The dynamic soaring of salmon

How salmon gain upstream thrust from pressure gradients and extract energy from velocity shears. Plus other strategies for upstream energy minimization.

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Abstract

Salmon migrating upstream have three sources of energy in addition to their stored body fat. Two are unrecognized: salmon extract velocity energy from pressure gradients and velocity shears. The third has been shown: drag reduction and thrust from the vortices behind rocks. Salmon senses, physiology, and brains have evolved to take advantage of each. Several stream features create pressure gradients that speed or slow flows, including partial venturi flows between or around rocks. Where upstream pressure gradient forces slow flows they put upstream thrust on salmon, or equivalently, lower pressure drag on a salmon's body. Salmon will rush through or avoid downstream pressure gradients and higher velocity flows. And using the same 'dynamic soaring' that albatross use to circle the southern hemisphere without flapping, salmon extract energy from velocity shears within streams. As a salmon exits slower flows behind a rock, in shallows, or near the bottom of a stream, the veer into faster current multiplies its water speed. With a turn water speed is turned to ground speed. The salmon is whipped across current, perhaps to dart to a more sheltered part of a stream where that speed can be turned into upstream progress. A turn downstream and then upstream through slower water will bring it back to its starting point, or further, effortlessly. It is unavoidable that salmon use dynamic soaring of the velocity shears between plunging water and turbulent pools to leap waterfalls. I also integrate established salmon behaviors into a more complete picture of salmon upstream energy management.

In a video of an Icelandic stream, six salmon hover in a tight group just upstream of a boulder, barely moving their tails against the current.[1] Other videos show sea trout or salmon holding position while barely moving tails.[2] The usual explanations apply, a local eddy downstream of a boulder, or water slowed near a rocky bottom. But there is a third explanation not visible to human senses. In each video the salmon may have found a local upstream pressure gradient.

Our six salmon may be surfing a rock's pressure-bow wave, or they may have found a well-known situation downstream of a channel narrowing, where the same upstream pressure gradient push that slows flows gives an upstream push on fish, thrust. We'll look at several such situations. For stream fish, upstream pressure gradients are as important an energy source as food.

And there is another generally unrecognized source of energy for salmon migrating upstream. As a salmon verges from slowed flows behind a rock into faster current it instantly gains water speed. This gain in water speed from transitioning velocity shears, where faster water slides past slower, is so unavoidable that salmon would have to fight to not benefit from it. Sometimes they merely take advantage of slower flows behind a rock or near a streambed to gain the speed to charge through faster current. But water speed gained from a shear transition into faster current can be combined with a turn, an angle to onrushing flow that whips them sideways, perhaps to escape a predator, perhaps to cross into a slower part of their stream in which they may turn that cross-stream velocity upstream – free energy.

Velocity shears are a source of energy for various species, including humans. Windmills and sailboats take energy from the shears between wind and land or water. Salmon and other fish species share the ability of many bird species, from albatross, northern fulmars, and swallows, to extract energy from velocity shears. Albatross circle the southern hemisphere without flapping by 'dynamic soaring' (DS), curving between lower velocity air close to the ocean surface and higher speed winds above. Salmon cannot avoid doing something similar in the velocity shears within water. That they do so well is a tribute to highly adapted senses and brains.

Strategically 'flying' pressure gradients and velocity shears are two generally unrecognized means that help salmon migrate hundreds of miles upstream consuming only their body fat.

There are many recognized salmon strategies for upstream migration: Salmon use the upstream vortex flows around plunging water to gain the velocity to leap falls.[3] Similar to the takeoff of flying fish, they can achieve higher leap velocities than underwater swimming velocities as drag disappears while their body emerges from the surface but their tail still provides thrust.[4] Liao and Akanyeti, with a short video and pdf, have shown that trout gain thrust and extract energy from the alternating vortices downstream of rocks.[56] Salmon swim upstream where flow velocities are lowest, in the shallows near banks or near the inside shore of curves, and in eddies behind rocks. Flows also slow close to streambeds – over a wing surface this slowed region is called a 'boundary layer' and may thicken from millimeters to centimeters or more toward the trailing edge, but above a rocky streambed significant slowing may persist upwards for feet, slowing in which a salmon may rest or make better progress than in faster flows. Salmon will usually swim well below the surface to avoid surface wave drag.[7]

Fish evolved specialized brains, senses, and physiologies to optimize responses to each of these environmental conditions, including pressure gradients and velocity shears:

Salmon upstream sensory and bio-computer sophistication

Fish emerged in the Cambrian explosion, 542 million years ago. In early shared and then parallel evolution, fish and birds have developed sophisticated sensory systems and bio-flight-computer brains. Like gliders, powered planes, and dirigibles, salmon 'fly' in a three-dimensional environment similar to that of mountainous terrain with a headwind. The energy management strategies of human pilots are reinventions of what fish and then birds developed over half an eon.

Fish intelligence is beyond the scope of this article, but a web search should help combat the common assumption that fish are primitive lower life forms. Recent studies show that fish have spatial and social learning capabilities and memories similar to other vertebrates.[8] They also perceive what humans cannot:

A fish's lateral line is composed of sensory receptors called neuromasts. They are often in a visible row down its sides, supplemented by more scattered single receptors on its body and head. Fish use their lateral line pressure sensors for awareness of obstacles, predators, and prey. This much is parallel to the echolocation of bats. Fish also use their lateral lines for communication and schooling with their species, and to synchronize with the rhythms of turbulence and vortices within flows, to minimize drag and gain thrust.[9][10] And lateral lines sense flow speed, a second clue to sensing pressure gradients, since varying velocities along a fish's length are partly resultant from pressure gradients.

Other studies show that various fish species develop geometric maps of their environment and retain those memories.[11] In its 'map' a river salmon will include more than rocks. With its lateral line, hearing, and sight, the salmon brain will build a three-dimensional map of the stream ahead and around it, including the perceived and expected pressure and velocity gradients, vortices, and velocity shears surrounding the obstacles of their stream.

With this sensory input, salmon implement sophisticated strategies for upstream navigation and energy management in a highly varied environment of flows and pressures. Responses to this 3D map of obstacles, flows, pressures, and shears will be a blend of learning and instinctual programming, each requiring practice.

For salmon, none of this will be abstract. It will experience an upstream pressure gradient push much like we feel a slight downgrade on a sidewalk or trail. It will experience its environment of pressures, shears, proximity to stream surfaces or streambed, velocities and vortices, in about the same way we experience any varied terrain. But its streamlining must make the experience more like we are a boarder sliding the curving terrain and pipes of a skateboard park during a windstorm.

Salmon upstream navigation requires a different brain capability from that used for ocean navigation. As returning salmon acclimate to freshwater in the brackish water of estuaries they adjust their osmoregulation, the fluid-electrolyte balance that controls cellular osmosis pressures, so they don't dehydrate in freshwater.[12] Hypothesis: It is likely that the parts of their brains devoted to river navigation also develop and expand in this period. This would parallel how the song centers of the brains of migratory birds expand as they enter times of territorial and mating singing.

Disclaimer: verification is needed. Much of what I present is hypothetical, though highly probable. Quantitative studies of how the pressure gradients along the streamlines around obstacles increase and decrease drag forces on salmon are beyond this article but should be easily accomplished. Pressure and skin friction components of drag versus velocity of a model salmon can be compared in steady flows with and without upstream and downstream pressure gradients. Pressure drag will be increased within pressure gradients that accelerate flows downstream. Pressure drag will be decreased within pressure gradients that slow flows. Videos targeting salmon and trout use of shear transitions would be invaluable. In streams with measured velocities, shears, and pressure gradients around rocks, videos and telemetry would help verify salmon upstream strategies.

Pressure gradient basics

The surface of water is always at local atmospheric pressure, so pressure gradients parallel to flows mostly disappear right at the surface of water. But within surface waves, pressure gradients make ‘restorative forces’, perpetuating the wave. Pressure gradients along and across streamlines in flows develop more strongly at greater depths, where there is less leakage of pressure and kinetic energy into surface wave formation. The vertical pressure gradient from depth is irrelevant to fishes of neutral buoyancy.

In addition to accelerations or decelerations from the slope of flow, there are a number of situations where pressure gradients slow or accelerate water. These include where rocks set up immersed bow and stern pressure waves; partial venturis (discussed soon); one-sided venturis (where streambed features set up pressures gradients similar to those above or below a wing); where water plunging into a pool and decelerating raises local pressures; and where lowered wake pressures behind rocks make eddies and even upstream flows.

When a salmon has its tail in ambient pressure and its head in lower pressure it gets squeezed forward much like when you squeezed that cherry pit between thumb and forefinger and it shot across the living room to stain your mother’s favorite lace doily.

But there's a difference: The cherry pit or a solid model of a salmon is pushed by pressures on its surface. A real salmon is pushed by a pressure gradient that pervades its body, just as fluid is pushed by internal pressure differences. Migrating upstream through an upstream pressure gradient, our salmon can have lower pressures within its head than within its tail. Or in a downstream pressure gradient, it will have higher pressures within its head. Still, the result is the same as when you squeezed the cherry pit. It gets a push that can fight or add to drag.

With the addition of pressure drag, skin friction drag, and pressure thrust terms to the pressure gradient term, one could use the Bernoulli equation (discussed soon), normally used for fluid flows, directly on fish. This would yield fish velocities from pressures as if fish were liquid. The Bernoulli equation predicts higher velocities where pressures are lower. In an upstream pressure gradient this would indicate higher velocities for a fish’s head than tail. That can’t happen. Even as drag may slow it, the fish will stretch slightly, its head pulling its tail upstream.

