Feeding preferences of herbivores in a relatively pristine subtropical seagrass ecosystem

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Abstract.   Understanding forage choice of herbivores is important for predicting the potential impacts of changes in their abundance. Such studies, however, are rare in ecosystems with intact populations of both megagrazers (sirenians, sea turtles) and fish grazers. We used feeding assays and nutrient analyses of seagrasses to determine whether forage choice of grazers in Shark Bay, Australia, are influenced by the quality of seagrasses. We found significant interspecific variation in removal rates of seagrasses across three habitats (shallow seagrass bank interior, shallow seagrass bank edge, deep), but we did not detect variation in gazing intensity among habitats. In general, grazers were more likely to consume fast-growing species with lower carbon : nitrogen (C : N) and carbon : phosphorus (C : P) ratios, than the slower-growing species that are dominant in the bay. Grazer choices were not, however, correlated with nutrient content within the tropical seagrasses. Slow-growing temperate seagrasses that experienced lower herbivory provide greater habitat value as a refuge for fishes and may facilitate fish grazing on tropical species. Further studies are needed, however, to more fully resolve the factors influencing grazer foraging preferences and the possibility that grazers mediate indirect interactions among seagrass species.

Additional keywords: *Amphibolis*, *Cymodocea*, diet selection, dugong, food choice, green turtle, *Halodule*, *Halophila*, *Pelates*, *Posidonia*.

Introduction

Herbivores can play an important role in structuring primary-producer communities in terrestrial, freshwater and marine habitats. In marine settings, green turtles (*Chelonia mydas*; Bjorndal 1997; Moran and Bjorndal 2005; Fourqurean *et al.* 2010; Lal *et al.* 2010), dugongs (*Dugong dugon*; Aragones and Marsh 2000; de Iongh *et al.* 1995; Preen 1995; Masini *et al.* 2001) and fishes (Kirsch *et al.* 2002; Tomas *et al.* 2005; Armitage and Fourqurean 2006) can modify the structure and biomass of seagrass communities. The relative importance of herbivory in structuring seagrass ecosystems, however, has traditionally been underappreciated, likely because populations of large-bodied grazers have been greatly reduced in many ecosystems worldwide (e.g. Heck and Valentine 2007).

Understanding herbivore forage choice is critical for predicting ecosystem effects of changing population densities of herbivores. For example, experimental addition of nutrients or removal of herbivorous fish on Conch Reef in the Florida Keys resulted in increased algal cover and algal biomass, and suppressed cover of crustose coralline algae (Burkepile and Hay 2009). Around the fringing reefs of the Florida Keys, *Sparisoma aurofrenatum* (redband parrotfish) selectively grazes on the higher nutrient-content, faster-growing seagrass *Halodule wrightii* rather than on the lower nutrient-content, slower-growing *Thalassia testudinum*. Fish herbivory facilitates the dominance of *T. testudinum* in areas near reefs (Armitage and Fourqurean 2006). In addition to showing preference among functional forms and species of primary producers, the nutrient content of individual species can also influence the grazing rates of herbivores; e.g. parrotfishes prefer grazing on *Thalassia testudinum* with high rather than lower N content (Goecker *et al.* 2005). In general, higher N and P content in primary producers is associated with higher grazing rates within and among species. For example, manipulating nutrient content of primary producers resulted in plots with higher nutrient content experiencing fish foraging rates 3–13 times higher than those in the control plots (Burkepile and Hay 2009). Also, Boyer *et al.* (2004) found that increased tissue N and P of the macroalgae *Acanthophora spicifera* resulted in increased fish herbivory across multiple habitats (coral, seagrass and mangrove), with increases as high as 91% in mangrove habitats. Such preferences for high-nutrient content also appear to drive preferences for particular species and can influence the composition of primary-producer communities. For example, in the Wantamu Marine

Park in Kenya, herbivorous fish foraged more on fast-growing seagrass species, including *Cymodocea rotundata*, with lower carbon content (i.e. low C : N) than on slow-growing species with higher carbon fibre content (Mariani and Alcoverro 1999). Preferential grazing of highly palatable *Halodule wrightii* by juvenile parrotfish may help explain its relatively low abundance in Florida Bay and the Florida Keys compared with that of the less palatable *Thalassia testudinum* (Armitage and Fourqurean 2006). Similar preferences for fast-growing species with high N and P content have been suggested for both dugongs (de Iongh *et al.* 1995; Preen 1995) and green turtles (Moran and Bjorndal 2005).

