Hydrodynamic Design of the Humpback Whale Flipper

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ABSTRACT The humpback whale (Megaptera novaeangliae) is reported to use its elongate pectoral flippers during swimming maneuvers. The morphology of the flipper from a 9.02-m whale was evaluated with regard to this hydrodynamic function. The flipper had a wing-like, high aspect ratio planform. Rounded tubercles were regularly interspersed along the flipper's leading edge. The flipper was cut into 71 2.5-cm cross-sections and photographed. Except for sections near the distal tip, flipper sections were symmetrical with no camber. Flipper sections had a blunt, rounded leading edge and a highly tapered trailing edge. Placement of the maximum thickness placement for each cross-section varied from 49% of chord at the tip to 19% at mid-span. Section thickness ratio averaged 0.23 with a range of 0.20-0.28. The humpback whale flipper had a cross-sectional design typical of manufactured aerodynamic foils for lift generation. The morphology and placement of leading edge tubercles suggest that they function as enhanced lift devices to control flow over the flipper and maintain lift at high angles of attack. The morphology of the humpback whale flipper suggests that it is adapted for high maneuverability associated with the whale's unique feeding behavior. © 1995 Wiley-Liss, Inc.

The humpback whale, Megaptera novaeangliae, has the longest flipper of any cetacean (True, '83). Flipper length varies from 0.25 to 0.33 of the total body length (Tomilin, '57; Winn and Winn, '85; Edel and Winn, '78). Flipper shape is long, narrow, and thin (True, '83), although shape is variable among individuals (Winn and Winn, '85). The humpback whale flipper is also unique because of the presence of large protuberances or tubercles located on the leading edge, which gives this surface a scalloped appearance (Winn and Reichley, '85). Locations of the tubercles correspond to the positions of the cartilages of the manus (Tomilin, '57; Edel and Winn, '78; True, '83).

The unusual length of the pectoral flippers has been hypothesized to provide benefits to the humpback whale including 1) the ability of these whales to navigate in much shallower waters than other whales (Tomilin, '57; Perkins and Whitehead, '77), 2) use for thermoregulation as heat dissipaters because of the high surface-to-volume ratio (Scholander and Schevill, '55; Brodie, '77), 3) production of sound signals by slaps on the water surface (Tomilin, '57; Tyack, '81), 4) use of the light coloration on the underside of the flipper in herding prey into the mouth (How-

ell, '30; Brodie, '77; Hain et al., '82), 5) use of the light coloration as a cue to others on the orientation and movement of the whale (Madsen and Herman, '80), 6) use of the flippers during mating (Howell, '30; Evans, '87), and 7) increased maneuverability (Jurasz and Jurasz, '79; Edel and Winn, '78). This latter function suggests that the flippers act as biological hydroplanes. The humpback whale is the most "acrobatic" of baleen whales (Howell, '30; Tomilin, '57; Edel and Winn, '78; Winn and Reichley, '85; Leatherwood et al., '88). This species is capable of performing underwater somersaults (Jurasz and Jurasz, '79). If the flippers of the humpback are adapted for maneuverability, they should display a morphology for high hydrodynamic performance. There are limited data on the amount of streamlining displayed in appendages of cetaceans and its affect on hydrodynamic performance (Howell, '30; Felts, '66; Lang, '66; Edel and Winn, '78; Bose et al., '90; Fish and Hui, '91). A single cross-section

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cut from the tip of a humpback whale flipper indicated a symmetrical streamlined profile with a rounded leading edge and tapering

trailing edge (Edel and Winn, '78).

The present study was initiated to characterize the design of the humpback whale flipper and quantitatively describe the shape in terms of hydrodynamically relevant parameters. Using this approach, the flipper design can be compared to well-streamlined, engineered hydrofoils or aerofoils with known performance capabilities. It was expected that the morphology of the humpback flipper would display similarities with engineered designs for enhanced maneuverability.

MATERIALS AND METHODS

The left pectoral flipper was removed from a 9.02-m male humpback whale, Megaptera novaeangliae Borowski, (Marine Mammal Stranding Center Field Number 91-108) that beached on Island Beach State Park, New Jersey. The flipper was in good condition with some surface abrasion. Flipper span was 2.5 m as measured from the distal tip to the anterior insertion of the flipper with the body. The flipper was cut into three approximately equal segments (distal, medial, proximal), wrapped in plastic sheeting, and subsequently frozen.

