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Herbivory in multi-species, tropical seagrass beds

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ABSTRACT: Very little is known about the characteristics of herbivory and selection by various grazers in tropical, multi-species seagrass beds. We used an *in situ* shoot tethering method to quantify grazing on 3 dominant seagrass species (*Thalassia hemprichii*, *Cymodocea rotundata*, and *C. serrulata*) that co-inhabit extensive seagrass beds surrounding Dongsha Island in the South China Sea. We measured the amount of seagrass grazing as well as leaf production in different habitats and seasons. The dominant seagrass grazers in Dongsha Island were parrotfish, followed by meso-invertebrates, suggesting that herbivory by small invertebrates may also be critical in tropical seagrass ecosystems. Our results revealed significant spatial and seasonal differences in leaf biomass losses. The level of grazing was 3.6× higher in the subtidal than in the intertidal zones, and 2.6× higher in the warm than in the cool season. Leaf biomass losses were positively associated with parrotfish density, water depth, leaf production, and starch content. However, the nitrogen and total sugar contents did not affect the preferences of the grazers. The 2 *Cymodocea* species were preferred by most grazers. Collectively, all grazers typically removed <10% of the leaf production in Dongsha Island, which indicates that most seagrass biomass was not directly used by herbivores and flows into detrital pathways.

KEY WORDS: *Cymodocea rotundata* · *Cymodocea serrulata* · Herbivory · Parrotfish · South China Sea · *Thalassia hemprichii*

INTRODUCTION

Seagrass production represents an important carbon source in coastal ecosystems (Duarte & Chiscano 1999). Although seagrasses fix CO_2 into organic carbon, they are considered to be a poor-quality food source, unlike algae, because their cellulose-rich leaves are difficult for most herbivores to digest (Thayer et al. 1984, Duarte 1990). It is often believed that most seagrass production is not directly used by herbivores and ultimately flows into detrital pathways in ecosystems (Nienhuis & Groenendijk 1986, Pergent et al. 1994, Cebrián 2002). Nevertheless, certain herbivores (e.g. fish and sea urchins) can directly consume seagrasses and become important grazers in seagrass beds (Ogden et al. 1973, Rose et al. 1999, Alcoverro & Mariani 2002, 2004, Heck & Valentine 2006). Several large animals (e.g. green turtles and dugongs) can consume large amounts of seagrass (Preen 1995, Aragones et al. 2006, Fourqurean et al. 2010). These grazers represent important top-down controls on seagrass production, and their grazing may affect the growth and canopy succession of seagrass beds (Valentine et al. 1997, Cebrián & Duarte 1998, Rose et al. 1999, Valentine & Heck 1999).

Herbivory in seagrass beds varies over both spatial and temporal scales as well as in response to a variety of factors: (1) Grazer density. The degree of herbivory may differ as a function of grazer density, which could be affected by bed structures and sea-

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*Corresponding author: hjlin@dragon.nchu.edu.tw scapes. Densities of herbivorous fish (Maciá & Robinson 2005, Prado et al. 2007, Gullström et al. 2011, Lee et al. 2014) and sea urchins (Tertschnig 1989, Klumpp et al. 1993, Rose et al. 1999, Alcoverro & Mariani 2002) are known to vary significantly with tides, depth and seascapes in different seagrass beds; (2) Seagrass characteristics. A variety of environmental factors can also affect the shapes, bed structures, leaf production, and seagrass species in beds (Alcoverro et al. 1995, Cebrián et al. 1996a, 1996b, Lan et al. 2005), leading to differing amounts of food availability for grazers (Aragones et al. 2006, Unsworth et al. 2007); and (3) Seagrass nutrient content. Nutrient content in seagrass leaves can also affect grazing preferences (Zieman et al. 1984, Valentine & Heck 2001, Goecker et al. 2005).

It is believed that seagrass herbivory is higher in the tropics than in temperate regions (Heck & Valentine 2006, Valentine & Duffy 2006). In tropical seagrass beds (especially in the Indo-Pacific region), several species may be integrated within the same bed (Vermaat et al. 1995, Lin et al. 2005, Unsworth et al. 2007). In multi-species seagrass beds, each seagrass species may have different characteristics and growth forms, leading to a wide variety of structures within the same bed. Under such conditions, grazers may be more selective, and their grazing may be influenced by the complex factors described above. In addition to parrotfish and sea urchins, which are commonly known to be important grazers in tropical seagrass beds, other meso-invertebrates can also feed on seagrass leaves. In tropical regions, crustaceans and gastropods can also directly consume seagrass leaves (Mukai & Iijima 1995, Holzer et al. 2011, Unabia 2011). However, very little is known about seagrass herbivory and food selection by diverse grazers in these multi-species seagrass beds (but see Mariani & Alcoverro 1999, Prado & Heck 2011).

Counting bite marks and comparing the leaf biomass with the maximum possible biomass are 2 approaches that have been used to estimate the loss of biomass due to grazing on seagrass leaves (Zieman et al. 1984, Cebrián et al. 1996b, Cebrián & Duarte 1998). The results of these studies have indicated that very limited portions of leaf production are consumed by grazers. However, these methods have been found to yield underestimates of seagrass grazing (Heck & Valentine 2006). More recently, methods based on direct estimation, such as leaf marking (via tethering), have been used to record grazing activities and quantify biomass losses in seagrass beds (Kirsch et al. 2002, Tomas et al. 2005, Unsworth et al. 2007, Chiu et al. 2013). By marking ungrazed seagrass *in situ*, biomass losses due to grazing were estimated more accurately by pre- and post-grazing comparison of leaves. Furthermore, the losses were compared with the biomass produced by the leaves, and the size and shape of the bite marks themselves were used to determine the predominant grazing fauna. These studies have found that grazers can remove larger amounts of leaf biomass than previous studies have shown, and the amounts of biomass removed were sometimes even greater than the amount of seagrass production (e.g. Kirsch et al. 2002, Unsworth et al. 2007).

However, these studies have also left several questions on seagrass herbivory unanswered: (1) *Spatial/temporal scales*. Many tethering studies were conducted at a particular time, and the sites chosen may have contained various seascapes. Herbivory could vary at different spatial/temporal scales; (2) *Unknown for multi-species seagrass beds*. Most of the studies employing tethering methods were conducted in mono-specific seagrass beds. To date, little is known about grazing in multi-species seagrass beds (but see Unsworth et al. 2007); (3) *Contribution of meso-invertebrates*. Although a significant amount of research has focused on seagrass herbivory by large herbivores (e.g. turtles, fish, and sea urchins), fewer have documented the contribution, or lack thereof, by smaller invertebrates (Heck & Valentine 2006); and (4) *Relationship with seagrass characteristics*. Few studies have focused on how both environmental factors and seagrass characteristics (e.g. leaf features or nutrient content) can affect the grazing preferences of herbivores in multi-species, tropical seagrass beds (but see Prado & Heck 2011). Quantifying the relationship between grazing preference and seagrass characteristics can help us better understand grazing behavior in tropical seagrass beds.

In this study, we applied *in situ* tethering methods to mark the leaves of various seagrass species in multi-species seagrass beds of Dongsha Island, which is a remote coral island in the South China Sea. Because Dongsha Island is a relatively pristine tropical island, the seagrass beds are extensive in both area and coverage (see detail below). The aims of this study were to: (1) quantify *in situ* herbivory rates on different seagrass species by various grazers in the multi-species beds, (2) explore temporal variability in the herbivory rates, (3) determine the preferences of various grazers in these multi-species beds, and (4) examine which factors may be affecting the grazing preferences of herbivores. We hypothesized that habitats of higher grazer density would be characterized by higher levels of herbivory and that seagrass leaf features and nutrient content would influence the overall preference of herbivores in these multi-species seagrass beds.

MATERIALS AND METHODS

Study site

Dongsha Island (20°42′ N, 116°43′ E) is a 1.74 km^2 coral island on the east side of Dongsha atoll (Fig. 1a) in the South China Sea. In 2007, the atoll was incorporated into the Dongsha Marine National Park and fishing activities have been prohibited within a 12 nautical mile radius of the atoll. A semi-enclosed lagoon (0.64 km^2) occupies the central part of Dongsha Island (Fig. 1b). An open inlet located on the western side of the island is the only channel that permits seawater exchange between the inner lagoon and the open ocean, and the degree of water exchange is dependent on the tidal cycle (tidal ranges: 0.85 ± 0.21 m). The water surrounding Dongsha Island is <5 m deep, and large seagrass beds (11.85 km^2) extend from the intertidal to the subtidal zones around the entire island. Although Dongsha Island is dominated by a tropical climate and water temperatures around the island average 27.6°C, the intense northeast monsoons from October to early March can markedly decrease water temperatures to 19°C. In this study, 4 surveys were conducted over 4 mo: 2 in the warm season (April and August 2010), and 2 in the cool season (October 2010 and February 2011).

