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Turning performance of batoids: Limitations of a rigid body

Jana M. Parson [a], Frank E. Fish [a,*], Anthony J. Nicastro [b]

[a] Department of Biology, West Chester University, West Chester, PA 19383, USA
[b] Department of Physics, West Chester University, West Chester, PA 19383, USA

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ABSTRACT

The ability to maneuver is an important aspect of the locomotor performance of fishes, but can be constrained by the inflexibility of the body, such as in batoid rays. Turning radius (maneuverability) and turning rate (agility) were measured from overhead video recordings of rays in a large pool during unrestricted swimming. The rays that were observed swam by oscillatory movements of the pectoral fins (*Aetobatus narinari*, *Myliobatis freminvillii* and *Rhinoptera bonasus*) or by undulations of the fins (*Dasyatis americana* and *Dasyatis centroura*). Oscillatory rays maneuvered by either powered or unpowered gliding turns, whereas undulatory rays turned using asymmetrical undulations of both pectoral fins. Underwater observations showed that both rays used banking while turning, where bank angle ranged from 15–70°. No differences were found between mean turning parameters between the two locomotor types. Minimum turn radius and maximum turning rate based on the extreme 20% of measurements were respectively smaller and larger for oscillatory rays (0.7 m; 44.4° s^{-1}) compared to undulatory rays (1.0 m; 30.4° s^{-1}). Compared to other aquatic animals, the turning performance of rays is lower than flexible bodied animals, but similar to other animals with rigid bodies.

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1. Introduction

Maneuvering is particularly important for negotiating obstacles in complex spatial environments, catching prey, escaping predators, and ritualistic display and mating (Howland, 1974; Webb, 1976; Weihs and Webb, 1984; Domenici and Blake, 1997; Biewener, 2003; Walker, 2004). The morphologies and locomotor modes of aquatic animals are expected to have an effect on maneuverability (Webb, 1978, 2002, 2004, 2006; Walker, 2000, 2004; Fish, 2002; Weihs, 2002; Danos and Lauder, 2007). The design and position of control surfaces determine how maneuverable a body will be in a fluid environment (Fish, 2002; Singh et al., 2004). Fish utilize an assortment of fins as control surfaces to regulate changes in translational (slip, heave, and surge) and rotational (pitch, yaw, and roll) movements (Fig. 1; Fish, 2002; Walker, 2004; Webb, 2006). These fins generally comprise a small proportion of the entire surface area of the body. Possession of multiple fins (e.g., pectoral, pelvic, anal, dorsal, and caudal) allows for the fish to simultaneously execute motions associated with maneuvering, stabilization, and propulsion (Walker, 2004; Webb, 2006). In contrast, the dominant pectoral fins of rays must perform all of these functions.

Batoids are a monophyletic group of elasmobranchs that possess dorsoventrally flattened bodies and expanded pectoral fins that are fused to the head to form a broad flat planform (Lindsey, 1978; Rosenberger, 2001; Douady et al., 2003). Rays swim with the pectoral fins by undulatory or oscillatory mechanisms for thrust generation (Breder, 1926; Clark and Smits, 2006). The pectoral fins are highly flexible, although constrained at the base (Klausewitz, 1964; Lindsey, 1978; Heine, 1992; Rosenberger, 2001; Schaefer and Summers, 2005). Undulatory locomotion (rajiform mode) is performed by various benthic species (e.g., *Dasyatis* and *Raja*) and involves passing short wavelength traveling waves along the fin margin from anterior to posterior (Breder, 1926; Campbell, 1951; Klausewitz, 1964; Webb, 1975; Daniel, 1988; Rosenberger and Westneat, 1999; Rosenberger, 2001). The pelagic rays (e.g., *Manta*, *Myliobatis*, and *Rhinoptera*) use oscillatory locomotion (mobuliform mode). These rays swim by flapping the pectoral fins dorsoventrally to produce lift to generate thrust analogous to the flight of birds (Breder, 1926; Klausewitz, 1964; Lighthill, 1969; Heine, 1992; Webb, 1994, 1998; Rosenberger, 2001; Kato, 2005). An undulation–oscillation continuum exists within the diversity of batoid species between these two locomotor extremes. Position in the continuum is based on the number of waves present in the pectoral fin (Rosenberger, 2001). Undulation is defined as more than one wave present on the fin at one time, whereas, oscillation is having less than one-half of a wave present on the fin (Rosenberger, 2001).

