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Consumption of Aquatic Plants by the West Indian Manatee

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ABSTRACT

Because manatees (*Trichechus manatus*) are large aquatic herbivores they have often been considered as potential control agents for aquatic plants. Several problems are associated with this concept, and a major one has been the gap in knowledge concerning food consumption rates of manatees. We estimated food consumption by measuring chews per unit time, chews per amount of food consumed, and time spent chewing food. Data were collected on captive manatees of various sizes and used to construct regression equations that predict consumption rates based on body size. Time budget data were obtained by radiotelemetry of free-ranging animals. Estimates of consumption rates for manatees eating hydrilla (*Hydrilla verticillata* Royle) were compared to the estimated biomass of hydrilla in Kings Bay, Florida, the overwintering site for a large manatee population (116 in the winter of 1980-1981). Estimates show that nearly ten times as many manatees would have been needed just to consume the standing biomass of hydrilla. The inefficiency of manatees as control agents for aquatic plants becomes even more apparent when plant productivity is included in these estimates.

Key words: Hydrilla, aquatic herbivores, biological control, food intake.

INTRODUCTION

Knowledge of food consumption rates is essential in understanding the energetics and ecology of any animal. This information is especially important in the case of the endangered West Indian manatee (*Trichechus manatus* Linnaeus), because food requirements must be known for successful habitat management, and because these aquatic herbivores have often been considered as potential control agents for aquatic plants.

Interest in the West Indian manatee as a biological control agent of aquatic macrophytes became a topic of international interest (Dill, 1961) when it was revealed that manatees had been used to clear weed-choked canals in Guyana (formerly British Guiana) since 1885 (Allsopp, 1960, 1961). In the 1960's several qualitative experiments were undertaken to determine the effectiveness of manatees as control agents of aquatic plants (Sguros, 1966; MacLaren 1967; Allsopp, 1969). These trials indicated that manatees could keep limited areas clear of aquatic weeds, but several problems were identified that limited their broader use. The more important of these problems were that manatees required year round warm water (Sguros, 1966), they had to be confined to the specific area requiring clearing (Allsopp, 1969), and their density had to be greater than 0.74 individuals per hectare (Dill, 1961). Despite widespread optimism for using manatees to control aquatic plants (Bertram and Bertram, 1966, 1968; Vietmeyer, 1974), the problems have not been overcome and manatees have not been widely used for this purpose.

Actually, little attention has been given to the biological factors that cause manatees to be ineffective control agents of aquatic plants. Perhaps the most basic question that has received little attention is "how much do manatees eat?" Estimates for wet weight food consumption by captive manatees range from 5 to 11% of body weight per day (Best, 1981), but these data cannot be extrapolated to free-ranging animals, which eat different foods and have higher activity levels. Until recently (Bengtson, 1983), no one has attempted to quantify food consumption in free-ranging manatees. The techniques used by Bengtson and in our study are similar to those employed by others investigating the consumption rates of large herbivores in which the number of times an animal chews its food is related to food consumption (Belovsky and Jordan, 1978). Our study differs from Bengtson's in two major ways. First, we measured consumption rates of hydrilla, whereas Bengtson measured consumption rates of waterhyacinth (*Eichhornia crassipes* Solms.), water lettuce (*Pistia stratoites* Linnaeus), and vallisneria (*Vallisneria americana* Michx.). Hydrilla is a major pest plant in Florida, and it forms a large portion of the diet of the manatees that aggregate during the winter in the head waters of the Crystal River in Citrus County, Florida (Hartman, 1979). Second, we adjusted consumption rates based on body size, whereas Bengtson (1983) determined a mean consumption rate for a sample of animals of undetermined body size.

METHODS

Feeding manatees make audible chewing noises that can be monitored with a hydrophone. We attempted to determine relationships between the amount of food that is ingested, number of chews per unit time, and total number of chews. We measured the number of chews per unit time in both free-ranging and captive manatees. Chew rates of manatees in Crystal River were monitored from November 1980 through March 1981, on 12 occasions. Feeding manatees were approached quietly by boat and a hydrophone was lowered into the water such that the chewing sounds of an individual manatee could be heard. Approximately 12 to 15 manatees were observed at different times, but because individuals were not identified, some manatees may have been sampled more than once. (The chances of sampling an animal more than once were small because more than 100 animals were present in Kings Bay that winter.) Chews per

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unit time were counted during bouts of chewing and a mean chew rate for these manatees was obtained. In addition, three free-ranging, radio-telemetered manatees. Gus (CR#108), Pickle (CR#41) and Bert (CR#23), were followed and chew rates were recorded for these animals. Six captive manatees (four adults and two juveniles) kept at Sea World in Orlando, Florida, were individually tested between January 1981 and June 1981 (see Table 1).

