

Swimming Strategies for Energy Economy

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INTRODUCTION

The laws of physics are rigid and fixed. Animals, therefore, are restricted in their use of available energy in accordance to the constraints of mechanics and thermodynamics. Evolutionary success dictates that a large proportion of the available energy reserves be allocated to reproductive effort despite the demand by other energy consuming functions. Therefore, mechanisms that reduce energy costs for non-reproductive functions relative to total energy reserves have an adaptive benefit for individuals (Fausch, 1984). As the laws of physics are inflexible and the available energy limited, animals have found ways to exploit these laws for their own benefit.

Locomotion is an energy demanding activity. Swimming by fishes permits them to seek out new energy resources, but comes at a cost to transport the body mass over a distance. For movement in water, the kinetic energy is transferred from the movement of the body to the fluid medium, both to replace momentum losses associated with viscosity and induced energy losses associated with this replacement. This energy loss from the animal is due to the high density and viscosity of the water in conjunction with the shape and texture of the body surface, and the animal's propulsive movements (Webb,

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1988). The rate of energy loss, sometimes considered the “drag” power, P_D , for a body relative to a water flow can be determined according to the equation:

$$P_D = 0.5 \rho S C_D U^3 \quad (1)$$

where ρ is the density of the water (freshwater, 1000 kg/m³; salt water, 1025 kg/m³), S is the wetted surface area of the body, U is the velocity, and C_D is the dimensionless drag coefficient (Webb, 1975; Vogel, 1994). While arguments of energy saving by maintaining laminar versus turbulent flow conditions in the boundary layer have occurred (Webb, 1975; Fish, 2006a), body shape has a greater influence in determination of the drag and energy consumption while moving through water. Drag power is minimized primarily by streamlining the shape of the body and the appendages. However, even with the most optimized of streamlined forms, advantageous geometry of the surface texture, and control of flow around the body, drag can only be minimized and never eliminated. The consequences for a fish are that energy must be allocated to overcome power loss, this being actively generated by the fish as “thrust” power. The propulsive movements of the swimming fish further draw upon available energy reserves. Propulsive movements of the body and appendages are expected to increase C_D by a factor of 3–5 (Lighthill, 1971).

How can swimming animals gain an energetic advantage when subjected to the unrelenting demands associated with the drag power? As P_D is dependent on the cube of U , the velocity becomes the important factor in determining the rate of energy expended in swimming. For some fishes, energetic gain can be maximized relative to locomotor costs by adopting a sit-and-wait or ambush predator strategy, reducing translocation to very short periods. In this strategy, energy cost=0 while $U=0$. By choosing among velocities of the flow, a swimming fish or a fish in a current can similarly reduce the energy cost of locomotion. Fishes use advantageous flow conditions as a behavioral strategy to reduce drag.

This review will examine behavioral strategies to minimize drag and energy expenditure. The primary thrust of most research on swimming fishes has been concerned with the interaction of morphology, muscle physiology, and hydrodynamics. The carefully executed experiments for these examinations constrained fish to swim against constant flows in linear flow tanks or annular swimming rings without interference with the solid walls of the test chamber (Webb, 1975). The results of these studies have benefited understanding of physiological mechanisms, but have been more limited in an ecological context. Steady rectilinear swimming may be more the exception than the rule. By using alternative means of swimming, fishes “cheat” in order to reduce costs due to swimming and maximize net energy resources. Fishes, therefore, use a variety of behavioral mechanisms to take advantage of local flow conditions.

Optimal speed and gaits

As the mechanical power due to drag of a fish increases with the cube of the velocity (equation 2), the metabolic cost, representing the power input, also increases curvilinearly with increasing swimming velocity according to the power function (i.e., $y = ax^b$) with an exponent $b > 1$ (Brett, 1964, 1965; Webb, 1975; Videler and Nolet, 1990; Videler, 1993). The intersection of the curve, expressed by this power function, and the tangent that passes through the origin indicates the minimum cost of transport (CT) (Fig. 4.1; Tucker, 1975; Videler, 1993).

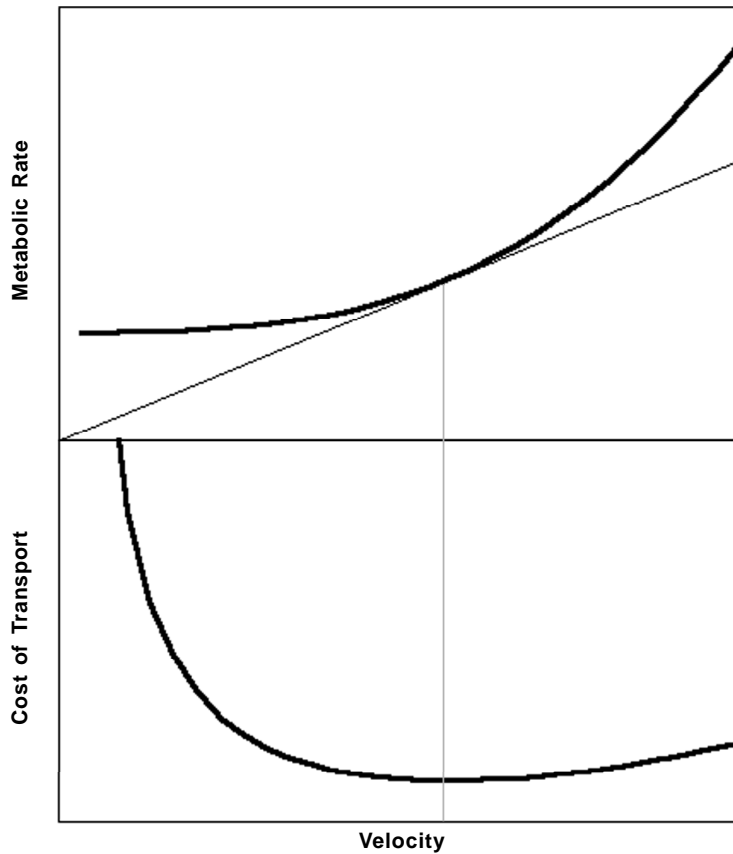


Fig. 4.1 Relationship between metabolic rate and cost of transport (CT) of a swimming fish and velocity. The optimal swimming speed, where the greatest energy efficiency is realized, occurs at a velocity where the tangent line intersects with the curve of the metabolic rate. This corresponds to the velocity of the minimum cost of transport, which is indicated by the vertical line.

CT is defined as the metabolic energy required to transport a unit mass a unit distance. When plotted against velocity, CT displays a U-shaped curve (Brett, 1965; Videler and Nolet, 1990; Videler, 1993). At low swimming speeds, the metabolic cost is high relative to locomotor costs and the total costs per unit distance are high (Webb, 1975). At high swimming speeds, CT is high due to the disproportional rise in drag. The minimum CT corresponds to the velocity where the distance traveled for the energy available is maximized (i.e., maximum range).

The optimal swimming speed should coincide with the speed of minimum CT. Weihs (1973) predicted a theoretical optimal cruising speed of approximately one body length/s. An ultrasonic telemetry study on migrating sockeye salmon (*Oncorhynchus nerka*) showed that estimated ground speed corresponded to a mean 1.0 lengths/s in open waters (Quinn, 1988). The optimal speed predicted by Weihs (1973) was considered low when compared with the maximum endurance speeds of fishes. A review of CT based on metabolic studies showed a range of optimal swimming speeds of 0.7 to 5.8 lengths/s for a variety of fishes (Videler, 1993). Scombrids cruise at about 0.3 to 2.2 lengths/s (Magnuson, 1978). Dewar and Graham (1994a) found the optimal swimming speed of 2.0 lengths/s for yellowfin tuna (*Thunnus albacares*) measured in a water tunnel to be close to the mean swimming speed of yellowfin tuna tracked at sea (Holland *et al.*, 1990).

