

## Balancing Requirements for Stability and Maneuverability in Cetaceans<sup>1</sup>

FRANK E. FISH<sup>2</sup>

Department of Biology, West Chester University, West Chester, Pennsylvania 19383

**SYNOPSIS.** The morphological designs of animals represent a balance between stability for efficient locomotion and instability associated with maneuverability. Morphologies that deviate from designs associated with stability are highly maneuverable. Major features affecting maneuverability are positions of control surfaces and flexibility of the body. Within odontocete cetaceans (i.e., toothed whales), variation in body design affects stability and turning performance. Position of control surfaces (i.e., flippers, fin, flukes, pectoral) provides a generally stable design with respect to an arrow model. Destabilizing forces generated during swimming are balanced by dynamic stabilization due to the phase relationships of various body components. Cetaceans with flexible bodies and mobile flippers are able to turn tightly at low turning rates, whereas fast-swimming cetaceans with less flexibility and relatively immobile flippers sacrifice small turn radii for higher turning rates. In cetaceans, body and control surface mobility and placement appear to be associated with prey type and habitat. Flexibility and slow, precise maneuvering are found in cetaceans that inhabit more complex habitats, whereas high-speed maneuvers are used by cetaceans in the pelagic environment.

### INTRODUCTION

#### **Stability and maneuverability**

The morphologies displayed by animal species represent compromises between structural materials, evolutionary constraints, and diverse functional requirements. For mobile animals, two of these functional requirements concern stability and maneuverability for animals in motion. Stabilizing systems self-correct for disturbances and maintain a desired postural attitude; whereas maneuvering systems do the opposite by producing controlled instabilities allowing a change in direction, stopping, and starting (Webb, 1997). Although these functions appear to be quite different, they are closely related (Webb, 1997). Stability promotes steady movement along a predictable trajectory, whereas changes in rate of movement and trajectory characterize maneuverability, which represents a controlled instability. A maneuvering body undergoes translation or rotation as opposed to a stable body in which the sum of all forces and all turning moments are zero.

Animals are at constant odds to balance the competing requirements of stability and maneuverability. Stability for animals reduces the energetic cost of locomotion. Stable gaits operate economically within narrow ranges of speed (Hoyt and Taylor, 1981; Webb, 1994). Movement in a rectilinear manner decreases the resistive forces associated with the locomotor activity and minimizes the distance traveled. Therefore, from an evolutionary perspective, one might conjecture that stability would have a positive selection value in such behaviors as migration over prolonged distances and time. However, animals rarely move continuously in straight lines. For example, complex movements are

required when a potential prey must out-maneuver a predator or for a predator to turn fast enough to catch its prey (Howland, 1974; Webb, 1983). In addition, some search patterns employed by animals use episodic turning maneuvers (Marler and Hamilton, 1966).

Stability and maneuverability are controlled in concert both actively and passively in animals. Active mechanisms include activation of musculo-skeletal components under neurological control to internally induce perturbations for maneuverability or compensate for external perturbations acting against stability (Webb, 1997). While active mechanisms effectively manage stability and maneuverability, these come at the expense of energy. Passive mechanisms, which are dependent upon the morphology of the animal, require no additional energy. Depending on the specific morphology, stability or maneuverability can be accentuated. Body designs that are adapted for stable movement are not suitable for high maneuverability and vice versa (Weihs, 1993). As animals are multi-tasking entities, a "compromise" morphology between one optimized for stability or maneuverability is necessary, although depending on the habits of a particular organism, the morphology may be more polarized toward one extreme.

How can one identify specific morphological designs that promote either stability or maneuverability? An important consideration in functional design is the environment in which the morphology operates. Figure 1 illustrates a series of cross-sectional morphologies from a circular profile to a flat plate with gradations of elliptical forms as intermediates. In a terrestrial situation with the object contacting the ground, the circular form would be more unstable than the flat plate. Only a small perturbation, and thus little energy, would be required to remove the circular form from its static equilibrium while in contact with a rigid substrate. With transition to a flat plate, increasing forces are required to displace and accelerate the body against

<sup>1</sup> From the Symposium *Stability and Maneuverability* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 3–7 January 2001, at Chicago, Illinois.

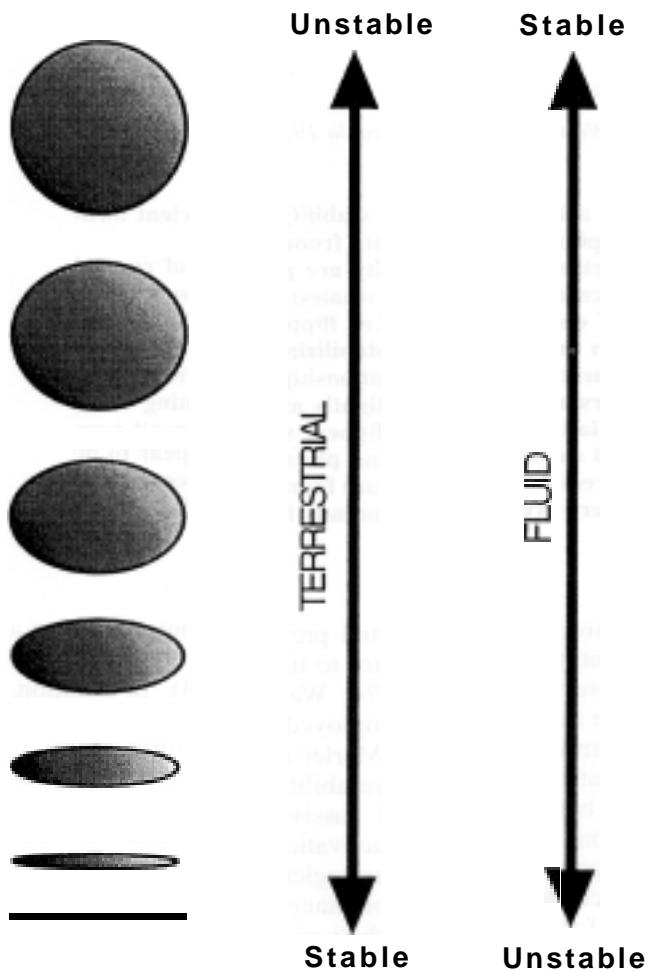


FIG. 1. Gradient of cross-sectional morphologies. In a terrestrial environment, stability is gained in transition from a circular to flattened design. The reverse occurs in a fluid environment (i.e., air, water) with the flatten profile being unstable. If canted at angle, the flat plate will produce lift which will destabilize its position, whereas no lift is incurred for the circular profile.

frictional forces and the reduced tendency to roll. In a fluid environment, the stability of the design gradient is opposite to the terrestrial situation (Fig. 1). For a given angle of attack, a flow can produce a larger lift inducing displacement on a flat plate compared to elliptical designs approaching a circular form.

