

STABILIZATION MECHANISM IN SWIMMING ODONTOCETE CETACEANS BY PHASED MOVEMENTS

F. E. FISH

J. E. PEACOCK

Department of Biology
West Chester University
West Chester, Pennsylvania 19383, U.S.A.
E-mail: ffish@wcupa.edu

J. J. ROHR

Space and Naval Warfare Systems Center,
RDT&E Division, Code D363,
53560 Hull Street
San Diego, California 92152-6004, U.S.A.

ABSTRACT

Propulsive movements of the caudal oscillating flukes produce large forces that could induce equally large recoil forces at the cranial end of the animal, and, thus, affect stability. To examine these vertical oscillations, video analysis was used to measure the motions of the rostrum, pectoral flipper, caudal peduncle, and fluke tip for seven odontocete cetaceans: *Delphinapterus leucas*, *Globicephala melaena*, *Lagenorhynchus obliquidens*, *Orcinus orca*, *Pseudorca crassidens*, *Stenella plagiodon*, and *Tursiops truncatus*. Animals swam over a range of speeds of 1.4–7.3 mlsec. For each species, oscillatory frequency of the fluke tip increased linearly with swimming speed. Peak-to-peak amplitude at each body position remained constant with respect to swimming speed for all species. Mean peak-to-peak amplitude ranged from 0.02 to 0.06 body length at the rostrum and from 0.17 to 0.25 body length at the fluke tip. The phase relationships between the various body components remain constant with respect to swimming speed. Oscillations of the rostrum were nearly in phase with the fluke tip with phase differences out of -9.4° – 33.0° of a cycle period of 360°. Pectoral flipper oscillations trailed fluke oscillations by 60.9° – 123.4° . The lower range in amplitude at the rostrum compared to the fluke tip reflects increased resistance to vertical oscillation at the cranial end, which enhances the animal's stability. This resistance is likely due to both active and passive increased body stiffness, resistance on the flippers, phased movements of body components, and use of a lift-based propulsion. Collectively, these mechanisms stabilize the body of cetaceans during active swimming, which can reduce locomotor energy expenditure and reduce excessive motions of the head affecting sensory capabilities.

Key words: swimming, dolphin, stability, recoil, kinematics, cetaceans, *Delphinapterus leucas*, *Globicephala melaena*, *Lagenorhynchus obliquidens*, *Orcinus orca*, *Pseudorca crassidens*, *Stenella plagiodon*, *Tursiops truncatus*.

Animals that swim by body and caudal fin propulsion must balance the large forces generated at the tail with recoil forces at the cranial portion of the body (Webb 1992, Fish and Shannahan 2000). Recoil forces can produce large movements in the cranial region of the animal. Head deflections result in increased drag, deviation from a desired trajectory, potential interference of sensory apparatus, and a reduction in stability (Lighthill 1975, Webb 1992, Fish 2002, Weihs 2002). A stable body resists changes in direction and velocity due to forces either externally or internally generated (Weihs 1993, 2002; Webb 2002). Balancing both forces and their associated torques acting at the ends of the body can reduce recoil movements. Stabilizing systems self-correct for disturbances and maintain a desired postural attitude (Webb 1997). These systems stabilizing the body can be passive or active and can effectively dampen perturbations that generate instabilities. Passive mechanisms require no additional energy to provide stability and are largely a function of body morphology (Fish 2002). Active mechanisms can compensate for destabilizing movements by neurological activation of musculo-skeletal components in concert with sensory feedback at the expense of energy (Webb 1997).

Cetaceans swim by the generation of large forces from the dorso-ventral oscillations of broad, caudal flukes (Lang 1975; Fish 1993, 1998; Williams *et al.* 1993). Such forces could be destabilizing at the head and result in movements in the pitching direction. If cetaceans swam as a rigid beam, the body would oscillate around the center of gravity with the rostrum and fluke tips moving 180° out of phase (*i.e.*, moving in exactly opposite directions) and with large dorso-ventral displacements. Cetaceans are not rigid bodies and exhibit varying degrees of flexibility along the body (Pabst 1993, 2000; Long *et al.* 1997). Flexibility in cetaceans and other aquatic animals, however, is associated with increased maneuverability, a controlled instability (Fish and Rohr 1999, Fish 2002). How then do cetaceans control stability? Stability in the cranial portion of swimming cetaceans would require relatively small pitching deviations of the head compared to the flukes.

Few studies have measured the displacements of the various body components of cetaceans other than at the flukes. Reports on dolphin swimming have indicated substantial displacements of points along the body that oscillate in the vertical plane. Steady swimming cetaceans exhibited a range for peak-to-peak fluke amplitudes of 0.18–0.21 (Fish 1993, 1998). Outlines of a bottlenose dolphin (*Tursiops truncatus*) swimming at a routine speed of 2.63 m/sec exhibited dorso-ventral excursions of 0.08 and 0.35 body length at the rostrum and at the fluke tip, respectively (Videler and Kamermans 1985). The maximum bending angle of the entire caudal peduncle of a swimming *Tursiops* was 46° (Pabst 1993), although a captive dolphin giving birth (Parry 1949) was determined to bend its peduncle into an arc of 65° . Lang (1975) showed the outline of an accelerating dolphin (*Lagenorhynchus obliquidens*) with a dorso-ventral displacement at the rostrum of approximately 0.05 body length. Skrovan *et al.* (1999) found the peak-to-peak amplitudes of the fluke tip of *Tursiops truncatus* to be as high as 0.5 body length when accelerating, but only 0.2 body length at steady swimming speeds of 1.5–3.7 m/sec.

