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Three-dimensional geometry of the narwhal (*Monodon monoceros*) flukes in relation to hydrodynamics

JANET E. FONTANELLA

FRANK E. FISH¹

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

NATALIA RYBCZYNSKI

Canadian Museum of Nature,
Ottawa, Ontario K1P 6P4, Canada

MARTIN T. NWEEDIA

Harvard University,
School of Dental Medicine,
Boston, Massachusetts 02115, U.S.A.
and
Smithsonian Institution,
Washington, D.C. 20227, U.S.A.

DARLENE R. KETTEN

Biology Department,
Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543, U.S.A.
and
Department of Otology and Laryngology,
Harvard Medical School,
Boston, Massachusetts 02114, U.S.A.

Cetaceans (whales, porpoises, and dolphins) use only their flukes for propulsion. Flukes are distally located extensions of the tail, and from a biomechanical standpoint, function as a pair of wings (Vogel 1994). Flukes function to produce thrust generated as an anteriorly directed lift force as flukes oscillate vertically (Fish 1998*a, b*). Their cross-sections resemble hydrofoils. For a hydrofoil to be effective, a large lift must be produced while drag is minimized; this, in turn, increases the thrust generated (Weihs 1989, Vogel 1994).

The hydrodynamic implications of fluke design can be studied by examining the cross-sections (*i.e.*, parasagittal) of the flukes. Cross-section profiles taken along the horizontal axis exhibit what is a typical streamlined hydrofoil profile with a rounded leading edge and a long, tapered trailing edge. This shape is critical for the generation of lift for thrust, while minimizing induced drag (*i.e.*, drag due to lift production;

¹ Author to whom correspondence should be sent.

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Lighthill 1970, Vogel 1994). The flukes are symmetrical about the chord (Lang 1966, Bose *et al.* 1990). The cross-sectional profile of the flukes is similar to symmetrical engineered foils (Fish 1998*b*). The similarity to engineered foils would imply that cetacean flukes would be capable of effectively generating large lift with low drag at higher angles of attack.

The typical planform shape of cetacean flukes is characterized as a tapered wing with sweepback (*i.e.*, rearward inclination of the leading edge). Such a wing shape can achieve improved efficiency by reducing induced drag by 8.8% compared to a wing with an elliptical planform (van Dam 1987). Minimal induced drag occurs in swept wings with a triangular planform approximating the design of most cetacean flukes (Chopra and Kambe 1977, Fish 1998*b*). Aspect ratio (*AR*) measures the relationship between the span and planform area of a hydrofoil and is related to the effectiveness of the hydrofoil's design. A low *AR* is characterized as a short, broad wing, whereas a high *AR* wing is long and narrow. A combination of low sweep with high *AR* allows for high-efficiency rapid swimming, whereas high sweep may compensate for the reduced lift production of low-*AR* flukes (Azuma 1983, Liu and Bose 1993). Highly swept, low-*AR* wings produce maximum lift when operating at high angles of attack, when low-sweep, high-*AR* designs would fail (Hurt 1965). This feature aids in the maintenance of high efficiency at slow, sustained speeds (Magnuson 1978), as observed in *Monodon monoceros*, the narwhal. In general, narwhals are regarded as very slow swimmers that seldom exceed speeds of 1.7 m/s (Minasian *et al.* 1984). Although increasing efficiency, the high sweep angle will reduce thrust. Maintenance of thrust would be facilitated by a higher *AR* hydrofoil planform.

The external morphology of flukes is generally considered constant among the Cetacea. An acute departure from the typical fluke shape is found in the narwhal. Narwhals are regionally circumscribed cetaceans that inhabit the Atlantic sector of the Arctic Ocean (Heide-Jørgensen 2009). They are widely distributed in the ice-packed stretches of waters bordering Greenland and the Canadian High Arctic (Laidre *et al.* 2003). The flukes of mature male narwhals have a slightly concave leading edge without sweepback (Fig. 1; Hay and Mansfield 1989). A female narwhal generally has a fluke very similar in shape to that of a dolphin, which is swept back (Fig. 1). Whether or not the differing fluke morphology is an evolved adaptation that coincides with the long, tapering tusk present on most males is unknown (Fish *et al.* 2007).

