

REVIEW

Seagrass herbivory: evidence for the continued grazing of marine grasses

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ABSTRACT: Unlike the majority of marine plants, seagrasses are believed to experience little damage from the feeding activities of marine herbivores. Based on our previous work, plus a review of the literature, we suggest that this paradigm significantly underestimates the importance of seagrass herbivory in nearshore environments. In this review, we provide evidence from over 100 publications, showing that grazing on seagrasses is widespread in the world's oceans. Overwhelmingly, reports of grazing on seagrasses are based on observations, laboratory measurements, and bioenergetic calculations. To date, few field experiments have been conducted to evaluate the importance of seagrass grazing in the nearshore environment. Of these, even fewer have considered the possibility that herbivores may stimulate rates of primary production or the role of belowground nutrient reserves in determining the impacts of grazers on seagrasses. We contend that the currently accepted view that herbivory plays a minor role in the energetics of seagrass habitats needs to be reexamined by measuring seagrass responses to grazer induced tissue losses in controlled field manipulations. Only then will we be able to determine the importance of the seagrass-grazing pathway in marine food webs.

KEY WORDS: Seagrass · Herbivory · Waterfowl · Fishes · Sea urchins · Food webs

INTRODUCTION

Herbivores often greatly influence the productivity and abundance of plants in aquatic and marine environments (e.g. Porter 1973, 1977, Lynch & Shapiro 1981, Lewis 1985, Vanni 1987a, Mallin & Paerl 1994). For example, in freshwater lakes, zooplankton grazing can reduce the abundance of small or naked phytoplankton species, favoring the survival of larger phytoplankton species with gelatinous sheaths or other structures that reduce their vulnerability to grazing (e.g. Porter 1973, 1977, McCauley & Briand 1979, Demott & Kerfoot 1982, Vanni 1987b). In marine

environments, grazing by coral reef fishes and invertebrates can cause shifts in macroalgal community structure from dominance by highly competitive, fast-growing, edible algae to competitively inferior, slower growing, but chemically defended algae (reviewed by Hay & Steinberg 1992). Similarly, gastropod grazing can alter macroalgal community structure in temperate rocky intertidal zones by removing competitively dominant, fast-growing, more palatable species, which are then replaced by competitively inferior, slower growing, less palatable species (reviewed by Lubchencho & Gaines 1981, Gaines & Lubchencho 1982). In one of the most dramatic examples of herbivore impacts on primary producers, sea urchin grazing can convert macroalgal kelp forests to grazer resistant coralline dominated algal pavements in temperate and boreal settings (reviewed by Lawrence 1975).

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The seagrass-detritus paradigm

In contrast, marine vascular plants or seagrasses, which are common in coastal waters along every continent except Antarctica, are reported to experience very low levels of herbivory because their leaves are thought to be of poor nutritional value, owing to high C/N ratios (e.g. Bjorndal 1980, Duarte 1990, Lalli & Parsons 1993, Valiela 1995), and the inability of most invertebrate grazers to digest cellulose (Lawrence 1975). Current levels of seagrass herbivory are also thought to be low because of the historical overharvesting of larger vertebrate herbivores (e.g. green turtles, dugongs, manatees, fishes, and waterfowl; Randall 1965, Heinsohn & Birch 1972, Lipkin 1975, Charman 1979, Bjorndal 1980, Kiorboe 1980, Jacobs et al. 1981, Thayer et al. 1984, Dayton et al. 1995). As a result, the amount of seagrass production entering food webs via grazing is believed to be small, usually less than 10% of annual net aboveground primary production, with most macrophyte production thought to enter food webs through the detrital pathway (e.g. Fenchel 1970, 1977, Kikuchi & Peres 1977, Nienhaus & Van Ierland 1978, Kikuchi 1980, Thayer et al. 1984, Nienhaus & Groenendijk 1986, Zieman & Zieman 1989). Consequently, investigations of the factors controlling seagrass growth and biomass have emphasized the primacy of nutrient supply (e.g. Patriquin 1972, Short 1987, Powell et al. 1989, Fourqurean et al. 1992, Short et al. 1993), light availability, and/or physical factors (e.g. Patriquin 1975, Backman & Barilotti 1976, Dennison & Alberte 1985, Thom & Albright 1990).

COUNTER EVIDENCE

There are, however, few actual tests of this paradigm, and there is an existing body of evidence which shows that its underlying assumptions need reevaluation. For example, several investigators have provided evidence that nitrogen concentrations in seagrasses are similar to those of algae (e.g. Lowe & Lawrence 1976, Lobel & Ogden 1981, reviewed in Thayer et al. 1984). There is also substantial evidence that detrital seagrass leaves are an even poorer source of nutrition (i.e. have higher C/N ratios) for consumers than are living leaves (Klumpp & Van der Walk 1984), as seagrass detritus resists decay, requiring long periods of conditioning time before detritivores can use it (Harrison & Mann 1975, Zieman 1975, Fenchel 1977, Thayer et al. 1977, Rice 1982).

