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Plant–herbivore interactions in seagrass meadows

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Abstract

During the past two decades we have gained much insight into the factors that regulate the productivity of seagrass dominated ecosystems, especially those at low latitudes. Here, we review and reassess the importance of plant–herbivore interactions in seagrass meadows, focusing on recent studies that have examined: 1) grazing on live seagrass leaves; 2) consumption of epiphytic algae growing on seagrass leaves; and 3) consumption of planktonic algae from the waters surrounding seagrass meadows. The major conclusion is that, in contrast to what has been reported in much of the literature on food webs in seagrass meadows, a diverse grazing pathway continues to represent an important conduit for the transfer of energy from the primary producers to higher order consumers. This remains true, although in many areas consumption of seagrasses is reduced in an historical context, owing to the overharvesting of many large species of herbivorous waterfowl, turtles and mammals.

We also summarize our view of the important gaps in understanding the broadly defined topic of herbivory in seagrass-dominated ecosystems. We suggest that future studies should focus on: understanding the foraging strategies of seagrass herbivores; quantifying the impact of herbivory on seagrass demography, including effects on sexual reproduction, the fate of flowers, and the production of fruits and seeds; and documenting the commonness of compensatory responses to grazing. In addition, the role of chemical defenses in seagrass species remains inadequately investigated. Studies of the roles of nutritional content (as measured by C/N/P ratios) and chemical defenses are also fertile grounds for future studies of epiphytes and their grazers, as are additional experiments to quantify the relative roles of top-down and bottom-up factors as they determine algal growth and abundance. There is also a need to expand the geographical scope of studies of epiphyte–grazer interactions from cold temperate to sub-tropical and tropical waters. Suspension feeders also need to be studied more broadly, with additional experiments required to quantify their effects on water clarity and their ability to fertilize pore waters, and whether benefits from these activities balances the costs of shading and competition for space that can result from both epifaunal and infaunal suspension feeders.
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1. Introduction

The growing understanding that seagrass meadows serve as "nursery habitats" for a variety of economically important finfish and shellfish (see recent meta-analysis by Heck et al., 2003), coupled with the global decline of seagrasses during the last several decades (Short and Wylie-Echeverria, 1996), has stimulated interest in understanding the factors that contribute to healthy seagrass meadows and led to an increasing number of studies of seagrass species (Duarte, 2002) and the animals that inhabit them. Many of these studies have been carried out in warm temperate, sub-tropical or tropical latitudes, and much new information has been

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obtained about the ecology of low-latitude seagrass meadows. Some of this information is at odds with the conventional wisdom about the structure and dynamics of food webs in temperate seagrass meadows, while other studies have produced findings consistent with earlier efforts.

In this paper we summarize what is currently known about plant–herbivore interactions in seagrass meadows, emphasizing the new information that has been gathered during the last two decades. Included are estimates of the magnitude of direct consumption of seagrasses, which at present seem to be much greater in low latitudes than in the temperate zone, the dominant role of small grazers (mesograzers) in controlling the biomass of algae growing epiphytically on seagrass leaves, and the effect of suspension feeders in linking the overlying water column with the benthos and sediments of seagrass meadows.

2. Herbivory on seagrasses

While the importance of grazing in algal-dominated communities is well documented (Strong, 1992), the premise that the ingestion of living seagrass biomass is infrequent and inconsequential remains one of the central tenets of current food web theory (Kikuchi and Peres, 1977; Thayer et al., 1984; Zieman and Zieman, 1989; Cebrian, 2002). This idea has been so widely accepted that it is found in most of the marine ecology textbooks used in North America. As an example, Levinton's (2001) widely used marine biology text reports that: "One of the most interesting aspects of sea grasses is their apparent unpalatability to grazers." Similarly Nybakken's (2001) text instructs students to conclude that: "Despite the obvious position of seagrass beds as primary production units in inshore waters surprisingly few animals consume seagrasses directly." The generality of this hypothesis has been largely accepted without question but the available evidence suggests that this is a gross oversimplification of the importance of grazing in both modern-day and historical seagrass food webs (Valentine and Duffy, 2005).

Below, we contrast this well worn canon of food web theory and its key conceptual underpinnings with an accumulating body of evidence showing that it is inaccurate to minimize the importance of the grazing pathway as a conduit for the transmission of seagrass production to higher order consumers in nearshore food webs. In addition, we identify what we believe to be critical gaps in our understanding of the interaction between seagrasses and their consumers.

2.1. Origins and the inconsistencies of the existing seagrass grazing paradigm

The grazing paradigm for seagrass meadows is strikingly similar to the view once held by terrestrial ecologists (e.g., Karban and Baldwin, 1997; Lowman, 1984, 1985; McNaughton, 1985; McNaughton et al., 1996) who emphasized the importance of the detrital pathway over that of the grazing pathway in terrestrial food webs. This conclusion was based on the observed presence of large volumes of detritus in terrestrial ecosystems. Put simply, ecologists asked: how could grazing be important if plant detritus was so abundant? The abundant detrital seagrass leaves seen on some sediments and shorelines also appear to have led ecologists to conclude that grazing on seagrasses must also be low in marine ecosystems (Fenchel, 1970).

The proposed mechanism underpinning the primacy of the detrital pathway was that the nutritional quality of detritus was believed to be superior to that of living leaves. In part, the basis for this belief was the notion that the C/N ratios of detrital seagrass leaves would become lower than the C/N ratios of living leaf tissues following the development of microbial gardens on the surfaces of detached leaves (Fenchel, 1977), as had been shown in terrestrial ecosystems. As a result, it was assumed that lower order consumers would preferentially consume detrital leaves over live leaves (Bjorndal, 1980; Duarte, 1990). Yet comparisons of the nutritional quality of plants using C/N ratios can provide only crude insights into the foraging patterns of marine consumers (Thayer et al., 1977; Hatcher, 1994; Cebrian and Duarte, 1998; Kirsch et al., 2002). Furthermore, detrital seagrass leaves rapidly leach soluble nitrogen following detachment from a ramet and the detached tissues take a very long time to break down (e.g., Harrison and Mann, 1975; Rice, 1982). As such, the C/N ratio of detrital leaves remains much higher than that of the remaining attached leaves for long periods following detachment (Klumpp and Van der Walk, 1984). Moreover, because detrital seagrass leaves behave essentially as passive particles whose distribution is determined by tidal exchanges, waves and currents (Cebrian and Duarte, 2001), the nutritional enrichment of detached leaves frequently takes place at sites far removed from the source bed (Menzies et al., 1967; Suchanek et al., 1985; Vetter, 1995, 1998). It should also be noted that some authors cite support for the hypothesis that seagrass grazing is of little importance to nearshore food webs based on a passage in Russell-Hunter (1970), who concluded that food with a C/N ratio <17 was required to satisfy the protein requirements of consumers. This

conclusion has been cited out of context, as Russell-Hunter was referring to the protein requirements of humans for growth, not those for marine herbivores. In fact, he made no mention of seagrass herbivory (Thayer et al., 1977). Thus, the conceptual underpinnings of the view that the detrital pathway is the key conduit for the transfer of seagrass production to higher trophic levels are not strongly supported by the existing evidence.

