

## Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay

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**Abstract.** Seagrass meadows in Florida Bay and Shark Bay contain substantial stores of both organic carbon and nutrients. Soils from both systems are predominantly calcium carbonate, with an average of 82.1% CaCO<sub>3</sub> in Florida Bay compared with 71.3% in Shark Bay. Soils from Shark Bay had, on average, 21% higher organic carbon content and 35% higher phosphorus content than Florida Bay. Further, soils from Shark Bay had lower mean dry bulk density ( $0.78 \pm 0.01 \text{ g mL}^{-1}$ ) than those from Florida Bay ( $0.84 \pm 0.02 \text{ mg mL}^{-1}$ ). The most hypersaline regions of both bays had higher organic carbon content in surficial soils. Profiles of organic carbon and phosphorus from Florida Bay indicate that this system has experienced an increase in P delivery and primary productivity over the last century; in contrast, decreasing organic carbon and phosphorus with depth in the soil profiles in Shark Bay point to a decrease in phosphorus delivery and primary productivity over the last 1000 y. The total ecosystem stocks of stored organic C in Florida Bay averages  $163.5 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$ , lower than the average of  $243.0 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$  for Shark Bay; but these values place Shark and Florida Bays among the global hotspots for organic C storage in coastal ecosystems.

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### Introduction

Seagrass meadows are significant contributors to the carbon, nitrogen and phosphorus cycles in the ocean. Seagrasses grow on subaqueous soils – sedimentary deposits modified and structured by the input of organic matter from the rooted seagrasses (Demas *et al.* 1996). The annual rate of carbon accumulation in seagrass meadows:  $83 \text{ gC m}^{-2} \text{ year}^{-1}$  and global carbon burial rates of  $27\text{--}44 \text{ Tg C yr}^{-1}$  are an important component (10–18%) of the total carbon burial in the ocean (Duarte *et al.* 2005). High rates of C burial, combined with the stability of organic matter buried in the anoxic soils below seagrass meadows because of slow decomposition rates, lead to large deposits of organic carbon ( $C_{\text{org}}$ ), nitrogen (N) and phosphorus (P). The  $C_{\text{org}}$  storage on an areal basis is comparable in magnitude to that of terrestrial forests, mangroves and salt-marshes (Fourqurean *et al.* 2012). However, accounting of the total accumulated organic C and related storage of nitrogen and phosphorus in the world's seagrass meadows has only been done

in a handful of locations, and based largely on the  $C_{\text{org}}$  of surficial sediments. Here, we examine the depth distribution of  $C_{\text{org}}$  and nutrients in seagrass meadow soils from two of the best-studied subtropical seagrass-dominated regions, Florida Bay in south Florida, USA, and Shark Bay, Western Australia.

A plethora of data exists on the  $C_{\text{org}}$  (reviewed in Bouillon and Boschker 2006; Kennedy *et al.* 2010), N and P content as a percentage of dry mass of seagrass sediments, but data on the dry bulk density (DBD) of soils needed to convert these concentrations into volumetric storage in seagrass soils are more rarely published. Sediments generally undergo compaction after they are deposited, but the degree of compaction is largely a function of the rate of sediment deposition, weight of overlying soils, and the chemical composition and size of the sediment grains (Berner 1980), so it is problematic to assume general patterns in the changes in DBD with depth across systems. Further, direct measurements of  $C_{\text{org}}$  of seagrass soils are relatively rare in the literature compared with estimates based on loss on ignition

(LOI) and assumptions about the C content of the mass lost on ignition (Fourqurean *et al.* 2012). Further studies of the patterns in DBD with depth will enable a better understanding of the relationships between directly-measured  $C_{org}$  and values estimated from LOI, resulting in a more reliable accounting of C storage in the world's seagrass ecosystems.

Florida Bay and Shark Bay are two of the larger seagrass-dominated subtropical systems in the world. Florida Bay, a roughly 2000 km<sup>2</sup> area, is in the middle of a larger, ~18 000 km<sup>2</sup> area of semi-continuous seagrass beds in the south Florida region (Fourqurean *et al.* 2002). *Thalassia testudinum* is the dominant seagrass species in Florida Bay (Zieman *et al.* 1989). Seagrass meadows of south-west Australia are widely distributed across the region, from Shark Bay in the north to the Great Australian Bight in the south-east, occupying ~20 000 km<sup>2</sup> of shallow coastal habitat in this region (Carruthers *et al.* 2007). Shark Bay has ~4300 km<sup>2</sup> of seagrass meadows, of which ~85% are dominated by *Amphibolis antarctica* (Walker *et al.* 1988). Both bays have sediments dominated by carbonates, but they have very different hydrologic regimes: Florida Bay is downstream of the wetlands of the greater Everglades watershed, whereas the Shark Bay watershed is largely desert.

Both Shark Bay (Smith and Atkinson 1983; Smith 1984) and Florida Bay (Fourqurean *et al.* 1992; Fourqurean *et al.* 1993) are recognised as phosphorus-limited ecosystems with the major supply of P that contributes to ecosystem productivity coming from ocean water either brought in by tides or advection driven by the surplus of evaporation over precipitation and freshwater runoff responsible for the hypersaline nature of both systems. Down-core changes in the N and P content of sediment in Florida Bay cores are thought to correspond to historical changes in the availability of those nutrients, with more recent, higher P content of Florida Bay soils corresponding with an increase in P availability in Florida Bay beginning in the latter half of the twentieth century (Orem *et al.* 1999). Because climate controls the relative delivery of seawater and freshwater to these coastal ecosystems, and local climate has varied in the past and will continue to vary in the future, down-core changes in N and P content may help us to use historical patterns of nutrient deposition to predict how these systems will respond to future climate change.

We examine changes in bulk density,  $C_{org}$ , and N content and P content with depth in soils, and integrate this information over the area of seagrasses in these ecosystems to estimate ecosystem storage of  $C_{org}$ , N and P. We then use the down-core patterns in  $C_{org}$ , N and P content to make hypotheses about changes in ecosystem functioning in Florida Bay and Shark Bay over the period of record covered by the cores.

## Methods

### Site descriptions and site selection

#### Florida Bay

In August 1998, we collected surficial soil cores from 51 sampling stations on the south-west Florida Shelf and 24 stations in Florida Bay (Fig. 1). The P, S and Fe content of these samples have been published elsewhere (Chambers *et al.* 2001). Also deep cores of Holocene sediments that had accumulated

on Pleistocene bedrock were collected near Bob Allen Bank, Ninemile Bank, Trout Cove and Russell Key in Florida Bay in June and August 2002. At each location, two cores ~100 m apart were collected from the leeward sides of seagrass-covered accreting banks, which minimised the potential for inclusions of periods of low or no sedimentation. *Thalassia testudinum* dominated the seagrass meadows at the coring sites, but lesser amounts of *Halodule wrightii* and *Syringodium filiforme* were present at some of the sites. To sample a wide range of environments, we chose sites that have historically different sources of freshwater runoff and water exchange (Fourqurean and Robblee 1999). Paleontological and biomarker studies of these cores have been published elsewhere (Xu *et al.* 2006; Xu *et al.* 2007; Wachnicka *et al.* 2010; Cheng *et al.* 2012).

#### Shark Bay

During April 2011, we collected surficial soil cores from 61 sites on Wooramel Bank and Faure Sill (Fig. 1). These site locations were a combination of 20 sites at which prior studies had been conducted and 41 randomly-selected new sites. If no seagrass was present at the target coordinates, sampling was conducted in the seagrass bed nearest the target coordinates. A subset of eight of these locations was haphazardly selected for collecting deeper soil cores.

#### Seagrass biomass estimation

Large-diameter core tubes (15 cm in Florida Bay, 25 cm in Shark Bay) were inserted through the rhizome mat of seagrasses at each coring site to sample the seagrass biomass. Living seagrass material was separated from epiphytes, sediment and detritus, and separated by species. These samples were dried at 70°C and weighed, with total seagrass biomass (above and below ground components combined) expressed as g of dry weight m<sup>-2</sup>.

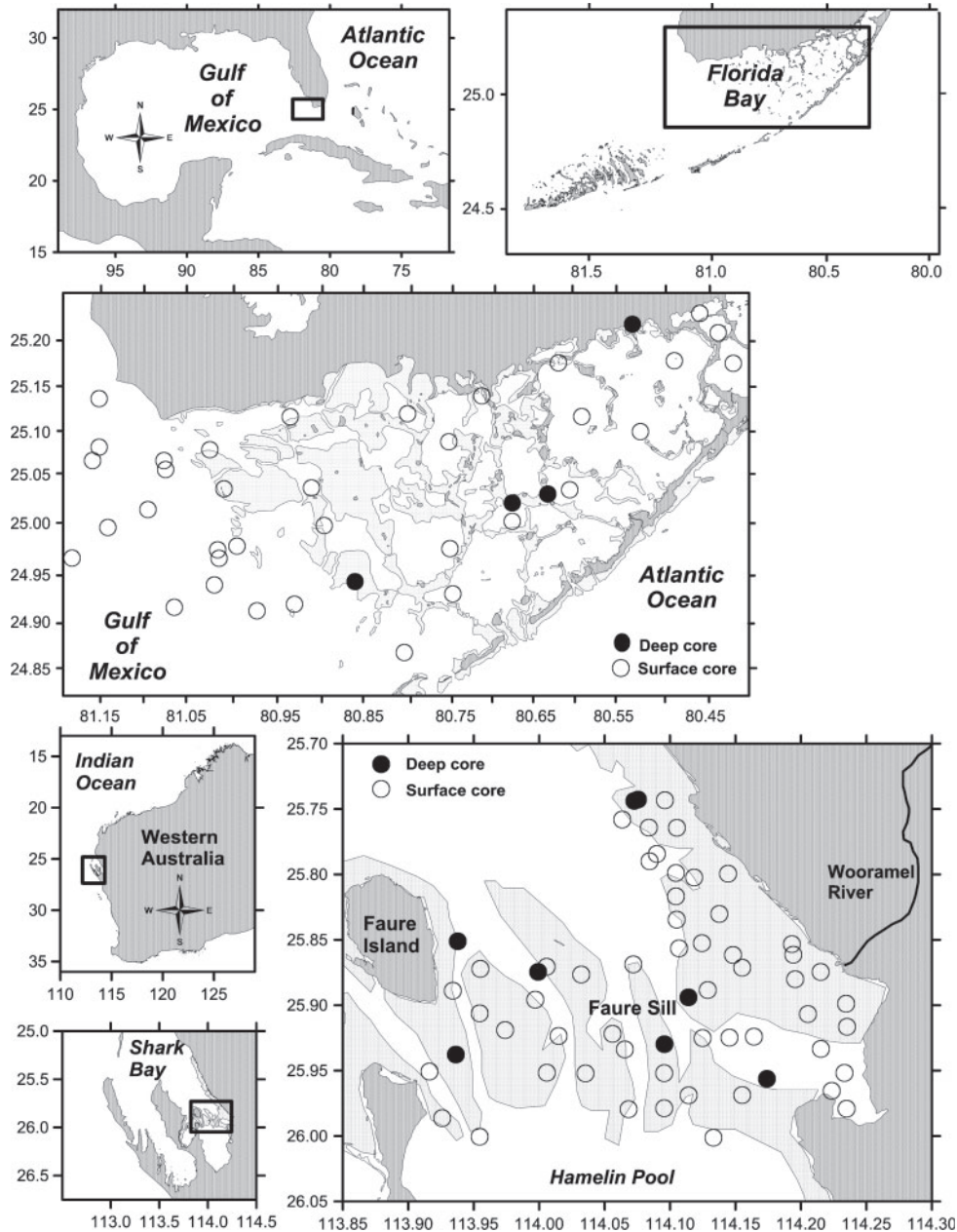
#### Core collection

##### Florida Bay

In August 1998, we collected surficial cores of the top 1 cm of soil from each site using duplicate piston corers made from cut-off polyethylene syringes (~1 cm diameter) that were inserted 1 cm into the soil, capped, retrieved and frozen until later analysis. We collected eight deep profile soil cores using a barge-mounted tripod and PVC piston corer (10.25 cm diameter, using the methods of Sansone *et al.* 1994). Cores were pushed through the soil until they reached the underlying Pleistocene rock. Cores were between and 96 and 244 cm long. The cores were sliced completely into 2-cm-thick samples for analysis.

