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PERSISTENCE OF STREAM FISH ASSEMBLAGES: EFFECTS OF ENVIRONMENTAL CHANGE

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The impact that environmental perturbation has on community structure is of major relevance to our understanding of the importance of biotic interactions such as competition and predation, and responses of species assemblages to these factors (e.g., Connell 1975; Wiens 1977; Peckarsky 1983). Studies of lotic invertebrate assemblages (Peckarsky 1983), as well as fish assemblages in general, suggest that stability and/or persistence of communities is greater in benign than in harsh environments. We follow Connell and Sousa (1983) in considering stability as constancy in the numbers of organisms over time, and persistence as a qualitative measure of existence. Constanz (1981), for instance, documented high population variability of fish species in desert arroyo environments in contrast to more consistent desert springs, thus illustrating decreased stability in the harsh environment.

Rather than comparing fish assemblage stability or persistence over time in harsh and benign habitats, most studies instead have focused on only one habitat type. Tyler (1971) suggested that thermal variability created instability in a north-temperate marine demersal fish assemblage, resulting in a decreased number of resident species, and Quinn (1980), working in Australian tidal creeks, obtained similar results. Harrell (1978) ascribed the absence of permanent species associations in Devil's River, Texas, to the generally harsh and unpredictable environment, and Kushlan (1976) found that species composition of Everglades fish assemblages varied with water-level constancy. Grossman et al. (1982), working in a more constant environment, also documented significant changes in community structure illustrative of low stability, but Grossman (1982) documented high stability of an intertidal fish assemblage. In addition to changes in species composition of a system, specific habitat use by fishes may be less structured in physically harsh than in benign systems (Harrell 1978; Tyler 1978; Matthews and Hill 1980).

In this study we contrast fish assemblage stability and persistence in an inter-

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STOCHASTICITY AND ASSEMBLAGE ORGANIZATION IN AN INDIANA STREAM FISH ASSEMBLAGE

In 1982, Grossman et al. purported to demonstrate that a stream fish assemblage was probably affected more by unpredictable environmental disturbances than by interactive processes such as competition. The main purpose of that paper was to interest ecologists in the possibility that stream fish and invertebrate assemblages may be organized through processes fundamentally different from those addressed by the bulk of ecological theory. Grossman et al. (1982) provoked a series of critical rebuttals (Herbold 1984; Rahel et al. 1984; Yant et al. 1984), and our purpose here is to clarify some of the issues raised by these critiques.

METHODOLOGICAL CRITICISMS

Adequacy and Generality of the Study Site

The study site below Markles Dam was chosen because it has not displayed major physical changes for 150 yr and it possesses high species diversity (Whitaker 1976). Although this site may not be typical of others in the Otter Creek drainage, mill dams are common in streams of the eastern and midwestern United States. There is also ample evidence suggesting that the dynamics of fish assemblages in undammed streams are very similar to those observed in Otter Creek (Grossman et al. 1982). Consequently, our study site possesses some generality, and results derived from it cannot be considered unique.

Yant et al. believed that our 120-m × 23-m study site was too small to ensure that individual fishes would have spent a great proportion of their lives within this site. They criticized the references cited by Grossman et al. (1982) and stated "However, in reviewing the relevant literature up to 1959, Gerking [1959] did not find any cyprinid showing such restricted movements" (p. 574). What Yant et al. failed to mention is that Gerking (1959) did not present any data whatsoever on cyprinids, so that the question of whether stream cyprinids move great distances remains unanswered. Yant et al. then cited several references that "indicate [that] cyprinids in streams are unlikely to remain within a 120-m site (Ruhr 1956; Moshenko and Gee 1973; Fraser and Sise 1980; Storck and Momot 1981)" (p. 574). None of these studies, however, directly assessed the movements of individuals; hence, they cannot be used to estimate movement patterns and home ranges for individual fishes. Since May 1983, Grossman and Hill have individually marked eight species of fishes as part of a long-term study of assemblage dynamics in North Carolina streams. We have obtained sufficient data for home-range

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estimates for three species: one cottid (*Cottus bairdi*, $N = 22$) and two cyprinids (*Clinostomus funduloides*, $N = 14$, and *Rhinichthys cataractae*, $N = 12$). To date, 87% of the recaptures occurred in the original section of capture ($\bar{x} \pm 1$ SD $= 13.4 \pm 1.5$ m), even over substantial time periods (range of days from original marking to recapture: *Cottus*, 5–232; *Clinostomus*, 8–297; *Rhinichthys*, 7–81). To our knowledge, these are the first home-range estimates for North American stream cyprinids, and these data indicate that the 120-m × 23-m site was of sufficient size to quantify the dynamics of assemblage regulation.

Yant et al. also stated that "Whitaker (1976) implied that individuals of at least two common species (*Notropis atherinoides* and *N. spilopterus*) moved to the site from the Wabash River" (p. 574). Whitaker (1976, p. 195) stated that the abundance of these species probably can be explained both by the proximity to the Wabash and by the presence of a riverine habitat in the study site. This does not imply that individuals move between the sites, but rather that there are nearby populations from which individuals could have dispersed to the study site and that sufficient habitats were available at the study site for colonization by these individuals. Whitaker and Wallace (1973) also stated that *N. atherinoides* was "abundant in the Wabash River and lower portions of major streams" (p. 456) and that *N. spilopterus* was reported to be "abundant and widespread . . . [with the] greatest occurrence in streams" (pp. 456–457). Similar statements are found in Smith (1979) and Becker (1983). Hence, the evidence indicates that these species are expected members of fish assemblages in stream reaches like the one studied.

Sampling Methods and Adequacy

Detailed information on sampling methods and adequacy are presented in Grossman et al. (1982, pp. 425–426) and Whitaker (1976, p. 192). To ensure that samples were comparable, we always started at the lower end of the same pool and ended at the dam. Approximately the same amount of sampling effort was expended during each collection. Yant et al. criticized our methods by stating that "seining was in an upstream direction, contrary to standard practice (Hendricks et al. 1980)" (p. 574). Hendricks et al. emphasized, however, that the skill, effort, and knowledge of the investigator are most important for determining sampling techniques. Other methodological references (Everhart et al. 1975; Bagenal 1978; Nielsen and Johnson 1983) also fail to make any claim for the general efficiency of downstream seining.

Both Yant et al. and Rahel et al. suggested that much of the variability upon which our conclusion of stochastic organization was based resulted from sampling variability rather than actual assemblage variability. We performed a correlation analysis of intraseasonal samples before submitting the original paper (Grossman et al. 1982) and found that four of five samples were significantly correlated at the 0.1 level or below (Sept. & Nov. 1966, $r_s = 0.709$, $P < 0.01$; July 1967 [3 samples], $W = 0.776$, $P \ll 0.0001$; Sept. & Nov. 1966, $r_s = 0.776$, $P < 0.01$; Sept. & Oct. 1968, $r_s = 0.473$, $0.05 < P < 0.10$); only one was not (Oct. & Nov. 1964, $r_s = 0.370$, $P > 0.02$). Examination of these calculations also indicated that significant correlations were not caused by shared absences of species. We viewed these results as equivocal and decided to pool samples because such pooling reduces variability and hence would make our tests conservative. Although four of five

[ca, 1985]

24. Factors Influencing Changes in Fish Assemblages of Pacific Northwest Streams

Hiram W. Li, Carl B. Schreck, Carl E. Bond, and Eric Rexstad

Abstract

Recent structural alterations to watersheds of the Pacific Northwest have changed the ecological setting for fish assemblages. Dams have acted as physical zoogeographic barriers and may have increased the importance of fish diseases both as zoogeographic barriers and as mechanisms structuring fish assemblages. The impoundments favor the establishment of exotic, temperate mesotherms and eurytherms from the Midwest. Forestry, grazing, and bank-stablization practices have changed the morphology of watersheds and diminished the role of large woody debris and riparian vegetation, which are important regulators of physical change and stream metabolism. Fishing has depleted juvenile *Oncorhynchus tshawystscha*, a formerly very abundant fish in large tributaries of major watersheds, and certain other species no longer support commercial fisheries. Harvesting of salmonids has led to a significant reduction of nutrient input to nutrient-poor stream complexes. Stock depletion has given rise to hatcheries that now produce fish that are different genetically from the ancestral populations.