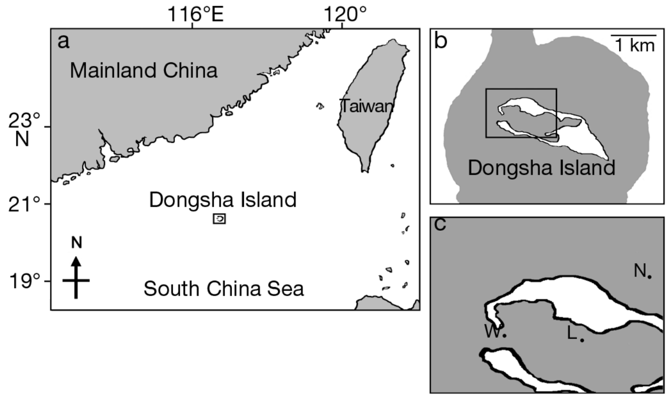

Fig. 1. (a) Location of Dongsha Island within the South China Sea, and (b) seagrass beds (shaded area) surrounding Dongsha Island. In (c), the inset in (b) has been magnified to reveal the 3 study stations

There are 7 seagrass species in Dongsha Island (Lin et al. 2005). Our study focused only on the 3 most dominant species: *Thalassia hemprichii* (TH), *Cymodocea rotundata* (CR), and *C. serrulata* (CS). Other seagrass species (*Halodule uninervis*, *Halophila ovalis*, *Syringodium isoetifolium*, and *Thalassodendron ciliatum*) were excluded in this study because their overall biomass (<10%) and coverage (<5%) were rather low in most beds.

We set up 3 study stations at Dongsha Island: the lagoon (L), the west inlet (W) and the north coast (N), as the seagrass species composition differs among these 3 stations (Fig. 1c, Table 1). The L station is located on the north coastline of the inner lagoon. It is shallow (<0.3 m at low tide), and some seagrass canopies are exposed to air during ebb tides. The W station is located near the inlet at the west side of Dongsha Island, where large amounts of seawater are exchanged during the tidal cycle. Some deeper channels (0.5–1.3 m at low tide) shaped by tidal flux are located there. The seagrasses at this station are never exposed to air, and the beds have a higher canopy due to the deeper water. The dominant seagrass species at both L and W are TH and CR. The N station is located in the subtidal zone of the north coastline of Dongsha Island. Vast and continuous seagrass beds characterize both the intertidal and subtidal zones of the north coast. The canopies are a mix of TH, CR, and CS.

Seagrass leaf features

We deployed 3 permanent 50 m transects for seagrass surveys at each station. All transects were parallel and separated from each other by at least 5 m. Water depth was randomly measured (10 replicates) along each transect during ebb tides. To estimate seagrass cover (%) and canopy height, 5 quadrats (50 × 50 cm) divided into 25 squares (10 × 10 cm) were randomly deployed and separated from each other by 5 m within each transect. In each quadrat, canopy height was measured, and percent cover was assessed based on the frequency of the mid-point percentage of 6 cover classes in the 25 squares following the methods of Saito & Atobe (1970). Shoot density was counted from 5 randomly selected squares within each of the 5 quadrats within each transect at each station. A total of 15 replicate measurements of seagrass cover, canopy height and shoot density were recorded at each station in each survey month. Another 5 replicate 10 × 10 cm quadrats were randomly deployed near each transect to collect sea-

Table 1. Environmental and seagrass characteristics of the 3 stations in Dongsha Island. Values are pooled averages (±SE) across 4 survey months. Stations are L: lagoon, W: west inlet, and N: north coast. Seagrass species are TH: *Thalassia hemprichii*, CR: *Cymodocea rotundata*, and CS: *Cymodocea serrulata*. DW: dry weight

Stn	Water depth during ebb tides (m)	Studied seagrass species	Total seagrass biomass (g DW m^{-2})	Total seagrass production (g DW m^{-2})	Seagrass cover (%)	Canopy height (cm)	Shoot density (shoots m^{-2})
L	0.25 ± 0.03	TH, CR	827.4 ± 74.8	4.65 ± 1.05	85.14 ± 6.33	20.62 ± 1.52	2920 ± 639
W	1.25 ± 0.13	TH, CR	807.7 ± 34.6	7.87 ± 1.68	81.19 ± 5.87	24.83 ± 0.31	745 ± 85
N	1.85 ± 0.32	TH, CR, CS	949.4 ± 62.1	8.47 ± 2.92	81.91 ± 2.13	22.36 ± 1.22	2677 ± 485

grass shoots for leaf feature (length, width, and nutrient content) determination and biomass assessment.

Seagrass leaf production was quantified by the leaf marking method (Zieman 1974). We randomly deployed three 10 × 10 cm quadrats (not on the transects) within each seagrass species bed at each station and marked each seagrass shoot through the sheath with a needle. In each quadrat, 9–29 shoots of TH, 11–24 shoots of CR, or 6–17 shoots of CS were marked in each survey month, depending on the shoot density of each seagrass species. Damaged or withered leaves were not used for this process. These marked seagrass shoots were collected after 5 d. In the laboratory, the epiphytes on the leaves were scraped off with razors, and the newly grown leaves were dried overnight at 60°C and weighed to calculate leaf production per shoot. For comparison, the specific growth rate (SGR hereafter) was calculated by dividing leaf production by leaf biomass per shoot (Hillman et al. 1989, Cebrián & Duarte 1998). The total leaf production per unit area was calculated by summing the average leaf production of different seagrass species per unit area at each station.

Seagrass nutritional features

To determine the nutrient content of each seagrass species, we collected 3 replicate shoots per species at each station in each survey month. Damaged, withered, or too small (shoot height <3 cm) leaves were not used, and the epiphytes on the leaves were carefully scraped off with razors. The recovered seagrass leaves were dried for 48 h at 60°C and ground to a fine powder. An Elementar Vario EL III CHN-O-S-Rapid Analyzer (Elementar Analysensysteme) was used to determine the carbon (C) and nitrogen (N) contents. Leaf samples were also analyzed for crude fiber content using the gravimetric method, and for total sugar and starch contents using the anthrone method (Yemm & Willis 1954).

Grazer abundances

We documented the number, density and behavior of grazers in seagrass beds at each station. Densities of herbivorous fishes and macro-invertebrates were determined by underwater visual censuses within 3 random parallel transects (20 × 2 m) at each station. All transects were separated from each other by at least 5 m. Only herbivorous fishes >5 cm in total length were counted as grazers because their juveniles feed primarily on algae and detritus before ontogenetic dietary shifts (Lee et al. 2014). To record herbivorous meso-invertebrates (body size < 1 cm), a 7.5 cm diameter core tube (n = 3 replicates per transect) was pushed into the sediment to a depth of 10 cm. The core samples were sieved through a 0.5 mm mesh screen, and the number of individuals of each species was counted. Additionally, these invertebrates were maintained in an aquarium with seagrass to visualize their bite marks.

Seagrass tethering experiments

To track daily seagrass biomass losses due to grazing in seagrass beds, we modified the tethering method of Kirsch et al. (2002). We randomly deployed 15 replicate 10 × 10 cm quadrats of ungrazed seagrass shoots within the multi-species beds at each station (15 replicated quadrats × 2 repeats [see below] = 30 quadrats at each station in each survey month). Each quadrat was at least 5 m away from the one previously deployed. Within each quadrat, seagrass shoots of 2 (L and W) or 3 (N) species were deployed, with the shoot densities of each seagrass species approximating the natural densities at each station as described above. Before deployment, ungrazed seagrass shoots were collected from each station, and their leaf areas were recorded with a digital camera and analyzed using the Image-Pro Plus software (Media Cybernetics, ver. 4.5) following the methods of Unsworth et al. (2007). Damaged, withered, or small shoots (shoot height <3 cm) were excluded from the tethering process. Sessile organisms such as epiphytes, sea anemones, and tunicates were removed from the leaves. Seagrass shoots were attached within each quadrat by plastic ropes, and the quadrats were then attached to the sediment with wire stakes. All seagrass shoots were left *in situ* and retrieved after a 1 d deployment, and we then deployed another 15 replicate quadrats nearby (at least 5 m away) to repeat the experiment and retrieved them the next day. In total, we had 30 replicates at each station in each survey month.