Feedbacks in grazed ecosystems can influence species composition of communities. For example, excavation grazing by dugongs facilitates the dominance of their preferred seagrass species because these high-N content species are fast-growing (Preen 1995). Therefore, understanding forage choice of marine herbivores is important for predicting the consequences of changes in their abundance for primary-producer communities. This may be particularly true for subtropical embayments, which can contain a diverse array of seagrass species with variable life histories, nutrient content and resilience to grazing disturbance. For example, the seagrass communities in Shark Bay, Western Australia, are a mix of slow-growing, low nutrient-content species of temperate origin (e.g. *Amphibolis antarctica*, *Posidonia* spp.) and more rapidly growing, high nutrient-content species of primarily tropical origin (e.g. *Cymodocea* sp., *Halodule* sp, *Halophila* sp.) (Walker *et al.* 1988; Burkholder *et al.* in press).

We set out to investigate whether the large populations of herbivores in Shark Bay – which include dugongs, sea turtles and fishes – would selectively forage on high nutrient-content, fast-growing tropical species when given a choice. Because the abundance of these large-bodied grazers in Shark Bay can vary in space and time (e.g. Heithaus 2004; Heithaus *et al.* 2007a; Wirsing *et al.* 2007a, 2007b), we conducted forage-choice assay trials across multiple habitat types.

Materials and methods

Study site

The study was conducted in the Eastern Gulf of Shark Bay, Western Australia (~25°45′S, 113°44′E). Located ~800 km north of Perth, Shark Bay is a shallow (<15 m) subtropical bay dominated by extensive seagrass beds, which cover ~4000 km² (Walker *et al.* 1988). Our study site in the Eastern Gulf is characterised by a series of shallow (<4.5 m) seagrass banks, separated by deeper channels (6–11 m) mostly covered by sand. Shallow habitats can be further subdivided into two microhabitats – interior portions of banks and bank edges – that vary in the abundance of some herbivorous species as well as seagrass community structure and biomass (see Heithaus *et al.* 2007a; Wirsing *et al.* 2007b; Burkholder *et al.* in press).

Shark Bay is perhaps one of the most pristine remaining seagrass ecosystems in the world and affords a unique opportunity to examine the effects of large herbivores on seagrass ecosystems (Heithaus *et al.* 2007b, 2008). Dominant herbivores in the system include green turtles (*Chelonia mydas*), dugongs (*Dugong dugon*) and teleosts (including the very common

striped trumpeters, *Pelates octolineatus*; previously, *P. sexlineatus*); these species are likely to be at or near population densities expected in the absence of anthropogenic impacts (Preen *et al.* 1997; Heithaus 2004; Heithaus *et al.* 2005). The seagrass community in our study area is a diverse assemblage. The dominant species, *Amphibolis antarctica* and *Posidonia australis*, are large and slow-growing. Smaller, faster-growing seagrasses, including *Halophila ovalis*, *H. spinulosa*, *Halodule uninervis*, *Cymodocea angustata*, *Syringodium isoetifolium*, *Halophila decipiens* and *H. minor*, are found in lower abundances (Walker *et al.* 1988; Burkholder *et al.* in press). Duarte (1991) estimated that the leaf turnover rates (in units per year) for the species in our study at 3.86 units per year for *Posidonia australis*, 3.94 units per year for *Amphibolis antarctica*, 8.14 units per year for *Cymodocea angustata*, 13.87 units per year for *Halodule uninervis*, 20.85 units per year for *Halophila ovalis* and 21.00 units per year for *H. spinulosa*. Relevant figures present species in order of growth rates from slowest to fastest.

