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Swimming kinematics of the Florida manatee (*Trichechus manatus latirostris*): hydrodynamic analysis of an undulatory mammalian swimmer

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Summary

The submerged swimming of the Florida manatee (*Trichechus manatus latirostris*), a subspecies of the West Indian manatee, was studied by filming individuals as they swam rectilinearly in a large pool at several rehabilitation centers. The swimming was analyzed using videography to detail the kinematics in conjunction with a hydromechanical model to determine the power output (P_t) and propulsive efficiency (η_p). Manatees swam at velocities of 0.06–1.14 m s^{-1}. Locomotion was accomplished by undulation of the body and caudal fluke. Undulatory locomotion is a rapid and relatively high-powered propulsive mode involved in cruising and migrating by a variety of swimmers. Manatees displayed an undulatory swimming mode by passing a dorso-ventrally oriented traveling wave posteriorly along the body. The propulsive wave traveled at a higher velocity than the forward velocity of the animal. The frequency of the propulsive cycle (f) increased linearly with increasing swimming velocity (U). Amplitude at the tip of the caudal fluke (A) remained constant with respect to U and was 22% of body length. P_t increased curvilinearly with U. The mean η_p, expressing the relationship of the thrust power generated by the paddle-shaped caudal fluke to the total mechanical power, was 0.73. The maximum η_p was 0.82 at 0.95 m s^{-1}. Despite use of a primitive undulatory swimming mode and paddle-like fluke for propulsion, the manatee is capable of swimming with a high efficiency but lower power outputs compared with the oscillatory movements of the high-aspect ratio flukes of cetaceans. The swimming performance of the manatee is in accordance with its habits as an aquatic grazer that seasonally migrates over extended distances.

Key words: manatee, swimming, *Trichechus manatus*, power output, efficiency.

Introduction

Fish (Fish, 1996; Fish, 2000; Fish, 2001) proposed a model for the sequence of transitional stages in swimming mode from primitive to derived aquatic mammals. According to Fish's model, the evolution of mammals that swim using oscillations of pointed, wing-like caudal flukes (i.e. cetaceans, dugong) was immediately preceded by a transitional locomotor stage using dorso-ventral undulations of broad, flattened tail. Within the Sirenia, manatees employ the more primitive swimming mode [dorso-ventral undulation (Hartman, 1979)] and propulsive morphology (Fig. 1) compared to the related dugongs. Dugongs and cetaceans swim by caudal oscillation, also described as thunniform or carangiform with lunate tail (Lighthill, 1969; Webb, 1975; Fish, 2001). As differences exist between the morphologies and movements of manatees and these caudal oscillators (Fish, 2001) it is, therefore, expected that there are corresponding differences in swimming characteristics. Compared to the cetaceans, manatees were considered inefficient swimmers due to their inability to reach and maintain high speeds, a less streamlined body shape, broad paddle-like tail flukes and a lack of the peduncular musculature necessary to generate thrust (Hartman, 1979; Fish, 1996).

The Florida manatee (*Trichechus manatus latirostris* L.) is a fully aquatic mammal of the order Sirenia that inhabits temperate, tropical and subtropical waters commonly along the coasts of Florida and Georgia (Hartman, 1979; Reynolds and Powell, 2002). The manatee migrates between fresh, brackish and saltwater habitats; they rarely remain in deep ocean waters (Hartman, 1979; Reynolds and Odell, 1991). In one case, a male manatee tracked by a satellite transmitter tag traveled over 4800 km at 20–35 km per day (Reid, 1996).

Hartman (Hartman, 1979) described the gross swimming movements of the Florida manatee. He noted that the propulsive forces were produced by dorso-ventral undulation of the horizontally flattened and rounded tail (Fig. 1). No motion anterior to the peduncle was observed to be involved in forward propulsion. Stroke cycle frequencies observed (Hartman, 1979) ranged from 0.30 to 0.83 Hz depending on whether the individuals were idling, cruising or fleeing. Manatees have been reported to swim at speeds of 0.6–13.3 m s^{-1}, but tend to swim in a leisurely manner at 0.6–0.8 m s^{-1} and cruise at 0.8–1.9 m s^{-1} (Hartman, 1979; Charnock-Wilson, 1968).