The dorsal surface of the flipper was marked with a reference grid and photographed. Intertubercular distances were measured from photographs as the linear distance between the centers of adjacent leading edge tubercles. The intertubercular distances were expressed as a percentage of the flipper span. The distal and medial segments were cut with an industrial bandsaw into 2.5-cm cross-sections. Cross-sections were numbered sequentially starting from the flipper tip. A total of 71 cross-sections (S1-S73) were cut from the distal and medial flipper segments with S8 and S22 lost. The proximal segment was not sectioned, because of extensive damage to the axial region of this segment during the flipper's removal from the whale carcass.

Each cross-section was photographed with a 35-mm SLR camera. Outlines from photographs of the flipper planform and of the flipper sections were measured using a GTCO digitizer (Digi-Pad 21A71D4) interfaced to an IBM PC microcomputer.

Aspect ratio (AR) was calculated as flipper span squared divided by flipper area (von Mises, '45; Hurt, '65; Lighthill, '77). AR is associated strongly with the lift and drag performance of a wing. Dimensions of the

cross-sectional profiles included chord length (C), maximum thickness (T), and position of the maximum thickness with respect to leading edge of the chord (X) (Fig. 1). Quantitative indication of streamlining for sections were computed from the thickness ratio (TR) = T/C and position of maximum thickness (PMT) = X/C (Hoerner, '65; Vogel, '81).

RESULTS

The pectoral flipper was 28% of the total length of the whale. The flipper planform was elliptical and tapered distally. A slight sweep-back of 19° relative to the longitudinal axis of the flipper was measured for the distal third of the flipper. AR was 6.1.

Eleven tubercles were found along the leading edge of the flipper (Fig. 1). The tubercles (T1-T11) were confined to the distal and medial segments of the flipper. T1 was the largest tubercle and was located proximally on the flipper at 33% of the flipper span. The smallest tubercle, T11, was located near the flipper tip at 99.1% of span. Intertubercular distances decreased distally (Fig. 2). A large decrease of 31.2% was measured between intertubercular distance from T1 to T2 and T2 to T3. Despite the overall decrease of intertubercular distances over the entire flipper span, intertubercular distances remained relatively constant at 6.5-8.5% of span over the mid-span of the flipper between T2-T3 and T7-T8. Distal to T8, intertubercular distance declined steadily over the distal 12.4% of span. Barnacles were found attached to the distal tubercles, but barnacles were not observed to have attached in the spaces between tubercles.

In cross-section, the flipper displayed a large, blunt, and rounded leading edge and a thin, tapering trailing edge. Bones were present in both anterior and median portions of the sections, but were not observed near the posterior trailing edge. Cross-sections were symmetrical about the chord proximal to S10 (Fig. 1). Distal tip sections (S1-10) were scooped out along the ventral surface of the leading edge producing a concavity. This tip concavity was reported previously by Tomilin ('57). Chord (C), maximum thickness (T), and maximum thickness position (X) showed a non-uniform decrease distally (Fig. 3). The largest decrease of C, T, and X occurred at the flipper tip with sections S1-7. Sections with tubercles had longer chords than adjacent distal non-tubercle sections (t = 5.23, df = 9, P < .05).

TR ranged from 0.28 at section S2 to 0.20 at section S37 (Fig. 4). Mean TR for the

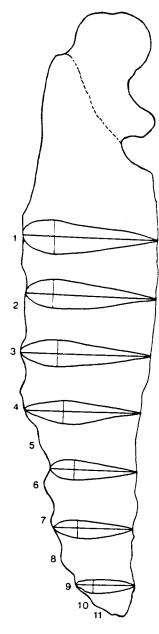


Fig. 1. Megaptera novaeangliae. Flipper planform showing representative cross-sections at intervals of five sections. Flipper is oriented with its distal tip pointed down. Horizontal line through each cross-section represents the chord length (C), and vertical line represents the maximum thickness (T). Distance from the leading edge (left side) to T represents the position of maximum thickness (X). Numbers located along the leading edge indicate the center for each of the tubercles. Ten intertubercle intervals occur between adjacent tubercles.

cross-sections was 0.23 ± 0.02 (SD). TR of flipper sections decreased from midspan distally to the tip. The TRs of tip sections (S1-3) were 21% greater than the mean TR for the majority of flipper sections. The increase in TR occurred in tip sections because these sections had smaller chords relative to the thickness. A distinct demarcation in TR was observed between sections S34 and S35. Sections distal to S35 had a mean TR of 0.24 ± 0.01 (SD), whereas the more proximal sections had a mean of 0.22 ± 0.01 (SD). PMT decreased steadily from a maximum of 0.49 at the flipper tip to a minimum of 0.19 at the midspan (Fig. 5).