This study makes a systematic comparison of the movements of various body components for a variety of cetacean species. The goals of the paper are (1) to measure the dorso-ventral displacements of positions along the body of odontocete cetaceans, (2) to determine whether the dorso-ventral displacements are affected by body morphology and swimming speed, and (3) examine the phase relationships between different body components. It was hypothesized that cetaceans would not act as a rigid beam producing large vertical displacements at the rostrum, and

Table 1. Morphometrics of odontocete cetaceans.

Species	Sex	Body mass (kg)	Body length (m)	Fineness ratio	Fluke span (m)	Fluke area (m ²)	Flipper length (m)	Flipper area (m ²)
<i>Stenella plagiodon</i>	male	81.6	1.83	5.41	0.49	0.061	0.38	0.050
<i>Lagenorhynchus obliquidens</i>	male	130.6	2.18	4.98	0.67	0.081	0.37	0.055
<i>Lagenorhynchus obliquidens</i>	female	139.7	2.25	5.05	0.55	0.072	0.38	0.057
<i>Tursiops truncatus</i>	female	192.0	2.51	5.10	0.58	0.089	0.34	0.048
<i>Tursiops truncatus</i>	female	229.5	2.60	5.00	0.50	0.112	0.46	0.026
<i>Tursiops truncatus</i>	female	263.1	2.70	4.69	0.65	0.117	0.37	0.063
<i>Pseudorca crassidens</i>	female	367.4	3.55	6.72	0.74	0.109	0.51	0.108
<i>Delphinapterus leucas</i>	female	698.5	3.25	4.66	0.77	0.165	0.33	0.113
<i>Globicephala melaena</i>	female	764.3	3.99	5.86	0.96	0.196	0.71	0.192
<i>Orcinus orca</i>	female	929.9	4.16	4.89	1.10	0.269	0.64	0.349
<i>Orcinus orca</i>	female	1124.3	4.46	4.78	1.05	0.226	0.70	0.339
<i>Orcinus orca</i>	female	1995.8	5.16	4.91	1.33	0.356	0.79	0.510

animals with large flipper areas relative to fluke areas would exhibit smaller dorso-ventral oscillations at the cranial portion of the body. Large displacements at the cranial portion of the body may be indicative of instabilities generated by the muscles and translated from the propulsive movements at the caudal flukes. Small oscillations would indicate stabilization mechanisms.

METHODS

The swimming motions of twelve individuals of seven species of trained odontocete cetaceans (Table 1) were recorded at Sea World parks in Orlando, FL; San Antonio, TX; San Diego, CA, and the National Aquarium in Baltimore, MD. The species examined included the spotted dolphin (*Stenella plagiodon*), striped dolphin (*Lagenorhynchus obliquidens*), bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*), beluga whale (*Delphinapterus leucas*), pilot whale (*Globicephala melaena*), and killer whale (*Orcinus orca*). Experiments were performed in large elliptical pools with maximum lengths of 27.4–48.8 m. The curved portions of each pool were constructed of glass panels. A water depth of 1.4–2.1 m was visible through the panels. Depths of the pools were 7.3–11.0 m and water temperatures ranged between 12°C and 22°C. Animals were directed to swim by human trainers or routinely swam along the wall of the pool. All animals were trained to swim near the water surface. The speed of the animals varied in response to cues from trainers.

Morphological measurements were obtained from direct measurement with a tape measure or from photographs and video images with a scalar in the image. Measurements included body length (L , m) as the linear distance from rostral tip to fluke notch, flipper length as the linear distance from anterior flipper insertion to flipper tip, fluke span as the linear distance between fluke tips, total planar surface area of flukes, total planar area of the flippers, and maximum body depth. Maximum body depth was measured from photographic and video images of the

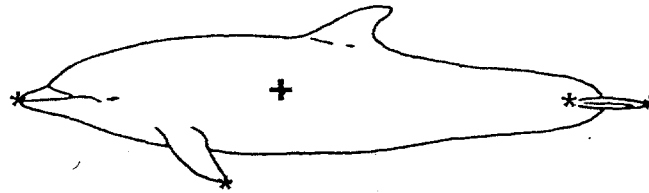


Figure 1. Bottlenose dolphin showing digitized points on rostrum, flipper, peduncle, and flukes. The symbol + indicates the position of the center of mass. Center of mass was determined from Fish (2002).

lateral aspect of the body as the animal floated in the water. Flipper length was reported as the average length for the two flippers. Fineness ratio (FR) was calculated as the body length divided by the maximum body depth.

The swimming motions were recorded with a Panasonic VHS camcorder (DV-510) at 60 Hz. Sequential positions of the rostral tip, flipper tip, caudal peduncle (*i.e.*, position of tail fluke insertion), and fluke tips (Fig. 1) were digitized from individual fields of videotape with the Peak Motus video analysis system (Version 4.3.1; Peak Performance Technologies, Englewood, CO) input from a Panasonic AG-7300 video recorder. Kinematic data from videotape records included mean swimming velocity (U , m/sec), stroke cycle frequency (f , Hz) and peak-to-peak amplitude (A , m) for each digitized point, and phase differences between the motion of the flukes and the motion of the other three body components. Both U and A were computed using L as a scalar. A is the maximum vertical displacement for the oscillatory motion of each digitized point on the body. Due to size differences between species, comparisons were made using length-specific values U/L and A/L .

Phase differences in degrees with respect to movements of the fluke tip were calculated as the time difference between the maximum vertical movement of the fluke tip and each of the other body points divided by the cycle period of the fluke tip and multiplied by 360° . A phase difference of 0° indicated synchronous movement (*i.e.*, body components move simultaneously in the same direction in the vertical plane), whereas, a phase difference of 180° indicated the opposite phase (*i.e.*, body points move exactly opposite to one another in the vertical plane). Movements of body points were considered asynchronous with respect to the fluke tip when the phase difference was statistically different from 0° . Negative values indicated the cycle of the body point trailed the cycle of fluke tip; whereas, positive values indicated the cycle of the body point led the fluke tip.