In addition, many herbivorous fishes are 'extreme' generalists that feed on vegetation in proportion to its abundance (Ogden 1980, Hay & Steinberg 1992, Hay

1997). In fact, field palatability testing using both seagrasses and marine macroalgae has found that seagrasses are of intermediate palatability among several species of algae offered to marine herbivores throughout the Caribbean Sea and Indian Ocean (e.g. Hay 1981, 1984a, b, Lewis 1985, MacIntyre et al. 1987). If true, seagrasses are likely to contribute to the diets of many of marine herbivorous fishes in some significant way.

More importantly, we and others have shown, from field observations and short-term experiments, that the variegated sea urchin *Lytechinus variegatus* (Lamarck) consumes from 50 to 100% of the aboveground seagrass biomass produced in some areas of the eastern Gulf of Mexico and Caribbean Sea (Moore et al. 1963, Camp et al. 1973, Greenway 1976, 1995, Zimmerman & Livingston 1976, Bach 1979, Valentine & Heck 1991, Heck & Valentine 1995). At densities of 10 ind. m⁻², *L. variegatus* can reduce turtlegrass habitats to barren unvegetated substrates from fall through early spring (Valentine & Heck 1991). If grazing is persistent throughout the winter and spring, sea urchins can reduce these vegetated habitats to permanently barren unvegetated substrates (Heck & Valentine 1995). In summer, turtlegrass persists under severe grazing pressure and regrows to levels that either equal or exceed the standing crop of nearby ungrazed turtlegrass. The apparent mechanism by which turtlegrass overcomes the effects of this grazing is to increase the production or recruitment of new shoots in the grazed area rather than to increase the production of existing shoots (Valentine et al. 1997). Similarly, the sea urchins *Tripneustes ventricosus* can, and *Diadema antillarum* did, until recently, consume large quantities of seagrass in some Caribbean settings (e.g. Ogden et al. 1973, Lilly 1975, Vicente & Rivera 1982, Keller 1983, Tertschnig 1984 in Tertschnig 1989). Although it was once thought that grazing on seagrasses was predominantly a Caribbean phenomenon (Ogden & Zieman 1977, Ogden 1980, Ogden & Ogden 1982), observations elsewhere show that sea urchins also consume significant amounts of seagrass in the tropical Pacific and Indian Oceans (Bak & Nojima 1980, Kirkman & Young 1981, Hulings & Kirkman 1982, Verlaque & Nedelec 1983, Jafari & Mahasneh 1984, Larkum & West 1990, Klumpp et al. 1993, Jernakoff et al. 1996).

In tropical settings where fishing pressure is low, herbivorous fish, not sea urchins, are the dominant herbivores (e.g. Ogden 1976, 1980, Hay 1981, 1984a, Carpenter 1986, but see Jackson 1997). More than 30 species of Caribbean fishes, predominantly parrotfishes and surgeonfishes, have been found with seagrasses in their guts (Randall 1967, McAfee & Morgan 1996, Lewis & Wainwright 1985, but see Hay 1984a). It is likely that even more species draw nutrition from

these plants, as investigators have typically considered the presence of seagrass leaves in the guts of fishes to be incidental intake associated with the capture of animal prey (e.g. Thompson 1959, Carr & Adams 1973, Bell et al. 1978). When seagrass leaves are isotopically labeled or fishes have been presented with seagrass in laboratory studies, it has been found that seagrasses leaves can contribute to fish growth (e.g. Conacher et al. 1979, Montgomery & Targett 1992). Using stable isotopes, Fry et al. (1982) found that seagrasses and benthic algae contributed significantly to the diets of many fishes in the seagrass beds of St. Croix, USVI. Fry & Parker (1979) also found that seagrasses and other benthic plants contributed significantly to the diets of shrimps and fishes in some areas of Texas.

In some locations, fish grazing on seagrasses is so intense that 'halos' are created and maintained within seagrass habitats at the base of coral reefs (e.g. Randall 1965, Ogden & Zieman 1977, Hay 1984a, McAfee & Morgan 1996). Not all foraging in and on seagrasses is near the base of coral reefs, however (Ogden & Zieman 1977). While many herbivorous fishes seek shelter on coral reefs at night, they commonly forage in nearby seagrass habitats throughout the day (Randall 1965, Ogden & Zieman 1977, Zieman et al. 1984, McAfee & Morgan 1996). For example, the parrotfish *Scarus guacamaia* and *S. coelestinus* have been reported to move up to 500 m inshore from coral reefs to feed (Winn & Bardach 1960, Winn et al. 1964). Juvenile and smaller species of parrotfish also feed on seagrasses away from the reef (Ogden & Zieman 1977, Handley 1984, MacIntyre 1987, McGlathery 1995, McAfee & Morgan 1996). Once large enough, many juvenile fish abandon structurally simpler seagrass habitats for more structurally complex coral reefs where it has been hypothesized that they find increased protection from large piscivorous fishes (Springer & McErlean 1962, Ogden & Zieman 1977, Dubin & Baker 1982, Handley 1984, Carpenter 1986). These observations suggest that the flow of energy from seagrass habitats to coral reefs can be substantial, but quantitative estimates are constrained by the limited amount of information on coral reef food webs (cf. Polunin 1996).