Recent debate has rekindled interest in the nature of fish taxocene structures in streams (Moyle and Li, 1979; Grossman et al., 1982; Herbold, 1984; Rahel et al., 1984; Yant et al., 1984). The heart of the controversy is whether the fish fauna is the result of independent physiological responses to physical gradients by each species or the result of biological interactions. If the composition of the fish assemblage is relatively constant through time, it is deterministically governed, and biological interactions are important mechanisms determining its structure (Grossman et al., 1982). We will argue that the problems of temporal and spatial scaling will affect the interpretation of variations in relative composition of fish assemblages. The problem of scale is linked with anthropogenic change and the difficulties in separating its confounding influences from natural, periodic disturbances. The goal of this chapter is to recount the forces that have changed faunal composition in the Pacific Northwest and to relate them to the current controversy.

Faunal Characteristics in Relationship to Spatial Scale

Connell and Sousa (1983) have made us more aware that scaling is important when we are examining the stability of populations and communities. Their criteria state that the area of study must encompass the home ranges of the organisms throughout their life cycles and through at least one complete generation. For river systems such as those of the Pacific Northwest, any investigation of assemblage dynamics requires that entire basins be considered the unit of study. Approximately 40% of the native fish fauna is anadromous, and a high degree of potadromy is exhibited by various species (Moring et al., 1981). Anadromous fishes can be found in the Snake and Columbia rivers throughout the entire year, migrating upstream to spawn or downstream to the sea (Allen et al., 1976; Northwest Power Planning Council, 1981; Everest and Sedell, 1983).

The suggestion that the river basin is the most meaningful spatial unit in which to study fish communities is theoretically supported by the River Continuum Concept (RCC) of Vannote et al. (1980) and the hierarchical stream structure proposed by Warren and Liss (1983). We believe that these frameworks can explain the distribution of fish guilds as they do functional groups of insects. For instance, the distribution of chiselmouth (*Acrocheilus alutaceus*), an herbivorous minnow, corresponds well with stream order as predicted by RCC (D. R. Lassuy, unpub. data; fig. 24.1).

Figure 24.2 displays native fishes along a continuum of a generalized Pacific Northwest river system. Much of this information was derived from the computerized data base of the Department of Fisheries and Wildlife, Oregon State University, which has stored collection records since 1900 that

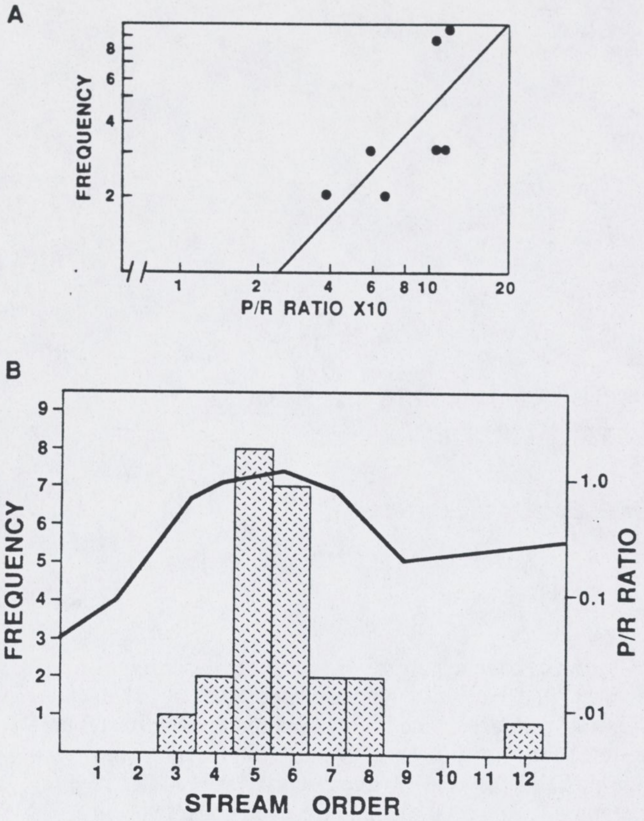

Fig. 24.1. A: Frequency of occurrence of chiselmouth plotted against the P/R (productivity/respiration) ratio. The solid line is the theoretical distribution of P/R ratios by Vannote et al. (1980). B: Frequency of occurrence of chiselmouth by stream order. The solid line is the theoretical distribution of *P/R* ratios by Vannote et al. (1980).

are highly oriented toward an Oregonian perspective. However, the shared species pool of Pacific Northwest river systems is substantial (Miller, 1958; Reimers and Bond, 1967; McPhail, 1967; McPhail and Lindsey, 1970; Moyle, 1976). From this figure one observes that the fauna was composed mostly of salmonids and cottids, which constituted 39–50% and 20–30%, respectively, of the fishes collected from 1900 to the mid-1940s. Figure 24.2 is analogous to a canonical function with three important physical factors: gradient, temperature, and stream size. In general, species are added to the system as gradient lessens and as water temperature rises and stream size increases. Temperate stenotherms are physiologically most efficient at temperatures < 20° C (Hokanson, 1977) and are found, therefore, primarily in lower-order streams. Temperate mesotherms and temperate eurytherms form larger fractions of the fauna when water temperatures increase. Hence, some species replacement may occur as a result of physiological specialization for temperature. For instance, mountain suckers (*Catostomus platyrhynchus*) and longnose suckers (*Catostomus catostomus* are gradually replaced by the bridgelip sucker (*Catostomus columbianus*) and the largescale sucker (*Catostomus macrocheilus*) as the gradient becomes less steep, and water temperatures increase. The mountain sucker and the longnose sucker are stenotherms; the bridgelip sucker, a mesotherm; and the largescale sucker, a eurytherm. The pattern of down stream species addition also follows a trophic gradient consistent with the RCC; surface insect feeders are found in the headwaters, followed by small benthic invertebrate feeders, herbivore-detritivores, omnivores, and large invertebrate-piscivores in higher-order streams.

The impacts of interactions among native fishes on distributional patterns are highly localized, resulting primarily in shifts in microhabitat use. The presence of torrent sculpin (*Cottus rhotheus*) alters habitat choice by the reticulate sculpin (*Cottus perplexus*) and the Piute sculpin (*Cottus beldingi*; Finger, 1982). Numerous studies have documented interactions among various species of salmonids that cause shifts in microhabitat use (Lister and Genoe, 1970; Andrusak and Northcote, 1971; Schultz and Northcote, 1972; Stein et al., 1972; Everest and Chapman, 1972; Allee, 1974; Glova, 1978). Competitive dominance plays a major role in microhabitat use where several salmonid species are found locally. Coho salmon (*Oncorhynchus kistuch*) is the most aggressive species, followed in order by steelhead trout (*Salmo gairdneri*), cutthroat trout (*Salmo clarki*), and chinook salmon (*Oncorhynchus tshawytscha*).

Impacts of Fishing

Before commercial fishing, the dominant fish in the Columbia River was the summer run of chinook salmon. By 1889–90 this run was badly depleted, and the fishery shifted to the spring and fall runs of chinook salmon, steelhead trout, sockeye salmon *Oncorhynchus nerka*), coho salmon, and chum salmon (*Oncorhynchus keta*), in order of importance. By 1975 the total catch of chinook salmon had dropped eightfold from historical peaks, coho salmon by tenfold, and steelhead trout and chum salmon by one hundredfold. Sockeye salmon were no longer capable of supporting commercial fishing (Allen et al., 1976). Sturgeon stocks were also overfished. The catch was 2,500,000 kg in 1895 and declined to 36,000 kg in 1934 (Craig and Hacker, 1940).