The objectives of this study were to analyze the swimming kinematics of manatees with greater fidelity than originally

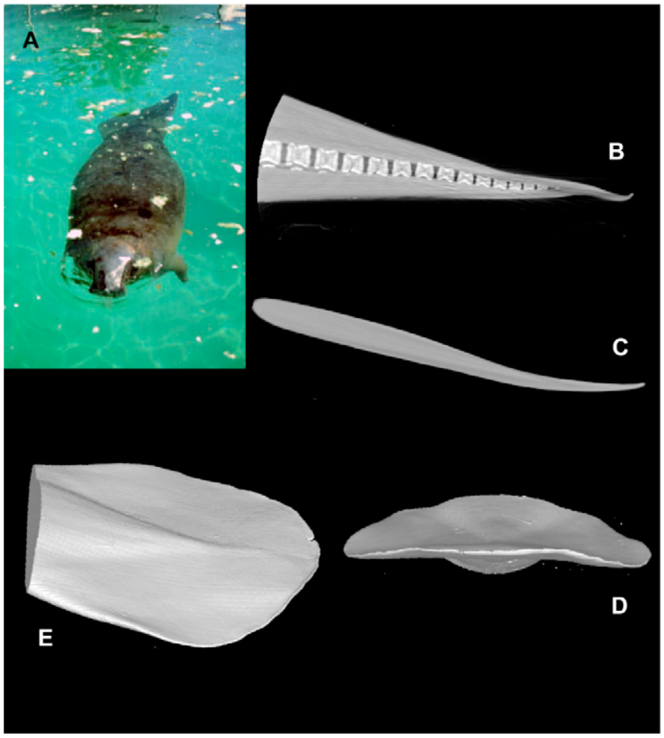

Fig. 1. Structure of the caudal flukes of the manatee. (A) Photograph of manatee showing position of caudal flukes. (B) Midsagittal section of tail flukes from CT (computer tomography) scan. Vertebrae are shown as dense blocks with flattened anterior and posterior ends. (C) Parasagittal section from CT scan of fluke at approximately 50% position midway between the central body axis and lateral tip. (D,E) Three-dimensional construction of fluke blades from CT scans.

described (Hartman, 1979) and to use this information to estimate thrust power output (P_t) and propulsive efficiency (η_p). Based on previous observations of manatee swimming and propulsive morphology, it was hypothesized that values of P_t and η_p would to be less than those for evolutionarily more derived swimmers (i.e. caudal oscillators such as cetaceans). From an evolutionary perspective, manatees swimming by undulation can represent functional analogues for the ancestors of more derived, lift-based oscillatory swimmers (Fish, 1996) and demonstrate swimming capabilities of transitional forms.

Materials and methods

Experimental animals

Nine Florida manatees (*Trichechus manatus latirostris* L.) were observed at Sea World in Orlando, FL, USA (SW), Lowry Park Zoological Gardens in Tampa, FL, USA (LP) and Columbus Zoo in Columbus, OH, USA (CZ) during 2001. All the manatees were held for rehabilitation.

The SW facility consisted of oblong pool of approximately 42 m×9 m with a maximum depth of 5.5 m and total volume of about 1.36×10^6 liters. Manatees were visible from an underwater viewing area that extended along the length of the pool with 7.3 m×2.5 m glass windowpanes. The water temperature in the pool was maintained at 24–25°C. All pools were filled with freshwater. The CZ manatee habitat consisted of one oblong pool with dimensions 33 m×12 m and volume of 7.2×10^5 liters. The maximum depth was 3.6 m. The water temperature in the exhibit was maintained at 26–27°C and the salinity of the pool was 14.36 p.p.t. The LP facility consisted of two pools with viewing windows that were approximately 3 m×2 m. Access to each facility was gained before normal hours of operation to facilitate video recording without interference from park visitors.

The staff members at SW, CZ and LP provided the morphometrics of the individual animals that are summarized in Table 1. Body length (*BL*, m) was the linear distance from the tip of the nose to the tip of the tail fluke. Fluke span (*d*, m) was the linear distance of the widest section of the tail fluke perpendicular to the central axis of the body.

Video analysis

The animals were videotaped with a Sony Digital 8 video camera recorder (model DCR-TRV530) that allowed for continuous recording of the gross movements at 60 Hz. The video camera was held stationary on a tripod that was placed at 5.5–6 m from the glass viewing window at each facility. Lateral views of the animals were recorded as the animal normally swam parallel to a viewing window. Animals swam at various depths and distances from the window. Data were acquired only from those video records in which the whole body or posterior portion of the steadily swimming manatee was in view for at least one stroke cycle, with no apparent accelerations or deviations from a horizontal trajectory. In most sequences, the animals were swimming alone (i.e. the other individuals were out of view of the camera).

Sequential body and fluke positions were digitized from individual fields of videotape with a computerized video analysis system (Motus 2000; Peak Performance Technologies, Inc., Centennial, CO, USA). In some cases, video was transferred to VHS tapes from Hi-8 tapes prior to analysis. In order to digitize this footage, a Panasonic AG-7300 video recorder and Sony PVM 1341 monitor were used. The specific anatomical features that were digitized included the nose, eye, flipper tip, peduncle and fluke tip (Fig. 2). The body length, *BL*, for each animal served as its own scale.

