Journal of Mammalogy, 81(3):649–658, 2000

FOOD-HANDLING ABILITY AND FEEDING-CYCLE LENGTH OF MANATEES FEEDING ON SEVERAL SPECIES OF AQUATIC PLANTS

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Food-handling ability was examined in Florida manatees (*Trichechus manatus latirostris*) feeding on different species of aquatic plants during controlled feeding trials. Subjects were presented with freshwater (*Hydrilla verticillata, Myriophyllum spicatum,* and *Vallisneria americana*) and marine species (*Syringodium filiforme* and *Thalassia testudinum*) of aquatic plants. Food handling was quantified by measuring length of cyclic movements (or feeding cycles) of perioral bristles that manatees use to introduce food into the mouth. Mean feeding-cycle lengths varied, depending on body size of the subject and species of plant being consumed. Rates of food introduction derived from mean feeding-cycle lengths were similar to chewing rates reported by other researchers. Manatees consumed plants with tubular stems and numerous branches faster than plants with flat blades. Food-handling time using perioral bristles differed, depending on the species of plants consumed and was reflected in the mean feeding-cycle length.

Key words: consumption, feeding behavior, herbivory, manatees, perioral bristles, Sirenia

Florida manatees (*Trichechus manatus latirostris*) are obligate herbivores and one of the best-studied sirenians (O'Shea et al. 1995). These herbivores are known for their generalized feeding habits and may ingest >60 species of freshwater and marine plants (Bengtson 1983; Best 1981; Etheridge et al. 1985; Hartman 1979; Ledder 1986). They possess a short muscular snout that is covered by short sinus hairs and modified vibrissae or bristles. These bristles are short, thick, and robust and are organized in several discrete fields in the perioral region (Reep et al. 1998). Among mammals, manatees are unique in using these perioral bristles in a prehensile manner in conjunction with elaborated facial musculature to bring plants into the mouth (Marshall et al. 1998a, 1998b). Manatees use this vibrissal–muscular complex to manipulate a diverse range of structural forms among aquatic angiosperms. Our objective was to examine food-handling ability in captive manatees when presented with 5 species of aquatic plants that represented a wide range of variation of plant morphologies that manatees consume in the wild. We hypothesized that food-handling time (using the perioral bristles) differed, depending on species of plants consumed, and that these differences would be reflected in the mean feeding-cycle length (MFCL).

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Feeding-cycle length was defined as the length of time required to complete 1 cyclic, grasping motion using perioral bristles and associated facial musculature. A typical feeding episode consisted of a repetitive and continuous series of individual feeding cycles. A detailed description of this behavior is given by Marshall et al. (1998b).

MATERIALS AND METHODS

Feeding trials.—Feeding trials were conducted at 3 facilities: Homosassa Springs State Park, Homosassa, Florida; Lowry Park Zoological Gardens, Tampa, Florida; and Sea World of Florida, Orlando. Seventeen animals (5 females, 12 males) were used in our study. Manatees were fed 3 species of freshwater aquatic plants (*Hydrilla verticillata, Myriophyllum spicatum*, and *Vallisneria americana*) and 2 species of sea grasses (*Syringodium filiforme* and *Thalassia testudinum*). Each feeding trial presented 1 species of aquatic plant to a single manatee by use of a Plexiglas feeder; individuals had to consume about 80–90% of all plants presented for a single feeding trial to be considered complete. All plant species were normally consumed by free-ranging Florida manatees.

Feeding trials were conducted between May and August in 1993, 1994, and 1995. A total of 449 feeding trials were conducted once a week at each facility between 0900 and 1500 h. Fresh aquatic plants were novel foods for the captive manatees, and they found them preferable to their normal diet (Romaine lettuce, cabbage, miscellaneous vegetables). Satiation of individuals did not appear to occur during trials. Preliminary trials (in 1993) were conducted using 5 males (Lowry Park Zoological Gardens) and 5 females (Homosassa Springs State Park) during 120 feeding trials. During those trials, freshwater plants (*Hydrilla, Myriophyllum*, and *Vallisneria*) were presented without regard to order, and manatees were allowed to feed randomly. Feeding trials during 1994 were conducted using 3 males (Lowry Park Zoological Gardens) and 3 females (Homosassa Springs State Park). Two hundred and eighty feeding trials were conducted for 10 weeks at Lowry Park Zoological Gardens and 9 weeks at Homosassa Springs State Park. During those experiments, each plant species was presented, 1 at a time, to each individual for 5 feeding trials per animal per day. Feeding trials ($n = 49$) were conducted at Sea World of Florida during 1995. Five male manatees were presented with the same feeding regime as in the 1994 feeding trials. Because of the release of several captive manatees from this facility, individuals were sampled only twice over 6 weeks.