Overharvest of anadromous salmonids has had several ecological impacts. The overharvest of salmonid stocks denied a substantial amount of nutrients to the Columbia system. The diminution of nutrients destined for natal streams can be appreciated by the pattern of nutrient loss to the fishery (fig. 24.3). Salmonids actively transport nutrients against a gradient when they migrate from the relatively nutrient-rich ocean environment to relatively poor-nutrient headwater stream systems (Nikolskii, 1969). We calculate that the amount of nutrients in a spawning adult population is roughly four times that of seaward-migrating juveniles from the same stream. Nitrates and phosphates are rapidly sequestered by the periphyton during the height of carcass decomposition. Decaying carcasses can elevate primary production tenfold (Richey et al., 1975). Bacterial heterotrophy is also stimulated and hastens decomposition of leaf litter, thereby enriching the food base for shredder insects (Durbin

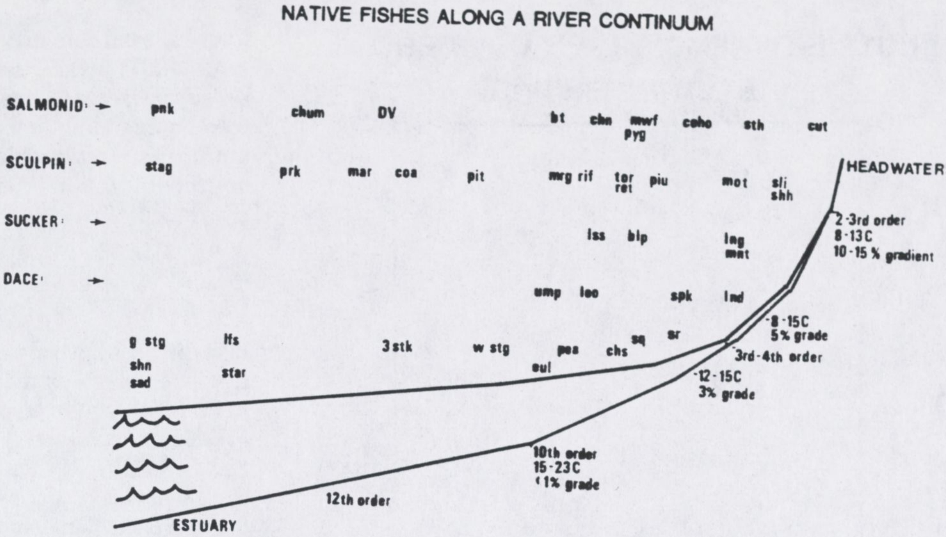

Fig. 24.2. Generalized distribution of selected native fishes along a river continuum of the Pacific Northwest. bt = bull trout, blp = bridgelip sucker, chum = chum salmon, chn = chinook salmon, chs = chiselmouth, coa = coastrange sculpin, cut = cutthroat trout, coho = coho salmon, DV = Dolly Varden, eul = eulachon, g stg = green sturgeon, leo = leopard dace, lfs = longfin smelt, lng = longnose sucker, lnd = longnose dace, lss = largescale sucker, mar = marbled sculpin, mnt = mountain sucker, mot = mottled sculpin, mrg = margined sculpin, mwf = mountain whitefish, pea = peamouth, pit = pit sculpin, piu = piute sculpin, pnk = pink salmon, prk = prickly sculpin, pyg = pygmy whitefish, ret = reticulate sculpin, rif = riffle sculpin, sad = saddleback gunnel, shh = shorthead sculpin, shn = shiner perch, sli = slimy sculpin, spk = speckled dace, sq = squawfish, sr = sandroller, stag = staghorn sculpin, star = starry flounder, sth = steelhead, 3 stk = three-spined stickleback, tor = torrent sculpin, ump = umpqua dace, w stg = white sturgeon.

et al., 1979). The loss of nutrients consequent to depletion of the stocks must have had profound impacts on the trophic system, and greater competition among species may have been one consequence.

We have attempted to mitigate for decreased natural production through hatchery supplementation. Hatcheries significantly contributed to salmonid production during the mid-1960s (Allen et al., 1976; Raymond, 1979; Northwest Power Planning Council, 1981). Runs of coho salmon entering the lower Columbia River increased from 72,000 fish in 1960 to 2,606,000 in 1970. It is debatable whether hatcheries will continue to produce well over the long term because the percentage of fish returning to hatcheries has decreased (Gunsolus, 1978).

Studies of different salmonids show that hatcheries profoundly change stock gene pools (Kincaid, 1976; Allendorf and Phelps, 1980; Ryman and Stahl, 1980). Hatchery coho salmon are distinguishable from wild stocks irrespective of geographic origin, on the basis of electrophoretic, morphological, and life-history characteristics; moreover, the progeny of wild fish reared in hatcheries differ from those reared in the wild (Hjort and Schreck, 1982). Reisenbichler and McIntyre (1977) found that growth and survival of juvenile steelhead trout to a migratory status is best in wild × wild progeny, intermediate in wild × hatchery progeny, and worst in offspring of hatchery fish. Hatchery practices have significantly altered run timing in coastal steelhead trout (Peterson, 1978).

Hatchery fishes behave differently from those reared in the wild. Their behavioral repertoire is more limited and is disruptive to wild inhabitants (G. Glova, pers. comm.). Territories of resident salmonids may be swamped by introductions of hatchery fish, which forces them to leave preferred microhabitats (Stein et al., 1972).

Impacts of Dams

There are now more than 100 high dams within the Columbia River basin. From the first recorded construction in 1850, numbers of dams grew exponentially through the 1960s. They have primarily had an impact on the system by inundating spawning areas and blocking migration runs. The dams have changed river conditions to increase migration difficulty for anadromous fishes, possibly increase the role of fish disease as a zoogeographic barrier, and favor exotic fishes to the detriment of native fishes.

Dams as Physical Barriers

The demise of the "June Hogs," large chinook salmon that once migrated into the upper basin of the Columbia River, is attributed to the lack of fish ladders at Grand Coulee Dam (Chaney, 1978). More than 50% of the basin is now blocked by dams. Counts at existing fish ladders indicate that white sturgeon appear to be declining in the Snake River system

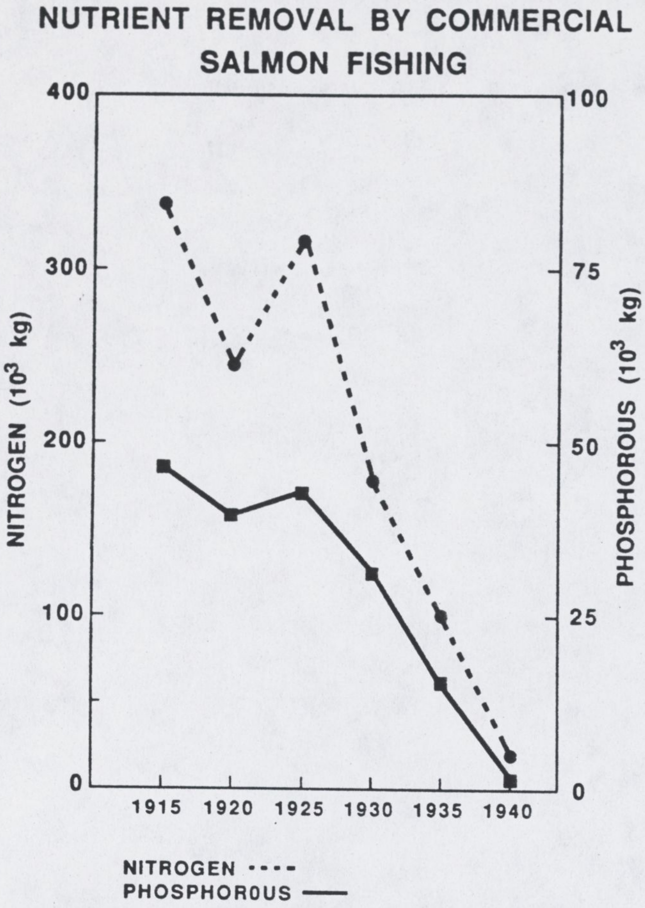

Fig. 24.3. Nutrients removed by commercial harvest of salmonids, 1915–45. Annual harvest by the aboriginal Indian fishery, estimated to be 8 million kg, was discounted (Craig and Hacker, 1940). Conversion values of Bull and Mackay (1976) were used to calculate nitrogen and phosphorus values from biomass of the catch.

