

Parrotfish grazing on turtlegrass *Thalassia testudinum*: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary

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ABSTRACT: The widespread occurrence and persistence of modern day seagrass habitats has led many to hypothesize that grazing on seagrasses is minimal. On a global scale this may well be true as the numbers of large vertebrate herbivores (e.g. sea turtles, manatees and dugongs) and waterfowl, grazers that can greatly alter seagrass density, have been dramatically reduced in coastal ecosystems. Nonetheless, numerous observations indicate that smaller herbivores (e.g. the bucktooth parrotfish *Sparisoma radians*), grazers that may not be able to reduce seagrass density substantially, still commonly feed on seagrasses in the subtropical and tropical western Atlantic Ocean. These observations led us to quantify the role that seagrass herbivory plays in modern-day seagrass food webs. In the first phase of this study, digitally scanned seagrass leaves were clipped to ropes and placed at 3 sites in Hawk Channel, in the northern Florida Keys (USA). Areal loss from the tethered leaves provided a daily estimate of seagrass grazing rates. These losses, coupled with local estimates of net aboveground primary production, allowed us to determine the proportion of seagrass production consumed at our study sites during 4 separate seasons. We found that seagrass grazing varied greatly both spatially and seasonally at our sites but, on average, grazers consumed virtually all of the aboveground production at 2 of the 3 sites. When experiments were repeated in the summer of a second year at 6 sites, seagrass grazing again varied greatly among sites, but at 3 of the sites most of the daily production of seagrass shoots was consumed by small herbivorous fishes. These results suggest that while it is undoubtedly true that modern day grazing by mammals, turtles and waterfowl on seagrass is reduced, small vertebrate grazers consume substantial amounts of seagrass production in the northern Florida Keys.

KEY WORDS: Carbon · Nitrogen ratios · Florida Keys · Herbivory · Parrotfish · Production · Seagrass · Tethering · *Thalassia testudinum*

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INTRODUCTION

The proportion of seagrass production reaching higher order consumers via the grazing pathway is reported to be low in most locations (<30% of annual net aboveground primary production) (e.g. Fenchel

1970, 1977, Kikuchi & Peres 1977, Nienhuis & Van Ierland 1978, Kikuchi 1980, Thayer et al. 1984, Nienhuis & Groenendijk 1986, Valiela 1995). While this may be true in some areas, seagrasses are readily consumed in many others (Randall 1965, 1967, Lawrence 1975, Kirkman & Reid 1979, Lobel & Ogden 1981, Klumpp & Nichols 1983a,b, Valentine & Heck 1991, 1999, Montgomery & Targett 1992, Klumpp et al. 1993, Mitchell et al. 1994, Cebrián et al. 1996, Pinto & Punchihewa 1996,

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Havelange et al. 1997, Valentine et al. 1997, 2000). In some cases, grazing by herbivorous fishes, waterfowl, and sea urchins can be so intense as to control both seagrass productivity and density (see Lodge et al. 1998, Valentine & Heck 1999). Clearly, in these areas the importance of seagrass grazing is great, and there remains a need to better understand the factors that control spatial and temporal variability in seagrass consumption.

The historical overharvesting of green sea turtles, sirenians, and waterfowl has undoubtedly led to reduced grazer impacts on seagrass density in many areas (Jackson 1997, Valentine & Heck 1999). It has also been hypothesized that the threat of predation from both pelagic and reef-resident piscivorous fishes limits seagrass grazing in pristine reef environments (Ogden et al. 1973, Morse 1977, Ogden & Zieman 1977, Dubin & Baker 1982, Macintyre et al. 1987). Evidence supporting this hypothesis, however, remains elusive. Observational data suggest that while predation risk may limit grazing by larger herbivorous fishes on seagrasses to the base of coral reefs, it does not seem to limit feeding by smaller species of parrotfishes (e.g. bucktooth parrotfish *Sparisoma radians*) that hide within, and feed on, seagrasses far removed from coral reefs (Randall 1965, Ogden & Zieman 1977, Robertson & Warner 1978, Weinstein & Heck 1979, Lobel & Ogden 1981, Macintyre et al. 1987, Greenway 1995, Montague et al. 1995, McAfee & Morgan 1996). Macintyre et al. (1987), for example, showed that the size of parrotfish bites on seagrass leaves in Belize decreased with distance from a reef. Grazing, however, remained high as far as 100 m away from the reef where some 80% of leaves were bitten by small parrotfish. Similarly, Ogden & Zieman (1977) discovered that while bite size on seagrass leaves decreased with increasing distance from a reef in the Virgin Islands, an overfished location (Ogden et al. 1973, Hay 1984a), the number of parrotfish bites did not decrease significantly with distance, but instead increased with distance from the reef. Although data exist for only these 2 locations in the Caribbean Sea, it seems that small parrotfish grazing on seagrasses may still represent an important energy pathway.

We believe that seagrasses have characteristics that have led investigators to underestimate the magnitude of grazing by smaller grazers such as juvenile parrotfish and sea urchins (Valentine & Heck 1999). Unlike wholly exposed marine macroalgae, which are often very heavily grazed, many seagrass species possess rhizome and short shoot meristems that are located within the sediment. This means that regenerative tissues are probably not accessible and easily damaged by most small grazers. This partial refuge from consumption may allow seagrasses to quickly overcome

grazer-induced damage to aboveground tissues (cf. Valentine et al. 1997, 2000). It is noteworthy, however, that when meristems are exposed, grazers can dramatically reduce seagrass density and biomass (Maciá & Lirman 1999, Rose et al. 1999).

In contrast to estimating grazing rates on macroalgae, accurate estimates of consumption by small grazers may be further hindered by the sequential leaf growth of many seagrasses. Put simply, while an outer leaf is being consumed another leaf is being produced in the interior of the leaf bundle (Tomlinson & Vargo 1966, see also Valentine & Heck 1999). When taken together, these characteristics illustrate some of the difficulties in accurately estimating seagrass consumption by smaller marine herbivores such as sea urchins (Valentine et al. 2000) and herbivorous fishes (this study) that do not usually consume whole shoots. They also suggest that estimates of energy flow from seagrasses to higher order consumers based solely on changes in seagrass density may be too low (Valentine & Heck 1999).

In this paper, we directly estimate the proportion of seagrass production consumed by parrotfishes in the Florida Keys National Marine Sanctuary (USA). Using tethered leaves, we show that grazing on seagrasses varies greatly both spatially and temporally, but that the proportion of living seagrass consumed at our study sites is much greater than currently thought. From our data it seems clear that the importance of seagrass grazing in food web dynamics has been greatly underestimated in subtropical settings like the Florida Keys.

MATERIALS AND METHODS

Description of the study sites. Our study sites were haphazardly located within Hawk Channel, which is located along the southeastern coast of the Florida Keys, USA, in an area included in the Florida Keys National Marine Sanctuary (Fig. 1). Experiments were begun in December 1995 and repeated in May, July, and November of 1996. These months were selected to evaluate the degree to which grazing on seagrasses varies seasonally in this subtropical setting.

Our first experiment was conducted at 2 sites in December 1995. One site was located within Hawk Channel and called the Mid-Channel site. The Mid-Channel site (25° 00.17' N, 80° 25.43' W) was characterized by a large, monospecific stand of turtlegrass *Thalassia testudinum* located in approximately 6 m of water. The second site was just inshore of a low-relief reef known as Pickles Reef (the Pickles Site). The Pickles Site was located approximately 100 m north of Pickles Reef (24° 59.28' N, 80° 25.02' W). This grassbed, located in ap-

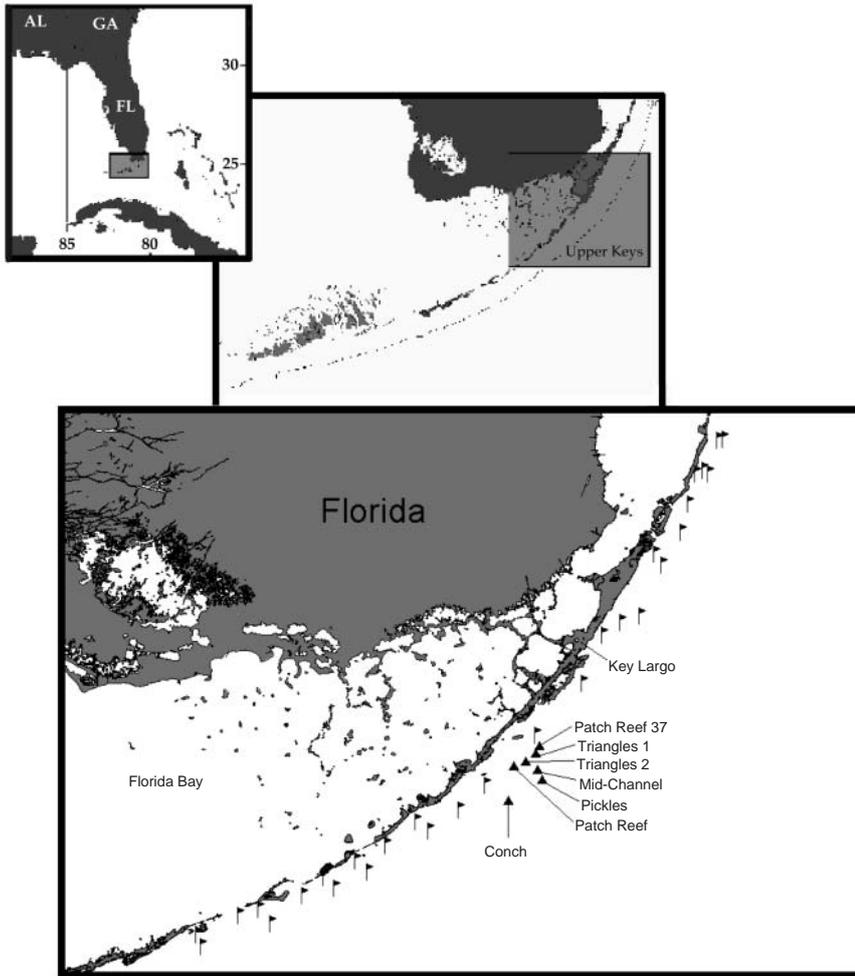


Fig. 1. Study site locations in the northern Florida Keys. Flags indicate transect station locations

proximately 3 m of water, was dominated by turtlegrass as well. Interspersed within this seagrass meadow were unvegetated sand patches of varying sizes.

