Balancing Requirements for Stability and Maneuverability in Cetaceans

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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 the order of odontocete cetaceans (i.e., toothed whales), variation in body design affects both stability and turning performance. Position of control surfaces (i.e., flippers, fin, flukes, and pectoral flukes) provides a generally stable design with respect to an arrow model. Destabilizing forces generated during swimming are balanced by dynamic stabilization due to phase relationships of various body components. Cetaceans with flexible bodies and mobile flippers are able to turn low turning rates, whereas fast-swimming cetaceans with less flexibility and relatively immobile flippers sacrifice small radii for higher turning rates. In cetaceans, body and control surface mobility and placement appear to be associated with prey 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 (Weibol, 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...
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 (Alleyev, 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 (Alleyev, 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
recoil by changes in the distribution of 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 larger whales. However, a whale holds an advantage in its absolute swimming speed typically substantially greater than the speed of its 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 an arrow model, it also appears to be nearly coincident to the center of buoyancy (Slijper, 1979; Weihls, 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 Ali, 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

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**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

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**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.
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 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 (Slijper, 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 (Slijper, 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...
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 lateral 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
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°/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°/sec during unpowered turns (Table 1).

**Table 1. Summary of differences in powered (P) and unpowered (U) turning performance of odontocete cetaceans.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Minimum radius (m)</th>
<th>Minimum radius (lengths)</th>
<th>Maximum velocity (m/s)</th>
<th>Maximum centripetal acceleration (g)</th>
<th>Maximum turning rate (deg/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cephalorhynchus</em></td>
<td>P 0.47</td>
<td>0.37</td>
<td>5.40</td>
<td>3.72</td>
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<tr>
<td></td>
<td>P20% 0.59 ± 0.02</td>
<td>0.46 ± 0.01</td>
<td>4.59 ± 0.09</td>
<td>3.20 ± 0.05</td>
<td>1.99 ± 0.15</td>
</tr>
<tr>
<td></td>
<td>U 0.19</td>
<td>0.15</td>
<td>2.21</td>
<td>1.72</td>
<td>1.44</td>
</tr>
<tr>
<td></td>
<td>U20% 0.21 ± 0.01</td>
<td>0.16 ± 0.01</td>
<td>2.14 ± 0.04</td>
<td>1.66 ± 0.05</td>
<td>1.29 ± 0.11</td>
</tr>
<tr>
<td><em>Delphinapterus</em></td>
<td>P 0.73</td>
<td>0.23</td>
<td>2.57</td>
<td>0.80</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>P20% 0.85 ± 0.05</td>
<td>0.26 ± 0.02</td>
<td>2.40 ± 0.06</td>
<td>0.70 ± 0.03</td>
<td>0.38 ± 0.02</td>
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<tr>
<td></td>
<td>U 0.50</td>
<td>0.15</td>
<td>2.58</td>
<td>0.76</td>
<td>1.01</td>
</tr>
<tr>
<td></td>
<td>U20% 0.56 ± 0.03</td>
<td>0.17 ± 0.01</td>
<td>2.41 ± 0.04</td>
<td>0.67 ± 0.02</td>
<td>0.68 ± 0.09</td>
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<tr>
<td><em>Ini</em></td>
<td>P 0.63</td>
<td>0.25</td>
<td>0.99 ± 0.01</td>
<td>0.39</td>
<td>0.14 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>P20% 0.65 ± 0.01</td>
<td>0.25 ± 0.00</td>
<td>0.99 ± 0.01</td>
<td>0.39 ± 0.00</td>
<td>0.14 ± 0.01</td>
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<tr>
<td></td>
<td>P20% 0.80 ± 0.02</td>
<td>0.25 ± 0.00</td>
<td>0.86 ± 0.02</td>
<td>0.33 ± 0.01</td>
<td>0.15 ± 0.01</td>
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<tr>
<td></td>
<td>U 0.26</td>
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<td>0.92</td>
<td>0.36</td>
<td>0.20</td>
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<tr>
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<td>0.16 ± 0.01</td>
<td>0.86 ± 0.02</td>
<td>0.33 ± 0.01</td>
<td>0.15 ± 0.01</td>
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<td><em>Lagenorhynchus</em></td>
<td>P 1.61</td>
<td>0.74</td>
<td>3.20</td>
<td>2.73</td>
<td>225.00</td>
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<tr>
<td></td>
<td>P20% 1.86 ± 0.05</td>
<td>0.86 ± 0.02</td>
<td>2.80 ± 0.06</td>
<td>1.74 ± 0.13</td>
<td>171.63 ± 7.30</td>
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<tr>
<td></td>
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<td>0.23</td>
<td>2.27</td>
<td>1.25</td>
<td>453.33</td>
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<tr>
<td></td>
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<td>2.08 ± 0.53</td>
<td>0.32 ± 0.01</td>
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<td><em>Orcinus</em></td>
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<td>0.95</td>
<td>1.49</td>
<td>1.25</td>
<td>148.13</td>
</tr>
<tr>
<td></td>
<td>P20% 2.08 ± 0.09</td>
<td>0.41 ± 0.02</td>
<td>1.28 ± 0.05</td>
<td>0.87 ± 0.08</td>
<td>114.3 ± 8.67</td>
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<tr>
<td></td>
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<td>0.62</td>
<td>0.16</td>
<td>232.50</td>
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<tr>
<td></td>
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<td>0.18 ± 0.01</td>
<td>0.96 ± 0.09</td>
<td>1.00 ± 0.02</td>
<td>1.09 ± 0.04</td>
</tr>
<tr>
<td><em>Pseudorca</em></td>
<td>P 1.64</td>
<td>0.42</td>
<td>5.04</td>
<td>1.42</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>P20% 2.03 ± 0.12</td>
<td>0.52 ± 0.03</td>
<td>4.88 ± 0.07</td>
<td>1.31 ± 0.04</td>
<td>0.97 ± 0.04</td>
</tr>
<tr>
<td></td>
<td>U 0.52</td>
<td>0.13</td>
<td>3.40</td>
<td>0.88</td>
<td>1.16</td>
</tr>
<tr>
<td></td>
<td>U20% 0.59 ± 0.02</td>
<td>0.15 ± 0.01</td>
<td>3.18 ± 0.08</td>
<td>0.83 ± 0.01</td>
<td>0.96 ± 0.07</td>
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<tr>
<td><em>Tursiops</em></td>
<td>P 0.56</td>
<td>0.22</td>
<td>5.28</td>
<td>2.12</td>
<td>1.31</td>
</tr>
<tr>
<td></td>
<td>P20% 0.76 ± 0.04</td>
<td>0.32 ± 0.02</td>
<td>5.03 ± 0.09</td>
<td>1.99 ± 0.03</td>
<td>1.07 ± 0.07</td>
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<td>4.76</td>
<td>1.82</td>
<td>1.56</td>
</tr>
<tr>
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<td>0.19 ± 0.01</td>
<td>3.88 ± 0.15</td>
<td>1.55 ± 0.05</td>
<td>1.21 ± 0.07</td>
</tr>
</tbody>
</table>

# 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 (Youm et al., 1978).

* Values 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.

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., *Ini*, *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.

*Ini* 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; Simila et al., 1993; Simila, 1997; Berta 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).
maneuverability of the large cetaceans. For example, killer whales (Orcinus orca) will herd herring into edged. This research was supported by the Office of Naval Research, grant number N00014-95-1-0145 (program manager Teresa McMullen).

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.

References