Kinematic data from video records included swimming velocity (U, m s^{-1}), peak-to-peak amplitude at the eye, nose, flipper, peduncle and fluke tip (A, m), stroke frequency (f, Hz),

Table 1. *Morphometrics of manatees*

Individual[1]	Sex	Age (years)	Mass (kg)	Body length (m)	Fluke span (m)
SW1	F	17	962	3.15	0.76
SW2	F	22–24	1388	3.53	0.97
SW3	F	16	959	3.17	0.78
CZ1	M	15	534	3.16	0.86
CZ2	M	26	839	3.39	0.82
CZ3	M	17	569	3.44	0.88
LP1	F	N/A	590	3.07	N/A
LP2	F	10	821	3.02	N/A
LP3	M	15	572	3.10	N/A

[1] SW, Sea World; CZ, Columbus Zoo; LP, Lowry Park Zoological Gardens.

N/A, not available.

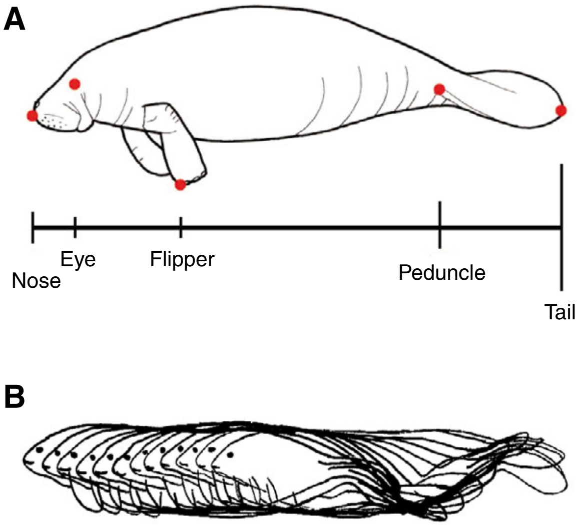

Fig. 2. Outlines of swimming manatee. (A) The position of points (red circles) on body used for kinematic analysis. The horizontal line represents the body length of the manatee and vertical lines represent the peak-to-peak amplitude of each point. (B) Sequential outlines of the lateral view of a swimming manatee during one complete stroke cycle. Maximum vertical displacement is confined to the tip of the caudal flukes moving along a sinusoidal pathway.

fluke tip velocity (W, m s^{-1}) and propulsive wave velocity (V, m s^{-1}). U was calculated as the horizontal displacement during one complete stroke cycle divided by duration of the stroke cycle. A at the eye, nose, flipper tip, peduncle and fluke tip were calculated as the vertical displacement between successive peaks of the sinusoidal trajectory followed by the feature. f was calculated from the inverse of the stroke cycle period. W was calculated as A divided by the time of the tail tip to make the excursion. V was determined from the distance from the peduncle position to the tail tip divided by the time difference between when peduncle and tail tip reached their maximum amplitudes. The wavelength (λ) was calculated from simple harmonic motion as V/f.

To adjust for size differences, data were analyzed with respect to length-specific velocity (U/BL) and length-specific amplitude (A/BL). To maintain hydrodynamic similarity, data were also analyzed with respect to Reynolds number (Re):

$$Re = BL \times U/v\,, \tag{1}$$

where v is the kinematic viscosity (1.044×10^{-6} m^2 s^{-1}).

Thrust power and efficiency calculations

The thrust power and propulsive efficiency were calculated using Lighthill's 'bulk momentum' model based on 'slender body theory' model (Lighthill, 1969; Webb, 1975). The model can be applied to anguilliform and carangiform swimmers, which includes the swimming motions of the manatee (see Results). The advantage of using this model for the manatee is that propulsive force is estimated from movements at a defined trailing edge. Therefore, discrete movements of the thick body sections are unnecessary. However, the model has assumptions including a small tail stroke amplitude, neglecting forces of viscous origin, except for viscous drag, and a propulsive efficiency that is always greater than 0.5 (Webb, 1975). Large amplitude motions, like those in the manatee (Hartman, 1979), were found to have little effect on total power compared to small amplitude motions (Lighthill, 1971). In addition, corrections to propulsive efficiency for large amplitude movements are only necessary at low efficiencies. Propulsive efficiencies in the range of 0.75–0.9 only have a 5% error when a small amplitude is assumed for the model (Webb, 1975).

