

Anadromous Fishes as Ecological Links between Ocean, Fresh Water, and Land

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Oceans, freshwater streams and lakes, and terrestrial "ecosystems" are usually thought of as separate entities, studied by different sets of scientists who seldom interact. Interactions among these systems are commonly seen as unidirectional: a flow of materials from land to fresh water to sea. For instance, stream ecologists often emphasize the importance of terrestrial inputs such as large woody debris for stream structure and allochthonous litter and insects as food for freshwater organisms. Marine ecologists note that streams carry silt and sediment to estuaries (e.g., Jickells 1998). The possibility of reverse flow patterns has received relatively little attention, although it has long been recognized (Leopold 1941, cited in Likens and Bormann 1974). This volume, and the relatively recent investigations that stimulated it, are proof that the long-lived classic paradigm of unidirectional flow is being overturned thoroughly.

Our thesis is that anadromous fishes form ecological links from ocean to fresh water to land. Anadromous fishes, returning from the ocean to freshwater streams to spawn, enrich the freshwater food chain. Terrestrial carnivores and scavengers, foraging on these fishes, transport marine-derived nutrients in the form of fish carcasses and digesta from fresh water to land, enriching the riparian food chain and influencing the biology of major terrestrial consumers.

Table 19.1 Taxonomic distribution of anadromy in fish families

Family	Anadromous species	Total species	% anadromous	Common names
Petromyzontidae	9	37	24	Lamprey
Acipenseridae	8	27	30	Sturgeon
Salmonidae	28	68	41	Salmon, trout, whitefish
Osmeridae	6	12	50	Smelt
Salangidae	13	14	93	Noodlefish
Retropinnidae	3	4	75	New Zealand smelt
Aplochitonidae	3	3	100	Whitebait
Clupeidae	<16	180	<9	Herring
Ariidae	1	120	<1	Sea catfish
Syngnathidae	1	175	<1	Pipefish, seahorse
Gasterosteridae	2	8	25	Stickleback
Gadidae	1	55	2	Cod
Percichthyidae	<3	40	8	Temperate perch
Cottidae	<3	300	<1	Sculpin
Gobiidae	<14?	800	<2	Goby

SOURCE: McDowall 1987; taxonomy mostly according to Nelson 1994.

That anadromous fishes contribute to the productivity of fresh waters has been known for decades (Gilbert and Rich 1927; Juday et al. 1932; Nelson and Edmondson 1955). Occasional papers on this subject appeared throughout the ensuing decades, but concerted approaches to understanding the cascading interactions based on anadromous fishes have appeared only recently. Popular articles have even appeared in newspapers and popular journals about the increasing evidence that "it takes a salmon to make a salmon," not only genetically but ecologically (e.g., Hunt 1997; Levy 1997a, 1997b). Nevertheless, we have a long way to go before we comprehend the detailed workings of these interactive systems, including their numerous and important variations in time and space, and the relationships between aquatic and terrestrial habitats in systems enriched by nutrient subsidies from anadromous fishes.

ANADROMOUS FISHES: DISTRIBUTION AND LIFE HISTORIES

"Anadromous" means "to run up," thus including any organism that regularly migrates upstream. In general usage, the term is restricted to organisms that migrate from ocean to fresh water to spawn. We use the second meaning of the term here, although many of the principles we set out could be applied to the first meaning.

About fifteen fish families have anadromous representatives (table 19.1; McDowall 1987, 1988). Of these, the lamprey, sturgeon, salmon and

