



The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific

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Received 19 February 2007; accepted 2 April 2007

Abstract

The functional importance of herbivory is well established within terrestrial ecosystems yet within marine ecosystems, specifically seagrass beds, consumption by herbivores has generally been considered to be of little importance due to its minor contribution to turnover of growth. The present paper challenges this assumption within the Indo-Pacific and shows that scarid (parrotfish) herbivory may have a functionally important role in the export of seagrass detrital material. Estimation of scarid herbivory on dominant Indo-Pacific seagrass species was conducted using a three pronged approach. We estimated: background levels of scarid seagrass bites; *in-situ* rates of grazing using tethering experiments; and seagrass grazing effect per individual scarid, which was scaled up to estimate the grazing effects of the local scarid population. All research was carried out within the Wakatobi Marine National Park, Indonesia. Research found scarid herbivory to be an important process within an Indo-Pacific seagrass bed causing the loss of up to ten times (average, four times) the daily seagrass growth. *T. hemprichii* was found to be lost at a rate of 0.28 ± 0.08 g DW day⁻¹, while *E. acoroides* was lost at a rate of 2.85 ± 0.43 g DW day⁻¹. We propose that such high rates of seagrass consumption are the combined effects of seasonally high grazing rates by resident scarids and short-term effects from shoals of juvenile reef scarids. Scarid grazing was indiscriminate between seagrass species and grazing was dependant on seagrass availability rather than nutritional quality. In conclusion, the present research finds scarids to be major herbivores within an Indo-Pacific seagrass bed; they not only take up carbon into the food chain through direct seagrass consumption, but also make an important indirect contribution to the detrital food chain through the export of discarded decaying seagrass material.

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Keywords: seagrass; herbivory; parrotfish; scarids; Indo-Pacific; Indonesia; Wakatobi

1. Introduction

The functional importance of herbivory in controlling plant productivity and abundance in terrestrial ecosystems is well established (Crawley, 1985; Whitham and Mopper, 1985) yet within marine seagrass ecosystems, consumption by herbivores has generally been considered to be of little functional importance due to its minor contribution to the turnover of growth (Nienhuis and Van Ierland, 1978; Thayer et al., 1984; Nienhuis

and Groenendijk, 1986). This assumption is based on seagrasses being a poor-quality food source (Bjorndal, 1980).

Recent research has highlighted that the importance of fish herbivory has probably been underestimated in the Caribbean and Mediterranean seas, as substantial grazing has been reported relative to the total annual seagrass production (Kirsch et al., 2002; Tomas et al., 2005). These researchers also found that herbivory caused periods of overgrazing. At small scales, simulated herbivory has been found to influence the shoot growth and density of a number of key Indo-Pacific seagrass species (Cebrian et al., 1998). If herbivory in the Indo-Pacific region is as high as that suggested in the Caribbean and Mediterranean seas it may have major ecological consequences for the management of seagrass food webs as herbivores such as

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scarids are a common human food source in the Indo-Pacific (May, 2005). Seagrass herbivory can also be important to reef fish at different stages of their life cycle (McAfee and Morgan, 1996). Seagrass food webs are important as seagrass shoots support epiphytes that may make major contributions to food chains (Yamamuro, 1999), they provide shelter and habitat for larger fauna (Bell and Westoby, 1986; Larkum et al., 2005; Jackson et al., 2006; Unsworth et al., 2007), and they also play a major role in nutrient cycling and sea defence (Hemminga and Duarte, 2000).

Currently, the importance of herbivory in the Indo-Pacific by scarids is poorly understood as data exists from only a number of preliminary studies that utilised only basic methodology (Alcoverro and Mariani, 2004). Such studies found that herbivores consume only a small proportion of seagrass production (10–15%), indicating that herbivory may not be as important within this region compared to other bio-regions (Klumpp et al., 1989; Hemminga et al., 1991). A thorough assessment of scarid herbivory as a proportion of seagrass growth is required to determine the importance of herbivory in the Indo-Pacific (Parrish, 1989).

Traditionally the Green Turtle (*Chelonia mydas* Linnaeus) (Jackson, 1997) and the Dugong (*Dugong dugon* Müller) were the largest herbivores inhabiting Indo-Pacific seagrass beds (Marsh et al., 2005) and in areas where Dugongs are still abundant, research suggests that they exert a considerable herbivorous pressure on seagrass (De Iongh et al., 1995). Within the Indo-Pacific, herbivorous fish such as scarids and siganids, and sea urchins (particularly *Tripneustes gratilla* Linnaeus and *Diadema* spp.) are the remaining key herbivores that directly consume seagrass (Alcoverro and Mariani, 2004). These herbivores make an important contribution to the diet of human communities throughout the Indo-Pacific (de la Torre-Castro and Rönnbäck, 2004; May, 2005). With exploitation of seagrass fauna at unsustainable levels in many areas of the Indo-Pacific (Fortes, 1988, Fortes, 1990; Rollon and Fortes, 1991), populations of important functional groups such as herbivores may be locally threatened.

In addition to the importance of seagrass grazing possibly supplying energy to other levels of the food chain, the total loss of seagrass caused by scarids is also important; this can often be much greater than the amount consumed directly (Unsworth, personal observation). This is because when a scarid takes a bite from a leaf it leaves a hemispherical bite mark, which if large enough may cut the leaf causing the loss of the upper leaf section (Kirsch et al., 2002). The upper leaf section may then be exported away from the seagrass bed or decay locally and move to nearby habitats along alternative food chains. Gases within the leaves of seagrass can cause them to remain buoyant after detachment from the plant (Hemminga and Duarte, 2000). This potentially results in the widespread dispersal of seagrass material in surface waters. Detached seagrass may also be cast onto the shore where it decays and may re-enter the system as detritus (Christiansen et al., 1981; Hemminga and Nieuwenhuize, 1990).