##### Shark Bay

In April 2011, we collected surficial sediment cores from each site using duplicate piston corers made from cut-off 60 mL polyethylene syringes (2.9 cm diameter) that were inserted ~8 cm into the soil, capped, retrieved and frozen until later analysis. The top 5 cm of these cores were analysed, and the means of the duplicates were calculated to represent each site. During the same field trip, we collected deep sediment cores using a 5.2 cm diameter, diver-operated piston corer that was driven in to the sediments until refusal using a sledge hammer. The deep cores in Shark Bay did not penetrate the entire

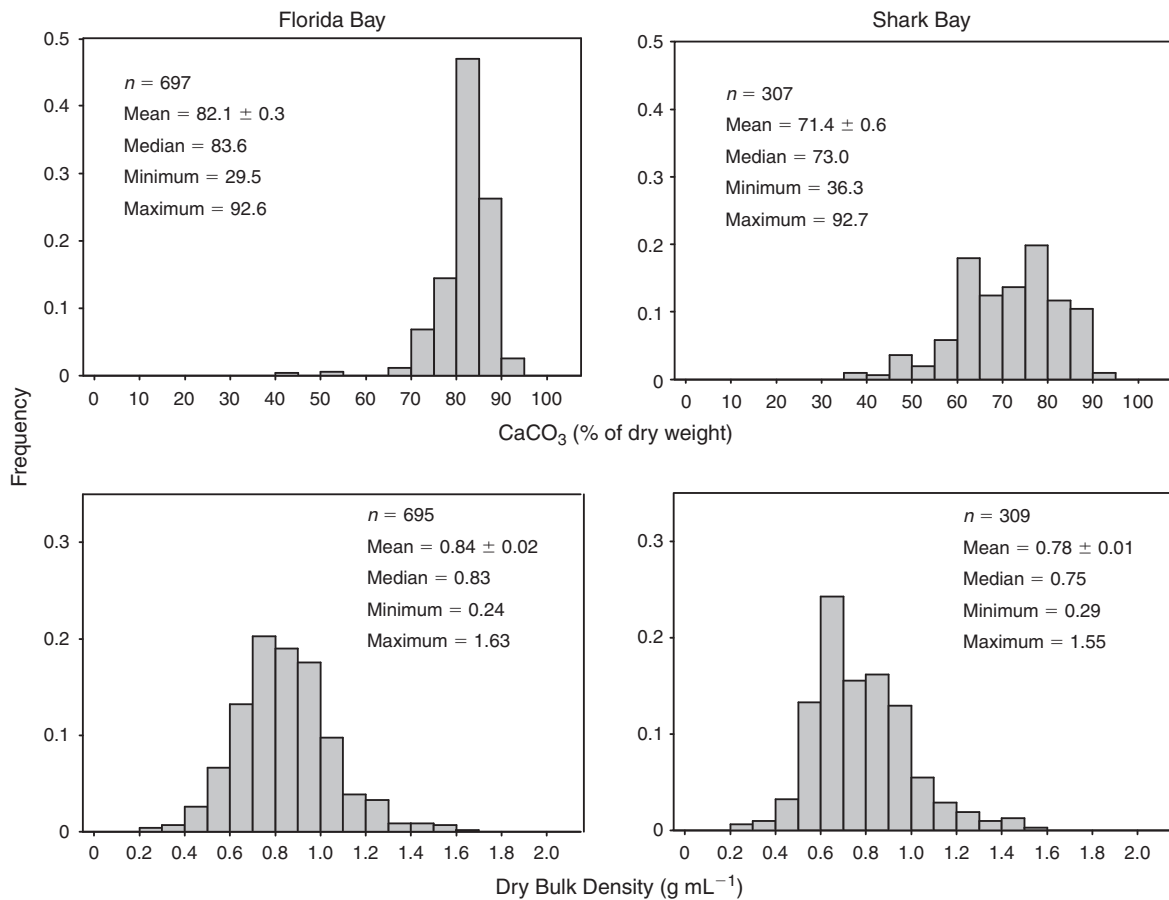


**Fig. 1.** Location maps and details of coring locations for seagrass soil cores taken from Florida Bay, Florida, USA (top panels) and Shark Bay, Western Australia, Australia (bottom panels). Filled circles indicate locations of cores taken for depth profiles, open circles indicate locations of surficial cores of the top 5 cm. Light stippled areas on the detail maps indicate shallow (<1 m deep) mud and sand banks.

thickness of accumulated soil as was the case for the Florida Bay cores. These deeper Shark bay cores ranged from 55 to 138 cm long. The core tube was pre-drilled with 2.5 cm diameter sampling ports at 3 cm intervals, these ports were covered with duct tape during the coring process. Cores were extracted from the sediment, kept upright, and returned to shore for subsampling. The tape was slowly peeled downward to reveal the sampling ports; a piston sub-corer made of a 25 mL cut-off polyethylene syringe (2.0 cm diameter) was inserted into each port to extract a sample of known volume.

#### Sample analyses

Samples from each depth layer were used to analyse sediment porosity, dry bulk density, organic content and elemental content (C, N, P). Soil samples of known volume were transferred into pre-weighed 20 mL glass scintillation vials and wet weight was calculated. The sample was dried at 70°C for a minimum of 48 h to obtain a dry weight. Dry bulk density (DBD) was calculated as the dry weight of the sediment divided by the volume of the original soil sample. A subsample of each sample was



**Fig. 2.** Frequency distributions for Dry Bulk Density (DBD) and calcium carbonate (CaCO<sub>3</sub>) content of seagrass soils from Florida Bay and Shark Bay. Data from both surficial and deep cores are included in the plots. Confidence intervals around mean are 95% CI.

ashed at 500°C for five hours and organic content was calculated as loss on ignition (LOI). Dry soil samples were ground using a ceramic mortar and pestle and total nutrients (C, N and P) were determined. Powdered samples were analysed in duplicate for total carbon (TC) and nitrogen content using a CHN analyzer (Fisons NA1500). Ashed soils were also analysed for total inorganic carbon (IC) and the percentage of organic carbon (C<sub>org</sub>) was calculated as the difference between IC and total carbon (TC). Estimation of the calcium carbonate content of the samples was performed using the IC values and assuming a molecular formula of CaCO<sub>3</sub>. Phosphorus content was determined by a dry-oxidation, acid hydrolysis extraction followed by a colourimetric analysis of phosphate concentration of the extract (Fourqurean *et al.* 1992). Elemental content was calculated on a dry weight basis; elemental ratios were calculated on a molar basis.

We calculated the mass of C<sub>org</sub>, N and P stored in the top metre of the soil profile at each deep coring site in Florida Bay and Shark Bay using for each core slice the volume, bulk density, and the C<sub>org</sub>, N and P contents, from the surface to 1 m deep. For two cores that did not extend to 1 m deep, we assumed that the bulk density and elemental content for the part of the profile below the depth of the core but above

1 m deep were constant at the values of the bottommost core slice in that profile.

#### Statistical analyses

Distributions of data were tested for normality before analyses. Distributions of measured sediment parameters in general were not normal, so tests for differences in sediment characteristics between bays were performed using the Mann–Whitney U test (PASW Statistics 18, SPSS Inc., IBM Corporation, Armonk, NY, USA). Correlations among sediment characteristics within bays were conducted using the nonparametric Spearman's  $\rho$  test (PASW Statistics 18). Linear regression tested for the ability of LOI to predict C<sub>org</sub> within each bay and for trends in soil properties with depth in the cores (PASW Statistics 18).

#### Results

The distribution of seagrasses in Florida Bay has been well described elsewhere (Zieman *et al.* 1989; Fourqurean *et al.* 2002); the seagrasses in our sampling area were dominated by *Thalassia testudinum* in the eastern parts of the system and by *Syringodium filiforme* and *Halophila decipiens* in the western parts of our study area. *Halodule wrightii* was a common species