Much of aerodynamics and fluid dynamics is devoted to mapping or predicting the pressure gradients and velocities (flow fields) around various shapes in flows – wings, streamlined and non-streamlined objects, and venturis. We can intuitively translate that to stream flows around and between rocks, depressions, and bridge pylons. The resulting pressure gradients can also be measured and mapped. In relatively simple situations they can be derived.

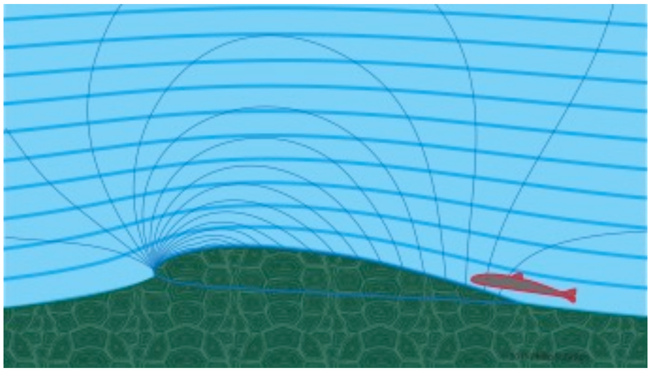

Figure 1: Lowered pressures over a deeply submerged airfoil-shaped rock. Aerofoil Fish has his nose in lower pressure than his tail, reducing pressure drag, gaining thrust. Trout probably fight as much over such energy-saving locations as for food.

A standing wave over a deeply submerged airfoil-shaped rock has about the same pattern of pressures and velocities as over a wing: Flows centrifuge upper, low pressures (inner pressure isolines), that briefly accelerate and narrow flows. Original pressures and velocities are nearly restored near the trailing edge.[13]

Where a pressure gradient is what slows flow, that pressure gradient is putting an upstream force on the flow. But a salmon holding its place or swimming upstream in that pressure gradient has no downstream speed to be slowed. It experiences the same upstream forces as does the water around it, which opposes the drag of water streaming down its sides. A salmon is so incredibly streamlined that the upstream force of a pressure gradient can be significant, a major energy source.

Figure 2: Raised pressures and slowed flows around an inverted airfoil-shaped depression in a creek bed. Aerofoil fish deux has her tail in higher pressures than her head and is taking advantage of lowered boundary-layer flow velocities close to the streambed.

The pattern of pressures and velocities around this dip is the same standing wave as we'd see under a wing, upside down. Flows centrifuge slightly higher pressures, especially 'under' a wing's leading edge. Where flows approach higher pressures they thicken and slow, a pressure gradient that puts upstream thrust on a fish. Flip the picture for flight orientation.[14]

Note that Ms. Salmon could have scooped out this depression as her redd (her nest). In its slowed flows and maybe an upstream eddy more of her eggs will remain until she can scoop gravel over them.

This is not the sort of thing a human experiences, and so is counterintuitive. I have occasionally enjoyed swimming into current as it sweeps around a large rock and slows. But my experience is entirely different from that of a salmon or trout. Being a primate I'm not very streamlined. The major force on my body is always drag from flow, dwarfing any of the stream's pressure forces. If I were to dive to the bottom, the effects of even a strong pressure gradient on my progress would be negligible compared to drag from flow. But for a salmon, pressure gradient forces are important.

For example, at 1:52, a YouTube video shows salmon barely moving their tails upstream of a submerged rock. It is taking advantage of the rock's bow-wave upstream pressure gradient and slowed boundary layer flows close to the streambed.[15]

It will intuitively seem strange that a salmon could get upstream thrust from a pressure gradient, thrust that at least fights the drag of flows down its side. But this phenomenon is well established, for wings. Near stall, air above the back part of a wing is pulled forward by an 'adverse pressure gradient' in the same way a salmon may be pulled forward by an upstream pressure gradient. Over the back three-fourths or so of a lifting wing there is always a forward pressure gradient that slows flows that were temporarily accelerated further ahead. Near stall that forward pressure gradient over the back part of a wing slows, thickens, and may even reverse a 'boundary layer' of air close to the wing's surface. That's much like how the pressure gradient behind a rock can drag water upstream, in which a salmon may rest or add upstream swimming speed. But those are flow reversals. In some situations the salmon is the eddy pressured upstream while flows down its sides are only slowed. In upstream pressure gradients salmon get at least a reduction in pressure drag, and sometimes net thrust.

Quantitative pressure gradient forces within a fish:

Imagining the varying pressures on a salmon's surfaces as similar to the squeeze of fingers on a cherry pit is an appealingly intuitive way to visualize the upstream push on a salmon. But a cherry pit is more like a submarine, on which pressures don't penetrate its interior. And quantitatively using surface pressure forces on something as oddly shaped as a salmon is difficult.

Every molecule of a salmon's body is pushed by the pressure gradients that pervade its flesh, just as the water around it is pushed by internal pressure differences.

Quantitatively, the upstream pressure gradient force on a fish is approximately equal to the average deceleration of flow surrounding the fish times its mass. That's just Newton's F = ma, where the F is the pressure gradient force.

More precisely, the pressure gradient force on the fish is locally proportional to its cross-sectional area, since force equals pressure times area:

$F = \sum_0^L dp/dx * dA/dx$

This reads: Force on the fish is the sum over its length of the local pressure gradient strengths times its local cross-sectional areas.

The Bernoulli equation and pressure gradients

The Bernoulli equation shows how pressure gradients in streams develop more strongly at depths, and how at depth, when we see a velocity gradient around an obstruction we can expect a proportionally larger opposite pressure gradient. That pressure change is what a salmon uses or fights.

The famous Bernoulli equation was actually derived in its modern form by Leonhard Euler in 1752. He named it after his friends, Daniel Bernoulli, who diagrammed a physical relationship between container depth and velocity of leak, and his father, Johan Bernoulli, who is generally credited for the concept of internal fluid pressures, though they had been described by Newton.[16]

$\frac{1}{2}\rho v^2 + \rho g h + p = \text{constant}$

This reads, (half the density x the velocity squared) plus (density x gravity x height) plus (pressure] equals a constant.

In energy terms Bernoulli says that along any streamline there is an exchange of pressure gradient energy, the potential energy of mass at raised elevation, and kinetic energy.

Bernoulli is not complete for energy in flows around fish, where there are drag losses to vortices and turbulence around fins and body, and when a salmon swims within a few body thicknesses of the surface, losses to surface wave formation. More inclusive:

$\frac{1}{2}\rho v^2 + \rho g h + p + \text{losses} = \text{constant}$

Bernoulli exchanges can explain why salmon, given a choice, will swim at least several body diameters below the surface. Near the surface tail-thrust pressures partly leak into wave crest elevation and wave motion, which doesn't do a salmon any good. At depth, the inertia of water above largely contains the pressures of tail thrust, with some losses to stirred up water and vortex pressure drag.

The Bernoulli equation also makes it explicit that where we see a velocity change around an obstruction we can expect a larger change in some combination of pressure or wave crest height, depending on depth.

Velocities are what we can observe with human eyes, but with the Bernoulli exchange, we can infer pressure gradients. In a moderately pure Bernoulli exchange of pressure for velocity, as in a venturi narrowing of a pipe, when we see a small percentage increase in velocity we can infer a larger percentage drop in pressure. Pressure is ideally inversely related to velocity squared. For example, over a given distance, if we see velocity double we can expect at a drop to one-quarter the original pressure, though less in real situations. (See Figure 3.)

In streams, velocity changes are due to a mix of elevation changes as well as the pressure gradients around obstacles. But still, and increasingly with depth, the Bernoulli equation shows that where we see a velocity change we can expect a strong pressure gradient.

Venturi

The venturi effect usually refers to the increased speed and lowered pressure in an idealized, gradual narrowing and expansion in a pipe. But it applies at least partially to any narrowing of flow. Note the term, 'effect.' The venturi effect says what we can expect in a flow constriction, not why it happens. Leonardo da Vinci's approximately 1590 continuity equation observes that for liquids, flow velocity must be inversely proportional to flow cross-sectional area. (Av = constant.)[17]