The extent of herbivory within seagrass habitats may be related to fish density; therefore it is important to consider

how factors associated with larger spatial scales can influence the density and behaviour of fish assemblages as this variability will have potential consequences on herbivory rates. At local scales, variable habitat structural complexity and the continuity of vegetation (often referred to as 'landscape effects') have been determined as being important in controlling seagrass fish densities (Salita et al., 2003; Verweij et al., 2006). For example scarid herbivory was found to increase away from patchy seagrass areas (Maciá and Robinson, 2005), whilst increasing distance from a reef reduced the rate of herbivory due to reduced fish migration (Kirsch et al., 2002). Research has found that seagrass shoot abundance and biomass can be highly variable within Indo-Pacific seagrass beds often over small spatial scales (Kuriandewa et al., 2003). Variable seagrass habitat structure may therefore have important impacts on herbivory rates and remains un-quantified.

Estimating fish herbivory is difficult as direct observations are not effective due to observer interference and the necessary times scales required to make observations. A number of alternative experimental methodologies have been used to assess herbivory such as experimental leaf tethering (Kirsch et al., 2002), observations of small experimental plots (Alcoverro and Mariani, 2004) and the use of aquaria (Maciá and Robinson, 2005). Combining these methods provides an opportunity to accurately assess herbivory and allows comparisons between methodologies (Mulder and Ruess, 1998). Estimating seagrass grazing effects for individual fish is important as it provides an alternative measurement of herbivory and enables observed levels to be scaled up to the population level. Although such estimates have been successfully conducted using habitat enclosures in terrestrial environments (Mulder and Ruess, 1998) no studies have attempted such estimations for fish in seagrass ecosystems.

This study provides the first quantitative assessment of the rates and patterns of the herbivory of seagrass by scarids in an Indo-Pacific seagrass bed relative to seagrass growth. Evidence is provided from the use of a combination of direct and indirect methodological approaches to quantify scarid seagrass consumption within the Wakatobi Marine National Park, Indonesia.

2. Materials and methods

2.1. Study sites

Estimation of scarid seagrass herbivory was conducted using three methods: (1) estimating current impact of grazing on existing seagrass flora by surveying background levels of scarid seagrass bites; (2) estimating *in-situ* rates of grazing as a proportion of growth using seagrass tethering experiments; and (3) estimating the grazing impact of the scarid population by developing estimates of seagrass grazing effect for individual scarids within seagrass enclosures and then scaling up this information to the population level.

Tethering and bite surveys were conducted at three intertidal seagrass sites (Hoga Beach, Boat Bay and Mushroom Bay) around Hoga Island, Wakatobi Marine National Park

(MNP), SE Sulawesi, Indonesia (Fig. 1). These are all sandy bays that contain inter-tidal to sub-tidal swaths of seagrass leading onto fringing reefs that as with all areas of the Wakatobi MNP are subject to small scale fishing. Overall habitat and environmental characteristics for these sites are described in Table 1. Seagrass beds of the Wakatobi MNP are subject to a maximum tidal amplitude 2.3 m (Unsworth et al., 2007).

Habitat complexity is defined as ‘consisting of many different and connected parts’ (Oxford English Dictionary, 2006). The present study quantified seagrass cover, biomass, leaf density and height as measures of habitat complexity as these have successfully been used in other studies (Heck and Wetstone, 1977; Stoner, 1980; Attrill et al., 2000). Each of the three sites were categorised into levels of increasing complexity (hereafter referred to as high, mid and low complexity). These three levels were based upon the extreme and middle values of the local seagrass beds observed in pilot studies.

A fourth site (Bounty Bay) was used exclusively to conduct enclosure experiments. All sites comprised a mixed assemblage of four seagrass species (*Thalassia hemprichii*, *Enhalus acoroides*, *Cymodocea rotundata*, and *Halophila ovalis*), although *Halodule univernis*, *Syringodium isoetifolium* and *Thalassodendron ciliatum* have been infrequently recorded around Hoga. All sites were standardised for distance from shore (≈ 30 m) and reef (≈ 200 m) and were in a depth range of 1.5–2 m (high tide).

Species leaf abundance and percentage cover was estimated at all sites (five 0.25 m² quadrats placed arbitrarily). Dry weight biomass (g DW) was estimated from the mean biomass per leaf (20 leaves per quadrat were cleaned, dried and weighed) and then by multiplying this by the total density of leaves per quadrat. The 20 leaves were collected randomly within the quadrat and assumed to be representative (cut at the internode). For the tethering and growth experiments, the mean dry weight per cm² of leaf tissue was calculated by digitally photographing leaves of each species and calculating their area (using UTHSCSA ImageTool v3.0) relative to its dry weight.

2.2. Estimation of scarid grazing: surveying bite levels

The number of residual natural bites (pre-existing hemispherical bite marks visible on seagrass leaves) was determined at all three sites by counting bite numbers appearing on all seagrass species present in five 0.25 m² quadrats.

