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PRIMARY RESEARCH PAPER

Sensitivity of dissolved organic carbon exchange and sediment bacteria to water quality in mangrove forests

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Abstract Poor water quality affects the biogeochemistry functions and the biological community structure of coastal ecosystems. In this study we investigated the effect of water quality on: (a) The exchange of dissolved organic carbon (DOC) between floodwater and mangrove forests, (b) the abundance of sediment bacteria, (c) the microbial community composition, and (d) the microbial catabolic activity. We selected six mangrove forests that were flooded by creeks with differing water qualities to test for thresholds of nutrient concentrations associated with changes in DOC dynamics and the microbial community. Our results show that in sites flooded by water high in soluble reactive phosphorus (SRP) (>20 μg l^{-1}) and NH_4^+ (>30 μg l^{-1}) the DOC concentrations in the floodwater were higher than in ebb water, suggesting DOC import by the mangroves. In contrast, in sites flooded by water low in SRP (<20 μg l^{-1}) and NH_4^+ (<30 μg l^{-1}), DOC concentrations in the floodwater were lower than in the ebb water, suggesting DOC export by the mangroves. Bacterial abundance was higher in sediments with low bulk density, high organic carbon and when flooded by water with low N:P (1–2), but the microbial composition and total catabolic activity assessed using Biolog Ecoplates™ did not differ among sites. The relationship between water quality, microbial communities and DOC exchange suggests that, at least during some periods of the year, poor water quality increases bacterial abundance and modifies DOC exchange of mangrove forests with floodwater and thus, their role in supporting near-shore productivity.

Keywords Nutrients · Wetlands · Eutrophication · Phosphorus · Moreton Bay · *Avicennia marina*

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Introduction

Poor water quality and eutrophication of estuaries has been recognised as one of the most widespread and serious environmental problem in the coastal zone (Nixon, 1995; Cloern, 2001). The addition of human-derived nutrients to the coastal zone has caused dramatic changes in coastal ecosystems, such as changes in benthic communities (Díaz & Rosenberg, 1995; Lapointe, 1997), changes in phytoplankton composition, altered trophic interactions, and increase in toxic algal blooms (Valiela et al., 1997; Cloern, 2001). More subtle effects of eutrophication include changes to the species composition of microbial

communities and biogeochemical processes, such as nutrient cycling (Nixon et al., 1986).

In the past few decades, there has been a significant increase in the delivery of human derived nutrients to wetlands, such as mangroves. Mangroves have a high capacity for nutrient retention (Valiela & Cole, 2002), and many forests are being used as sites for sewage treatment, receiving nutrient concentrations several orders of magnitude above their critical loads (Verhoven et al., 2006). Consequently, drastic changes in wetland composition and ecosystem function have occurred in many sites (Verhoven et al., 2006).

There are many processes in mangrove forests that can be affected by an increase in nutrients in the floodwater. For example, increases in nutrients can increase mangrove production, but also mortality rates (Lovelock et al., 2009). Increase in nutrient concentrations in the floodwater results in enhanced nutrient import by the mangrove forest during tidal inundation (Adame et al., 2010). Furthermore, an increase in nutrient availability can modify mangrove belowground production and the accumulation of soil volume (McKee et al., 2007), increase endophytic hervibory, and enhance growth of epiphytic pneumatophore algae (Onuf et al., 1977; Feller, 1995; Melville & Pulkownik, 2006). It is also likely that an increase in nutrients in the floodwater will increase, and probably modify, sediment bacteria communities, as has been observed in manipulated experiments in mangrove sediments (Tam, 1998) and in estuaries adjacent to polluted mangrove forest (Al-Sayed et al., 2005). Bacteria and microalgae are extremely responsive to eutrophication and are sensitive indicators of ecological change in coastal ecosystems (Paerl et al., 2003).

The modification of sediment bacterial communities is likely to have cascading effects on the sediment biogeochemistry and on the general performance of the mangrove forest in moderating nutrient and carbon exchange (Alongi, 1994; Holguin et al., 2001). For example, bacteria are highly efficient in assimilating dissolved organic carbon (DOC) from the floodwater, thus DOC assimilation is likely to be enhanced if bacterial populations increase (Benner et al., 1986, Boto et al., 1989). Understanding DOC dynamics is important as DOC can fuel the microbial loop in creeks and rivers adjacent to mangrove forests, facilitating movement of dissolved carbon to the particulate phase through bacterial assimilation and making it available to higher trophic levels (Bano et al., 1997). Thus, investigating the microbial processes influencing DOC exchange in mangrove forests will increase our understanding of pathways of carbon transfer in coastal ecosystems.

In this study we tested whether water quality affects DOC exchange during tidal inundation, bacteria abundance, microbial community composition and catabolic activity in mangrove sediments. We studied six mangrove forests in Southeast Queensland, Australia that were flooded by tidal water with different levels of water quality. We hypothesised that at sites with high levels of nutrients (poor water quality) we would observe an increase in the concentration of bacteria in the sediment, higher microbial diversity, increases in the catabolic activity of microbial communities and an increase in the net import of DOC within the mangrove forest.

Materials and methods

Study sites

Six mangrove sites in Southeast Queensland, Australia were chosen for the study (Fig. 1). The sites were chosen to reflect a gradient of floodwater quality: from relatively "good" to relatively "poor". From the six sites selected, Mooloolah River has the best water quality and Nudgee Creek the poorest (EHMP, 2010). For each site we calculated: (1) Eutrophication score (ES) based on guidelines set by Karydis (1995). Numerical scores were given to reflect the average and range of each nutrient concentration (NO_x^-–N, SRP and NH_4^+). Based on these guidelines (Karydis, 1995) we calculated a score for each nutrient, for each site. The sum of scores for all the nutrients considered resulted in a number for each site which ranged from 0 to 50. High scoring values represented sites with poor water quality, i.e. the ones with high nutrient concentrations; and (2) a Water Quality Index (WQI) which takes into consideration not only nutrient concentration (NO_x^-–N, SRP and NH_4^+), but also total suspended solids concentrations [TSS and chlorophyll *a* (Chl *a*)], which are common measurements of water quality. With this information a Principal Component Analysis (PCA) (Statistica 7.0; StatSoft In., Tulsa, USA) was performed. The principal factor (Factor 1) of variability was numerically transformed (−(Factor 1) + 2.1) to facilitate the visualisation of the index (to