Investigators have used tethering, stable isotope, gut content studies, and reconstructive sampling techniques to show that seagrasses are readily consumed by fishes, at times in large quantities, in some areas of the Mediterranean Sea, the Indian and Pacific Oceans (Kirkman & Reid 1979, Hay 1981, 1984a, b, Klumpp & Nichols 1983a, b, Lewis 1985, Nichols et al. 1985, Nojima & Mukai 1990, Cebrián et al. 1996a, b, Pinto & Punchedewa 1996, Marguillier et al. 1997). In virtually every study seagrass leaves were readily consumed by herbivores, thereby demonstrating the susceptibility of seagrasses to herbivores across broad geographic

areas. We have so far emphasized the importance of sea urchin and fish grazing on seagrasses, but several species of waterfowl have also been shown to consume large quantities of seagrass production (both above- and belowground) during their seasonal migrations through subtropical, temperate and boreal estuaries (e.g. Charman 1977, Wilkins 1982, Tubbs & Tubbs 1983, Baldwin & Lovvorn 1994, Michot & Chadwick 1994, Mitchell et al. 1994). In addition, green turtles *Chelonia mydas* (Linnaeus) and sirenians (manatees and dugongs), which are still abundant in some areas, are intense seagrass grazers (Heinsohn & Birch 1972, Spain & Heinsohn 1973, Lipkin 1975, Heinsohn et al. 1976, Anderson & Birtles 1978, Nietschmann & Nietschmann 1981, Marsh et al. 1982, Ogden et al. 1983, Nishiwaki & Marsh 1985, Lanyon et al. 1989, Nietschmann 1990, Provancha & Hall 1991, de Iongh et al. 1995, Preen 1995). These large herbivores can have even greater impacts on seagrass productivity and abundance than sea urchins or fishes (Zieman et al. 1984). All of the examples cited above show that seagrass herbivory, although probably reduced in a historical context, continues to represent an important and underestimated trophic pathway in many areas, and not a highly localized anomalous event.

SEAGRASS-HERBIVORE INTERACTIONS

If this view is correct, how do seagrasses persist in the face of such grazing pressure? We believe that part of the answer lies in the unrecognized potential of seagrasses to compensate for grazing losses, and the belowground location of much seagrass biomass. During the summer months we have shown that turtlegrass responds to sea urchin grazing by increasing the production of new shoots, which leads to increased areal aboveground primary production (Valentine et al. 1997). Because of the increased production of new shoots, aboveground biomass in grazed areas does not change when compared to nearby ungrazed plots during the growing season. We suggest that this increased turnover of leaf material allows seagrasses to compensate for tissue lost to herbivores and enables seagrass to persist during intense grazing (Valentine et al. 1997). Since new shoots are produced only at rhizome apices (Tomlinson & Vargo 1966), we hypothesized that sea urchin grazing should also lead to increased belowground production (Valentine et al. 1997). Our data suggest that focussing solely on seagrass biomass without accounting for the material produced between sampling periods can lead to large underestimates of the amount of seagrass consumed by herbivores (cf. Jacobsen & Sand-Jensen 1994, Sand-Jensen et al. 1994).

Table 1. Summary of selected studies or reports of herbivory in seagrasses. W: waterfowl; U: urchin; G: gastropod; C: crustacean; F: fish; R: reptile; M: mammal

