Denitrification efficiency for defining critical loads of carbon in shallow coastal ecosystems

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Abstract Denitrification efficiency [DE; ($N_2 - N$/($DIN + N_2 - N$) × 100%)] as an indicator of change associated with nutrient over-enrichment was evaluated for 22 shallow coastal ecosystems in Australia. The rate of carbon decomposition (which can be considered a proxy for carbon loading) is an important control on the efficiency with which coastal sediments in depositional mud basins with low water column nitrate concentrations recycle nitrogen as N_2. The relationship between DE and carbon loading is due to changes in carbon and nitrate (NO_3) supply associated with sediment biocomplexity. At the DE optimum (500–1,000 μmol m^{-2} h^{-1}), there is an overlap of aerobic and anaerobic respiration zones (caused primarily by the existence of anaerobic micro-niches within the oxic zone, and oxidized burrow structures penetrating into the anaerobic zone), which enhances denitrification by improving both the organic carbon and nitrate supply to denitrifiers. On either side of the DE optimum zone, there is a reduction in denitrification sites as the sediment loses its three-dimensional complexity. At low organic carbon loadings, a thick oxic zone with low macrofauna biomass exists, resulting in limited anoxic sites for denitrification, and at high carbon loadings, there is a thick anoxic zone and a resultant lack of oxygen for nitrification and associated NO_3 production. We propose a trophic scheme for defining critical (sustainable) carbon loading rates and possible thresholds for shallow coastal ecosystems based on the relationship between denitrification efficiency and carbon loading for 17 of the 22 Australian coastal ecosystems. The denitrification efficiency "optimum" occurs between carbon loadings of about 50 and 100 g C m^{-2} $year^{-1}$. Coastal managers can use this simple trophic scheme to classify the current state of their shallow coastal ecosystems and for determining what carbon loading rate is necessary to achieve any future state.

Keywords Carbon loading · Critical loads · Eutrophication · Nutrient enrichment · Trophic state · Indicator · Threshold

Introduction

Eutrophication associated with nutrient over-enrichment is a global problem in shallow coastal ecosystems

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(Nixon, 1995). General conceptual models are available that show the response of coastal systems to nutrient enrichment (Cloern, 2001; Kemp et al., 2005) and central to these models is the importance of benthic–pelagic coupling in shallow systems. In brief, coastal systems with small nutrient loads typically have low pelagic productivity and low light attenuation in the water column (Nielsen et al., 2002). These oligotrophic systems support a diverse range of benthic habitats and communities (e.g., seagrass, benthic microalgae) which retain nitrogen in microbial and metazoan biomass and grazing of these communities represents a flow of nitrogen up the food chain (Eyre & Ferguson, 2005). Little nitrogen is recycled from the benthic system to the water column, with most of the benthic nitrogen load lost through denitrification and/or passed up the food chain. As nutrient loads increase there is an associated increase in pelagic productivity and an increase in light attenuation in the water column (Nielsen et al., 2002). The decrease in light reaching the sediment surface results in a loss of benthic habitats (e.g., seagrass and benthic microalgae; Short & Wyllie-Echeverria, 1996) and less nitrogen flowing up the food chain. Increased organic loading from phyto-detritus leads to an increase in benthic carbon decomposition and oxygen consumption, with more nitrogen recycled to the water column as ammonium and less nitrogen lost to the atmosphere via denitrification (Kemp et al., 1990). The combination of an increased benthic flux of ammonium and less nitrogen flowing up the food chain results in a negative feedback loop with the stimulation of more pelagic production. These bottom-up changes have flow-on effects that alter the structure of higher trophic levels such as fish and invertebrate communities (Kemp et al., 2005).