(Coon et al., 1977). There are 8,000 to 12,000 white sturgeon between Lower Granite Dam and Hells Canyon Dam, but they are growing slower now than formerly, apparently because new dams are trapping nutrients upstream. Runs of lampreys are declining both in the Sanke Basin and in the mid-Columbia, again presumably because of the dams (Coon et al., 1977; J. Mullan, unpub. data). Splash dams used by the timber industry to store logs for drives downstream blocked substantial amounts of spawning area of coastal streams in Oregon and Washington, estimated to be as much as 60 percent in some areas (Wendler and Deschamps, 1955; Sedell and Luchessa, 1982).

Changes in discharge patterns have changed the timing and increased the duration of migrations by salmonid smolts two- to threefold in the Columbia River system because the fish are no longer aided by the fast currents that were once present (Raymond, 1979). The mortality of juvenile salmonids varies inversely with discharge through each dam: 5% at high levels of spill and 15% at low levels of spill (Northwest Power Planning Council, 1981). During the 1973 drought losses at each dam may have reached 45 percent. Buchanan et al. (1981) suggest that northern squawfish (*Ptychocheilus oregonensis*) may concentrate in large numbers at dams to feed on migrating juvenile salmonids. Gas-bubble diseases are no longer a problem in the Columbia River because corrective "flip-lip" structures have been installed at dams (Raymond, 1979).

Dams and Fish Diseases

Fish diseases have always been a potent force in structuring fish assemblages in the Pacific Northwest. For instance, 14 million fish of three species succumbed to an epizootic of *Flexibacter columnaris* in Klamath Lake, Oregon (Rohovec and Fryer, 1979). Native fishes differ in susceptibility to these diseases because of differential immunity and because the virulence of endemic diseases is temperature-dependent. *Flexibacter columnaris* becomes virulent to salmonids at temperatures above 10° C; however, catostomids and cyprinids are relatively unaffected at temperatures below 20° C (Becker and Fugihara, 1978). Infectious hematopoietic necrosis is responsible for epizootics in sockeye salmon, chinook salmon, and steelhead trout when temperatures rise above 15° C, but coho salmon are immune. *Ceratomyxa shasta* affects various species differently (Sanders et al., 1970). Infected coho salmon show an increasing susceptibility as temperature rises: mortality below 10° C is 2% at most, 22% at 15° C, and 84% at 20.5° C. In contrast, mortality of infected juvenile steelhead trout can be as high as 80% and is independent of temperature.

The distribution of *C. shasta* is well known, and its role as a zoogeographic barrier has been documented (Sanders et al., 1970; Hoffmaster, 1985). Chinook salmon and steelhead trout that evolved in drainages with *Ceratomyxa* are less susceptible than are fishes that evolved in its absence (Zinn et al., 1977; Buchanan et al., 1983). Immunity to some of these diseases has a heritable basis. Suzumoto et al. (1977) and Winter et al. (1980) showed that resistance to bacterial kidney disease is correlatable to the genotype for transferrin in coho salmon. Transferrin may limit endogenous iron by binding it and making it unavailable for bacterial use.

Disease problems may have been exacerbated by the installation of dams on the Columbia River. Becker and Fugihara (1978) concluded that fish ladders were epicenters for epizootic outbreaks of *F. columnaris*. They suggested that relatively unaffected resident species such as that large scale sucker inhabit the fish ladders and disperse spores that infect migrating adult salmonids. Chinook salmon of the summer run are severely infected because of a lack of immunity and because they migrate when water temperature is high and disease most virulent. Spring chinook, in contrast, are relatively unaffected because they migrate when the water is cold.

Ratliff (1983) found that the hypolimnions of reservoirs now harbor dense concentrations of *Ceratomyxa shasta*. Spores from carcasses of infected fish lodge and age in the reservoir mud, becoming infective when temperatures rise. He speculated that diseased carcasses are retained to a greater degree because of dams.

Table 24.1. Classification of Selected Native Freshwater Fishes of the Pacific Northwest According to Hokanson's (1977) Thermal Guilds (Stenotherms, Mesotherms, Eurytherms) and Trophic Guilds, Maximum Mandible Length, Maximum Total Length, and Maximum Age*

Species	Age	Trophic (Primary Prey)								Jaw:TL Ratio	TL (mm)	Jaw (mm)
		S	*M*	*B*	Plt.	Det.	Mic.	Mac.	Fish			
Stenotherms												
Lampetra richardsoni	Ammocoete			*c*	*d*	*X*	*x*					
L. ayresi	Ammocoete			*c*	*d*	*X*	*x*					
Cottus beldingi	4			*c*				x		0.035	60	2.0
C. marginatus	?			*c*				x		0.039	60	2.5
C. bairdi	5			*c*				*x*	YOY	0.029	130	3.7
C. cognatus	4			*c*				*x*	YOY	0.045	80	3.8
C. gulosus	4			*c*				*x*	YOY	0.049	90	4.2
C. confusus	4			*c*				*x*		0.046	100	4.7
C. aleuticus	4			*c*				*a*		0.067	80	5.1
C. rhotheus	6			*c*				*X*	*x*	0.056	150	8.5
Catostomus catostomus	14			*c*	*D*	*x*	*x*	*x*				
C. platyrhynchus	9			*c*	*D*	*x*	*x*	*x*				
Lota lota	10		*c*	*C*				*x*	*X*	0.035	790	27.9
Spirinchus thaleichthys	3		*c*	*C*				*Z*		0.087	110	9.7
Thaleichthys pacificus	4		*c*	*C*				*Z*		0.092	200	18.4
Steelhead	5	*c*	*c*	*C*				*x*		0.072	790	56.7
Steelhead	Juvenile	*c*	*C*	*c*				*x*		0.436	50–130	2.2–5.7
Oncorhynchus nerka	Juvenile	*c*	*C*	*c*				*z*		0.682	50–130	3.1–8.9
Salmo gairdneri	4	*c*	*C*	*c*				*x*		0.081	300	24.7
Salvelinus confluentus	7	*c*	*C*	*c*				*x*	*X*	0.071	720	51.7
O. kisutch	Juvenile	*C*	*c*	*c*				*x*		0.102	50–130	5.1–13.3
O. tshawytscha	Juvenile	*C*	*c*	*c*				*x*		0.110	50–130	5.5–14.2
Salmo clarki clarki	6	*C*	*c*	*c*				*X*	*x*	0.079	430	34.2
Mesotherms												
Cottus perplexus	6			*c*				*A*	*x*	0.040	70	2.8
Novumbra hubbsi	?			*c*				*X*	*x*	0.052	70	3.4
C. asper	7			*c*				*X*	*x*	0.038	130	5.1
Rhinichthys cataractae	5			*c*				*x*		0.033	160	5.2
R. falcatus	5			*c*				*x*		0.051	120	6.2
Percopsis transmontana	?			*c*				*x*	*x*	0.083	80	6.3
Mylocheilus caurinus	9			*c*				*x*	YOY	0.021	340	7.3
Acipenser transmontanus	82			*c*	*x*	*x*	*x*	*X*	*x*	0.038	3660	139.1
A. medirostris	?			*c*	*x*	*x*	*x*	*X*	*x*	0.025	2300	57.5
Catostomus columbianus	17			*c*	*D*			*x*			430	
Lampetra tridentata	Ammocoete			*c*	*x*		*X*	*x*				
Eurytherms												
Rhinichthys osculus	3			*c*				*x*		0.030	70	2.0
Acrocheilus alutaceus	6			*c*	*D*			*x*			300	
Catostomus macrocheilus	11			*c*	*D*	*x*	*x*	*x*			600	
Couesius plumbeus	5		*c*	*C*	*P*			*Z*	*x*	0.037	230	8.3
Ptychocheilus oregonensis	19	*c*	*c*	*C*				*x*	*x*	0.082	740	60.1
Gasterosteus aculeatus		*c*	*C*	*c*				*x*		0.070	80	5.6
Richardsonius balteatus	5	*c*	*C*	*c*				*x*		0.044	180	7.8
Hybopsis crameri	?	*c*	*C*	*c*			*X*			0.034	70	2.3
Gila bicolor	7	*c*	*C*	*c*	*X*		*X*		YOY	0.050	410	20.7

*Age = maximum life span; *S* = surface feeder; *M* = midwater feeder; *B* = bottom feeder; Plt. = plant; Det. = detritus; Mic. = microinvertebrate; Mac = macroinvertebrate; Jaw = maximum mandible length; TL = maximum total length; *c* = location in the water column; *d* = diatom; *x* = feeds on entire array within prey class; YOY = young-of-the-year; *z* = zooplankton; *a* = aquatic insect; *p* = phytoplankton. Capital letters denote dominant mode.