Certain features of the experimental design were intended to minimize introduction of systematic bias into our observations. We randomized the order in which plant species were presented to each manatee during each experimental day. That was intended to decrease the possibility that response of a manatee to the presentation of a particular food during a feeding trial might be influenced by number or type of other species already presented during the same trial (i.e., a species-ordering effect). To avoid confounding effects of plant species and general day-to-day variation in manatee feeding behavior, all 5 plant species were presented to each manatee during each experimental day, except in the pilot study at Homosassa Springs State Park in 1993. For each manatee, experimental day could be regarded as complete blocks with respect to plant species, in the context of a randomized block design.

During 1993 at Homosassa Springs State Park and Lowry Park Zoological Gardens and during 1994 at Lowry Park Zoological Gardens, plants were presented to manatees on a square sheet of Plexiglas (about 80 by 90 cm) with holes drilled at 10-cm intervals. Pieces of plants were pushed into the holes, and the Plexiglas was placed on an underwater viewing window using suction cups. Feeding behavior then was recorded through the window using a video camera. Feeding trials at Homosassa Springs State Park (1994) and Sea World of Florida (1995) utilized a mobile underwater window constructed of polyvinyl chloride plumbing pipe (PVC) and Plexiglas (Fig. 1). A video camera within an underwater video housing (Yashica model KD-H170u Hi8 format video camera; Amphibico underwater housing) was placed within the PVC frame. Four floats were attached to the top of the frame that allowed it to hang just below the water surface. A sheet of Plexiglas with holes drilled through it was attached to the frame in front of the video camera. The video camera recorded movements of the perioral bristles, lips, and jaws while manatees fed from the Plexiglas. That apparatus was used at locations where attaching a sheet of