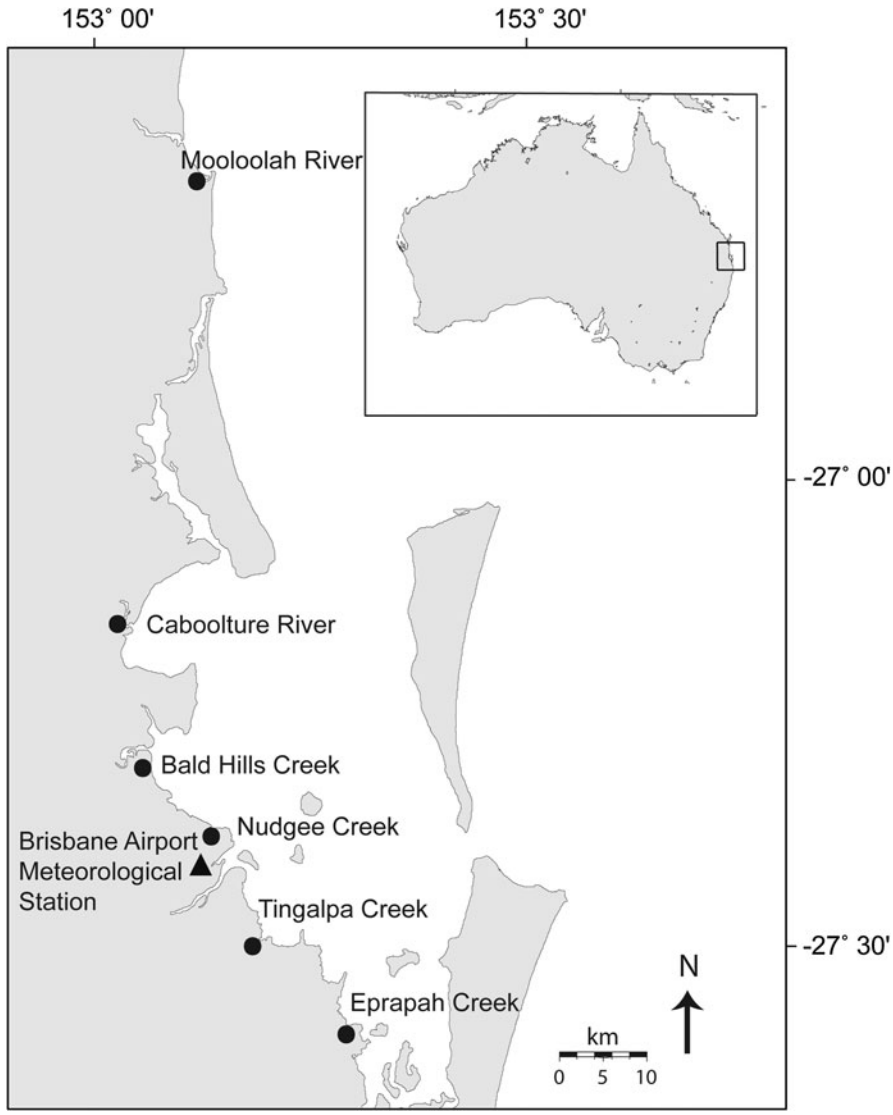

Fig. 1 Study sites in Southeast Queensland, Australia and location of the Brisbane Airport Meteorological Station

eliminate negative and decimal numbers). The WQI ranged from 1 to 4, with low values representing "good" water quality (low nutrients, TSS and Chl *a* concentrations) and high values representing relatively "poor" water quality (high nutrients, Chl *a* and TSS concentrations) (Tables 1, 2).

The sites chosen for this study are located in the Southeast Queensland biogeographic region. Each site was a creek or river within Moreton Bay, with the exception of the Mooloolah River, which lies 40 km north of the Bay (Fig. 1). The tidal regime in the region is semidiurnal with mean amplitude <2 m (Australian Estuarine Database Survey, 1998, OzCoasts, Geoscience Australia). The region is classified as subtropical, experiencing moderate temperatures all year round. The mean annual maximum temperature of the area is 25°C and the minimum is 15°C (Australian Bureau of Meteorology, Brisbane Airport Station). The climate is characterised by a dry winter (average of 44 mm from June to August) and a hot summer with rainfall (average of 356 mm from December to February). The average total annual precipitation is 996 mm (Australian Bureau of Meteorology; 1992–2006).

The shoreline of Southeast Queensland has extensive mangrove forests ($\sim$533 km^2), with *Avicennia*

Table 1 Nutrient (soluble reactive phosphorus; SRP, NO_x^-–N and NH_4^+; mg l^{-1}), Chlorophyll *a* (Chl *a;* μg l^{-1}) and total suspended solids concentrations (TSS; mg l^{-1}) (mean ± standard error) of floodwater in six estuaries in Southeast Queensland, Australia

	Salinity (ppt)	TSS (mg l^{-1})	SRP (μg l^{-1})	NO_x^-–N (μg l^{-1})	NH_4^+ (μg l^{-1})	Chl *a* (μg l^{-1})	N:P	ES	WQI	WQS 2008/2010
Mooloolah	30 ± 4	90.7 ± 13.2	27 ± 4	12 ± 19	20 ± 22	2.2 ± 0.7	1.5	27	1.0	B/B
Bald Hills	37 ± 7	113.0 ± 3.7	25 ± 9	10 ± 10	18 ± 7	3.5 ± 2.7	1.4	29	1.3	C/C−
Eprapah	35 ± 2	119.2 ± 6.2	9 ± 11	17 ± 20	28 ± 4	6.0 ± 4.2	6.3	31	1.5	C/C−
Caboolture	33 ± 1	127.4 ± 16.5	17 ± 26	41 ± 25	39 ± 14	18.8 ± 5.4	5.1	39	2.4	F/D
Tingalpa	29 ± 4	123.1 ± 9.0	32 ± 78	86 ± 68	84 ± 19	1.9 ± 1.4	5.9	42	3.2	C/C+
Nudgee	31 ± 12	134.4 ± 22.4	80 ± 8	23 ± 16	55 ± 16	5.6 ± 4.9	1.3	39	3.3	D/D−

From these data an Eutrophication Score (ES) was calculated based on guidelines by Karydis (1995), a Water Quality Index (WQI) was obtained from the principal factor of variability of a PCA, which included nutrients, TSS and Chl *a* values. Water Quality Score (WQS) were obtained from Healthy Waterways, Queensland (2008/2010) and indicate: A = excellent condition; B = good; C = fair; D = poor; F = fail. Salinity data was previously reported in Adame et al. (2010)

Table 2 Contribution of parameters (NO_x^-–N, SRP, NH_4^+, TSS and Chl *a*) obtained from a PCA describing the water quality of six sampling locations

	Factor 1	%
NO_x^-–N	0.632	17.6
SRP	0.773	26.3
NH_4^+	0.950	39.8
TSS	0.600	15.9
Chl *a*	0.084	0.3
	Factor 1	WQI
Mooloolah River	1.149	1.0
Bald Hills Creek	0.786	1.3
Eprapah Creek	0.628	1.5
Caboolture River	−0.291	2.4
Tingalpa Creek	−1.093	3.2
Nudgee Creek	−1.178	3.3

Each factor represents the percentage of variability that is explained by each parameter (NO_x^-–N, SRP, NH_4^+, TSS and Chl *a*). The Factor 1 for each site was transformed to a relative value to facilitate its visualisation (WQI = (−Factor) + 2.1). The resulting WQI was used for further analysis of the data

marina being the dominant species in our study sites and in most communities of the area (Duke, 2006). The study sites had similar forest structure with relatively sparse trees (300 trees ha^{-1}) of 5–10 m height. Three of our study sites are located within river-dominated estuaries (Mooloolah River, Caboolture River and Tingalpa Creek), and three within tidal dominated estuaries (Eprapah Creek, Bald Hills Creek and Nudgee Creek) (OzCoasts, Geoscience Australia).

Carbon exchange with the floodwater

Three tidal cycles were sampled at each of the six sites for a total of 18 tidal cycles. Sampling was conducted during the austral summer months of January to March 2008. The tidal cycles were selected to be of amplitude >2.2 m in all sites except Mooloolah river, which was sampled during tides >1.7 m, which is the minimum required to flood the entire mangrove forest (M.F. Adame, personal observation). Water was collected in front of the mangrove forest during complete tidal cycles as the water moved in and out of the forest (Adame et al., 2010). We sampled at the beginning of the flood tide, during the high tide, and at the end of the ebb tide ($n = 54$ for total organic carbon (TOC) and $n = 54$ for DOC). During field sampling, salinity of the floodwater was sampled using a hand-held refractometer (model 300011 w/ATC, SPERScientific, Scottsdale, USA) and used as a tracer of water moving in and out of the mangrove forest (Ridd et al., 1997) (see Adame et al., 2010 for further details on field methodology). The difference in concentration between the flood and ebb tide provides an approximation of carbon exchange: higher concentrations in the floodwater compared to the ebb water suggest carbon import, while lower concentrations in the floodwater compared to the ebb water suggest carbon export (Roman & Daiber, 1989; Wang et al., 2010). There are no significant underground water intrusions in the area (Abal & Dennison, 1999). Analysis of nutrient concentration in the water column over different depths was not significant ($F_{2,\ 3} = 0.41$;

$P = 0.70$) suggesting a well-mixed water column. Based on this, samples were collected at one depth: 20 cm below the water surface. Samples were collected in 200 ml nitric acid washed polyethylene terephthalate (PET) containers (Labtek Pty Ltd, Australia). For DOC, water was filtered at the moment of collection through a 0.45-μm MF filter (Millex-HA, Millipore, MA, USA). Samples were acidified in the field with 200 μL (0.1%) of HCl for preservation and kept in ice during transportation to the laboratory where they were frozen. Both TOC and DOC were analysed within the first month of collection by high temperature oxidation using an ELEMENTAR Analyser (Queensland Health Forensic and Scientific Services, Queensland Government, Australia).

