## 1

# The Role of Sirenians in Aquatic Ecosystems

LEMNUEL V. ARAGONES, IVAN LAWLER, HELENE MARSH,
DARYL DOMNING, AND AMANDA HODGSON

The role of sirenians in aquatic ecosystems is largely a function of their feeding ecology. Sirenians are large herbivorous aquatic mammals that often congregate and, being mammals, have high energetic requirements relative to other marine herbivores. An adult dugong can weigh from 250 to 600 kg[1], while the West Indian and West African manatees both range between 350 and 1,400kg[2], and the Amazonian manatee from 200 to 480kg[3]. Consequently, sirenians consume significant amounts of aquatic vegetation. They also display dietary preferences in regard to plant species, individual plants, and parts of plants[4,5]. Thus dugongs and manatees have the capacity to alter the nutritional quality and species composition of the plant communities upon which they feed[6].

In this chapter we provide an overview of the geographic ranges of sirenians, their food types, and their adaptations to utilizing these foods. We then consider the effects of sirenians feeding on plant communities based on small-scale studies and experiments. Finally, we discuss the likely significance of these effects when scaled up to the level of populations, and the consequential impacts on plant communities.

### Distribution and Abundance

Extant sirenians range from the tropics to the subtropics, their distribution largely determined by a species' thermal tolerance and the distribution of their food (map 1.1).

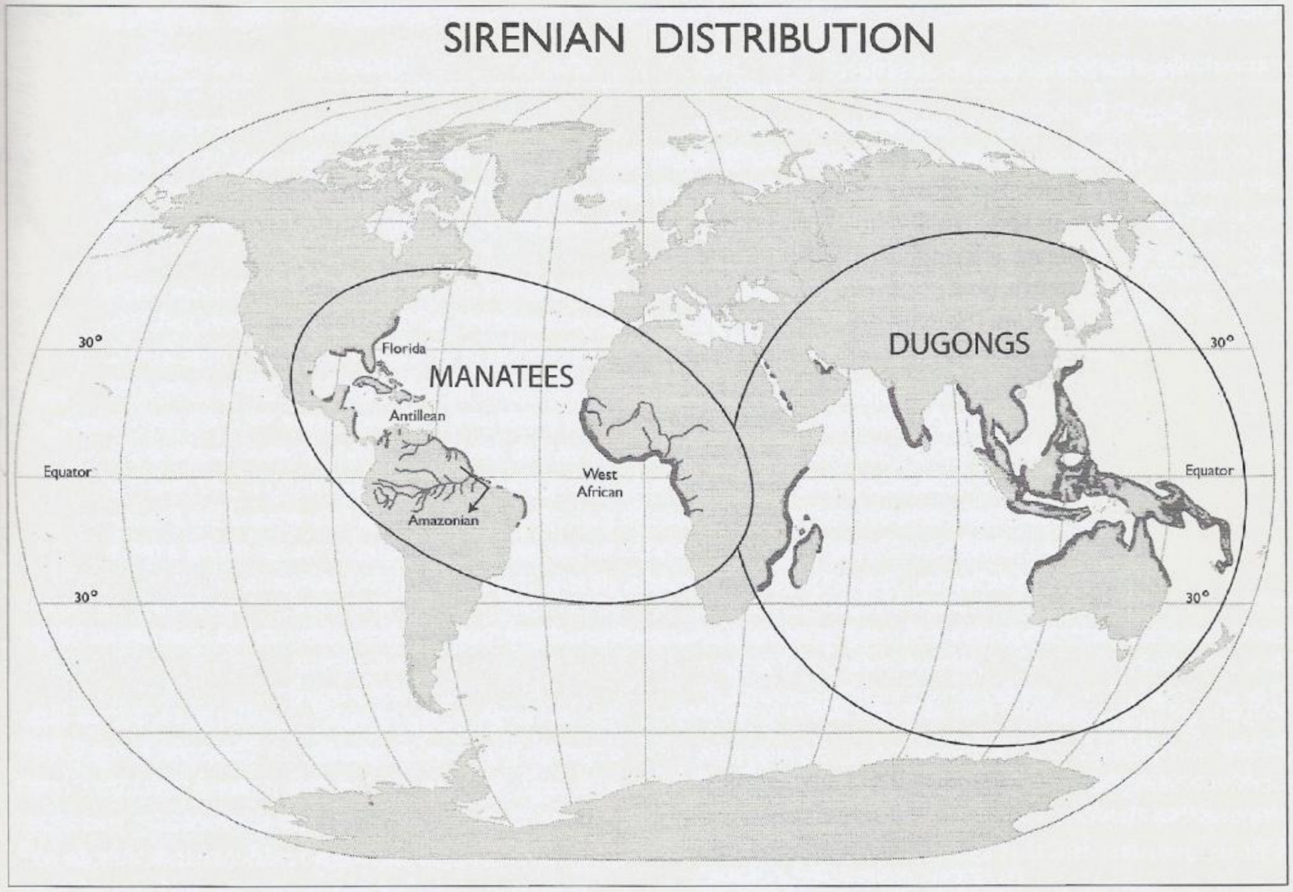
The present population sizes of all sirenian species are believed to be significantly smaller than they were in even the recent past[7]. While it is reasonable to assume a consequential reduction in the role of sirenians, we believe they still significantly affect the ecology. An individual sirenian must consume about 4–25% of its body weight per day[8]. It is estimated that a dugong consumes 28–40 kg of seagrass per day[9]. In the Moreton Bay region of Australia the calculated median biomass of seagrasses on which dugongs feed is 12.3 g dry matter/$m^2$; each dugong overturns on the order of 401.5 $m^2$ of seagrass each day[10]. In the Great Barrier Reef region the biomass of the seagrasses on which dugongs feed ranges from 5.8 to 10.4 g dry matter/$m^2$ [11] and a dugong is estimated to overturn 263–904 $m^2$ of seagrass each day[12]. An adult manatee can consume about 5.9 kg/day dry weight of the seagrass *Syringodium filiforme* each day, an amount equivalent to about 50 $m^2$ per day[13]. Thus even an individual sirenian has some capacity to influence the dynamics of the plant community on which it feeds.