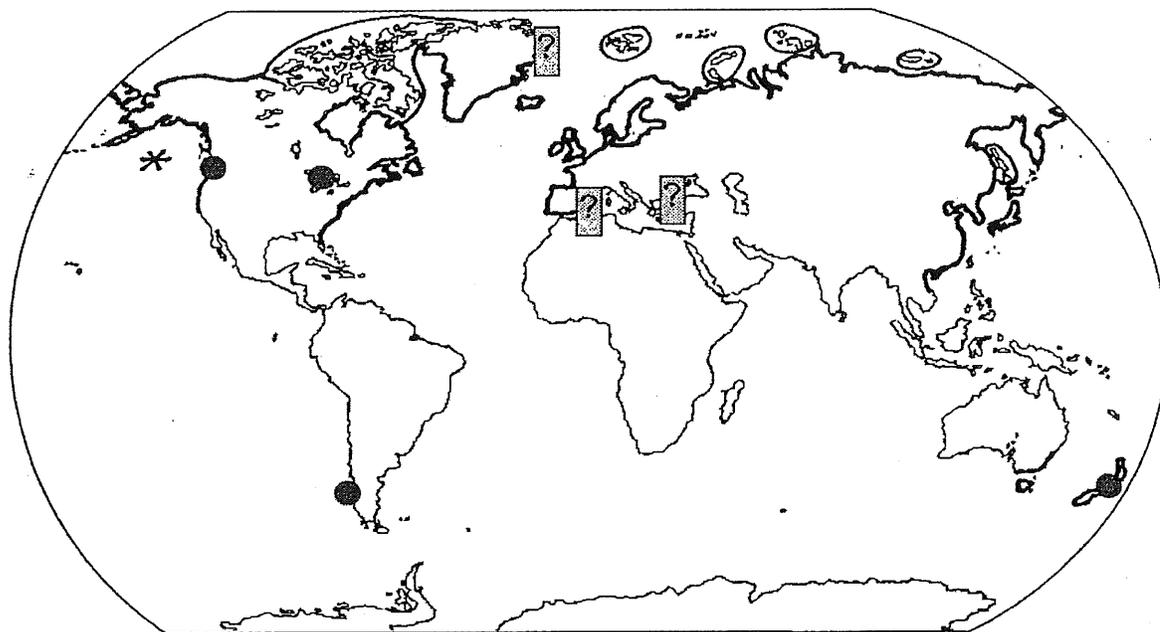


Figure 19.1 Global distribution of anadromous fish species. Heavy continental outlines indicate historical distributions; solid circles, introduced populations; asterisks, regions still retaining large populations of native anadromous fishes; ?, no information available. (From McDowall 1987, 1988.)

whitefish, smelt, noodlefish, and herring families contribute the most species, but the habit is most widely expressed (as a percentage of species in species-rich families) in the sturgeon, salmon, smelt, and noodlefish families. Anadromy is well developed in some ancient lineages but also occurs sporadically in more recently evolved groups. In short, it has evolved independently many times but remains a relatively uncommon life history (< 1% of fish species).

Anadromy is overwhelmingly most common in the north-temperate and boreal regions and occurs at low frequency in the tropics and the Southern Hemisphere (McDowall 1987, 1988). The extensive coastline along the large northern land masses may have contributed to its high frequency there. In North America, the frequency of anadromy changes little with latitude but constitutes an increasingly dominant proportion of the life histories at higher latitudes. Similar latitudinal patterns of frequency and proportion usually occur within single species (McDowall 1987, 1988). Thus, on a global scale (fig. 19.1), most of what we say about the ecological importance of anadromous fishes pertains to north-temperate and boreal zones, and perhaps especially to the far north, because soils and freshwater streams are more often nutrient-poor there (e.g., Ulrich and Gersper 1978; Matthews 1992; Oswald 1997).

Life histories of anadromous fishes vary from fully iteroparous (sturgeon) to fully semelparous (five species of Pacific salmon, *Oncorhynchus*). Presumably the evolutionary choice between these life history patterns was set by the relative mortality rates of adults and juveniles: if adults have a low probability of living to reproduce again, semelparity may be favored (reviewed in Stearns 1992). A low probability of surviving to reproduce again is thought to be related to the cost of the spawning migration and the risks of freshwater reproduction—including the risk of predation by terrestrial carnivores (Willson 1997).

Most of the biomass of anadromous fishes accumulates during their growth at sea and therefore is composed of marine-derived materials. At maturity, these fishes return to fresh water to spawn. When semelparous fishes senesce and die, their carcasses often accumulate on rocks, woody debris, and gravel bars in streams (e.g., Cederholm and Peterson 1985; Cederholm et al. 1989). There they rapidly dwindle away (Minshall et al. 1991; Piorkowski 1995; M. F. Willson, S. M. Gende, and P. A. Bisson, personal observations), fed upon by scavenging vertebrates (eagles, corvids, gulls, carnivorous mammals), macroinvertebrates, and microorganisms. Both semelparous and iteroparous spawners may be preyed upon by terrestrial carnivores and scavengers, including bears, wolves, coyotes, and foxes (and many others of lesser size) (e.g., Willson and Halupka 1995; Marston et al. 2002). These consumers often carry fish from fresh water to land, where they cache or consume part of the prey, leaving the remnants and excreta to decompose in terrestrial, chiefly riparian, habitats. The input from semelparous species is potentially greater than that from iteroparous species because all adults die and decompose in or near fresh water and, within the salmon family, because the semelparous *Oncorhynchus* apparently maintain larger population sizes than their more iteroparous relatives (e.g., *Salmo*; T. P. Quinn, personal communication).

Thus, anadromous fishes bring marine-derived nutrients to fresh water, and terrestrial consumers carry some of those nutrients to land. Some proportion of those nutrients is recycled from land to fresh water and from fresh water back to the sea, but we focus here on the flow of materials from ocean to land.

NUTRIENT TRANSFER BETWEEN HABITATS

Nutrient Content of Anadromous Fishes

Little has been published on the nutrient content of anadromous fishes. Just as most studies of the effects of artificial fertilization on fresh waters (e.g.,

Table 19.2 Nutrient content of some anadromous fishes (g/fish)

	Unspawned	Spawned
Sockeye salmon (<i>Oncorhynchus nerka</i> ; male + female)		
C	392	162
N	73	50
P	13	9.5
S	3.5	2.5
Atlantic salmon (<i>Salmo salar</i> ; female)		
N	67	60
P	8	11.5
Alewife (<i>Alosa pseudoharengus</i>)		
C	33	21
N	6	5
P	1	0.9

SOURCES: Sockeye salmon, Mathisen et al. 1988; Atlantic salmon, Talbot et al. 1986; alewife, Durbin et al. 1979.

