SEDIMENT STRUCTURE IN TROPICAL INTERTIDAL ENVIRONMENTS?

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ABSTRACT

Seagrass meadows are considered important for sediment trapping and sediment stabilisation. Deposition of fine sediments and associated adsorbed nutrients is considered an important part of the chemical and biological processes attributed to seagrass communities. This paradigm was based on work in temperate regions on *Zostera marina* and in tropical regions on *Thalassia testudinum,* two species that maintain relatively high biomass, stable meadows. The current study investigates this concept for three species of intertidal tropical seagrass meadows in northeastern Australia. Sediment structure and nutrient status did not differ between vegetated and unvegated habitats in intertidal areas within the central region of the Great Barrier Reef World Heritage Area. The 'trapping' functions that have been attributed to seagrasses need to be re-assessed for a variety of locations and species before they can be accepted as dogma. In tropical Australia, intertidal meadows are predominantly ephemeral and comprised of structurally small species of low biomass. Consequently, sediment trapping within these meadows is largely insignificant.

Seagrass meadows have traditionally been considered important for sediment trapping, sediment stabilisation and as nutrient sinks (Hemminga and Duarte, 2000). The concept of seagrass meadows acting as a sink for particles (sediments and adsorbed nutrients) is due to a reduction of flow velocities by the plant canopy (Gacia et al., 1999). As the flow velocity drops, the capacity of the water to hold particles decreases, resulting in the deposition of fine sediments and their adsorbed nutrients. This paradigm is based on historical accounts of differences in sedimentation patterns, sediment structure and nutrient content between seagrass areas and bare sand (Wilson, 1949; Odum, 1959; McRoy and McMillan, 1977; Christiansen et al., 1981). The sediment-trapping paradigm has made an important contribution in understanding how seagrass meadows function, as many chemical and biological processes are related to the sedimentary environment in which seagrasses grow.

Nitrogen cycling, (Iizumi and Hattori, 1982; Howarth, 1988; Blackburn, 1990; Caffrey and Kemp, 1990), nutrient parameters (McRoy, 1970; Orth, 1977; Kenworthy et al. 1982; Thayer et al., 1984; Pulich 1985; Boon, 1986; Moriarity and Boon, 1989) and sediment structure (Scoffin, 1970, Almasi et al., 1987; McGlathery et al., 1994) are all related to fine scale sediment movement and have been measured as being different between seagrass and associated unvegetated substrates. Seagrass species and meadows come in a variety of functional forms ranging from small leafed species that form ephemeral, low biomass beds to large leafed species forming stable, high biomass beds (Walker et al., 1999). Historically much of the research on the 'trapping' paradigm was undertaken at locations characterized by *Zostera marina* (Scoffin, 1970; McRoy, 1970; Orth, 1977). Thus, the dogma relating to sediment trapping and nutrient status of seagrass meadows is based on the results of a single Northern Hemisphere temperate species, usually studied at one

location (small spatial scale). In more recent years research has expanded, but the literature is still dominated by studies devoted to *Thalassia testudinum*, *Posidonia oceanica* and *Zostera marina*, and research effort concentrated in the Caribbean, Mediterranean and North Atlantic (Duarte, 1999). Studies on these species perpetuate the dogma, as they are all structurally large species that tend to form stable meadows of high biomass (see Walker et al., 1999).

Diversity of seagrass form coupled with the requirement to examine processes on larger spatial scales for management, necessitates a re-assessment of the attributes that have become universally ascribed to seagrasses. This study aimed to investigate the nutrient status and sediment trapping paradigm for tropical intertidal seagrass meadows on the northeastern coast of Australia (145º46′E 16º53′S–148º 25′E 19º56′S). To do this, nutrient status and sediment structures were compared between seagrass-vegetated areas that were low in biomass, and comprised of structurally small species and adjacent non-vegetated intertidal areas.

MATERIAL AND METHODS

STUDY AREA.—The intertidal locations selected for this study are on the mainland coast within the central region of the Great Barrier Reef Lagoon between Cairns and Bowen, spanning approximately 556 km of coastline (Fig. 1). Sediments along this coastline are comprised of terrigenous–derived mud and sand (Maxwell, 1968). For a location to be included in this study, which aimed to test the influence of established seagrass meadows, seagrass presence had to be consistent for 3 yrs (see Table 1 for species present at each location).

Sampling within the vegetated sites was restricted to areas of monospecific, homogenous seagrass-cover. Disturbed areas and bare patches within the meadows were avoided. Unvegetated sites were identified within the same geographical confines as the vegetated site for each location. Vegetated and unvegetated sites were generally separated by (ca) 100 m and were sampled at approximately the same distance from the shoreline to ensure that each site was subjected to the same light, tidal and wave regimes. Fifteen porewater samples, five random sediment cores (nutrient analysis), and an additional three random sediment cores (grain size analysis) were collected concurrently from a vegetated and parallel non-vegetated site at each location. Sediment pH (15 replicates) was also measured and averaged to characterize locations.