Grazer	Seagrass, location, study type	Description of results	Source
<i>Branta bernicla bernicla</i> (W), <i>Anas penelope</i> (W), <i>Anas crecca</i> (W)	<i>Zostera noltii</i> and <i>Z. marina</i> . Solent, England. Field study, percent cover recorded at 5 stations. Enclosures used to monitor seagrass change due to grazing.	Large reductions in seagrass areal coverage attributed to brent geese feeding.	Tubbs & Tubbs (1983)
<i>B. bernicla</i> (W), <i>A. acuta</i> (W), <i>A. penelope</i> (W), <i>A. platyrhynchos</i> (W)	<i>Z. noltii</i> and <i>Z. marina</i> . Dutch Wadden Sea. Field-based bioenergetic study and field experiment where change in submerged aquatic vegetation (SAV) shoot density, biomass, and percent cover were monitored.	An estimated 1426 kg DW of seagrass (~50% of all SAV production) consumed, mostly by <i>A. acuta</i> and <i>A. penelope</i> .	Jacobs et al. (1981)
<i>B. bernicla</i> (W), <i>Anas americana</i> (W), <i>A. platyrhynchos</i> (W), <i>A. acuta</i> (W)	<i>Zostera japonica</i> and <i>Z. marina</i> . Boundary Bay, British Columbia. Collections and field based bioenergetic study. Above- and below-ground standing stock were monitored. Waterfowl use days were estimated. Some birds were collected and esophagus contents recorded.	Bird density positively correlated with SAV distribution. Dabbling ducks and geese consumed some 362 t of <i>Z. japonica</i> leaves and rhizomes (~50% of aboveground and 43% of belowground biomass) at the study site. Lesser amounts of <i>Z. marina</i> consumed.	Baldwin & Lovvorn (1994)
<i>Aythya americana</i> (W)	<i>Halodule wrightii</i> . Lower Laguna Madre, TX. Two years of field collections and 1 experiment at 3 sites were used to assess impacts of redhead ducks on SAV biomass.	Rhizome biomass was 75% lower in grazed areas than where grazers were excluded. When rhizome biomass was grazed below 0.18 g DM ⁻¹ core ⁻¹ (at 1/3 of the sites), grass did not recover.	Mitchell et al. (1994)
<i>B. bernicla</i> (W), <i>Anas penelope</i> (W), <i>A. crecca</i> (W)	<i>Zostera noltii</i> and <i>Zostera marina</i> . Dutch Wadden Sea. Field surveys plus an enclosure experiment were used to quantify impacts of wildfowl grazing on seagrass biomass.	Brent geese and widgeon reduced aboveground biomass some 30% faster than in areas where grazers were excluded. Belowground biomass in grazed cages was 48% lower than in ungrazed plots.	Madsen (1988)
<i>Cygnus olor</i> (W), <i>Anas penelope</i> (W), <i>A. platyrhynchos</i> (W), <i>A. acuta</i> (W), <i>A. crecca</i> (W), <i>Aythya ferina</i> (W), <i>Branta bernicla</i> (W), <i>Fulica atra</i> (W), <i>Idotea chelipes</i> (C)	<i>Zostera marina</i> . Lake Grevelingen, SW Netherlands. Field-based bioenergetic study and laboratory experiment.	An estimated 7.5% of <i>Zostera marina</i> production consumed by waterfowl and a single species of isopod.	Nienhuis & Groenendijk (1986)
<i>Branta bernicla hrota</i> (W), <i>Anas penelope</i> (W)	<i>Zostera</i> sp. Strangford Slough, Northern Ireland. Field study. The impact of grazers was documented by monitoring changes in seagrass biomass at the study area along with the use of exclusion cages in grassbeds with uniform coverage.	Grazing led to faster rates of seagrass loss than was occurring due to weathering in ungrazed areas. Belowground biomass was 48% lower in grazed plots than measured in ungrazed plots.	Portig et al. (1994)
<i>Aythya americana</i> (W)	<i>Halodule wrightii</i> . Chandeleur Sound, LA. Field monitoring of seagrass biomass to document the impact of waterfowl grazing on seagrass.	Waterfowl grazing was found to reduce above-ground and belowground biomass by 90 and 49% respectively.	Michot & Chadwick (1994)
<i>Lytechinus variegatus</i> (U)	<i>Thalassia testudinum</i> . Miskito Cays, Nicaragua. Laboratory measurements, field collections and observations. Feeding preferences determined by turning over urchins. Urchin gut contents examined at 1 station.	Sea urchins were estimated to consumed some 0.5 g DW per urchin d ⁻¹ of seagrass. However, gut contents indicated that 40% of this urchin's diet was detrital turtlegrass. Less than 5% of the diet was live grasses.	Vadas et al. (1982)
<i>L. variegatus</i> (U), <i>Sparisoma radians</i> (F), <i>Archosargus rhomboides</i> (F), <i>Monocanthus setiferus</i> (F), <i>Acanthurus chirurgus</i> (F), <i>Sphaeroides spengleri</i> (F), <i>Acanthostracion quadricornis</i> (F)	<i>Thalassia testudinum</i> . Kingston Harbour, Jamaica. Laboratory measurements, field sampling, stomach content analysis, and field experimentation to estimate herbivory on grazers on seagrass.	5 species of fish found to feed on both live and detrital seagrass along with algae and crustaceans. Only the sea urchin <i>Lytechinus</i> and the bucktooth parrotfish <i>S. radians</i> were found to feed predominantly on seagrass. <i>Lytechinus</i> was estimated to consume some 49% of the SAV leaf tissue produced each day. A small fraction of this production was consumed by fishes.	Greenway (1975, 1995)
<i>L. variegatus</i> (U)	<i>Thalassia testudinum</i> . Offshore grass beds of west Florida. Field observations and measurements.	An episodic settlement of sea urchins led to significant reductions of seagrass coverage. Grazing was found to have denuded an estimated 20 ha area of seagrass habitat.	Camp et al. (1973)
<i>L. variegatus</i> (U), <i>Tripneustes ventriosus</i> (U)	<i>Thalassia testudinum</i> . Discovery Bay, Jamaica. Field experiment tested for intraspecific and interspecific competition between 2 species of urchins. Above ground biomass within cages was used to document the effects of urchin manipulations.	<i>Tripneustes</i> grazing had a highly significant effect on seagrass biomass in enclosure treatments. <i>Lytechinus</i> had a moderate effect on seagrass biomass.	Keller (1983)

Table 1 (continued)