NOTE: Values are rounded.

Elser et al. 1990; Hart and Robinson 1990; Jorgenson et al. 1992; Peterson et al. 1993; Stockner and MacIsaac 1996; Perrin and Richardson 1997) and many studies of soil nutrients (e.g., Tarrant and Miller 1963; Russell 1966; Wollum and Davey 1975; several papers in Tieszen 1978) emphasize N and P, so do most of the available data on the nutrient content of fish or fish-fed vertebrates on land (table 19.2, Lyle and Elliott 1998; but see also Sugai and Burrell 1984; Talbot et al. 1986; Williams et al. 1978; Shearer et al. 1994). In general, the N content of whole salmon ranges between 2% and 4%, and the P content is less than 1% (Haywood-Farmer 1996; S. M. Gende et al., unpublished data). Many studies have documented the ecological effects of N and P enrichment (see below).

Some micronutrients in anadromous fish bodies may also have important ecological effects. For example, calcium (< 1% of whole-fish biomass; S. M. Gende et al., unpublished data) reduces the acidity of water, and streams flowing over limestone are often relatively productive (Egglshaw and Shackley 1985; Bryant et al. 1997). Ca in solution may directly benefit developing juvenile salmonids (McCay et al. 1936). Soil acidity and availability of base cations influences soil fertility (Vitousek, Aber et al. 1997), the productivity and composition of boreal forests (Giesler et al. 1998), and tree mortality (e.g., Likens et al. 1998). The effects of soil Ca from anadromous fishes on higher trophic levels are unknown but could include eggshell thickness in birds and bone density (Barclay 1994; Eeva and Lehtikoinen 1995; Graveland and Drent 1997).

Sizes and Numbers of Anadromous Fishes

The size of the individual package of marine-derived nutrients represented by an anadromous fish varies enormously: anadromous fishes range in size from less than 40 g (smelt, alewife) to many kilograms (some chinook salmon, *Oncorhynchus tshawytscha*; sturgeon). The number of such nutrient packages that arrive from the ocean also varies greatly. Run sizes of wild salmon range from just a few fish in a tiny stream to over 40 million (and perhaps as many as 100 million) in the Fraser River system, often with considerable annual variation within a system (e.g., Ricker 1987; Northcote and Larkin 1989; Roos 1991; National Research Council 1996; Larkin and Slaney 1997; Halupka et al. 2000), although many runs are now seriously depleted, especially south of Alaska (Roos 1991; National Research Council 1996; Nehlsen 1997; Regier 1997). Less is known about the density of fish in spawning reaches, but estimates range from fewer than 300 coho salmon (*O. kisutch*) per kilometer in Washington (Cederholm et al. 1989; Washington Department of Fisheries, Washington Department of Wildlife, and Western Washington Treaty Indian Tribes 1993) and Oregon (Nickelson et al. 1992) to about 170,000 sockeye salmon (*O. nerka*) per kilometer in the Adams River in a peak year (Lewis 1994) to perhaps almost a million sockeye salmon per kilometer in another part of the Fraser system (Ricker 1987).

Delivery of Nutrients from One Habitat to Another via Anadromous Fish Bodies

Ocean to Fresh Water (and Back)

British Columbia and the Yukon Territory once had over 9,660 anadromous salmon stocks, of which over 100 are recently extinct (Slaney et al. 1996). Southern British Columbia alone has over 900 salmon streams with 2,300–2,400 distinct runs (Larkin and Slaney 1997). Larkin and Slaney estimate that salmon can increase regional levels of P by 200 times and levels of N by 18 times over the levels that would prevail without salmon. In southeast Alaska, over 5,200 anadromous fish streams, with a total length of over 40,000 km (Halupka et al., unpublished data), support several anadromous species: seven salmon and trout (*Oncorhynchus*), a char (*Salvelinus*), and three anadromous smelts (including the eulachon, *Thaleichthys pacificus*). The levels of fertilization (per unit area) provided by these fishes to fresh waters often exceed those of most agricultural ecosystems. Perhaps 100 million adult salmon return to southeast Alaska streams to spawn each year (Alaska Department of Fish and Game 2003), bringing an estimated 100 million kg of carbon, 10 million kg of N, and 2 million kg of P to freshwater

streams. An additional 150–200 million fish, which would have returned to spawn, are harvested, thus reducing the nutrient input to about a third of what it would be without commercial harvest; most are wild fish, as only some (about 7% over all species; Alaska Department of Fish and Game 2003) of the harvested fish are hatchery-bred in southeast Alaska. On a local scale, a small run of salmon (e.g., 1,000 fish km⁻¹) would provide an estimated 9.4 kg P km⁻¹ to its natal stream, assuming that all fish died and decomposed in situ (Willson et al. 1998). Salmon-enriched fresh waters exhibit enhanced productivity of aquatic phytoplankton, invertebrates, and fish (table 19.3) and would be expected to exhibit more rapid breakdown of allochthonous litter (e.g., Webster and Benfield 1986). The magnitude of the fertilization effect varies enormously among fresh water bodies (e.g., Mathisen 1972; Stockner 1987; Stockner and MacIsaac 1996; Gross et al. 1998) and among potentially responding organisms (e.g., Hershey 1992).