According to Lighthill (Lighthill, 1960; Lighthill, 1969; Lighthill, 1970), for a hypothetical fish swimming with increasing small amplitude motions, a reaction force is generated for each segment of the body. This reaction force is proportional to the velocity of the segment and mass of the water affected by the segment (virtual mass). Considering a fish of constant depth, the mass of water passed along the body remains constant between body segments. The momentum, however, increases as each body segment increases in amplitude and velocity posteriorly. The more posterior segments move through greater distances at a faster velocity, producing a relatively greater force that is more aligned with the direction of movement of the animal. Eventually, the water is shed into the wake with a momentum, which is defined by the motions of the trailing edge of the caudal fin (Webb, 1975). The thrust is proportional to the rate of momentum shed into the wake and the P_t is equal to the rate of work performed by the trailing edge against the shed momentum.

The mean thrust power (P_t) is the power output generated by the flukes to propel the manatee forward (total power – kinetic energy), which is calculated as:

$$P_t = m\omega UW - 1/2(m\omega^2U)\,, \tag{2}$$

where m is the virtual mass per unit length and ω is the relative velocity of the tail. The virtual mass per unit length represents the relatively large mass of fluid accelerated by the tail (Webb, 1975) and is given as:

$$m = (k_t\rho\pi d_t^2) / 4\,, \tag{3}$$

where k_t is a constant equal to 1.0 (Lighthill, 1970), ρ is the density of water equal to 1000 kg m^{-3}, and d_t is the maximum width of the tail. The relative velocity of the flukes, ω, was calculated from:

$$\omega = W[(V-U) / V]\,. \tag{4}$$

The propulsive efficiency (η_p) for thrust generation is:

$$\eta_p = \{m[\omega WU - 1/2(\omega^2U)]\} / m\omega UW\,, \tag{5}$$

which is equivalent to the ratio of P_t to the total power produced by the system.

Statistical procedure

Statistical analysis of the data was performed using Statistica for Windows (Version 5.1, Statsoft) in conjunction with Microsoft Excel 2000 for Windows. Swimming trials for each individual were not considered to be independent. Variation about means was expressed as ± one standard deviation (s.d.). Regressions were computed using least-squares regression. Simple repeated-measures ANOVA was used to determine differences in peak-to-peak amplitude A at specific body positions. *Post hoc* analysis was performed using the Scheffe test. In all statistical analyses, a significance level of $P=0.05$ was maintained.

Results

Fifty-seven swimming sequences in which the animals maintained continuous propulsive motions of the tail fluke were recorded and used for kinematic analysis. Acceptable sequences were supplied by only seven of the animals. Twenty-five of the sequences were recorded at SW and 32 sequences were videotaped at CZ. Due to the configuration of the LP facility, which prevented observation of the body through one full stroke cycle, no useful video data were obtained and the animals were not included in the analysis.

Swimming velocity

Healthy, adult manatees swam at U ranging from 0.3 to 1.1 m s^{-1} (0.1–0.4 BL s^{-1}) (mean 0.6±0.2 m s^{-1}; 0.2±0.1 BL s^{-1}). Reynolds number (Re) ranged from 7.0×10^5 to 2.8×10^6 with a mean of $1.6\times10^6\pm0.5\times10^6$ (Fig. 3).

Kinematics

Swimming by manatees was produced by dorso-ventral undulations as a sinusoidal wave moved posteriorly along the body (Fig. 2). The pectoral flippers were held motionless either appressed against the body or hanging vertically. The peak-to-peak amplitude (A) of the wave generally increased along the length of the body (Figs 2, 3). Maximum A was confined to the tip of the tail and ranged from 0.3 to 1.1 m with a mean of 0.8±0.2 m. A/BL ranging from 0.10 to 0.33 with a mean of 0.2±0.04. A/BL at the tip of the caudal fluke was not significantly correlated with U or U/BL for any category of animals. A/BL at other positions on the body ranged from 0.01 to 0.15 (mean 0.1±0.03) at the nose, 0.01–0.1 (mean 0.04±0.02 BL) at the eye, 0.01–0.1 (mean 0.04±0.02) at the flipper, and 0.03–0.17 (mean 0.10±0.03) at the peduncle (Fig. 2).

The nose, eye, peduncle and tail fluke all followed a sinusoidal pathway (Fig. 2). Cyclic movements at the peduncle lead corresponding movements of the tail tip by 100.3±22.4°. λ of the sinusoidal wave measured in the fluke was shorter than the body length of the healthy manatees ($\lambda/BL=0.9\pm0.2$).

The kinematic parameters f, W, and V showed a significant linear increase with increasing U (N=57; $P<0.001$) (Fig. 4), according to the regression equations:

$$f = 0.24 + 0.22U\,, \qquad r = 0.68\,, \tag{6}$$

$$W = 0.36 + 0.40U\,, \qquad r = 0.52\,, \tag{7}$$

$$V = 0.51 + 1.09U\,, \qquad r = 0.62\,. \tag{8}$$

f varied from 0.26 to 0.55 Hz.

