

Spatial pattern in seagrass stoichiometry indicates both N-limited and P-limited regions of an iconic P-limited subtropical bay

Derek A. Burkholder^{1,*}, James W. Fourqurean^{1,2}, Michael R. Heithaus¹

¹Department of Biological Sciences, Marine Sciences Program, Florida International University, North Miami, Florida 33181, USA

²Southeast Environmental Research Center, Florida International University, Miami, Florida 33199, USA

ABSTRACT: We investigated seagrass species distribution and nutrient content in the iconic phosphorus-limited Shark Bay, Western Australia. We found the slower-growing, temperate species *Amphibolis antarctica* and *Posidonia* spp. had lower N and P content compared to the faster-growing tropical species *Halodule uninervis*, *Syringodium isoetifolium*, *Cymodocea angustata*, *Halophila ovalis* and *Halophila spinulosa*. Further, by comparing elemental content of different seagrass species at sites where species co-occurred, we were able to standardize seagrass elemental content across sites with different species composition. This standardization allowed us to make ecosystem-scale inferences about resource availability despite taxon-specific distributions and elemental content. We found a marked spatial pattern in N:P of seagrasses across the system, indicating that P limitation occurred, despite calcium carbonate sediments, only in the most isolated portions of the bay. Large areas closer to the mouth of the bay were either N limited or were not limited by N or P availability. Our results suggest that large-scale nutrient budgets may oversimplify our understanding of limiting factors in a system, resulting in management decisions that may have unforeseen effects on different areas within the same ecosystem.

KEY WORDS: Seagrass distribution · Nutrient limitation · Shark Bay

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Estuaries and bays were once considered by biologists to be universally N limited (despite the conclusions of Redfield 1958), but in the 1980s it became clear that systems with long water residence times and high N:P in freshwater runoff could be P limited (Smith 1984, Howarth 1988). Shark Bay, a subtropical, hypersaline embayment in Western Australia, was one of the first coastal systems for which P limitation was asserted (Smith & Atkinson 1983, Smith 1984, Atkinson 1987). It was argued that little freshwater runoff, long water residence times and high rates of N fixation led to this P-limited state. Since that time, other coastal ecosystems with long water residence times have also been shown to be P limited (e.g. coastal China, Harrison et al. 1990; the eastern Medi-

terranean, Krom et al. 1991; Florida Bay, Fourqurean et al. 1992; Moreton Bay, Australia, Wulff et al. 2011).

Phosphorus limitation is commonly reported in systems with sediments composed chiefly of calcium carbonate, which is the case for Shark Bay (Atkinson 1987, Walker & Woelkerling 1988). This relationship has been attributed to the high phosphate binding capacity of carbonate sediments and the resultant low mobility of P in carbonate systems (de Kanel & Morse 1978). However, not all carbonate ecosystems are P limited, and, in fact, adjacent N and P limited regions in carbonate sediment ecosystems have been identified (Fourqurean & Zieman 2002), suggesting that the carbonate content of sediments does not alone determine whether N or P will limit benthic primary production. The generality of this result, however, remains unclear. Given the observed N-limited

*Email: derek.burkholder@fiu.edu

nature of many phytoplankton communities offshore of Shark Bay (Hanson et al. 2005) and the strong tidal mixing of nearshore ocean waters into Shark Bay, it is likely that regions of Shark Bay closer to the mouth with lower water residence times could be N, rather than P, limited despite carbonate sediments.

Understanding the nature of nutrient limitation in coastal water bodies is critical to their management. Coastal ecosystems in the United States and around the world have been modified dramatically by rapidly increasing human populations and anthropogenic impacts (e.g. Lotze et al. 2006, Orth et al. 2006). Among the most prevalent anthropogenic impacts is nutrient pollution, which can drastically alter the structure of ecological communities (Nixon 1995). As different management strategies are employed to control the discharge of N and P, efficient management requires identifying the limiting nutrient of a system.

Nutrient-limited estuaries and bays often have relatively transparent water columns and support seagrasses and other benthic primary producers in areas where sufficient light can reach unconsolidated sediments. Seagrasses are important benthic primary producers and form critical habitats in many coastal ecosystems. Seagrass ecosystems are highly productive habitats, providing primary productivity rates comparable to agricultural fields in annual primary production (Zieman & Wetzel 1980). Seagrass ecosystems also provide critical habitat for a multitude of species including many of economic importance (Short & Wyllie-Echeverria 1996). Despite their importance, seagrass ecosystems are one of the most threatened ecosystems on the planet today, estimated to be lost at a rate of $110 \text{ km}^2 \text{ yr}^{-1}$ since 1980 (Waycott et al. 2009). The most often cited impact leading to decline in seagrass meadows around the world is impaired water quality, often driven by increases in the delivery of the limiting nutrient to the ecosystem (Short & Wyllie-Echeverria 1996, Orth et al. 2006).

Since the ratios of elements in tissues of marine primary producers respond to the relative availability of nutrients and light, N:P ratios of primary producer biomass can be used to assess the relative importance of N and P in limiting biomass and productivity (Redfield 1958). While phytoplankton communities can be advected around an ecosystem, obscuring the spatial pattern in the availability of different resources, benthic primary producers are fixed in place and, therefore, can be used to integrate nutrient availability over long time periods. Consequently, spatial patterns in the N:P ratios of benthic primary

producers have been used to deduce the landscape of resource limitation for benthic primary producers within ecosystems (e.g. Fourqurean et al. 1992, Fourqurean & Zieman 2002, Johnson et al. 2006).

In this paper, we revisit the question of P limitation in Shark Bay, the iconic P-limited coastal ecosystem, by analyzing spatial patterns in the N:P of the bay's seagrasses and epiphyte communities. Shark Bay supports some of the world's most extensive seagrass meadows, covering approximately 4000 km^2 , and, with 12 species of seagrasses, it is also one of the most diverse seagrass ecosystems (Walker et al. 1988). Given that no one species of seagrass is distributed across all of the seagrass meadows of Shark Bay and that seagrasses in other regions have species-specific differences in elemental content (Campbell & Fourqurean 2009), we aimed to describe the distributions of the most common seagrass taxa across the system and determine whether there were taxon-specific differences in N:P. We then analyzed the large-scale spatial pattern in N:P of seagrasses across the $13\,000 \text{ km}^2$ of Shark Bay to determine whether the relative importance of N and P as limiting nutrients varies across the system.

MATERIALS AND METHODS

Study site

Shark Bay, Western Australia, is a $13\,000 \text{ km}^2$ embayment located about 800 km north of Perth. It is a relatively shallow bay (<15 m generally) that is divided by Peron Peninsula into an Eastern and Western Gulf (Fig. 1). The Western Gulf features greater connectivity to waters of the Indian Ocean than the Eastern Gulf. Circulation to the southern portions of the Eastern Gulf, particularly Hamelin Pool, are further restricted by the shallow carbonate bank of the Faure Sill, which runs from the eastern coast of Peron Peninsula to the mainland coast. For regional comparisons, we divided the study area into the (1) Western Gulf, defined as the area from the tip of Dirk Hartog Island to the tip of Peron Peninsula south, (2) the Eastern Gulf, defined as the area from the tip of Peron Peninsula east to the mainland and south and (3) Northern Region, which was defined as the area north of the 2 gulfs (Fig. 1).

Seagrasses are broadly distributed across the bay and are particularly abundant in water shallower than 4 m. Both the Eastern and Western Gulfs of Shark Bay and coastal waters in the Northern Region were surveyed for seagrass distribution and nutrient

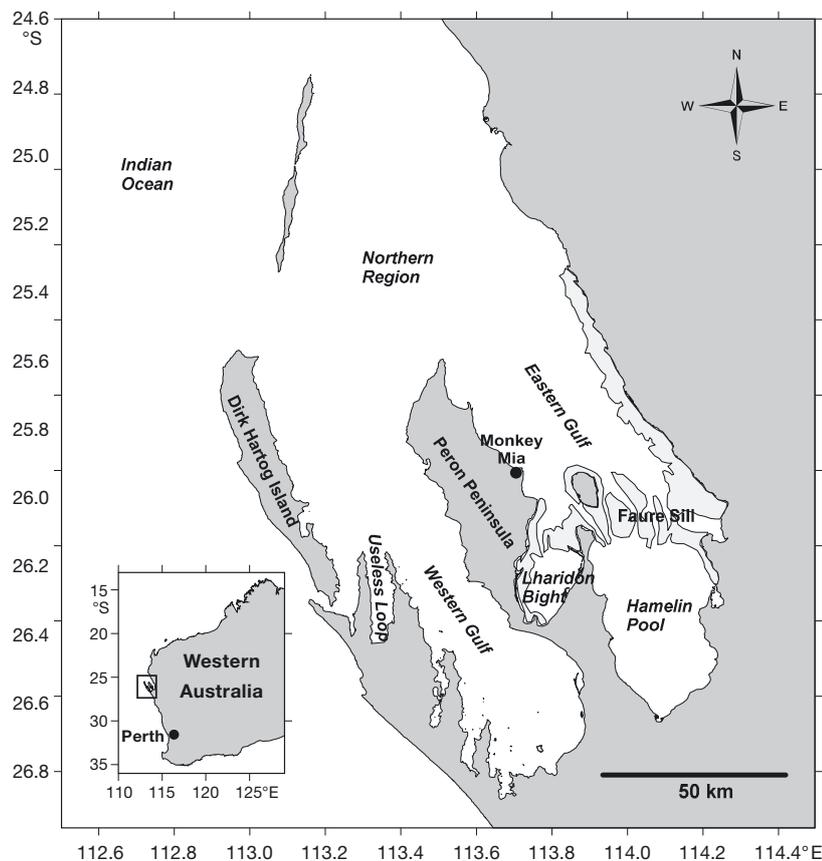


Fig. 1. Shark Bay study site, Western Australia, with Eastern Gulf, Western Gulf and Northern Regions outlined, and major landmarks