In this study, we compared the fluke geometries of male and female narwhals, which may be associated with hydrodynamic effects. Computerized tomography (CT) scanning was used to obtain data for analyses of the three-dimensional geometry of the flukes.

The flukes from four narwhals (two males and two females) were obtained from aboriginal hunters in the vicinity of Broughton Island, Canada. The body lengths of the animals ranged from 2.98 to 3.60 m (Table 1). Both males had erupted, upper left tusks. Standard body measurements were made including the span of the fluke (*i.e.*, linear distance between fluke tips).

The flukes were frozen and shipped to the Canadian Museum of Nature (CMN) in Ottawa, Canada. The frozen flukes were later transported to the Woods Hole

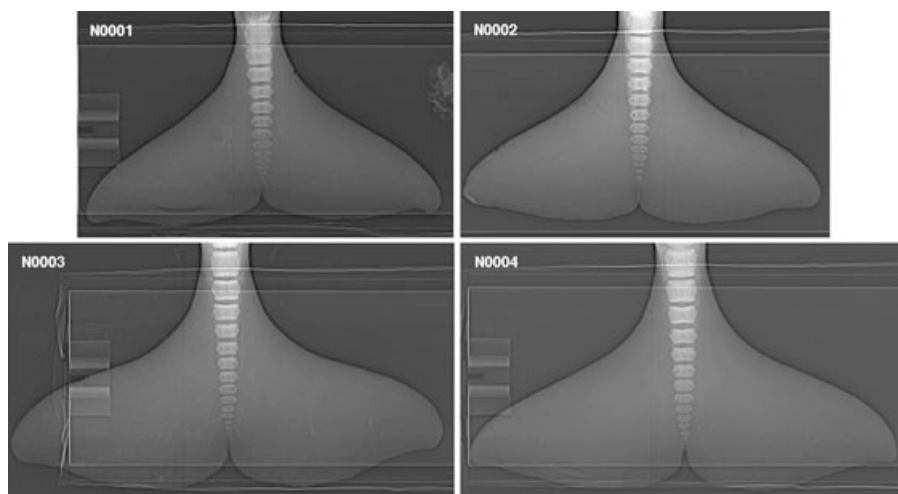


Figure 1. CT topograms illustrating the differences between female (N0001, N0002) and male (N0003, N0004) fluke planforms.

Oceanographic Institution CT imaging facility for scanning. The flukes were placed flat, dorsal side up, on the scanner table, stabilized with plastic wedges and Styrofoam sheets, and scanned tip to tip with span-wise parasagittal cross-sections.

CT scans were obtained on a Siemens Volume Zoom CT scanner. Spiral protocols for data acquisition with 0.5–1.0 mm detector collimation at 1 mm/s table feeds were used. All images were reconstructed in both soft tissue and ultra-high resolution kernels with extended attenuation scales to improve discrimination of high-density elements. Images were obtained in DICOM formats, and for some data, were reconstructed at 100 μ slice intervals that provide 100 μ isotropic voxels needed for finer grain structural analyses. With these parameters, the maximum in-plane resolution was 0.35 mm at 2% of the modulation transfer function. Prior studies suggest 25 μ in-plane pixel resolutions are possible, but a conservative nominal resolution is 50 μ .

Because true data base magnifications cannot be obtained from enlargements of processed image files, raw attenuation data were archived onto magneto-optical disks for all scans in order to allow additional post-scan processing as needed. Image files were archived in DICOM format and 512 matrices on CD. The DICOM images

Table 1. Morphometrics of fluke planforms.

Specimen	Sex	Body length (m)	Fluke span (m)	Planform area (m ²)	Aspect ratio	Sweepback angle	Tusk length (m)
N0001	F	3.09	0.71	0.13	3.88	33.7°	N.A.
N0002	F	2.98	0.70	0.13	3.63	29.0°	N.A.
N0003	M	3.60	0.87	0.19	3.90	16.8°	1.00
N0004	M	3.57	0.85	0.19	3.86	24.2°	0.44