SEDIMENT STRUCTURE.—Grain Size Analysis: The grain size output, derived by laser diffraction, was collated into particle size categories and subcategories according to the scheme of Udden (1914) and Wentworth (1922) as presented in Gale and Hoare (1991). Patterns in sediment structure between vegetated and unvegetated sites were similar across all grain size classes within location. Only the results from the fine silt fraction (15.625 µm to 7.813 µm) for sandy locations and the results from the very fine silt fraction (7.182 µm to 3.906 µm) for muddy locations are presented.

CHEMICAL ANALYSES.—Interstitial nutrients: Porewater samples were taken from the rhizosphere (2 cm *Halophila ovalis*, 10 cm *Halodule uninervis* and *Zostera capricorni)*. The same depth range was used in the adjacent unvegetated sites. The porewater samples were placed on dry ice in the field to minimize further chemical transformation and microbial activity. The samples were analyzed for dissolved inorganic nutrients, ammonium (NH_4^+), nitrite + nitrate ($NO_2^- + NO_3^-$), and phosphate (PO_4^{3-}) (Strickland and Parsons, 1972; Ryle et al., 1981).

Adsorbed nutrients: Sediment samples were collected to the depth of the rhizosphere at each location (2 cm *H. ovalis*, 10 cm *H. uninervis* and *Z. capricorni*). The same core depth was used at the corresponding unvegetated site. Sediment core samples to be analysed for exchangeable inorganic nutrients were placed on ice then refrigerated until they could be analysed the following day. These samples were analyzed for extractable inorganic NH_4^+ and PO_4^{3-}. Cores were homogenized
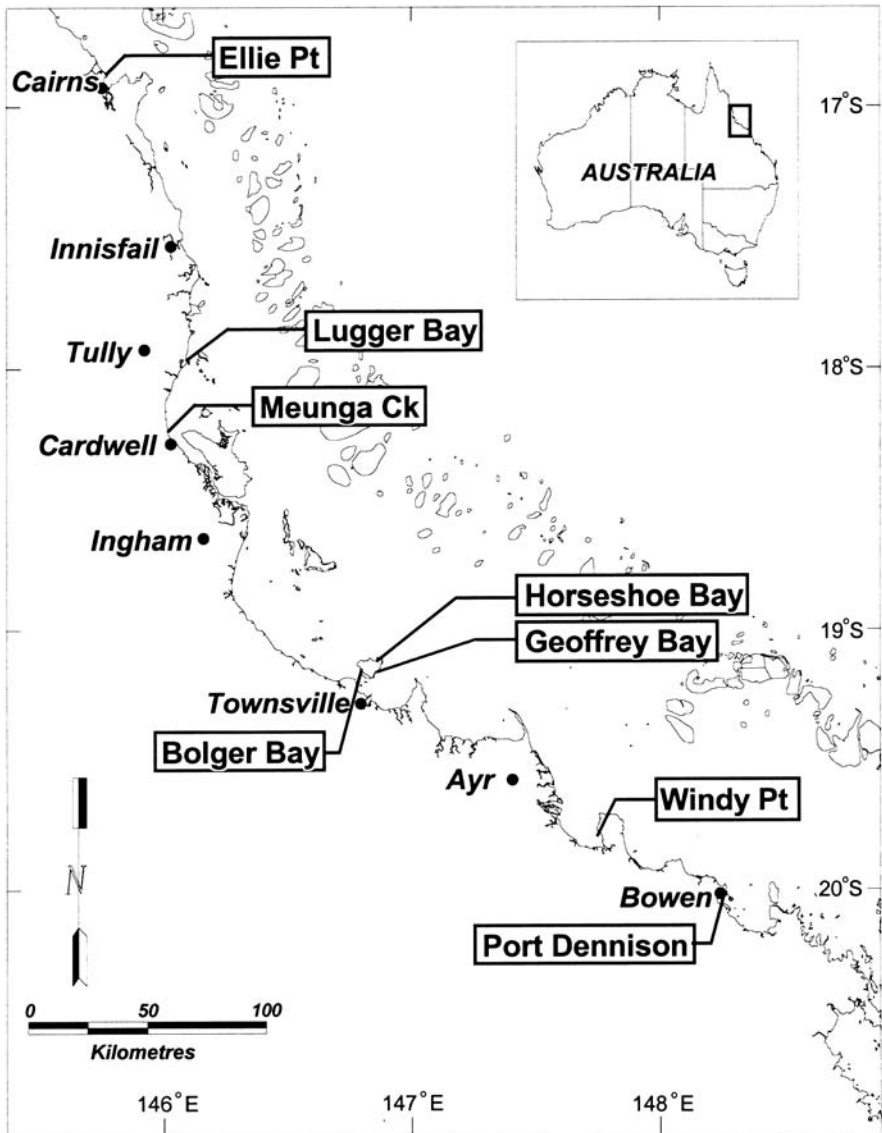
Figure 1. Locations sampled during a survey of nutrients and sediments in the central region of the Great Barrier Reef World Heritage Area.