When the fish die, some are carried downstream to the estuary (Brickell and Goering 1970; Sugai and Burrell 1984; Reimchen 1994). The quantity of fish carcasses and dissolved nutrients thus returned to the sea is seldom known for any system but undoubtedly varies from almost 100% in short streams with few obstacles to retain carcasses (e.g., Brickell and Goering 1970) to a very small proportion in inland streams with ample woody debris and boulders (or lakes) to hold carcasses (Cederholm and Peterson 1985). Estuarine scavengers such as halibut, crabs, and snails gather to take advantage of the influx of salmonid material (e.g., Reimchen 1994). Decomposing carcasses increase the growth of estuarine algae, a principal food of harpacticoid copepods, which in turn are fed upon by juvenile salmonids (Fujiwara and Highsmith 1997). Some carcasses may decompose in intertidal meadows, fertilizing the growth of sedges and other major foods of herbivorous migratory waterfowl on the west coast of North America (Hutchinson et al. 1989; Verbeek and Butler 1989; R. H. Armstrong, personal communication).

Fresh Water to Land (and Back)

The Tongass National Forest occupies 16.9 million acres (about 6.8 million ha), covering most of southeast Alaska; about 59% of this area is forested (> 10% tree cover; Everest et al. 1997). Of the forested land, about 47% is within 0.5 km of an anadromous fish stream (G. Fisher, personal communication, from GIS maps); we estimate that over 90% of the forested land may lie within 5 km of an anadromous fish stream. Plainly, most of the anadromous fish streams in this region are within easy reach of terrestrial vertebrate predators and scavengers.

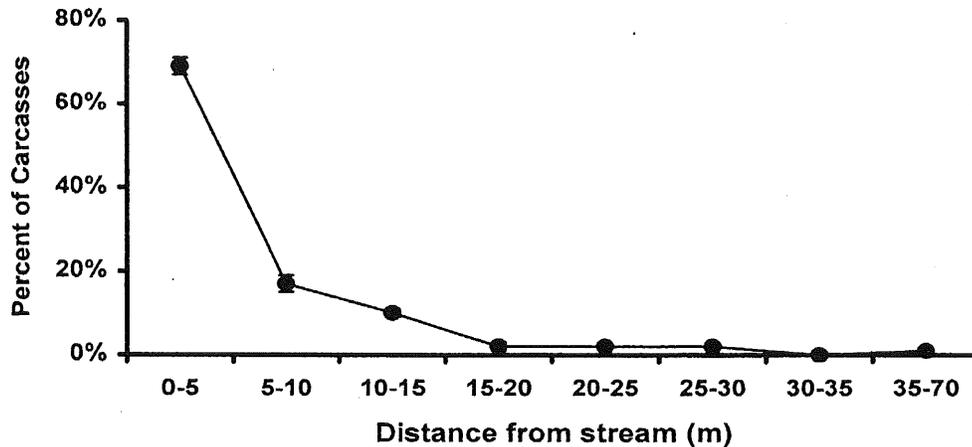


Figure 19.2 Distribution of salmon carcasses near spawning streams in southeast Alaska. Data points are the average proportions of carcasses ($N = 900$) at given distances from several streams. (From S. M. Gende and M. F. Willson, unpublished data.)

Many vertebrates forage on living, dying, or dead fish (Willson and Halupka 1995; Willson et al. 1998; Marston et al. 2002). These foragers include bears, canids, eagles, and corvids, which often carry whole fish, fish parts, or digested fish to land. Both undigested and digested fish are deposited, sometimes at high densities, on the soil, where this nutrient-rich material usually is quickly decomposed.

Estimates of the proportion of spawners captured by terrestrial foragers range up to 60–70% or even 100% in small streams (Shuman 1950; Gard 1971; T. P. Quinn, personal communication), although it commonly must be much less (e.g., Frame 1974). The amount of salmon eaten daily by a black bear (*Ursus americanus*) may be about 21 kg (Reimchen 1994). Even more may be taken from the stream to land, especially by large brown bears (*U. arctos*) when they are selectively foraging on particular portions of the carcass (Gende et al. 2001).