For this paper, I will focus on the effect of various morphological designs on stability and maneuverability in a fluid environment. This focus will permit an understanding of the association between animal morphology and the limitations on behavior. In particular, stability and maneuverability issues for cetaceans (e.g., whales, dolphins) will be explored with regard to their ecology.

#### Arrow model

To understand how variation in the morphology of animals can affect maneuverability, consideration should be given to parameters associated with stability. Maneuverability represents a controlled instability, and

morphological characters that deviate from those of a stable design are expected to enhance maneuvering performance. Perhaps the simplest model to use as a standard to assess a stable morphology of an animal in a fluid environment is an arrow. An arrow represents a relatively simple technology that is extremely stable for movement through a fluid (Wegener, 1991). Upon being shot from a bow, an arrow becomes self-stabilizing with respect to yaw, pitch and roll. The stabilizing feathers, located at the posterior end of the shaft, produce lift forces to counteract destabilizing turning moments around the center of gravity (CG). Based on analysis of aerodynamics, a number of design features associated with stability are represented in the arrow (Fig. 2).

Features associated with placement and design of control surfaces provide stability by producing turning moments in response to changing flow direction (Aleyev, 1977; Webb, 1984; Weihs, 1993; Bandyopadhyay et al., 1997; Fish, 1997). Control surfaces located far from the CG can generate large directionally correcting moments, because of their long lever arm. The relative size of the control surface in relation to its location also will determine the magnitude of the moments (Aleyev, 1977). Stable movement occurs with posterior placement of the control surfaces relative to CG (Wegener, 1991). Both dihedral and sweep of the control surfaces act similarly to stabilize motion (Hurt, 1965; Webb, 1975; Weihs, 1993). Dihedral is a tilting of the control surface relative to the body and sweep is rearward sloping of the leading edge of the control surface. Because the velocity of a fluid oriented obliquely to the trajectory of the arrow encounters each member of a paired control surface differently, the control surface with a more perpendicular orientation to the flow will generate larger forces than the other control surface and produce stabilizing moments (Smith, 1992). Sweep results in a backward shift in the center of lift providing increased stability (Weihs, 1993). Reduced motion of the control surface and reduced flexibility of the body restrict self-generated perturbations (Fish, 1997, 1999; Walker, 2000).

The same features that control stability for an arrow are present in the morphology of animals. Unlike the arrow, the animal body is responsible for producing its own propulsive forces. Flexibility of the body and the appendages, by undulation and oscillation, are necessary in the generation of thrust (Lighthill, 1975; Webb, 1975; Fish, 1996). These propulsive motions produce transverse recoil forces that must be balanced along the body to maintain stability and minimize energy expenditure during locomotion (Lighthill, 1975; Webb, 1992). Although the increased flexibility for propulsion can produce its own destabilizing perturbations, the various forms of cyclical and symmetrical movements of the body and appendages can act as dynamic stabilizers (Fish, 1982; Ferry and Lauder, 1996; Fish et al., 2000). In elongate animals, recoil forces are balanced by multiple body flexures (Webb, 1975; Blake, 1983). Animals with short or inflexible bodies reduce

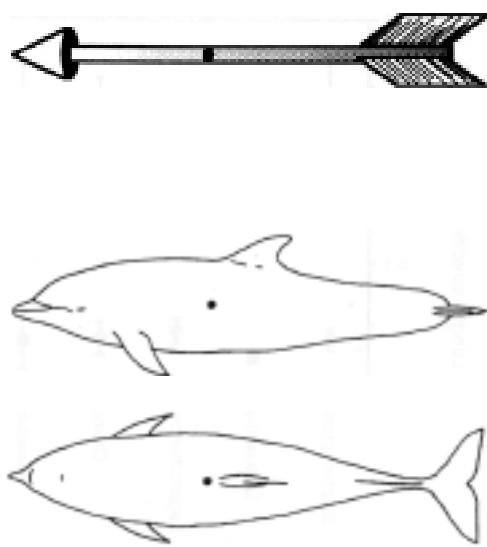


FIG. 2. Comparison of the stable arrow design with the dolphin morphology. Factors associated with stability from an arrow model are listed. The center of gravity on the arrow and dolphin is indicated by the black dot.

recoil by changes in the distribution of the projected area in the direction normal to flexure (Lighthill, 1975; Aleyev, 1977).

#### DIVERSITY, DESIGN AND PERFORMANCE OF CETACEANS

Within the marine mammals, there are divergent body designs that suggest differences in performance regarding stability and maneuverability. Of the fastest swimming marine mammals, cetaceans display considerable variation in their morphology (Fig. 3). The diversity of morphological designs have been related to the swimming speed and propulsive efficiency of whales and dolphins (Fish, 1998; Fish and Rohr, 1999). A body design adapted for stability when swimming would aid in minimizing energy expenditure and increase propulsive efficiency. In addition, a stable body design would reduce transverse movements of the body that could interfere with effective use of sensory systems. Odontocete cetaceans (i.e., toothed whales including dolphins and porpoises) rely upon echolocation to sense the environment and detect prey. As both emission and reception of the acoustic signal is located in the head (Berta and Sumich, 1999), reduced transverse motion may be necessary to focus the signal.

The ability of many cetaceans to maneuver (i.e., turn) with speed becomes imperative in the acquisition and capture of nektonic prey (e.g., fish, pinnipeds, squid). With some exceptions (Silber et al., 1990), the prey of a cetacean is smaller than it is. Small animals have an advantage with respect to turning performance (i.e., turn radius, turn rate) compared to large animals (Howland, 1974; Fish, 1999). Turn radius increases di-

#### Stability Factors

1. Control surfaces located far from center of gravity
2. Concentration of control surface area posterior of center of gravity
3. Anterior position of center of gravity
4. Dihedral of control surfaces
5. Sweep of control surfaces
6. Reduced motion of control surfaces
7. Reduced flexibility of body

rectly with body mass (Howland, 1974). Escape by small prey animals is possible as they are able to turn in smaller radii and with higher angular velocities than the larger whales. However, the whale holds an advantage in that its absolute swimming speed typically is substantially greater than the speed of the prey.

#### Morphological design of cetaceans

The center of gravity (CG) is located at a position of 41% of body length in *Tursiops truncatus* (Fish unpublished; Fig. 2). Although this position appears to enhance stability as determined from the arrow model, it also appears to be nearly coincident with the center of buoyancy (Slijper, 1979; Weihs, 1993). As a result, cetaceans can be unstable with respect to roll, which is exemplified by their ability to side-swim, swim upside down, and barrel-roll (Layne and Caldwell, 1964; Klima et al., 1987).

