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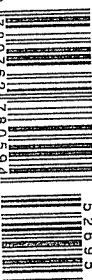
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Waldman

Running Silver

Restoring Atlantic Rivers and Their Great Fish Migrations

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John Waldman

LYONS
PRESS

Chapter 1

Running Silver and Ghost Fishes

The herring are running!

—John Hay, *The Run* (1959)

Henry David Thoreau was not pleased with the changes he saw occurring along the Concord and Merrimack Rivers as he and John paddled. The voyage that was the basis for *A Week on the Concord and Merrimack Rivers* actually took two weeks, not one. Each chapter in the book constituted a “day,” but was really a compendium of observations made along the rivers, together with ruminations on religion, poetry, and history. Thoreau may be celebrated for his philosophical insights, but he was also an acutely perceptive observer of the natural world. In fact, his data on the timing of the flowering of Massachusetts flora are being used as a baseline for measuring climate-change effects today. In *A Week*, Thoreau foretold many of the oncoming environmental consequences of the nascent Industrial Revolution on the rivers he so admired. The book’s first draft was written while Thoreau lived at Walden Pond. When completed, he could not find a publisher for it, and so he had it produced at his own expense. *A Week* was not a smash success; only a few copies were sold of the hundreds Thoreau had printed, and he was driven into debt.

Thoreau was familiar with the great abundances of anadromous fishes as they drove inland, and it’s possible he witnessed a migration so pronounced as to justify use of the term *running silver*, a description of times when there were so many metallic-scaled bodies churning their way up a river that it seemed the fish had become the water. I have collected testimony, written accounts of the reactions of early colonists to these runs when they ran silver. The language often approaches the hyperbolic, as if the possibility of such abundances could not have been conceived, never mind witnessed. To

pore over these quotations is to read of awesome plethora, number orders of magnitudes higher than we are accustomed to today.

A sampling:

We are set down eighty miles within a river, for breath, sweetness of water, length navigable up into the country, deep and bold channel, so stored with sturgeon and other sweet fish as no man's fortune has ever possessed the like.

Yea, when a heape of stones is reared up against [the alewives during their spawning runs] a foot high above the water, they leap and tumble over and will not be beaten back with cudgels.

We had more sturgeon than could be devoured by dog or man . . .

In the spring of the year, herrings come up in such abundance into their brooks and fords to spawn that it is almost impossible to ride through without treading on them. Thus do these poor creatures expose their own lives to some hazard out of their care to find a more convenient reception for their young, which are not yet alive. Thence it is that at this time of the year, the freshest of the rivers, like that of the Broadwick, sink off fish.

[T]he greate smells passé up [the Smelt River, near Blymouth, Massachusetts] to spawn likewise in troops innumerable, which with a scoupe, or a boule, or a peece of bark, a man may cast upon the bank . . .

There are such multitudes, that I have scene stopped into the river close adjoining to my house with a sand at one tide, so many as will load a ship of a 100 Tonnes. Other places have greater quantities in so much, as wagers have bin layed, that one should not throw a stone in the water, but that hee should hit a fish. I my selfe at the turning of the tyde, have scene such multitudes passé out of a pound, that it seemed to mee, that one might goe over their backs dishod.

The sturgeons be all over the country, but the best catching of them is upon the shoals of Cape Cod and in the river of Merrimac, where much is taken, pickled, and brought for England. Some of these be 12, 14, 18 foot long. I set not down the price of fish there because it is so cheap . . .

[D]uring one month the fish ascend the river in so great numbers that a man could fill fifty thousand barrels with them in a day, if he could be equal to the work.

And my favorite, a veritable festival of superlatives:

When they spawn, all streams and waters are completely filled with them, and one might believe, when he sees such terrible amounts of them, that there was as great a supply of herring as there is water. In a word, it is unbelievable, indeed, indescribable, as also incomprehensible, what quantity is found there. One must behold oneself.

This sampling extends from 1607 to the early 1800s. They reflect the perceptions of European colonists who had recently arrived in the New World, from an Old World where its fishes had been overharvested for centuries. Their view of “normal” abundances was already altered by the insidious declines long suffered by their fish stocks. Yes, Native Americans had fished the American runs for millennia, but to help feed human populations that were diminutive compared with the numbers of people in Europe. Walking “dishod” over the backs of migrating fish is, of course, an exaggeration, but one expressed in wonderment by colonists who were overwhelmed, both with the sheer spectacle and with their own good fortune.



One December day in 2007, my colleague Karin Limburg and I sat with our laptop computers in her dining room in Syracuse, New York, an ad hoc war room, to try to take stock of the status and trends of the Atlantic's diadromous fishes. Both of us had worked on these species long enough to know

we'd end up painting a grim picture, but until then, no one had synthesized so much of this bad news quantitatively. An early snow fell hard outside as we began to merge diverse streams of information.

The news was not good; in fact, it was downright dismal. The resultant article, published in the journal *Bioscience*, covered two dozen species of fish. We had examined their abundances as far back in time as possible, realizing that the numbers they would show likely were already reduced, probably substantially in many cases, from the pristine profusion seen before anyone was inspired to try and enumerate them. Nonetheless, the declines were astonishing: For thirty-five species, each considered as a whole, or of populations of a species, relative abundances had dropped more than 98 percent, from historic peaks in thirteen, and more than 90 percent in another eleven. Most had reached their lowest levels at the present, and many showed trend lines that sloped slowly toward zero.