In southeast Alaska, bears usually deposit the partially eaten bodies of salmon near the stream, although some carcasses are carried over 75 m away (fig. 19.2). Elsewhere, carcasses may be carried up to 150 m into the forest (Reimchen 1994), or “several hundred yards” from the stream (Shuman 1950). Females may be more likely than males to be carried to land by black bears (Reimchen 1994), especially if they are still gravid (Frame 1974). Both black and brown bears are likely to carry large salmon farther into the forest than small ones (Reimchen 1994, 2000; S. M. Gende and M. F. Willson, unpublished data), and fresh kills are more likely to be carried into the forest than are carcasses of senesced fish

Table 19.3 Effects of anadromous fish carcasses on aquatic systems: some examples of "biogenic eutrophication" from the literature

Water body	Location	Fish biomass or abundance	Species	Nutrients		Effect on			Reference
				N	P	Microorganisms/ plankton	Invertebrates	Fish	
Karluk Lake	South-western Alaska	2 x 10 ⁶ kg	Sockeye salmon		5,000 kg	Increase		Increase	Juday et al. 1932; Nelson and Edmondson 1955; Koenings and Burkett 1987
Iliamna Lake	South-western Alaska	340,000 to 24 million	Sockeye salmon		3.6-170 metric tons	Uptake of MDN ^a		Uptake of MDN	Donaldson 1967; Hartman and Burgner 1972; Kline et al. 1993
Nushagak system	South-western Alaska	Up to 5.9 million	Sockeye salmon					Increase	Mathisen 1971, 1972
Dalinee Lake	Russia	Up to 15% of energy input	Sockeye salmon						Krokin 1968, 1969, 1975; Sorokin and Paveljeva 1978
Pausacaco Pond	Rhode Island	4,530 kg C	Alewife	728 kg	115 kg	Increase		Increase	Durbin et al. 1979
Skagit River	Washington	Up to 0.7 million = 1.6 million kg	Pink salmon					Increase coho, decrease chum?	Michael 1995

Chulitna River tributaries	South-central Alaska	?	Various salmon	Increase of some taxa	Piorowski 1995
Margaret Creek	South-eastern Alaska	75,000	Pink salmon	Increase of some taxa	Wipfli et al. 1998
Sashin Creek	South-eastern Alaska	30,000	Pink salmon	Uptake of MDN	Kline et al. 1990
Various streams	British Columbia	Various	Various salmon	Increase	Johnstone et al. 1997; Larkin and Slaney 1997
Snoqualmie River tributaries	Washington	?	Coho salmon	Increase	Bilby et al. 1996

^aMDN = marine-derived nutrients

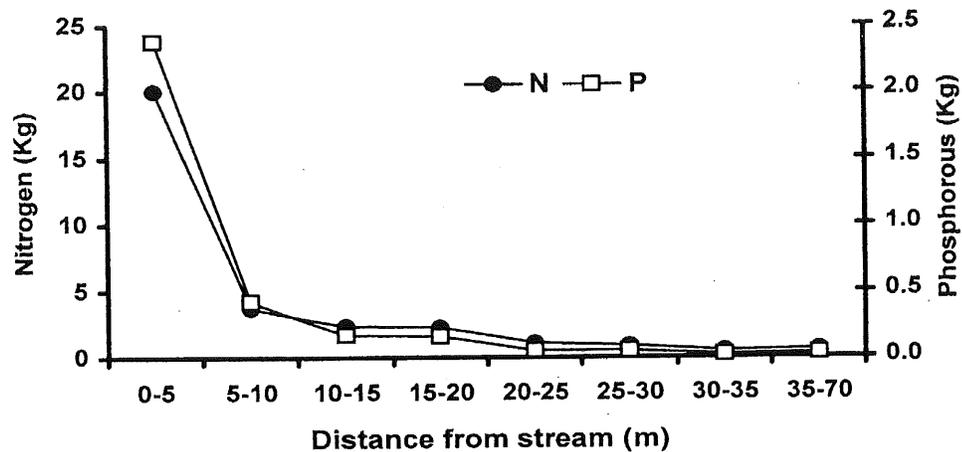


Figure 19.3 Distribution of nutrients (N and P) from salmon carcasses near spawning streams in southeast Alaska. Data points were calculated from figure 19.2.

(Reimchen 1994, 2000). The distribution of carcasses on the shore can be influenced by the abundance of spawning fish, the numbers of bears present, and social interactions among the bears (Luque and Stokes 1976; Egbert and Stokes 1976; Reimchen 1998; Gende 2002).

As a result of bear transport, salmon-derived nutrients are added to the terrestrial riparian system (Hilderbrand, Hanley et al. 1999) (fig. 19.3). Although nutrient deposition is clearly greatest near the stream, the long tail on the distribution indicates that some deposition occurs at some distance from the stream. In actuality, the tail of the distribution is more attenuated than illustrated in figure 19.3 because large carnivores range widely and some excreta will be deposited at greater distances. Furthermore, scavenging eagles (*Haliaeetus leucocephalus*), ravens (*Corvus corax*), and crows (*C. caurinus*) commonly carry salmon pieces (and smaller forage fishes) into the forest, sometimes over 100 m; some food items are stored in trees or meadows by corvids, dropped en route, or taken to nestlings.