To be able to effectively manage nutrient over-enrichment of coastal systems, environmental managers need criteria to define critical (sustainable) nutrient loads. Since excess nutrients disrupt the delicate balance between carbon production and metabolism in coastal systems, management criteria are probably best based on carbon loading rates rather than loadings of inorganic nutrients (Nixon, 1995). In shallow coastal systems, pelagic and benthic compartments are tightly coupled and much of the carbon production and metabolism occurs in the sediments. As such, sediments and benthic communities are probably the most sensitive part of the coastal ecosystem to nutrient enrichment, making them ideally suited as an indicator of change and for defining management criteria such as critical (sustainable) carbon loading rates. Benthic denitrification is particularly important with respect to nutrient enrichment because it permanently removes fixed nitrogen and, as such, counteracts the processes of nitrogen over-enrichment (commonly the limiting nutrient). More important than the actual denitrification rate is the percentage of the total inorganic nitrogen released from the sediments as di-nitrogen gas (N_2), which can be expressed by the term denitrification efficiency [DE; ($N_2 - N/(DIN + N_2 - N) \times 100\%$)] (Berelson et al., 1998; Eyre & Ferguson, 2002). Because of the link among carbon loading and decomposition, oxygen consumption, and coupled nitrification–denitrification, the DE of shallow coastal systems should decrease as the carbon loading increases, making DE useful for defining critical loads (Eyre & Ferguson, 2002). The purpose of this article is to demonstrate how the DE of shallow coastal systems changes as carbon loading rates change and to use these changes in DE for defining critical loads.

Materials and methods

Data from 22 Australian coastal systems were used in this study (Table 1; Fig. 1). These systems covered a range of different trophic states from oligotrophic to hypertrophic, each of the seven major geomorphic types of Australian estuaries (Harris & Heap, 2003), as well as artificial ponds, and a range of climate zones from temperate to tropical. With the exception of Port Phillip Bay (Berelson et al., 1998), the methods used for the measurement of the benthic ΣCO_2, dissolved inorganic nitrogen (DIN), and N_2 fluxes in all the systems were similar. Details of these methods are given in the published studies (Table 1) and similar methods were used in the unpublished studies. In brief, all fluxes were measured in plexiglass cores (95 mm internal diameter), except for Heron Island Sands, Southern Moreton Bay Sands, and two sites in Southern Moreton Bay where chambers were used. Cores and chambers were pre-incubated for 24 h and then incubated over a 24-h dark–light cycle (only the dark data were used in this study). Typically, three samples were taken during the dark for ΣCO_2 (pH and alkalinity), DIN (flow

Table 1 Shallow coastal ecosystems used in this study and the total number of core/chamber incubations, the number of sites studied, and the frequency of study for each system

Location	Total number of cores/chambers	Sites	Frequency	Source
Bramble Bay	9	3	Summer, Winter	Ferguson et al. (2007)
Bremer River	7	4	Summer	Cook et al. (2004)
Brunswick Estuary	74	1	Monthly for 2 years	Eyre & Ferguson (2005)
Cairns Prawn Effluent Pond	6	2	Summer	Unpubl. data
Cairns Prawn Grow-out Pond	6	2	Summer	Unpubl. data
Curl-Curl Lagoon	8	4	Summer, Winter	Eyre & Ferguson (2002)
Deception Bay	216	6	3-Monthly for 18 months	Ferguson & Eyre (2007)
Dee Why Lagoon	8	4	Summer, Winter	Eyre & Ferguson (2002)
Edmunds Bay	4	1	Summer	Eyre & Ferguson (2002)
Fennell Bay	4	1	Summer	Eyre & Ferguson (2002)
Great Sandy Straits	6	2	Summer	Unpubl. data
Kooroora Bay	4	1	Summer	Eyre & Ferguson (2002)
Heron Island	27	1	Summer	Eyre et al. (2008); Glud et al. (2008)
Manly Lagoon	8	4	Summer, Winter	Eyre & Ferguson (2002)
Mary River	9	3	Summer	Unpubl. data
Mission Beach Prawn Effluent Pond	6	2	Summer	Unpubl. data
Mission Beach Prawn Mangrove Treatment Pond	6	2	Summer	Unpubl. data
Mud Pit, Moreton Bay	9	3	Summer, Winter	Ferguson et al. (2007)
Ord River	15	5	Summer	Unpubl. data
Port Phillip Bay				Berelson et al. (1998)
Southern Moreton Bay	40	8	Summer, Winter	Ferguson et al. (2004)
Southern Moreton Bay Sands	30	1	Summer	Ferguson et al. (2004)
Waterloo Bay	6	2	Summer, Winter	Ferguson et al. (2007)