Many individual populations had been lost, too. In North America for Atlantic salmon, only 135 of some 600 original runs were left. American shad were extirpated in almost half the rivers where they once occurred. The Atlantic whitefish lost only one population, but it only had two to begin with, and it reeters near extinction. In Europe the sea sturgeon, which had swum in as many as twenty rivers from the Baltic all the way to the Black Sea, hung on only in France's Gironde River, and in grim numbers. For some other species significant losses of populations are suspected (such as sea lamprey), but because they lack commercial value, no one had bothered to collect the appropriate data. The conservation status of these fishes echoed our more specific data. The International Union for the Conservation of Nature convenes panels that deliberate at length about the state of a species; most were now listed with a designation of at least some concern, or worse: "vulnerable," "near threatened," "endangered," and "critically endangered." The only encouraging news Karin and I extracted is that true species extinctions haven't yet occurred. Overall take-home message: *Abundances for most species decimated, numbers of populations sometimes severely reduced, but firiations with extinctions still uncommon.* A set of findings that simultaneously seem even beyond the point of urgency while revealing a modicum of hope.



Whether as severely diminished numbers or as populations lost, what's happened to these freshwater-sea migratory fishes has left both ecological and sociological voids: *ghost fishes*. "Ghost species" is a new concept in conservation biology. Concerning the freshwater-sea migratory fishes, ghost fishes are those that are either completely lost as a population in a river or region where they once occurred, or those that persist at such low numbers that in ecological terms, they are essentially absent. Though now missing in reality or in effect, these fishes once did play a role, and usually a highly important one, in the broader food web as prey, predator, and competitor, one that evolved with the other organisms that compose that network. And so their absence resonates as holes, or "ghosts," in the ecological machinery of those environments.

In the absence of these fishes, their importance to society naturally faded, also to ghost-like roles. The task today is to exorcise these ghosts, not through the supernatural but by filling the empty spaces in nature they represent through the hard work of applied restoration via all possible avenues. But to muster the wherewithal, their fates first need to matter; in our minds, they need to pass from poorly remembered specters to living creatures in need of a fair chance. Or, as Thoreau put it, "Poor shad! Where is thy redress?"



Chapter 2

Diadromy 101:

Swimming the Great Migratory Circuit

[A]nd the riverbank talks of the waters of March,
it's the promise of life, it's the joy in your heart.

—“*Waters of March*,” Antonio Carlos Jobim
and Cassandra Wilson

Alaska at last! I rejoice as an East Coast conservation biologist and angler finally in salmon paradise. My buddies and I have arrived in the quaint coastal village of Cordova too late in the day to go fishing, but we can't help but drive at last light to a small stream to look at a spawning run of pink salmon. Everywhere in the current the dark backs of the pinks are showing above the surface as fish either pass farther upstream, dig pits in the gravel called “redds” with their tails to mate in place, or just loiter. Others appear less lively and actually “torn,” white flesh showing as these spawned-out individuals literally rot alive as preprogrammed death advances. And dead salmon line the banks, decaying and leaving a powerful but not completely unpleasant organic stench in the air.

I want to touch and handle a salmon, so we find a curved tree branch and steer a female pink onto shore. I hold my pink lady high to admire her and some large golden eggs trickle out, so I put my mouth to her vent and taste a few—they burst and provide me with the subtle and salty flavors of a life spent wandering the Pacific. When I slip her back into the flow, she immediately rejoins the salmon parade. On another day, while driving I look down along the shore and spot a run of pink salmon streaming through a culvert. I stop the car and see that the landward side of the road has a small flow in its gutter and it is filled with salmon with their backs

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out of the water. Where they are headed amazes me; a short distance away the source of this runoff is nothing but a trickle down a 45-degree rock-strewn slope. But the pinks are ascending from wet pocket to wet pocket like drunken mountain climbers, raking a harsh physical beating to place their eggs in the relative safety of this otherwise inhospitable environment.

I've spent much of my career in New York working on regional and international issues concerning freshwater-sea migratory or “anadromous” fishes, but no sight ever revealed so baldly the sheer force of the spawning drive as in these Alaska fishes. This is anadromy illustrated, and I am in awe. And yet, I realize it's no different for their Atlantic Coast analogues; the combination of this instinctual impulse plus overwhelming plentitude is just either more cryptic, or it's a legacy that's been squandered through mismanagement and obliviousness. A 300-pound sturgeon that slides past Manhattan to spawn in the Hudson is responding to the same imperative; it's just that the fish is forty feet below in a murky river. Likewise



A Hudson River commercial fishing station. Note that all fish species shown are anadromous, demonstrating their high importance.
From *The Hudson: From the Wilderness to the Sea* (Benson Lossing, 1866).

for an American shad in Georgia's Ogeechee, or a striped bass in Maine's Kennebec. In fact, most rivers of the Atlantic Seaboard did run silver with alewives and other fishes before the Industrial Revolution, obeying the same imperative; it's just that those days are long gone and barely remembered.



There are more than 20,000 species of fish alive on the planet today. Imagine an experiment: Take one of each of them and slowly change their dwellings from freshwater to salt water, or salt water to freshwater, to see how many survive. The overwhelming majority should perish—most when crossing the barrier of about five to ten parts per thousand salinity from either direction. Of those that can make the physiologically demanding transition between the zero parts per thousand salinity of freshwater and the thirty-five parts per thousand of seawater (or vice versa), a select group of only about 250 do this as a routine and predictable part of their life cycle. These are the *diadromous* fishes.

Some more essential terminology: *Anadromous* fishes are those diadromous fishes that are spawned in freshwater and then migrate to the sea. *Catadromous* fishes do the opposite; they start life in the ocean and migrate to freshwater. A little more "Intro to Ichthyology": "Fish" are the individuals you have in your bucket after your successful fishing trip. Perhaps you had a good day on the water and brought home twenty mixed flounder, porgy, and hake that you plan to eat; you have twenty "fish" at hand. But if a scientist described how many different species made up that catch, they would say three "fishes"; the word *fishes* describes diversity.

Just a dozen or so diadromous fishes occur on the East Coast of North America. Only one is catadromous: the American eel. The best-known anadromous species of this region are Atlantic salmon, striped bass, American shad, alewife, and Atlantic sturgeon; others include sea lamprey, shortnose sturgeon, blueback herring, hickory shad, rainbow smelt, Atlantic tomcod, and Atlantic whitefish. Striped bass are also found along the Gulf of Mexico coast, together with the Alabama shad, skipjack herring, and a subspecies of Atlantic sturgeon.