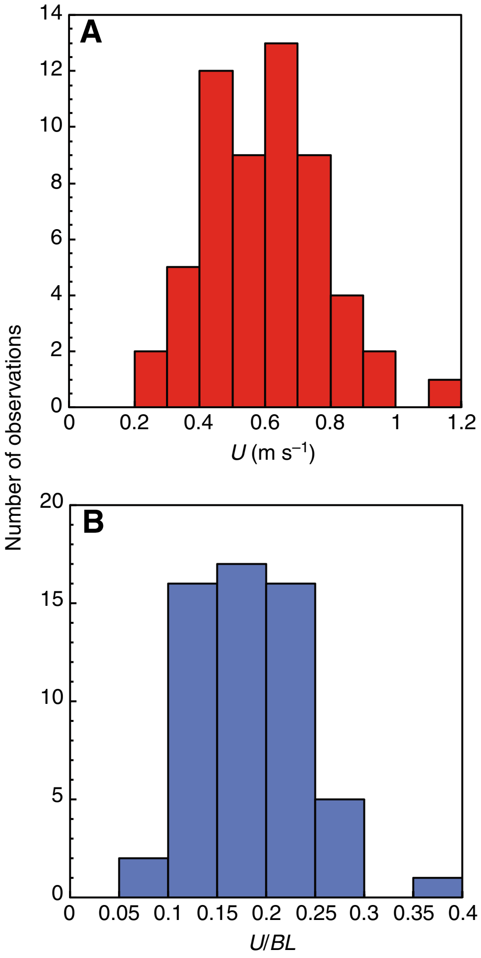

Fig. 3. Frequency distribution of absolute (A) and length-specific (B) swimming speeds of captive manatees.

Thrust power and efficiency

The calculated P_t and η_p were based on an average adult manatee (length=3.34 m; mass=857.8 kg; fluke span=0.86 m) and kinematic statistics of f, W and V. P_t displayed a curvilinearly with increasing U. The polynomial equation, which describes the relationship between P_t and U, is:

$$P_\mathrm{t} = 1.30 + 41.16U + 77.57U^2\,, \tag{9}$$

ranging from 18.1 W at 0.27 m s^{-1} to 149.0 W at 1.14 m s^{-1} (Fig. 5). Values of P_t for manatees were lower than for cetaceans, although manatees swam at comparatively lower speeds (Fig. 5). Mass-specific P_t was 2.1×10^{-2} to 1.8×10^{-1} W kg^{-1} over the range of U.

Manatees swam with η_p of 0.67–0.81 (Fig. 6). η_p showed a curvilinear increase with increasing U. Unlike cetaceans. no plateau in η_p was displayed by manatees, although this may have been a function of the relatively low swimming speed of the manatees in this study.

Discussion

Swimming velocity

Generally, manatees are slow swimmers, although high speeds are possible when the animal is provoked. Sirenians may sprint up to 6 m s^{-1} during an escape from a predator but more routinely swim at speeds of 0.6–0.8 m s^{-1} (Hartman, 1979; Nishiwaki and Marsh, 1985). During migration, manatees may cruise at speeds of 0.8–1.89 m s^{-1}. Charnock-Wilson (Charnock-Wilson, 1968) reported that a fisherman in British Honduras had observed manatees swimming at speeds up to 13.33 m s^{-1}; however, as this speed is exceptional even for more

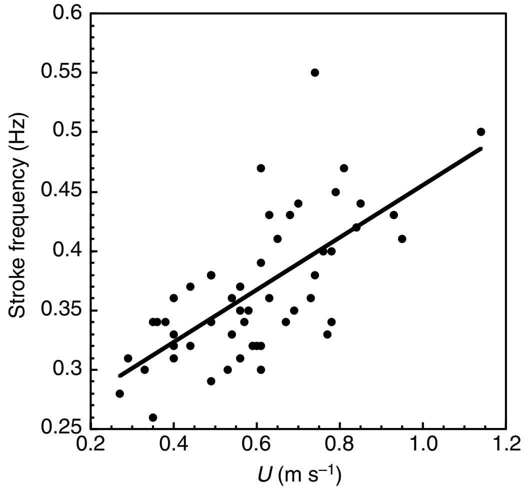

Fig. 4. Relationship of stroke frequency (f) with respect to swimming speed (U). The line is a least-square regression; see text for regression equation.

streamlined dolphins (Fish and Rohr, 1999), the record is questionable. A wide range of swimming velocities have been reported (Hartman, 1979), with idling manatees swimming at speeds of 0.56–0.83 m s^{-1}, cruising animals at 0.83–1.94 m s^{-1}, and sprinting animals at 5–6.94 m s^{-1}. Dugongs, a close but more derived relative of the manatee, cruise at speeds of 2.67 m s^{-1} (Jarman, 1966). The speeds observed in this study are indicative of animals that were idling and cruising but not fleeing. This was reasonable considering that all individuals were in the confines of a pool.