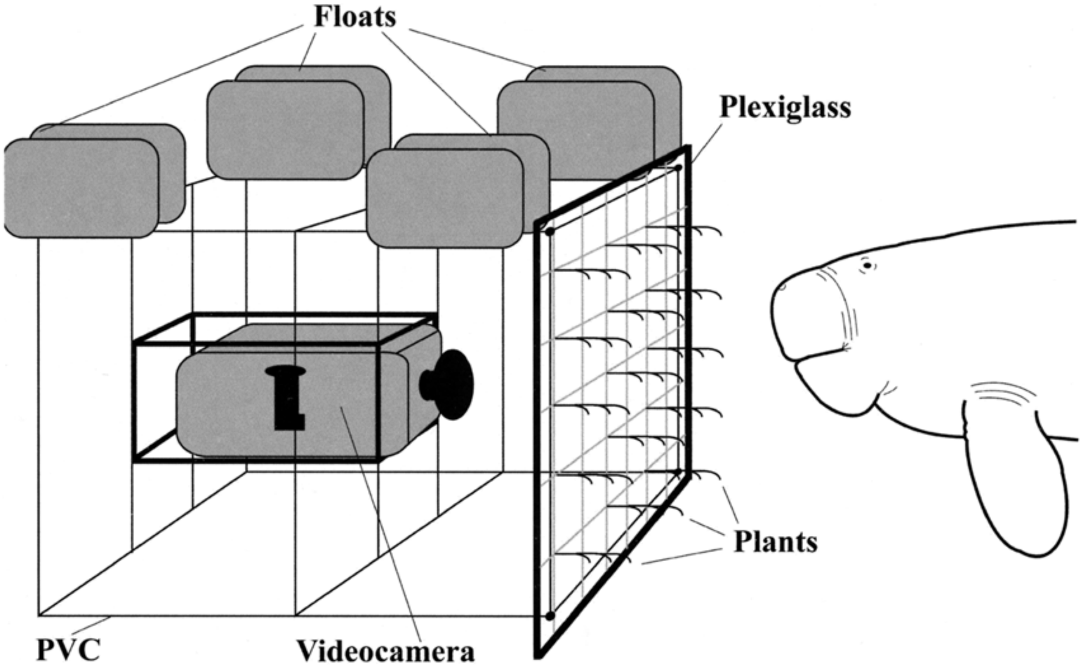

FIG. 1.—Experimental setup using a mobile underwater window to present plants to manatees. The PVC frame holds an underwater video camera directed at a piece of Plexiglas in which vegetation is pushed through the holes. Manatees are videotaped while feeding from the Plexiglas. Floats positioned the apparatus just below the surface of the water.

Plexiglas with suction cups to an underwater viewing window was logistically difficult. It also was useful in leading a single manatee away from several other hungry manatees in the same tank. Manatee feeders were placed in a vertical position. Wild manatees often feed on the surface, in the mid-water column, or on the bottom (Hartman 1979); however, it has been suggested that they prefer to feed on the bottom (Domning 1980). To ensure that feeding on a vertical surface did not generate results that differed from bottom feeding, we videotaped free-ranging manatees feeding on the bottom and captive manatees feeding on an apparatus designed to present plants on the bottom (i.e., PVC frame surrounding a wire mesh through which long stems of plants were woven). Analysis of feeding-cycle length did not produce any significant differences. We chose the vertical manatee feeder because of its logistical ease in capturing close-up footage of the entire perioral region and controlling manatee and order of plant species. In general, free-ranging manatees feed on leaves of aquatic plants; however, they will often feed on rhizomes of sea grasses. Collection and presentation of aquatic plants to manatees were intended to collect data regarding feeding on leaves only.

Analysis of feeding trials.—Videotape was analyzed frame by frame, in slow motion and in real time, to quantify duration of each feeding-cycle for each individual manatee feeding on each plant species. Frame-by-frame analysis was conducted using a Panasonic model AG-7300 S-VHS editor in conjunction with either an IBAS computer imaging system (Kontron Image Analysis Division, Munich, Germany) that supported a black-and-white imaging monitor or a Sony Trinitron model PVM-1350 color video monitor. The MFCL for an individual manatee feeding on a single aquatic plant species was obtained by determining number of video frames that spanned a single grasping event, multiplying that number of frames by the time span of a single frame (1/30 s). Fifty feeding-cycle lengths were averaged per subject per aquatic plant species consumed per day. All measurements were obtained during a consistent period of uninterrupted feeding.

Statistical analyses.—Descriptive and multivariate statistical analyses were performed. Linear-mixed-effects-model analysis (PROC MIXED, SAS Version 6.12—Littell et al. 1996) was used to assess influence of various experimental factors and manatee characteristics on MFCL. Plant species, body length, sex, week of observation, and interactions among those factors and characteristics were modeled as fixed effects. Initial univariate assessment of the association between body length and feeding-cycle length for each plant species revealed a relatively strong exponential relationship in animals >230 cm in body length, which could be linearized by transforming body length to $\ln(\text{body length} - 230 \text{ cm})$. That transformation (TBL) was used in place of body length as a fixed-effects covariate, and the focus of our analysis shifted to the 9 animals (6 from Homosassa Springs State Park and Lowry Park Zoological Gardens in 1994 and 1995, 3 from Sea World of Florida in 1995) with body lengths >230 cm. Year of observation, site of captivity (nested within year of observation), manatee (nested within site of captivity and observation year), and relevant interactions between those factors and fixed effects were modeled as random effects. In modeling the covariance of feeding-cycle length among observation weeks within individual manatee–plant species combinations, we evaluated both compound symmetry and 1st-order autocorrelation structures. In modeling manatee as a random effect, a compound symmetry structure was imposed on the within-manatee covariance of responses among plant species. Modeling began with a core model that included plant species as a fixed effect and manatee-by-plant interaction as random effects. Other fixed or random effects and relevant interaction terms were added individually or in combination and evaluated with regard to the degree to which they accounted for additional variation in feeding-cycle length. The F-test, with approximate degrees of freedom of the denominator determined by the Satterthwaite method (Fai and Cornelius 1996), was used to assess significance of fixed effects and interactions in the model. Contribution of a random effect was evaluated by looking at the change in Akaike's Information Criterion (AIC—Bozdogan 1987) after adding the random effect to a given model. The random effect was retained in the model if its inclusion resulted in a decrease in the absolute value of the AIC. Alternate covariance structures for observation week also were evaluated in that manner. Histograms and normal probability plots of residuals were used to check goodness of fit for the various mixed-effects models considered in the model-building process. A ''final'' model was considered to consist of the core model plus additional significant fixed or random effects and interactions. Standard errors (*SE*) estimated in the final TBL by plant species model were used to generate pointwise 95% confidence bands for TBL regression lines and 95% confidence intervals (*CI*) for MFCL predicted for selected body lengths. Tukey's multiple pairwise comparison procedure was used to maintain an experimentwise significance level of 0.05 for all pairwise comparisons of TBL slopes or predicted MFCL among plant species. To assess and contrast the strength of association between MFCL and TBL among plant species, r^2 was estimated for each plant species by applying inverse-variance–weighted least-squares linear regression to the final mixed-effects-model subject-specific MFCL estimates and *SE*s.

