
Anadromous Fish as Keystone Species in Vertebrate Communities

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Abstract: *Many wildlife species feed on anadromous fishes of several life-history stages. There is evidence for some wildlife species that the availability of anadromous fish is critically important for survival or reproduction. In some regions anadromous fishes in fresh water appear to be keystone food resources for vertebrate predators and scavengers, forging an ecologically significant link between aquatic and terrestrial ecosystems. The spatial distribution of anadromous fish in fresh water, including the occurrence of runs in very small streams, has important consequences for wildlife biology (social interactions, distribution, activity patterns, possibly survivorship) and conservation of biodiversity.*

Peces anádromos como especies claves en las comunidades de vertebrados

Resumen: *Muchas especies se alimentan de varios de los estadios de desarrollo de peces anádromos. Existe evidencia que indica que para algunas especies silvestres la disponibilidad de peces anádromos es de suma importancia para su supervivencia o su reproducción. En algunas regiones, los peces anádromos en aguas dulces parecen ser recursos alimenticios claves para los predadores vertebrados y los carroñeros, constituyendo un eslabón ecológicamente significativo entre los sistemas acuáticos y terrestres. La distribución espacial de los peces anádromos en aguas dulces, incluyendo la presencia de "corridas" en arroyos muy pequeños, tiene consecuencias importantes para la biología de la vida silvestre (interacciones sociales, distribución, patrones de actividad, posibilidades de supervivencia) y la conservación de la biodiversidad.*

Introduction

Aquatic and terrestrial ecosystems are usually studied separately, by different sets of researchers using different methods and, often, different approaches. In some regions of the world, however, it is clear that ecological interactions between the two ecosystems are central to regional ecology. One such region is the north Pacific coast of North America, where anadromous fish return to spawn, often in huge numbers, and where they

fall prey to numerous species of terrestrial wildlife. Anadromy is common throughout the northern cool-temperature and subarctic region, and it also occurs—less commonly—in south-temperature regions (McDowall 1987), suggesting that the potential for important interactions between anadromous fishes and wildlife predators is widespread. Although any field biologist could readily note that herons and mink eat fish, thus making the aquatic-terrestrial link, the magnitude of the interaction in some regions warrants special examination and calls attention to the pervasive occurrence of important aquatic-terrestrial linkages in many other areas. The loss or severe depletion of anadromous fish stocks could have major effects on the population biology of many species of wildlife consumers and, thus,

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on terrestrial animal communities, but these possibilities have not been examined and indeed have seldom been addressed at all.

The link between fish populations and their vertebrate consumers has received some attention, usually of a one-sided nature. Almost all of the existing studies stem from fisheries biology, in which a central concern is how many fish remain for humans to harvest. Harvest by humans and other consumers has so profoundly affected the perception of salmon populations that adult population size is customarily referred to as "escapement"—those individuals that escape from their enemies. Our approach here is to reverse the perspective and to focus on the importance of fish populations for wildlife. There is precedent for such a change in perspective. Some years ago Gould (1981) addressed the seemingly silly question of whether a zebra is basically a white animal with black stripes, or perhaps a black animal with a white overlay. The question is, in fact, anything but silly for scientists interested in development and evolution, because posing the alternatives permits a more perceptive analysis of some basic biological processes. The initial effect of our shift in perspective on fish-wildlife interactions may be to complicate the study of ecological systems by insisting on linkages among systems, but in the long run the change of focus should allow us to comprehend things that could not be understood otherwise.

We focus on direct interactions between anadromous fish and their vertebrate consumers in and near freshwater, but anadromous fish also have important—though less apparent—indirect interactions with both plants and wildlife through nutrient dynamics. A growing body of evidence indicates that chemical nutrients delivered by spawned-out carcasses can play a critical role in sustaining the productivity of riparian and lacustrine ecosystems, perhaps including the next generations of juvenile salmon (see Richey et al. 1975; Kline et al. 1990, 1993; R. Bilby et al., unpublished manuscript).