Changes in optimal swimming speed can be exploited by using different gaits. Changes in gait are considered to minimize energy costs when moving at a particular speed or increase stability (Hoyt and Taylor, 1981; Arreola and Westneat, 1996; Hove *et al.*, 2001; Alexander, 2003). Many fishes swim with various kinematics patterns of combinations of median and paired fins (Webb, 1994, 1998b). As defined by Alexander (1989), a gait is “a pattern of locomotion characteristic of a limited range of speeds described by quantities of which one or more change discontinuously at transitions to other gaits.” While gaits are typically associated with terrestrial locomotion, the description of gaits is also applicable to swimming (Webb, 1994). The swimming gaits of fish are median-paired fin (MPF) gaits and body-caudal fin (BCF) gaits (Webb, 1998b). MPF gaits involve undulatory or oscillatory movements of the paired (e.g., pectoral) or median (e.g., dorsal, anal) fins. These fins can be used singly or in combination. MPF swimmers hold the body rigid. BCF gaits involve undulations of the body and caudal fin, or oscillations confined to the caudal fin (Breder, 1926; Webb, 1975, 1994, 1998b; Lindsey, 1978; Hale *et al.*, 2006). MPF gaits are generally associated with relatively slow swimming, particularly used for precise maneuvering and stability control. BCF gaits involve generally more rapid swimming for cruising and high-speed accelerations (e.g., burst swimming, fast-starts).

Gait transition with changing swimming speed is common in fish. As the power requirement for swimming increases with the cube of the speed

(equation 1), a given gait that is powered with a restricted muscle mass can only generate sufficient power efficiently over a small range of speeds (Webb, 1994). Therefore, varied gaits are necessitated to swim over an extended performance range. The sequence of gait changes is MPF swimming, burst and coast BCF swimming (see below) powered by red muscle, steady BCF swimming with red muscle, burst and coast BCF swimming with white muscle, and steady BCF swimming with white muscle (Alexander, 1989; Webb, 1994; Hale *et al.*, 2006). For MPF swimmers, the pectoral fins are beat synchronously at low speeds and alternately at high speeds or vice versa (Hove *et al.*, 2001; Hale *et al.*, 2006).

MPF swimming is used in hovering and station holding (i.e., zero ground speed) (Webb, 1994, 1998b). Sustained low-speed swimming also employs MPF gaits. At higher swimming speeds, MPF gaits are abandoned in favor of BCF swimming, with the exception of labriform fishes that use almost exclusively MPF swimming which is supplemented with BCF swimming (Drucker and Jensen, 1996a, b; Mussi *et al.*, 2002). The MPF gaits use a small mass of propulsive appendicular muscle to power the fins. In transition to BCF swimming, power is generated from the myotomal muscle mass. At low BCF swimming speeds, power is generated by red muscle, which comprises a small proportion of the entire myotomal muscle mass (Greer-Walker and Pull, 1975; Jayne and Lauder, 1995; Coughlin and Rome, 1996; Knower *et al.*, 1999). However with increasing speed, a greater proportion of the musculature is recruited in the form of pink and white muscle fibers (Rome *et al.*, 1990, 1993).

The energy cost of swimming is low for MPF swimming compared to BCF gaits (Korsmeyer *et al.*, 2002; Cannas *et al.*, 2006). CT decreases with increasing speed using MPF swimming until gait transition. Above the gait transition speed, CT increases with the shift to BCF swimming. The difference in energy cost between gaits is likely due to the relatively smaller muscle mass required to swim at low speeds and reduced drag due to a rigid body. Gait transition is necessary as the forces (e.g., drag, acceleration reaction, lift) involved in the production of thrust for each of the gaits is maximal for only a limited range of speeds (Vogel, 1994; Webb, 1994; Sfakiotakis *et al.*, 1999). It has been assumed that gait transition is associated with a change from aerobic to anaerobic swimming (Drucker and Jensen, 1996, Cannas *et al.*, 2006). Increases in speed require shifting to different muscle masses to take advantage of different optimum muscle shortening velocities (Drucker and Jensen, 1996).

Burst and Coast Swimming

The use of intermittent locomotion has been demonstrated to reduce the energy cost of locomotion. Burst and coast swimming is a two-phase periodic

behavior (Weihs and Webb, 1983). Alternating bouts of active swimming movements (burst phase) with passive coasts or glides (coast phase) conserves on the energy by reducing the amount of muscular effort over a prolonged time period (Fig. 4.2). The burst phase accelerates the body forward, while in the coast phase, the body decelerates. Burst and coast swimming is a behavioral strategy that exploits the lower drag of a rigid, non-flexing animal during the coast compared to when it is actively swimming (Weihs and Webb, 1983). Many fish swim using alternating bursts and coasts. Fish that use this behavior have a body morphology within a range of fineness ratio (body length/maximum girth) of 4.0 and 6.5 (Blake, 1983). The hydrodynamic drag of a flexing fish body is three to five times higher than when the fish is straight and coasting at the same speed (Lighthill, 1971; Webb, 1975). Therefore, the advantage of this swimming strategy would be realized by BCF swimmers using subcarangiform and carangiform swimming. As MPF swimmers such as labriform fishes (e.g., wrasse) and to a lesser extent thick-bodied thunniform swimmers (e.g., tuna) already maintain a rigid body, little advantage would be gained by adopting burst and coast swimming.

Weihs (1974) developed a theoretical model that estimates that efficiency on the initial and final speeds and the difference between the drags associated with active swimming and coasting. The optimal condition

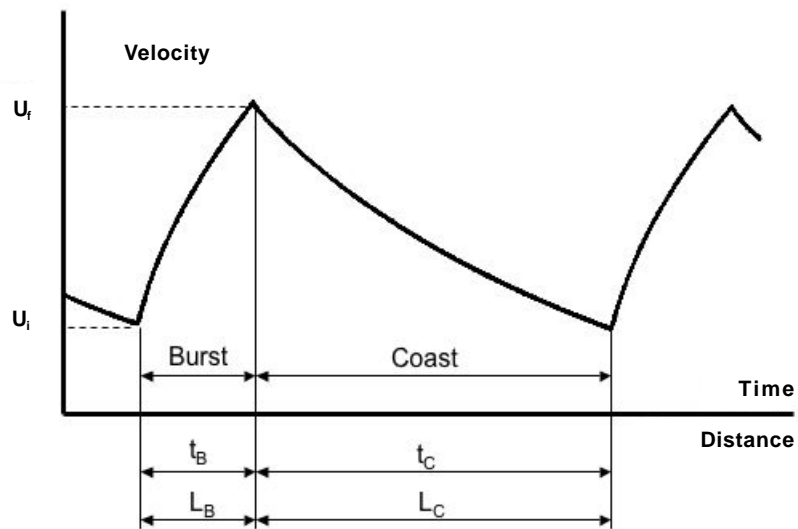


Fig. 4.2 Burst and coast swimming. During the burst phase, there is a rapid increase in velocity from a low initial velocity (U_i) to a final velocity (U_f). The burst is short in duration (t_B) and propels the fish a relatively short distance (L_B). During the coast phase, the fish decelerates over a long time (t_C) and is transported a relatively long distance (L_C). Figure based on Weihs (1974).

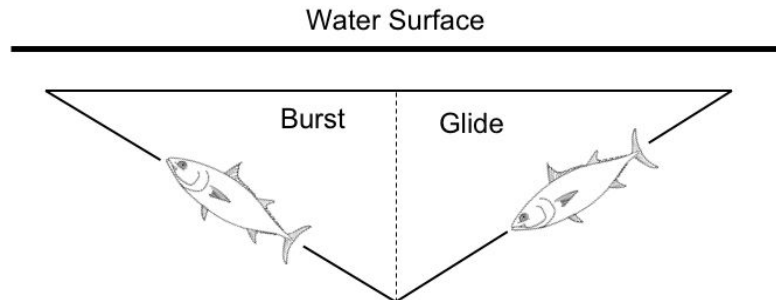


Fig. 4.3 Hypothetical path of negatively buoyant fish during burst and glide swimming. The fish sinks to a lower depth using a passive glide. During the burst phase, the fish actively swims to power itself to a higher depth. Figure based on Weihs (1973a).

was obtained at low average speeds, but for gadids, energetic advantage also accrues when using high-speed anaerobically powered sprints (Videler and Weihs, 1982). Weihs (1974) estimated that an energy savings of over 50% was possible by alternating accelerated motion with powerless glides. Burst-and-coast swimming becomes more economical as the animal's size or speed increases (Videler and Weihs, 1982). In addition, burst time is reduced by a fish trailing between and behind other fish in a school, resulting in a 29% energy savings compared to burst-and-coast swimming by solitary fish (Fish *et al.*, 1991).

