by multiplying the tidal prism for each system (Webb, McKeown and Associates 1998, 1999; Patterson Britton and Partners 1999) by the average nearshore total N concentration (152 ug L⁻¹; (Eyre 2000). Based on the gross annual ocean inputs of N to Camden Haven (1,665.5 t) and Wallis Lake (1242.8 t) the N deficits would require 11.5% and 66.5% of the ocean N to be retained respectively. The required retention of ocean N is reasonable for Camden Haven but quite high for Wallis Lake, suggesting there may also be other missing sources of N. An additional source of N could be unmeasured benthic N-fixation in the light. Net denitrification measurements in the light were excluded from a number of sites with high rates of benthic production due to the formation of bubbles in the incubation cores and chambers (Eyre et al. 2013a), which reduces the N₂/Ar ratio giving a pseudo-rate of N-fixation (see Discussion in Eyre et al. 2002). As such, there may have been unmeasured benthic N-fixation that could account for some of the N deficit (Eyre et al. 2013b). Additional unmeasured sources could be groundwater inputs of N and pelagic N-fixation. Groundwater inputs have been shown to be a significant source of N to other east Australian estuaries (Santos et al. 2013; Makings et al. 2014).
Budget comparisons

Net input of N from the ocean (assuming this equals the missing N) was the largest N flux in the Camden Haven and Wallis Lake budgets (Fig. 3). This contrasts with the river dominated Hastings and 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; Eyre et al. 2011) and tropical (Burford et al. 2008) coastal systems. Differences in the importance of ocean exchange to the N 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 to the north of the study area (McKee et al. 2000; Ferguson et al. 2004). However, the ratio of ocean to terrestrial input is much higher in Camden Haven (3.2:1) and Wallis Lake (16.9:1), than these sub-tropical river dominated estuaries, which can be easily explained by the much smaller catchment inputs compared to the Richmond and Brunswick estuaries. In contrast, Southern Moreton Bay has almost the same terrestrial input (47.7 t N yr⁻¹) as Wallis Lake (48.8 N yr⁻¹) and a very similar ratio of ocean to terrestrial input (15:1) (Eyre et al. 2011).

N loss via net denitrification was the largest output term in the N budget of all three systems (Fig. 3). About 27%, 60% and 62% of the total annual N load (missing N plus other N inputs) was denitrified (and > 100% of the land and atmosphere load) for the Hastings River Estuary, Camden Haven and Wallis Lake, which is very high for a coastal
systems with residence times of 10, 45 and 60 days (Eyre and Maher 2010), respectively. (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 times of the three systems about 10 to 25% of the total N load should have been denitrified. The high efficiency of N removal via denitrification most likely reflects the high denitrification rates in the seagrass beds, which accounted for 27%, 62% and 70% of the annual system denitrification, in the Hastings River Estuary, Camden Haven and Wallis Lake respectively. In addition, the overall shallowness of the systems (average 1.8 m) increases the sediment surface area:volume ratio allowing greater contact between N in the water column and the sediments where denitrification takes place than in deeper coastal systems.