2.3. Estimation of scarid grazing: tethering experiments

An adaptation of the tethering method successfully tested and utilised by Kirsch et al. (2002) was used to measure the area of seagrass lost per day from natural leaves of the two most abundant seagrass species (*Thalassia hemprichii* and

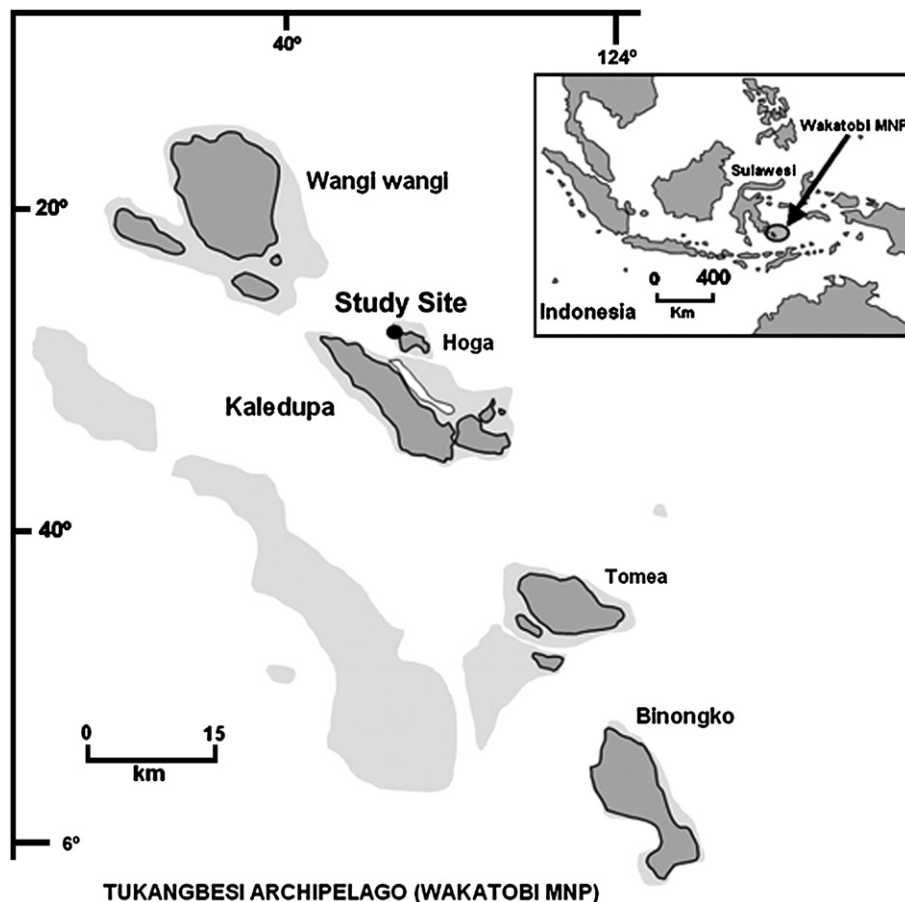


Fig. 1. Location of the study sites, close to Hoga Beach in the Wakatobi Marine National Park, S.E. Sulawesi, Indonesia.

Table 1
Mean (\pm SE, $n = 5$) habitat characteristics, total fish densities (adults and juveniles) and coordinates of the four sites (high complexity seagrass, mid complexity seagrass, low complexity seagrass and the enclosure site) used for tethering experiments within intertidal seagrass beds of Wakatobi Marine National Park, Indonesia

		High complexity	Mid complexity	Low complexity	Enclosure site
Leaf density (leaves/m ²)	Total seagrass	773.1 \pm 65.2	667.2 \pm 148.5	645.3 \pm 24.8	670.4 \pm 42.2
	<i>Thalassia hemprichii</i> Ehrenberg	640.0 \pm 47.5	402.7 \pm 59.6	458.7 \pm 37.0	542 \pm 32.0
	<i>Enhalus acoroides</i> L.f. Royle	133.1 \pm 14.8	104.5 \pm 15.3	8.0 \pm 2.6	40.2 \pm 4.6
	<i>Cymodocea rotundata</i> Ehrenb and Hempr. ex Asch	3.7 \pm 2.7	171.4 \pm 29.1	178.7 \pm 39.0	55.7 \pm 22.1
	<i>Halophila ovalis</i> Ehrenb and Hempr. ex Asch	1.6 \pm 0.9	1.6 \pm 0.9	1.1 \pm 0.5	1.9 \pm 0.4
% cover	% seagrass cover	82.5 \pm 7.2	64.7 \pm 16.5	48.0 \pm 1.8	65.0 \pm 8.0
	% vegetation cover	83.2 \pm 6.8	64.7 \pm 16.5	48.6 \pm 1.8	75.6 \pm 11.3
	% algae cover	0.0 \pm 0.0	0.0 \pm 0.0	0.6 \pm 0.4	9.5 \pm 0.7
Biomass (g DW m ⁻²)	Total seagrass	438.4 \pm 81.8	94.8 \pm 26.7	31.5 \pm 2.3	84.5 \pm 4.5
	<i>Enhalus acoroides</i>	260.2 \pm 68.4	52.4 \pm 20.1	1.5 \pm 0.4	33.1 \pm 4.6
	<i>Thalassia hemprichii</i>	178.2 \pm 29.3	28.8 \pm 8.0	19.3 \pm 1.3	22.4 \pm 3.1
Fish density (fish ha ⁻¹)	Parrotfish (<i>Scaridae</i> spp.)	2000 \pm 537	500 \pm 406	125 \pm 65	

Enhalus acoroides). Tethering has been commonly used in a range of habitats to estimate herbivory rates (see Macintyre et al., 1987; Micheli, 1993).