Fishes with depressed body morphologies, such as flatfishes, skates and rays are associated with benthic habits in which the fishes are in contact or in close proximity with the ocean bottom with one side of their bodies (Brainerd et al., 1997). The depressed body
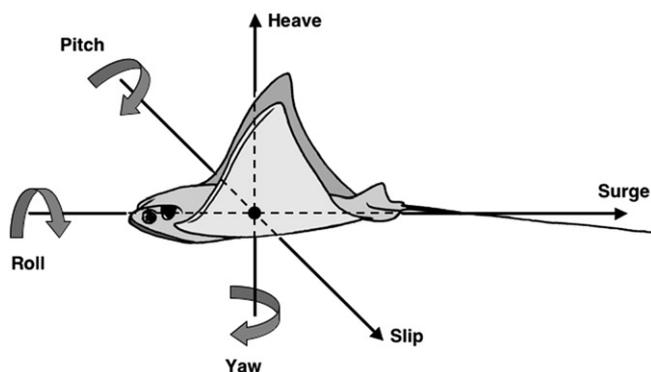
Fig. 1. Translational and rotational movements associated with a three-dimensional axis system superimposed on *R. bonasus*. Rotational movements include roll (rotation around the longitudinal axis), pitch (rotation around the transverse axis), and yaw (rotation around the vertical axis). Translational movements along the three axes include surge (longitudinal axis), heave (vertical axis) and slip (transverse axis).

morphology of flatfishes enhances stability, particularly in station holding (Arnold and Weihs, 1977; Brainerd et al., 1997; Fish, 2002). For a body in a stable state, the sum of all forces and all turning moments is zero. Maneuvering, however, is characterized by changes in rate of movement and trajectory in which a body undergoes translation and rotation (Fig. 1; Fish and Nicastro, 2003).

Body rigidity is particularly important in determining stability and maneuvering performance (Walker, 2000; Fish, 2002; Fish and Nicastro, 2003; Rivera et al., 2006). The flexible vertebral column possessed by many animals permits a substantial amount of maneuverability (Fish, 2002; Fish and Nicastro, 2003). A flexible body is thought to enhance turning performance in two ways, by enabling the organism to turn about a small radius of curvature and by decreasing the rotational inertia (Fish, 1999; Walker, 2000; Fish, 2002; Rivera et al., 2006). However, many aquatic animals including rays have bodies that are constrained by a stiff/rigid spinal column or are encased in a rigid exoskeleton (Klausewitz, 1964; Summers, 2000; Fish and Nicastro, 2003; Schaefer and Summers, 2005; Dougherty et al., 2010). An inflexible body restricts rigid and thus maneuvering by increasing the moment of inertia (Giancoli, 1991). Although turning performance has been studied in a number of diverse flexible-bodied species, explicit evaluations of turning performance among rigid-bodied animals have been limited (Walker, 2000; Fish and Nicastro, 2003; Rivera et al., 2006; Dougherty et al., 2010).

Rays like other fishes must be able to execute turning maneuvers. Breder (1926) observed functional differences among families of rays in executing turning maneuvers. In the family Rajidae, the small but functional tail is used to steer. However in the families Trygonidae and Myliobatidae, the tail is reduced to a whip-like appendage. Turning by rays in these families is accomplished by differential movements of the pectoral fins with the propulsive movements of the outboard fin being faster than the inboard fin.

The dichotomy between morphologies associated with stability and maneuverability places constraints on performance. To examine these constraints for a stable body design, the turning performance of five species of rays was examined using videography to quantify the spatial (i.e. radius) and rate (i.e. angular velocity) characteristics of turning. The rays were examined to assess the differences between oscillatory and undulatory locomotors and the effects of their dorsoventral flattened morphologies on turning performance. As oscillatory swimmers are characterized as having relatively stiffer propulsors and swimming speeds than undulatory swimmers (Webb, 1975), it was expected that oscillatory swimming rays would exhibit higher turning rates but larger turn radii than undulatory swimming rays. In addition, it was expected that rigid bodied rays should show lower turning performance compared to flexible bodied swimmers (Fish, 2002).

2. Materials and methods

2.1. Experimental animals

The turning performance of five species of batoid rays from the Myliobatidae and Dasyatidae was examined at the National Aquarium in Baltimore, MD, USA. The rays present at the facility included 18 cownose rays (*Rhinoptera bonasus*), 12 southern rays (*Dasyatis americana*) two bullnose rays (*Myliobatis freminvillii*), two roughtail rays (*Dasyatis centroura*), and one spotted eagle ray (*Aetobatus narinari*). Based on their method of propulsion, the rays were categorized as either oscillatory swimmers (Myliobatidae: *A. narinari*, *M. freminvillii*, and *R. bonasus*) or undulatory swimmers (Dasyatidae: *D. americana*, and *D. centroura*) (Rosenberger, 2001).

The dasyatid rays, *D. americana* and *D. centroura*, have a disk shaped body and pectoral fins, which terminate distally with a blunt and rounded shape. Myliobatid rays, *A. narinari*, *M. freminvillii*, and *R. bonasus*, have pectoral fins that are pointed distally and broaden proximally. Dasyatid rays have fin shapes with relatively low aspect ratios (the ratio of span to chord) compared to the myliobatid rays, which have longer fin spans with a narrower width (Rosenberger, 2001).