Means were calculated for values that did not vary with L and U/L . Variation about means was expressed as \pm one standard deviation (SD). Statistical analyses were performed using software packages Statistica (Version 4.1; StatSoft) and DataDesk (Version 3.0). Linear relationships were estimated by least-squares regression. The phase difference in the timing of rostrum and fluke tip was tested against zero using a paired Student *t*-test. All tests were 2-tailed and differences were considered significant at $P < 0.05$.

RESULTS

Body length among species varied 2.80-fold from 1.83 m (*Stenella*) to 5.16 m (*Orcinus*). FR varied from 4.66 (*Delphinapterus*) to 6.72 (*Pseudorca*) (Table 1). Across

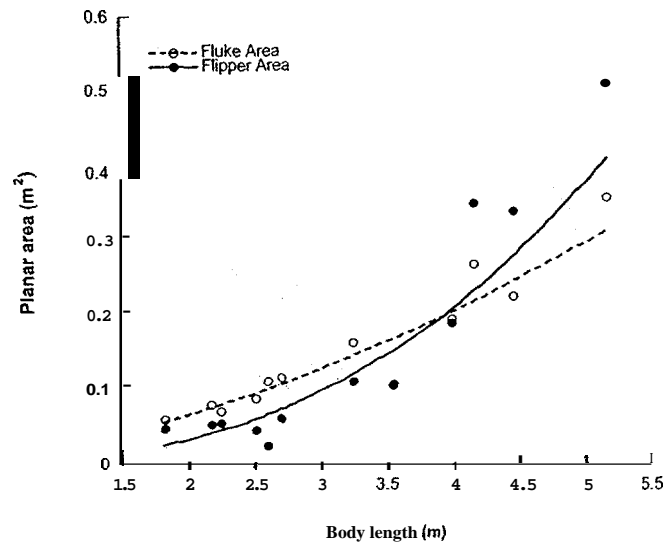


Figure 2. Relationships of planar areas of flukes and flippers with body length. Equations for regression lines are provided in the text.

species, flipper length, total flipper area, fluke span, and fluke area increased with body length, according to the following equations:

$$\text{Flipper length (m)} = 0.035 + 0.144L \quad r = 0.900; P < 0.001 \quad (1)$$

$$\text{Flipper area (m}^2\text{)} = 0.006L^{2.619} \quad r = 0.968; P < 0.001 \quad (2)$$

$$\text{Flukespan (m)} = -0.009 + 0.246L \quad r = 0.955; P < 0.001 \quad (3)$$

$$\text{Fluke area (m}^2\text{)} = 0.021L^{1.642} \quad r = 0.952; P < 0.001 \quad (4)$$

The planar areas of the appendages (Fig. 2) were not statistically different from each other (paired t-test; $t = -0.229$; $P < 0.823$). However, animals under 3.6 m tended to have fluke areas greater than flipper areas and those longer than 3.6 m had fluke areas less than flipper areas.

A total of 143 swimming trials were analyzed. Video recordings showed that all the species swam steadily in a manner similar to previous descriptions of cetacean locomotion (Lang 1975; Videler and Kamermans 1985; Fish 1993, 1998; Skrovan *et al.* 1999). All measured body components moved along sinusoidal pathways (Fig. 3A, B). Regression analysis showed that the frequency of the propulsive cycle (f) increased linearly with increasing U/L ($r = 0.90$; $P < 0.001$) (Fig. 4), according to the equation:

$$f = 0.538 + 0.902U/L \quad (5)$$

The vertical excursion, A , was greatest for the flukes (A_f) followed in decreasing order by the peduncle (A_p), rostrum (A_r), and flipper (A_{β}) (Fig. 3). The flipper was located closest to the center of mass of the body (Fish 2002). For all species, A for all body points was found to be independent of U/L (Fig. 5). Peak-to-peak amplitude for the body components varied linearly with L across a wide range of