injection analysis), and N_2 (membrane inlet mass spectrometer with oxygen removal; Eyre & Ferguson, 2002) analysis and the concentration changes over time were used to calculate flux rates. In Port Phillip Bay, N_2 was estimated using measured dissolved inorganic nitrogen and carbon efflux ratios and assuming Redfield stoichiometry, with some direct N_2 measurements (Berelson et al., 1998). Denitrification efficiency (DE) was expressed as the proportion of the total inorganic nitrogen released as N_2 ($N_2 - N/(DIN + N_2 - N) \times 100\%$) (Eyre & Ferguson, 2002). Only dark ΣCO_2, DIN, and N_2 flux rates were used and flux rates less than zero were excluded. DE was calculated for individual cores before averaging. For individual sites and sampling times, the DE and ΣCO_2 efflux are typically the average of triplicate core or chamber incubations. Sites and times were averaged for the DE of individual systems; the number of core or chamber incubations averaged is given in Table 1. A Loess curve was fitted to the data using SPSS v11. The Loess curve uses iterative weighted least squares to determine values that best fit the data. An Epanechinov kernel was used to smooth the data.

Results

The Loess curve fitted to the system average data indicates that the maximum DE occurred between ΣCO_2 efflux rates of about 500 and 1,500 μmol m^{-2} h^{-1} (Fig. 2). DE then decreased rapidly to less than 10% at ΣCO_2 effluxes above about 6,000 μmol m^{-2} h^{-1}. Permeable quartz (Southern