The rays were maintained in an indoor facility consisting of a large saltwater pool. Except for a single individual of *A. narinari* and *D. centroura*, individual animals could not be identified.

2.2. Video recording and analysis

A dorsal view of the turning rays was recorded with a Sony Digital 8 Handycam at 60 Hz. The camera was positioned at a height of 8.2 m above a cul-de-sac in the tank (approximately 7.3 m wide) with a depth of 2.1 m, where the rays freely exhibited volitional turning behaviors. Surface distortions of the water were minimal as the rays tended to stay submerged. A meter stick was placed on the water surface in the field of view to act as a scale. Although an object on the bottom of the tank would appear 20% smaller than at the surface, the refractive index of water (1.33) would magnify the object so that its apparent size on the bottom would be 5.9% larger than actual size.

Video records of the turns were analyzed frame-by-frame using the Peak Motus video analysis system (version 4.3.1: Peak Performance Technologies, Englewood, CO, USA). Points were placed manually on the end of the rostrum and base of the tail for each individual frame. The scaled distance between these two points represented the body length (L). The Peak Motus system was used to calculate the x- and y-coordinates of a virtual midpoint along a line joining the two digitized points. Portions of a path where a turning maneuver exhibited the sharpest turn were chosen for analysis. The x- and y-coordinates of the virtual midpoint ($0.5L$) was used to define the path of the ray. This midpoint approximated the center of mass of the rays (Fish, unpublish. data). The coordinate data were smoothed by fitting a second or third order polynomial to the data using Microsoft Excel. Values for r^2 for all polynomial fitted paths averaged 0.99 ± 0.01 (S.D.).

Once a smoothing polynomial was fitted to the path of a turning maneuver, the radius of curvature along the path could be determined by computing the radius (R) from x- and y-coordinates (Koshtoev, 1973; Sandor and Richter, 1987; Larson et al., 1994; Walker, 2000):

$$R = \frac{\left[1 + (dy/dx)^2\right]^{3/2}}{|d^2y/dx^2|}. \tag{1}$$

For this analysis, the polynomial function replaces the original data. The location of the minimum value of the radius of curvature can be located to whatever precision is needed by simply using sufficiently small steps in the x-coordinate.

From scaled coordinates' data, the speed along the path was calculated from the x- and y-components of the speed, v_x and v_y, by determining the difference in respective coordinates and dividing by the time between frames. The resultant speed (v) was calculated using $v = \sqrt{v_x^2 + v_y^2}$. With the location of the radius of curvature (R) of the path determined by using Eq. (1), the average angular speed (ω) in radians per second as a measure of turning rate was computed from $\omega = v/R$ and converted to degrees per second by multiplying by $180/\pi$. Centripetal acceleration (a_c) as a multiple of gravitational acceleration ($g = 9.8 \, \mathrm{ms}^{-2}$) was computed according to (Fish and Nicastro, 2003; Fish et al., 2003a, 2003b):

$$a_c = v^2 / Rg. \tag{2}$$

2.3. Banking

Anterior and posterior views of the rays were video recorded through a square underwater viewing window to describe the gross movements of the rays when turning. Rays turned in a 7 m square section of the pool that was 4 m deep. Maximum bank angles of the oscillatory and undulatory rays executing a turn were measured from video with a protractor when the ray was oriented with the tips of the pectoral fins perpendicular to the camera view. To indicate the action of the pectoral fins during turning, the convention used by Fish and Nicastro (2003) was used. The inboard fin was the fin closest to the center of rotation of the turn, whereas the outboard fin was furthest from the center of the turn.

2.4. Turning performance variables

To examine turning performance by the rays, data were expressed as maximum and minimum values, means ± 1 standard deviation (S.D.), and the means of the extreme 20% of values (i.e., minimum radius and maximum turning rate). Choice of the extreme 20% of values was considered arbitrary but was used previously for comparisons of turning performance (Webb, 1983; Gerstner, 1999; Fish, 2002; Fish et al., 2003a, 2003b; Fish and Nicastro, 2003; Maresh et al., 2004; Rivera et al., 2006).

As individual animals could not be determined, only relative comparisons of means of performance parameters between species and swimming mode (undulatory and oscillatory swimming) were

made. Regression equations and correlation coefficients were computed using KaleidaGraph (version 3.0) software. To adjust for size differences between species, data were analyzed with respect to length-specific velocity (v/L) and length-specific turning radius (R/L).

3. Results

3.1. Swimming patterns

A total of 29 dorsal views of turns by rays were analyzed (oscillatory n = 21; undulatory n = 8). Only dorsal views by *D. americana* (n = 6), *D. centroura* (n = 2), *M. freminvillii* (n = 6) and *R. bonasus* (n = 15) were available as *A. narinari* avoided turning in the cul-de-sac. In most cases, the turns were made as 90° or 180° turns. In one case, a cownose ray (*R. bonasus*) sequentially completed two 360° turns. All curved trajectories by the *D. americana* and *D. centroura* were executed as powered turns, whereby thrust was continually generated by fin undulations. *M. freminvillii* and *R. bonasus* executed powered turns by oscillations of the fins, but these oscillatory rays also executed unpowered turns in which the ray glided through the turn with no oscillatory motions.