content. The diversity of seagrasses in Shark Bay is partly attributable to the overlap of temperate and tropical floras. Seagrasses of temperate origin are the most abundant. *Amphibolis antarctica* (Aa) is the most common species, followed by *Posidonia australis*. *P. coriacea*, also of temperate origin, is less common. In the field, we did not differentiate between these *Posidonia* species, so we will refer to *Posidonia* species (*Psp*) for the remainder of this paper, although *P. australis* was by far the most common *Posidonia*. Tropical seagrasses also occur within the study area, but are confined to shallow sandy patches and deep water. These include *Halophila ovalis* (Ho), *H. spinulosa* (Hs), *Halodule uninervis* (Hu), *Syringodium isoetifolium* (Si) and *Cymodocea angustata* (Ca) (Walker et al. 1988).

Field methods

From 2007 to 2009, we surveyed seagrasses at 475 stations (summer 2007, N = 168 sites; winter

2007, N = 188 sites; summer 2008, N = 123 sites; winter 2008, N = 163 sites; summer 2009, N = 179). General sample locations were selected to distribute stations widely throughout Shark Bay. Specific stations were selected haphazardly by stopping the vessel after 5 min of travel time (at ca. 30 km h⁻¹) between sites along pre-determined routes. Each sampling site was surveyed either using snorkel or SCUBA. A 60 × 60 cm quadrat with grid was dropped haphazardly off the side of the anchored vessel. Percent cover for each seagrass species was visually estimated in the quadrat where it settled on the bottom. One observer made all visual assessments throughout the study for uniformity. The quadrat was then flipped end over end 3 times moving toward the front of the boat and visually sampled for percent seagrass cover for each species. The process was repeated for a third quadrat reading at each site. Data were averaged into a mean percent cover for each sample station. Water temperature, salinity (refractometer), water depth (vessel depth sounder) and GPS location were recorded at each site.

Seagrass samples were collected by hand at each site for elemental analysis. At least 5 shoots and their roots/rhizome tissue were collected for each species at the sample station. All seagrass species encountered, even if they were not represented in the quadrat-sampling regime, were collected for nutrient analysis. All samples were stored on ice in the field. Samples were immediately frozen to -20°C upon return to shore. Samples remained frozen until they could be processed.

Sampling sites were visited once in the warm season (September to May), and once in the cold season (June to August). Species abundance estimates represent pooled data from both seasons. Seagrass nutrient limitation is most prevalent in the warm season during the period of highest seagrass primary production and resource use (Walker & McComb 1988, Fourqurean et al. 2005). Since even temperate seagrass species show peak growth rates during the warm season in Shark Bay (Walker & McComb 1988), we limited our elemental analyses to samples collected in the warm (high productivity) season.

Laboratory methods and analysis

Seagrass samples were thawed, rinsed in DI water and each leaf was gently scraped with a razorblade to remove all epibiota. The epibiota were combined from all seagrass species collected at a site to obtain enough epiphyte material for analysis and were run separately from leaf tissue. This pooling procedure assumed that the elemental content of the epibionts was the same across seagrass species. We did not test this assumption. We separated leaves from stems and belowground tissue (roots and rhizome) and restricted our analysis to leaf tissue of each species. Leaves from each of the 5 plants collected for each site were dried using a food dehydrator (Ezidri Ultra FD1000) for at least 24 h. Once dry, samples were crushed into powder for analysis using mortar and pestle. C and N content of samples were measured using an elemental analyzer (Fisons NA1500) and P content was measured using a dry-oxidation/acid hydrolysis method (Fourqurean et al. 1992)

Statistical analyses

We used ANOVA with Tukey's post-hoc tests on log transformed data to test for mean differences in the elemental content of the seagrass taxa and epiphytes for all data pooled across the study area. Since differences in nutrient availability across the study could interact with different species distributions to lead to differences in mean elemental content among species, we further tested whether the elemental content of seagrass taxa and epiphytes differed predictably at sites where they co-occurred by using paired *t*-tests to test for significant pairwise differences.

Using the results of the comparisons of N:P of seagrass taxa at sites where the taxa co-occur, we generated a standardized seagrass N:P ratio for each sampling station by using the observed value of N:P for

each taxon, then adjusting each value by the average difference between that taxon and *Amphibolis antarctica* (see Table 4), the most widely distributed taxon, so that $N:P_{\text{standardized}} = \text{mean}(N:P_{Aa}, N:P_{Psp} - 4.6, N:P_{Hu}, N:P_{Ho} + 8.5, N:P_{Hs} + 7.9, N:P_{Ca} - 5.6, N:P_{Si})$ (see 'Results'). To visualize the pattern in $N:P_{\text{standardized}}$ across the study area, we generated a contour plot using a kriging routine (Surfer v9, Golden Software) to interpolate between our sampling locations. Our kriging routine assumed a linear variogram with a slope of 1 and no anisotropy and calculated predicted values using up to 64 nearest neighbors within 60 km of each grid position. We calculated the root mean square error (RMSE) of this kriged map as a measure of the reliability of the depicted pattern

We used a general linear model to explore the influences of water depth (based on readings from the vessel's depth sounder), distance from the Indian Ocean and region (Northern, Eastern Gulf, Western Gulf) on N:P ratios of each species. We also included the interaction of region and distance in models because of differences in water flow among regions. This interaction was removed for species if $p > 0.10$. Main effects were retained in final models regardless of significance level.

RESULTS

Samples were collected from 475 stations for point samples of seagrass species composition, percent cover and nutrient content. Of these, 470 were sampled in the warm season (daily temperature range 19.5 to 31.5°C) and 351 were sampled in the cold season (daily temperature range 15.8 to 23.2°C). Variation in winter versus summer sample site numbers resulted from mechanical/weather constraints during the winter months in 2008 limiting sampling in some areas. Summer sampling with the Department of Environment and Conservation in 2009 allowed for

Table 1. Bottom cover of seagrasses at 475 sites in Shark Bay, Western Australia. Values are based on averages of 3 subplots per site. Med. = median, FO = frequency of occurrence

Species	All sites			When present		
	Mean ± SD	Med.	FO	Mean ± SD	Med.	Max.
<i>Amphibolis antarctica</i>	44.25 ± 43.63	35	58.9	74.53 ± 30.74	90	100
<i>Cymodocea angustata</i>	0.55 ± 4.21	0	9.1	5.80 ± 12.66	2.5	80
<i>Halophila ovalis</i>	0.15 ± 1.16	0	5.1	2.70 ± 4.31	1.1	15.8
<i>Halodule uninervis</i>	1.21 ± 4.32	0	25.7	4.62 ± 7.49	1.6	48.35
<i>Halophila spinulosa</i>	0.61 ± 4.08	0	8.0	7.19 ± 12.39	1.7	65
<i>Posidonia</i> spp.	7.65 ± 20.74	0	22.1	33.98 ± 31.93	26.6	100
<i>Syringodium isoetifolium</i>	0.09 ± 0.63	0	3.4	2.34 ± 2.35	1.6	9

the expansion of sample sites into locations, including Hamelin Pool, that were otherwise inaccessible due to permit regulations and vessel restrictions. Salinity ranged from 25 ppt (warm season 2008 in Useless Loop) to 65 ppt (warm season 2009 in Hamelin Pool).

