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Hydrodynamic patterns associated with echelon formation swimming by feeding bowhead whales (*Balaena mysticetus*)

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Various species of animals organize into defined aggregates while traveling (*e.g.*, schools, pods, flocks, queues, herds, swarms). The suggested functions of these social groupings include sharing information, aero/hydro-dynamic efficiency, antipredator tactics, increased probability of finding mates, and increased foraging efficiency (Shaw 1978, Partridge *et al.* 1983, Fish 1999). Prey herding is not uncommon among cetaceans, such as humpbacks feeding on euphasiids (Heithaus and Dill 2002). Certain locomotor aggregates are arranged as highly structured formations, whereby individuals are oriented in the same direction, maintain a defined spacing and are organized in discrete patterns. For example, tuna swimming together can be arranged in a parabolic shape and in an elongate diamond formation to take advantage of hydrodynamic effects (Weihs 1973, Partridge *et al.* 1983).

Large groups of cetaceans have been observed swimming in side-by-side and echelon formations (Norris and Prescott 1961, Leatherwood and Walker 1979, Norris and Johnson 1994). In addition, bowhead whales (*Balaena mysticetus*) and southern right whales (*Eubalaena australis*) have been observed swimming in echelon formation while surface feeding (Richardson *et al.* 1985, Würsig *et al.* 1985, Würsig and Clark 1993, Landino *et al.* 1994). Bowhead whales swim in a V-formation with the trailing whales positioned laterally (Würsig *et al.* 1985). Speculation on the occurrence of echelon formations focused on feeding efficiency (Würsig *et al.* 1985, Würsig and Clark 1993). This formation is thought to allow a trailing whale to capture food that spilled from the mouth of a leading whale or to channel prey toward a trailing whale

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by having the body of a lead whale function as a “wall.” While these are plausible explanations for moving in an echelon formation when feeding, they do not take into account the hydrodynamics of swimming in a closely organized formation. The discussion below considers alternative causations for echelon swimming by bowhead whales based on hydrodynamics and aerial photographs of feeding bowhead whales.

In the summer bowhead whales feed on copepods and euphausiids in the western Beaufort Sea near Barrow, Alaska, sometimes in large groups (Lowry and Burns 1980, Würsig *et al.* 1985). Aerial photography from a NOAA Twin Otter (N56RF) was used by researchers from the National Marine Mammal Laboratory (NMML) to obtain information on residence times, feeding behavior, and age classes of whales as part of the Bowhead Whale Feeding Ecology Study (BOWFEST). A fully automated, triple-camera system (Canon EOS-1DS Mark III cameras with Zeiss 85 mm f1/4 lenses) was used for photogrammetry and photo-identification. The cameras, firing at a rate of 1.4 photos/second, were aimed out of a large belly window and held in a forward motion-compensating (FMC) mount with a rocker mechanism to counter the forward velocity of the aircraft. This system provided a photographic footprint with 20% overlap between images horizontally and 60% overlap vertically (along the flight line). Altitudes during photographic passes over whales were generally between 210 and 270 m (700–900 ft). A laser altimeter (Universal Laser Sensor) provided altitudes accurate to within a few centimeters. A calibration target was used to test the laser, radar, and GPS altimeters and provided a correction factor for whale body length estimates relative to aircraft altitude.

On 12 September 2010, BOWFEST aerial observers flew over a feeding group of more than 60 whales located 40 km east of Point Barrow in water approximately 8 m deep. This large group was observed intermittently across a period of 27 min. Individual whales were in a view for only a few seconds at a time. Many were in pairs or trios, and up to five whales were observed in an echelon formation while swimming at the surface (Fig. 1; whales numbered 1–5). The five whales swam on their sides with their right side² facing downward and mouths agape. One whale swimming just lateral and aft of the lead whale was oriented upright with its venter positioned downward. The whales were positioned in classic echelon formation, closely together, with approximately 3.4–6.2 m from the tip of one head to the tip of the following whale. Most of the whales in this formation were within touching distance with a spacing of <1 body width apart. The orientation of the whales described here was different from the whales observed by Würsig *et al.* (1985). The latter animals swam upright and maintained a distance of 0.5–3 body widths between individuals. However, one group of three whales located at the top of Figure 1, as seen during the BOWFEST survey, swam with two whales in the “normal” orientation and one whale swimming on its left side.