Video records from the underwater view were available for the ray species (n = 38), excluding *D. centroura*. Oscillatory rays initiated the turn by raising the outboard pectoral fin, while dropping the inboard fin and banking with the dorsum facing into the turn (Fig. 2). During powered turns, the outboard fin was observed to have oscillations with larger amplitudes at the tip than the inboard fin. Oscillatory rays were also seen gliding through 20% of turns after an initial power stroke was made. In unpowered turns, the fins were held dorsally and motionless throughout the entire turn with the outboard fin tip curled over the body toward the midline. The bodies and tails of the oscillatory rays remained straight and rigid throughout all turning maneuvers.

For the undulatory swimmer *D. americana*, the rays constantly undulated their pectoral fins throughout the turn (Fig. 3). The waves of each fin were in phase during straight swimming. As the ray turned, the outboard fin increased in amplitude, whereas, undulations of the inboard fin appeared smaller in amplitude and less frequent. For small radius turns, the inboard fin beat only once or not at all. The outboard fin tip remained raised and curled toward the midline throughout the entire turn. The tail bent in the direction of the turn creating a C-shape, whereas the body of the ray remained straight throughout all turns.
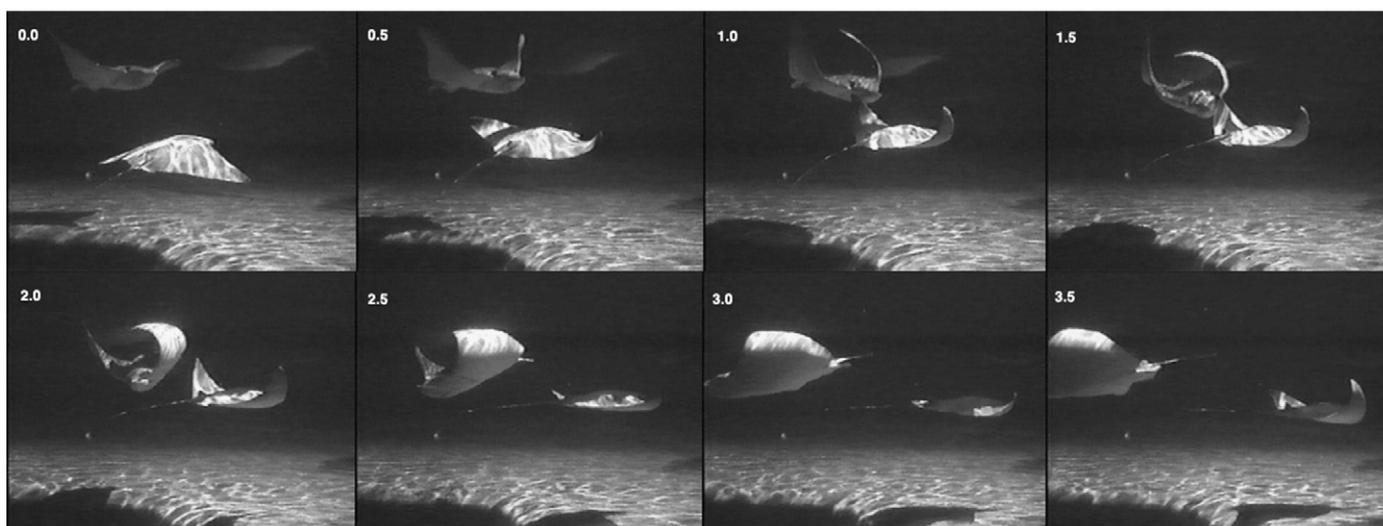