A variant of the burst and coast behavior was applied to negatively buoyant fish as swim and glide (Weihs, 1973a, 1984). Energy is conserved by gliding downward with no propulsive motions and then regaining altitude by active swimming (Fig. 4.3; Weihs, 1973a; Weihs and Webb, 1983). Weihs (1973a) calculated an energy savings of 20% for a kawakawa using this technique to traverse the same horizontal distance in 7% more time. Energy savings for other tuna were estimated at 7% for skipjack tuna and 16% for albacore (Magnuson, 1978). Increased energy savings are possible if the angle between the plane of the surface and downward trajectory of the fish on the glide is kept small (Weihs, 1973a).

Schooling

Energy economy for swimming by fish has been suggested as a possible advantage to schooling. Increased energy savings would be advantageous by permitting faster swimming speeds during foraging or increasing range particularly for migration. The pattern of the school is hypothesized to be dependent on the undulatory movements of the fish, which produce a series of counter-rotating vortices in its wake as a thrust-type vortex street (reverse Kármán vortex street) (Belyayev and Zuyev, 1969; Weihs, 1972a, 1973b).

The vorticity in thrust production is necessary to transport momentum from the propulsor into the fluid. Each vortex is formed from the reversal in direction of the propulsor, requiring a reversal in circulation of the bound vortex. At the end of each half-stroke, the bound vortex is shed from the propulsor and as the propulsor is reaccelerated in the opposite direction a new bound vortex is formed with a reversed circulation (Vogel, 1994). The shed vortex is known as the “stopping vortex.” The oscillating motion of the propulsor thus produces two parallel trails of staggered vortices perpendicular to the plane of oscillation and with opposite circulations. The direction of the circulation is oriented so that the tangential velocity is parallel to the trails and directed posteriorly between the trails and anteriorly on the outside of the trails.

The thrust-type vortex street is a two-dimensional representation of the flow field shed from an oscillating propulsor. In three dimensions, the stopping vortices are actually connected by tip vortices, forming a folded chain of vortex rings (Videler, 1993; Vogel, 1994). Such a flow field is essential to the generation of thrust in swimming fish. Although the vorticity convected into the wake represents an energy loss, the vortex street has possibilities for reduction in energy costs by schooling fish (Weihs, 1973b, 1975). The thrust-type vortex system reduces the drag on individuals positioned parallel and lateral to the street. Thus, a fish swimming diagonally behind another achieves a low relative velocity and high energetic advantage. Due to the rotation of the vortices, a fish following directly behind another will experience a higher relative velocity and would have to expend a greater amount of energy (Weihs, 1973b).

A three-dimensional, inviscid flow model by Weihs determined the optimal configuration between fish in a school for energy conservation (Weihs, 1973b, 1975). The model considered the structure of an infinite array of identical fish swimming in an oncoming flow. The fish were organized in discrete layers and in evenly spaced rows so that fish in the trailing row were staggered and centered between two fish in the leading row. The three-dimensional arrangement of fish in the theoretical school is like a crystal lattice (Weihs, 1975). The stationary position of the fish in the flow is maintained by the oscillatory sideways propulsive motions of the fish from its body and caudal fin. The propulsive motions produce the vortex wake in which the rate of change of momentum in the water is equal and opposite to the thrust, which opposes the total drag on the body. The equality of thrust and drag is maintained as the fish swims at constant velocity.

Considering only one layer of the theoretical school, the model predicted that the relative velocity directly behind a fish would be high, whereas the relative velocity would be lowest outside the vortex street (Breder, 1965; Belyayev and Zuyev, 1969; Weihs, 1972a, 1973b, 1975). Because the vortex wake takes time to fully develop and then dissipate further downstream, the

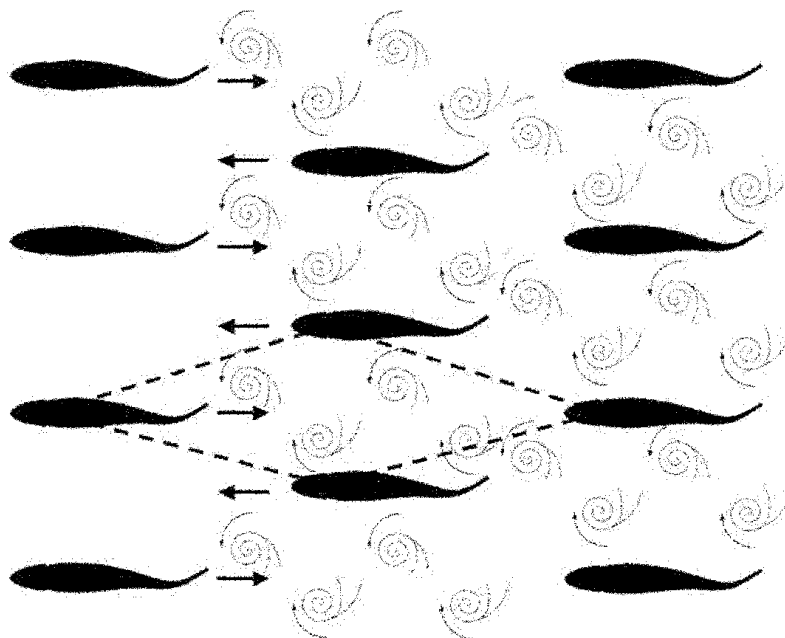


Fig. 4.4 Optimal arrangement for maximum energy savings of a fish school swimming in a horizontal layer. Vortex patterns in the wake of the fish are illustrated. Arrows show direction of induced flow relative to vortices. The diamond configuration of fish is shown by the dashed lines. Based on illustration from Weihs (1973b).

optimal configuration is a diamond or shallow rhombus pattern with a leading fish, two fish in the second row, and a fish in the third row (Fig. 4.4). The angles within the pattern are 30° and 150° (Weihs, 1973b).

The first row of fish swimming into undisturbed water will have the same relative and absolute velocities. Fish in the second row experience a relative velocity 40–50% of the free stream velocity and a reduction of the force generated for swimming by a factor of 4–6 (Weihs, 1973b, 1975). However, the decrease in relative velocity is not maintained with each successive row due to destructive interference. The vortex wakes of two successive rows will cancel because the vortices from each row are in line and have opposite vorticity when the lateral distances between adjacent fish is twice the width of the vortex street. The third row thus encounters undisturbed flow and incurs no reduction in relative velocity and drag. The reduced relative velocity occurs with alternate rows. Integrated over the entire formation, the school will have only a 50% savings in energy of the second row (Weihs, 1973b).

Individual fish in alternate rows not experiencing reduced drag from the interaction of the vortex wake of the previous row may still contract a

benefit from effects due to lateral spacing. As spacing decreases there is a channeling effect so that the force produced by a fish in a row may be twice that of a single fish (Weihs, 1975). The channeling effect is not added to the energy savings of the row encountering the effects of the vortex wake. The two effects may not be superimposed, because the trailing row has a reduced relative velocity, which decreases lateral interactions.

In addition, Weihs (1973b, 1975) suggested that tip vortices from the pectoral fins could be exploited for lift by trailing fish. Tip vortices are produced from the movement of fluid caused by the pressure difference over a three-dimensional foil generating lift (Vogel, 1994; Fish, 1999). A foil that is directed into a flow with a positive angle of attack (i.e., angle to the incipient flow) will have a relatively faster flow on the upper surface (suction side) than the lower surface (pressure side). The difference in velocity translates into a pressure difference due to the Bernoulli effect, which generates lift. Fluid moves around the foil tip from the pressure side (high pressure) to the suction side (low pressure). The induced flow around the tip creates the tip vortex. The tip vortex encounters the main flow over the foil and is sheared. As the tip vortex is shed from the foil, it leaves a vortex trail. The vortex is positioned slightly inboard of the tip.

Fish such as tuna are negatively buoyant and maintain trim from lift generated by the pectoral fins (Magnuson, 1978). The spin of tip vortices from leading fish would provide an upwash lateral and posterior of the pectoral fin tips. Trailing fish would benefit by being in the tip vortex wake. This is analogous to the mechanism used by birds flying in V-formations, which for the trailing individual reduces induced drag, increases lift, and reduces the energetic cost of locomotion (Fish, 1999).