A similar high loss of total N via denitrification (10% with a 1 day flushing time) was also seen in Southern Moreton Bay where seagrasses accounted for 48% of the annual system denitrification (Eyre et al., 2011). There was also a high loss of total N via denitrification (78%) for a given residence time (116 days; Basta et al., 1990) in the shallow Bogue Sound where seagrasses accounted for 24% of the annual system denitrification (Smyth et al. 2012). 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 (1 m) allowing for greater N turnover. Fifty percent of the N load in Galveston Bay was removed via denitrification which is also high for a system with a flushing time of 50 days (An and Joye 2001). This
high N removal via denitrification was thought to be due to enhanced dentrification in the
light (An and Joye 2001), but may also reflect the shallow water column (3 m). Plotting
the percentage loss of total N load via denitrification versus flushing time for Southern
Moreton Bay, Bogue Sound, Ochlockonee, Galveston Bay, Hasting River, Camden
Haven and Wallis Lake shows a significantly higher N removal rate via denitrification for
a given residence time (p<0.001; covariance analysis) than the 10 (the shallow
Ochlockonee Bay was excluded) deeper temperate estuaries in Nixon et al. (1996)(Fig.
4). In addition, the amount of total N load removed via denitrification for a given flushing
time is also slightly higher for the four systems with extensive seagrass coverage (r² =
0.995; p<0.05; n=4) where denitrification has been measured in the seagrasses and scaled
to the whole ecosystem (Wallis Lake, Camden Haven, Southern Moreton Bay and Bogue
Sound). This suggests that overall N loss via denitrification for a given residence time
may be higher in shallow and oligotrophic coastal systems with extensive seagrass
habitats than deeper temperate systems.
Seagrass communities were clearly important benthic habitats for N loss via net
denitrification and burial. Overall N loss via denitrification for a given residence time
may be higher in shallow and oligotrophic coastal systems with extensive seagrass
habitats than deeper temperate systems. Because denitrification and deep burial
permanently remove nitrogen from an ecosystem they are key ecosystem processes. As
such, seagrass lost during eutrophication (McGlathery et al. 2007) will be a negative
feedback, with less nitrogen loss via denitrification and burial. Changes in the type
(quality), and maybe the mixture, of organic matter (detritus) associated with seagrass
loss are also expected to impact system level losses of nitrogen via denitrification (Eyre
et al. 2013a). Further work using both isotope pairing and N2/Ar techniques simultaneously to better determine denitrification rates, and N-fixation measurements using 15N-labelled gas (Mohr et al. 2010), in different seagrass communities would be fruitful areas for further research.

References


Table 1. Characteristics of the three study estuaries (modified from Eyre and Maher, 2010)

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Hastings</th>
<th>Camden Haven</th>
<th>Wallis Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evolutionary Stage</td>
<td>Mature</td>
<td>Intermediate</td>
<td>Immature</td>
</tr>
<tr>
<td>Catchment area (km²)</td>
<td>3,395</td>
<td>440</td>
<td>1,420</td>
</tr>
<tr>
<td>Open water area (km²)</td>
<td>18.62</td>
<td>30.05</td>
<td>90.45</td>
</tr>
<tr>
<td>Average depth (m)</td>
<td>2.5</td>
<td>1.2</td>
<td>1.8</td>
</tr>
<tr>
<td>Rainfall (mm)</td>
<td>1,533</td>
<td>1,540</td>
<td>1,220</td>
</tr>
<tr>
<td>Annual discharge (ML)</td>
<td>503,471</td>
<td>251,483</td>
<td>147,883</td>
</tr>
<tr>
<td>Mean residence time (days)</td>
<td>10</td>
<td>45</td>
<td>60</td>
</tr>
<tr>
<td>Total Seagrass Area (km²)</td>
<td>1.2 (6)</td>
<td>11.4 (38)</td>
<td>32.7 (36)</td>
</tr>
<tr>
<td>(% of open water area)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zostera Seagrass Area (km²)</td>
<td>1.2 (6)</td>
<td>5.6 (19)</td>
<td>22.9 (25)</td>
</tr>
<tr>
<td>(% of open water area)</td>
<td></td>
<td></td>
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</table>
Table 2. Nitrogen loss via net denitrification and burial in different benthic habitats in the Hastings River Estuary, Camden Haven and Wallis Lake. Net denitrification rates are the average of the seasonal rates measured over a diel cycle (mean±SE).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Area km$^2$</th>
<th>Net denitrification (µmol m$^2$ d$^{-1}$)</th>
<th>Net denitrification (t N y$^{-1}$)</th>
<th>Burial (g m$^2$ y$^{-1}$)</th>
<th>Burial (t N y$^{-1}$)</th>
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<td>2,772±384</td>
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<td>5.3±0.5</td>
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<td><em>Zostera</em> community</td>
<td>1.2</td>
<td>3,712±219</td>
<td>22.2±1.3</td>
<td>8.0</td>
<td>3.9±3.9</td>
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<td>Subtidal muds/ degraded <em>Halophila</em></td>
<td>0.4</td>
<td>445±59</td>
<td>0.9±0.1</td>
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<td>4.1±4.1</td>
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<td>Total</td>
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<td>87.0±8.1</td>
<td>32.4±32.4</td>
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<td>Camden Haven</td>
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<td>301±24</td>
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<td>Halophila community</td>
<td>Subtidal muds</td>
<td>Fluvial muds and sands</td>
<td>Intertidal muds</td>
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<td>Ruppia community</td>
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<td>1,672±347</td>
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<tr>
<td>Total</td>
<td>29.9</td>
<td>164.8±18.0</td>
<td>102.7±102.7</td>
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Wallis Lake