The placement and design of control surfaces of cetaceans indicates a relatively stable configuration (Figs. 2, 3; Fish, 1997), although there are marked differences between species. The control surfaces of cetaceans are represented by paired pectoral flippers, paired caudal flukes, a dorso-ventrally deep caudal peduncle, and a dorsal fin. The flippers, flukes, and peduncle are associated with mobile joints that permit changes in orientation. These mobile control surfaces are located at a distance from the CG and provide the major percentage of area for control (Slijper, 1961; Aleyev, 1977; Edel and Winn, 1978; Fish and Battle, 1995; Fish, 1997). The mobility of flippers of dolphins capable of rapid sprints and fast cruising appears to be more constrained when compared to the flippers of

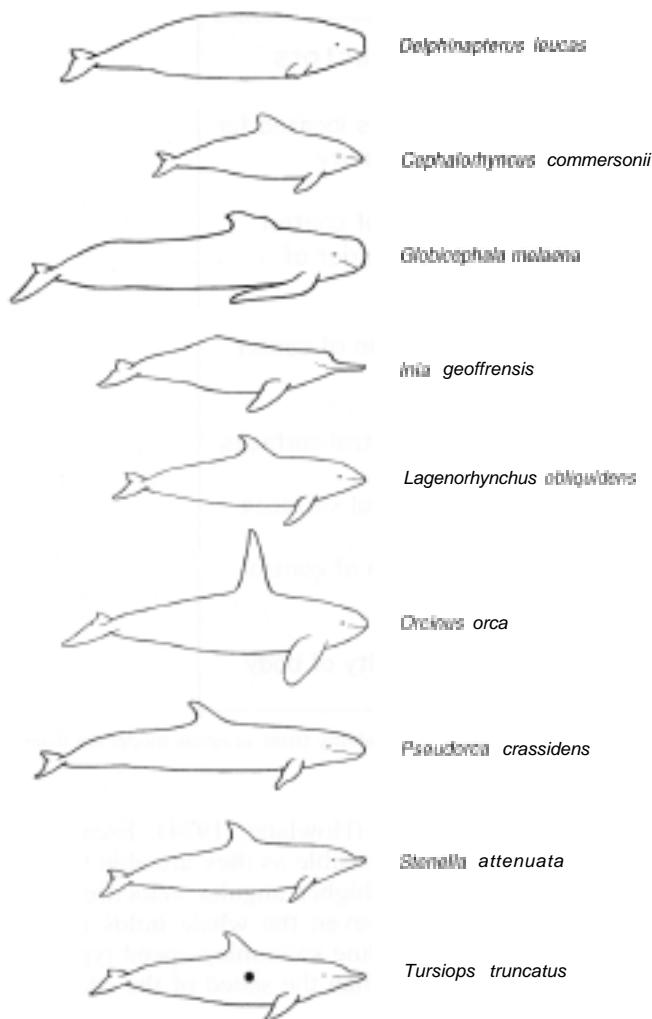


FIG. 3. Outlines of various odontocete cetaceans illustrating body form, and control surface design and position. The control surfaces are represented by the pectoral flippers, dorsal fin, caudal peduncle, and caudal flukes. The black dot on the outline of *Tursiops truncatus* indicates the position of the center of gravity. Outlines redrawn from Minasian et al. (1984).

slow-swimming, highly maneuverable animals (Howell, 1930; Vasilevskaya, 1974; Pilleri et al., 1976; Klima et al., 1987). The shoulder musculature of *Inia geoffrensis* is highly differentiated in contrast to the faster swimming *Lagenorhynchus albirostris*, *Phocoena phocoena*, and *Tursiops truncatus* (Klima et al., 1987). The dorsal fin, when present, is located approximately over the center of gravity and is immobile (Fish and Rohr, 1999). This position limits the dorsal fin's effectiveness in developing a turning moment, but allows the fin to prevent side-slip. The flippers, flukes, and dorsal fin can be highly swept, particularly in the faster species (Azuma, 1983; Fish and Rohr, 1999).

Flexibility in the body of cetaceans is generally constrained (Long et al., 1997). The highly compressed cervical vertebrae and streamlined body form restrict bending in the neck, although some species have mobile necks (e.g., *Delphinapterus leucas*, *Inia geoffrensis*) (Ridgway and Harrison, 1989). Bending stiffness

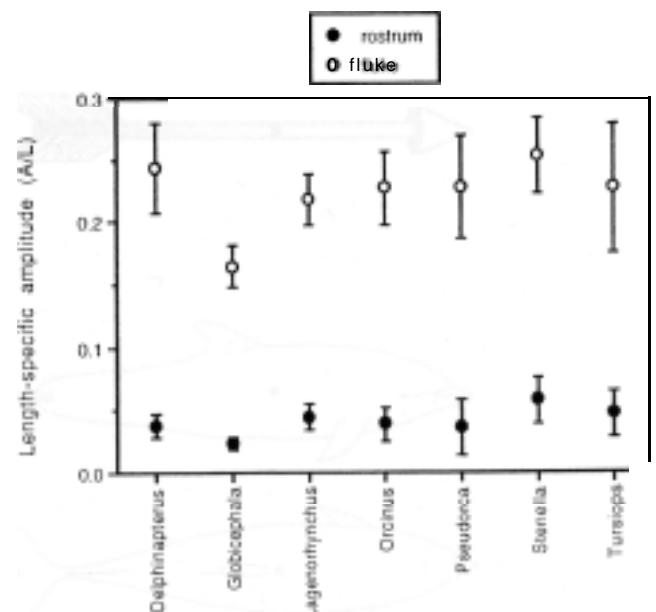


FIG. 4. Mean length-specific amplitude ( $A/L \pm SD$ ) for the rostrum and fluke tip for several species of odontocete cetacean (Fish et al., 2000). The amplitude ( $A$ ) refers to the total vertical excursion of the body.

is greatest in the lumbar region of the vertebral column compared to the adjacent thoracic and caudal regions, although *in situ* the thoracic vertebrae are stiffened by the ribs. The vertebral joints are less stiff in flexion than in extension due to the ligamentous attachments between vertebrae (Long et al., 1997). A strongly developed longitudinal ventral ligament runs beneath the spine and acts in a supportive role (Slipper, 1979). Lateral flexion is constrained by articular processes on the vertebrae that straddle the adjacent neural spines, particularly in the cervical, thoracic, and anterior lumbar regions of the spine (Slipper, 1979; Rommel, 1990; Long et al., 1997).

An additional constraint on flexibility is due to the specialized feeding system exhibited by many cetaceans. Mysticete whales with their expanded oral cavities for filter feeding and river dolphins with their elongate pincer-like jaws possess rigid skulls that comprise 26–30% of the body length (Ridgway and Harrison, 1985, 1989).

#### Dynamic stabilization

The vertical recoil movements of the head result from large transverse forces generated at the caudal flukes. Analysis of the swimming kinematics for various cetaceans showed that mean vertical excursions of the rostrum were only 2–7% of body length, whereas the mean excursion of the fluke tips was 17–25% of body length (Fig. 4; Fish et al., 2000). Such movements at the head are similar to those of subcarangiform fish in the order of 4–7% of body length (Webb, 1975).