Fig. 2. Video sequence of a cownose ray (*R. bonasus*) executing an unpowered gliding turn. The uppermost individual performs the turn, while the lower ray swims in a straight line. The numbers in each image indicate seconds.
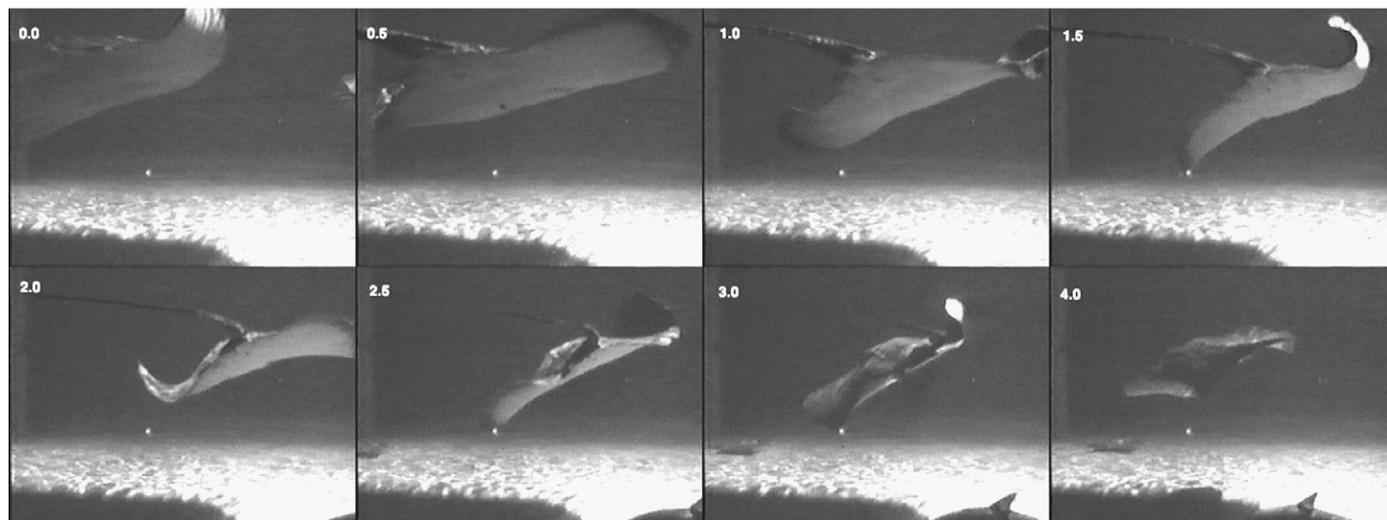
Fig. 3. Video sequence of a southern ray (*D. americana*) executing a powered turn. The numbers in each image indicate seconds.

Both oscillatory and undulatory rays banked (i.e., rotation about roll axis, Fig. 1) throughout their turns. The mean bank angles for oscillatory rays (*A. narinari*, n = 5; *M. freminvillii*, n = 2; *R. bonasus*, n = 14) and undulatory rays (*D. americana*, n = 17) were 30.6 ± 16.2° (n = 21; range: 15–70°) and 31.4 ± 4.7° (n = 17; range 26–42°), respectively. Comparison of mean bank angle for the two types of rays showed less than a 3% difference. However when considering maximum performance values, two *R. bonasus* banked at angles of 65° and 70°, which was 1.5–1.7 times higher than the maximum bank angle of 42° observed for a *D. americana*. The other species displayed lower maximum bank angles (*A. narinari*, 31°; *M. freminvillii*, 28°).

3.2. Turning performance

Summary data on turning performance of the swimming batoids are presented in Table 1. Overall, differences in means for oscillatory and undulatory rays for all parameters were small indicating no difference in performance between the two swimming modes. As the means for oscillatory and undulatory rays were similar, all data were combined (Table 1).

However, there were some differences between oscillatory and undulatory swimming rays for the extreme 20% of turning performance parameters (Table 1). The minimum turn radius was 30% smaller for oscillatory rays compared to undulatory rays. Despite similar maximum swimming velocities, oscillatory swimmers had 22% higher values of v/L than undulatory swimmers. This resulted in 32% and 37% higher ω and a_c, respectively, for oscillatory swimmers versus undulatory swimmers.

The mean turning rate, ω, for all rays was 23.5 ± 11.2°. The highest ω of 44.2° s^{-1} was found at R of 0.8 m (1.3L) for *R. bonasus*. ω

decreased curvilinearly with increasing R (Fig. 4) according to the relationship:

$$\omega = 26.80 R^{-0.77} (r = 0.71). \tag{3}$$

The increase in ω with decreasing R occurred because, over an equivalent range of v, rays would transverse similar arc lengths. With smaller radius turns, rays would move through a larger angular displacement for a given time compared to larger-radius turns. As the rays swam steadily, ω approaches an asymptote with increasing R.

Turning rate was linearly related to a_c (Fig. 4; $r = 0.89$). The regression equation describing this relationship was:

$$a_c(g) = -5.70 \times 10^{-4} + 1.27 \times 10^{-4} \omega. \tag{4}$$

4. Discussion

4.1. Turning maneuvers by rays

The batoid rays were able to execute turns by unpowered glides and powered flapping motions. Unpowered turns were confined to the oscillatory rays, *M. freminvillii*, *R. bonasus*, and *A. narinari*. These rays held their fins dorsally and motionless as they glided through the turn. Gliding behavior has been observed in rays with high aspect ratio fins that have an oscillatory-based propulsion (Rosenberger, 2001). Similarly, unpowered, gliding turns are performed by other oscillatory lift-based swimmers (Hui, 1985; Fish, 2002; Fish et al., 2003a, 2003b). In powered turns, propulsive motions of the pectoral fins were evident through the entire turn. These turns were

Table 1
Turning performance data (means ± S.D.) for oscillatory and undulatory swimming batoids.