Boat-based sampling of hydrography and plankton was conducted in the same region near Barrow, also a part of the BOWFEST program. Data showed that upwelling-favorable winds followed by weak winds, particularly from the south-southwest, can result in large quantities of euphausiids being upwelled and then “trapped” on the Beaufort Sea shelf (Okkonen *et al.* 2011). An observation of diel vertical migration (DVM) in acoustic backscatter records in the area supported the evidence of occasional high abundance of euphausiids (Ashjian *et al.* 2010). At the time of the

²Gray whales apparently feed on the right side as well based on evidence from wear on their baleen (Kasuya and Rice 1970).



Figure 1. Aerial photograph of bowhead whales feeding in the western Beaufort Sea near Barrow, Alaska. Whales are numbered 1 through 9. Two groups of whales are observed in echelon formations with six of the nine whales (1, 2, 3, 4, 5, 7) displaying a side-swimming behavior.

sighting, the average winds were from the west-southwest at 5.3 m/s (~10 kn), creating favorable conditions for trapping large quantities of euphasiids on the Beaufort Sea shelf. Also, the clearest DVM occurred between 7 and 13 September providing further evidence of high prey abundance in the Barrow area at the time of the sighting.³

As the whales were swimming at the ocean surface at an approximated speed of 1.1–2.5 m/s (Mayo *et al.* 2001, Baumgartner and Mate 2003, Werth 2004), flow patterns were apparent. Despite moving at the water surface, surface tension would have a negligible effect on the pattern of vorticity by the whales due to the scale of the system (Vogel 1994). Analysis of Figure 2 shows four hydrodynamic patterns associated with various body parts of the whales. These hydrodynamic patterns include: (1) a prominent bow wave anterior to the mouth, (2) thrust-type vortices associated with the oscillating caudal flukes, (3) separation vortices emanating from the margins of the upper and lower jaws, and (4) channeled flow between the bodies. The presence of the hydrodynamic patterns can have bearing on feeding efficiency in concert with echelon swimming. A schematic of the hydrodynamic features is provided in Figure 3.

Bow wave (BW)—A bow wave is generated by a pressure differential between the anterior of the whale and the open water. The position of the bow wave anterior of the mouth indicates a high pressure and low flow velocity inside the oral cavity. Despite the flow-through nature of the baleen filtration apparatus in the oral cavity

³Personal communication from S. R. Okkonen, Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK, 15 October 2010.

