

Effects of manatee herbivory on seagrasses

Sirenian are large marine mammal feeding exclusively on plants. West Indian manatees are widely distributed, exploit all available habitats (marine, estuarine and freshwater systems), and are known for their diverse feeding habits. Adult specimens are able to ingest 4-9% of their body weight daily (Bengtson, 1983).

Seagrasses support major detritus-based food chains in many coastal waters, providing nutrients for a number of invertebrates and fish (Short et al., 2007). Only a few species of animals graze on living seagrasses, and apparently only a small portion of the energy and nutrients in seagrasses is usually channeled through these herbivores. The general paucity of direct seagrass grazers may be a function of several factors in the composition of seagrasses, including availability of nitrogen compounds, presence of relatively high amounts of structural cell walls and presence of toxic or inhibitory substances (Thayer et al., 1984). The widespread occurrence and persistence of modern day seagrass habitats has led many to hypothesize that grazing on seagrasses is minimal. On a global scale this may well be true as the numbers of large vertebrate herbivores (e.g. sea turtles, manatees and dugongs) and waterfowl, grazers that can greatly alter seagrass density, have been dramatically reduced in coastal ecosystems. Nonetheless, numerous observations indicate that it can be different at smaller scale (Kirsch et al., 2002). Sirenians graze destructively by uprooting seagrasses or by cropping their leaves (Marsh et al., 1999). Due the large size of the manatee, and its great capacity of feeding on seagrasses, a concern is raised about the effects of reintroducing manatees in a seagrasses ecosystem. The objective of this document is to summarize the potential effects of manatee feeding on seagrass meadows and associated fauna (see also the explanatory chart). A comprehensive review on this matter have been previously done by Marsh et al (2011).

Reduction of seagrasses biomass and compensatory responses

Two modes of manatee feeding behavior on seagrasses have been observed: rooting and grazing. While rooting, manatees consume entire plants; the vegetation is grasped with the mouth at the edge of a shallow ridge of sediment and the forelimb is used to dig into the sediment at the side of the mouth. While grazing, manatees consume blades without disturbing roots or sediments. (Packard, 1984).

The obvious effect of manatee grazing is the substantial reduction of plant biomass (Packard, 1984). However, plants can develop induced responses (changes that occur as a result of herbivore damage), involving both tolerance and resistance traits (Vergés et al., 2008). Low and moderate fish herbivory has demonstrated to induce substantial compensatory responses in marine seagrasses, such as enhanced growth through mobilization of internal resources (Vergés et al., 2008). It is expected that the same is true for the plant species eaten by sirenians (Marsh et al., 2011). Aragonés and March (2000) showed that a seagrass community under dugong feeding pressure exhibited a relatively rapid recovery, even when the grazing was intensive.

Natural disturbances such as sedimentation water scouring, or "die-off" from disease, flooding or cyclones may cause a uniform loss of tropical seagrasses over large areas. Meadows suffering such losses take years to recover (Preen et al., 1995). In contrast, grazing disturbance is limited by the feeding behavior of the grazer. Manatees appear to prefer feeding patches with relatively high biomass (Hartman, 1979), moving to another patch when the biomass overpasses the nutrient threshold, thus allowing the recovery of impacted areas. This behavior would tend to reduce further impact areas previously disturbed (Bengtson, 1983), and to favor disturbance on abundant species over rare plant species (Packard, 1984). Preen (1995) observed that the presence of seagrass patches of less than 1m² interspersed across quite large areas which have been severely disturbed by dugongs. These patches of seagrasses survive even the most intensive regime of grazing, forming a reserve which is not accessible to dugongs. This "ungrazable reserve" is the key to seagrasses recovering within months from intensive dugong grazing.

(Aragones & Marsh 2000). That 'cultivation grazing' maximizes the abundance of seagrass species that are preferred by dugongs, at the expense of less preferred species. Heavy grazing pressure converts the meadows to a lower serial stage, dominated by a more palatable, grazing tolerant species, probably resulting in a higher carrying capacity. This grazing pattern appears to be a deliberate strategy to improve the quality of the dugong's diet (Preen, 1995b). Nevertheless, there is some indication that, when the biomass is reduced below some threshold level, recovery is hampered (Lefebvre and Powell, 1990).

Species composition

Herbivory by manatees could also change species composition of seagrass communities where rooting occurs more frequently than grazing. The creation of gaps can alter the composition of seagrass communities by favoring the growth of pioneer genera of seagrass (Aragones and Marsh, 2000). For example, in Florida when *Thalassia* rhizomes are removed, bare patches are invaded more quickly by *Syringodium* and *Halodule*. Thus, manatee disturbance would tend to maintain species diversity in seagrass communities by creating bare patches favoring species common to early successional stages (Packard, 1984).