RESULTS

The MFCL of all subjects feeding on all plants from all trials was 613.7 ms (±8.73). Manatees eating *Hydrilla* possessed the shortest MFCL, followed by (in increasing order) *Myriophyllum*, *Syringodium*, *Vallisneria*, and *Thalassia*. The MFCLs for each species are as follows: *Hydrilla* = 593 ms, *Myriophyllum* = 595 ms, *Syringodium* = 615 ms, *Vallisneria* = 618 ms, and *Thalassia* = 646 ms (Fig. 2).

The linear-mixed-effects-model analyses examined the influence of other variables (season of observation, week of observation, site of study, sex, and length of body) on MFCL. The TBL ($P = 0.027$) and sex ($P = 0.048$) interacted with plant species. However, neither interaction remained significant when both were included together in the core model because of a confounding of sex and body length in the study animals (the 3 female manatees in the study also had the 3 longest body lengths: 322, 322, and 328 cm). Because TBL appears to have

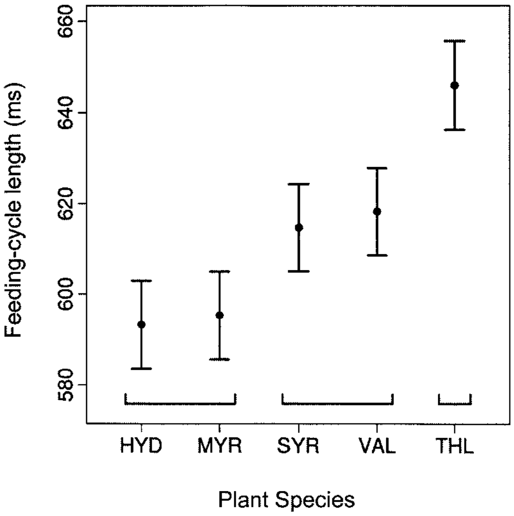

FIG. 2.—Least-squares estimates of MFCL (ms) from a mixed-effects model and corresponding standard errors for 9 Florida manatees feeding on 5 plant species. The MFCL estimates are those that would be predicted at a body length equal to the mean body length for the experimental animals (279.3 cm). Horizontal brackets span MFCLs that do not differ from one another ($P = 0.05$). HYD = *Hydrilla,* MYR = *Myriophyllum,* VAL = *Vallisneria,* SYR = *Syringodium,* THL = *Thalassia.*