Field methods

Because the abundance of megaherbivores (dugong and green sea turtle) and mesograzers (striped trumpeters) varies among habitats (deep *v.* shallow) and within shallow ones (seagrass interior *v.* seagrass edge) for at least megagrazers (see Heithaus 2004; Heithaus *et al.* 2007a; Wirsing *et al.* 2007a, 2007b), we conducted a total of 35 forage-preference assays across multiple habitats (shallow interior, bank edges, deep). Five assays were conducted during March 2007 and 30 were conducted February–March 2009. Each trial consisted of a series of servings of seagrasses (see below) that were woven into a 7-mm, three-strand nylon rope, with servings spaced every 50 cm along the line. Seagrasses were secured to the line with paperclips to stand vertically to simulate live seagrasses. The lines were placed over sand bottoms parallel to the edge of a seagrass patch at a distance of 1 m from the sand to seagrass margin and secured to the sediment with bent metal-wire stakes. For each trial, we included three replicate 'servings' of each abundant seagrass species ($n = 18$ total servings per trial – 3 replicates $\times$ 6 seagrass species – in 2007; $n = 15$ total servings per trial – 3 replicates $\times$ 5 seagrass species – in 2009). During 2007, we conducted all five trials in interior habitats using *Halophila ovalis*, *H. spinulosa*, *Amphibolis antarctica*, *Posidonia australis*, *Halodule uninervis* and *Cymodocea angustata*. In 2009, we conducted 30 trials ($n = 10$ per habitat), with all species used in 2009 except for *Halophila spinulosa*, which was not present in adequate abundances for collection in 2009.

Prior to an assay, we collected leaves of all available seagrass species from one of two 'donor beds', depending on seagrass species, and separated collections into replicate servings. Each serving was photographed individually, with a numbered plate identifying the serving number and position in the line and a ruler making it possible to match leaves before and after trials. The number of leaves per serving varied across species so as to approximately match servings for total biomass (i.e. servings of species with large leaves contained fewer leaves than servings of species with small leaves). Three leaves were used for *Posidonia australis*, five leaves were used for *Amphibolis antarctica*, *Halophila spinulosa*, *H. ovalis* and *Cymodocea angustata*, and 10 leaves were used for *Halodule uninervis*. Seagrass species

order on each line was assigned haphazardly and the pattern was repeated for each of the three servings per species on an assay. Therefore, the nearest neighbours of a particular species varied across lines within habitats. Each assay was run for 24 h and then the lines were removed. Servings were removed from the paperclips, laid flat and re-photographed, all leaf material (total serving) was assessed in the before and after photographs to calculate total percentage leaf area lost. Although no specific controls were run during the time of herbivory assays, seagrass species used in the present study were transplanted into cages that prevented herbivory for another study. All species maintained or increased their biomass (C. Bessey, K. Gastrich, M. Heithaus, D. Burkholder and J. Fourqurean, unpubl. data), suggesting that the loss or damage to leaf material in our study was from herbivores and not handling.

In some systems, herbivores leave distinctive bite marks on seagrass leaves when they forage; for instance, bucktooth parrotfish, *Sparisoma radians*, leaves distinctive curved bite-marks (Goecker *et al.* 2005). We were unable to use such approaches in the present study because dugongs and turtles would be expected to remove entire servings in many cases and the stomach-content analysis of *P. octolineatus* suggests that rather than removing small bites from blades, it consumes the entire width of blades in many cases (C. Bessey and M. Heithaus, unpubl. data). Although we encountered some bitemarks of herbivorous fish on the larger seagrass species, smaller tropical species in the present study exhibited marks that were characterised by large portions of the leaves missing and the bite consuming the entire width of the leaf. Such bites could be due to either turtle or fish herbivory. Behavioural observations while deploying assay lines suggest that herbivorous fish, specifically *P. octolineatus*, may have played a significant role in seagrass removal for some seagrass species. Stomach-content analysis of green sea turtles (Burkholder *et al.* 2011) and *P. octolineatus* (C. Bessey, unpubl. data) in Shark Bay suggested that they eat multiple species of seagrass, including some *Amphibolis antarctica*.