But the boundaries among diadromous fishes and non-diadromous fishes are not well defined. Some view the Atlantic tomcod as anadromous, though they tend to migrate only as far as the saltier extremes of their home estuaries, and not into true marine waters. Then there are those that are "facultative," meaning that they can lead an anadromous life-history pattern if they want to, but it's not obligatory. Native brook trout and nonnative brown trout both may drop down rivers and go to sea, but most don't; the majority of striped bass in mid-Atlantic rivers migrate to the ocean, but some never leave fresh waters. Finally, almost all of these species may "landlock," completing their life cycles in fresh waters, such as lakes and reservoirs.

To view these fishes as a group is to be struck by their diversity of size and shape, a clue that there is little evolutionary commonality among them. "Primitive" sea lamprey have no bones and are jawless. Sturgeons also are considered primitive, have only cartilaginous skeletons, but display armored plates of bone on their flanks. Salmon and shads are intermediate on the evolutionary tree, lacking fin spines, with spiny-rayed striped bass being the most "advanced" among the entire East Coast lot. It's important, though, to not misunderstand the significance of loaded-sounding terms like *primitive* and *advanced*. *Primitive* is not a value judgment, and it does not mean such species are slow and dim-witted; lamprey and sturgeons would not have survived for hundreds of millions of years if that were the case. This term means only that these highly successful groups appeared early in fish evolution; *advanced* means they evolved relatively recently.

This begs the question: If diadromy is rare, and is a characteristic that is spread across the evolutionary spectrum of fishes, under what conditions did it evolve? And are diadromous fishes sea creatures that adapted to freshwater, or vice versa? Here our understanding gets shakier. It's commonly accepted that in temperate latitudes, fresh waters are "safer" than the sea as places to leave eggs, to hatch, and to live as larvae and juveniles. Marine waters undoubtedly are more ecologically productive, but beware—there are many more hungry mouths and sharp teeth there.

A population of an anadromous species can claim the benefits of higher survival for its young by placing them in freshwater where they rear to a

size large enough to enter the sea to grow further and mature—but this strategy does not come without costs. The spawning adults need to expend considerable energy migrating to a suitable river, make the physiological adjustment to freshwater, expend further energy moving upriver against the current, in many cases feed little or not at all while in the river, expose themselves to river-based predators, complete the act of spawning and then migrate downstream, undergo another physiological adjustment, and then migrate back to their marine feeding grounds. That this grand but highly demanding life cycle is worth the costs is clear from the plenitudes that once existed for undulcerated populations, but the scope and complexity of this strategy leaves them especially vulnerable to the hand of man.

Interestingly, whereas anadromy dominates temperate latitudes, catadromy is more often seen in the tropics. The relative productivity of fresh and marine waters switches there; in these warm regions, fresh waters offer richer food webs than does the sea, and many species drop down rivers to the salt to spawn, with the young later penetrating inland. This is taken to an extreme with the Hawaiian gobies, marine fish that evolved to climb torrential rivers and waterfalls soon after transforming from larvae in seawater, this after being spawned at high elevations and washing downriver. The gobies' pelvic fins have transformed to sucking discs that allow them to inch along wet rocks, and the mouth of one species actually moves in only thirty-six hours from the fish's front end as a larva to the bottom of its head as a juvenile, to serve as an extra sucking disc. Some of these gobies were found above a 1,148-foot-tall waterfall, a feat of climbing more than five thousand times its body length. In human terms that's like scaling Mount Everest.

If gobies win the award for mountain climbing, eels are the winners for epic distances. My personal epiphany about the intense migratory drive of eels occurred in Iran. I was being shown around a sturgeon hatchery on the shore of the Caspian Sea. On one wall was a poster of the "Fishes of the Caspian," which included the European eel, a species that spawns a hemisphere away in the middle of the Atlantic Ocean. I asked, "How is this possible? The Caspian Sea is landlocked and sits one hundred feet below ocean level." The answer amazed me. Some eels, born in the Sargasso, loop around the Gulf Stream for 300 days, swim through the Straits of Gibraltar,

down the Mediterranean past Sicily, past Istanbul and through the Bosphorus Strait, across most of the Black Sea, and through the Strait of Kerch, before entering the Don River and locking through to the Volga, at long last gaining entry to the Caspian to the south, or farther upriver toward Moscow. Altogether, about a 4,000-mile trip—one way.

So how did the rare but supremely successful life-history mode of diadromy evolve? Mart Gross, a conservation biologist at the University of Toronto, hypothesized that in the case of anadromy, there is an in-between stage called *amphidromy*, much like for the tomcod mentioned above. In one scenario, a freshwater species makes occasional forays into brackish waters to feed, realizes some benefits (such as increased food availability), and this positive selection results first in amphidromy, where a population ventures to higher-salinity estuarine waters as part of its life cycle, with this adaptation eventually leading to anadromy, with migrations to the sea. And vice versa for catadromous fishes.

These concepts are appealing and make sense. But are they true? The late Robert McDowall, a prominent New Zealand fish biologist, thought not. When he looked at the evolutionary trees within taxonomic groupings of fishes, he found a mixed signal—that anadromy likely arose from both freshwater and marine origins. He also found no evidence for amphidromy being a precursor to catadromy. Indeed, McDowall believed that for some fish, diadromy may even be the ancestral condition.



Regardless of how it evolved, it is common knowledge that salmon "home" to the river they were born in. In fact, it's known or safe to assume that each of the Atlantic anadromous fishes homes, with one major exception: sea lamprey. What does it mean, to "home"? And to "stray"? Why should homing even occur?