| Swimmer	n	Turn radius (m)	Turn radius (L)	Velocity (m s^{-1})	Velocity (L s^{-1})	ω (deg s^{-1})	Centripetal acceleration (m s^{-2})
Oscillatory	21	1.4 ± 0.6	2.1 ± 1.0	0.5 ± 0.2	0.8 ± 0.2	24.8 ± 12.2	0.020 ± 0.020
Range		0.5–3.0	0.9–4.9	0.3–0.9	0.4–1.1	9.3–48.0	0.008–0.056
Extreme 20%	4	0.7 ± 0.1	1.1 ± 0.2	0.8 ± 0.1	1.1 ± 0.0	44.4 ± 2.7	0.052 ± 0.004
Undulatory	8	1.8 ± 0.9	2.2 ± 1.7	0.6 ± 0.2	0.6 ± 0.2	20.1 ± 7.8	0.022 ± 0.012
Range		1.0–3.5	0.9–6.1	0.3–0.8	0.2–0.8	7.8–32.0	0.006–0.035
Extreme 20%	2	1.0 ± 0.1	1.0 ± 0.1	0.8 ± 0.1	0.8 ± 0.0	30.4 ± 2.3	0.033 ± 0.003
All data	29	1.5 ± 0.7	2.1 ± 1.2	0.5 ± 0.2	0.7 ± 0.2	23.5 ± 11.2	0.024 ± 0.016
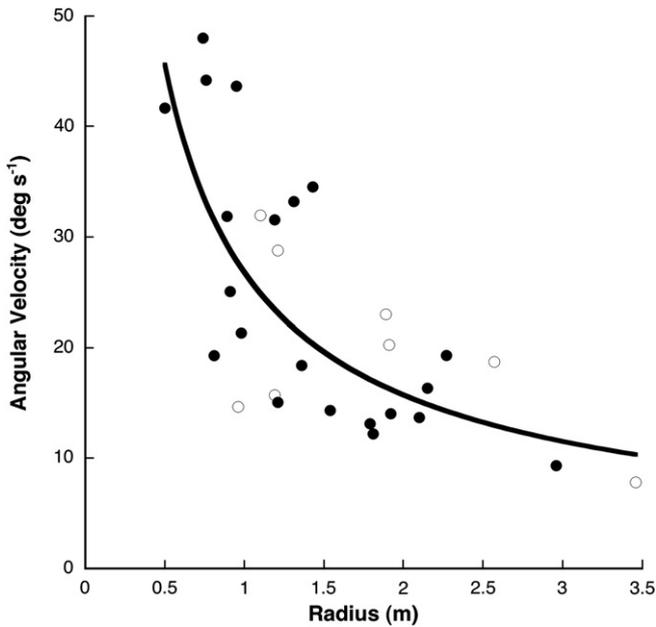
Fig. 4. Relationship of angular velocity, ω, and turning radius, *R* for oscillatory rays (solid circles) *M. freminvillii* and *R. bonasus* and undulatory rays (open circles) *D. americana* and *D. centroura.*

accomplished by asymmetrical motions of the pectoral fins. Powered turns were observed for both undulatory and oscillatory swimming rays (Fig. 5).

No difference in mean turning performance was observed between rays using the two swimming modes. In that the freely swimming rays were not induced to perform maximally and turned in a relatively unconfined space, performance differences may not have been expressed. Indeed when the extreme 20% of turn variables were compared, distinct differences in performance were noted. Oscillatory rays displayed smaller turning radii than larger undulatory ray. The
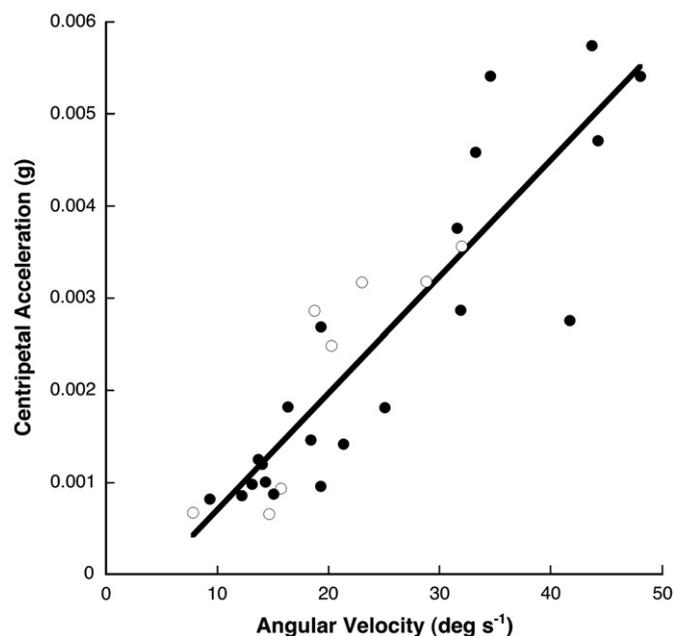
greater agility and centripetal acceleration of oscillatory swimmers compared to undulatory rays may be a function of the absolute size and turning radius differences. Turning rate is inversely proportional to body size (Fig. 6); thus, larger animals turn at a slower angular velocity than do smaller animals (Howland, 1974; Fish and Nicastro, 2003).