Early seagrass ecologists also followed the lead of their terrestrial counterparts and relied predominantly on the use of indirect approaches (e.g., either by counting grazing marks on leaves, comparing leaf density or biomass at grazed and ungrazed sites or laboratory ingestion studies), rather than direct field estimates of grazing rates on seagrass leaves (Valentine and Duffy, 2005). Terrestrial ecologists came to view that utilization of such indirect approaches as flawed and they adopted more direct approaches to estimate rates of herbivory (Lowman, 1984, 1992; McNaughton, 1985; McNaughton et al., 1996; McGuinness, 1997). The shift in their approach led to consistently higher estimates of herbivory than had been previously reported (Lowman, 1984, 1985). From early studies conducted in seagrass meadows it was estimated that, depending on the location, somewhere between ~3% and 100% of seagrass net primary production enters food webs via the grazing pathway (Fig. 1). This extraordinarily wide range demonstrates that grazing on seagrasses varies greatly in time and space, as it does in most other ecosystems (cf. Louda and Collinge, 1992; Hacker and Bertness, 1995, 1996), not that grazing on seagrasses is, on average, inconsequential. As such, the relevant question to be asked is why does grazing on living seagrass tissue vary so greatly in time and space?

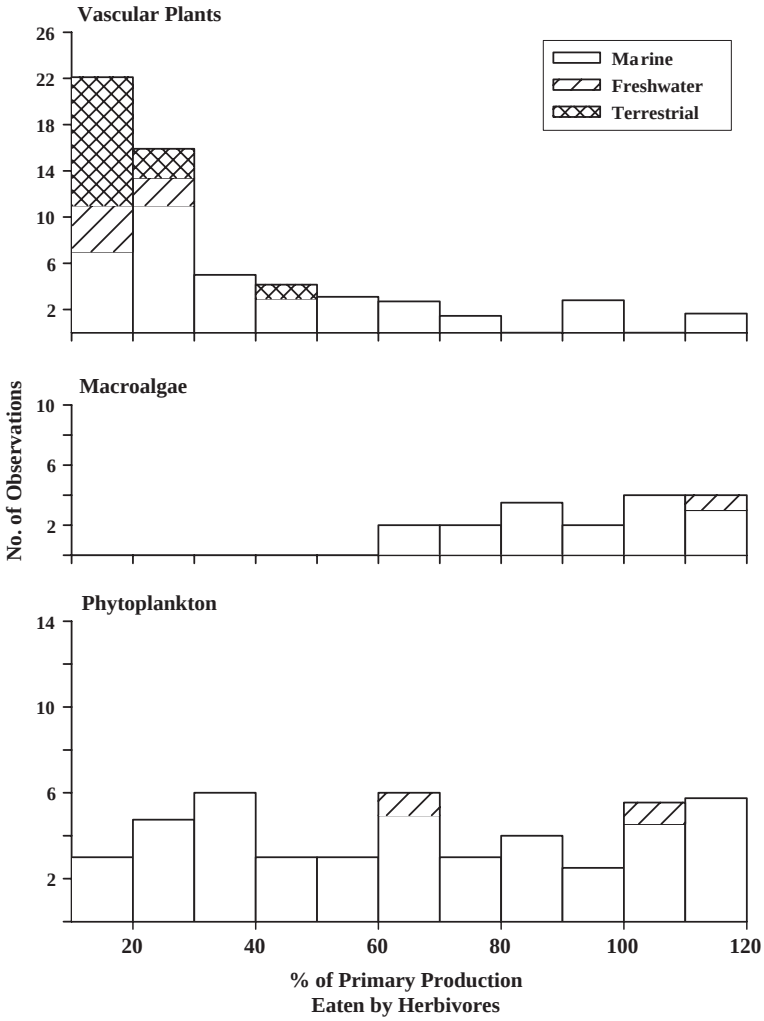

Fig. 1. Frequency distribution of the amount of net primary production consumed by herbivores for vascular plants (top), macroalgae (middle) and phytoplankton (bottom). Reprinted with permission from Valiela (1995).

We should also be aware that many of the most basic canons of ecological theory were based on studies conducted long after most ecosystems were depleted of larger consumers (e.g., Dayton et al., 1995; Domning, 2001; Myers and Worm, 2003; Springer et al., 2003). The recent, high-profile discussions of the impacts of the over harvesting of the once abundant seagrass-consuming green turtles, manatees and dugongs (Jackson, 1997, 2001; Jackson et al., 2001) need to be broadened to include the effects of large reductions of the once abundant herbivorous waterfowl by hunters (Madsen, 1988, 1998a,b). This is important, since the remaining populations of herbivorous waterfowl have been demonstrated to be effective grazers of seagrass production (Charman, 1977; Wilkins, 1982; Tubbs and Tubbs, 1983; Baldwin and Lovvorn, 1994; Michot and Chadwick, 1994; Mitchell et al., 1994; Ganter, 2000).

2.2. Historical interaction between grazers and seagrass

It is generally appreciated that the plants of terrestrial grassland ecosystems share a long and close evolutionary history with large vertebrate grazers, and that many important traits of the grasses represent, at least in part, adaptations to their historical interactions with herbivores (Barnard and Frankel, 1964; Mack and Thompson, 1982; McNaughton, 1984; Coughenour, 1985). Larger vertebrate seagrass herbivores were once very abundant and more diverse than their modern-day counterparts. Moreover, they relied extensively on seagrass production to meet their nutritional needs (Domning, 2001; Jackson et al., 2001). Since enormous grazers such as marine mammals and turtles were abundant throughout most of the evolutionary history of seagrasses (Jackson, 1997), seagrasses in the lower latitudes in the Atlantic Ocean must have experienced the same kind of intense grazing pressure that the unrelated terrestrial grasses did (Domning, 2001). In temperate latitudes, waterfowl (ducks, geese and swans) appear to have been important seagrass herbivores (see references cited above) that may have also exerted important selective pressures on seagrass traits in higher latitudes. As a result, it is likely that grazers played a more important role in the development of seagrasses and the meadows they form than we are familiar with today. While seagrasses developed independently of terrestrial grasses (Larkum and den Hartog, 1989; Les et al., 1997), they possess many of the same traits considered to be grazer-derived adaptations (Valentine and Duffy, 2005). Among these traits are: clonal propagation and the resultant physiological integration of ramets; the possession of largely inaccessible belowground basal meristems and branching rhizomes; an abundance of small deciduous shoots; and the ability to rapidly regenerate defoliated tissues (Valentine and Heck, 1999).