Homing means that after spending months to years at sea, maturing, possibly far from its natal river, there is an overwhelming propensity that an individual will return to spawn in that same river. How these fish navigate in the sea to find the river they were born in is not completely understood,

but research with salmon has shown that they "imprint" on the odor of their natal system before they go to sea, and that they detect that odor once again as they approach their river from the seaward side. Homing over the short term has been studied directly by tagging fish and seeing how many turn up again in their natal rivers, versus other rivers. (However, scientists have discovered that attaching tags to fish can alter their behavior.) Homing also has been studied indirectly using genetics; the more different two populations are genetically, the less gene flow between them is indicated, meaning that straying is therefore rare. This approach provides a long-term signal but not much present-day information. Either way, though, homing rates of about 98 to 99 percent or more seem to be the norm.

What then of the 1 percent, give or take a little, that end up spawning in a river other than the one they hatched in? This might seem maladaptive, but it's not. Consider perfect homing. If a river's population went extinct, it would *never* be recolonized—there would be no source of new individuals. Nor would colonization occur in any new, suddenly accessible habitat.

But the tendency to come back to the same river for generation after generation does have consequences—good ones from the fish's point of view. This is the engine for the exquisite fine-tuning of anadromous fish to their own life-history circuit. Different stocks of a single species, say, shad or salmon, mix in the sea, yet there may be noticeable differences among them in various characteristics, telling us that these differences are driven primarily by their particular freshwater conditions. How so?

The answer is that the fish become physically sculpted to the unique demands and opportunities provided by their fresh waters. Anadromous fishes once displayed remarkably recognizable variation below the species level, tuning expressed strongly enough to constitute a variety of groups that were seasonally or geographically sufficiently different to be termed "substocks," "races," or "runs," with many given colloquial names. Commercial shad fishermen in the Hudson were particularly attuned to variations, recognizing yellowback, blueback, greenback, golden, pink, pink-faced, locust, chunker (exceptionally deep-bodied), chunk head, and red-finned (possibly due to slight damage to capillaries in the skin) shad. Farther south in the Potomac and North Carolina, fishermen in the 1800s noted "May shad" late

in the run that were fatter and deeper-bodied, with a thicker tail section than the earlier fish.

Atlantic salmon are especially adaptable in their physical and life-history characteristics, and the differences that emerge can often be linked to their migratory challenges. The salmon of the Grand Caspédia in Quebec are large and powerful, reflecting qualities of that river. The Sevogle, a small branch of the Northwest Miramichi in New Brunswick, has small but very stocky fish. The Serpentine River, a tributary of the Tobique, also in New Brunswick, produces strong, wiry fish from its shallow, rocky stream. Maine's greatest river, the Penobscot, has good-size, muscular salmon. From Scotland, the Tweed produces bulky salmon. But salmon from Scottish Highland rivers, such as the Dee, with its upstream rapids, are lean but nicely proportioned. New Brunswick's Restigouche people adopted the salmon as their tribal symbol, adorning their canoes, clothing, and bodies with images of the fish. So intimate were they with salmon that it was said they could immediately identify which river a fish came from.

Salmon in long, fast rivers such as the Ala and Vosso in Norway require a large amount of energy to reach the spawning grounds, but larger rivers also are more likely to have enough water each year to support reproduction, so these rivers will select for a longer period of feeding at sea, and hence, for delayed breeding, with less repeat reproductions. Salmon in short, more easily traversed rivers with more uneven flows are typified by reproduction at an earlier age, but with more repeat spawnings, they are more apt to hedge by spreading reproductive risks across years (e.g., the small salmon of the little "spare" rivers of Cape Breton, Nova Scotia). Most Atlantic salmon rivers worldwide also have some proportion of "grilse," which are individuals that spend only one winter at sea. Though quite small and composed mostly of males, they do help assure that some portion of the population returns to continue it.

Just how fine do anadromous fish take this fine-tuning? Late-run spawning salmon on the Miramichi enjoy post-spawning survival rates substantially higher than those of early-run counterparts, with early-run fish pushing into the headwaters and late-run fish spawning farther downstream. Within all the sections of only one large drainage, New Brunswick's Saint

John River, researchers found as much variation in reproductive characteristics of shad as found among all East Coast populations. For anadromous fishes there also are energetic demands on how often an individual spawns in its lifetime. The cost in energy of migration, plus the act of spawning, is about 60 percent of that stored in Atlantic salmon. For American shad it is as much as 70 to 80 percent in Florida's warmish St. Johns River, where there are no repeat spawners. In a northern river such as the Connecticut, where shad may spawn multiple times, the cost in energy on a spawning run is 35 to 60 percent. Nature's knife puts the slice between life histories where a fish spawns once instead of twice or more within the 60 to 70 percent energy-depletion range. Darwin would not have found these adjustments as dramatic as those seen in his Galapagos finches, but natural selection works on river fishes just the same.

Fortunately for their management, the effects of the particular environments on these fish that home—and thus build up slight but important differences through natural selection—can be used to identify the population of origin where they mix in the wild. Striped bass, in particular, have received enormous attention toward discriminating between individuals from the Hudson versus the Chesapeake, and sometimes North Carolina's Roanoke River, too. In a sense, this science of stock identification has taken these fish apart, looking for useful differences.

In 1989 I drove some five thousand miles on coastal highways collecting about five hundred striped bass for a study, to look for differences among populations using the same specimens by different researchers employing their own approaches—genetics, body shape, scale and fin-ray counts, scale shape, and fatty acids—allowing me a unique opportunity to see many fish from different rivers during the same season. Though I could not have assigned individuals with certainty to their rivers of origin like the Restigouche with their salmon, some generalized differences were visible to my naked eye: Hudson River specimens were a distinctly mixed lot, Roanoke River stripers were compact, Choptank River fish seemed like

classic "textbook" stripers, but the ones from the Rappahannock were long and sleek, like graceful athletes.

Gathering these specimens often meant meeting state biologists and helping to net the waters with them or picking up at the dock fish already caught. Either way, though, I needed to process and preserve the critical portions of the fish for the researchers. This meant creating "laboratories" on the fly. One time I obtained about thirty large stripers from the Choptank River and then rented a motel room in southern Maryland, spreading them over every horizontal surface and working them up. I sometimes wonder what the motel owners thought went on in that room when the next morning they discovered a guy with New York license plates on his van had left trash cans overflowing with bloody newspapers and dozens of syringes.