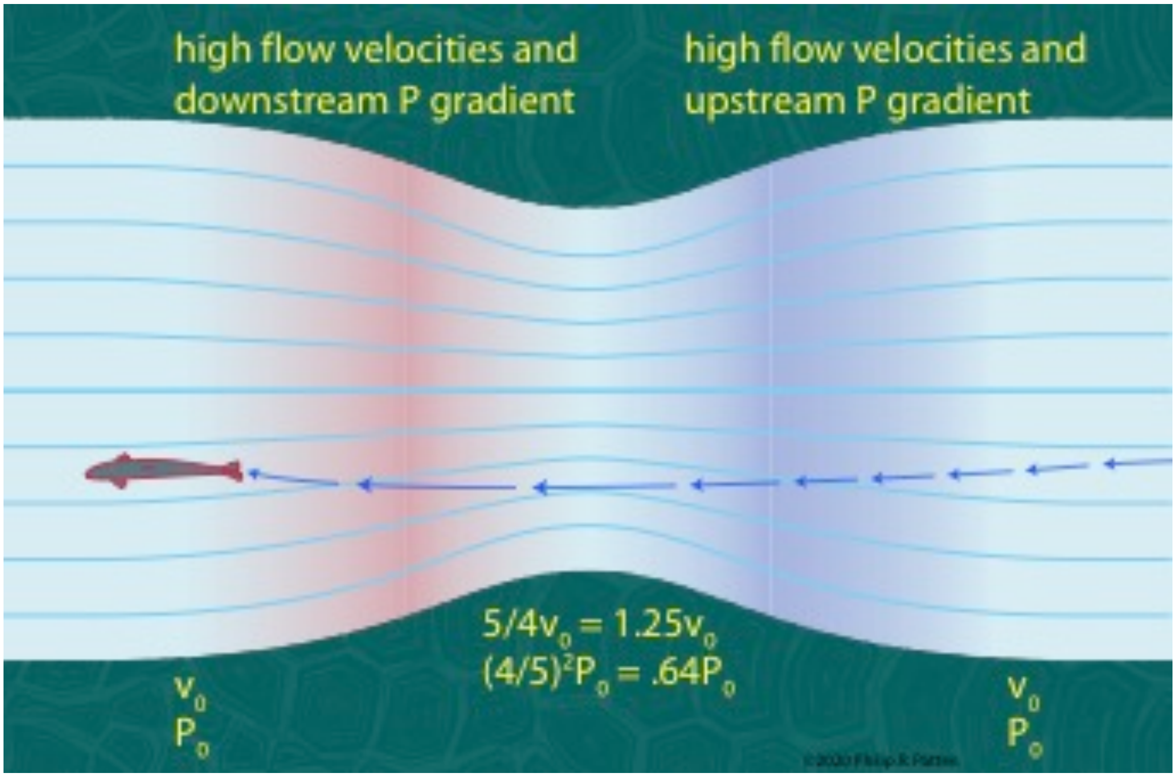

Figure 3: Venturi: In a venturi narrowing, velocity changes inversely with the cross-sectional area of flow. But pressure changes are inversely proportional to the square of velocity changes. So where we see a velocity drop we can expect a proportionally larger pressure increase. Velocity changes around rocks are partly from pressures, partly from the elevation of water into wave crests, and partly from slope. Even so, pressure gradients around rocks in streams are powerful.

Salmon swimming speeds in venturi flows: Red areas are downstream pressure gradient forces. Blue areas are upstream pressure gradient forces. Flow speeds are highest where streamlines are closest together. At most flow speeds, as a salmon swims into increasing flow speeds coupled with an increasingly helpful pressure gradient drag might not change much. The upstream pressure gradient is strongest far from the surface, so a salmon approaching a swimmable venturi may swim near the streambed, where turbulence also slows flows. Rising closer to the surface would lose thrust energy to surface wave creation, but to avoid faster flows ahead it may rise and leap. During the second quarter of the venturi the pressure gradient decreases to zero at the narrowing, while flow velocities increase. The salmon's speed of minimum energy expenditure per upstream progress is higher. It will attempt to further increase water speed as it verges past the narrowest fastest point into slowing flows into an increasingly strong downstream pressure gradient. In the last quarter of the venturi it encounters decreasing flow velocities and a lessening downstream pressure gradient, so it again slows.

The relation between flow velocity and pressure is usually predicted, approximately, by the Bernoulli equation. Bernoulli asserts a lossless exchange along streamlines between pressure, velocity, and elevation of flow. It's useful for its simplicity but does not recognize losses to turbulence, friction, bow or stern surface waves, work, or energy exchanges across streamlines. Real venturis have higher pressures ahead than aft.

Downstream from the narrowest throat of a venturi pressures increase and flow slows. At depth, the narrowing between two rocks has at least a partial venturi effect: Water speed increases between two submerged rocks and then slows. Downstream of the narrowing, an upstream-pressure-gradient-push slows flows and pushes upstream on a salmon, a push that fights the downstream drag on its body.

The pressure-gradient benefit ends when the salmon transitions into the downstream pressure gradient upstream from the narrowest point between the two submerged rocks. There salmon fight both high flow velocities and increasing pressures. And that's where salmon use the same strategies as glider and powered plane pilots in sink or headwinds, to go fast through adverse situations.

Upstream of a narrowing between two rocks a bow-wave forms. Increased downhill slope and increase of pressures from the weight of the wave crest help speed water through the gap. But at depth, upward deflection of water is mostly blocked by the mass (inertia) of water above, so the flows act more like they are going through a venturi restriction in a pipe.

It has long been debated whether the upper curve of a wing is a half-venturi. I'll assert that it is. The other part of the flow restriction is the inertia of the surrounding air. It's the same around a rock in a river. The flow is squeezed between the rock and the inertia of the surrounding water. Water's inertia isn't as rigid as the surface of a second rock, but it still makes a similar constriction and has a partial venturi effect on flow speeds and pressures.

However, venturis depend on a cone or bell-shaped exit profile, which helps lower pressures and increase velocities in the throat.

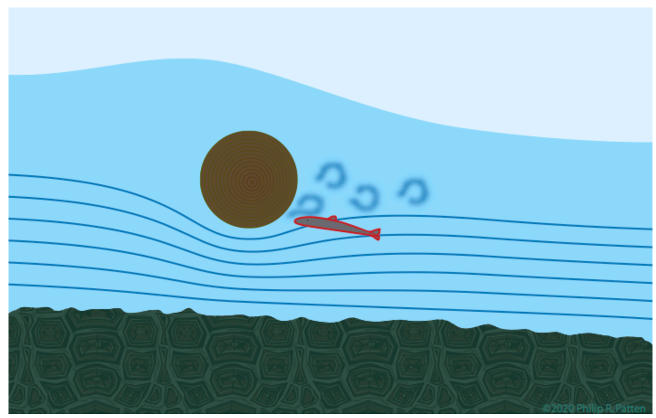

Figure 4: A trout resting in the upstream pressure gradient and Kármán vortices behind a submerged log.

A physical explanation of venturis

Venturi's are counterintuitive. Usually, explanation of the exchange between pressure and velocity along streamlines is limited to quoting the Bernoulli equation. But the Bernoulli equation is non-causal. It predicts but doesn't explain. I will:

In the cone-shaped profile downstream from a venturi narrowing, flows widen out. As da Vinci's continuity equation observes, there isn't enough volume of flow to keep the velocities up. The inertia of slowing fluid drops pressures upstream. It's a little like when you suddenly turn a quarter-turn hose bib off on a translucent garden hose. The water keeps going for a few inches, leaving a strong vacuum behind it that sucks the water back. Plumbers call this a 'water hammer.' But a venturi is more like if you suddenly turned the valve half off. The inertia of the water creates low pressure downstream of the narrowing and an increase in pressure upstream.

Unlike a simple hole in a plate, cone or trumpet-bell exit profiles are good at preserving fairly uniform velocities across each cross-sectional area, uniformity of flow that inertially 'contains' the pressure gradient and lets it build upstream. Upstream toward the narrowing, pressures lower cumulatively, from ambient pressures aft to lowest near the narrowing. That pressure gradient force doesn't just stop at the narrowing, but continues its pull well upstream.

Upstream of the narrowest area, flows are accelerated toward that lowest pressure. That would be sufficient to create an accelerating pressure gradient in the upstream part of the narrowing in a pipe or stream. That accelerating gradient may be enough to disguise a bow wave, or not.

'Bow wave' usually refers to the elevated wave ahead of a ship's prow. But that's a result of the raised pressures ahead of an object in flow. If the object is near a surface, 'immersed bow wave' pressures will escape into elevation. So I use 'bow wave' or 'immersed bow pressure wave' to refer first to raised pressures ahead of an immersed object or flow constriction, and secondly to a visible surface wave, if any.

Bow waves in pipes are not predicted by the traditional Bernoulli equation, but they are often obvious where a stream flows between two boulders. A narrowing acts like a partial dam, sometimes visually raising water levels upstream. At least ahead of each rock, water levels are raised, wave crests whose weight increases pressures below and increases the slope of flow, each contributing to velocity through the narrowing. A raised bow wave ahead of the narrowing may or may not be visible, depending on the slope of the water and the pull of the pressure gradient spreading upstream from below the narrowing, but is always present and raises water levels ahead of the opening above what they would be if bow waves didn't exist.

Downstream of the venturi narrowing, pressures may be lowered further by losses of energy to turbulence. Turbulence and vortex formation absorbs kinetic energy that is then not available to raise pressures. Turbulence often forms in decelerating flows. But large-scale turbulence or vortices may leak volumes of fluid into exiting flows, breaking the 'inertial containment' of the low-pressure gradient, raising pressures in the venturi throat. Similarly, an abrupt exit profile, like a hole in a plate, results in a jet of water that doesn't immediately widen and slow to inertially lower pressures in the orifice upstream.

I noted that bow waves are not predicted by traditional Bernoulli analyses. In a different article, "Isaac Newton's falsely dismissed theory of inertially caused pressure resistance," I show how a more complete Bernoulli equation allows bow waves. But that's another story.