to provide a depth-integrated sample. Adsorbed exchangeable ammonium was extracted using KCl (Rayment and Higginson, 1993). Two techniques were used to extract phosphate: the Bray method (Bray and Kurtz, 1945; Rayment and Higginson, 1993) and the Olsen/Colwell/Bicarbonate method (Mengel and Kirkby, 1987; Rayment and Higginson, 1993). The extracted nutrients (NH_4^+ and PO_4^{3-}) where then chemically analysed (Strickland and Parsons, 1972).

Calcium carbonate and plant organic matter: Sediment samples were prepared for analysis by air drying and were homogenized prior to carbonate and plant organic matter determinations. The

carbonate from any biological source (e.g., shells) was also included in the carbonate analysis. The samples were then analysed for carbonate content using a weight loss method involving hydrochloric acid (Blakemore et al., 1987). Plant organic matter was determined using a weight loss method by ignition (Gale and Hoare, 1991).

STATISTICAL ANALYSES.— Principal Components Analysis (PCA) was used as an exploratory tool to identify the existence of relationships within the data set. After grouping the data according to the PCA, sediment grain size and nutrient data were analysed using analysis of variance. Locations were considered as blocks. Measurements taken within a site were considered as samples rather than true replicates. Thus the location by site interaction term was considered the appropriate error for testing the site term. Distributional assumptions for the analyses were assessed by inspection of residual and normal probability plots. Data were log transformed where appropriate.

RESULTS

LOCATION CHARACTERIZATION.—All vegetated sites were monospecific stands of seagrass. *H. uninervis* (narrow morph) was the predominant species found at five locations; two locations were dominated by *Z. capricorni*, and one location, *H. ovalis* (Table 1). Biomass measurements were extremely variable between locations. The highest biomass was recorded at Ellie Point, a meadow dominated by *Z. capricorni,* (252.16 g DW m^{-2}), the lowest biomass was recorded at Bolger Bay, a location dominated by *H. ovalis* (0.2 g DW m^{-2}). Sediment pH measurements were indicative of marine influences (over pH 8.0) with the exception of Bolger Bay and Horseshoe Bay with recordings of pH 7.1 and pH 6.8 respectively (Table 1). These measurements are characteristic of a freshwater influence, possibly from ground water intrusion. Carbonate content ranged from 1.44% at Ellie Point to 75.97% at Geoffrey Bay (Table1). Only Geoffrey Bay could be considered to have carbonate sediments (carbonate content ≥ 50%, Scoffin, 1987). Organic matter ranged from 0.51% at Port Dennison to 2.14% at Windy Point (Table 1).

Locations within the central region of the Great Barrier Reef World Heritage Area where seagrass beds occurred were categorized by sediment type as either muddy or sandy (PCA, Fig. 2, Table 1). The muddy location group was comprised of data points that were more widespread across both axes in the PCA than the sandy locations, indicative of muddy locations being more variable (Fig. 2). Sandy sites were inhabited predominantly by the narrow morph of *H. uninervis*. The muddy sites were inhabited by a variety of species, including *H. uninervis*, *H. ovalis* and both locations dominated by *Z. capricorni* (Table 1). Consequently, analyses were conducted separately on each sediment type, because of the differences in sediment type that can influence sediment geochemistry (see Short, 1987, Erftemeijer and Middleburg, 1993). The data from muddy locations were variable with respect to sediment grain size proportions and nutrient concentrations than those collected from sandy locations. This variability may be related to the more complex mineralogy associated with clay minerals found in muddy sediments compared to the more uniform mineralogy at sandy sites.

SANDY LOCATIONS.—Sediment Structure: Analysis of the fine silt fraction of the sediment (as a representative of all sediment analyses) showed that there was no significant difference in percent fine silt between vegetated and unvegetated sites ($F_{(1,3)}$ = 0.24, P = 0.656, Fig. 3A). There were however, large differences between locations (Fig. 3A). Lugger Bay and Geoffrey Bay had proportionately higher percentages of fine silt present than the other two sandy locations, Horseshoe Bay and Port Dennison (Fig. 3A).