Grazed seagrass shoots were then transported to the laboratory, and all leaves for each species were digitally scanned and the leaf areas again analyzed using the Image-Pro Plus software. We traced bite marks and estimated the areal losses to grazers based on comparisons with the original ungrazed leaf images. The bite mark types were assigned to 1 of the 4 main types shown in Fig. 2: (1) semilunar-shaped bites, typically from parrotfish, especially *Leptoscarus vaigiensis* and *Calotomus spinidens*; (2) serrated bites, typically from sphaeromatid isopods; (3) irregularly shaped bites, typically from sea urchins (the most numerically dominant sea urchin species in Dongsha Island being *Tripneustes gratilla*); and (4) eroded bites characterized by scars in which only leaf veins remained on the leaves. These bites were typically from emerald nerites (herbivorous gastropods belonging to the genus *Smaragdia*) (Holzer et al. 2011, Unabia 2011). The most numerically dominant of these species was *S. rangiana*. Bite marks that could not definitively be assigned to a particular type of grazer were excluded from the analysis (<0.1%). After scanning, all leaves were dried overnight at 60°C and weighed to determine the regression equation between the leaf area and biomass in terms of dry weight (DW) for each seagrass species. Bite areas of different seagrass species contributed by each of the 4 types of grazers were calculated and then transformed to biomass losses due to grazing based on the regression equations relating leaf area to DW. Because the areal biomass of the 3 seagrass species differed at most stations, we divided the daily leaf biomass losses per unit area by the seagrass leaf biomass per unit area to estimate the proportion of relative biomass loss (RBL) by grazing in terms of% d^{-1} on each of the 3 seagrass species at each station in each survey month.

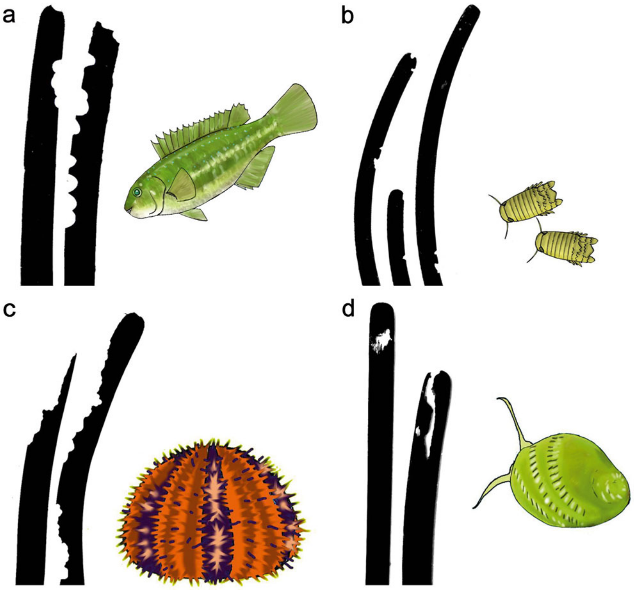

Fig. 2. Four types of grazers in Dongsha Island and the shapes of their bite marks: (a) parrotfish – semilunar-shaped bites, (b) isopods – serrated bites, (c) sea urchins – irregularly shaped bites, and (d) gastropods – eroded bites

Seagrass preferences

To determine whether the 4 types of grazers had preferences for particular seagrass species, we used Chesson's index (Chesson 1983):

$$\alpha = (r_i/p_i)/\Sigma(r_i/p_i) \qquad (1)$$

where r_i is the proportional biomass loss due to grazers feeding on seagrass species i, and p_i is the proportional biomass of seagrass species i in the source sample. The α value is between 0 and 1. If α = 1/n, selective feeding does not occur; n is the total number of seagrass species included in the analysis. There were 2 seagrass species at L and W (n = 2, 1/n = 0.50), and 3 seagrass species at N (n = 3, 1/n = 0.33). If α > 1/n, it is probable that grazers have a preference for seagrass species i, whereas if α < 1/n, seagrass species i is probably avoided.

Grazing to production ratios

To represent the grazing pressure on each of the 3 seagrass species sampled at the 3 stations over the 2 seasons, we calculated the grazing:production ratio (G:P ratio) as:

$$\text{G:P ratio} = (\text{areal leaf biomass loss by grazing}) / (\text{areal leaf production}) \times 100\% \qquad (2)$$

G:P ratios >100% suggest that consumption by grazers is higher than leaf production. The total G:P ratios at each station were calculated by adding the G:P ratios of the different seagrass species weighted by the areal biomass present at each station.

Data analysis

Three-way ANOVAs were used to test the effects of station (n = 3; L, W, and N), season (n = 2; warm and cool seasons), and seagrass species (n = 3; TH, CR, and CS) on seagrass leaf features (leaf length, leaf width, and SGR) and nutrient content (C:N ratio, crude fiber, total sugar, and starch). However, the results showed a significant interaction between seagrass species and station. Thus, 1-way ANOVAs were further used to test the differences in leaf features and nutrient contents among each of the species at each station individually, with the measurements collected in different months as replicates. A 2-way MANOVA was used to test the effects of station and season on the densities of the 4 types of grazers. If significant differences were detected at $p \leq 0.05$, the means were compared using Scheffé post-hoc test, or alternatively, the Games-Howell post-hoc test as a non-parametric method if the variances were still nonhomogeneous after data transformation. All data were tested for homogeneity of variances using Levene's test. The square-rooted or log transformed data were analyzed in SPSS 12.0 if a nonhomogeneous variance was detected before the ANOVA.

Because all our grazing data were heteroscedastic and non-normally distributed, we examined grazing differences using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) in PRIMER ver. 6.1.13 and PERMANOVA+ ver. 1.0.3 (Clarke & Gorley 2006, Anderson et al. 2008). The grazing data were log-transformed to downweigh the influence of large values before analysis. Euclidean distance was used to create the resemblance distance matrix. The total biomass losses and total G:P ratios were tested using a 2-factor PERMANOVA, with station and season as the 2 fixed factors. The RBL values and G:P ratios of different seagrass species were tested using a 3-factor PERMANOVA, with station and season as the 2 fixed factors and seagrass species as a random factor. Three-factor PERMANOVAs were also used to test whether the RBL values varied by season, station or seagrass species among the 4 types of grazers.

A stepwise multiple regression was used to analyze the relationship between total biomass loss by grazing and water depth, seagrass production and coverage, and the densities of the 4 types of grazers. A stepwise multiple regression was also used to test whether water depth, seagrass characteristics (leaf length, leaf width, and SGR) and nutrient content (C:N ratio, crude fiber, total sugar, and starch) affected the amounts of leaf biomass loss produced by the 4 types of grazers.

RESULTS

Seagrass leaf and nutritional features

Extensive seagrass beds were present in our study areas (Table 1). Water depth was shallower at L and deeper at N. At all stations, seagrass coverage was >80%, canopy height was >20 cm, and mean biomass was >800 g DW m^{-2}. Shoot densities at L and N averaged over 2600 shoots m^{-2}, whereas the mean density at W was 745 shoots m^{-2}. Mean total seagrass production was ~2× as high at W and N than at L.

Among the leaf features, only SGR showed seasonal effects. Higher SGRs were found in the warm than in the cool season for all seagrass species (3-way ANOVA: $F = 98.81$, $p < 0.05$). Other leaf features varied among seagrass species but not among stations (1-way ANOVA; Table 2). No spatial differences were found in crude fiber and total sugar content in TH or CR. Leaf length, crude fiber, and total sugar content were also not different among the 3 seagrass species. However, CS had the widest leaves (mean: 1.00 cm), followed by TH (mean: 0.72 cm) and CR (mean: 0.39 cm). The 2 *Cymodocea* species had significantly higher SGRs (mean: 0.026), C:N ratios (mean: 16.27), and starch contents (mean: 1.40%) than TH (mean: 0.017, 14.32, and 0.96% for SGR, C:N ratio, and starch content, respectively).