For each of the two species of seagrass, at each site, four 5 m long tethers made of coloured string were staked out perpendicular to the shore using four metal stakes. Tethers were placed parallel to each other 3 m apart, therefore tethers covered an area of 45 m². Five wooden pegs were equally spaced along the tethers and a group of three leaves of one species was attached to each peg. This created 20 repeat samples (groups of leaves) at each site. All stakes, tethers and pegs were buried within the sand to prevent any interference to the experiment. These were treated as 20 independent samples of the one locality. Tethers were positioned in the seagrass for 6 days at each of the three sites and the protocol was repeated for *Thalassia hemprichii* and *Enhalus acoroides*. All experiments were completed within a 6-week period (June to August 2005).

Seagrass was collected from each locality and returned to the laboratory for shoot area analysis. All groups of three leaves originated from one seagrass shoot, so leaves were mixed ages and therefore representative of the overall population. Only intact leaves were used in this study. The total leaf surface area of each group of three leaves was calculated prior to tethering by taking digital photographs using an Olympus C4000 zoom camera fixed on a modified tripod, which enabled the horizontal angle to be kept consistent between photographs. Total leaf area was calculated using the UTHSCSA ImageTool v3.0 software.

Grazed leaves were defined as those containing hemispherical bite marks or those that had been cut with a curved mark due to the unique mouth shape created by the fused teeth of scarids (Kirsch et al., 2002). It was anticipated that a large proportion of the leaves would be grazed by siganids or echinoderms (*Tripneustes gratilla*, *Protoreaster nodosus*, *Diadema* sp. or *Echinothrix* sp.), *Calotomus spinidens* (the only seagrass spiny-toothed parrotfish) or possibly species of Labridae. Such bites would be distinguished from that of parrotfish by the presence of tear marks, rather than hemispherical bite marks. Parrotfish bites make a clean accurate mark whilst other fish and urchins do not (for pictures see Kirsch et al., 2002). Such tears

were very infrequently observed. Any non-hemispherical marks were not included in the analysis. Tethers were examined and replaced every 24 h and those that had been grazed were collected and returned to the laboratory for recalculation of the area consumed and percentage of seagrass lost.

In order to calculate the grazing rate as a percentage of seagrass growth, the net above-ground seagrass production (NAPP) was calculated for both species at each site using a modification of the hole-punch technique described by Kirkman and Reid (1979). At all three sites 30 leaves of *Thalassia hemprichii* and *Enhalus acoroides* were punched at their base using a pin and then a small 4 cm section of very fine fishing wire was inserted as a marker. The movement of this marker up the leaf over 4 days was measured three times at each site for each species. The increase in leaf area was calculated by measuring the width of the plant and its increase in length. Leaf biomass increase (g DW) was calculated by multiplying the increase in seagrass leaf area by the mean seagrass area biomass (g DW cm⁻²) for each species at each site.

2.4. Estimation of scarid grazing: enclosure estimates per individual

The grazing rate of individual scarids (*Leptoscarus vaigiensis*) was determined in 5 m \times 5 m enclosures of natural seagrass. This species is common within Wakatobi seagrass beds (Unsworth, personal observation) and is known from stomach contents analysis to be a seagrass herbivore (Almeida et al., 1999). Enclosures were built from wooden poles, bamboo strips and dark green nylon meshing (mesh size 3 mm). Grazing rates of 10 individual scarids placed separately within the enclosure were calculated over 4 days. To prevent cumulative repeat effects on the seagrass within the enclosure area, a period of 4 days was left between experiments to allow for recovery of the enclosure. Repeat measures of seagrass cover and density were taken throughout the experiment and no change was found. Fish were caught by fishermen by hand at low tide and only adult fish in the range 20–30 cm were used.

Biomass loss per individual scarid was estimated by determining the average number of leaves bitten per day. This was

achieved by first removing all damaged or bitten seagrass from $3 \times 1 \text{ m}^2$ sub-plots within the enclosure prior to the experiment. After 4 days the number of leaves exhibiting signs of scarid herbivory was determined within the sub-plots. The average amount of total biomass lost when a leaf was bitten by a scarid was determined for each species from the tethering experiments (averaged across all sites). For each species the respective values were multiplied by the number of bitten leaves within the sub-plots to calculate the biomass lost within each of the three sub-plots for each species over 4 days. A daily consumption rate was then calculated per sub-plot (1 m^2) and a mean calculated for the three. This rate was extrapolated to the whole enclosure (25 m^2) by multiplying by 25 enabling a total consumption rate per fish per day to be calculated for each species and for total seagrass.

Due to its presence within the enclosures *Cymodocea rotundata* was also included in this experiment (Table 2), allowing total seagrass biomass loss per individual fish to be estimated. No data was available to extrapolate *C. rotundata* data from the tethering studies to the enclosure. To estimate loss of *C. rotundata*, a value of half that of the *Thalassia hemprichii* leaf loss was used as this species was found to have approximately half the dry weight biomass per cm of leaf of *T. hemprichii*.