The number of chews required to ingest a specific amount of hydrilla was measured for each of the captives at Sea World. Plants were collected fresh within 24 hours of feeding trials. Each sample was shaken to remove excess water and weighed to the nearest gram in 25 g, 50 g, 100 g, and 200 g portions. Ten samples of each weight were fed to an isolated manatee and the number of chews required to consume each sample was recorded. Trials in which manatees appeared to be satiated were discarded. Using the data from captive animals, regression equations were developed to predict chew counts from body weight. One captive manatee was also fed vallisneria to obtain comparative values for this plant species.

In January, February, and March of 1981, the three radio-tagged manatees at Crystal River were followed and their behavior observed to obtain an estimate of the amount of time spent feeding. Each animal's behavior was monitored 24 hours a day for 7 days during tracking. The radio signal occasionally was attentuated when a manatee entered salt water, and at other times behavioral observations were impossible due to fog, darkness, or other factors. Time budget data therefore indicate only the minimum amount of time an individual manatee spent feeding.

RESULTS

Mean chew rates (chews/second) were similar for free-ranging and captive manatees (Table 2). Except for Marina, captive manatees showed an increase in chew rate with a decrease in body size. Statistical correlation was not significant however, possibly due to small sample size.

The mean number of chews required to consume *Hydrilla* (Table 3) varied inversely with body weight. The strongest relationship was between chews per 25 g and body weight, which is stated as follows ($r^2 = 0.755$, $p = 0.02$):

$$\log \text{chews per } 25 \text{ g} = 3.14 - 0.67 (\log \text{body weight}).$$

TABLE 1. CAPTIVE MANATEES USED FOR FEEDING EXPERIMENTS AT SEA WORLD, ORLANDO, FLORIDA.

Name	Date of capture	Capture locality	Age at capture	Mass at time of testing (kg)
Violet	13 Aug. 1980	Homosassa River, FL	newborn	120
Caloosa[1]	27 June 1980	Fort Myers, FL	1-2 years	148
Marina	9 Aug. 1979	Daytona Beach, FL	newborn	181
Lucy[1]	27 June 1980	Fort Myers, FL	adult	421
Gene[2]	16 Feb. 1977	Satellite Beach, FL	adult	431
Nerdine	18 Sept. 1977	Crystal River, FL	adult	1066

[1]Mother and calf.
[2]Gene was the only captive male.

TABLE 2. CHEW RATES OF FREE-RANGING AND CAPTIVE MANATEES.

	Number of chewing bouts[1]	Mean chews/second ± SD
Free-ranging manatees:		
Pickle	8	1.94 ± 0.06
Burt	6	1.80 ± 0.05
Others[2]	54	1.85 ± 0.12
Captive manatees:		
Violet	13	2.20 ± 0.11
Caloosa	17	1.99 ± 0.08
Marina	10	1.59 ± 0.06
Lucy	33	1.83 ± 0.11
Gene	10	1.80 ± 0.10
Nerdine	10	1.68 ± 0.11

[1]Chewing bouts were periods of continuous chewing lasting a minimum of 30 seconds.
[2]Includes 12 to 15 unidentified animals in Kings Bay, Crystal River, Florida.

Table 4 summarizes the results of a two-way factorial ANOVA that compares consumption rates for four quantities of hydrilla and vallisneria eaten by a captive manatee (Nerdine). Mean chew counts were higher for wild celery at all four quantities, but differences were significant ($p < 0.05$) only at 100 g and 200 g.

The amount of time during which radio-telemetered animals were observed feeding is shown in Table 5. Bert was the only animal for which consistent data were obtained, and he fed for a mean of 267 ± 70 minutes per 24 hour period. Radio signals from the other two animals often were lost, and only the minimum amount of time spent feeding could be determined. Individual manatee behavior varied from day to day, and much variability in habits was noted among the three manatees.