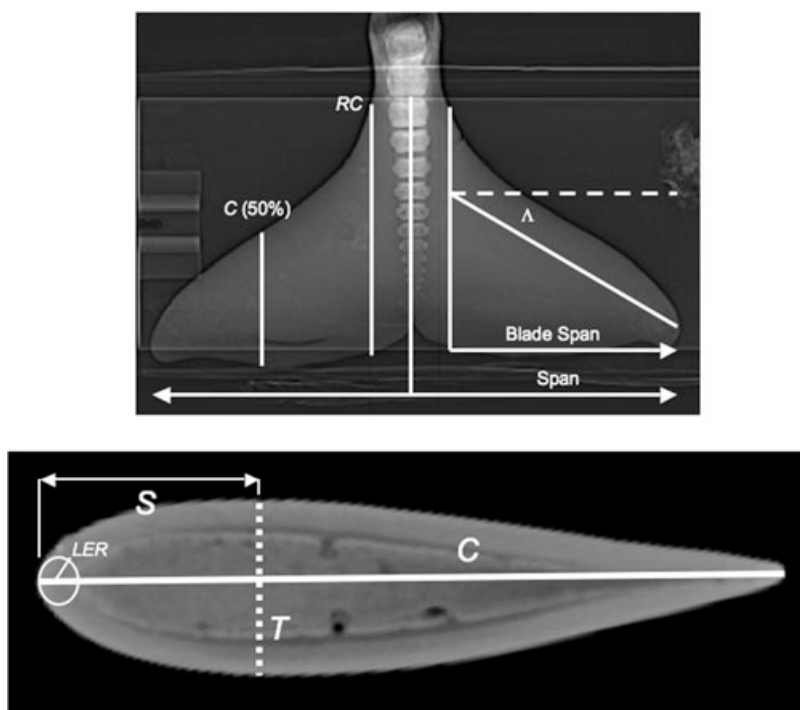


Figure 2. Planform and sectional fluke dimensions. The upper figure shows a fluke planform. The vertical solid lines show the root chords (RC) and the chord (C) at 50% of the blade span. The blade span extends horizontally from RC to the fluke tip and the span is the horizontal distance between fluke tips. The sweep angle (Δ) is the angle subtended from a line at the 25% of RC and the horizontal dashed line. The lower figure shows a CT image of a fluke section. The horizontal line (C) illustrates the chord at 50% of blade span, the dashed vertical line is the maximum thickness (T), and the distance from the leading edge to the maximum thickness is the shoulder (S). The line within the circle indicates the LER that is determined from the radius of the white circle that connects tangent points of the leading edge with the upper and lower surfaces of the section.

of fluke cross-sections were analyzed using OsiriX (OsiriX Foundation, Geneva, Switzerland, version 2.7.5). A total of 2,715 fluke cross-sections were examined for all four specimens; this figure excludes the tailstock cross-sections, for which leading and trailing edges of the flukes were not visible.

Measurements of the fluke planforms (Fig. 2) included the span (FS , distance from fluke tip to fluke tip), fluke blade span (BS , distance from root fluke chord; RC , to tip of fluke), planform area (F_a , total planar area of flukes on the dorsal surface), and sweepback (Δ). RC is the chord at the intersection of the fluke blade and the tailstock. The sweepback was measured as the angle between a line extending from 25% of the fluke chord extending from the cranial end of RC and to the maximum lateral extension of the fluke tip and a line perpendicular to RC (Hurt 1965; Fish 1998a, b). The AR of each fluke was calculated as FS^2/F_a .

Measurements of fluke sections for each CT slice (Fig. 2) were made for the chord length (C), maximum thickness (T), shoulder (S), and leading edge radius (LER) (Fish *et al.* 2006, 2007). C was measured as the linear distance from the leading to trailing edge of the fluke. T was the maximum vertical distance between the upper and lower side of the fluke perpendicular to the chord line. S was measured as the distance from the leading edge to the maximum thickness line. For comparison of narwhals of different sizes, C , T , and S measurements were presented as a percentage of BS , starting at 0% at RC to 100% at the fluke tip. LER was the radius of the curvature of the leading edge as determined from the radius of a circle that connects tangential points of the leading edge and the upper and lower surfaces of the cross-section (Hurt 1965). A circle template was used on images taken at 50% of the BS on the two flukes for each individual narwhal to determine radius of the leading edge. LER was presented as a proportion of C (Fish *et al.* 2007).

The thickness ratio ($TR = T/C$) and shoulder position ($SP = S/C$) of each cross section were used as indicators of flow structure and the hydrodynamic performance relating to the generation of lift and drag for foils (von Mises 1945, Hoerner 1965).