While sirenians have been reduced over most of their ranges, they may still occur at locally high densities. Herds in excess of 200 dugongs are seen in Moreton Bay (Queensland), where they were estimated to dig up more than a square kilometer of seagrass every week[14]. The winter aggregations of Florida manatees, in warm-water areas, may also cause significant grazing impacts in nearby vegetation[15].

Prehistoric sirenians were not only more abundant than modern sirenians, but they were also much more diverse in the numbers of species and morphological variation among those species. For example, five or more sympatric (occurring in overlapping geographical areas) lineages of dugongids inhabited the West Atlantic–Caribbean region during the later Tertiary (approximately 25 million years ago)[16]. Such diversity implies greater and more complex impacts on plant communities than occur today, including faster recycling of nutrients, with less primary productivity passing through the detrital (where decomposition takes place) pathway; consequent increases in plant species diversity and biological productivity; and selection pressures favoring evolutionary adaptations of plants to herbivory (including changes to growth forms, chemical defenses, life strategies, and modes of reproduction, germination, and dispersal)[17].

### Diet

Dugongs are seagrass specialists, feeding almost exclusively on marine angiosperms rooted to the sea bottom[18]. In contrast, manatees tend to vary their habitat and diet.



Map 1.1. Global sirenian distribution. (Map by Ellen McElhinny.)

The West Indian manatee (and presumably the West African manatee) feeds on a wide array of freshwater and marine plants[19] (see table 1.1); indeed the Florida manatee has been documented to feed on more than 60 species of freshwater, marine, and even terrestrial plants[20]. The Amazonian manatee feeds mainly on emergent freshwater plants, as the rapid reduction of light penetration inherent in the Amazonian system limits the growth of submerged vegetation[21]. The marine/freshwater dichotomy has a strong influence on the foods used by sirenians.

The facial morphology of sirenians reflects their feeding strategies and diets[22]. Dugongs have the strongest rostral deflection and are specialized for bottom feeding. The Amazonian manatee has the least deflection and prefers to forage at the surface[23], while the Antillean and the West African manatees have intermediate rostral deflections, which enable them to feed throughout the water column, from bottom feeding on seagrasses[24] to cropping emergent terrestrial grasses and herbs growing on banks[25].