Table 1. Categorization of intertidal seagrass beds within the central region of the Great Barrier Reef World Heritage Area. (Mean ± S.E.).

| Location (n = 3)	Sediment Type	Dominant Species	Total Biomass (DW m^{-2}) mean ± S.E.	pH	% carbonate	% plant organic matter
Ellie Point, Cairns	Mud	Zostera capricorni	252.16 ± 24.52	8.0 ± 0.16	1.44 ± 0.24	1.30 ± 0.35
Meunga Creek, Cardwell	Mud	Halodule uninervis	5.01 ± 0.31	8.2 ± 0.07	1.85 ± 0.51	2.05 ± 0.23
Bolger Bay, Magnetic Island	Mud	Halophila minor	0.20 ± 0.12	7.1 ± 0.00	12.66 ± 1.62	1.82 ± 0.20
Windy Point, Cape Upstart	Mud	Zostera capricorni	72.34 ± 3.96	8.1 ± 0.05	14.40 ± 0.98	2.14 ± 0.20
Lugger Bay, Mission Beach	Sand	Halodule uninervis	5.38 ± 2.32	8.8 ± 0.05	1.94 ± 0.22	0.55 ± 0.04
Geoffrey Bay, Magnetic Island	Sand	Halodule uninervis	11.89 ± 0.73	8.9 ± 0.17	75.97 ± 0.46	2.00 ± 0 04
Horseshoe Bay, Magnetic Island	Sand	Halodule uninervis	2.92 ± 0.87	6.8 ± 0.05	14.39 ± 0.19	0.96 ± 0.05
Port Dennison, Bowen	Sand	Halodule uninervis	25.10 ± 5.56	8.7 ± 0.03	4.45 ± 0.78	0.51 ± 0.02
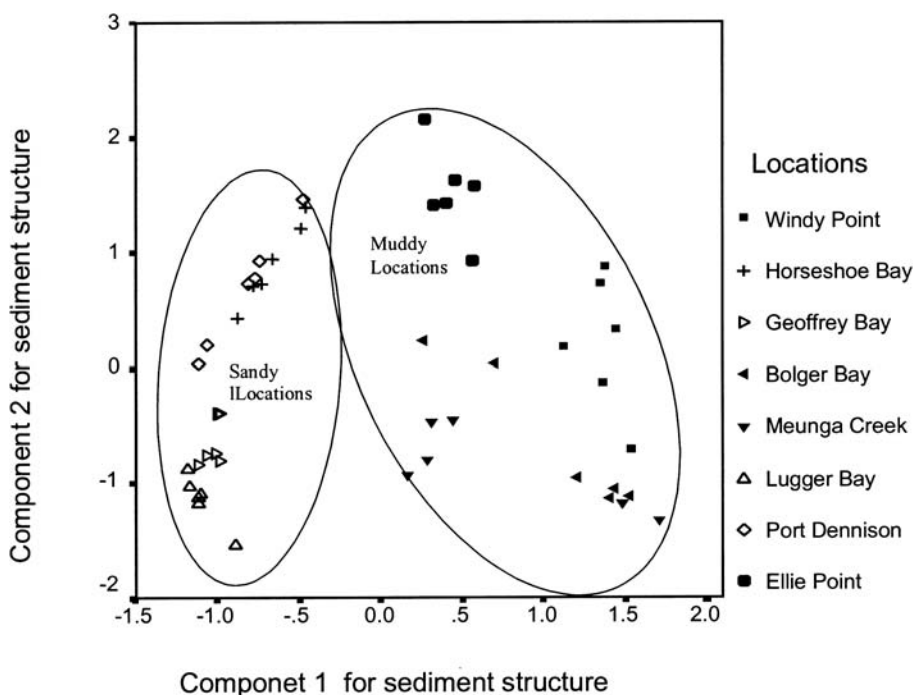
Figure 2. Intertidal areas (locations) categorized by sediment types (muddy or sandy) using Principle Component Analysis.

Nutrients: Mean interstitial $NO_2^- + NO_3^-$ ranged from 0.02 μM (Horseshoe Bay) to 1.27 μM (Port Dennison) (Table 2). Conversely, Port Dennison recorded the lowest mean interstitial NH_4^+ (6.31 μM),while Horseshoe Bay recorded the highest mean concentration (144.43 μM).

Measurements of mean interstitial PO_4^{3-} ranged from 0.69 μM (Horseshoe Bay) to 3.15 μM (Geoffrey Bay). Geoffrey Bay recorded the highest mean concentration of adsorbed NH_4^+. The lowest concentration of adsorbed NH_4^+ was recorded from Lugger Bay (Table 2). The highest and lowest concentrations (a 30 fold difference) of adsorbed PO_4^{3-} were recorded from Geoffrey Bay and depended on the method of extraction used (Table 2). The Bray technique tends to extract phosphate incompletely in an alkaline environment due to the presence of calcium carbonate (Pailles and Moody, 1995). The bicarbonate method is not affected by pH and is more appropriate for alkaline soils pH > 7.8 (Baker and Eldershaw, 1993). This large difference in adsorbed PO_4^{3-} concentrations from the same site using different extractive techniques demonstrates the need to consider sediment type and to choose appropriate analytical methods for adsorbed PO_4^{3-}.