Reduced motion of the head of cetaceans is in part a result of passive stabilization mechanisms, including

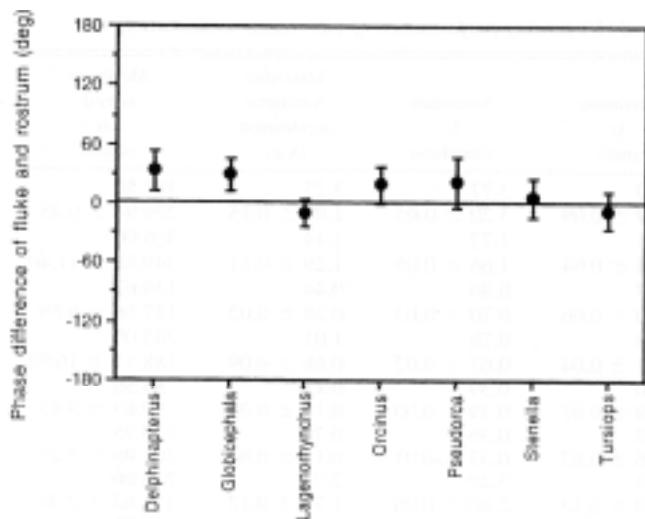


FIG. 5. Phase difference (deg  $\pm$  SD) between flukes and rostrum for several species of odontocete cetacean (Fish *et al.*, 2000). Negative values indicate that the rostrum follows flukes; positive values indicate rostrum leads flukes.

the rigidity, projected area and mass of the anterior body, and narrow necking of the tail (Lighthill, 1975; Webb, 1975). However, further oscillatory dampening is a result of active control of pitching movements by the phase relationship between body components. The phase difference between fluke oscillation and those of the rostrum is small, indicating near synchrony (Fig. 5; Fish *et al.*, 2000). Conversely, large phase differences (60.9–123.4°) between the oscillations of the flukes and flippers generate resistance forces at the flippers that counter the vertical forces produced by the flukes.

#### Turning performance

Cetaceans use a lift-based maneuvering system, which has the advantage of producing a centripetal force to effect turning without incurring a large decelerating drag (Watts, 1961; Fish and Battle, 1995; Fish, 1997). Lift-based maneuvering is the primary system used by ships, fish and other marine mammals (Manning, 1930; Howland, 1974; Hoerner and Borst, 1975; Weihs, 1981; Webb, 1983, 1997; Marchaj, 1988; Fish and Battle, 1995; Fish, 1997) and the control surfaces that work best are those with a high aspect ratio, wing-like morphology. The effectiveness of lift-based mechanisms varies with speed (Marchaj, 1988). Lift used by the control surfaces to create destabilizing moments and to produce a curved trajectory varies directly with the square of the velocity (Weihs, 1981). As speed decreases, the lift also decreases relative to the required force necessary to turn so that maneuvering is more difficult at low velocity. Small turns at low speed can be effected by increased bending of the body and mobility of the control surfaces.

Cetaceans swimming with their bodies in the horizontal plane used either powered or unpowered turning gaits (Fish, 1997). A powered turn was defined as a

turn in which the animal was continuously propelling; whereas in an unpowered turn, the animal glided through the turn without apparent use of propulsive mechanisms. Although in powered turns thrust is maintained throughout the maneuver, the use of unpowered turns limits speed and acceleration after the turn. This limitation can be reduced by propulsive movements of mobile flippers as the animal comes out of the turn (Layne and Caldwell, 1964; Fish, 1997).

Generally, turns are initiated anteriorly with lateral flexion of the head, and adduction and rotation of the flippers into the turn (Fish, 1997). During unpowered turns, substantial lateral flexion of the peduncle is observed in addition to twisting at the base of the flukes. At the beginning of a turn, *Tursiops* will twist the inside fluke blade downward by 15–45° from the horizontal, before reversing the rotation of the flukes by 58–88° as the animal exits the turn. The elongate *Pseudorca* flexes its body during the turn and only twists its flukes at the end of turn by 18–53° with the outside fluke blade depressed. The twisting action allows the animal to use the flukes in conjunction with the peduncle as a rudder. This action is only possible in unpowered turns because the control surfaces are uncoupled from propulsion permitting increased flexibility of the spine.

Various cetaceans bank toward the inside of a turn, although the degree of banking is small (Fish, 1997). The highly flexible river dolphin, *Inia*, shows no tendency to bank. However, *Delphinapterus*, which lacks a dorsal fin, banks at an angle of 90° with its ventral surface facing into the turn. A high bank angle is characteristic of penguins and sea lions which also lack a dorsal fin and turn using elongate pectoral flippers (Godfrey, 1985; Hui, 1985).

Unpowered turns for cetaceans have smaller minimum radii than powered turns (Table 1; Fish, 1997). When the animals are not actively swimming the increased flexibility of the body in conjunction with mobility of the flippers and twisting of the flukes permits smaller turns. When scaled to body length, cetaceans generally demonstrate unpowered turning radii of <50% of body length (Fig. 6) with minimum radii ranging from 11 to 17% of body length. These radii are slightly higher than the minimum radii reported for many fish (Domenici and Blake, 1997; Gerstner, 1999), are comparable to maneuvers by sea lions and penguins, but considerably smaller than those for engineered devices (Webb, 1983; Hui, 1985; Domenici and Blake, 1991; Bandyopadhyay *et al.*, 1997). Submarines with inflexible hulls have turning radii of 200–300% of body length (Maslov, 1970).

Differences in performance between species are indicated when data for turning radius are plotted as a function of velocity (Fig. 7). *Inia* and *Delphinapterus* produce low-speed, small radius turns. Faster speed but larger radius turns are performed by *Lagenorhynchus* and *Cephalorhynchus* and intermediate performance is displayed by *Orcinus*, *Pseudorca* and *Tursiops*. Smaller radius turns are possible by reorienta-

TABLE 1. Summary of differences in powered (P) and unpowered (U) turning performance of odontocete cetaceans.<sup>#</sup>