DISCUSSION Hydrodynamic design

The flippers of the humpback whale represent control surfaces that can maintain both stability and create force imbalances for maneuvering (Felts, '66; Edel and Winn, '78; Weihs, '93). The effectiveness of humpback whale flippers as biological hydrofoils or wings is determined by the hydrodynamic design, which influences lift and drag characteristics (Hurt, '65; Webb, '75; Vogel, '81). An effective hydrofoil produces a large lift (force acting perpendicular to the direction of flow) while minimizing drag (force acting parallel to fluid flow) (Vogel, '81; Weihs, '93). For symmetrical foil sections, lift is generated as a foil is canted at an angle to the water flow (angle of attack). Above a critical attack angle, the hydrofoil stalls (losses lift) because of separation of the boundary layer near the leading edge (Webb, '75). Drag on a foil is derived from profile drag and induced drag (Vogel, '81; Weihs, '93). Profile drag results from pressure and frictional forces and occurs even when no lift is generated, whereas induced drag is produced in lift generation from kinetic energy imparted to the water from pressure differences between the two surfaces of the hydrofoil (Webb, '75). Leakage of fluid from high pressure to low pressure around the distal tip of a lifting surface results in the formation of tip vortices (Hurt, '65; Vogel, '81).

The planform and symmetrical cross-sectional designs of the flipper indicate hydrodynamic adaptations for generating lift and minimizing drag. The elliptical planform of the flipper provides the optimal shape for uniform distribution of lift over the span and for incurring the least induced drag (von Mises, '45; Hurt, '65). Cross-sectional profiles of the humpback whale flipper had a

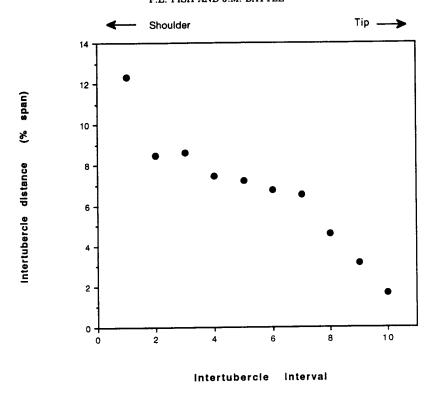


Fig. 2. Megaptera novaeangliae. The distance between centers of adjacent tubercles (intertubercle distance) is expressed as a percentage of total flipper span. Intertubercle distance is plotted against the intertubercle intervals (1-10).

thickness ratio similar to fluke sections from other whales and dolphins (Bose et al., '90). Humpback cross-sections had a streamlined, fusiform design analogous to engineered highperformance aerofoils and hydrofoils. Midspan sections were similar in design to the NACA 634-021 foil (Abbott and von Doenhoff, '49). A streamlined shape is characterized by a blunt, rounded leading edge, maximal thickness located one-third to one-half body length posterior of the leading edge, and narrowing toward the trailing edge. This configuration reduces profile drag by reduction of the flow-induced pressure gradient around the section (Webb, '75; Vogel, '81; Blake, '83). The pressure gradient reduction delays separation of the boundary layer to a point downstream on the section, thus maintaining a small wake and ultimately minimizing the energy lost to drag (Hurt, '65; Streeter, '66; Webb, '75; Vogel, '81).

The magnitudes of lift and drag on the

The magnitudes of lift and drag on the flipper are influenced also by the position of the maximum thickness (PMT). Adverse pres-

sure gradients (i.e., pressure increases in the downstream direction), downstream of PMT, facilitates boundary layer separation with an associated increase in pressure drag (Webb, '75; Vogel, '81). Separation can be delayed by downstream displacement of PMT which maintains a longer favorable pressure gradient (i.e., pressure decreases in the downstream direction). In addition, PMT determines the percentage of the flipper where laminar flow occurs due to a favorable pressure gradient upstream of PMT (Blake, '83). Laminar flow in the boundary layer produces less drag than turbulent flow until boundary layer separation (Webb, '75; Vogel, '81; Blake, '83).