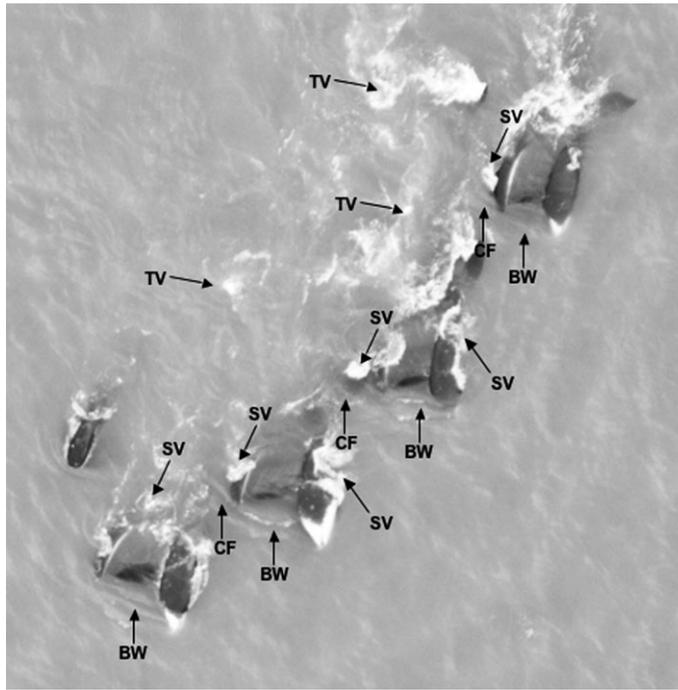


Figure 2. Close-up from Figure 1 of whales 1–4 showing hydrodynamic features associated with an echelon formation of side-swimming bowhead whales at the water surface. The hydrodynamic features include bow waves (BW), channeled flow (CF), separation vortices (SV), and thrust-type vortices (TV).

(Pivorunas 1979, Werth 2004), the pressure wave is indicative of increased resistance to flow. The rate of flow through the mouth and magnitude of the pressure differential would be dependent on the porosity of the baleen sieve.⁴ A high-pressure head at the mouth could transport prey away from the oral cavity, reducing feeding efficiency. Particularly fast swimming prey or prey near the edges of the mouth could escape. Such escape is mitigated by the forward extension of the lower jaw and lower lateral lips that could provide a barrier to escape. In addition, the high pressure in front of the head will increase the drag on the body, making swimming while feeding energetically expensive compared to swimming with the mouth closed. High drag when feeding requires additional thrust production from the flukes and reduces swimming speed.

Thrust-type vortices (TV)—The presence of vortices (*i.e.*, fluid circulating rapidly around a center; whirlpool) at the caudal flukes (Fig. 2) is indicative of thrust-type vortices (Weihs 1972). When the flukes oscillate, a vortex is shed from the flukes at the end of each half-stroke (Vogel 1994). As the flukes are reaccelerated in the opposite direction, a new vortex is formed that is bound to the flukes with a reversed circulation (Vogel 1994). Thus, each vortex is formed from the reversal in direction

⁴Personal communication from A. J. Werth, Department of Biology, Box 162, Hampden-Sydney College, Hampden-Sydney, VA, 2011.

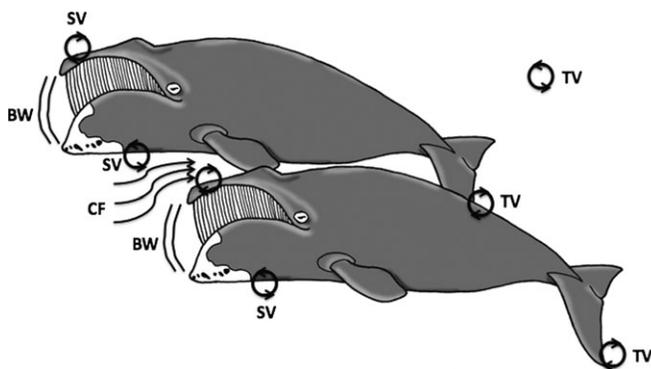


Figure 3. Schematic of flow pattern of two whales swimming in echelon formation based on Figures 1 and 2. The hydrodynamic features include bow waves (BW), channeled flow (CF), separation vortices (SV), and thrust-type vortices (TV). The direction of the spin of the vortices and flow are indicated by the arrow heads.

of the propulsor (Fish and Lauder 2006). As the whale progresses, the oscillating motion of the flukes produces two parallel trails of staggered vortices perpendicular to the plane of oscillation and with opposite circulations.

These thrust-type vortices transport momentum from the flukes into the fluid. The momentum imparted to the fluid is concentrated in a jet of fluid directed on average opposite to the swimming direction (Weihs 1972, Rayner 1985, Videler 1993). Thrust is derived from the reaction of the jet stream. The jet induces the resting water around it to generate the vortex wake.

The thrust-type vortex wake is a two-dimensional representation of the flow field shed from an oscillating propulsor. The wake is a trail of connected alternating clockwise and anticlockwise vortices. In three dimensions, the vortices are actually connected by tip vortices generated at the distal ends of the flukes, forming a folded chain of vortex rings with the momentum jet directed posteriorly through the center of the rings (Videler 1993, Vogel 1994, Fish and Lauder 2006). Such a flow field is essential to the generation of thrust in swimming whales.