Table 24.2. Classification of Fishes Introduced into the Pacific Northwest According to Hokanson's (1977) Thermal Guilds (Stenotherms, Mesotherms, Eurytherms), Trophic Guilds, and Maximum Mandible Length, Maximum Total Length, and Maximum Age*

Species	Age	Trophic (Primary Prey)								Jaw:TL Ratio	TL (mm)	Jaw (mm)
		S	*M*	*B*	Plt.	Det.	Mic.	Mac.	Fish			
Stenotherms												
Coregonus clupeaformis	10		c	C				X	x	0.018	610	10.8
Salvelinus fontinalis	5	c	C	c				X	x	0.079	410	32.4
Salmo trutta	9	c	C	c				x	x	0.117	550	63.9
Mesotherms												
Stizostedion vitreum vitreum	10		c	C				x	X	0.064	760	48.9
Morone saxatilis	9		C	c					x	0.061	760	46.4
Esox americanus vermiculatus	7		C					x	X	0.075	360	26.8
Perca flavescens	7	c	C	c				Z	x	0.045	330	15.1
Micropterus dolomieui	10	c	c	C				x	x	0.066	470	31.2
Eurytherms												
Noturus gyrinus	2?			C				x		0.106	90	9.4
Ictalurus punctatus	40			C				d	x	0.04	860	15.9
I. nebulosus	7			C	x	x	x	X	x	0.053	360	18.7
Tinca tinca	?			C	x			X		0.036	610	22.0
Ictalurus natalis	5			C	x	x	x	D	x	0.052	430	22.3
I. melas	6			C	x			X		0.074	460	33.7
Cyprinus carpio	15			C	x	x	x	X		0.048	710	33.9
Pylodictus olivaris	19			C				d	X	0.049	1040	50.9
Carrassius auratus	20?		c	C	P	x	x			0.057	250	14.4
Ambloplites rupestris	7		c	C				x	x	0.072	290	21.1
Lepomis gibbosus	6		C	c				X	YOY	0.04	180	7.2
L. cyanellus	7		C	c				x	x	0.071	130	9.1
L. gulosus	7		C	c				X	x	0.071	250	18.1
L. macrochirus	9	c	C	c				Z	YOY	0.045	150	6.9
Pomoxis nigromaculatus	9	c	C	c				z	x	0.481	300	14.4
P. annularis	10	c	C	c				z	x	0.051	330	16.8
Micropterus salmoides	14	c	C	c				x	X	0.071	510	36.3
Gambusia affinis	1.25	C	c					x		0.064	60	4.1

*Age = maximum life span; *S* = surface feeder; *M* = midwater feeder; *B* = bottom feeder; Plt. = plant; Det. = detritus; Mic. = microinvertebrate; Mac. = macroinvertebrate; Jaw = maximum mandible length; TL = maximum total length; *c* = location in the water column; *x* = feeds on entire array within prey class; *d* = diatom; *P* = phytoplankton; YOY = young-of-the-year; *z* = zooplankton. Capital letters denote dominant mode.

Dams and Exotic Species

Dams have created conditions that favor warmwater fishes, largely introduced from the Midwest. This has greatly increased the numbers of piscivorous fishes and greatly increased the risk of predation to the native fauna in the Columbia River. This was judged from an index of predatory capability (Maximum jaw size; tables 24.1, and 24.2) and dietary studies (Wydoski and Whitney, 1979; Hjort et al., 1981; Bennett et al., 1983; Stainbrook, 1982; Gray et al., 1984; Maule and Horton, 1984).

Before the introduction of exotic predators, most predation affected young-of-the-year fishes (fig. 24.4). Bull trout (*Salvelinus confluentus*), cutthroat trout, and burbot (*Lota lota*) are native fishes most able to prey on adult fishes in coldwater streams of the Columbia basin. The northern squawfish was probably the most abundant large predator in warmwater streams, although the omnivorous white sturgeon (*Ascipenser transmontanus*) was and is able to ingest large prey on occasion. Consequently, being a large species served to reduce chances of predation. Fish larger than 200 mm were seldomly preyed on, and most predation pressure was probably exerted on the young-of-the-year.

Food-web patterns changed after the introduction of warmwater game fishes (fig. 24.5). Sculpins, cyprinids, and catostomids are subject to more predation because large size no longer confers immunity from predation. Only the squawfish among the native fauna is known to prey to any extent on exotic fishes, and its diet overlaps substantially with that of exotic species, suggesting that competition for food is possible.

Walleyes (*Stizostedion vitreum vitreum*) have recently invaded the lower Columbia River from the reservoir of Grand Coulee Dam, where they are now extremely abundant (Harper et al., 1980; Hjort et al., 1981; Nigro et al., 1981). Growth rates of walleyes in the mid- and lower Columbia are comparable to the highest published values, suggesting that rapid population growth may soon follow (Maule and Horton, 1985). This fish is a large, schooling predator, unlike any in the native fauna. Its impact on juvenile salmonids

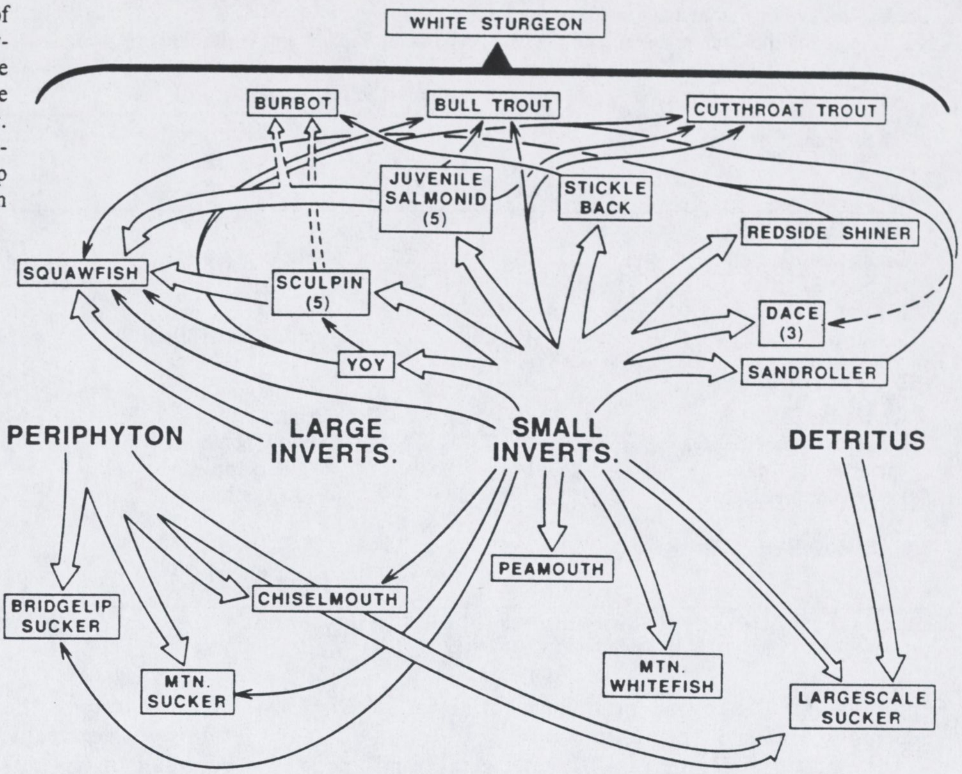

Fig. 24.4. Hypothetical food web of the middle and lower Columbia River before 1800. The width of the trophic link represents the relative importance of prey to the predator. Dashed arrows denote the assumption that burbot preys mostly in deep lakes within the drainage. Sturgeon is capable of eating anything.

