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PREHENSILE USE OF PERIORAL BRISTLES DURING FEEDING AND ASSOCIATED BEHAVIORS OF THE FLORIDA MANATEE *(TRICHECHUS MANATUS LATIROSTRIS)*

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Abstract

The use of perioral bristles (modified vibrissae) by 17 captive Florida manatees and approximately 20 wild manatees was analyzed. Captive manatees were fed six species of aquatic vegetation normally eaten in the wild (four freshwater species and two seagrasses). Inanimate objects were placed in the holding tanks with manatees at Lowry Park Zoological Gardens (Tampa, FL) to determine the degree to which perioral bristles were used in exploration and to define the range of manipulative behavior. In addition, behavioral observations were made on the use of perioral bristles during social interactions with conspecifics. Observations were recorded using a Hi8-format video camera. Florida manatees possess an unusually large degree of fine motor control of the snout and perioral bristles. The large and robust perioral bristle fields of the upper lip were used in a prehensile manner during feeding. Bristle use by manatees feeding on submerged vegetation differed from that seen during feeding on floating vegetation. Other behavioral use of the perioral bristles shows variation depending upon the situation encountered. The degree of plasticity of perioral bristle use supports our hypothesis that the

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vibrissal-muscular complex of the Florida manatee has evolved to increase the efficiency of grazing and browsing on aquatic vegetation and to fully maximize the potential of the manatee as a generalist feeder. The manipulative and sensitive nature of the manatee snout is likely a manifestation of a complex sensory and motor system which has evolved for marine mammal aquatic herbivores living in shallow turbid habitats.

Key words: Florida manatee, *Trichechus manatus latirostris*, perioral bristles, vibrissae, feeding behavior.

The order Sirenia (manatees and dugongs) is the only living taxon of marine mammal herbivores. The Florida manatee (*Trichechus manatus latirostris*), a subspecies of the West Indian manatee, is one of the best-studied sirenians (O'Shea *et al.* 1995). Florida manatees are known for their generalist feeding habits and may feed on over 60 species of freshwater and marine vegetation (Best 1981, Packard 1981, Bengtson 1983, Packard 1984, Etheridge *et al.* 1985, Ledder 1986, Hurst and Beck 1988, Provancha and Hall 1991).

Like other sirenians, Florida manatees have an unusual facial anatomy that reflects their aquatic herbivory. Manatees possess a short muscular snout which is covered by short sinus hairs and modified vibrissae or bristles (Reep *et al.* 1998). These modified vibrissae are short, thick, and robust compared to those of terrestrial mammals and are found in the perioral region. Florida manatees use this vibrissal-muscular complex in a prehensile manner to bring vegetation into the oral cavity and to manipulate inanimate objects in their environment. This function of the perioral bristles was first mentioned by Chapman (1875). He described feeding manatees as "fanning" food into their mouths using "bristles situated on their upper and lower lips." Later, Garrod (1877) described the feeding behavior of a captive manatee in greater detail. He referred to the bristle fields as pads and stated that when an animal is about to grab a piece of vegetation, ". . . the pads are diverged transversely in such a way as to make the median gap of considerable breadth." The two lip 'pads' are approximated, grasping the food and drawing it into the mouth by a ". . . backward movement of the lower margin of the lip . . . ." Garrod (1877) described the feeding behavior as being similar to that of a caterpillar feeding upon a leaf. Murie (1880) described the action of perioral bristles as ". . . seize[-ing] {food} with its bristle-clad lips . . . " and having ". . . great mobility and special use of the inner circumscribed bristle-clad portions of the upper lip." Allsopp (1961) compared the feeding behavior to that of ungulates and as moving in a sideways fashion. Ling (1977) simply mentioned that manatee vibrissae are "very mobile." Hartman (1979) stated that the lips are bilobed and covered with bristles and described the action of feeding: "The lobes are everted, projecting the bristles into the food source, then closed laterally, forcing the bristles to grasp the vegetation, tuck it in the cleft between the lobes and funnel it to the mouth."

The use of vibrissae by manatees to manipulate objects in their environment is a departure from the classical function of mammalian vibrissae. Other mammals use vibrissae to detect tactile cues; many pinnipeds employ "whisking" movements for more directed tactile exploration. For example, California sea lions (*Zalophus californianus*) possess extremely mobile vibrissae which can be rotated from the resting position along the side of head to extend almost directly forward from the muzzle (Peterson and Bartholomew 1967). The sniffing behavior and related vibrissal movements during exploration by albino rats involves sweeping of the mystacial vibrissae forward and backwards in conjunction with protraction and retraction of the rhinarium and head (Welker 1964). The modification of manatee perioral vibrissae (bristles) to manipulate food and other objects in a prehensile manner appears to be unique to sirenians. Previous descriptions of the function of Florida manatee perioral bristles are brief and lacking in detail. Our objective was to explore the range of behaviors involving the vibrissal-muscular complex of Florida manatees and to determine the importance of bristle use to the feeding ecology and sensory perception of the animal.