Detritus cycle and nutrients

Through rooting, sirenians can modify intensively the substrate structure, which eventually can lead to an increase in nitrogen fixation rates. Excavating dugongs aerate the substrate and mix some of the detritus with sediment, producing a substrate for bacterial nitrogen fixation (Perry, 1996). There are also some clues that seagrasses productivity, especially underground (rhizome and roots), may be facilitated by increased nitrogen fixation stimulated by dugong rooting (Masini et al., 2001). Green sea turtles, which graze only on shoots and not rhizomes, are believed to have a positive effect on the seagrass community by short-circuiting the detritus cycle and increasing the rate of return of nutrients to the seagrasses (Thayer et al., 1984). Seagrasses respond to cropping or clipping of leaves by increasing nitrogen levels and decreasing levels of fiber. Grazing and

cropping has the capacity to alter the subsequent nutrition quality of seagrass regrowth (Aragones & Marsh 2000). Aragones et al., 2006 examined the effects of simulated light and intensive grazing on eight nutritionally relevant measures of seagrass chemical composition. Some species showed an increase in the leaf N concentration of 30% after a year, while the fiber concentration decreased. Also, it has been speculated that the clouds of suspended sediment caused during feeding by dugongs may redistribute nutrients stimulating productivity surge (Masini et al., 2001)

The potential importance of nutrients returning to grassbeds in manatee fecal material is probably high in some areas (Lefebvre and Powell, 1990). Defecation could provide a rapid recycling path for nutrients (Thayer et al., 1984). However, this source of nutrients is perhaps less important in areas where the tidal flushing is rapid (Lefebvre and Powell, 1990), and may be functionally more important in transferring nutrients to adjacent ecosystems than in supplying nutrients to the seagrass beds (Castelblanco-Martínez et al., 2012).

Effects on associated fauna

There have been few studies on the effects of sirenian feeding on benthic animals in seagrass communities (Marsh et al., 2011). Sirenian feeding effects on benthic fauna could be direct (by ingestion) or indirect (by affecting the substrate structure or by competition). Dugongs often deliberately feed on benthic invertebrates, such as ascidians, polychaetes and bivalves (Preen, 1995a). Also, some observations have suggested that manatees actively or incidentally consume invertebrates (Courbis and Worthy, 2003). However, it is unlikely that invertebrate ingestion by manatees would be important enough to impact negatively benthic fauna. Manatees affect seagrass community structure through intense herbivory and disturb the sediment by rooting (Heinsohn et al., 1977), consequently affecting the community structure of small benthic organisms (Thayer et al., 1984). In addition, because the feeding scars remain for weeks or months, it is possible that this disturbance may induce secondary indirect effects on the benthic community by altering habitat structure (Marsh et al., 2011), or by fragmentation of benthic population. Nakaoka et al., 2002

investigated the effect of dugong grazing on benthic organisms, and found a decreasing in abundance after grazing. However, delayed and/or indirect effects of dugong herbivory on benthic communities have not been detected. The effects of manatee grazing on benthic fauna is not clear.

An artificial trophic model created to analyze the impact of West Indian manatees in an estuary suggested that competition for resources between manatees and other groups is insignificant owing to the fact that other groups are exploiting a variety of energy sources, while manatees exclusively exploit primary producers (Castelblanco-Martínez et al., 2012). For instance, most of the species of benthic invertebrates in this specific ecosystem were detritivorous or omnivorous; and only a few of fish species were exclusively herbivorous.

Additional observations

There is an important geographical variation in the foraging strategies of manatees, as shown by its diet composition (Reich and Worthy, 2006). This is due to the wide distribution and large variety of habitats where manatees occurs (Lefebvre et al., 2001). The more elaborate dentition of manatees may be one of the factors enabling it to exploit a wider variety of food plants than the dugong (Marsh et al., 1999), which diet consists almost entirely of seagrasses (Marsh et al., 1982). Also, the vibrissal-muscular complex of manatees has evolved to increase the efficiency of browsing on aquatic vegetation and to fully maximize the potential of the manatee as a generalist feeder (Marshall et al., 1998). Differently to the seagrass-eater dugongs, manatees are generalist/opportunist herbivores feeding on submersed, floating and riparian vegetation. In estuary areas, manatees can exploit riparian vegetation like mangrove (Castelblanco-Martínez et al., 2009). Thus, impact of manatees feeding would not be exclusively on seagrasses but also on other types of vegetation available.

Conclusions

- Although the notion that herbivory invariably has a negative impact on plant communities has been raised, manatees may have significant positive effects on grazed area by (1) their role in enhancing nutrient recycling or short-circuiting the detritus cycle, (2) the maintenance of seagrasses diversity by allowing the creation of successional stages, (3) the increase of nutritional quality of grazed seagrasses through changes in the nutrient concentration of regrowth.
- The negative impacts on seagrasses due to manatee feeding can be attenuated by several processes: (1) seagrasses under intensive grazing may produce compensatory responses such as enhancing growth through mobilization of internal resources in seagrasses, (2) manatees feed on patches with higher biomass, moving to another patch when the biomass overpasses the nutrient threshold, thus allowing the recovery of low biomass areas/species ('cultivation grazing'), (3) manatees are opportunistic feeders, and are able to exploit several type of vegetation, and not exclusively seagrasses beds.
- The impacts of manatee herbivory on all types of primary producers are not completely described. In the future, more manipulative experiments are needed to explain the effects of manatee herbivory on seagrasses. Seagrasses ecosystems dynamic could vary depending on the location, therefore local experiments should be conducted.
- It is even less understood how manatee feeding affects associated fauna in seagrasses communities and further studies should be addressed in this regard. However, it is possible to speculate that the effect by direct consumption is not considerable.
- The present sizes of most populations of manatee species are believed to be significantly smaller than they were in the early nineteenth century (Marsh et al., 2011). For that reason, it is believed that extant manatee populations are far to reach the carrying capacity of the ecosystems. Even though manatees are large-body

exclusively herbivorous aquatic mammals, it seems unlikely that a small population could negatively impact the seagrass communities and associated fauna.