During May, July, and November of 1996 we conducted experiments at 3 haphazardly selected sites. The sites included the original Mid-Channel, and Pickles sites, plus 1 new site located further inshore near the southern end of Key Largo (the Patch Reef 37 site). The Patch Reef 37 study site was near Channel Marker 37 ($25^{\circ} 02.24' N$, $80^{\circ} 25.25' W$) in approximately 4 m of water. Turtlegrass was the only seagrass at this site and it extended to the edge of a small, isolated patch reef. The addition of this third site provided the opportunity to examine how seagrass grazing varies along an offshore-onshore gradient.

Experiments were repeated again in August 1998 to replicate testing conducted in the summer 1996. The goals of this final experiment were to assess the degree to which seagrass grazing varies annually and to in-

crease the spatial scale of our previous experiments. This time 6 haphazardly selected sites were used. They included a new site located approximately 200 m west-northwest of Conch Reef ($24^{\circ} 57.45' N$, $80^{\circ} 28.00' W$). This reef has a more developed crest than does the Pickles Site and was located in a mixed stand of seagrasses consisting of both turtlegrass and manatee grass *Syringodium filiforme*. Two additional sites were located near patch reefs in Hawk Channel. One was the original Patch Reef 37 site, and the second site was near another isolated patch reef site (Patch Reef 39). Patch Reef 39 was located near channel marker 39 ($25^{\circ} 00.49' N$, $80^{\circ} 27.47' W$) which was also within a continuous turtlegrass habitat. Water depth was approximately 4 m at this site.

Two more sites were located in an area of Hawk Channel known as the Triangles. Both the Triangles 1 site ($25^{\circ} 01.60' N$, $80^{\circ} 25.61' W$) and the Triangles 2 site ($25^{\circ} 00.92' N$, $80^{\circ} 26.48' W$) were located in monospecific stands of turtlegrass. Both Triangles sites were near the original Mid-Channel site, which was used again in August 1998.

Estimates of seagrass grazing by fishes. We modified a previously used tethering approach to estimate grazing on seagrasses. Macrophyte tethering has been used to study how herbivores control macroalgal distribution and community structure on coral reefs (e.g. Hay 1981, 1984b, Lewis 1985, Macintyre et al. 1987) and to estimate herbivore consumption of mangrove leaves (Robertson 1986, Micheli 1993).

In our study, turtlegrass leaves were attached to 60 cm lengths of sisal rope with clothespins. We chose to tether turtlegrass leaves because *Thalassia testudinum* is the dominant seagrass species in the tropical and subtropical western Atlantic Ocean and covers much of the bottom in the northern Florida Keys (Zieman 1982, Fourqurean et al. 2002). Sisal rope was chosen because it is a natural fiber whose color (light tan) blended well with the sandy sediments at our study sites. Each tether consisted of 3 seagrass shoots attached to a single sisal rope. Each tethered shoot

consisted of all of the undamaged leaves (usually 3) from individual turtlegrass shoots. Leaves were considered to be undamaged if no signs of grazing (i.e. jagged edges indicative of urchin grazing or crescent shaped bite marks indicative of small parrotfish grazing) were found (cf. Hay 1984a). The shoots used in all of these experiments were collected from a boat channel located just north of Rodriguez Key (Fig. 1). Undamaged shoots were readily available in all seasons at this location.

Four replicate tethers (totaling 12 shoots at Site 1) were placed within a continuous seagrass habitat, at each study site, for 24 h. The tethers were secured to the bottom with wire stakes inserted at both ends of the sisal line. Tethers were placed approximately 0.5 m apart. Care was taken to ensure that the ends of the clothespins were pushed in the sediments such that the shoots were held upright, thus simulating natural shoot orientation. After 24 h, the tethers were collected and replaced with new ones. The process continued for 5 to 7 d, except in November 1996 when inclement weather reduced the experimental period to 3 d.

We estimated tethered leaf losses to grazers with the aid of a Scanman digital hand scanner (Logitech, Fremont, CA). Once scanned, leaf surface area was determined using Sigma-Scan image analysis software (SPSS, Chicago, IL). Leaf tissue lost to grazers during the 24 h period was determined by subtracting the initial measurement of leaf area (Fig. 2a) from leaf area remaining after 24 h (Fig. 2b). Leaves that appeared to be torn, rather than grazed, were excluded from statistical analyses. Such damage was infrequent in this study.

The net aboveground turtlegrass production (NAPP) was measured at each site using a modified hole punch technique (Kirkman & Reid 1979). All turtlegrass short shoots within 3 haphazardly placed 0.01 m² quadrats were marked by punching a hole, with a blunt point probe, through all leaves at the top of each short shoot sheath. After 6 d, all marked shoots within each quadrat were collected and returned to the laboratory. In the laboratory, the leaves were separated from the shoots at the top of each short shoot sheath. Once removed, the surface area of all leaves in each shoot was measured as described above. The area of new leaf growth (recorded in cm² d⁻¹) was defined as the distance between the initial marking scar and bottom of the leaf, plus any new unmarked leaves formed during the 6 d period. Growth was summed from all marked shoots and, then calculated both on a per meter square and a short-shoot specific basis to standardize our estimates with the work of others. Shoot-specific growth (cm² shoot⁻¹ d⁻¹) was calculated by dividing NAPP by the number of shoots within each quadrat. This value was compared to the amount of

area lost to herbivores to provide an estimate of the daily proportion of shoot-specific production consumed by fishes. Estimates of areal NAPP and short shoot specific growth were then converted to biomass (both as g m⁻² d⁻¹ and g shoot⁻¹ d⁻¹) by drying scanned leaf material to a constant weight at 60°C. We also recorded the number of parrotfish bites on all marked leaves.

In addition, aboveground seagrass biomass (dry mass, DM: g m⁻²) was estimated from the harvested shoots. Aboveground seagrass biomass for each site was estimated by averaging all the dried aboveground leaf material from the 3 quadrats.

Spatial extent of fish grazing: To determine the extent to which the study sites were representative of parrotfish grazing on seagrasses throughout the northern Florida Keys, in July 1996 turtlegrass shoots were collected at 29 stations along a 96 km transect through the center of Hawk Channel (see Table 1 for station locations). The transect started southeast of Elliot Key and followed Hawk Channel southwest to just offshore of Duck Key. Stations were located at approximately 4.8 km intervals along the transect. At each station, haphazardly chosen turtlegrass shoots were collected

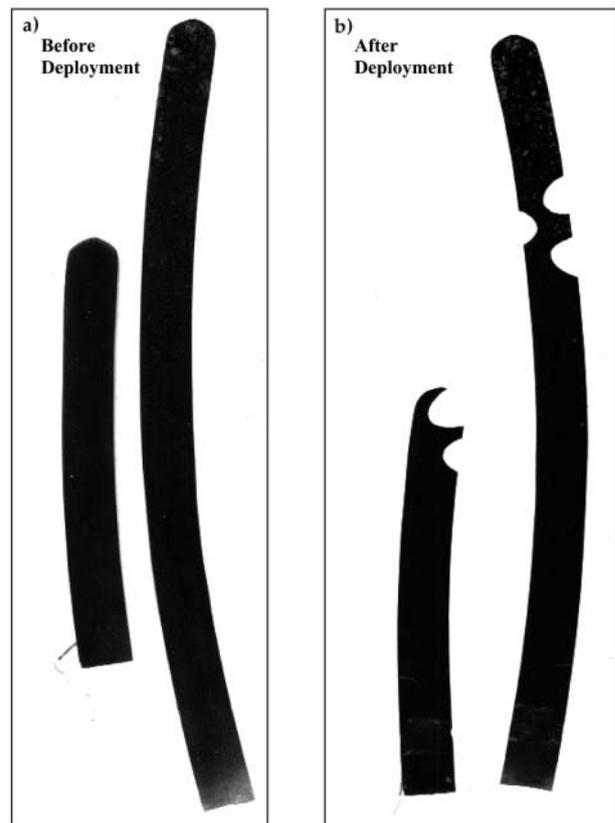


Fig. 2. Digital images of tethered leaves (a) before and (b) after being deployed in the field for 24 h

and returned to the lab for analysis. In the laboratory, all leaves were examined for evidence of parrotfish grazing based on the incidence of a clearly distinguishable crescent-shaped bite mark (cf. Hay 1984a).