Methods

The range of behavioral plasticity of the muscular snout and perioral bristles of Florida manatees was elucidated using several methods and study sites. Captive manatees were presented with several species of aquatic plants and inanimate objects. Wild manatees were observed at the Crystal River Refuge (CRR), Crystal River, FL, and in the headwaters of the Homosassa River (HR), Homosassa, FL. At these latter study sites, individuals were observed feeding upon aquatic vegetation and interacting with inanimate objects, as well as with conspecifics.

We define a feeding trial as the presentation of a single species of vegetation to a single subject. Feeding trials were conducted at three facilities where manatees are kept in captivity: Homosassa Springs State Park (HSP), Homosassa, FL; Lowry Park Zoological Gardens (LPZ) in Tampa, FL; and Sea World of Florida (SWF), Orlando, FL. A total of 17 animals, 5 females and 12 males, were used in this study. Four species of freshwater vegetation, *Hydrilla verticillata* (hydrilla), *Myriophyllum spicatum* (Eurasian watermilfoil), *Vallisneria americana* (tapegrass or wild celery), and *Eichhornia crassipes* (water hyacinth), and two species of seagrass, *Syringodium filiforme* (manatee grass) and *Thalassia testudinum* (turtle grass), were used for feeding trials. All plant species used in this study are normally consumed by free-ranging Florida manatees.

Feeding trials employed a piece of plexiglass (80 cm × 90 cm) into which 1-cm holes were drilled at 10-cm intervals. Prior to each feeding trial, stems of vegetation were pushed into the holes of the plexiglass. Only one species of aquatic vegetation was presented during any single trial. An underwater viewing window was used at LPZ for the duration of the study and at HSP for the first field season. Suction cups were fixed to each corner of the plexiglass, which was then affixed to the underwater viewing window inside the display tank. Manatees were videotaped from the opposite side. By placing the plexiglass on the window in this manner, we were able to obtain a close-up view of the perioral region through the plexiglass while the animals fed.

Manatees at LPZ (three males) and HSP (three females) were fed each of the six species of vegetation between the months of May and August during two years (1993 and 1994). Each species of plant was presented to each manatee at LPZ and HSP once a week for a total of ten weeks. Manatees at SWF (five males) were also presented with the same species of plants once a week for a total of five weeks during the summer months (1995). A total of 514 feeding trials was conducted over the three-year sampling period.

We attempted to control the order in which plant species were presented to specific individuals. An ordered sequence of feeding trial presentations helps to ensure that any vegetation type has an equal chance of being in any presentation to a given manatee. The daily sequence in which each plant species was presented was changed for each session. Logistically this often proved to be difficult. Under certain circumstances, feeding trials were conducted opportunistically; our desire to present a certain type of aquatic plant to a particular individual was often compromised by manatee behavior. For example, during the feeding trials, we attempted to present a specific species of plant to a specific individual. Often this individual would wander away and a different individual would approach the plexiglass and try to eat the plants. If the second individual had not fed on that plant species for that day, we would allow it to feed. When attempting to present a specific plant to a specific individual, occasionally that individual would be distracted and decide not to eat. A second piece of plexiglass filled with a different species of vegetation was often ready and would be switched with the first piece of plexiglass. Most of the time the individual would eat the vegetation from the second plexiglass. The first plexiglass with the original vegetation would then be replaced and the same individual would immediately consume the desired vegetation. Specific information regarding handling time and consumption rates for the individual species of aquatic plants presented will be presented in a separate report.

Feeding trials were conducted between 0900 and 1500, although most trials were completed by 1300. At LPZ, morning feeding schedules conducted by zookeepers were delayed until after the feeding trials were completed. Normal feeding regimens were not altered at HSP and SWF; feeding trials were conducted around these times.

Manatees in the study quickly learned that feeding trials involved novel food items. Usually, manatees appeared to find freshly collected aquatic plants preferable to their normal diet (romaine lettuce, cabbage, carrots, *etc.*). Satiation of individuals was not a problem. Individual preferences were qualitatively observed to occur. Preference varied among individuals, and individual preferences appeared to change from day to day. Only feeding trials in which manatees ate approximately 80%–90% of the vegetation were used for data analysis and calculation of overall average feeding rates.