The current use of the term "anadromous" refers specifically to populations in which the adults migrate from the sea to fresh water for spawning (McDowell 1987). The derivation of the word itself, however, refers more broadly to a habit of running upstream (to spawn), and therefore in a broad sense can be applied to any population that moves from a large body of water (ocean or lake) to a stream environment for breeding. We use the narrower sense of the word here, but because the ecological relationships between the migrating fish and their wildlife consumers is similar, whether the fish come to a stream from the sea or a lake, we briefly discuss the relationships for inland populations restricted to fresh water.

We have chosen to use the term "keystone species" for anadromous fish in these interactive systems, despite

some possible difficulties (Mills et al. 1993). We find the term useful to emphasize our point about the likely importance of anadromy for the many predators that use anadromous fish. We submit that interactions between anadromous fish and terrestrial wildlife are important components of regional biodiversity, and that they deserve a far greater consideration in land-management schemes, fishery management practices, ecosystem-management plans, and ecological studies of ecosystems than they have received in the past.

Background

Research on predator-prey interactions in which anadromous fish are the prey has strongly emphasized the effects of predation on the fish populations. For example, a literature search of Wildlife and Fisheries Review, 1971–1993 (using keywords salmon, predator, predation, and scavenger), revealed 80 papers on interactions in fresh water. Only 10 of these papers contained some mention of the consequences of the interactions for the consumers. Further inspection of the literature reveals the general lack of studies on the relationship of anadromous fish to the communities of vertebrate consumers. The utility of seabird data (especially rates of energy acquisition) as indicators of the population size of oceanic fish has been suggested (Cairns 1992). The focus is usually still on the economically important fish, however, although the potential impact of overharvesting of fish on seabird populations may be serious (references in Cairns 1992). One exception to this trend is a poster produced by the U.S. Fish and Wildlife Service, entitled "Alaska's Salmon Resource: Importance to the Ecosystem", which illustrates the variety of wildlife that use salmon as a food resource. In addition, the implications of fisheries management for fish-feeding birds in inland waters have been emphasized by Dombeck et al. (1984).

Many existing studies emphasize fish-hunting wildlife species as competitors of human harvesters and often address the question of how to reduce the effect of such predators on the numbers of anadromous fish. The answers to the question range from adjusting the timing of hatchery releases (Mace 1983; Wood 1985a; Bayer 1986) to more draconian programs of wildlife slaughter (Shuman 1950; Anderson 1986, cited in Mills 1989). We present two examples to illustrate some of the drastic measures used against wildlife consumers and the attitudes that have led to these measures.

Some programs of wildlife "control" have been conducted despite their dubious efficacy and uncertain ramifications. For example, Elson (1962) reported that merganser (*Mergus merganser*) populations would need to be reduced from the estimated natural average of 5–10 birds per 15 miles (24 km) of stream to about

one bird per 15 miles, in order to increase significantly the production of Atlantic salmon (*Salmo salar*) smolt in eastern Canada. Elson's program destroyed an average of 54 adult mergansers per year for six years in a 10-mile stretch of river and achieved an estimated increase of 20,000 smolts. Stocking rates also increased during this time, however, so the estimated gain in smolt abundance cannot be attributed solely and clearly to the removal of mergansers. Furthermore, Elson's estimates were based on relatively high densities of hatchery-released juveniles, and hatchery stocks are often more susceptible to predation than wild stocks (Beamish et al. 1992; see also Patten 1977; Wood & Hand 1985; Bayer 1986). Where the merganser population is more abundant, when mergansers recruit to waters with increased densities of juvenile salmonids (Elson 1962; Wood 1985a, 1985b), and where the regional supply of mergansers is able to recolonize an area of merganser control (Mace 1983), the toll in wildlife death would be even higher. Merganser control programs in eastern Canada have continued in more recent times, although the correlation between merganser control and returns off adult salmon appears to be uncertain (Hunter 1959; Parker 1960; Anderson et al. 1985; Anderson 1986; or Mills 1989; Wood 1987b). Furthermore, the decline of Atlantic salmon abundance in recent decades has been caused directly by excessive exploitation by humans, not by merganser predation, so the killing of mergansers to increase populations of salmon is scientifically dubious (Anderson et al. 1985).