The length-specific velocity for manatees in this study was 0.08–0.38 $BL\,\text{s}^{-1}$. This range of velocity is substantially slower than cetaceans, which swim by oscillation of a highly derived wing-like fluke (Fish, 1998a). The manatee's relative velocity was also slower than the sea otter (0.47–1.08 $BL\,\text{s}^{-1}$), which swims by undulation of the body and hind feet (Williams, 1989).

Swimming kinematics

Hartman briefly described the kinematics of swimming in manatees (Hartman, 1979). He did not observe undulation of the body, and considered all movement to be confined to the tail. He reported that during the full stroke the tail moved through an arc of 130° (Hartman, 1979), which was substantially less than the arc of 200° described for the fluke of a dolphin (Slijper, 1962).

Observations of Florida manatees in this study suggest that swimming is accomplished using an undulatory mode. Manatees have previously been listed among caudal oscillators (Fish, 1993a; Fish, 1996). Undulatory swimming entails throwing the body and tail into a traveling wave. The wave is propagated in the direction opposite of forward motion of the animal. For organisms that undulate the body and tail, the propulsive wave may be produced over different lengths of the body. Body and tail undulators are characterized along a continuum as anguilliform, subcarangiform, carangiform or thunniform, where the propulsive wave is confined more posteriorly, respectively (Breder, 1926; Webb, 1975; Lindsey, 1978). This undulatory continuum has functional implications.

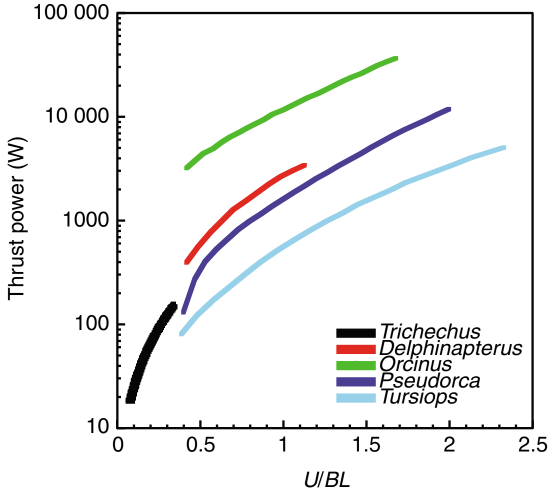

Fig. 5. Comparison of thrust power (P_t) as a function of swimming speed (U/BL) for the manatee and four cetaceans. The black line represents the calculated thrust power for an average manatee using Lighthill's bulk momentum model (see text). Colored lines show P_t for beluga *Delphinapterus leucas*, killer whale *Orcinus orca*, false killer whale *Pseudorca crassidens* and bottlenose dolphin *Tursiops truncatus* (from Fish, 1998b).

Thunniform swimmers, such as cetaceans, are characterized as high speed, high efficiency swimmers, whereas lower swimming performance is associated with anguilliform and subcarangiform swimmers.

Manatees swim using the paddle-like flukes (Figs 1, 2) with subcarangiform mode. In this swimming mode, the body and caudal flukes are thrown into a wave with more than one half-wavelength within the length of the body and the A of the wave rapidly increases over the posterior half of the body (Lindsey, 1978). Wavelength for the manatee was determined to be equal

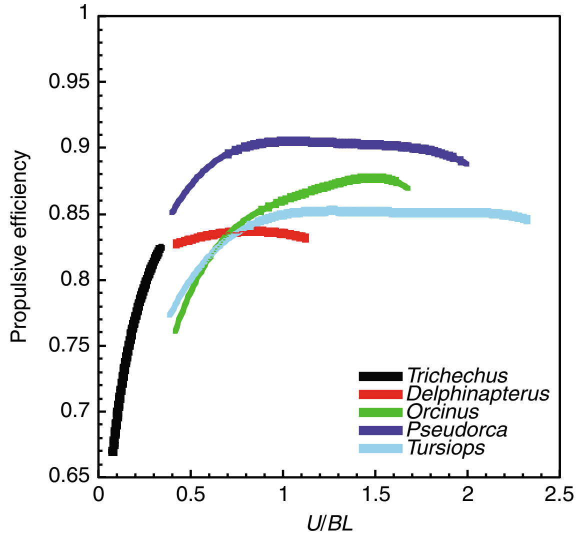

Fig. 6. Relationship of propulsive efficiency (η_p) and swimming speed (U/BL). The black line represents the calculated efficiency for an average manatee using Lighthill's bulk momentum model (see text). Color lines show P_t for beluga *Delphinapterus leucas*, killer whale *Orcinus orca*, false killer whale *Pseudorca crassidens* and bottlenose dolphin *Tursiops truncatus* (from Fish, 1998b).