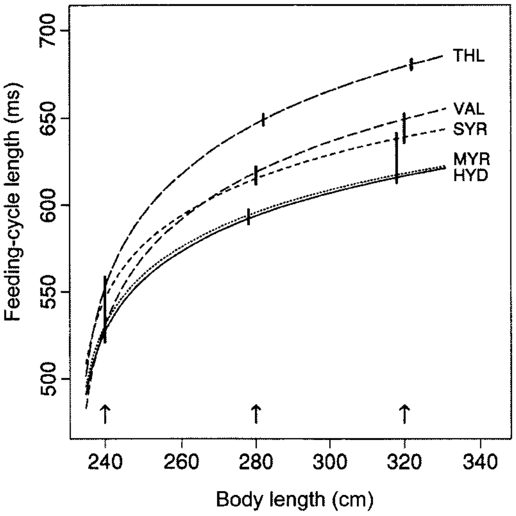

FIG. 3.—Mixed-effects-model regressions for body length (cm) versus MFCL (ms) estimated from observations of 9 Florida manatees feeding on 5 plant species. Regression lines were determined by the linear equation MFCL = $B_0 + B_1 \times \ln(\text{body length} - 231.5 \text{ cm})$, rescaled to body length on the x-axis. Vertical bars span predicted MFCLs that do not differ from one another ($P = 0.05$) at body lengths of 240, 280, and 320 cm (represented by arrows).

a strong linear association with MFCL for each plant species, it was not surprising that sex also would have an association with MFCL. The final TBL by plant model included plant species, TBL, and plant species by TBL as fixed effects ($P = 0.513$, 0.0007, and 0.027, respectively) and manatee by plant as random effects. Season of observation, week of observation, and site of captivity did not account for any additional significant variation or covariance structure in length of feeding cycle beyond that explained by the core model. The choice of the constant to be subtracted from body length in the TBL covariate was adjusted by refitting a series of final models in which the constant varied between 225 and 235 cm at 0.5-cm increments. A constant of 231.5 cm yielded the best-fitting model in that series (the model with the overall smallest random-effects variance and residual variance). The significance of the interaction between TBL and plant species implied that the slope characterizing the linear association between TBL and MFCL differed among plant species. Similarly, the significance of the interaction between sex and plant species implied that the effect of sex in MFCL differed among plant species.

Body length >231.5 cm was the best single predictor of MFCL. The MFCL observed in the 3 manatees with body lengths <231.5 cm did not adhere to the exponential relationship seen in the larger manatees. Overall, differences in MFCL among plant species being consumed increased as body length increased to 320 cm (Fig. 3; Table 1). No differences in MFCL among plants were observed at 240 cm (Table 2), but at a body length of 280 cm, 3 statistically distinct groupings of aquatic plants emerged (*Hydrilla-Myriophyllum, Syringodium-Val-*

TABLE 1.—Mixed-effects-model statistics by plant species for the regression equation: feeding-cycle length = $B_0 + B_1 \times \ln(\text{body length} - 231.5\text{ cm})$.

	B_0 = (ms)			B_1 = (ms/cm)					
Plant	*r*	*SE*	*P*	*r*	PWD[a]	*SE*	*P*	95% *CI*	r^2
Myriophyllum	451.0	31.1	0.0001	37.3	X	8.5	0.001	18.4, 56.2	0.86
Hydrilla	445.1	31.4	0.0001	38.3	XX	8.6	0.001	19.4, 57.2	0.86
Syringodium	461.1	31.1	0.0001	39.7	XX	8.5	0.001	20.8, 58.6	0.79
Vallisneria	422.4	31.1	0.0001	50.6	XX	8.5	0.001	31.8, 69.5	0.85
Thalassia	437.0	31.1	0.0001	54.0	X	8.5	0.001	35.2, 72.9	0.89

[a] Pairwise differences among slopes; columns (X) span slopes that do not differ significantly from one another ($P = 0.05$).

lisneria, and *Thalassia*; Fig. 3). Order of plant species from shortest to longest MFCL was *Hydrilla*-*Myriophyllum*, *Syringodium*-*Vallisneria*, and *Thalassia.* At a body length of 320 cm, *Hydrilla*, *Myriophyllum*, and *Syringodium* did not differ; *Syringodium* and *Vallisneria* did not differ, but *Vallisneria* was significantly different from *Hydrilla* and *Myriophyllum.* Again, *Thalassia* differed from the other plants (Fig. 3). However, the order of ascending MFCLs still was similar (*Hydrilla*-*Myriophyllum*-*Syringodium*, *Syringodium*-*Vallisneria*, *Thalassia*). Predicted values of MFCL extrapolated to 400 cm showed a nonsignificant grouping between *Vallisneria* and *Thalassia*; otherwise, the extrapolation did not produce increased differences in MFCL among plant species.