For fast swimming dolphins, fins and flukes have maximum thicknesses at 32–36% of chord posterior of the leading edge (Lang, '66). Without bony supports, the unpaired appendages of dolphins may minimize drag by optimizing the length of laminar flow. For the humpback flipper, the average PMT of 28% of chord is reminiscent of conventional

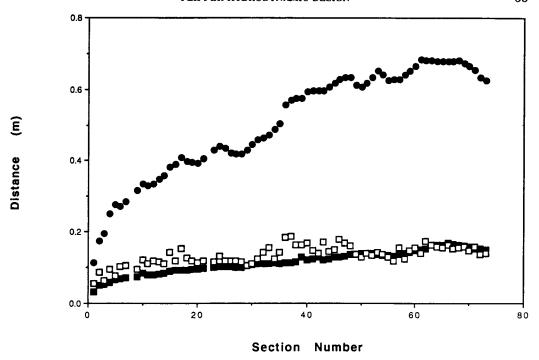


Fig. 3. Megaptera novaeangliae. Spanwise variation in cross-sectional dimensions, chord (C: solid circles), maximum thickness (T: solid squares), and distance from leading edge to maximum thickness (X: open squares). Section numbers increase from the flipper tip toward the shoulder of the whale.

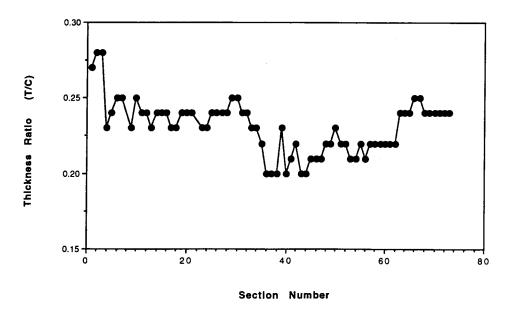


Fig. 4. Megaptera novaeangliae. Variation of thickness ratio (TR = T/C) with flipper cross-section. Section numbers increase from the flipper tip toward the shoulder of the whale.

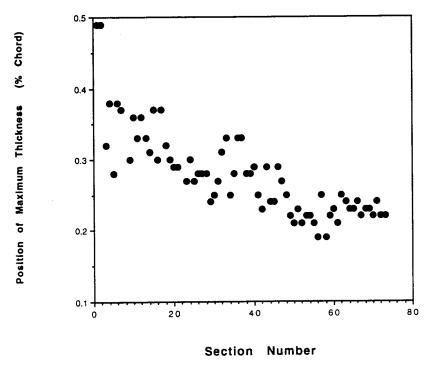


Fig. 5. Megaptera novaeangliae. Spanwise variation of position of maximum thickness from leading edge (PMT). Section numbers increase from the flipper tip toward the shoulder of the whale.

foil designs (Hurt, '65). Maximum thickness of the flipper is determined by bones of the manus and antebrachium which provide strength against transverse loading to the leading edge and medial portion of the flipper (Howell, '30; Felts, '66).

Maximum lift/drag is proportional to the square-root of the AR (Lighthill, '77). High AR indicates long narrow planforms with high lift to drag characteristics. A longer span produces more lift than a shorter span by deflecting a greater mass of fluid (Vogel, '81). Less induced drag is produced with a high AR, because less kinetic energy is imparted to the fluid. Induced drag predominates in sharp turns at low speed (Hurt, '65). High AR wings are favored for sharp, highspeed banking turns because of their high lift/drag characteristics (Lambie, '84). In a banking turn, the body rolls or tilts toward the inside of the turn. The lift force developed by the wings has a horizontal component that supplies the centripetal force necessary to maintain the turn (Alexander, '83; Weihs, '81, '93). Weihs ('81) showed banking to be an economical method of turning for negatively buoyant fish. Lift and bank angle are inversely related to turn radius (Alexander, '83; Norberg, '90). Shorter wings can produce a quicker roll into a turn but produce less lift and thus a wider circle (Lambie, '84). The high AR flippers of penguins and sea lions allow the rapid execution of smallradius turns (Godfrey, '85; Hui, '85). In comparison to all other rorquals (Balaenopteridae), humpback whale flippers display greater AR, longer span to body length, and greater range of mobility (Tomilin, '57; Edel and Winn, '78). These features indicate that humpbacks should display greater maneuverability than other rorquals.

