

Resident Fish Assemblages in Shallow Shorelines of a Columbia River Impoundment

Abstract

During May-September 1995, we replicated an earlier (1984-85) study of fishes in shoreline habitats of the John Day Reservoir, Columbia River, to investigate fish assemblage structure at several spatial and temporal scales. A total of 37,400 resident fishes representing 24 taxa was collected in 359 beach seine hauls. Fish catch composition during 1984 and 1985 was very similar, but was greatly different from catch in 1995. During 1984-1985, four native taxa (chiselmouth, northern pikeminnow, suckers, and sand rollers) constituted more than 90% of the combined main-channel catch, with introduced taxa comprising only 1.3% of the main-channel catch. In contrast, during 1995 only 37.7% of the main-channel catch comprised chiselmouth, northern pikeminnow, suckers, and sand rollers, while 33.9% were introduced taxa, primarily sunfishes and yellow perch. This shift in catch composition was greatest in the lower reservoir where the 1995 catch was 61% introduced taxa. Although changes in species composition of near-shore reservoir fish assemblages over the 10-yr period appeared to be substantial, we are unsure of annual variability since we have only one season of sampling for comparison with the earlier study. The differences we observed could be a long-term response to reservoir aging, a short-term reaction to annual differences in hydrologic and thermal regimes, or simply the naturally varying reproductive success of some species.

Introduction

Fish assemblages in the Columbia River Basin were historically dominated by salmonids and cottids, which were 39-50% and 20-30% of the fishes collected in Oregon streams and rivers from 1900 to the mid-1940s (Li et al. 1987). In the past century, however, aquatic environments have been greatly altered by land-use practices such as farming, timber harvesting, and hydroelectric development (Lichatowich 1999). In the United States portion of the Columbia River Basin for example, 11 large hydroelectric dams were constructed between 1933 and 1968 (Ebel et al. 1989), creating reservoirs where the average water velocity is lower, water temperature increases earlier in the season and remains high longer into the fall (Quinn and Adams 1996), and fine sediments have accumulated behind dams, thus changing substrate composition. Concurrent with these changes in aquatic habitats, introduced non-native warmwater and coolwater fishes, such as centrarchids and percids, have proliferated (Li et al. 1987, Poe et al. 1994).

Despite these large-scale changes in basin aquatic habitats and biotic assemblages, few multi-taxa accounts of resident fishes (non-anadromous) in main-stem impoundments exist. Li et al. (1987) and Poe et al. (1994) provide descriptive accounts of historic and recent fish assemblages, with some data on temperature preferences and trophic relationships. Gray and Dauble (1977) estimated the relative abundance of fishes in the unimpounded Hanford Reach of the Columbia River. Species lists with abundance data are available for some reservoirs in agency reports (Nigro 1988). Research in the basin has primarily focused on salmonids and white sturgeon (*Acipenser transmontanus*), with some studies on predators of juvenile salmonids such as northern pikeminnow (*Ptychocheilus oregonensis*) and smallmouth bass (*Micropterus dolomieu*).

Identifying the composition and dynamics of reservoir fish assemblages is important to fishery managers who must develop strategies for recovering endangered species, but still allow for sport, tribal, and commercial fisheries along with other competing uses of waterways in the basin. Management agencies within the Pacific Northwest are currently considering several changes to the hydrosystem and its operation (e.g., dam breaching, reservoir drawdowns, seasonal water budgeting) and to fishery management strategies (e.g., liberalized harvest of introduced taxa) in

¹Current address: Tribal Fisheries, Confederated Salish and Kootenai Tribes, Box 278, Pablo, MT 59855

²Author to whom correspondence should be addressed. E-mail: dena_gadomski@usgs.gov

an attempt to recover severely depressed salmonid populations. These proposed management actions could greatly alter the habitat and fish species composition of impounded reaches.

The objective of this study was to examine the temporal and spatial composition of shoreline fish assemblages in John Day Reservoir, the largest impoundment (123 km in length) on the lower Columbia River (Figure 1). Shorelines are important habitats for all life stages of resident fishes, often providing shelter and abundant food resources. However, shallow shoreline habitats may be particularly vulnerable to hydrosystem operations, and changes in water levels and flows that result in altered environmental conditions may subsequently cause changes in fish assemblages. We determined if changes in fish assemblage structure have occurred in John Day Reservoir, which was impounded in 1968, by examining fish composition in four main-channel locations and two backwater areas at three temporal scales: within-year (spring compared to summer), annual (1984 compared to 1985), and over a long time interval

(1984-1985 compared to 1995). Changes in fish assemblages over time were additionally determined at two spatial scales. We examined the six John Day Reservoir locations individually, and also pooled sites by either main-channel or backwater area.

