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Sources and fate of organic matter in constructed versus natural coastal waterways

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ABSTRACT

Coastal wetlands are increasingly being converted into canal estates with potential consequences for ecosystem functioning. We compared the sources and fate of organic matter and water quality at four types of canal habitats (entrances and ends of canals, canal lakes and lake edges) and shallow and deep natural habitats (four replicates of each habitat). The fate of labile organic matter was assessed by measuring rates of scavenging of carrion. Surface sediments were analysed for organic carbon content and stable carbon isotopes, fatty acid biomarkers and compound specific stable isotope analysis of selected fatty acids were used to elucidate sources of sedimentary organic matter. Canal lakes differed from other habitats and were characterised by negligible scavenging, larger quantities of organic matter comprised of higher contributions from diatoms, and hypoxia. Despite some trends, natural habitats were statistically indistinguishable from canal entrances and ends. Variation among replicate habitats was large.

1. Introduction

Coastal wetlands, such as mangroves, saltmarshes and seagrass meadows, provide important ecosystem services. For example, they are habitat for macrofauna, support coastal food webs, maintain water quality by trapping sediments and organic matter, and efficiently recycle organic matter or sequester it (Barbier et al., 2011; McLeod et al., 2011). Growing demand for waterfront residential property has seen increasing areas of coastal wetlands being converted to residential canal estates and 4000 linear km of canal estates now occur globally (Waltham and Connolly, 2011). Understanding the sources and fates of organic matter in artificial versus natural coastal systems is a key aspect of determining how the proliferation of artificial waterways affects coastal ecosystem functioning and is needed to inform policy on the design and construction of artificial waterways (Harvey and Stocker, 2015).

Canal estates are an extreme form of coastal modification because the natural complex, vegetated coastline is converted to narrow, blind-ending channels and deep lakes (Waltham and Connolly, 2013) that limit tidal exchange and are prone to sedimentation, the accumulation of organic matter and hypoxia (Azzoni et al., 2015; Cosser, 1989; Waltham and Connolly, 2011). These conditions make canal estates less hospitable for fish and macroinvertebrates and the biomass of these taxa is usually less than in nearby unmodified coastal waterways (Maxted et al., 1997; Morton, 1989).

Several of the important primary producers in coastal wetlands, including mangroves, saltmarsh plants and seagrasses are usually absent in constructed waterways. Primary producers in canal estates are thus dominated by phytoplankton, benthic microalgae and some novel sources, such as urban grasses (Connolly, 2003). This can lead to food webs within constructed waterways being supported by basal carbon sources that are different from those in natural waterways (Connolly, 2003; Waltham and Connolly, 2006). Moreover, the particulate organic matter that is deposited in sediments in constructed vs natural waterways may differ in lability, since phytoplankton and microalgae typically have lower C:N than highly refractory mangrove leaves and seagrasses (Enriquez et al., 1993).

A variety of methods can be used to identify the sources of carbon within sediments including stable isotopes and lipid biomarkers. Stable isotopes are useful when different sources have distinct isotopic signatures (Fry, 2013). Fatty acid biomarkers can usually identify a larger range of sources than stable isotopes (e.g. bacteria and different types of

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algae) but the assignment of different types of fatty acids to their sources is sometimes ambiguous (Dalsgaard et al., 2003). Isotopic analysis of particular fatty acids (i.e. compound-specific isotope analysis) can more reliably resolve the sources of different fatty acids. Moreover, isotopic analysis of fatty acids unique to bacteria (e.g. odd carbon-numbered and branched-chain fatty acids and the mono-unsaturated fatty acid (MUFA) 18:1ω7) can help elucidate the source of organic matter being used by bacteria (Boschker et al., 1999).

Recycling of particulate organic matter is a critical ecosystem function. Particulate organic matter that accumulates on the benthos may have several fates: it may be consumed by scavengers or re-mineralised by microbes and thus recycled to the environment, or it may be buried in sediments. In natural waterways that support an abundant and diverse community of scavengers, most detritus is probably consumed. Because canals support fewer fish and macro-invertebrates overall and fewer detritivores (Maxted et al., 1997; Morton, 1989), less detritus is probably scavenged and a larger proportion of the decaying organic material may be remineralised by microbes or accumulate in sediments. Scavenging rates may vary through time, however, as consumption rates of organisms often vary seasonally (e.g. Micheli, 1997). Moreover, deep lakes and the ends of canals that are poorly flushed may act as sinks for fine sediments and organic matter (Cosser, 1989) and if the organic matter content is high, the deep lakes may experience net respiration and hypoxia. Consequently, compared to natural waterways sediments in artificial waterways potentially contain more organic matter and bacterial biomass, have a different composition of organic matter and their bottom waters may be more prone to hypoxia.

The Gold Coast region of southeast Queensland, Australia, supports > 150 linear km of artificial waterways (Waltham and Connolly, 2011). Canal systems have been established within the Nerang River, Tallebudgera River and Currumbin River estuaries and have replaced extensive mangrove forests, saltmarshes and seagrass meadows. The canal estates are comprised of flow-through and dead-end canals and deep lakes (some exceeding 25 m depth). The lakes were created when sediment was excavated during the construction of the canal system and used to elevate the adjacent low-lying residential land. The hydrology of the lakes is different to the canals and natural waterways since they are much deeper and some are located behind tidal gates that restrict tidal flows (Zigic et al., 2002; Waltham and Connolly, 2013).

Similar species of fish inhabit the Gold Coast canals and nearby natural waterways but the relative abundances of species vary (Morton, 1989; Morton, 1992; Morton et al., 1987). In particular, the dead-ends of canals support fewer macrobenthic carnivores (e.g. sparids and tetraodontids) and detritivores (mugilids) than canal entrances or rivers (Morton, 1989; Morton, 1992) and abundances of these groups are also reduced compared to nearby natural waterways (Morton et al., 1987). The ends of canals also support reduced species richness and diversity of benthic macroinvertebrates (Cosser, 1989). Fish assemblages are depauperate and sometimes absent in the deep lakes (Waltham and Connolly, 2013). Consequently, rates of scavenging in the canal system, and in the deep lakes in particular, are likely to be lower than in natural waterways.