A second example may be even more telling. Between 1917 and 1953, a bounty, ranging from 50 cents to two dollars a bird, was placed on Bald Eagles (*Haliaeetus leucocephalus*) in Alaska (Imler & Kalmbach 1955; Robards & King 1966). Records were kept on the numbers of eagles killed during this time, except for 1941–1945, when the bounty was in effect but not funded, and 1945–1949, when it was briefly repealed. Between 100,000 and 128,000 eagles were recorded in the bounty books during the years for which data are available, and an unknown number were killed and not retrieved or wounded and died later (Robards & King 1966). About 80% of these birds came from southeast Alaska (Robards & King 1966). Casual observations indicated that this mayhem was associated with a reduced number of eagles in coastal Alaska (Imler & Kalmbach 1955), but no assessments of the effects of reduced eagle numbers on prey populations were made (M. Jacobson, W. G. Meehan, personal communication), although a major initial motivation for the bounty was the reduction of predation by eagles. During this time, the nuisance value of eagles as possible competitors was clearly considered to be more important than their ecological value, so much so that the effect of "nuisance" reduction was not even worth measuring.

Wildlife and Anadromous Fish on the Northwest Coast of North America

The Prey Resource in Fresh Water

Between southern California and the Arctic Ocean there are over 15 native species of dramatically anadromous fishes (see Scott & Crossman 1973). These include three species of lamprey (Petromyzontidae), several species of smelt (Osmeridae), at least one species of charr (*Salvelinus*), and seven species of *Oncorhynchus* (Salmonidae). The diversity of anadromous species is especially high between northern California and southwestern Alaska. Some species, especially of *Oncorhynchus*, have sea-run populations that spawn in inland waters located hundreds of kilometers from the sea. Spawners of several species may use the same streams, at either similar or different times. Therefore, any given stream at any one time of year may harbor adults of one or several species. The total number of streams supporting stocks of anadromous fish in this region is enormous. For example, in southeast Alaska alone, coho (*O. kisutch*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon each occur in over 2000 stream systems, sockeye (*O. nerka*) utilize over 200, and chinook (*O. tshawytscha*) about 100 (Alaska Department of Fish and Game, Anadromous Waters Catalog, unpublished).

The time of spawning varies considerably, both among species and among populations in different locations (Scott & Crossman 1973, references in Groot & Margolis 1991). The lampreys enter fresh water in the late summer and fall but do not spawn until the following spring. Some of the smelt spawn in spring, but others spawn in fall and winter. The charr are typically fall (and occasionally spring) spawners. In general, the five species of Pacific salmon spawn in summer and fall, but spawning of coho, chum, and sockeye salmon may extend into winter in some places. Both steelhead (*O. mykiss*) and cutthroats (*O. clarki*) are generally spring spawners. For conspecific populations, significant differences are found among locations in the time of spawning and the time of adult entry into fresh water, perhaps especially in steelhead and chinooks. But adult migrations and spawning times and smolt out-migration times for any particular species in any one river system are usually less variable from year to year than among locations.

Thus, the diversity and abundance of anadromous adults in a stream display enormous variation in both time and space. In addition, the size of the populations (and the body size of the individual fish) varies in response to many factors, including human harvest. High variability of prey density is reflected in the opportunistic foraging of many wildlife consumers—but "opportunistic" is not a synonym for biologically unimportant. In many freshwater drainages, the presence of anadromous

fish is sufficiently reliable that the biology of some wildlife species seems to be geared to their exploitation.