Grazer abundances

The recorded grazer species were more diverse at N than at L (Table 3). Among the 4 types of grazers, gastropods had the highest density (Fig. 3). Their mean density reached over 14 ind. m^{-2} at N. Five parrotfish species were observed to directly consume seagrass leaves in Dongsha Island (Table 3). *Leptoscarus vaigiensis* and *Calotomus spinidens* were the most dominant parrotfish species. The density of parrotfish was significantly higher at N and W than at L (MANOVA: $F = 19.54$, $p < 0.001$). Isopods also showed a significantly higher density at N than at W and L (MANOVA: $F = 19.14$, $p < 0.001$). Gastropods, however, had a higher density at L and N than at W

Table 2. Characteristics of the 3 target seagrass species collected at the 3 stations in Dongsha Island. Values are pooled averages (±SE) across 4 survey months. Letters next to values denote post-hoc differences ($p \leq 0.05$) if an overall difference was detected in 1-way ANOVA. Abbreviations for stations and seagrass species as in Table 1. SGR: seagrass specific growth rate

Seagrass species	Stn	Leaf length (cm)	Leaf width (cm)	SGR	Carbon:nitrogen ratio	Crude fiber (%)	Total sugar (%)	Starch (%)
TH	L	12.11 ± 1.71	0.68 ± 0.06^b	0.010 ± 0.001^a	14.22 ± 0.16^a	2.46 ± 0.38	0.38 ± 0.15	0.98 ± 0.11^a
TH	W	15.83 ± 2.35	0.79 ± 0.05^b	0.017 ± 0.003^{ab}	14.06 ± 0.09^a	2.60 ± 0.28	0.36 ± 0.06	0.97 ± 0.10^a
TH	N	13.58 ± 1.21	0.70 ± 0.06^b	0.024 ± 0.004^b	14.67 ± 0.16^a	2.65 ± 0.55	0.34 ± 0.12	0.94 ± 0.10^a
CR	L	13.41 ± 1.25	0.39 ± 0.05^a	0.024 ± 0.002^b	16.31 ± 0.23^b	2.84 ± 0.64	0.34 ± 0.14	1.43 ± 0.15^b
CR	W	14.29 ± 1.12	0.39 ± 0.02^a	0.025 ± 0.005^b	16.38 ± 0.24^b	2.52 ± 0.20	0.35 ± 0.05	1.39 ± 0.09^b
CR	N	13.52 ± 0.95	0.40 ± 0.04^a	0.027 ± 0.004^b	15.44 ± 0.93^b	2.79 ± 0.42	0.42 ± 0.17	1.40 ± 0.15^b
CS	N	13.74 ± 0.71	1.00 ± 0.05^c	0.028 ± 0.003^b	16.96 ± 0.47^b	2.74 ± 0.50	0.50 ± 0.21	1.37 ± 0.14^b

Table 3. Numerically dominant species of the 4 types of grazers and their occurrence at the 3 stations in Dongsha Island. Station abbreviations as in Table 1

Grazer type	L	W	N
Parrotfish (semilunar-shaped bites)			
Calotomus spinidens		★	★
Leptoscarus vaigiensis	★	★	★
Hipposcarus longiceps			★
Scarus ghobban			★
Scarus spp.		★	★
Isopods (serrated bites)			
Sphaeromatidae spp.	★	★	★
Sea urchins (irregularly shaped bites)			
Mespilia globulus			★
Pseudoboletia maculata			★
Toxopneustes pileolus			★
Tripneustes gratilla	★	★	★
Gastropods (eroded bites)			
Smaragdia spp.	★	★	★

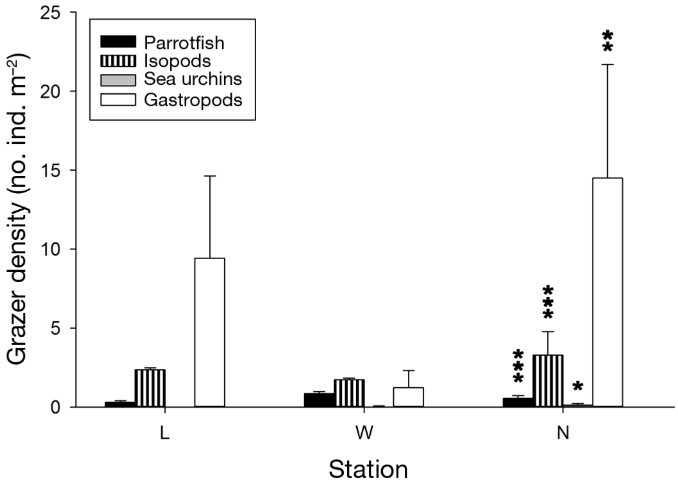

Fig. 3. Mean densities (±SE) of 4 types of grazers at 3 stations in Dongsha Island across 4 survey months. (*)Significant differences among the 3 stations (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$). For parrotfish, only individuals with body length >5 cm were included. Station abbreviations as in Table 1

(MANOVA: $F = 6.34$, $p = 0.002$). Four species of sea urchins were observed, but their mean densities were low at all stations (<0.1 ind. m $^{-2}$). The density of sea urchins (MANOVA: $F = 3.82$, $p = 0.019$) were significantly lower at L than at N. Among the 4 types of grazers, only parrotfish showed a significant seasonal difference in density, with a higher density in the warm season (MANOVA: $F = 12.92$, $p < 0.001$; data not shown).

Seagrass consumption

There were significant effects of station and season on daily total biomass losses by grazing (Fig. 4, Table 4a). Grazers removed more biomass in the warm season (mean: 0.18 g DW m^{-2} d^{-1}) than in the cool season (mean: 0.07 g DW m^{-2} d^{-1}). Moreover, daily total biomass losses by grazing were higher at N (mean: 0.11 g DW m^{-2} d^{-1}) and W (mean: 0.07 g DW m^{-2} d^{-1}) than at L (mean: 0.03 g DW m^{-2} d^{-1}).

RBL values differed between seasons and among seagrass species but not among stations (Table 4b). The RBL values of the 2 *Cymodocea* species (mean: 0.08 % d^{-1} for CR and 0.11 % d^{-1} for CS) were higher than that for TH (mean: 0.04 % d^{-1}). RBL values were also significantly higher in the warm than in the cool season.

Seagrass preferences

Among the 4 types of grazers, parrotfish consumed a high proportion of the seagrass biomass losses (Fig. 5). In general, parrotfish contributed over 50 % of grazing on seagrasses in Dongsha Island (mean: 50.63, 78.22, and 75.93 % for L, W, and N, respec-

