

The Role of Competition and Predation in the Decline of Pacific Salmon and Steelhead

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Abstract

In this paper, I examine the role of competition and predation in the decline of Pacific salmon and steelhead (*Oncorhynchus* spp.) populations along the Pacific coast of North America. Few studies have clearly established the role of competition and predation in anadromous population declines, especially in marine habitats. A major reason for the uncertainty in the available data is the complexity and dynamic nature of competition and predation; a small change in one variable (e.g., prey size) significantly changes outcomes of competition and predation. In addition, large data gaps exist in our understanding of these interactions. For instance, evaluating the impact of introduced fishes is impossible because we do not know which nonnative fishes occur in many salmon-producing watersheds. Most available information is circumstantial. While such information can identify where inter- or intraspecific relationships may occur, it does not test mechanisms explaining why observed relationships exist. Thus, competition and predation are usually one of several plausible hypotheses explaining observed results.

Competition and predation should not be considered primary causes of population declines. For competition and predation to contribute to anadromous population declines, something must occur to alter the outcomes of these interactions (e.g., predation mortality increases). Competition and predation are altered as a result of the following: introductions of nonnative, non-salmonid fishes, introductions of artificially produced salmonids, environmental changes, and non-environmental changes in predator or competitor populations (e.g., from fishing). Efforts to restore salmon populations must direct action at identifying and eliminating primary causes of population declines and not simply treating secondary effects (i.e., competition and predation) of these causes.

Introduction

Many populations of naturally spawning Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*O. mykiss*) along the west coast of North America have declined to critically low levels (Konkel and McIntyre 1987, Nehlsen et al. 1991, Brown et al. 1994). One recently published assessment of the status of salmon and steelhead in California, Oregon, Washington, and Idaho

(The Wilderness Society 1993) concluded that salmon were extinct in 40% of their combined ranges and threatened or endangered in 27%.

To restore depressed populations and maintain viable populations in the future, we must understand why declines have occurred. Overfishing, freshwater habitat loss, water quality alterations, loss of genetic integrity of wild fish, and biological interactions (e.g., competition and predation) have been identified as factors causing anadromous population declines (Nehlsen et al. 1991, Hilborn 1992, The Wilderness Society 1993, Brown et al. 1994, Botkin et al. 1995). The purpose of this paper is to examine the role that competition and predation in freshwater and marine habitats have had in the decline of Pacific salmon and steelhead. Competition among adults for space and mates during reproduction was not included as part of this review.

I first summarize what is known about competition and predation for anadromous salmonids. Second, I discuss how these biological interactions have contributed to decreases in abundance of anadromous populations. Finally, I consider the effects of competition and predation within the context of restoration of salmonid populations.

Competition

Competition is the demand by two or more individuals of the same or different species for a resource that is actually or potentially limiting (Larkin 1956). As a result of competition, some competing individuals obtain less of the scarce resource than is optimum. These individuals may experience declines in reproductive rates, they may die, or they may be forced to emigrate from where they are living.

STREAMS

Stream-dwelling juvenile salmonids appear to compete primarily for space rather than for food or other resources (Chapman 1966, Hearn 1987). Individuals compete for positions based upon their importance for food acquisition and as cover (Fausch and White 1981). Competition for space is most critical during seasonally occurring periods of low flow (late spring to early fall) while in winter space is less critical owing to the fishes' lower metabolic requirements and levels of aggression (Hartman 1965, Glova 1986). Intraspecific competition is often of greater intensity than interspecific competition (Fraser 1969, Allee 1974, Lonzarich 1994). Aggressive interactions between individuals of the same species (i.e., interference competition) result in the formation of social hierarchies. The dominant individuals occupy preferred positions and are less likely to be displaced from territories, thereby having the highest growth rates (Chapman 1962, Mason and Chapman 1965, Allee 1974, Nielsen 1992).

Interspecific competition occurs between non-salmonids and salmonids as well as between different species of salmonids. Competition between salmonids and non-salmonids occurs infrequently (Moyle 1977, Brown and Moyle 1981, Baltz and Moyle 1984, Reeves et al. 1987, Lonzarich 1994), and is probably most significant in larger streams where non-salmonids are more abundant (Li et al. 1987). Interspecific competition is one mechanism used to partition scarce resources in streams (e.g., Hartman 1965, Glova 1986, Fausch and White 1986, Hearn 1987). Effects of aggressive interactions between competing individuals are highly localized

and may result in shifts in microhabitat use by one or both of the interacting species (Li et al. 1987). Outcomes of interspecific competitive interactions vary with the species involved (Fausch and White 1986, Li et al. 1987), size differences among competing individuals (Fausch and White 1986), and numerous environmental factors such as temperature and streamflow (Hearn 1987, Reeves et al. 1987, Fausch 1988). Competition among sympatric salmonid species is minimized by species-specific differences in habitat preference, emergence timing, body morphology, environmental tolerances, or a combination of these factors (Hearn 1987, Bisson et al. 1988, Dolloff and Reeves 1990).

LAKES

The most extensive use of lakes by anadromous salmonids along the west coast of North America is by juvenile sockeye salmon (*O. nerka*), which rear for ≤ 3 years in lakes before migrating to sea. Intraspecific competition is considered the most important interaction involving sockeye juveniles. Burgner (1991) concluded that intraspecific competition for food among juvenile sockeye occurs when there are large numbers of sockeye in one year class, two or more year classes use the same resources, or species other than sockeye utilize the same resources. For example, in the Wood River Lakes, Alaska, the size (mean weight in g on September 1) of sockeye salmon fry rearing in the nursery lakes is inversely related to the number of parent spawners per rearing lake area (Fig. 1). One explanation for this relationship is that food supplies are limiting and, as a result, growth declines as density of rearing fry increases (indexed by changes in numbers of parent spawners per nursery lake area).

MARINE HABITATS

Food is the most limiting resource in marine habitats. Because measuring the amount of food available in coastal or open ocean habitats is difficult, evaluations of when, where, and what stocks might encounter food limitations during marine life have relied upon studies of food habits and dietary overlap, measures of stomach fullness and daily ration, simulation models, and evaluations of abundance, survival, and age composition from salmon management databases (Walters et al. 1978; Healey 1980; McCabe et al. 1983; Nielsen et al. 1985; Nickelson 1986; Peterman 1984, 1987; Fisher and Percy 1988; Emlen et al. 1990; Percy 1992; Beamish and Bouillon 1993; Cooney 1993; Rogers and Ruggerone 1993). One frequently used approach to identify where competition occurs is to test for density-dependent growth and survival (Peterman 1984, Emlen et al. 1990, Cooney 1993, Rogers and Ruggerone 1993). Evidence of a carrying capacity effect (e.g., decreased growth or survival as salmon densities increase) suggests food is limiting and competition is occurring. Regardless of the difficulty in proving that food is limiting, the carrying capacity of the ocean for salmonids is not unlimited; at some point, food supplies will be limiting.