No significant differences were detected between vegetated and unvegetated sites for any of the nutrient parameters (Table 3). Comparison of the Location sums of squares in relation to the Site sums of squares indicated that the majority of the variance within these data sets was the result of differences between locations (Table 3).

MUDDY LOCATIONS.—Sediment Structure: The amount of very fine silt (as a representative of sediment grain size analyses) was not significantly different between vegetated and unvegetated sites ($F_{(1,3)} = 0.13$, P = 0.738, Fig. 3B). However at locations dominated
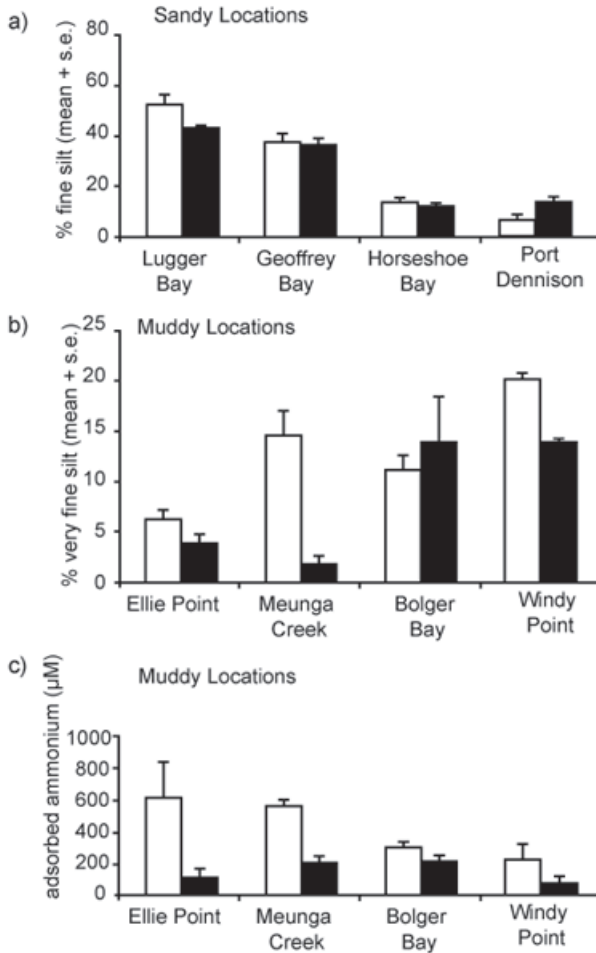
Figure 3. a) very fine silt at muddy locations for vegetated and unvegetated sites, b) Fine silt at sand locations for vegetated and unvegetated sites, c) adsorbed NH_4^+ at muddy locations for vegetated and unvegetated sites. Means and standard errors presented. vegetated = filled. unvegetated = unfilled. The patterns observed here are representative of the patterns observed for all grain size and nutrient analyses.

by *Z. capricorni* (Windy Point and Ellie Point) there was an apparent species effect with respect to percentage presence of very fine silt (Fig. 3B). Although the two vegetated sites both had a higher proportion of very fine silt than the unvegetated sites, the effect was significant only at Windy Point ($F_{(1,4)}$ = 181.43, P = 0.001).

Nutrients: Windy Point (*Z. capricorni*) recorded the lowest interstitial $NO_2^-+NO_3^-$, adsorbed NH_4^+ and adsorbed $PO_4^{3-}{}_{(bray)}$ (Table 2). The lowest concentrations of interstitial NH_4^+, PO_4^{3-} and adsorbed $PO_4^{3-}{}_{(bicarbonate)}$ were reported from Ellie Point, (also *Z. capricorni*, Table 2). The highest concentrations of all nutrients were recorded from Meunga Creek (Table 2).

Table 2. Concentrations of sediment nutrients (mean ± S.E.) recorded for each location at unvegetated (unveg) and vegetated (veg) sites.