The constant washing of a watershed with rainfall and snowmelt slowly depletes the nutrients that sustain its ecological productivity. But the relentless circularity of the anadromous life-history cycle helps return some minerals from richer marine waters back to rivers. Anadromous fish themselves are bundles of nutrients—that's why we eat them. Once having left their natal rivers as young individuals just large enough to have a chance to survive in the richer but also more dangerous sea waters, they feed heavily and put on weight, eventually maturing and becoming egg- or milk-laden and ready to spawn. And so a river trades numerous young sent to sea fueled by river-derived nutrients for fewer but much larger adults that are themselves laden with marine-derived nutrients upon their return.

These migrating spawners bleed some of these chemical compounds to a river as they excrete waste products. More are contributed in the many eggs and sperm cells that don't find partners or that perish after fertilization. But the largest nutrient inputs originate from the adults that die in the river, more often during the post-spawning phase of life. For some anadromous fishes death soon after spawning is programmed into their genes. For Pacific salmon, in which decomposition seems to precede death, nutritious hunks of salmon are so commonly seen in the flow during spawning runs

that fly fishermen use "flesh flies"—feathers tied to resemble ragged pieces of salmon—to draw strikes from the salmon that have yet to spawn.

The contribution of dead salmon to the fertility of Pacific rivers cannot be overstated. Qualitatively, it seems obvious. Visit the spawning reaches of an unadulterated stream during a run and carcasses lie in the water and on the banks in various stages of rot as still more fresh bodies beat their way monomaniacally past them, only hours to days behind but in lock-step. Juvenile salmon already can be seen nibbling on the bare flesh of their deceased relatives, part of a suite of insects, fish, birds, and mammals that will scavenge them.

Quantitatively, their importance ripples through the Pacific slope ecosystems. Ninety percent of a Pacific salmon's weight is gained at sea. In *King of Fish*, David Montgomery writes: "Up to a third of the nitrogen in valley-bottom forests swam up the river as a fish." Trees growing along salmon-bearing streams grow up to three times faster than those living along salmon-free streams. Higher in the food chain, more than 90 percent of the nitrogen contained in Alaskan brown bears comes from salmon. Circularity—relentless circularity. The hordes of salmon smolts sent seaward could never reach both the abundances and sizes without the lagged enrichment provided by their parents. Salmon essentially extend the fertility of the oceans inland for their own purposes, but also to the benefit of a host of other species tightly entwined in these special ecosystems.

Atlantic salmon did not evolve with that same death switch. And New England and Canadian forests along salmon rivers—as verdant as they are—do not display the grandeur of their cross-continent counterparts. No one has really satisfactorily answered why the salmon of two ocean basins don't share the same life cycle. But because a phenomenon doesn't reach an extreme doesn't mean that it's unimportant. In fact, for Atlantic salmon, surviving first spawning and then returning appears to be the exception; a rough rule of thumb is that one in ten comes back to spawn a second time.

Other East Coast anadromous fish contribute essential nutrients to rivers too. Phosphorus is usually the limiting element in fresh waters. A dead adult alewife adds more than one-half a gram of phosphorus to the ecosystem, while a spawner that survives excretes about one-third of that amount.

This may not be much on an individual basis, but pristine runs that number in the tens to hundreds of thousands to millions would have mightily enriched the river ecosystems they spawned in. In fact, for one small Connecticut pond, Yale researchers estimated that at moderate abundances, more than 40 percent of the phosphorus found there arrived in the form of alewives. Likewise, in a modest stream in Massachusetts, sea lamprey, which always die after spawning, were found to add about a fifth of all the phosphorus that entered that reach annually. In these and other Eastern Seaboard rivers, anadromous fishes when they still ran silver did much to extend the influence of the Atlantic inland. But Atlantic rivers are different today; ghosts aren't corporeal, and ghosts don't migrate.



Chapter 4

On the Nature of Rivers

Water is the driving force of all Nature.

—Leonardo da Vinci

There are two fundamental ways to perceive, to study, or to simply enjoy a river. If you sit on a rock and watch the flow or stand in a stream with a fly rod and observe drowning mayflies pass you on the water's surface while you watch for trout to feed on them, you are a *Eulerian* observer. But if you hop into an inner tube or canoe and drift with the current, you are in the *Lagrangian* camp. Fortunately, there is no need to take sides; each has its pros and cons, and any ardent river scientist or aficionado practices both.

This simple description glosses over important findings in the 1750s by the Swiss mathematician Leonhard Euler and his Italian counterpart, Joseph-Louis Lagrange. The resultant Euler-Lagrange calculation is a rather imposing set of differential equations that is said to be analogous to Fermat's theorem. But they also developed independent equations to describe flow in these two frames of reference, and both have spawned large bodies of sophisticated work—sometimes combining the two approaches—that allows us to comprehend and to predict how water moves.

Before Euler and Lagrange there was Leonardo da Vinci. The Renaissance master was captivated by water, especially in flowing forms. Da Vinci devoted enormous effort to understanding the most basic properties of flowing water, such as bubbles and vortices. He worked both in his laboratory and in nature, where he studied stream hydraulics using a weighted rod held afloat by an inflated animal bladder. In fact, da Vinci wrote more about water than any other subject. It is our loss, though, that da Vinci never followed through on an outline for a treatise on water found in the margin of one of his papers. Anyone who loves rivers would want to learn about

his thoughts and view his sketches on chapters titled "Of Water in Itself," "Of Rivers," "Of the Surface of Water," "Of Things Moving in It," and "Of Things Worn Away by Water," among ten other chapters. Nonetheless, he left behind many remarkably original insights.