Behavior was recorded using a Yashica model KD-H170u Hi8-format video camera and evaporated Hi8 videotape. All Hi8 videotapes were backed up using S-VHS videotape. Feeding trials at HSP and SWF differed slightly in methodology from those at LPZ. At the former sites, using the underwater

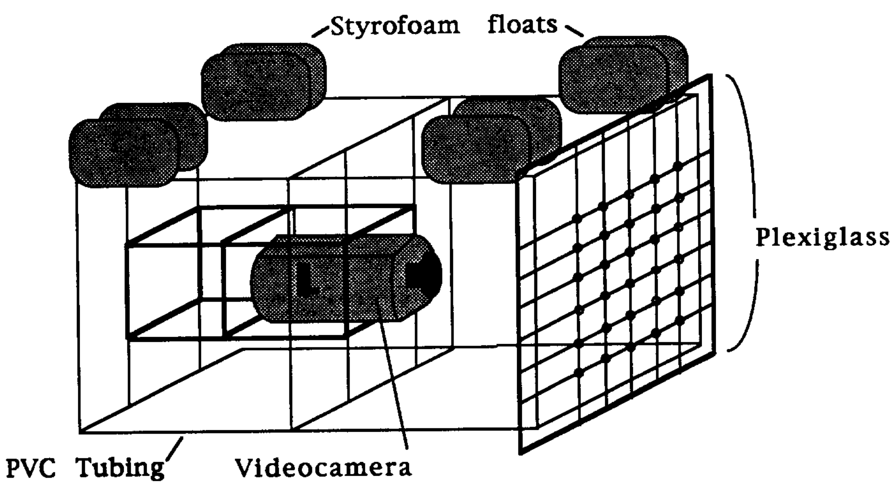

Figure 1. Schematic of mobile underwater window. Top of structure floated just below water line. Manatees fed off plexiglass while video camera recorded behavior.

viewing windows was impractical. Instead, a mobile underwater viewing window was constructed from PVC plumbing pipes, in the shape of a cube in which the Hi8 video camera (in an Amphibico underwater housing) was positioned (Fig. 1). The underwater video camera faced one side of the cube which was covered with a removable piece of plexiglass. Holes were drilled into this piece of plexiglass and vegetation was placed in the plexiglass as described above. Styrofoam floats were attached to the top of the PVC cube, enabling the underwater window to float just below the water's surface. This apparatus proved to be invaluable in helping to isolate and present vegetation to a single animal in the presence of many other hungry manatees. In addition, manatees were videotaped feeding upon free-floating water hyacinth using the underwater video camera alone to determine if differences existed between feeding upon floating vegetation versus submerged vegetation.

During the summer months of 1995 (May through August), inanimate objects were presented to captive manatees at LPZ. Manipulation of non-food objects by manatees was videotaped in order to better understand the range of manipulative behavior involving perioral bristles. Several items were placed in the manatee holding tank. Two identical sets of polygons of seven different shapes (triangle, circle, square, rectangle, pentagon, star, and modified square) were attached to two separate sheets of plexiglass (Fig. 2). Polygons were constructed of 1.25 cm thick acrylic with approximate dimensions of 12.5 cm in height and width. One set of polygons had roughened surfaces and one set had smooth surfaces. Each polygon was affixed to the plexiglass sheet with acrylic cement. In addition, a hole was drilled through each polygon and the sheet of plexiglass, and a brass nut and bolt were fastened to provide additional strength. The polygon sets were placed on different underwater windows in the same manner as in the feeding trials.

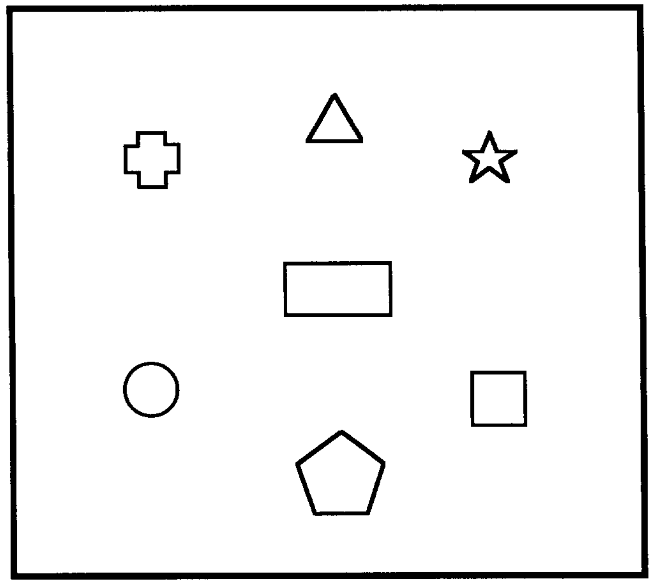

Figure 2. Schematic of plexiglass with affixed three-dimensional polygons presented to manatees.

Videotapes of manatee behavior were analyzed in real time, slow motion, and frame-by-frame to determine the component movements of the bristles, snout, and associated structures. Analysis of videotape was performed on a Panasonic model AG-7300 S-VHS editor in conjunction with either an IBAS computer imaging system (Kontron Image Analysis Division), which supported a black-and-white imaging monitor, or a Sony Trinitron model PVM-1350 color video monitor.