Microsoft Excel 2004 and KaleidaGraph (Synergy Software, version 4.03) were used to statistically and graphically analyze the data collected. Because of differences in fluke sizes of the individual narwhals, comparisons were made using means (± 1 standard deviation). The linear measurements from each CT slice (C , T , S) were averaged for the corresponding slice for each fluke blade for an individual animal. The mean values of each measurement and morphological parameter were calculated for each sex. The small sample size precluded statistical analysis beyond descriptive statistics.

The FS and F_a were both greater for the male narwhals, due to their larger size. The calculated values for AR did not show significant differences for male and female narwhals. The main difference was the difference in Λ between the sexes (Table 1, Fig. 1). Females had a mean sweepback angle of 31.4 ± 3.3 degrees and males had a mean sweepback angle of 20.5 ± 5.2 degrees.

It was noted that male N0004 was slightly immature, judging by its overall smaller body size and tusk and the fluke morphology was slightly swept back. Measurements of the S for female N0001 were lower than expected at approximately 15% of span (Fig. 3, 5) because of depressions on the ventral side of the cross-sections.

For both sexes, the fluke cross-sections were highly streamlined, having a rounded leading edge and a tapering, trailing edge; fluke sections were also symmetrical about the chord (Fig. 2). Both right and left fluke blades were apparently symmetrical. From the root of the fluke, C , T , and S showed an approximately linear decrease to about 95% of span in which these measurements decreased more rapidly toward the tip (Fig. 3). Differences between male and female narwhals for C , T , and S were only observed near the fluke root. Interestingly, there was no discernable difference in sectional values for C between males and females despite the difference in Λ (Fig. 3).

TR decreased proximally toward the tailstock (Fig. 4). The maximum values of TR occurred at the fluke tip. Over the fluke span, males had a mean TR of 0.23 ± 0.02 , whereas the females had a mean TR of 0.24 ± 0.02 . Differences in TR between

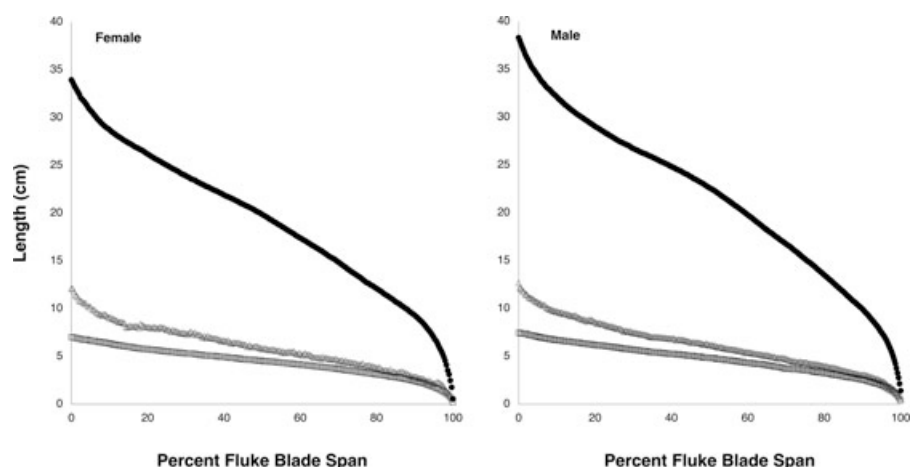


Figure 3. Linear measurements of male and female flukes of the chord (*C*, solid circles), maximum thickness (*T*, open squares) and shoulder (*S*, open triangles) as a percentage of the fluke blade span, where 0% is at the RC and 100% is at the fluke tip.

male and female narwhals were apparent from 20% to 90% of *BS*. Within this range, *TR* for females was 5% greater than for the males.

SP had a U-shaped distribution along the fluke blade span with the highest values at the tip and root of the flukes and lowest at approximately mid-span (Fig. 5). Between 20% and 65% of span, males and females had means for *SP* of 0.28 ± 0.00 and 0.30 ± 0.01 , respectively. Over this range of span the females averaged a 10% greater *SP* than males.

No apparent difference of *LER* was found between males and females. Mean *LER* values were 0.05 ± 0.01 and 0.05 ± 0.00 for males and females, respectively.