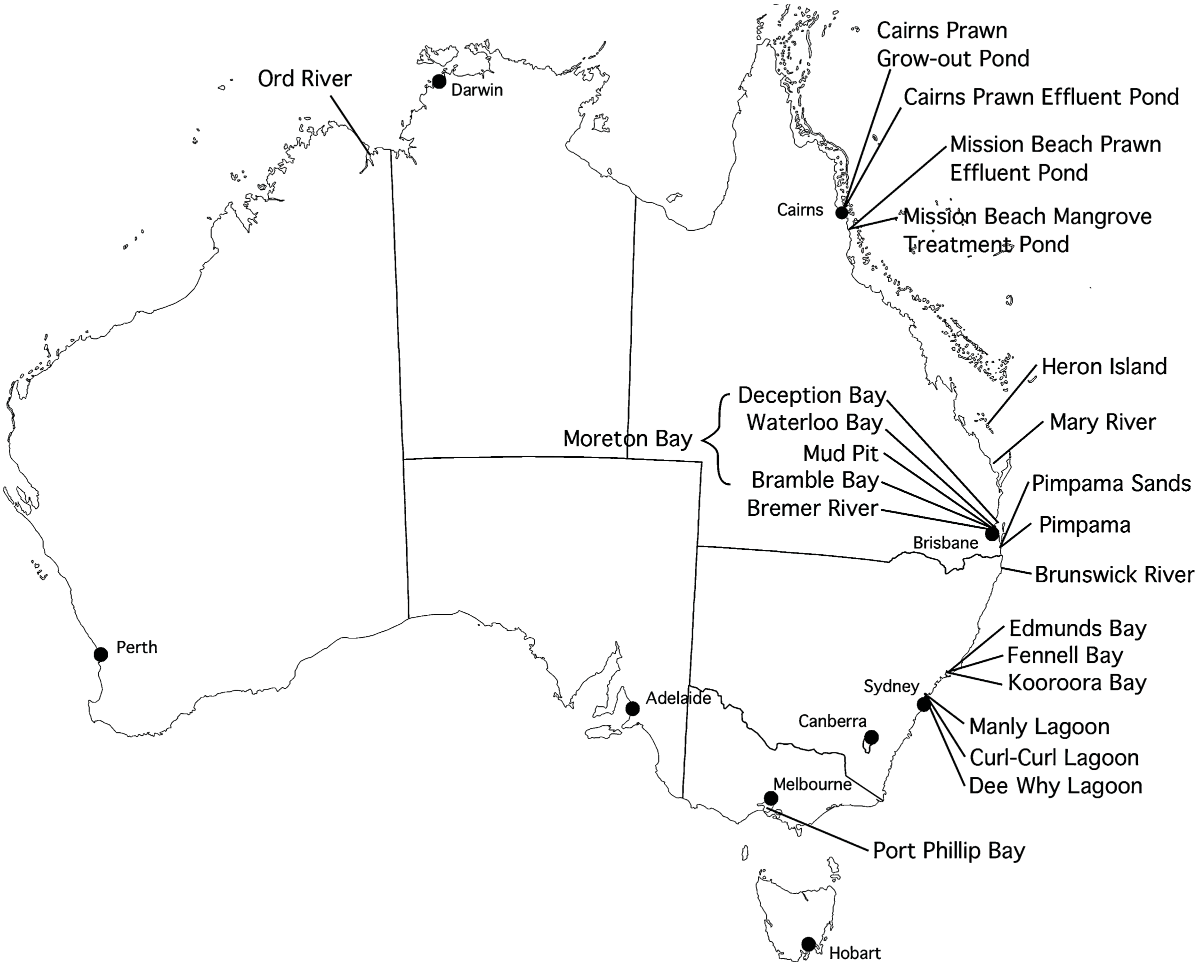

Fig. 1 Locations of the systems studied. The 22 systems studied covered a range of different trophic states from oligotrophic to hypertrophic, each of the seven major geomorphic types of Australian estuaries, as well as artificial ponds, and a range of climate zones from temperate to tropical

Moreton Bay Sands) and carbonate sands (Heron Island), seagrass sites (Kooroora Bay, Waterloo Bay) and the Bremer River were outliers to this general relationship, with a much higher DE for a given ΣCO_2 efflux.

The Loess curve fitted to the individual site data was similar to the system average curve, showing that the maximum DE occurred between ΣCO_2 efflux rates of about 500 and 1,000 μmol m^{-2} h^{-1} (Fig. 3). However, it also suggests that DE decreased on either side of the maximum, not just with increasing ΣCO_2 effluxes. The relationship between DE and ΣCO_2 efflux was quite variable between individual systems. In some systems, the relationship between DE and ΣCO_2 efflux for individual sites (e.g., Port Phillip Bay) and sample times (e.g., Bramble Bay) followed the Loess curve (Fig. 3). On the other hand, in other systems, the relationship between DE and ΣCO_2 efflux for individual sites (e.g., Southern Moreton Bay) and sample times (e.g., Brunswick Estuary) showed little resemblance to the Loess curve (Fig. 3).

Discussion

Since much of the organic matter supplied to shallow coastal ecosystems is decomposed in the sediments, benthic ΣCO_2 efflux is a useful proxy for organic