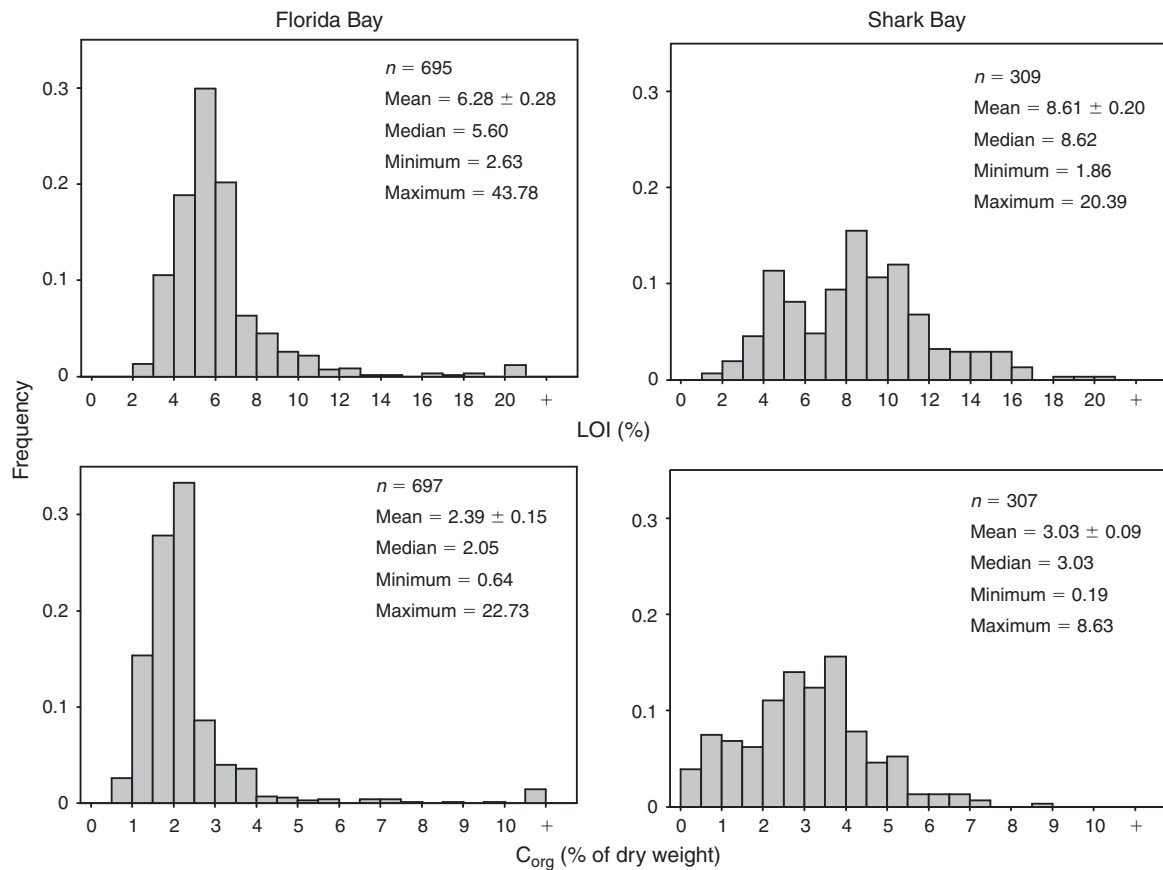


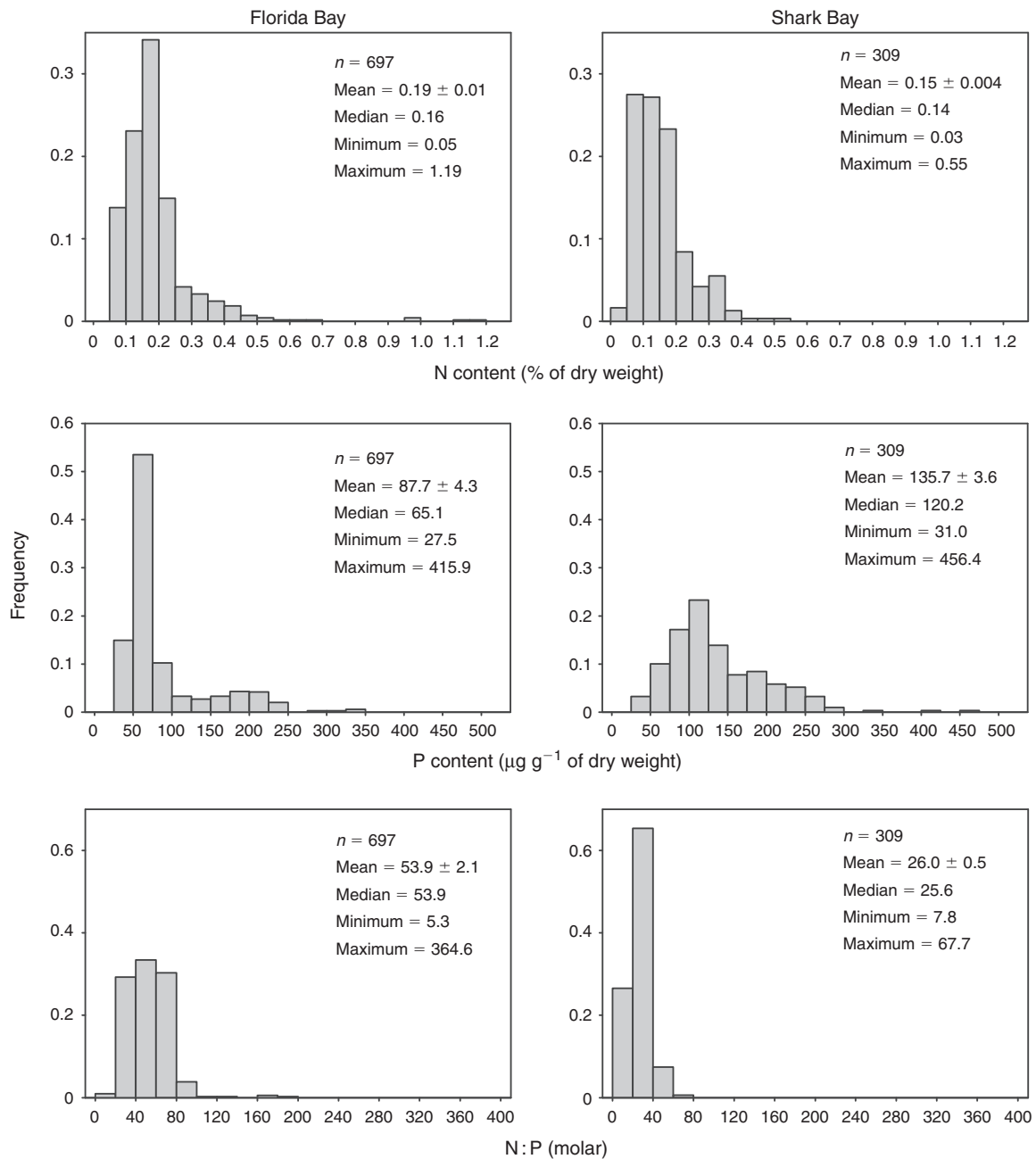
Fig. 3. Frequency distributions for Loss on Ignition (LOI) and Organic Carbon content ( $C_{org}$ ) of seagrass soils from Florida Bay and Shark Bay. Data from both surficial and deep cores are included in the plots. Confidence intervals around mean are 95% CI.

encountered but rarely was the dominant seagrass at a site. Unfortunately we did not collect seagrass species composition or biomass estimates at our surface sediment coring sites in Florida Bay. We did collect seagrass biomass estimates at our eight sediment profile deep core sites, where the communities were dominated by *T. testudinum* with a range in biomass (above and below ground combined) of 104–205  $g\ m^{-2}$ , with a mean of 144  $g\ m^{-2}$  ( $n = 8$ ). Although the seagrass meadows of all of Shark Bay are among the world's most diverse (Walker *et al.* 1988; Burkholder *et al.* in press), seagrass biomass in our study area was dominated by *Amphibolis antarctica*, which occurred at densities from 0–2414  $g\ m^{-2}$  with a mean of 468  $g\ m^{-2}$  ( $n = 47$ ). *Halodule uninervis* was also commonly encountered, but at much lower biomass, with a range of 0–63  $g\ m^{-2}$ , with a mean of 7  $g\ m^{-2}$  ( $n = 47$ ). We did observe other seagrass species in the study area, including *Halophila ovalis*, *Syringodium isoetifolium*, *Cymodocea angustata* and *Posidonia australis*, but none of these species occurred in our biomass samples.

The inorganic fraction of the soil in both Shark Bay and Florida Bay was composed predominantly of calcium carbonate grains. Florida Bay sediments ranged from 29.5 to 92.6%  $CaCO_3$ , with a mean of  $82.1 \pm 0.3\%$  ( $\pm 1\ s.e.$ ). The low- $CaCO_3$  samples from Florida Bay coincided with high organic content. A similar range was found in the  $CaCO_3$  content of Shark Bay sediments (36.3 to 92.7%), but the low- $CaCO_3$  in Shark Bay

samples was caused by siliceous grains contributing to the sediment, especially along the eastern shore of the bay.  $CaCO_3$  content in Shark Bay sediments (mean of  $71.3 \pm 0.6\%$ ) was significantly lower than Florida Bay sediments (median test,  $P < 0.001$ ). Sediments from Florida Bay had significantly higher DBD, by an average of  $0.06 \pm 0.01\ g\ mL^{-1}$  than sediments from Shark Bay (Fig. 2, Mann–Whitney U test,  $P < 0.001$ ). This higher DBD corresponded with a significantly higher average  $CaCO_3$  content in Florida Bay soils compared with Shark Bay soils (Fig. 2, means test,  $P < 0.001$ ). Most soil samples were greater than 50% by weight composed of  $CaCO_3$  in both bays. Concomitant with the differences in DBD and  $CaCO_3$  content, the LOI of Florida Bay soil was significantly lower than to Shark Bay sediments (Fig. 3, Mann–Whitney U test  $P < 0.001$ ). The lower DBD, higher LOI sediments from Shark Bay had, on average,  $C_{org}$  values  $0.6 \pm 0.1\%$  higher than the Florida Bay sediment (Fig. 3, Mann–Whitney U test,  $P < 0.001$ ).

Soils from Florida Bay had slightly, but significantly, higher N content compared with sediments from Shark Bay (Fig. 4, mean average difference =  $0.034 \pm 0.006\%$ , Mann–Whitney U test,  $P < 0.001$ ). The difference in P content of the soils was much larger than the differences in N content; P content of Shark Bay sediments was  $48.0 \pm 4.2\ \mu g\ g^{-1}$  higher than the Florida Bay sediments (Mann–Whitney U test,  $P < 0.001$ ). The higher



**Fig. 4.** Frequency distributions of Nitrogen and Phosphorus content and molar N:P for seagrass soil samples from Florida Bay and Shark Bay. Data from both surficial and deep cores are included in the plots. Confidence intervals around mean are 95% CI.

N content and lower P content of Florida Bay sediments resulted in N:P values for the Florida Bay sediments almost twice as high as the N:P of Shark Bay sediments (Mann-Whitney U test,  $P < 0.001$ ).

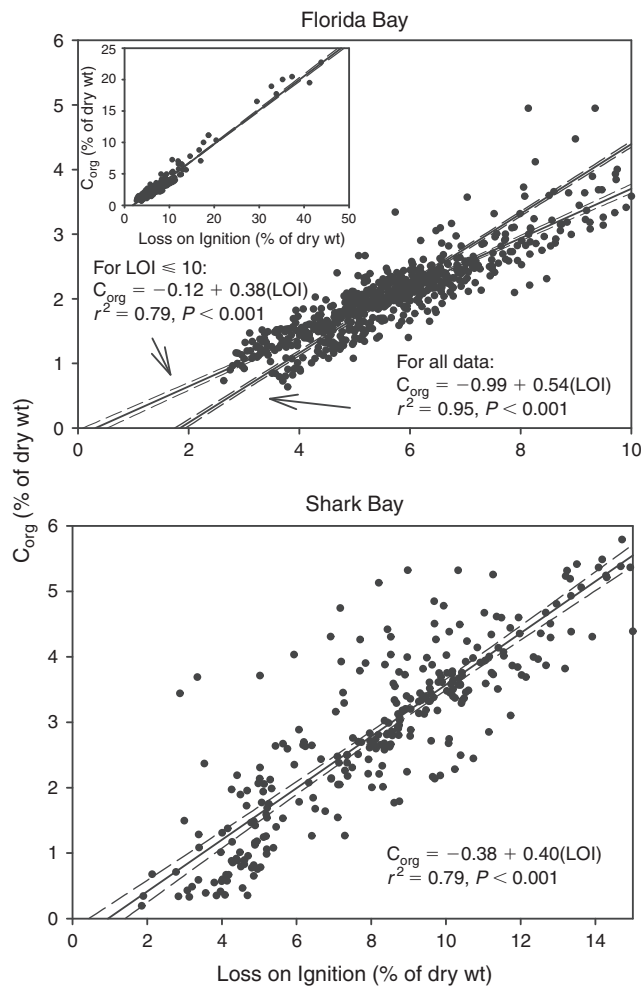
Many of the sediment property measures were correlated within the sampling areas (Table 1). In both systems, DBD was positively correlated with  $\text{CaCO}_3$  content, but negatively correlated with  $C_{\text{org}}$ , Soil N and Soil P.  $C_{\text{org}}$ , Soil N and Soil P were all positively correlated. Hence, samples with high  $\text{CaCO}_3$  content had low  $C_{\text{org}}$ , Soil N and Soil P. In Shark Bay, porosity was

negatively correlated with DBD, but there was no significant relationship between porosity and DBD in Florida Bay.