DISCUSSION

Food consumption rate. Data from the captive animals indicate an inverse relationship between body size and number of chews per unit food consumed. Calves may chew faster than adults, but must chew many more times to consume the same amount of food. Larger animals can get more food into their mouths at one time, have a larger grinding surface area, and presumably a more forceful chewing motion. Bengtson (1983) reported a slower mean chew rate of 1.05 chews per second (compared with a pooled mean of 1.86 chews per second in this study) for manatees at Blue Spring in Volusia County, Florida. This could be due to the fact that he fed test animals a variety of plants including waterhyacinth and water lettuce, both of which float and require more manipulation by manatees than submersed vegetation. Manatees feed on hydrilla in a grazing manner and may chew it faster than waterhyacinth, which they often manipulate in their flippers and eat by cropping off the leaves (Hartman, 1979).

The variation in observed feeding times among the three radio-telemetered animals is due to differences in their movement patterns. Gus was difficult to follow because he moved long distances and often ventured into salt water where the radio signal was lost. However, when he was ob-

TABLE 3. MEAN NUMBER OF CHEWS REQUIRED BY CAPTIVE MANATEES TO CONSUME HYDRILLA. SAMPLE SIZE WAS 10 UNLESS OTHERWISE INDICATED.

Manatee	Body mass (kg)	Mean number of chews per plant mass ± S.D. 25 g	50 g	100 g	200 g
Violet	120	120.6 ± 13.6[1]	269.0 ± 21.0[2]	—	—
Caloosa	148	45.3 ± 5.2	87.7 ± 8.7	192.5 ± 21.2	—
Marina	181	34.7 ± 3.0	78.8 ± 13.8	—	—
Lucy	421	20.3 ± 2.3	26.4 ± 3.5[3]	46.0 ± 5.3	85.6 ± 5.4
Gene	431	24.8 ± 2.0	44.2 ± 5.3	93.2 ± 4.3	—
Nerdine	1066	16.4 ± 3.2[4]	27.3 ± 3.9	39.2 ± 3.1	78.9 ± 4.2

[1]n = 5
[2]n = 6
[3]n = 9
[4]n = 9

served closely, he spent less time feeding than the other two animals. The signal from Pickle was also lost several times due to prolonged forays into salt water. Bert was the easiest to follow since he restricted his movements to a smaller area in fresh water. Bert spent an average of four and one half hours each day feeding, an amount of time similar to the mean of 5 hours/day spent feeding by Blue Spring manatees from January to March (Bengtson, 1983).

It has been reported that manatees feed 6 to 8 hours per day (Bertram and Bertram, 1964; Hartman, 1979). The longest we observed any radio-telemetered animal feeding in a 24 hour period was 6 hours and 10 minutes. As we have shown, vallisneria requires more chews/gram for consumption than hydrilla. Varying nutrient levels in different food plants could also affect the amounts consumed. Bengtson (1983) reported that the number of hours manatees fed varied seasonally, possibly due to changes in their nutritional needs, to temperature, or to forage quality.

The data obtained on food consumption rates and time spent feeding can be combined to calculate an estimate of total daily food consumption for individual manatees of known body size (Table 6). Food consumption rates were calculated using the mean chew rate for free-ranging manatees, and the regression equation relating body weight to number of chews per 25 g of hydrilla consumed by captives. Error in these estimates may be introduced by the small sample size of captive animals available, and by the limited success in obtaining a time budget from radio-telemetered manatees. For our calculations, feeding time was estimated to be 5 hours per day based on our data and Bengtson's study (1983).

Adult manatees can eat approximately 7.1% of their own body weight in wet weight hydrilla in 5 hours of chewing time (Table 6). Bengtson (1983) estimated that manatees feeding an average of 5 hours per day would consume 4 to 9% of their body weight in wet vegetation. Feeding time is not equivalent to chewing time however, because some time is spent moving to new patches of vegetation and

TABLE 4. CHEWS ($\bar{x}$ ± SD) REQUIRED BY NERDINE TO CONSUME VARIOUS QUANTITIES OF HYDRILLA AND VALLISNERIA.