Methods

Study Area and Field Methods

During 1995 we replicated an earlier (1984-1985) study (Gray et al. 1984, Palmer et al. 1986) of resident fish assemblages in shoreline areas of the John Day Reservoir. The upper third of the reservoir contains extensive shallow-water habitat in main-channel and backwater areas. Farther downriver, banks become steep-sided with limited shallow-littoral habitat. Substrate is mud, sand, gravel, and cobble (Parsley et al. 1993). Dominant substrates at the sample sites ranged from fine sediment to cobble. Growths of aquatic macrophytes, primarily water milfoil (*Myriophyllum* spp.), are seasonally abundant in littoral areas, particularly in shallow embayments and backwater habitats.

We sampled fishes with a beach seine at four shoreline sites at each of four main-channel locations: the tailrace, forebay, and the upper and lower pool (pool is defined as the area of the reservoir excluding the tailrace and forebay); and in two backwaters: Plymouth and Paterson sloughs (Figure 1). This typically resulted in 24 beach seine hauls per sampling period, with the four sites at each location considered a sample. In 1984 and 1985, fish samples were collected on a monthly basis from April through August (except July) at each of the six study locations. In 1995 we sampled on a biweekly schedule from May through August. During late June through August of 1995, we were unable to sample at any site in the Paterson Slough backwater location because of water milfoil abundance.

Fish samples were collected at night using 30.5 x 2.4 m beach seines with a 2.4 m² central bag and 6.4-mm knotless nylon mesh. Leads (15.2 m) and weighted brails were attached to both ends of the seine. To conduct a seine haul, one end of the seine was anchored to the shoreline by attaching the lead to streamside vegetation or to a metal stake driven into the ground, and the opposite lead was attached to a cleat on the bow of a

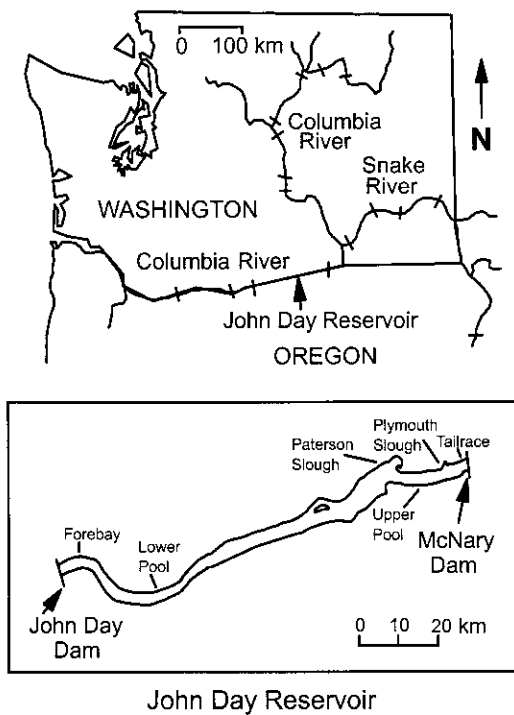


Figure 1. Beach seine sample sites in the John Day Reservoir, Columbia River. Fishes were sampled at six major locations in the reservoir.

boat. The seine was deployed by backing the boat in a semicircle until water depth was insufficient for boat operation; the seine was then manually pulled to shore using the lead ropes. This method of sampling is not without biases, i.e., capture efficiency can be influenced by the habitat types being sampled, and by size- and species-specific behavioral differences. We attempted to minimize or maintain the consistency of these problems by sampling only at night, by restricting the size of the fish included in the analyses, and by sampling at the same sites across years with generally equal effort among locations within a year.

For comparison with the 1984-85 data sets (Gray et al. 1984, Palmer et al. 1986), only fish 250 mm or less in fork length were retained. These were measured to the nearest mm and identified to the lowest possible taxon. Most fishes were released after sampling, however, large catches of small fish were preserved in 10% formalin and returned to the laboratory for processing. Some suckers (*Catostomus* spp.), bullheads (*Ameiurus* spp.), sculpins (*Cottus* spp.), and sunfishes (*Lepomis* spp. and *Pomoxis* spp.) were inconsistently identified to species between the two study periods. Because of this, these fishes were grouped into their respective genera for analysis (Table 1).

To describe environmental conditions during each season, we obtained daily discharge and temperature information from StreamNet (2001).