Species	Gait*	Minimum radius (m)	Minimum radius (lengths)	Maximum (m/s)	Maximum U (length/s)	Maximum centripetal acceleration (x g)	Maximum turning rate (deg/s)
<i>Cephalorhynchus</i>	P	<b>0.47</b>	<b>0.37</b>	<b>5.40</b>	<b>3.72</b>	<b>3.25</b>	<b>337.50</b>
	P20%	<b>0.59 ± 0.02</b>	<b>0.46 ± 0.01</b>	<b>4.59 ± 0.09</b>	<b>3.20 ± 0.05</b>	<b>1.99 ± 0.15</b>	<b>279.94 ± 9.45</b>
	U	<b>0.19</b>	<b>0.15</b>	<b>2.21</b>	<b>1.72</b>	<b>1.44</b>	<b>366.00</b>
<i>Delphinapterus</i>	U20%	<b>0.21 ± 0.01</b>	<b>0.16 ± 0.01</b>	<b>2.14 ± 0.04</b>	<b>1.66 ± 0.05</b>	<b>1.29 ± 0.11</b>	<b>349.88 ± 11.40</b>
	P	<b>0.73</b>	<b>0.23</b>	<b>2.57</b>	<b>0.80</b>	<b>0.44</b>	<b>139.62</b>
	P20%	<b>0.85 ± 0.05</b>	<b>0.26 ± 0.02</b>	<b>2.40 ± 0.06</b>	<b>0.70 ± 0.03</b>	<b>0.38 ± 0.02</b>	<b>117.56 ± 6.59</b>
<i>Inia</i>	U	<b>0.50</b>	<b>0.15</b>	<b>2.58</b>	<b>0.76</b>	<b>1.01</b>	<b>245.00</b>
	U20%	<b>0.56 ± 0.03</b>	<b>0.17 ± 0.01</b>	<b>2.41 ± 0.04</b>	<b>0.67 ± 0.02</b>	<b>0.68 ± 0.09</b>	<b>188.11 ± 16.92</b>
	P	<b>0.63</b>	<b>0.25</b>	<b>1.00</b>	<b>0.39</b>	<b>0.15</b>	<b>85.50</b>
<i>Lagenorhynchus</i>	P20%	<b>0.65 ± 0.01</b>	<b>0.25 ± 0.00</b>	<b>0.99 ± 0.01</b>	<b>0.39 ± 0.00</b>	<b>0.14 ± 0.01</b>	<b>80.63 ± 3.45</b>
	U	<b>0.26</b>	<b>0.10</b>	<b>0.92</b>	<b>0.36</b>	<b>0.20</b>	<b>123.75</b>
	U20%	<b>0.41 ± 0.03</b>	<b>0.16 ± 0.01</b>	<b>0.86 ± 0.02</b>	<b>0.33 ± 0.01</b>	<b>0.15 ± 0.01</b>	<b>101.96 ± 5.25</b>
<i>Orcinus</i>	P	<b>1.61</b>	<b>0.74</b>	<b>6.81</b>	<b>3.20</b>	<b>2.73</b>	<b>225.00</b>
	P20%	<b>1.86 ± 0.05</b>	<b>0.86 ± 0.02</b>	<b>6.00 ± 0.13</b>	<b>2.80 ± 0.06</b>	<b>1.74 ± 0.13</b>	<b>171.63 ± 7.30</b>
	U	<b>0.42</b>	<b>0.20</b>	<b>4.83</b>	<b>2.27</b>	<b>3.56</b>	<b>453.33</b>
<i>Pseudorca</i>	U20%	<b>0.49 ± 0.05</b>	<b>0.23 ± 0.02</b>	<b>4.08 ± 0.53</b>	<b>1.91 ± 0.25</b>	<b>3.12 ± 0.31</b>	<b>433.67 ± 13.91</b>
	P	<b>1.76</b>	<b>0.35</b>	<b>6.55</b>	<b>1.49</b>	<b>1.25</b>	<b>148.13</b>
	P20%	<b>2.08 ± 0.09</b>	<b>0.41 ± 0.02</b>	<b>5.98 ± 0.14</b>	<b>1.28 ± 0.05</b>	<b>0.87 ± 0.08</b>	<b>111.43 ± 8.67</b>
<i>Tursiops</i>	U	<b>0.55</b>	<b>0.11</b>	<b>6.02</b>	<b>1.26</b>	<b>1.74</b>	<b>232.50</b>
	U20%	<b>0.94 ± 0.04</b>	<b>0.18 ± 0.01</b>	<b>5.06 ± 0.09</b>	<b>1.00 ± 0.02</b>	<b>1.09 ± 0.04</b>	<b>154.04 ± 5.04</b>
	P	<b>1.64</b>	<b>0.42</b>	<b>5.04</b>	<b>1.42</b>	<b>1.08</b>	<b>138.00</b>
	P20%	<b>2.03 ± 0.12</b>	<b>0.52 ± 0.03</b>	<b>4.88 ± 0.07</b>	<b>1.31 ± 0.04</b>	<b>0.97 ± 0.04</b>	<b>121.42 ± 5.07</b>
	U	<b>0.52</b>	<b>0.13</b>	<b>3.40</b>	<b>0.88</b>	<b>1.16</b>	<b>252.86</b>
	U20%	<b>0.59 ± 0.02</b>	<b>0.15 ± 0.01</b>	<b>3.18 ± 0.08</b>	<b>0.83 ± 0.01</b>	<b>0.96 ± 0.07</b>	<b>200.03 ± 12.01</b>
	P	<b>0.56</b>	<b>0.22</b>	<b>5.28</b>	<b>2.12</b>	<b>1.31</b>	<b>252.00</b>
	P20%	<b>0.76 ± 0.04</b>	<b>0.32 ± 0.02</b>	<b>5.03 ± 0.09</b>	<b>1.99 ± 0.03</b>	<b>1.07 ± 0.07</b>	<b>202.18 ± 8.11</b>
	U	<b>0.30</b>	<b>0.13</b>	<b>4.76</b>	<b>1.82</b>	<b>1.56</b>	<b>405.00</b>
	U20%	<b>0.47 ± 0.03</b>	<b>0.19 ± 0.01</b>	<b>3.88 ± 0.15</b>	<b>1.55 ± 0.05</b>	<b>1.21 ± 0.07</b>	<b>251.98 ± 21.98</b>

# Data obtained from overhead views of trained cetaceans swimming in large pools. Animals were videotaped at 60 Hz and the sequential position of the center of gravity was recorded from the videotape. Turn radius was determined geometrically (Youn *et al.*, 1978).

\* Values are provided for minimum individual and minimum 20% of performance data for turn radius and maximum individual and maximum 20% of performance data for velocity (U), centripetal acceleration, and turning rate. Variation expressed as ± one standard error.

tion of the body. An *Orcinus* (1725.2 kg, 5.05 m) was observed to produce a turn radius of 4% of body length by ventrally flexing the posterior half of the body (Fish, 1997). The flukes were used to pivot the animal around its longitudinal axis.

The performance limits for turning are illustrated in Figure 8. Most data for cetaceans are clustered at accelerations <1.5 g with turning rates <200 deg/sec. Individuals of *Cephalorhynchus* and *Lagenorhynchus* are able to exceed these lower values for cetaceans with *Lagenorhynchus* displaying the maximum performance with an acceleration of 3.6 g and turning rate of 453 deg/sec during unpowered turns (Table 1).