Testing for seagrass tethering artifacts: As the use of tethering has increased in ecology, so has its criticism (Barbeau & Scheibling 1994, Zimmer-Faust et al. 1994, Peterson & Black 1994, Micheli 1996, Benedetti-Cecchi & Cinelli 1997, Curran & Able 1998). While critiques have focussed on the experimental artifacts associated with animal tethering, it is possible that the tethering of marine macrophytes also has, as yet, unrecognized artifacts (cf. Aronson & Heck 1995, McGuinness 1997). We hypothesized that the tethered leaves represented a novel prey that might differ either nutritionally or morphologically from leaves growing at the study sites. If true these differences could have led, depending on the nature of the artifact, to either over- or underestimates of seagrass grazing.

To obtain clear images, seagrass leaves were blotted dry, then scanned. Some herbivorous fishes (i.e. buck-

tooth parrotfish are reported to forage preferentially on seagrasses with elevated epiphyte coverage (Lobel & Ogden 1981, Montague et al. 1995). Therefore, either blotting or scanning may have resulted in the loss of attached epiphytes, possibly producing an underestimate of fish grazing. To assess the importance of this potential artifact, we placed pairs of scanned and unscanned shoots at Conch Reef in August 1998. Leaves were replaced at 24 h intervals for 4 consecutive days. A comparison of the number of bites on each of the scanned and unscanned leaves was used to assess the degree to which the scanning process affected grazing preferences.

The C:N ratio of seagrass leaves varies greatly throughout the Florida Keys (Fourqurean et al. 1992). Because leaf nutritional quality (expressed as the carbon:nitrogen or C:N ratio) has been suggested to influence fish grazing on seagrasses (cf. McGlathery 1995), we also compared the C:N ratios of turtlegrass leaves collected from each study site and leaves collected from Rodriguez Key in May 1996 and August 1998. The leaves used for the tethering experiments were always collected from the boat channel at Rodriguez Key, where we found little evidence of seagrass grazing. Thus, it was possible that potentially important nutritional differences (in terms of the C:N ratio) could exist between the leaves growing at Rodriguez Key and those at our study sites. If true, it was again possible that our estimates of seagrass grazing might be biased.

To test the hypothesis that the C:N ratios of leaves used for our tethers varied from the leaves growing at each of the study sites, we collected leaves from 10 shoots selected from the experimental sites and eleven shoots from those collected at Rodriguez Key. Epiphytes were removed, the shoots were dried to a constant weight at 60°C, and then they were ground into a powder using a Wiley Intermediate Grinding Mill™. The C:N ratios of these leaves were determined using an NA1500 N/C/S analyzer™ (Carlo Erba, Milan).

Leaves collected from the boat channel at Rodriguez Key appeared to be longer and wider, than the seagrass leaves at our study sites. We considered the possibility that these larger leaves might attract grazers, possibly leading to exaggerated estimates of grazing. Therefore the lengths and widths of tethered leaves collected from Rodriguez Key were compared to the lengths and widths of leaves harvested from the production quadrats at each study site. These comparisons were made during each season of this study.

To further consider the possibility that grazers were preferentially feeding on tethered leaves, we compared the number of bites on tethered leaves with the number of bites per leaf on shoots collected from the production quadrats in each season. We hypothesized

Table 1. Stations location for July 1996 transect survey of grazing in the Hawk Channel and percentage of grazed shoots

Station ID	Location	% of shoots suffering herbivory
N1	25° 25.8' N, 80° 25.3' W	60
N3	25° 07.8' N, 80° 21.2' W	40
N4	25° 15.6' N, 80° 19.5' W	40
N5	25° 13.1' N, 80° 17.9' W	0
N6	25° 13.6' N, 80° 16.2' W	30
N7-D	25° 19.1' N, 80° 15.0' W	60
N7-S	25° 19.0' N, 80° 14.3' W	60
N8-S	25° 21.0' N, 80° 12.6' W	90
N9-D	25° 23.5' N, 80° 12.0' W	60
N9-S	25° 26.2' N, 80° 11.3' W	0
N10-D	25° 26.5' N, 80° 10.7' W	50
N10-S	25° 26.2' N, 80° 10.2' W	10
N11-D	25° 29.2' N, 80° 09.0' W	80
N11-S	25° 29.1' N, 80° 09.4' W	20
S1	24° 58.8' N, 80° 29.7' W	60
S2	24° 56.7' N, 80° 32.1' W	30
S3-D	24° 55.7' N, 80° 35.7' W	10
S3-S	24° 54.9' N, 80° 34.6' W	40
S4-D	24° 53.6' N, 80° 38.4' W	10
S5-D	24° 52.2' N, 80° 41.0' W	10
S5-S	24° 51.3' N, 80° 40.0' W	10
S6-D	24° 50.8' N, 80° 43.8' W	80
S6-S	24° 49.8' N, 80° 42.9' W	0
S7-S	24° 49.2' N, 80° 45.7' W	60
S8-D	24° 48.0' N, 80° 49.5' W	0
S8-S	24° 46.7' N, 80° 48.5' W	30
S9-S	24° 47.3' N, 80° 51.3' W	10
S10-D	24° 45.7' N, 80° 54.9' W	0
S10-S	24° 44.6' N, 80° 54.5' W	0
Mean		32.76 ± 28.27

that if the tethered leaves were grazed at some anomalously high rate than there would be significantly more bites on our tethered leaves than on the leaves harvested from our production quadrats.

Finally, to ensure that losses on tethered leaves were due to parrotfish grazing and not to unidentified physical processes, 2 sisal ropes containing tethered shoots were placed in a wire mesh cage at the Triangles 2 site in August 1998. The shoots were left in the cage for 7 d and on each day the leaves were inspected to determine if any damage of any kind had occurred during the preceding 24 h.

Statistical analysis. Seasonal and spatial scales of fish grazing on turtlegrass: Prior to testing the hypotheses that grazing varied both seasonally and spatially in the northern Florida Keys, leaf losses were averaged (on a per shoot basis) for the shoots on each rope. Thus, each replicate was the average amount of leaf loss per shoot on each rope. Losses were then converted to the proportion of daily shoot production consumed at each site. Since many of the proportions were greater than 1 (due to the extraordinarily high grazing rates recorded at some sites), all were divided by 100, then arcsine square root transformed (Sokal & Rohlf 1981) before statistical analysis.

To test the hypothesis that grazing varied seasonally in the northern Florida Keys, we pooled the estimated proportions of leaf tissue grazed at all sites in each month. In this comparison, time was considered to be the treatment. Results from Levene's test indicated that these transformed data violated the homogeneity of variance assumption for ANOVA. Therefore, a nonparametric Kruskal-Wallis 1-way ANOVA was used to compare the ranked transformed daily proportions of production removed each month. When significant differences were detected, the nonparametric Games-Howell multiple comparison test was used for a posteriori comparisons among months. The Games-Howell test is a conservative pairwise comparison that is used when the variance is unequal (Games & Howell 1976, Sokal & Rohlf 1981).

To determine if grazing varied spatially, a separate Kruskal-Wallis 1-way ANOVA on ranks was also performed for each month, except December, comparing the mean proportions of daily production consumed at each site. In this case, each day was considered to be a replicate and each replicate represented the average leaf loss (per shoot) on each tether. Nonparametric tests were again used due to violations of the homogeneity of variance assumption. When significant differences were found, the Games-Howell multiple comparison test was again used to make post-hoc comparisons. Because there were only 2 sites (Pickles and Mid-Channel) in December, the nonparametric Mann-Whitney test was used.

Spatial differences in NAPP, short shoot density and aboveground biomass, collected from the marked quadrats, were compared using a 1-way ANOVA with sites as treatments, following the examination of the data for the validity of the model's assumptions. The equality of variance assumption of ANOVA was tested using Levene's test for homogeneity. Normality was tested using the Shapiro-Wilk test. When significant treatment effects were detected, post-hoc comparisons were made using a least significant difference's procedure.

p-values less than 0.05 were considered to be significant. p-values between 0.05 and 0.10 were considered to be marginally significant.

Analysis of tethering artifacts: We used a series of four, 2 sample *t*-tests to determine the degree to which the scanning of the seagrass leaves might have altered grazing estimates. Again each rope containing multiple shoots represented an individual replicate. Similarly, we used 2 sample *t*-tests, conducted for each season, to determine whether parrotfishes may have attacked tethered leaves at higher rates than the leaves collected in our production quadrats occurring at our sites. We did this by comparing the average number of leaf bites per tethered shoot to the average number of bites per leaf collected from the production samples. To further assess the degree to which grazing on tethered seagrass leaves reflected grazing on leaves growing at the study sites, we also calculated the correlation between the total number of leaf bites on each rope with the number of bites on leaves collected from production quadrats.

Finally, to assess the degree to which the nutritional artifacts associated with the use of leaves collected from Rodriguez Key boat channel, we used ANOVA to determine if the C:N ratios of the tethered leaves varied significantly from the leaves growing at our study sites. When significant differences were detected we used a least significant difference (LSD) test to compare differences in either the leaf C:N ratios or leaf morphology among sites. We used a series of 2 sample *t*-tests, conducted for each month and site of the survey, to determine if the morphology of the leaves used in our tethers was different from the morphology of leaves growing at our study sites. The results were again considered to be significant when $p < 0.05$ and marginally significant when p was between 0.05 and 0.10.