Inter- and intraspecific competition involving juvenile salmonids is more likely to occur in estuarine and nearshore coastal areas. In these habitats, juvenile salmon can encounter food limitations that reduce growth and survival because they are spatially and temporally concentrated and have similar diets (e.g., Healey 1980; Peterman 1982, 1987; Nielsen et al. 1985; Percy and Fisher 1988; Brodeur and Percy 1990; Brodeur et al. 1992; Thomas and Mathisen 1993). Adult salmon also may encounter carrying capacity limitations when passing through nearshore coastal areas during their return migrations to natal streams (Rogers and Ruggerone 1993).

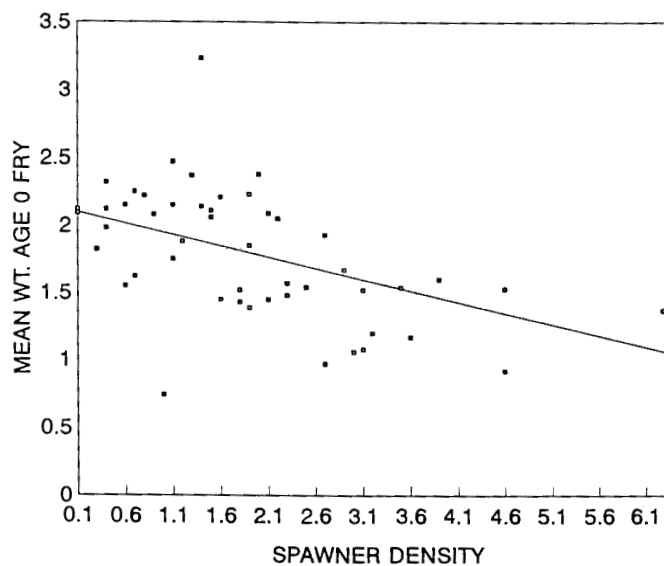


Figure 1. Relationship between mean size of sockeye salmon fry (weight in grams on September 1) and the relative density of parent spawners (numbers of spawners per km² of nursery lake area) from the previous year in the Wood River Lakes, Alaska. Data represent different lakes and years combined into one plot (after Burgner 1991). Source: Rogers (1977).

Predation

A large number of species eat salmon throughout their life cycle. The available literature indicates that 33 fish species, 13 bird species, and 16 marine mammal species are predators of juvenile and adult salmon (Table 1).

FRESHWATER

Numerous estimates of predation mortality in freshwater have been made (Table 2). Freshwater predators often consume large numbers of pink (*O. gorbuscha*) and chum (*O. keta*) salmon fry during their downstream migration. Up to 85% of pink and chum fry are eaten in some systems (e.g., Hooknose Creek, British Columbia; see Hunter 1959) even though fry need only migrate a short distance to reach the estuary (several km) and can accomplish this within one night. The small size of newly emerged pink and chum fry (typically <40 mm) and their minimal avoidance capabilities make them especially vulnerable to predators.

Sockeye salmon juveniles are eaten by predators throughout their freshwater life (Foerster 1968, Burgner 1991). Similar to pink and chum fry, sockeye fry are particularly vulnerable to

Table 1. Predators of juvenile and adult Pacific salmon in freshwater and estuarine/marine habitats.

Common name	Species	Freshwater predator	Marine predator	Selected references
	Scientific name			
Fish predators				
River lamprey	<i>Lampetra ayresi</i>	x	x	Beamish and Neville (1995)
Spiny dogfish	<i>Squalus acanthias</i>		x	Beamish et al. (1992)
American shad	<i>Alosa sapidissima</i>	x		Wendler (1967)
Pacific herring	<i>Clupea harengus pallasii</i>		x	Ito and Parker (1971)
Coho salmon	<i>Oncorhynchus kisutch</i>	x	x	Fresh and Schroder (1987), Hargreaves (1988)
Chinook salmon	<i>O. tshawytscha</i>	x	x	Dunford (1975), Sholes and Hallock (1979)
Cutthroat trout	<i>O. clarki</i>	x	x	McCart (1967), Fresh et al. (1981)
Rainbow trout	<i>O. mykiss</i>	x	x	Fresh et al. (1981), Fresh and Schroder (1987)
Arctic char	<i>Salvelinus alpinus</i>	x		Meacham and Clark (1979)
Dolly Varden	<i>S. malma</i>	x	x	Lagler and Wright (1962), Foerster (1968)
Lake trout	<i>S. namaycush</i>	x		Gilhouse and Williams (1989)
Lake whitefish	<i>Coregonus clupeaformis</i>	x		Gilhouse and Williams (1989)
Mountain whitefish	<i>Prosopium williamsoni</i>	x		Gilhouse and Williams (1989)
Northern squawfish	<i>Ptychocheilus oregonensis</i>	x		Rieman et al. (1991), Tabor et al. (1993)
Sacramento squawfish	<i>P. grandis</i>	x		Brown and Moyle (1981)
Channel catfish	<i>Ictalurus punctatus</i>	x		Poe et al. (1994)
Pacific cod	<i>Gadus macrocephalus</i>		x	Simenstad et al. (1979)
Tomcod	<i>Microgadus proximus</i>		x	Cooney et al. (1978)
Walleye pollock	<i>Theragra chalcogramma</i>		x	Armstrong and Winslow (1986)
Pacific hake	<i>Merluccius productus</i>		x	Hargreaves et al. (1990, cited by Wood et al. 1993)
Burbot	<i>Lota lota</i>	x		Gilhouse and Williams (1989)
Striped bass	<i>Morone saxatilis</i>	x	x	Stevens (1966), Johnson et al. (1992)
Smallmouth bass	<i>Micropterus dolomieu</i>	x		Tabor et al. (1993)
Largemouth bass	<i>Micropterus salmoides</i>	x		Poe et al. (1994)
Yellow perch	<i>Perca flavescens</i>	x		Dahle (1979)
Walleye	<i>Stizostedion vitreum vitreum</i>		x	Rieman et al. (1991), Poe et al. (1994)
Chub mackerel	<i>Scomber japonicus</i>		x	Washington Dep. Fish and Wildlife (unpubl. data)

Table 1—cont.