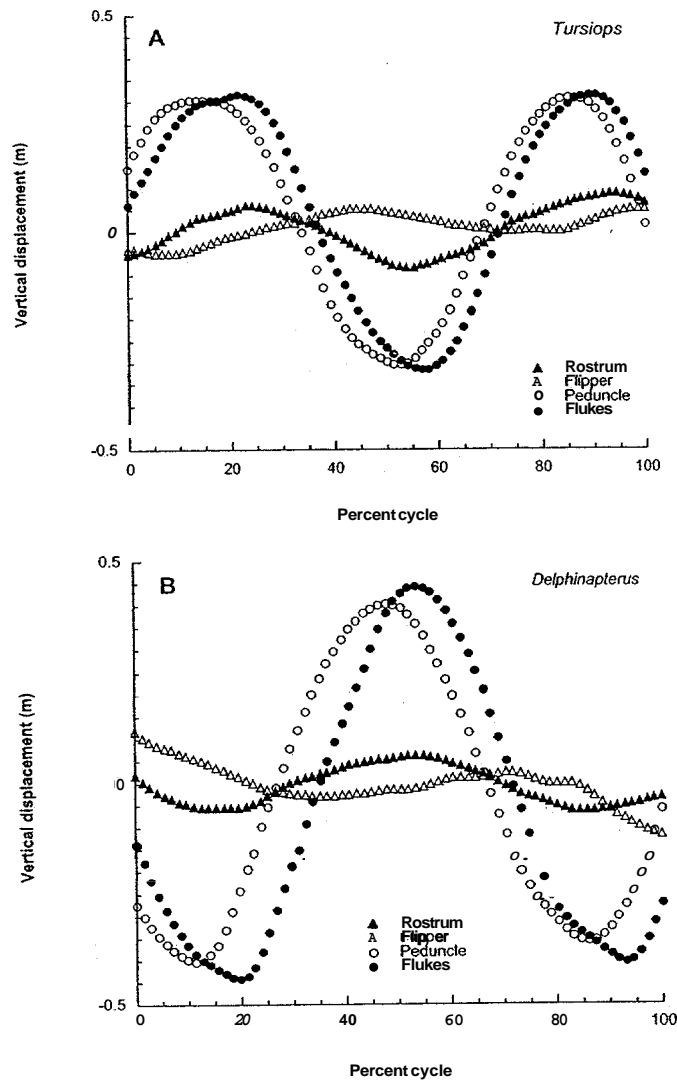


Figure 3. Oscillations of **body** components for swimming cetaceans. A. *Tursiops* swimming at 2.0 mlsec. B. *Delphinapterus* swimming at 2.5 mlsec.

species of different **body** lengths (Fig. 6). Regressions on means for individuals for each body component were statistically significant for the equations:

$$A_r = 0.071 + 0.017L \quad r = 0.601; P < 0.05 \quad (6)$$

$$A_f = -0.014 + 0.037L \quad r = 0.785; P < 0.01 \quad (7)$$

$$A_p = 0.026 + 0.196L \quad r = 0.936; P < 0.001 \quad (8)$$

$$A_f = 0.071 + 0.199L \quad r = 0.936; P < 0.001. \quad (9)$$

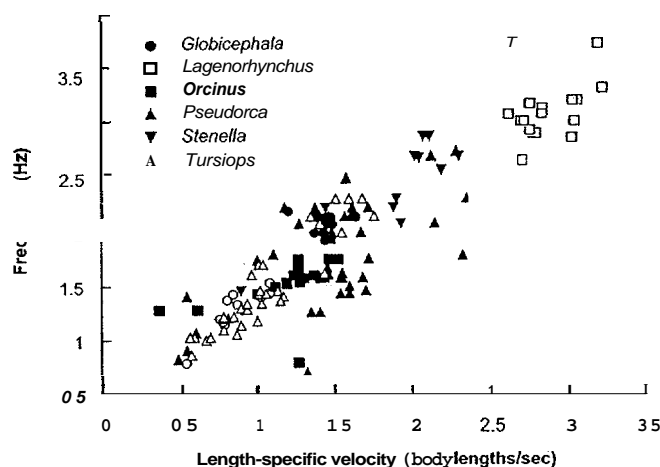


Figure 4. Frequency of swimming strokes as a function of length-specific velocity for the odontocete cetaceans investigated in this study.

Differences between mean A_r/L between species were small (Fig. 7), varying from 0.02 ± 0.01 to 0.06 ± 0.02 . For the vertical excursions of the flukes, mean A_f/L varied from 0.17 ± 0.02 to 0.25 ± 0.03 (Fig. 6). Both the fluke and rostrum mean A/L values were found to be smallest for *Globicephala* and largest for *Stenella*.

The ratio of A_f/A_r varied from 4.34 to 6.76 for the cetaceans. The smaller species (*Lagenorhynchus*, *Stenella*, *Tursiops*) exhibited a lower range of A_f/A_r (4.34–4.89) compared to the larger cetaceans (5.94–6.76).

There were differences among species in the phased movements of the flukes with the rostrum and peduncle. No relationship was observed for phase relationships among the body points and U .

The phase differences between the fluke oscillations and those of the rostrum were consistently small for all species (Fig. 8). Phase differences between the fluke tip and rostral tip were not statistically different from zero for *Stenella* ($t = 1.07$, $df = 13$, $P < 0.303$) and *Tursiops* ($t = 2.00$, $df = 31$, $P < 0.054$), indicating near synchrony in time and direction between rostrum and flukes. Phase differences between the rostrum and the flukes ranged from $-9.4^\circ \pm 13.8^\circ$ for *Lagenorhynchus* to $33.0^\circ \pm 21.3^\circ$ for *Delphinapterus*. With the exception of the negative mean values for *Lagenorhynchus* and *Tursiops*, the mean phase differences were positive for the other cetaceans, indicating that the motion of the rostrum led the fluke motion.

In all cases the motion of the peduncle led the flukes ranging from $18.9^\circ \pm 5.9^\circ$ to $48.7^\circ \pm 26.9^\circ$; whereas the flippers were out of phase by exhibiting phase relationships of $-60.9^\circ \pm 24.8^\circ$ to $-123.4^\circ \pm 29.9^\circ$ following the flukes (Fig. 9). The phase relationship between the motions of the flukes and the peduncle in cetaceans is associated with control of the angle of attack of the flukes in accordance with a lift-based propulsive system (Fierstine and Walters 1968, Fish 1998).