The three-dimensional complexity of fish schools has made data collection to validate the model difficult. Schools of 20–30 individuals of saithe (*Pollachius virens*), herring (*Clupea harengus*) and cod (*Gadus morhua*) were tested in a circular tank (Partridge and Pitcher, 1979). Although the fish generated vortices in their wake as predicted by Weihs, the schools were not organized according to the model. In all cases the fish exhibited non-random spacing but did not mimic the optimal configuration predicted by Weihs' model. Trailing fish often swam with their snout ahead of the tail of the leading fish. Despite the lack of data supporting energy reductions by trailing fish, the observed lateral separation was about 0.9 body lengths and could still provide a 35% reduction in energy.

There are few examples of fish that swim in the hydrodynamically advantageous arrangement predicted by Weihs (1975) (Pitcher and Partridge, 1979). Golden shiners (*Notemigonus crysoleucas*) were not observed to swim in the theoretical arrangement when in groups of 30 individuals (Boyd and Parsons, 1998). However, Fish *et al.* (1991) found that groups of three golden shiners did swim in positions that would benefit a trailing individual.

Observations on scombrid and salmonid fish do support the configuration predicted from the model. Jack mackerel (*Trachurus symmetricus*) and pink salmon (*Oncorhynchus gorbuscha*) swam in formations, which approximated the diamond shape (Breder, 1976; Keenleyside and Dupuis, 1988). Estimates of lateral distance by scombrids show relatively narrow spacings of less than one body length in which propulsive force is increased. Pacific mackerel (*Scomber japonicus*) and bluefin tuna (*Thunnus thynnus*) in schools had lateral distances of 0.4–0.6 body lengths (Belyayev and Zuyev, 1969; van Olst and Hunter, 1970; Partridge *et al.*, 1983).

Indirect measures of energy economy of fish schools have been based on the kinematics of propulsive movements. Maximum duration of fish swimming in schools is 2–6 times longer than for a single fish (Belyayev and Zuyev, 1969), which suggests energy economy and reduced metabolic effort. As fish increase tail beat frequency with increasing swimming speed and thus experience an increased drag, the frequency reflects the relative energy expenditure (Parrish and Kroen, 1988). Tail beat frequency was demonstrated to be lower for some individuals of Pacific mackerel (*Scomber japonicus*) when schooling than when swimming alone (Fields, 1990). The tail beat frequency was higher for sea bass (*Dicentrarchus labrax*) swimming at the front of a school than for fish at the rear of the school (Herskin and Steffensen, 1998). Individual fish at the rear of the school displayed frequencies that were 9–14% lower than fish swimming in the front. Svendsen *et al.* (2003) swam schools of eight roach (*Rutilus rutilus*) at velocities of 2, 3 and 4 body lengths/s. The roach showed consistent intra-school positional preferences. Tail beat frequencies of trailing fish were 7.3–11.9% lower compared to roach in leading positions.

In addition to the use of vortices from leading fish in a school, the reduced swimming effort of trailing fish has been hypothesized to be due to shed mucus from leading fish (Breder, 1976; Herskin and Steffensen, 1998). The addition of dilute solutions of long-chain polymers into flow is well established as a means of drag reduction (Rosen and Cornford, 1971; Bushnell and Moore, 1991). Drag reduction by introduced polymers is possible under the following conditions: (1) turbulent or pulsed laminar flow in the boundary layer, (2) the polymer is linear and soluble, (3) the polymer has a molecular weight of 50,000 or more and (4) the density and viscosity of the fluid from the surface outwards must be constant (Hoyt, 1975; Daniel, 1981). The mucus secreted by fish over the body surface is considered to meet these conditions. Mucus is a combination of mucopolysaccharides, nucleic acids, proteins, and surfactants in the form of lipids, phospholipids and lipoproteins (Bushnell and Moore, 1991). Reductions in drag of 50–65% were observed with fish mucus (Rosen and Cornford, 1971; Hoyt, 1975; Daniel, 1981). While these drag reducing properties were measured for the mucus of several species of

fish, Parrish and Kroen (1988) found no advantage for the mucus of silversides (*Menidia menidia*).

Oxygen consumption by fish schools was reported to be significantly lower than the collective consumption of an equivalent number of solitary fish (Belyayev and Zuyev, 1969; Parker, 1973). However, this effect has been attributed more to group effect than to formation swimming. Parker (1973) argued that the decrease in metabolic rate of schooling fish compared to individuals tested in isolation resulted from a “calming effect” by the group. Schooling and nonschooling species both exhibited the effect when swimming in a rotating annular tank. However, nonschooling *Micropterus salmoides* swam in a single file formation and demonstrated no discernable reduction in metabolic cost between solitary and grouped fish. Obligate schoolers such as *Dorosoma cepedianum* and *Mugil cephalus*, however, showed 42–58% reductions in metabolic rate when swimming in schools as opposed to solitary swimming. The reduction of tail beat frequency for trailing sea bass over a range of swimming speeds (see above) was correlated with a reduction in oxygen consumption corresponding of 9–23% (Herskin and Steffensen, 1998). To remove the possibility of group effect, three fish were tested as a school in a water current of 0.07 m/s (Abrahams and Colgan, 1985). Oxygen consumption was measured for the entire school and on individuals separated from the other two by a clear partition. The partition allowed the fish to maintain visual contact without experiencing flow distortion. A 13% reduction in oxygen consumption was found for the school compared to the sum for the individual fish. However, only schools of large individuals (approximately 60 mm in length) demonstrated measurable energy savings. The small diameter (50 mm) of the test chamber may have introduced errors due to blocking and wall effects.

The possibility that fish swimming in schools reduces the energy cost of swimming assumes that all the fish in the school are swimming continuously to use a constant vortex pattern. Fish such as scombrids beat their tails continuously when swimming; however, many fish swim intermittently using a burst-and-coast strategy (Weihs, 1974; Weihs and Webb, 1983; Fish *et al.*, 1991). In burst-and-coast swimming, the fish alternates bouts of active accelerated swimming with passive glides or coasts. The fish realizes an energy savings by decreasing its drag during the coast phase. Lower total energy expenditure to travel a given distance thus is achieved when compared to a fish, which is constantly undulating over the same distance.

When three fish were examined swimming in the formation predicted by Weihs (1973b, 1975) for energy savings, the lead fish had equivalent mean times for bursting and coasting with solitary fish; whereas, the trailing fish demonstrated a reduced burst time and an increased coast time (Fish *et al.*, 1991). Coast time for trailing fish was 58 and 115% greater than coast time for leading and solitary fish, respectively. Coast and burst phases of trailing fish

were nearly equal in duration. An energy reduction of 29 and 21% was estimated for the trailing fish relative to solitary fish swimming continuously and leading fish, respectively. Although the combination of formation swimming and burst-and-coast strategies allows for increased energy savings, the simultaneous use of both behaviors reduces the effectiveness of either strategy alone. The interaction of the two strategies would negate attainment of the optimal configuration, because as the trailing fish coasts it moves backward relative to the leading fish. The trailing fish must then accelerate to return to its original position. In addition, coasting by a leading fish does not generate the vortex pattern exploited by trailing fish. Such conditions may explain the deviation in natural formations from the model (Partridge and Pitcher, 1979; Fish *et al.*, 1991).

Position within a school relates to competing strategies associated with responses to stimulus detection and energetics. Location at the periphery of a school will allow individuals to more readily detect predators and sources of food. However in this position, the fish are more exposed to predators and leading fish can incur higher energy requirements to swim. Fish in the middle of the school are less likely a direct target for predators and can experience a reduction in drag when swimming in the wake of leading fishes. However, the energetic price for trailing in a school can be influenced by a delay in food procurement and a reduction in oxygen availability (McFarland and Moss, 1967; Domenici *et al.*, 2002).

Hitchhiking

Hitchhiking is a mechanism to reduce locomotor costs by direct physical attachment to another animal in motion. As the hitchhiker is passively towed along, it saves considerable amounts of energy that it would have to expend by muscular contraction to swim. For this behavior to be of benefit to the hitchhiker without being a detriment to the other animal, the hitchhiker must be much smaller in body size compared to the host animal.