In Florida Bay, LOI was a good predictor of  $C_{\text{org}}$ . Regression of the entire range of LOI values yielded a slope of  $0.54 \pm 0.01$  (95% confidence interval) and a significantly ( $P = 0.007$ ) non-zero intercept suggesting loss of  $\sim 1\%$  of the dry weight on ignition of the samples that was not caused by the oxidation of organic compounds (Fig. 5). The relatively few high LOI data from mangrove peat soils at the base of the cores had a large influence on the slope of the relationship between LOI and  $C_{\text{org}}$ .

**Table 1. Spearman's  $\rho$  correlations between soil properties**Florida Bay correlations are above the diagonal, Shark Bay correlations are below the diagonal. \*\* indicates a significant correlation at  $P < 0.001$ 

	Porosity	DBD	CaCO <sub>3</sub>	C <sub>org</sub>	Soil N	Soil P
Porosity (%)		-0.037	-0.492**	0.516**	0.554**	0.544**
DBD	-0.767**		0.334**	-0.584**	-0.680**	-0.262**
CaCO <sub>3</sub>	-0.249**	0.403**		-0.796**	-0.542**	-0.501**
C <sub>org</sub>	0.527**	-0.722**	-0.655**		0.854**	0.494**
Soil N	0.756**	-0.871**	-0.491**	0.811**		0.550**
Soil P	0.605**	-0.648**	-0.395**	0.652**	0.730**	

**Fig. 5.** Relationship between Loss on Ignition (LOI) and independently measured organic carbon content of seagrass soils. In both bays, the  $y$ -axis intercepts were significantly different than zero, indicating that a small amount of mass is lost on ignition that is not associated with C<sub>org</sub>.

Restricting the analysis to the bulk of the seagrass soil samples with  $\text{LOI} \leq 10\%$  resulted in a lower slope ( $0.38 \pm 0.01$ ) compared with that for the entire dataset and a lower, but significantly non-zero, intercept ( $0.12\% \pm 0.04\%$ ). Similarly, in Shark Bay, LOI was a good predictor of C<sub>org</sub> (Fig. 5). The slope of the relationship for Shark Bay samples was  $0.40 \pm 0.02$ ,

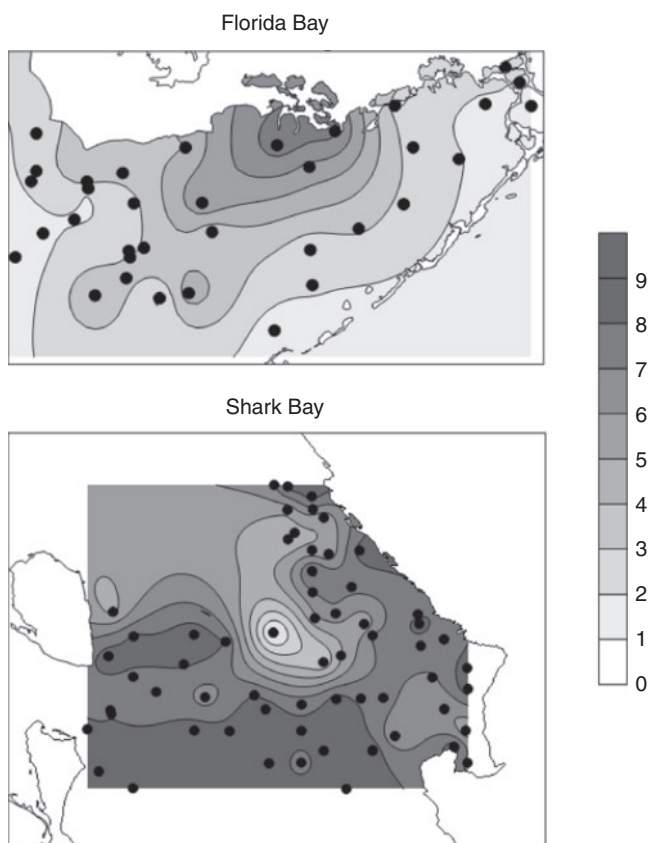
indistinguishable from the slope for low LOI samples from Florida Bay. The statistically significant ( $P = 0.031$ ) non-zero intercept of  $-0.38\% \pm 0.21\%$  indicates that Shark Bay samples also lost  $\sim 1\%$  of their mass on ignition unrelated to the combustion of organic matter.

Soil properties of the surface cores varied considerably across both bays (Table 2). Phosphorus content of surficial soil from Florida Bay averaged  $99.5 \pm 20.0 \mu\text{g g}^{-1}$  ( $\pm 95\%$  CI), compared with  $125.7 \pm 19.8 \mu\text{g g}^{-1}$  for Shark Bay. Spatial pattern in P content of these soil samples have been presented elsewhere: in general, P content of surface sediment decreases from west to east as distance to the Gulf of Mexico increases in Florida Bay (Chambers *et al.* 2001); similarly, P content decreases from N to S in Shark Bay as distance from the Indian Ocean increases (Atkinson 1987; Fraser *et al.* 2012). In Florida Bay, C<sub>org</sub> of surficial soil was highest in the central area of the bay adjacent to the coastline, where C<sub>org</sub> was in excess of 8% (Fig. 6). The pattern in C<sub>org</sub> in the surface soils in Shark Bay was more complex, with a general increase towards the south and towards the coastline (Fig. 6). Location within the bay was more important than seagrass density in determining the C<sub>org</sub> of the surface soil. In Shark Bay, where we had data on seagrass biomass and C<sub>org</sub> of surficial cores from the same sites, biomass was not a predictor of C<sub>org</sub> (linear regression,  $r^2 < 0.01$ ,  $P = 0.942$ ).

DBD was lowest at the top of the soil profiles in Florida Bay and increased gradually down core at a rate of between 0.155 and  $0.286 \text{ g mL}^{-1}$  per metre of core depth (Table 3), reflecting the compaction normally seen in sediment profiles and the general increases in CaCO<sub>3</sub> content with depth (Fig. 7a, Fig. 8a). At the bottom of the Ninemile 2, Bob Allen 1 and Bob Allen 2 cores, DBD and CaCO<sub>3</sub> content decreased, concomitant with peaks in C<sub>org</sub> (Fig. 9a). The bottoms of all of these cores were composed of mangrove peats, a common feature of the bottoms of cores from Florida Bay (Davies and Cohen 1989). Owing to the strong negative correlation between DBD and C<sub>org</sub> (Table 1), C<sub>org</sub> decreased down-core in six of the eight Florida Bay soil profiles (Table 3). Unlike in Florida Bay, no general pattern in DBD in the Shark Bay sediment profiles was observed: in three of the eight profiles, DBD increased with depth, but DBD decreased with depth in four and had no trend with depth in another (Fig. 7b, Table 3). Also, in contrast to the Florida Bay cores, there was not a general increase in CaCO<sub>3</sub> content with depth in Shark Bay; rather, at five of the eight cores, CaCO<sub>3</sub> content decreased with depth. Further, C<sub>org</sub> significantly increased with depth in seven of the eight Shark Bay cores

**Table 2. Soil properties of the shallow surface cores collected across Shark Bay and Florida Bay**  
Means are given  $\pm 95\%$  confidence interval, ranges of observed values are enclosed in parentheses. No nitrogen determinations were performed on the Florida Bay surface soil core samples.

	Florida Bay ( $n = 75$ )	Shark Bay ( $n = 62$ )
P content ( $\mu\text{g g}^{-1}$ )	$99.5 \pm 20.0$ (0.4–344.1)	$125.7 \pm 19.8$ (31.0–456.4)
N content (% of dry weight)	n.d.	$0.13 \pm 0.02$ (0.03–0.54)
$C_{\text{org}}$ (% of dry weight)	$2.1 \pm 0.3$ (0.4–7.6)	$1.9 \pm 0.4$ (0.2–8.6)
Dry Bulk Density ( $\text{g mL}^{-1}$ )	$1.0 \pm 0.1$ (0.3–1.5)	$0.9 \pm 0.1$ (0.3–1.6)



**Fig. 6.** Spatial pattern in the  $C_{\text{org}}$  content (in % of dry weight) of surface soil cores from Florida Bay and Shark Bay. Black spots indicate sample locations.

(Fig. 9b, Table 3), in contrast to the general decreases observed in the Florida Bay cores.

In the top metre of the soil profile, the Florida Bay core sites stored between  $124.3 \text{ Mg C ha}^{-1}$  and  $210.4 \text{ Mg C ha}^{-1}$ , with a mean of  $163.0 \text{ Mg C ha}^{-1}$  (Fig. 10). The core sites in Shark Bay had higher storage of  $C_{\text{org}}$ , ranging from  $115.3 \text{ Mg C ha}^{-1}$  to  $335.1 \text{ Mg C ha}^{-1}$ . The mean for Shark Bay sites was  $241.3 \text{ Mg C ha}^{-1}$ . In both systems, soil storage of  $C_{\text{org}}$  is higher than the  $C_{\text{org}}$  of the living seagrass biomass. Assuming that seagrass biomass is 35% organic carbon (Fourqurean *et al.* 2012), seagrass biomass  $C_{\text{org}}$  averaged  $0.5 \text{ Mg C ha}^{-1}$  at our Florida Bay sites and  $1.7 \text{ Mg C ha}^{-1}$  at our Shark Bay sites.

Soil N and P content decreased down-core in all of the Florida Bay cores (Figs. 11a, 12a, Table 3), paralleling the general decrease in the  $C_{\text{org}}$  of those cores. In Shark Bay, though, the pattern in N and P profiles was markedly different than those from Florida Bay, as was the case for  $C_{\text{org}}$  profiles. Phosphorus content significantly increased with depth in the cores at five of the eight Shark Bay cores with no cores showing significant decreases in P content with depth (Fig. 11b, Table 3). Nitrogen content showed no general trend with depth in the Shark Bay cores, with a significant decrease in N in core F17b, significant increases in cores F10b, 11–2 and 431, and no significant linear trend in the other four cores (Fig. 12b, Table 3).