Common name	Species Scientific name	Freshwater predator	Marine predator	Selected references
Fish predators—cont.				
Coastrange sculpin	<i>Cottus aleuticus</i>	x		Hunter (1959)
Prickly sculpin	<i>C. asper</i>	x		Hunter (1959)
Shorthead sculpin	<i>C. confusus</i>	x		K. Fresh (Washington Dep. Fish and Wildlife, unpubl. data)
Reticulate sculpin	<i>C. perplexus</i>	x		Patten (1972)
Torrent sculpin	<i>C. rhotheus</i>	x		Patten (1972)
Staghorn sculpin	<i>Leptocottus armatus</i>		x	Dunford (1975)
Bird predators				
Double crested cormorant	<i>Phalacrocorax auritus</i>		x	Robertson (1974)
Harlequin duck	<i>Histrionicus histrionicus</i>	x		McCart (1967)
Common merganser	<i>Mergus merganser</i>	x	x	Simenstad et al. (1979), Wood (1987a, b)
Bald eagle	<i>Haliaeetus leucocephalus</i>	x	x	Simenstad et al. (1979), Angell and Balcomb (1982)
Short-billed gull (mew)	<i>Larus canus</i>	x		McCart (1967)
Ring-billed gull	<i>L. delawarensis</i>	x		Ruggerone (1986)
Glaucous-winged gull	<i>L. glaucescens</i>	x		Meacham and Clark (1979)
Bonaparte's gull	<i>L. philadelphia</i>	x		Meacham and Clark (1979)
Black tern	<i>Chlidonias niger</i>	x		McCart (1967)
Arctic tern	<i>Sterna paradisaea</i>	x		Meacham and Clark (1979)
Caspian tern	<i>Sterna caspia</i>		x	Simenstad et al. (1979)
Common murre	<i>Uria aalge</i>		x	Varoujean and Mathews (1983)
Rhinoceros auklet	<i>Cerorhinca monocerata</i>		x	D. Manuwal, University of Washington, Seattle, unpubl. data)

Table 1—cont.

Common name	Species Scientific name	Freshwater predator	Marine predator	Selected references
Mammal predators				
River otter	<i>Lutra canadensis</i>	x		Dolloff (1993)
California sea lion	<i>Zalophus californianus</i>		x	Simenstad et al. (1979), Fiscus (1980)
Northern sea lion	<i>Eumetopias jubatus</i>		x	Simenstad et al. (1979), Fiscus (1980)
Northern fur seal	<i>Callorhinus ursinus</i>		x	Simenstad et al. (1979), Fiscus (1980)
Harbor seal	<i>Phoca vitulina</i>	x	x	Beach et al. (1985), Olesiuk (1993)
Larga seal	<i>P. largha</i>		x	Fiscus (1980)
Fin whale	<i>Balaenoptera physalus</i> ^a		x	Fiscus (1980)
Humpback whale	<i>Megaptera novaeangliae</i> ^a		x	Fiscus (1980)
Pacific whiteside dolphin	<i>Lagenorhynchus obliquidens</i>		x	Fiscus (1980)
False killer whale	<i>Pseudorca crassidens</i> ^a		x	Fiscus (1980)
Killer whale	<i>Orcinus orca</i>		x	Fiscus (1980)
Harbor porpoise	<i>Phocoena phocoena</i>		x	Fiscus (1980)
Dall's porpoise	<i>Phocoenoides dalli</i>		x	Fiscus (1980)
Beluga whale	<i>Delphinapterus leucas</i>		x	Meacham and Clark (1979), Fiscus (1980)
Sperm whale	<i>Physeter catodon</i> ^a		x	Fiscus (1980)
Bear	<i>Ursus spp.</i>	x	x	Gard (1971)

^aConsidered by Fiscus (1980) to be an accidental occurrence.

Table 2. Some estimates of freshwater predation mortality. Examples were selected to show the range of life history stages, locations, and time intervals where predation mortality has been quantified. Outmig. = period of outmigration.

Prey, stage	Habitat	Time period	Mean loss (%)	Range (%)	Source
Chum, fry	Stream	Outmig.	47	35-62	Neave (1953)
Chum, fry	Stream	1 week	58	33-55	Hunter (1959)
Chum, fry	Stream	Outmig.	37	2-68	Semko (1954)
Pink, fry	Stream	Outmig.	34	5-86	Neave (1953)
Pink-chum, fry	Stream	Outmig.	45	23-85	Hunter (1959)
Sockeye, fry	Stream	Migrate to lake	84	67-98	Foerster (1968)
Sockeye, smolt	Lake	Outmig.	63	—	Rogers et al. (1972)
Sockeye, fingerlings	Lake	May-Sept.	59	—	Ruggerone and Rogers (1992)
Chinook and steelhead, smolts	Lake	Outmig.	14	9-19	Rieman et al. (1991)
Coho, fingerlings	Stream	Outmig.	—	24-65	Wood (1987b)
Coho, smolts	River	Outmig.	<1	—	Fresh (Washington Dep. Fish and Wildlife, unpubl. data)

predators as they emerge from the gravel and migrate downstream, but in this case, fry are migrating to rearing lakes (Table 2); some estimates of predation mortality during this period exceed 95%. Predators also consume large numbers of juvenile sockeye while they rear in lakes and as the smolts leave rearing lakes (Foerster and Ricker 1941, Eggers 1978, Burgner 1991). In the Chignik Lakes, Alaska, Ruggerone and Rogers (1992) found that 59% of the average population of sockeye fry was consumed by juvenile coho (*O. kisutch*) between May and September. In the Agulowak River, Alaska, Arctic char (*Salvelinus alpinus*) ate 33-66% of the outmigrating sockeye smolts in 1 year (Rogers et al. 1972).

Compared with pink, chum, and sockeye, there are few estimates of predation mortality of chinook (*O. tshawytscha*) and coho salmon in freshwater. Available data suggest that predation rates on wild populations are low under natural conditions (Patten 1971; Buchanan et al. 1981; Brown and Moyle 1981; Wood 1987a, b) but are much higher in non-natural situations, such as around dams and diversions during downstream migration (Brown and Moyle 1981). In the John Day Reservoir on the Columbia River, predators ate an annual average of 14% of migrating juvenile salmonids (mostly chinook) (Rieman et al. 1991); 21% of this loss occurred in a small area immediately below McNary Dam. Because both hatchery and wild fish were mixed, it was not possible to determine predation on wild populations.

MARINE

The impact of predation on salmonids during marine life is poorly understood. A significant portion of the total natural marine mortality of salmon occurs during the estuarine and early marine period of juvenile life (Parker 1968, Ricker 1976, Bax 1983, Fisher and Percy 1988);

the extent to which this loss is due to predators is unclear. Few studies have estimated predation mortality of juvenile salmon during early marine life (Wood 1987a, Beamish et al. 1992, Wood et al. 1993). Instead, most assessments of predation during marine life have been limited to analyses of predator stomach contents (Fresh et al. 1981, Hargreaves 1988). Interpreting stomach contents data alone without accompanying data on the size of predator and prey populations can lead to erroneous conclusions. A low incidence of salmon smolts in predator stomachs can reflect a high predation mortality if the predator population is large and the smolt population size is low.