to *BL* of the individual. Subcarangiform swimmers have a fusiform body and deep caudal peduncle (Webb, 1975; Lindsay, 1978). Subcarangiform swimming is a rapid and relatively high-powered propulsive mode (Webb et al., 1984). This mode is used for durations of a few seconds to several weeks. It is involved in behaviors such as cruising, sprinting, patrolling, station holding as well as migrating (Fish, 1993b).

Estimates of stroke cycle frequency, f, for the swimming adult Florida manatees in this study were within the range previously reported (Hartman, 1979) for adult manatees idling and cruising. Adult free-ranging manatees swim at f of 0.3–0.33 Hz when idling, 0.4–0.6 Hz when cruising and 0.75–0.83 Hz when fleeing (Hartman, 1979). f for the Florida manatee was less than f for several species of cetaceans (Fish, 1998b). f for the bottlenose dolphin *Tursiops truncatus*, a marine mammal approximately one-third the mass of the Florida manatee, is approximately 1–3 Hz (Fish, 1993b). f should be lower, however, in the manatee, which is not able to reach and maintain higher U of the dolphin.

The linear increase of f with U for the Florida manatee was consistent with results from previous studies of other marine mammals using body and tail propulsion (Pyatetsky and Kayan, 1975; Kayan and Pyatetsky, 1977; Kayan et al., 1978; Fish, 1993b; Fish, 1998b). In fully aquatic marine mammals, f is the major determinant of U. Modulation of f as opposed to A is preferred in aquatic mammals because it prevents excessive body distortion, which would increase overall drag and thus decrease η_p (Fish et al., 2003).

The analysis of A at several body positions for the Florida manatee was consistent with previous studies for subcarangiform swimmers (Bainbridge, 1958; Webb, 1975; Wardle and Videler, 1980; Fish, 1993b; Fish, 1998a; Dewar and Graham, 1994; Long et al., 1994; Wassersug and Hoff, 1985). A for subcarangiform fishes ranges from 0.04 to 0.07 *BL* at the nose and 0.20 *BL* at the tail (Bainbridge, 1958; Webb, 1975; Webb, 1986; Webb and Keyes, 1982). For cetaceans, A at the rostrum ranges from 0.02 *BL* to 0.08 *BL* and A ranges from 0.17 *BL* to 0.25 *BL* at the fluke tips (Lang and Daybell, 1963; Videler and Kamermans, 1985; Fish et al., 2003).

The small A observed at the anterior end of animals that swim *via* body and tail propulsion is displaced as a result of the movements of the tail (Fish et al., 2003). The propulsive motions at the tail produce transverse forces that need to be balanced at the anterior end of the body. This is necessary to reduce drag, increase propulsive efficiency and maintain stability. Large deviations at the rostrum will increase the added mass of the system as the water adjacent to the body is accelerated by its movement (Lighthill, 1971). Additionally, transverse movements increase instability, which can potentially cause the animal to deviate from it's chosen trajectory. The animal must increase its energy output in order to maintain its course (Fish et al., 2000). These recoil forces are balanced by throwing the body into at least one complete wavelength (Webb, 1975; Blake, 1983). As the wave travels posteriorly down the body, the opposing lateral forces are cancelled out (Fish et al., 2000).

Thrust power output and propulsive efficiency

The Florida manatee produces less thrust power than other highly derived marine mammals (Fig. 5). A maximum P_t for the bottlenose dolphin exceeds 7600 W or 30.5 W kg^{-1} at 5.9 m s^{-1} (2.2 *BL* s^{-1}) (Fish, 1993b). This P_t was obtained for animals at higher speeds than those observed for the manatees in this study. However, when compared to the beluga *Delphinapterus leucas* of equivalent size (length=3.55 m; mass=664.2 kg) and swimming speed (0.35 *BL* s^{-1}) (Fish, 1998b), the cetacean had a P_t that was 70% greater than for the manatee. Such power outputs may reflect differences in both physiological and morphological mechanisms for sirenians and cetaceans. In particular, the paddle-like fluke and undulatory swimming mode of the manatee are less effective in power generation than the oscillations of the wing-like flukes of cetaceans.