DISCUSSION

The planar area of the flippers and the flukes were surprisingly similar for the cetaceans examined. Only *Orcinus* displayed flippers with combined areas larger

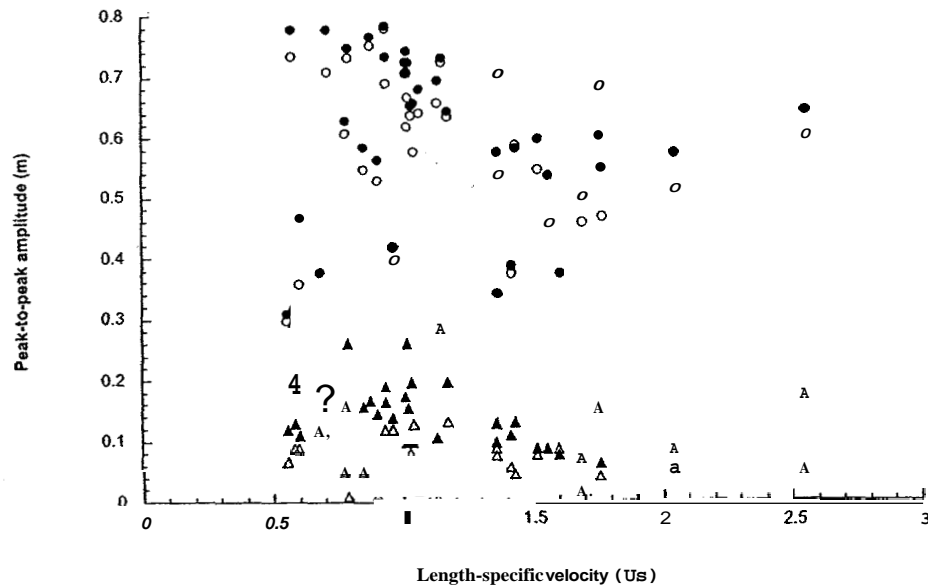


Figure 5. Peak-to-peak amplitude plotted as a function of length-specific swimming speed (L/sec) for *Tursiops*. Symbols represent the rostrum (solid triangles), flipper (open triangles), peduncle (open circles), and fluke tip (solid circles).

than their flukes. The flippers for *Orcinus* were 1.3–1.5 times larger than the flukes. The flippers of *Orcinus* are subject to increased size due to sexual dimorphism (Dahlheim and Heyning 1999), but the animals examined for this study were all females. Despite the larger flipper area for *Orcinus*, there is no indication of enhanced performance for stability (this study) or maneuverability (Fish 2002).

The kinematics of cetaceans examined were consistent with previous studies of cetacean locomotion (Videler and Kamermans 1985; Fish 1993, 1998). Swimming speed in cetaceans was controlled by modulation of f , whereas A_f remained constant over the range of swimming speeds. Frequency modulation by cetaceans was similar to results found for fish and other marine mammals that swim by oscillations of a high aspect ratio hydrofoils (Bainbridge 1958, Hunter and Zweifel 1971, Webb et al. 1984, Feldkamp 1987, Fish et al. 1988, Scharold et al. 1989).

Amplitude (A_f) remained a constant proportion of L for each of the species examined. These results were similar to previous results for *Tursiops* ($A_f/L = 0.16$ – 0.21 ; Kayan and Pyatetskiy 1977; Fish 1993, 1998), *Orcinus* ($A_f/L = 0.21$; Fish 1998), and *Pseudorca* ($A_f/L = 0.18$; Fish 1998). *D. leucas* exhibited a decrease in A_f/L from 0.27 to 0.13 with increasing U/L . Despite the change in A_f/L for *D. leucas*, the values for the cetaceans examined are typical for thunniform swimmers in which A_f/L is 0.16–0.34 (Fierstine and Walters 1968, Fish et al. 1988, Dewar and Graham 1994).

Propulsive oscillatory motions of the flukes should produce forces that are perpendicular to the direction of motion by a swimming dolphin (Webb 1975; Fish 1993, 1998). The time-average of these transverse forces and the generated torques must be balanced at the cranial end of the animal. If a dolphin acted as a simple rigid beam, the transverse forces at the flukes would be balanced by a pitching movement at the cranial end of the animal in a direction within the vertical plane

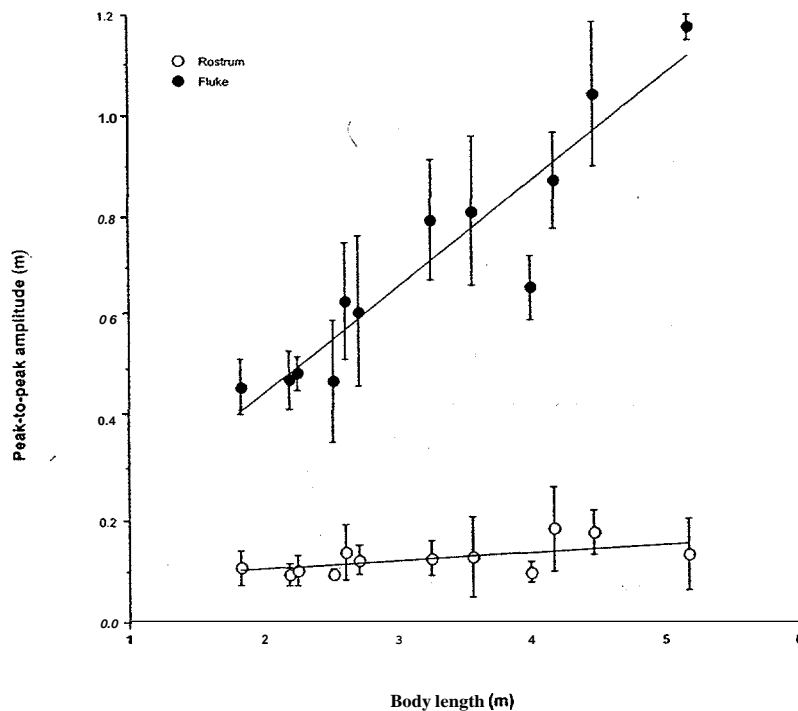


Figure 6. Mean (\pm SD) peak-to-peak amplitude measured at the rostrum (A_r) and fluke tip (A_f) if individuals plotted as a function of body length (L). Equations for regression lines are provided in the text.

immediately opposite to direction of the flukes. The dolphin would act like a seesaw with the rotational center of the pitching motion located at the center of mass. However, observations of cetaceans in this study showed that the animals did not act as simple rigid beams. As a result, the vertical displacement of the rostrum in all species was small in comparison to the movement of at the flukes. In addition, the rostral end of the animals moved in the same direction as the flukes exhibiting near synchrony. Indeed, the movements of the ends were synchronous for *Stenella* and *Tursiops*.