We also suggest that the species-rich seagrass assemblages in the Indo-Pacific Ocean may be a product of the past grazing activities of large vertebrate herbivores (Preen, 1995; Peterken and Conacher, 1997). Using comparisons between grazer exclusion cages and varying degrees of mechanical simulations of dugong grazing in nearby open areas, Preen (1995) concluded that dugongs prevent fibrous, low nitrogen *Zostera capricorni* from competitively dominating the submerged landscape. Instead, dugong feeding was hypothesized to allow their preferred forage, *Halophila ovalis*, a rapidly growing less fibrous plant with higher leaf nitrogen content, to persist. Similarly, Aragones and Marsh (2000) showed that modest levels of green turtle grazing could trigger dramatic shifts in the relative abundances of *Z. capricorni* and *H. ovalis*. These findings suggest that grazing can have important impacts on the species composition of seagrass communities. As such, large grazers would have played an important role in determining the life-history characteristics of modern-day seagrasses. For example, green turtles cultivate the nitrogen content of their forage by pruning away older more fibrous turtlegrass leaves, allowing them access to a greater abundance of younger more nitrogen rich leaves (Bjorndal, 1980).

2.3. Modern seagrass food webs: evidence for the importance of the grazing pathway

While it seems clear that the historical alteration of nearshore food webs has reduced the magnitude of energy transfer from living seagrasses to higher trophic levels, this does not mean that the seagrass grazing pathway has been functionally eliminated. This is because seagrass food webs are characterized by high levels of functional redundancy, as shown by a review of the literature that described the numbers of herbivores that feed on seagrass production (Fig. 2). This means that there has been a shift from larger herbivores that are strong interactors (sensu Paine, 1992) to smaller herbivores who are weak interactors (i.e., McCann et al., 1998; Berlow, 1999). Smaller grazers (weak interactors) can consume substantial quantities of seagrass production yet have modest impacts on seagrass density (Kirsch et al., 2002; Tomas et al., 2005). This may explain the seeming contradiction between recent reports of high herbivory in what remain

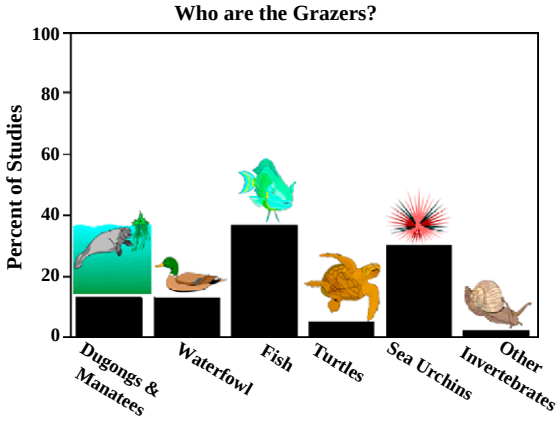

Fig. 2. Frequency distribution of studies carried out on various types of seagrass herbivores (after Valiela, 1995).

lush, high biomass seagrass meadows (Valentine and Duffy, 2005).

Grazers that are strong interactors, however, continue to be present in many seagrass meadows. Studies over the last two decades have shown that a number of sea urchins and herbivorous fish species in lower latitudes ingest large amounts of aboveground seagrass biomass. The purple urchin (*Lytechinus variegates*) can consume from 50% to 100% of the aboveground biomass of turtlegrass (*Thalassia testudinum*) in the northern Gulf of Mexico when present at densities commonly observed (Valentine and Heck, 1991), and this can result in the local extinction of seagrasses (Camp et al., 1973; Heck and Valentine, 1995; Rose et al., 1999; see Fig. 3). Similarly, tropical urchins in the Atlantic, Pacific and Indian Oceans can consume large amounts of seagrass biomass (Keller, 1983; Klumpp et al., 1993; Alcoverro and Mariani, 2002) and an Atlantic species (*Diadema antillarum*) can produce overgrazed, unvegetated "halos" around coral reefs (Ogden et al., 1973). Several species of herbivorous fishes can also consume large amounts of seagrass. These taxa shelter on reefs but forage in the surrounding seagrass meadows and can also contribute to the formation of "halos" around reefs (Randall, 1965; McAfee and Morgan, 1996; Valentine and Duffy, 2006). These are but a few examples from an accumulating body of evidence that the complex interactions between these rooted macrophytes and their consumers are important in regulating the dynamics of seagrass meadows.

2.4. Estimation of grazing intensity in seagrass food webs: shifts in methodology are required

Methodological differences among the varying approaches used to calculate rates of seagrass herbivory may explain the wide range of grazing estimates in the literature. Indirect approaches to estimating grazing on seagrasses have consistently led to low rates of herbivory, and all of them are based on static measures of leaf loss to grazers made once or a few times annually. In one common approach, the estimates of leaf damage caused by herbivores are made on haphazardly selected shoots collected once a year (Cebrian et al., 1996a). These estimates are compared with areal estimates of aboveground production at the same site and the ratio of the estimate of grazer induced leaf tissue loss to production is used to estimate grazing intensity. Estimates of grazing made using this method are bound to be low as they do not account for leaves completely consumed by grazers (Lowman, 1984), nor do they account for grazer-induced shoot mortality.