Data Analysis

We examined the similarity of resident fish assemblages at various temporal scales by calculating Spearman's rank correlation coefficients (r_s) on the ordered abundances of the most commonly collected fish taxa. The anadromous fishes American shad (*Alosa sapidissima*) and juvenile salmonids (*Oncorhynchus* spp.) were not included in these analyses because of large temporal variations in abundance. Rank correlation analyses are commonly used to assess temporal concordance of fish assemblages (Ross et al. 1985, Bass 1990). However, the use of such analyses has been questioned because the strength of the association and the significance of the test can be influenced by including large numbers of rare species. Since all species are equally important in the analysis, small changes in the rank orders of uncommon species could outweigh relatively large changes in the ranks of more abundant species (Grossman

et al. 1982). Thus, we restricted our analyses to the 10 overall most abundant taxa for the sample periods being compared. Since this restriction always retained an average abundance of at least 90% of the fishes collected, the analyses still included those taxa that were the most important in the assemblage structure (Matthews et al. 1988).

We examined seasonal, annual, and long-term continuity of assemblage structure. Seasonal continuity was assessed by comparing spring (April-May in 1984 and 1985; May in 1995) with summer (June and August in 1984 and 1985; June-August in 1995) catches to determine if temporal changes in fish habitat use or an increased abundance of young-of-the-year fishes in the summer caused large shifts in the rank orders of the most common taxa. Annual assemblage continuity was examined by comparing 1984 taxa ranks to 1985 ranks, and long-term continuity was assessed by comparing the ranks of the pooled 1984-85 catches to the 1995 taxa ranks. Seasonal and annual assemblage changes were compared at each of the six sample locations of the reservoir, while long-term changes were only examined at main-channel locations because of some backwater sample site differences in 1995. Changes in assemblage structure were also examined at larger spatial scales by comparing catches pooled across all main-channel locations of the reservoir and by comparing catches pooled across both backwater locations.

We also examined assemblage similarities using Schoener's (1968) proportional similarity index (PSI) (Meffe and Sheldon 1990). The index varies from zero to one, with a value of zero indicating no similarity. Indices are not statistical tests, but they do provide a relative assessment of assemblage similarity (Matthews et al. 1988, Meffe and Sheldon 1990). In addition, PSI values, unlike rank order analyses, may not be as sensitive to the inclusion of rare taxa in the calculations. Thus, we computed PSI values on the entire taxa list for each of the periods being compared.

We used principal components analysis (PCA) to identify fish taxa associations and to assess assemblage composition in time and space (Rose and Echelle 1981, Moyle et al. 1986, Finger and Stewart 1987, Ross et al. 1987, Meng et al. 1994, Mahon et al. 1998, Hoff and Bronte 1999). The PCA was conducted on a correlation matrix of the 10 overall most abundant taxa; these made

up an average of $\approx 97\%$ of the reservoir-wide annual catch and excluded those taxa that generally made up $< 1\%$ of the total annual catch. We first averaged the individual seine haul data by month for each of the six locations. Input data were the arcsine-square root transformed proportions of each taxon for each year-month-location combination (3 yr x 4 mo x 6 locations). Samples were not available for the forebay and lower pool locations during April 1984, or for the Paterson Slough location during July and August 1995; thus, the PCA was conducted on 68 monthly samples. Fish taxa associations were identified by plotting taxa loadings on the first and second principal components (PC) (Carpenter et al. 1981). We then graphically examined temporal and spatial relations of catches at the sample locations by plotting the scores of each year-month-location combination on the first two principal components (Finger and Stewart 1987, Ross et al. 1987).

Results

Overview of Resident Fish Catch

During the 3 yrs of sampling (1984, 1985, 1995), 37,400 resident fishes representing 9 families and 24 taxa were collected in 359 seine hauls. Although young age classes were important in the catch, length frequency information for the 10 overall (pooled across years and locations) most abundant taxa indicated that most species were represented by two or more year classes. The exception to this was smallmouth bass, which were almost all age-0 individuals (Figure 2). Of the 24 resident fish taxa collected, 13 species were introduced (Table 1). The same taxa were collected in all years, except goldfish (*Carassius auratus*) was absent in 1985, and speckled dace (*Rhinichthys osculus*), an uncommon species in 1984-1985, was not collected in 1995.