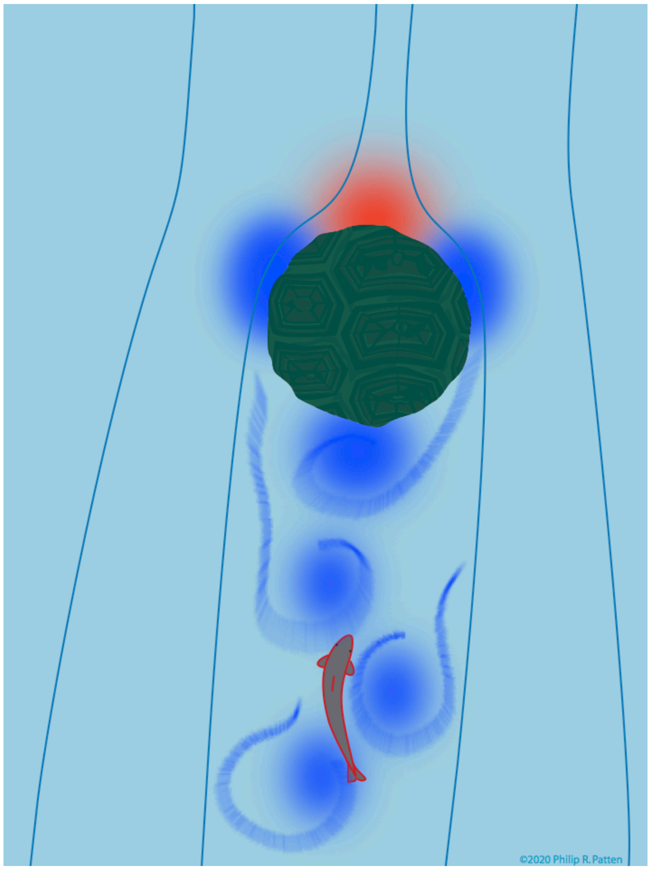

Figure 5: A salmon gaining thrust and minimizing drag in the vortices behind a rock. Its tail gets a push from the inner, forward motion and the centrifugal force of a vortex, while it aligns its body with flows to minimize drag. Ahead of the rock is a bow wave with some combination of raised pressures, raised water levels, and slowed flows. To the sides of the rock, pressures drop and flows accelerate. Downstream of non-streamlined objects expect low-pressures and alternating von Kármán vortices. Such wake eddies dramatically lower pressures right behind the rock and may reverse parts of flow and even the surface slope. An outstanding simulation of Kármán vortex shedding is at http://apps.amandaghassaei.com/VortexShedding/[18]

Kármán vortices downstream of rocks

The strongest slowing or reversing of flows is in the wakes downstream of boulders or bridge pylons. Flows behind blunt objects are more complex than flows behind streamlined objects. Both will have an upstream pressure gradient downstream of their widest points and in wakes, but behind a blunt object alternating vortices often form. As one is swept downstream another of opposite rotation is formed. These are Kármán vortices, eponymously self-named by the late aerodynamicist Theodore von Kármán. They make alternating pulses of low pressure. In a small plane executing a standard power stall, you will feel these as thudding pulses. They are what make a flag wave. In the deep water behind a rock they are invisible to human eyes, being made of transparent water, but not to fish lateral lines.

The slowing of flows behind rocks is more obvious to human senses than pressure gradients or (usually) Kármán vortices. The outer flow in each vortex will be downstream, but the inner flow will be in an upstream direction, or at least slowed. Within these alternating slowings and pulsing upstream pressure gradients a fish can minimize its expenditure of energy until ready to charge into current. It may even be able to bat its tail against the inner, forward moving part of a swirl to extract thrust, while it aligns the forward part of its body to the next vortex flow, minimizing drag.[19]

Salmon as similar to airplanes and airships

The primary definition of ‘navigate’ implies two-dimensional plotting of courses over long distances. That applies to salmon ocean migration, but with the exception of forks, where smell dictates, a stream supplies course.

The second definition of 'navigate' is to lay a course through local, often difficult conditions. While in the ocean salmon are like submarines, salmon upstream migration is more like airplanes or airships flying the eddies of rough terrain against an ambient headwind.

Technically, salmon are very maneuverable bio-dirigibles. Like most fish, salmon use neutral buoyancy to avoid the energy expenditure and drag of maintaining altitude. Like the historic Zeppelin airships, salmon are moderately rigid structures with gas sacs for neutral buoyancy. In fish, these are called swim bladders and don't need to be as disproportionally large as airship bladders. The bladder gas only needs to be lighter than the medium in which a dirigible 'swims,' so airships use gasses lighter than air (hydrogen, helium, or hot air) while fish bladders usually contain air or oxygen,[20] also available against brief hypoxia.[21]

Neutral buoyancy in airships and salmon eliminates the need for wings to maintain altitude and so eliminates the wingtip-vortex drag caused by lift. Similar to propeller tip vortex drag, there will still be vortex drag around fins during propulsion and maneuvering.

For airplanes, lift drag is highest at lower speeds. Form drag (friction and non-lift pressure drag) increases with speed, with minimum total drag at some moderate flying speed. But a salmon doesn't have lift drag. As with a dirigible, a salmon's energy expenditure per speed follows a steepening curve with minimum drag at zero speed.

Against headwinds, airplane minimum fuel usage per distance requires a higher speed than in still air or a tailwind. Decades ago a bush pilot friend described flying a Super Cub at 45 mph into a 50 mph headwind over Kotzebue, Alaska. His ground speed was negative. A salmon has to swim faster than the current to make progress, and significantly faster than current to achieve minimal energy expenditure per travel. But bursts of maximum speed exhaust a salmon in seconds. It will swim at speeds that minimize expenditure-per-upstream-distance, but where that speed is greater than its maintainable speed it will periodically rest. It will charge through a fast current or downstream pressure gradient. It will then seek slower flows near a streambed, shallows, or an eddy in which to recoup.

Just as a glider will increase speed through sinking air or a powered plane may increase airspeed in a headwind to maximize mpg, a salmon will increase swimming speed through higher velocity water and downstream pressure gradients. Within similar patterns of dissimilar forces, similar strategies apply. A salmon works its way to supporting pressure gradients and areas of lowered or reversed velocities in the same way a sailplane pilot hunts thermals. Each searches for supporting energy and avoids or rushes through challenges.

The upstream salmon's energy minimization algorithms

A salmon's form drag is the sum of skin friction and pressure drag. Pressure drag is from speed, turbulence, vortices, and the surrounding pressure gradient.

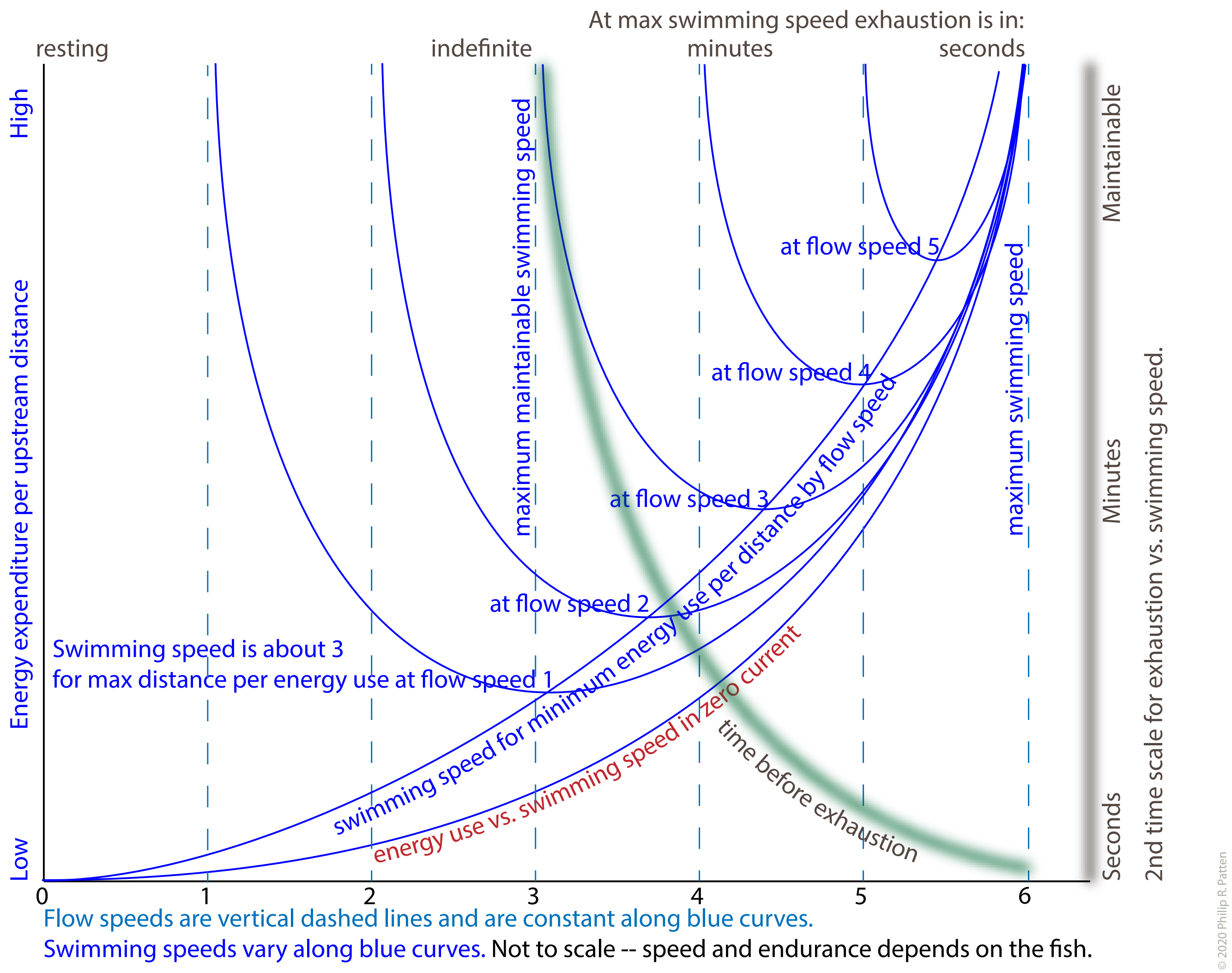

Figure 6: Swimming speeds for minimum energy expenditure per upstream distance increase with stream flow velocity. Unlike airplanes, neutral buoyancy means that fish energy expenditure increases from about zero with zero swimming speed. The time before exhaustion decreases with speed. Increased thrust or drag from pressure gradients are not shown but act like decreased or increased flow velocity.