The magnitude of predation mortality of salmon in freshwater and marine habitats is a function of characteristics of predators, prey (i.e., the salmon), and their environment. Examples of these characteristics include predator and prey abundance, the size and number of individuals, condition or health of predators and prey, light intensity, and water temperature (Mead and Woodall 1968, Coutant et al. 1979, Hargreaves and LeBrasseur 1986, Fresh and Schroder 1987, Gregory 1993, Mesa 1994, Mesa et al. 1994). Depending on the direction of change of these factors, the magnitude of predation mortality increases or decreases. For instance, as prey size decreases, predation increases (Taylor and McPhail 1985, Hargreaves and LeBrasseur 1986). Similarly, predation increases as salmon become more visible to predators because of increased light intensity, decreased streamflows, or decreased turbidity (Ginetz and Larkin 1976).

Declines in Salmonid Stocks: Role of Competition and Predation

Competition and predation are natural processes that have influenced the abundance of salmon and steelhead throughout their evolutionary history. Anadromous salmonids have evolved characteristics that minimize both predation mortality and the loss of fitness due to effects of competition; otherwise, they would have gone extinct long ago. For competition and predation to contribute to the decline of an anadromous population, something must alter the outcome of biological interactions (e.g., predation mortality must increase). Moreover, this change must result in decreased numbers of reproducing adults. Ways in which this can happen include the following: introductions of nonnative, non-salmonid fish; introductions of artificially produced salmonids; environmental changes; and changes in population sizes of predators and competitors caused by non-environmental factors such as fishing. Although each of these factors is discussed separately in the following sections, several may operate simultaneously on any one salmonid stock. I have also focused on human-induced changes because understanding their effects will be most useful in helping to restore declining populations.

INTRODUCTIONS OF NON-SALMONID FISHES

Overview

Since the arrival of Europeans, numerous species of plants, invertebrates, and fish have been introduced throughout North America (Taylor et al. 1984, Moyle et al. 1986). While ecosystem effects of plant and invertebrate introductions can be severe (Li and Moyle 1981, Nichols et al. 1990, Northcote 1991), I focus here on introductions of non-salmonid fishes.

The successful establishment of a nonnative fish alters the physical or biological nature of the receiving environment (Taylor et al. 1984, Brown and Moyle 1991). As a result, growth, survival, or abundance of native species can decline owing to parasites and diseases, inhibition of reproduction, changes in the nature of existing biological interactions, or environmental alterations (Moyle 1976, Taylor et al. 1984, Moyle et al. 1986, Ross 1991). Effects on native species are difficult to predict because they depend on two factors: (1) physiological, behavioral, and ecological potentialities of the introduced species; and (2) physical and biological properties of the ecosystem (Taylor et al. 1984, Herbold and Moyle 1986, Ross 1991). In general, the successful establishment of nonnative species and subsequent displacement of native fish is greater in habitats that have been extensively modified, especially by anthropogenic factors (Ross 1991, Baltz and Moyle 1993).

To my knowledge, there is no comprehensive assessment for fish species introductions into anadromous salmonid-producing watersheds of the North American west coast. Introductions into some areas, such as California (Moyle 1976) and the Columbia and Sacramento rivers (Moyle 1976, Li et al. 1987, Bisson et al. 1992, Poe et al. 1994), have been well documented. However, in most areas, little or no information exists on the extent to which nonnative fish introductions have negatively impacted native salmon and steelhead because of the effects of competition and predation (Table 3).

Competition

Considerable concern has been expressed about potential impacts on salmonids of American shad (*Alosa sapidissima*) because they are present in various river systems along the North American west coast (Table 3) that also have depressed populations of salmon and steelhead. However, in most West Coast rivers American shad are not abundant, suggesting that they have not caused population declines in those river systems.

American shad are abundant in two rivers, the Sacramento and Columbia, although in the Sacramento River, the numbers of shad have declined considerably from peak levels in the early 1900s (Stevens et al. 1987). Conversely, in the Columbia River, numbers of American shad recently increased to their highest historical levels (Fig. 2) at the same time as some salmon and steelhead runs declined to critically low levels. As a result, competition between American shad and juvenile salmon and steelhead has been hypothesized as one cause of anadromous population declines in the Columbia River system (Kaczynski and Palmisano 1992, Bevan et al. 1994). Other than the inverse relation between shad abundance and salmon runs, evidence supporting this hypothesis results primarily from high dietary overlaps between shad and juvenile salmonids in some habitats (e.g., estuaries; see McCabe et al. 1983). Even though dietary overlaps are often cited as evidence of interspecific competition, they are inconclusive without accompanying information on food supplies and spatial and temporal overlap of the potentially interacting species. To my knowledge, estimates of the amount of food available do not exist for the estuary or reservoirs associated with the Columbia River. Some overlap of shad and several anadromous species in reservoirs occurs, but overlap in the estuary appears to be minimal (Dawley et al. 1986).

Table 3. Examples of non-salmonid fish species introduced into anadromous salmonid-producing watersheds along the Pacific coast of North America. Species selected were those where available information suggested they could be predators or competitors of naturally produced salmon and steelhead. (Note: Lake Washington sockeye salmon were included as a naturally reproducing population even though they have both native and introduced portions. Since their introduction, the non-native portion has been sustained largely by natural production.)

Species/watershed	Species potentially impacted			
	Chinook	Coho	Steelhead	Sockeye
Potential Competitors				
American shad ^a				
Sacramento River, California	x	x	x	
Russian River, California	x	x		
Klamath River, Oregon	x		x	
Coos River, Oregon	x	x		
Columbia River	x	x	x	x
Chehalis River, Washington	x	x	x	
Threadfin shad				
Sacramento River, California	x	x	x	
Longfin smelt ^b				
Lake Washington, Washington				x
Bluegill				
Russian River, California	x	x		
Columbia River	x	x	x	
Lake Washington, Washington				x
Yellow perch				
Columbia River	x	x	x	
Lake Washington, Washington				x
Potential Predators				
American shad				
Sacramento River, California	x			
Klamath River, Oregon	x			
Columbia River	x			
Yellow perch				
Lake Washington, Washington				x
Channel catfish				
Columbia River	x	x	x	
Striped bass				
Sacramento River, California	x	x	x	
Coos River, Oregon	x			
Smallmouth bass				
Russian River, California	x	x		
Umpqua River, Oregon	x		x	
Mid-Columbia River	x	x	x	x
John Day River, Oregon	x			
Lake Osoyoos, Washington				x
Lake Washington, Washington				x

Table 3—cont.

Species/watershed	Species potentially impacted			
	Chinook	Coho	Steelhead	Sockeye
POTENTIAL PREDATORS—CONT.				
Largemouth bass				
Lake Washington, Washington				x
Russian River, California	x	x		
Walleye				
Columbia River	x	x	x	x
White bass/striped bass hybrid				
Tenmile Lakes, Oregon		x		

*Shad are present in many North American west coast rivers; these were selected to show the range of systems in which they are found.

^bThe exact origin of longfin smelt in Lake Washington is unknown, but they were probably strays from an adjacent watershed.