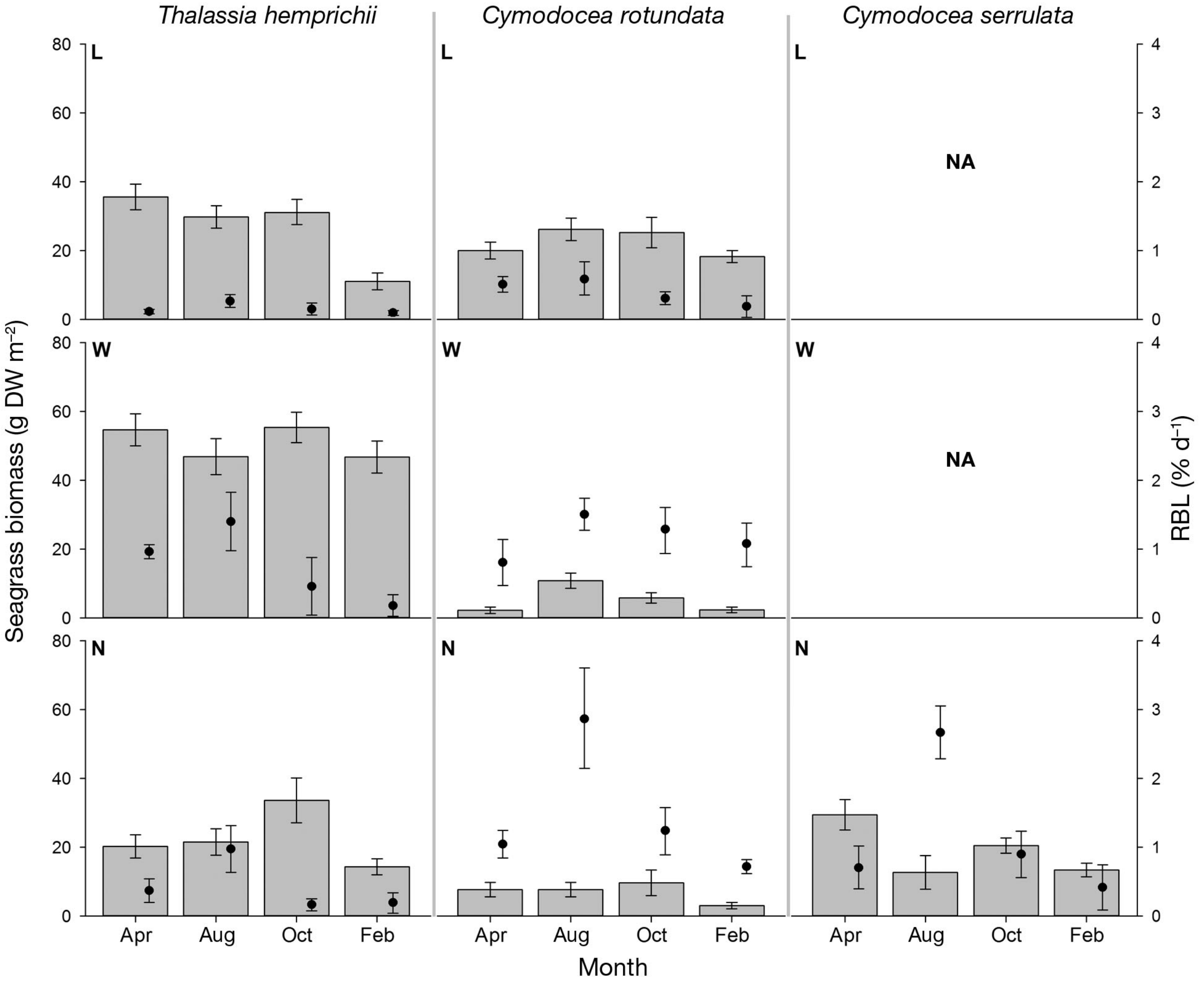

Fig. 4. Mean seagrass biomass (±SE, n = 30) (gray bars, left *y*-axis) and relative biomass losses by grazing (RBL, black dots, right *y*-axis) of 3 seagrass species at 3 stations in Dongsha Island in 4 survey months. DW: dry weight; NA: not applicable. Station abbreviations as in Table 1

tively), followed by isopods (mean: 31.26, 19.52, and 8.51% for L, W, and N, respectively) and gastropods (mean: 16.24, 0.90, and 10.65% for L, W, and N, respectively). Sea urchins contributed a rather low proportion of grazing (<5%) across all stations and seasons.

The RBL values due to grazing by the 4 types of grazers varied significantly with seagrass species but showed no seasonal and station variations (Table 5). However, interactions among season, station, and seagrass species were detected for grazing by parrotfish and isopods. Briefly, parrotfish and isopods consumed more biomass of the 2 *Cymodocea* species than of TH across all stations (Fig. 6). However, sea urchins consumed more biomass of TH at W and N, and gastropods consumed more biomass of TH and CS only at N. Chesson's indices also revealed similar patterns for the 4 types of grazers (Table 6). At L and W, most grazers preferred CR, whereas sea urchins preferred TH. At N, all grazers preferred CS. However, sea urchins and gastropods also preferred TH.

A stepwise multiple regression showed that total seagrass biomass losses by grazing were strongly positively affected by seagrass leaf production and parrotfish density (Table 7a; Global R = 0.80, F = 40.25, $p < 0.001$). For parrotfish, SGR and water depth were the most important positive factors affecting grazing (Table 7b; Global R = 0.68, F = 15.75, $p < 0.001$). Starch content and SGR were more important in enhancing grazing by isopods (Table 7c; Global R = 0.46, F = 10.35, $p < 0.05$). No factors were shown to significantly affect grazing by sea urchins and gastropods.

Table 4. PERMANOVAs on (a) total seagrass biomass losses, (b) relative seagrass biomass losses (RBL), (c) total grazing to production ratio (G:P ratio) with pair-wise comparisons for stations, and (d) G:P ratios of different seagrass species with pair-wise comparisons for seagrass species. Abbreviations for stations and seagrass species as in Table 1. Significant differences at p ≤ 0.05 in bold text

a

Source	df	MS	Pseudo *F*	p
Season (SE)	1	6.541	25.865	**0.001**
Station (ST)	2	2.738	10.825	**0.001**
SE × ST	2	0.661	2.614	0.080
Residual	594			
Total	599			

b

Source	df	MS	Pseudo *F*	p
Season (SE)	1	5.209	28.167	**0.002**
Station (ST)	2	2.007	4.620	0.208
Seagrass (GR)	2	3.378	14.230	**0.001**
SE × ST	2	0.538	0.748	0.574
SE × GR	2	0.164	0.691	0.516
ST × GR	2	0.435	1.831	0.178
SE × ST × GR	2	0.719	3.032	0.059
Residual	586			
Total	599			

c

Source	df	MS	Pseudo *F*	p
Season (SE)	1	0.076	9.596	**0.002**
Station (ST)	2	0.343	43.040	**0.001**
SE x ST	2	0.048	6.062	**0.002**
Residual	594			
Total	599			

d

Source	df	MS	Pseudo *F*	p
Season (SE)	1	0.635	32.868	**0.013**
Station (ST)	2	0.293	4.210	0.211
Seagrass (GR)	2	0.240	14.692	**0.001**
SE × ST	2	0.046	0.468	0.689
SE × GR	2	0.021	1.259	0.289
ST × GR	2	0.070	4.272	**0.016**
SE × ST × GR	2	0.098	5.978	**0.003**
Residual	586			
Total	599			

Pair-wise groups (Station)

Warm season	*t*	p
L, W	3.332	**0.002**
L, N	6.110	**0.001**
W, N	3.598	**0.001**

Cool season	*t*	p
L, W	2.515	**0.013**
L, N	3.943	**0.001**
W, N	3.056	**0.005**

Pair-wise groups (Seagrass)

Warm season	*t*	p
TH, CR (at L)	4.597	**0.001**
TH, CR (at W)	5.884	**0.001**
TH, CR (at N)	0.078	0.948
TH, CS (at N)	2.540	**0.013**
CR, CS (at N)	2.697	**0.009**

Cool season	*t*	p
TH, CR (at L)	1.524	0.132
TH, CR (at W)	1.102	0.260
TH, CR (at N)	1.303	0.204
TH, CS (at N)	1.694	0.108
CR, CS (at N)	3.098	**0.004**

Grazing to production ratios

Although seagrass biomass losses by grazing varied between seasons and among stations, the G:P ratios for all seagrass species were generally <10 % (mean: 1.63, 3.45, and 6.67 % for L, W, and N, respectively; Fig. 7). A 2-way PERMANOVA showed that total G:P ratios differed significantly between seasons and among stations (Table 4c). A 3-way PERMANOVA further showed that G:P ratios differed between seasons and among seagrass species (Table 4d). The G:P ratios for CS (mean: 8.01 % for N) were higher than those for CR (mean: 2.18, 1.57, and 4.91 % for L, W, and N, respectively) and TH (mean: 1.08, 4.39, and 5.51 % for L, W, and N, respectively). Moreover, CS and TH showed significantly higher G:P ratios in the warm season than in the cool season.