The objective of this study was to investigate the sources and fate of particulate organic matter in different types of habitats within artificial and natural waterways of southeast Queensland, Australia to determine how the proliferation of artificial waterways affects coastal ecosystem functioning. We tested the following hypotheses:

1. That rates of scavenging of carrion would be greater in natural than canal habitats and lowest in deep lakes and that rates of scavenging would be greater in summer than in winter.
2. That canal habitats would contain more sedimentary organic matter, finer sediments and be more prone to hypoxia than natural habitats, with the most extreme values occurring in the deep lakes.
3. That sediment organic matter within the constructed waterways would have greater contributions from bacteria and microalgae and less from macrophytes than natural waterways.

2. Materials and methods

The study was done in the Gold Coast region of southeast Queensland, Australia. Six types of habitat were sampled: 1) canal lakes (depth range 8–23 m); 2) edges of canal lakes (< 2 m); 3) entrances of canals (where a canal intersected the river; depth range 1.4–5 m); 4) ends of canals (> 500 m from the canal entrance; depth range 1.5–2.1 m); 5) natural deep habitats (depth range 3.5–4.3 m); and 6) natural shallow habitats (depth range 0.7–1.0 m) (for examples see Fig. 1). Four independent replicate locations were sampled for each type of habitat from across the Gold Coast region (24 locations overall spread over 40 km of coastline). Except for deep lakes and edges of deep lakes, all locations were > 500 m apart. Latitude and longitudes of all 24 locations are provided in Supplementary Table 1. Natural habitats were located within the Broadwater of southern Moreton Bay and consisted of a network of channels containing extensive seagrass meadows (predominantly *Zostera muelleri*) fringed by mangroves (predominantly *Avicennia marina*) and saltmarsh flats (predominantly *Sporobolus virginicus*).

2.1. Rates of scavenging

Rates of scavenging were assessed at all habitats and locations, except for the edges of the deep lakes. Scavenging rates were measured twice during summer (December 2009 and February/March 2010) and twice during winter (June and July/August 2010) to assess temporal variation within one year. Scavenging was assessed using a commonly-employed assay (e.g. Porter and Scanes, 2015) by quantifying the mass of carrion consumed over 1 h. Fifteen 'dillies' (300 mm diameter flat rings covered in 20 mm mesh) were baited with a known mass (~50 g) of dead pilchards (*Sardinops sagax*) and lowered to the benthos. Any carrion remaining on the dillies was re-weighed after retrieval.

2.2. Sampling and analyses of sediments

Surface sediments (~15 cm depth) were sampled between December 2012 and January 2013 for analysis of % of particulate organic matter (%POM), percentage of organic carbon (%OC), $\delta^{13}C$, atomic C:N, sediment grain size distributions, profiles of fatty acid methyl esters (FAMES) and compound-specific isotopic analyses (CSIA; $\delta^{13}C$) of selected bacterial fatty acids. At every location, five samples of unvegetated surface sediment were collected using a van Veen grab and immediately cooled and then frozen when returned to the laboratory.

The percentage of organic matter was determined by wet-sieving sub-samples of sediment through a 2 mm sieve. Organic material retained on the sieve and sediments < 2 mm that passed through the sieve were retained and dried in an oven at 60 °C until constant weight. The %POM was determined as the proportion of the organic material relative to the total weight of the dried sample. Sediments analysed for %OC, $\delta^{13}C$ and atomic C:N were dried at 60 °C until constant weight, homogenised and subsamples were extracted. Sub-samples were acidified with 1 M HCl to remove inorganic carbonates and redried. Samples were then ground using a mortar and pestle, weighed and combusted on a Sercon Hydra 20–22 mass spectrometer. Isotope results were presented using standard δ notation (per mil ‰), defined as:

$$\delta^{13}C = ([R_{sample}/R_{standard}] - 1) \times 10^3$$

where R represents $^{13}C/^{12}C$. PDB limestone was the standard reference for carbon. Atomic C:N was calculated based on percentage dry weight of the two elements. Sediment grain size distribution was determined from volumetric particle size distribution (0.1–2000 μm) measurements. The five replicate samples collected at each location

Fig. 1. Examples of the six types of habitat (four canal habitats and two natural habitats) sampled within the canal system and within unmodified natural waterways of the Gold Coast, Australia. Four replicate locations were sampled for each type of habitat from across the Gold Coast region. See Supplementary Table 1 for geographic coordinates of all 24 locations.

were pooled and homogenised. A sub-sample was taken, ultrasonically treated and measured using laser diffraction particle size analysis (Malvern Mastersizer, 3000).