Additional hydrological information (tidal height and currents) were measured during each sampling campaign. The methodology and hydrological description of each site has been described in detail in Adame et al. (2010).

Water quality parameters

In order to obtain a value of the water quality for each site sampled, we measured dissolved nutrients, Chl *a* and TSS of the floodwater for three tidal cycles at each site. For nutrient analysis water samples were collected during the summer months of January to March 2008, simultaneously with the DOC samples, and Chl *a* and TSS were collected in the summer of 2007. Nutrient concentrations in the six sampling sites have been described in detail in Adame et al. (2010). Samples were collected from 20 cm below the water surface at three points in the creek or river adjacent to the mangrove forest during the flood tide ($n = 108$ nutrients, $n = 54$ for Chl *a* and TSS). For nutrient analysis, water was filtered directly after collection through a 0.45-μm MF-filter (Millex-HA, Millipore, MA, USA) and stored in 20 ml acid washed high-density polyethylene scintillation vials. For Chl *a* and TSS, 200 ml of water was filtered in the field through pre-filtered 47 mm glass microfibre GF/C Whatman filters (1.2 μm pore size). The samples were kept on ice during transportation to the laboratory where water samples and filters for Chl *a* were frozen, and filters for TSS analysis were oven dried at 60°C.

Ammonium (NH_4^+) was analysed the same day of collection by the fluorescence method (Holmes et al., 1999), and nitrogen oxides ($NO_3^- + NO_2^-$–N = NO_x^-–N) and SRP were measured within the first 28 days from collection using colorimetric analysis with a nutrient analyser AQ-2 SEAL (A.I. Scientific, Australia; APHA methods). Chl *a* was extracted in methanol and measured in a UV–visible spectrophotometer Cintra 10e (GBC, Scientific Equipment, Victoria, Australia) using conventional methodology (Murrell & Lores, 2004). TSS were calculated by weight differences in filter papers before and after filtration (Pejrup, 1988).

Long-term measurements of nutrient concentrations (1996–2007) provided by the Queensland Environmental Protection Agency (QEPA, Queensland Government, Australia) from stations close to our sampling points were also used to compare the nutrients analysed during our sampling campaign to the long-term water quality status of the sites.

Sediment characteristics

Surface sediments (15 cm depth) were sampled within the mangrove forest adjacent to the creek or river. We sampled three replicates for each site. To calculate bulk density, cores of 50 cm^3 (3 cm in diameter) were taken and the sediment was weighed after being oven dried at 55°C. For assessment of soil organic carbon (OC), 2 g of dry sediment were combusted at 550°C for 4 h and weighted. OC was calculated as the difference between the pre- and post-combusted sample (Heiri et al., 2001). Interstitial salinity was measured with a hand-held refractometer at each site from interstitial water extracted from 30 cm deep soil using a suction device (McKee, 1993).

Bacteria abundance, microbial composition and metabolic activity

Three triplicate surface sediment samples of 2 cm depth (core of 3 cm diameter) were taken from the mangrove forest fringe at five of the six sampling sites. The sampling was conducted during November 2010, when moderate rains were falling and temperatures were high (~30°C) and similar to those when nutrients and DOC were sampled. The samples were preserved at 4°C and analysed within 7 days of collection.

Interstitial water suspensions from each sample were extracted by gentle centrifugation to settle large

soil particles. In order to enumerate live bacteria, 0.01% neutral red was added to ten aliquots of supernatant for each sample and left in the dark for 10 min. The stained bacteria were spread thinly on a hemacytometer slide and viable bacteria (stained dark red) were counted at ×1,000 magnification using a light microscope (Olympus BX41). Bacteria concentrations are expressed as number of cells per ml of supernatant and per gram of dry sediment.

In order to assess variation in bacterial community composition Biolog Ecoplates™ (BIOLOG Inc., Hayward, CA, USA) were inoculated with 130 µl of the supernatant from the samples following the manufacturer's instructions. Each plate had 32 wells that contained three replicates of 31 different carbon sources. Bacteria that can utilise carbon sources within wells in the Biolog Ecoplates™ respire and produce NADH. This in turn reduces a dye producing colour that can be quantitatively measured using a spectrometer source. Each Biolog Ecoplate™ was assigned to a soil sample. The plate was read at 595 nm on a plate reader (Bio-Rad Laboratories, Model 680 Microplate Reader, using Microplate Manager 5.2 software, PA, USA). The first reading was designated as time zero. The plates were incubated in the dark at room temperature (24°C) and absorbance values were read again at 12, 24, 36, 48, 72 and 108 h to monitor colour development, which indicated carbon utilisation. The 108-h measurements were used for data analysis. The number of carbon sources used and the development of colour intensity in each well by each of the inoculums is an indicator of species richness and diversity in the sample. Total catabolic activity was estimated as the sum of the corrected absorbance for each carbon source relative to the well containing water as the carbon source.

Data analysis

Linear regression was used to determine the relationships between DOC exchange, nutrient concentration, DOC concentration, eutrophication score, WQI, bacteria abundance, sediment characteristics and catabolic activity. The differences between flood and ebb DOC concentrations, used as a measure of DOC import or export, was tested using repeated-measures ANOVA, where our sampling points in front of the mangroves were the repeated measures over time. Normality was assessed using Shapiro–Wilk tests and bacteria numbers were log transformed to conform to normality requirements. Differences of catabolic activity among sites were tested using multivariate statistics; to test whether communities of microbes varied significantly among sites, we compared the patterns of carbon source use on the Biolog Ecoplates™ by calculating Bray Curtis similarity between samples followed by analysis of similarity (ANOSIM). Post hoc honestly significant difference (HSD) analyses were conducted to visualise differences within sites. Univariate analyses were performed using STATISTICA (8.0 StatSoft In., Tulsa, USA) and multivariate statistics were performed in Primer 6.0 (PRIMER-E Ltd, Plymouth, UK).

Results

Carbon exchange during tidal inundation

During the sampling campaign the mean concentration of TOC in floodwater was (mean ± standard error) 6.3 ± 0.9 mg l^{-1} (range of 2–12.5 mg l^{-1}) and DOC was 5.9 ± 0.9 mg l^{-1}. Most of the carbon in the water sampled was DOC, accounting for 85.1 ± 2.1% of the total carbon (Fig. 2). TOC and DOC were significantly correlated ($F_{1,\ 16} = 362.2$; $R^2 = 0.88$; $P = 0.00001$).

The concentrations of DOC in the floodwater were variable among sites. Sites with poor water quality (Nudgee Creek, Caboolture River and Tingalpa Creek) had the highest DOC concentrations (11.1 ± 0.8, 8.9 ± 0.4 and 7.5 ± 1.0 mg l^{-1}, respectively), while sites with higher water quality (Eprapah Creek, Bald Hills Creek and Mooloolah River) had the lowest (2.3 ± 0.2, 2.6 ± 0.0 and 3.2 ± 0.2 mg l^{-1}, respectively) (Fig. 2).