In other cases, grazing estimates are based on comparisons of the expected lengths of undamaged leaves with the actual lengths of leaves collected at a given sample site. The difference between the actual and expected lengths of leaves is assumed to be the amount of leaf tissue lost to grazing. In this, as well as the previous method, the numbers of herbivores are not counted nor is the proportion of leaf tissue that is lost to disturbances such as storms quantified (Cebrian et al., 1996b). Such indirect calculations are also unable to account for grazer-induced increases in plant production or leaf turnover rate (e.g., Zieman et al., 1984; McNaughton et al., 1996). This is significant since increased rates of aboveground production (via either increased production by surviving shoots or via increased recruitment of new shoots) can prevent accurate measurements of production consumed when estimates are based on differences in biomass between

Fig. 3. Overgrazed manatee grass (*Syringodium filiforme*) meadow in Florida Bay, USA, caused by the purple urchin (*Lytechinus variegatus*). Photo by Bill Sharp, Florida Department of Natural Resources.

grazed and ungrazed plots (Valentine and Heck, 1999). Increased plant production following grazing is significant in many ecosystems (Lehman and Scavia, 1982; Cargill and Jeffries, 1984; Bianchi, 1988; Williams and Carpenter, 1988; Littler et al., 1995; McNaughton et al., 1996) and more recently has been shown to be substantial in grazer dominated seagrass ecosystems (Valentine et al., 1997, 2000; Valentine and Heck, 2001). When the positive impacts of grazing on plant growth were included in estimates from other ecosystems, grazing was almost always found to be substantially greater than previously estimated (e.g., Karban and Baldwin, 1997; Lowman, 1984, 1992; McNaughton, 1985; McNaughton et al., 1996; McGuinness, 1997; Valentine and Heck, 2001).

Surprisingly, a comprehensive review of the seagrass literature found only two studies that directly estimated the proportion of seagrass production consumed by herbivorous fishes (Kirsch et al., 2002; Tomas et al., 2005). In the first study, Kirsch et al. (2002) used a digital scanner and commercially available software to directly estimate the amount of turtlegrass (*T. testudinum*) tissue lost to small parrotfish (*Sparisoma radians*) in the Florida Keys (Fig. 4). The areal losses of leaf tissue were then compared to the amount of leaf tissue produced. From these efforts, Kirsch et al. (2002) found that, on average, fishes consumed some 80% of the net aboveground production of turtlegrass. To evaluate whether grazers were preferentially feeding on tethered leaves, the numbers of bites on tethered leaves were compared to the numbers of bite marks on leaves harvested from quadrats placed at the same locations. In all comparisons, there were significantly fewer bite marks on the tethered leaves than on leaves harvested from the quadrats (Kirsch et al., 2002), indicating that the tethering technique did not lead to exaggerated estimates of rates of herbivory. Using similar techniques, Tomas et al. (2005) estimated that as much as 70% of the production of seagrasses (*Posidonia oceanica*) in some areas of the Mediterranean Sea was consumed by herbivorous fish (*Sarpa salpa*). Because Cebrian and Duarte's (1998) conclusion, that grazing intensity was very low at the same study sites used by Tomas et al. (2005), was based on measurements of herbivorous fish bite marks on a single set of haphazardly selected shoots, it seems clear that indirect estimates of grazing should be viewed with caution. We suggest that many, if not most, prior estimates of grazing on seagrasses developed using indirect methods are far too low.

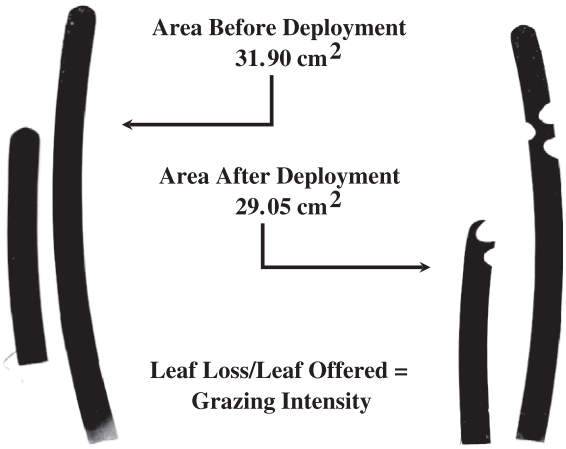

Fig. 4. Example of method used by Kirsch et al. (2002) to estimate the daily amount of leaf tissue lost to grazers. Leaves were digitally scanned before and after deployment for 24 h, and the daily amount of tissue lost was calculated.

2.5. New avenues of investigation: herbivore foraging strategies

Current understanding of the sensory capabilities and foraging patterns of marine herbivores is limited. Compared to the well-studied role of terrestrial plant nitrogen content in determining herbivore feeding preferences, the effects of seagrass leaf nutritional quality (in the case of both leaf nitrogen content and the seeming indigestibility of leaf carbon) in determining food selection is inadequately investigated. Correlative field studies have, however, found a significant, positive relationship between leaf nitrogen content and grazing by vertebrates, including parrotfishes, sea turtles, and dugongs. This suggests that some herbivores preferentially feed in areas where seagrass leaves are enriched in nitrogen, or that grazers may in some way be cultivating the nutritional content of their food (Bjorndal, 1980; Zieman et al., 1984; McGlathery, 1995; Preen, 1995; but see Cebrian and Duarte, 1998). There is also recent experimental evidence that supports the idea that vertebrate grazers preferentially feed on nitrogen-rich seagrass leaves. Goecker et al. (2005) used a series of controlled choice tests to show that one abundant specialist seagrass herbivore, the bucktooth parrotfish (*S. radians*), selectively forages on seagrass leaves of high nitrogen content. Both field and laboratory experiments in which seagrass leaves of varying leaf nitrogen content were offered to parrotfish at multiple locations in the Florida Keys showed that the bucktooths consumed nearly all the enriched leaves while they consumed few of the low nitrogen leaves. A follow-up laboratory experiment in which the tissues of high and low nitrogen leaves were embedded in agar and offered to the bucktooths gave the same results: parrotfish

consumed substantially more of the agar that was impregnated with high rather than low nitrogen leaves. It is intriguing to speculate how grazers can differentiate between plants of high and low leaf nitrogen content, and whether these fishes possess undiscovered sensory capabilities that allow them to select seagrass leaves based on their nutritional content. These finding also suggest that the dominance of subtropical and tropical seagrass meadows by plants of low nitrogen content may be the result of the preferential removal of high nitrogen plants by herbivores, rather than some form of low nitrogen defense strategy against herbivores.

The preferential feeding reported for vertebrate grazers has not been found for the smaller and more sluggish invertebrate herbivores, which may use other mechanisms, such as compensatory feeding, to compensate for the low nutritional quality of their forage. Only one experimental study, to our knowledge, has considered the possibility of compensatory feeding on seagrasses. Valentine and Heck (2001) manipulated the in situ nitrogen content of seagrass leaves within cages where urchins (*Lytechinus variegatus*) were stocked at a range of densities reported in the field. Using Osmocote™ nutrient stakes, we raised the nitrogen content of turtlegrass leaves in one treatment by 20%. It was anticipated that urchins placed in the nutrient enriched cages would consume greater amounts of enriched than unenriched seagrass leaves. Interpretation of the results of this experiment was confounded by the fact that the urchins stimulated aboveground seagrass production within the unenriched urchin cages. As a result, the anticipated differences in aboveground seagrass biomass between nitrogen-enriched and unenriched urchin enclosure treatments were not observed. Relying instead on a mass balance estimate of urchin consumption in the nitrogen-enriched and unenriched cages, and on estimates of urchin consumption of nitrogen-enriched and unenriched seagrass leaves embedded in agar, we concluded that urchins increased their consumption of leaves with low nitrogen to meet their nutritional needs. That is, they ate more of the seagrass production in the unenriched cages than they did in the enriched cages.