Plant species	Plant mass 25 g	50 g	100 g[1]	200 g[1]
hydrilla	16.4 ± 3.2 (n = 9)	27.3 ± 3.9 (n = 10)	39.2 ± 3.1 (n = 10)	78.9 ± 4.2 (n = 8)
vallisneria	20.1 ± 2.4 (n = 10)	30.2 ± 2.8 (n = 10)	51.0 ± 4.8 (n = 10)	91.0 ± 5.5 (n = 10)

[1]Differences between consumption rates of hydrilla and vallisneria were significant only at 100 g and 200 g quantities (2-way factorial ANOVA, $p < 0.05$).

TABLE 6. ESTIMATED RATES OF HYDRILLA CONSUMPTION FOR THREE SIZE CLASSES OF WEST INDIAN MANATEE.

Size class	Estimated mean weight (kg)[1]	Chews/ 25 g hydrilla[2]	Kg/hr hydrilla[3]	Kg/5 hrs hydrilla	% Body weight consumed in 5 hrs
calf (≤175 cm)	54	95.3	1.7	8.5	15.7
juvenile (176-275 cm)	271	32.3	5.2	26.0	9.6
adult (>275 cm)	637	18.2	9.1	45.5	7.1

[1]Calculated using regression equation from the Sirenia Project, U. S. Fish and Wildlife Service: log weight = −4.700 + 3.012 log length.
[2]Calculated from regression equation: log (chews/25 g) = 3.14 − 0.67 log (body weight).
[3]Hydrilla consumption in kg/hr = $\frac{1.85 \text{ chews/sec} \times 3600 \text{ sec/hr} \times 0.025 \text{ kg/25 g}}{\text{chews/25 g}}$.

TABLE 5. TIME SPENT FEEDING BY RADIO-TELEMETERED MANATEES AT CRYSTAL RIVER.

Manatee	Sex	Feeding time (min/24 hrs) for days 1-7: 1	2	3	4	5	6	7	Total	Mean min/ 24 h
Bert	Male	300	145	220	280	290	265	370	1869	267 ± 70
Gus[1]	Male	230	65	65	0	0	55	65	480	68 ± 77
Pickle[2]	Female	380	160	65	60	—	115	—	780	—

[1]Gus moved more than the other two manatees, and on some days he did not appear to feed at all.
[2]Pickle was "lost" for long periods after the first four days of tracking, and may have fed on days 5 and 7.

manipulating plants. The food consumption of manatees can most accurately be estimated using this technique if the amount of time spent chewing and the body weights of the manatees are known.

Manatees as plant control agents. Because numerous data are available on both the manatee population and macrophyte biomass in Kings Bay, Florida, this system will serve as our model for a discussion of manatees as control agents for aquatic plants. Kings Bay is the clear, spring-fed headwater of the Crystal River, and is used by a large number of manatees as a warm-water refuge from November through March (Kochman et al., 1983). Kings Bay supports several species of submersed aquatic plants, including coontail (*Ceratophyllum demersum* Linnaeus), water lettuce, Eurasian watermilfoil (*Myriophyllum spicatum* Linnaeus) and Southern naiad (*Najas guadalupensis* Magnus). However, about 80% of the bay's plant biomass is composed of the introduced hydrilla (Haller and Shireman, 1982), which is the principal food of manatees in Kings Bay (Hartman, 1979).

During the winter of 1980-81, a maximum aerial count of 116 manatees was made in Crystal River (Powell and Rathbun, in press). Based on individually recognized manatees in the bay during the same winter, the number of animals in each of three relative age classes was estimated to be 55 adults (>275 cm), 49 juveniles (176-275 cm), and 12 calves (≤175 cm) (U.S. Fish and Wildlife Service, unpubl. data). Using the estimated mean body weights for manatees in each size class (U.S. Fish and Wildlife Service, unpubl. data) the total biomass of the 116 manatees in Kings Bay was calculated to be 48,962 kg for the 1980-1981 winter. Using predicted rates of hydrilla consumption for each size class (Table 6), we estimated that the 116 manatees in Kings Bay would consume about 3878 kg wet weight of submersed aquatic plants per day, or an average of about 33.4 kg per manatee. Haller and Shireman (1982) estimated the standing biomass of submersed aquatic plants in Kings Bay in December 1980 as 5,916.65 metric tons fresh weight (95% confidence limits = 4,224.05 to 7,619.18). Since 80% of this was hydrilla, the average consumption rates for this species were used for our calculation. Using the lower confidence limit as a conservative estimate there was a standing biomass of at least 4.2×10^6 kg wet weight submersed plants. The 116 manatees that wintered in Kings Bay for 120 days (November-March) in 1980-1981 would have had to remain an additional 963 days in order to consume the standing biomass of submersed aquatic plants present in December 1980. Conversely, it would have required 1,050 manatees to consume the standing biomass within 120 days. By some estimates this would constitute nearly the entire Florida manatee population (Brownell et al., 1981).