The dentition of sirenians is also adapted to their diets. Steller's sea cows had no teeth[26]. The dugong's dentition is suggested to be of little use, with the horny pad playing the major role in breaking down food[27]. In contrast, the six to eight cheek teeth in each manatee (*Trichechus* spp.) jaw quadrant are constantly being replaced horizontally in an apparently limitless monophyodont (having only one set of teeth) series of supernumerary molars[28]. Despite its simple dentition, the dugong is as effective at masticating seagrasses of the genera *Thalassia* and *Halodule* as the Florida manatee[29], an achievement that presumably reflects the efficiency of its entire masticatory apparatus[30]. Domning suggested that the elaborate system of molar replacement of the three manatee species evolved in response to the tooth wear caused by siliceous phytoliths in the true grasses (Gramineae)[31]. Together with their more horizontal mouths, the more elaborate dentition of the manatees may be one of the factors enabling them to exploit a wider variety of food plants than the dugong.

### Diet in Marine Environments

Seagrasses, the predominant food of dugongs and manatees, are marine vascular flowering plants (angiosperms) rather than true grasses. There are 50–60 known species

**BOX 1.1**

## Rostral Deflection in Sirenians

Daryl P. Domning

A prominent feature of the sirenian skull is the enlarged snout, or rostrum, formed mainly by the premaxillary bones. This structure supports the nostrils and nasal passages; the large, fleshy upper lips and their tactile and prehensile vibrissae; and, on its underside, the horny pad that (with its counterpart on the lower jaw) serves as a cropping mechanism in feeding.

This rostrum is bent downward to varying degrees, relative to the plane of the palate and cheek teeth, in different species. The degree of deflection reflects the typical diet: 15°–40° in African manatees and 25°–41° in Amazonian manatees (both of which feed largely on floating or emergent freshwater vegetation), and 29°–52° in West Indian manatees (which feed on seagrasses). The bottom-feeding dugong, a seagrass specialist, has the most downturned snout at around 70°. For swimmers with a low metabolic rate such as sirenians, constantly tipping the head up to breathe and down to feed wastes energy, while keeping the body axis horizontal as much as possible is economical. Hence, the position of the mouth is permanently adjusted to minimize movements of the body. A mouth that opens almost straight downward like the dugong's is suited to bottom-feeding, while a diet located higher up in the water column selects for a more moderate rostral deflection. This principle also provides clues to the diets of extinct sirenians.

worldwide[32]; dugongs and manatees eat about 15 species of them[33] (table 1.1).

Most information on sirenian diets comes from the dugong and the West Indian manatee, particularly the Florida manatee, and that bias is reflected in the information presented here. Dugongs show strong and consistent preferences among species of seagrasses[34]; manatees are more generalist browsers and appear to forage opportunistically but selectively where their preferred seagrass is available[35].

Generally, dugongs show preferences for species characteristic of lower seral (intermediate phase found in ecological succession) stages of seagrass communities, especially species of the genera *Halophila* and *Halodule* (see table 1.1). These genera respond well to disturbance, grow quickly[36], and invest little in structural material. The seagrass species favored by dugongs are typically lower in fiber and higher in protein than climax species such as *Zostera* or *Enhalus*[37]. When dugongs feed on *Halophila* and *Halodule*, they typically consume the whole plant, uprooting it from the substrate and leaving characteristic feeding trails[38] (figure 1.1).

In some regions dugongs feed on higher-biomass species of seagrass such as *Syringodium*, *Cymodocea* and *Thalassia*, and consume mostly the aboveground leaf material, especially if the substrate is too compact or the seagrass too robust to allow them to uproot whole plants. For example, in winter in Shark Bay, Western Australia, dugongs move into deeper, warmer water where their usual food species are unavailable. In these areas they switch to feeding on *Amphibolis* and strip the leaves from the stems[39]. Similarly, in Torres Strait dugongs may feed primarily on *Thalassia hemprichii*[40]. Although adult male dugongs possess tusks that could potentially be used to break up the substrate and access seagrass rhizomes, there is no evidence that they do so[41].

Manatees may choose seagrass on the basis of its accessibility and availability. *Halophila* spp. and *Halodule wrightii* are often found in shallower waters and are often easily accessible[42]. In Jupiter Sound (Florida), manatees have been observed to graze on mixed seagrasses, including *Halodule*, *Syringodium*, and *Thalassia*[43]. In areas devoid of seagrass because of high turbidity, and during the winter season, manatees feed opportunistically on any available vegetation including algae, mangrove leaves, and other terrestrial vegetation[44], especially when they aggregate in warm-water refuges. The seagrasses in winter refuges are at their lowest seasonal biomass[45] and are vulnerable to depletion by feeding manatees. Freshwater plants such as *Ruppia maritima* and cord grass are other possible alternatives[46].