RESULTS

Seagrass production and biomass

Although seagrass growth, shoot density and biomass varied greatly among seasons, with only a few exceptions these parameters did not vary significantly

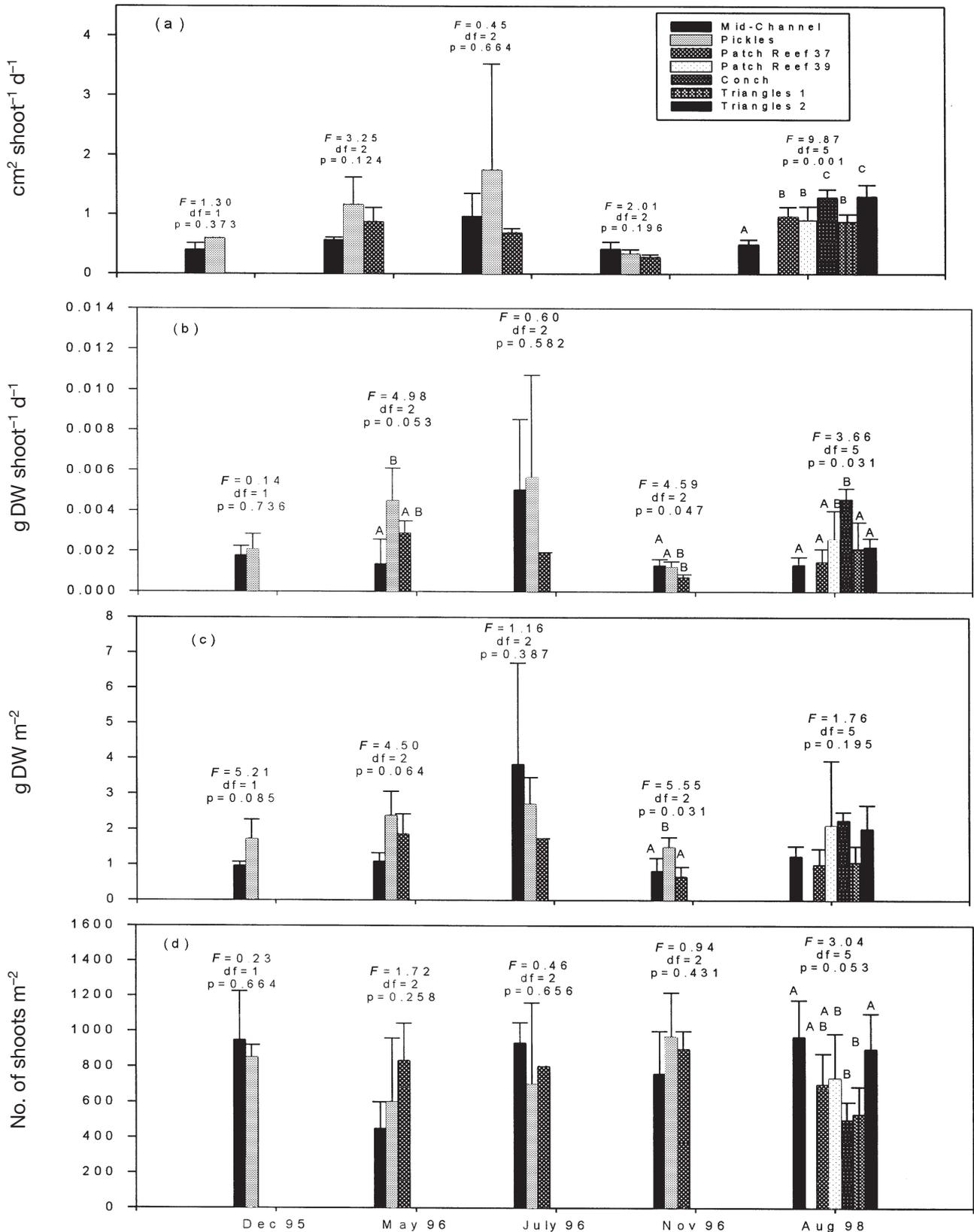


Fig. 3. Net aboveground turtlegrass short shoot production measured by (a) leaf area and (b) biomass produced, (c) net aboveground primary production and (d) short shoot density at the study sites by month (mean \pm 1 SD). Uppercase lettering indicates sites that were statistically significantly different within the respective month. DW = dry weight

among sites. For example, shoot-specific leaf growth (in terms of leaf area) ranged from a low of $0.28 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ in November 1996 to a high of $1.74 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ in July 1996 (Fig. 3a). However, only one significant difference in leaf growth among sites was detected, when in August 1998 we found that leaves were growing faster at the Triangles 2 and Conch sites, and slower at the Mid-Channel site, than at any of the other sites. Shoot-specific production (in terms of biomass) mirrored that of shoot-specific leaf growth (Fig. 3b), with biomass production lowest in November 1996 ($0.66 \text{ gDW m}^{-2} \text{ d}^{-1}$) and highest in July 1996 ($3.84 \text{ gDW m}^{-2} \text{ d}^{-1}$) (Fig. 3c). Significant differences among sites were noted only twice, in November 1996 and August 1998, and a marginally significant difference was noted in May 1996. Clear patterns of habitat-specific growth, however, were lacking (e.g. higher production at the shallower sites and lower at the deeper sites) as shoot-specific production was highest at the deepest site (Mid-Channel site) in November 1996 and the shallowest site (Conch Reef) in August 1998.

In 3 of the first 4 visits, NAPP was higher at the Pickles site than at the other sites, but only once was it significantly higher (in November 1996) (Fig. 3c). NAPP differed significantly among sites again in August 1998, with higher values at Conch Reef than any of the other study sites. Shoot density was lowest in May 1996 (450 shoot m^{-2}) and highest in November 1996 (966 shoot m^{-2}) (Fig. 3d). Again only one marginally significant difference was noted among sites (in August 1998). Aboveground biomass ranged from a

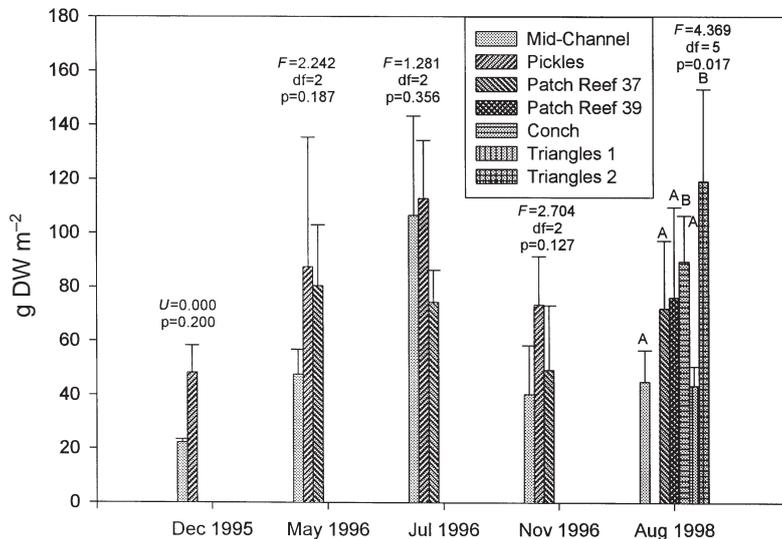


Fig. 4. Aboveground turtlegrass biomass at the study sites by month (mean \pm 1 SD). Uppercase lettering indicates sites that are statistically significantly different within the respective month. The Mann-Whitney U -test used in December 1995 because of heterogeneity of error variances. DW = dry weight

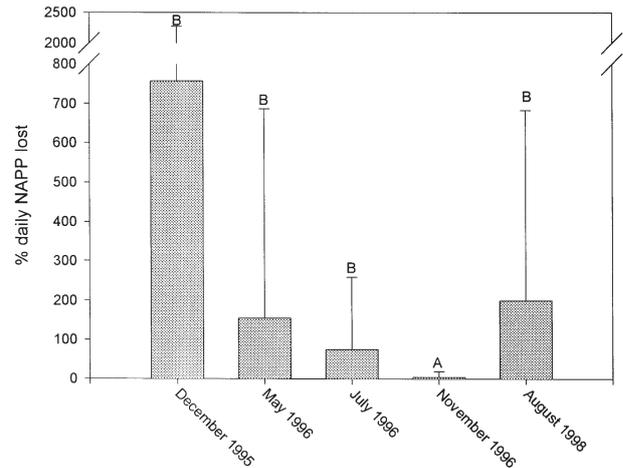


Fig. 5. Average percentage of daily NAPP lost at the study sites by month (mean \pm 1 SD). Uppercase lettering indicates statistically significant differences between months

low of $\sim 22 \text{ gDW m}^{-2}$ in December 1995 to a high of $\sim 119 \text{ gDW m}^{-2}$ in August 1998 (Fig. 4). Significant differences in aboveground biomass among sites were detected in only 1 mo (August 1998).

Estimates of parrotfish grazing

While the proportion of seagrass production consumed by parrotfish also varied with season, only 1 significant difference among months was detected (Fig. 5). A pairwise comparison found that the estimated loss of seagrass production to parrotfish grazing was significantly higher in December 1995 ($\sim 750\%$ of daily NAPP on average) than in November 1996, when less than 5% of the average daily shoot production was grazed by parrotfish ($p \leq 0.03$). No other significant seasonal differences in grazing intensity were detected.