We analysed seagrasses collected from our donor beds between 2007 and 2009 to determine nutrient content. At least five shoots were collected for each species. All samples were stored on ice in the field and immediately frozen to $-20°C$ on return to shore. Samples remained frozen until they could be processed.

Laboratory methods

Seagrass samples for elemental analysis were thawed, rinsed in deionised water, and each leaf was gently scraped with a razorblade to remove all epibiota. 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 five plants collected for each site were dried using a food dehydrator (Ezidri Ultra FD1000, EziDri, Moorabbin, Australia) for at least 24 h. Once dry, samples were crushed into powder for analysis with a mortar and pestle. The contents of C and N in samples were measured using an elemental analyser (Fisons NA1500, UK) and P content was measured using a dry-oxidation/acid hydrolysis method (Fourqurean *et al.* 1992).

Analyses

We investigated species differences in elemental composition (C : N, C : P) of seagrasses at the sites from which the plants were collected (i.e. donor beds) to determine whether herbivore preferences might partially be explained by interspecific variation in nutrient composition. These included *Amphibolis antarctica*, *Posidonia australis*, *Halodule uninervis* and *Cymodocea angustata* samples from edge habitat and *Halophila ovalis* and *H. spinulosa* samples from deep habitats. Only samples from warm months (October–May) were included in analyses because nutrient content can vary seasonally (Fourqurean *et al.* 2005) and our trials were conducted during these times.

Because it is difficult to ensure that all leaves of certain seagrass species are perfectly flat during photographs and extensive handling could damage seagrass leaves, we estimated the proportion of leaf area lost for each serving by comparing photographs of each serving before and after a trial. All serving photographs were viewed by five independent observers who recorded the estimated percentage area loss during the trial. For analyses, we used the average estimated percentage loss for each serving across the five observers and then collapsed the data for the three servings of each species in each trial to a single mean value. This accounted for non-independence of the three replicate servings within an assay line.

We used a conditional approach to analyses because of the large number of zeros in the dataset. In this approach, we first conducted a logistic regression to investigate variation in the probability that any of the three servings were grazed at all on a line. Then, we used ANOVA on arcsin square-root transformed data to investigate factors affecting the proportion of seagrass removed from servings if any grazing occurred during the trial (i.e. we did not include zeros in the dataset). Because of differences in species used during the 2 years of trials we analysed these data separately. In 2007, we investigated variation only among species of seagrasses (because all trials occurred within interior microhabitats). In 2009, we investigated the effects of species, microhabitat (interior, edge, deep) and their interaction. The interaction term was removed and the model re-run if $P > 0.10$. Although individual lines may experience different overall levels of herbivory, we did not account for non-independence of species within a line because variance in overall herbivory pressure among lines should obscure results and non-parametric tests (e.g. Friedman's test) do not allow for independent contrasts among species.

Results

There was significant variation among seagrasses in C : N and C : P ratios ($F_{5,289} = 59.4$, $P < 0.0001$; $F_{5,289} = 49.7$, $P < 0.0001$, respectively). N content was higher in all of the faster-growing species than in *Amphibolis* or *Posidonia*, with *Cymodocea* and *Halodule* having the highest relative N content (Fig. 1*a*). Similarly, P concentration was lowest (i.e. highes C : P ratios) in *Amphibolis* and *Posidonia* and highest in *Halophila ovalis* (Fig. 1*b*). All other species had similar, and intermediate, values.