Results

Bristle field designations and descriptions follow Reep *et al.* (1998). There is a total of six discrete bristle fields; four (U1–U4) are located on the upper lip and two (L1–L2) on the lower lip. The U2 bristle fields are contiguous with the ventrolateral area of the oral disk. The oral disk is the region between the orofacial ridge (a prominent ridge on the dorsum of the snout, rostral to the nares) and the mouth (Reep *et al.* 1998). Bristle fields U1–U4 are located bilaterally along the margin of the oral cavity in a rostral to caudal series. Bristle fields L1–L2 are located in a similar manner on the lower lip margin.

Submerged vegetation—Florida manatees are able to feed at any position in the water column (Hartman 1979, Domning 1980). However, because much of the vegetation encountered is submerged, submerged feeding behavior may be considered more common than surface feeding. Manatee feeding involves rhythmic movements of the lips, perioral bristles and jaws. The most common

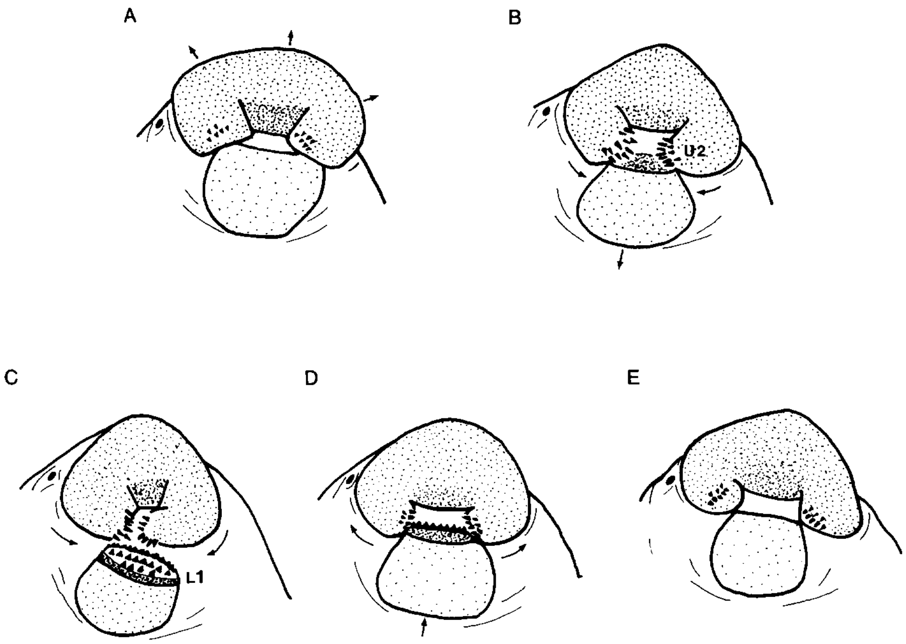

Figure 3. Schematic from five representative videotape frames of a manatee feeding on submerged vegetation positioned in plexiglass. Arrows indicate direction of movements of the oral disk (A), U2 bristle fields (B, C, and D), and lower jaw (B and D). A–E correspond with component movements of feeding on submerged vegetation described in detail in text. Short video segment of this figure is available at http://www.vetmed.ufl.edu/manatee/mana.html.

sequence of movements observed when manatees ingest submerged vegetation is as follows (Fig. 3):

A. The most rostral muscular portion of the snout contracts in the rostrocaudal direction. This action pulls the oral disk dorsocaudally and exposes the U2 bristles to the vegetation.

B. The U2 bristles evert forward, then are moved medially to bring the plant material toward the midline of the body in a lateral-to-medial sweeping motion. The lower jaw begins to open at this time.

C. The right and left U2 bristles reach apposition at the midline and push vegetation into the oral cavity; the lower jaw is now maximally open. The L1 bristles evert from their fleshy pad.

D. The U2 bristles diverge laterally and the lower jaw begins to close.

E. As the lower jaw closes, the L1 bristles sweep vegetation farther caudally into the mouth. The U2 bristles arrive at their original and lateral position. A new grasping cycle then begins.

We define each sequence of events (A through E) as a single feeding cycle. The mean feeding-cycle length was 610 ms (SD ± 52.9, $n = 17$). Together, the right and left U2 bristle fields act in a prehensile manner during feeding. The L1 bristle field actively pushes vegetation farther into the oral cavity. The

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actions of the U2 and L1 bristle fields alternate temporally with each other, resulting in the continual movement of vegetation into the oral cavity. The U1 bristle fields are naturally everted throughout the cycle but play no active role in food gathering. These bristle fields may be involved in tactile exploration during feeding. The remaining bristle fields (U3, U4, L2) are difficult to visualize from the video because of their more caudal locations in the oral cavity. However, visual observations of these fields were made during occasions where one of the authors (CDM) was in close proximity to feeding manatees. The U3, U4, and L2 bristle fields appear to passively aid in the movement of food farther into the oral cavity. For example, as the U2 fields reach out to grasp vegetation, the lateral margins of the upper bristle pad (which contain U3 and U4 bristle fields) are raised and moved forward. As the U2 bristles introduce vegetation into the mouth, the bristle pad margins are lowered and moved in a caudal direction. Therefore, the U3 and U4 bristles are moved in a circular fashion; this motion directs food farther into the mouth in a passive manner relative to the U2 bristle fields. This same action occurs in conjunction with the L1 bristle field, allowing the L2 bristle fields to passively move vegetation into the oral cavity.