The turns performed by all the rays in this study were generally of large radii that were produced by a combination of translational and rotational movements. These turns may not represent the minimum radius that could potentially be accomplished. Minimum circular turns of fish typically have radii of less than 0.2*L* (Webb, 1983; Domenici and Blake, 1997; Gerstner, 1999). Fast-start experiments demonstrated that fish could turn with radii down to 5.5% of body length (Domenici and Blake, 1997).

Rays are capable of small radius turns. A video by M. Ball of a bat ray, *Myliobatus californica*, (http://ad.id.ucsb.edu/quicktime/video.asp?movie=Mylobatls01.mov) showed a 90° turn from a resting position. The turn was nearly all rotational with a zero-radius displacement until the ray accelerated away from the observer. This turn was accomplished by asymmetrical motions of the pectoral fins. The initial motions had a wave move laterally along the leading edge of the fin with the trough of the wave in the proximity of the substrate. This motion raised the anterior of the body off the substrate. The inboard fin was then pitched ventrally with the tip curled dorsally, while the outboard fin was pitched dorsally and the body rolled slightly toward the inboard fin. The crest of the traveling wave moved toward the outboard fin tip, causing the ray to yaw. With the ray turning, the fin tips were brought into apposition over the dorsum of the ray. Finally, simultaneous downstroke of the pectoral fins accelerated the ray with a new trajectory.

Purely rotational, zero-radius turns are performed by fish with inflexible bodies and active motions of fins that are positioned close to
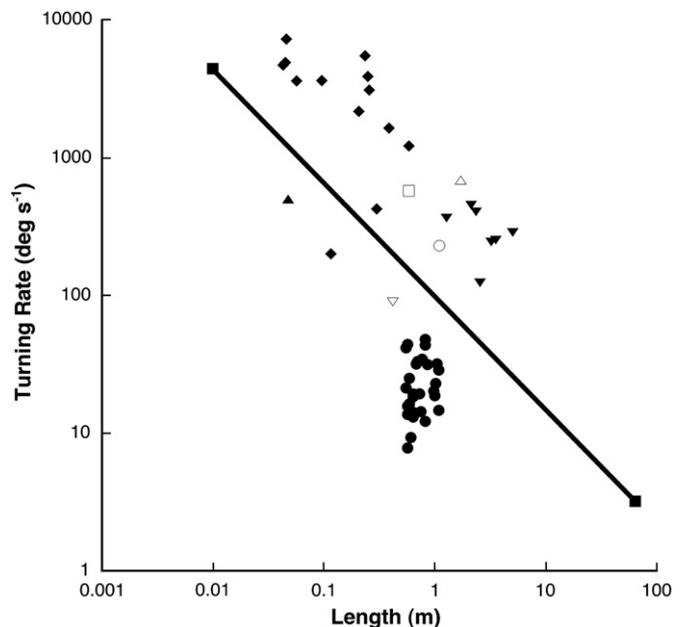

Fig. 6. Comparison of turning rate, ω, with respect to body size. The line connecting the whirligig beetle (upper ■) and submarine (lower ■) represents a limit to turning performance for rigid bodies. The other symbols are for rays (●), crocodile (○), fish (♦), penguin (□), sea lion (△), squid (▽), turtle (▲), and whales (▼). Symbols above the line represent flexible-bodied animals, whereas symbols below the line are for rigid-bodies. The only fish to have a turning rate below the line was the boxfish, which has a rigid body.

Data from Webb (1976, 1983), Hui (1985), Foyle and O'Dor (1988), Miller (1991), Blake et al. (1995), Gerstner (1999), Walker (2000), Frey and Salisbury (2001), Fish (1997, 2002), Fish and Nicastro (2003), Fish et al. (2003a, 2003b), Domenici et al. (2004), and Rivera et al. (2006).

Fig. 5. Relationship between centripetal acceleration, a_c, and turning rate, ω, for rays. Solid circles represent data for oscillatory rays *M. freminvillii* and *R. bonasus* and open circles are for undulatory rays *D. americana* and *D. centroura.* The regression equation for the combined data from oscillatory and undulatory rays is provided in the text.

the center of mass (Breder, 1926; Blake, 1977; Walker, 2000). Breder (1926) stated that turns by fish could be accomplished by either abducting one pectoral fin into the flow or using only one fin for propulsion. Blake (1977) and Walker (2000) observed rotational turns by the boxfishes (Ostraciontidae) using a combination of asymmetrical pectoral fin motions and motions of the dorsal and anal fins.