Wildlife Predation on Anadromous Fish in Alaskan Coastal Streams

As an example of the multiple linkages that occur in a relatively restricted region, we first summarize the wildlife species of coastal southeast Alaska that are known or expected to feed on salmon. We focus on southeast Alaska because this is one of the few places in North America that contain abundant stocks of anadromous fishes and a relatively unmodified terrestrial vertebrate fauna.

The regional list of wildlife consumers of anadromous fish is impressive (Table 1). Not surprisingly, all carnivorous mammals in the region take advantage of anadromous adult fish, as do a number of large carnivorous birds. In some cases, predation occurs on live adults (especially by bears and eagles). The spawned-out, moribund kelts and the carcasses of dead adults (many species of anadromous fishes are semelparous and die shortly after spawning) are scavenged by carnivores.

Perhaps surprisingly, carcasses are also eaten by species such as squirrels and deer, which are typically considered to be herbivorous (see also Cederholm et al. 1989). Juveniles fall prey to otters and many species of birds, as well as to predatory fishes. Eggs are eaten by many birds, and by Dolly Varden charr, juvenile salmonids, and sculpins (see Armstrong 1965; Moyle 1977; F. H. Everest, personal communication). Many of the eggs consumed by these animals are drifting eggs that have been displaced from redds by subsequent spawning activity or other disturbances, although sculpins may take eggs from the gravel as well (Moyle 1966; Reed 1967; Armstrong 1970). Gulls sometimes tread over redds in shallow water to stir up eggs (Moyle 1966) or prod the belly and vent area of gravid female salmon to force them to release eggs before spawning (our observation; R. H. Armstrong, G. Streveler, personal communication).

Two lacunae in Table 1 deserve some exploration: there is a dearth of mammalian egg-eaters and of piscine scavengers. We know that mammals will eat salmon eggs because bears often forage preferentially on roe (and brains) from captured females (Frame 1974; our observation). Therefore, it is not likely that eggs are

Table 1. Wildlife consumers of salmon in or near fresh waters of southeast Alaska.*

Consumers	Salmon Life-History Stage		
	Eggs	Juveniles	Adults (including carcasses)
Mammals		river otter (<i>Lutra</i>) mink (<i>Mustela</i>)	bears (<i>Ursus</i> spp.) mink, weasels (<i>Mustela</i> spp.) wolverine (<i>Gulo</i>) wolf, coyote (<i>Canis</i> spp.) red fox (<i>Vulpes</i>) seals (<i>Phoca</i>) sea lions (<i>Eumetopias</i>) deer mouse (<i>Peromyscus</i>) shrew (<i>Sorex</i>) red squirrel (<i>Tamiasciurus</i>) flying squirrel (<i>Glaucomys</i>) black-tailed deer (<i>Odocoileus</i>)
Birds	Mallard (<i>Anas</i>) Canada Goose (<i>Branta</i>) goldeneyes (<i>Bucephala</i> spp.) gulls (>4 <i>Larus</i> spp.) American Dipper (<i>Cinclus</i>) American Robin (<i>Turdus</i>)	loons (<i>Gavia</i>) mergansers (<i>Mergus</i> spp.) Great Blue Heron (<i>Ardea</i>) scaup (<i>Aythya</i> spp.) gulls Arctic Tern (<i>Sterna</i>) Belted Kingfisher (<i>Megaceryle</i>) crow Black-billed Magpie	Bald Eagle (<i>Haliaeetus</i>) Red-tailed Hawk (<i>Buteo</i>) Northern Harrier (<i>Circus</i>) gulls Black-billed Magpie (<i>Ptca</i>) crow, raven (<i>Corvus</i> spp.) Steller's Jay (<i>Cyanocitta</i>) Winter Wren (<i>Troglodytes</i>) American Dipper
Fishes	Dolly Varden (<i>Salvelinus</i>) sculpins (<i>Cottus</i> spp.) coho salmon (<i>Oncorhynchus</i>) suckers (<i>Catostomus</i>) grayling (<i>Thymallus</i>)	Dolly Varden sculpins coho, chinook salmon rainbow trout/steelhead cutthroat trout walleye pollock (<i>Theragra</i>) Pacific herring (<i>Clupea</i>)	