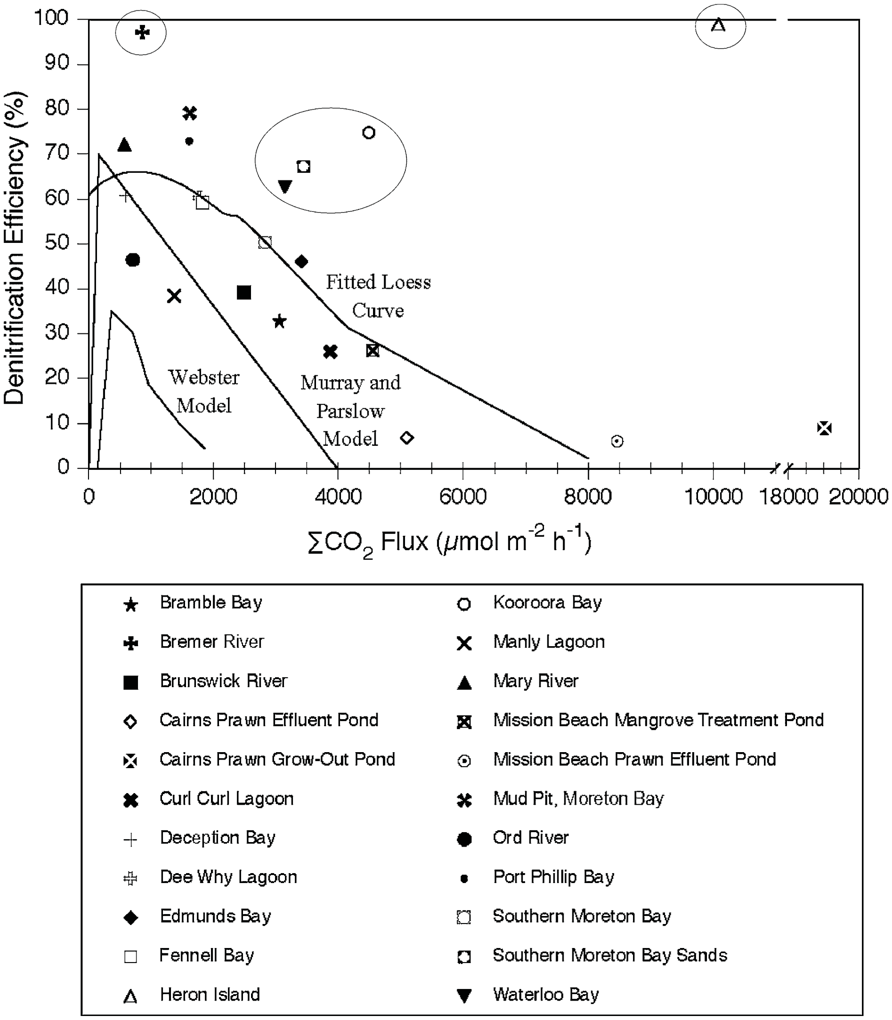

Fig. 2 System average denitrification efficiency (DE) as a function of ΣCO_2 efflux for 22 shallow coastal Australia systems. A Loess curve has been fitted to the data which uses iterative weighted least squares to determine values that best fit the data. The mechanistic modeled DE versus respiration curves of Murray & Parslow (1997) and Webster (2001) are also shown. *Circled points* are outliers to the Loess curve

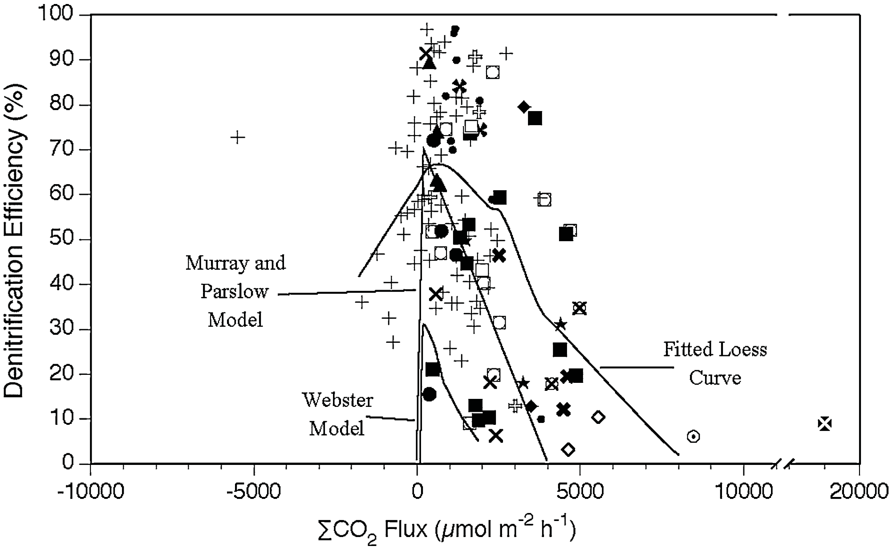

Fig. 3 Denitrification efficiency averaged for individual sites and sample times as a function of ΣCO_2 efflux for 17 shallow coastal Australia systems (outliers from Fig. 2 were excluded). A Loess curve has been fitted to the data. The mechanistic modeled DE versus respiration curves of Murray & Parslow (1997) and Webster (2001) are also shown. For symbols legend, see Fig. 2

carbon loading (both autochthonous and allochthonous), although part of the flux may be from the dissolution of $CaCO_3$ (see Exceptions to the Rule). In addition, benthic ΣCO_2 efflux is an easier measurement to make than quantifying both benthic and pelagic productivity and allochthonus carbon loads. The impact of carbon loading on DE in this study (i.e., above a carbon decomposition rate (threshold) of about 1,000 to 1,500 μmol CO_2 m^{-2} h^{-1}, there was a large decrease in DE) was similar to that in a number of previous studies. For example, in Port Phillip Bay sediments, DE decreased rapidly above a carbon decomposition rate of 1,250 μmol CO_2 m^{-2} h^{-1} (Berelson et al., 1998), in the Bremer River sediments, above a carbon decomposition rate of 1,000 μmol CO_2 m^{-2} h^{-1} (Cook et al., 2004), and in the sediments of warm temperate lagoons, above a carbon decomposition rate of 1,500 μmol CO_2 m^{-2} h^{-1} (Eyre & Ferguson, 2002); all of these data sets are included in this study. Blackburn & Blackburn (1993) also noted a drop in coupled nitrification–denitrification rates at DOC loads above about 1,500 μmol m^{-2} h^{-1}. In an experimental system with different organic loadings, the DE was highest at a carbon decomposition rate of 890 μmol CO_2 m^{-2} h^{-1} and decreased to near zero at a carbon decomposition rate of 1,350 μmol CO_2 m^{-2} h^{-1} (Sloth et al., 1995). There clearly appears to be an optimum carbon loading that managers need to maintain to maximize DE in shallow coastal systems.