There are important exceptions to the sirenians' focus on seagrasses. At the high latitude limits of their range, dugongs have been recorded feeding on ascidians and polychaetes during winter and spring, perhaps a response to their increased energy requirements due to lower temperatures and the seasonal reduction in seagrass biomass[47]. While animal material may be found in the stomach contents of tropical dugongs, analysis of stomach contents suggests that it is consumed incidentally while seagrass foraging[48]. West Indian manatees have also been reported to consume

**Table 1.1. General summary of the distribution, habitats, and diet of sirenians.**

| Species | IUCN Status | Distribution | Habitats | Diet | Source of Information |
|---|---|---|---|---|---|
| Dugong (*Dugong dugon*) | Vulnerable | Tropical and subtropical Indian and Pacific Oceans | Seagrass meadows; coastal waters | Seagrasses: *Halophila ovalis, H. minor, H. spinulosa, H. decipiens, Halodule uninervis, H. pinifolia, Syringodium isoetifolium, Thalassia hemprichii, Zostera capricorni, Cymodocea serrulata, C. rotundata, Enhalus acoroides*<br>Algae (intermittently) | Wake 1975; Marsh et al. 1978, 1982; Lanyon 1991; Preen 1993; Aragones 1994, 1996; de Iongh 1995; Suwanpanid 1999; Spain and Heinsohn 1973; Heinsohn 1981; Whiting 2002 |
| Steller's sea cow (*Hydrodamalis gigas*) | Extinct | Subtropical to cold temperate Pacific Ocean | Kelp beds | Algae likely included in diet: *Agarum cribrosum, A. pertusum, Thalassiophyllum clathrus, Nereocystis luetkeana, Halosaccion glandiforme, Constantinea rosa-marina, Alaria praelonga, Laminaria saccarhina* | Domning 1978 |
| West Indian manatee (*Trichechus manatus*) | Vulnerable | Tropical to subtropical western Atlantic Ocean (southeastern USA to southern Brazil), including Orinoco basin | Riverine and coastal waters | Seagrasses: *Halophila ovalis, H. decipiens, H. johnsoni, Halodule wrightii, Syringodium filiforme, Thalassia testudinium, Zostera marina*<br>Algae (genera only): *Acetabularia, Chaetomorpha, Chara, Cladophora, Ectocarpus, Enteromorpha, Gracillaria, Halimeda, Hypnea, Oscillatoria, Penicillus, Polysiphonia, Sargassum, Spirogyra, Udotea, Ulva*<br>Other vegetation: *Alternanthera, Eichhornia, Hydrilla, Lemna, Pistia, Ruppia, Salvinia, Spartina* | Hartman 1971, 1979; Thayer et al. 1984; Lefebvre et al. 1989; Provancha and Hall 1991; Lefebvre and Powell 1990; Hartman 1971; Campbell and Irvine 1977; Bengtson 1981; Ledder 1986; Hurst and Beck 1988 |
| West African manatee (*T. senegalensis*) | Vulnerable | Tropical to subtropical eastern Atlantic Ocean (Senegal to Angola and Niger-Benué basin) | Riverine & coastal waters | Seagrasses: *Cymodocea nodosa, Halodule wrightii*<br>Grasses (genera only): *Alternanthera, Echinochloa, Paspalum, Pennisetum, Phragmites, Pistia, Polygonum, Rhizophora, Ruppia, Typha, Vossia* | Reeves et al. 2002 |
| Amazonian manatee (*T. inunguis*) | Vulnerable | Amazon River and its tributaries | Riverine | Aquatic and semi-aquatic vascular plants | |

ascidians[49], bryozoans and hydroids[50], and to scavenge fish from nets[51].

Marine sirenians feed incidentally on algae[52] when seagrass resources are reduced. Following cyclones, which cause seagrass losses from wave action and sedimentation or turbidity blocking light, dugongs in Australia have been recorded eating significant amounts of algae[53]. However, large undigested fragments in stomach contents and in feces indicate that these are poorly digested[54]. Whiting provides the only account of tropical dugongs consistently feeding on algae in Australia, but the number of dugongs involved was very low and seagrass was locally scarce[55].