The general morphology of cetacean flukes influences the requirements of energy for swimming. A highly streamlined fluke is characterized by the symmetrical nature of the cross-sections in the sagittal plane. A rounded leading edge and a tapering, trailing edge are characteristics shown in the cross-sections that are fundamental in the generation of lift, while also reducing drag (Webb 1975, Vogel 1994).

The parameters *TR* and *SP* influence the pressure distribution of flow over the surface of the flukes. A favorable gradient has pressure decreasing in the downstream direction, which aids in flow over the fluke surface. An unfavorable gradient has pressure increasing in the downstream direction. This ultimately delays the flow over the fluke's surface. The favorable and unfavorable pressure gradients are located upstream and downstream of *SP*, respectively (Fish *et al.* 2007). An increase in drag results from an unfavorable pressure gradient, because flow will tend to separate from the fluke surface (Webb 1975, Vogel 1994). Thrust increases with lift until a critical point when the fluke stalls due to the separation of flow from the surface. Thus, the displacement of the *SP* further downstream on the fluke section impedes the separation of flow by extending the favorable pressure gradient. However, downstream displacement of *SP* will foster separation, particularly when the section is canted

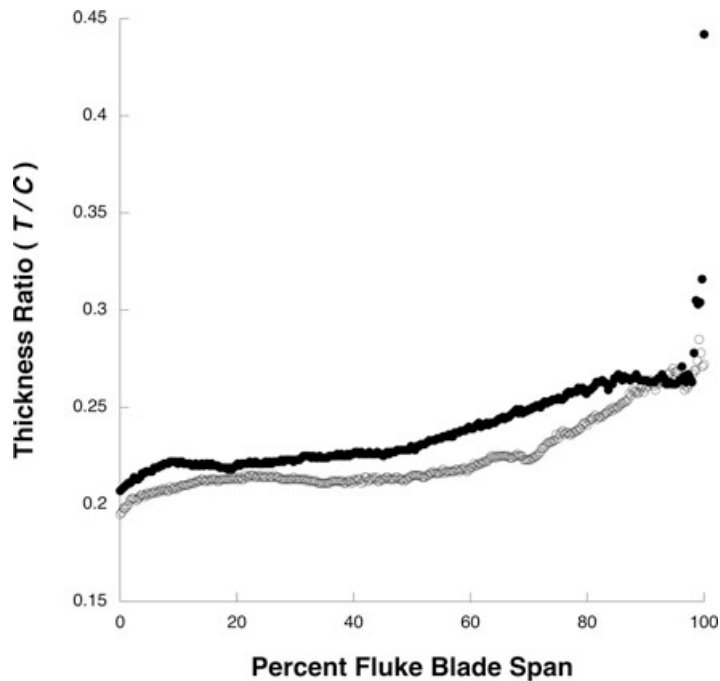


Figure 4. TR as a function of fluke blade span for male (open circles) and female (solid circles) narwhals.

at an angle to the flow. Mean SP values ranged from 0.29 to 0.38 for females and male values ranged from 0.27 to 0.36. Female narwhals had a higher SP than male narwhals (Fig. 5), indicating that SP was placed further downstream on the fluke section.

Male narwhals had lower TR values when compared to female narwhals. Average TR values for male narwhals ranged from 0.195 to 0.285, while female narwhals ranged from 0.207 to 0.442. Streamlined foil sections have lower drags with low TR values than high TR foils (Abbott and von Doenhoff 1959). Low TR foils have a small pressure gradient magnitude, which reduces drag (Fish *et al.* 2007). Conversely, as the TR values increase, as observed in female narwhals, lift is enhanced and stall is delayed. This hydrodynamic performance would be possible because the shape of the cross-section would allow the flow of water to move smoothly over the fluke surface. Similarly, a high SP value leads to delayed stall. Consequently, it would appear that the flukes of male narwhals have a hydrodynamic advantage in reducing drag; however, the cross-sectional design of the flukes of female narwhals would tend to increase lift and delay stall.

Other limiting factors of induced drag include the sweep of a fluke (Fish 1998*b*). Female narwhals have a greater sweepback in fluke planform compared to males. Sweepback of a wing or hydrofoil can reduce the induced drag (*i.e.*, drag due to lift) by as much as 8.8% compared to a wing without sweepback (van Dam 1987).