* Compiled from unpublished observations, personal communications, and from species listed in Cederholm et al. (1989) and Groot and Margolis (1991) that also occur in this region. The list undoubtedly omits some species of consumers; for instance, many other birds are likely to utilize salmon carcasses. In other regions the variety of consumers is still greater because some amphibians and reptiles prey on eggs or juvenile fish.

unsuitable food for mammals. Probably most of the mammals capable of entering the water are so big relative to the size of the eggs that egg-foraging, especially for single eggs, is not profitable. The absence of piscine scavengers may be attributed principally to the limited species diversity (and foraging habits) of fishes in these streams. It is also possible that mammalian use of eggs and piscine use of carcasses are under-recorded.

Although bears are widely recognized as salmon predators, the consequences of salmon predation for bear biology are virtually unknown. The large size of coastal brown bears (*Ursus arctos*), compared to the conspecific grizzlies in the interior, is sometimes attributed to the great availability of anadromous fish (Nowak & Paradiso 1983). Salmon consumption probably contributes to the fat deposition required for hibernation and to the reproductive success of female bears (references in Willson 1993) but the relative importance of salmon compared to other food resources has not been assessed. Mink (*Mustela vison*) may adjust the phenology of reproduction to match the seasonal availability of spawning salmon (M. ben David, personal communication). Salmon carcasses may be critical to the overwinter survival of Bald Eagles and, in some areas, to their reproductive success (Hansen 1987). In addition, the accessibility of carcasses probably also facilitates the survival of fledgling eagles, which are just learning how to forage for themselves at about the time when salmon carcasses are readily available. Late runs of salmon and spring runs of eulachon (*Thaleichthys pacificus*) draw eagles from all over the region and contribute to the maintenance of regional populations (our observation; Hansen et al. 1984; R. H. Armstrong, unpublished report). Consumption of high-energy eggs may be critical to the survival of juvenile salmonids reared in fresh water at high latitudes, where the growing season is very short (F. H. Everest, personal communication).

Juvenile salmon probably influence the breeding biology of several predators. The phenology of migration and reproduction of mergansers may be coordinated with fry emergence and smolt out-migration (Wood 1987b; Marquiss & Duncan 1993). For mammals, the lactation period is energetically costly, and the mobility of females with young in the den may be limited. During this time, juvenile salmon may provide an important food resource for river otters (Dolloff 1993). Out-migrations of juvenile salmon often attract large numbers of birds, including immature individuals (Mace 1983; Wood 1985a, 1985b), and the nesting density of mergansers has been correlated with the abundance of juvenile salmon (Wood 1986).

Some marine mammals pursue their anadromous prey far up freshwater rivers: for example, beluga whales (*Delphinapterus leucus*) have been found hundreds of kilometers up the Yukon river, following the salmon run

(*Juneau Empire*, September 14, 1993), and salmon-hunting seals and sea lions move more than 100 km upstream in large rivers in Oregon and Washington (F. H. Everest, personal communication; *Juneau Empire*, April 26, 1994). As adult anadromous fish approach the coast, and as the juveniles leave freshwater (or at high tides), their congregations are often subject to high levels of predation by several species of marine birds and mammals, including seals, sea lions, and small whales (Fiscus 1980; *Juneau Empire*, December 6, 1993), and some saltwater fishes (for example, walleye pollock [*Theragra chalcogrammus*]—see Armstrong (1968)—and Pacific herring (*Clupeus pallasii*)).