In addition to AR, sweep-back and taper can improve lift generation and drag reduction (Hurt, '65; van Dam, '87). However swept-back, tapered wings carry more lift near the tips which stall before the root of the wing (Hopkins, '51; Hurt, '65; Lambie, '84). Pronounced stall at the distal wing can lead to instability in roll (Hopkins, '51; Hurt, '65). In aircraft design this problem is recti-

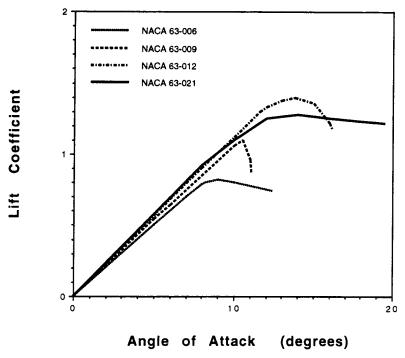


Fig. 6. Lift performance as a function of angle of attack for different manufactured foil sections. Foil NACA 63_4 -021 is similar to cross-sections from the whale flipper. In order of increasing thickness, NACA 63-016 (TR = 0.06), NACA 63-019 (TR = 0.09), NACA 63-012 (TR = 0.12), NACA 63-021 (TR = 0.21). Foil sections

were tested at the same Reynolds number (6×10^6) which would be equivalent to the flipper of *Megaptera novaeangliae* in this study moving through water at 8.8 m/s. Data were redrawn from Abbott and von Doenhoff ('49).

fied by installing twist or "washout" at the wing tip (Hurt, '65; Lambie, '84). Twist decreases the local angle of attack at the tip so lift is spread elliptically over the entire wing. A similar function can be suggested for the ventral concavity displayed in the distal cross-sections of the humpback flipper. This would provide the whale with sufficient lift and stability at the high angles of attack required in maneuvering.

Tubercle function

The position and number of tubercles on the flipper suggest analogues with specialized leading edge control devices associated with improvements in hydrodynamic performance. Bushnell and Moore ('91) suggested that humpback tubercles may reduce drag on the flipper. The occurrence of "morphological complexities" on a hydroplane could reduce, or use, tip bleed flow to decrease drag and improve lift generation to prevent tip stall. Alternatively, various biological wings utilize leading edge control devices to main-

tain lift and avoid stall at high attack angles and low speeds (Norberg, '90). Hydroplanes used in turning must operate at high angles of attack while maintaining lift.

The tubercles of the humpback whale flipper may function to generate vortices by unsteady excitation of flow to maintain lift and prevent stall at high angles of attack (Wu et al., '91). The function of the tubercles may be analogous to strakes used on aircraft. Strakes are large vortex generators that change the stall characteristics of a wing (Hoerner, '65; Shevell, '86). Stall is postponed because the vortices exchange momentum within the boundary layer to keep it attached over the wing surface. Lift is maintained at higher angles of attack with strakes compared to wings without strakes, although maximum lift is not increased by strakes. Increased angle of attack is necessary during turning maneuvers to generate the lift force for the turn (von Mises, '45; Hurt, '65; Weihs, '93). The ability to maintain lift at high angles of attack would be advantageous for humpback

whales in maneuvering, and the pattern of tubercles on the flipper suggests a morphology associated with rapid maneuvers.

Flow visualization experiments conducted on a model wing section with leading edge tubercles similar to those on humpback flippers showed that vorticity was produced (Wallace and Smith, personal communication). The effect of these vortices on sustaining lift

and reducing drag was unclear.

Although no direct evidence from humpback whales exists for vortex generation and water channeling by leading edge tubercles, the pattern of barnacle attachment indicates non-uniform flow patterns. The velocity gradient of water over a solid surface is a major determinate of attachment success of barnacle larvae (Crisp, '55). Cyprids of balanomorph barnacles fail to attach to areas of strong water flow (Crisp, '55; Crisp and Stubbings, '57; Lewis, '78). At water velocities exceeding 1-2 m/s, attachment by cyprids does not occur; attachment above 2 m/s is possible in areas of surface irregularities forming local eddies with reduced velocity gradients (Crisp, '55). Typically, barnacles are found on the upper leading edge of the tubercles of humpback whales (Edel and Winn, '78; True, '83; Winn and Reichley, '85). Lack of barnacles between tubercles as observed in this study indirectly supports a hypothesis of flow modification by the tubercles where water is channeled at high speeds.

Swimming pattern

Humpback whale flippers may be used for swimming by rowing and sculling (Edel and Winn, '78). These swimming modes, however, are confined to slow movements and positional changes (Edel and Winn, '78).