Location	Site	Interstitial $NO_2^- + NO_3^-$ μmols L⁻¹ n = 15	Interstitial NH_4^+ μmols L⁻¹ n = 15	Interstitial PO_4^{3-} μmols L⁻¹ n = 15	Adsorbed NH_4^+ μmols kg⁻¹ n = 5	Adsorbed PO_4^{3-} (bray) μmols kg⁻¹ n = 5	Adsorbed PO_4^{3-} (bicarb) μmols kg⁻¹ n = 5
Sandy locations							
Lugger Bay	unveg	0.56 ± 0.14	27.36 ± 6.76	1.40 ± 0.07	27.90 ± 9.76	123.31 ± 3.36	126.55 ± 3.07
	veg	0.67 ± 0.23	13.75 ± 2.58	1.57 ± 0.14	43.10 ± 12.51	147.3 ± 12.30	130.37 ± 11.85
Port Dennison	unveg	1.27 ± 0.70	47.57 ± 5.69	2.92 ± 0.51	115.23 ± 36.75	133.20 ± 15.19	135.66 ± 11.10
	veg	0.76 ± 0.29	6.31 ± 0.87	1.60 ± 0.16	38.64 ± 14.66	85.57 ± 4.46	66.44 ± 12.39
Geoffrey Bay	unveg	0.04 ± 0.01	31.73 ± 5.81	2.63 ± 0.18	183.30 ± 43.49	11.40 ± 3.61	394.22 ± 25.17
	veg	0.09 ± 0.02	28.68 ± 4.01	3.15 ± 0.45	252.49 ± 34.65	17.59 ± 3.78	408.30 ± 32.51
Horseshoe Bay	unveg	0.02 ± 0.003	73.47 ± 18.74	0.95 ± 0.09	191.02 ± 13.16	96.48 ± 5.08	153.13 ± 5.53
	veg	0.03 ± 0.007	144.43 ± 25.12	0.69 ± 0.10	229.96 ± 10.27	124.41 ± 13.22	144.72 ± 8.32
Muddy locations							
Ellie Point	unveg	0.44 ± 0.15	45.27 ± 6.94	2.82 ± 0.48	88.00 ± 31.65	312.80 ± 28.75	228.66 ± 22.03
	veg	0.41 ± 0.13	1.84 ± 0.09	0.84 ± 0.06	532.47 ± 152.66	353.19 ± 47.81	142.57 ± 12.10
Meunga Ck	unveg	2.28 ± 0.78	66.75 ± 9.39	6.08 ± 1.04	299.66 ± 60.58	459.04 ± 21.89	286.47 ± 22.68
	veg	3.12 ± 1.08	86.85 ± 7.15	2.65 ± 0.46	563.11 ± 40.67	820.08 ± 61.85	471.21 ± 64.92
Bolger Bay	unveg	0.66 ± 0.16	70.04 ± 6.52	1.32 ± 0.22	210.55 ± 15.08	439.98 ± 45.65	341.94 ± 29.27
	veg	0.32 ± 0.13	59.35 ± 6.34	2.20 ± 0.47	257.72 ± 24.71	482.83 ± 75.81	328.36 ± 42.40
Windy Point	unveg	0.43 ± 0.16	18.99 ± 3.04	0.99 ± 0.13	91.77 ± 21.63	167.72 ± 12.21	251.11 ± 16.88
	veg	0.17 ± 0.09	2.47 ± 0.25	0.85 ± 0.16	203.11 ± 59.16	225.34 ± 21.78	240.36 ± 34.10

Table 3. The results of univariate ANOVAs for nutrient parameters from sandy and muddy locations.

Variable	Location SS[1]	Site SS	F(df)	P
Sandy locations				
adsorbed PO_4^{3-} (bicarbonate)	307,206.9	1,399.00	0.30	0.620
adsorbed PO_4^{3-} (bray)	51,089.8	12.00	0.001	0.934
adsorbed NH_4^+	132,664.0	2,678	0.20	0.686
interstitial PO_4^{3-}	0.77	0.014	2.05	0.284
interstitial NH_4^+	1.7822	0.0018	0.02	0.908
interstitial $NO_2^- + NO_3^-$	4.1486	.2346	0.14	0.736
Muddy locations				
adsorbed PO_4^{3-} (bicarbonate)	0.58	0.002	0.03	0.879
adsorbed PO_4^{3-} (bray)	1.38	0.13	5.04	0.111
adsorbed NH_4^+	1.60	1.58	5.76	0.096
interstitial PO_4^{3-}	5.83	1.21	1.84	0.268
interstitial NH_4^+	28.41	8.50	2.35	0.223
interstitial $NO_2^- + NO_3^-$	1.94	0.019	0.47	0.540

[1]Sums of squares.

No significant differences were detected between vegetated and unvegetated sites for any of the nutrient parameters (Table 3). Comparison of the Location sums of squares and the Site sums of squares showed that, with the exception of adsorbed NH_4^+, most of the data variance was allocated to differences between locations (Table 3). For adsorbed NH_4^+ the variance was partitioned equally between Location and Site (Table 3) and a trend was obvious, with concentrations of adsorbed NH_4^+ being greater in vegetated sites (Fig. 3C), although the difference is not significant (Table 3, P = 0.096).

Discussion

Across a range of mud and sand localities in a tropical intertidal habitat, the paradigm of seagrass meadows trapping sediments and nutrients did not hold. Interstitial and adsorbed nutrient concentrations and sediment grain size distributions were not significantly different between seagrass meadows and adjacent unvegetated sites. Seagrass functional form and biomass were considered important in determining sedimentation processes. The relatively high biomass and stable *Z. capricorni* meadows showed trends towards an increase in sedimentation and a decrease in nutrient concentration (increases in nutrient utilisation) in vegetated than in unvegetated areas (Fig. 3B,C). In contrast, no trends were evident in the low biomass meadows of *H. uninervis* and *H. ovalis* (Fig. 3A,B,C).