Seven seagrass taxa were commonly encountered throughout the study area. There was, however, a large amount of variation in taxa richness across the bay as well as the frequency of occurrence and cover of seagrass species (Table 1, Fig. 2). Stations where seagrass was absent were concentrated south of the

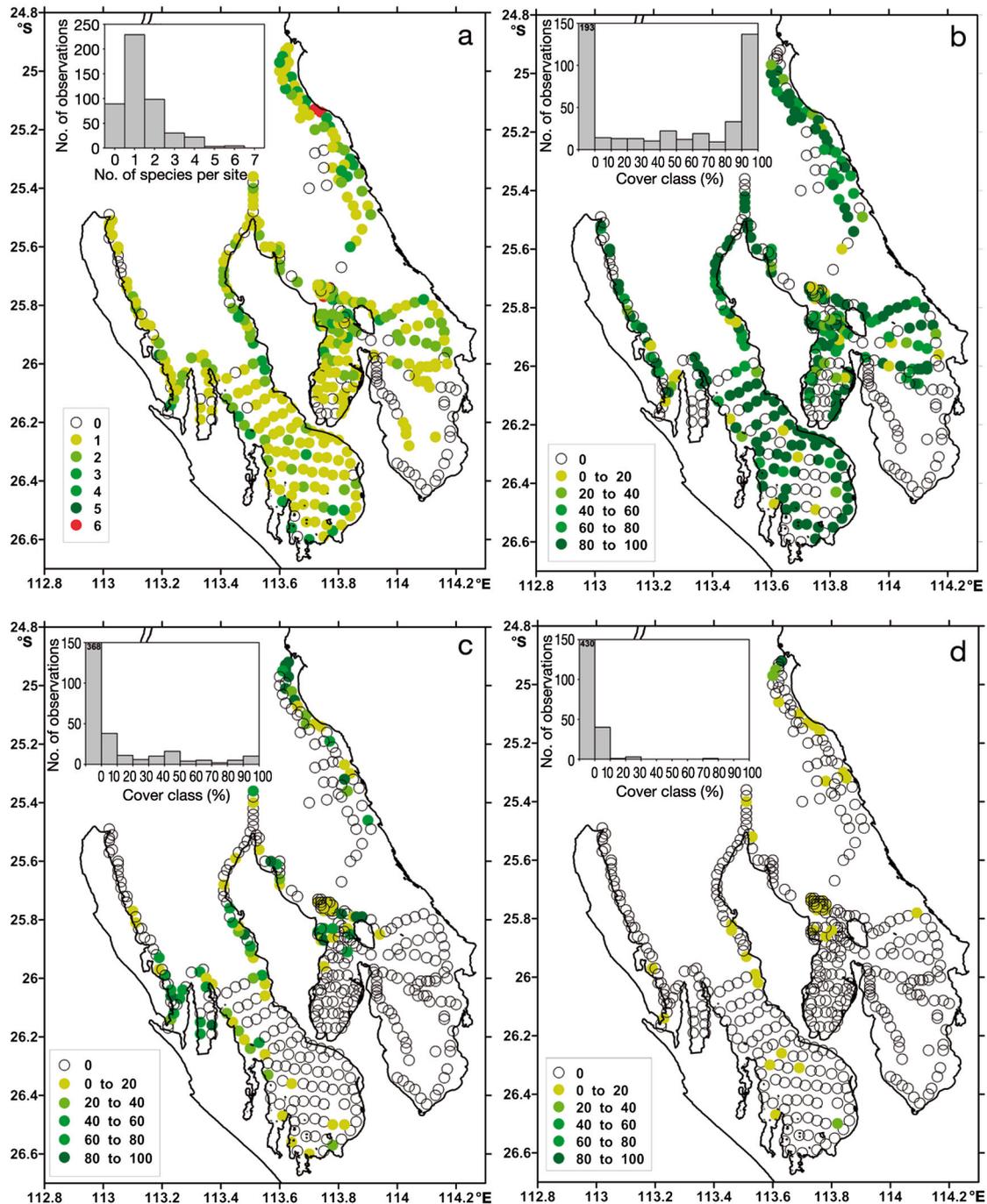


Fig. 2. Seagrass taxa diversity across Shark Bay, Australis, from (a) both summer and winter sampling effort, and average abundances of seagrass species across Shark Bay; (b) *Amphibolis antarctica*; (c) *Posidonia* spp.; (d) *Cymodocea angustata*; (e) *Halophila ovalis*; (f) *Halophila spinulosa*; (g) *Halodule uninervis*; and (h) *Syringodium isoetifolium*. Positions of the symbols indicate sampling locations. Insets show frequency histograms of species richness (a) or percent cover (b–h)

(continued on next page)

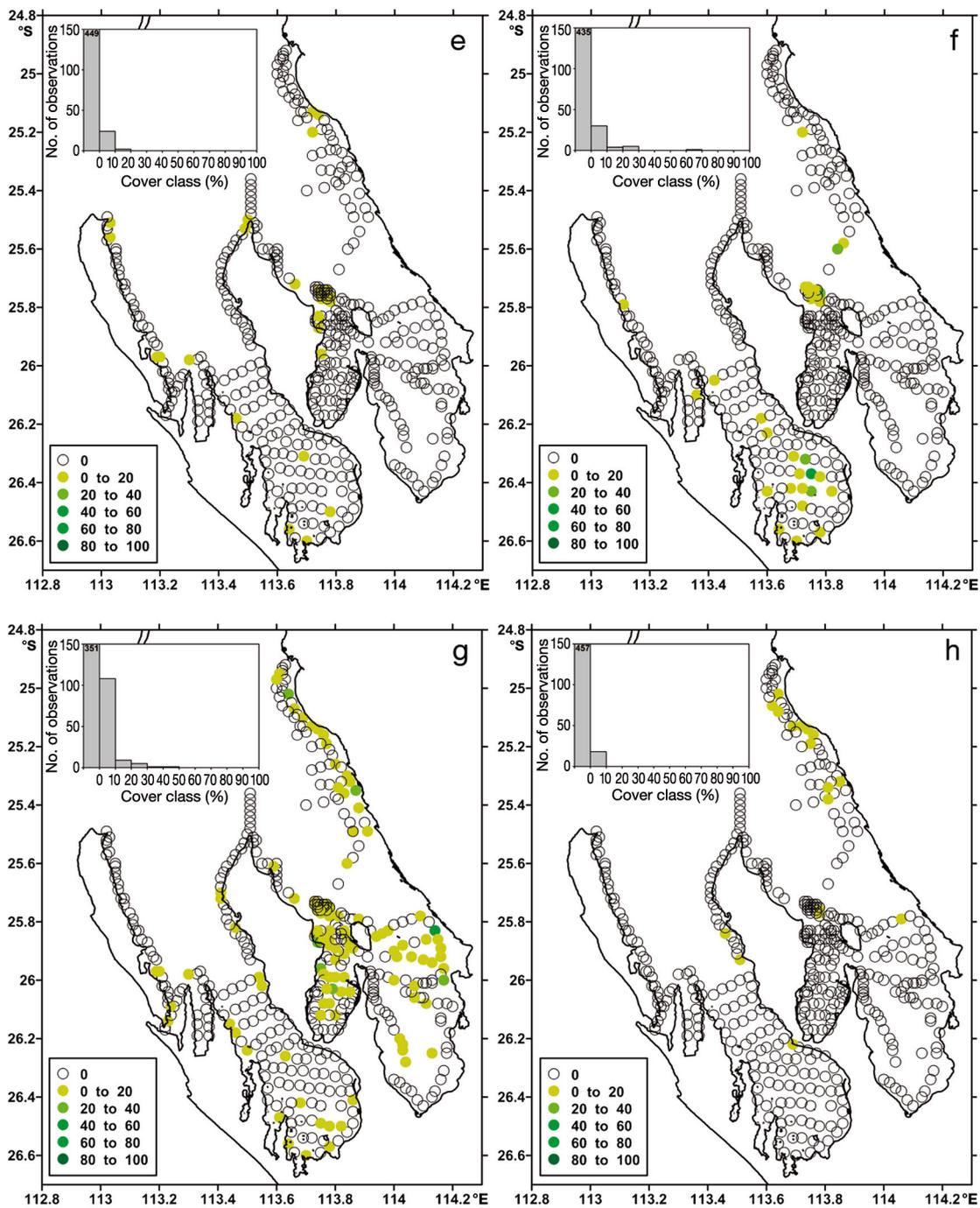


Fig. 2 (continued)

Faure Sill, especially in the hypersaline Hamelin Pool. At more than half of the stations where seagrass was present, there was only a single species (Fig. 2a). There were, however, several hotspots of diversity, where up to 6 taxa of seagrass were found at individual stations, including in the central Eastern Gulf where there are numerous offshore seagrass banks

(<4 m) surrounded by deeper channels (7–11 m depth) and along the shallow coastal waters of the Northern Region. Several coastal areas in the southern Western Gulf and along the northeast Western Gulf had 4 or 5 taxa of seagrass at individual stations, but these concentrated in nearshore areas. Stations in the middle of the gulf generally had only a single taxon.

Amphibolis antarctica was the most widespread species and was generally found in dense stands, usually with mean cover exceeding 90%, (Fig. 2b) and canopy heights up to 130 cm tall. *A. antarctica* was notably absent from Hamelin Pool and was encountered less often in deeper waters of Freycinet Basin in the southern Western Gulf, and restricted areas including Lharidon Bight in the Eastern Gulf and Useless Loop in the Western Gulf. The other temperate species in Shark Bay, *Posidonia* spp., were absent from large portions of the southern areas of the Eastern and Western Gulf (Fig. 2c), but were found (primarily *P. australis*) in some dense stands north of the Faure Sill, in northern portions of the Northern Region and along southern Dirk Hartog Island.

Tropical species, with the exception of *Halodule uninervis*, were generally distributed patchily and were found in low percent cover when encountered (Fig. 2d-h). Most tropical species, however, were found along the northern coast of the Northern Region and associated with the offshore seagrass banks of the central Eastern Gulf. Although generally occurring in sparse stands, *H. uninervis* was widely distributed in the bay, including the more restricted waters of the southern Eastern Gulf. It was, however, absent from most of the coast of Dirk Hartog Island (Fig. 2g).