The exchange of DOC during tidal inundation, estimated as the difference between flood and ebb concentrations, was also variable among sites. Sites with poor water quality consistently had higher concentrations of DOC in the flood compared to the ebb water (Nudgee Creek, Tingalpa Creek and Caboolture River), suggesting DOC import. While sites with better water quality had higher DOC concentrations in the ebb compared to the floodwater (Mooloolah River, Bald Hills Creek and Eprapah Creek), suggesting DOC export (Fig. 3; Table 3). Thus, the difference in concentration between the

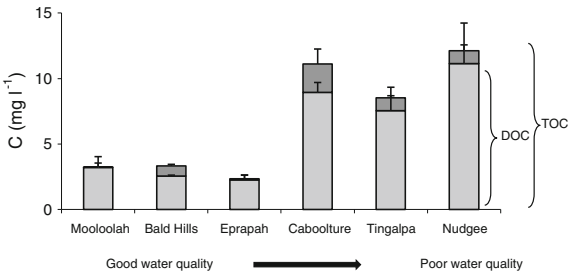

Fig. 2 Total organic carbon (TOC) and dissolved organic carbon (DOC) in the floodwater of six mangrove forests in Southeast Queensland. Values are means ± standard errors of three tidal cycles per site ($n = 18$)

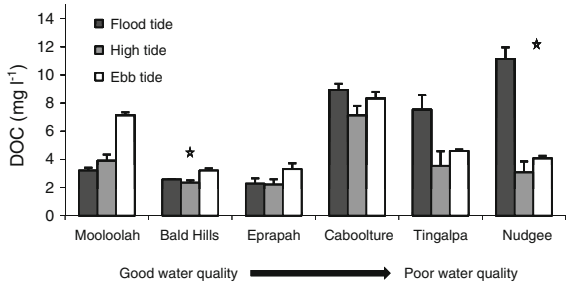

Fig. 3 Dissolved organic carbon (DOC) during flood, high, and ebb tide in six mangrove forests in Southeast Queensland. Values are means ± standard errors of three tidal cycles per site ($n = 54$)

flood and ebb water (positives for import and negative for export) was significantly correlated with the WQI ($F_{1,\ 4} = 12.2$; $R^2 = 0.75$; $P = 0.025$) (Fig. 4B) and with SRP concentration of the floodwater ($F_{1,\ 4} = 40.9$; $R^2 = 0.91$; $P = 0.003$) (Fig. 4C). The concentrations of DOC in the floodwater were also significantly correlated to the percentage of DOC export ($F_{1,\ 4} = 11.5$; $R^2 = 0.74$; $P = 0.027$). When correlating the DOC concentrations with long-term averages of nutrient data (1996–2007, QEPA), we found that long term mean NH_4^+ concentrations were significantly correlated to DOC export measured in 2008 ($F_{1,\ 4} = 19.9$; $R^2 = 0.83$; $P = 0.01$).

Sediment characteristics

Surface sediment of the mangrove forest had a mean bulk density of 0.78 ± 0.10 g cm^{-3} with a range of 0.47–1.06 g cm^{-3} for Nudgee Creek and Caboolture River, respectively. The percentage of OC in the sediment had a mean of 11.36 ± 6.38%, ranging from a site mean of 3.22% in Caboolture River to 20.72% in Nudgee Creek (Table 4).

Bacteria abundance

Bacteria concentrations had a mean of 1.2E6 ± 5.5E5 cells ml^{-1} or 2.9E7 ± 2.5E7 cells g^{-1}. Lowest values were found at the Caboolture River (0.7E6 ± 0.2E6 cells ml^{-1}, 1.0E7 ± 0.2E7 cells g^{-1}) and highest values were found at Nudgee Creek (1.7E6 ± 0.4E6 cells ml^{-1}, 6.3E7 ± 2.3E7 cells g^{-1}; Table 4), which were twice as high as the other sites. We found a significant correlation between bacteria abundance and the water quality of floodwater with higher bacteria abundance where the mangrove was flooded with water high in SRP ($R^2 = 0.36$, $F_{1,\ 13} = 8.75$ $P = 0.011$). The correlation between bacteria and SRP was driven by high bacteria abundance and high SRP concentrations of Nudgee Creek. The N:P of the floodwater was significantly correlated with bacterial abundance. Low N:P in the floodwater (1–2) was associated with high bacteria abundance (~3–6E7 cells g^{-1}), while high N:P (5–7) was associated with

Table 3 Differences in concentration of dissolved organic carbon (DOC; mg l^{-1}) (mean ± standard error) between flood and ebb tide for six mangrove forests in Southeast Queensland

	Flood-ebb (mg l^{-1})	%	df	*F*	MS	*P*
Mooloolah River	−0.70 ± 0.32	−21.9	1,4	5.88	0.74	0.07
Bald Hills Creek	−0.63 ± 0.15	−24.7	1,4	13.60	0.60	0.015*
Eprapah Creek	−1.03 ± 0.22	−45.6	1,4	4.98	1.60	0.09
Caboolture River	0.60 ± 0.55	6.7	1,4	0.88	0.40	0.54
Tingalpa Creek	2.93 ± 1.77	25.2	1,4	4.76	10.3	0.12
Nudgee Creek	7.07 ± 0.44	63.5	1,4	69.2	74.9	0.001**

Positive values represent import to the mangrove forest and negative values represent export from the mangrove forest

*$P < 0.05$; **$P < 0.01$

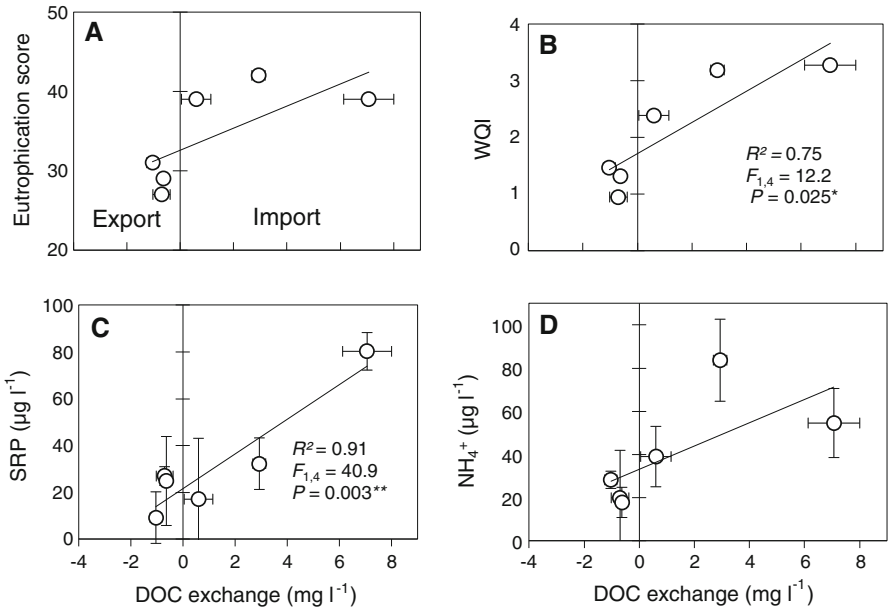

Fig. 4 Correlation between the difference in dissolved organic carbon (DOC concentration; mg l^{-1}) (flood–ebb) as an indicator of carbon exchange (positive for import, negative for export) and: **A** Eutrophication score (Karydis, 1995) (n.s.), **B** Water Quality Index (WQI) (See methods) ($F_{1,4} = 12.18$; $R^2 = 0.75$; $P < 0.05$), **C** Soluble reactive phosphorus (SRP; µg l^{-1}) ($F_{1,4} = 40.9$; $R^2 = 0.91$; $P = 0.003$), and **D** NH_4^+ (µg l^{-1}) (n.s.)

Table 4 Sediment characteristics (mean ± standard error) and bacterial concentrations in six mangrove forests that are flooded by a range of water qualities in Southeast Queensland

	Bulk density (g cm^{-3})	OC (%)	No. carbon sources	Bacteria (E6 cells ml^{-1})	Bacteria (E7 cells g^{-1} sediment)
Mooloolah	0.66 ± 0.02	9.12 ± 0.95	16 ± 5	1.5 ± 0.4	3.1 ± 0.5
Bald Hills	0.88 ± 0.13	8.57 ± 1.61	n.a.	n.a.	n.a.
Eprapah	n.a.	12.75 ± 1.43	19.3 ± 13.4	1.2 ± 0.1	2.4 ± 0.1
Caboolture	1.06 ± 0.06	3.22 ± 0.79	13.7 ± 3.7	0.7 ± 0.2	1.0 ± 0.2
Tingalpa	0.84 ± 0.08	10.60 ± 1.79	22.3 ± 4.9	1.0 ± 0.2	1.8 ± 0.4
Nudgee	0.47 ± 0.20	20.72 ± 1.78	22.7 ± 2.9	1.7 ± 0.4	6.3 ± 2.3

lower bacterial abundance (~1–2E7 cells g^{-1}; Fig. 5A). Bacterial abundance was in turn associated with DOC exchange (Fig. 5B); higher DOC import was measured at sites with high bacterial abundance. Bacteria abundance was also correlated with sediment characteristics, with higher abundance in sediments with low bulk density and rich in OC ($R^2 = 0.66$, $F_{1,9} = 17.4$, $P < 0.0001$; $R^2 = 0.64$, $F_{1,13} = 26.1$, $P = 0.0002$, Fig. 6A, B).