In 2007 in interior habitats, there was significant variation among species in the probability that at least one serving of a species would be grazed ($\chi^2 = 19.9$, d.f. = 5, $P = 0.001$) and the
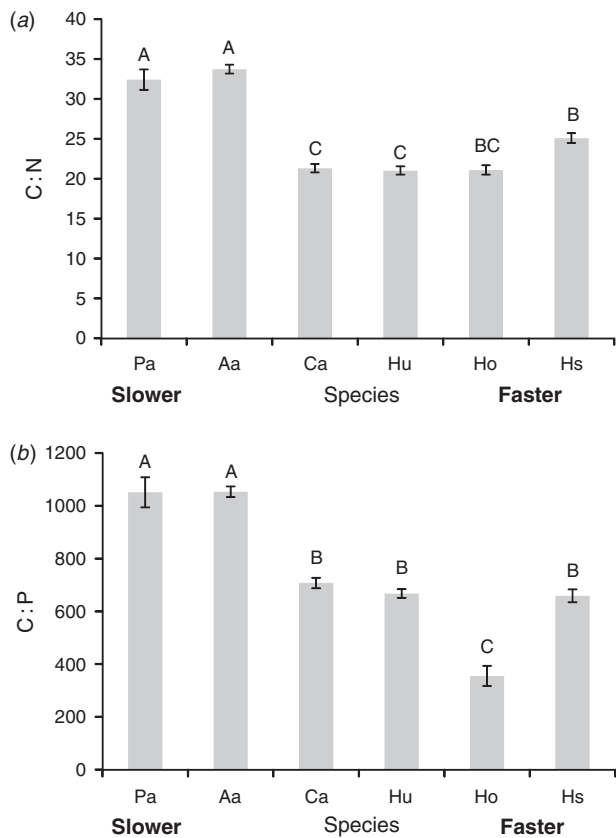
Fig. 1. Interspecific variation in (*a*) carbon : nitrogen (C : N) and (*b*) carbon : phosphorus (C : P) ratios of seagrasses collected for feeding preference trials. Error bars are ±s.e. Bars labelled with the same letter are not significantly different from one another. Note that lower values should indicate species of greater quality from an herbivores perspective (i.e. higher relative N or P content). Seagrass species are arranged along the *x*-axis according to leaf turnover rates from slowest to fastest. Aa = *Amphibolis antarctica* (*n* = 166), Ca = *Cymodocea angustata* (*n* = 32), Hu = *Halodule uninervis* (*n* = 43), Ho = *Halophila ovalis* (*n* = 12), Hs = *Halophila spinulosa* (*n* = 43) and Pa = *Posidonia australis* (*n* = 36).

Fig. 2. (*a*) Proportion of lines with at least some grazing on seagrasses during 2007 trials in interior microhabitats. (*b*) Proportion of leaf area removed for lines and species that experienced at least some grazing of at least one serving. Bars with the same letter are not significantly different from each other. Error bars are ±s.e. Seagrass species are arranged along the *x*-axis according to leaf turnover rates from slowest to fastest. Aa = *Amphibolis antarctica*, Ca = *Cymodocea angustata*, Hu = *Halodule uninervis*, Ho = *Halophila ovalis*, Hs = *Halophila spinulosa* and Pa = *Posidonia australis*.

proportion of leaf area that was removed if grazing occurred ($F_{5,47} = 15.7$, $P < 0.0001$). *Halophila spinulosa* and *Halodule uninervis* always had at least one serving grazed and *Amphibolis antarctica* and *Posidonia australis* were grazed relatively infrequently (Fig. 2*a*). When grazed, *H. spinulosa* experienced the greatest amount of leaf-area loss, followed by *H. uninervis* (Fig. 2*b*).