In contrast, grazing varied greatly among sites. In December, consumption at the Mid-Channel site was significantly higher than recorded at the Pickles site where parrotfishes did not graze on the tethered leaves (Mann-Whitney $U = 35$, $p < 0.001$; Fig. 6). At the Mid-Channel site, over 20%, on average, of the tethered leaf surface area was removed daily. Because NAPP was low at this site in December (Fig. 4), our estimate of the proportion of daily shoot production consumed by small parrotfish was extraordinarily high, some 15 times more than was produced.

Grazing varied significantly among the 3 sites in May ($\chi^2 = 36.95$, $df = 2$, $p < 0.001$, Fig. 6) and July 1996 ($\chi^2 = 7.96$, $df = 2$, $p < 0.019$). Losses to grazers were significantly higher at the Mid-Channel site (exceeding 450% of daily short shoot NAPP) than at the Pickles site (~1.8% of the daily NAPP per shoot). Grazing at Patch Reef 37 was also low in May (~2.5% of the daily NAPP per shoot), but was higher at Patch Reef 37 than at the other sites in July (Fig. 6), with shoots losing ~5% of the surface area offered per day (representing over 170% of the daily production per shoot). Grazing

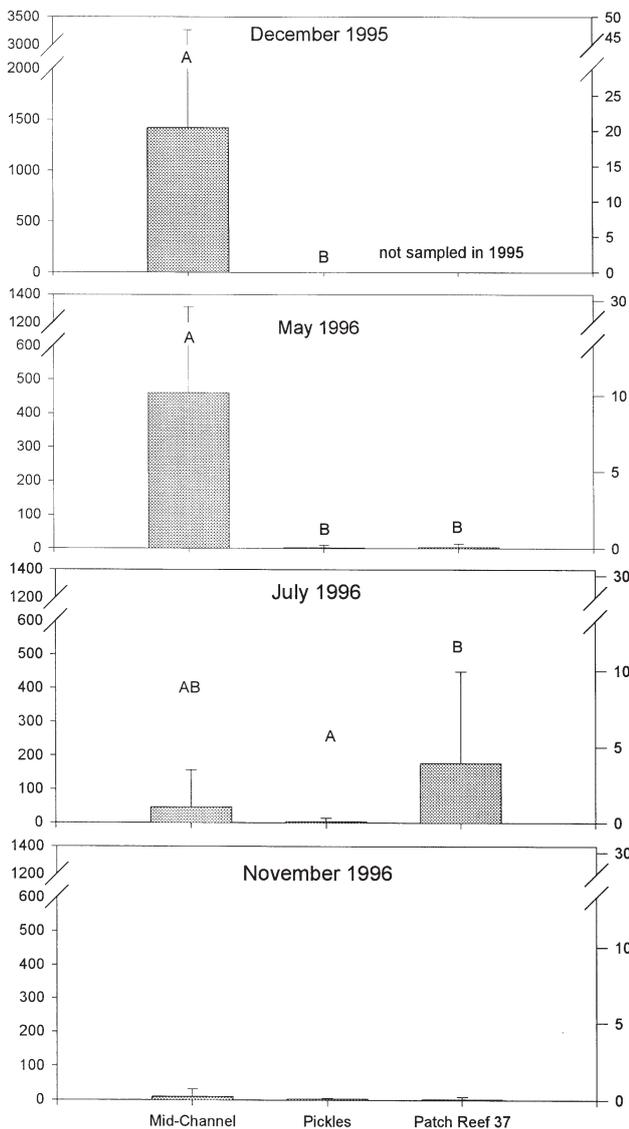


Fig. 6. Percentage of daily production consumed by fish (left y-axis) and percentage of biomass offered removed (right y-axis) at 3 locations in 1995 and 1996 (mean \pm 1 SD). Uppercase lettering indicates sites that were statistically significantly different within the respective month at $p < 0.05$

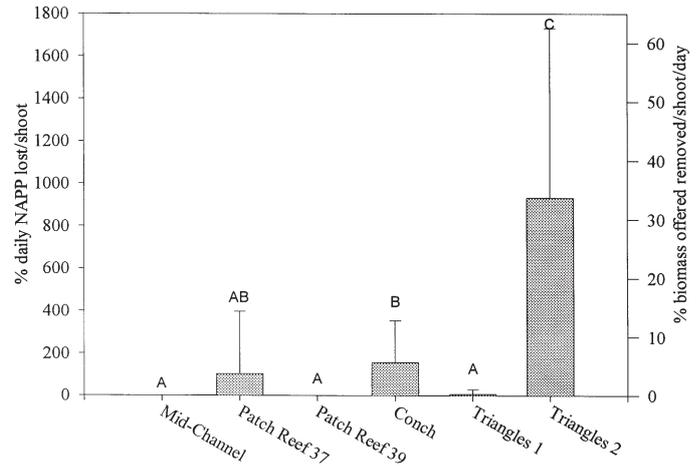


Fig. 7. Percentage of NAPP consumed by fish and the percentage of offered/removed biomass shoot⁻¹ d⁻¹ at 6 locations in August 1998 (mean \pm 1 SD). Uppercase lettering indicates sites that were statistically significantly different at $p < 0.05$

at the Pickles site (~3% daily production per shoot) was significantly lower than at the Patch Reef 37 site in July. In November 1996, there were no significant differences among sites ($\chi^2 = 0.74$, $df = 2$, $p > 0.10$) as grazing was uniformly low at all sites (Fig. 6).

In August 1998, neither the leaves placed at the Mid-Channel or the Patch Reef 39 sites were grazed at all (Fig. 7). Grazing on the leaves placed at the Triangles 2 site was significantly greater than at any other sites ($p \leq 0.003$), with losses estimated at over 900% of daily NAPP per shoot.

When averaged across all sites and months (excluding our estimates from the Triangles 2 site which were more than 3 standard deviations from the mean), we estimate that the small parrotfishes can consume some 85% of seagrass production within the northern reaches of Hawk Channel.

Highly significant correlations between short shoot-specific growth and NAPP ($r = 0.87$, $n = 17$, $p < 0.001$), and between the number of bites on tethered shoots and the average number of bites on shoots harvested from the production quadrats ($r = 0.631$, $n = 15$, $p < 0.012$) indicate that our estimates of grazing on tethered leaves (on a per shoot basis) were comparable to grazer-induced tissue losses on leaves harvested from our study sites. A small, nonsignificant negative correlation ($r = -0.15$, $n = 17$, $p > 0.57$) between the proportion of leaf tissue lost to grazers on our tethered shoots and aboveground biomass suggests that, while the proportion of seagrass production consumed by small parrotfishes was high, grazers did not seem to have a significant negative impact on aboveground biomass.

Survey of spatial extent of herbivory

Evidence of parrotfish grazing on seagrasses was found throughout Hawk Channel, and leaves at 23 of the 29 stations had been bitten by parrotfish (Table 1). On average, 3 of 10 shoots collected at each station had been grazed. At 1 site (N-8-5), leaves on 9 of 10 shoots had been grazed. Moving from northeast to the southwest, there appeared to be a reduced incidence of fish herbivory that seemed to coincide with increasing distance from reef habitat.

Test of tethering artifacts

With the exception of the last day of this comparison, there were fewer parrotfish bites on tethered leaves that had been scanned than on those that had not (Table 2). On only 1 day, however, did we find a marginally significant difference between the number of bites on scanned leaves and the number of bites on unscanned leaves. On this day, there were significantly more bites on the unscanned leaves (3.5 bites shoot⁻¹) than on scanned leaves (1.4 bites shoot⁻¹). This suggests that if the scanning process impacted our estimates of seagrass grazing it did not lead to a gross overestimate of grazing on seagrass leaves.

Leaf C:N ratios varied significantly both among sites and tethers in May 1996 ($F = 7.45$, $df = 3$, $p < 0.001$). Post-hoc analysis showed that leaves growing at Patch Reef 37 had significantly lower C:N ratios than those growing at the other 2 sites or of the tethered leaves (LSD, $p < 0.05$, Fig. 8a). Even so, grazing at Patch Reef 37 was low in May and the number of bites on the tethered leaves was lower than the number of bites on leaves growing at the site (Table 3). C:N ratios of the tethered leaves were also significantly lower than those growing at the Pickles site but significantly higher than those at Patch Reef 37 ($p < 0.03$). Again, losses to grazers on our tethers

Table 2. Statistical comparisons of the number of parrotfish bites on scanned and unscanned leaves placed at Conch Reef in August 1998

Date	Treatment	n	Mean no. of bites per shoot	SD	<i>t</i>	df	<i>p</i> (2-tailed)
12–13	Not scanned	12	5.67	4.03	1.141	22	0.27
	Scanned	12	3.50	5.20			
13–14	Not scanned	12	3.50	3.21	2.038	22	0.059
	Scanned	12	1.42	1.51			
14–17	Not scanned	12	1.58	1.56	1.085	22	0.29
	Scanned	12	0.92	1.44			
17–18	Not scanned	12	0.42	0.90	-0.392	22	0.7
	Scanned	12	0.58	1.16			