DISCUSSION

Our results showed significant seasonal variation in seagrass biomass consumption in Dongsha Island. This pattern was positively related to parrotfish density within each station, suggesting that parrotfish abundance in the seagrass beds can influence the

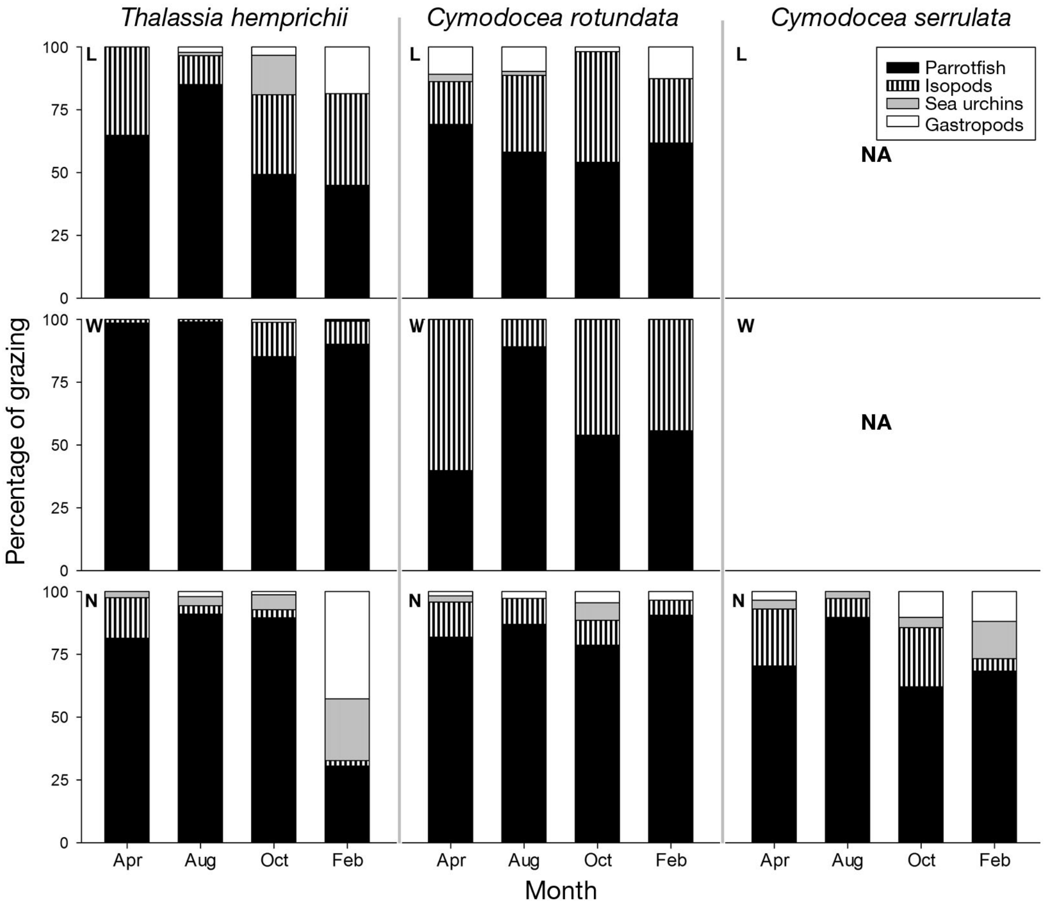

Fig. 5. Relative contribution to total grazing on 3 different seagrass species by 4 types of grazers at 3 stations in 4 survey months. NA: not applicable. Station abbreviations as in Table 1

Table 5. PERMANOVAs on seagrass biomass removal by (a) parrotfish, with pair-wise comparisons for seagrass species, (b) isopods, with pair-wise comparisons for seagrass species, (c) sea urchins, and (d) gastropods. Grazing by urchins and gastropods was too small for pair-wise comparisons. Significant differences at p ≤0.05 in bold text. Abbreviations as in Table 1

Source	df	a			b			c			d		
		MS	Pseudo *F*	p	MS	Pseudo *F*	p	MS	Pseudo *F*	p	MS	Pseudo *F*	p
Season (SE)	1	1.050	0.420	0.058	5.255	2.158	0.316	0.058	1.668	0.347	0.003	0.041	0.900
Station (ST)	2	6.813	3.271	0.148	6.582	1.189	0.441	0.014	0.729	0.611	0.050	1.477	0.423
Seagrass (GR)	2	1.147	12.426	**0.001**	3.482	29.646	**0.001**	0.117	4.645	**0.006**	0.204	5.235	**0.005**
SE × ST	2	3.464	0.642	0.611	6.145	0.971	0.555	0.061	1.715	0.360	0.034	4.311	0.178
SE × GR	2	3.462	37.519	**0.001**	3.363	28.631	**0.001**	0.039	1.544	0.208	0.094	2.405	0.088
ST × GR	2	2.083	22.572	**0.001**	5.534	47.118	**0.001**	0.020	0.790	0.448	0.034	0.865	0.456
SE × ST × GR	2	5.395	58.461	**0.001**	6.326	53.857	**0.001**	0.036	1.415	0.254	0.008	0.202	0.820
Residual	586												
Total	599												

Pair-wise groups (Seagrass)

Warm season	*t*	p	*t*	p
TH, CR (at L)	2.346	**0.020**	4.569	**0.001**
TH, CR (at W)	7.966	**0.001**	2.342	**0.011**
TH, CR (at N)	3.687	**0.001**	1.125	0.289
TH, CS (at N)	2.047	**0.047**	3.241	**0.003**
CR, CS (at N)	5.692	**0.001**	2.542	**0.010**
Cool season	*t*	p	*t*	p
TH, CR (at L)	3.276	**0.003**	4.711	**0.001**
TH, CR (at W)	4.788	**0.001**	5.249	**0.001**
TH, CR (at N)	1.247	0.201	1.377	0.158
TH, CS (at N)	2.115	**0.033**	3.324	**0.001**
CR, CS (at N)	1.231	0.221	2.412	**0.025**

Table 6. Chesson's α for the 3 seagrass species grazed by the 4 types of grazers at the 3 stations in Dongsha Island. (*) Preference for seagrass species. Abbreviations for stations and seagrass species as in Table 1

Stn	Seagrass species	Parrotfish	Isopods	Sea urchins	Gastropods
L	TH	0.40	0.28	0.84*	0.39
	CR	0.59*	0.69*	0.15	0.59*
W	TH	0.33	0.22	0.89*	0.54*
	CR	0.66*	0.78*	0.10	0.44
N	TH	0.16	0.13	0.42*	0.54*
	CR	0.35*	0.23	0.16	0.07
	CS	0.49*	0.64*	0.41*	0.39*

amount of grazing. Parrotfish contributed nearly ⅔ of the seagrass grazing in Dongsha Island. The 2 most dominant parrotfish species (*Leptoscarus vaigiensis* and *Calotomus spinidens*) are often the major seagrass grazers in the Indo-Pacific region (Mariani & Alcoverro 1999, Unsworth et al. 2007). Similarly, in the Mediterranean Sea, the leaf biomass consumption of *Posidonia oceanica* was also strongly influenced by the abundance of a species of sea bream, *Sarpa salpa* (Prado et al. 2007, 2008). The water conditions around Dongsha Island can be easily affected by weather or tides due to the shallow water. The cold northeast monsoons could significantly decrease water temperatures and reduce parrotfish density in Dongsha Island. In the warm season, however, parrotfish density increases in the beds due to the recruitment of juveniles. Consequently, their foraging behavior contributed to the high seagrass biomass consumption during the warm season.

Our results also showed significant spatial variation in seagrass biomass consumption in Dongsha Island. Lee et al. (2014) showed that parrotfish density increased with increasing depth as well as during flood tides. These authors observed that deeper water or flood tides can provide more space for herbivores. In the present study, total seagrass biomass losses by grazing were highly positively affected by parrotfish density. In particular, water depth was an important factor positively affecting grazing by parrotfish. The subtidal habitats (W and N) supported a greater abundance of parrotfish and more herbivory on seagrasses than the shallower intertidal habitats (L) in Dongsha Island. Parrotfish abundance in seagrass beds can also be affected by distance to a neighboring reef (Kirsch et al. 2002, Valentine et al. 2007), bed complexity (Unsworth et al. 2007, Gullström et al. 2011) and bed heterogeneity (Salita et al. 2003, Maciá & Robinson 2005). In the present study, the high parrotfish densities at W and N may also be related to the shorter distance to the neighboring coral reefs, which may increase habitat heterogeneity and support a greater abundance of parrotfish within the beds.

Substantial variability in the amount of seagrass consumption by sea urchins has been reported in tropical seagrass beds (Ogden et al. 1973, Tertschnig 1989, Valentine et al. 2000, Alcoverro & Mariani 2002, 2004). In the present study, sea urchins had a relatively lower contribution to total seagrass consumption than parrotfish. The reason for this difference is evidently the low abundance of sea urchins (mostly *Tripneustes gratilla*) in the seagrass beds. Their bite marks were rarely recorded in our surveys and experiments (as discussed below). Instead, small meso-invertebrates, e.g. sphaeromatid isopods and emerald nerites (*Smaragdia* spp.), were the numerically dominant invertebrate grazers in Dongsha Island. Their body sizes were generally <1 cm, and their bite marks on leaves were also small in area (but often numerous). Most likely, the grazing contribution of these species has been rarely recorded or has been underestimated in field surveys.