The DE versus ΣCO_2 efflux relationship of low DE at low carbon loadings, increasing to a maximum DE between a carbon loading of about 500 and 1,000 μmol CO_2 m^{-2} h^{-1} (optimum) and then decreasing rapidly at higher carbon loadings can be explained by changes in carbon and NO_3 supply associated with sediment biocomplexity. At the DE optimum, there is probably an overlap of aerobic and anaerobic respiration zones, caused primarily by the existence of anaerobic micro-niches within the oxic zone, and oxidized burrow structures penetrating into the anaerobic zone, which enhances denitrification by improving both the organic carbon and NO_3 supply to denitrifiers (Middelburg et al., 1996; Kristensen, 2000; Ferguson & Eyre, 2007). Although there is little direct evidence of anoxic microsites, recent studies suggest that short-lived anoxic micro-niches can evolve in marine snow aggregates (Glud, 2008). On either side of the DE optimum zone (500–1,000 μmol CO_2 m^{-2} h^{-1}), there is most likely a reduction in denitrification sites as the sediment loses its three-dimensional complexity. At low organic carbon loadings, a thick oxic zone (Blackburn & Blackburn, 1993) with low macrofauna biomass (Herman et al., 1999) would exist, resulting in limited anoxic sites for denitrification. In contrast, at high carbon loadings, there would be a thick anoxic zone and a resultant lack of oxygen for nitrification and associated NO_3 production (Kemp et al., 1990). The lack of coupled nitrification–denitrification sites at higher carbon loadings is exacerbated by the reduction or change in macrofauna biomass and species due to hypoxia (Gray et al., 2002) and possibly an inhibition of nitrification by exposure to sulfide (Joye & Hollibaugh, 1995). Increased organic loading has also previously been shown to decrease nitrification and denitrification in an experimental system, most likely also due to a decrease in oxygen supply and inhibition by sulfide (Caffrey et al., 1993). In addition, dissimilatory nitrate reduction to ammonium (DNRA) may become quantitatively more important as the organic matter loading increases (Kaspar et al., 1988; Gilbert et al., 1997; Christensen et al., 2000).

The influence of sediment biocomplexity on DE is further illustrated by changes in macrofauna biomass (Ferguson & Eyre, 2007; unpublished data). For example, the biomass of burrowing deposit-feeding macrofauna (e.g., bristle crabs and bivalves) in Deception Bay (Fig. 4b, c; Ferguson & Eyre, 2007; unpublished data) shows the same pattern as DE (Fig. 4a), increasing to a maximum at a carbon loading of about 1,000 μmol CO_2 m^{-2} h^{-1} (optimum) and then decreasing at higher carbon loadings. This results in a more two-dimensional sediment profile with less effective overlap between nitrification and denitrification zones and reduced areal extent of oxic-anoxic boundaries (Ferguson & Eyre, 2007; unpublished data).

The shape of our Loess curve of DE versus ΣCO_2 efflux (Figs. 2, 3) is consistent with the shape of simple mechanistic modeled relationships of DE versus respiration (Murray & Parslow, 1997; Webster, 2001; see Figs. 2, 3). However, the Webster model had a maximum DE of only 34% at a respiration rate of 18 mg N m^{-2} day^{-1} (ΣCO_2 efflux of 350 μmol m^{-2} h^{-1}) and the Murray and Parslow model had a maximum DE of 70% at a respiration