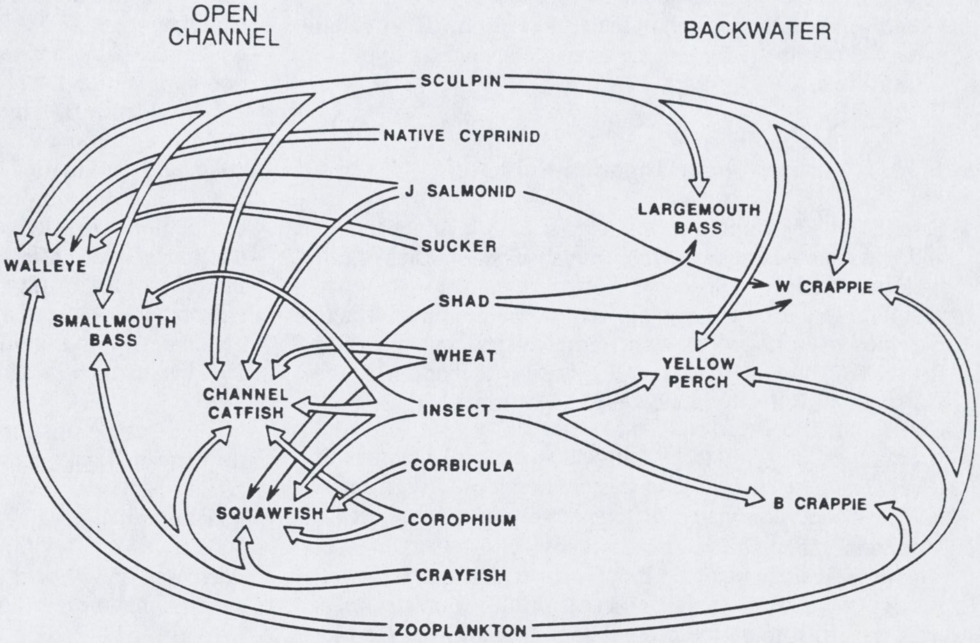

Fig. 24.5. Major changes in the food web of the middle and lower Columbia River ca. 1888–1983.

Table 24.3. Exotic Fishes as a Percent of the Total Catch per Unit Effort (CPUE), as a Fraction of the Total Species Assemblage (No.) Exotics/No. Total), and the Common Name of the Most Abundant Species and Its Ranking of Abundance in the Entire Assemblage (in Parentheses)

Area Sampled*	Seines			Gill Nets		
	Percent Exotics, CPUE	No. Exotics/ Total No.	Highest-ranked Exotic	Percent Exotics, CPUE	No. Exotics/ Total No.	Highest-ranked Exotic
Upper Columbia River						
Grand Coulee Dam	53	7/11	Yellow perch (1)	54	7/15	Walleye (1)
Hanford Reach						
Km 605–13	0	0/9	None	5	1/11	Carp (7)
Km 557–66	< 1	1/9	Yellow perch (9)	6	3/13	Yellow perch (7)
Snake River						
Ice Harbor Dam	65	10/17	Centrarchids (1, 2, 3)	62	7/14	Carp (1)
Lower Monumental Dam	86	7/11	Yellow perch (1)	41	9/17	Carp (2)
Little Goose Dam	63	12/18	White crappie (1)	40	10/20	Yellow perch (2)
Lower Granite Dam	75	5/9	Brown bullhead (1)	24	9/16	Yellow perch (4)
Mainstem Columbia River						
John Day Dam	63	13/27	Black crappie (2)	36	11/23	Yellow perch (1)

Sources: Gray and Dauble (1977), Harper et al. (1980), Hjort et al. (1981), Nigro et al. (1981), Bennett et al. (1983).
*All areas except those in the Hanford Reach are reservoirs.

could be great because of the potential for density-depensatory predator-prey interactions.

The impact of dam-related habitat changes and exotic introductions on fish assemblages of the Columbia Basin is shown in table 24.3. Note the difference between the reservoir assemblages and that of the Hanford Reach, the last free-flowing reach above Bonneville and below Priest Rapids Dams. Few exotics inhabit the Hanford Reach, a seminatural stretch of the Columbia River. However, exotic species have become dominant elements in reservoir assemblages. For example, walleye and yellow perch were twice as numerous as the next most abundant species in gill-net catches and seine hauls at Grand Coulee Reservoir. The overall pattern is that the fish fauna now resembles faunas found in the Midwest.

Impacts on Riparian Habitats

Essentially, the impact of logging, stream channelization, and grazing are similar. As the watershed becomes physically less complex, it loses its buffering capacity to retain runoff, trap and retain organic and inorganic material, and provide cover to protect fish from physical injury during floods (Bustard and Narver, 1975a, b; Tschaplinski and Hartman, 1983; Rodnick, 1983; Bottom et al., 1985; Cederholm and Peterson, 1985).

Stands of old-growth (450–to–500-year-old) Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) once dominated watersheds west of the Cascade Mountains, shaping stream morphology and development as well as influencing trophic input: primary productivity versus organic detritus (Swanson et al., 1982). Forestry practices have disrupted these regulatory processes of the old-growth conifer forest and have simplified the physical structure of watershed by changing the amount of large woody debris in streams. Beaver dams function like large woody debris in watersheds and are important in creating habitats for coho salmon (Everest and Sedell, 1983). They act as retention devices and receive nutrient input from the beavers but do not impede fish movement during high flows (C. Dahm and J. Sedell, in prep.). Destruction of beaver dams is one of the reasons why habitat for coho is now more limited in coastal streams of Oregon (Bottom et al., 1985).

Removal of the forest canopy by logging can influence changes in the faunal assemblage through temperature-mediated effects on competitive ability and differential disease resistance of various species. Reeves (1985) found that at temperatures of 19–22° C redside shiners (*Richardsonius balteatus*) displace juvenile steelhead trout through exploitation competition for food resources: at temperatures of 12–15° C juvenile steelhead trout dominate redside shiners through aggressive challenges. Infection from *Flexibacter columnaris* led to high mortality among the less competitive species at those temperature ranges; however, the dominant competitor was relatively unaffected. In contrast, the production of aquatic insects and cutthroat trout dramatically increases as a result of the increase in sunlight entering stream reaches affected by clear-cut timber harvests in smaller, colder, higher-gradient streams (Hawkins et al., 1982; Hawkins et al., 1983; Murphy and Hall, 1981; Murphy et al., 1981).

Overgrazing riparian vegetation in the dry interior east of the Cascade Range causes higher water temperatures, greater stream-bank erosion, loss of spawning habitat, and deleterious changes in stream-channel structure (Hall and Baker, 1982; Bottom et al., 1985). Porosity of the soils decrease, and stream banks slump because of trampling; streams may become intermittent because of these changes (Winegar, 1977).

Bank-stablization practices reduce the amount of riparian vegetation, especially large trees. It causes another negative

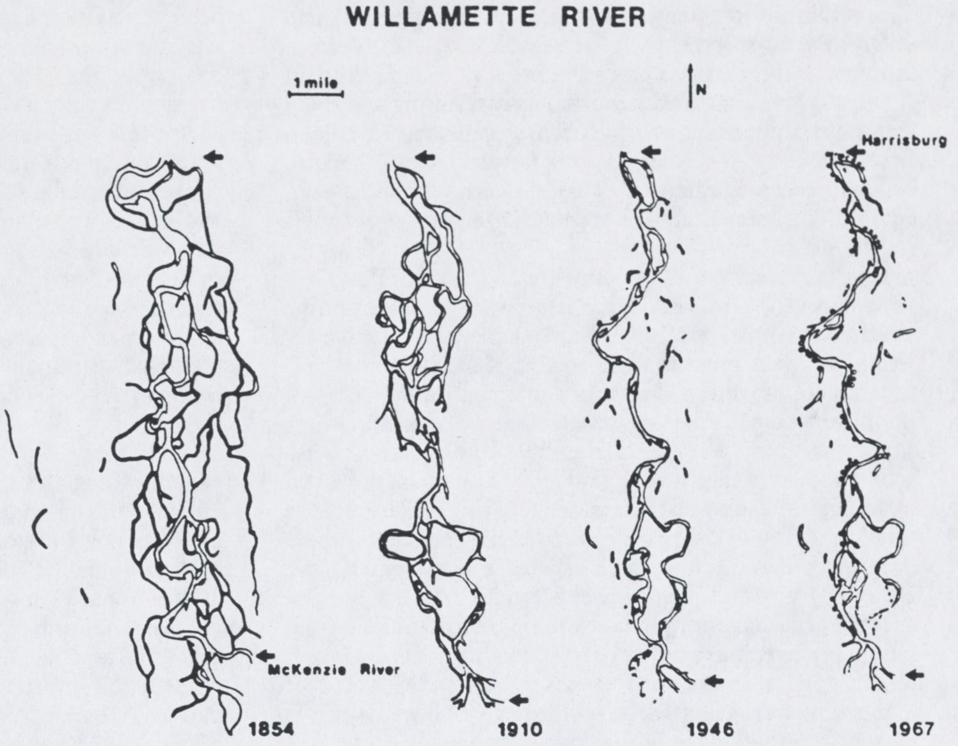

Fig. 24.6. Changes in the Willamette River floodplain caused by revetments. Open circles along the 1967 river channel indicate location of revetments.