Grazer	Seagrass, location, study type	Description of results	Source
<i>L. variegatus</i> (U)	<i>Thalassia testudinum</i> . Biscayne Bay, FL. Laboratory estimate of sea urchin ingestion rates and preferences when fed live seagrass and seagrass detritus.	Urchins ingested decayed leaves at a significantly higher rate than when fed green leaves. No evidence of a significant preference for decayed leaves over green ones was found.	Montague et al. (1991)
<i>L. variegatus</i> (U)	<i>Thalassia testudinum</i> . Card Sound, FL. Observations.	A large population of sea urchins consumed all benthic plants in a several hectare area of Card Sound.	Bach (1979)
<i>Tripneustes gratilla</i> (U), <i>Salmacis sphaeroides</i> (U)	<i>Thalassia hemprichii</i> . Bolinao, Philippines. Field and laboratory measurements of sea urchin consumption of seagrass biomass. Food preferences for several plant species also examined.	Preferences tests showed <i>Tripneustes</i> chose live SAV alternative food choices. <i>Salmacis</i> consumed equal quantities of all plant species. Both urchins efficiently digested and absorbed seagrass (>60%). Estimates of total SAV consumption by both sea urchins was 240 to 400 g DW m ⁻² d ⁻¹ , an average of ~17% of SAV produced with a range from 3 to 100% of SAV production.	Klumpp et al. (1993)
<i>Paracentrotus lividus</i> (U)	<i>Posidonia oceanica</i> . Mediterranean Sea. Field experimentation used to determine grazing impacts on seagrass biomass, shoot density, and production.	Loss of seagrass biomass was directly proportional to grazing intensity.	Kirkman & Young (1981)
<i>Astropyga magnifica</i> (U)	<i>Zostera marina</i> . Tomioka Bay, Amakusa, Japan. Eelgrass patch size, density and biomass used to document the impact of a sea urchin aggregation on seagrass density. Urchin gut contents were recorded as well.	A seagrass patch was reduced from ~71 to <3 m ² in 3 mo by grazing. Urchin stomachs were completely full of seagrass. No other plants were observed. The seagrass standing crop decreased from 7789 to 375 g DW.	Bak & Nojima (1980)
<i>Heliocidaris erythrogramma</i> (U)	<i>Posidonia australis</i> . Botany Bay, Australia. Field observations and mapping from 1930 to 1985 were used to document the impact of urchin grazing on a seagrass meadow.	Urchins completely denuded 20 ha of seagrass from 1979 to 1982 before being dispersed by a storm. Urchin aggregations reappeared in late 1982 and an additional 25 ha of <i>Posidonia</i> was lost from 1982 to 1984. Up to 1987 no regrowth had occurred.	Larkum & West (1990)
<i>Tripneustes gratilla</i> (U)	<i>Halophila stipulacea</i> . Sinai, Northern Red Sea and the Jordanian coast of the Gulf of Aqaba. Observational.	Heavy urchin grazing was recorded on seagrasses at depths ranging from 5 to 9 m. Grazing on seagrass was subsequently verified by gut content analysis.	Lipkin (1979), Bouchon (1980), Hulings & Kirkman (1982), Jafari & Mahasneh (1984)
<i>Temnopleuris michaelsonii</i> (U)	Cockburn Sound, Warnbro Sound, Australia. Field sampling and seagrass mapping were used to document urchin denudation of a seagrass habitat.	In Cockburn Sound, seagrasses were grazed by locally abundant <i>Temnopleuris michaelsonii</i> . Most heavy damage was localized. Where grazing was heavy, plants had not recovered 2 to 4 yr later. Urchins invaded a second site, reducing remnants of one healthy seagrass meadow to bare sand. Intense grazing was noted in fall of 3 different years. Outbreaks were also reported from a third site, where sea urchins removed all of the leaves in deeper portions of a seagrass bed.	Cambridge et al. (1986)
<i>Tectura depicta</i> (G)	<i>Zostera marina</i> . Monterey Bay, CA. Lab experiment. <i>Zostera</i> transplanted into plastic flower pots, at natural densities of limpets were maintained on 8 plants while 8 others were kept grazer free. Seagrass growth was determined weekly along with total leaf length. At the end of the experiment, plants were harvested and analyzed for biomass (shoot, rhizome, root), rates of leaf photosynthesis, respiration, and sucrose enzymes were measured in leaves and shoots, plus protein and sugar contents. Chlorophyll <i>a</i> was extracted from leaf segments.	Growth rates, carbon reserves, root proliferation, and net photosynthesis of grazed plants were 50 to 80% lower than on ungrazed plants. The carbon allocated to the roots of ungrazed plants was 800% higher for ungrazed plants than for grazed plants. Limpet grazing induced carbon limitation in eelgrass growing in an otherwise light replete environment.	Zimmerman et al. (1996)
<i>Littorina sitkana</i> (G), <i>Margarites helicanus</i> (G), <i>Lacuna variegata</i> (G), <i>Telmessus chieragonus</i> (C), <i>Microcottus sellaris</i> (F), <i>Branta canadensis</i> (W), <i>Anas carolinensis</i> (W), <i>Anas acuta</i> (W)	<i>Zostera marina</i> . Izeimbek Lagoon, AK. Sampling and ¹³ C: ¹² C analysis.	Eelgrass was found to be incorporated into the local food chain through herbivory by at least 7 species.	McConnaughey & McRoy (1979)