The use of caged enclosures within natural aquatic systems has commonly been utilised to understand the ecological interactions between different trophic groups (Vanni and Layne, 1997; Cronin et al., 2006; Hereu, 2006). Such artificial enclosures have the potential to induce experimental artefacts on fish behaviour. This has been found to be the case in small enclosures ($<1 \text{ m}^2$) (Vanni and Layne, 1997) but with larger enclosures artefacts are considered negligible (Maciá and Robinson, 2005; Hereu, 2006).

Local populations of scarids were estimated at all sites allowing data on individual scarid grazing rates (biomass consumed per fish per day) to be extrapolated to field densities of fish and estimate total seagrass consumption at each site. To survey fish a stationary point-count method by means of snorkelling was used (Polunin and Roberts, 1993; Watson and Quinn, 1997). This method has been commonly used to assess fish assemblages (including scaridae) within tropical seagrass beds (Nakamura and Sano, 2004; Dorenbosch et al., 2006). This method used a 16 m^2 ($4 \times 4 \text{ m}$) quadrat delineated by tape measures laid out 15 min prior to sampling. The quadrat size was chosen as visibility within the sampling locality is at least 5 m for 90% of the

time (calculated during preliminary observations). At each site five independent sample observations haphazardly placed were conducted. As these observations were conducted by an observer conducting wider fish monitoring programs, numerous study training exercises had been conducted prior to sampling (see English et al., 1997). During the first 10 min of the 15 min period, the observer was situated on the edge of the quadrat, while during the last 5 min, the observer moved through the quadrat to search for scaridae hiding behind or under seagrass leaves. Care was taken not to count individuals or groups of fish more than once that regularly moved in and out of the quadrat (Dorenbosch et al., 2006). All observations were conducted at high tide. Scarid densities per 16 m^2 were scaled up to densities per hectare.

Leptoscarus vaigiensis is known to feed on seagrass detritus when a small juvenile ($<6 \text{ cm}$) rather than directly on fresh seagrass, presumably as a response to the developing strength of its beak (Nakamura et al., 2003). As a result visual observations aimed to exclude all individuals $<8 \text{ cm}$, however none were observed.

2.5. Statistical analysis

General linear model (GLM) ANOVA utilising MINTAB v13 was conducted to determine any differences between treatments in all experiments (including habitat data). Differences were compared using Tukey's pair-wise comparisons. One-way PERMANOVA (PERMANOVA v6, University of Auckland) was used as an alternative to GLM where data was found to be heteroscedastic and deviated from a normal distribution following transformation. PERMANOVA is not reliant on the assumptions of ANOVA, and it tests the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design (Anderson, 2001; McArdle and Anderson, 2001). PERMANOVA enabled a conventional ANOVA style univariate two-way analysis to be conducted using the assumptions of a multivariate method.

3. Results

3.1. Habitat and seagrass growth characteristics

All sites had different habitat characteristics that reflected the high, mid and low habitat complexity categories (Table 1). This was particularly evident from the significant differences

Table 2

ANOVA tables for two-way permutational multivariate analysis of variance (PERMANOVA) for total seagrass biomass loss (g DW day^{-1}) and two-way ANOVA of $\log_{10} (+1)$ transformed % seagrass proportional loss ($\% \text{ day}^{-1}$) following seagrass grazing experiments utilising controlled tethers of natural seagrass placed at three sites (high, mid and low complexity seagrass) in the Wakatobi Marine National park, Indonesia. PERMANOVA used Euclidean distances with no transformation or standardisation of data and 999 permutations

Source	Degrees of freedom	PERMANOVA seagrass total loss			ANOVA seagrass % loss		
		Mean squares	F statistic	p value (permutational)	Mean squares	F statistic	p value
Complexity	2	10181	9.185	0.001	0.398	3.94	0.030
Species	1	12808	11.555	0.001	0.001	0.00	0.961
Complexity \times species	2	7340	6.621	0.001	1.125	11.15	0.001
Residual	30	1108			0.101		
Total	35						

in the seagrass % cover ($F_{2,14} = 5.15, p < 0.03$) and mean of the seagrass biomass ($F_{2,14} = 56.59, p < 0.001$) (Table 1). All inter-site comparisons were significantly different for seagrass % cover and seagrass biomass (Tukey's pair-wise comparisons). *Thalassia hemprichii* and *Enhalus acoroides* were the most abundant species at all sites, while *Cymodocea rotundata* was only abundant at the mid-complexity site. *Halophila ovalis* had low abundance at all sites. Seagrass growth rates were significantly higher at the high complexity site (*E. acoroides*: $F_{3,269} = 26.4, p < 0.001$; *T. hemprichii*: $F_{2,149} = 12.3, p < 0.001$) compared with the other two sites, while no significant differences were found between the mid and low complexity sites (Tukey's pair-wise comparisons < 0.001).

3.2. Estimation of scarid grazing: surveying bite levels

Evidence of grazing was found on three of the four seagrass species (*Thalassia hemprichii*, *Enhalus acoroides* and *Cymodocea rotundata*) at all three sites (Fig. 2b), with no grazing being found on *Halophila ovalis*. Bite mark density was significantly higher on *T. hemprichii* at the high complexity site ($F_{2,17} = 43.61, p < 0.001$) and *E. acoroides* ($F_{2,17} = 3.56, p = 0.05$), followed by the mid complexity site. Differences for *E. acoroides* were only present between the high and low complexity sites (Tukey's pair-wise comparisons). Bite densities on *C. rotundata* were lower than for the other two species at all sites, with the highest number being found at the sites of mid and low complexity where this species had its highest abundance.