2.3. Preparation of fatty acid methyl esters

Lipids were extracted from sediments using an accelerated solvent extractor. 10 g (dry weight) of sediment was transferred to an 11 ml extraction cell and any void was filled with glass beads or acid-washed sand. ASE extraction was performed at 100 °C and 1500 psi using a chloroform:methanol ratio of 2:1. The extract was concentrated to 1 ml by rotary evaporation at 50 °C and the extracts were transferred to clean tubes and dried under nitrogen gas. Samples were saponified by adding 1 ml of NaOH and 2 ml of methanol. Tubes were heated in boiling water for 2 h and cooled before being acidified with 0.4 ml of 37.5% HCl. 2 ml of chloroform was added and samples were centrifuged at 3000 rpm for 5 min. Samples were transferred to new tubes and the aqueous phase was extracted again with another 2 ml of chloroform. The chloroform extracts were combined and evaporated and dried under nitrogen gas. Samples were methylated by adding 1 ml of 14% BF_3-methanol into the liquid residue. The tube was purged with N_2, closed, heated at 90 °C for 10 min and cooled. To isolate FAMEs 2 ml of hexane and 2 ml of water were added and the samples mixed on a vortex for 1 min and centrifuged at 2500 rpm for 3 min. The upper hexane layer was extracted and the extraction was repeated with another 2 ml of hexane. The combined hexane phases were stored together and concentrated under nitrogen before being stored at −20 °C until analysed. Samples were analysed by a gas chromatograph using an Omegawax 320 *Supelco column (30 m × 0.32 mm internal diameter, 0.25 μm film thickness). N_2 was used as the carrier gas with a flow rate of 1.5 ml min^{-1}. After injection at 24 °C the oven temperature was raised to 60 °C for 1 min, 150 °C at 40 °C min^{-1} and held for 3 min, then 240 °C at 2 °C min^{-1} and held for 10 min. Bacterial fatty acids were identified by comparing the samples with that of bacterial acid methyl ester (BAME, Sigma) and the percentage contribution of each bacterial FAME to total FAMEs extracted from each sample were calculated as following:

$$FA\% = (A_{FA}/A_T) \times 100 \text{ where } A_{FA} = \text{Area of FAME of interest and } A_T = \text{Total area of all FAMEs in the sample.}$$

CSIA of 15:0 *iso* and 15:0 *anteiso* was done at the Stable Isotope Facility at the University of California, Davis USA. Replicate samples from within each location were pooled and locations were used as replicates. FAME extracts were combusted to gas and analysed on a Thermo GC/C-IRMS coupled to a Delta V Advantage isotope ratio mass spectrometer.

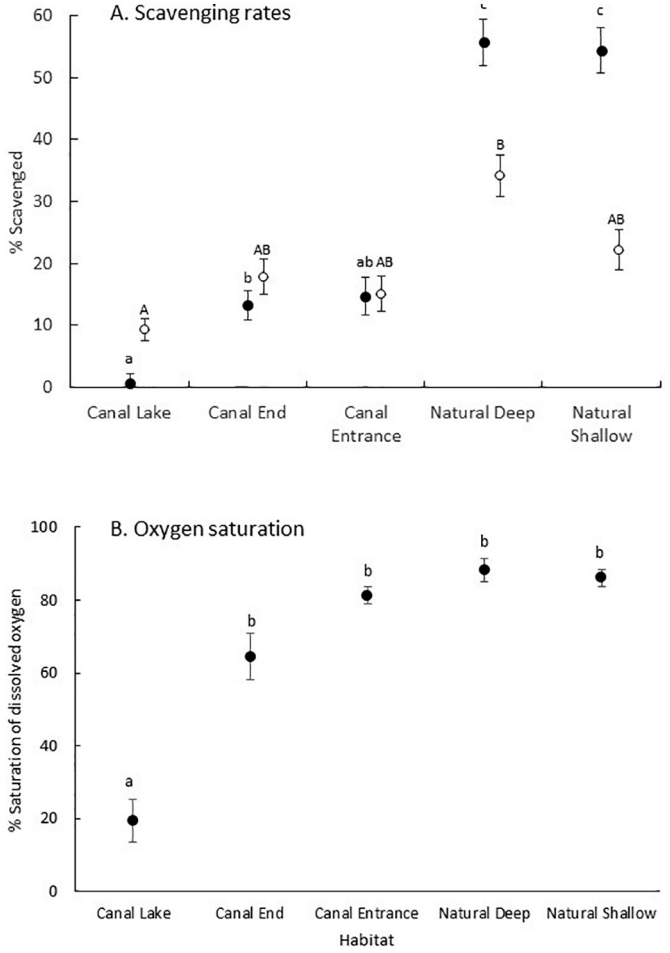

Fig. 2. (A) Scavenging rates (mean ± SE) among habitats during summer (black) and winter (white). Letters denote results of post-hoc comparisons among habitats during summer (lower case) and winter (upper case) where the same letter indicates no significant difference. (B) Dissolved oxygen saturation (mean ± SE) among habitats during the 2009/2010 sampling period.

2.4. Water quality parameters

Dissolved oxygen saturation (%DO), temperature and salinity were measured 0.5 m above the benthos at all habitats and locations, except for the edges of the deep lakes, twice during summer (December 2009 and February/March 2010) and twice during winter (June and July/August 2010) to coincide with measurements of scavenging. Triplicate measurements were taken approximately 50 m apart to characterise the conditions at each location. Water quality was measured again during summer 2012/13 to coincide with sediment sampling. During 2012/13 measurements were taken at all habitats and locations (including the edges of the deep lakes) and pH was measured in addition to %DO, temperature and salinity. All measurements were made using a YSI water quality meter.

2.5. Analyses of data

Patterns of variability were analysed using permutational analysis of variance (PERMANOVA), which is a non-parametric analogue of ANOVA (Anderson, 2001). PERMANOVAs were used to analyse both univariate and multivariate data sets since univariate data sets frequently violated the assumption of homoscedasticity and variances could not be stabilised using transformations. All analyses were based on Euclidean Distance similarity matrices. When significant differences among levels of fixed factors were detected, a posteriori pair-wise tests were used to identify which levels differed.

Spatial and temporal variability in rates of scavenging and water quality parameters measured during 2009/2010 (%DO, temperature and salinity) were analysed using four-way PERMANOVAs. The factors were Season (a fixed factor with two levels; summer and winter); Time (a random factor that was nested within season and had two levels); Habitat (a fixed factor with five levels) and Location (a random factor that was nested within habitat and had 4 levels).