Separation vortices (SV)—The pattern of vortices occurring along the margins of the upper and lower jaws is due to the separation of water from the surface of the whale (Fig. 2). This separation occurs because an adverse pressure gradient develops along the body surface (*i.e.*, low pressure upstream and high pressure downstream) (Webb 1975, Vogel 1994). The flow along the body decelerates as it has insufficient energy to overcome the adverse pressure gradient. Water next to the surface accelerates in the opposite direction of the flow and causes separation (Webb 1975). The separated flow produces eddies and vortices.

As a bluff (nonstreamlined) body moves through a fluid, the flow about the body is nonsteady. Flow separates alternately from each side of the body producing two staggered rows of vortices in the wake. Like the thrust-type vortex wake, all the vortices in one row rotate in the same direction, but opposite to that of the other row. However, the rotation of the vortices is opposite to the pattern found in the thrust-type vortex wake (Weihs 1972). This flow pattern around a bluff body is a drag-type vortex wake (Vogel 1994).

Channeled flow (CF)—The position of the whales swimming on their sides in the echelon formation will form restricted channels between adjacent animals (Fig. 2). The constriction of flow between the whales will cause a decrease in pressure (Venturi Effect) as a consequence of an increase in flow velocity (Bernoulli Principle) (Vogel 1994). This faster flow is evident as it is ejected behind the lower jaw of the leading whale and upper jaw of the immediate trailing whale. The bow wave is deflected posteriorly along with the separation vortices. The reduced fluid pressure within the channels will produce a mutually attractive force between adjacent whales (Kelly 1959).

Würsig *et al.* (1985) interpreted bowhead whales swimming in an echelon formation as a feeding strategy in which trailing whales would capture prey that was missed or had evaded a leading animal. A trailing whale would gain an advantage by having an adjacent whale act as a “wall” to guide the prey into its mouth (Würsig and Clark 1993). While this represents a plausible explanation of the behavior, it does not take into consideration the hydrodynamic factors associated with the whales feeding on their sides. In the original description by Würsig *et al.* (1985), the bowhead whales were in a normal gravity-orientated position (*i.e.*, ventral side oriented downward). In addition, the distance between whales was 8 m apart (Würsig and Clark 1993), which is greater than the distance between the side-swimming whales described in this note.

Swimming in an echelon formation avoids hydrodynamic interference. By swimming alongside another whale, each whale would be moving through a region of undisturbed water so that a following whale is not in the shadow of a lead whale through the food patch. Thus, prey may not be deflected away from a trailing whale due to the flow pattern produced by a leading whale. However, the optimal formation to forage through undisturbed water would be by swimming abreast and arranged as a long line.

In an echelon formation, the leading whale induces a flow that could be taken advantage of by a trailing whale. The separation vortex generated from the lower jaw (Fig. 2) could aid in concentrating prey (*e.g.*, copepods, euphausiids) into its center and directing the prey toward the mouth of the following whale. The way that particles are dispersed by a vortex is dependent on the size and density of the particles relative to the size of the vortex and viscosity of the medium (Green 1995). Small particles with densities below or close to the medium of the vortex will be transported into the vortex core, whereas large particles with densities greater than the medium will be accelerated away from the vortex. Copepods are of a small size (1–2 mm) with a density of 1,027–1,045 kg/m³ and euphausiids (10–60 mm) have a body density of 1,042–1,068 kg/m³ (Greenlaw 1977). As copepods and euphausiids are of small size, with a body density similar to seawater (1,024 kg/m³), the vortices will tend to concentrate the prey into the center of the vortex for intake by the following whale (Green 1995, Knutsen *et al.* 2001).