Floating vegetation—The grasping pattern of the feeding cycle differs when manatees are feeding upon *Eichhornia crassipes* (water hyacinth). The U2 bristle fields were observed acting individually or together (right and left sides) in a raking fashion. The upper lip or lips reached out for the vegetation with the upper bristles extended and pointed downward. The individual then reached for the vegetation and attempted to drag it closer to the mouth. Multiple reaching motions were usually required to accomplish this act. When the plant was firmly held by the bristles, the manatee almost always grasped the plant with both flippers and sank below the surface to feed. The usual cyclic grasping movements seen when manipulating submerged vegetation were then employed to pass the vegetation into the oral cavity.

Other manipulative behavior—We have made many observations of other manipulative behavior involving the perioral vibrissal-muscular complex. The left and right U2 bristle fields can act independently under certain conditions. During feeding upon submerged vegetation, both U2 bristle fields were normally brought together in a prehensile manner at the midline in a lateral-to-medial sweeping motion. The orientation and medial extension of each U2 bristle field appeared equivalent during this event. However, when grasping food that was difficult to free from the plexiglass, manatees often used only one U2 bristle field, or both right and left U2 bristle fields but in a nonprehensile manner such as dragging the vegetation from the hole. Another variation was the use of both U2 bristle fields in a prehensile manner in which the bristle fields did not meet at the midline, but overlapped in order to free the object of interest. For example, a portion of a whole carrot was wedged between the plexiglass and the underwater viewing window at LPZ. One individual spent approximately two minutes tugging and pulling on the end of the carrot until it was freed from behind the plexiglass (Fig. 4C). During the manipulation of the carrot, this individual displayed a wide range of pre-

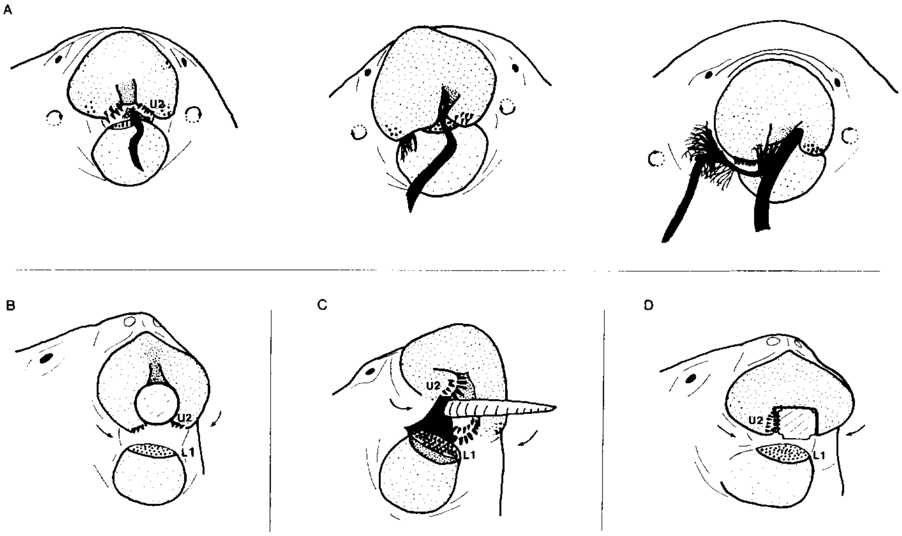

Figure 4. Schematics from representative videotape frames. Arrows indicate direction of movement of U2 bristle fields. A. Reversal of direction of U2 bristle movement. Left panel shows plant leaf and root in mouth at begining of reversal movement; center panel shows position of bristles as same plant and root appear outside the oral cavity; right panel shows final extraction of plant material from oral cavity. B. Non-perioral, muscular grasping behavior; note that U2 bristles are not used. C. Independent use of left and right U2 bristle fields. D. Use of U2 bristles during exploration of novel object.

cise, coordinated movement and prehensile ability not previously documented. In such cases the orientation and medial extension of each U2 bristle field appeared to be markedly independent. In addition to this strategy, the L1 bristle field was often used alone to scrape vegetation off the plexiglass as the animal moved from the bottom of the plexiglass to the top.