A salmon creates vortex pressure drag from using its body, tail, and fins for propulsion and maneuvering. An aircraft in flight is in a mushing sink that causes air to spill up around wingtips making tip vortices. Body, fin, and tail forces build trailing vortices much like the airplane wingtip trailing vortices caused by lift. The rotation of such vortices centrifuges their low-pressure centers, which pull back on skin surfaces (for vortex pressure drag) and pull forward on trailing water. But tailfin vortices are more parallel to propeller tip vortices, as each is for thrust. The salmon expends energy on propulsion with losses to the kinetic energy of stirred up wake and to pressure drag as byproducts. Pressure drag from a salmon's motion is a balance between bow-wave pressures ahead pushing back and ‘recovered’ pressures on its aft surfaces pushing forward. Swimming several body thicknesses below the surface also prevents bow-wave and thrust pressures from leaking into wave formation, moving the surface instead of the salmon. Larger species swim deeper and in the faster currents further from shallows than do smaller species, to avoid bow wave pressures leaking into surface wave formation instead of into drag-lowering pressure recovery on their aft surfaces.[22] Tip vortex losses around the tail will be partially blocked if the salmon’s tail is close to the streambed. That’s like a wingtip against the side of a wind tunnel or an albatross touching water’s surface with a wingtip.

A salmon’s upstream swimming speed algorithm is a complex balance between energy for the whole upstream journey and the limited energy available for handling local conditions. For its complete river migration it must balance the drive to get to the spawning ground on time for mating with swimming speeds that don’t prematurely use up its limited supply of fat. If it goes too fast it will run out of fat and won’t reach the spawning grounds. Hypotheses: We can expect that salmon with shorter upstream migrations will travel faster on average than those with longer runs. In slow flows, they will swim at their maximum maintainable speed rather than at minimum energy expenditure per upstream distance. Salmon with the longest stream migrations will swim at speeds that in local conditions minimize energy expenditure per upstream distance, given a couple of constraints: maximum swimming speeds and exhaustion after bursts of speed above a maintainable speed.

The normal component of a centrifuged pressure gradient around a rock

A flow curving around a rock centrifuges a pressure gradient across streamlines with the lowest pressure close to the rock. (Such centrifugally lowered pressures near the widest point of an object are also a major cause of the pressure gradients along streamlines.) A salmon swimming upstream is subject to the same pressure gradient as the water, but its velocity is different so the centrifugal forces on it are independent of the centrifugal forces on the water. If its upstream progress is slower than the downstream speed of water and follows the same curve it will experience less centrifugal force than the water it is immersed in. If not close to the surface that means it will get sucked toward the rock by the pressure gradient, right into the highest velocity flows. It will likely angle away from the rock to avoid those, or blast through them.

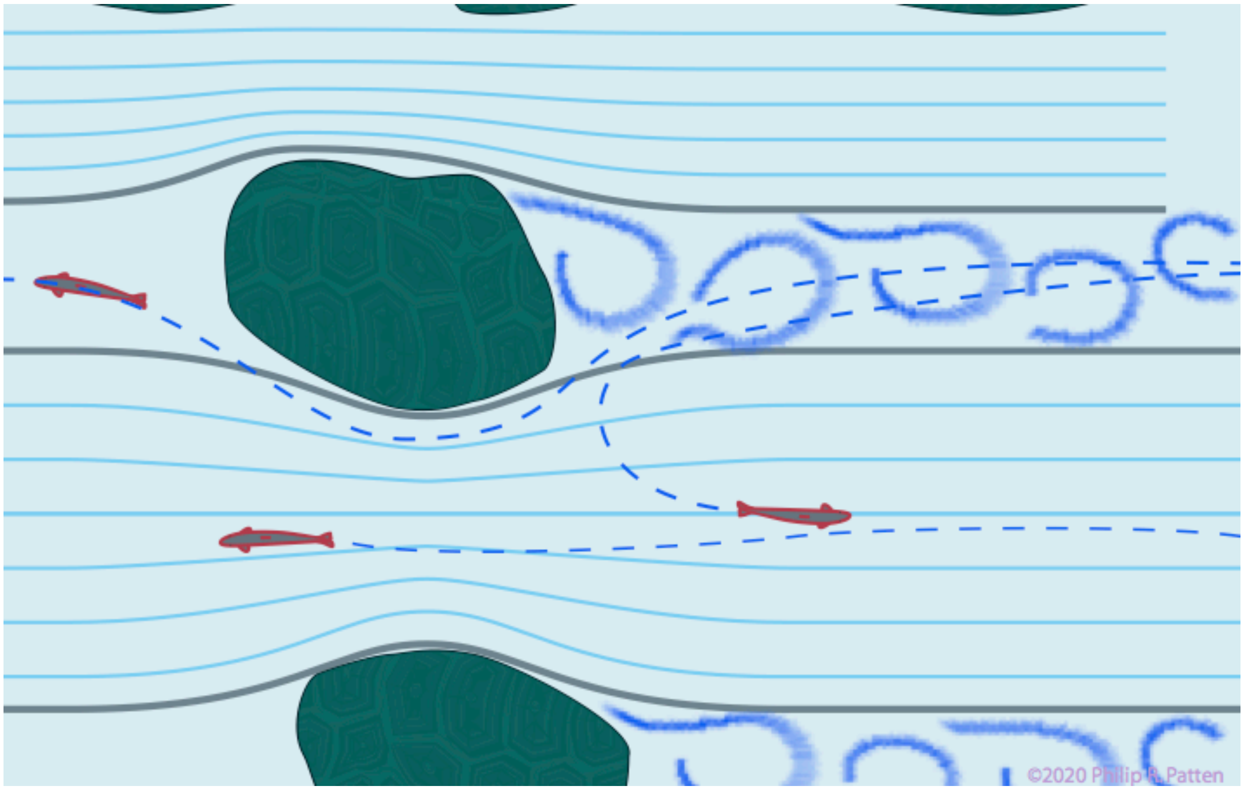

Figure 7: Salmon shear transitions. The salmon that gains speed in the eddies behind a rock before entering faster flows will get further upstream with less energy use than if it charged up the middle of the flow. The shear transition increases its water speed, giving it maneuvering speed should a threat appear. The turn downstream adds its freshly bumped water speed to the speed of the stream, helpful if Brer Bear charges.

Transitioning shear layers: the dynamic soaring of salmon.

There are at least three ways salmon can gain from transitioning shear layers. The first is simply by running upstream in the eddy behind a rock and keeping that momentum as it slides into the higher velocity flows around the rock. Second, the same transition adds water speed, which can be used for maneuvering -- a turn across current turns that bumped water speed into ground speed. The third adds turns and shear transitions for more complex maneuvers, including using dynamic soaring to gain the velocity to leap a waterfall.

The dynamic soaring of birds was first postulated in 1883 by Lord Rayleigh.[23] A good explanation and DS animation is at Wikipedia.[24] There is energy in velocity shears, free for the taking. Sailboats and windmills continuously extract energy from the shear between wind and water or land, but DS extraction from shears is sequential. Each crossing into opposing flows is like a ping-pong ball batted between opposing paddles, gaining higher and higher speeds.

It's what allows albatross to circle the southern hemisphere without flapping. In the last couple decades, model glider pilots have learned to fly circles with a double punch through velocity shears over sharp ridges, increasing airspeed and ground speed at each half-circle until: The world record for a dynamic soaring model glider (no motor) is now 545 mph.[25] (Search on 'dynamic soaring speed record video.') That's 26 mph slower than the historic muzzle velocity of a Colt 1911 .45 pistol bullet!

As DS has become more widely understood it has been observed in many bird species,[26] including fulmars, frigate birds, and swallows.[27] Where there is a source of energy a few hundred million years of bio-flight-computer evolution will have learned how to exploit it. Ditto for fish.

Dynamic soaring of salmon

The three elements of dynamic soaring are shear transitions to gain water speed (unavoidable for salmon), turns to gain ground speed, and multiple turns and shear transitions.

If it has an option, a salmon won't approach a rock within faster stream flows. It may rest in the eddy behind the rock, then gain ground speed (a flight term) in those slow or reversed eddy currents, and charge into the faster flow. It gains more ground speed within the eddy than if it had fought straight up the middle of the faster current. Being streamlined, its momentum, with some tail-waggling, will help carry it around the rock.

That salmon gain water speed as they cross a shear into faster flow is a characteristic of their environment, unavoidable, as are the limited choices of what to do next – continue upstream, turn across flow, or turn downstream. Each has benefits, with evolutionary pressure to optimize brain, sensory, and physiological capabilities for extracting energy or maneuvering speed from velocity shears in a variety of situations.

After a shear transition, adding a turn to increase ground speed is the second element of dynamic soaring.

On our salmon's shear transition into a faster flow, even though its speed relative to the streambed may be moderate, it can use its sudden boost in water speed for maneuvering. If it turns its relatively flat side at an angle to the flow, it is whipped sideways by the current, perhaps crossing to easier upstream conditions, slower flows or another eddy. If it turns 180° its 'ground speed' downstream will be its shear-bumped water speed plus the speed of the flow. Either maneuver may help it escape Brer Bear.

56 seconds into a video, a trout rises from shelter through slowed bottom flows into faster flows, and turns 360° back into slow bottom flows, gulping something in the process.[28] The shear transition up into faster flows gives it a bump in water speed. Its turn downstream adds this water speed to flow speed. It then verges down into slower flows and and turns upstream, turning all that downstream velocity into upstream velocity, to effortlessly arrive upstream next to its starting point.