Some marine-derived nutrients are recycled from the enriched land back to fresh waters via leaching and runoff, terrestrial insects that fall into the stream (Hunt 1975; Wipfli 1997; Nakano and Murakami 2001), riparian zone vegetation litter, which is often a major nutrient source for streams (e.g., Durbin et al. 1979; Sidle 1986), and vertebrate excreta deposited in streams.

Our emphasis on biological agents of nutrient transfer should not obscure the fact that some transfer, of variable magnitude, also occurs by abiotic means, such as hyporheic flow (Gende et al. 2002).

EFFECTS OF NUTRIENT TRANSFER

In Fresh Water

Increased nutrients commonly increase the productivity of freshwater food chains, especially in oligotrophic waters. Most information on this subject comes from studies in which inorganic supplements were added (e.g., Nelson and Edmondson 1955; Ashley and Slaney 1997; Kyle et al. 1997; Perrin and Richardson 1997; Budy et al. 1998). Some studies, however, focused specifically on nutrients arriving via anadromous fishes (see table 19.3; Lyle and Elliott 1998; Wipfli et al. 1999) or their analogs in strictly freshwater systems (Richey et al. 1975; Rand et al. 1992; Kraft 1993; Schuldt and Hershey 1995). In general, salmon subsidies are incorporated into aquatic organisms (Chaloner et al. 2002; Bilby et al. 1996) and can increase productivity at all trophic levels, including fish. Future work should disentangle the relative effects of different nutrients and nutrients following different pathways (Gende et al. 2002) as well as the interactions among nutrient subsidies (Treseder and Vitousek 2001).

On Land

Marine-derived nutrients (from decomposed salmon carcasses or carnivore excreta) can be taken up by streamside vegetation (Bilby et al. 1996; Reimchen et al., in press; Ben-David, Hanley, and Schell 1998; Ben-David, Bowyer et al. 1988), and some riparian plants exhibit enhanced growth (Helfield and Naiman 2001, 2002), but their possible effects on reproductive output or succession have not yet been assessed. Herbivorous and detritivorous invertebrates that forage on salmon-enriched vegetation and leaf litter accumulate salmon-derived nutrients (Reimchen et al., in press; Hocking and Reimchen 2002). Several species of invertebrates (flies, beetles) colonize salmon carcasses soon after deposition on land, rapidly turning such carcasses into a seething mass of maggots and beetle larvae (Johnson and Ringler 1979; M. F. Willson, S. M. Gende, and P. A. Bisson, personal observations). These invertebrates are not known to be eaten by terrestrial insectivores (Reimchen 1994) but, when washed into the stream, are fed upon by fish (Johnson and Ringler 1979; Wipfli 1997).

Dozens of species of vertebrates feed directly on anadromous fish bodies, carcasses, or eggs (Willson and Halupka 1995; Marston et al. 2002), sometimes gathering in large numbers near spawning streams (e.g., Luque and Stokes 1976; Marston et al. 2002). Vertebrates may also respond to salmon

enrichment of terrestrial vegetation (and insects): in southeast Alaska, breeding bird density (in the spring) tended to be higher along salmon streams than along streams lacking salmon runs (Willson and Gende 2001), possibly because of increased arthropod abundances (Nakano and Murakami 2001). That breeding bird density might increase in response to salmon fertilization is plausible, given that bird density in the nearby Yukon Territory increased following aerial application of inorganic fertilizer (Folkard and Smith 1995).

The breeding biology and body size of consumers may also be affected by this rich food resource. The abundance of salmon in summer may increase survival of fledgling and juvenile bald eagles, as well as subsidizing the very high eagle densities in southeast Alaska. Spring foraging on eulachon probably helps pay the reproductive costs of Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*) and the migration and prereproductive costs of red-breasted mergansers (*Mergus serrator*) and several species of gulls (*Larus* spp.) (Marston et al. 2002). Mink (*Mustela vison*) in southeast Alaska give birth earlier than other high-latitude populations, perhaps because the lactation period then coincides with salmon availability (Ben-David 1997). Coastal bears with regular access to abundant fish runs grow bigger, mature earlier, have larger litters, and reproduce more often than interior bears (Herrero 1978; Spraker et al. 1981; Nowak and Paradiso 1983; reviewed by Welch et al. 1997; Willson et al. 1998), and they reach very high densities (over 200 bears 1,000 km⁻²; Miller et al. 1997). Indeed, the large body size of coastal brown bears apparently cannot be supported by a diet of fruit (Welch et al. 1997), and the abundant food supply provided by salmon may have permitted their large size (Hilderbrand, Schwartz et al. 1999). However, inland bears with regular access to (formerly) large salmon runs on the Columbia, Fraser, and Yukon river systems (Hilderbrand et al. 1996) seem to have remained relatively small.