While purely rotational turns accentuate maneuvering, the combination of rotation and translational movements can foster increased agility when speed is maximized while simultaneously minimizing turning radius. Such turns require the simultaneous generation of thrust and centripetal forces. However, development of both these forces by the pectoral fins of rays may be limited for a flat body form with respect to the horizontal plane. The dorsoventral compressed body provides little ability to generate the lateral forces necessary to prevent slip and maintain the turn. A lateral compressed body shape or the addition of median fins produces hydrodynamic forces from flow to maintain the turn (Webb and Keyes, 1981; Fish, 2002; Webb, 2002, 2006). The laterally compressed body form allows the angelfish (*Pterophylum*) to have a minimum turning radius (Domenici and Blake, 1991) that is smaller than predicted by Howland (1974). The relatively large lateral surface of the angelfish permits large turning moments with a minimum of slip.

Movement of the paired pectoral fins of rays can aid in the generation of a centripetal force to bank the body and reduce slip. Banking is a rolling maneuver that provides a greater projected area facing the axis of the turn (Fish et al., 2003a, 2003b). By banking through the turn, the body and fins would be canted at an angle to the incident water flow (i.e., angle of attack). Lift is generated as a force acting perpendicular to the direction of flow that is resolved into vertical and horizontal vector components. The horizontal component of the lift generated from the pectoral fins and body produces a centripetal force, which turns the ray. The vertical component counters the gravitational force and keeps the negatively buoyant animal from losing altitude. Banking is a more economical means of moving in a circular path than generating an asymmetric thrust (Weihs, 1981). High bank angles are characteristic of aquatic animals that lack median fins and turn using elongate pectoral flippers (Godfrey, 1985; Hui, 1985; Fish and Battle, 1995; Fish, 2002; Fish et al., 2003a, 2003b).

4.2. Effects of a rigid body on turning performance

An animal's morphology is a compromise between competing behavioral requirements and phylogenetic history. Various morphologies that encourage maneuverability or stability have evolved within aquatic animal lineages (Webb, 1983, 2002, 2006; Webb et al., 1996; Fish, 1999, 2002; Weihs, 2002; Fish and Nicastro, 2003). In particular, body and fin morphology of fish and other aquatic animals are associated with stability and maneuverability (Fish, 2002).

Compared to animals with flexible bodies, the relative minimum turning radii of batoids are constrained due to their rigid body (Webb, 1976; Webb and Keyes, 1981; Domenici and Blake, 1991, 1997; Gerstner, 1999; Webb and Fairchild, 2001; Fish, 2002; Fish et al., 2003a, 2003b; Domenici et al., 2004; Rivera et al., 2006). In the absence of a large number of highly mobile control surfaces, the ability to flex the body promotes rotation ability (Fish, 2002; Fish et al., 2003a, 2003b; Maresh et al., 2004). Fish and Nicastro (2003) compared the ω of flexible- and rigid-bodied swimmers of different body lengths (Fig. 6). When a line was drawn between the maximum ω for a whirligig beetle ($4437.5°\,s^{-1}$), the smallest rigid bodied animal measured, and for the experimental submarine USS Albacore ($3°\,s^{-1}$), the largest rigid bodied entity measured, flexible-bodied animals were positioned above the line, whereas rigid-bodied animals were positioned below the line. The distribution of data indicated that for equivalent body sizes, flexible-bodied swimmers had higher turning rates than rigid-bodied animals. The ω for rigid-bodied swimmers was at least six to eight times lower than predicted for flexible animals (Walker, 2000).

Batoids had a low ω compared to various other flexible-bodied animals. Both oscillatory and undulatory rays fell below the line between beetles and the submarine along with other rigid-bodied swimmers. The values of ω for rays were slower than for other rigid bodied animals (Foyle and O'Dor, 1988; Walker, 2000; Rivera et al., 2006). These data support the hypothesis that the rigid body of rays limits turning performance.

Walker (2000) argued that rigid-bodied organisms had relatively lower turning performance than flexible-bodied animals due to the inability to reduce the body's moment of inertia (second moment of area) about the yawing axis, resulting in high inertial resistance to rotation. Rotational inertia is a measure of the resistance to changes in rotation about an axis (Frohlich, 1980; Carrier et al., 2001; Walter and Carrier, 2002). The contribution to a body's rotational inertia by a particle of the body is computed from the product of the particle's mass and the square of the distance from the axis of rotation (Giancoli, 1991). The more mass that is positioned far from the center of rotation, the greater the rotational inertia, and the more force needed to turn. Animals with laterally flexible bodies can redistribute their mass to effectively lower the inertia resistance to turning. The geometry of the ray and the restrictions of the skeleton prevent lateral bending. In addition, the tails of rays, although capable of lateral bending, are long and narrow. The tail is not of sufficient mass compared to the body to change the moment of inertia. In addition, the caudal fin of dasyatid rays is too small to generate sufficient force to overcome the inertia of the body. With the fins bent dorsally and in apposition, the mass of the animal was effectively concentrated closer to the yawing axis and inertial resistance would be reduced.

Acknowledgments

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