Native fishes dominated the combined main-channel catches in all 3 yrs, but to a much lesser extent in 1995 (Table 2). In the earlier sampling period (1984-1985) four native taxa (chiselmouth, northern pikeminnow, suckers, and sand rollers) constituted more than 90% of the combined main-channel catch, with introduced taxa comprising only 1.3% of the catch. In contrast, during 1995 only 37.7% of the main-channel catch comprised chiselmouth, northern pikeminnow, suckers, and sand rollers, while introduced taxa made up 33.9% of the catch. The greater percentage of introduced

TABLE 1. Scientific and common names of resident fishes collected by beach seining in the John Day Reservoir, Columbia River, during 1984, 1985, and 1995. ^a = Introduced species.

Scientific name	Common name
Cyprinidae	Carps and minnows
<i>Acrocheilus alutaceus</i>	Chiselmouth
<i>Carassius auratus</i>	Goldfish ^a
<i>Cyprinus carpio</i>	Common carp ^a
<i>Mylocheilus caurinus</i>	Peamouth
<i>Ptychocheilus oregonensis</i>	Northern pikeminnow
<i>Rhinichthys osculus</i>	Speckled dace
<i>Richardsonius balteatus</i>	Redside shiner
Catostomidae	Suckers
<i>Catostomus columbianus</i>	Bridgelp sucker
<i>Catostomus macrocheilus</i>	Largescale sucker
Ictaluridae	Bullhead catfishes
<i>Ameiurus natalis</i>	Yellow bullhead ^a
<i>Ameiurus nebulosus</i>	Brown bullhead ^a
<i>Ictalurus punctatus</i>	Channel catfish ^a
Salmonidae	Trouts
<i>Prosopium williamsoni</i>	Mountain whitefish
Percopsidae	Trout-perches
<i>Percopsis transmontana</i>	Sand roller
Gasterosteidae	Sticklebacks
<i>Gasterosteus aculeatus</i>	Threespine stickleback
Cottidae	Sculpins
<i>Cottus</i> spp.	Sculpin spp.
Centrarchidae	Sunfishes
<i>Lepomis gibbosus</i>	Pumpkinseed ^a
<i>Lepomis macrochirus</i>	Bluegill ^a
<i>Micropterus dolomieu</i>	Smallmouth bass ^a
<i>Micropterus salmoides</i>	Largemouth bass ^a
<i>Pomoxis annularis</i>	White crappie ^a
<i>Pomoxis nigromaculatus</i>	Black crappie ^a
Percidae	Perches
<i>Perca flavescens</i>	Yellow perch ^a
<i>Stizostedion vitreum vitreum</i>	Walleye ^a

fish in the 1995 catch was primarily due to an increase in the relative abundance of sunfishes and yellow perch. In pooled backwater catches, the percentage of introduced fishes remained similar between the earlier sampling period (28.4%) and 1995 (33.6%). The dominant introduced taxa, however, differed between periods, with crappies dominating backwater catches in the earlier period, and yellow perch dominating in 1995.

General patterns of assemblage composition also varied among individual sample locations. In all years, fish abundance and species richness were highest at Plymouth Slough, and lowest at the forebay location, which was characterized by catches of only a few numerically dominant taxa.