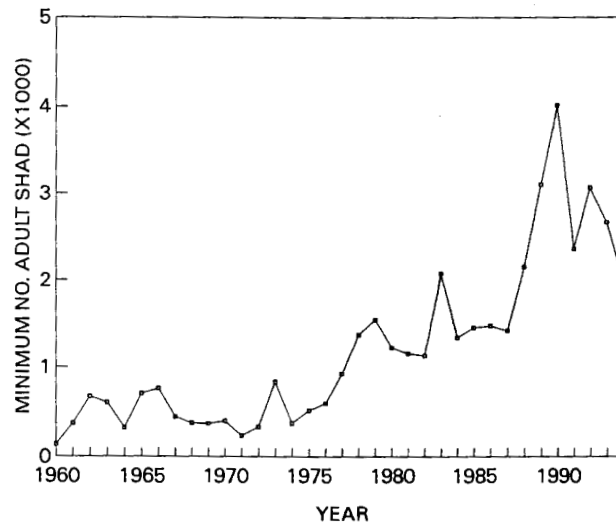


Figure 2. Minimum numbers of adult American shad entering the Columbia River. Source: Washington Department of Fish and Wildlife and Oregon Department of Fish and Wildlife, unpubl. data.

Predation

Introduction of a piscivorous species can impact native fish directly as a result of consumption or indirectly by affecting habitat use and competitive interactions (Brown and Moyle 1991, Rieman et al. 1991). Various salmon- and steelhead-producing river systems have introduced piscivores (Table 3). For instance, striped bass (*Morone saxatilis*) were introduced into the Sacramento River in 1879. Even though striped bass prey on salmon (Stevens 1966) and have historically been abundant in the system, I am unaware of any study that evaluates their impact on native anadromous populations in the basin.

In 1914, striped bass were introduced into the Coos River, Oregon. Since their introduction, the abundance of striped bass and fall chinook in the system has been inversely related, suggesting striped bass were negatively impacting native chinook (Johnson et al. 1992). However, changes in habitat occurred simultaneously, making it difficult to isolate effects of the striped bass. A predation model developed by Johnson et al. (1992) estimated that striped bass in this system could consume between 42,000 and 383,000 juvenile salmonids or an equivalent of 1,000 to 46,000 adult salmon. Despite this information, a decision was made to enhance the striped bass fishery to a level of 20,000 adults, potentially resulting in the loss of 15,000 adult salmonids (Johnson et al. 1992).

The most rigorous evaluation of predation by nonnative species on anadromous populations has been in the Columbia River. Smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum vitreum*), and adult American shad are introduced species known to prey on juvenile salmon (Poe et al. 1994). Rieman et al. (1991) calculated that smallmouth bass and walleye in the John Day Reservoir ate ~3% of the outmigrating salmonids annually (a mixture of hatchery and wild). Although overall predation appears low, some specific salmon populations may be more heavily impacted by nonnative species. Tabor et al. (1993) found a high incidence of subyearling chinook in smallmouth bass stomachs just below the last natural spawning area of wild salmon in the mainstem Columbia River. They speculated that many of the chinook being eaten were juveniles from wild spawners.

INTRODUCTION OF ARTIFICIALLY PRODUCED SALMONIDS

Overview

The use of artificially produced fish is widely believed to be a major factor contributing to the decline in abundance of salmon and steelhead along the North American west coast (Marnell 1986, Nehlsen et al. 1991, Hilborn 1992, Brown et al. 1994). Competition and predation between native and cultured fish are two types of impacts that may result from artificially cultured fish introductions (Marnell 1986, Steward and Bjornn 1990, Nehlsen et al. 1991, Hilborn 1992, Brown et al. 1994).

Artificially produced salmonids are equivalent to nonnative species introductions even when conspecifics are already present in the receiving environment. As mentioned previously, impacts of nonnative species will depend upon physiological, ecological, and behavioral characteristics of the introduced fish. For artificially cultured fish, these characteristics are a function of their genetic origin and how they are reared and released (Mead and Woodall 1968, Fenderson and Carpenter 1971, Hume and Parkinson 1987, Swain et al. 1991). Cultural practices influence many attributes

of hatchery fish that affect outcomes of biological interactions, including the following: size and morphology (Swain et al. 1991), behavior (Fenderson and Carpenter 1971, Mesa 1991, Nielsen 1994), habitat utilization patterns (Dickson and MacCrimmon 1982, Levings et al. 1986, Petrosky and Bjornn 1988), and movements (Levings et al. 1986, Hume and Parkinson 1987).

Competition

Competition between hatchery-produced and wild salmonids is often cited as a mechanism to explain how hatchery fish introductions have impacted native salmonids in streams (Marnell 1986, Fausch 1988, Brown et al. 1994). Although studies show that hatchery fish can disrupt the growth, survival, and abundance of native salmonid communities in streams (Bjornn 1978, Nickelson et al. 1986), competition's role in causing these changes is unclear (Fausch 1988, Steward and Bjornn 1990). For instance, Nickelson et al. (1986) reported a 44% decline in abundance of wild juvenile coho salmon in Oregon coastal streams following the release of hatchery-produced coho juveniles. The authors speculated that hatchery coho were able to outcompete wild coho because they were larger and thus could evict wild fish from their territories.

Flagg et al. (1995) concluded that the over tenfold reduction in densities of wild coho spawners in the lower Columbia River resulted, in part, from the large size of juvenile coho used in hatchery programs as well as stocking hatchery coho at densities $\leq 7X$ the carrying capacity of the receiving environment. As a result, wild juvenile coho were competitively displaced by the larger-sized (hence, competitively superior) and abundant hatchery coho. In the Eagle River, British Columbia, Perry (1995) found that the return per spawner of wild coho and the survival of hatchery coho fry declined as hatchery coho fry abundance was increased; he attributed these trends to the effects of competition between the hatchery and wild coho in freshwater. Similarly, Bjornn (1978) and Tripp and McCart (1983) concluded that competitive interactions between native and hatchery fish caused the decline in native salmonid populations they studied. Even though competition was a plausible explanation for the results of the previous studies, none of them specifically measured mechanisms responsible for changes in the native salmonid populations.

Both intra- and interspecific competition can occur as a result of hatchery fish introductions (Allee 1974, Fausch and White 1986, Kennedy and Strange 1986, Spaulding et al. 1989, Nielsen 1994). Nielsen (1994) provides an excellent example of the effects of intraspecific competition between hatchery and wild salmonids. Following the introduction of hatchery coho salmon in the Noyo River, California, Nielsen (1994) found that agonistic encounters between hatchery and wild coho resulted in the displacement of 83% of the wild coho from their usual microhabitats. Foraging behavior of the wild fish was also altered as a result of aggressive encounters. Production of wild coho salmon in the Noyo River declined following the introduction of the hatchery coho although this decline did not appear to be significant when compared with concurrent changes in other wild populations where hatchery fish were not used.