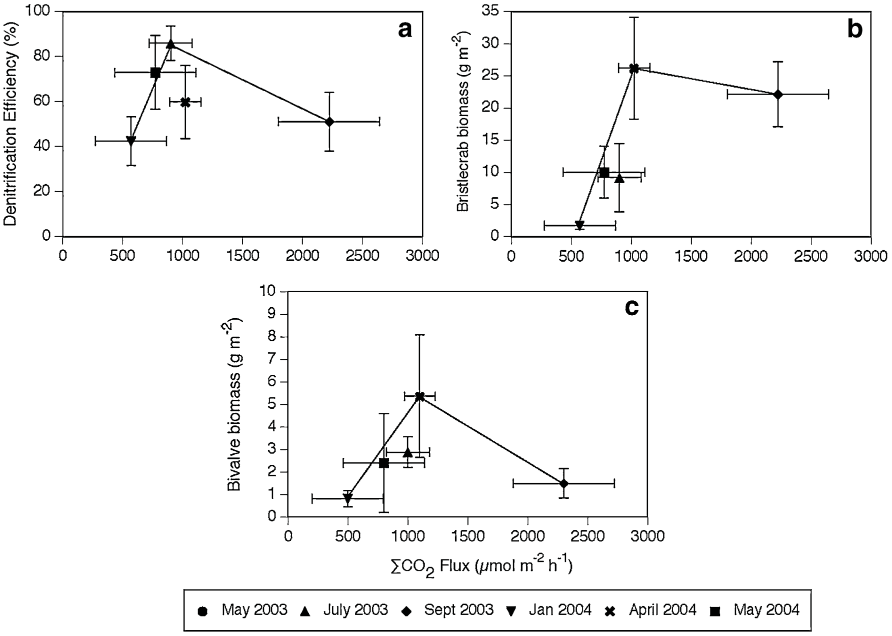

Fig. 4 **a** Denitrification efficiency (site averages), **b** bristle crab biomass, and **c** bivalve biomass in Deception Bay as a function of ΣCO_2 efflux ($n = 6 \times 36$; Ferguson & Eyre, 2007; unpublished data)

rate of 10 mg N m^{-2} day^{-1} (ΣCO_2 efflux of 200 μmol m^{-2} h^{-1}). The maximum modeled DE occurred at lower respiration rates than our measured DE most likely because the models used net diel respiration, whereas our analysis only used dark respiration rates (Murray & Parslow, 1997). Some individual measurements of DE were also much higher than the modeled predicted maximum DE, most likely because the bioturbation and bioirrigation behavior of the macro- and meiofauna was poorly presented in the models and hence coupled nitrification–denitrification would be underestimated (Webster, 2001; also see above). Overall, the Murray and Parslow model average maximum DE of 70% compared well to the measured median DE of about 68%. The next step is to use our extensive field measurements to conceptualize, calibrate, and verify a more detailed mechanistic benthic model that more realistically includes the effects of macrofauna.

Exceptions to the rule

Despite moderate carbon decomposition rates in the Bremer River and high carbon decomposition rates in the permeable quartz sands (Southern Moreton Bay Sands), carbonate sands (Heron Island), and seagrass sites (Kooroora Bay, Waterloo Bay), they all had high DE (Fig. 2). Seagrass beds appear to be able to maintain high rates of coupled nitrification–denitrification even under high carbon loadings (Eyre & Ferguson, 2002) probably due to the transport of oxygen down to the rhizosphere (Frederiksen & Glud, 2006). Denitrification rates as high as 412 μmol N_2 m^{-2} h^{-1} were measured in the seagrass beds. Similarly, high rates of porewater flushing enhance the downward transport of oxygen into permeable sands (Booij et al., 1991), and this probably enhances coupled nitrification–denitrification even under high respiration rates. In addition, some of the ΣCO_2 efflux in the carbonate sands would consist of $CaCO_3$, resulting in an over-estimation of the respiration rates. In systems like the Bremer River with high water column nitrate concentrations, denitrification of water column nitrate is more important than coupled nitrification–denitrification (Cook et al., 2004) and carbon loading has little impact on DE. As such, DE as an indicator of change, and for defining critical carbon loads, is most appropriately measured in the depositional mud basins of coastal systems with low water column nitrate concentrations.

Spatial and temporal variability within an individual system

Application of the system-averaged DE versus ΣCO_2 efflux relationship to an individual system requires consideration of the controlling factors at each site and for each sample period. For example, sandy and seagrass sites need to be excluded from any analysis (as discussed above) and some sample periods may also need to be excluded due to episodic increases in nitrate and an associated switch from coupled nitrification–denitrification to water column nitrate-driven denitrification (see Eyre & Ferguson, 2005, 2006). Some sites in depositional mud basins with low water column nitrate concentrations still have a low DE for a given carbon loading (e.g., Brunswick Estuary; Deception Bay; Fig. 3), suggesting that other factors may be limiting the nitrate supply (i.e., reduced coupled nitrification–denitrification). Possibilities include competition for DIN by benthic microalgae (Risgaard-Petersen, 2003) and bacterial assimilation of DIN during the decomposition of high C:N carbon (Eyre & Ferguson, 2005). In addition, the sites in the Brunswick Estuary with a low DE for a given carbon loading (Fig. 3) also had low respiratory quotients (RQ = dark ΣCO_2 efflux/dark O_2 consumption; Eyre & Ferguson, 2005), suggesting that coupled nitrification–denitrification may be inhibited due to oxygen consumption when reduced sulfides are oxidized. In the Brunswick Estuary, and other systems, low RQs typically occur in winter (see Eyre and Ferguson, 2005) under conditions of low carbon loading, suggesting that the DE versus ΣCO_2 efflux relationship may be best applied using spring and summer data when maximum carbon loadings occur.