Discussion

The few systems about which we have found published information all suggest that wildlife species capitalize on available concentrations of anadromous fish and may change their distribution and even breeding biology in response to the abundance of these fish. Most reports of wildlife responses to anadromous fish have emphasized trout and salmon as the prey, perhaps because of their considerable commercial and recreational interest. The relationships between anadromous fish and wildlife on the northwest coast of North America can also be found, with regional variations, on the north Pacific coast of Asia and on both sides of the north Atlantic.

Wildlife in inland areas also make extensive use of migratory fish resources. Both black and grizzly bears in Yellowstone National Park prey on spawning cutthroats; the level of bear activity was often correlated with the density of fish in the stream (Reinhart & Mattson 1989). Almost all the studied streams with spawning runs were visited by bears, and there was evidence that bears often tended to avoid each other by using different streams (Reinhart & Mattson 1989).

Eagles utilize the spring runs of suckers (Catostomidae) in midwestern streams (M. F. Willson observation). Inland eagles whose nests are close to spawning streams have higher nesting success than those whose nests are more distant (Gerrard et al. 1975). Eagles in the non-breeding season often congregate near good fishing sites, and the number of eagles is often correlated with the availability of fish (see Fitzner & Hanson 1979; Spencer et al. 1991, Hunt et al. 1992; McClelland et al. 1994). In several cases, the prey fish were not native to the waters in the region, but the eagles readily incorporated the new food source into their foraging patterns. Exotic rainbow trout populations in the highly modified aquatic ecosystem of the Grand Canyon probably benefit the eagle population but may further damage the community of native fishes (Brown 1993). In a profoundly modified system in western Montana, the num-

ber of introduced kokanee salmon declined sharply after 1986. The numbers of eagles and other wildlife species that gathered to harvest kokanee declined in parallel with those of their prey (Spencer et al. 1991). Possible alternative food sources for eagles, such as carcasses of bison or elk, are no longer available.

Sometimes the activities of one major consumer initiate a chain of interactions for other wildlife species. On the Kamchatka peninsula, for example, sea-run sockeye salmon in Kuril Lake and its tributaries are extraordinarily numerous and spawn over a nine-month period in waters that commonly remain ice-free (Ladigin 1994). This sockeye population supports a diverse aggregation of wildlife species similar to that in southeast Alaska, and resident eagles usually gain weight over the winter. Perhaps the most conspicuous of the wildlife species is Steller's Sea-eagle (*H. pelagicus*), a large relative of the North American Bald Eagle. The massive bill of Steller's Sea-eagles enables them to open efficiently the tough skin of salmon carcasses that smaller birds cannot pierce. The presence of two smaller species of eagle at Kuril lake in winter has been attributed to the availability of salmon carcasses opened by Steller's Sea-eagles (Ladigin 1994). When exceptionally severe weather covers the spawning grounds with ice, the interspecific congregation of eagles disbands; the consequences of being forced to forego this rich winter resource are unknown.

The biological relationships between anadromous fish and a diverse array of wildlife consumers seems to stand out from many terrestrial predator-prey interactions. Food resources for almost all kinds of animals are variable in space and time, but the anadromous fish system is an extreme case in which prey is temporarily very abundant, spatially constrained, relatively easy to capture, and more or less predictable. It is different from predator-prey interactions with irruptive species (locusts, lemmings) because of its interannual predictability. It is similar in some respects to tropical frugivore-fruit interactions in which some fruits serve as keystone food resources at certain times (Terborgh 1986), but it is not clear when or where anadromous fish fill a seasonal gap in other resources. Some parallels exist with ant swarms and ant-following birds in tropical forests, but the ants themselves are not the prey and the swarm may be somewhat less predictable than the fish. Better comparisons can perhaps be found with migratory ungulates as the prey species. Long-range movements of the American bison were surely used by carnivorous mammals, vultures, cowbirds, and humans, and the migrations of Arctic caribou are still utilized by an array of carnivores. But the diversity of vertebrate predators and scavengers supported by bison and caribou may be less than that for anadromous fish. Perhaps the closest parallel comes from the hordes of migratory antelope in Africa, on which many species of predators and scavengers de-

pend. None of these sets of interactions, however, is based on a link between ecological communities that are usually treated separately.