There was significant variation among taxa in P content ($F_{7,1516} = 115.2$, $p < 0.0001$; Fig. 3a) and N content ($F_{7,1516} = 271.7$, $p < 0.0001$; Fig. 3b). *Halophila ovalis* had the highest P content, followed by *Halophila spinulosa* and *Halodule uninervis*. *Amphibolis antarctica* and epiphytes had the lowest P and N content. *Cymodocea angustata* had the highest N content, followed by *H. uninervis*, *H. ovalis* and *Syringodium isoetifolium*.

The ratios of C:N ($F_{7,1516} = 194.8$, $p < 0.0001$; Fig. 4a), C:P ($F_{7,1516} = 168.9$, $p < 0.0001$; Fig. 4b) and N:P ($F_{7,1516} = 49.6$, $p < 0.0001$; Fig. 4c) varied across species. C:N and C:P ratios were highest in *Amphibolis antarctica*, followed by *Posidonia* spp. Mean N:P ratios for all seagrass sampled were around 30, indicating that neither N nor P is limiting (Atkinson & Smith 1983, Duarte 1990). However, N:P at individual sites could vary markedly, from clearly N-limited lows of 12.2 for *A. antarctica* and 12.8 for *Posidonia* spp. to clearly P-limited highs of 66.5 and 63.5, respectively. The highest ratios were in *Cymodocea angustata* and *Halodule uninervis*, and suggested that they were growing in P-limited conditions, while *Halophila spinulosa* and *Halophila ovalis* exhibited the lowest N:P ratios, which were indicative of N limitation.

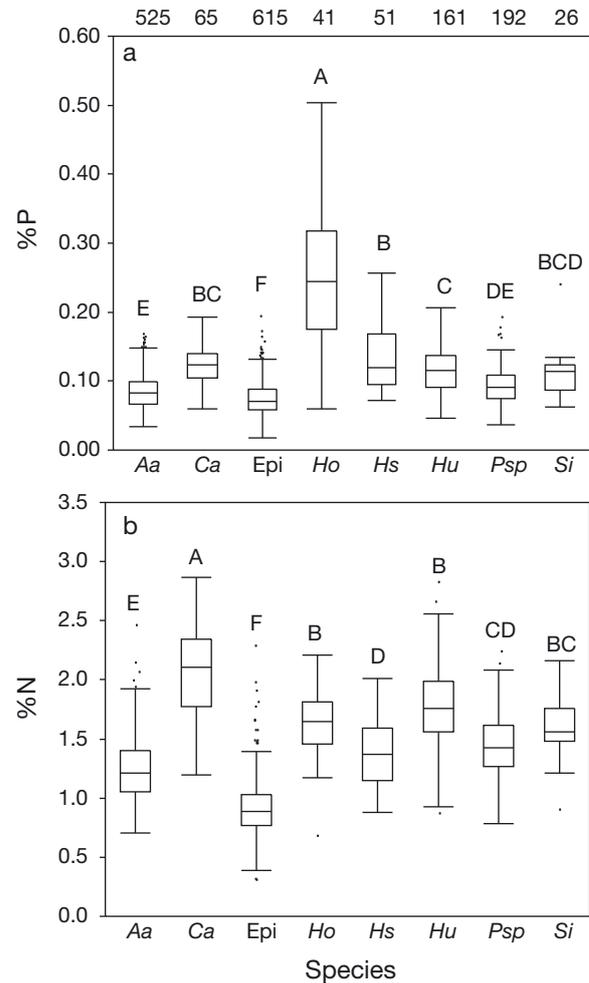


Fig. 3. (a) P and (b) N content of seagrass and epiphytes in Shark Bay, Australia, during the warm season. Boxes with the same letter indicate no significant differences at $p < 0.05$ for Tukey's test. Sample sizes are provided above panel a. Aa = *Amphibolis antarctica*, Ca = *Cymodocea angustata*, Epi = epiphytes, Ho = *Halophila ovalis*, Hs = *Halophila spinulosa*, Hu = *Halodule uninervis*. Psp = *Posidonia* spp. (primarily *P. australis*), Si = *Syringodium isoetifolium*. Mid-line is the median, box limits are the 25th and 75th quantiles, whiskers are 5th and 95th% confidence intervals, and dots are outliers

Based on paired comparisons at sites where species co-occurred, the epiphytes collected from seagrasses always had lower P content than the seagrasses on which they were growing (Table 2). *Amphibolis antarctica* had lower P content than all other seagrass taxa when growing with those other taxa. *Posidonia* spp. had lower P content than *Halodule uninervis*, *Halophila ovalis*, *Cymodocea angustata* and *Syringodium isoetifolium*, but there was no difference in the P content of *Posidonia* spp. and *H. spinulosa*. *H. uninervis* had lower P content than *H. ovalis*, but higher P content than *H. spinulosa*. *H. ovalis* had

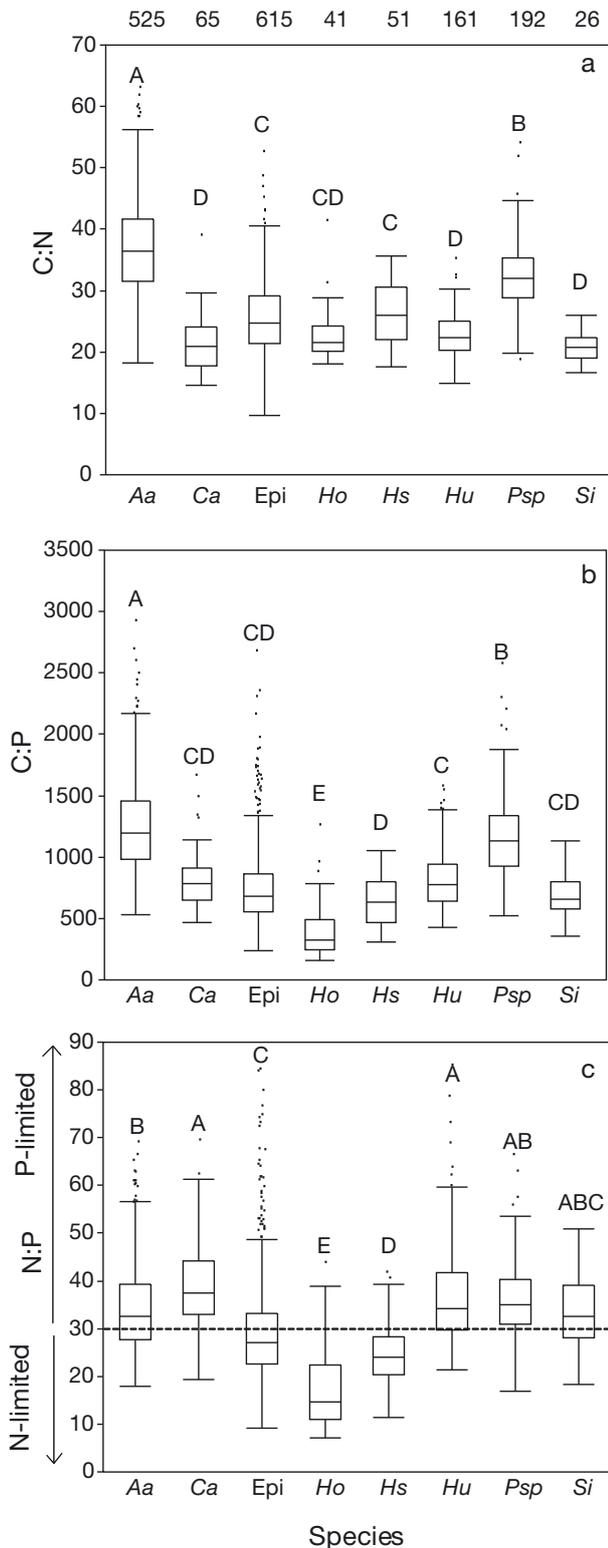


Fig. 4. Ratios of (a) C:N, (b) C:P, and (c) N:P for 7 species of seagrass and epiphytes in Shark Bay, Australia, during the warm season. Boxes with the same letter indicate no significant differences at $p < 0.05$ for Tukey's test. Sample sizes are provided above panel (a). See Fig. 3 for species abbreviations and box definitions

higher P content than its congener *H. spinulosa*, but lower P content than *C. angustata*.

Similar to the P content, the N content of epiphytes was lower than any of the seagrasses on which they grew (Table 3). *Amphibolis antarctica* had lower N content than any of the other seagrass taxa. *Posidonia* spp. had lower N content than *Halodule uninervis*, *Halophila ovalis* and *Cymodocea angustata*. *H. uninervis* had higher N content than *H. ovalis*, *H. spinulosa* and *Syringodium isoetifolium*, but lower than *C. angustata*. *H. ovalis* had higher N content than its congener *H. spinulosa*, but lower N content than *C. angustata*. *H. spinulosa* had lower N content than either *C. angustata* or *S. isoetifolium*, but *C. angustata* had higher N content than *S. isoetifolium*.