Interspecific competition between artificially produced and native salmonids has been the focus of a great deal of research (Allee 1974, Kennedy and Strange 1986, Marnell 1986, Moyle et al. 1986, Fausch 1988, Nielsen 1994). Unfortunately, we lack the ability to reliably predict which combinations of sympatry will produce intense interspecific competition and which will not (Fausch 1988). Because species that have not co-evolved do not possess behavioral and morphological mechanisms to reduce competition, intense interspecific competition can occur

when an introduction brings together species that are not naturally sympatric (Hearn 1987, Fausch 1988). Introductions that produce sympatry in species that have co-evolved elsewhere but not in the system where the introduction occurs may also result in interspecific competition (Hearn 1987). This occurs because in allopatry, a species can exhibit ecological release, a process whereby the niche of the species expands in the absence of competition. When a new species is introduced, intense interspecific competition occurs because the two species in that particular system did not co-evolve. Thus, they lack mechanisms to reduce effects of competition, even though they co-occur elsewhere.

In marine habitats, evidence that competition occurs between hatchery and wild fish consists primarily of density-dependent declines in survival or growth of wild salmonids simultaneously with increasing numbers of hatchery fish (Thomas and Mathisen 1993, Perry 1995). For example, Hilborn (1992) suggested that sockeye salmon juveniles produced by the Babine Lake, British Columbia, spawning channels depressed smolt-to-adult survival of wild sockeye owing to competition (Fig. 3). While this suggests a density-dependent interaction (e.g., competition for food), no specific evaluation of causative mechanisms was conducted.

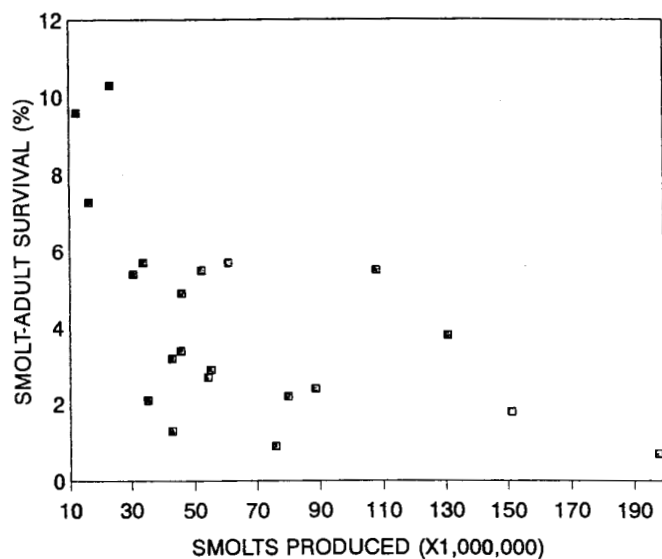


Figure 3. The relationship between total sockeye salmon smolt production and smolt-to-adult survival from Babine Lake, British Columbia (after Hilborn 1992). Smolt production represents the total number of juvenile sockeye produced in a year and includes both wild and artificially produced fish. Survival declines as more artificially produced fish are released. Source: McDonald and Hume (1984) and Macdonald et al. (1987).

One situation where competition between hatchery and wild salmonids during the marine life phase likely occurs is in populations of pink and chum salmon in Washington and southern British Columbia (Gallagher 1979, Peterman 1987, Beachum 1993). Many chum populations in this region exhibit strong odd-even year cyclicity in abundance and age composition (Gallagher 1979). This between-year variability has been hypothesized to result from chum competing with pink salmon during early marine life (Belford 1978, Gallagher 1979, Peterman 1987, Beachum 1993). Such an interaction is plausible because the number of adult pink salmon that return to spawn in the region is much greater in odd-numbered years; thus, pink fry are abundant in even-numbered years, but scarce in odd-numbered years. Moreover, the two species have similar distributions and food requirements during early marine life (Simenstad et al. 1980, Peterman 1987).

Evidence of the pink salmon effect on chum is exhibited in Puget Sound where chum salmon survival declines as pink salmon escapement increases (Fig. 4). For Fraser River pink and chum salmon, Peterman (1987) concluded, based on survival rate correlations, that most of the between-year variability in marine survival of chum salmon occurs during early ocean life when pink and chum juveniles are sympatric for a prolonged period. If competition between these two species occurs during early marine life, then increasing numbers of pink salmon juveniles with

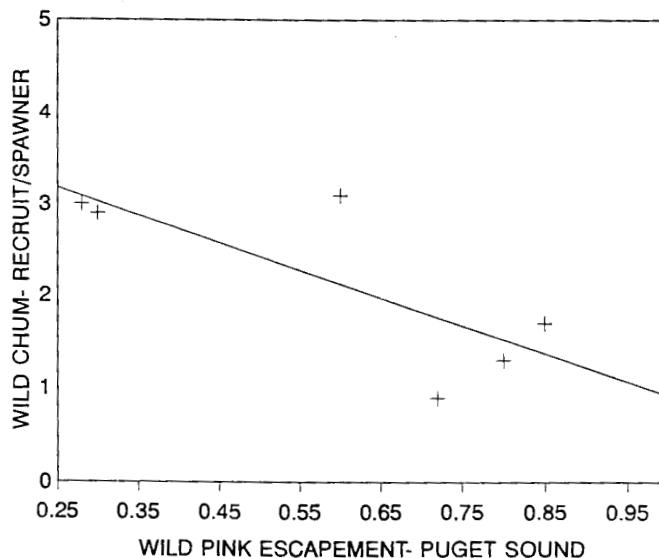


Figure 4. Relationship between pink salmon escapement and chum salmon survival (as measured by recruit per spawner) in Puget Sound, Washington ($r^2 = 0.62$). Each data point is a separate year from 1959 to 1979. Source: Washington Department of Fish and Wildlife (WDFW), unpubl. data; J. Ames, WDFW, pers. comm.

enhancement programs will depress chum survival. This can occur if high densities of hatchery fish depress growth rates of wild fish and increase the period when wild fry remain vulnerable to predators (Belford 1978).

Predation

Compared with competition, less is known about predation by hatchery fish on wild salmonids (Fausch 1988). Several studies have used data on stomach contents, predator abundance, etc., to estimate consumption of juvenile wild salmon by hatchery-produced fish (Table 4). For example, Evenson et al. (1981) calculated that the average annual loss of wild chinook and steelhead over a 3-year period in the Rogue River, Oregon, due to predation by hatchery fish was 9.7%. Martin et al. (1993) evaluated predation on juvenile chinook in the Tucannon River, Washington, from a release of 119,082 juvenile steelhead; they estimated ~10,000 of these fish remained in the study area and ate 456 wild fish (95% CI = 4–3,117) in the first 4.5 months following their release in April.