Observations of swimming performance by humpback whales show them to be highly maneuverable (Tomilin, '57; Nishiwaki, '72), using the extremely mobile flippers for banking and turning (Edel and Winn, '78; Madsen and Herman, 780). This maneuverability is associated particularly with the feeding behavior of humpback whales. These whales feed on patches of plankton or fish schools including euphausiids, herring, and capelin (Jurasz and Jurasz, '79; Winn and Reichley, '85; Dolphin, '88). Although the elongate flippers have been observed in scooping prey into the mouth, this method is uncommon (Howell, '30; Jurasz and Jurasz, '79). Swimming is more widely used in feeding employed in

conjunction with lunging and bubbling behaviors (Hain et al., '82).

In lunge feeding, whales rush (approximately 2.6 m/s) toward their prey from below while swimming up to the water surface at a 30°-90° angle (Jurasz and Jurasz, '79; Hain et al., '82). In "inside loop" behavior, the whale swims away rapidly from the prey aggregate with its flippers abducted and protracted (Edel and Winn, '78), then rolls 180° making a sharp U-turn ("inside loop"), and lunges toward the prey (Hain et al., '82). The entire "inside loop" maneuver is executed in 1.5–2 body lengths of the whale. Rapid turning maneuvers are required also for "flick feeding" which is performed in approximately 3 s (Jurasz and Jurasz, '79).

In "bubbling" behaviors, underwater exhalations from the blowhole produce bubble clouds or columns which concentrate the prey (Winn and Reichley, '85). Columns of bubbles arranged as rows, semicircles, and complete circles form "bubble nets" (Jurasz and Jurasz, '79; Hain et al., '82). Bubble nets are produced as the whale swims toward the surface in a circular pattern from a depth of 3-5 m. At completion of the bubble net, the whale pivots with its flippers and then banks to the inside as it turns sharply into and through the center of the net (Ingebrigtsen, '29; Hain et al., '82). Bubble net size varies from a minimum diameter of 1.5 m for corralling euphausiids to a maximum diameter of 50 m to capture herring (Jurasz and Jurasz,

The turning radius (R) achieved by the humpback whale flippers alone can be found by setting the centripetal force acting on the whale equal to the lift force generated by the flippers (Howland, '74; Weihs, '81). Using equation 2 of Weihs ('81), $R = m_v/0.5 \rho \ A \ C_L$ sin φ, where m_v is the whale's virtual mass, A is total planar area of the flippers (2.04 m²), C_L is maximum lift coefficient (1.3), and ϕ is the bank angle (Alexander, '83). Turning radius is speed independent, because both centripetal and lift forces scale with the square of speed. Assuming neutral buoyancy, m_v equals the sum of the whale's mass and the whale's mass times an added mass coefficient (0.082 for a 4:1 spheroid; Vogel, '81). From data on mysticete whales (Tomilin, '57; Wahrenbrock et al., '74; Sumich, '83; Winn and Reichley, '85; Bose et al., '90; Curren, '92), the mass of a 9-m whale was estimated as 9231 kg. According to the above equation, the whale's minimum turning radius equals 7.4 m when ϕ equals 90°. The calculated minimum turning radius falls between the minimum and maximum radii for turns during bubbling behaviors (Jurasz and Jurasz, '79). Maximum bubble net radius (25 m) may be achieved by the humpback whale with ϕ of

745°. Considering that other surfaces of the whale (e.g., flukes, peduncle, body) are employed in turns (Edel and Winn, '78), the actual minimum turning radius is assumed to be smaller. Fluke span is 27–38% of total body length (True, '83; Tomilin, '57). The relatively large size of the flukes would contribute to maneuverability by increasing the lift force. However, the restricted range of motion of flukes and body in conjunction with their use in thrust production limits their effectiveness to control maneuverability during powered swimming.

The plankton-feeding behavior of other baleen whales is different from that of the humpback whale. Whales of the Balaenopteridae, exclusive of the humpback, swim rapidly forward and engulf prey-laden water (Ridgway and Harrison, '85). Whales of the Balaenidae swim slowly and use their elongate baleen to skim the water surface for food (Burns et al., '93). For both families, the typical feeding behavior is to swim rectilinearly with little maneuvering. Differences in feeding behaviors and swimming patterns are reflected morphologically by the relatively smaller size of the flippers of baleen whales compared to the humpback whale. The feeding behavior of humpbacks is considered more energetically demanding than the skim feeding of bowhead whales (Balaena mysticetus) (Dolphin, '87). However, faster swimming and individual foraging by finback whales (Balaenoptera physalus) was suggested by Whitehead and Carlson ('88) to be less advantageous for feeding success than maneuverability by groups of humpback whales.