The remora or sharksucker (Echeneididae) include eight species that rely upon hitchhiking. These fishes attach onto much larger fish, turtles, and whales (Fertl and Landry, 1999; Guerrero-Ruiz and Urbán, 2000; O'Toole, 2002; Brunnschweiler and Sazima, 2006; Sazima and Grossman, 2006). Even larger sharksuckers (*Echeneis naucrates*) can be a host for juveniles (Brunnschweiler and Sazima, 2006). Attachment onto large mobile hosts minimizes the energy expenditure to locomote by remoras. When attached to a moving object or in a current, remoras use the water flow for respiration, switching from active branchial ventilation of the gills to passive ram gill ventilation (Parin, 1968; Steffensen and Lomholt, 1983). Oxygen consumption is 3.7–5.7% lower for ram gill ventilation compared to branchial pumping. As the cost of gill ventilation can be 5–28% of the standard

metabolism in fish (Cameron and Cech, 1970; Edwards, 1971), the shift to ram gill ventilation can significantly reduce the total energy cost of the remora. The association with larger hosts provides the remora, in addition to a reduction in locomotor costs, with feeding opportunities. Remoras will forage on food scraps left by their host, the host's feces and vomit, parasites on the host's body, and plankton from ram-feeding while attached to the host (Sazima *et al.*, 1999, 2003; O'Toole, 2002; Sazima and Grossman, 2006).

Remoras attach onto their larger host with a suction disk (Fig. 4.5). The sucking disk of remoras is a modified dorsal fin with slat-like transverse ridges, which are modified spines (Moyle and Cech, 1988). Muscles erect or depress the spines on the disk. During suction, the spines are erected creating a sub-ambient chamber and a pressure differential for suction (Fulcher and Motta, 2006). The suction pressure generated by *E. naucrates* has been recorded up to -103 kPa. The pressure difference is highest when the sharksucker is attached to a smooth surface, but decreases to -47 kPa on sharkskin. However, more force is required to dislodge the sharksucker from rough sharkskin

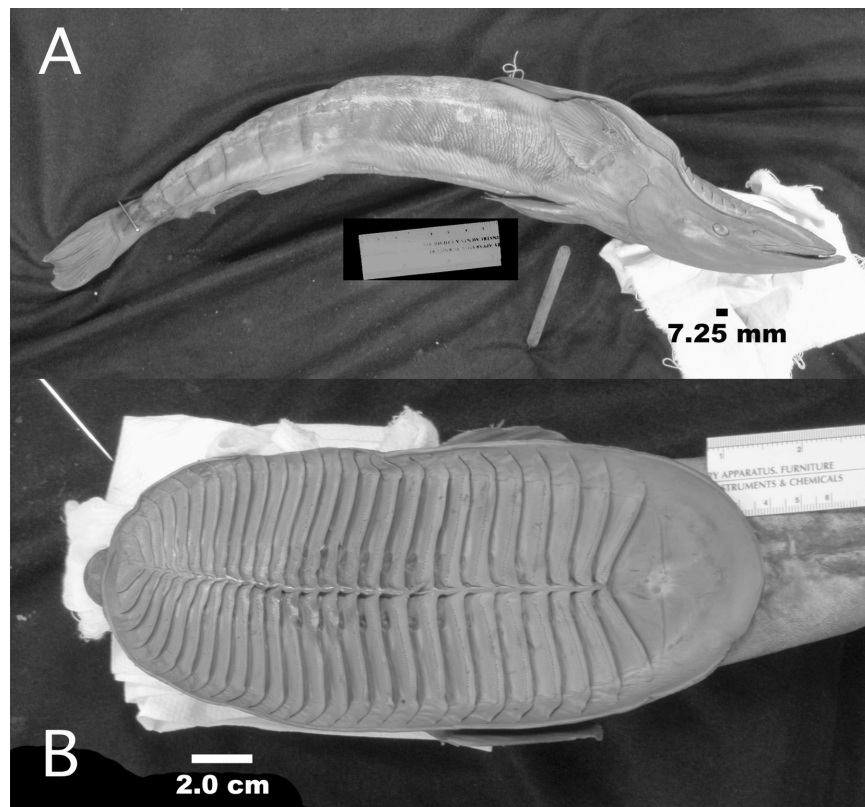


Fig. 4.5 A photograph of a remora showing a lateral view (A) and close-up of the sucker (B).

compared to a smooth surface as friction is increased to the sucker spines (Fulcher and Motta, 2006). Townsend (1915) found that 0.61 and 0.67 m long specimens of *E. naucrates* could lift pails of water weighing 93.4 and 107.9 N, respectively.

The association can negatively impact the remora's host. Remoras are considered a hydrodynamic parasite as they disrupt the flow of water over the body of their host and potentially increase the host's drag (Moyle and Cech, 1988). In addition, the suction developed by the disk and presence of the disk spines can act as an irritant on the skin of the host. Schwartz (1992) observed an open sore on a sheephead (*Archosargus probatocephalus*) due to the attachment of a remora. Remoras would be particularly irritating to a highly sensitive and naked skin, such as in dolphins (Fish *et al.*, 2006). The spinning aerial leaps that are executed by spinner dolphins (*Stenella longirostris*) were suggested to be a mechanism in the removal of remoras (Hester *et al.*, 1963; Fish *et al.*, 2006). The spinning may be a behavioral response to remora attachment necessitated by an inability to remove parasites by use of traditional mechanisms of biting, combing, scratching and rubbing (Gunter, 1953). The high rotation rates could aid in peeling away the suction disk from the dolphin's body and the orientation of the dolphin's body during re-entry into the water could produce enough hydrodynamic force to shear off the unwanted remoras (Fish *et al.*, 2006; Weihs *et al.*, 2007). Sharksuckers appear to irritate sharks and induce rotational and non-rotational behavioral patterns. Jumping by blacktip sharks (*Carcharhinus limbatus*) was proposed as a means of dislodging attached remoras (Ritter, 2002; Ritter and Brunschweiler, 2003).

Drafting

A fish can take advantage of the thrust produced by a larger animal by swimming in a hydrodynamically favorable region. The close proximity of the two bodies induces an interaction of their pressure and flow fields. The presence of the neighboring bodies causes the flow between them to increase, which produces a pressure drop (Bernoulli effect). The pressure drop creates a suction force resulting in a mutual attraction that exerts an equal and opposite force on each animal (Kelly, 1959; Weihs, 2004). Due to the difference in masses of the animals, the smaller fish is pulled along with the larger. A smaller individual can swim with reduced energy costs at the expense of the larger. This free-riding behavior is associated with drafting or slipstreaming, and bow-riding (Lang, 1966; Fish, 1999; Weihs, 2004).

Drafting uses the flow field along the sides of a large animal to "pull" the smaller fish forward, whereas, bow-riding uses the high pressure generated in the anterior region of a large individual to "push" a smaller fish forward without physical contact. This latter mechanism is often observed by dolphins

swimming in front of ships (Fish and Hui, 1991). The pilotfish (*Naucrates*) swims in the flow field in front and along the sides of larger fish like sharks (Parin, 1968; Magnuson and Gooding, 1971; Clark and Nelson, 1997). Although a reduction in energy expenditure by pilotfish has been ascribed to swimming in the boundary layer of the shark, such is not the case. The boundary layer is generally too thin relative to the size of the pilotfish. It is rather the interaction of the mutual pressure fields of the fishes that permits drafting. Trout (*Oncorhynchus mykiss*) are able to hold station in front of a cylinder in a water current (Liao *et al.*, 2003b). The trout displays reduced tail-beat amplitudes and body wave speeds, indicating low energy costs. This effect is due to the same mechanism as bow wave riding.

A variant of drafting is the use by animals of the wake from obstructions in a flow stream (Webb, 1998a). By swimming behind an object shedding a vortex wake, an animal could extract energy from the flow (Fig. 4.6). The flow behind a rigid, bluff (non-streamlined) body is non-steady. The pressure on the downstream side of the bluff body is low forming a suction and drawing fluid back toward the body. This reversal in flow direction leads to instabilities in the boundary flow adjacent to the body and causes flow separation from its surface. Flow separates alternately from each side of the body producing two staggered rows of vortices, which are shed into the wake. All the vortices in one row rotate in the same direction, but opposite to that of the other row. This flow pattern around a bluff body is a drag-type of vortex street or Kármán vortex street (Fig. 4.6). The vortex pattern is stable for a long distance downstream if the distance between successive vortices on the same side is 3.56 times the distance between the two rows (Vogel, 1994). Due to the direction of rotation in the vortex street, the flow in the center of the street is directed anteriorly. By swimming between the parallel vortex rows of the Kármán vortex street, the cost of locomotion can be reduced (Fish, 1999). The trailing fish will experience a reduced relative velocity compared to the free stream velocity. As drag is proportional to the square of the velocity, the fish will expend a reduction in energy to maintain position between the bluff body.