Because several generalist herbivores increase ingestion rates when feeding on marine plants of low nutritional value (Lares and McClintock, 1991), it seems likely that many invertebrate grazers may be able to compensate for low nutritional quality of their forage as well. Similarly, most herbivorous fishes have high consumption rates and rapid gut throughput times (Horn, 1989), and can maintain large populations and high growth rates on diets low in protein (Russ, 1984; Russ and St. John, 1988). Thus, these fishes process large amounts of organic material quickly and could consume significant quantities of seagrass production when herbivore biomass is high. At this time, however, it is impossible to draw firm conclusions about how the variability of the nutritional content of seagrass determines the foraging strategies and feeding preferences of different types of herbivores.

2.6. Impacts of grazing on seagrass demography and reproduction: can herbivores trigger shifts in the age structure and reproduction of seagrass populations?

Given the continued presence of strong interactors in seagrass dominated ecosystems and the increased recruitment of new shoots that can be triggered by grazing (Valentine et al., 1997), it seems likely that some seagrass herbivores can still exert a controlling influence over seagrass demography. Recently, Dormsjo (unpublished) showed that survival of young shoots was lower near reefs. To test the hypothesis that the low survival of young shoots near reefs was the result of grazing, she conducted a field preference test. The results of paired young and old shoots placed near and away from reefs found that the numbers of bite marks and loss of tissue from young shoots near reefs were significantly greater than they were from older shoots (Fig. 5). Thus, it seems likely that herbivores control the age-structure of seagrasses near reefs. The same effect was not observed on shoots placed away from the reef, as no bite marks were detected on young shoots, suggesting that the large reef-associated grazers were causing the damage. This also suggests the smaller herbivores, which are at greater risk of predation, do not attack young shoots.

This study needs to be repeated, but if these results can be generally extended, they would explain why there are significant impacts of grazing on young shoots

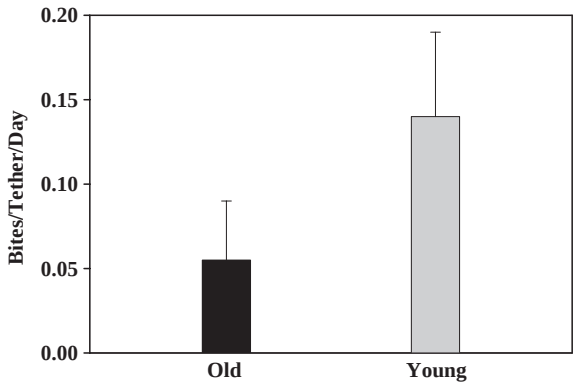

Fig. 5. Rates of herbivory on different-aged turtlegrass shoots near coral reefs in the Florida Keys, USA (data from Dormsjo, unpublished).

in some locations and not others. Among the important effects could be changes in the frequency of sexual reproduction, as grazing can have both inhibitory and stimulatory effects on flower production. In some cases, grazer-induced increases in the production of new shoots (Zieman et al., 1984, Valentine et al., 1997) may also stimulate flowering and seed production (Valentine and Heck unpublished data; Peterken and Conacher, 1997). In other cases, grazers may prevent shoots from reaching sexual maturity, or feed directly on inflorescences, thereby reducing sexual reproduction (Piazzi et al., 2000; Williams and Heck, 2001).

Although there remains much to do, recent evidence also suggests that the consumption of seagrass flowers and seeds is more widespread and important than has been previously reported (Wigand and Churchill, 1988; Williams, 1995; Nakaoka, 2002; Holbrook et al., 2002; Orth et al., 2002). In a novel study, Orth et al. (in press) used laboratory studies and field video recordings to document that *Posidonia australis* seed predators were primarily small crustaceans that fed most heavily on seeds in densely vegetated areas. If these findings are supported by future studies, then herbivores are more important than previously considered in determining the survival of seagrasses at the earliest stages of their lives (Orth et al., in press). Additional information from other areas and for other species of seagrasses is needed to evaluate the impacts of herbivores on seed production, seed survivorship and germination.

2.7. Physiological responses to herbivores

While we know that seagrasses can persist while being grazed (Ogden and Zieman, 1977; Zieman et al., 1984; Mitchell, 1987; Valentine et al., 1997, 2000; Cebrian et al., 1998), the mechanisms by which they respond to grazer-induced leaf loss remain unknown (Valentine and Heck, 1999). Based on studies in other ecosystems, we know that plants can compensate for losses to grazers either by increasing nutrient uptake from the surrounding environment (Lehman and Scavia, 1982; Cargill and Jeffries, 1984; Bianchi, 1988; Williams and Carpenter, 1988; Day and Detling, 1990; Seagle et al., 1992; Sand-Jensen et al., 1994; McNaughton et al., 1996) or by translocating nutrients among physiologically integrated ramets (Jónsdóttir and Callaghan, 1990). While seagrasses compensate for leaf loss via the rapid recycling of stored nitrogen (Dawes and Lawrence, 1979; Bjorndal, 1980; Iizumi and Hattori, 1980; Short and McRoy, 1984; Zieman et al., 1984; Pedersen and Borum, 1993) and the transport of carbohydrates along common rhizomes (Libes and Boudouresque, 1987; Tomasko and Dawes, 1989a,b), it is not known whether grazing also triggers these same responses in surviving tissues (Valentine and Heck, 2001; Valentine et al., 2004). In general, the physiological effects of grazer-induced leaf loss are not well understood (Dawes and Lawrence, 1979; Valentine et al., 1997, 2000; Cebrian et al., 1998; Valentine and Heck, 1999, 2001), and since grazing damages and reduces photosynthetic tissues, it is critical to strengthen understanding of how seagrasses rebuild these tissues to sustain growth (Kraemer et al., 1997; Hemminga et al., 1999; Stapel and Hemminga, 1997).