#### Ecological relations

In general cetaceans possess a morphological design (*i.e.*, anterior position of CG, concentration of control surfaces posterior of CG, dihedral and sweep of control surfaces) that enhances stability thereby potentially constraining turning performance. However, flexible bodies and mobile control surfaces provide mechanisms to induce instabilities for turning maneuvers. Cetaceans with more flexible body designs (*e.g.*, *Inia*, *Delphinapterus*) sacrifice speed for maneuverability, whereas species with more restricted flexibility (*e.g.*, *Lagenorhynchus*, *Cephalorhynchus*) produce faster but

wider turns (Brodie, 1989; Fish, 1997). As morphological differences can be correlated with behavioral differences (Gerstner, 1999), features that effect stability and maneuverability of cetaceans appear to be associated with their prey type and habitats.

*Inia* inhabits rivers, lakes, and flooded forests and grasslands. These habitats are structurally complex, where decreased turn radius and precise, slow maneuverability would be necessary. Similarly, the distribution of *Delphinapterus* is in complex environments including shallow waters, coastal habitats, rivers, and pack ice. *Delphinapterus* feeds on less mobile prey such as bottom organisms and large zooplankton (Brodie, 1989).

The more stable design of fast swimming cetaceans may limit these animals to locomoting and foraging in pelagic habitats. Despite the potential disadvantage in turning performance compared to smaller fish (Howland, 1974), cetaceans have developed a number of behavioral strategies to capture their elusive prey. Pelagic species often use cooperative foraging behaviors that often involve encirclement of prey and division of labor during an attack (Silber *et al.*, 1990; Simill and Ugarte, 1993; Simill, 1997; Bertu and Sumich, 1999). In some instances, stunning behaviors are employed to compensate for the relatively poor acceleration and

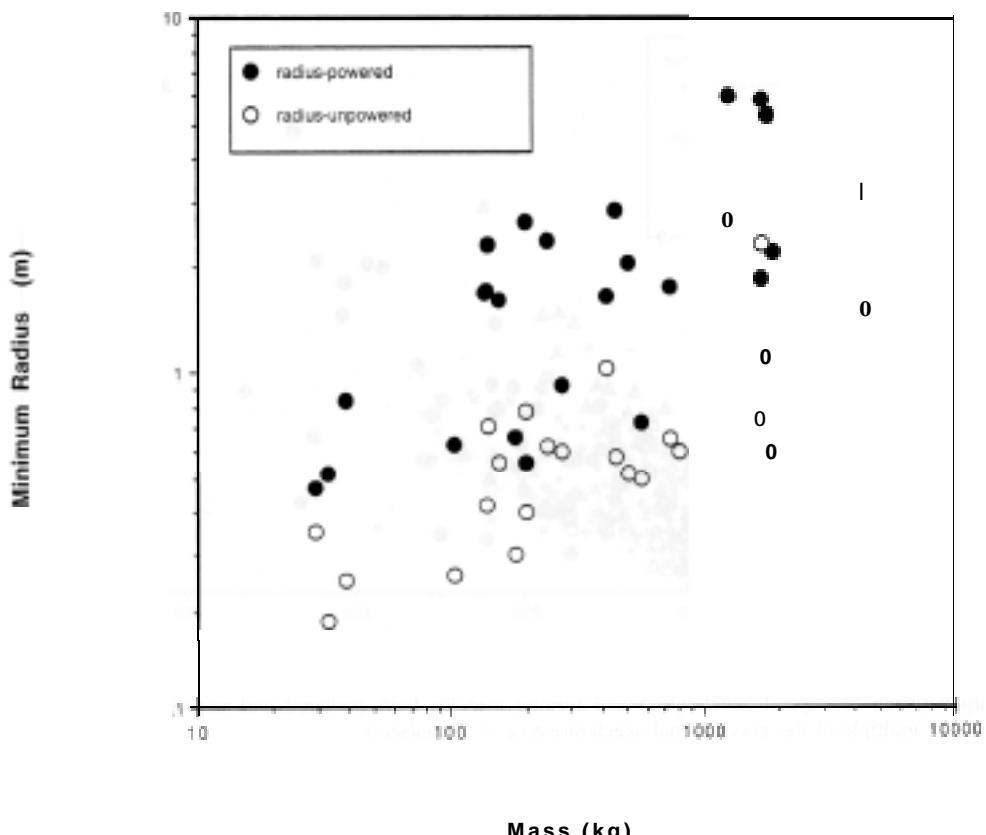


FIG. 6. Minimum turning radii for powered (solid circles) and unpowered (open circles) turns plotted against body mass for individuals from seven species of odontocete cetaceans (Fish, 1997).

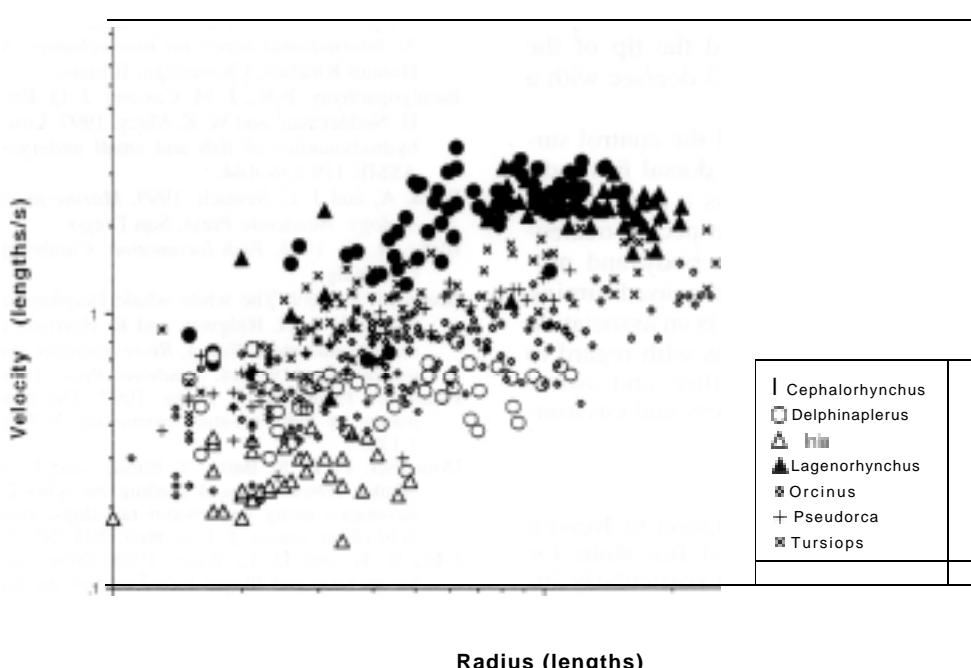


FIG. 7. Length-specific velocity in relation to length-specific turning radius for cetaceans performing horizontal powered and unpowered turns (Fish, 1997).