The last whale in the echelon that is shown in Figure 1 (whale 5) is aligned with the trail of separation vortices shed from the previous whale in the formation. In this position, the whale is optimally placed to feed on copepods concentrated by the vortex wake. Similarly, the spoonbill (*Platalea leucordia*) uses vortices to transport prey. This bird sheds vortices from the tip of its bill as it is swept through the water to generate hydrodynamic suction on the bottom to move prey (Weihs and Katzir 1994).

Echelon formations by cetaceans have been suggested to have an effect on the flow dynamics to lower the energetic cost of swimming (Kelly 1959, Lang 1966, Brodie

1977, Norris and Johnson 1994). Formation swimmers influence water flow around adjacent individuals (Weihs 1973, Fish 1999). Use of separation vortices or thrust-type vortices can produce a flow regime that reduces the relative velocity on an individual in a formation when swimming in the optimal position (Fish 1999). As drag is directly related to the velocity squared, a reduced relative velocity will substantially reduce the drag and energy cost to swim. Because swimming at the water surface incurs higher energy costs than submerged swimming (Hertel 1966, Fish 2000) and the feeding apparatus can increase pressure drag, mechanisms to reduce the total drag on the whale when surface feeding would be highly advantageous (Woodward *et al.* 2006).

For separation vortices produced by a leading body, the optimal formation is a closely spaced single file (Fish 1994, 1995, 1999). A thrust-type vortex system has the opposite rotation of the vortices (Weihs 1972). In this case optimal position to reduce drag is for trailing individuals to be parallel and lateral to the vortex wake in the plane of oscillation of the flukes. Thus, an individual swimming diagonally behind another achieves a low relative velocity and high energetic advantage (Weihs 1973). Due to the rotation of the vortices, however, an individual following directly behind another will experience a higher relative velocity and would have to expend a greater amount of energy (Weihs 1973). Because the thrust-type vortex wake takes time to fully develop and then dissipate further downstream, the optimal configuration is an elongate diamond or shallow rhombus pattern (Weihs 1973), such as seen in schools of fish (Partridge *et al.* 1983). Geese will also fly in echelon or V-formations to reduce energy costs when migrating (Fish 1999).

The positions of the bowhead whales seen in Figure 1 do not take advantage of vortices to achieve drag reduction. The diagonal configuration of the echelon precludes drag reduction from separation vortices and distance between whales is too small to take advantage of the thrust-type vortices from the oscillating flukes. However, the close spacing can induce a rapid channeled flow between adjacent whales, which can reduce drag by drafting. The channeled flow would produce an attractive force by a Bernoulli suction between the bodies with the leading body having additional drag and a reduced drag on the trailing body (Kelly 1959, Lang 1966, Weihs 2004). The dynamic nature of the echelon formation may be associated with different drags on leading and trailing whales. When individual whales leave or enter the echelon, the relative position of the whales will change (Würsig and Clark 1993).

Drafting is used by small whales that often position themselves beside and slightly behind the maximum diameter of a larger animal (Tavolga and Essapian 1957, Norris and Prescott 1961, Dohl *et al.* 1974, Reid *et al.* 1995, Marino and Stowe 1997, Gubbins *et al.* 1999, Noren 2008, Noren *et al.* 2008, Noren and Edwards 2011). Weihs (2004) estimated that a neonatal dolphin could have savings of 60%–90% of the thrust required to maintain a position alongside of the mother.

In conclusion, the occurrence of side-swimming whales while foraging represents an unusual behavior that has implications for the hydrodynamics of the whales. There are potential benefits to the echelon formation of side-swimming whales based on observations of the vortices produced and proximity and location of the whales. The vortices shed from the surface of a leading whale could help to concentrate prey to be consumed by a trailing whale. The location of adjacent whales would produce a flow field that would aid in pulling along each trailing whale by the Bernoulli effect. Side-feeding of bowhead whales in concert with echelon formation swimming can increase feeding efficiency and/or decrease the overall energy cost of locomotion when foraging.