Overall differences among habitats were analysed using a composite multivariate data set comprising 2012/2013 data on water quality (% DO, temperature, salinity, pH) and sediment characteristics (%POM, % OC, $\delta^{13}C$, C:N, median grain size and the scores of the first axis of the principle components of FAMES (which explained 41% of the total variation in FAMEs)). Average values of each variable were compiled for each location and locations were used as replicates in the analysis. Data were normalised to account for differences in units of measurement among variables. Differences among habitats were analysed using a one-way PERMANOVA. Canonical analysis of principal coordinates (CAP) was used to graphically represent differences among habitats. CAP is a constrained ordination of multivariate points that uses a priori hypotheses to produce the plot (Anderson and Willis, 2003).

Two-way PERMANOVAs were used to analyse overall FAME profiles. Univariate two-way PERMANOVAs were also used to analyse 2012/2013 water quality parameters (%DO, temperature, salinity and pH), sediment parameters (%POM, %OC, C:N, $\delta^{13}C$), total bacterial fatty acids (Σ 15:0 + 15:0 *iso* + 15:0 *anteiso* + 16:0 *iso* + 17:0 + 17:0 *iso* + 18:1ω7), the ratio of even-numbered very long chain fatty acids (VLCFA; Σ 22:0 + 24:0) to even-numbered long chain fatty acids (LCFA; Σ 14:0 + 16:0 + 18:0; an indicator of the relative contribution of aquatic and terrestrial organic matter; (Meyers, 1997)) and the ratio of 16:1/16:0 (which reflects differences between diatom and dinoflagellates sources and values > 1.6 indicate a predominance of diatom sources (Budge and Parrish, 1998)). The factors were 'Habitat', a fixed factor, and 'Location', a random factor that was nested within habitat. CSIA of 15:0 *iso* and 15:0 *anteiso* and sediment grain size distributions among habitats were analysed using a one-way PERMANOVAs.

3. Results

Rates of scavenging varied among habitats but patterns were not consistent between summer and winter (Supplementary Table 1). During summer average rates of scavenging in natural habitats exceeded 50% during the one-hour deployments but scavenging rates were < 15% in artificial waterways and were negligible in the canal lakes (Fig. 2A). Rates of scavenging were lower and more variable during winter. Average rates of scavenging were greatest and exceeded 30% in deep natural habitats and were lowest in canal lakes (8%) but varied between 15 and 20% across all other habitats (Fig. 2A).

During the 2009/2010 sampling period, dissolved oxygen saturation was consistently lower in the canal lakes than in all other habitats (Fig. 2B; Supplementary Table 1). Patterns of %DO were consistent between summer and winter but varied among times and locations within habitats (Supplementary Tables 1, 2). Water temperature was cooler in winter than summer (18.2 ± 0.2 °C vs 26.7 ± 0.3 °C) at all habitats, except for the deep lakes, where the temperature of bottom waters did not differ significantly between seasons (summer = 24.3 ± 1.1 °C; winter = 21.4 ± 0.9 °C; Supplementary Tables 1 and 2). Salinity varied among locations but patterns were not consistent through time (Supplementary Tables 1 and 2).

Analysis of the composite multivariate dataset of sediment and water quality parameters collected in 2012/13 indicated variation among habitats (Pseudo-F = 3.187; Pseudo-P = 0.007; Fig. 3). Post-hoc analyses revealed that canal lakes differed from all other habitats, except the edges of the canal lakes. No significant differences were detected among the remaining habitats although there was a trend for ends of canals to differ from both deep (Pseudo-P = 0.055) and shallow

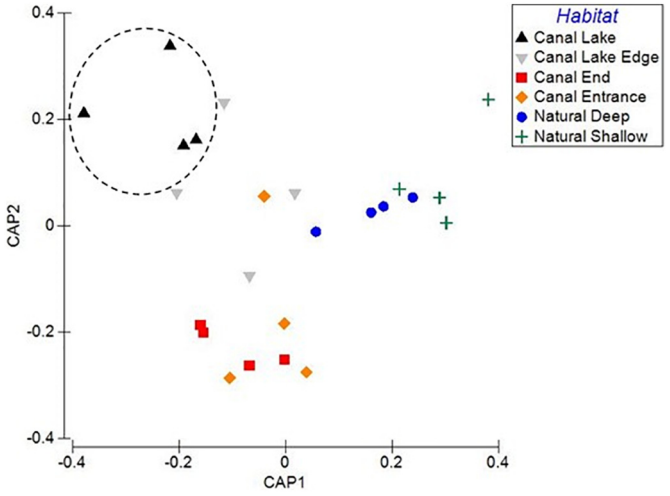

Fig. 3. CAP plot indicating differences among habitats in water quality and sediment characteristics. Hatched polygon highlights the four canal lakes.

(Pseudo-P = 0.084) natural habitats and for canal entrances to differ from deep natural habitats (Pseudo-P = 0.06).

Sediments were dominated by silt (2–50 μm; 40%), medium sand (250–500 μm; 29%) and fine sand (100–250 μm; 21%). Clays (< 2 μm), very fine sand (50–100 μm) and coarse sand (500–1000 μm) contributed < 5% each, on average. The distribution of grain sizes did not vary among habitats (Pseudo-F = 1.513; Pseudo-P = 0.231). The %POM varied greatly among habitats and locations within habitats (Table 1). Canal lakes contained large amounts of POM (> 70%) whereas both natural locations and canal entrances contained relatively little (< 20%; Fig. 4A). The spatial variability in the %OC in sediments among habitats mirrored that of the %POM and was lowest in the natural habitats and at the entrances of canals (< 0.75%), greatest in the deep lakes (> 2%), and intermediate at the ends of canals and at the edges of the deep lakes (Table 1; Fig. 4B). Sediments in deep natural waterways were most enriched in ^{13}C (−21.5‰) but were similar across all other habitats (range from −23.4‰ to −24.6‰) (Table 1; Fig. 4C). C:N did not vary among habitats but varied substantially among locations within habitats. C:N ranged between 5.6 and 17.2 (average 10.6) across all habitats.