Not all effects of anadromous fish on their predators are necessarily beneficial to individual consumers. For instance, when bears congregate along salmon streams, intense social strife sometimes leads to competitive displacement of subordinate individuals or to the death of cubs (S. Morello, K. Titus, personal communication). Dense aggregations in salmon-foraging season might increase the transmission of pathogens within or even among species. Furthermore, a disease known as salmon poisoning afflicts some species of carnivore in certain parts of the west coast of North America (Schwabe et al. 1977). The disease is caused by a rickettsia, which is transmitted by a trematode vector whose life cycle passes through one species of freshwater snail as the first intermediate host, then through certain fishes (including salmonids) as second intermediate hosts, and finally into fish-eating mammals and birds. Of the final hosts, only canids and raccoons become ill, but the infection can be fatal to canids.

We have been concerned, so far, chiefly with the effects of anadromous fish on their wildlife consumers. But predators can have effects on their prey in addition to potentially reducing their abundance. Predation, in general, is seldom random, and predation on anadromous fish is no exception. Trade-offs between foraging benefits and predation risks are thought to contribute to patterns of habitat use by Arctic charr and other species (see Huntingford et al. 1988; Magnhagen 1988; L'Abbe-Lund et al. 1993) and are probably relevant to many anadromous fishes. Size-selective predation on juvenile salmonids is known to occur, but the direction of selection appears to vary with circumstances (Parker 1971; Wood & Hand 1985; Wood 1987a). The juveniles of some species may be more susceptible than others to predation by certain wildlife species in some experimental situations (Patten 1975; Hoar 1976; Hargreaves & LeBrasseur 1985); whether this is true when each prey species occupies its own natural habitat is apparently not known. Black bears favored chum over pink salmon, perhaps because of their greater size (Frame 1974). Furthermore, predation can be sex-specific, but the sex most at risk varies. Glaucous-winged Gulls (*Larus glaucescens*) have been reported to prey or scavenge differentially on female salmon (Mossman 1958; Moyle 1966). Bears and otters prey selectively on male salmon in some cases (Gard 1971; Carss et al. 1990; Burgner 1991) but on females in others (Frame 1974). Reports of selective predation are too few and scattered to allow us to examine the causes and consequences of the variation. Nevertheless, it is clear that potentially important effects of selective predation may be exerted on the life history of anadromous fishes.

The distribution of anadromous fish on the landscape

has several important implications for wildlife conservation. Temporary local declines of anadromous fish populations must be relatively common in nature, because many small-scale disturbances and stochastic events can make a stream inaccessible or inhospitable to anadromous fish. Some predators, such as bears, may be capable of consuming the entire run of salmon in very small streams (Shuman 1950), leading to depressed future returns. If a stream loses its anadromous fish population, the spatial distribution of wildlife consumers or their nutritional status and, ultimately, their reproductive success are likely to be altered. The severity of these effects depends in large part on how long the fish population is depressed and on the availability of alternative resources.

Commercial fisheries have great potential for persistently altering the spatial distribution of anadromous fish resources, in particular by eliminating small stocks. Fisheries for anadromous salmon are generally managed at the scale of regulatory districts encompassing multiple watersheds, and migratory salmon are often intercepted in multiple districts before reaching their spawning stream. Fishing regulations for each district are typically based on the estimated ability of the largest or most productive local stocks to sustain harvest, with an additional allowance for intercepted fish. This management strategy is economically expedient, but it tacitly accepts that smaller or less productive stocks, or those with migratory paths that expose them to a gauntlet of harvest may be overexploited or extirpated. If the populations of anadromous fishes in small streams are severely reduced, this management policy is potentially detrimental to wildlife for several reasons. For many terrestrial wildlife species, fish are typically easier to catch in small, shallow streams (or at riffles and rapids in larger ones) than in lakes or large rivers (see Shuman 1950; Reinhart & Mattson 1989). Moreover, the presence of anadromous fish in numerous tributary streams permits intraspecific spacing of at least some predators, such as bears. Female bears with cubs, and young bears newly independent of their mothers, all avoid mature males, and family groups may also tend to avoid one another (Reinhart & Mattson 1989). Thus, "escapements" sufficient to maintain a fishery in a management district may be inadequate from a wildlife perspective. The fish populations of small streams are not entirely substitutable resources for many species of wildlife, although they may be for commercial fishers.