DISCUSSION

We demonstrated a clear correlation between body length $>$231.5 cm and MFCL. Plots of MFCL versus body length ($>$231.5 cm) resemble a mammalian growth curve. Notably, the approximate body length at which manatees are weaned from their mothers is reported to be 230 cm (O'Shea and Reep 1990). No differences in MFCL among aquatic plants were observed in subjects possessing a body length $\leq$231.5 cm. Subjects with greater body length demonstrated greater differences among plant species overall. Predicted values of MFCL for all aquatic plants increased as body length increased (Table 2). Etheridge et al. (1985: 22) also reported an inverse relationship between manatee consumption (as measured from chewing rates) and body length; "calves may chew faster than adults, but must chew many more times to consume the same amount of food." This difference in chewing rates was attributed to calves having a smaller grinding surface area and smaller mouths. It also is likely that normal allometric and physiological changes in the manatee feeding apparatus (lips, bristles, tongue, jaw, and associated musculature) during growth can explain the correlation between consumption and body length in both studies. For example, Reep et al. (1998:267) noted that "face area [including the oral disk] was strongly correlated with body weight ($r^2 = 0.86$) and length ($r^2 = 0.83$)." As the oral disk increases in size, distance between U2 bristle fields and the gape also increase. The increase in size of the oral disk, distance between perioral bristles and gape, and larger facial and masticatory musculature likely act in concert to alter timing of feeding mechanics.

Although we report on manatee feeding and refer to consumption rates, our data (MFCL) are not rates but durations. Bengtson (1983) and Etheridge et al. (1985) reported consumption rates of manatees based on hydrophone recordings of mastication. Bengtson (1983) reported a mean chewing rate of 1.05 chews/s in free-ranging manatees feeding on water hyacinth (*Eichhornia crassipes*), water lettuce (*Pistia stratiotes*), and *Vallisneria.* Etheridge et al. (1985) reported a pooled mean rate of 1.86 chews/s for manatees feeding on *Hydrilla* and *Val-*

TABLE 2.—Predicted mean feeding-cycle length from the mixed-effects model and pairwise differences among plant species at 4 selected body lengths.

Body length (cm)	Plant	Predicted mean (ms)	PWD[a]			*SE*	95% *CI*	Predicted mean (ms)
240	*Hydrilla*	527.1	X			14.8	495.0, 559.1	537.5
	Vallisneria	530.8	X			14.6	498.9, 562.6	
	Myriophyllum	530.9	X			14.6	499.0, 562.7	
	Syringodium	546.1	X			14.6	514.2, 578.0	
	Thalassia	552.6	X			14.6	520.8, 584.5	
280	*Hydrilla*	539.8	X			9.7	572.2, 615.3	614.1
	Myriophyllum	595.9	X			9.7	574.3, 617.5	
	Syringodium	615.3		X		9.7	593.7, 636.8	
	Vallisneria	618.9		X		9.7	597.4, 640.5	
	Thalassia	646.8			X	9.7	625.2, 668.4	
320	*Hydrilla*	616.8	X			12.5	588.9, 644.7	640.6
	Myriophyllum	618.3	X			12.5	590.4, 646.2	
	Syringodium	639.1		X		12.5	611.2, 667.0	
	Vallisneria	649.4		X		12.5	621.5, 677.2	
	Thalassia	679.3			X	12.5	651.4, 707.2	
400	*Hydrilla*	641.5	X			16.8	604.1, 678.9	668.9
	Myriophyllum	642.3	X			16.8	604.9, 679.7	
	Syringodium	664.7	X	X		16.8	627.3, 702.1	
	Vallisneria	682.0		X	X	16.8	644.6, 719.3	
	Thalassia	714.1			X	16.8	676.7, 751.4	

[a] Pairwise differences among predicted means; columns (X) span means that do not differ significantly from one another ($P = 0.05$).