Microbial composition and catabolic activity

The number of carbon sources consumed by the microbial community on the Biolog Ecoplates™ can be used as an indicator of bacterial diversity while the total colour development of the Biolog Ecoplates™ is an indicator of total community catabolism. Bacterial community diversity (the number of carbon sources used at each site) was strongly correlated to the total catabolic activity at that site ($\beta = 0.54$, $R^2 = 0.75$, $P < 0.0001$, Fig. 7A) but not to bacterial abundance measured in the soils (see Table 4) ($\beta = 0$, $R^2 = 0.07$, $P = 0.37$, Fig. 7B). Soils with higher levels of OC had higher catabolic activity ($\beta = 3.03$, $R^2 = 0.30$, $P = 0.03$, Fig. 7C) than sites with low OC in the sediment, but they did not have significantly higher community diversity ($\beta = 4.2$, $R^2 = 0.23$, $P = 0.07$).

The diversity of carbon sources used by bacterial communities and the total catabolic activity did not vary significantly over sites ($F_{4,14} = 0.70$, $P = 0.60$, and $F_{4,14} = 1.66$, $P = 0.23$, Table 4; Fig. 8). A test of differences in bacterial community composition over sites also did not reveal significant differences among sites (ANOSIM, global $R = 0.08$, $P = 0.19$).

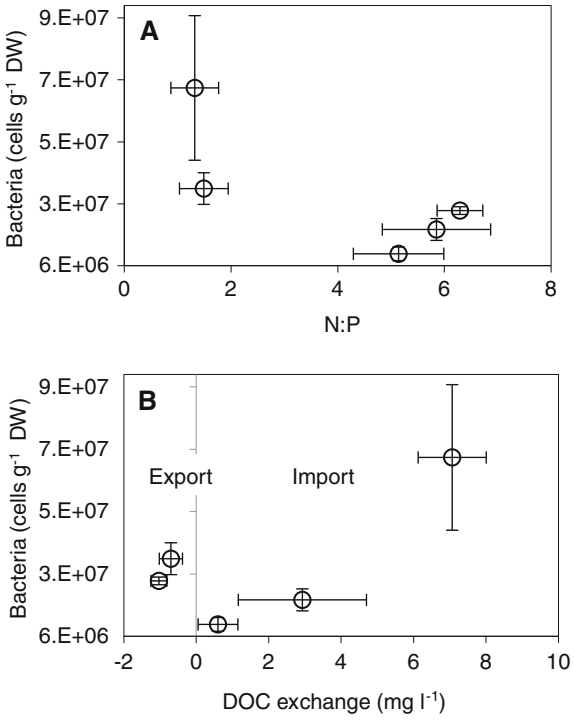

Fig. 5 Correlations between bacterial abundance (cells g^{-1} DW sediment) and **A** N:P of floodwater and **B** DOC exchange (mg l^{-1}) (flood–ebb) in five mangrove forests in Southeast Queensland. Values are means ± standard errors of three tidal cycles per site ($n = 15$) and three sediment samples per site ($n = 15$)

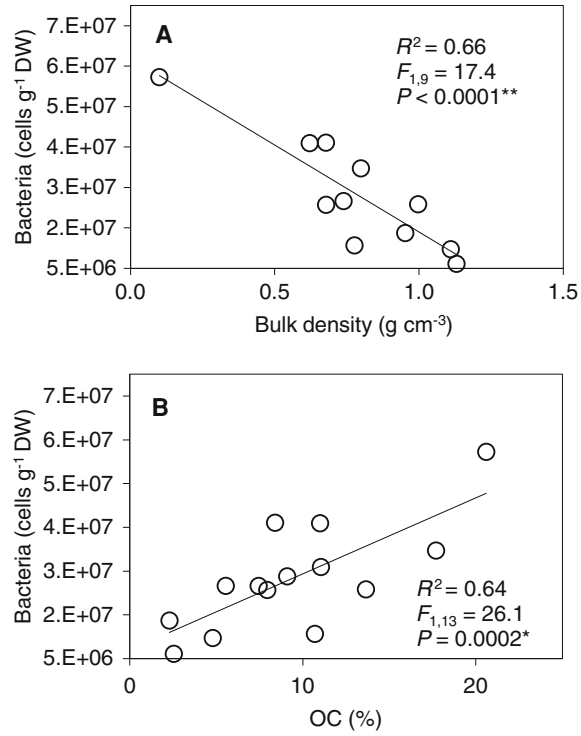

Fig. 6 Correlations between bacterial abundance (cells g^{-1} DW sediment) and **A** soil bulk density (g cm^3), and **B** soil organic carbon (OC) content (%). Each value represents a sediment sample

Discussion

Nutrient enrichment and eutrophication of aquatic systems can modify biogeochemical processes in wetlands (Vymazal, 1995). Our data suggests that a decrease in the quality of the floodwater can affect DOC exchange in mangrove forests; forests flooded by relatively poor water quality imported DOC from the floodwater, while forests flooded by high water quality exported DOC to the floodwater (Fig. 3). Additionally, high SRP concentrations and low N:P of the floodwater, and high OC in the sediment were associated with higher bacteria abundance, which was in turn associated with DOC import. The range of water quality tested in this study did not significantly affect the microbial community diversity or their catabolic activity measured under aerobic conditions using the Biolog Ecoplate™ method.

Bacteria are abundant in mangrove soils (Alongi, 1988), especially in nutrient rich environments (Kirchmann, 1990, 1994; Vymazal, 1995). Mangrove bacteria can effectively assimilate DOC (Boto et al., 1989). Thus, changes in the quality (nutrient and DOC concentrations) of the water flooding mangroves can have an important effect on bacteria and on DOC dynamics. Our data set suggests that poor water quality results in an increase of DOC import by the mangrove forest. An increase in DOC import may be a component of a positive feedback process that mitigates nutrient and carbon enrichment in the coastal zone: High nutrients and DOC concentrations in the floodwater favour high mangrove bacterial abundance, which consume nutrients and DOC, which in turn improve floodwater quality. Similar results have been shown for mangrove forests with semi-intensive shrimp farming in China, where mangroves imported almost 15% of the DOC that entered in the floodwater during a tidal cycle (Wang et al., 2010) (7–64% DOC import in our nutrient rich sites). The proposed mechanism is also supported by previous studies that have shown that in Southeast Queensland, high nutrient concentrations in the floodwater result in