Differences in the amount of P and N stored in the top metre of the seagrass meadows of Florida Bay and Shark Bay were not significant (t-test,  $P > 0.05$ ). On average, the top metre of soil contained  $0.82 \pm 0.09 \text{ Mg P ha}^{-1}$ , ranging from  $0.41 \text{ Mg P ha}^{-1}$  at the Trout 2 site to  $1.53 \text{ Mg P ha}^{-1}$  at the Ninemile 2 site, both in Florida Bay. Nitrogen stores were larger than the P stores, averaging  $12.4 \pm 1.1 \text{ Mg N ha}^{-1}$  across both bays. The lowest N store ( $6.5 \text{ Mg N ha}^{-1}$ ) was measured at the F17b site in Shark Bay, and the highest N store was measured at the Ninemile 2 site in Florida Bay.

## Discussion

The amounts of  $C_{\text{org}}$  and nutrients stored in the seagrass meadows of Florida Bay and Shark Bay are very large, and conservation of these ecosystems should be of high priority. The consequences of release of stored nutrients would have an impact on a regional scale, while the consequences of the release of  $C_{\text{org}}$  would have a global impact. Measuring the mass of accumulated materials is largely straightforward, and we found that methodologically simple techniques can be used to estimate the accumulated  $C_{\text{org}}$ . The patterns in down-core changes in  $C_{\text{org}}$ , N and P content of seagrass soils from Florida Bay and Shark Bay suggest very different histories of ecosystem function. In Florida Bay,  $C_{\text{org}}$ , N and P content all are higher in present-day surface soils than they are in the older sediments buried deeper in the soil profile, supporting previous work that has shown recent increases in P delivery, and therefore primary productivity, of this P-limited ecosystem (Orem *et al.* 1999). In sharp contrast, the soil cores from Shark Bay show a general increase in  $C_{\text{org}}$ , N and P with depth in the cores, suggesting that primary productivity of this system has decreased over time as P availability has declined.

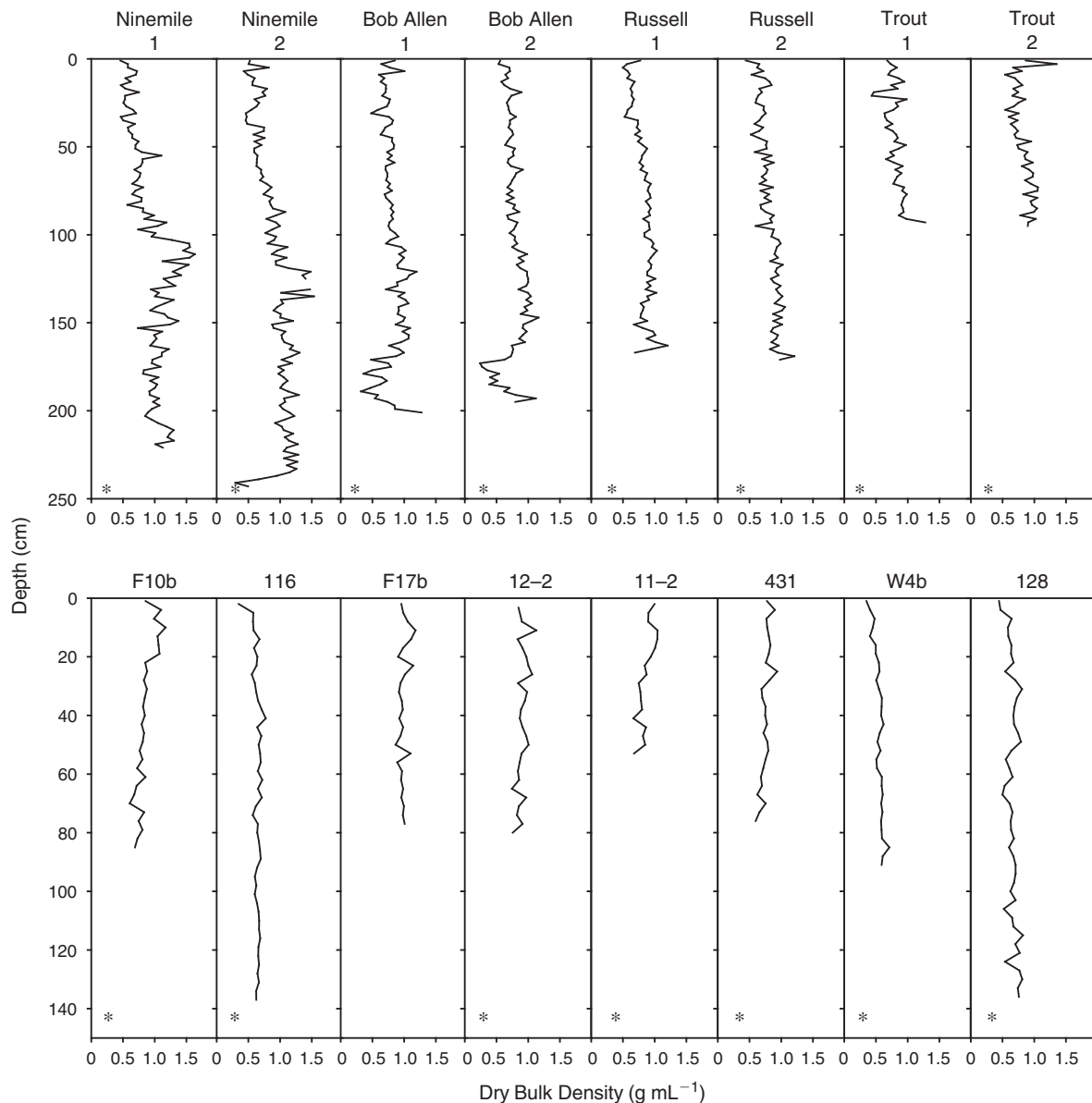
We attribute the general pattern of increasing DBD in our Florida Bay cores to be a result of compaction of the muds that make up most of the soils of Florida Bay (Bosence 1989), a well



**Table 3. Rates of change of soil properties with depth in the cores**

Values given are the estimates  $\pm 1$  s.e. for the slope from linear regression analyses of the property as a function of depth. Negative slopes indicate values that decrease with depth in the core. Asterisks indicate estimates significantly different from 0 (\* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ ). Values in parentheses are the  $r^2$  for the regression analyses. NS = so statistically significant linear trend with depth. For the two Bob Allen and the Ninemile Bank 2 sites from Florida Bay, the data were censored to remove the effect of the mangrove peat deposits in the bottoms of those cores

Core site	Rate of change with depth				
	DBD (g mL <sup>-1</sup> ) m <sup>-1</sup>	CaCO <sub>3</sub> % (dry wt) m <sup>-1</sup>	C <sub>org</sub> % (dry wt) m <sup>-1</sup>	N content% (dry wt) m <sup>-1</sup>	P content (µg g <sup>-1</sup> ) m <sup>-1</sup>
<b>Florida Bay</b>					
Ninemile Bank 1	0.269 ± 0.033*** (0.379)	5.1 ± 0.7*** (0.347)	-0.999 ± 0.092*** (0.522)	-0.137 ± 0.007*** (0.764)	-96.0 ± 3.8*** (0.853)
Ninemile Bank 2	0.238 ± 0.031*** (0.325)	2.7 ± 0.5*** (0.215)	-0.988 ± 0.078*** (0.581)	-0.132 ± 0.012*** (0.491)	-98.1 ± 3.7*** (0.857)
Bob Allen Bank 1	0.155 ± 0.024*** (0.324)	2.7 ± 0.4*** (0.332)	NS	-0.046 ± 0.007*** (0.307)	-15.3 ± 2.0*** (0.399)
Bob Allen Bank 2	0.171 ± 0.021*** (0.432)	2.7 ± 0.4*** (0.168)	-0.498 ± 0.084*** (0.297)	-0.029 ± 0.005*** (0.282)	-7.2 ± 1.66*** (0.185)
Russell Key 1	0.197 ± 0.023*** (0.484)	2.3 ± 0.7*** (0.120)	-0.330 ± 0.095*** (0.129)	-0.051 ± 0.005*** (0.581)	-8.8 ± 2.0*** (0.184)
Russell Key 2	0.225 ± 0.019*** (0.614)	2.9 ± 0.3*** (0.500)	-0.434 ± 0.052*** (0.453)	-0.054 ± 0.003*** (0.764)	-14.2 ± 1.4*** (0.544)
Trout Cove 1	0.286 ± 0.064*** (0.305)	NS	NS	-0.056 ± 0.010*** (0.417)	-161.3 ± 26.7*** (0.453)
Trout Cove 2	0.273 ± 0.073*** (0.234)	NS	-0.860 ± 0.147*** (0.428)	-0.049 ± 0.010*** (0.358)	-26.6 ± 4.4*** (0.446)
<b>Shark Bay</b>					
F10b	-0.421 ± 0.062*** (0.630)	11.7 ± 4.8* (0.347)	2.927 ± 0.568*** (0.496)	0.146 ± 0.016*** (0.754)	204.7 ± 22.6*** (0.752)
F116	0.048 ± 0.022* (0.096)	-3.1 ± 0.9*** (0.222)	0.482 ± 0.184* (0.135)	NS	68.1 ± 8.5*** (0.591)
F17b	NS	-6.9 ± 0.2** (0.319)	0.891 ± 0.371* (0.194)	-0.027 ± 0.004*** (0.645)	NS
I2-2	-0.165 ± 0.071* (0.186)	-10.7 ± 2.4*** (0.465)	2.107 ± 0.407*** (0.528)	NS	NS
I11-2	-0.527 ± 0.120*** (0.547)	-29.9 ± 7.4*** (0.347)	5.470 ± 1.176*** (0.575)	0.068 ± 0.025* (0.314)	127.1 ± 21.8*** (0.680)
431	-0.223 ± 0.049*** (0.461)	NS	2.713 ± 0.572*** (0.484)	0.103 ± 0.023*** (0.452)	79.8 ± 12.5*** (0.627)
W4b	0.210 ± 0.032*** (0.606)	7.1 ± 2.3** (0.252)	NS	NS	NS
128	0.087 ± 0.031** (0.154)	-8.0 ± 1.5*** (0.409)	0.904 ± 0.228*** (0.263)	NS	49.7 ± 6.7*** (0.556)