2.8. Chemical deterrents in seagrasses

An issue at the forefront of recent grazing studies is the seeming disconnect between the persistence of large lush seagrass meadows in the tropics and the large estimates of seagrass herbivory referenced above. As suggested previously, perhaps the grazing compartment of modern-day seagrass food webs is simply dominated by a diverse assemblage of weak interactors (sensu Paine, 1992) that has little overall impact on seagrass density. Alternatively, seagrasses may have an undiscovered repertoire of capabilities that can deter grazing. Chemical compounds such as phenolic acids and condensed tannins are commonly used by marine macroalgae to reduce palatability or increase toxicity to herbivores (e.g. Steinberg, 1985; Hay et al., 1987, 1994; Hay and Fenical, 1988; Steinberg et al., 1991; Arnold et al., 1995; Targett et al., 1995; Hay, 1996). Many of these same compounds are also present in the leaves of seagrasses and McMillan (1984) and others (Zapata and McMillan, 1979, McMillan et al., 1980, Harrison, 1982, 1989, Buchsbaum et al., 1984) have postulated that they may well make seagrass leaves unpalatable and toxic to some herbivores (Thayer et al., 1984). With one exception (see Goecker et al., 2005), little consideration has been given to the potential role of chemical feeding deterrents in determining the foraging patterns of seagrass herbivores.

3. Grazing on algal epiphytes

Despite their small biomass, the algae attached to seagrass leaves are extraordinarily productive (Morgan and Kitting, 1984; Moncreiff et al., 1992), owing to their short generation times and rapid rates of growth. In some instances, the productivity of seagrass epiphytes equals that of the seagrass leaves to which they are attached to (Morgan and Kitting, 1984; Thom, 1990; Williams and Heck, 2001). Stable isotope studies have

revealed that a large number of seagrass-associated organisms feed heavily on epiphytic algae (see review by Jernakoff et al., 1996). These abundant smaller grazers are characterized by high levels of secondary production (Valentine and Heck, 1993) and in turn are an important source of prey for higher order consumers (Heck et al., 2000). Thus, in agreement with the changing paradigm for seagrass meadows described above, there is growing recognition of the importance of grazing by smaller seagrass associated animals (such as gastropods, amphipods, isopods and caridean shrimp) in the dynamics of nearshore food webs.

3.1. Grazing, nutrients and the abundance of epiphytes on seagrass leaves

With regard to the factors that determine epiphyte abundance on seagrass leaves, investigators have historically stressed the importance of elevated inputs of anthropogenically supplied nutrients in stimulating algal production in coastal waters. These investigators also suggested that the rapid overgrowth of the seagrass leaves by epiphytic algae lead to the eventual disappearance of seagrasses from eutrophic bays and near-coastal waters in North America (Duarte, 1995; Bricker et al., 1999; Howarth et al., 2000; NAS, 2000; Hauxwell et al., 2001; Orth and Moore, 1983; Neundorfer and Kemp, 1993; Short et al., 1995; Tomasko et al., 1996), Europe (Giesen et al., 1990; den Hartog, 1994) and Australia (Cambridge and McComb, 1984; Shepherd et al., 1989). Given this consensus among scientists worldwide, we were surprised to find that in studies where the effects of nutrient enrichment and grazing on epiphytic algal abundance were considered simultaneously, researchers have come to a very different conclusion; namely, that the presence of grazers can explain as much, or more of the observed variance in algal biomass on seagrass leaves as can nutrient concentration or loading rate (Heck et al., 2000, Hughes et al., 2004). Below we describe some of these studies and provide an update on the most recent data on this subject.

In a series of unrelated experiments, investigators have consistently and independently demonstrated that grazing plays a key role in controlling algal overgrowth of seagrass leaves. Neckles et al. (1993), for example, found that grazing by amphipods prevented the overgrowth of eelgrass leaves by epiphytic algae in nutrient-enriched mesocosms. This led the authors to conclude that the effects of grazers on epiphyte biomass were stronger than those of nutrient enrichment. Similarly, Williams and Ruckelshaus (1993) found that isopod grazing reduced epiphyte biomass on eelgrass leaves in Washington (USA) by as much as one-third. Moreover, they found that nutrient enrichment led to increased epiphyte biomass only when grazers were absent. They concluded that epiphytes have the potential to control eelgrass growth only in warmer nitrogen-enriched environments where small grazers are absent. Similarly, we (Heck et al., 2000) too found few significant nutrient effects on either epiphytic algae or seagrass density. In contrast, the presence of omnivorous pinfish led to significant effects on mesograzer density, epiphyte biomass and the production, leaf length and shoot density of *Thalassia* within our enclosures. In addition, Nixon et al. (2001) reported that their work in mesocosms over many years did not show significant increases in epiphyte biomass following nutrient enrichment, although they did observe changes in epiphyte composition. In aggregate, the results from these studies show that when grazers are present the stimulatory effects of increased nutrient loading on epiphyte abundance are greatly reduced, and that mesograzers can control the abundance of epiphytes, even in highly enriched conditions.

A recent meta-analysis (Hughes et al., 2004) of all of the existing studies, including those cited above, that have compared the relative effects of nutrients and grazers on the epiphytic biomass support the qualitative conclusion that grazers are a key determinant of the extent to which epiphytes can overgrow living seagrass leaves. As they state: “The positive effects of epiphyte grazers were comparable in magnitude to the negative impacts of water column nutrient enrichments, suggesting that the 2 factors should not be considered in isolation of each other.”

Thus, at locations where epiphyte loads on seagrass leaves are large, it seems to us that important questions to ask are “Why aren’t grazers controlling epiphytic algae?”, or perhaps, “What happened to the grazers?”. We also suggest that reductions of nutrient inputs alone will not result in the increased coverage of seagrasses if other conditions prevent grazers from existing at historically common densities.

This conclusion differs from the paradigm of nutrient-based seagrass decline summarized by Duarte (1995) and others (Bricker et al., 1999; Howarth et al., 2000; NAS, 2000; Hauxwell et al., 2001). We hypothesize that the reason for this difference is that the paradigm is largely based on data from either observational studies or experimental studies that did not include manipulations of grazers in their design. Thus, because the effects of grazers were not considered in the studies, they were unlikely to have been part of

their conclusions. This difference in emphasis is another example of the on-going debate among ecologists about the relative importance of top-down and bottom-up factors in controlling ecosystem structure and function (see Williams and Heck, 2001; Valentine and Duffy, 2006 for recent discussions in a marine context).