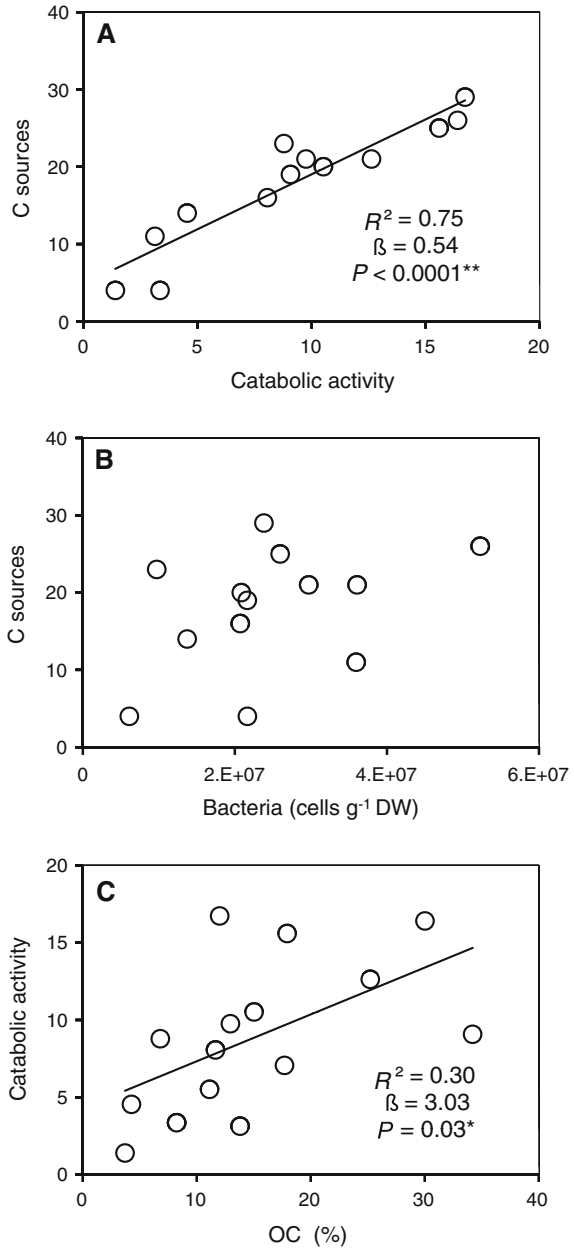

Fig. 7 The number of carbon sources used by the microbial community in three locations at five mangrove forests in Southeast Queensland as a function of: **A** Total catabolic activity of the sample (relative units) ($\beta = 0.3$, $R^2 = 0.3$, $P = 0.033$); **B** bacterial abundance in the soil (cells g^{-1} DW sediment), and **C** the total catabolic activity of the sample as a function of soil organic content ($\beta = 1.37$, $R^2 = 0.74$, $P < 0.001$). Each value represents a sediment sample

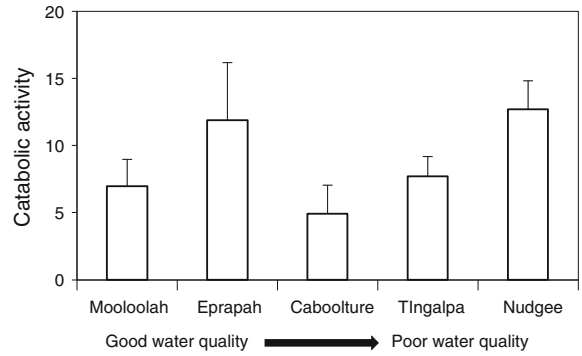

Fig. 8 Catabolic activity of sediment bacteria (in relative units) for five mangrove forests in Southeast Queensland. Values are means ± standard errors of three sediment samples per site

increased nutrient import (Adame et al., 2010), thereby supporting the idea that nutrients stimulate bacteria growth and consequently, nutrient import in mangrove sediments. Mangrove bacteria could be acting in a similar way to benthic organisms, which by removing nutrients and organic matter mitigate eutrophication of shallow aquatic ecosystems (Officer et al., 1982).

The exchange of DOC of mangrove forests with the coastal zone is highly variable (from an import of 67 g m^2 $year^{-1}$ to an export of 138 g m^2 $year^{-1}$; Adame & Lovelock, 2010 and references therein). Variation in water quality and bacteria abundance may explain some of this variability. For example, the water quality of mangrove creeks in Malaysia with intensive aquaculture was not significantly different from creeks without aquaculture (Alongi et al., 2003). It is possible that abundant bacteria in this nutrient rich environment contributes to mitigate eutrophication by consuming nutrients and DOC. Intensive bacterial consumption could also result in decreased DOC export from these mangrove forests. Another example is the Great Barrier Reef in Australia, where mangrove forests along the coast seem to retain nutrients and DOC, thereby mitigate eutrophication of adjacent corals reefs (Alongi & McKinnon, 2005). It is possible that DOC dynamics have been altered globally in areas where nutrients and DOC loads have increased above levels that occurred prior to intensive agriculture and fertiliser use. Changes of DOC dynamics are likely to have important consequences for coastal ecosystems, as DOC exchange is a key pathway of carbon coastal budgets (Dittmar & Lara, 2001). Future studies in other sites that include long-term measurements will enable generalisations of the influence of water quality on DOC export in mangrove forests around the world.

Annual DOC fluxes could potentially vary from the results presented here. Our field sampling only occurred in one season and we speculate that the effect of water quality on DOC export is stronger during periods of rainfall, when pulses of nutrients (Eyre & McKee, 2002) may stimulate fast growing bacteria and algae, and thus nutrient (Adame et al., 2010) and DOC import. Although in some sites interstitial DOC concentrations can be constant throughout the year (Boto et al., 1989), in other areas large seasonal variations have been observed (Marchand et al., 2006). Spatial and temporal factors are likely to modify DOC dynamics, such as the timing of litter fall, the extent of tidal inundation, rainfall (Lee et al., 2008), evapotranspiration (Marchand et al., 2006), and changes in bacterial composition, abundance and productivity (Alongi, 1994, Al-Sayed et al., 2005).

Increases in nutrient concentrations (especially phosphorus) in the floodwater can modify the microbial community by increasing bacterial biomass, but can also modify the biomass of phytoplankton, micro- and macroalgae (Caron, 1994, Melville & Pulkownik, 2006), which may also influence nutrient and DOC dynamics. Algae can be sources of DOC (Pregnall, 1983), as well as competing with bacterial for nutrients (Caron, 1994). The abundance of benthic algae is influenced by light availability at the sediment surface which is affected by nutrient enrichment though effects on forest canopy development and phytoplankton abundance. Thus, in mangrove forests where nutrients and C are abundant, the abundance and activity of algae could strongly influence DOC fluxes.

In our study sites, bacteria abundance was enhanced in OC rich soils and when flooded by water high in SRP and low in N:P, results that suggest that bacteria are carbon and phosphorus limited. Heterotrophic bacteria account for a large fraction of the uptake of phosphorus ($\sim$60%) and ammonium ($\sim$30%) in aquatic systems (Kirchmann, 1994). The high demand for phosphorus by bacteria is a result of the high phosphorus content in bacterial membrane (phospholipids) and as nucleic acids (Kirchmann, 1994). Bacteria in mangroves of Papua New Guinea (Alongi et al., 1993), and in Hong Kong (ammonia-oxidizing beta-proteobacteria; Huiluo et al., 2011) were observed to be phosphorus limited. It has been suggested that phosphorus limitation could be a common trait of mangrove forest bacteria (Alongi, 1991). In one of our study sites, Nudgee Creek, the association between DOC exchange, bacteria and water quality was strong. There were very high SRP concentrations in the floodwater (80 $\mu g\ l^{-1}$), very low N:P (1–2), high bacterial abundance (6.3E7 cells g^{-1}), and strong DOC import to the mangrove forest (64% import). However, in other sites, the association among water quality with bacterial abundance and DOC exchange was not so clear. For example in Mooloolah River, bacterial concentrations were relatively high (3.1E7 cells g^{-1}), N:P ratios were low (1–2) but DOC was exported from the mangroves (22% export), rather than imported. Thus, while low N:P ratios appear to favour high bacterial abundance, and high bacterial abundance seem to be associated to DOC import, the process is likely to involve multiple biotic, (e.g. microbial competition, nutrient limitation; Cotner & Wetzel, 1992; Kirchmann, 1994) and abiotic factors (e.g. hydrology, temperature, salinity; Lebo, 1990, Al-Sayed et al., 2005, Gonzalez-Acosta et al. 2005).

A change in benthic community composition is one of the most sensitive responses of coastal ecosystems to eutrophication (Jørgensen, 1996). However, over the range of water qualities tested, we did not find a significant effect on bacterial community composition, and bacterial abundance was not an indicator of community richness. Similar results have been found in Bangkok, Thailand, where microbial communities in highly nutrient polluted mangroves were not significantly different from natural ones (Wickramasinghe et al., 2008). While higher OC of sediments led to higher bacterial catabolic activity (Fig. 7A), it did not result in a more diverse soil bacterial assemblage. Thus, in our study sites the difference between a site that exports DOC and one that imports DOC appears to be bacterial abundance and not modifications of community composition.

Mangrove soils are typically saline, anoxic, acidic and frequently waterlogged. Thus, anaerobic bacterial processes have an essential role in mangrove soil metabolism (Alongi, 1994). The Biolog Ecoplates™ used to measure bacterial community diversity and catabolic activity in this study only assessed aerobic catabolism. Thus, the effect of water quality on bacterial community composition and catabolic activity of anaerobic microorganisms may reveal different results from the ones observed in this study.