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<th>Subtidal sands</th>
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<th>Halophila community</th>
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<td>12.5±12.5</td>
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<td>Fluvial muds and sands</td>
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<td>Depositional mud basin</td>
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<td>Macroalgae</td>
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<td>7.8±0.8</td>
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<tr>
<td>Total</td>
<td>90.5</td>
<td>593.5±32.8</td>
<td>317.5±317.5</td>
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Table 3. Annual nitrogen budget for the Hastings River Estuary, Camden Haven and Wallis Lake.

<table>
<thead>
<tr>
<th></th>
<th>Hastings</th>
<th>Camden Haven</th>
<th>Wallis Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inputs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Point Source (t N y(^{-1}))</td>
<td>0.1±0.0</td>
<td>0.0±0.0</td>
<td>0.0±0.0</td>
</tr>
<tr>
<td>Atmosphere (t N y(^{-1}))</td>
<td>9.6±9.6</td>
<td>16.3±16.3</td>
<td>41.5±41.5</td>
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<tr>
<td>Diffuse (t N y(^{-1}))</td>
<td>299.5±299.5</td>
<td>60.1±60.1</td>
<td>48.8±48.8</td>
</tr>
<tr>
<td>Missing N (t N y(^{-1}))</td>
<td></td>
<td>192.1</td>
<td>826.1</td>
</tr>
<tr>
<td><strong>Outputs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burial (t N y(^{-1}))</td>
<td>32.4±32.4</td>
<td>102.7±102.7</td>
<td>317.5±317.5</td>
</tr>
<tr>
<td>Net denitrification (t N y(^{-1}))</td>
<td>87.0±8.1</td>
<td>164.8±18.0</td>
<td>593.5±32.8</td>
</tr>
<tr>
<td>Fisheries (t N y(^{-1}))</td>
<td>0.9±0.9</td>
<td>1.0±1.0</td>
<td>5.4±5.4</td>
</tr>
<tr>
<td>Ocean Export (t N y(^{-1}))</td>
<td>188.9</td>
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Table 4. Sensitivity analysis on the nitrogen budgets for Camden Haven and Wallis Lake.

<table>
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<th>Nitrogen budget term adjusted</th>
<th>Net ocean exchange (t N y(^{-1}))</th>
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<tbody>
<tr>
<td></td>
<td>Camden Haven</td>
</tr>
<tr>
<td>Error adjusted down</td>
<td>Error adjusted up</td>
</tr>
<tr>
<td>Diffuse</td>
<td>131.9</td>
</tr>
<tr>
<td>Atmosphere</td>
<td>175.7</td>
</tr>
<tr>
<td>Burial</td>
<td>294.7</td>
</tr>
<tr>
<td>Net denitrification</td>
<td>210.1</td>
</tr>
<tr>
<td>Fisheries</td>
<td>193.1</td>
</tr>
</tbody>
</table>

The sensitivity analysis was done by adjusting each of the terms in the budget (e.g. overall N burial) up or down by their estimated error, determine if the overall conclusions derived from the budget changed.
Fig. 1. Nitrogen burial rates in the Hastings River Estuary, Camden Haven and Wallis Lake. Only surface nitrogen burial rates were available for the sub-tidal muds in the Hastings River Estuary and Camden Haven and the Depositional Mud Basin in Wallis Lake.