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LITERATURE CITED

Abbott, I.H., and A.E. von Doenhoff (1949) Theory of Wing Sections. New York: Dover Publ.

Alexander, R.M. (1983) Animal Mechanics. Oxford: Blackwell Scientific Publ.

Blake, R.W. (1983) Fish Locomotion. Cambridge: Cambridge University Press.

Bose, N., J. Lien, and J. Ahia (1990) Measurements of the bodies and flukes of several cetacean species. Proc. R. Soc. Lond. [Biol.] 242:163-173.

Brodie, P.F. (1977) Form, function and energetics of cetacea: a discussion. In R.J. Harrison (ed): Functional Anatomy of Marine Mammals, Vol. 3. London: Academic Press, pp. 45–58.

Burns, J.J., J.J. Montague, and C.J. Cowles (1993) The Bowhead Whale. Special Publication Number 2: The Society for Marine Mammalogy.

Bushnell, D.M., and K.J. Moore (1991) Drag reduction in nature. Annu. Rev. Fluid Mech. 23:65-79.

Crisp, D.J. (1955) The behaviour of barnacle cyprids in relation to water movement over a surface. J. Exp. Biol. 32:569–590.

Crisp, D.J., and H.G. Stubbings (1957) The orientation of barnacles to water currents. J. Anim. Ecol. 26:179– 196.

Curren, K.C. (1992) Designs for swimming: morphometrics and swimming dynamics of several cetacean species. M.S. Thesis. Memorial University of Newfoundland.

Dolphin, W.F. (1987) Ventilation and dive patterns of humpback whales, Megaptera novaeangliae, on their Alaskan feeding grounds. Can. J. Zool., 65:83-90.

Dolphin, W.F. (1988) Foraging dive patterns of hump-back whales, Megaptera novaeangliae, in southeast Alaska: cost-benefit analysis. Can J. Zool. 66:2432-2441.

Edel, R.K., and H.E. Winn (1978) Observations on underwater locomotion and flipper movement of the hump-back whale Megaptera novaeangliae. Mar. Biol. 48:279–287

Evans, P.G.H. (1987) The Natural History of Whales & Dolphins. New York: Facts On File.

Felts, W.J.L. (1966) Some functional and structural characteristics of cetacean flippers and flukes. In K.S. Norris (ed): Whales, Dolphins, and Porpoises. Berkeley: University of California Press, pp. 255–276.

Fish, F.E., and C.A. Hui (1991) Dolphin swimming—a review. Mamm. Rev. 21:181-195.

Godfrey, S.J. (1985) Additional observations of subaquaeous locomotion in the California sea lion (Zalophus californianus). Aqu. Mamm. 11.2:53-57.

Hain, J.H.W., G.R. Carter, S.D. Kraus, C.A. Mayo, and H.E. Winn (1982) Feeding behavior of the humpback whale, Megaptera novaeangliae, in the western North Atlantic. Fish. Bull. 80:259-268.

Hoerner, S.F. (1965) Fluid-Dynamic Drag. Brick Town, NJ: Published by author.

Hopkins, E.J. (1951) Lift, pitching moment, and span load characteristics of wings at low speed as affected by variations of sweep and aspect ratio. NACA Tech. Note 2284.

Howell, A.B. (1930) Aquatic Mammals. New York: Dover Publ.

Howland, H.C. (1974) Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. J. Theor. Biol. 47:333-350. Hui, C.A. (1985) Maneuverability of the Humboldt penguin (Spheniscus humboldti) during swimming. Can. J. Zool. 63:2165-2167.

Hurt, H.H., Jr. (1965) Aerodynamics for Naval Aviators. The Office of the Chief of Naval Operations Aviation Training Division, U.S. Navy. NAVWEPS 00-80T-80.

Ingebrigtsen, A. (1929) Whales caught in the North Atlantic and other seas. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 56:1-26.

Jurasz, C.M., and V.P. Jurasz (1979) Feeding modes of the humpback whale, Megaptera novaeangliae, in southeast Alaska. Sci. Rep. Whales Res. Inst. 31:69-83 Lambie, J. (1984) Composite Construction for Homebuilt

Aircraft. Hummelstown, PA: Aviation Publ.