Sixteen individual fatty acids were isolated and expressed as a percentage of the overall FAMEs extracted from each sample. FAMEs comprised saturated fatty acids (SAFAs), including long chain (LCFAs;

Table 1
Results of two-way PERMANOVAs of sediment parameters, FAMEs and water parameters among habitats and locations sampled in 2012/2013. DF = degrees of freedom. Number of unique permutations = 999.

Variables		Habitat DF = 5		Location (habitat) DF = 18	
		Pseudo-F	Pseudo-P	Pseudo-F	Pseudo-P
Sediment	%POM	2.865	0.043	57.722	0.001
	%OC	2.935	0.049	26.868	0.001
	$\delta^{13}C$	3.485	0.021	35.746	0.001
	C:N	2.448	0.071	25.863	0.001
FAMEs	Overall FAME profile	1.601	0.067	14.042	0.001
	Total bacterial FAMEs	2.973	0.035	10.073	0.001
	15:0 *anteiso*	6.210	0.001	4.666	0.001
	14:0	3.088	0.035	13.555	0.001
	VLFAs/LCFAs	0.657	0.662	4.074	0.001
	16:1/16:0	1.006	0.428	33.684	0.001
Water	%DO	9.535	0.003	15.258	0.001
	pH	3.248	0.026	23.179	0.001
	Salinity	1.041	0.403	793.81	0.001
	Temperature	1.275	0.282	90.726	0.001

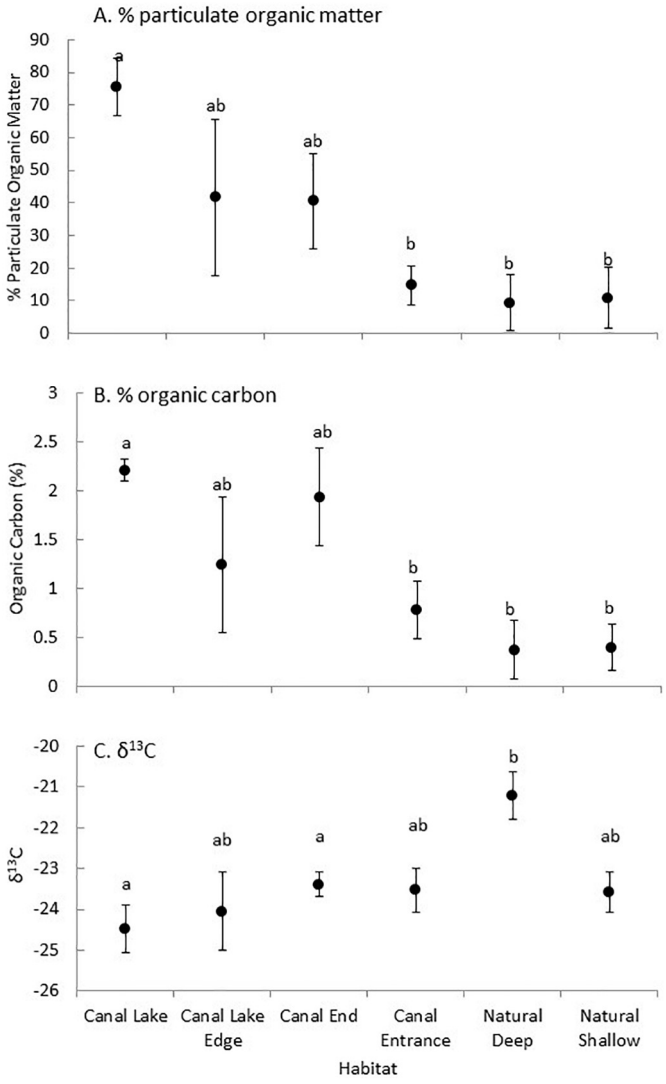

Fig. 4. Percentage of organic particulates (A), organic carbon content (B) and carbon isotope ratios (C) within sediments among habitats (mean ± SE). Letters as per Fig. 2.

C_{14}–C_{20}) and very long chain fatty acids (VLCFAs C_{22}–C_{24}), four branched fatty acids (BAFAs) and four monounsaturated fatty acids (MUFAs). No polyunsaturated fatty acids were detected. FAMEs were dominated by palmitic acid (16:0), which contributed, on average, 41% of all FAMEs. Bacterial fatty acids (15:0, *iso*- and *anteiso*-15:0, *iso* 16:0, 17:0, *iso*-17:0, 18:1ω7) were also abundant and contributed 15.9% of total FAMEs. VLCFAs were relatively scarce (5.9% of total FAs).

Despite a strong trend, overall FAME profiles did not vary significantly among habitats but did vary among locations within habitats (Table 1). Total bacterial FAMEs varied among habitats and locations within habitats but pair-wise comparisons were unable to determine which habitats differed (Table 1; Fig. 5A). The bacterial marker 15:0 *anteiso* was the only individual bacterial FAME that varied among habitats and locations (Table 1). The percentage contribution of 15:0 *anteiso* in the deep natural habitat was lower than all other habitats, except the lake edge (Fig. 5B). The diatom marker 14:0 varied among habitats and locations within habitats (Table 1). 14:0 contributed a greater percentage of the FAME profile in the deep lakes compared to the canal entrances and both shallow habitats (Fig. 5C). Neither the ratio of SCFA to VLCFAs nor the ratio of 16:1/16:0 varied among habitats but both varied among locations within habitats (Table 1). $\delta^{13}C$ of the bacterial markers 15:0 *iso* (Pseudo-F = 1.143; Pseudo-P = 0.393)