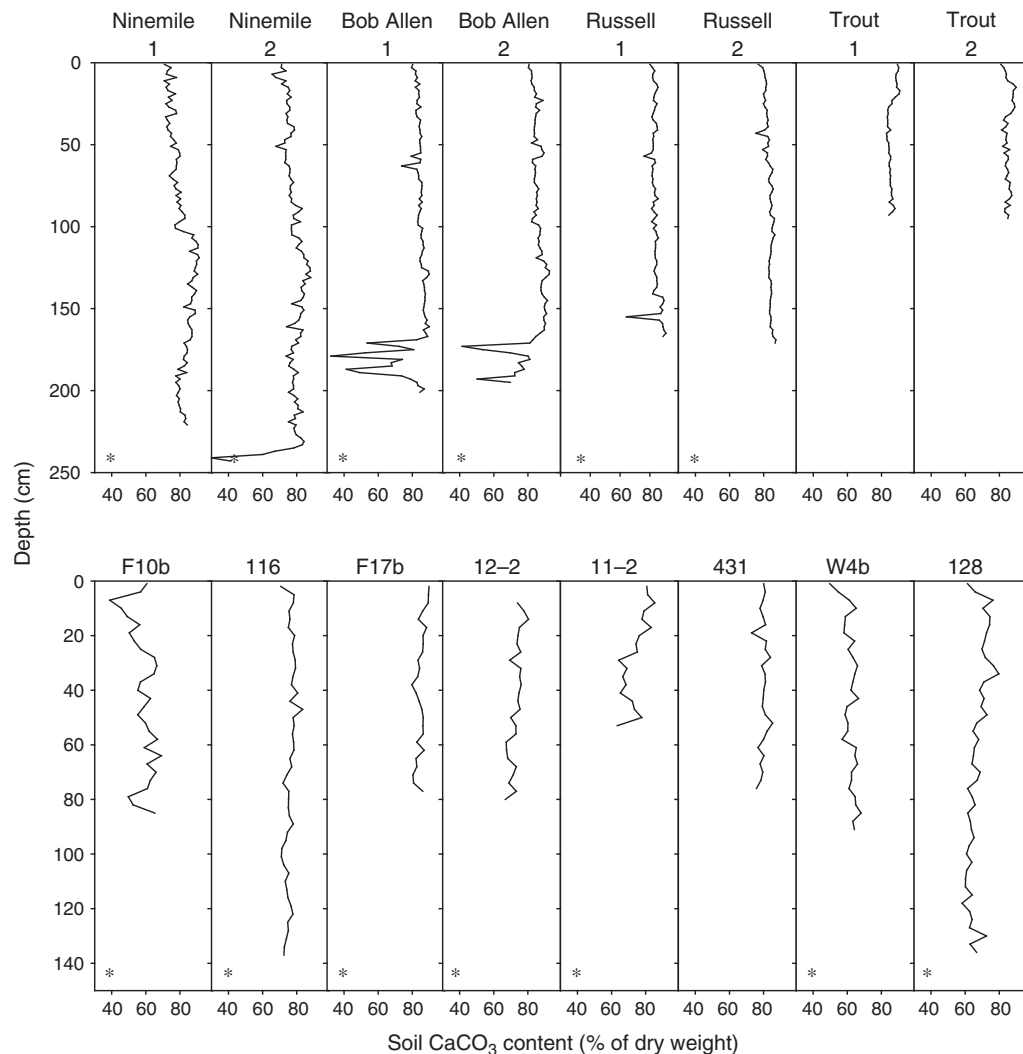


**Fig. 7.** Dry Bulk Density (DBD) changes with depth in the cores from Florida Bay (top panel) and Shark Bay (bottom panel). Cores are arranged from westernmost on the left to easternmost on the right within each bay. Asterisks indicate significant linear trends with depth (see Table 3). Note the different scales of the Y axes between top and bottom panels.

known phenomenon in muds (Berner 1980). The lack of a consistent pattern in DBD with depth in Shark Bay is likely a consequence of the coarser, sand-sized sediments characteristic of the Faure Sill (Logan *et al.* 1970; Logan *et al.* 1974), less compaction of sands (Berner 1980), and the increase in organic content down-core at some of the sites.

Decreases in  $C_{org}$  and N with depth in the soil, as we observed in Florida Bay, are to be expected owing to the mineralisation of organic matter produced by the benthic communities and allochthonous organic matter deposited in surficial sediments. Microbial degradation of labile organic compounds into  $CO_2$  consumes soil organic matter, and the anaerobic soils of seagrass meadows are important sites for denitrification and loss of fixed

nitrogen (Hemminga *et al.* 1991). Because over time respired C and N can outgas, the observed decreases in  $C_{org}$  and N with depth are not unequivocal signs of lower productivity in the past. The pattern of elevated P content in near-surface soils in Florida Bay, however, does suggest a recent increase in P delivery, and therefore productivity, through time. In surface soils of Florida Bay, 56% of the total P pool is carbonate-bound P, whereas 42% is composed of P in organic matter (Koch *et al.* 2001), and our data show that organic matter, and therefore the proportion of organic P, decreases down-core. Microbial respiration leads to remineralisation of the organic P, as well as dissolution of calcium carbonate in the soils, releasing P sorbed onto those particles (Jensen *et al.* 1998; Burdige and

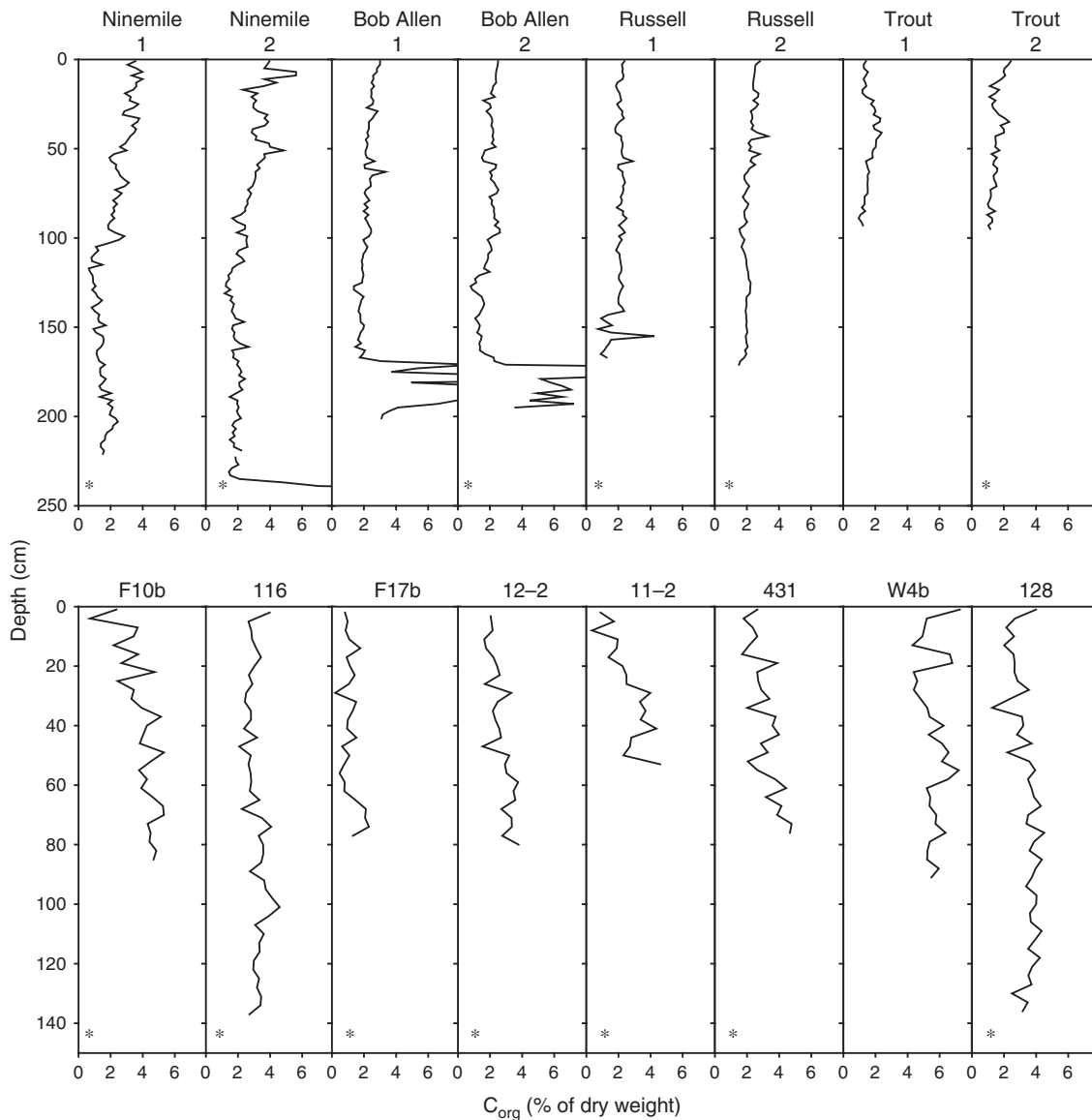


**Fig. 8.** Calcium carbonate ( $\text{CaCO}_3$ ) content changes with depth in the cores from Florida Bay (top panel) and Shark Bay (bottom panel). Cores are arranged from westernmost on the left to easternmost on the right within each bay. Asterisks indicate significant linear trends with depth (see Table 3). Note the different scales of the Y axes between top and bottom panels.

Zimmerman 2002; Burdige *et al.* 2008; Jensen *et al.* 2009). Carbonate dissolution, desorption and resorption of  $\text{PO}_4^{3-}$  onto carbonate particles would not lead to the observed increases in P concentration in surficial strata unless pore water flowed upward, which is not likely in the fine-grained, low hydraulic conductivity muds of Florida Bay. Further, the general increases we observed in carbonate content down-core in Florida Bay suggest that there has not been a significant net dissolution of  $\text{CaCO}_3$  in Florida Bay soils over the time represented by our cores. In the absence of any mechanism to remove respired P from deeper sediment, we believe the most parsimonious explanation for increases in P content in the most recent Florida Bay soils is increasing P supply. Given that microbial degradation of organic matter and denitrification should lead to decreases in  $\text{C}_{\text{org}}$  and N down-core in seagrass soils, the patterns we observed of increasing  $\text{C}_{\text{org}}$  and N down-core in Shark

Bay are particularly striking, and when coupled with the observations of increasing P content down-core, suggest that P supply and consequently productivity in Shark Bay have decreased over time. We don't think that increases in other environmental stresses, leading to decreased seagrass productivity and burial of seagrass-derived organic matter, in the recent in Shark Bay is a likely explanation of the decreases in  $\text{C}_{\text{org}}$  in the tops of the cores. Hypersalinity is the most pervasive environmental stress to seagrasses in the near-pristine Shark Bay ecosystem, and our surface sediment patterns show that in the present, more  $\text{C}_{\text{org}}$  is deposited in the surficial soils of the more hypersaline regions in our study site.