Like P and N content, the N:P ratio of epiphytes was lower than most of the seagrasses on which it grew. *Halophila spinulosa* N:P, however, did not differ significantly from its epiphytes and *Halophila ovalis* had a lower N:P ratio than its epiphytes (Table 4). *Amphibolis antarctica* had a higher N:P ratio than *H. ovalis* and *H. spinulosa*, but lower than *Posidonia* spp. and *Cymodocea angustata*. *Posidonia* spp. had a higher N:P ratio than *H. ovalis*, *H. spinulosa* and *Syringodium isoetifolium*. *Halodule uninervis* had a higher N:P ratio than *H. ovalis*, *H. spinulosa* and *S. isoetifolium*, but a lower N:P ratio than *C. angustata*. *H. ovalis* had a lower N:P ratio than *H. spinulosa* and *C. angustata*. *H. spinulosa* had a higher N:P ratio than *S. isoetifolium*.

N:P ratios varied with distance from oceanic waters, sample region and water depth, as well as the interaction between distance and region (i.e. the effect of distance from the ocean varied among regions), but there was variation among species in how these factors influenced N:P ratios (Table 5). *Amphibolis antarctica*, *Halodule uninervis* and epiphyte N:P ratios varied with distance from the Indian Ocean, but the nature of this relationship varied across regions (Fig. 5). In general, within each region, N:P ratios increased with increasing distance from the ocean, but values for the Eastern Gulf were generally lower at further distances from the ocean and the slope of the relationship varied among regions. The Northern Region had higher N:P than the Eastern and Western Gulfs for *Cymodocea angustata*, *Halophila ovalis* and *Syringodium isoetifolium* (Table 5, Fig. 6). For both *Halophila* species, the N:P ratio increased with increasing distance from the ocean, but the nature of this relationship did not vary among regions (Table 5, Fig. 6). For epiphytes, *S. isoetifolium* and *Posidonia* spp., there was a significant negative relationship between N:P ratio and depth (Table 5).

Table 2. Differences in phosphorus concentration (%P) among co-occurring seagrass species and epiphytes. Numbers above the diagonal represent the difference in P content of the species in the first column minus the species across the top (e.g. %P of *Aa* – %P of *Psp* = –0.006). Numbers below the diagonal are sample sizes. *Aa* = *Amphibolis antarctica*, *Ca* = *Cymodocea angustata*, *Epi* = epiphytes, *Ho* = *Halophila ovalis*, *Hs* = *Halophila spinulosa*, *Hu* = *Halodule uninervis*, *Psp* = *Posidonia* spp. (primarily *P. australis*), *Si* = *Syringodium isoetifolium*. **p* < 0.05, ***p* < 0.01, ****p* < 0.001, ns = not significant (*p* > 0.05)

	<i>Aa</i>	<i>Psp</i>	<i>Hu</i>	<i>Ho</i>	<i>Hs</i>	<i>Ca</i>	<i>Si</i>	<i>Epi</i>
<i>Aa</i>	–	–0.006*	–0.036***	–0.115***	–0.034***	–0.035***	–0.039***	0.013***
<i>Psp</i>	77	–	–0.032***	–0.011**	ns	–0.036***	–0.032*	0.008***
<i>Hu</i>	78	53	–	–0.098***	0.027**	ns	ns	0.042***
<i>Ho</i>	17	16	22	–	0.145***	–0.137***	ns	0.139***
<i>Hs</i>	18	6	15	11	–	ns	ns	0.040***
<i>Ca</i>	32	24	30	11	6	–	ns	0.045***
<i>Si</i>	20	12	16	6	4	12	–	0.040***
<i>Epi</i>	265	109	92	27	26	41	21	–

Table 3. Differences in nitrogen concentration (%N) among co-occurring seagrass species and epiphytes (above the diagonal). Numbers above the diagonal represent the difference in nitrogen content of the species in the first column minus the species across the top (e.g. %N of *Aa* – %N of *Psp* = –0.273). Numbers below the diagonal are sample sizes. See Table 2 for species abbreviations. **p* < 0.05, ***p* < 0.01, ****p* < 0.001, ns = not significant (*p* > 0.05)

	<i>Aa</i>	<i>Psp</i>	<i>Hu</i>	<i>Ho</i>	<i>Hs</i>	<i>Ca</i>	<i>Si</i>	<i>Epi</i>
<i>Aa</i>	–	–0.273***	–0.565***	–0.446***	ns	–0.761***	–0.518***	0.296***
<i>Psp</i>	77	–	–0.391***	–0.436***	ns	–0.665***	ns	0.421***
<i>Hu</i>	76	53	–	0.142*	0.710***	–0.215**	0.174*	0.822***
<i>Ho</i>	17	16	22	–	0.543***	–0.269***	ns	0.729***
<i>Hs</i>	18	6	15	11	–	–0.828***	–0.377*	0.421***
<i>Ca</i>	32	24	31	11	6	–	0.331**	1.143***
<i>Si</i>	20	12	16	6	4	12	–	0.747***
<i>Epi</i>	265	108	90	27	26	41	21	–

Table 4. Differences in N:P among co-occurring seagrass species and epiphytes (above the diagonal). Numbers above the diagonal represent the difference in N:P of leaf tissues of the species in the first column minus the species across the top (e.g. N:P of *Aa* – N:P of *Psp* = –4.6). Numbers below the diagonal are sample sizes. See Table 2 for species abbreviations. **p* < 0.05, ***p* < 0.01, ****p* < 0.001, ns = not significant (*p* > 0.05)

	<i>Aa</i>	<i>Psp</i>	<i>Hu</i>	<i>Ho</i>	<i>Hs</i>	<i>Ca</i>	<i>Si</i>	<i>Epi</i>
<i>Aa</i>	–	–4.6***	ns	8.5**	7.9***	–5.6*	ns	2.4***
<i>Psp</i>	77	–	ns	8.1*	11.9*	ns	7.3*	8.2***
<i>Hu</i>	76	53	–	13.1***	6.3**	–4.7*	5.6*	4.6***
<i>Ho</i>	17	16	22	–	–8.8**	–20.0***	ns	–5.3*
<i>Hs</i>	18	6	15	11	–	–11.3**	ns	ns
<i>Ca</i>	32	24	31	11	6	–	9.1**	12.5***
<i>Si</i>	20	12	16	6	4	12	–	7.0**
<i>Epi</i>	261	108	90	27	26	41	21	–

Normalizing N:P ratios to that of *Amphibolis antarctica* allowed us to investigate spatial patterns of nutrient limitation across Shark Bay (Fig. 7). The average deviation of our kriged surface of normalized N:P from the observed values at a location was 2.8 (RMSE). In general, N:P >> 30, indicating strong P limitation, was limited to the Eastern Gulf, south of the Faure Sill. There are regions of 30 < N:P < 50, indicating moderate P limitation, in the southern area

of the Western Gulf, along the mainland coast, and along the northeast coast of Peron Peninsula. The central portions of the bay had N:P ratios near 30, suggesting that these areas are not nutrient-limited. The waters along Dirk Hartog Island and the Northern Region have low N:P ratios suggestive of N-limitation; however, due to sampling logistics, sample sites are limited in the center of the mouths of the Eastern and Western Gulfs.

Table 5. Effects of region, distance to the Indian Ocean, depth and the interaction of region and distance on N:P. Non-significant interactions (ns) ($p > 0.10$) were removed from final models. Significant values are in **bold**. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant ($p > 0.05$). See Table 2 for species abbreviations

Species	Region		Distance to ocean		Depth		Region × Distance	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
<i>Aa</i> ***	41.9	0.0001	61.1	0.0001	1.9	0.17	3.1	0.05
<i>Psp</i> *	1.3	0.27	3.7	0.06	6.2	0.01	ns	ns
<i>Hu</i> ***	10.4	0.0001	33.9	0.0001	0.0	0.95	10.4	0.0001
<i>Hs</i> **	6.9	0.003	12.6	0.001	1.5	0.23	ns	ns
<i>Ho</i> ***	18.0	0.0001	18.8	0.0002	0.3	0.57	ns	ns
<i>Ca</i> **	8.2	0.001	0.1	0.93	0.6	0.46	ns	ns
<i>Si</i> *	4.7	0.02	0.3	0.55	4.8	0.04	ns	ns
<i>Epi</i> ***	59.9	0.0001	94.9	0.0001	5.4	0.02	16.5	0.0001

Final models: *Aa*: $F_{6,271} = 40.3$, $p < 0.0001$, $R^2 = 0.48$; *Psp*: $F_{4,113} = 2.5$, $p = 0.04$, $R^2 = 0.08$; *Hu*: $F_{6,113} = 30.6$, $p < 0.0001$, $R^2 = 0.63$; *Hs*: $F_{4,37} = 4.7$, $p = 0.004$, $R^2 = 0.36$; *Ho*: $F_{4,33} = 16.3$, $p < 0.0001$, $R^2 = 0.69$; *Ca*: $F_{4,42} = 4.1$, $p = 0.008$, $R^2 = 0.30$; *Si*: $F_{6,21} = 4.2$, $p = 0.02$, $R^2 = 0.50$; *Epi*: $F_{6,315} = 51.2$, $p < 0.0001$, $R^2 = 0.50$