The seagrass biomass values reported here are comparable to those reported elsewhere in tropical Queensland (Lee Long et al., 1993). These values are less than values quoted for temperate Australian waters (see Hillman et al., 1989), and do not approach the recorded maxima for Caribbean seagrass beds (Bauersfield et al., 1969), North American beds (McRoy, 1970) or Mediterranean seagrass beds (Gacia et al., 1999). Most seagrass species in the central region of the Great Barrier Reef World Heritage Area are structur-

ally small and bed formations are ephemeral compared with temperate seagrass communities and some other tropical regions. Regardless of their diminutive state, these seagrasses play a central role in supporting grazing by large populations of macro-herbivores (dugongs and green turtles)(Aragones and Marsh 2000).

In some of the nutrient and sediment parameters, differences between vegetated and unvegetated sites were evident, but these differences were not significant once the influence of location was removed. The two *Z. capricorni* meadows had the highest biomass (1200 times that of *H. ovalis*) and occurred in areas low in interstitial nutrients while *H. uninervis* was associated with high interstitial nutrients suggesting a difference in these species nutritional requirements or their ability to modify their nutrient environment.

This study shows that seagrass meadows of structurally small species do not act in accordance with the paradigm that seagrasses trap sediments and nutrients. Within these beds, none of the measured nutrient parameters demonstrated evidence for detrital cycling in sediments. All measurements showed low organic content and no difference in sediment structure or nutrient state between vegetated and unvegetated sites. However, the paradigm was partially supported in the meadows of *Z. capricorni* (high biomass) that are similar in functional form to the meadows and species that have contributed to the 'trapping' paradigm.

CONCLUSION

Within the central region of the Great Barrier Reef World Heritage Area, *Zostera capricorni* has maintained beds of relatively high biomass that have persisted for decades (Coles et al.,1985). Seagrass beds of this species are more comparable to those that have been shown to alter the sediment in their habitat than the more empheral species that dominate this region. *H. uninervis* and *H. ovalis* meadows were not found to trap sediments or nutrients. The functional form model of Walker et al. (1999) allows conceptualization of how different seagrass species form functionally different meadows and should be tested over a variety of seagrass habitats. In tropical Australia, the 'trapping' paradigm is largely insignificant as this region is typified by species that create low biomass ephemeral seagrass meadows in the intertidal coastal regions of the central section of the Great Barrier Reef World Heritage Area.

ACKNOWLEDGMENTS

Literature Cited

Almasi, M. N., G. M. Hoskin, J. K. Reed and J. Milo. 1987. Effects of natural and artificial *Thalassia* on rates of sedimentation. J. Sed. Petro. 57: 901–906.

Aragones, L. and H. Marsh. 2000. Impact of dugong grazing and turtle cropping on tropical seagrass ecosystems. Pac. Conserv. Biol. 5: 277–288.

Blackburn, T. H. 1990. Elemental cycles. Pages 167–176 (Chapt. 29) *in* R. C. Phillips and C. P. McRoy, eds. Seagrass research methods UNESCO, Paris.

Blakemore, L .C., P. L. Serale and B. R. Daly. 1987. Methods of chemical analysis of soils. New Zealand Soil Bureau, Scientific Rpt. 80.

Baker, D. E. and E. J. Eldershaw. 1993. Interpreting soil analysis for agricultural land use in Queensland. (Department of Primary Industries: Queensland) Project Rpt. Ser. QO93014.

Boon, P. I. 1986. Nitrogen Pools in seagrass beds of *Cymodocea serrulata* and *Zostera capricorni* of Moreton Bay, Australia. Aquat. Bot. 25: 1–19.

Bray, R. M. and L. T. Kurtz. 1945. Determination of total organic and available forms of phosphorus in soils. Soil Sci. 59: 39–45.

Bauersfield, P., R. R. Kifer, N. W. Durrant and J. E. Skyes. 1969 Nutrient content of Turtle grass (*Thalassia testudinum*). Proc. Int'l. Seaweed Symp. 6: 637–645.

Caffrey, J. M. and W. M. Kemp. 1990. Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliates* and *Zostera marina*. Mar. Ecol. Prog. Ser. 66: 147–160.

Christiansen, C., H. Christoffersen, J. Dalsgaard and R. Norberg. 1981. Coastal and nearshore changes correlated with die-back in eelgrass (*Zostera marina* L.). Sed. Geol. 28: 163–173.