For the moment, we can only speculate on the reasons why the density of mesograzers might be low in some areas. There may have been failed recruitment, or it may be that elevated concentrations of toxic materials or persistent hypoxia kept grazer densities low. Alternatively, higher order food web alterations resulting from the overharvesting of large predatory fishes may have indirectly led to reductions in grazer density. In the latter scenario, the overharvesting of large predators is predicted to lead to increased numbers of their prey, small predatory fishes. Increases in these small predators in turn will produce reductions in the density of their prey which are mostly smaller grazers such as caridean shrimp, amphipods, gastropods and small fish. If the interactions between trophic levels are strong at each step along the way, reductions in small grazer density should in turn lead to accumulation of epiphytic algae biomass on seagrass leaves (Fig. 6). Because nearshore areas experiencing nutrient enrichment are also areas that are likely to have experienced overfishing, we suggest that this food web alteration hypothesis may be broadly applicable and deserves more study (see Williams and Heck, 2001; Heck and Orth, 2006).

Another important recent finding is that different species of herbivores have different effects on algal density and composition, due to the diversity of feeding methods employed by mesograzers along with their predilections for feeding on different epiphyte species (Jernakoff et al., 1996; Gacia et al., 1999; Hillebrand et al., 2000; Duffy and Harvilicz, 2001; Duffy et al., 2003). The implication here is that different suites of herbivores (e.g., gastropods versus amphipods, caridean shrimp or small herbivorous fishes) could have different effects on the accumulation and composition of algae in areas that are enriched with nutrients, and that the taxonomic composition of these herbivores may be the key determinant of which algae can overgrow seagrass leaves. At this time, however, we have insufficient knowledge to predict just how differences in herbivore species composition will influence algal species composition or abundance.

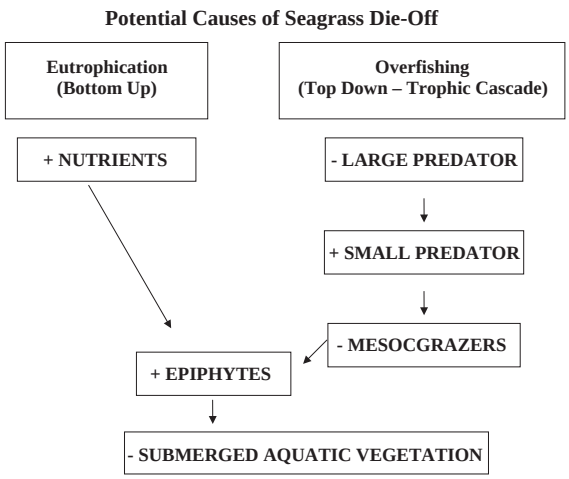

Fig. 6. Simplified comparison of how trophic cascades induced by overharvesting top predators and bottom-up effects due to nutrient enrichment could both lead to the same end result–the disappearance of seagrasses.

3.2. Generality of our assessment

We conclude this section by noting that similar conclusions about the impacts of epiphytic grazers have been reached by other investigators working in diverse marine environments. For example, grazing intensity can determine the biomass of algae on coral reefs to a greater extent than does nutrient enrichment (Larkum and Koop, 1997; Miller et al., 1999; Szmant, 2002). Similarly, the overgrowth of ceramic tile substrates by microalgae was determined to a greater extent by amphipod and gastropod consumption than by nutrient delivery (Hillebrand et al., 2000; Lotze and Worm, 2002). In addition, a meta-analysis conducted by Shurin et al. (2002) showed that manipulations of the density of marine benthic predators produced stronger indirect effects on primary production, via shifts in herbivore abundance, than did predator manipulations in terrestrial, marine or lake planktonic, or stream or lake benthic systems. In addition, a more recent meta-analysis of the factors determining the strength of trophic cascades (Borer et al., 2004) confirmed that marine benthic species exhibited the strongest trophic cascades of any system tested. Thus, a substantial body of evidence suggests that the accumulation of algal biomass in shallow benthic habitats is more likely to be controlled by grazers than by nutrients. As such, benthic food webs would appear to be more strongly affected by top-down effects than any others.

3.3. Future investigations of epiphyte–grazer interactions

Among the general issues and topics for future study in the area of epiphyte–herbivore interactions is

the need to evaluate the generality of these results as sites beyond temperate North America, Europe and Australia. In addition, we need to determine the extent to which the findings of studies conducted in laboratory or field mesocosms can be extrapolated to predict the effects of epiphyte–grazer interactions at the ecosystem level. To date, large-scale manipulations (e.g., at the size of an embayment) of consumers and nutrients have not been conducted in marine ecosystems. Limnologists have learned a great deal by manipulating entire lake ecosystems (e.g., Schindler, 1998; Carpenter et al., 2001), although replication and controls are often difficult to include in such study designs, and we feel strongly that marine ecologists could benefit from seriously considering this approach.

Other unanswered questions that remain to be addressed include the following: If algal grazers prefer nitrogen-rich plants, as noted in Section 2, and demonstrated experimentally for algae by Hemmi and Jormalainen (2002) and Boyer et al. (2004), how can filamentous green algae, which are characteristic of eutrophic waters, accumulate in nitrogen-rich waters when grazers are present? One possible answer is that since most filamentous green algae seem to be palatable to a wide range of grazers, persistent accumulations of green algae are only possible if there are few grazers present.

Are there effects of nutrient enrichment on the consumers of algae with high nitrogen content and altered C/N/P ratios? One tenet of the emerging discipline of ecological stoichiometry is that elemental ratios of consumers remain constant, despite the make-up of their food sources. To accomplish this constancy, consumers adjust their assimilation and excretion efficiencies in accord with the elemental composition of their food (Elser and Urabe, 1999). Because food quality can play a major role in determining the growth and fecundity of consumers, we might expect positive effects on these factors in eutrophic waters that contain nitrogen-rich algae. To date, we are not aware that anyone has addressed this issue in benthic marine environments.

Can chemically defended algae (e.g., red and brown algal species) become abundant on the surface of seagrass leaves where grazing is intense? Possibly so. Drift algal mats commonly found in North and Central American seagrass meadows may be an example, as may be the algal accumulations often associated with eutrophic waters. This can be easily tested experimentally, using both nitrogen-enriched and unriched algae with a variety of consumers.

Are there latitudinal differences in the stimulatory effects of elevated nutrient inputs on epiphytic algae (e.g., more impacts in cold than warm climates because grazers may not be able to "catch up" to algae in environments with short growing seasons)? This may be the case, and there is an on-going multi-investigator study of the relative effects of top-down and bottom-up effects in Swedish waters (Baden and Moksnes, personal communication) that can help answer this question.