(Table continued overleaf)

Table 1 (continued)

Grazer	Seagrass, location, study type	Description of results	Source
<i>Ampithoe</i> spp. (C)	<i>Syringodium</i> . Fiji. Laboratory determinations of ingestion rates of manatee grass.	Initially amphipods fed at the top of the leaf. One day later they made nests from fragments of grazed grass. Grazing rates ranged from 1.7 to 26.4 mg WW ind. ⁻¹ d ⁻¹ . Using a carbon budget approach, the authors estimated that the amphipods grazed 1/2 of the material produced and further assimilated 1/2 of it.	Mukai & Iijima (1995)
<i>Monacanthus chinensis</i> (F)	<i>Posidonia oceanica</i> . Quibray Bay, Botany Bay, New South Wales. Stomach analysis and field sampling ¹⁴ C labeled seagrass used to assess seagrass assimilation by fishes.	Gut analysis showed fish ate SAV, along with 5 spp. of algae, crustaceans, and other invertebrates. Seagrass and amphipods were most abundant in fish guts. Microscopic examination of ingested plant material suggested that plants were untouched. (i.e. no cell wall damage observed). However, radioactive labeling showed that ~22% of labeled SAV was in the liver and gut wall of the fish, 32 to 33% in the feces. The remaining label may have been in other tissues. This is significant as it shows that microscopic examination of the cell walls does not necessarily provide a complete picture. The actual % of SAV production removed was low.	Conacher et al. (1979)
<i>Monacanthus chinensis</i> (F), <i>Meuschenia freycineti</i> (F), <i>Meuschenia trachylepis</i> (F)	<i>Posidonia australis</i> . Port Hacking, New South Wales. Field sampling and stomach contents. The entire fish community in a 400 m ² area of <i>P. australis</i> was collected twice each in 2 seasons. Stomachs of all leatherjackets were dissected and the contents identified. The relative percentages of food items was determined. Rectal items were identified using microscope to determine which items were used as food.	Leatherjackets dominated the fish community, averaging 26% of the number and 34% of the biomass. Seagrasses ingested were small pieces leaf material which were covered with epibionts. <i>M. freycineti</i> consistently bit off pieces in neat semicircular bites. Juveniles of all species of fed principally on encrusting animals listed above with little seagrass being present. Microscopic rectal contents from several ind. of each species found that <i>Posidonia</i> was undigested.	Bell et al. (1978)
<i>Monacanthus ciliatus</i> (F) <i>Stephanolepis hispidus</i> (F)	<i>Thalassia testudinum</i> . Apalachee Bay, FL. Field sampling and stomach contents of filefish collected over a 9 yr period.	These fish fed on a wide variety of prey, however, seagrass and invertebrates accounted for 80% of the stomach contents. As fish grew, the dietary importance of seagrasses and associated epifauna increased. Approximately 1/2 of the diet of larger fishes was <i>Thalassia</i> . The pattern was the same for both species of filefishes. The incidence of SAV in the diets of <i>Monacanthus</i> was greatest in late summer and early fall coincident with peak SAV productivity. The incidence of SAV in <i>Stephanolepis</i> increased between summer and fall.	Clements & Livingston (1983)
<i>Hyporhamphus unifasciatus</i> (F)	<i>Ruppia maritima</i> and <i>Halodule wrightii</i> . Crystal River, FL. Shallow water fish collected with a bag in approximately 1 m of water.	Volume of SAV in gut ~50% in large halfbeaks.	Carr & Adams (1973)
<i>Hyporhamphus melanochir</i> (F)	<i>Zostera muelleri</i> and <i>Heterozostera tasmanica</i> . Cirib Point, Western Port Bay, and Duck Point, Corner Inlet, Australia. Field sampling and stomach contents.	During the day green eelgrass tissue was in the guts of 93% of the fish, making up almost 70% of the total volume. Insects, amphipods, and shrimp larvae made up most of the remaining food. Amphipods were far more important prey at night. Eelgrass tissue was consumed by 1/2 of fish and was only 18% of total volume at night. All eelgrass material in the guts was macerated by pharyngeal teeth. Eelgrass in the foregut was undigested, while material in the hindgut was colorless. Microscopic examination of the material found most plant cells were empty.	Robertson & Klumpp (1983)
<i>Lagodon rhomboides</i> (F)	<i>Zostera marina</i> . Field sampling and laboratory bioenergetic and radioactive labeling study. Pinfish (>65 mm SL) were fed diets of either eelgrass or frozen grass shrimp. Assimilation efficiency for plants (either eelgrass or algae) and shrimp and labeled seagrass.	Pinfish found to assimilate a substantial portion of the organic material from eelgrass, but with less efficiency than shrimp. Specific growth rates of pinfish fed grass shrimp partially substituted with either eelgrass or digestible carbohydrates were not significantly different from growth rates when feeding solely on shrimp. Pinfish appeared to increase feeding rates when offered low calorie seagrass.	Montgomery & Targett (1992)