Manatees were observed to reverse the direction of the U2 bristle fields either together or independently. This often occurred when an individual appeared to dislike the taste or texture of the vegetation or part of the vegetation ingested. Several individuals were observed to reverse the direction of one U2 bristle field from a lateral-to-medial direction to a medial-to-lateral direction while the other U2 bristle field maintained the original direction (lateral-to-medial). During these events, individuals were able to extract the undesirable food item from within the oral cavity (Fig. 4A). This suggests that manatees possess a high level of perioral tactile discrimination and dexterity.

Often the perioral bristles and associated bristle-like hairs of the oral disk (Reep *et al.* 1998) appeared to be used in a tactile, exploratory fashion. As vegetation was consumed during the feeding trials, individuals began exploring the rest of the plexiglass for additional vegetation. This behavior involved quick side-to-side movements of the snout region in a quivering motion while the animal swept the entire head side to side as well as up and down. When a piece of vegetation was encountered, the individual often used both U2 bristle fields to grasp the vegetation from the side, position the mouth over the piece of vegetation, or attempted to drag the vegetation toward the mouth with one or both U2 fields or the L1 fields. The oral disk and its bristle-like hairs are sensitive to human touch; if one touched any portion of the oral disk, the U2 bristles grasped for the stimulus.

Pectoral flipper use was greatest when feeding upon floating vegetation. However, flippers were used occasionally to pull or push off the plexiglass during feeding trials. In fact, the original design of the plexiglass feeding apparatus inadvertently enabled some manatees to place their flipper behind it and pull it off the window. Once individuals learned that the plexiglass could be removed, this behavior was repeated again and again until we changed the method of anchoring the suction cups to allow the plexiglass to be positioned closer to the window (a change in distance of approximately 2 cm).

Inanimate objects—Three manatees at LPZ were presented with objects designed to aid in the understanding of the range of manipulative behavior. Two sets of acrylic polygons (smooth and roughened) and several ropes of varying fiber type and diameters were placed in the holding tanks. Manatees did not seem to prefer any set of inanimate objects over another. Animals explored the plexiglass, presumably for vegetation (or out of curiosity). Once the plexiglass was discovered to contain no vegetation, the individual usually moved on. During such directed exploration of polygons, the U2 bristle fields moved back and forth over the edges of the polygons and the head was moved side to side in a sweeping manner (Fig. 4D). Manatees also seemed to brush the objects with bristle-like hairs which are distributed over the oral disk (Reep *et al.* 1998). Such behavior was also observed when hand-feeding manatees monkey biscuits (used to supplement the diet and as a vehicle to administer multivitamins). Individuals approached the hand, touched the biscuit with the bristle-like hair on the oral disk (occasionally moving their head back and forth and up and down if necessary) and then grasped the biscuit with the U2 bristles. Occasionally, an individual grasped a polygon with the entire vibrissal-muscular complex, wrapping the muscular lips and perioral bristles around the perimeter, tightening its grip and attempting to remove the polygon from the plexiglass (Fig. 4B).

Manipulation of ropes by manatees was observed in the wild and in captivity. During one occasion while using a mask and snorkel observing wild manatees at CRR, one of the authors (CDM) was followed by a small calf for 30 min, during which it grasped for and chewed at the rope attached to a dive flag which trailed behind. It is not uncommon for manatees to spend long periods of time 'chewing' or manipulating anchor lines at CRR. Two types of behavior were noted in wild and captive animals: they brought parts of the rope into the mouth, and they used their muscular lips and bristles to manipulate knotted portions of it. Both the U2 bristles and the L1 fields were used as if feeding on submerged aquatic vegetation. On one occasion a wild individual was observed to take an anchor line into its mouth, gently touch, explore, and manipulate the rope as it moved down along the length of the rope. When the individual encountered a knotted loop of rope, it spent a considerable amount of time moving the knotted loop around inside the mouth using the U2 and L1 perioral bristles. In other instances individuals brought the rope into the mouth perpendicular to the long axis of the body, pushed the rope to the corners of the mouth using the U2 and L1 bristle fields, and presumably chewed the rope with the teeth.

Comparisons with other taxa—Several pinnipeds, including the harbor seal (*Phoca vitulina*), ringed seal (*Phoca hispida*), southern elephant seal (*Mirounga leonina*), California sea lion (*Zalophus californianus*), Steller sea lion (*Eumetopias jubatus*), northern fur seal (*Callorhinus ursinus*), and walrus (*Odobenus rosmarus divergens*) were observed in captivity to determine if vibrissal use was prehensile in nature. On several occasions, trainers placed objects and/or food near the animals' vibrissae to test for prehensile ability. All pinnipeds observed possessed remarkable "whisking" ability, but no prehensile behavior was seen. Of the pinnipeds observed, the orofacial anatomy of the walrus most closely resembles that of the manatee. Six walruses from SWF and Futami Sea Paradise Aquarium, Futami City, Japan (Mie Prefecture) were observed. Walruses are able to use the vibrissae to move food in the direction of the mouth. This is accomplished by passing food particles from vibrissa to vibrissa in a wavelike manner until the food either falls into the mouth and is grasped by the muscular lips (but not vibrissae) or brought close enough to the mouth to allow the animal to use its suction ability to feed. At no time were walruses observed to grasp the food particles by opposing their vibrissae; walruses observed relied principally upon suction to introduce food into the mouth.