These estimates do not consider productivity, however, and if even modest productivity is included it becomes quite evident why manatees are not effective plant control agents. Dry weight productivity rates for hydrilla under controlled conditions average 4.9×10^{-3} kg/m²/day (Ryther et al., 1978), and since hydrilla has a 92% water content (Boyd and Scarsbrook, 1975), the wet weight productivity is 6.1×10^{-2} kg/m²/day. If an "average" manatee eats 33.4 kg of hydrilla per day, one manatee could consume the daily productivity of about 550 m² (0.055 ha). Haller and Shireman (1982) determined that 165 ha of Kings Bay were occupied by submersed aquatic plants in December 1980, therefore about 3,000 manatees (18 manatees per hectare) would be required just to maintain the hydrilla at a constant biomass by consuming daily productivity.

Manatees do not rely on emergent or natant aquatic vegetation for food in Kings Bay (Hartman, 1979; pers. obs.), but in other areas, such as South America, natant plants are an important dietary component (Best, 1981). Natant aquatic vegetation has a much greater productivity than submersed plants (Westlake, 1965). For example, an average productivity figure for water hyacinth is about 1.7×10^{-2} kg dry weight/m²/day or about 3.5 times that of hydrilla (Ryther et al., 1978). When this figure for water hyacinth is used in calculations similar to those for hydrilla above, the impracticality of using manatees as the sole means of controlling emergent or natant aquatic plants becomes quite apparent.

How, then, were manatees "successfully" used in Guyana (Allsopp, 1969) and southern Florida (Sguros, 1966) to control aquatic plants? Early proponents of manatees as aquatic plant control agents failed to distinguish between crude and ecological densities (Odum, 1971). Dill (1961) calculated that a crude density of 0.73 manatees/ha would be necessary to achieve aquatic plant control. Unfortunately, data or estimates on the standing biomass of plants and their productivity in the canals where manatees were confined are not available. It is likely that the canals in Guyana and southern Florida were deep and turbid, restricting growth of aquatic plants to the waterway margins. The density of manatees required to keep the canals weed-free probably was calculated using the water surface area (crude density) rather than the water surface area containing food plants (ecological density). Based on "crude density", the estimate of manatees needed to control aquatic plants (0.73 manatees/ha) is much lower than our estimate based on "ecological density" (18 manatees/ha), which was calculated as manatees per hectare of plant cover.

Lastly, the basic ecological limitations of manatees must be taken into consideration. Manatees require warm water year-round, which precludes their use outside of tropical waters or warm springs. Manatees have a low reproductive rate of approximately 1 calf every 2 to 3 years (U.S. Fish and Wildlife Service, unpub. data), and are currently listed as an endangered species throughout their range, so the numbers necessary to successfully control aquatic plants are not available. Finally, manatees have a metabolic rate that is 15 to 20% lower than expected based on body mass (Irvine, 1983). Although manatees are large and impressive animals that appear to eat vast quantities of food, smaller herbivores such as coots, with their higher metabolic rate and greater reproductive output, may actually be more efficient at aquatic plant control.

Although manatees are inefficient at controlling aquatic plants, this should not be interpreted as a mandate to abandon any concern for conserving adequate food supplies for them. Current management practices for hydrilla attempt to achieve maximum chemical control in the fall in order to reduce the following spring's growth. This man-

agement technique applied to Kings Bay would result in a potentially catastrophic depletion of the manatees' food sources during the winter when they are in the bay. Obviously, careful planning and management must be exercised in order to achieve control of aquatic plants while maintaining an adequate food supply for wintering manatees.

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