DISCUSSION

It may be a matter of semantics whether to discuss aquatic-terrestrial interactions as part of the ecological richness associated with ecotones (Naiman and Décamps 1990, 1998) or as integrated systems in and of themselves. Clearly, in any event, close integration of land and water ecology is potentially important wherever anadromous fish run. To illustrate the relationships between land and water, we present a simplified version of the food web that links anadromous fishes to the terrestrial system (fig. 19.4). Although there are other interactors in this web (fleshy

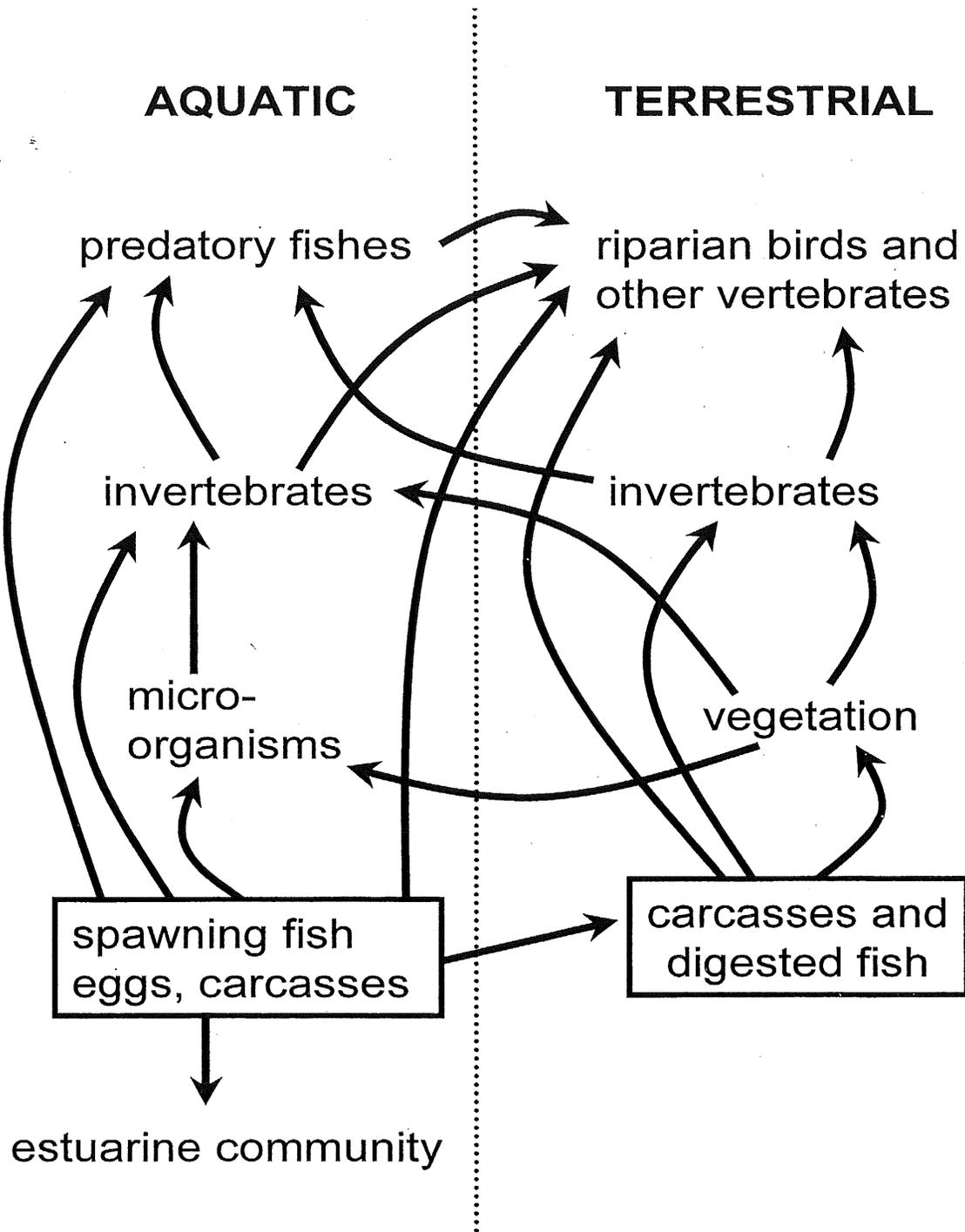


Figure 19.4 A simplified general food web linking aquatic systems containing anadromous fishes with terrestrial systems. Note the number of arrows that cross the border between land and water. Some locations may have additional aquatic-terrestrial interactions; for example, northern pike (*Esox lucius*) may feed on small mammals and birds. (From Willson et al. 1998.)

fruits and frugivores, for instance), we emphasize relationships centered on the fishes. Particularly noteworthy are the numbers of arrows that cross the border between the aquatic and terrestrial sides of the diagram and the numbers of types of organisms that in some way depend on anadromous fishes.

These integrated systems are still quite functional (though not without anthropogenic influences) in most of Alaska, but they are seriously impaired in most of the rest of the world. In most of the contiguous United States, southern Canada, and Eurasia, heavy fishing pressure, habitat destruction, and other factors have caused severe declines in many wild anadromous fish populations (e.g., Palmisano et al. 1993; National Research Council 1996). Historically, fish stocks were harvested very intensely—for example, over 80% of the returning Pacific salmon were commonly harvested, often wastefully (e.g., Ricker 1987). In addition, urbanization, other developments, and intense hunting have often led to the extirpation or near-extirpation of the carnivore populations that formerly served as nutrient transport agents between water and land (e.g., Storer and Tevis 1955; Kadosaki 1983; Miller 1989). Therefore, these highly modified systems will probably never be able to return to anything like their original ecological state.