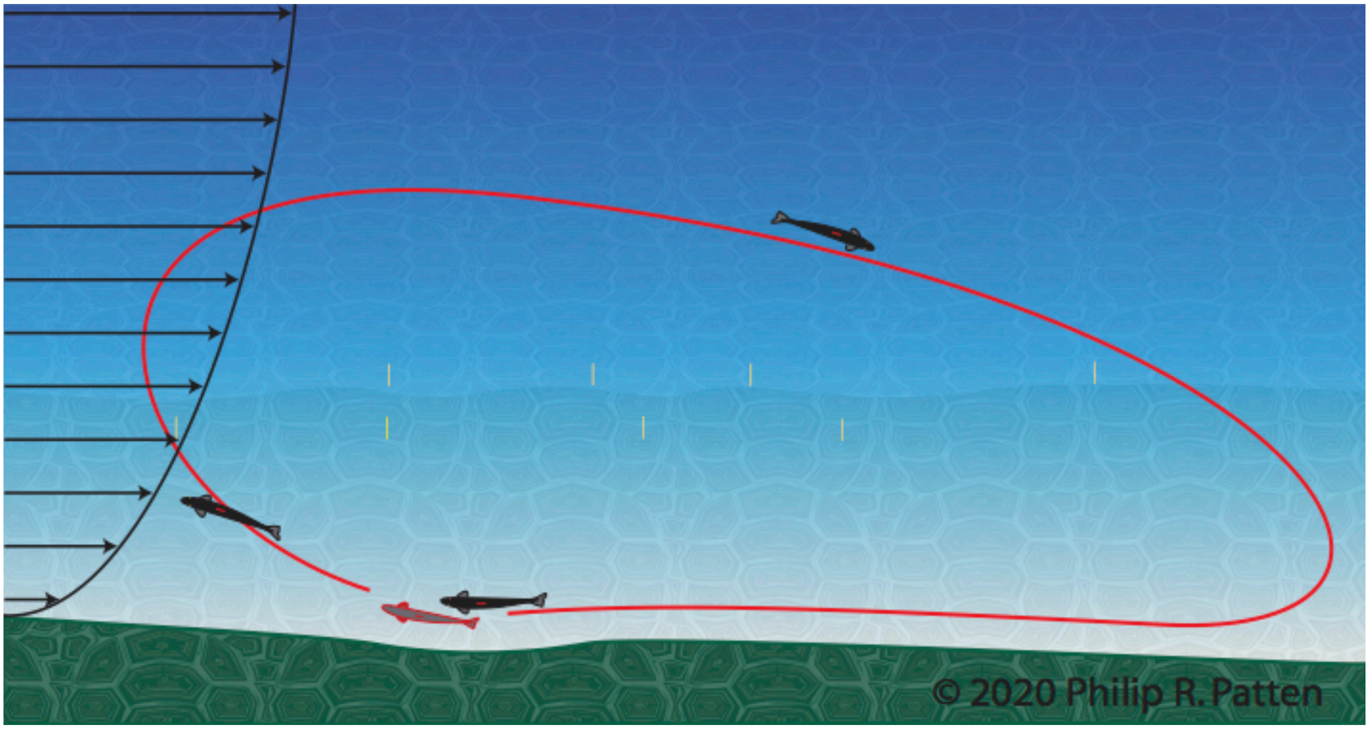

Figure 8: The most easily observable dynamic soaring of a salmonid. Our male salmon protects his hen, at her redd, where they rest in slower shallows (birds-eye view). The male veers sideways into deeper, faster current, to chase an interloper. That bumps his water speed. He turns downstream to add his water speed to the speed of the faster flow for high downstream speed. He veers into the slow shallows where he turns his downstream speed upstream, effortlessly arriving back at his hen.

Viewed from the side, in deeper water: The salmonid performs the same maneuver vertically, from slow flows near the streambed into faster flows above, and with turns arrives back at his starting point.

This is exactly what an albatross does, punching up from slow surface flows, perhaps even from the shelter behind a wave, into faster flows fifty feet up, gaining airspeed. It may turn downwind, adding airspeed to windspeed, or not. It again dives into slower flows below, where with a turn its airspeed becomes groundspeed it uses to repeat, even moving upwind. Our trout has done the same.

A salmon may rise through the velocity gradient from slow flows near a rocky streambed into faster flows above or may veer from slower spawning shallows into the faster main stream. If it turns downstream it adds the bump in water speed to stream speed. It turns back into slower flows, using its residual speed to almost effortlessly glide back to its mate, perhaps having chased an interloper. See Figure 8. [Dear reader, videos would be welcome.]

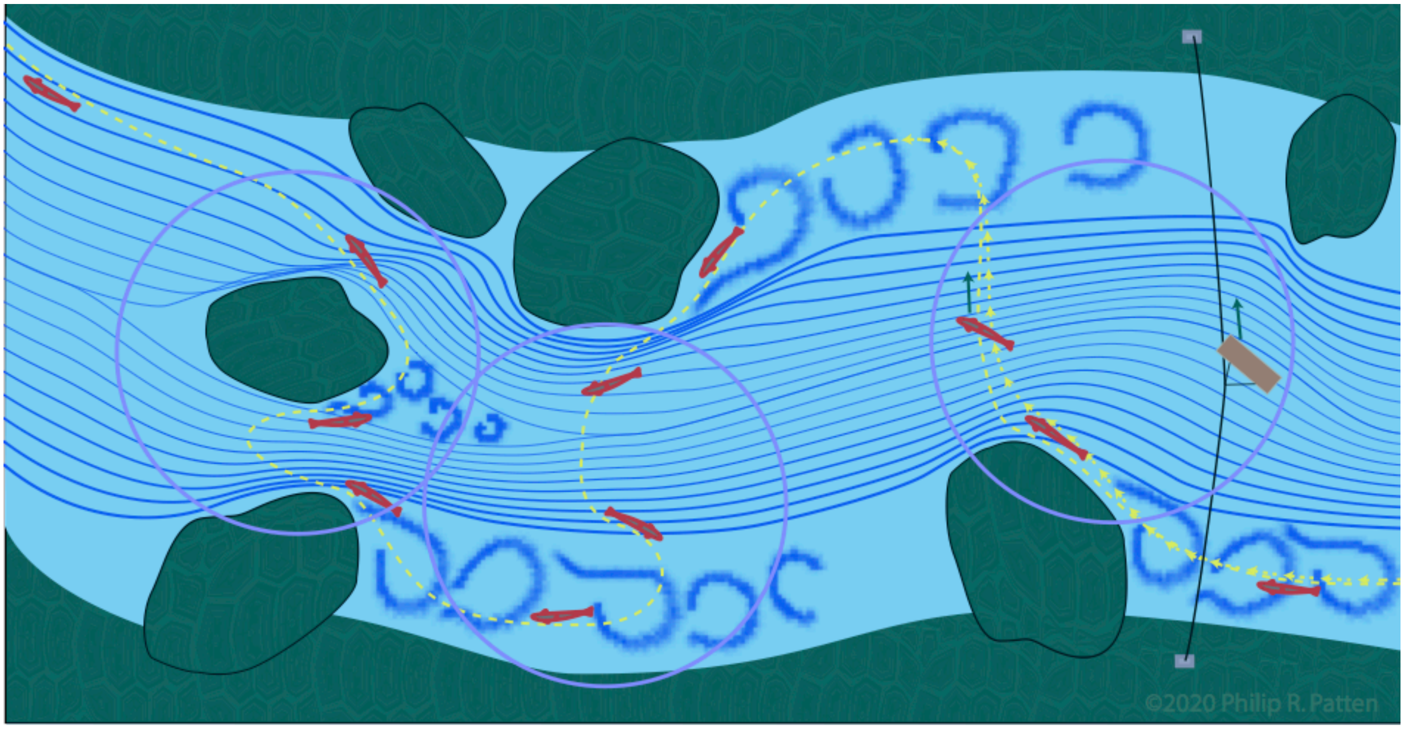

Figure 9, Shears, ferries, and DS turns: Rocks in an alternating pattern offer free upstream energy to salmon. Such a pattern could help salmon ascend fish ladders or steep streambeds.

Right: A cable ferry angles against current. Fish and kayakers substitute upstream momentum for a cable.

• Lower right circle—The water speed bump from crossing a shear from an eddy into oncoming flow
• The salmon's groundspeed plus the speed of the oncoming water give it a high water speed. Kayakers call this 'peeling out.'
• Mid-right: Turning water speed into groundspeed by angling across current: Salmon angles its body so that the current and water speed whip it across the stream to slower flows or into the eddy behind another rock.
• Upper right: Salmon turns its cross-stream groundspeed into water speed as it busts into relatively slow water. With a turn this water speed carries it upstream, perhaps even carrying momentum through the next shear transition. Free energy!

River and ocean kayakers do just what Brer Salmon has done in this illustration. Kayakers call shears 'eddy lines.' Exiting an eddy across the line is a 'peel out.' The combination of forward momentum and angle that gets the kayak to shoot across the current is a 'ferry,' for good reason: historic cable ferry operators would crank the angle of the ferry so the current would pull it across the river. I had the pleasure once of crossing the Snake River in Eastern Washington on Lyon's Ferry. The site is now underwater.

Center circle—Gaining even more upstream speed with a downstream turn:
• Salmon follows the same process, gaining water speed crossing a shear from an eddy into oncoming flow and angling to be whipped across the main current. Then:
• The salmon turns downstream. It adds its water speed to the speed of the flow for a very high groundspeed.
• As it crosses a shear line into an eddy, that groundspeed becomes very high water speed, which it turns upstream. Note: If the current forces the salmon downstream until it can duck into an eddy this maneuver is dictated by the environment. But in the illustration this appears to be a situation where the fish has choice, to turn downstream for extra final speed, or to just barge into the eddy. Such situations are a test of whether salmon shear-management bio-programming is as sophisticated as that of albatross or swallows. Probable, but unknown.

Left circle—Dynamic soaring a rock in the middle of a rapids or falls:
• Salmon powers out of an eddy into a rapids. Its momentum and waggling don't carry it past the rapids.
• It is forced to turn downstream. Its ground speed is then its swimming speed plus the speed of the rapids flow, = fast.
• It immediately tries to get out of fast rapids flows into the eddy behind a rock. The shear transition into the eddy behind the rock turns that fast groundspeed into water speed.
• The salmon turns upstream in the eddy, so its new water speed becomes upstream groundspeed sufficient to help it past the rapid.
Note: This situation has forced the behavior of the salmon. Its senses and brain make success more likely.