Da Vinci's sketch of a free jet of water issuing from a square hole captures the leonine liquidity but also the sheer complexity of its flow. He likened the motion of the surface of the water to hair, noting two motions: one caused by the weight of the hair, and the other, by the direction of the curls. Or, to put it another way, water has eddying motions, one due to the principal current and the other to the random and reverse motion. Indeed, some hydrologists believe his realization anticipated the well-known Reynolds's formula for the decomposition of turbulence by almost four hundred years. Da Vinci also accurately sketched the pair of the nearly stationary counter-rotating vortices in the wake of an object, commenting on how water wends its way past obstacles, and how large and small eddies are related—observations that presaged important modern hydrological concepts. If these notions appear relevant only to a hydrologist, consider that this is what a kayaker must navigate, and that it is a fish's world, too.

Da Vinci may have been the first to recognize the relationship between earth forms and waterborne erosion generated by these motions, writing in his *Coder Atlanticus*: "Water gnaws at mountains and fills valleys. If it could, it would reduce the earth to a perfect sphere." This physical and progressive wearing and transport of the very vessels of rivers is another link to their biology. Water carves the Earth and, in the process, gives the river its form.



"Study of Water Passing Obstacles and Falling"
Leonardo da Vinci, c. 1508–1509

Rivers also carry their bounty of minuscule particles—organic and inorganic shavings and forsam—along with them, resulting in anywhere from chemically uninhabitable to paradisiacally rich and biodiverse flowages.



Some four centuries after da Vinci, there is a substantial but still-emerging science on the nature of rivers. Some river fundamentals: Water flows downhill. Rain and snow falls on the land, and rain and snowmelt run into brooks and streams or percolate underground to emerge as springs. Unless withdrawn for human needs or by intense evaporation in serene landscapes, the waters that run downstream through their catchments are cumulative, as minor tributaries add water to the main stem and as larger trunks merge.

There are exceptions, but the pattern is for the steeper upland slopes at the heads of watersheds to have many small brooks, and for the number of links to lessen downstream as the watercourses become larger. The most upstream rivulets may be ephemeral, visible only during periods of precipitation, and ending at divides—boundaries on the spines of hills and mountains that demark adjoining watersheds. But gravity and water flow make high-relief regions geologically and hydrologically dynamic, and “stream captures” can occur, where an erosively upcutting stream slices into the bed of another, commandeering its flow. Not only does the capturing stream gain more water, but it may acquire new species. This is one mechanism that allows fish and other aquatic creatures to cross mountains and jump drainage basins.

Larger rivers resolutely are “rivers,” but smaller watercourses sport a variety of regional names: A “brook” in New England; a “run” in Pennsylvania; a “kill” in New York; a “branch” in the Southeast; and a “creek” out west. The divisions between these terms—streams and rivers—are subjective. But because smaller watersheds normally flow into and contribute to larger systems, catchments by their nature are arranged hierarchically. This hierarchy offers opportunity for a descriptive framework. The most well-known is “stream order,” using Strahler’s system. In 1952 Arthur Newell Strahler, a geoscience professor at Columbia University, defined a first-order stream as having no tributaries, a second-order stream

as formed by the meeting of two first-order tributaries, a third-order stream as formed by the meeting of two second-order tributaries, and so on, a useful but somewhat “dry” way of describing the great melding of waters in which little brooks become mighty rivers.



Describing the physical geography of rivers is far simpler than characterizing the myriad commonalities and differences in ecology among them. Beginning in the 1970s, as the still-young field of ecology matured, conceptual models of rivers began to be developed. The *River Continuum Concept* proposed by Robin Yarnote and colleagues has been influential. They noted that the metabolisms of smaller, headwater streams of the first to third orders are dominated by what falls or is carried into the water (like mayflies mating and dying above a stream), with photosynthesis playing only a minor role because of the shading by the tree canopy. But the importance of production from rooted vegetation and plankton increases moving downstream to higher-order links. This in-river productivity becomes more significant farther downstream at even higher orders, but can be decreased by the sunlight-blocking turbidity that often characterizes the lowest reaches of rivers and, especially, estuaries—those important reaches where fresh and salt waters meet. And so many anadromous fishes have evolved to capitalize on the river continuum, depositing their eggs in food-poor waters that also can support relatively few predators, but leaving them in position, after they absorb the nourishing yolk sacs they are born with, to drift downstream into food-rich estuaries.

How are these minerals and other essential chemicals processed within flowing water? The conservationist Aldo Leopold recognized the essential role of the retentiveness of nutrients by rivers when he wrote: “All land represents a downhill flow of nutrients from the hills to the sea.” And that this flow has a “rolling motion,” meaning that plants and animals “suck nutrients out of the soil and air and pump them upward through food chains; the gravity of death spills them back.” That is, without nutrients “spiraling” through temporary captivity in food webs of animals and plants in rivers,

these building blocks of life would be carried rapidly downstream and then be shot out to sea.

But today most rivers do not follow the idealized gradients that shape the River Continuum Concept. Hence, the more realistic *Serial Discontinuity Concept*, a corollary which better describes the ubiquitous, less-pristine rivers that are broken up by dams and impoundments. In these kinds of systems, regulating structures such as dams "reset" the river continuum, and not always in the low-order to high-order direction. Because of this, a given stream reach may "behave" ecologically in ways that the River Continuum Concept would predict *should* occur for a different stream order, generating rivers that no longer make ecological "sense."

Add to these concepts the critical notion of scale in ecology. Christopher Frissell and his colleagues at Oregon State University developed a framework of the different evolutionary events and developmental processes that occur at various spatial scales in watersheds. An anadromous fish moving upriver in spring may have only the fierce instinctual drive to reproduce on its mind, but it will "sample" the river as it proceeds at a suite of scales ranging from the river system itself, on the order of thousands of linear yards, created by tectonic forces, governed by erosional planation of the landscape, and persisting for millions to tens of millions of years, all the way down to microhabitat patches of river of less than a yard, created by annual sedimentation, governed by weather-controlled velocity changes, and persisting for weeks to months.