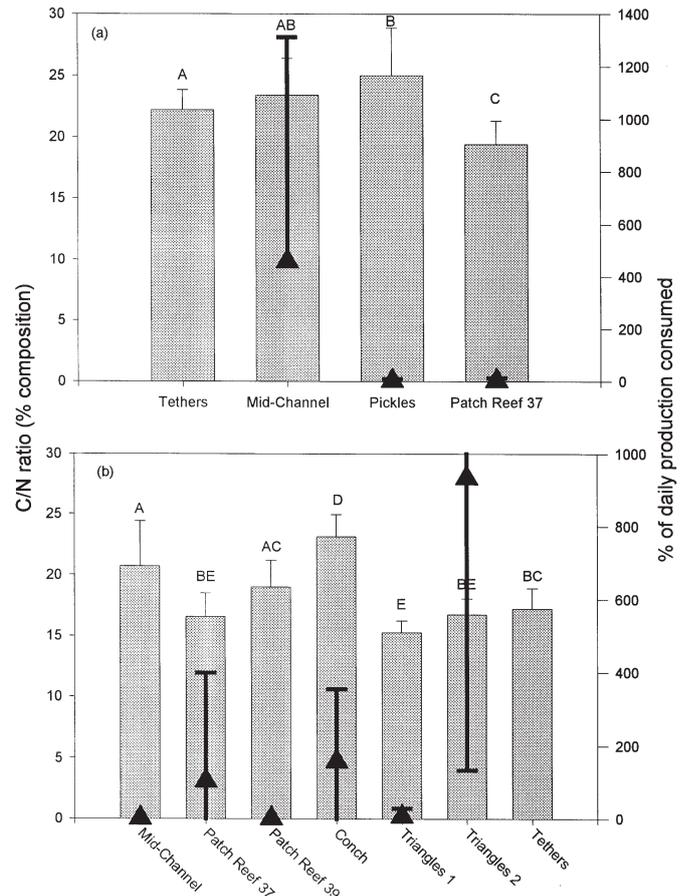


Fig. 8. C:N ratios of leaves collected (a) at the 3 sites and on the tethers used in May 1996 versus the percentage of daily production consumed at each site (indicated by \blacktriangle), and (b) at the 6 sites and the tethers used in August 1998 comparing ratios of leaves with epiphytes removed versus leaves with epiphytes and ratios versus the percentage of daily production consumed at each site (indicated by \blacktriangle) (mean \pm 1 SD). Uppercase lettering indicates sites with significantly different C:N ratios at $p < 0.05$

were negligible at Pickles Reef. A highly significant difference was also found between the C:N ratios of leaves growing at the sites and those of tethered leaves in August 1998 ($F = 17.54$, $df = 6$, $p < 0.001$; Fig. 8b). Post-hoc analysis indicated that tethered leaves had a significantly lower C:N ratio than leaves collected from the Triangles 2, Patch Reef 39 and Conch sites. Grazing estimates were high at both the Triangles 2 and Conch reef sites. Nonetheless, there were still fewer parrotfish bites on the tethered leaves than on the leaves growing at these sites, suggesting that differ-

Table 3. T-test for the difference in number of bites per leaf on the tethers and the shoots used in production measurements. *Equality of error variance not assumed

Month	Site	Production or tether	n	Mean bites blade ⁻¹	SD	t	df	p (2-tailed)
May 96	Mid-Channel	Production	65	0.23	0.55	3.5*	220.3	0.001
		Tether	161	0.64	1.20		8	
	Pickles	Production	99	0.0707	0.29	1.67*	134.6	0.098
		Tether	176	0.0170	0.17		8	
	Patch Reef 37	Production	76	0.0789	0.36	1.23*	107.87	0.223
		Tether	168	0.0238	0.24		7	
Jul 96	Mid-Channel	Production	69	0.30	0.88	1.49*	99.38	0.137
		Tether	155	0.13	0.62			
	Pickles	Production	79	0.37	1.10	2.35*	88.78	0.021
		Tether	150	0.0667	0.40			
	Patch Reef 37	Production	48	0.27	0.61	0.76	197	0.451
		Tether	151	0.20	0.57			
Nov 96	Mid-Channel	Production	73	0.25	0.55	3.13*	90.49	0.002
		Tether	60	0.0333	0.18			
	Pickles	Production	71	0.79	1.99	3.26*	70.86	0.002
		Tether	54	0.0185	0.14			
	Patch Reef 37	Production	56	0.32	1.16	1.80*	58.18	0.077
		Tether	53	0.0377	0.19			
Aug 98	Mid-Channel	Production	56	0.0983	0.29	2.32*	55	0.024
		Tether	130	0.00	0.00			
	Patch Reef 37	Production	42	1.14	2.14	1.1	165	0.273
		Tether	125	0.66	2.54			
	Patch Reef 39	Production	54	0.26	0.68	2.81*	53	0.007
		Tether	127	0.00	0.00			
	Conch	Production	31	7.35	7.99	4.53*	30.6	0.000
		Tether	125	0.82	1.60			
	Triangles 1	Production	39	0.72	1.67	2.56*	38.59	0.014
		Tether	134	0.0299	0.27			
Triangles 2	Production	68	4.29	7.99	1.41*	79.62	0.162	
	Tether	139	2.86	3.47				

ences in C:N ratios did not lead to exaggerated grazing rates.

Leaves collected for tethering tended to be longer and wider than leaves growing at the study sites (Figs. 9, 10 & 11). Again, however, in only 1 month and at only 1 site were there significantly more bites on tethered leaves than on leaves growing at a site (Mid-Channel site in May 1996: 0.23 bites per leaf from production quadrats versus 0.64 bites per tethered leaf (Table 3). At all other sites, and in all months, leaves harvested from the production quadrats had more bites than recorded from the tethered leaves, with half being significantly higher ($p < 0.05$, Table 3). This indicates that morphological differences between tethered leaves and those growing at the study sites did not lead to a large overestimate of the proportion of NAPP production consumed by grazers.

Finally, tethered leaves placed inside cages remained undamaged during the 7 d of deployment, whereas tethers outside the cage suffered substantial amounts of herbivory. This, in conjunction with the easily distinguishable crescent-shaped bite marks, demonstrated that the removal of leaf material from the tethers was the direct result of grazers.

DISCUSSION

We found that parrotfish grazing on turtlegrass was significant in the northern portions of the Florida Keys National Marine Sanctuary. Although grazing varied spatially, our estimates of consumption often exceeded local daily turtlegrass production. When averaged across all sites and seasons, we estimate that small herbivorous fishes can consume much of the production of turtlegrass in the northern reaches of Hawk Channel. These estimates are among the highest reported in the literature, and they suggest that the current paradigm regarding the minimal importance of seagrass herbivory in nearshore food webs is inaccurate.

If our estimates of grazing are accurate, why does seagrass persist in areas such the Mid-Channel site, where grazing is intense? Marine herbivores

have never been observed to graze a single habitat or landscape uniformly, either temporally or spatially (Ogden et al. 1973, Ogden & Zieman 1977, Bjorndal 1980, Lobel & Ogden 1981, Handley 1984, Hay 1984a, Carpenter 1986, Polunin 1996, Overholtzer & Motta 1999), and this was certainly the case in our study. While grazing was consistently high (i.e. >50% of NAPP) at the Mid-Channel site in December, July, and May 1996, little grazing was detected at this site in August 1998. Intense grazing at Patch Reef 37 was limited to July 1996 and August 1998. Grazing also varied among similar, nearby, habitats. For example, tethers placed in a turtlegrass meadow on one side of the Triangle Reef (Triangles 2) were heavily grazed but there was little evidence of grazing in a similar meadow on the other side of the reef (Triangles 1). Little grazing was recorded in a turtlegrass meadow on the north side of Pickles Reef (a back reef environment) at any time in

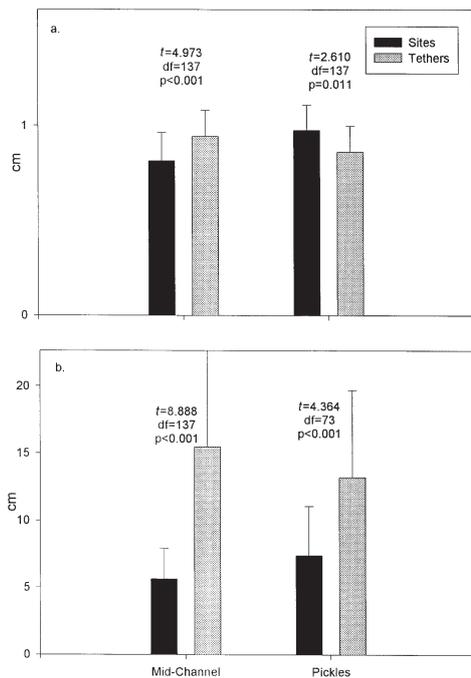


Fig. 9. Average (a) width and (b) length of leaves used on tethers versus leaves at experimental sites for December 1995 (mean \pm 1 SD)

1995 or 1996, yet grazing was heavy in a similar habitat on the north side of Conch Reef in 1998. On a broader geographic scale, leaves collected at almost 90% of the stations, along the ~96 km of Hawk Channel surveyed had been grazed by small fish. Grazing was more common at the more northerly stations than at the more southerly stations that corresponds with changes in the amount of reef structure in the upper Florida Keys.

The lack of a significant negative correlation between the proportion of NAPP consumed by grazers and aboveground biomass, coupled with the observed variability in grazing suggests either that periods of intense grazing are followed by periods of low grazing and seagrass biomass accrual or that seagrass production is stimulated by grazing and that this increased production replaces biomass lost to parrotfish, as we have shown previously for sea urchins (Valentine et al. 1997, 2000).