Note: In each of the above maneuvers a salmon could exit with more upstream speed than at entry. Our salmon could conceivably make it from the lower right rock to the upper left of the illustration without using its tail for thrust.

There's another example that shows that at least some fish, like birds, can dynamically soar velocity shears. Photographers and dorado prefer to chase flying fish under calm conditions. There we see a flying fish fleeing in a straight line, usually decreasing air drag by gliding close to the surface in 'ground effect,' a term for riding a partially trapped cushion of air. When it slows and sinks it will waggle its tail in the surface to gain the speed to get back into another glide.[29] But in the occasional windy video we watch a flying fish launch upwind, like any small plane, through the velocity shear of wind over water. Its airspeed is its water speed plus the wind speed. The oncoming wind makes it easier to take flight. And some videos show a turn shortly after launch.[30] Again, that turn is the second element of dynamic soaring. The fish's airspeed is in relation to the air in which it flies. If it turns across the wind that airspeed whips it sideways. If it turns downwind its airspeed adds to the wind's speed for a very high downwind ground speed. Thus it gains distance from the maw of a hungry dorado.

Extracting energy from fluid shears: windmills, sailboats, and cable ferries vs. kayak and salmon.

To extract energy from a velocity shear there must be a way to at least briefly keep velocity relative to the flow. Windmills anchor to earth to work the shear between earth and wind. Sailboat keels hold against sideslip forces of wind shearing across water. Cable ferries are held against the current by a cable across their river. The angle of the ferry to flow pulls them across. Fish and kayakers do the same, but substitute upstream momentum gained in an eddy to hold them against flow, briefly, but for long enough to be 'ferried' sideways.

Do hatchery fish gain the same upstream capabilities as wild fish?

Are salmon capabilities for managing complex stream environments entirely instinctual, or partly learned? At least some behaviors are partly learned – hatchery fry have been shown to improve feeding behaviors by imitating adult salmon.[31] Is a salmon fry released from a hatchery on par with its wild cousin? Is there a formative period in salmon learning? Salmon fry fight over prime feeding territory, but they also must fight over energy-conserving eddies and pressure gradients, gaining experience a hatchery fish misses. A salmon hatchery is a sterile environment compared to a stream. Would the common zoo policy of environmental enrichment help the survival of hatchery salmon? Do even salmon instinctive behaviors require practice? If the bottom of a circular circulating pen had alternating bumps and protrusions would salmon fry gain useful experience in extracting energy from pressure gradients and velocity shears?

Dynamic soaring to leap a waterfall?

For salmon the simpler energy extractions from shear transitions are as low-hanging fruit. Salmon may have leaped further. Gaining velocity in a fluid by transitioning a shear and then turning that velocity into ground speed is sufficient to technically be dynamic soaring. But usually the term refers to sequential links of shear transitions and turns, by which an albatross may even make upwind progress. A model plane punches in a circle through the fast flow over a ridge, down into the relatively still air behind, and back up into the fast flow, gaining airspeed with each shear transition and groundspeed with each turn. There is at least one way salmon could do something similar to gain the speed to leap a waterfall.

A falls into even a tumultuous pool combined with the salmon's upstream drive make the following occasionally inevitable, but salmon evolution has optimized senses and bio-programming to make success more likely and frequent.

As water falls into a pool there will be a velocity shear between the rapidly plunging flow and the relatively low velocity of the pool. When this is the case no salmon in its right mind will attempt to struggle right up the high-velocity water. Instead, it charges through the slower water above and leaps. It will be helped in its leap if the surrounding water flows in a vortex with an upstream component.[32] That much is well established.

Our salmon leaps nearly to the top of the falls, where it is instantly caught in the downstream current. (It may gain water speed in this first shear transition.) It immediately powers its way downstream

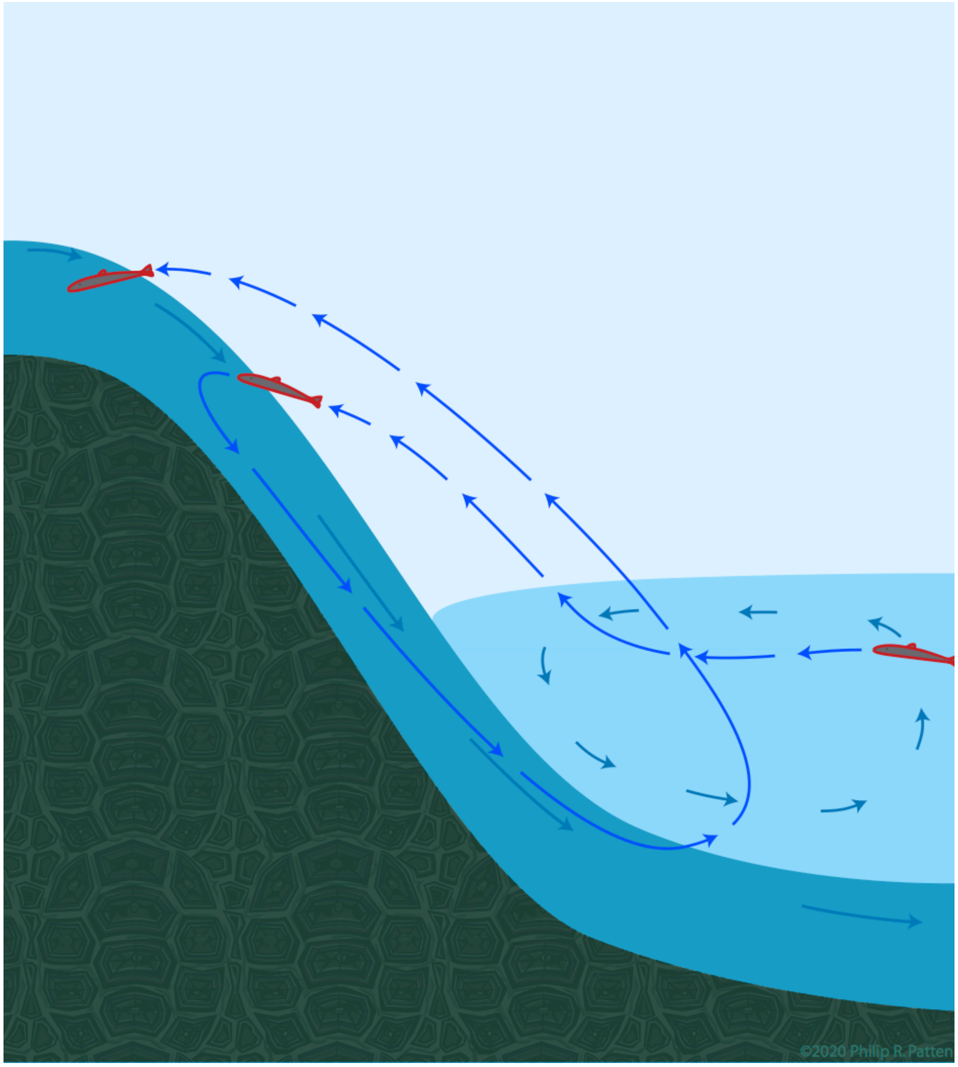

Figure 10: A salmon using the downstream velocity it gets from its first leap at a waterfall for a successful second leap.

within the plunge, gaining enough headway to maneuver. Its ‘ground speed’ is much higher than its swimming speed within the falling water, equal to its downstream swimming speed plus the speed of the falls water. And then:

What makes dynamic soaring of a waterfall likely is that the salmon will want to get out of the high-velocity water sweeping it downstream as soon as possible. Just after the falling water plunges through the surface of the pool the salmon turns and punches through the velocity shear into the relatively slow waters of the pool. It’s headed downstream even faster than the plunging falls, but now through comparatively slow water. To end its downstream rush, it continues its turn until much of that extreme velocity is pointed upstream, at the surface. It may get a further boost from local vortex upwelling. With a last burst of power, it leaps again and is perhaps successful.

If a salmon does this, it has done exactly what albatross do to circle the southern hemisphere without flapping. It has done exactly what a few radio-controlled model gliders do to gain bullet speeds. It has demonstrated that what works for a variety of bird species in air also works in water.