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EFFECTS OF MANATEES ON SEAGRASSES COMMUNITIES

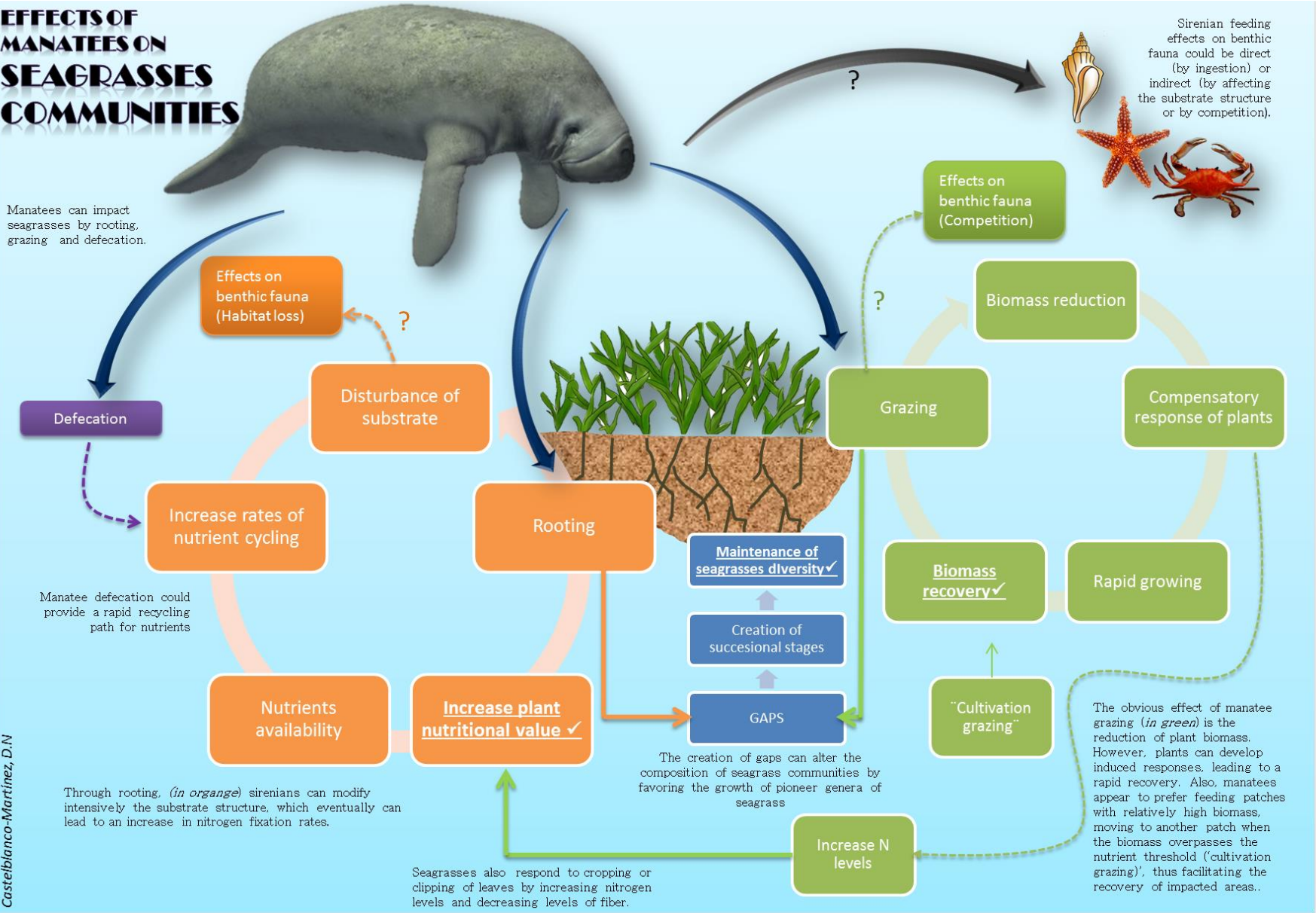
Manatees can impact seagrasses by rooting, grazing and defecation.

Manatee defecation could provide a rapid recycling path for nutrients

Through rooting, (*in organge*) sirenians can modify intensively the substrate structure, which eventually can lead to an increase in nitrogen fixation rates.

Seagrasses also respond to cropping or clipping of leaves by increasing nitrogen levels and decreasing levels of fiber.

Sirenian feeding effects on benthic fauna could be direct (by ingestion) or indirect (by affecting the substrate structure or by competition).



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