3.3. Estimation of scarid grazing: tethering experiments

Grazing by scarids on the seagrass tethers was very high (Fig. 2c) with *Thalassia hemprichii* being lost at a rate of 0.28 ± 0.08 g DW day^{-1} , while *Enhalus acoroides* was lost at a rate of 2.85 ± 0.43 g DW day^{-1} (averaged across 60 leaves). *Enhalus acoroides* has the greatest loss of biomass at the high complexity site (Fig. 2c) (approximately three times greater than all other species at all sites); the greatest loss of *T. hemprichii* occurred at the mid complexity site. Significant differences were found in the amount of seagrass biomass lost per day between sites ($F_{2,35} = 9.1852, p < 0.001$) and seagrass species ($F_{1,35} = 11.56, p < 0.001$). The high complexity site did not always have the greatest seagrass biomass loss.

Tethering experiments indicated that *Thalassia hemprichii* lost an average 64% of its daily leaf growth whilst *Enhalus acoroides* lost 787%. These rates were highly variable and ranged from $16.7 \pm 1.4\%$ for *T. hemprichii* at the low complexity site to $1893 \pm 447\%$ of *E. acoroides* at the high complexity site (Fig. 2d). Seagrass loss was greater than seagrass growth for *E. acoroides* irrespective of site, but only at the mid complexity sites for *T. hemprichii* (Fig. 2d). We found a significant difference in the proportional loss of seagrass between sites ($F_{2,35} = 3.94, p < 0.05$), but not between species (Table 2). Consumption of seagrass was not always highest at the high complexity site. This was indicated by a significant interaction term between site and species ($p < 0.001$).

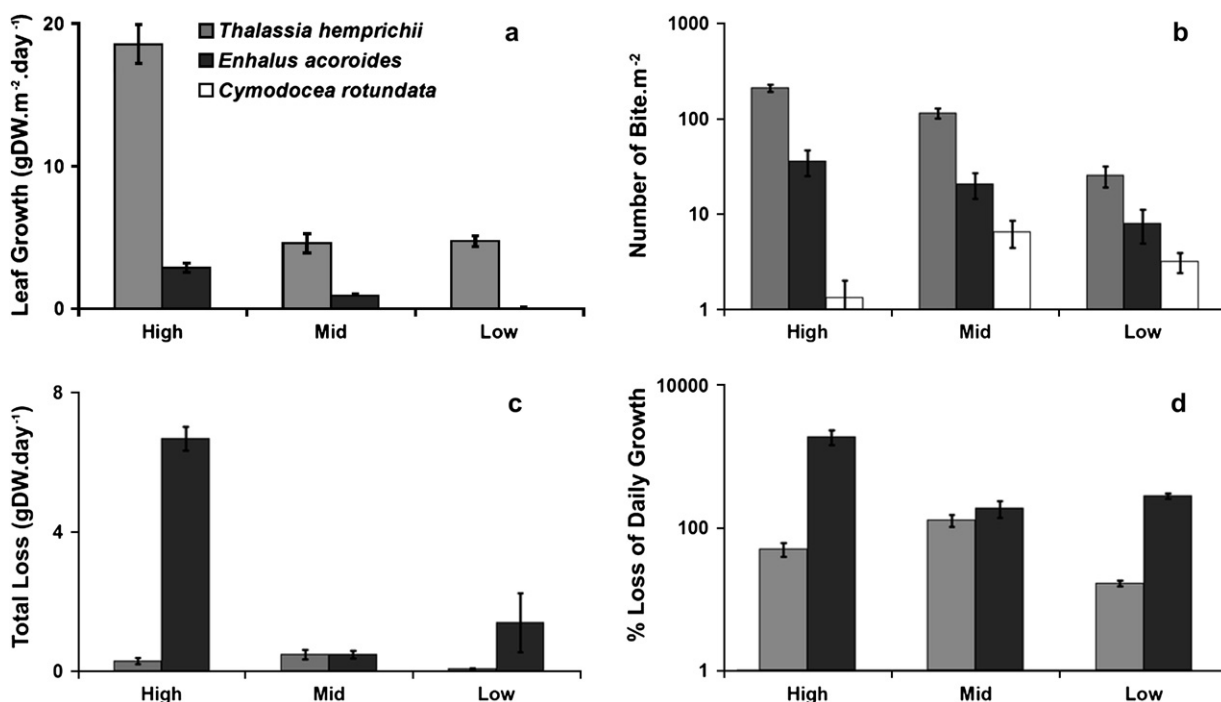


Fig. 2. Seagrass tethering experiments and habitat data for three seagrass sites (high, mid and low complexity seagrass) within the Wakatobi Marine National Park, Indonesia. (a) Mean (\pm SE, $n = 30$) seagrass growth (measured as biomass accumulation g DW m^{-2}) per unit area (g DW m^{-2}) (b) Mean number (\pm SE, $n = 5$) of residual scarid bites per unit area (bite. m^{-2}) (c) Mean (\pm SE, $n = 6$) total loss of seagrass caused by scarids relative to growth (biomass accumulation as g DW m^{-2}) (d) Mean (\pm SE, $n = 6$) proportional loss of seagrass per unit area (% m^{-2}) relative to seagrass growth (biomass accumulation as g DW m^{-2}).