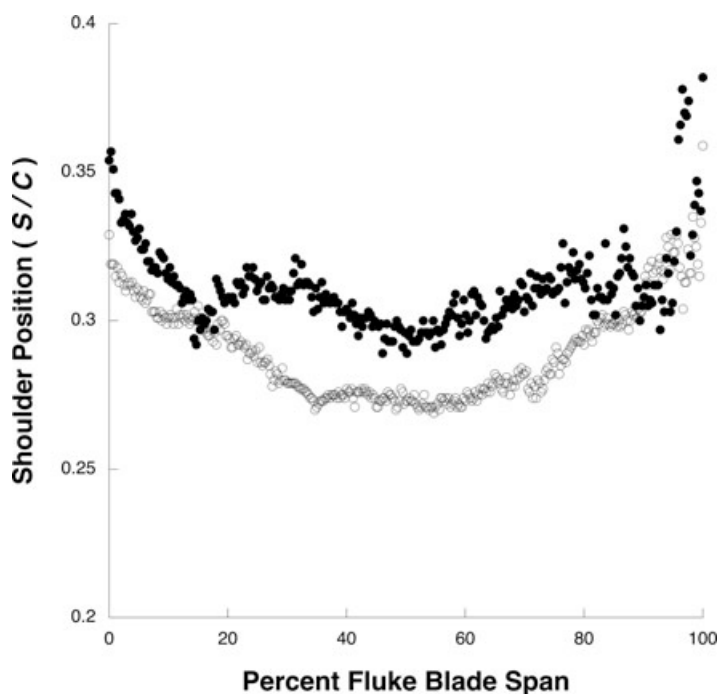


Figure 5. *SP* of male (open circles) and female (solid circles) narwhals as a function of fluke blade span.

Swept back wings produce maximum lift generation at high angles of attack (Fish 1998*b*). This would be advantageous particularly at low swimming speeds when the angle of attack of the flukes is high (Fish 1993). However, low sweep angles allow for high-efficiency, rapid swimming (Azuma 1983). Based on this information, it is deduced that females would have increased lift but at low swimming speeds, whereas males would have high efficiency at higher swimming speeds.

The hydrodynamic effects produced from differences in the geometries of the flukes, which were stated above, are largely associated with steady flow conditions. The flukes of cetaceans are oscillated incurring the dominance of unsteady flow conditions (Webb 1975; Fish 1993, 1998*a*). Unsteady effects can incur lower lift than for steady motion (Lighthill 1970). Further analysis of narwhal fluke geometry would require examination of unsteady effects, although results based on steady flow conditions can provide an indication of differences in hydrodynamic performance.

The differences in fluke design between the sexes of narwhals could have hydrodynamic consequences associated with swimming performance. No differences in swimming speeds between male and female narwhals have been reported, when transiting between locations as during migrations (Dietz and Heide-Jørgensen 1995, Dietz *et al.* 2001; Heide-Jørgensen *et al.* 2002, 2003). However, Laidre *et al.* (2003) found that female narwhals made more dives to deeper depths than males. Deeper destination depths were related to increased swimming speed (Laidre *et al.* 2003),

indicating that at least during foraging dives, females could be swimming faster than males. The design of the flukes of females, thus, may be associated with the need to transit to greater depths at fast speed. For males, the increased lift and concomitant thrust production from the low sweepback fluke design may aid in compensating for the increased drag that might accompany the possession of the elongate tusk. Swimming performance by narwhals (*i.e.*, overcoming drag, swimming speed) is associated with the hydrodynamically complex and conflicting relationships of lift and thrust production, reduction in drag, delay in stall, and efficiency, which are dependent on the fluke geometry and kinematics.