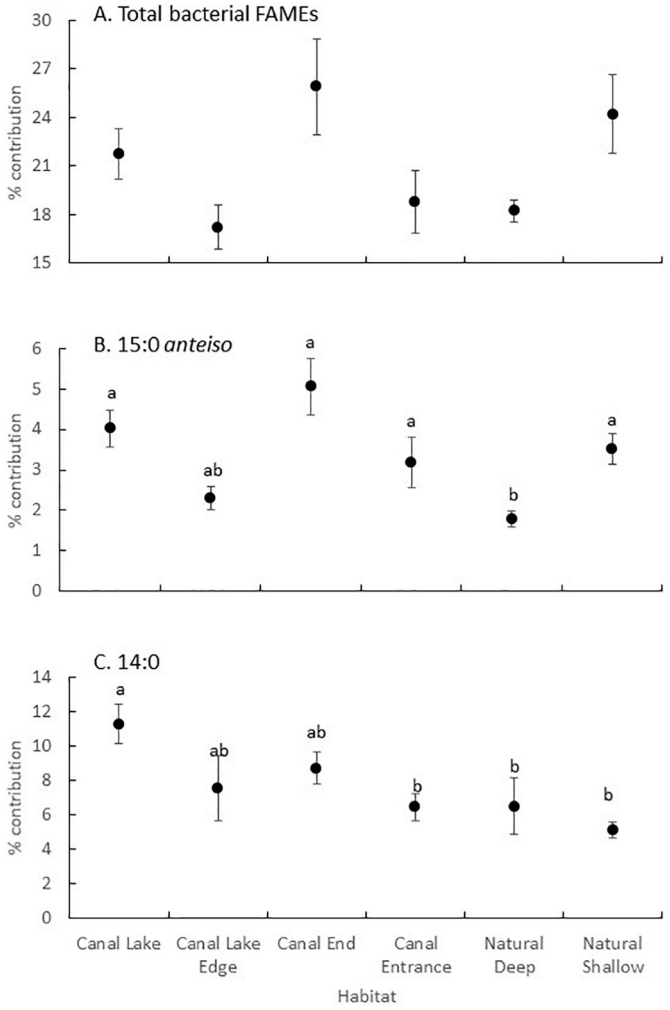

Fig. 5. Percentage contribution of total bacterial FAMEs (A), the bacterial marker 15:0 *ante-iso* (B) and the dinoflagellate marker 14:00 (C) among habitats (mean ± SE). Pairwise tests for total bacterial FAMEs were unable to determine which habitats differed therefore no post-hoc lettering is shown.

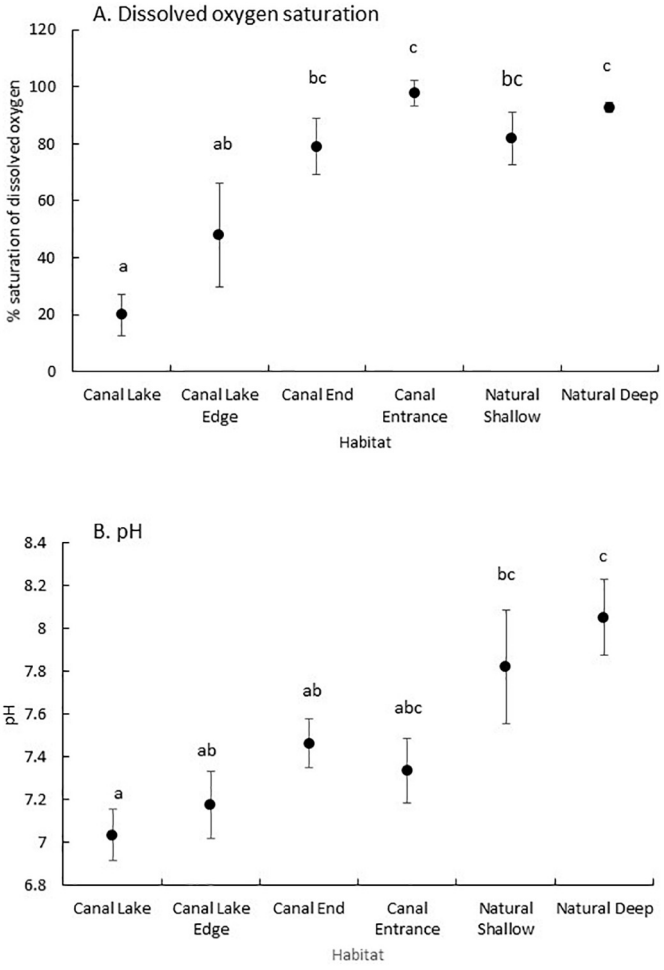

Fig. 6. Dissolved oxygen saturation (A) and pH (B) (mean ± SE) among habitats during the 2012/2013 sampling period. Letters as per Fig. 2.

and 15:0 *anteiso* (Pseudo-F = 0.670; Pseudo-P = 0.687) did not vary among habitats. The average $\delta^{13}C$ of 15:0 *anteiso* was −26.4‰ (± 0.65) and of 15:0 *iso* was −34.4‰ (± 1.49).

Trends in dissolved oxygen saturation sampled in 2012/2013 were similar to those sampled in 2009/2010, with oxygen saturation of canal lakes being lower than all other habitats, except the edges of the lakes (Table 1; Fig. 6A). pH was lowest in the canal lakes (< 7.1) and highest in the two natural habitats (> 7.8; Fig. 6B). Salinity and temperature did not vary among habitats, but varied among locations within habitats (Table 1; Supplementary Table 2).

4. Discussion

Canal lakes stood out as being different from all other habitats, except the edges of the lakes. The environmental conditions in the bottoms of lakes were characterised by almost negligible amounts of scavenging, large quantities of organic matter, low levels of dissolved oxygen and very low pH. Hence our hypothesis that environmental conditions would be most extreme in the canal lakes was supported. Despite strong trends in some variables, the entrances and ends of canals and the edges of the canal lakes were statistically indistinguishable from the natural habitats, indicating that the overall environmental conditions of those canal habitats were not significantly different to those in unmodified waterways.