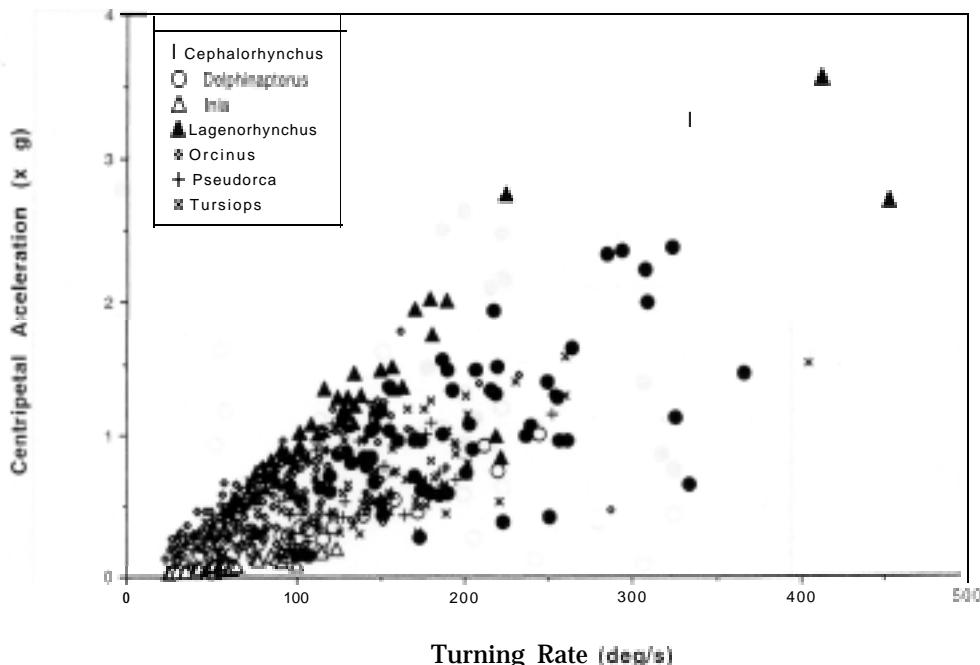


FIG. 8. Relationship between centripetal acceleration and turning rate for both powered and unpowered turns (Fish, 1997). Centripetal acceleration is given as a multiple of the gravitational acceleration ( $g = 9.8 \text{ m/sec}^2$ ).

maneuverability of the large cetaceans. For example, killer whales (*Orcinus orca*) will herd herring into tight schools and slap the fish with the underside of the tail (Domenici *et al.*, 2000).

The ability to roll permits cetaceans to reorient their body to take advantage of the increased flexibility by ventral flexing of the body. Aerial views showed foraging dolphins (*Tursiops truncatus*) rolling 90° during the final lunge for fish (Nowacek and Fish, unpublished). Bending of the body allowed the tip of the rostrum to turn at a rate of up to 656.3 deg/sec with a radius of 0.1 body lengths.

In summary, design and position of the control surfaces (e.g., flukes, peduncle, flippers, dorsal fin) indicate that odontocete cetaceans possess a morphology that is hydrodynamically stable with respect to maneuverability. However, flexibility of the body and mobility of the control surfaces permit increased turning performance. It is suggested that there is an association between the variation among cetaceans with regard to body flexibility, control surface mobility, and swimming speed and their foraging behaviors and environments.

#### ACKNOWLEDGMENTS

I would like to express my appreciation to Kendra Heron, Jen Holak, John Peacock, and Jim Rohr for their contributions to this work. I am particularly indebted to the fine editing performed by the two reviewers. Much of the manuscript was based on research performed at Sea World, University of California Santa Cruz, Pittsburgh Zoo, and the National Aquarium and the cooperation of the trainers and sup-

port staff at those institutions is gratefully acknowledged. This research was supported by the Office of Naval Research, grant number N00014-95-1-1045 (program manager Teresa McMullen).

#### REFERENCES

- Aleyev, Y. G. 1977. *Naukova*. Junk, The Hague.
- Annum, A. 1983. Biomechanical aspects of animal flying and swimming. In H. Matsui and K. Kobayashi (eds.), *Biomechanics VIII-A: International series on biomechanics*, Vol. 4A, pp. 35-53. Human Kinetics, Champaign, Illinois.
- Bandyopadhyay, P.R., J. M. Costano, J. Q. Rice, R. B. Philips, W. H. Nedderman, and W. K. Macy. 1997. Low-speed maneuvering hydrodynamics of fish and small underwater vehicles. *Trans. ASME* 119: 136-144.
- Berth, A. and J. L. Sumich. 1999. *Marine mammals: Evolutionary biology*. Academic Press, San Diego.
- Blake, R. W. 1983. *Fish locomotion*. Cambridge University Press, Cambridge.
- Brodie, I? E. 1989. The white whale *Dolphinapterus leucas* (Pallas, 1776). In S. H. Ridgway and R. Harrison (eds.), *Handbook of marine mammals*, Vol. 4, *River dolphins and the larger toothed whales*, pp. 119-144. Academic Press, London.
- Domenici, I? and R. W. Blake. 1997. The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* 200: 1,165-1,178.
- Domenici, I?, R. S. Batty, T. Simill, and E. Ogami. 2000. Killer whales (*Orcinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps: kinematics analyses of field observations. *J. Exp. Biol.* 203: 283-294.
- Edel, R. K. and H. E. Winn. 1978. Observations on underwater locomotion and flipper movement of the humpback whale *Megaptera novaeangliae*. *Mar. Biol.* 48: 279-287.
- Ferry, L. A. and G. V. Lauder. 1996. Heterocercal tail function in leopard sharks: A three-dimensional kinematic analysis of two models. *J. Exp. Biol.* 199: 1,253-1,268.
- Fish, F. E. 1982. Function of the compressed tail of surface swimming muskrats (*Ondatra zibethicus*). *J. Mamm.* 63: 591-597.