Despite the more primitive morphology and swimming mode used by manatees, η_p was higher than expected (0.67–0.81) (Fig. 6) and consistent with the performance of other undulatory swimmers. Animals that swim by undulating the body and/or caudal appendage (anguilliform to carangiform) have η_p of 0.45–0.85 (Webb, 1975; Webb, 1978; Wardle, 1975; Wardle, 1977; Videler and Hess, 1984; Webb et al., 1984; Vogel, 1994). However, the more derived thunniform swimming mode of cetaceans and phocid seals has a higher range for η_p of 0.75–0.90 (Fig. 6) (Fish et al., 1988; Fish, 1998b). Using computational fluid dynamics, Schultz and Webb (Schultz and Webb, 2002) indicated that carangiform swimmers with a wavelength equal to one body length were less efficient than thunniform swimmers. This result was due to the large power consumption predicted for carangiform swimmers.

Relationship of manatees to evolution of derived swimming modes

Recent studies on swimming in aquatic mammals focused on how propulsive modes have changed throughout evolution, resulting in more derived forms (Fish, 1996; Fish, 2000; Thewissen and Fish, 1997; Domning, 2001). The evolution of fully aquatic mammals (cetaceans, sirenians) represents the culmination of a series of transitional stages that have resulted in morphologies and propulsive modes providing high swimming speeds with high energetic efficiency (Gingerich et al., 1983; Barnes et al., 1985; Fish, 1996). However, unlike cetaceans or the dugong, the manatee does not possess a high-efficiency, wing-like caudal fluke.

Evolutionarily, the manatee has a swimming mode that occupies a position just below the high-derived oscillatory swimming using the thunniform mode (Fish, 1996; Fish, 2000). The manatee represents a transitional morphology and swimming mode to more derived oscillatory swimmers. The undulatory mode, while providing sufficient thrust with generally high efficiency, is limited in performance compared to use of oscillating flukes. Furthermore, the rounded, paddle-like flukes of the manatee are not specialized for steady high-speed swimming. Although thrust increases with the span of a caudal propulsor, the drag on the propulsor increases with its surface area in similar proportion to the increased thrust (Webb, 1978). Fast swimmers, therefore, have narrow propulsors with large spans (i.e. high aspect ratio). Such flukes are found in dugongs *Dugong dugon*, which have converged with cetaceans. Compared to the manatee, dugongs are found in more open water habitats and undergo daily and seasonal movements (Nishiwaki and Marsh, 1985).

The evolution of sirenians parallels that of cetaceans. Both groups evolved over 50 millions years ago from quadrupedal terrestrial ancestors (Thewissen and Fish, 1997; Domning, 2001). Upon entry into water these aquatic mammals are believed to have first used paddle propulsion and subsequently simultaneous pelvic paddling combined with spinal undulation (Fish, 1996). Later loss of the hind limbs and exclusive undulatory propulsion were due to maintenance of horizontal trim (Domning and de Buffrénil, 1991) and reduced drag (Fish, 1996). Propulsion exclusively by spinal undulation required expansion of the tail flukes oriented perpendicular to the plane of the traveling wave. Eventually, the flukes were modified into wing-like structures for lift-based propulsion (Fish, 1996; Fish, 1998a). Diet does not appear to have played a key role in the evolution of wing-like flukes as sirenians are strictly herbivores and cetaceans are piscivores or carnivores. Movements in pelagic habitats and high cruising speeds by the efficient generation of thrust are presumed to be the important parameters in the evolution of highly derived flukes and swimming modes (Webb and de Buffrénil, 1990; Fish, 2000). Such behaviors and morphologies are associated with foraging for patchy resources.

Manatees have very little need for powerful steady swimming (Domning, 1978). Unless migrating, speed and thrust are less important to the manatee that has very few threats outside of humans (Reynolds and Odell, 1991; Gerstein, 2002; Reynolds and Powell, 2002; Rommel et al., 2007). The majority of their daily activities involve feeding on sessile aquatic plants and resting (Hartman, 1979; Best, 1981; Bengston, 1983; Etheridge et al., 1985; Marshall et al., 2000). Similarly, another undulatory swimming mammal is the sea otter *Enhydra lutra*, which also forages on stationary prey. If the morphology and ecology of the sea otter are compared to that of the manatee, several key similarities emerge. Both species swim by vertical undulations of the caudal region of the body. They both inhabit structurally complex environments. Much like the manatee, the sea otter spends a large portion of its day resting. Although the sea otter is a carnivore, its diet consists mainly of sedentary or slow-moving invertebrates (Kenyon, 1969). Rather than using speed to capture elusive prey, the sea otter maneuvers through rocky shores, barrier reefs and dense kelp to locate food. The similar foraging ecology of these species may be associated with similar swimming kinematics.

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