Dugongs (*Dugong dugon*) also possess structures which appear similar in structure and function to perioral bristles in manatees (Domning 1977, Anderson 1979). We observed two captive dugongs at the Toba Aquarium, Toba City, Japan (Mie Prefecture). Dugongs, like manatees, also possess a prehensile ability to introduce vegetation into the mouth using perioral bristles. However, the manner in which dugongs accomplish this is different from manatees. The details of perioral bristle use by dugongs will be discussed in detail in a subsequent report.

Discussion

Aquatic vegetation is a ubiquitous but low-quality food source, and manatees may spend 5–8 h a day feeding and may consume between 5% and 15% of their body weight per day (Best 1981, Bengtson 1983, Etheridge *et al.* 1985); younger animals (calves and juveniles) consume a greater percentage of aquatic vegetation per body weight per day than adults (Etheridge *et al.* 1985). Our mean feeding cycle length for manatees is best compared with feeding trials conducted by Bengtson (1983) and Etheridge *et al.* (1985). Since the introduction of food into the mouth is likely to be intimately linked with mastication, feeding cycle length may be considered to be inversely related to chewing rate. Therefore, our mean feeding cycle length of 610 ms (1.64 feeding cycles per second) falls between chewing rate values reported by Bengtson

(1983; 1.05 chews per second) and Etheridge *et al.* (1985; 1.86 chews per second).

It is of interest that the eyes were often closed during feeding and exploratory behavior. Closing the eyelids would protect the eyes when feeding upon a silty substrate or among plant stalks. In addition, shutting down one sensory system (vision) that has limited value in a particular situation may enhance other sensory modes such as touch.

It has been demonstrated that evolution of supernumerary teeth (as well as other adaptations) is a result of selection pressures aimed at a particular kind of aquatic herbivory (Domning 1982). Selection pressure to maximize ingestion of aquatic plants is apt to have been high throughout the evolutionary history of sirenians. It is reasonable to assume that natural selection was not acting on tooth morphology or rostrum deflection alone, but also upon the entire feeding apparatus, including soft tissue structures such as the perioral bristles and surrounding musculature. The functional significance of the manatee feeding apparatus may be that it allows the manatee to exploit many types of habitats as a generalist herbivore. The vibrissal-muscular complex and associated behavior are likely an adaptation that allows manatees to maximize the efficiency of grazing and browsing on large quantities of a variety of aquatic vegetation.

Hartman (1979) described several interactions (sexual and nonsexual) between conspecifics that involved perioral bristles. Sexual and nonsexual behaviors were often difficult to distinguish. Most interactions included mouthing, nuzzling, nudging, and embracing (Hartman 1979). Of these behaviors reported by Hartman, we have observed that mouthing and nuzzling involve perioral bristles. Mouthing predominantly involved the U2 bristle fields but also occasionally the L1 bristle fields. We agree with Hartman (1979) that mouthing and nuzzling behaviors are social in nature. Manatees occasionally pushed and shoved at each other in order to better position themselves to feed upon presented vegetation. During these events some individuals used the U2 bristles to pinch the back, flipper, or tail of a conspecific. On a number of occasions one of the authors (GDH) was pinched in tender areas by the U2 bristles and can attest to the force used and discomfort incurred. Often individuals in captivity and in the wild (CRR and HR) were observed to explore the back of a conspecific, gently caressing or scratching the dorsum and often picking off algae or loose skin. The action of the robust bristle fields (U2 and L1) was similar to that observed during feeding on submerged vegetation. However, the degree to which they were used varied. Nuzzling is defined by Hartman (1979) as " . . . minor variations of mouthing." Muzzle-to-muzzle contact, often termed "kissing behavior," was observed occasionally. During such contacts, only the tactile bristle-like hairs on the oral disk are usually used; the U2 and L1 bristles appeared to have little or no function during this behavior.

Manatees are known to "chew" on non-food objects naturally in the wild (Hartman 1979), as well as in captivity (personal observation). The manipulative nature of the perioral bristles and the ablility to extract items from the mouth as demonstrated in Figure 4A speaks to the problem of ingestion of debris, which contributes to manatee mortality (Beck and Barros 1991). If manatees are able to extract undesirable food items from the mouth, why is debris ingested at all? Such questions are difficult to answer. However, it is possible that manatees are either unable to detect certain types of debris (*e.g.*, monofilament line) when entangled in aquatic vegetation (*e.g.*, *Hydrilla*) or are unable to extract such debris once introduced into the oral cavity.