Fishes are able to use vortices shed by objects in flowing water and radically alter their locomotor kinematics to maintain station well downstream of any suction region (Webb, 1998; Liao *et al.*, 2003a, b; Liao 2004; Beal *et al.*, 2006). The fish can extract sufficient energy from the oncoming vortices to develop thrust and overcome the drag on the body (Beal *et al.*, 2006). Fish coordinate the swimming motions with the alternating vortices of the Kármán street. This locomotor gait, termed the Kármán gait, was observed in fishes swimming 3–6 fish body lengths downstream of a cylindrical object in the Kármán vortex street shed by this object.

Trout (*Oncorhynchus mykiss*) swimming in a Kármán street alter the body kinematics. Large lateral oscillations of the center of mass occur as the body

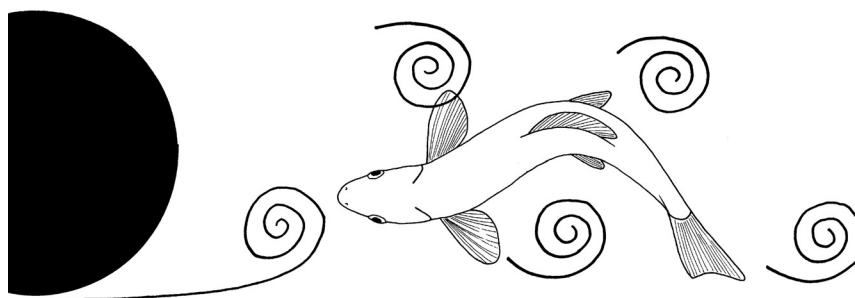


Fig. 4.6 Karman vortex gait. The fish is swimming directly behind a bluff body, which is alternately shed vortices. The fish stays between the two rows of vortices.

is buffeted from side to side in the vortex street (Fig. 4.6). The amplitude of lateral body movement and body curvature are both much greater than during free-stream locomotion (Liao *et al.* 2003b). Tail-beat frequency is lower than when swimming in the free stream and matches the frequency of vortex shedding by the cylinder (Liao *et al.*, 2003b).

Trout can maintain position in the central downstream flow between vortices with very little activity of body musculature (Liao *et al.*, 2003a). This reduction in muscle activity when swimming in a Kármán vortex street strongly suggests that fishes are experiencing a considerable energy savings compared to free-stream locomotion. In effect, the fish can capture energy from vortices generated by the environment. The strength of this mechanism was demonstrated when a dead fish was towed behind a cylinder (Liao, 2004; Beal *et al.*, 2006). With no muscular effort, the dead fish “swam” against the water current and moved forward passively into the suction region behind the cylinder.

Naturally formed vortices are generated by obstructions in a flow (e.g., stones, tree branches) and interactions with surface interfaces (i.e., river bottom, stream banks). For fish holding station, the vortices need to be predictably shed (Webb, 1998; Liao *et al.*, 2003a, b). Unsteady perturbations will require greater energy allocation for stability.

Vorticity control

The production of vorticity is a consequence of the propulsive motions of animals in a fluid. As a shearing action is imposed on a separating flow, it induces a rotation in the form of a vortex. A vortex functions to transport momentum into the fluid, which can be used in the generation of thrust (Rayner, 1985, 1995). However, the vorticity will demand the expenditure of energy and lower propulsive efficiency. Thus, there has been interest in using vorticity to enhance propulsive performance.

Rosen (1959) developed the vortex peg hypothesis. He observed cross flows around the dorsal and ventral surfaces of a sprinting fish. The cross flows produced vortices on alternate sides of the body. Rosen postulated that the fish actively produced the vortices to act as quasi-static pegs. The fish could push off the vortices to affect propulsion. Rosen (1959) concluded that the drag on the fish was near zero. However, the velocity of flow adjacent to the fish from the vorticity would be higher than the free stream velocity, resulting in higher drag (Webb, 1975).

More recently, the idea that vorticity generated along the body or leading edge of the tail of a swimming fish upstream of the trailing edge of the propulsive caudal fin could enhance thrust production and increase efficiency (Ahlborn *et al.*, 1991; Triantafyllou *et al.*, 1993, 1996; Gopalkrishnan *et al.*, 1994; Anderson, 1996; Anderson *et al.*, 1998; Bandyopadhyay and Donnelly, 1998; Barrett *et al.*, 1999; Wolfgang *et al.*, 1999). Ahlborn *et al.* (1991) developed the vortex excitation/ destruction model. In the model, a starting vortex is produced before being acted upon as the fin is quickly reversed. This action produces new vortices on the opposite side of the fin, which gain strength at the expense of the primary vortex. Higher power is achieved (Ahlborn *et al.*, 1991). This mechanism is particularly applicable to starts from rest.

Using digital particle image velocimetry (DPIV), Anderson (1996) and Wolfgang *et al.* (1999) were able to demonstrate the development of vorticity along the sides of an undulating fish. This vorticity was developed in a manner similar to flow along an undulating plate (Wu, 1971a). The bound vorticity was conducted toward the trailing edge of the caudal fin. The bound vortices combined as they were being shed into the wake to produce an amplified vortex. The next set of vortices shed into the wake had the opposite rotation. This produced a pair of counter-rotating vortices and a thrust jet. Continuous vortex shedding produces a wake with the thrust type reverse Karman vortex street (Weihs, 1972; McCutchen, 1977; Müller *et al.*, 1997; Wolfgang *et al.*, 1999; Lauder, 2000). The interaction of vorticity generated along the body and shed at the caudal fin conformed to the mechanism discussed by Gopalkrishnan *et al.* (1994). A similar pattern of vorticity was observed for fish executing a turn (Anderson, 1996; Wolfgang *et al.*, 1999). It was postulated that this mechanism of propulsion was dependent on active control involving coordination of the body undulation and caudal fin motion (Wolfgang *et al.*, 1999).

Use of vorticity generated along the body to enhance wake structure is limited in high-performance thunniform swimmers. These animals are relatively stiff anteriorly, have nearly circular or elliptical cross-sections, and display extreme narrow-necking (Webb, 1975; Lindsey, 1978). These morphological features should not promote the production and conduction of bound vorticity along the body. However, the heaving and pitching motions

of the relatively stiff, high-aspect ratio caudal propulsor could produce leading-edge vortices, which would impact the wake structure (Anderson *et al.*, 1998). The development of leading edge vortices from dynamic stall has been experimentally demonstrated to produce high-lift forces (Ellington, 1995; Dickinson, 1996; Ellington *et al.*, 1996; Dickinson *et al.*, 1999). The leading edge vortex would interact with the trailing edge vortex to produce thrust. This vorticity control is the principle mechanism by which high efficiency is achieved (Anderson, 1996; Anderson *et al.*, 1998). Anderson *et al.* (1998) demonstrated propulsive efficiencies of over 85% for a rigid flapping foil.

Experiments with the biologically-inspired RoboTuna showed that under a particular set of kinematic conditions the swimming robot could reduce its drag in excess of 70% compared to the same body towed straight and rigid (Barrett *et al.*, 1999). The conditions, which produced this reduction in drag, deviated from the kinematics found in living thunniform swimmers. In particular, the lateral excursion of the caudal propulsor was 12% of body length (Barrett *et al.*, 1999), whereas the typical excursion of the caudal propulsor in animals is approximately 20% of body length (Fierstine and Walters, 1968; Webb, 1975; Lindsey, 1978; Fish *et al.*, 1988; Fish, 1993b, 1998a; Dewar and Graham, 1994b; Gibb *et al.*, 1999). Deviation from the optimal settings of kinematic parameters for RoboTuna resulted in a drag augmentation of 300% (Barrett *et al.*, 1999).