During 2009, the probability that at least one serving of a species was grazed during a trial varied among species ($\chi^2 = 40.9$, d.f. = 4, $P < 0.0001$). There were not statistically significant differences across habitats ($\chi^2 = 3.9$, d.f. = 2, $P = 0.14$) and we did not detect an effect of the interaction between habitat and seagrass species ($\chi^2 = 10.4$, d.f. = 8, $P = 0.24$). *Halodule uninervis* and *Halophila ovalis* were the most likely species to be grazed and *Amphibolis antarctica* and *Posidonia australis* were the least likely species to be grazed, and probabilities of at least some grazing occurring was higher for these temperate species in 2009 than they were in 2007 (Fig. 3*a*). The amount of seagrass removed from servings that
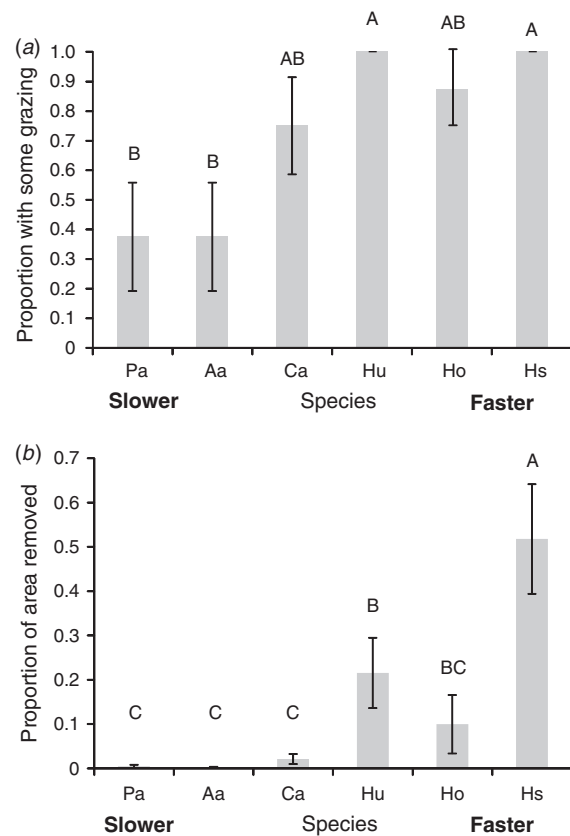
were grazed varied among species ($F_{4,111} = 13.60$, $P < 0.0001$), but there was no statistically significant effect of habitat ($F_{2,111} = 0.5$, $P = 0.59$) or the interaction of seagrass species and habitat ($F_{8,111} = 1.0$, $P = 0.42$). *Halodule uninervis* and *Halophila ovalis* had substantially higher proportions of servings removed than did the three other species, which did not differ significantly (Fig. 3*b*).

Discussion

In the relatively pristine seagrass ecosystem of Shark Bay, fast-growing, smaller, high nutrient-content seagrasses were consumed by herbivores at a faster rate than were slow-growing, larger, low nutrient-content seagrasses. For the individual seagrass species, removal rates of seagrass species were generally similar across years in warm seasons and did not appear to vary across habitat types. The lack of detected spatial variation, however, may be explained by relatively low sample sizes, the short duration of trials, the relative importance of fish grazing, or
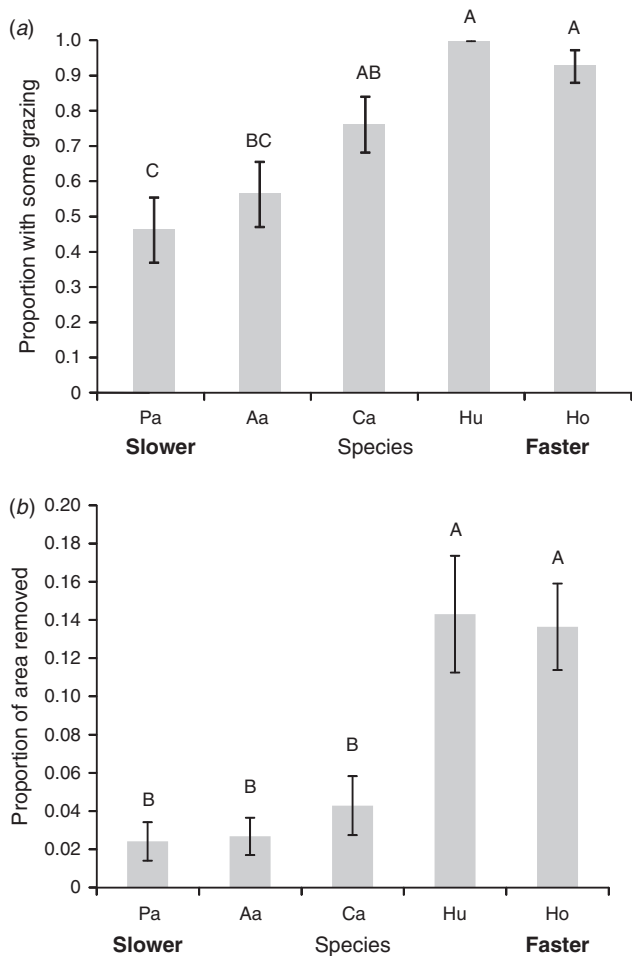
Fig. 3. (*a*) Proportion of lines with at least some grazing on seagrasses during 2009 trials in interior, edge and deep microhabitats. There was no detectable effect of habitat or the interaction of habitat and species. (*b*) Proportion of leaf area removed for lines and species that experienced at least some grazing of at least one serving. There was no detectable effect of habitat or the interaction of habitat and species. Bars with the same letter are not significantly different. Error bars are ±s.e. Seagrass species are arranged along the *x*-axis according to leaf turnover rates from slowest to fastest. Aa = *Amphibolis antarctica*, Ca = *Cymodocea angustata*, Hu = *Halodule uninervis*, Ho = *Halophila ovalis*, Hs = *Halophila spinulosa* and Pa = *Posidonia australis*.