In temperate seagrass beds, small amphipods (Duffy & Harvilicz 2001, Lewis & Anderson 2012), isopods (Williams & Ruckelshaus 1993, Duffy et al. 2003), and gastropods (Zimmerman et al. 1996, Fredriksen et al. 2004, Lewis & Anderson 2012) have

Table 7. Stepwise multiple regression on (a) the relationship between total seagrass biomass losses by grazing, parrotfish density and seagrass production; and the effects of water depth, seagrass characteristics, and nutrient content on seagrass biomass losses by (b) parrotfish and (c) isopods. SGR: seagrass specific growth rate

	Unstandardized coefficient (β)	SE	Standardized coefficient (β)	*t*	p
(a) Total seagrass biomass losses by grazing					
Parrotfish density	2.041	0.322	0.895	6.344	<0.001
Seagrass production	0.416	0.092	0.818	4.499	0.001
(b) Seagrass biomass losses by parrotfish					
SGR	1.870	0.428	0.552	4.363	<0.001
Water depth	0.000	0.011	0.263	2.082	0.044
(c) Seagrass biomass losses by isopods					
Starch content	0.014	0.004	0.463	3.218	0.003
SGR	0.002	0.001	0.400	2.692	0.011

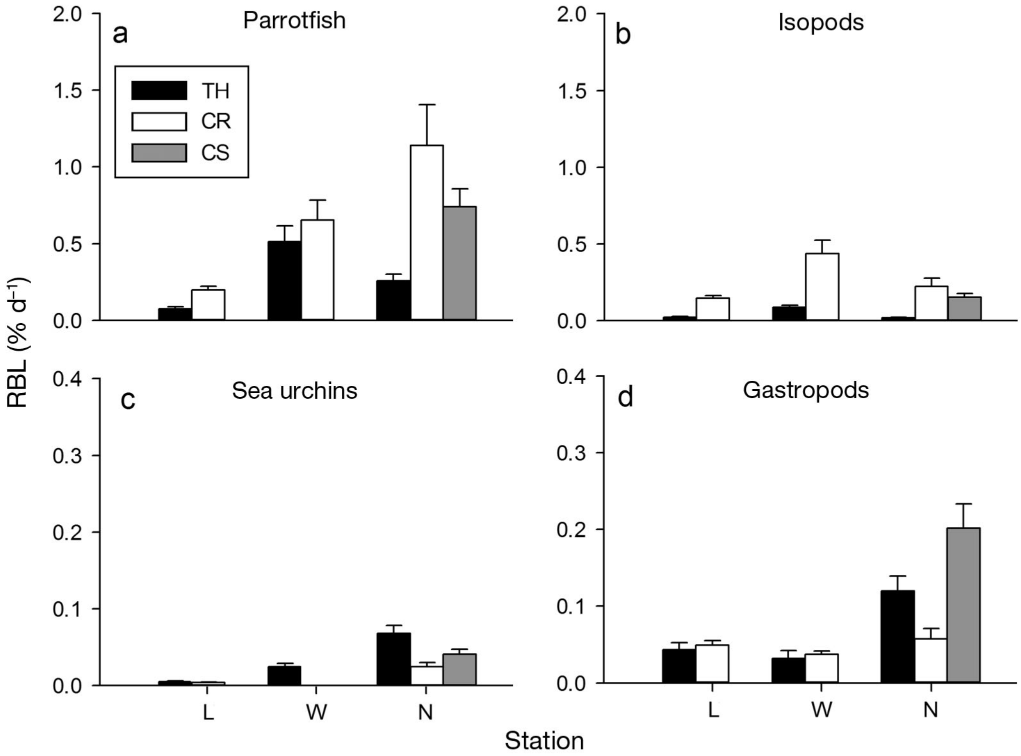

Fig. 6. Daily relative seagrass biomass losses (RBL,% d^{-1}) due to grazing by 4 types of grazers on 3 seagrass species at 3 stations. Abbreviations for stations and seagrass species as in Table 1

been observed to graze directly on seagrass leaves. Recently, emerald nerites (*Smaragdia* spp.) have been found to consume young seagrass leaves in tropical regions (Rueda et al. 2009, Holzer et al. 2011, Unabia 2011). In the present study, we found that these meso-invertebrates can be crucial grazers, as they contributed ~10 to 20 % to total seagrass grazing in Dongsha Island. Although the overall grazing contribution by these small invertebrates was much smaller than that contributed by parrotfish (>50 %), we propose that grazing by these small invertebrates may impact seagrass growth. The basis for this proposal is the frequent occurrence of their bite marks on actively growing young leaves, which could reduce leaf production. Small invertebrate grazers have also been reported to damage the leaves of eel-

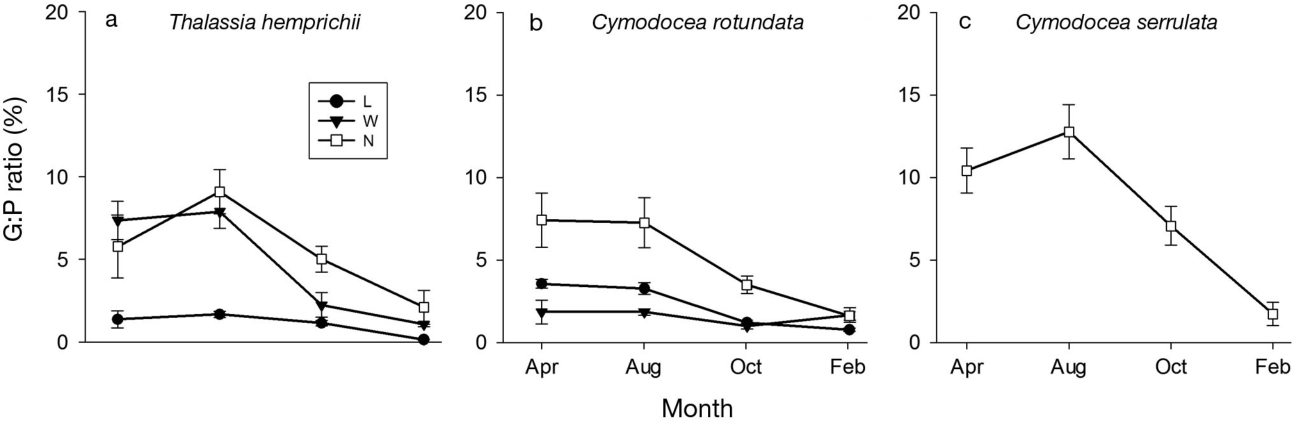

Fig. 7. Temporal changes in grazing to production (G:P) ratios (mean ± SE, n = 30) for (a) *Thalassia hemprichii*, (b) *Cymodocea rotundata*, and (c) *Cymodocea serrulata* at 3 stations. Station abbreviations as in Table 1

grass (*Zostera marina*) and restrict their production rate (Zimmerman et al. 1996, Lewis & Anderson 2012). Therefore, grazing by these small invertebrates may act to decrease leaf growth and influence the overall production of the seagrass beds.

Seagrass leaf production plays a critical role in herbivory in Dongsha Island because the seasonal variation in grazing was correlated with leaf production. Similar seasonal variation of grazing was found on TH in southern Taiwan (Chiu et al. 2013), where seagrasses had more biomass losses by grazing during seasons of high production. The documented grazing preferences were also positively related to leaf production. Generally, rapidly growing seagrass species are preferred more strongly by most grazers (Cebrián & Duarte 1998, Heck & Valentine 2006). Our results indicated that parrotfish and isopods preferred to graze on the 2 *Cymodocea* species rather than on TH. The 2 *Cymodocea* species demonstrated a higher SGR and higher production in our studies. Feeding on rapidly growing seagrass would provide grazers with more opportunities to feed on young leaves, which are lower in cellulose but higher in carbohydrate content. Heck & Valentine (2006) also indicated that young shoots are more strongly preferred by grazers in tropical seagrass beds. However, we found that the preferences of sea urchins and nerites differed from those of other grazers. Most grazing by sea urchins was found on TH. Both Klumpp et al. (1993) and Tertschnig (1989) indicated that sea urchins preferred to graze on slow growing/long-lived seagrass species such as *Thalassia* spp. Higher densities of sea urchins in long-lived seagrass species can be explained by their preference for well-developed canopies that provide protection from predation and for the rhizome structure that enhances recruitment (see Prado et al. 2009). However, we expected nerites to show passive preferences due to their sluggish grazing (Heck & Valentine 2006).