These dynamic smaller-scale changes form much of the basis for the ancient Greek philosopher Heraclitus's famous observation that "you can't step into the same river twice." Recently, some have taken this notion further, saying that even the best Eulerian observer can't step into the same river once! Regardless, watersheds evolve at a series of spatial scales, but not necessarily (and perhaps not even normally) at a steady pace. Yes, over eons erosion appears to be a constant grind, but sediments don't readily dislodge at low flows; it is easier to transport and deposit particles than to first displace them. Interestingly, medium-size particles are most easily eroded. Large ones are heavy, whereas tiny, clay-like particles are "sticky" because of molecular bonding among them. However, the force of water increases geometrically with velocity, meaning that rare but extreme events often

have far greater consequences to a river's form than the ongoing but soft drumbeat of average flows.

This "punctuated equilibrium" for rivers, to borrow from evolutionary biology, was well illustrated in an East Coast watershed in 1972. That June, an unusually early hurricane, Agnes, visited the Chesapeake Bay watershed. Though only a Category 1 cyclone in wind speed, it dropped torrential rains of six to twelve inches over a short time, resulting in catastrophic flooding. I still recall driving on a bridge over the Susquehanna River in Harrisburg after the waters receded and looking down at an island to see an aluminum canoe wrapped like a U around a tree some twenty feet up in the air. So much freshwater was flushed into Chesapeake Bay that the seafood industry was damaged for several years. The storm caused the Susquehanna River alone to carry over 31 million metric tons of sediment into the Bay—some thirty times the annual average!



Although one might think the relationship between flow and sediments and, thus, the very nature of rivers is eternal, how rivers functioned was different in the Cambrian Period, half a billion years ago. For decades scientists who thought deeply about rivers entertained a surprising but difficult-to-prove hypothesis: that land plants created the shape of modern rivers hundreds of millions of years ago. Recently, researchers at Dalhousie University strengthened the case for this. The Cambrian's geologic record shows that rivers were shallow but wide, like floods that allowed rainwater to run sheetlike off the barren land. In fact, sediment sizes and distributions suggested that rivers then were one thousand times or more as wide as they were deep.

When these researchers looked at river sediment deposits from the Silurian-Devonian boundary, some 420 million years ago, the patterns changed. The unconsolidated sediments characteristic of the Cambrian appear less frequently, while the depositional footprints of more complex and diverse rivers are seen. There also is more mud, probably due to the enhanced chemical weathering that plants assist. But, most significantly,

the shapes of rivers change to highly sinuous, single-thread channels. How could this happen? Plants bind the soil of riverbanks, creating new dynamics between flow and erosion. This was demonstrated experimentally in a laboratory at the University of Minnesota. Alfalfa sprouts were allowed to germinate on the banks of a channel that flowed between multiple sandbars. Over time the system was transformed into one that self-organized into a single-thread channel. The strength of the alfalfa roots was enough to completely change the pattern. Another river researcher commented that these findings “may be considered significant progress in the comprehension of one of the most critical phases in the coupling between physical and biological processes on Earth.”



Science proceeds according to well-supported but imperfect paradigms that occasionally are overturned through new findings or new ways of thinking, or a mix of both, as so eloquently outlined by Thomas Kuhn in his 1962 classic, *The Structure of Scientific Revolutions*. A paradigm shift in our comprehension of the form of Piedmont rivers occurred with the publication of a paper in *Science* in 2008 by Robert Walter and Dorothy Merritts of Franklin & Marshall College in Lancaster, Pennsylvania. Until then, river restoration was based on a notion of a characteristic pristine form where water flowed in a single meandering channel through a floodplain. In other words, an archetypical normal river looked much like many assume a healthy river looks today—one main channel with picturesque bends and a sandy or muddy bottom. This form, of course, had become the goal for river restoration.

Examining many lines of evidence, Walter and Merritts showed how wrong that thinking was—how centuries of milldam construction, together with the geophysical cycles they wrought, had radically altered the nature of many East Coast rivers. Walter and Merritts mounted one of those multipronged investigations that are becoming the *sine qua non* of environmental history these days, surveying archived early accounts and maps of milldams along with historical geochemical and geophysical records of river valleys during the period of early land clearing, making their own

field observations. Ironically, much of this work was conducted on the same streams and reaches examined in the studies that pioneered earlier fundamental ideas about how rivers behaved through time.

A little milldam history: Europeans had used milldams since as early as 1100 BC, and they quickly applied their know-how in the New World, beginning in the late 1600s. Dams and races that delivered water from the newly formed ponds powered iron forges, furnaces, and mining operations, but most often mills. Indeed, before the advent of steam engines, every mill required a reliable source of dammed water to power it. This resulted in a proliferation of milldams, with peak construction occurring between 1780 and 1860. Walter and Merritts’s analysis of 872 counties in the eastern United States revealed more than 65,000 water-powered mills by 1840. Water-powered milling was especially intensive in the Mid-Atlantic Piedmont region, along and west of the fall line. In fact, by the late 1700s the Brandywine Valley had the most notable concentration of milldams in the colonies, with sixty paper mills alone.

This density was achieved despite a less-than-steep gradient—the faster water runs downhill, the more milldams are possible. Even with this modest slope, the investigators found there was one milldam every 1.5 to 3 miles along the Brandywine and its neighboring watersheds. With most milldams ranging between about eight and twelve feet in height, calculations showed that flows would be reduced by 60 percent from about a half-mile to two miles upstream, allowing heavy siltation from the logged and farmed surroundings.

Once the milldams were erected, the accompanying sediments became pale brown and fine-grained, reflecting erosion from the land. These deposits were thickest in the deeper waters near the dams, and thinned upstream from them. Over time, the ponds filled in at the bottoms and sides, with many reaching full sediment storage capacity by about 1850. The investigators repeatedly observed groves of large trees that provided a time marker of up to about 150 years old on valley fill deposits. From then on, the ponds gradually diminished in size and became stable swamps and meadows until the dams breached, causing the waters to cut into the deposits, creating the kinds of simple linear and steeply sided riparian environments we took for

normal until this research occurred. Much of today's problematic suspended sediment and nutrient loads in East Coast rivers may be due to this legacy.