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LITERATURE CITED

- Ashjian, C., R. Campbell and S. Okkonen. 2010. Broad-scale oceanography component. Pages 35–40 in Bowhead whale feeding ecology study (BOWFEST) annual report for 2010. National Marine Mammal Lab, NOAA Fisheries Service, 7600 Sand Point Way NE, Seattle, WA.
- Baumgartner, M. F., and B. R. Mate. 2003. Summertime foraging ecology of North Atlantic right whales. *Marine Ecological Progress Series* 264:123–135.
- Brodie, P. F. 1977. Form, function and energetics of cetacea: A discussion. Pages 45–58 in R. J. Harrison, ed. *Functional anatomy of marine mammals*. Volume 3. Academic Press, London, U.K.
- Dohl, T. P., K. S. Norris and I. Kang. 1974. A porpoise hybrid: *Tursiops* x *Steno*. *Journal of Mammalogy* 55:217–221.
- Fish, F. E. 1994. Energy conservation by formation movement: Metabolic evidence from ducklings. Pages 193–204 in Q. Bone, L. Maddock, and J. M. V. Rayner, eds. *Mechanics and physiology of animal swimming*. Cambridge University Press, Cambridge, U.K.
- Fish, F. E. 1995. Kinematics of ducklings swimming in formation: Energetic consequences of position. *Journal of Experimental Zoology* 272:1–11.
- Fish, F. E. 1999. Energetics of swimming and flying in formation. *Comments on Theoretical Biology* 5:283–304.
- Fish, F. E. 2000. Biomechanics and energetics in aquatic and semiaquatic mammals: Platypus to whale. *Physiological and Biochemical Zoology* 73:683–698.
- Fish, F. E., and G. V. Lauder. 2006. Passive and active flow control by swimming fishes and mammals. *Annual Review of Fluid Mechanics* 38:193–224.
- Green, S. I. 1995. *Fluid vortices*. Kluwer, Dordrecht, Netherlands.
- Greenlaw, C. F. 1977. Backscattering spectra of preserved zooplankton. *Journal of the Acoustical Society of America* 62:44–52.
- Gubbins, C., B. McCowan, L. K. Spencer, S. Hooper and D. Reiss. 1999. Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science* 15:751–765.
- Heithaus, M. R., and L. M. Dill. 2002. Feeding strategies and tactics. Pages 412–422 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. Academic Press, New York, NY.
- Hertel, H. 1966. *Structure, form, movement*. Reinhold, New York, NY.
- Kasuya, T., and D. Rice. 1970. Notes on baleen plates and on arrangement of parasitic barnacles of gray whales. *Science Reports of the Whales Research Institute, Tokyo* 22:39–43.
- Kelly, H. R. 1959. A two-body problem in the echelon-formation swimming of porpoise. Technical Note 40606-1. U.S. Naval Ordnance Test Station, China Lake, CA.
- Knutsen, T., W. Melle and L. Calise. 2001. Determining the mass density of marine copepods and their eggs with a critical focus on some of the previously used methods. *Journal of Plankton Research* 23:859–873.