The only other modern dugongid is the giant (9–10 m in length) Steller's sea cow (*Hydrodamalis gigas*), which was exterminated by 1768, 27 years after its discovery. Steller's sea cow was also exclusively marine but mainly browsed on kelp, the large brown and red algae that dominates the cold-water, high-energy habitats of its former North Pacific range[56]. Steller's sea cows followed

Figure 1.1. Dugong feeding trail. (Courtesy of Taro Hosokawa.)

the general sirenian pattern of resorting to an algal diet only when angiosperms were unavailable: the ancestors of *Hydrodamalis* ate seagrass before this resource was eliminated by habitat change in the North Pacific[57].

### Diet in Freshwater Environments

In freshwater systems, manatees have access to a variety of aquatic plants ranging from floating and emergent to submerged forms[58]. Species of terrestrial true grasses and shoreline plants are also potential food items, especially when they are plentiful. These grasses are rooted macrophytes found underwater and along river banks. Other available plant parts, such as tree leaves, are also eaten[59].

The only exclusively freshwater sirenian, the Amazonian manatee, eats a wide variety of aquatic and semi-aquatic vascular plants[60]. Food availability in the Amazon basin is affected by seasonal changes in water levels. In the rainy season (December to June), water levels are high and food is abundant. In the dry season (July to November), water levels drop drastically, making food scarce[61]. In response, Amazonian manatees may feed on dead vegetation or fast[62].

Both West Indian and West African manatees are capable of thriving in freshwater systems for extended periods and are even thought to be dependent on access to freshwater[63]. The West African manatee feeds primarily on emergent grasses from the genera *Vossia*, *Echinochloa*, and *Paspalum*[64]. In freshwater systems, Florida manatees apparently feed on any dense vegetation they can access[65], including *Hydrilla*, a not-so-nutritious submerged aquatic plant (~92% water)[66], eelgrasses (*Vallisneria*), and cord grass (*Spartina*) (see table 1.1, and see Hurst and Beck[67] for a comprehensive list). Manatees in the Blue Spring area, a natural spring with sparse floating and submerged vegetation, will even feed on acorns (mast) from the oak (*Quercus virginiana*)[68]. Mast (fruit) is a good source of fats, sugar, starch, and protein and apparently augments the low nutritional quality of freshwater vegetation.

## Effects of Grazing

The main role of sirenians in the aquatic ecosystem is herbivory; that is, grazing and/or browsing. Grazing is the act of ingesting a large proportion (≥90%) of the plant structure in grasses and other monocotyledons. Browsing is the act of ingesting leaves and branches of trees, shrubs, and forbs. Most if not all sirenians are capable of destructive grazing and browsing. Grazing is the more damaging, and bottom feeders such as the dugong and the West Indian and African manatees can uproot whole plants. Amazonian manatees are accomplished grazers and browsers on submerged and emergent aquatic vegetation.

Herbivory influences plant morphology, productivity, distribution, and community structure in terrestrial[69] and aquatic[70] systems. The effect of sirenian herbivory on seagrass depends on grazing intensity.

### Effects of Grazing on Plants

Our main approach in explaining the role of sirenians in the ecosystem is to draw generalizations and parallels from information on dugong-seagrass interactions. Most of this information comes from field experiments conducted by Preen[71] and Aragones[72]. Full details of the experimental design and effects on seagrass communities are more widely available in Aragones and Marsh[73], and effects on nutrient composition are in Aragones et al.[74]. In these experiments two levels of dugong grazing and turtle cropping were simulated in seagrass beds in tropical Queensland, Australia. One level was "intensive dugong grazing," which represented a favored dugong feeding site, wherein almost all aboveground biomass was removed, leaving a small amount of belowground biomass. Another level, "light intensity dugong grazing," was simulated by removing three evenly-spaced 15 cm wide feeding strips (each resembling a typical dugong muzzle width) within each experimental unit (1.0 $m^2$).

### Effects of Grazing on Biomass

The herbivory experiments showed that dugong grazing can change the biomass of seagrass beds, sometimes in counterintuitive ways. A favorite seagrass species, *Halophila ovalis*, increased its aboveground biomass, almost equaling its belowground biomass 10 months after intensive grazing[75]. The leaves of *H. ovalis* are some of the most important food items for dugongs, based on stomach content analysis[76] and observational data[77]. Also, it has one of the highest concentrations of nitrogen among tropical seagrasses[78].