Much of the information on predation by hatchery fish on wild salmonids is circumstantial in nature, such as that obtained from analyses of fishery management databases (Table 4). One example of this type of data is from Washington, where Johnson (1973) proposed that predation by hatchery coho salmon had caused the decline of several wild pink and chum populations. His conclusion was based on circumstantial evidence such as a comparison of adult returns of chum and coho at various hatcheries. Johnson (1973) observed that at a number of hatcheries, adult chum returns declined dramatically shortly after the initiation of hatchery coho programs. Further, he found that wild chum populations did not decline in areas where hatchery coho programs had not been established (e.g., South Puget Sound or on larger streams). This and other circumstantial evidence led Johnson (1973) to conclude that hatchery coho were responsible for the declines of a number of chum populations.

ENVIRONMENTAL CHANGES

Considerable attention has been focused on the role that human-induced environmental changes have had in the decline of Pacific salmon and steelhead populations (e.g., Nehlsen et al. 1991). For >150 years, humans have altered or eliminated access to freshwater habitats (Li et al. 1987, Raymond 1988); modified the quantity, type, and quality of freshwater and marine habitats (Scott et al. 1986, Hicks et al. 1991, Bisson et al. 1992, Simenstad et al. 1992, Reeves et al. 1993); and changed the physiochemical nature of waters the fish use (e.g., Seiler 1989, Hicks et al. 1991). Many authors regard environmental changes, especially impacts to freshwater habitats, as a major cause of the decline of anadromous populations in the Pacific Northwest (Nehlsen et al. 1991, The Wilderness Society 1993, Brown et al. 1994).

One way environmental changes cause salmon abundance to decline is by altering outcomes of biological interactions, such as by changing availability of resources, abundance of predator and competitor populations, condition (e.g., stress levels) of interacting individuals, and sizes of interacting individuals (Ginetz and Larkin 1976, Coutant et al. 1979, Fisher and Pearcy 1988, Brodeur and Pearcy 1990, Gregory 1993, Mesa 1994). Changes in water temperatures (e.g., caused by removing riparian vegetation along streams) altered competitive interactions between redband shiner (*Richardsonius balteatus*) and juvenile steelhead trout (Reeves et al. 1987). At

Table 4. Examples of situations where hatchery salmonids are potentially preying upon wild salmonids. Two general types of data analysis were used: (1) fishery management databases, and (2) stomach contents.

Wild population	Predator	Evidence	Source
Fishery database analyses			
PUGET SOUND CHUM AND PINK SALMON			
Samish River	Coho salmon	Decline in rack returns	Johnson (1973)
Skykomish River	Coho salmon	Decline in rack returns	Johnson (1973)
Green River	Coho salmon	Spawner abundance index	Johnson (1973)
Minter Creek	Coho salmon	Decline in rack returns	Johnson (1973)
Nemah River	Coho salmon	Decline in rack returns	Johnson (1973)
Willapa River	Coho salmon	Decline in rack returns	Johnson (1973)
Stillaguamish River	Coho salmon	Decline in terminal run size	J. Ames (Washington Dep. Fish and Wildlife, unpubl. data)
Stomach contents analyses			
CHINOOK SALMON			
Rogue River, Oregon	Chinook, steelhead	\bar{X} = 9.7% salmon juveniles eaten per year	Evenson et al (1981)
Salmon River, Idaho	Steelhead	~13% of juveniles eaten in 1 year	Bevan et al. (1994)
Feather River, California	Chinook, steelhead	7.5 million wild fish eaten in 1 year	Sholes and Hallock (1979) ^a
Tucannon River, Washington	Steelhead	Mean predation loss = 456 fish	Martin et al. (1993)
Nicola River, British Columbia	Chinook	No predation observed	Levings and Lauzier (1989)
SOCKEYE			
Lake Washington, Washington	Rainbow trout	2% of sockeye eaten per year	Beauchamp (1987)

^aNo method was provided for how the predation loss was derived.

higher temperatures, the redbreasted sunfish were able to competitively displace steelhead from their territories. A higher incidence of disease also led to higher mortality among the less competitive species while the dominant competitor was unaffected.

Another example of how environmental changes alter biological interactions is in the Columbia River where damming and impounding the river has created favorable habitat conditions for a number of nonnative piscivorous species, most of which originated from the midwestern United States (US) (Li et al. 1987). These nonnative piscivores prey on native salmonids and have altered the native fish community structure and food web in the Columbia River system (Li et al. 1987, Tabor et al. 1993, Poe et al. 1994).

While it is clear that human-induced environmental changes can alter competition and predation, such changes will not always cause the abundance of salmonid populations to decline. Salmon have lived in naturally changing freshwater and marine environments throughout their evolutionary history and, thus, have adapted to some level of environmental changes (e.g., Taylor 1991). For instance, juvenile salmon in some rivers move in the fall to habitats that provide greater protection from winter flood conditions (Bustard and Narver 1975, Peterson 1982, Nickelson et al. 1992). It is when salmonids cannot adapt to environmental changes that abundance levels can decline.

One example of how environmental changes, biological interactions, and declines in salmonid populations can be linked is predation around dams and diversions, such as in the Columbia and Sacramento rivers (Hall 1979, Rieman et al. 1991). In the Columbia River, predation by fish and birds is a particularly significant cause of dam-related mortality (Ruggerone 1986, Rieman et al. 1991). Detailed studies of predation in one reservoir (John Day Reservoir) demonstrated that the average annual loss of salmonid smolts due to fish predators, especially northern squawfish (*Ptychocheilus oregonensis*), was 14% (Rieman et al. 1991). High predation losses of smolts are also associated with other mainstem dams and reservoirs in the Columbia River system (Uremovich et al. 1980).

I speculate that losses of salmonids to northern squawfish and other fish predators in the Columbia River are higher now than they were historically. What was once a free-flowing system has been converted into a series of dams and impoundments. Squawfish predation is especially high around dams, diversions, and in lakes; in free-flowing rivers, predation rates are typically lower (Brown and Moyle 1981, Rieman et al. 1991). It is not possible to quantify how predation losses in the Columbia River may have changed as a result of damming the river because historical data on pre-dam predation rates do not exist. Also, without knowledge of stock-specific mortality rates, it is impossible to know how mortality varies among stocks (e.g., is it more severe on certain stocks?).

OTHER FACTORS CAUSING CHANGES IN PREDATOR AND COMPETITOR POPULATIONS

Factors other than environmental variability (e.g., diseases, parasites, and fishing) can also alter biological interactions. For example, since the early 1970s, pinniped abundance, particularly harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus californianus*), has increased to near historical levels because the harvest of these animals was prohibited by the Canadian and US governments (Olesiuk et al. 1990a, Calambokidis and Baird 1994). Because

marine mammals have recently increased in abundance, are known to prey on adult and juvenile salmon and steelhead, and tend to aggregate at river mouths (Beach et al. 1985, Olesiuk et al. 1990b), it is believed that these animals are contributing to declines in some anadromous populations (Kaczyinski and Palmisano 1992). The most comprehensive evaluation of marine mammal predation on salmon is a study by Olesiuk (1993) of harbor seals in the Strait of Georgia, British Columbia. Olesiuk (1993) calculated that nearly 386 mt of salmon or 3% of the mean annual escapement in the area in recent years was consumed by harbor seals in 1988.