Age at depth for soils from Florida Bay have been estimated with  $^{210}\text{Pb}$  methods (Xu *et al.* 2007), allowing us to estimate the time course of the recent increase in P in Florida Bay. The last 100 years of the soil record are represented by the top 37 cm

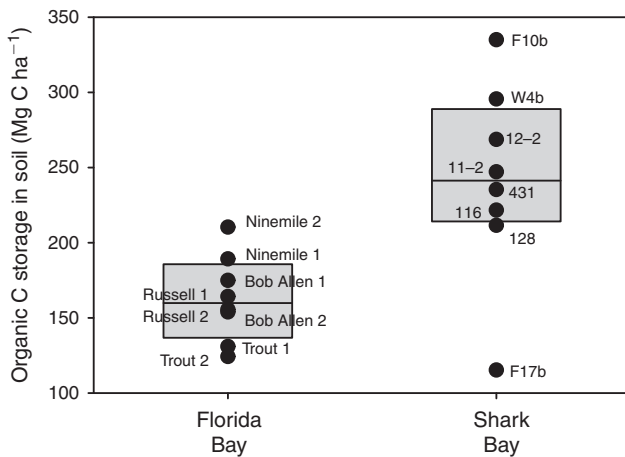


**Fig. 9.** Organic Carbon concentration ( $C_{org}$ ) changes with depth in the cores from Florida Bay (top panel) and Shark Bay (bottom panel). Cores are arranged from westernmost on the left to easternmost on the right within each bay. Asterisks indicate significant linear trends with depth (see Table 3). Note the different scales of the Y axes between top and bottom panels.

of the cores from the Bob Allen site, ~55 cm from the Trout Cove and Ninemile sites, and 112 cm for the Russell Key site. Using the slopes of the change in P content with depth we derived, P concentrations in the sediment have increased as much as  $50 \mu\text{g g}^{-1}$  in the last century at the seaward (Ninemile) and landward (Trout Cove) parts of Florida Bay, while increasing at a slower rate ( $4.2 \mu\text{g g}^{-1}$  at Bob Allen,  $12.6 \mu\text{g g}^{-1}$  at Russel Key) in the interior of Florida Bay. The increases in P content at Nimemile and Trout Cove are remarkable, considering the median measured P concentration for all Florida Bay samples was  $65.1 \mu\text{g g}^{-1}$ . This pattern in relative rates of increase across Florida Bay are what we would expect if increases in P availability in the last century were driven by changes in water-borne delivery of P to the system from both

the Gulf of Mexico and the Everglades watershed. Given the hydrological isolation of the interior of Florida Bay from both of these water and P sources by the anastomosing web of intertidal mudbanks of the interior of Florida Bay (Fourqurean *et al.* 1993; Nuttle *et al.* 2000; Swart and Price 2002), we would expect the interior parts of the bay to be more isolated from changes in these P sources.

Unfortunately, we do not have an age model for our Shark Bay cores, so the period over which productivity has declined is highly speculative. Faure Sill, the sedimentary feature from which our cores were collected, probably formed roughly 4200 ybp (Playford 1990), so our cores contain a record  $\leq 4200$  years and given that they are all 1 m or less in length and the deeper sediments on the Faure Sill are up to 4 m, they are at least



**Fig. 10.** Mass of organic C stored in soils at the Florida Bay and Shark Bay coring sites. The boxes indicate the median, 25th and 75th percentiles of the distribution within each bay; the values for the individual core sites are labelled.

1000 years old. Given the mobile nature of the sands that make up the sill (Logan *et al.* 1970; Logan *et al.* 1974) and the fact that we only sampled the top m or less of the soil, it is likely that our cores have recorded changes that have taken place over a considerably shorter interval than 4200 y. Given this constraint, we interpret our core data as suggesting that the delivery of P, the limiting nutrient for primary production in this system (Smith and Atkinson 1983; Smith 1984), to the Faure Sill region of Shark Bay, has declined markedly over the last millennium, leading to less primary production and less storage of  $C_{org}$  in soils in the present compared with the past. Currently, the main source of P to support primary production in Shark Bay is thought to be water brought into the bay from the Indian Ocean both by tidal excursion and because of net loss of water from the bay because evaporation exceeds precipitation (Smith and Atkinson 1983; Smith 1984; Atkinson 1987). Modern day P delivery may have been reduced due either to increased isolation of this part of the bay from the Indian Ocean caused by the vertical growth of the Faure Sill, by reduction in terrestrial runoff, or by reductions in atmospheric deposition of P.

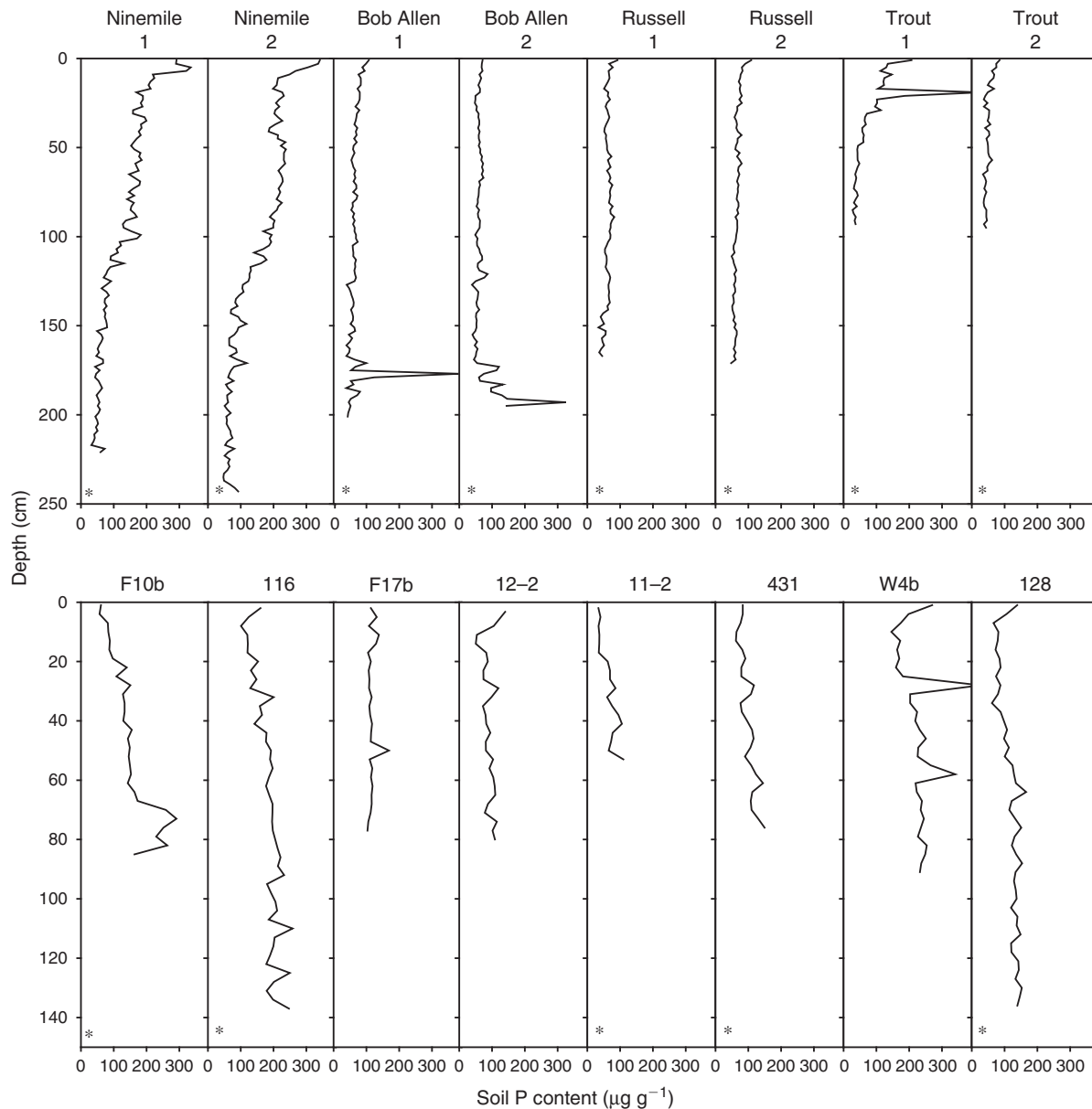
The quaternary evolution of the Faure Sill was well described by Logan *et al.* (1974) and their observations from cores suggest that seagrasses (*Posidonia australis*, *Amphibolis antarctica*) were more extensive in distribution and responsible for the formation of up to 10 m depth of sediments across the region when it was deeper water <8000 years b.p. The characteristic steep sides and flat-top of the contemporary Faure Sill developed as seagrasses trapped sediment and grew seaward and shallowed. The combined shallowing and heavy physical reworking of sediments resulted in an environment that is less suited for seagrass growth, and present day seagrasses account for less than 10% of the edges and tops of the banks and meadows are restricted to deeper channels and basins (Walker *et al.* 1988). Combined reduction in seagrass cover and increased physical reworking over millennia may thus account for the pattern of reduced  $C_{org}$  and nutrients in surface sediments, versus deeper sediments. There are no clear trends in palaeoclimate during this time that would suggest a wetter

environment and it appears generally the area was dryer in the past.

In addition to climate change over the last few millennia, human management actions may also be partly responsible for the patterns in P supply to Florida Bay and Shark Bay. Any management activity that alters freshwater inflow into either of these bays could impact P availability, because tidal exchange and the net inflow of ocean water into both systems to replace water lost from evaporation exceeding rainfall and runoff in both ecosystems are the main sources of P that drive productivity (Smith and Atkinson 1983; Fourqurean *et al.* 1992; Rudnick *et al.* 1999). Currently, stream flow is a small source of P in each system, but for different reasons: in Florida Bay, large amounts of terrestrial runoff enter the bay but the watershed effectively removes P, and P concentrations are extremely low (Fourqurean *et al.* 1993; Childers *et al.* 2006); whereas in Shark Bay, concentrations of P in freshwater runoff could be large but the volumes of freshwater discharge are very small so that loading rates of P via terrestrial runoff are currently unimportant at the systems scale (Smith and Atkinson 1983). Consequently, increases in terrestrial runoff would decrease P supply to Florida Bay because increased freshwater discharge would decrease advective flux into Florida Bay from the Gulf of Mexico (Childers *et al.* 2006) but increase P supply to Shark Bay because of increased river discharge. Flooding in the Gascoyne watershed for the Wooramel is predicted to increase under present climate change modelling for Western Australia. Future climate change is likely to have further influence on P supply and ecosystem productivity, as local relationships between rainfall, runoff and precipitation change.