Peering below the sediments of the Colonial Era for a view of undisturbed rivers, Walter and Merritts found their natural bottoms contained seeds, nuts, branches, roots, peat, and even tree trunks. These rivers passed through forested wetlands with small branching flows around low vegetated islands that united and separated to form broad necklaces of water. They also contained vastly more woody debris, with natural "snags" and logjams of limbs and branches likely causing new side channels to form, contributing to the dominant braided pattern of flow. The ubiquity of this alternative, natural form was also demonstrated by old maps of European rivers, and today, in the River Lee, flowing through a rare patch of ancient forest near Cork, Ireland. The traditional stream archetype was dead wrong: in the United States two generations of milldam construction inundated and buried presentment wetlands and drastically altered stream functions and ecology.



But before European colonists modified Atlantic rivers, there were beavers. They also built dams and had been building them for millennia. Still, beavers are often viewed as cute curiosities instead of the remarkable ecosystem shapers they are. Beavers are among the world's most unlikely creatures—oversize rodents imbued with idiot-savant-level abilities to perform hydrological engineering. When I was in graduate school, a fellow student from Taiwan, Moses Chang, refused to acknowledge that the existence of beavers was anything but apocryphal; he insisted that no rodent could perform such dam-building feats. It wasn't until we showed him an actual beaver dam in the Adirondacks, with its carefully woven wall of sticks holding back a substantial pond, that Chang said, "Okay, I admit it; beavers do exist."

In fact, they once existed in extraordinary numbers. Before the arrival of Europeans, some 60 to 400 million beaver were estimated to be gnawing wood from the Arctic tundra to the deserts of northern Mexico. In New England and along much of the Eastern Seaboard, nearly every water body

was inhabited and, of course, modified by beaver. But their handsome and useful fur was their downfall, with massive hunting and trapping in the early 1600s sending them into a steep decline, a demand perhaps driven by its coinciding with the coldest portion of the Little Ice Age. Between 1620 and 1630, in Connecticut and Massachusetts alone, more than 10,000 beavers per year were killed for the fur trade. Likewise, between 1630 and 1640 in the Hudson Valley and western New York, approximately 80,000 were killed annually. So great was the taking of beaver, perhaps 50 million in North America alone, that it is hypothesized the resultant drastic reduction from an estimated original 25 million beaver ponds with consequent lowered methane and carbon dioxide discharges instigated a "reverse-greenhouse effect," reinforcing the Little Ice Age and, ironically, creating an even greater need for warm beaver-fur coats.

Today, after a comeback that has brought their numbers to perhaps 6 to 12 million, beavers are often viewed as little more than suburban annoyances whose dams flood backyards. But healthy beaver populations once had a profound influence on otherwise-undisturbed landscapes; their woodcutting and barrier-building retained sediment and organic matter in river channels, created and maintained wetlands, increased nutrient cycling, and helped to shape associated plant and animal communities. Healthy streams may have fifteen or more beaver dams per mile, each dam holding back thousands of cubic yards of sediment and enlarging the wetted area several hundredfold. One beaver dam, however, became notorious in 2010 when it was seen from space. Most beaver dams are tens to hundreds of feet long, but the beavers in Wood Buffalo National Park in Alberta, Canada, have been working since the 1970s on a structure that now stretches for 2,800 feet. When beaver colonies existed serially along watershed corridors, they were the dominant controlling force across many landscapes. Colonists in eastern North America encountered streams that were broad and ponded, swampy, slow-flowing, and highly productive because of the relentless efforts of forty-pound rodents.



The author of the fly-fishing novel *A River Runs Through It*, Norman Maclean, was “haunted by waters.” He is not alone. A river speaks many languages. When I stand in a river, survey the currents, and cast a trout fly to what might be called the edge of a “quasi-stationary counter-rotating vortex,” or, more simply, to “nice-looking water,” many thoughts pass through my mind, among them, the fact that I am cuing to the end result of many millennia of evolutionary fine-tuning between a remarkably dynamic environment and superbly adapted fishes. A glint of nature worthy of a da Vinci sketch.



Interlude I

A Shad's Journey, circa 1600

The shad wriggles and then pops through the membrane that was her waterborne capsule for ten days as she drifted along as an egg. Her female parent, a medium-size American shad on her second spawning run, had immediately departed the mating area upriver and was working her way back to the sea and its rich food stores to begin another migratory lap along the Atlantic coast. Barely an eighth of an inch long and a feeble swimmer, the shad carries three weeks' worth of provisions—a yolk sac, minuscule but packed with nutrition, to kick-start survival as a speck in the big river.

The shad lives in a soupy world. The flow contains inorganic and organic detritus washed by rains and the melting snowpack from high in the watershed, bacteria that feast on these nutrients, and algae that bloom under the strengthening sun. At her size, though, the world is measured only in inches—flocks of minerals are like boulders; a phytoplankton cell is a beach ball. She drifts with multitudes of her tribe, some hatched earlier than she, some later, and with the eggs and larvae of other fishes—all sharing an evolutionary course where spawning takes place in accord with an instinctual memory of the approximate time and place that often enough in the past led to a good-enough match with the peaking of microbial food production in the river to ensure perpetuation of her kind.

This burst of life near the sunny surface of the river positions the shad in the middle of the food chain. As she finishes depleting her yolk, she begins to graze on minute plankton, obeying the most elemental law of nature—to eat or be eaten. With tens of thousands in her cohort, she coasts along in a defenseless and yet ironical state—there is a sort of safety in numbers—but those high abundances also attract predators. Shad after shad is picked off by perch, sunfish, and minnows as the survivors struggle to eat and grow.

In four weeks the shad has matured considerably, transforming to a diminutive version of her adult form, graduating to larger prey such as insect larvae, and