- Landino, S. W., S. D. Treacy, S. A. Zerwick and J. B. Dunlap. 1994. A large aggregation of bowhead whales (*Balaena mysticetus*) feeding near Point Barrow, Alaska in late October 1992. *Arctic* 47:332–335.
- Lang, T. G. 1966. Hydrodynamic analysis of cetacean performance. Pages 410–432 in K. S. Norris, ed. *Whales, dolphins and porpoises*. University of California Press Berkeley, CA.
- Leatherwood, S., and W. A. Walker. 1979. The northern right whale dolphin *Lissodelphis borealis* Peale in the eastern North Pacific. Pages 85–141 in H. E. Winn and B. L. Olla, eds. *Behavior of marine animals*. Volume 3. Plenum Press, New York, NY.
- Lowry, L. F., and J. J. Burns. 1980. Foods utilized by bowhead whales near Barter Island, Alaska, autumn 1979. *Marine Fisheries Review* 42:88–91.
- Mayo, C. A., B. H. Letcher and S. Scott. 2001. Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis*. *Journal of Cetacean Research and Management Special Issue* 2:225–229.
- Marino, L., and J. Stowe. 1997. Lateralized behavior in two captive bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology* 16:173–177.
- Noren, S. R. 2008. Infant carrying behaviour in dolphins? Costly parental care in an aquatic environment. *Functional Ecology* 22:284–288.
- Noren, S. R., G. Bledenbach, J. V. Redfern and E. F. Edwards. 2008. Hitching a ride: Formation locomotion strategy of dolphin calves. *Functional Ecology* 22:278–283.
- Noren, S. R., and E. F. Edwards. 2011. Infant position in mother-calf dolphin pairs: A social interaction with hydrodynamic benefits. *Marine Ecology Progress Series* 424:229–236.
- Norris, K. S., and C. M. Johnson. 1994. Schools and schooling. Pages 232–242 in K. S. Norris, B. Würsig, R. S. Wells and M. Würsig, eds. *The Hawaiian spinner dolphin*. University of California Press, Berkeley, CA.
- Norris, K. S., and J. H. Prescott. 1961. Observations on Pacific cetaceans of California and Mexican waters. University of California Publications in Zoology 63:291–401.
- Okkonen, S. R., C. J. Ashjian, R. G. Campbell, J. T. Clarke, S. E. Moore and K. D. Taylor. 2011. Satellite observations of circulation features associated with a bowhead whale feeding ‘hotspot’ near Barrow, Alaska. *Remote Sensing of Environment* 115:2168–2174.
- Partridge, B. L., J. Johansson and J. Kalish. 1983. The structure of schools of giant bluefin tuna in Cape Cod Bay. *Environmental Biology of Fishes* 9:253–262.
- Pivorunas, A. 1979. The feeding mechanisms of baleen whales. *American Scientist* 67:432–440.
- Rayner, J. M. V. 1985. Vorticity and propulsion mechanics in swimming and flying animals. Pages 89–118 in J. Riess and E. Frey, eds. *Konstruktionsprinzipien lebender und ausgestorbener Reptilien*. University of Tübingen, Tübingen, Germany.
- Reid, K., J. Mann, J. R. Weiner and N. Hecker. 1995. Infant development in two aquarium bottlenose dolphins. *Zoo Biology* 14:135–147.
- Richardson, W. J., M. A. Fraker, B. Würsig and R. S. Wells. 1985. Behaviour of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: Reactions to industrial activities. *Biological Conservation* 32:195–230.
- Shaw, E. 1978. Schooling fishes. *American Scientist* 66:166–175.
- Tavolga, M. C., and F. S. Essapian. 1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. *Zoologica* 42: 11–31.
- Videler, J. J. 1993. *Fish swimming*. Chapman & Hall, London, U.K.
- Vogel, S. 1994. *Life in moving fluids: The physical biology of flow*. 2nd edition. 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.
- Weihls, D. 1972. Semi-infinite vortex trails, and their relation to oscillating airfoils. *Journal of Fluid Mechanics* 54:679–690.
- Weihls, D. 1973. Hydromechanics of fish schooling. *Nature* 241:290–291.
- Weihls, D. 2004. The hydrodynamics of dolphin drafting. *Journal of Biology* 3:8.1–8.16.

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- Weih, D., and G. Katzir. 1994. Bill sweeping in the spoonbill, *Platalea leucordia*: Evidence for a hydrodynamic function. *Animal Behavior* 47:649–654.
- Werth, A. J. 2004. Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. *Journal of Experimental Biology* 207:3581–3590.
- Woodward, B. L., J. P. Winn and F. E. Fish. 2006. Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology* 267:1284–1294.
- Würsig, B., and C. Clark. 1993. Behavior. Pages 157–199 in J. J. Burns, J. J. Montague and C. J. Cowles, eds. *The bowhead whale*. Special Publication Number 2, The Society for Marine Mammalogy.
- Würsig, B., E. M. Dorsey, M. A. Fraker, R. S. Payne and W. J. Richardson. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: A description. *Fishery Bulletin, U.S.* 83:357–377.

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