Table 1 (continued)

Grazer	Seagrass, location, study type	Description of results	Source
<i>Sparisoma rubripinne</i> , <i>Sparisoma chrysopterum</i>	<i>Thalassia testudinum</i> . Carrie Bow Cay, Belize. Field tethering study using clean freshly collected pieces of <i>T. testudinum</i> blades along with algal species.	Each study found that herbivorous fishes readily consumed seagrass leaves but the intensity varied according to coral reef habitat and depth. Lewis found that tethered <i>Thalassia</i> was entirely consumed by 2 parrotfish— <i>Sparisoma rubripinne</i> and <i>Sparisoma chrysopterum</i> . Lewis also found that <i>Thalassia</i> was among the preferred sources of food during feeding trials.	Hay 1981, Lewis (1985)
<i>Scarus</i> spp. (F), <i>Sparisoma</i> spp. (F), <i>Acanthurus</i> spp. (F)	<i>Thalassia testudinum</i> , <i>Halodule wrightii</i> . US Virgin Islands. Field experiment, stomach content and observation. Three separate transplantations of mixed plots <i>T. testudinum</i> and <i>H. wrightii</i> were placed into a halo zone next to a coral reef used to assess the impact of herbivores on seagrass abundance. In addition, an artificial reef was built in a mixed turtlegrass and <i>H. wrightii</i> habitat.	Parrotfish totally consumed seagrass patches transplanted into a halo zone next to a coral reef. Parrotfish (<i>Scarus</i> and <i>Sparisoma</i>) all seem to feed to some degree on the grass; <i>Scarus guacamaia</i> had 95% of the gut volume filled with <i>Halodule</i> . <i>Acanthurus chiurugis</i> and <i>A. bahamensis</i> had 40 and 80% gut volume filled with seagrass.	Randall (1965)
<i>Scarus guacamaia</i> , <i>Sparisoma radians</i> (F)	<i>Thalassia testudinum</i> . St. Croix, USVI. Sampling. Seagrass leaves collected and fish bites marks identified along a transect running from the base of a coral reef into an adjacent seagrass habitat.	Leaves collected closest to a reef showed bites resulting from a population of large parrotfishes (<i>Scarus guacamaia</i>) whereas the stations 20 and 60 m from the reef had bites characteristic of <i>Sparisoma radians</i> . The station 4 m from the reef showed mixed feeding.	Ogden & Zieman (1977)
<i>Scarus croicensis</i> (F), <i>Sparisoma aurofrenatum</i> (F), <i>Acanthurus chiurugis</i> (F), <i>A. bahianus</i> (F)	<i>Syringodium filiforme</i> and <i>Thalassia testudinum</i> . San Blas Islands, Panama. Field tethering study measured both feeding selectivity and intensity.	Each species of seagrass was heavily grazed but herbivory on these grasses was variable spatially.	Tribble (1981)
Scarid and siganid fishes	<i>Enhalus</i> , <i>Thalassia hemprichii</i> , <i>Halodule uninervis</i> , <i>Cymodocea rotundata</i> , <i>Syringodium isoetifolium</i> . Palau, Western Carolina Islands. Field-based monitoring.	All samples of <i>Thalassia</i> and <i>Cymodocea</i> had bite marks. At one site approximately 30 to 40% of leaves of all species except <i>Enhalus</i> , had at least 1 bite taken. <i>Enhalus</i> had bite marks on at least 75% of blades.	Ogden & Ogden (1982)
<i>Trichechus manatus</i> (M)	<i>Syringodium filiforme</i> . Cape Canaveral, FL. Field experimentation percent cover, and aboveground biomass used to document herbivore impact on seagrass.	Grazing led to significant reductions in seagrass coverage, biomass and leaf length. Manatees were highly aggregated but their distribution was positively correlated with the <i>Syringodium</i> and <i>Halodule</i> density.	Provancha & Hall (1991)
<i>Dugong dugong</i> (M)	<i>Halodule uninervis</i> . Nang Bay, Moluccas, East Indonesia. Observation and biomass monitoring.	Dugongs were found to remove some 75% of the belowground biomass in the upper 4 to 5 cm of sediment. Vegetation biomass recovered to nearby ambient levels in just 4 to 5 mo following grazing during the wet season, no such recovery was noted during the dry season.	de Jongh et al. (1995)
<i>Dugong dugong</i> (M)	<i>Zostera capricorni</i> , <i>Halophila ovalis</i> and <i>Halophila uninervis</i> . Moreton Bay, east Australia. Aerial and boat surveys, monitoring along with field experiments used to document dugong grazing on seagrass habitats.	Dugongs appear to spend most of their time grazing. In one area, shoot density, aboveground biomass and belowground biomass were reduced by 65, 73 and 31% respectively over 3.5 mo. Grazing impacts were variable, in one area shoot density was reduced by 85% in 12 d, 95% in 17%. In another area biomass was reduced by 96% (aboveground) and 71% belowground.	Preen (1995)
<i>Chelonia mydas</i> (R)	<i>Thalassia testudinum</i> . Great Iguana, Bahamas. Field-based observations and bioenergetic study. A 3 ha area of turtlegrass was impounded along with 12 turtles and changes in seagrass biomass were noted.	Turtles grazed grass blades by biting the lower parts of the leaves and allowing the upper portion to float away, creating a patch of closely cropped patches with leaves averaging 2.5 cm in length. The grazed areas were recropped while adjacent stands of tall blades remained untouched. There were no sharp boundaries between grazed and ungrazed areas.	Bjorndal (1980)
<i>Diadema antillarum</i> (U), <i>Chelonia mydas</i> (R)	<i>Thalassia testudinum</i> . St. Croix, USVI. Field experiments where changes in seagrass growth and biomass were recorded along a grazing gradient.	Turtle grazing had a significant negative impact on seagrass production. Urchins were ineffective in controlling the abundance of seagrass. However, urchin grazing did increase the rate at which seagrass biomass turned over within enclosures.	Zieman et al. (1984)