DISCUSSION

Spatial patterns in the stoichiometry of seagrasses from Shark Bay indicate broad areas of the bay that appear to be N limited and P limited, and areas that are not nutrient limited despite the asserted general P limitation of the system derived from budget calculations for the Eastern Gulf of the bay (Smith & Atkinson 1983, 1984). We do not see our results as contradictory to the conclusions drawn by Smith & Atkinson (1983, 1984). That work, based on system-scale budgets, suggested the mechanism driving P limitation is the stripping of P out of relatively P-replete Indian Ocean source water as that water is advected into the system to replace water lost due to evaporation from the surface of the bay in this arid ecosystem. It stands to reason, then, that regions of the bay close to the P-replete source water receive ample P supply, while those distant from that source experience increased P-limitation stress—precisely the pattern our stoichiometric map revealed. We suggest that within a system that as a whole appears limited by one resource, there can exist broad areas where biomass and primary production can be limited by another resource. We found that strong evidence for P limitation was restricted to the southern ends of both the Eastern and Western Gulfs (Fig. 7). These areas are most distant from the oceanic P source that fuels net production and have long water residence times (Smith & Atkinson 1983, Atkinson 1987, Price et al. in press). Thus, our results support

for the contention that water residence time is a main driver of the relative importance of N and P in limiting biomass and net production in aquatic systems (Smith & Atkinson 1984, Smith 1984). Areas within Shark Bay less isolated from the oceanic P source were N limited and areas in the middle reaches of the system were neither N nor P limited.

Phosphorus in the system is delivered by tidal water exchange with the relatively P-rich waters of the Indian Ocean. Indeed, seagrasses showed moderate P limitation near the primary freshwater input to the bay, despite upstream agriculture. Therefore, distance from the mouth of the bay serves as a reasonable proxy for P availability throughout the system, although the strength of the distance effect varied somewhat across the 3

broad regions of the bay. In the Western Gulf, P limitation appeared to occur at closer distances to the ocean than in the Eastern Gulf or Northern Region. Overall, the gradient of P limitation, with the highest levels occurring in the most isolated areas, is very similar to findings in Florida Bay, USA (Fourqurean & Zieman 2002, Fourqurean et al. 2005). However, some species showing Redfield-like N:P from deep sites suggest that some areas of the bay are not nutrient limited and other factors (e.g. light limitation, depth limitation, herbivore limitation, etc) also play an important role in ecosystem dynamics in this system. Combined with the bioassay work on nutrient limitation of the phytoplankton communities (Segal et al. 2009), our results also suggest that spatial patterns of N and P limitation with distance from the mouth may operate differently for benthic and pelagic portions of the water column. Segal et al. (2009) found that within Useless Loop (Western Gulf), phytoplankton were N limited near the open bay and P limited deeper into the embayment. In contrast, although we found evidence for moderate N limitation of the benthos near the open bay, the remainder of the benthic system in Useless Loop/central Western Gulf appears to not be nutrient limited.

The finding of elevated N:P ratios in the most isolated parts of Shark Bay, with low N:P ratios further offshore, mirrors the patterns in stoichiometry of the seagrasses of south Florida (Fourqurean & Zieman 2002, Fourqurean et al. 2005), as well as the onshore-offshore pattern observed in Sulawesi, Indonesia

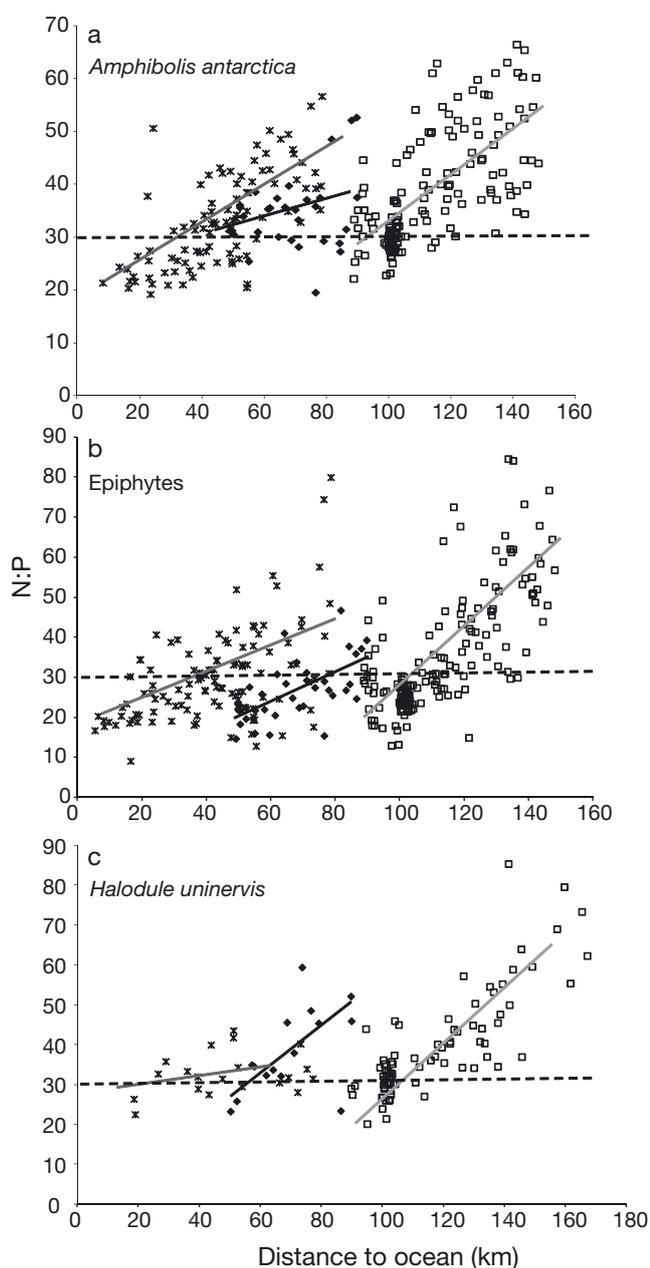


Fig. 5. Regional variation in the influence of distance from the Indian Ocean on N:P ratios. \times = Western Gulf, \blacklozenge = Northern Region, \square = Eastern Gulf. Values above the dashed line suggest P limitation while those below the line suggest N limitation. See Table 5 for statistical results

(Erftemeijer 1994) and in the mangrove-lined creeks of the Bahamas (Allgeier et al. 2011). The inferences about resource limitation derived from these stoichiometric spatial patterns—N limitation offshore, P limitation in more isolated bays—have been verified with nutrient addition experiments in south Florida (Ferdie & Fourqurean 2004, Armitage et al. 2011).

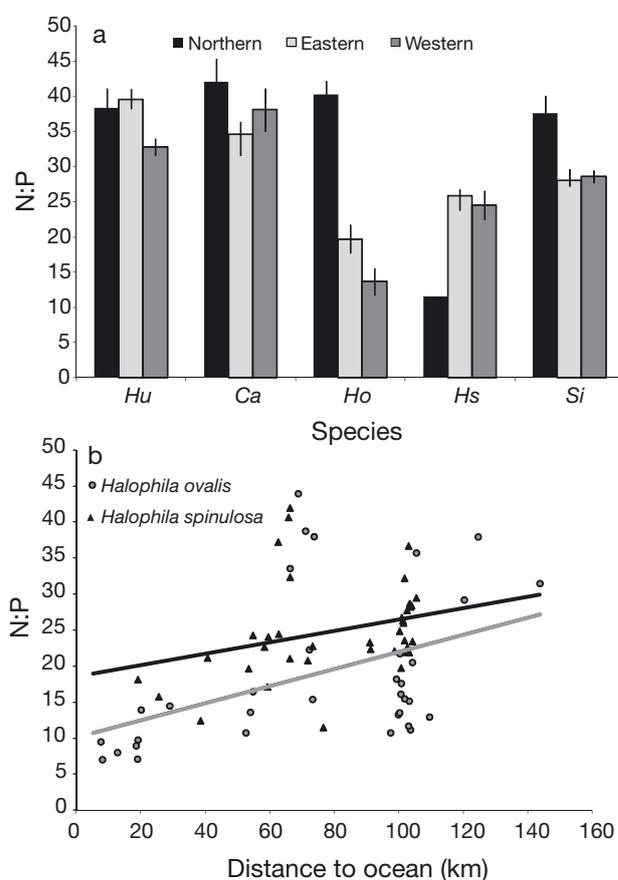


Fig. 6. Variation among (a) regions and (b) with distance from the Indian Ocean in N:P ratios of seagrasses in Shark Bay. Only species with significant main effects and no significant interaction between region and distance are included (see Table 5). N:P ratios >30 suggest P limitation, and values <30 suggest N limitation. See Fig. 3 for species abbreviations