Table 1. Relationship between estimated proportion of leaf area removed (i.e. proportion grazed at all × mean area removed when grazed), mean carbon : nitrogen ratio (C : N) and mean carbon : phosphorus ratio (C : P) content of seagrass species

Aa = *Amphibolis antarctica*, Ca = *Cymodocea angustata*, Hu = *Halodule uninervis*, Ho = *Halophila ovalis*, Hs = *Halophila spinulosa* and Pa = *Posidonia australis*

Species	Year	C : N	C : P	Estimated proportion removed
Aa	2007	34.56	1071.62	0.001
Ca	2007	21.13	746.35	0.016
Hu	2007	20.99	682.23	0.215
Ho	2007	21.09	359.92	0.087
Hs	2007	25.68	666.25	0.518
Pa	2007	33.84	1102.28	0.002
Aa	2009	34.56	1071.62	0.015
Ca	2009	21.13	746.35	0.033
Hu	2009	20.99	682.23	0.143
Ho	2009	21.09	359.92	0.127
Pa	2009	33.84	1102.28	0.011

(D. Burkholder, pers. obs.), observations of seagrasses in the stomachs of *P. octolineatus* (C. Bessey and M. Heithaus, unpubl. data), fatty acid analysis consistent with substantial seagrass herbivory in 1/3 of the surveyed *P. octolineatus* individuals in the study area (Belicka *et al.* 2012), and the presence of partially removed servings in many situations. We would have expected turtles or dugongs to have completely, or largely, removed individual servings. The relatively small servings probably are more likely to attract teleosts than they are to attract turtles or dugongs and future studies should include video recording of trials as well as designs that might be more likely to attract turtles and dugongs.

The expectation that fast-growing species, with higher N and P contents, would be grazed more heavily than are slow-growing lower-quality forage species (*Amphibolis* and *Posidonia*) was generally upheld during our study. Variation in grazing patterns on fast-growing species are harder to explain. *Cymodocea angustata* had the highest N content, along with *Halodule uninervis*, whereas *Halophila ovalis* had the highest P content. *C. angustata*, however, experienced the least grazing of the faster-growing species, whereas *Halophila spinulosa* experienced the heaviest grazing, despite having lower N and P contents than for several other species (Table 1). Nutrient content and more specifically N content (food quality) is only one factor that may drive herbivore forage choices. Many marine plants employ both morphological and chemical defences that may reduce their palatability or forage quality to herbivores. These include morphological defences such as concentrated compounds in cell walls or increased fibre content, making them hard to digest (Fritz and Simms 1992). Plant chemical defences also can play an important role in herbivore food choice. Condensed tannins can affect protein-binding properties of the plant material, making protein less available to consumers, and phenolic compounds can reduce palatability or even increase toxicity to herbivores (Jones and Mangan 1977; McMillan 1984; Hay *et al.* 1987; Robbins *et al.* 1987; Hay and

grazing saturation on some species thus limiting the ability to detect more intense grazing. Unfortunately, we could not identify the species responsible for grazing on our seagrass servings, which makes it impossible to determine species-specific foraging patterns with our data. It is unlikely that all three grazer types (sea turtle, sirenians and teleosts) contributed equally to observed removals because of variation in their abundance and the likelihood that fish, turtles and dugongs respond differently to the sizes of servings in our assays. Although at the outset of the study we assumed that most grazing would be by green turtles and dugongs, it appears that the teleost *Pelates octolineatus* likely was responsible for most grazing. This is supported by observations of *P. octolineatus* removing entire servings of *H. spinulosa* before an assay was completely deployed

Fenical 1988; Hagerman *et al.* 1992; Arnold *et al.* 1995). In addition, epibiotic growth can also affect herbivory on marine plants (Wahl and Hay 1995; Karez *et al.* 2000; Jormalainen *et al.* 2008).