The hydrology and the characteristics of tidal inundation of the mangrove forests could be an important factor for determining bacteria concentrations and DOC export. Our study sites have different hydrological characteristics, firstly, because some sites are dominated by riverine forces (Mooloolah River, Caboolture River and Tingalpa Creek) and others by tidal forces (Nudgee Creek, Bald Hills Creek and Eprapah Creek). The difference in hydrology results in differing salinity of the floodwater with mean values during our field sampling of 29–33 ppt for riverine sites and 31–37 ppt for tidal sites (Table 1), which may affect bacterial abundance, composition and DOC exchange (Al-Sayed et al., 2005). Additionally, water residence time and tidal flushing may also affect sediment–water column processes (Alongi 1988; Al-Sayed et al., 2005). From our study sites, Nudgee Creek had the lowest inundation height, shortest inundation period, and slowest tidal flows. Conversely, Eprapah Creek had the highest inundation height, longest inundation period, and fastest tidal flows (Adame et al., 2010). Although we expected that the hydrological characteristics of tidal inundation would be important in determining bacteria abundance and DOC exchange, we did not find a clear relationship among hydrology, bacterial abundance or DOC exchange.

The measured DOC concentrations in the selected estuaries for this study (5.9 ± 0.9 mg l^{-1}; 2–12.5 mg l^{-1}) are within the range of to those measured in mangrove estuaries in Andhra Pradesh, India (2.0 ± 3.0 mg l^{-1}; Bouillon et al., 2003) and Florida, US (10–20 mg l^{-1}; Twilley, 1985). The trophic states of the sites (from low mesotrophic to low eutrophic) are also comparable to other estuaries around the world that have been affected by nutrient and carbon enrichment derived from anthropogenic activities. Nutrient concentrations in the floodwater from our sampling locations during the rainy season (0.3–3 μM SRP, 0.3–3 μM NO_x^-–N and 1–5 μM NH_4^+) are similar than those found in Peninsular Malaysia (0–2 μM PO_4, 1–20 μM NO_x^-–N and 1–12 μM NH_4^+; Alongi et al., 2003) and in Southeast India (0.3–1 μM P, 1.9–5 μM NO_3^-–N and 0.1–0.2 μM NH_4^+; Ashokkumar et al., 2011). Thus, it seems plausible that conditions of nutrient enrichment in floodwater of mangrove forests around the world have resulted in modified bacteria abundance and altered DOC exchange within their coastal zones. For example, Machiwa & Hallberg's (2002) model predicted that 40% of DOC available is consumed within a mangrove affected by anthropogenic activity. In our study sites, mangroves at Nudgee and Tingalpa Creek (sites with poor water quality) imported 64 and 25% of DOC, respectively.

The effects of eutrophication and poor water quality in the coastal zone have negative consequences for the marine environment resulting in decreased light penetration to the benthos, increase in algal blooms, and declines in benthic oxygen concentrations (Cloern, 2001). The Southeast Queensland coast has had considerable human impacts in the last century that have resulted in a decrease in coastal ecosystem health of the region (Lotze et al., 2006). Mangrove forests with sediments that are rich in C and subject to high nutrient inputs in the floodwater could be important in reducing the impacts of nutrients and DOC enrichment in the marine environment.

Nutrient thresholds of change

Based on the comparison of sites with differing water qualities, we calculated approximate thresholds of the shift of DOC export to import in a mangrove forest in relation to nutrient concentrations. When SRP concentrations are lower than 20 μg l^{-1} in the floodwater DOC export from the mangrove forests is expected, while when concentrations are higher than 20 μg l^{-1}, DOC import is predicted (Fig. 4C). We also calculate that the NH_4^+ threshold of shift between import and export of DOC is approximately 30 μg l^{-1} (Fig. 4D). It is also likely that in addition to nutrient concentrations, total nutrient loads, and the seasonal variation of nutrient delivery are important in determining bacteria abundance and DOC exchange.

Currently there are no guidelines to define critical nutrient values in coastal wetlands in this region of Australia (ANZECC, 2000). For estuarine water it has been determined that nutrient concentrations should not be higher than 15 μg l^{-1} of SRP and NH_4^+. To the north of our study sites, in the Great Barrier Reef lagoon, it has been determined, based on the reference condition of the area, that wetlands should not have concentrations higher than 5-25 μg l^{-1} of SRP and 10 μg l^{-1} of NH_4^+ (ANZECC, 2000). Our estimated values of 20 μg l^{-1} for SRP and 30 μg l^{-1} for NH_4^+ in Southeast Queensland mangrove forests could be

critical thresholds of changes in bacterial abundance and DOC dynamics of mangrove forest in the region.

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References

Abal, E. G. & W. C. Dennison, 1999. Moreton Bay study: a scientific basis for the healthy waterways campaign. South East Queensland Regional Water Quality Management Strategy, Brisbane, Australia.

Adame, M. F. & C. E. Lovelock, 2010. Carbon and nutrient exchange of mangrove forests with the coastal ocean. Hydrobiologia 663: 23–50.

Adame, M. F., D. Virdis & C. E. Lovelock, 2010. Effect of rainfall and geomorphological setting in nutrient exchange in mangroves during tidal inundation. Marine and Freshwater Research 61: 1197–1206.

Alongi, D. M., 1988. Bacterial productivity and microbial biomass in tropical mangrove sediments. Microbial Ecology 15: 59–79.

Alongi, D. M., 1991. The role of intertidal mudbanks in the diagenesis and export of dissolved and particulate materials from the Fly Delta, Papua New Guinea. Journal of Experimental Biology and Ecology 149: 81–107.

Alongi, D. M., 1994. The role of bacteria in nutrient recycling in tropical mangrove and other coastal benthic ecosystems. Hydrobiologia 285: 19–32.

Alongi, D. M. & A. D. McKinnon, 2005. The cycling and fate of terrestrially-derived sediments and nutrients in the coastal zone of the Great Barrier Reef shelf. Marine Pollution Bulletin 51: 239–252.

Alongi, D. M., P. Christoffersen & F. Tirendi, 1993. The influence of forest type on microbial–nutrient relationships in tropical mangrove sediments. Journal of Experimental Biology and Ecology 171: 201–223.

Alongi, D. M., V. C. Chong, P. Dixon, A. Sasekumar & F. Tirendi, 2003. The influence of fish cage aquaculture on pelagic carbon flow and water chemistry in tidally dominated mangrove estuaries of peninsular Malaysia. Marine Environmental Research 55: 313–333.

Al-Sayed, H. A., E. H. Ghanem & K. M. Saleh, 2005. Bacterial community and some physico-chemical characteristics in a subtropical mangrove environment in Bahrain. Marine Pollution Bulletin 50: 147–155.

ANZECC, Australian and New Zealand Environment and Conservation Council and Agriculture and Resource Management Council of Australia and New Zealand, 2000. An introduction to the Australian and New Zealand Guidelines for fresh and marine water quality. National Water quality management strategy. No. 4a. Australia.

Ashokkumar, S., G. Rajaram, P. Manivasagan, S. Ramesh, P. Sampathkumar & P. Mayavu, 2011. Studies on hydrographical parameters, nutrients and microbial populations of Mullipallam, Creek in Muthupettai mangroves (southeast coast of India). Research Journal of Microbiology 6: 71–86.

Australian Bureau of Meteorology, Australian Government. www.bom.gov.au/.

Bano, N., M.-U. Nisa, N. Khan, M. Saleem, P. J. Harrison, S. I. Ahmed & F. Azam, 1997. Significance of bacteria in the flux of organic matter in the tidal creeds of the mangrove ecosystem of the Indus River delta, Pakistan. Marine Ecology Progress Series 157: 1–12.

Benner, R., E. Peele & R. Hodson, 1986. Microbial utilization of dissolved organic matter from leaves of the red mangrove, *Rhizophora mangle*, in the Fresh Creek Estuary, Bahamas. Estuarine, Coastal and Shelf Science 23: 607–619.

Boto, K. G., D. M. Alongi & A. L. J. Nott, 1989. Dissolved organic carbon–bacteria interactions at sediment-water interface in a tropical mangrove system. Marine Ecology Progress Series 51: 243–251.