These findings examine the utility of using stoichiometry of long-lived, sessile benthic primary producers for generating hypotheses about the functioning of ecosystems. Nutrient addition assays have not yet been conducted in Shark Bay to test these hypotheses. It is interesting to note, however, that in general the N:P ratios of Shark Bay seagrasses are lower than those from the severely P-limited regions of Florida Bay, which are often in excess of 96, suggesting that the scarcity of P in Shark Bay is not as severe as in Florida Bay. It is not just in carbonate-dominated, tropical locations that the spatial pattern in stoichiometry of seagrasses has been shown to be an indicator of relative nutrient availability across an ecosystem. For example, N content of the temperate seagrass *Zostera marina* decreases with increasing N limitation in Tomales Bay, California (Fourqurean et

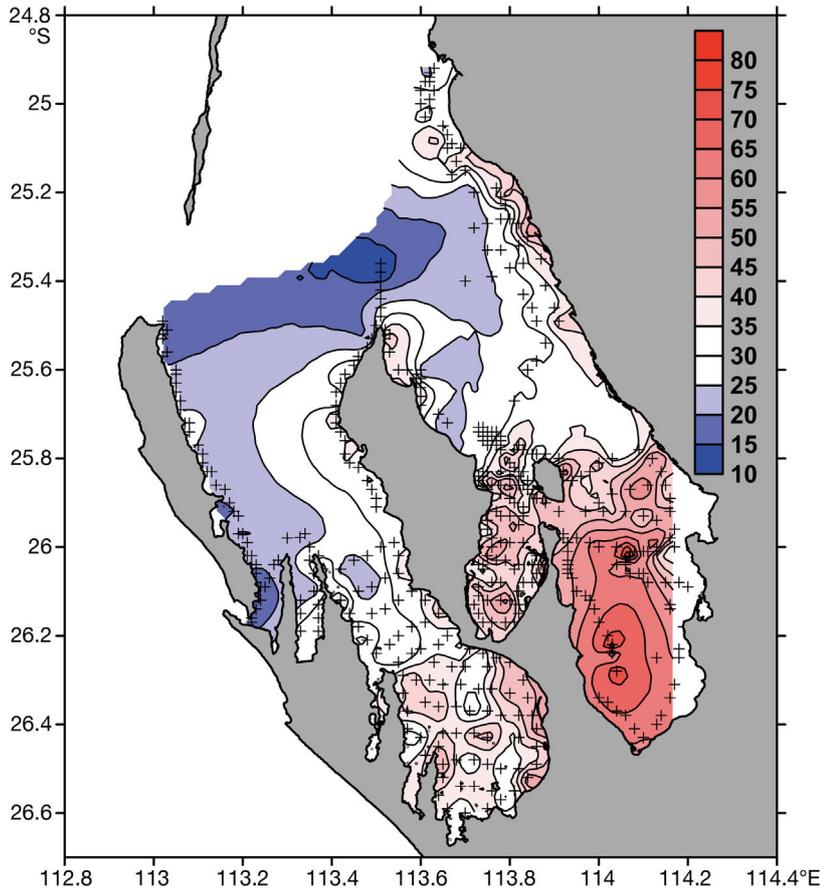


Fig. 7. Isopleth of nutrient availability according to N:P ratios. Blue represents N limitation (N:P < 30), red represents P limitation (N:P > 30), regions plotted in white show no N:P values consistent with nutrient limitation. (+) sample sites used for kriging map generation

al. 1997) and variation in C:N:P in the seagrasses and epiphytes of the northern Gulf of Mexico indicates distinct regions of N and P limitation (Johnson et al. 2006).

The spatial patterns in the relative importance of N and P in Shark Bay suggest that changes in N and P delivery to Shark Bay would have different consequences depending on the location within the bay. In the southern reaches of both the Eastern and Western Gulfs, P addition would likely cause increases in benthic primary production and change the community structure of the benthic primary producers and consumers, while N addition would likely have few effects. However, N inputs in the southern reaches of the system could potentially be transported towards the ocean and effect the seagrass communities of the less isolated, N-limited parts of the system. If management decisions about changes in nutrient delivery to a system were made on the basis of the whole-system nutrient budgets as done for Shark Bay (Smith & Atkinson 1984), such far-field effects could

not be anticipated, suggesting a need for understanding the resource availability landscape.

This spatial variation in the importance of P as a limiting nutrient in Shark Bay occurred despite the distribution of carbonate sediments across the entire bay. Owing to the high phosphate binding capacity of carbonate sediment and the resultant low mobility of P in carbonate systems (de Kanel & Morse 1978) and the common observations of P limitation of benthic primary production in carbonate sediment ecosystems (e.g. Short et al. 1985, Fourqurean et al. 1992), a paradigm of the general P limitation of primary production in carbonate sediment ecosystems arose. However, not all carbonate ecosystems are P limited; in fact, adjacent N- and P-limited regions in carbonate sediment ecosystems have now been identified in Shark Bay (Fig. 7) and south Florida (Fourqurean & Zieman 2002). This suggests that the carbonate content of sediments does not alone determine whether N or P will limit benthic primary production. While P does strongly bind to carbonate sediments (de Kanel & Morse 1978), respiration that generates acidity dissolves carbonate sediments (Jensen et al. 1998, Burdige et al.

2008), releasing the bound P (Jensen et al. 2009). Further, organic acids produced by seagrasses can also dissolve carbonates and release P (Long et al. 2008). Clearly, factors like N:P ratio of loadings and rates of N fixation and denitrification interact with sediment type to determine whether N or P are limiting factors in carbonate sediments.

Prior to this study, limited data on the N and P content of seagrasses from Shark Bay have been reported. The seasonally averaged N:P of *Posidonia australis* was reported as 25 and *Amphibolis antarctica* as 32 in a study of growth and nutrient content of these species near Monkey Mia, midway up the Eastern Gulf of Shark Bay (ratios calculated from data in Walker et al. 1988); our data from this same area indicates N:P ratios in the same range. These values suggest balanced N and P availability (Atkinson & Smith 1983, Duarte 1990); we interpret this to indicate that nutrients are not the limiting factor of biomass and primary production in the dense meadows characteristic of this area. We document a great range in the

N:P for these 2 taxa across the ecosystem, however, from 12.2 to 66.5 for *A. antarctica* and 12.8 to 63.0 for *Posidonia* spp. (Fig. 4), suggesting the relative availability of N and P for these species varies greatly across the system. Published data on the elemental content of other taxa from Shark Bay are lacking.

Elemental content of organisms is, of course, taxon-specific, as differences in architecture of organisms requires differing relative amounts of the various biomolecules needed to build and maintain morphologically and metabolically diverse organisms (Sterner & Elser 2002). It is now becoming clear that morphologically similar organisms, like the seagrasses for example, have distinct elemental ratios even when they are growing intermixed with other seagrasses. In south Florida in the subtropical Atlantic, which in general has seagrass N:P values suggestive of nutrient limitation across the landscape, slower growing species generally showed less nutrient-limited N:P ratios than fast growing species from the same locations, even though fast-growing species had higher N and P content than the slow-growing species (Campbell & Fourqurean 2009). In Shark Bay, we also found that the taxa with the faster relative growth rates had higher average N and P contents than the slower growing taxa. The slow-growing seagrasses *Amphibolis antarctica* and *Posidonia* spp. have biomass turnover rates of 3.8 to 3.9 yr⁻¹, compared to the smaller, faster-growing taxa like *Cyrtosira* spp. (11.7–12.0 yr⁻¹), *Syringodium* spp. (11.0–13.7 yr⁻¹), *Halodule* spp. (13.9 yr⁻¹) and *Halophila* spp. (17.2–32.4 yr⁻¹) (Duarte 1991). Averaged across all collections, the slow-growing taxa had lower N and P content, as indicated by higher C:N and C:P ratios, than the faster-growing taxa (Fig. 4a,b). Within sites where species co-occurred, there were consistent differences between species pairs (Tables 2 to 4), allowing us to calculate a standardized seagrass elemental content across sites with different species composition. Such standardization allowed us to make ecosystem-scale inferences that would not have been possible otherwise because of the taxon-specific distributions and elemental contents.

We also found that seagrass species varied considerably in their nutrient content, and possibly palatability to herbivores. Nutrient content is one of many key drivers of herbivore forage selection (e.g. Bjornald 1980, Boyer et al. 2004, Armitage & Fourqurean 2006), and appears to play a role in forage choice of herbivores in Shark Bay (Burkholder et al. in press). However, further investigation is needed to fully elucidate herbivore forage choice in this system. Spe-

cies-specific differences in nutrient content can lead to species-specific herbivory. Since seagrass species in Shark Bay with lower nutrient content (especially *Amphibolis antarctica*) provide shelter for some herbivores (e.g. *Pelates octolineatus*¹; Heithaus 2004), these low-quality forage species (Burkholder et al. in press) may enhance herbivory rates on more palatable species. In conclusion, by normalizing N:P ratios across seagrass species, we were able to elucidate spatial patterns of nutrient-limitation in an iconic P-limited coastal ecosystem. We found that P limitation occurred, despite calcium carbonate sediments, only in the most isolated portions of the bay and large areas were either N limited or not nutrient limited, where we believe light limitation is the most likely driver. Therefore, management decisions aimed at avoiding eutrophication should consider potential meso-scale variation in nutrient limitation within coastal ecosystems. The low rainfall, low runoff nature of Shark Bay and the very low human population densities in its watershed suggest that large-scale eutrophication from terrestrial anthropogenic sources of this system is not likely in the near future, but nonetheless, the broad parts of the system that are nutrient limited are at risk to eutrophication if the human population grows markedly in this area.