lisneria. Mean chew rates between captive and free-ranging manatees were found to be similar. For the sake of comparison, MFCLs can be converted to rates by calculating their inverse. Because manatees use perioral bristles in a grasping manner, we refer to this value as a mean grasping rate. Feeding data from Bengtson (1983), Etheridge et al. (1985), and our study and their conversions are summarized in Table 3. Mean grasping rate derived from MFCL herein is 1.63 grasps/s. This value falls between those reported by Bengtson (1983) and Etheridge et al. (1985) and is similar to the mean of these 2 studies (1.45 chews/s). Our calculations are based on manatees feeding on a greater variety of aquatic plants (3 freshwater and 2 marine species) and include 2 species (*Hydrilla* and *Vallisneria*) examined by Bengtson (1983) and Etheridge et al. (1985). It was reported that *Vallisneria* required many more chews per unit time to process compared with *Hydrilla* (Etheridge et al. 1985). The similar finding in this study—a divergent MFCL between *Hydrilla* and *Vallisneria* and between *Hydrilla* and *Thalassia*—suggests that surface area of teeth (or mastication in general) is not the sole variable involved in explaining dif-

TABLE 3.—Summary of manatee feeding data and conversions.

Report	Mean chew/s	Mean grasps/s[a]	Mean feeding-cycle length (ms)
Bengtson (1983)	1.05		952[b]
Etheridge et al. (1985)	1.86		537[b]
This study		1.63	614
Hydrilla		1.69	593
Myriophyllum		1.68	595
Syringodium		1.63	615
Vallisneria		1.62	618
Thalassia		1.55	646

[a] Calculated from mean feeding-cycle length.

[b] Calculated from chews per second.

ferences in consumption rates between species of aquatic plants. It may be that some inherent characteristic (e.g., morphology or number of branches) of *Vallisneria* in the Etheridge et al. (1985) study or *Vallisneria* and *Thalassia* in this study resulted in greater difficulty in introducing these plants into the oral cavity compared to *Hydrilla.* Because mastication requires that food be present in the oral cavity, it is intuitive that introduction of food into the mouth (MFCL) is linked intimately with mastication (chewing rate). Introduction of food into the mouth and mastication each may independently constrain rate of consumption (swallowing). For example, manatees feeding on aquatic plants in this study were observed to introduce plants into the oral cavity and masticate (verified visually and audibly) without interruption. This may imply that aquatic plants were masticated as fast as or faster than introduction of food into the mouth. In contrast, manatees feeding on nonaquatic foods, such as carrots, were observed to introduce food into the oral cavity for a certain period and then stop yet continue to chew. We interpret this behavior to mean that potential rate of food introduction into the oral cavity exceeded rate of mastication. In this case, food must be chewed further before introduction of additional food can occur. Each step toward swallowing (introduction and mastication) may be a rate-limiting step. Manatees feeding only on aquatic plants were never observed to interrupt food introduction into the oral cavity; even while expelling food from 1 side of the mouth, manatees often introduced food into the other side (Marshall et al. 1998b).

Consumption rates of terrestrial herbivores are reported to be influenced by morphological characteristics of plants and anatomical characteristics of feeding apparatus (Cooper and Owen-Smith 1986; Shipley and Spalinger 1992; Spalinger et al. 1988). Other factors, such as fiber content, plant anatomy, and material properties, also may affect handling time and mastication and therefore consumption rates. Our data show a consistent trend such that certain plants require a longer handling time than others. We hypothesize that *Hydrilla* and *Thalassia* are 2 possible endpoints of a spectrum of plant morphologies that influence handling time for the manatees in this study. The MFCLs of *Hydrilla* and *Thalassia* were consistently the lowest and highest, respectively. Structurally, *Hydrilla* possesses a tubular stem and many branches. *Thalassia* lacks a complex branching pattern, and its leaves are flat in cross section (rather than tubular). *Vallisneria* also shares these characteristics with *Thalassia.* Although flattening of blades presumably would increase surface area overall, this increase would occur predominantly in only 2 dimensions; surface area would actually be decreased in the 3rd dimension. We consider *Hydrilla* to be complex in its gross morphology relative to the flat blades of *Vallisneria* and *Thalassia,* which appear simple in comparison. A tubular stem could result in easier grasping by the perioral bristles because of a substantial surface area in all 3 dimensions, whereas a flat, unbranched blade could be more difficult to manipulate from certain directions. Indeed, *Hydrilla, Myriophyllum,* and *Syringodium* all possess tubular stems, and manatees generally exhibited lower MFCLs when feeding on these plants compared to *Vallisneria* and *Thalassia.* Although a tubular versus flat structure among aquatic plants may help to explain variation in MFCL of manatees, it is likely that increased branching is important for ease of manipulation. This would explain differences between *Hydrilla* and *Myriophyllum* (tubular stems and many branches) and *Syringodium* (tubular stem with little relative branching). However, there are many other underlying factors that possibly could account for the observed variation in consumption among aquatic plants by Florida manatees (e.g., material properties, fiber content, and plant morphology).