### Effects of Grazing on Community Structure and Composition

The experiments showed that dugong grazing can also have significant effects on seagrass community structure and dynamics. The structure of a tropical seagrass meadow in Australia was altered by both intensive and less intensive dugong grazing. A meadow at Ellie Point, Queensland, changed its species composition from predominantly *Zostera* and *Cymodocea* to *Halophila ovalis*[79]. Likewise, a monospecific seagrass meadow in Moreton Bay shifted from *Zostera* to *Halophila* and *Halodule* after it was intensively grazed by several hundred dugongs[80]. *Halophila* and *Halodule* species are adapted to disturbance because of their relatively short, opportunistic life histories (see table 1.2) which enable them to colonize spaces opened up by grazing. Areas where manatees feed regularly and intensively would be expected to show similar response. Thus grazing by sirenians on seagrass beds can short-circuit the detrital cycle, resulting in mosaics of young plants.

### Effects of Grazing on Detrital Matter

Grazing by dugongs in tropical Australia altered the relative abundance of detrital matter in a seagrass meadow[81]. Intensive dugong grazing resulted in less detritus, presumably because most of the plant material was eaten instead of dying and decaying. We hypothesize that, in contrast, seagrass beds with few or no large grazers are likely detrital-based meadows. The detritus in seagrass meadows is an important source of organic matter and other nutrients, particularly in coastal areas. However, herbivory results in more rapid recycling of nutrients than does decomposition, so it should be even more beneficial to a community's productivity. Feeding by sirenians aerates the soil and mixes some of the detritus with soil, providing a substrate for bacterial nitrogen fixation[82], increasing seagrass productivity.

### Effects of Grazing on Nutritional Quality

The response of seagrasses to grazing disturbance also initiates physiological processes that alter the chemical

**Table 1.2. Relative growth rates, from published literature, of some Australian tropical seagrasses (from Aragones and Marsh 2000).**

| Species | Specific growth rate (% per day) | Turnover time (days) | Source |
|---|---|---|---|
| *Halophila ovalis* | 4.0–9.0 | 11–24 | Hillman and McComb 1988 |
| *Zostera capricorni* | 0.8–3.5 | 33–67 | Kirkman et al. 1982 |
| *Cymodocea rotundata* | 2.5–4.0 | 25–40 | Brouns 1987 |

composition of the plants. These changes are likely to complement the detrital cycling enhancement. However, the lack of a definitive set of determinants of food quality is a barrier to understanding the impacts of their grazing on seagrass nutritional quality. As for most herbivores, all chemical measures of food are only proxies for animal performance. For sirenians, obstacles to determining the effects of feeding strategies more precisely are ethically and logistically prohibitive as this would require experiments using captive animals. We measured a range of chemical constituents widely held to be important for a range of herbivores. We considered carbohydrates (energy), nitrogen (protein), and *in vitro* dry matter digestibility (IVDMD—a functional measure inversely related to levels of indigestible fiber). We also observed behavioral indicators from the dugongs themselves, assuming that preference for a feeding area indicates the presence of higher quality food.

In our experiments, *Halophila* and *Halodule* were the main genera that showed interesting changes in nutritional qualities as a result of grazing. The whole-plant nitrogen concentrations of *Halophila ovalis* and *Halodule uninervis* increased by 35 and 25%, respectively, even after almost a year of recovery from intensive grazing. However, these gains were tempered by diminishing returns in starch concentrations, making it difficult to conclude decisively whether the nutritional quality of these seagrasses increased or decreased.

Despite our imperfect knowledge of the determinants of nutritional quality for dugongs, we can interpret the above changes as improvements. The key nutrients for herbivores are usually energy (as starch, carbohydrates, etc.) and/or protein (measured as nitrogen, N). However, the relative importance of each will vary. Simulated and actual grazing consistently lead, broadly speaking, to reduced starch concentrations but higher N concentrations. Dugongs show a common tendency to re-graze areas[83], suggesting that they take advantage of the increased nitrogen concentration despite the concomitant decrease in starch.

Why does dugong grazing alter nitrogen and starch concentrations? The causes are twofold. First is the plant growth response. After grazing there is a simple increase in the proportion of new foliage with less structural material, which leads to increased N concentrations, while mobilization of energy reserves in rebuilding the aboveground biomass leads to reduced starch concentrations. Second, detrital cycling leads to higher bacterial N fixation rates in grazed areas[84] and, presumably, to enhanced tissue N concentrations in seagrasses.