The P-limited nature of both of these ecosystems has implications for the long-term effects of changes in nutrient delivery. P loading to seagrass beds in carbonate systems can be effectively trapped by a combination of biological uptake and abiotic adsorption onto carbonate particles (de Kanel and Morse 1978; Short *et al.* 1985). On the other hand, fixed nitrogen is lost from the system through denitrification (Hemminga *et al.* 1991). Both N and P can be lost from the system by export of organic matter from the seagrass beds, but the net loss of organic matter by export seems to be quite small in carbonate sediment seagrass meadows. In south Florida, budgetary analyses from fertilisation experiments suggests that, over the course of a few years, all of added P is retained in seagrass meadows but only ~25% of added N is retained (Ferdie and Fourqurean 2004; Armitage *et al.* 2011). Indeed, P retention in Florida Bay is so great that elevated P contents in surface sediments are still measurable decades after short-term fertilisation experiments whereas N concentrations return to ambient. Primary productivity, species composition and biodiversity are still elevated in plots of a three-year fertilisation experiment in Florida Bay seagrass beds over 20 years after the cessation of fertilisation (Herbert and Fourqurean 2008). Even short-term changes in P delivery in such P-limited systems can have long-lasting effects on ecosystem structure and function. In N-limited systems, however, short-term increases in N availability are likely to have transitory impacts.

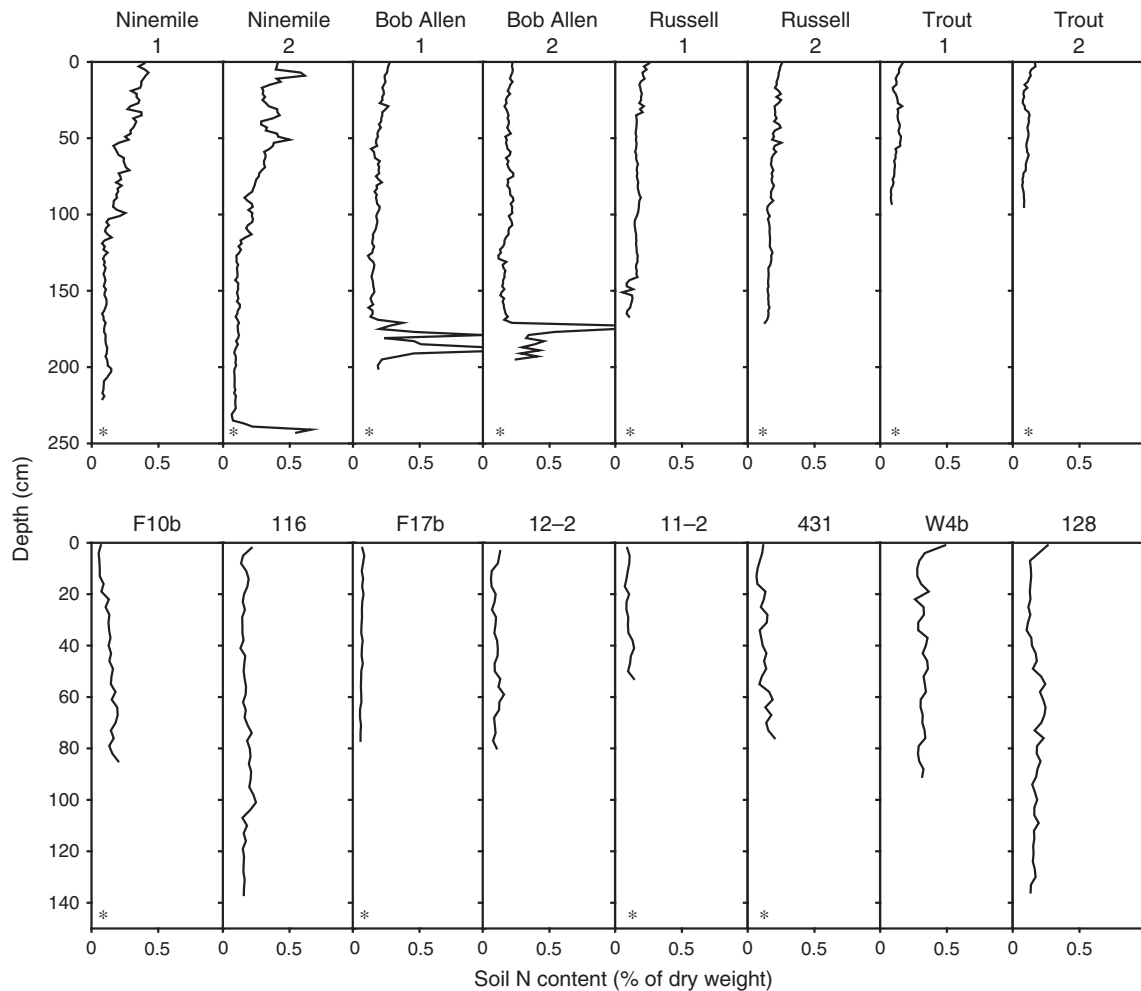
Accumulation of autogenic carbonate sediments suggests a net precipitation of  $CaCO_3$  from the water column in both bays. Mineral precipitation would drastically alter seawater pH,



**Fig. 11.** Phosphorus concentration changes with depth in the cores from Florida Bay (top panel) and Shark Bay (bottom panel). Cores are arranged from westernmost on the left to easternmost on the right within each bay. Asterisks indicate significant linear trends with depth (see Table 3). Note the different scales of the Y axes between top and bottom panels.

$p\text{CO}_2$ , and carbonate saturation in carbonate accumulating systems like Florida Bay and Shark Bay but for the production of organic matter by primary producers (Smith and Veeh 1989). The oxidation of organic matter, conversely, dissolves  $\text{CaCO}_3$ . Hence, net autotrophic systems, where primary production exceeds respiration, should produce more organic matter and  $\text{CaCO}_3$  than they consume; and, net heterotrophic ecosystems should consume organic matter and  $\text{CaCO}_3$ . Given the propensity of inorganic P to be immobilised by sorption onto  $\text{CaCO}_3$ , net autotrophic ecosystems should then be storing P as P sorbed to carbonates, whereas net heterotrophic systems should liberate inorganic P sorbed to carbonates. Therefore, changes in the

balance of autotrophic and heterotrophic processes have the potential to not only change the storage of organic matter in ecosystems, but also the storage and mobility of P. Hence, the large quantity of P stored in the sediments of P-limited Florida and Shark Bays could be remobilised out of the soils if rates of primary production in the benthos were reduced below respiration rates. P mobilisation has the potential to either fuel additional primary production of phytoplankton and macroalgae in these bays or to become sources of nutrients for adjacent ecosystems. Given the importance of low-nutrient, clear water in the coral reef ecosystems adjacent to both bays, maintenance of the net autotrophic state of the seagrass beds of Florida Bay



**Fig. 12.** Nitrogen concentration changes with depth in the cores from Florida Bay (top panel) and Shark Bay (bottom panel). Cores are arranged from westernmost on the left to easternmost on the right within each bay. Asterisks indicate significant linear trends with depth (see Table 3). Note the different scales of the Y axes between top and bottom panels.

and Shark Bay should be of utmost importance to local resource managers in those adjacent systems.

Surface soils had higher  $C_{org}$  in the more hypersaline, hydrographically-isolated regions of both bay systems, perhaps suggesting storage of  $C_{org}$  and P in soils could be affected by the tendency of the ecosystem to be hypersaline. However, we believe this correlation between surficial  $C_{org}$  and hypersalinity is really a consequence of the current coincidence of hypersalinity and relatively low-energy, protected sedimentary environments. We base this belief on the apparent decline in productivity of Shark Bay as the Faure Sill was deposited and the evidence that our region of Shark Bay did not become hypersaline until the Sill was deposited (Playford 1990). We also found the lack of correlation between seagrass biomass and surficial  $C_{org}$  in Shark Bay interesting, because many have found  $C_{org}$  to be higher in dense seagrass meadows compared with adjacent bare areas (reviewed in Kennedy *et al.* 2010). Our lack of correlation may be caused by the present patchy nature of the dense seagrass meadows in this part of Shark Bay and a general redistribution of organic matter among seagrass patches and

unvegetated areas of this relatively high-energy environment. In contrast, in the generally lower-energy environment of Florida Bay, seagrass has a more continuous distribution, and the unvegetated areas in Florida Bay are likely the result of disturbances of previously vegetated areas (Robblee *et al.* 1991). Surficial unvegetated sediments have lower  $C_{org}$  than adjacent vegetated areas, but these differences in  $C_{org}$  disappeared down-core so that deeper sediments had the same  $C_{org}$  whether they were overlain by seagrasses or not (Orem *et al.* 1999). It may be that the presence of seagrass over an accumulated soil has little effect on the longer-term diagenesis of sediment provided that the unvegetated sediment does not erode.

$C_{org}$  of soils from coastal ecosystems is more often reported as loss on ignition (LOI) than as  $C_{org}$  (Fourqurean *et al.* 2012), but use of LOI as a proxy has been suggested to be problematic because of mass lost on ignition that is independent of  $C_{org}$  content in some samples, especially those high in calcium carbonate (Leong and Tanner 1999). We found, in Shark Bay and Florida Bay, that there was indeed mass lost on ignition

unrelated to  $C_{\text{org}}$  content, but that this mass lost could be accounted for in a regression analysis of the data so that LOI could indeed serve as a proxy for  $C_{\text{org}}$  in these systems with relatively high  $C_{\text{org}}$  content, similar to conclusions drawn for an analysis of the value of LOI as a  $C_{\text{org}}$  predictor from a global data compilation and analysis (Fourqurean *et al.* 2012). This should allow for estimation of  $C_{\text{org}}$  stores in seagrass meadows using simpler LOI methodology, but caution should be exercised in systems with low  $C_{\text{org}}$ .

The total storage of  $C_{\text{org}}$  and nutrients in the soils of Shark Bay and Florida Bay is large when compared with other ecosystems. Seagrasses in general have been shown to store, on average, about as much  $C_{\text{org}}$  on an areal basis as terrestrial forests (Fourqurean *et al.* 2012). The median estimate for seagrass  $C_{\text{org}}$  storage in the top m of seagrass soils is  $139.7 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$ , with extreme values of  $C_{\text{org}}$  storage in the mat-forming *Posidonia oceanica* beds of the Mediterranean of up to  $829.2 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$ . We found that the  $C_{\text{org}}$  stores in Florida Bay and Shark Bay were substantially higher than the median values for the world's seagrass ecosystems: Florida Bay seagrasses stored, on average,  $163.5 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$  and Shark Bay stored on average  $243.0 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$ . These stores are comparable to those of boreal, temperate and tropical forests that average  $\sim 300 \text{ MgC}_{\text{org}} \text{ ha}^{-1}$  total  $C_{\text{org}}$  storage in the living biomass and top metre of the soil (IPCC 2003). The maintenance of terrestrial  $C_{\text{org}}$  stores in forests is recognised as a vital component of climate change mitigation (Agrawal *et al.* 2011). Owing to the rapid and accelerating losses of seagrass meadows on a global scale (Waycott *et al.* 2009), it has been argued that global loss rates of seagrass meadows could be responsible for a  $\text{CO}_2$  flux to the ocean-atmosphere  $\text{CO}_2$  pool at a rate equivalent to 10% of the total flux driven by terrestrial land use changes (Fourqurean *et al.* 2012). Clearly, conservation of the  $C_{\text{org}}$  stores of seagrass communities, including those of Florida Bay and Shark Bay, is of global importance.

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