- Fish, E. E. 1996. Transitions from drag-based to lift-based propulsion in mammalian swimming. Amer. Zool. 36:628-641.
- Fish, E. E. 1997. Biological designs for enhanced maneuverability: Analysis of marine mammal performance. *Proceedings of the Tenth International Symposium on Unmanned Untethered Submersible Technology: Proceedings of the special session on bio-engineering research related to autonomous underwater vehicles*, pp. 109-117. Autonomous Undersea Systems Institute, Lee, New Hampshire.
- Fish, E. E. 1998. Comparative kinematics and hydrodynamics of odontocete cetaceans: Morphological and ecological correlates with swimming performance. J. Exp. Biol. 201:2,867-2,877.
- Fish, E. E. 1999. Performance constraints on the maneuverability of flexible and rigid biological systems. *Proceedings of the Eleventh International Symposium on Unmanned Untethered Submersible Technology*, pp. 394-406. Autonomous Undersea Systems Institute, Durham, New Hampshire.
- Fish, E. E. and J. M. Battle. 1995. Hydrodynamic design of the humpback whale flipper. J. Morph. 225:51-60.
- Fish, E. E. and J. Rohr. 1999. Review of dolphin hydrodynamics and swimming performance. *SPA WARS System Center Technical Report* 1801, San Diego, CA. <http://www.sparcwar.navy.mil/SPAWAR/publications/pubs/tr/1801/tr1801.pdf>
- Fish, E. E., J. E. Peacock, and J. Rohr. 2000. Phase relationships between body components of odontocete cetaceans in relation to stability and propulsive mechanisms. *Zn N.* Kato and Y. Suzuki (eds.), *Proceedings of the 1st International Symposium on Aqua Bio-Mechanisms/International Seminar on Aqua Bio-Mechanisms*, pp. 57-60. Tokai University Pacific Center, Honolulu, Hawaii.
- Gersner, C. L. 1999. Maneuverability of four species of coral-reef fish that differ in body and pectoral-fin morphology. Can. J. Zool. 77:1,102-1,110.
- Godfrey, S. J. 1985. Additional observations of subaqueous locomotion in the California Sea Lion (*Zalophus californianus*). Aqu. Mamm. 11:53-57.
- Hoerner, S. F. and H. V. Borst. 1975. *Fluid-dynamic lift*. L. A. Hoerner and H. V. Borst, Bricktown, New Jersey.
- Howell, A. B. 1930. *Aquatic mammals*. Charles C. Thomas, Springfield, Illinois.
- Holland, H. C. 1974. Optimal strategies for predator avoidance: The relative importance of speed and manoeuvrability. J. Theor. Biol. 47:333-350.
- Hoyt, D. E. and C. R. Taylor. 1981. Gait and the energetics of locomotion in horses. Nature 292:239-240.
- Hui, C. A. 1985. Maneuverability of the Humboldt penguin (*Spheniscus humboldti*) during swimming. Can. J. Zool. 63:2,165-2,167.
- Hurt, H. H., Jr. 1965. *Aerodynamics for naval aviators*. U. S. Navy, NAVWEPS 00-BOT-80.
- Klima, M., H. A. Oelschläger, and D. Wiinsch. 1987. Morphology of the pectoral girdle in the Amazon dolphin *Zinia gufraensis* with special reference to the shoulder joint and the movements of the flippers. Z. Saugertierkunde 45:288-309.
- Lang, J. N. and D. K. Caldwell. 1964. Behavior of the Amazon dolphin, *Zinia gufraensis* (Blainville) in captivity. Zoologica, N.Y. 49:81-111.
- Lighthill, J. 1975. *Mathematical biodynamics*. Soc. Indust. Appl. Math., Philadelphia.
- Long, J. H., Jr., D. A. Pabst, W. R. Shepherd, and W. A. McLellan. 1997. Locomotor design of dolphin vertebral columns: Bending mechanics and morphology of *Delphinus delphis*. J. Exp. Biol. 200:65-81.
- Manning, G. C. 1930. *Manual of naval architecture*. van Nostrand, New York.
- Marchaj, C. A. 1988. *Aero-hydrodynamics of sailing*. International Marine Publ., Camden, Maine.
- Murphy, I? and W. J. Hamilton, III. 1966. *Mechanisms of animal Behavior*. Wiley, New York.
- Musilov, N. K. 1970. Maneuverability and controllability of dolphins. Bionika 4:46-50 (translated from Russian).
- Minasian, S. M., K. C. Balcomb, III, and L. Foster. 1984. *The world's whales*. Smithsonian Books, Washington, D.C.
- Pilleri, G., M. Gilhi, F. E. Purves, K. Zbinden, and C. Kraus. 1976. On the behaviour, bioacoustics and functional morphology of the Indus River dolphin (*Platanista gangetica* Blyth, 1859). Invest. Cetacea 6: 11-141.
- Ridgway, S. H. and R. Harrison. 1985. *Handbook of marine mammals*, Vol. 3, *The sirenians and baleen whales*. London, Academic Press.
- Ridgway, S. H. and R. Harrison. 1989. *Handbook of marine mammals*, Vol. 4, *River dolphins and the larger toothed whales*. London, Academic Press.
- Rommel, S. 1990. Osteology of the bottlenose dolphin. *Zn S.* Leatherwood and R. H. Reeves (eds.), *The bottlenose dolphin*, pp. 29-49. Academic Press, San Diego.
- Silber, G. E., M. W. Newcomer, and H. Perez-Cortes. 1990. Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). Can. J. Zool. 68: 1,603-1,606.
- Similä, T. 1997. Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools. Aqu. Mamm. 23: 119-126.
- Similä, T. and E. Ugarte. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Can. J. Zool. 71: 1,494-1,499.
- Slipper, E. J. 1961. Locomotion and locomotory organs in whales and dolphins (Cetacea). Symp. Zool. Soc. London 5:77-94.
- Slipper, E. J. 1979. *Whales*. Cornell University Press, Ithaca, New York.
- Smith, H. C. 1992. *Illustrated guide to aerodynamics*. McGraw-Hill, Blue Ridge Summit, Pennsylvania.
- Vasilevskaya, G. I. 1974. Structural features of the delphinid pectoral flippers. Bionika 8: 127-132 (translated from Russian).
- Walker, J. A. 2000. Does a rigid body limit maneuverability? J. Exp. Biol. 203:3,391-3,396.
- Watts, E. H. 1961. The relationship of fish locomotion to the design of ships. Symp. Zool. Soc. London 5:37-41.
- Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd. Can. 190:1-158.
- Webb, P. W. 1983. Speed, acceleration and manoeuvrability of two teleost fishes. J. Exp. Biol. 102: 115-122.
- Webb, P. W. 1984. Form and function in fish swimming. Sci. Amer. 251:72-82.
- Webb, P. W. 1992. Is the high cost of body/caudal fin undulatory swimming due to increased friction drag or inertial recoil. J. Exp. Biol. 162:157-166.
- Webb, P. W. 1994. Exercise performance of fish. *Zn J. H. Jones (ed.), Advances in veterinary science and comparative medicine*, 38B, pp. 1-49. Academic Press, Orlando.
- Webb, P. W. 1997. Designs for stability and maneuverability in aquatic vertebrates: What can we learn? *Proceedings of the Tenth International Symposium on Unmanned Untethered Submersible Technology: Proceedings of the special session on bio-engineering research related to autonomous underwater vehicles*, pp. 86-103. Autonomous Undersea Systems Institute, Lee, New Hampshire.
- Wegener, I? I? 1991. *What makes airplanes fly?* Springer-Verlag, New York.
- Weis, D. 1981. Effects of swimming path curvature on the energetics of fish motion. Fish. Bull. 79:171-176.
- Weis, D. 1993. Stability of aquatic animal locomotion. Cont. Math. 141:443-461.
- Youm, Y., R. Y. McMurry, A. E. Flatt, and T. E. Gillespie. 1978. Kinematics of the wrist. I. An experimental study of radial-ulnar deviation and flexion-extension. J. Bone Jt. Surg. 60A:423-431.