Lang, T.G. (1966) Hydrodynamic analysis of dolphin fin

profiles. Nature 209:1110-1111. Leatherwood, S., R.R. Reeves, W. Perrin, and W.E. Evans (1988) Whales, Dolphins, and Porpoises of the Eastern North Pacific and Adjacent Arctic Waters: A Guide to Their Identification. New York: Dover.

Lewis, C.A. (1978) A review of substratum selection in free-living and symbiotic cirripeds. In F.-S. Chia and M.E. Rice (eds): Settlement and Metamorphosis of Marine Invertebrate Larvae. New York: Elsevier, pp.

Lighthill, J. (1977) Introduction to the scaling of aerial locomotion. In T.J. Pedley (ed.): Scale Effects in Animal Locomotion. London: Academic Press. pp. 365-

Madsen, C.J., and L.M. Herman (1980) Social and ecological correlates of cetacean vision and visual appearance. In L.M. Herman (ed): Cetacean Behavior: Mechanisms & Functions. Malabar, FL: R.E. Krieger Publ. pp.

Nishiwaki, M. (1972) General biology. In S.H. Ridgway (ed): Mammals of the Sea: Biology and Medicine. Spring-

field, IL. C.C. Thomas, pp. 3-204. Norberg, U.M. (1990) Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution. Ber-

lin: Springer-Verlag. Perkins, J., and H. Whitehead (1977) Observations on three species of baleen whales off northern Newfoundland and adjacent waters. J. Fish. Res. Bd. Can. 34: 1436-1440.

Ridgway, S.H., and R. Harrison (1985) Handbook of Marine Mammals, Vol. 3: The Sirenians and Baleen Whales. London: Academic Press.

Scholander, P.F., and W.E. Schevill (1955) Countercurrent vascular heat exchange in the fins of whales. J. Appl. Physiol. 8:270-282.

Shevell, R.S. (1986) Aerodynamic anomalies: Can CFD prevent or correct them? J. Aircraft 23:641-649.

Streeter, V.L. (1966) Fluid Mechanics, Ed. 4. New York: McGraw-Hill.

Sumich, J.L. (1983) Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, Eschrichtius robustus. Can J. Zool. 61:647-

Tomilin, A.G. (1957) Mammals of the U.S.S.R. and Adjacent Countries. Vol. IX: Cetacea. Moscow: Nauk S.S.S.R. (English Translation, 1967, Israel Program for Scientific Translations, Jerusalem).

True, F.W. (1983) The Whalebone Whales of the Western North Atlantic. Washington, DC: Smithsonian Institution Press.

Tyack, P. (1981) Interactions between singing Hawaiian humpbacks and conspecifics nearby. Behav. Ecol. Sociobiol. 8:105-116.

van Dam, C.P. (1987) Efficiency characteristics of crescent-shaped wings and caudal fins. Nature 325:435-

Vogel, S. (1981) Life in Moving Fluids. Boston: Willard Grant Press.

von Mises, R. (1945) Theory of Flight. New York: Dover

Wahrenbrock, E.A., G.F. Maruschak, R. Elsner, and D.W. Kenney (1974) Respiration and metabolism in two baleen whale calves. Mar. Fish. Rev. 36:3-9.

Webb, P.W. (1975) Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd. Can. 190:1-159.

Weihs, D. (1981) Effects of swimming path curvature on the energetics of fish swimming. Fish. Bull. 79:171-176.

Weihs, D. (1993) Stability of aquatic animal locomotion. Cont. Math. 141:443-461.

Whitehead, H., and C. Carlson (1988) Social behaviour of feeding finback whales off Newfoundland: comparisons with the sympatric humpback whale. Can. J. Zool. 66:217-221.

Winn, H.E., and N.E. Reichley (1985) Humpback whale Megaptera novaeangliae (Borowski, 1781). În S.H. Ridgway, and R. Harrison (eds): Handbook of Marine Mammals, Vol. 3: The Sirenians and Baleen Whales. London: Academic Press, pp. 241-273

Winn, L.K., and H.E. Winn (1985) Wings in the Sea: The Humpback Whale. Hanover: University Press of New

England.

Wu, J.Z., A.D. Vakili, and J.M. Wu (1991) Review of the physics of enhancing vortex lift by unsteady excitation. Prog. Aerospace Sci. 28:73-131.