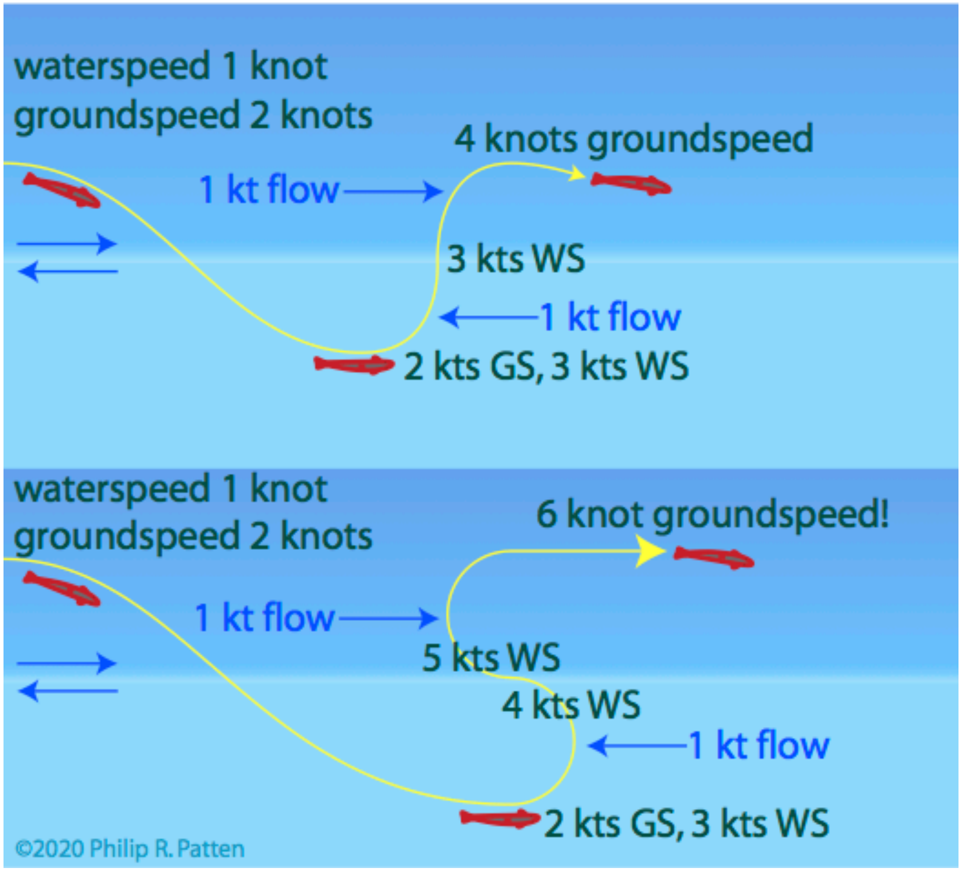

Figure 11: Salmon gaining speed without energy expenditure by crossing tidal shears. Upper: by crossing a tidal shear twice a salmon radically increases its ground and water speeds without tail waggling. Lower: In a more radical S turn, our salmon gains even more speed. Then it can coast for a while, until it repeats. Free energy! Autonomous winged aircraft should be able to do the same with the jet stream.

A major obstacle is that a salmon has to have the energy to make two leaps without a rest period. At maximum swimming speeds, salmon become exhausted within seconds. Verification will require underwater observation and perhaps telemetry in measured conditions.

Salmon could also gain velocity from dynamically soaring the velocity shears between tidal currents and calmer waters. This explains why, according to sport fishing lore, salmon often hang in tidal velocity shears. Perhaps they even play with these shears, building experience for the more volatile shears of their upstream migrations.

It would be surprising if energy-hungry migrating salmon hadn't developed 'dynamic soaring' capabilities for using the abundant energy of velocity shears within water. At least several bird species DS the velocity shears within air, but shears within any fluid work the same. I've illustrated a few ways a salmon can dynamically soar the velocity shears within water.

The question isn't whether salmon and other fish extract energy from velocity shears and pressure gradients. The question is how extensively they do so, how much this helps in their upstream migrations, and how sophisticated are their strategies for upstream energy management.

Summary

Half-a-billion-years of evolution have shaped upstream migrating fish senses, brains, and physiology to perceive, forecast, map, and extract energy from the pressure gradients, velocity shears, and vortices around the features of their three-dimensional environment. Salmon use a variety of strategies to minimize upstream energy expenditure. Pressure gradients form more strongly at depth around stream features. Salmon gain upstream thrust from pressure gradients that slow flows. They avoid or rush through the added pressure drag from pressure gradients that accelerate flows. Salmon and trout gain energy from velocity shears. As a salmon exits the slow flows behind a rock or near the bottom of a stream into faster current it gains water speed. With a turn, a salmon is whipped across current, perhaps to escape predators, or to dart to a more sheltered part of a stream where that speed can be turned into upstream progress. It is unavoidable that salmon will sometimes extract energy from velocity shears to leap waterfalls, in a process shared by albatross, other bird and fish species, and model gliders, called 'dynamic soaring.'

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[1] *Salmon Fishing in Iceland with Underwater Camera*, n. :30, 3:45, accessed January 11, 2020, https://www.youtube.com/watch?v=iEeYFhCdlas.

[2] Malcolm MacGarvin, *Underwater Video Salmon & Sea Trout River Avon, Strathspey, Scotland*, accessed July 25, 2018, https://www.youtube.com/watch?v=dpmM9cOIOIc.

[3] T. C. Bjornn and D. W. Reiser, "Habitat Requirements of Salmonids in Streams," in *Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats*, ed. William R. Meehan (American Fisheries Society, 1991), 81.

[4] WNY Tutor, *A Chinook Salmon Has a Maximum Underwater Speed of 3.0 m/s*, accessed July 25, 2018, https://www.youtube.com/watch?v=AjrpDq4WqAc.

[5] James C. Liao, *Fish Swimming: Why Trout Swim behind Rocks* (Fish code studios), accessed January 14, 2020, https://www.youtube.com/watch?v=aRWgqDi-ihs.

[6] James C. Liao et al., "Fish Exploiting Vortices Decrease Muscle Activity," *Science* 302, no. 5650 (November 28, 2003): 1566–69, https://doi.org/10.1126/science.1088295.

[7] Nicholas F Hughes, "The Wave-Drag Hypothesis: An Explanation for Size-Based Lateral Segregation during the Upstream Migration of Salmonids," *Canadian Journal of Fisheries and Aquatic Sciences* 61, no. 1 (January 1, 2004): 103–9, https://doi.org/10.1139/f03-144.

[8] Emily Gertz, "Are Fish As Intelligent As Crows, Chimps... Or People? | Popular Science," Popular Science, June 19, 2014, https://www.popsci.com/article/science/are-fish-intelligent-crows-chimps-or-people.

[9] Jared Harding, "Super Sense of Fish," *Ocean Blue Adventures* (blog), September 19, 2017, http://oceanadventures.co.za/super_sense_of_fish/.

[10] "A Fish Perspective: Detecting Flow Features While Moving Using an Artificial Lateral Line in Steady and Unsteady Flow," accessed February 8, 2019, https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4233726/.

[11] Joseph Stromberg, "Are Fish Far More Intelligent than We Realize?," Vox, August 4, 2014, https://www.vox.com/2014/8/4/5958871/fish-intelligence-smart-research-behavior-pain.

[12] E. Toolson, "Salmon Osmoregulation," accessed January 9, 2020, https://www.unm.edu/~toolson/salmon_osmoregulation.html.

[13] Randolph, "Frederick William Lanchester's Phenomenal, 1894, Wave Theory of Lift," 39.
[14] Randolph, 40.
[15] The Fish Finders, *Salmon Run - Bronte Creek Underwater HD*, accessed July 25, 2018, https://www.youtube.com/watch?v=dmKzczP5oHc.
[16] Isaac Newton, I. Bernard Cohen, and Anne Whitman, *The Principia: Mathematical Principles of Natural Philosophy* (Univ of California Press, 1999), 687.
[17] John D. Anderson Jr., *A History of Aerodynamics: And Its Impact on Flying Machines* (Cambridge University Press, 1999), 12.
[18] "AMANDA GHASSAEI: APPS," accessed July 22, 2018, http://www.amandaghassaei.com/apps/.
[19] James C. Liao et al., "Fish Exploiting Vortices Decrease Muscle Activity," *Science* 302, no. 5650 (November 28, 2003): 1566–69, https://doi.org/10.1126/science.1088295.
[20] "Swim Bladder | Fish Anatomy," Encyclopedia Britannica, accessed July 22, 2018, https://www.britannica.com/science/swim-bladder.
[21] Cornelis Groot, *Physiological Ecology of Pacific Salmon* (UBC Press, 2010), 447.
[22] Nicholas F Hughes, "The Wave-Drag Hypothesis: An Explanation for Size-Based Lateral Segregation during the Upstream Migration of Salmonids," *Canadian Journal of Fisheries and Aquatic Sciences* 61, no. 1 (January 1, 2004): 103–9, https://doi.org/10.1139/f03-144.
[23] J. W. S. Rayleigh, "The Soaring of Birds," *Nature* 27 (1883): 434–35, https://www.nature.com/articles/027534a0.pdf.
[24] "Dynamic Soaring," in *Wikipedia*, June 15, 2018, https://en.wikipedia.org/w/index.php?title=Dynamic_soaring&oldid=845938312.
[25] sll914, *FASTEST RC AIRPLANE IN THE WORLD! Transonic DP -- 545mph!!*, accessed September 21, 2018, https://www.youtube.com/watch?v=MoaWlKC3wIM.
[26] Peter Lissaman, "Wind Energy Extraction by Birds and Flight Vehicles," *Technical Soaring* 31, no. 2 (April 18, 2012): 52–60, http://journals.sfu.ca/ts/index.php/ts/article/view/165.
[27] Douglas R. Warrick et al., "Foraging at the Edge of the World: Low-Altitude, High-Speed Manoeuvering in Barn Swallows," *Philosophical Transactions of the Royal Society B: Biological Sciences* 371, no. 1704 (September 26, 2016), https://doi.org/10.1098/rstb.2015.0391.
[28] *Trout and Salmon II : Ambush*, accessed January 13, 2020, https://www.youtube.com/watch?v=9U8hIFAvB9s.
[29] "Winging It: Flying Fish Aerodynamics Directly Measured for the First Time - Scientific American," accessed July 23, 2018, https://www.scientificamerican.com/article/flying-fish-measured/.
[30] ODE, *Amazing Flying Fish!*, accessed July 22, 2018, https://www.youtube.com/watch?v=OmWRCdUw17E.
[31] Joseph Stromberg, "Are Fish Far More Intelligent than We Realize?," Vox, August 4, 2014, https://www.vox.com/2014/8/4/5958871/fish-intelligence-smart-research-behavior-pain.
[32] T. C. Bjornn and D. W. Reiser, "Habitat Requirements of Salmonids in Streams," in *Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats*, ed. William R. Meehan (American Fisheries Society, 1991), 87.