On the other hand, anadromous salmonids have been introduced to several places in the world where they are not native, including Chile, New Zealand, and the North American Great Lakes, and shad have been introduced to the Pacific coast (see fig. 19.1). Neither Chile nor New Zealand has native populations of large carnivores, but the Great Lakes region still has some black bears and wolves (*Canis lupus*) that may take advantage of this introduced food resource.

The relative contribution of fish-borne nutrients may be greater in the upper reaches than in the mainstem of a river. Although fish abundance is higher in the mainstem of the river than in tributaries and headwaters, in many cases the mainstem is too deep or turbid to permit much fish capture by terrestrial carnivores (Frame 1974). Furthermore, nutrients derived from non-fish sources are often less abundant in small-order streams than in the mainstem (e.g., Vannote et al. 1980), and shallower waters permit heavier predation by terrestrial predators (Heggenes and Borgstrøm 1988; Lonzarich and Quinn 1995).

The principles described here for anadromous fishes *sensu stricto* clearly apply equally well to upstream fish migrations within fresh waters. Thus, the spawning migrations of suckers, inland trout (and introduced salmon), and other freshwater fishes also may support important

components of the terrestrial community (e.g., Dombeck et al. 1984). These effects within fresh water may be more widespread in the world than the effects of strictly anadromous fishes.

Biotic aquatic subsidies of terrestrial communities have been described for islands in the Gulf of California (Polis and Hurd 1995, 1996b; Polis, Anderson, and Holt 1997; Polis et al., chap. 14 in this volume; Rose and Polis 1998), habitat and geographic islands in southern oceans (e.g., Atkinson 1964; Burger et al. 1978; Williams et al. 1978; V. R. Smith 1979; Siegfried 1981; Hureau 1985; Myrcha et al. 1985; Panagis 1985; Ryan and Watkins 1989), cays in the Coral Sea (Heatwole 1971), and migratory birds in the Great Lakes (Ewert and Hamas 1995). In addition, biotic vectors of nutrients have been previously described (e.g., Bosman and Hockey 1986; Bildstein et al. 1992; Polis and Hurd 1996b) and the role of consumers in nutrient cycling emphasized (e.g., Kitchell et al. 1979; Schindler et al. 1993; Vanni and Headworth, chap. 4 in this volume). Therefore, the ideas presented here are not new (e.g., Likens and Bormann 1974). Our discussion suggests, however, that biotic subsidies and biotic transport agents moving across habitat borders may be more common and more influential than previously recognized.

The consequences of the ecological interactions described here are wide-ranging. These interactions obviously cannot be maintained without both predators and prey (and their habitats). Thus, maintenance of the fish populations is important to both the populations of wildlife consumers and the integrated aquatic-riparian ecosystem, and the predator populations are essential as nutrient transport agents maintaining the flow of nutrients to the terrestrial part of the system. In terms of conservation, clearly the functioning of the system depends on the presence of its parts. In terms of management, a wide perspective is needed if a functioning system is to be maintained in the face of exploitation or depletion of some parts of the system. Just as fisheries biologists have called for changes in forestry practices to preserve fish habitat, wildlife biologists may now call for changes in fisheries practices to preserve wildlife populations. Much research is needed to quantify the relative importance of these aquatic-terrestrial interactions in different situations.

The "ecological goods and services" rendered by natural communities are hard to quantify monetarily and are therefore typically undervalued, but true self-sustainability in aquatic and riparian ecosystems is undoubtedly an important ecological service to human societies (National Research Council 1992). If biological resources in ecological systems linked by anadromous fishes can be managed to allow them to sustain

themselves without costly additions of fertilizer or artificially propagated fish, the long-term economic benefits in many cases could be great.

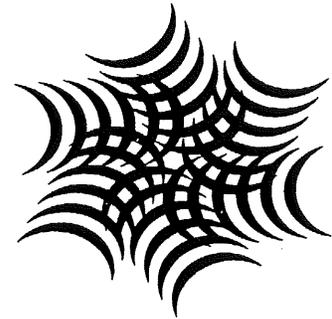
Naiman et al. (1995a, 1995b) discussed research priorities for North American freshwater ecosystems, urging an increased appreciation of the important trophic connections between water and land. We submit that reciprocal interactions between aquatic and terrestrial ecosystems mediated by the spawning migrations of anadromous fishes and their terrestrial consumers are important to all of the research priorities (ecological restoration, biodiversity, hydrological flow patterns, ecosystem services, predictive management, and future problem identification) recognized by Naiman et al. and should be considered in all of those contexts.

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Food Webs at the Landscape Level



Edited by Gary A. Polis, Mary E. Power, and Gary R. Huxel

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