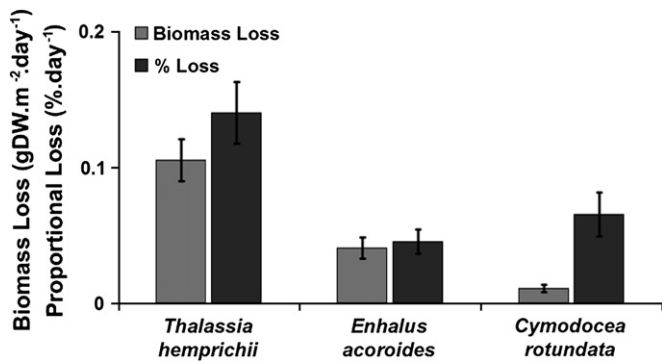


Fig. 3. Mean (\pm SE, $n = 10$) seagrass biomass loss ($\text{g DW m}^{-2} \text{ day}^{-1}$) and proportional loss of seagrass per unit area ($\% \text{ m}^{-2}$) caused by a single parrotfish of the species *Leptoscarus vaigiensis* on three seagrass species (*Thalassia hemprichii*, *Enhalus acoroides* and *Cymodocea rotundata*) within enclosures ($5 \text{ m} \times 5 \text{ m}$) of intertidal seagrass beds in the Wakatobi Marine National Park, Indonesia.

3.4. Estimation of scarid grazing: enclosure estimates per individual

On average one individual *Leptoscarus vaigiensis* removed $1.4 \pm 0.02\%$ of the available *Thalassia hemprichii*, $0.04 \pm 0.01\%$ of the *Enhalus acoroides*, and $0.06 \pm 0.01\%$ of the *Cymodocea rotundata* present each day (Fig. 3). We estimated that one individual *L. vaigiensis* caused the total loss of $3.94 \pm 0.44 \text{ g DW day}^{-1}$ of seagrass.

Loss of seagrass biomass was significantly higher on *Thalassia hemprichii* than on the other two species ($F_{2,20} = 23.08$, $p < 0.001$), whilst proportional loss of biomass was highest for *T. hemprichii* and *Enhalus acoroides* ($F_{2,20} = 5.11$, $p < 0.05$). By extrapolating this data to the information from the tethering experiments sites and combining it with observed scarid densities, the percentage of seagrass growth consumed by scarids was calculated (Table 3) and ranged between 0.7 and 2.6% of the growth each day. These figures were much lower than those calculated from the tethering study (Fig. 2d). After every 4-day period a large amount of loose floating seagrass appeared within the enclosures, presumably as a consequence of the scarid herbivory. This high biomass of floating seagrass, illustrated that not all of the seagrass lost from the benthos was actually consumed.

4. Discussion

Our research estimated that a large proportion of the growth of dominant Indo-Pacific seagrass species is grazed by

herbivorous scarids. Between 0.1 and 11 times the daily new growth of *Enhalus acoroides* was consumed suggesting that under some conditions more seagrass is lost than grown. The continuing persistence of these habitats (and this species) indicates that these high consumption rates cannot be continuous. High levels of scarid grazing are not unique to the Indo-Pacific and are unlikely to be an artefact of our experimental design, as the impacts of tethering methods used in the present study have been found to be minimal (Kirsch et al., 2002). Similar rates of scarid grazing of turtlegrass (*Thalassia testudinum*) to those in our study were reported in a sub-tropical Florida sanctuary (Kirsch et al., 2002). But as their study contained temporal variation they found such high rates to be a function of seasonality.

The role of scarid herbivory in the Indo-Pacific was first questioned by Ogden (1980) who suggested that scarids only consume a small proportion (10–14%) of seagrass growth, with was then supported by further studies (Klumpp et al., 1989; Hemminga et al., 1991). Despite the potential for herbivory to be highly variable, we have found it to be an underestimated process in structuring an Indo-Pacific seagrass community and this supports findings from other bioregions (Kirsch et al., 2002; Tomas et al., 2005). We found that seagrass scarid herbivory caused the loss of at least 16% of seagrass growth each day. This research is the first to estimate the seagrass loss caused per individual adult *Leptoscarus vaigiensis* ($3.94 \pm 0.44 \text{ g DW day}^{-1}$). When this figure is used to calculate grazing as a proportion of seagrass growth based on the estimated numbers of local scarids, levels of loss were much lower than recorded by tethering experiments. Both experimental procedures contain error that is inherent to experiments dependent on estimation and extrapolation rather than direct calculation. However, the large difference (two orders of magnitude) in observed tethering loss vs enclosure loss is too large to be the result of methodological variability and therefore warrants further discussion and interpretation.

Scaridae can be a difficult family to sample within seagrass beds due to some species remaining cryptic whilst some exhibit shoaling behaviour (Dorenbosch et al., 2006). We believe that our observed differences between techniques may reflect under-estimation of scaridae. We conducted our scarid population assessments at only one temporal interval during the day and only observed common seagrass resident scarids (*Leptoscaris vaigiensis* and *Calotomus spinidens*) (Dorenbosch et al., 2005). However, very large shoals of juvenile scarids (*Chlorurus sordidus*, *Calotomus spinidens* and *Leptoscarus vaigiensis*) have been infrequently observed in other tropical seagrass studies (Nagelkerken et al., 2000; Gratwicke and Speight, 2005;

Table 3

Extrapolation of consumption figures per individual parrotfish (*Scaridae* spp.) to calculate estimated percentage seagrass consumption based on observed daytime parrotfish densities and seagrass growth rates at three sites (high, mid and low complexity seagrass) in the Wakatobi MNP, Indonesia