Limiting the transverse movements of the head reduces drag, increases propulsive efficiency, and maintains stability (Weihs 1993, 2002). Large deviations at the cranial end will increase the added mass of the system as the water adjacent to the body is accelerated by its movements (Webb 1982). The drag (*i.e.*, the hydrodynamic resistance to forward movement) is dependent on the added mass and proportional to the kinetic energy dissipated into the water. Displacements at the cranial end of a swimming animal may induce instabilities of the pressure gradient along the body and foster conditions for premature boundary layer separation that can increase the total drag on the animal (Webb 1975, Vogel 1994). In addition, drag is increased due to large oscillations that increase the projected frontal area encountered by the ambient water flow. Deviation of body shape because of propulsive movements has been theoretically suggested to increase drag by five times over the drag of a rigid straight body (Lighthill 1975).

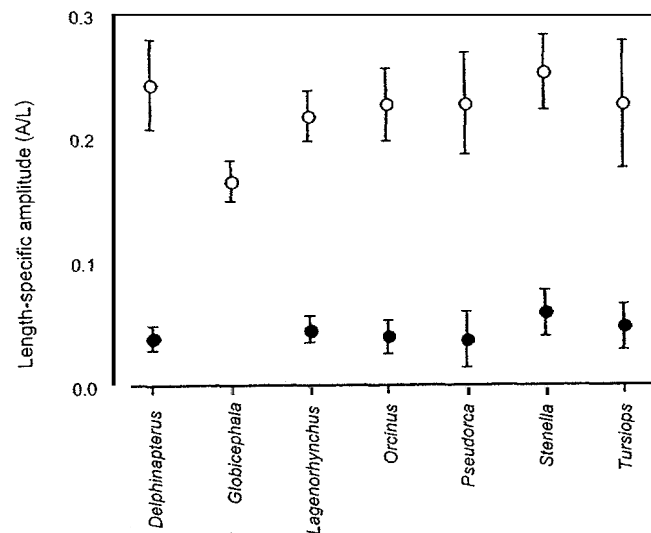


Figure 7. Mean Length-specific amplitude ($AIL \pm SD$) for the rostrum and flukes for each species.

The body motions of cetaceans create a tendency for instability by pitching (Aleyev 1977, Weihs 1993). The pitching movements potentially cause an animal to deviate from its chosen trajectory. Such a deviation will increase the energy expenditure to maintain course and increase time and effort in acquiring potential prey.

The body of cetaceans, particularly fast-swimming oceanic delphinids, has been considered a relatively stable morphological configuration (Fish 2002). Skrovan *et al.* (1999) found the vertical displacement of the rostrum of *Tursiops* to be $0.05 L$ during steady swimming at $1.5\text{--}3.7$ m/sec. Even when accelerating, a rostral displacement for *Lagenorhynchus* is still $0.05 L$ (Lang, 1975). Such pitching motions are in accordance with the results for the seven species examined in this study.

Morphological features associated with stability include an anteriorly located center of mass, control surfaces (*e.g.*, flukes, flippers, caudal peduncle) located far from the center of mass with most of the control surface area posterior to the center of mass, sweepback and dihedral of the control surfaces, reduced mobility of the flippers, and reduced flexibility of the body (Howell 1930, Klima *et al.* 1987, Smith 1992, Weihs 1993, Fish 2002). The increased stiffness of the anterior body due to skeletal mechanics limits pitching movements at the rostrum (Long *et al.* 1997). With the exception of *Delphinapterus*, the highly compressed cervical vertebrae and streamlined body of odontocete cetaceans restrict bending in the neck. The thoracic vertebrae are braced by the ribs, further restricting bending motions in the anterior of cetaceans.

The control surfaces of cetaceans act to passively dampen the rate of growth of a perturbation (Aleyev 1977). The position of the flippers increases both the area and span of the body anterior of the center of mass. Pitching movements will produce a force normal to the planar area of the flippers that will act to resist vertical motions of the head. This increased area would increase the added mass and inertia at the anterior end of the animal effectively dampening recoil movements (Webb 1975). The large phase differences between the motions of the flippers and

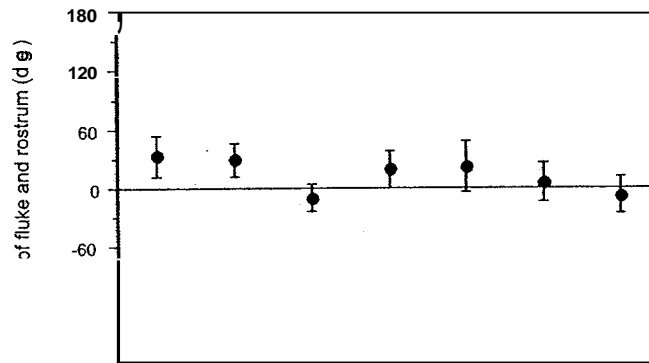


Figure 8. Phase difference (mean \pm SD) between flukes and rostrum for each species. Positive values indicate rostrum leads flukes; negative values indicate rostrum follows flukes. The horizontal line at a phase difference of 0° indicates synchrony between the fluke and the rostrum.

the flukes of the cetaceans in this study help to generate resistive forces at the flippers that would counter pitching rotations generated by the vertical forces produced by the flukes. However, flippers with relatively large areas had no effect on decreasing dorso-ventral excursions at the rostrum, contrary to the original hypothesis in this study. All animals tested maintained relatively small displacements at the rostrum ($A_r/L < 0.06$). *Orcinus* had the largest flipper areas, but this species did not show any difference in A_r/L with other species. One possible reason that the animals did not show differences is that the planar area of the flippers was statistically identical to the planar area of the flukes. Since fluke area is proportional to force production, the resistive force generated from recoil at the flippers would be proportionally similar.