### Cultivation Grazing

The effects on seagrasses described in the preceding section explain the phenomenon of cultivation grazing[85], which occurs when herbivory, such as by dugongs, enhances the chemical attributes and digestibility of plants. Grazing dugongs produce serpentine feeding trails approximately 20 cm wide and 3–5 cm deep[86] (see figure 1.1), a strategy that presumably enables them to sample the spatially heterogeneous seagrass beds typical of the tropics yet prevents overgrazing because some belowground biomass is left as a vegetative source of regrowth. Aragones et al.[87] consider the effect of bacterial nitrogen fixation in the seagrass beds created by grazing disturbance to be the key to cultivation grazing. This behavior introduces detritus into the sediment, aerating it and providing substrate for N fixation. Sediments from grazed areas show higher N fixation rates than those from matching ungrazed areas, and these differences are explained largely in terms of aerobic N fixation rates[88]. This process has no known terrestrial analogue.

Meadows with high-quality seagrass are easier to find if they are large—and the more animals that graze, the larger the grazed area they create, which enhances further grazing. This is the most likely reason dugongs go back to the same feeding grounds and/or regularly or intermittently rotate their feeding grounds. For dugongs grazing in Moreton Bay in Queensland, Preen[89] documents variable return times ranging from 17 days to 5 months.

### Dugongs and the Optimal Grazing Hypothesis

In terrestrial systems, there is a growing agreement that under some conditions, aboveground net primary productivity is maximized at some optimal grazing level[90]. The "grazing optimization hypothesis" can also apply in the marine environment, though the feedback loops may vary[91]. On land, herbivores may provide positive feedback to plants via local-scale inputs of feces and urine. In the marine environment these materials tend to be moved by currents, so positive feedbacks depend on the enhancement of the detrital cycle. Although total detritus may decrease in areas where grazing occurs, the physical action of dugong feeding introduces detritus and aeration into the sediment. Together, these two promote the activity of N-fixing bacteria. Nitrogen fixation rates in grazed seagrass are the highest recorded for any seagrass community[92].

In the study by Aragones and Marsh[93], *Halophila* *ovalis* showed an increase in aboveground biomass productivity, while *Zostera capricorni* showed a decrease. As *Halophila* is favored by dugongs, while *Zostera* is not, this shows that both *Halophila* and dugongs are benefited by this effect. Plants growing at a rate close to their maximum growth capability have less opportunity to respond positively to grazing than plants with growth rates below maximum. This result suggests that *H. ovalis* has a greater capacity to compensate for dugong grazing than the other species studied and may be a species tolerant of herbivory[94].

The effect of dugong grazing on seagrass community composition is determined by how soon the dugongs come back and the relative recovery rates of individual species. Recovery of seagrasses from grazing disturbance depends on the timing and intensity, species composition and location within the bed, and occurrence of any additional disturbance[95]. In a mixed seagrass bed, *Halophila ovalis* recovered fastest, followed by *Halodule uninervis*, and then *Z. capricorni*. As shown in table 1.2, *H. ovalis* has faster growth and turnover than *H. uninervis* or *Z. capricorni*. Tropical seagrasses appear to recover quickly from grazing even when they are grazed during the winter, when growth is supposedly slowest[96]. In subtropical Moreton Bay the effect of timing of grazing on recovery was more pronounced than in tropical areas, presumably because of the more pronounced seasonality.

## Conclusion: The Role of Sirenians

As we have shown for dugongs, sirenian grazing can have demonstrable effects on the community structure, productivity, and chemical composition of food plants. It seems likely that most sirenians are capable of producing similar grazing disturbances. Their importance is a function of the scale, both temporal and spatial, over their range and the numbers of animals occurring in local areas. Sirenians in the past presumably played a significant role in originally structuring the plant communities on which they feed, and they continue to do so in areas where their population densities remain high.

The widespread reduction in the sizes of most dugong and manatee populations has presumably altered plant communities, especially in areas not affected by other forms of physical disturbance. Presently, it is impossible to assess the ecosystem significance of the decline in populations as there are few data on the state of those systems prior to the reduction in sirenian populations. Perhaps the salient question is rather: do changes in plant communities after the removal of sirenians reach a threshold state beyond which sirenians are incapable of reinhabiting the area? We hope that conservation initiatives are sufficient to prevent that question from ever being answered.