Although sirenians are unique among marine mammals in the prehensile manner in which they use the snout, such behavior is common among herbivores. Whereas sirenians use modified vibrissae and facial musculature to grasp food, terrestrial herbivores exhibit a diversity of solutions to achieve prehensile functions. Elephants provide an interesting comparison because of their extreme facial elaboration among mammals and also due to their phylogenetic relationship (albeit distant) to sirenians. Recent anatomical investigations (Rasmussen and Munger 1996) document the existence of vibrissae at the trunk tips of Asian elephants (*Elephas maximus*). These vibrissae can be categorized into two groups: conventional long vibrissal hairs, and vellum vibrissae. Vellum vibrissae are hairs which barely protrude above the surface of the skin. The two types of vibrissae reported in the Asian elephant lack the conus innervation that is a prominent feature of vibrissae used for whisking behavior (Rice *et al.* 1986). In addition, there are no cutaneous muscles surrounding elephant vibrissae, which supports the contention that vibrissae in Asian elephants are not mobile (Rasmussen and Munger 1996). The similarities between sirenian vibrissae and elephant vibrissae are limited to the rostral location where vibrissae are found. Although Florida manatees possess at least two types of sinus hairs (bristles and bristle-like hairs), they do not possess vellum vibrissae. Furthermore, the large perioral bristles of Florida manatees (U2 and L1 fields) do lie just below the epidermis when relaxed; therefore, the degree to which they can be protruded when in use leaves no doubt that these are structures distinct from vellum vibrissae.

The giraffe (*Giraffe* sp.) uses its tongue and prehensile lips to grasp and browse foliage (Dagg and Foster 1976). The tongue can be as large as 54 cm long and 8 cm wide (Dagg and Foster 1976). During feeding the tongue is wrapped around groups of leaves or fruit to pull them to the lips, where the food is manipulated further, or pulled into the mouth directly (Dagg and Foster 1976). The giraffe tongue possesses greater mechanical power than that of any other ungulate (Sonntag 1922). The okapi (*Okapi johnstoni*), another giraffid, also possesses a manipulative tongue which can be up to 30 cm long and 4.5 cm wide (Burne 1917). Tapirs (*Tapirus* sp.) possess a long proboscis which is prehensile and is used in foraging to pull leaves and fruits from plants and to manipulate fallen fruit (Terwilliger 1978). Species of rhinoceroses exhibit differences in lip morphology which are correlated with browsing versus grazing feeding behavior. These features are exemplified in the resource partitioning of African rhinoceroses. Black rhinoceroses (*Diceros bicornis*) possess a narrow, beak-like upper lip structure and are considered adapted for browsing (Goddard 1968, Schenkel and Lang 1969, Owen-Smith 1975, Eisenberg

1981). White rhinoceroses (*Ceratotherium simum*) possess broad, wide lips and are considered to be adapted for grazing (Schenkel and Lang 1969, Eisenberg 1981). Such correlation in lip morphology and foraging ecology may also apply to manatees and dugongs.

The classical function of mammalian vibrissae is to obtain information from the environment using the sense of touch (Ling 1977). Tactile information is an important cue to all mammals. However, certain mammals have elaborated upon vibrissal form, density, and even function. As noted above, pinnipeds are a group known for their well-developed vibrissae (Peterson and Bartholomew 1967, Ling 1977, Fay 1982, Hyvärinen 1989). Most notably, the walrus and bearded seal have very dense arrays of elongated vibrissae (Burns 1981, Fay 1982, Kastelein and Van Gaalen 1988, Kastelein *et al.* 1990, Reidman 1990). As current data do not support a prehensile ability involving vibrissae for these two species, we contend that sirenians are the only mammals that use vibrissae in a prehensile manner.

The complexity and nuances of manatee behavior involving the vibrissal-muscular complex attest to the tactile nature of these animals. Manatees are often found in shallow turbid waters; in such systems, efficient acquisition of vegetation by vision alone is limited. In addition to the perioral bristles, manatees also possess short sinus hairs in the perioral region which are sensitive to tactile stimulation (Reep *et al.* 1998). It is likely that manatees rely heavily upon tactile cues to detect aquatic vegetation and perhaps even use tactile hairs to distinguish types of vegetation. Considering the tactile nature of Florida manatees and the habitats they frequent, is it reasonable to assume that manatees have developed complex sensory systems to detect tactile cues (Watkins and Wartzok 1985). Neuroanatomical data support this expectation. Manatees possess large trigeminal nerves, well-developed trigeminal-related somatic sensory nuclei (Johnson *et al.* 1986), and neural aggregations in the somatosensory cortex which are speculated to be related to processing sensory information from vibrissae (Reep *et al.* 1989, Marshall and Reep 1995).

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