Fig. 2. Nitrogen burial in the seagrass communities versus (a) respiration (Maher and Eyre 2011), and (b) net primary production (Maher and Eyre 2011), and (c) net denitrification versus burial in the seagrass communities, in the Hastings River Estuary, Camden Haven and Wallis Lake. The circled outlier in Fig. 2b is a *Ruppia* community in Wallis Lake and was excluded from the regression. This habitat is located at the upper edge of the other seagrass communities and collects at large amount of seagrass wrack. As such, in situ production is not reflective of the amount of N that is buried.

Fig. 3. Nitrogen budgets for the Hastings River Estuary, Camden Haven and Wallis Lake.

Fig. 4. The fraction of the total nitrogen input that is denitrified as a function of flushing time. The lower regression is through data from 10 coastal systems from around the world (after (Nixon et al. 1996) with the shallow Ochlockonee Bay excluded). The upper regression is through shallow and oligotrophic coastal systems with extensive seagrass habitats (this study; (Smyth et al. 2012); (Seitzinger 1987), data recalculated in (Nixon et al. 1996); (An and Joye 2001); (Eyre et al. 2011). The two regressions are significantly different (p<0.01).
Figure 1

Wallis Lake

Camden Haven

Hastings

- Posidonia community
- Depositional mud basin
- Ruppia community
- Intertidal muds
- Halophila community
- Subtidal muds/degraded Halophila
- Zostera community
- Subtidal muds

Burial (g N m$^{-2}$ yr$^{-1}$)
Figure 2

(a) Average N Burial (g N m⁻² yr⁻¹) vs. Respiration (μmol O₂ m⁻² h⁻¹)

(b) Average N Burial (g N m⁻² yr⁻¹) vs. Net Productivity (μmol O₂ m⁻² h⁻¹)

(c) Average N Burial (g N m⁻² yr⁻¹) vs. Net Denitrification (g m⁻² yr⁻¹)

- Camden Haven Ruppia
- Halophila
- Posidonia
- Zostera
- Wallis Lake Ruppia

- r² = 0.74
- r² = 0.69
- r² = 0.87
- r² = 0.95
Figure 3

Hastings

Denitrification 87.0 t N yr\(^{-1}\)
(4.7 t N km\(^{-2}\) yr\(^{-1}\))

Point Source 0.1 t N yr\(^{-1}\)

Atmosphere 9.6 t N yr\(^{-1}\)
(0.5 t N km\(^{-2}\) yr\(^{-1}\))

Groundwater ?

Ocean Exchange 188.9 t N yr\(^{-1}\)

River

Burial 32.4 t N yr\(^{-1}\)
(1.7 t N km\(^{-2}\) yr\(^{-1}\))

N-Fixation ?

309.5 t N yr\(^{-1}\)
(16.1 t N km\(^{-2}\) yr\(^{-1}\))

Camden Haven

Denitrification 164.8 t N yr\(^{-1}\)
(5.5 t N km\(^{-2}\) yr\(^{-1}\))

Atmosphere 16.3 t N yr\(^{-1}\)
(0.5 t N km\(^{-2}\) yr\(^{-1}\))

Groundwater ?

River

Burial 102.7 t N yr\(^{-1}\)
(3.4 t N km\(^{-2}\) yr\(^{-1}\))

N-Fixation ?

Ocean Exchange 192.1 t N yr\(^{-1}\)
(6.4 t N km\(^{-2}\) yr\(^{-1}\))

Wallis Lake

Denitrification 593.5 t N yr\(^{-1}\)
(6.6 t N km\(^{-2}\) yr\(^{-1}\))

Atmosphere 9.6 t N yr\(^{-1}\)
(0.5 t N km\(^{-2}\) yr\(^{-1}\))

Groundwater ?

River

Burial 317.5 t N yr\(^{-1}\)
(3.5 t N km\(^{-2}\) yr\(^{-1}\))

N-Fixation ?

Ocean Exchange 826.1 t N yr\(^{-1}\)
(39.1 t N km\(^{-2}\) yr\(^{-1}\))
Figure 4