Small differences in the C:N ratio of seagrass leaves over short distances have been correlated with changes in herbivore feeding patterns (Bjorndal 1980, McGlathery 1995). While the mechanisms by which chemical defenses affect plant feeding preferences in marine environments have been frequently reported

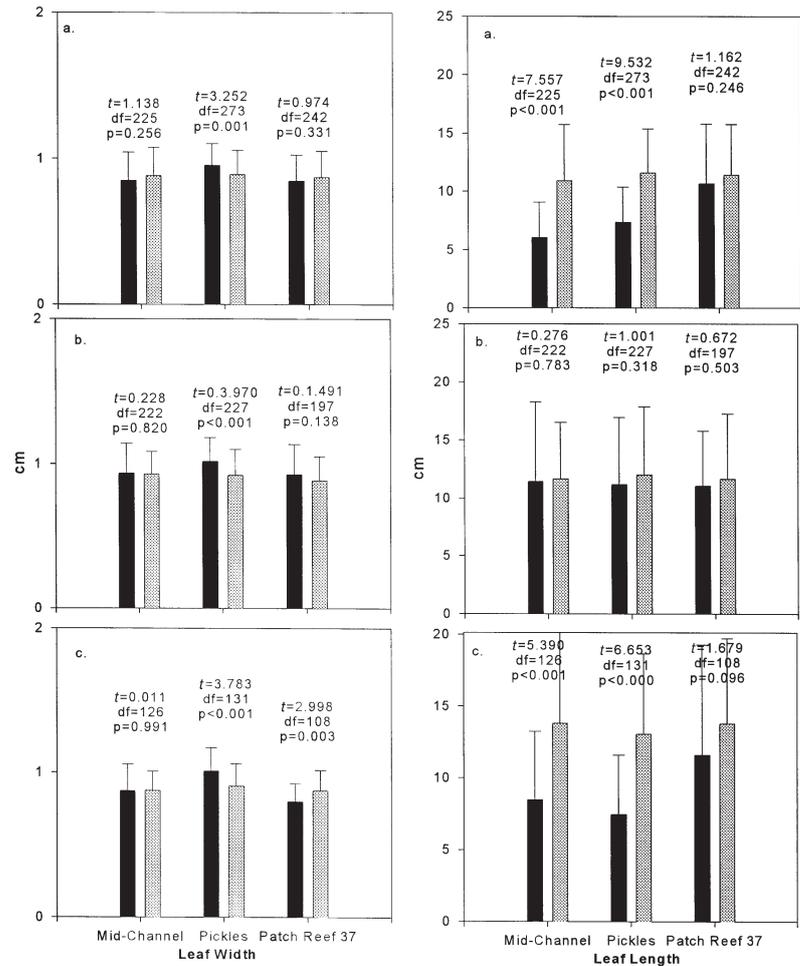


Fig. 10. Average width and length of leaves used on tethers versus leaves at experimental sites for (a) May 1996, (b) July 1996 and (c) November 1996 (mean \pm 1 SD)

(summarized in Hay & Steinberg 1992), we do not know how marine herbivores might preferentially select nitrogen-rich foods or avoid plants low in nitrogen. Certainly, such discriminating herbivores would need the ability to detect differences in plant nutritional quality so that they could preferentially feed on more nutritious plants (cf. Westoby 1974, 1978). To date, we know of no studies that have documented this capability in the marine realm. Indeed, it would be surprising if herbivores selected food based solely on nutritional value, given the lack of specialized feeding by most marine herbivores (Hay 1991, Hay & Steinberg 1992, Overholtzer & Motta 1999).

Nonetheless, we considered the possibility that differences between the C:N ratios of the leaves used in our tethers and the leaves growing at our study sites may have led to an overestimate of grazing on seagrasses. We found no evidence that the differences between the C:N ratios of turtlegrass leaves used for

our tethers and those growing at our study sites were related to the observed variability in grazing intensity. If C:N ratios had a significant effect on herbivore grazing patterns, sites with the lowest C:N ratios should have experienced the most herbivory because of their higher nitrogen content. That was not the case.

The possible alteration of epiphyte biomass did not seem to alter fish grazing preferences either, as we found no difference in the number of bites on scanned and unscanned leaves in 3 of 4 d. This, coupled with the fact that the average number of bites on tethered leaves was lower than observed on leaves harvested from our production quadrats, suggests that our estimates of grazing on seagrasses are not grossly exaggerated.

But can we accurately estimate the proportion of seagrass production consumed by grazers using tethered shoots? We think the answer is yes. A highly significant correlation between short shoot-specific productivity and NAPP suggests that we can extrapolate individual shoot production to areal estimates of NAPP. Additionally, we found a highly significant positive correlation between the number of bites on tethered leaves and

leaves harvested from our production quadrats (with the exception of 1 month at 1 site) further suggesting that our estimates of grazing were closely related to actual grazing intensity. We therefore believe that the proportional estimates of seagrass consumption on a per shoot basis can be extrapolated to estimate proportional losses of seagrass production to grazers on an areal basis.

Even so, we believe that relying on the use of proportional losses of seagrass production or changes in seagrass density to test the importance of grazing on seagrasses is an oversimplification of what appears to be a dynamic relationship between the growth patterns of these plants, the foraging patterns of small herbivorous fishes, and possibly the activities of their predators. From our study, it seems clear that the proportion of NAPP consumed by small herbivorous fishes varies with seasonal patterns of seagrass productivity. The proportional losses of seagrass production were greatest in winter when NAPP was lowest and lower in summer when NAPP was much higher. We propose that a better indicator of the importance of seagrass grazing to local food webs should be based on estimates of the absolute amount of seagrass production being consumed over a wide area.

Clearly the overharvesting of large seagrass herbivores which are strong interactors (sensu Paine 1992) has reduced the frequency with which herbivores control seagrass density. However, weak interactors that exert little control over community structure can still represent significant pathways for energy flow among trophic compartments (cf. Hall et al. 1990, Raffaelli & Hall 1996, Polis & Strong 1996). We believe that this is the case in modern day seagrass-dominated ecosystems. Even using the currently held paradigm (i.e. <30% of annual aboveground seagrass production is consumed), extrapolation to the area covered by seagrasses in the Florida Keys National Marine Sanctuary suggests that an extraordinary amount of energy is reaching higher order consumers through the grazing pathway.

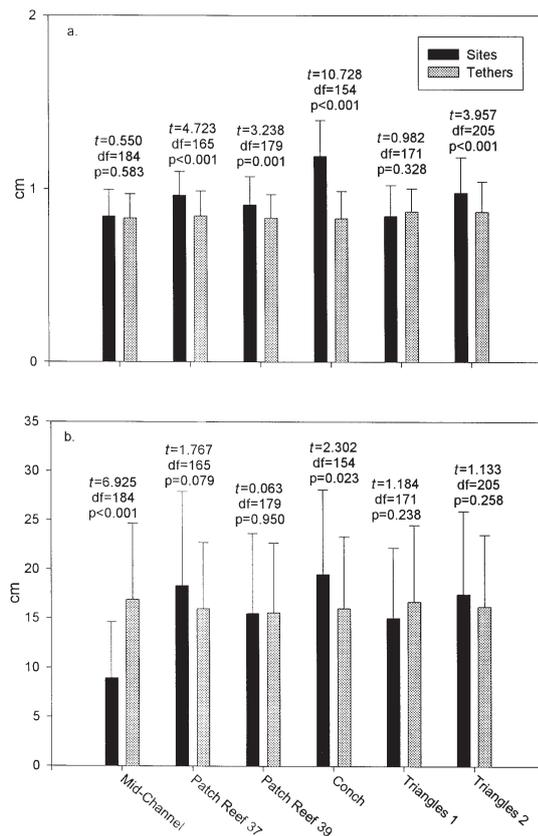


Fig. 11. Average (a) width and (b) length of leaves used on tethers versus leaves at experimental sites in August 1998 (mean \pm 1 SD)