impact: the hydraulic energy is redirected from lateral scour to downcutting. Since the first installation of a revetment in the Willamette River in 1888, there has been a tremendous loss of secondary side channels, backwaters, and oxbows (fig. 24.6)—important habitat for juvenile salmonids and the Oregon chub (*Hybopsis crameri*), a species now uncommon in the Willamette drainage. Revetments are poor habitat for most larval and postlarval fishes (Li et al., 1984). Five specimens appear to benefit from revetments: prickly sculpin (*Cottus asper*), redside shiners, northern squawfish, largescale suckers, and chiselmouths (Hjort et al., 1984; Li et al., 1984). The first three of these species are attracted by high densities of invertebrate prey living in the interstices. Chiselmouths and a largescale suckers graze on diatoms, and stone revetments provide good substrate for periphyton.

Discussion

The fauna of the Pacific Northwest was probably adapted to invade and exploit new or recently disturbed environments. Massive tectonic movements, volcanic eruptions, huge landslides (up to 5.4 km^2), large-scale glacial movement, and massive floods shaped several basins. This was especially characteristic of the Columbia basin, where some of the largest floods on record have occurred. It is estimated that 6 to 40 floods caused by the fracturing of ice dams occurred during a period 19,000–12,000 years ago. Each flood released an estimated 22 km^3 of water at a rate of 2.3 km^3/h for 40 h (Spranger, 1984). This may explain why much of the fish fauna is either anadromous or euryhaline. The ability to recolonize was clearly important. These events suggest that we should expect a fauna that has evolved primarily in response to physical gradients rather than to biological interactions. However, biological interactions are important in patterns of interactive segregation among salmonids and sculpins, and diseases can influence community assemblages. Certain disturbances have predictable outcomes. For example, a characteristic fauna results from the installation of stone revetments. It is evident, therefore, that both stochastic and deterministic forces shape the stream assemblages of Pacific Northwest streams, but their relative roles are unknown.

The streams of the Pacific Northwest, especially streams of the Columbia basin, operate very differently now from the way they once did because of all the man-made disturbances. Many of these perturbations caused secondary impacts (e.g., dams and fish disease, dams and exotic species). These disturbances have affected the fauna basinwide. Commercial fishing with gill nets at the mouth of the Columbia River affected nutrient inputs to oligotrophic streams of the upper basin. Logging of the upper watershed effected changes in species composition by limiting recruitment of young. This means that a basinwide perspective is needed to understand assemblage structure of this region. It also means that one must be very cautious about extrapolating present species assemblages to issues concerning regulation of assemblage or community structures.

Biological communities respond to disturbance as resetting mechanisms. Wiens (1984) suggests that the frequency of disturbances shapes the characteristics of natural communities so that they can be aligned on an equilibriumnonequilibrium gradient. If disturbances are frequent and severe, the environment will be unsaturated, and therefore biological interactions may be relatively insignificant (Wiens, 1984). Biased conclusions may result from a study that uses stability measures in stream systems from the Pacific Northwest. A species assemblage that may otherwise behave like an equilibrium community may mimic a nonequililbrium community as it responds to anthropogenic perturbations.

It is inappropriate to use time-series data from a single stream, even a relatively undisturbed one, to examine whether or not fish assemblages are stable in Pacific Northwest streams. A substantial proportion of the fauna is migratory, inhabiting different parts of a drainage during different life-history stages. The presence or absence of a species in a single stream may not be due entirely to physiological responses to shifting physical gradients but may be governed by biological events elsewhere in the basin. For example, a small year class of fish may be decimated by predators before it migrates into the study area. A species may spawn in an ecologically similar stream lower in the drainage that its natal stream because an oxygen block to migration resulted from failure of an overtaxed sewage treatment plant at the time of migration. The absence of a species is therefore an artifact of man's activities. When fish assemblages are viewed from the perspective of drainages rather than stream reaches, patterns appear less random because a reach is more homogeneous physically than are streams of different orders within a watershed. Large physical gradients between stream orders separate those fishes specialized for headwater environments from those better adapted for larger streams (see Matthews, chap. 14). Habitat use by stream fishes at the reach level may be plastic and dependent on spatiotemporal variability in habitat availability, which suggests that habitat electivity studies are needed (Angermier, chap. 7).

Connell and Sousa (1983) recommend a minimum time of one generation needed for stability analyses of populations. It is more difficult to choose a time span for communities. Should the generation time of the longest-lived species, such as the white sturgeon, be chosen? Should it be the life span of chinook salmon, the dominant species in the basin? Perhaps the time scale for the entire stream community should be adjusted to successional patterns of riparian vegetation, because the stream and its valley are an ecological unit (Hynes, 1975). Minimally, the time scale may be in the order of decades before noticeable recovery from anthropogenic disturbance is observed. Two examples follow: Dramatic improvement of habitat and shifts in species composition have been noticed in stream reaches of eastern Oregon 10 years after the use of fencing to limit cattle grazing near stream banks (see Hall and Baker, 1982). The riparian vegetation has not yet fully matured, and further changes can be expected following this time period. Native fishes now inhabit portions of the Willamette River not inhabited 35 years ago because minimum standards for dissolved oxygen were set in 1947, and the river has recovered from pollution from domestic and industrial sources (Hjort et al., 1984).

Can one determine how assemblages or communities are regulated in the Pacific Northwest? We think so, but it will require many approaches because of the problems outlined previously. It should be obvious that a historical perspective is important to the understanding of stream systems. We need to reconstruct, at least in part, how the system evolved. Mayden (chap. 26) argues persuasively that one needs to examine the zoogeographical record before interpreting present-day distributional patterns of the fauna. We need to establish how the stream systems we are studying have been affected by man (Sedell and Luchessa, 1982; Minshall et al., 1985). Some of this can be done through examination of historical records (past and present comparisons), while effects of other alterations can be examined through appropriate field comparisons. Biologists in the Pacific Northwest can use management agency experiments in stream rehabilitation as an approach to study factors affecting stream assemblages. Long-term surveys carefully designed along appropriate spatial and temporal scales will always be important, but studies that incorporate analyses of morphological and physiological limitations will provide a useful framework for generating null hypotheses concerning the influence of biological interactions on assemblage structure (see Matthews, chap. 14). Appropriate experiments that address the effects of biological processes on community structure should then be applied to test these hypotheses. Biological interactions are often limited to studies of predation and competition; the impacts of diseases, parasites, and symbionts are often overlooked. Stream systems from various regions may operate differently because they are on different evolutionary paths, and we must be cautious about generalizing findings from a particular system to all streams.[1]

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Long term persistence in a rocky intertidal fish assemblage

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Keywords: Community structure, Assemblage persistence, Deterministic systems, Equilibrium systems

Synopsis

A rocky intertidal fish assemblage at Dillon Beach, CA was persistent over 42 months. This time period represents greater than one mean generation time for residents. This result confirms an earlier conclusion of deterministic regulation based on 29 months of study. Additional work suggests that food resource partitioning is the organizational mechanism present in this assemblage. A correlation analysis of mean species ranks from collections where specimens were removed from the site, with those from collections where specimens were returned alive, exhibited a highly significant positive correlation ($r_s = 0.883$, $p<0.005$). Thus assemblage structure apparently was unaffected by collecting; validating previous conclusions based on control site-study site comparisons.