On large spatial scales, when regional spawning runs collapse (as from chronic overfishing or widespread habitat modification), the options for wildlife consumers are more limited. Long-distance emigrations, impaired reproductive success, and increased mortality become more probable. Spatial scale also affects the ability of wildlife consumers to recover from declines or extirpations of their prey. For instance, the current pat-

tern of salmon stock declines in southeast Alaska is haphazard, is limited to less than 10% of the stocks, and occurs primarily in small drainages (K. C. Halupka). This pattern resembles historical patterns of decline in the Pacific Northwest and British Columbia (Frissell 1993). If salmon runs are restored in these scattered systems, the probability of rapid recovery of wildlife populations or recolonization is high because source populations remain in nearby areas. In contrast, current salmon declines in the Pacific Northwest are more regional in scale (Frissell 1993), possibly compromising the viability of wildlife populations over broad areas. Furthermore, recovery times are likely to be protracted when immigration distances are large and source populations are small.

Scale is also important in recognizing the relevance of indirect disturbance events in a system characterized by many interconnections. For instance, destruction of headwater spawning grounds by landslides, earthquakes, road-building, logging, mining, or agriculture has consequences for the foraging ecology not only of the wildlife species that utilize these small streams but also of those that concentrate their activities far downstream. Furthermore, the subpopulations in lower-order streams may contribute to the genetic diversity of fish stocks, and extirpation of the subpopulations might reduce the long-term viability of the stock even when the numbers of fish remain temporarily unaffected (Northcote 1992). Likewise, downstream events obviously can have major effects on upstream ecology: Earthquakes and dams alter streamflow necessary for both upstream and downstream migration, water quality (especially temperature) that affects egg and juvenile survival, and the hydraulics of spawning areas (Roys 1971; Thorsteinson et al. 1971). Megaharvests (such as the capture of more than 80% of a sockeye run in one day; Rogers 1987) seriously deplete the number of spawners and can change their spatial distribution. Changing climates and oceanic cycles will have yet-to-be-determined effects on the availability of anadromous fish for both human and wildlife consumers.

Both harvesting practices and the prevalence of hatchery stocks in some areas may also affect the temporal availability of anadromous fish in fresh water by selecting for particular timing and duration of spawning runs. It is possible that temporal changes in prey availability have important effects on wildlife biology, but this possibility seems to be as neglected as the effect of spatial changes.

Many people will no doubt say that the importance of anadromous fish for wildlife is common knowledge, which is true at some level. Tourists and photographers flock to particular locations in coastal Alaska to watch bears capture salmon. Fish growers and harvesters are obviously aware of possible competition from wildlife. Sport fishers for anadromous fish in fresh water know

they must behave circumspectly in bear country, where ursine predators vie with humans for prey. We submit, however, that a change of perspective—to actively include the wildlife participants in the interaction—is long overdue. Variation in anadromous fish populations can have major effects on the productivity, phenology, and metapopulation dynamics of wildlife and hence on regional biodiversity. What is needed now, in terms of research, is some quantification of the interaction. Interactions among species are a central component of ecosystem function and, hence, of the maintenance of biodiversity in ecological systems (Willson 1995). Nowhere is this more evident than in the fish-wildlife interactions we have discussed here. Recognition of the keystone nature of anadromous fish populations should be incorporated into ecosystem-based plans for land management, fishery harvest, and conservation.

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