One of the clearest patterns to emerge was the difference in the amounts of organic matter among habitats. The canal lakes contained large amounts of POM but levels were low in the natural habitats and at the entrances of canals. Not surprisingly, the percentage of organic carbon in the sediments mirrored that of the particulate matter and exceeded 2% in the canal lakes, which is much greater than even the highest measurements made in a nearby shallow vegetated coastal lagoon with limited tidal exchange (Dunn et al., 2008). The bathymetry of the lakes, which are localised deep points in the canal system, would facilitate the accumulation of organic material. Indeed, extreme vertical stratification of salinity in the canal lakes indicates minimal exchange of bottom-waters (Lemckert, 2006), hence organic matter that accumulates in the basins is probably not removed via tidal flushing.

The accumulation of organic matter in poorly flushed systems facilitates hypoxia because microbial remineralisation of the organic material depletes oxygen from the water column (Cai et al., 2011). Our observations of oxygen saturation were consistent with this, with oxygen saturation being consistently lowest in the canal lakes, which had the highest organic loads, and highest in the natural habitats and canal entrances, where organic loads were smallest. The limited tidal flushing of the deep lakes, coupled with their depth and stratification (Lemckert, 2006), may limit replenishment of oxygen in the bottom waters through tidal movements or wind-driven reaeration. Moreover, although hypoxia can occur naturally, the dissolved oxygen saturation of the natural habitats always exceeded that of the canal lakes and the persistence of the trend suggests that the localised hypoxia in the canal lakes reflected their hydrological environment. The pH of the canal

lakes was also much lower than in the natural habitats and there was a trend (although not statistically significant) for it to be lower than the other canal habitats. This may have reflected the high rates of respiration that occur in hypoxic regions, which elevates pCO_2 and reduces pH (Cai et al., 2011). pH may also be reduced in canal systems because, during construction, canals may cut into aquifers and facilitate outgassing of CO_2 through the release of groundwater (Macklin et al., 2014). High concentrations organic acids (e.g. humic and fulvic), which were not measured in this study, might also reduce pH. Moreover, because measurements were made during daytime, photosynthesis of seagrasses in natural habitats may have enhanced O_2 and depleted CO_2 and exacerbated differences in dissolved oxygen and pH between natural and artificial habitats. Overall, the average pH of the canal system was comparable to previous measurements from the same canal system (Macklin et al., 2014).

A combination of stable isotopes, FAMEs, and compound specific stable isotope analyses were used to try to elucidate the sources of organic material in the sediments of the canal and natural habitats. Specifically, we had predicted that organic matter in the canal habitats would have a higher prevalence of bacteria and microalgae and a smaller contribution of macrophytes than the natural habitats. Sediments in all four canal habitats were depleted in ^{13}C, with $\delta^{13}C$ ranging from −23.3‰ to −24.3‰. Connolly (2003) sampled the $\delta^{13}C$ of the dominant autotrophs in natural waterways and the canal system of the Gold Coast and seston (including phytoplankton) and benthic microalgae were the most depleted sources in the canals (−24.8‰ and − 23.1‰ respectively). The strong similarity in the $\delta^{13}C$ of the sediments in the current study and seston and microalgae of canals reported by Connolly (2003) indicates that sedimentary organic pools were probably dominated by seston and/or microalgae and that macroalgae and urban grasses, both of which are enriched in ^{13}C, made minor or no contributions. Shallow natural habitats displayed similar values to those of artificial habitats and were consistent with contributions from seston, microalgae and, potentially, some input from mangroves, which are depleted in ^{13}C and are abundant in the natural waterways but very scarce in the canal system. However, despite not being statistically different to other habitats, deep natural habitats exhibited a strong trend (pairwise test = 0.057) to be more enriched in ^{13}C than the natural shallow habitats, which might reflect a greater contribution from seagrass or saltmarsh grasses, both of which are highly enriched in ^{13}C. Given that all habitats sampled were sub-tidal, however, seagrasses rather than saltmarsh grasses are more likely to have contributed to the enriched signature in deep natural habitats (Connolly and Waltham, 2015). The apparent difference between the deep and shallow habitats may reflect that deep areas may act as basins where seagrass detritus can accumulate whereas shallow areas do not.

Stable isotopes were limited in their ability to identify the organic sources in the sediments because the number of elements available for analysis was less than the number of possible sources (Fry, 2013). Isotope analyses were, therefore, complemented with FAME analyses to further elucidate carbon sources. The diatom marker 14:0 was abundant in all habitats (> 4%) but was most abundant in the canal lakes, which was consistent with our hypothesis that microalgae would comprise a larger proportion of organic matter in canal habitats compared to natural areas. The prevalence of diatom markers was also consistent with the large contribution of seston indicated by the $\delta^{13}C$ values. Despite extensive mangrove forests occurring in the natural habitats, FAME profiles indicated that mangroves contributed little to sedimentary organic matter in those regions. VLCFAs are considered a marker of terrestrial organic matter, including mangroves (Meziane and Tsuchiya, 2000). However, VLCFAs comprised only a small proportion of the total FAME profile and neither of the two VLCFAs present varied among habitats. Moreover, similarity in the ratio of even-numbered VLCFA to even-numbered LCFA indicated that the relative contribution of allochthonous to autochthonous organic matter did not vary across habitats (Meyers, 1997). Consequently, despite mangroves being abundant at all natural locations, mangroves did not appear to contribute substantially to sedimentary organic matter pools. This conclusion was further supported by the C:N values, which did not vary among habitats and fell within the lower end of the range of C:N values documented within Australian estuaries (10.1–24.3; Heap et al., 2001). The relatively low values were consistent with contributions from bacteria (C:N ~ 4; Goldman et al., 1987) and microalgae (C:N ~ 5–9; Meyers, 1994) and minimal contributions from vascular plants, which are characterised by high C:N (e.g. > 20; Meyers, 1994). Moreover, the bacterial fatty acids 15:0 *iso* and 15:0 *anteiso* were both quite depleted in ^{13}C and values did not vary spatially, which was consistent with our observation that the sources of organic matter available for degradation by bacteria were fairly similar across habitats.