4. Benthic–pelagic coupling in seagrass meadows

Early descriptions of the fauna of seagrass meadows noted the presence of many suspension feeders, including those attached to leaves such as hydroids, bryozoans and ascidians, as well as those living in and on the sediments, such as bivalves and polychaetes (see Kikuchi and Peres, 1977; Kikuchi, 1980; Ogden, 1980 for summaries of the early seagrass literature). However, the first attempt to assess the effect of suspension feeders on the phytoplankton in the waters bathing seagrass meadows was not conducted until 1996. In this study, Lemmens et al. (1996) used estimates of filtration rates and biomasses of suspension feeding animals, including those attached to seagrass leaves and those inhabiting the benthos, made from meadows dominated by three different species of seagrasses to calculate how much suspended material was being filtered from the water column in each. In the two meadows containing the greatest number of filter feeders, one dominated by *Posidonia sinuosa* and the other by *Amphibolis antartica*, Lemmens et al. (1996) concluded that the resident filter feeders could clear the overlying water column daily and at least partially control the density of suspended organic matter within these seagrass meadows.

Reusch et al. (1994), Reusch (1998) and Allen and Williams (2003) studied interactions between suspension-feeding mussels, both native and exotic, and seagrasses, and concluded that dense seagrass meadows could negatively affect the growth of mussels by as much as 2/3 via the baffling of water by the seagrass canopy and the subsequent reductions in food supply. Peterson and Heck (1999, 2001a,b) investigated interactions between semi-infaunal mussels and seagrasses and found that mussel feces and pseudofeces enriched the nutrient concentrations of pore waters, and this in turn enhanced the growth of turtlegrass, *T. testudinum*. At the same time, elevated numbers of mesograzers supported by mussel aggregations reduced the biomass of seagrass epiphytes through the feeding activities,

which also enhanced seagrass growth rates. In turn, the mussels received protection from predators by living in and among the seagrass root–rhizome layer and survived at higher rates that in unvegetated substrates (Fig. 7). However, none of these studies with mussels followed up on Lemmens et al. (1996) suggestion that suspension feeders reduce the volume of suspended materials in the waters surrounding seagrass meadows, and that this reduction in suspended materials could lead to the enhanced growth of seagrasses via increased light penetration of the water column.

A recent study by Peterson et al. (in press), however, has considered how reductions in the abundance of larger suspension feeders might have influenced water clarity and indirectly, the abundance of seagrasses in Florida Bay, USA. Peterson et al. (in press) hypothesized that a large seagrass die-off in the late 1980s in Florida Bay (Fourqurean and Robblee, 1999) could have been partially a result of a large die-off of filter feeding sponges. Using laboratory obtained filtration rates for the dominant sponge species in Florida Bay, combined with field surveys to obtain biomass estimates, Peterson et al. (in press) calculated that at previously reported densities, sponges could filter the water column every 3 days prior to the die-off, whereas after the die-off this would take around 15 days. They also suggest that the recent, on-going phytoplankton blooms in Florida Bay might be explained by the loss of sponges from the system, and this in turn could explain the failure of seagrasses to recolonize some portions of the Bay. This study was the first to establish the positive effects of suspension feeders on water clarity in seagrass meadows.

4.1. Future investigations of benthic–pelagic coupling

Much remains to be learned about how suspension feeders may influence water clarity and indirectly influence the growth and abundance of seagrasses. Among the most immediate needs are more field experiments with different species of filter feeders and seagrasses, and subsequent measurements of changes in water clarity. In addition, more studies are needed to quantify both the potential positive and negative interactions between different types of filter feeders and seagrasses, primarily due to shading by epiphytic filter-feeding species such as bryozoans and ascidians, and also by competing for space belowground by infaunal or semi-infaunal species of mussels and other suspension feeding bivalves. It seems most likely to us that low to moderate densities of suspension feeders of both types will be found to have positive effects on seagrasses but that very high densities of either are likely to produce negative effects. One could imagine that as negative effects led to reduced seagrass densities, recruitment of epiphyte suspension feeders would decline as the leaf area and substrate available for settlement declined, just as the survival of benthic species would decline as shoot and rhizome density decreased and the loss of structure allowed elevated success of predators such as crabs and predatory

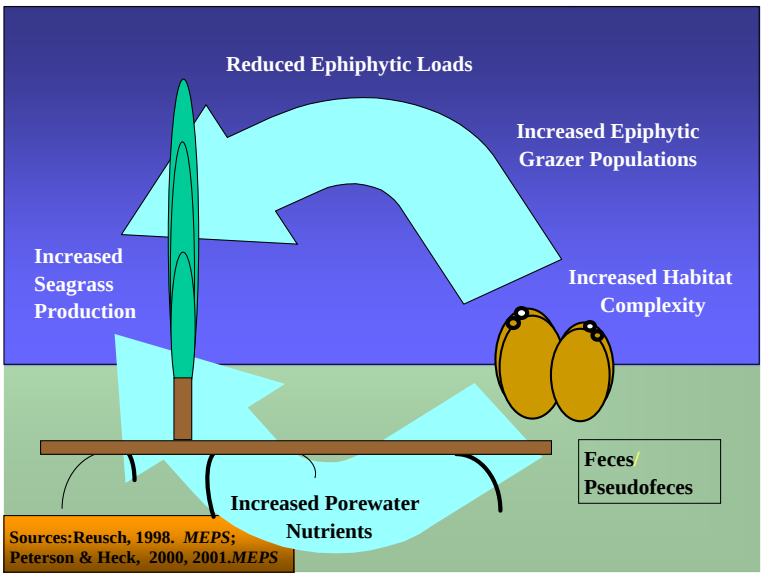

Fig. 7. Simplified representation of the effects of suspension feeding semi-infaunal mussels (*Modiolus americanus*) on turtlegrass (*Thalassia testudinum*) in the northern Gulf of Mexico (after Peterson and Heck, 2001b).

gastropods. The net result of these changes should be the stable coexistence of seagrasses and suspension feeders, including those that live attached to leaves and those living in the seagrass rhizosphere.

5. Conclusions

The impacts of herbivory on all types of primary producers associated with seagrass meadows have been previously underestimated, and this includes estimates of consumption of seagrasses themselves, as well as epiphytic and planktonic algae. In the future, more manipulative experiments are needed to elucidate the effects of nutritional quality and chemical defenses on the consumption patterns of diverse types of herbivores. In addition, the effects of herbivory on plant chemistry, morphology, reproductive biology and species composition need more study, as do the effects of both direct and indirect interactions among plants and herbivores, especially in sub-tropical and tropical locations. This list, while by no means complete, includes what we believe to be the priority topics for additional studies of plant–herbivore interactions in seagrass meadows.

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