Duarte, C. 1999. Seagrass ecology at the turn of the millennium: challenges for the new century. Aquat. Bot. 65: 7–20

Erftemeijer, P. L. A. and J. J. Middelburg. 1993. Sediment interactions in tropical seagrass beds: a comparison between a terrigenous and a carbonate sedimentary environment in South Sulawesi (Indonesia). Mar. Ecol. Prog. Ser. 102: 187–198.

Gacia , E., T. C. Granata and C. Duarte. 1999. An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. Aquat. Bot. 65: 255–268.

Gale, S. J. and P. G. Hoare. 1991. Quaternary sediments. Petrographic methods for the study of unlithified rocks. Belhaven Press Halsted Press, Toronto. 323 p.

Hemminga, M. A. and C. M. Duarte. 2000. Seagrass ecology. Cambridge Univ. Press, Cambridge. 298 p.

Hillman, K., D. I. Walker, A. W. D. Larkum and A. J. McComb. 1979. Productivity and nutrient limitation. Pages 635–685 *in* A. W. D Larkum, A. J. McComb and S. A. Shepherd, eds. Biology of seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region Elsevier, Amsterdam.

Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecol. 19: 89–110.

Iizumi, H and A. Hattori. 1982. Growth and organic production of eelgrass (Zostera marina L.) in temperate water of the Pacific Coast of Japan III. The kinetics of nitrogen uptake Aquat. Bot. 12: 245–256

Kenworthy, W. J., J. C. Zieman and G. W. Thayer. 1982. Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA) Oecologia (Berl) 54: 152–158

Lee Long, W. J., J. E. Mellors and R. G. Coles. 1993. Seagrasses between Cape York and Hervey Bay, Queensland, Australia. Aust. J. Mar. Freshw. 44: 19–31.

Maxwell, W. G. H. 1968. Atlas of the Great Barrier Reef. Elsevier Publ. Co., London.

McGlathery, K. J., R. Marino and R. Howarth. 1994. Variable rates of phosphate uptake by shallow marine carbonate sediment: Mechanisms and ecological significance. Biogeochem. 25: 127–146.

McRoy, C. P. 1970. Standing stocks and other features of eelgrass (*Zostera marina*) populations on the coast of Alaska. J. Fish. Res. Bd. Canada 27: 1811–1821

_____ and C. McMillan. 1977. Production ecology an physiology of seagrasses. Pages 53–87 *in* C. P. McRoy and C. Helfferich, eds. Seagrass ecosytems: A scientific perspective. Marine Science Series, vol. 4. Marcel Dekker, Inc., New York. 314 p

Mengel, K and E. A. Kirkby. 1987. Principles of plant nutrition. International Potash Institute, Switzerland. 687 p.

Moriarty, D. J. W. and P. I. Boon. 1989. Interactions of seagrasses with sediment and water. Pages 500–535 *in* A. W. D. Larkum, A. J. McComb and S. A. Shepherd, eds. Biology of seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.

Odum, E. P. 1959. Fundamentals of ecology. Saunders, Philadelphia. 521 p.

Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia , USA. Mar. Biol. 44: 187–194

Pailles, C. and P. W. Moody. 1995. Effect of experimental conditions on phosphorus extracted from estuarine and marine sediments Aust. J. Mar. Freshw. Res. 46: 435–440.

Pulich, W. M. Jr. 1985. Seasonal growth dynamics of *Ruppia maritima* L.s.l. and *Halodule wrightii* Aschers, in southern Texas and evaluation of sediment fertility status. Aquat. Bot. 23: 53–66.

Rayment, G. E. and F. G. Higginson. 1993. Australian laboratory handbook of soil and water chemical methods. Inkata Press, Sydney.

Ryle, V. D., H. R. Mueller and P. Gentein. 1981. Automated analysis of nutrients in tropical sea waters AIMS Data Rpt. III. AIMS OS 81 2, Townsville.

Scoffin, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. J. Sed. Petro. 40: 249–273.

_____. 1987. An introduction to carbonate cediments and rocks. Chapman and Hall, New York. 274 p.

Short, F. T. 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. Aquat. Bot. 27: 41–57.

Strickland, J. D. H. and T. R. Parsons. 1972. A practical handbook of seawater analysis. Fisheries Research Bd. Canada Bull. No. 167, 2nd. ed. Ottawa. 310 p.

Thayer, G.W., W.J. Kenworthy and M.S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic Coast : A community Profile. U.S. Fish Wildl. Serv. FWS/OBS-84/02 147 p.

Walker, D. I.., W. Dennison and G. Edgar. 1999. Status of seagrass research and knowledge. *In* A. Butler and P. Jernakoff, eds. 1999. Seagrass in Australia: Strategic review and development of an R & D plan (FRDC 1999)

Wilson, D. P. 1949. The decline of *Zostera marina* L. at Salcombe and its effects on the shore. J. Mar. Biol. Ass. UK 28: 395–412.

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