Bacterial fatty acids were major components of sedimentary organic matter. We had predicted that bacteria would contribute a greater proportion of organic matter in the canal habitats (particularly the lakes). Only two of the seven bacterial FAMEs present (15:0 and *anteiso* 15:0), however, varied among habitats and their pattern of variation was inconsistent with the hypothesis. Indeed 15:0 contributed an average of 7% in the shallow natural habitats but only 3.5% in the canal lakes and the percentage contribution of 15:0 *anteiso* in the canal habitats was not different to the shallow natural habitats. Although microbial processes generally dominate in hypoxic regions (Diaz and Rosenberg, 2008), the reduced pH that accompanies hypoxia (Cai et al., 2011) can retard microbial activity (Chelsky et al., 2015; Yamada and Suzumura, 2010), although results are equivocal (Liu et al., 2010; Piontek et al., 2010). The lower pH in the canal lakes compared to the other habitats, therefore, may have retarded microbial processes, and the overall magnitude of microbial activity in the lakes may have remained similar to, or been even less than natural waterways, resulting in similar contributions of bacterial FAMEs across most habitats.

PUFAs were not detected in any of the samples, despite being detected in relatively low abundances in nearby natural waterways (Dunn et al., 2008). PUFAs degrade rapidly (Smith et al., 1983) and so indicate recent deposits of organic matter (Carrie et al., 1998; Shaw and Johns, 1985). The absence of PUFAs, therefore, suggests that rates of deposition of new, labile organic material were quite low. Organic matter inputs are episodic and frequently occur when heavy rain transports terrestrial organic matter into waterways (Adame et al., 2012) or flushes nutrients into the system, thereby stimulating in-situ production (Patil and Anil, 2015). During the four months prior to sampling sediments (Aug–Nov 2012), the catchment received only 25% of its average rainfall for that period (Hinze Dam rain gauge, Bureau of Meterology) suggesting that minimal organic material may have been deposited during that time.

Scavenging is a critical ecosystem process that is likely to be affected by environmental conditions. Our hypothesis that greater amounts of carrion would be scavenged in natural waterways, the least in canal lakes and intermediate amounts at the ends and entrances of canals was supported during summer. Similar trends were also evident during winter although rates of scavenging were more variable and less carrion was consumed in the natural habitats, presumably because cooler water temperatures reduced the activity and feeding rates of scavengers, such as crabs (Barbeau and Scheibling, 1994). In natural systems, therefore, it appears that throughout the year most carrion would be rapidly consumed and that there would be limited opportunity for organic material from dead animals to be buried in sediments or remineralised by microbes. Although rates of scavenging were slower at the ends and entrances of canals than in natural waterways, during both seasons > 10% of the carrion was removed within 1 h indicating that, although it may take longer for the carrion to be consumed, a proportion of carrion would probably still be recycled by scavengers. Hence, although this important ecosystem service may be diminished in constructed waterways, it is not entirely lost. Such results are consistent with observations that although the biomass of detritivores is reduced in the canals, the species diversity of detritivores is similar in the canal

system and nearby natural waterways (Morton, 1989; Morton, 1992; Morton et al., 1987). During summer, deep lakes were the exception, with negligible amounts of carrion scavenged and organic matter in the canal lakes is more likely to be buried within sediments or recycled by microbes, creating a feedback that would perpetuate hypoxia and reduce pH. Animal organic matter, however, is typically more labile than plant organic matter and so further studies are needed to confirm whether similar patterns hold for less labile detritus.

Substantial variation among locations within habitats was detected for most variables measured indicating that local factors may have a greater influence on environmental conditions at a location than their overall position in the waterway. Habitats were defined by a rigid set of criteria (e.g. distance from river and depth) but the flushing rates of the locations sampled within each habitat type may have differed, which could influence water quality and sediment dynamics. Other factors that may have increased heterogeneity among locations include the proximity of the location to storm water discharges and the history of maintenance dredging. Although no dredging was observed during the study, differences in the history of maintenance dredging among locations may have influenced parameters such as sediment grain size, which did not vary among habitats, despite other studies reporting that finer sediments occur at the ends of canals (Cosser, 1989; Morton, 1989).

For some variables (e.g. C:N and overall FAME profiles) strong trends among habitats were apparent, despite not being statistically significant at $\alpha = 0.05$. In other cases, such as the composite multivariate dataset of water quality and sediment parameters (and, in particular for % organic matter and pH), statistically significant differences were detected only between the deep lakes and natural habitats, despite trends for canal ends and, sometimes, canal entrances to be intermediate between natural and deep lake habitats. In environmental impact studies, Type II errors (i.e. conclusion of no difference where one exists) are often considered more problematic than Type I errors (i.e. erroneous conclusion of differences where none exist) (Mapstone, 1995). This is because the consequences of not identifying an impact may be more detrimental for the environment than erroneously concluding one exists. Consequently, for those parameters where statistical power may have been limited, more detailed studies, such as comparing ends and entrances of canals with variable flushing rates or proximity to storm water discharges, may be required before concluding that no differences between canal ends and entrances and natural habitats exist.

5. Conclusions

The conversion of coastal wetlands into canal estates will continue. Whilst canal estates cannot function exactly like natural waterways they replace, their design should be maximised to optimise their ecological value. Canal developments must, therefore, avoid the inclusion of deep lakes since they act as traps for organic material, are characterised by hypoxia, and their ecological functioning is greatly compromised. Whilst rates of scavenging were also diminished in the remaining canal habitats, relative to natural habitats, scavenging still occurred and this important ecosystem process was preserved within the canal estates. Moreover, the sources of organic matter in the canal systems were mostly indistinguishable from nearby natural waterways. Designing canal estates to maximise their flushing rates and minimise areas prone to sedimentation and hypoxia is critical to maximise their ecological integrity.

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