The biological significance in observed differences in MFCL are best illustrated by considering the 2 extremes: *Hydrilla* and *Thalassia.* At a body length of 400 cm, predicted MFCL of these 2 plants differ by 72 ms, which can be converted to a difference of 0.16 grasps/s. Such apparently minor differences are important to a herbivore that spends large quantities of time each day feeding because differences are magnified the longer the animal feeds. West Indian and Amazonian manatees (*T. inunguis*) typically spend 6–8 h/day foraging (Best 1981); therefore, the difference between *Hydrilla* and *Thalassia* can be as great as 3,645–4,608 grasps/day (6–8 h, respectively). It is clear that over a day of feeding a manatee could consume much more *Hydrilla* than *Thalassia.* What is unclear is the nutritional differences between species of aquatic plants (which change seasonally) and whether manatees benefit energetically from more efficient foraging on *Hydrilla.*

Combined use of modified vibrissae and elaborated orofacial muscles by manatees is a unique mode of feeding among mammals. Organization of facial muscles as a muscular hydrostat (Marshall et al. 1998a) that controls discrete fields of modified vibrissae gives the snout of Florida manatees astounding prehensility and dexterity (Marshall et al. 1998b). Such dexterity could be responsible for success of these marine mammalian herbivores in the past. Foraging on aquatic plants is likely a greater physical and tactile challenge than feeding on terrestrial plants for any herbivore because of the difficulty in gathering large quantities in a short amount of time and constraints of movement within an aquatic environment. Sea grasses and freshwater aquatic plants are ubiquitous but poor-quality foods. The need to attain large body sizes (as an adaptation to the aquatic environment) and reproduce requires consumption of massive quantities of aquatic plants because of their poor nutritional quality. It is probable that sirenians, especially Florida manatees (which are at the northern limit of their range), live on the edge of their energetic needs. Fine-motor control and dexterity of the vibrissal–muscular complex are advantageous for efficient foraging on aquatic vegetation, particularly mixed stands of freshwater vegetation. Selection for a highly dexterous vibrissal–muscular hydrostat complex, which presumably increases aquatic foraging efficiency, is likely to have been as important as hard-structure adaptations (e.g., rostral deflection and tooth-replacement mechanisms) during sirenian evolution.

ACKNOWLEDGMENTS

We appreciate continuing cooperation and assistance of the Sirenia Project (United States Geological Survey), Homosassa Springs State Park, and Sea World of Florida. We thank M. Stoll and S. Paul for their time and assistance in conducting the feeding trials. Assistance with videotape analysis was provided by C. LeClear and L. White. We appreciate cooperation and support of Port Paradise Marina, Crystal River, Florida. This is University of Florida College of Veterinary Medicine journal series 564 and Seahorse Key Marine Laboratory Contribution 74. All work was conducted under United States Fish and Wildlife Service permit number PRT-791721. Freshwater aquatic plant collections were conducted under Florida Department of Environmental Protection permit number 419. Sea grasses were collected under Florida Department of Environmental Protection special permit number S-000308. This work has been sponsored by National Science Foundation grant IBN-9120450 to R. L. Reep.

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Submitted 30 April 1999. Accepted 22 December 1999.

Associate Editor was Renn Tumlison.