The distribution of body mass also plays a critical role in the passive dampening of recoil. Recoil forces at the head can be minimized by increasing the mass anterior to the center of mass. This configuration produces a large moment of inertia resisting recoil at the head. Furthermore, the peduncle region shows reduced mass that would assist in minimizing posterior vertical forces that would have to be balanced at the cranial end of the whale (Lighthill 1975). Thunniform swimmers (*i.e.*, cetaceans and tuna that swim by oscillating a caudal hydrofoil) reduce the posterior area of the body by narrow necking. In narrow necking, the projected area decreases progressively from the center of mass to the caudal peduncle, with a rapid increase in the span of the caudal propulsor (Fierstine and Waiters 1968, Lighthill 1975, Fish 1993). The peduncle is streamlined in its plane of oscillation. These modifications reduce the added mass effect posteriorly and corresponding recoil forces (Webb 1975, Blake 1983).

Active stabilization uses the body's own motions to counter the pitching force generated by the propulsive oscillations at the tail. The low A_r/L (0.02–0.06) despite the relatively large A_f (0.17–0.25) and phased movements between both

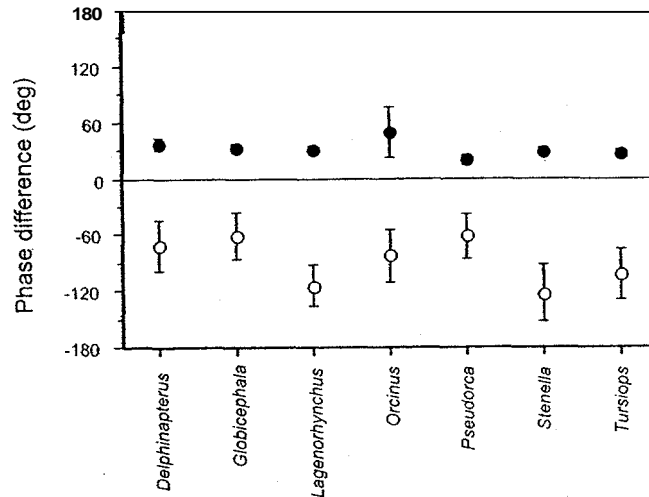


Figure 9. Phase difference (mean \pm SD) between flukes and flipper and peduncle. Peduncle always leads flukes (positive values); flippers always followed flukes (negative values). The horizontal line at a phase difference of 0° indicates synchrony between body components.

body components indicate control of pitching oscillations in cetaceans. By synchronously moving the rostrum in the same direction as flukes by muscular control, there is a reduction in the natural tendency of the rostrum to swing through a wide arc opposite the motion of the flukes. More control is afforded to the cranial end of the animal. Simultaneously, the flippers, which are out of phase with the flukes, oppose pitching (see above).

Similar to cetaceans, tuna can control displacement of the head. Tuna exhibiting sustained swimming limit A_r/L to 0.037–0.051 and A_f/A_r to 4.59–5.14 (Fierstine and Walters 1968, Dewar and Graham 1994). These fish with short or inflexible bodies reduce recoil by using the resistive force developed from the motions in the body in the direction normal to flexure in concert with the anteriorly located increased projected area (Lighthill 1975). Tuna, like cetaceans, use a lift-based propulsive system, whereby thrust is generated by an oscillating hydrofoil. The motion of the hydrofoil generates a large thrust force with relatively small transverse forces (Lighthill 1975, Webb 1975).

The resistance to pitching of the anterior body of cetaceans lowers the power requirements for swimming and increases stability. Mechanisms for pitch stabilization are associated with morphological features and kinematic control. The placement of the flippers and relatively inflexible cranial portion of cetaceans acts to provide a large inertial mass to resist recoil motions at the head. In addition, the phased movements of the various body components reduce pitching movement of the head. Minimizing pitch is an important requirement for cetaceans as fast-swimming aquatic predators. Stability is essential in minimizing energy consumption in swimming long distances while foraging and migrating (Fish and Rohr 1999). Pitch control in echolocating cetaceans can be important in targeting prey. Both emission and reception of an echolocation beam is confined to narrow range of elevation angles, particularly at high frequencies (Au 1993). Excessive pitching movements could

potentially reduce echolocation effectiveness in reception by signal loss from shadowing by the head and reduced directional control during emission.

ACKNOWLEDGMENTS

We wish to express our appreciation to curators and training staff of *Sea World* and the National Aquarium. Appreciation is also expressed to R. H. Baker, J. Holak, A. J. Nicasrro, T. M. Williams, and two reviewers for assistance in greatly improving the manuscript. This paper was based on research performed with support from the Office of Naval Research (N00014-95-1-1045; N00014-99-WX20135).