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LITERATURE CITED

- Aronson RB, Heck KL Jr (1995) Tethering experiments and hypothesis testing in ecology. *Mar Ecol Prog Ser* 121: 307–309
- Barbeau MA, Scheibling RE (1994) Procedural effects and the analysis of prey tethering experiments: predation of juvenile scallops by crabs and seastars. *Mar Ecol Prog Ser* 111:305–310
- Benedetti-Cecchi L, Cinelli F (1997) Confounding in field experiments: direct and indirect effects of artifacts due to the manipulation of limpets and macroalgae. *J Exp Mar Biol Ecol* 209:171–184
- Bjorndal KA (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar Biol* 56:147–154
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56:345–363
- Cebrián J, Duarte CM, Marbà N, Enriquez S, Gallegos M, Olesen B (1996) Herbivory on *Posidonia oceanica*: magnitude and variability in the Spanish Mediterranean. *Mar Ecol Prog Ser* 130:147–155
- Curran MC, Able KW (1998) The value of tethering fishes (winter flounder and tautog) as a tool for assessing predation rates. *Mar Ecol Prog Ser* 163:45–51
- Dubin RE, Baker JD (1982) Two types of cover-seeking behavior at sunset by the princess parrotfish, *Scarus taeniopterus*, at Barbados, West Indies. *Bull Mar Sci* 32: 572–583
- Fenchel T (1970) Studies on the decomposition of organic detritus derived from the turtlegrass *Thalassia testudinum*. *Limnol Oceanogr* 14–20
- Fenchel T (1977) Aspects of the decomposition of seagrasses. In: McRoy CP, Helfferich C (eds) *Seagrass ecosystems: a scientific perspective*. Marcel Dekker, New York, p 123–145
- Fourqurean JW, Zieman JC, Powell GVN (1992) Phosphorus limitation of primary production in Florida Bay: evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol Oceanogr* 37:162–171
- Fourqurean JW, Durako MD, Hall MO, Hefty LN (2002) Seagrass distribution in south Florida: a multi-agency coordinated monitoring program In: Porter JW, Porter KG (eds) *The Everglades, Florida Bay, and the coral reefs of the Florida Keys*. CRC Press LLC, Boca Raton, p 497–522
- Games PA, Howell JF (1976) Pairwise multiple comparison procedures with unequal N's and/or variances: a Monte Carlo study. *J Educ Stat* 1:113–125
- Greenway M (1995) Trophic relationships of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lyttechinus variegatus* (Lamarck). *Bull Mar Sci* 56:719–736
- Hall SJ, Raffaelli D, Turrell WR (1990) Predator-caging experiments in marine systems: a reexamination of their value. *Am Nat* 136:657–672
- Handley F (1984) Time-budgeting and foraging strategy of the stoplight parrotfish *Sparisoma viride* Bonnatere, in Jamaica. *J Exp Mar Biol Ecol* 83:159–177
- Havelange S, Lepoint G, Dauby P, Bouguegneau JM (1997) Feeding of the sparid fish *Sarpa salpa* in a seagrass ecosystem: diet carbon flux. *PSZN I: Mar Ecol* 18: 289–297
- Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat Bot* 11:97–109
- Hay ME (1984a) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous patterns typical? *Ecology* 65:446–454
- Hay ME (1984b) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64:396–407
- Hay ME (1991) Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, p 96–119
- Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal GA, Berenbaum MR (eds) *Herbivores: their interactions with secondary plant metabolites*. Academic Press, San Diego, p 371–413
- Jackson J (1997) Reefs since Columbus. *Proc 8th Int Coral Reef Sym*, Miami, p 97–106
- Kikuchi T (1980) Faunal relationships in temperate seagrass beds. In: Phillips RC, McRoy CP (eds) *Handbook of seagrass biology: an ecosystem perspective*. Garland STPM Press, New York, p 153–172
- Kikuchi T, Peres JM (1977) Consumer ecology of seagrass beds. In: McRoy CP, Helfferich C (eds) *Seagrass ecosystems: a scientific perspective*. Marcel Dekker, New York, p 147–194
- Kirkman H, Reid DD (1979) A study of the role of the seagrass *Posidonia australis* in the carbon budget of an estuary. *Aquat Bot* 7:173–183
- Klumpp DW, Nichols PD (1983a) Nutrition of the southern seagrass *Hyporhamphus melanochir*: gut passage rate and daily consumption of two food types and assimilation of seagrass components. *Mar Ecol Prog Ser* 12:207–216
- Klumpp DW, Nichols PD (1983b) A study of food chains in seagrass communities II. Food of the rock flathead, *Platycephalus laevigatus* Cuvier, a major predator in a *Posidonia australis* seagrass bed. *Aust J Mar Freshw Res* 34:745–754
- Klumpp DW, Salita-Espinosa JT, Fortes MD (1993) Feeding ecology and trophic role of sea urchins in a tropical seagrass community. *Aquat Bot* 45:205–229
- Lawrence JM (1975) On the relationship between marine plants and sea urchins. *Oceanogr Mar Biol Annu Rev* 13: 213–286
- Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* 65:370–375
- Lobel PS, Ogden JC (1981) Foraging by the herbivorous parrotfish *Sparisoma radians*. *Mar Biol* 64:173–183
- Lodge DM, Cronin G, Van Donk E, Froelich AJ (1998) Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and non-vascular plants, and among freshwater herbivore taxa. In: Jeppesen E, Søndergaard MA, Søndergaard MO, Christoffersen K (eds) *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, p 149–174
- Maciá S, Lirman D (1999) Destruction of Florida Bay seagrasses by a grazing front of sea urchins. *Bull Mar Sci* 65:593–601
- Macintyre IG, Graus RR, Reinthal PN, Littler MM, Littler DS (1987) The Barrier Reef sediment apron: Tobacco Reef, Belize. *Coral Reefs* 6:1–12
- McAfee ST, Morgan SG (1996) Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Mar Biol* 125:427–437
- McGlathery K (1995) Nutrient and grazing influences on a subtropical seagrass community. *Mar Ecol Prog Ser* 122: 239–252
- McGuinness KA (1997) Tests for artefacts in some methods used to study herbivory and predation in mangrove forests. *Mar Ecol Prog Ser* 153:37–44
- Micheli F (1993) Feeding ecology of mangrove crabs in north eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. *J Exp Mar Biol Ecol* 171: 165–186

- Micheli F (1996) Predation intensity in estuarine soft bottoms: between-habitat comparisons and experimental artifacts. *Mar Ecol Prog Ser* 141:295–302
- Mitchell CA, Custer TA, Zwank PJ (1994) Herbivory on shoalgrass by wintering redheads in Texas. *J Wildl Manag* 58:131–141
- Montague JR, Carballo JL, Valdes LM, Chacken M (1995) Analyses of decay and parrotfish grazing along attached leaves of turtlegrass (*Thalassia testudinum*) from two sites in Biscayne Bay. *Fla Sci* 58:206–215
- Montgomery JLM, Targett TE (1992) The nutritional role of seagrass in the diet of the omnivorous pinfish *Lagodon rhomboides*. *J Exp Mar Biol Ecol* 158:37–57
- Morse DH (1977) Feeding behavior and predator avoidance in heterospecific groups. *BioScience* 27:332–338
- Nienhuis P, Groenendijk P (1986) Consumption of eelgrass (*Zostera marina*) by birds and invertebrates: an annual budget. *Mar Ecol Prog Ser* 29:29–35
- Nienhuis P, Van Ierland E (1978) Consumption of eelgrass, *Zostera marina*, by birds and invertebrates during the growing season in Lake Grevekingen (SW Netherlands). *Neth J Sea Res* 12:180–194
- Ogden JC, Zieman JC (1977) Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. *Proc 3rd Int Coral Reef Symp*, Miami, p 377–382
- Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182:715–717
- Overholtzer KL, Motta PJ (1999) Comparative resource use by juvenile parrotfishes in the Florida Keys. *Mar Ecol Prog Ser* 177:177–187
- Paine RT (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75
- Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar Ecol Prog Ser* 111:289–297
- Pinto L, Punchihewa NN (1996) Utilization of mangroves and seagrasses by fishes in the Negombo Estuary, Sri Lanka. *Mar Biol* 126:333–345
- Polis GA, Strong DR (1996) Food webs complexity and community dynamics. *Am Nat* 147:813–846
- Polunin NVC (1996) Trophodynamics of reef fisheries productivity. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, p 113–135
- Raffaelli DG, Hall SJ (1996) Assessing the relative importance of trophic links in food webs. In: Polis GA, Winemiller K (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, New York, p 185–191
- Randall JE (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255–260
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr (Miami)* 5:655–847
- Robertson AI (1986) Leaf-burying crabs: their influence on energy flow and export from a mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *J Exp Mar Biol Ecol* 102:237–248
- Robertson DR, Warner RR (1978) Sexual patterns in the labroid fishes of the western Caribbean, II: the parrotfishes (Scaridae). *Smith Contrib Zool* 255:1–26
- Rose CD, Sharp WS, Kenworthy WJ, Hunt JH and 6 others (1999) Sea urchin overgrazing of a large seagrass bed in outer Florida Bay. *Mar Ecol Prog Ser* 190:211–222
- Sokal R, Rohlf F (1981) Biometry. WH Freeman, New York
- Thayer GW, Bjorndal KA, Ogden JC, Williams SL, Zieman JC (1984) Role of larger herbivores in seagrass communities. *Estuaries* 7:351–376
- Tomlinson PB, Vargo GA (1966) On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae) I. Vegetative morphology. *Bull Mar Sci* 16:748–761
- Valentine JF, Heck KL Jr (1991) The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. *J Exp Mar Biol Ecol* 154:215–230
- Valentine JF, Heck KL Jr (1999) Seagrass herbivory: evidence for the continued grazing of marine grasses. *Mar Ecol Prog Ser* 176:291–302
- Valentine JF, Heck KL Jr, Busby J, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. *Oecologia* 112:193–200
- Valentine JF, Heck KL Jr, Kirsch KD, Webb D (2000) Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadows in the Florida Keys (USA). *Mar Ecol Prog Ser* 200:213–228
- Valiela I (1995) Marine ecological processes, 2nd edn. Springer-Verlag, New York
- Weinstein MP, Heck KL Jr (1979) Ichthyofauna of seagrass meadows along the Caribbean Coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. *Mar Biol* 50:97–107
- Westoby M (1974) An analysis of diet selection by large generalist herbivores. *Am Nat* 108:290–304
- Westoby M (1978) What are the biological bases for varied diets? *Am Nat* 74:1939–1949
- Zieman JC (1982) The ecology of the seagrasses of South Florida: a community profile. FWS/OBS–82/25, Washington, DC
- Zimmer-Faust RK, Fielder DR, Heck KL Jr, Coen LD, Morgan SG (1994) Effects of tethering on predatory escape by juvenile blue crabs. *Mar Ecol Prog Ser* 111:299–303

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