Acknowledgements. We thank the Monkey Mia Dolphin Resort for providing lodging and logistical support throughout the study. Special thanks to the Department of Environment and Conservation (DEC) for logistical field support and an army of field assistants that made the project possible. K. Gastrich and the Seagrass Ecosystems Research Lab provided invaluable assistance in the lab. Funding for this project was provided by National Science Foundation grants OCE0526065 and OCE0745606, a Supplement to the Florida Coastal Everglades Long Term Ecological Research Project grant DBI0620409, and an FIU Dissertation Evidence Acquisition Fellowship to D.A.B. We thank Jopalo Boats, Bombadier Recreation Products, Humminbird, The Airline, and Submersible Systems for significant donations in the form of discounts on boats and equipment. Research was conducted under DEC permit numbers: CE001685, CE002300, CE001879, SW01147, SW012509, SW11794 and subsequent annual renewals. This is contribution #66 of the Shark Bay Ecosystem Research Project and #587 of the Southeast Environmental Research Center at Florida International University.

¹ *Pelates octolineatus* has previously been referred to as *P. sexlineatus* in the literature. *P. octolineatus*, a western Australian species, is now considered distinct from *P. sexlineatus*, which is now considered to be confined to eastern Australia

LITERATURE CITED

- Allgeier JE, Rosemond AD, Layman CA (2011) Variation in nutrient limitation and seagrass nutrient content in Bahamian tidal creek ecosystems. *J Exp Mar Biol Ecol* 407:330–336
- Armitage AR, Fourqurean JW (2006) The short-term influence of herbivory near patch reefs varies between seagrass species. *J Exp Mar Biol Ecol* 339:65–74
- Armitage AR, Frankovich TA, Fourqurean JW (2011) Long-term effects of adding nutrients to an oligotrophic coastal environment. *Ecosystems* 14:430–444
- Atkinson MJ (1987) Low phosphorus sediments in a hypersaline marine bay. *Estuar Coast Shelf Sci* 24:335–347
- Atkinson MJ, Smith SV (1983) C:N:P ratios of benthic marine plants. *Limnol Oceanogr* 28:568–574
- Bjorndal KA (1980) Nutrition and grazing behavior of the green turtle, *Chelonia mydas*. *Mar Biol* 56:147–154
- Boyer KE, Fong P, Armitage AR, Cohen RA (2004) Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. *Coral Reefs* 23:530–538
- Burdige DJ, Zimmerman RC, Hu XP (2008) Rates of carbonate dissolution in permeable sediments estimated from pore-water profiles: the role of sea grasses. *Limnol Oceanogr* 53:549–565
- Burkholder DA, Heithaus MR, Fourqurean JW (2012) Feeding preferences of herbivores in a relatively pristine subtropical seagrass ecosystem. *Mar Freshw Res* 63:1051–1058
- Campbell JE, Fourqurean JW (2009) Interspecific variation in the elemental and stable isotopic content of seagrasses in South Florida. *Mar Ecol Prog Ser* 387:109–123
- de Kanel J, Morse JW (1978) The chemistry of orthophosphate uptake from seawater onto calcite and aragonite. *Geochim Cosmochim Acta* 42:1335–1340
- Duarte CM (1990) Seagrass nutrient content. *Mar Ecol Prog Ser* 67:201–207
- Duarte CM (1991) Allometric scaling of seagrass form and productivity. *Mar Ecol Prog Ser* 77:289–300
- Erfteimeijer PLA (1994) Differences in nutrient concentrations and resources between seagrass communities on carbonate and terrigenous sediments in South Sulawesi, Indonesia. *Bull Mar Sci* 54:403–419
- Ferdie M, Fourqurean JW (2004) Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment. *Limnol Oceanogr* 49:2082–2094
- Fourqurean JW, Zieman JC (2002) Seagrass nutrient content reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys, USA. *Biogeochemistry* 61:229–245
- Fourqurean JW, Zieman JC, Powell GVN (1992) Phosphorus limitation of primary production in Florida Bay: evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol Oceanogr* 37:162–171
- Fourqurean JW, Moore TO, Fry B, Hollibaugh JT (1997) Spatial and temporal variation in C:N:P ratios, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. *Mar Ecol Prog Ser* 157:147–157
- Fourqurean JW, Escorcia SP, Anderson WT, Zieman JC (2005) Spatial and seasonal variability in elemental content, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of *Thalassia testudinum* from south Florida and its implications for ecosystem studies. *Estuaries* 28:447–461
- Hanson CE, Pattiaratchi CB, Waite AM (2005) Sporadic upwelling on a downwelling coast: Phytoplankton responses to spatially variable nutrient dynamics off the Gascoyne region of Western Australia. *Cont Shelf Res* 25:1561–1582
- Harrison PJ, Hu MH, Yang YP, Lu X (1990) Phosphate limitation in estuarine and coastal waters of China. *J Exp Mar Biol Ecol* 140:79–87
- Heithaus MR (2004) Fish communities of seagrass meadows and associated habitats in Shark Bay, Western Australia. *Bull Mar Sci* 75:79–99
- Howarth RW (1988) Nutrient limitation of net primary production in marine ecosystems. *Annu Rev Ecol Syst* 19:89–110
- Jensen HS, Mcglathery KJ, Marino R, Howarth RW (1998) Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. *Limnol Oceanogr* 43:799–810
- Jensen HS, Nielsen OI, Koch MS, De Vicente I (2009) Phosphorus release with carbonate dissolution coupled to sulfide oxidation in Florida Bay seagrass sediments. *Limnol Oceanogr* 54:1753–1764
- Johnson MW, Heck KL, Fourqurean JW (2006) Nutrient content of seagrasses and epiphytes in the northern Gulf of Mexico: evidence of phosphorus and nitrogen limitation. *Aquat Bot* 85:103–111
- Krom MD, Kress N, Brenner S, Gordon LI (1991) Phosphorus limitation of primary productivity in the eastern Mediterranean Sea. *Limnol Oceanogr* 36:424–432
- Long MH, Mcglathery KJ, Zieman JC, Berg P (2008) The role of organic acid exudates in liberating phosphorus from seagrass-vegetated carbonate sediments. *Limnol Oceanogr* 53:2616–2626
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809
- Nixon SW (1995) Coastal marine eutrophication—a definition, social causes and future concerns. *Ophelia* 41:199–219
- Orth RJ, Carruthers JB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. *Bioscience* 56:987–996
- Price RM, Skrzypek G, Grierson PF, Swart PK, Fourqurean JW (in press) The use of stable isotopes of oxygen and hydrogen to identify water sources in two hypersaline estuaries with different hydrologic regimes. *Mar Freshw Res* 63:952–966
- Redfield AC (1958) The biological control of chemical factors in the environment. *Am Sci* 46:205–221
- Segal RD, Waite AM, Hamilton DP (2009) Nutrient limitation of phytoplankton in solar salt ponds in Shark Bay, Western Australia. *Hydrobiologia* 626:97–109
- Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. *Environ Conserv* 23:17–27
- Short FT, Davis MW, Gibson RA, Zimmermann CF (1985) Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuar Coast Shelf Sci* 20:419–430
- Smith SV (1984) Phosphorus versus nitrogen limitation in the marine environment. *Limnol Oceanogr* 29:1149–1160
- Smith SV, Atkinson MJ (1983) Mass balance of carbon and phosphorus in Shark Bay, Western Australia. *Limnol Oceanogr* 28:625–639

- Smith SV, Atkinson MJ (1984) Phosphorus limitation of net production in a confined aquatic ecosystem. *Nature* 307: 626–627
- Sterner RW, Elser JJ (2002) *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, NJ
- Walker DI, McComb AJ (1988) Seasonal variation in the production, biomass and nutrient status of *Amphibolis antarctica* (Labill.) Sonder ex Aschers. and *Posidonia australis* hook.f. in Shark Bay, Western Australia. *Aquat Bot* 31:259–275
- Walker DI, Woelkerling WJ (1988) Quantitative study of sediment contribution by epiphytic coralline red algae in seagrass meadows in Shark Bay, Western Australia. *Mar Ecol Prog Ser* 43:71–77
- Walker DI, Kendrick GA, McComb AJ (1988) The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. *Aquat Bot* 30:305–317
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106:12377–12381
- Wulff F, Eyre BD, Johnstone R (2011) Nitrogen versus phosphorus limitation in a subtropical coastal embayment (Moreton Bay; Australia): implications for management. *Ecol Model* 222:120–130
- Zieman JC, Wetzel RG (1980) Productivity in seagrasses: methods and rates. In: Phillips RC, McRoy CP (eds) *Handbook of seagrass biology, an ecosystem perspective*. Garland STPM, New York, NY, p 87–116

*Editorial responsibility: Just Cebrian,
Dauphin Island, Alabama, USA*

*Submitted: January 13, 2012; Accepted: September 10, 2012
Proofs received from author(s): December 17, 2012*