Introduction

The identification of factors affecting assemblage organization in fishes has been a topic of interest for the past decade (Grossman 1982, Grossman et al. 1982, 1985, Sale 1984, Werner 1984). Although disagreement exists over the types and frequencies of processes responsible for assemblage organization, most investigators agree that long-term studies are necessary for the resolution of these issues. This brief communication presents data from the final 13 months of a study of assemblage organization on rocky intertidal fishes (Grossman 1982) and extends the previous finding of persistence from 29 to 42 months.

Methods

A team made 18 collections between January 1979 and June 1982 in a 30 m by 19 m mid- to lower rocky intertidal area at Dillon Beach, CA. This time period most likely represented greater than one mean generation time for assemblage residents (Grossman 1982). The site was of sufficient size to encompass home ranges of assemblage residents (Grossman 1982). During the first 29 months of the study, sampling involved the removal of all individuals from the study site whereas during the last 13 months, all specimens were returned alive to the site (with the exception of the July 1981 sample in which all individuals were retained). This represented an attempt to ascertain the effects of sampling on assemblage persistence. Previous comparisons between control and study sites, however, indicated that collecting did not exert a strong effect on assemblage structure (Grossman 1982). The experimental design and statistical techniques used were those of Grossman (1982) and Grossman et al. (1982) where a complete methodological description is presented. Herbold (1984), Rahel et al. (1984), and Yant et al. (1984) have criticized the approach of Grossman (1982) and Grossman et al. (1982), and these criticisms have been addressed in Grossman et al. (1985).

Results

A comparison of average species ranks from collections where individuals were removed (January 1979–February 1981, July 1981) with those from collections where specimens were returned (May 1981, October 1981–June 1982) yielded a highly significant positive correlation ($r_s = 0.883$, $p < 0.005$, $n = 9$). This indicated that collecting did not have a strong effect on assemblage structure; supporting earlier findings based on multiple control-study site comparisons (Grossman 1982).

The ranks of assemblage residents were highly concordant over the 42 months of the study (Table 1, $W = 0.621$, $p \ll 0.001$). The following values for W were obtained by sequentially deleting the stablest species: $W = 0.471$, $p \ll 0.001$ (*O. snyderi* deleted), $W = 0.324$, $p \ll 0.001$ (*O. snyderi* and *Sc. marmoratus* deleted), and $W = 0.274$, $p < 0.001$ (*O. snyderi, Sc. marmoratus* and *H. decagrammos*). Although statistically significant, these values were somewhat low. A lower level of concordance is to be expected, however, when sampling involves the removal of specimens from the study site. Nonetheless, the results indicate that assemblage structure was persistent and probably ordered through deterministic processes (Grossman 1982, 1985).

Discussion

A variety of mechanisms are capable of facilitating coexistence within first assemblages. For example, environmental disturbances can cause catastrophic mortality which prevents resource limitation and competition from occurring (Grossman et al. 1982). Environmental disturbance did not appear to be an important factor at Dillon Beach because this assemblage was persistent over a 42-month period (also see Grossman 1982, 1985). This persistence implies that assemblage structure probably is organized through some interactive mechanism. Previous work suggests that food limitation may exist in this system (Grossman 1982, Grossman & deVlaming 1984, Freeman et al. 1985). A 2.5 year study of food resource utilization in this assemblage demonstrated that intraspecific dietary overlap was high and stable, both between seasons and among years (Grossman 1985). In spite of little evidence of differential food availability, interspecific dietary overlap was low and stable, both between seasons and among years. These data strongly suggest that coexistence in this assemblage can be attributed to food resource partitioning (for a complete presentation of this argument see Grossman 1985). The results presented in this note support the findings of persistence and resilience observed during the initial 29 months of the study (Grossman 1982). Additional long term studies of persistence, resource utilization, and resource limitation in rocky intertidal fish assemblages will be necessary to determine the generality of these findings.

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Table 1. Stability analysis for the Dillon Beach intertidal fish assemblage. Data are the rank of species abundance and percent of the resident assemblage comprised by each

Table 1. Stability analysis for the Dillon Beach intertidal fish assemblage. Data are the rank of species abundance and percent of the resident assemblage comprised by each species (in parentheses).

Species	1/79	5/79	6/79	7/79	8/79	11/79	12/79	3/80	4/80	6/80	11/80	2/81	5/81	7/81	10/81	1/82	4/82	6/82
Oligocottus snyderi	1 (.50)	1 (.42)	1 (.39)	1 (.45)	1 (.80)	2 (.27)	1(.41)	1 (.36)	2(.23)	1 (.40)	1(.32)	1 (.41)	1(.40)	1 (.65)	1(.71)	1 (.89)	1 (.42)	1(.59)
Scorpaenichthys marmoratus	3 (.14)	3 (.13)	2 (.18)	2 (.13)	2 (.05)	3 (.20)	3(.20)	4 (.13)	4(.19)	3 (.17)	3(.13)	3 (.07)	3(.06)	4 (.03)	2(.11)	2 (.07)	2 (.27)	3(.10)
Apodichthys flavidus	6.5(.01)	7.5(.04)	8 (.03)	3 (.11)	5 (.03)	4 (.07)	4(.09)	3 (.14)	1(.31)	2 (.25)	2(.14)	2 (.17)	2(.28)	2 (.25)	4(.04)	3.5(.02)	3 (.17)	2(.15)
Sebastes rastrelliger	6.5(.01)	4 (.07)	4.5(.08)	5.5(0.5)	9 (.*)	1 (.36)	2(.24)	2 (.24)	3(.22)	4 (.08)	5(.07)	4 (.06)	5(.03)	6 (.*)	4(.04)	7 (.00)	7.5(.01)	5(.04)
Gibbonsia metzi	2 (.18)	2 (.15)	6 (.07)	5.5(.05)	4 (.03)	6.5(.03)	5(.04)	7.5(.01)	7(.01)	6 (.03)	4(.08)	5.5(.04)	4(.04)	7 (.*)	8(.01)	7 (.00)	7.5(.01)	4(.04)
Artedius lateralis	4 (.11)	5 (.06)	7 (.05)	8 (.03)	7.5(.01)	6.5(.03)	7(.01)	6 (.05)	7(.01)	8.5(.01)	7(.03)	5.5(.04)	7(.01)	5 (.01)	6(.03)	3.5(.02)	5 (.05)	9(.01)
Clinocottus globiceps	8.5(.00)	6 (.05)	3 (.09)	4 (.10)	3 (.04)	9 (.01)	7(.01)	9 (.00)	9(.00)	8.5(.01)	6(.04)	7 (.03)	6(.02)	3 (.06)	4(.04)	7 (.00)	6 (.02)	7(.02)
Clinoccottus analis	8.5(.00)	9 (.03)	4.5(.08)	7 (.04)	6 (.02)	8 (.02)	7(.01)	5 (.07)	7(.01)	5 (.05)	9(.00)	9 (.00)	8(.*)	8.5(.00)	7(.02)	7 (.00)	4 (.05)	8(.02)
Hexagrammos decagrammos	5 (.05)	7.5(.04)	9 (.03)	9 (.03)	7.5(.01)	5 (.03)	9(.00)	7.5(0.1)	5(.01)	7 (.01)	8(.01)	8 (.02)	9(.00)	8.5(.00)	9(.00)	7 (.00)	9 (.00)	6(.03)
Total numerical abundance	66	112	152	320	324	117	152	88	132	246	205	134	294	516	196	51	145	515
% of total community comprised by residents	0.93	0.89	0.57	0.61	0.90	0.89	0.93	0.92	0.88	0.74	0.82	0.84	0.83	0.87	0.94	0.88	0.91	0.44 $\bar{X}=$ 0.82

$W = 0.621$ df $= 9{,}18$ $p \ll 0.001$

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