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LITERATURE CITED

- Abbott, I. H., and A. E. von Doenhoff. 1959. Theory of wing sections. Dover, Mineola, NY.
- Azuma, A. 1983. Biomechanical aspects of animal flying and swimming. Pages 35–53 in H. Matsui and K. Kobayashi, eds. Biomechanics VIII-A. International Series on Biomechanics, Volume 4A. Human Kinetics Publishers, Champaign, IL.
- Bose, N., J. Lien and J. Ahia. 1990. Measurements of the bodies and flukes of several cetacean species. Proceedings of the Royal Society of London B 242:163–173.
- Chopra, M. G., and T. Kambe. 1977. Hydrodynamics of lunate-tail swimming propulsion. Part 2. Journal of Fluid Mechanics 79:49–69.
- Dietz, R., and M. P. Heide-Jørgensen. 1995. Movements and swimming speed of narwhals (*Monodon monoceros*) instrumented with satellite transmitters in Melville Bay, Northwest Greenland. Canadian Journal of Zoology 73:2106–2119.
- Dietz, R., M. P. Heide-Jørgensen, P. Richard, and M. Acquarone. 2001. Summer and fall movements of narwhals (*Monodon monoceros*) from northeastern Baffin Island towards northern Davis Strait. Arctic 54:246–263.
- 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. 1998a. Comparative kinematics and hydrodynamics of odontocete cetaceans: Morphological and ecological correlates with swimming performance. Journal of Experimental Biology 201:2867–2877.
- Fish, F. E. 1998b. Biomechanical perspective on the origin of cetacean flukes. Pages 303–324 in J. Thewissen, ed. The emergence of whales: Evolutionary patterns in the origin of Cetacea. Plenum Press, New York, NY.
- Fish, F. E., M. K. Nusbaum, J. T. Beneski and D. R. Ketten. 2006. Passive cambering and flexible propulsors: Cetacean flukes. Bioinspiration and Biomimetics 1:S42–S48.

- Fish, F. E., J. T. Beneski and D. R. Ketten. 2007. Examination of the three-dimensional geometry of cetacean flukes using computed tomography scans: Hydrodynamic implications. *The Anatomical Record* 290:614–623.
- Hay, K., and A. Mansfield. 1989. Narwhal *Monodon monoceros* Linnaeus, 1758. Pages 145–176 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Volume 4. Academic Press, San Diego, CA.
- Heide-Jørgensen, M. P. 2009. Narwhal, *Monodon monoceros*. Pages 754–758 in W. F. Perrin, J. G. M. Thewissen and B. Würsig, eds. *Encyclopedia of marine mammals*. Elsevier, San Diego, CA.
- Heide-Jørgensen, M. P., R. Dietz, K. L. Laidre and P. Richard. 2002. Autumn movements, home ranges, and winter density of narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island. *Polar Biology* 25:331–341.
- Heide-Jørgensen, M. P., R. Dietz, K. L. Laidre, P. Richard, J. Orr and H. C. Schmidt. 2003. The migratory behaviour of narwhals (*Monodon monoceros*). *Canadian Journal of Zoology* 81:1298–1305.
- Hoerner, S. 1965. Fluid-dynamic drag. Published by author, Brick Town, NJ.
- Hurt, H., Jr. 1965. Aerodynamics for naval aviators. US Navy, NAV-WEPS 00-80T-80. Department of the Navy, Washington, DC.
- Laidre, K. L., M. P. Heide-Jørgensen, R. Dietz, R. C. Hobbs and O. A. Jørgensen. 2003. Deep-diving by narwhals *Monodon monoceros*: Differences in foraging behavior between wintering areas? *Marine Ecology Progress Series* 261:269–281.
- Lang, T. 1966. Hydrodynamic analysis of dolphin fin profiles. *Nature* 209:1110–1111.
- Lighthill, J. 1970. Aquatic animal propulsion of high hydromechanical efficiency. *Journal of Fluid Mechanics* 44:265–301.
- Liu, P., and N. Bose. 1993. Propulsive performance of three naturally occurring oscillating propeller planforms. *Ocean Engineering* 20:57–75.
- Magnuson, J. J. 1978. Locomotion by scombrid fishes: Hydrodynamics, morphology and behaviour. Pages 239–313 in W. S. Hoar and D. J. Randall, eds. *Fish physiology*. Volume 7. Academic Press, London, UK.
- Minasian, S. M., K. C. Balcomb and L. Foster. 1984. *The world's whales*. Smithsonian Books, Washington, DC.
- van Dam, C. P. 1987. Efficiency characteristics of crescent-shaped wings and caudal fins. *Nature* 325:435–437.
- Vogel, S. 1994. *Life in moving fluids*. Princeton University Press, Princeton, NJ.
- von Mises, R. 1945. *Theory of flight*. Dover Publishers, Mineola, NY.
- Webb, P. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada* 190:1–158.
- Weih, D. 1989. Design features and mechanics of axial locomotion in fish. *American Zoologist* 29:151–160.

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