



Turning performance of batoids: Limitations of a rigid body

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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

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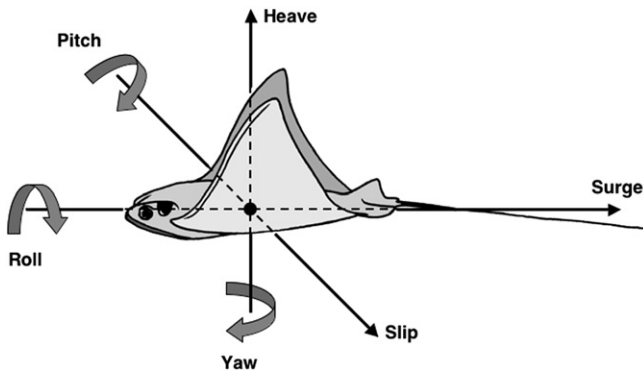


Fig. 1. Translational and rotational movements associated with a three-dimensional axis system superimposed on *R. bonasus*. Rotational movements include roll (rotation around the longitudinal axis), pitch (rotation around the transverse axis), and yaw (rotation around the vertical axis). Translational 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 Nicasro, 2003).

Body rigidity is particularly important in determining stability and maneuvering performance (Walker, 2000; Fish, 2002; Fish and Nicasro, 2003; Rivera et al., 2006). The flexible vertebral column possessed by many animals permits a substantial amount of maneuverability (Fish, 2002; Fish and Nicasro, 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 (Klauewitz, 1964; Summers, 2000; Fish and Nicasro, 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 Nicasro, 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, unpubl. 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):

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

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.

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