Large energy gains by vortex control can only be realized when the vortices are from energy sources external of the fish (e.g., schooling). A fish that is not subjected to external energy sources and the water immediately around it are a closed system with a finite amount of energy. The internally generated mechanical energy required for thrust production cannot be enhanced beyond the energy available in the system. Vorticity shed anterior of the caudal fin is essentially wasted energy. Capture of this wasted vorticity can reduce the total wasted energy and increase propulsive efficiency (Lighthill 1970; Wu, 1971b; Webb, 1975; Weihs, 1989; Barrett *et al.*, 1999). However, this increase in efficiency may only be marginal. In the case of vorticity shed from anterior fins (e.g., dorsal fin), a proportion of the additional thrust generated by the fin would be used to overcome the drag of the fin. Removal of the anterior fin, although affecting stability, may not adversely affect propulsive performance. Indeed, during steady propulsion, BCF swimmers will collapse highly flexible fins to reduce the lateral body profile and drag (Webb, 1977).

Aerial behavior

The high energy demand of movement in water can be reduced by leaving the water and entering an aerial phase. This behavior is performed by penguins and the fastest mammalian swimmers (Hui, 1987; Reidman, 1990;

Fish and Hui, 1991) in a series of rhythmic leaps, referred to as porpoising (Fish and Hui, 1991). At high speeds, the energy required to leap a given distance is considered less than the energy to swim at the water surface (Fig. 4.7; Weihs, 2002). Although they do not porpoise, flying fish (Exocoetidae) have the ability to launch themselves from the water and glide in the air (Aleyev, 1977; Fish, 1990; Azuma, 1992). Gliding has been considered as a behavior that decreases the energetic expenditure of locomotion with a low-drag aerial phase (Shoulejkin, 1929; Rayner, 1981, 1986; Davenport, 1994). Another possibility is that gliding is used to transport flying fish from food-poor to food-rich patches in the ocean (Davenport, 1994).

Flying fish possess wing-like surfaces to generate lift for flight. The wings are composed of elongate pectoral and pelvic fins, with the pectoral fins being the primary wing (Breder, 1930; Fish, 1990; Davenport, 1992). The morphological differences in wing structure were expressed by Breder (1930) as based on the airplane design at the time. A monoplane type was exemplified by the genus *Exocoetus*, which possessed a single set of long narrow pectoral fins, and the biplane type by *Cypselurus* with expanded pectoral and pelvic fins. These aerodynamic configurations displayed differences in flight performance for the two genera (Fish, 1990).

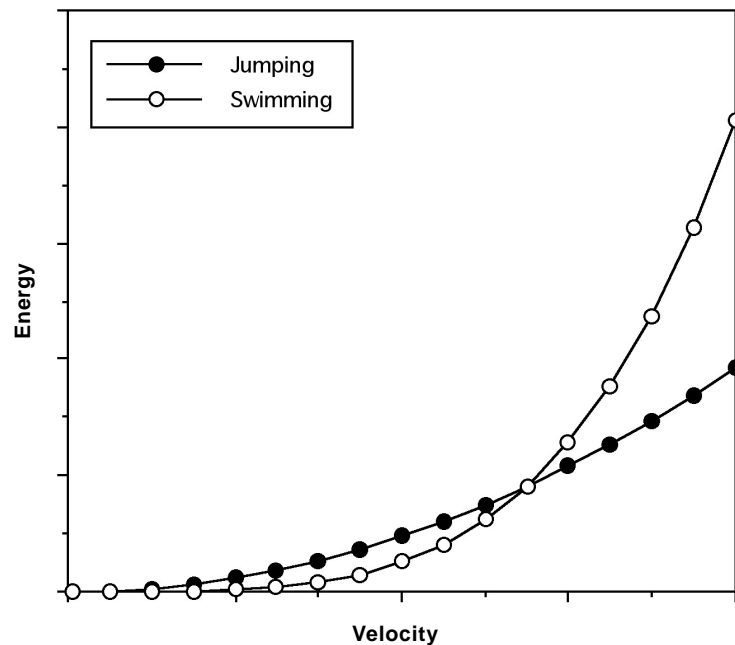


Fig. 4.7 The energies required for swimming close to the water surface and for jumping according to the model proposed by Au and Weihs (1980). The crossover velocity (i.e., where it becomes more economical to jump a given distance than to swim) occurs at the intersection of the two curves.

Take-offs vary with the genus of flying fish. *Cypselurus* uses a “taxiing glide” at the water surface for the initiation of flight (Breder, 1929; Hubbs, 1933, 1936; Hertel, 1966). The ventral surface of these fish is flat to act as a planing surface as the fish emerges from the water. During the taxi, the elongate lower or hypocaudal lobe of the caudal fin continues to remain in the water and generate thrust, increasing speed for take-off from 10 to 16–20 m/s (Shoulejkin, 1929; Mills, 1936a; Edgerton and Breder, 1941; Franzisket, 1965; Aleyev, 1977). The average taxi distance is 9 m (Hubbs, 1933). Once the trunk of the fish clears the water, the pectoral fins are opened and set at a small positive angle of attack to generate lift (Hubbs, 1933; Aleyev, 1977). The pectoral fins are opened lifting the tail from the water as the fish becomes airborne (Hubbs, 1933). Alternatively, initiation of the flight of *Exocoetus* is characterized by emergence from the water at an angle up to 45° (Shadbolt, 1908; Abel, 1926; Hubbs, 1933; Edgerton and Breder, 1941; Hertel, 1966).

The glide path of flying fish is regarded as relatively flat (Seitz, 1891; Breder, 1930, 1937). Maximum height of the glide is 6–7 m above the water (Ahlborn, 1897; Aleyev, 1977). Glide distances are generally greater for *Cypselurus* compared to *Exocoetus* and other flying fish genera that use a short taxi (Hubbs, 1933; 1936). Typical flights of 15 to 92 m for *Cypselurus* were reported. It was claimed that when flying with the wind flying fish could traverse 400 m in a single glide (Hubbs, 1918; Aleyev, 1977; Davenport, 1994). Total flight distance is extended by successive glides (Dahl, 1891; Breder, 1929; Hubbs, 1933, 1936; Forbes, 1936; Loeb, 1936, Mills, 1936a, b). At the end of a single flight, the flying fish will lower its hypocaudal lobe of the caudal fin into the water and accelerate the body to produce enough thrust for another glide. Successive glides, totaling as many as 12, can increase flight time and greatly increase the maximum flight distance (Hankin, 1920; Breder, 1929; Aleyev, 1977).

The reduction in drag in an aerial flight could minimize the energy expenditure in swimming over the same distance, particularly if swimming were to occur close to the water surface (Hertel, 1966). However, the increased drag incurred by wings and accelerated swimming during the taxi may limit any substantial energy savings. While energetic arguments at this time cannot be validated, a more probable use of an aerial phase by flying fish is the assertion that gliding is an anti-predator mechanism (Gill, 1905; Hubbs, 1933). In contrast to simple ballistic jumps, the aerial trajectory of a flying fish makes the position of reentry unpredictable to any predator confined to the water (Davenport, 1994).

Aerial behavior is also exemplified by the leaps of other fishes, including needlefishes (Belontiidae), halfbeaks (Hemiramphidae), silversides (Atherinidae), and salmon and trout (Salmonidae) (Gudger, 1944; Gunter, 1953; Stuart, 1962). Leaps by salmonids are used to negotiate obstacles and

waterfalls during upstream migrations (Osborne, 1961; Stuart, 1962; Lauritzen *et al.*, 2005). To make such jumps, the fish must accelerate quickly to a high take-off speed and expend considerable energy. A higher jump requires a higher take-off speed (Lauritzen *et al.*, 2005). However, a fish can be aided by using the upward tangential flow of the vortex produced by the water falling into a pool at the base of a waterfall (Stuart, 1962).

Currents and microhabitats

Fish will often migrate in areas where constant current or tidal currents are present (Weihs and Webb, 1983). When migrating downstream, the fish benefits by swimming with the current. The relative velocity between the fish and the water flow is reduced with a concomitant decrease in drag. Selective tidal stream transport by fish has been shown theoretically to provide a means of energy conservation (Weihs, 1978). When tidal current speeds are high, the fish can save 50% or more of its energy by swimming in midwater in the same direction of the current and resting on the bottom when the tide is moving in the opposite direction (Weihs, 1978; Weihs and Webb, 1983).