Grazer type also may affect how they select food types. For example, obligate herbivores appear to select potential foods on the basis of nutrient content, whereas omnivorous grazers may use other cues such as leaf manipulability and/or visual recognition of resources (Prado and Heck 2011). *Pelates octolineatus*, the numerically dominant fish grazer in the study area, is omnivorous (C. Bessey and M. Heithaus, unpubl. data). Therefore, the high rate of removal of *Halophila spinulosa* may be due in part to its morphology, with this species being more susceptible to complete removal of leaf tissue than are other tropical species. Indeed, during all trials in 2007 – the only year *H. spinulosa* was present in densities sufficient for grazing trials – grazers consumed at least a portion of *H. spinulosa* and *Halodule uninervis* during all trials and more than 70% of trials exhibited grazing on *Halophila ovalis* and *Cymodocea angustata* servings. *H. spinulosa*, however, exhibited higher proportions of leaf areas consumed from services that were grazed. The high rates of removal of fast-growing species raises the possibility that herbivores could be important in structuring seagrass communities in Shark Bay. Indeed, *H. spinulosa* was observed in high abundances in the study area only for relatively brief times after a storm event, and grazing on this highly preferred seagrass species could be responsible for observed declines in its abundance. Further work is needed to test this hypothesis.

The least-grazed species in our study – *Amphibolis antarctica* and *Posidonia australis* – are by far the dominant species in our study area (Burkholder *et al.* in press). *A. antarctica*, especially, forms large, dense, monospecific stands that can have canopy heights over 1 m. In a manner similar to the role that reefs can play in other near-shore ecosystems, the structural complexity of the dense *A. antarctica* canopies provides shelter for *Pelates octolineatus* (Heithaus 2004) and, therefore, may facilitate herbivory on more palatable tropical seagrasses in shallow habitats. Such apparent competition (i.e. negative effect of one species on another through the actions of a shared consumer; Holt 1977) among seagrass species may be an important feature in seagrass-community dynamics in Shark Bay. Grazers do not, however, completely overlook *A. antarctica* as a food source. Despite removing biomass of more palatable species during assays, some *A. antarctica* was consumed and observations of both green turtle and dugong foraging (e.g. Wirsing *et al.* 2007*c*), as well as stomach contents of striped trumpeters (C. Bessey, unpubl. data), show that *A. antarctica* is a component of their diets. Future trials, including those that incorporate video to identify grazers, larger sample sizes, trials in multiple seasons, as well as competition experiments between fast-growing and slow-growing species, are likely to provide interesting new insights into grazing dynamics in the bay.

Seagrasses stabilise coastal habitats, provide primary productivity and food for a system, and can serve as habitat for numerous invertebrates and fish species. Not all species, however, provide the same overall ecosystem services or value. For example, species composition of seagrass meadows in Florida

Bay strongly influences the structure and abundance of fish communities (Matheson *et al.* 1999). Because some seagrass species are preferred by herbivores over others and these herbivores can have large impacts on seagrass-community structure, it is important that managers incorporate an understanding of herbivore forage preferences and habitat use into management strategies. Whereas understanding forage preferences may not be as important in temperate environments where single seagrass species make up seagrass beds (e.g. *Zostera marina* in the North Atlantic temperate zone), it could be very important in areas with high seagrass species diversity, such as the subtropical embayments of Shark Bay or Florida Bay, where different management strategies can influence the species composition of seagrass beds in subtropical ecosystems (Fourqurean *et al.* 2003; Herbert *et al.* 2011).

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