LITERATURE CITED

- ALEYEV, Y. G. 1977. *Nekton*. Junk, The Hague.
- AU, W. W. L. 1993. The sonar of dolphins. Springer-Verlag, New York, NY.
- BAINBRIDGE, R. 1958. The speed of swimming fish as related to size and to frequency and amplitude of the tail beat. *Journal of Experimental Biology* 35:109-133.
- BLAKE, R. W. 1983. *Fish locomotion*. Cambridge University Press, Cambridge.
- DAHLHEIM, M. E., AND J. E. HEYNING. 1999. Killer whale *Orcinus orca* (Linnaeus, 1758). Pages 281-322 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Academic Press, San Diego, CA.
- DEWAR, H., AND J. B. GRAHAM. 1994. Studies of tropical tuna swimming performance in a large water tunnel. III. Kinematics. *Journal of Experimental Biology* 192:45-59.
- FELDKAMP, S. D. 1987. Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *Journal of Zoology, London* 212:43-57.
- FIERSTINE, H. L., AND V. WALTERS. 1968. Studies of locomotion and anatomy of scombrid fishes. *Memoirs of the Southern California Academy of Sciences* 6:1-31.
- FISH, F. E. 1993. Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology* 185:179-193.
- FISH, F. E. 1998. Comparative kinematics and hydrodynamics of odontocete cetaceans: Morphological and ecological correlates with swimming performance. *Journal of Experimental Biology* 201:2867-2877.
- FISH, F. E. 2002. Balancing requirements for stability and maneuverability in cetaceans. *Integrative and Comparative Biology* 42:85-93.
- FISH, F. E., AND J. ROHR. 1999. Review of dolphin hydrodynamics and swimming performance. SPAWARS System Center Technical Report 1801, San Diego, CA. <http://wnrw.spawar.navy.mil/sti/publications/pubs/tr/1801/tr1801.pdf>
- FISH, F. E., AND L. D. SHANAHAN. 2000. The role of the pectoral fins in body trim in sharks. *Journal of Fish Biology* 56:1062-1073.
- FISH, F. E., S. INNES AND K. RONALD. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. *Journal of Experimental Biology* 137:157-173.
- HOWELL, A. B. 1930. *Aquatic mammals*. Charles C. Thomas, Springfield, IL.
- HUNTER, J. R., AND J. R. ZWEIFEL. 1971. Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fisheries Bulletin, U.S.* 69:253-266.
- KAYAN, V. P., AND V. YE. PYATETSKIY. 1977. Kinematics of bottlenosed dolphins swimming as related to acceleration mode. *Bionika* 11:36-41 (translated from Russian).
- KLIMA, M., H. A. OELSCHLÄGER AND D. WÜNSCH. 1987. Morphology of the pectoral girdle in the Amazon dolphin *Inia geoffrensis* with special reference to the shoulder joint and the movements of the flippers. *Zeitschrift Saugtierkunde* 45:288-309.
- LANG, T. G. 1975. Speed, power, and drag measurements of dolphins and porpoises. Pages 553-571 in T. Y. Wu, C. J. Brokaw and C. Brennen, eds. *Swimming and flying in nature*. Volume 2. Plenum Press, New York, NY.

- LIGHTHILL, J. 1975. *Mathematical biofluid dynamics*. Society for Industrial and Applied Mathematics, Philadelphia, PA.
- 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*. *Journal of Experimental Biology* 200:65–81.
- PABST, D. A. 1993. Intramuscular morphology and tendon geometry of the epaxial swimming muscles of dolphins. *Journal of Zoology, London* 230:159–176.
- PABST, D. A. 2000. To bend a dolphin: Convergence of force transmission designs in cetaceans and scombrid fishes. *American Zoologist* 40:146–155.
- PARRY, D. A. 1949. The swimming of whales and a discussion of Gray's paradox. *Journal of Experimental Biology* 26:24–34.
- SCHAROLD, J., N. C. LAI, W. R. LOWELL AND J. B. GRAHAM. 1989. Metabolic rate, heart rate, and tailbeat frequency during sustained swimming in the leopard shark *Triakis semifasciata*. *Experimental Biology* 48:223–230.
- SKROVAN, R. C., T. M. WILLIAMS, P. S. BERRY, P. W. MOORE AND R. W. DAVIS. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. *Journal of Experimental Biology* 202:2749–2761.
- SMITH, H. C. 1992. *Illustrated guide to aerodynamics*. McGraw-Hill, Blue Ridge Summit, PA.
- VIDELER, J., AND P. KAMERMANS. 1985. Differences between upstroke and downstroke in swimming dolphins. *Journal of Experimental Biology* 119:265–274.
- VOGEL, S. 1994. *Life in moving fluids*. Princeton University Press, Princeton, NJ.
- WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada* 190:1–158.
- WEBB, P. W. 1982. Fast-start resistance of trout. *Journal of Experimental Biology* 96:93–106.
- WEBB, P. W. 1992. Is the high cost of body/caudal fin undulatory swimming due to increased friction drag or inertial recoil. *Journal of Experimental Biology* 162:157–166.
- 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. 86103, Autonomous Undersea Systems Institute, Lee, New Hampshire.
- WEBB, P. W. 2002. Control of posture, depth, and swimming trajectories of fishes. *Integrative and Comparative Biology* 42:94–101.
- WEBB, P. W., P. T. KOSTECKI AND E. D. STEVENS. 1984. The effect of size and swimming speed on locomotor kinematics of rainbow trout. *Journal of Experimental Biology* 109:77–95.
- WEIHS, D. 1993. Stability of aquatic animal locomotion. *Contemporary Mathematics* 141:443–461.
- WEIHS, D. 2002. Stability versus maneuverability in aquatic locomotion. *Integrative and Comparative Biology* 42:127–134.
- WILLIAMS, T. M., W. A. FRIEDL AND J. E. HAUN. 1993. The physiology of bottlenose dolphins (*Tursiops truncatus*): Heart rate, metabolic rate and plasma lactate concentration during exercise. *Journal Experimental Biology* 179:31–46.

Received: 18 April 2002

Accepted: 25 November 2002