In a variable current, such as in estuaries and coastal areas, the energetic cost of swimming is minimized if these variations are ignored and a constant speed is maintained (Trump and Leggett, 1980). The cost of swimming for migrating plaice (*Pleuronectes platessa*) using tidal stream transport is about 20% less than the cost for continuous swimming (Metcalf *et al.*, 1990). Even greater energy saving can be realized by these flatfish if burst-and-coast swimming is employed. An effective strategy used by flatfish is to rest on the bottom when the tidal current is flowing in a direction that is unfavorable for the fish (Weihs and Webb, 1983). The fish then swims when the tide is flowing in favorable direction. Even when the fish is swimming against the current reverse-flow vortices may be used to reduce the energy cost of swimming (Hinch and Rand, 2000). Such vortices would be more prevalent in river and stream habitats, where interactions between the water and solid interfaces would more readily shed vorticity into the flow.

Swimming near a solid surface, such as a river bottom or bank, can be advantageous when moving against a current. Despite the flow, the water at the interface with the solid has the same velocity as the solid (Vogel, 1994). Thus a hard river bottom will have a zero velocity as will the water adhering to its surface. This is the “no slip” condition. The layers of fluid adjacent to the interface are sheared due to viscous effects between the successive layers and the flow in the outer stream. This effect results in a velocity gradient within the fluid with the velocity varying with distance from the surface (Vogel, 1994). This layer of sheared flow is the boundary layer with a velocity gradient varying from zero at the interface to 99% of the free stream velocity. Fish

swimming near the interface and in the boundary layer experience a lower velocity relative to the current in the open water.

A number of behaviors described as “flow refuging” (Webb, 1998) minimizes or avoids the energy cost of swimming by taking advantage of low-flow microhabitats. By swimming in pools, behind physical obstructions, or within the boundary flow against a solid substrate, a fish takes advantage of the lower flow compared to swimming in the main stream or current (Feldmeth and Jenkins, 1973; Fausch, 1984; Webb, 1993a, 1998). Osborne (1961) argued that migratory fish would seek low-velocity water close to the bottom or shoreline. Rainbow trout (*Oncorhynchus mykiss*) and rosyside dace (*Clinostomus funduloides*) typically swim in microhabitats with velocities substantially lower than all the velocities available, avoiding energetically expensive microhabitats (Facey and Grossman, 1990, 1992). Osborne (1961) proposed that salmon migrating upstream could take advantage of irregularities in the bottom contour to reduce energy costs.

The flow patterns due to microhabitats are used to reduce energy costs in station holding. Mottled sculpin (*Cottus bairdi*) are a relatively inactive benthic fish (Grossman and Freeman, 1987). Sculpins have a strong preference for zero or low velocity microhabitats (Facey and Grossman, 1992). In a flow, the sculpin holds position by clinging to the substrate. The enlarged pectoral fins generate a downward force due to the water flowing over them. Similarly, plaice (*Pleuronectes platessa*) utilize changes in body and fin posture for station holding on the bottom and avoid active swimming in a flow (Arnold, 1969; Arnold and Weihs, 1978; Webb, 1989, 2002). Cod (*Gadus morhua*) and plaice are able to take advantage of substratum ripples to find areas of retarded flow to station-hold (Gerstner, 1998; Gerstner and Webb, 1998). With its compressed body form, the benthic plaice can be sheltered by bottom ripples with heights of 4% of total fish length or wavelengths of four times total fish length (Gerstner and Webb, 1998). Fusiform fishes, such as cod and cyprinids, require that bottom ripples have heights of 6–8% of total length (Gerstner, 1998; Webb, 2006).

In shallow water, the optimal position in a current may not always be close to a solid substrate, such as the bank of a stream. Fish swimming in deeper water experience less wave drag. Wave drag is the additional resistance from gravitational forces in the production of surface waves when moving at or near the air-water interface. Kinetic energy from the animal motion is lost as it is changed to potential energy in the formation of waves (Vogel, 1994). The wave drag can reach a maximum of five times frictional drag (Hertel, 1966). Maximum wave drag occurs when the body is just submerged at a relative depth of 0.5 of the maximum body diameter and negated at a depth of three times maximum body diameter (Hoerner, 1965; Hertel, 1966). Huges (2004) generated a wave drag model that accurately predicted that large chinook salmon (*Oncorhynchus tshawytscha*) swam further from the bank to avoid wave

drag. In addition, the model predicted that smaller sockeye salmon (*Oncorhynchus nerka*) should swim relatively closer to the bank to minimize migration costs.

Despite the energetic advantage of swimming or station holding in a flow near an interface with a solid body, there is a trade-off in remaining in a low velocity microhabitat. Under such flow conditions, the availability of prey items may be reduced. This is particularly the case in drift feeding, where the rate of prey availability is determined by the flow (Fausch, 1984; Facey and Grossman, 1992). Feeding in fast flowing currents may then facilitate a net gain in energy. Juvenile smallmouth bass (*Micropterus dolomieu*) increase the rate of net energy gain by moving into shallow-fast microhabitats (Sabo *et al.*, 1996). Stream salmonids were observed to take up positions in moderate current speeds that were close to faster flowing water (Everest and Chapman, 1972). This position was proposed to maximize the quantity of prey delivery, while minimizing the energy cost to maintain station.

CONCLUDING STATEMENT

The ability to control internal energy expenditures and exploit external energy sources permits fishes to reduce their energy for swimming (Table 4.1). While various behaviors for energy economy have been recognized, it has been mainly the mechanistic basis of the interaction between the fish and the water, which has been explored. These behaviors and their apparent energy savings have not been adequately investigated with respect to the muscle dynamics, total energy budget, or ecology. Are muscles tuned for particular species to operate efficiently with an energy saving behavior? If energy is a limited commodity for wild stocks, what are the savings as a proportion of total energy demands? Are energy savings by a particular behavior substantial enough that individuals not effectively using them are subject to reduced fitness or elimination by natural selection?

A uniform conceptual framework is lacking. While motion and theoretical studies have dominated the discipline (Weihs, 1973b, 1974; Lighthill, 1975; Webb, 1975), experiments using metabolic and muscle measures have been more limited (Belyayev and Zuyev, 1969; Liao *et al.*, 2003). Laboratory studies need to be performed in which metabolic measurements and electromyography are integrated with controlled flow tank experiments over a range of swimming speeds. Furthermore, field energetics need to be correlated with swimming behaviors.

Finally, work in this area has application to the development of nautical technologies that enhance increased efficiency and energy economy (Bandyopadhyay and Donnelly, 1997; Fish, 2006b; Fish and Lauder, 2006). The construction of biorobotic models provides a new direction for the development of engineered systems with improved propulsive performance

Table 4.1 Behavior and energy sources for energy economy by swimming fish.

<i>Behavior</i>	<i>Energy Source</i>	<i>Mechanism of energy savings</i>
Optimal swimming speed	Internal	Partitioning of metabolic and propulsive energy consumption
Gait transition	Internal	Gearing of muscle power
Burst and coast	Internal	Reduced muscular power and drag by maintaining a straight body
Swim and glide	External	Conversion of potential energy to kinetic energy and reduced muscular power and drag by maintaining a straight body
Schooling	External	Induced current from leading fishes reverses flow direction and reduces relative velocity on trailing fish
Hitchhiking	External	Direct attachment to a moving body
Drafting	External	Reduced relative velocity around drafting animal
Bow riding	External	High pressure behind fish from trailing body
Vorticity control	Internal	Constructive interference between vortices shed from anterior body and caudal fin of same fish
Aerial behavior	External	Change in medium reduces drag
Currents	External	Reduced relative velocity due to mass flow
Microhabitat	External	Induced current or vortices from physical obstructions

(Triantafyllou *et al.*, 1993; Barrett *et al.*, 1999; Bandyopadhyay, 2005; Long *et al.*, 2006; Lauder *et al.*, 2007; Pfeifer *et al.*, 2007; Bandyopadhyay *et al.*, 2008; Techet, 2008). The morphology and energy conservation strategies of fish can serve as model systems to design autonomous aquatic vehicles to function in remote, hostile environments for extended deployments. As the need for greater efficiency and energy economy are desired in engineered systems, imaginative solutions from nature can serve as the inspiration for new technologies (Fish, 2006b).

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