Bouillon, S., M. Frankignoulle, F. Dehairs, B. Velimirov, A. Eiler, G. Abril, H. Etcheber & A. Vieira Borges, 2003. Inorganic and organic carbon biogeochemistry in the Gautami Godavari estuary (Andhra Pradesh, India) during pre-monsoon: the local impact of extensive mangrove forests. Global Biogeochemical Cycles 17: 1114.

Caron, D. A., 1994. Inorganic nutrients, bacteria, and the microbial loop. Microbial Ecology 28: 295–298.

Cloern, J. E., 2001. Our evolving conceptual model of the coastal eutrophication model. Marine Ecology Progress Series 210: 223–253.

Cotner, J. B. Jr. & R. G. Wetzel, 1992. Uptake of dissolved inorganic and organic phosphorus compounds by phytoplankton and bacterioplankton. Limnology and Oceanography 37: 232–243.

Díaz, R. J. & R. Rosenberg, 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioral responses of benthic macrofauna. Oceanography and Marine Biology Annual Review 33: 245–303.

Dittmar, T. & R. J. Lara, 2001. Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River? Evidence from long-term flux measurements. Marine Ecology Progress Series 213: 67–77.

Duke, N. C., 2006. Australia's Mangroves. The authoritative guide to Australia's mangrove plants. University of Queensland, Brisbane.

Eyre, B. D. & L. J. McKee, 2002. Carbon, nitrogen, and phosphorus budgets for a shallow subtropical coastal embayment (Moreton Bay, Australia). Limnology and Oceanography 47: 1043–1055.

Feller, I., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf mangrove (*Rhizophora mangle*). Ecology Monographs 65: 477–505.

Gonzalez-Acosta, B., Y. Bashan, N. Y. Herandez-Saavedra, F. Ascencio & G. De la Cruz-Agüero, 2005. Seasonal seawater temperature as the major determinant for populations of culturable bacteria in the sediments of an intact mangrove in an arid region. FEMS Microbiology Ecology 55: 311–321.

Heiri, O., A. F. Lotter & G. Lemcke, 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25: 101–110.

Holguin, G., P. Vazquez & Y. Bashan, 2001. The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: an overview. Biology and Fertility of Soils 33: 265–278.

Holmes, R. M., A. Aminot, R. Kérouel, B. A. Hooker & B. J. Peterson, 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 56: 1801–1808.

Huiluo, C., M. Li, Y. Hong & J.-D. Gu, 2011. Diversity and abundance of ammonia-oxidizing archaea and bacteria in polluted mangrove sediment. Systematic and applied microbiology 34: 513–523.

Jørgensen, B. B., 1996. Eutrophication in coastal marine ecosystems. American Geophysical Union, New York: 243 pp.

Karydis, M., 1995. Quantitative assessment of eutrophication: a scoring system for characterizing water quality in coastal marine ecosystems. Environmental Monitoring and Assessment 41: 233–246.

Kirchmann, D. L., 1990. Limitation of bacterial growth by dissolved organic matter in the subarctic Pacific. Marine Ecology Progress Series 62: 47–54.

Kirchmann, D. L., 1994. The uptake of inorganic nutrients by heterotrophic bacteria. Microbial Ecology 28: 255–271.

Lapointe, B. E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 45: 1119–1131.

Lebo, M. E., 1990. Phosphate uptake along a coastal plain estuary. Limnology and Oceangraphy 35: 1279–1289.

Lee, R., P. William, I. Feller, K. McKee & S. Joye, 2008. Porewater biogeochemistry and soil metabolism in dwarf red mangrove habitats (Twin Cays, Belize). Biogeochemistry 87: 181–198.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson & J. B. C. Jackson, 2006. Depletion, degradation and recovery potential of estuaries and coastal oceans. Science 312: 1806–1809.

Lovelock, C. E., M. C. Ball, K. C. Martin & I. C. Feller, 2009. Nutrient enrichment increases mortality of mangroves. PLoS ONE 4(5): e5600.

Machiwa, J. F. & R. O. Hallberg, 2002. An empirical model of the fate of organic carbon in a mangrove forest partly affected by anthropogenic activity. Ecological Modeling 147: 69–83.

Marchand, C., P. Albéric, E. Lallier-Vergès & F. Baltzer, 2006. Distribution and characteristics of dissolved organic matter in mangrove sediment pore waters along the coastline of French Guiana. Biogeochemistry 81: 59–75.

McKee, K. L., 1993. Soil physicochemical patterns and mangrove species distribution—reciprocal effects. Journal of Ecology 81: 477–487.

McKee, K., D. Cahoon & I. Feller, 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Global Ecology and Biogeography Letters 16: 545–556.

Melville, F. & A. Pulkownik, 2006. Investigation of mangrove macroalgae as bioindicators of estuarine contamination. Marine Pollution Bulletin 52: 1260–1269.

Murrell, M. C. & E. M. Lores, 2004. Phytoplankton and zooplankton seasonal dynamics in a subtropical estuary: importance of cyanobacteria. Journal of Plankton Research 26: 371–382.

Nixon, S. W., 1995. Coastal marine eutrophication: a definition, social causes and future concerns. Ophelia 41: 199–219.

Nixon, S. W., C. A. Oviatt, J. Frithsen & B. Sullivan, 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. Journal of the Limnological Society of South Africa 12: 43–71.

Officer, C. B., T. J. Smayda & R. Mann, 1982. Benthic filter feeding: a natural eutrophication control. Marine Ecology Progress Series 9: 203–210.

Onuf, C. P., J. M. Teal & I. Valiela, 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58: 514–526.

OzCoast Australian Online Coastal Information. Geoscience, Australian. Australian Government. http://www.ozcoasts.gov.au/.

Paerl, H. W., J. Dyble, P. H. Moisander, R. T. Noble, M. F. Piehler, J. L. Pinckney, T. F. Steppe, L. Twomey & L. M. Valeds, 2003. Microbial indicators of aquatic ecosystem change: current applications to eutrophication studies. FEMS Microbiology Ecology 46: 233–246.

Pejrup, M., 1988. Suspended sediment transport across a tidal flat. Marine Geology 82: 187–198.

Pregnall, A. M., 1983. Release of dissolved organic carbon from the estuarine intertidal macroalga *Enteromorpha prolifera*. Marine Biology 73: 37–42.

Ridd, P., R. Sam, S. Hollins & G. J. Brunskill, 1997. Water, salt and nutrient fluxes of tropical tidal salt flats. Mangroves and Salt Marshes 1: 229–238.

Roman, C. & F. Daiber, 1989. Organic flux through a Delaware Bay salt marsh: tidal exchange, particle size distribution and storms. Marine Ecology Progress Series 54: 149–156.

Southeast Queensland Healthy waterways, Australia. www.healthywaterways.org/.

Tam, N. F., 1998. Effects of wastewater discharge on microbial populations and enzyme activities in mangrove soils. Environmental Pollution 102: 233–242.

Twilley, R. R., 1985. The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. Estuarine, Coastal and Shelf Science 20: 543–557.

Valiela, I. & M. L. Cole, 2002. Comparative evidence that salt marshes and mangroves may protect seagrass meadow from land-derived nitrogen loads. Ecosystems 5: 92–102.

Valiela, I., J. McCLelland, J. Hauxwell, P. J. Behr, D. Hersh & K. Foremean, 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42: 1105–1118.

Verhoven, J. T. A., B. Arheimer, Y. Chengqing & M. Hefting, 2006. Regional and global concerns over wetlands and water quality. Trends in Ecology and Evolution 21: 96–103.

Vymazal, J., 1995. Algae and element cycling in wetlands. Lewis Publishers, Boca Raton.

Wang, M., J. Zhang, Z. Tu, X. Gao & W. Wang, 2010. Maintenance of estuarine water quality by mangroves occurs during flood periods: a case study of a subtropical mangrove wetland. Marine Pollution Bulletin 60: 2154–2160.

Wickramasinghe, S., M. Borin, S. W. Kotagama, R. Cochard, A. J. Anceno & O. V. Shipin, 2008. Multi-functional pollution mitigation in a rehabilitated mangrove conservation area. Ecological engineering 35: 898–907.