Critical carbon loading rates

Based on the system relationship between DE and carbon loading for 17 of the 22 Australian coastal ecosystems (i.e., sands, seagrasses and Bremer River excluded; Fig. 2), the authors propose a trophic scheme for defining critical (sustainable) carbon loading rates for shallow coastal ecosystems (Fig. 5; Table 2). Oligotrophic systems have a carbon loading rate of less than about 200 g C m^{-2} $year^{-1}$ (2,000 μmol CO_2 m^{-2} h^{-1}) and are defined by a median DE of 68%; although DE did start to decrease above a carbon loading of about 150 g C m^{-2} $year^{-1}$ (1,500 μmol CO_2 m^{-2} h^{-1}), the median DE is similar to the curve fitted and previously modeled maximum DE. Mesotrophic systems have carbon loading rates between about 200 and 400 g C m^{-2} $year^{-1}$ (2,000–4,000 μmol CO_2 m^{-2} h^{-1}) and are defined by a median DE of 40%. Eutrophic systems have carbon loading rates between about 400 and 600 g C m^{-2} $year^{-1}$ (4,000–6,000 μmol CO_2 m^{-2} h^{-1}) with the median DE decreasing to 18%. Hypertrophic systems have carbon loading rates in excess of 600 g C m^{-2} $year^{-1}$ (6,000 μmol CO_2 m^{-2} h^{-1}) resulting in a very low median DE (8%). The cutoffs were arbitrarily chosen to give a systematic increase in the carbon loading ranges and a systematic decrease in DE. The cutoff for each trophic state is higher than those proposed by Nixon (1995), but Nixon's cutoffs were only based on pelagic production data and did not include benthic production and allochthonus sources.

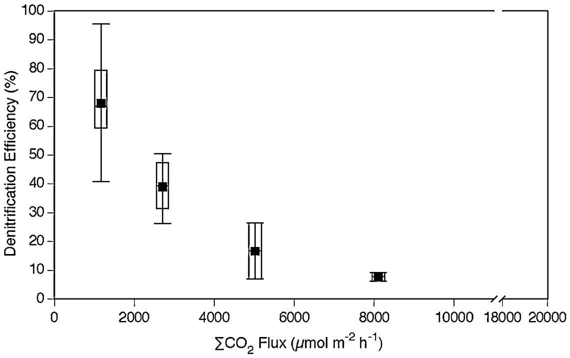

Fig. 5 Oligotrophic, mesotrophic, eutrophic, and hypertrophic box plots of system-averaged denitrification efficiencies

Table 2 A trophic scheme for shallow coastal systems based on the system relationship between denitrification efficiency (DE) and carbon loading

Trophic type	Organic carbon loading (g C m^{-2} $year^{-1}$)	Median denitrification efficiency (%)
Oligotrophic	<200	68
Mesotrophic	200–400	40
Eutrophic	400–600	18
Hypertrophic	>600	8

Coastal managers can use this simple trophic scheme to classify the current state of their shallow coastal ecosystems and to determine what carbon loading rate is necessary to achieve any future state. Benthic ΣCO_2 fluxes can be used as a reasonably simple integrated measure of organic carbon loading rates (both autochthonous and allochthonus). More importantly, because the DE relationship is exponential, it suggests that managers will be rewarded with greater return (i.e., increased denitrification for natural removal of nitrogen) for effort (i.e., reducing carbon loading rates) in the early stages of eutrophication (Eyre & Ferguson, 2002). We are currently measuring DE and ΣCO_2 effluxes in a coastal system where wastewater effluent has been removed to determine if there is any hysteresis in the DE/carbon loading relationship.

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