Unlike many species marine macroalgae and phytoplankton which are wholly exposed to marine grazers and often totally consumed by them (cf. Hay & Steinberg 1992 but see Steneck 1988 and Steneck & Dethier 1994), the stored reserves and sites of nutrient uptake for many seagrasses are located in a belowground 'refuge' which is not accessible to most grazers. This belowground refuge represents a stabilizing influence that allows seagrasses to persist where herbivory is intense and can, depending on the season, allow seagrasses to recover rapidly to levels that equal or exceed those in nearby ungrazed plots. What is unclear is what factors control seagrass responses to grazing, how long seagrasses can sustain higher levels of production post-grazing, and how they affect rates of energy flow through nearshore food webs.

FOOD WEB IMPORTANCE OF SEAGRASS HERBIVORY

We know of only a few attempts to estimate the amount of seagrass production directly entering nearshore food webs (Greenway 1976, 1995, Nienhaus & Groenendijk 1986, Klumpp et al. 1993). From these studies it has been estimated that somewhere between ~3 and 100% of seagrass net primary production enters food webs via the grazing pathway. All have relied on short-term laboratory measurements and anecdotal field observations to identify the levels of seagrass production entering local food webs. While laboratory-based efforts provide us with testable hypotheses, relying solely on such approaches allows only a rough estimate of the amount of material being consumed directly at a particular site. Accurately determining the density and the time spent grazing in a location, which would be required for such an approach, is likely to be limited to the amount of time a diver can spend underwater and involves an intensive effort. Moreover, in the case of vertebrate grazers, estimates may be low as fishes may avoid areas while divers are present. Such estimates must also be conducted seasonally as many of the vertebrate grazers exhibit seasonal migrations. In addition, laboratory approaches do not include the possibility that rates of plant regrowth following grazing can exceed those of ungrazed areas, which could lead to large underestimates of the amount of material grazed by these herbivores. This has been recognized to be significant in many ecosystems (Lehman & Scavia 1982, Cargill & Jeffries 1984, Bianchi 1988, Williams & Carpenter 1988, Littler et al. 1995, McNaughton et al. 1996), and more recently also shown to be substantial in seagrass ecosystems (Valentine & Heck 1991, Sand-Jensen et al. 1994, Valentine et al. 1997). To date, there have been no attempts to estimate the quantitative im-

pact of such compensatory responses to herbivory in seagrass systems. And while it has been recognized that we need to develop a better understanding of the role of sediment porewater nutrient concentrations and rhizome carbohydrate stores in determining seagrass production (cf. Zieman et al. 1984, Valentine et al. 1997), there have been no sustained experiments that have simultaneously considered the roles of each of these factors, how they could be influenced by herbivory, or what impact they may have on the transfer of energy to nearshore food webs.

In summary, while grazing on seagrasses is undoubtedly reduced in a historical context, herbivores still have significant effects on aboveground seagrass biomass in many areas (see Table 1 for a list of publications documenting grazing on seagrasses). Most importantly, previous studies of seagrass herbivory have not measured seagrass leaf turnover rates, which are essential to accurately estimate the amount of seagrass production actually consumed by herbivores (cf. Zieman et al. 1984, Sand-Jensen et al. 1994, Valentine et al. 1997). To date, there have been precious few field experiments which have simultaneously considered the multiple controlling factors that determine just how much energy actually flows from seagrasses to herbivores in nearshore food webs. We contend that the currently accepted hypothesis that herbivory plays a small role in the energetics of seagrass habitats and nearby coastal ecosystems needs to be reexamined using controlled field manipulations. Such studies will provide estimates of the amount of seagrass production directly entering nearshore food webs, and they will improve our understanding of the factors that control spatial and temporal variability of seagrass herbivory.

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