	Consumption per individual parrotfish (g DW)	Average (\pm SE) estimated seagrass growth (g DW ha^{-1})	Average (\pm SE) estimated parrotfish abundance (no fish ha^{-1})	Percentage consumption of seagrass growth
High complexity seagrass	3.94	307248 ± 23888	2000 ± 537.6	2.6
Mid complexity seagrass	3.94	78323 ± 11585	500 ± 643	2.5
Low complexity seagrass	3.94	71452 ± 5885	125 ± 643	0.7
All sites		152341 ± 13786	875 ± 297.6	2.3

Dorenbosch et al., 2006) and such infrequent, yet large shoals of juveniles and sub-adults (mainly the typical reef species *Hipposcarus longiceps* Valenciennes and *Scarus schlegeli* Bleeker) have also been found within seagrass beds of the wider locality of the present study (day and night) using netting techniques (Unsworth et al., unpublished data). The juveniles within these shoals may well be utilising seagrass habitats for only short periods of the year and have large spatial and temporal variability. This indicates that the observed high levels of herbivory may only be a short-term effect of irregular grazing by shoals of juvenile and sub-adult scarids. Large shoals of juveniles moving through the seagrass canopy rather than residents remaining hidden within dense lower foliage may additionally explain why the total consumption rate was much higher on the tall long leaved *E. acoroides* than other species. Such irregular and unpredictable patterns of marine herbivory (either temporally or spatially) have been observed in other localities and systems (Ogden and Buckman, 1973; Ogden and Ziemann, 1977; Bjørndal, 1980; Overholtzer and Motta, 1999; Kirsch et al., 2002) and may explain our results.

Seasonality could also be the cause of the high levels of herbivory. Despite an assumed lack of seasonality within the tropics, the weather can be split into a wet and a dry season, which may change the characteristics of seagrass habitats (Erfteheijer and Herman, 1994). Predictable seasonal changes in wind direction also occur and undergo a predictable pattern (Tomascik et al., 1997). Seasonal changes in habitats conditions and suitability could result in large changes in scarid density and cause large fluctuations in seagrass grazing. Seasonality within Indo-Pacific seagrass beds is poorly understood and should be a focus of future research.

A large proportion of scarid induced seagrass loss observed in the present study is not consumed but is lost (discarded) indirectly from grazing, as the scarid bites through the leaf. Although the present study has found that scarids are important herbivores within Indo-Pacific seagrass beds, we do not propose that all of this material is consumed by the fish. To the contrary we propose that scarids have an important functional role in discarding seagrass material that may end up in detrital food webs. Previous research has assumed that currents and adverse weather are primarily responsible for the loss and export of seagrass material from these habitats (Hemminga et al., 1991; Stapel et al., 1996; Hemminga and Duarte, 2000), but we propose that scarids may be equally important in influencing seagrass export from the system by the high rates of material discarded during consumption that becomes subsequently removed from the system by weather and currents. Seagrass loss from the system is estimated to be as high as 11% of seagrass growth (Stapel et al., 1996). Furthermore, we propose that scarids have an important role in supplying discarded seagrass material for export from the system. This may have an important role in the connectivity of seagrass beds with other habitats.

Previous analysis of seagrass nutritional quality (C:N ratios) showed no pattern in relation to herbivore activity (Kirsch et al., 2002); this demonstrates that herbivores do not select specific vegetation on the basis of nutritional quality as suggested previously (McGlathery, 1995). *Enhalus*

acoroides and *Thalassia hemprichii* have been found to have varied nutritional qualities in the Philippines and offer different nutritional benefits to herbivores (Duarte, 1990). We found no differences between proportional loss rates of *Enhalus acoroides* and *Thalassia hemprichii* despite *E. acoroides* containing preferential C, N, and P levels (Duarte, 1990). This indicates that grazing on seagrass is based on availability rather than active selection on the most nutritional seagrass.

We found that scarid herbivory was highest at the maximum habitat complexity site, which suggests that the increased shelter and food abundance provided by denser seagrass beds (Bell and Westoby, 1986; Hyndes et al., 2003) may have increased fish abundance resulting in high levels of herbivory. The relationship between habitat complexity and grazing rate was not clear, which probably reflects the complexity of process acting at larger spatial-scales in determining the distribution and consequential herbivory of scarids. Spatial variation in seagrass fish assemblages is common (Rollon and Fortes, 1991; Salita et al., 2003) and has been attributed to the influence of habitat connectivity (Dorenbosch et al., 2005), environmental variability (Bostrom and Bonsdorff, 1997) and the continuity of vegetation (often referred to as 'landscape-effects') (Salita et al., 2003; Hovel and Fonseca, 2005). As our study design only sampled three sites, and contained reduced replication of complexity this may have reduced the strength of these results and the effects may have been partially obscured by more influential local-scale variables. We suggest that future herbivory research should identify key factors that influence the spatial and temporal variation in Indo-Pacific seagrass herbivory (Maciá and Robinson, 2005).

In conclusion, we found that scarids are major herbivores in Indo-Pacific seagrass beds. They not only take up carbon into the food chain through direct consumption, but also make an important functional contribution to the detrital food chain through the export of seagrass material and its subsequent decay.

Acknowledgements

The authors thank the staff at the Hoga Marine Research Centre for their logistic support and Operation Wallacea who provided financial support for travel and fieldwork. Richard Unsworth is grateful to Dr Tim Coles and Operation Wallacea for providing a doctoral studentship.

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