In contrast, the nitrogen and sugar content of seagrass leaves did not appear to affect grazing preferences in our study. Previous studies have shown that grazers primarily select nitrogen-rich seagrass (Zieman et al. 1984, Goecker et al. 2005, Prado & Heck 2011). However, Kirsch et al. (2002) and Gullström et al. (2011) found this not to be the case. The nitrogen content or C:N ratios of seagrass leaves are site-specific. Many seagrass species in tropical regions are characterized by C:N ratios similar to those found in the current study (14.1–16.9) as well as a nitrogen content similar to that found in previous studies (Cebrián & Duarte 1998, Mariani & Alcoverro 1999). These characteristics may represent another reason for the lack of selectivity based on nitrogen content. In the present study, only starch content was found to be positively correlated with grazing by isopods. The starch content of the 2 *Cymodocea* species, which were preferred by all grazers, was higher than in TH. Accordingly, the small crustacean grazers in Dongsha Island may be preferentially choosing these species based on their relatively higher starch content.

All the G:P ratios indicated that only small portions of the leaf production of the 3 seagrass species were grazed in Dongsha Island. In general, seagrasses are considered a less important food for most marine grazers (Thayer et al. 1984, Duarte 1990). Our results were similar to those of many previous studies worldwide, which indicate that only a small quantity of leaf biomass and production is removed by grazers (Edgar & Shaw 1995, Cebrián & Duarte 1998, White et al. 2011). Cebrián & Duarte (1998) indicated that grazing removes only ~2 to 9% and 1 to 15% of seagrass leaf production in temperate and tropical regions, respectively. However, the indirect estimation methods might have severely underestimated the removal of biomass by grazing (Cebrián et al. 1996b, Cebrián & Duarte 1998, Heck & Valentine 2006). In recent decades, tethering methods have revealed that grazers can remove a greater amount of seagrass biomass than that estimated by previous studies (Table 8). For example, grazers have been documented to consume ~20% of seagrass production in southern Taiwan (Chiu et al. 2013), and >50%, sometimes even >100%, in certain parts of the Caribbean (Kirsch et al. 2002), Mediterranean (Prado et al. 2007, 2008) and Indonesia (Unsworth et al. 2007). However, the spatial/temporal scales of these studies varied in different ways. Certain cases of high consumption may occur only under occasional conditions in beds, such as a high density of grazers (Prado et al. 2007, Tomas et al. 2005), low seagrass production (Kirsch et al. 2002), and/or small meadow size (Prado et al. 2008) at a particular scale. We suggest that the evaluation of grazing impact should consider grazing across all seasons and microhabitats within seagrass beds to ensure unbiased estimation.

Compared with results obtained by other tethering studies, we found that the G:P ratios of the seagrass beds in Dongsha Island were extremely low (Table 8). The low G:P ratios in this case may be caused by 2 factors: (1) high seagrass production, and (2) top-down control by predators. In considering the first factor, it should be noted that the mean seagrass leaf production in Dongsha Island was high in comparison

Table 8. Comparison of seagrass production and proportional removal of production by grazing (G:P ratio) in this study and previous studies. Bold text in G:P ratio indicates occasionally more seagrass biomass grazed than was produced in the study. (*) Multi-species seagrass beds, DW: dry weight, NA: not applicable

Site Latitude	Study duration	Study method	Seagrass species	Leaf production (g DW m^{-2} d^{-1})	G:P ratio (%)	Source
Temperate region						
Spain, Mediterranean coast 36–42° N	Annual	Estimated	*Posidonia oceanica*	3.25 ± 0.48[a]	1.7 ± 0.2[a]	Cebrián et al. (1996a)
Spain, Mediterranean coast 36–42° N	Jun–Jul	Estimated	*Cymodocea nodosa*	1.02 ± 0.30[a]	8.5 ± 2.7[a]	Cebrián et al. (1996b)
Medes, Spain 42° N	Summer	Tethering	*Posidonia oceanica*	0.86[b]	**74**	Tomas et al. (2005)
Spain, Mediterranean coast 39–41° N	Annual	Tethering	*Posidonia oceanica*	1.63[b]	**57**	Prado et al. (2007)
Subtropical region						
Florida Keys 23–25° N	Annual	Tethering	*Thalassia testudinum*	0.66–3.84	**85**	Kirsch et al. (2002)
Florida Keys 23–25° N	Annual	Tethering	*Thalassia testudinum*	0.02–0.06	**48–100**	Valentine et al. (2007)
Tropical region						
Bolinao, Philippines 16° N	Spring	Estimated	*Enhalus acoroides*	0.31[a]	1[a]	Vermaat et al. (1995)*
	Spring	Estimated	*Cymodocea rotundata*	0.55	NA	
	Spring	Estimated	*Cymodocea serrulata*	0.71[a]	10[a]	
	Spring	Estimated	*Thalassia hemprichii*	2.31[a]	13.9[a]	
Wakatobi, Sulawesi, Indonesia 5° S	Jun–Aug	Tethering	*Enhalus acoroides*	2–4	**787**	Unsworth et al. (2007)*
	Jun–Aug	Tethering	*Thalassia hemprichii*	4–20	**64**	
Kenting, southern Taiwan 21° N	Annual	Tethering	*Thalassia hemprichii*	3.77 ± 0.91	20	Chiu et al. (2013)
Dongsha, South China Sea 20° N	Annual	Tethering	*Cymodocea rotundata*[c]	5.04 ± 0.44	2.0	This study*
	Annual	Tethering	*Thalassia hemprichii*[c]	4.00 ± 0.50	2.2	
	Annual	Tethering	*Cymodocea rotundata*[d]	4.50 ± 0.45	4.9	
	Annual	Tethering	*Cymodocea serrulata*[d]	3.77 ± 0.27	8.0	
	Annual	Tethering	*Thalassia hemprichii*[d]	2.26 ± 0.28	5.5	

[a] Values derived from Cebrián & Duarte (1998)
[b] Values estimated from Alcoverro et al. (1995)
[c] Seagrasses at lagoon and west inlet of Dongsha Island
[d] Seagrasses at north coast of Dongsha Island

with other tropical seagrass beds (Table 8), and the area occupied by seagrass beds is large. Seagrass species in Dongsha Island also showed higher production than the same species in other studies (Table 8). These characteristics may have resulted because multi-species beds could support more production than mono-specific beds, as the various seagrass species may fill different niches within the beds and form a more productive complex.

In terms of the second factor, previous studies have found that herbivory can be suppressed by primarily carnivorous fishes in tropical (Valentine & Duffy 2006, Valentine et al. 2007, 2008) and temperate regions (Lewis & Anderson 2012). Since fishing activities have been prohibited in the atoll, a variety of predators were found in relatively high abundance within the seagrass beds of Dongsha Island. The lemon shark *Negaprion acutidens* and the barracuda *Sphyraena barracuda* are the main predators of parrotfish in Dongsha Island (Lee et al. 2014). Numerous stingrays and triggerfish (Balistidae species) are important predators of sea urchins (pers. obs.). These predators were often found foraging during flood tides at the 3 stations. Even small fishes (e.g. emperors, wrasses, and gobies) sometimes also prey on small isopods and gastropods. The foraging of these invertebrate-feeding fish can also suppress herbivory by meso-invertebrates in seagrass beds (Lewis & Anderson 2012). These abundant carnivores may act as a strong top-down control on grazing pressure in Dongsha Island.

In conclusion, we found that seagrass biomass losses due to grazing were spatio-temporally variable in the multi-species seagrass beds of Dongsha Island.

Parrotfish density, seagrass production, water depth, and starch content were found to be the main factors affecting the degree of grazing. The most important seagrass grazers were parrotfish, followed by small isopods and nerites. Most grazers were shown to have a preference for particular seagrass species, generally preferring the 2 *Cymodocea* species, most likely because of their high production and/or starch content. All grazers, in combination, removed <10% of the total seagrass leaf production, and this low level of grazing in comparison with those found by other studies around the world may be due either to the relatively high seagrass production or to top-down predation-driven processes that act to control herbivore abundance in Dongsha Island.

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