Because information used by Olesiuk (1993) is unavailable for other areas of the North American west coast, comparable estimates cannot be computed for these regions. In a thorough review of the available information on salmon and steelhead in northern California and western Oregon, Botkin et al. (1995) concluded that, despite serious weaknesses in existing data and analyses, "marine mammals are a minor factor in the harvest of salmon." However, in some specific cases where stocks are already at critically low levels of abundance or where conditions exist that enhance predation, marine mammal predation can have a significant impact (Calambokidis and Baird 1994). For example, marine mammal predation adjacent to Lake Washington, Washington, is affecting winter-run steelhead. In recent years, California sea lions have annually consumed $\leq 65\%$ of the returning adults at the Hiram Chittendon Locks in Seattle (R. Leland, WDFW, Mill Creek, pers. comm.) and are considered a major factor responsible for the decline of this steelhead run.

General Discussion

EVALUATION OF AVAILABLE INFORMATION

Evaluating the role of competition and predation in the decline of salmon and steelhead populations depends upon the quantity and quality of available information. I found few instances where the contribution of these interactions to population declines could be clearly established. One reason for this was the existence of significant data gaps. For example, the lack of comprehensive surveys of nonnative fish introductions in western North American watersheds makes it impossible to fully assess effects of nonnative fishes on native salmonid communities.

Many of the data on competition and predation were circumstantial in nature, particularly in evaluations of interactions in marine habitats. Examples of such data include abundance or age composition data obtained from fishery management agencies, food habits and diet overlap (Peterman 1984, 1987). Analyses of this type of data identifies the potential for inter- or intra-specific relationships (Perry 1995) but does not directly measure or test potential mechanisms. Thus, competition and predation can be one of several plausible hypotheses explaining observed results. For example, the decline in the chum salmon populations observed by Johnson (1973) could have been due to predation by juvenile coho salmon from hatcheries on chum fry or habitat loss occurring at the same time as coho programs expanded.

Much of the uncertainty in the data stems from the inherent complexity and dynamic nature of biological interactions. Effects of competition and predation on a particular salmonid population depend upon a whole suite of variables (e.g., size of predators and competitors, environmental conditions, and abundance levels); a small change in one may dramatically change

mortality. This is particularly apparent when evaluating effects of hatchery fish introductions. As noted previously, numerous variables associated with rearing and releasing hatchery fish (e.g., numbers of hatchery fish that remain in the area, size of hatchery fish that are released) affect competition and predation with native salmonids. Thus, predicting what types of biological interactions may result from introducing hatchery fish and the associated impacts on native salmonids remains complex.

Data were especially ambiguous when assessing effects of interspecific competition. Competition is a difficult interaction to study and measure even in the best of conditions; for instance, effects of competition can be easily masked by a number of environmental factors (Taylor et al. 1984, Fausch 1988). Clear demonstration that interspecific competition is occurring requires evidence that a niche shift in one species occurs in the presence of another species (Hearn 1987). This necessitates manipulative experiments in either natural or controlled laboratory settings (Fausch 1988). These types of experiments have been successfully accomplished in stream environments while in marine habitats they have only been accomplished at very small scales (e.g., laboratory tanks). Stream habitats represent a better opportunity for competition experiments because we know more about the biology and ecology of the system, thus making it easier to design and conduct experiments; they can be more easily modeled in laboratory settings (e.g., laboratory stream channels); and sampling methods are relatively inexpensive. It is no accident that we know more about competition in streams than about competition in marine habitats. The reliance on circumstantial data to assess effects of biological interactions in marine habitats is undoubtedly a reflection of the difficulty associated with measuring biological interactions in such large systems.

BIOLOGICAL INTERACTIONS AND THE RESTORATION OF SALMONID POPULATIONS

Reviews by Nehlsen et al. (1991), Konkel and McIntyre (1987), The Wilderness Society (1993), Brown et al. (1994), and others have drawn attention to the depressed status of many Pacific salmon and steelhead populations. Clearly, once we have identified where depressed populations occur, we must next take action to restore populations and better maintain their future health. A major step in accomplishing this goal must be to identify reasons for population declines so that the appropriate corrective actions can be taken. In deciding what actions should be taken, it is important that we recognize that competition and predation are a secondary effect or symptom of other changes that have occurred. For biological interactions to have a role in the decline of an anadromous population, something must occur that alters the outcome of competition or predation (e.g., predation mortality must increase). For example, altering abundance levels of populations of salmon predators by changing harvest levels can affect overall predation mortality. In the Columbia and Sacramento rivers, dams and diversions, which kill salmon directly (e.g., as a result of passage through turbines) or indirectly (e.g., by increasing predation risk), are the underlying cause of salmon mortality while predation represents a secondary effect of the dams.

To effectively restore depressed populations, we must identify and eliminate the underlying causes of population declines and not simply treat secondary effects (Meffe 1992, Black 1994). This is analogous to a doctor treating a patient (Meffe 1992). To cure the patient, the doctor must

identify the disease that is responsible for the symptoms that he observes. If the physician treats only symptoms without understanding what is causing the symptoms, the patient may fail to recover because the doctor treats the wrong disease. Similarly, to restore a salmon population, the factors responsible for the deleterious biological interactions must be identified and corrective action directed at these factors. For example, while reducing the abundance of northern squawfish around dams in the Columbia River may increase abundance of salmon (Rieman and Beamesderfer 1990), it avoids the issue of why predation became a problem in the first place (the damming and impounding of the river). In this case, to cure the depressed salmon runs, a solution should involve the dams.

Establishing whether and how biological interactions have contributed to declines of specific salmonid populations will not be easy. The available data will rarely, if ever, be unequivocal. Uncertainty in decision making is not a unique feature of salmon populations or of competition and predation (Ludwig et al. 1993). It requires a willingness to use innovative, adaptive, and experimental management approaches in situations where many of our answers will come from experience (Walters 1986). A key part of these types of approaches must be monitoring both biological interactions and changes in salmon population abundance. For example, abundance levels of wild populations associated with hatchery programs should be carefully monitored; depending on the outcome of the monitoring efforts, managers can decide whether to proceed with additional enhancement (Olson et al. 1995, Perry 1995).

In some situations, decision makers will require additional data or a reanalysis of existing data using new methods before determining how to proceed. Such additional studies can be time-consuming and costly, may do little to reduce uncertainty, and might delay initiation of recovery actions, perhaps by many years. Such delays must be balanced against the likelihood that further work will reduce uncertainty and the status of the salmonid population. If no action is taken, already depressed salmonid populations may decline further or become extinct as a result of even a small change in predation or competition. Even populations that do not become extinct can be trapped at low levels of abundance by compensatory mortality (e.g., predation, Peterman 1987).

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~ please note ~~at~~ method for expenses on
Specimen: Sewer: Model