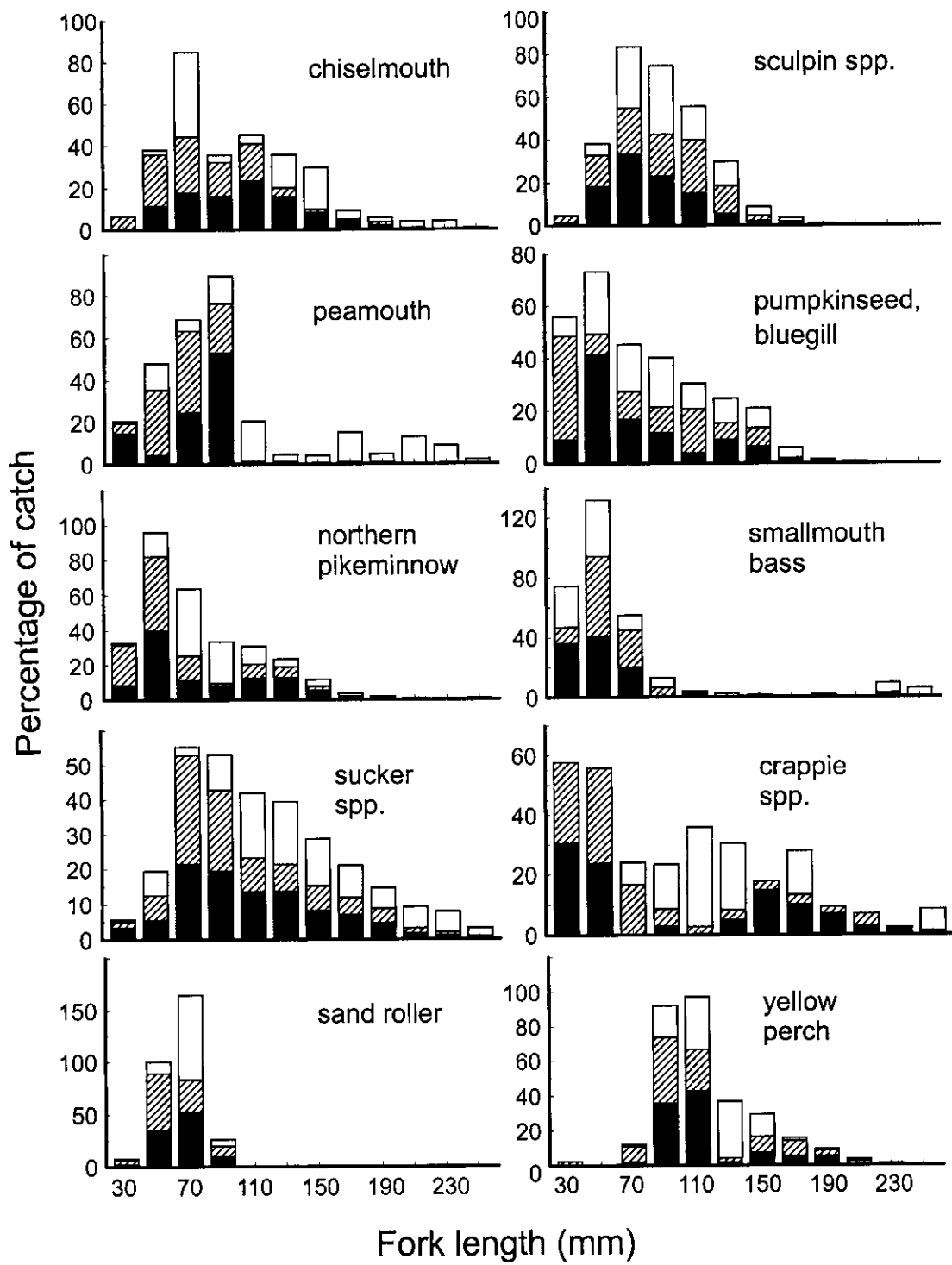


Figure 2. Length-frequency distributions of the 10 most abundant taxa collected by beach seining during May-September 1984 (black), 1985 (lines), and 1995 (white).

TABLE 2. Percent (%) composition of the 10 overall most abundant taxa collected by beach seining in the John Day Reservoir, Columbia River, during May-September 1984-1985 and 1995 in main-channel (MC) and backwater (BW) locations. Numbers of fish are sums of the 10 most abundant taxa only. CPUE=catch per unit effort. † = Introduced species.

	1984-1985		1995	
	MC	BW	MC	BW
Overview				
Number of hauls:	122	64	136	37
Number of fish:	14,102	12,743	5,701	3,739
CPUE:	116	199	42	101
% Composition				
Chiselmouth	15.3	1.7	2.4	3.3
Peamouth	2.3	11.8	8.1	12.5
Northern pikeminnow	13.3	18.6	6.7	29.9
Suckers	36.8	37.0	12.1	8.5
Sand rollers	28.3	3.3	17.5	9.0
Sculpins	3.0	1.2	20.8	3.8
Pumpkinseed, bluegill†	0.2	5.0	7.3	4.4
Smallmouth bass†	0.4	1.9	2.2	6.2
Crappies†	0.2	17.0	0.4	0.1
Yellow perch†	0.2	2.5	22.4	22.3

Although patterns of relative abundance varied somewhat between locations, during 1984 and 1985 a core group of native taxa (cyprinids, suckers, and sand rollers) dominated the catch at all individual locations except Paterson Slough, where introduced sunfishes and yellow perch made up a large percentage of the catch. Conversely, at nearly all main-channel sample locations during 1995, a larger percentage of the catch comprised introduced taxa, particularly yellow perch, than in the earlier sample. This shift in catch composition was greatest at the lower pool location where introduced taxa constituted 61% of the 1995 catch.

Assemblage Structure

Within-Year Comparisons

Based on rank correlation coefficients, catch composition did not vary greatly between seasons in main-channel habitats. Agreement between spring and summer resident fish taxa ranks of main-channel catches (pooled across locations) was strong ($r_s = 0.76-0.97$) and significant ($P < 0.05$) during all 3 yrs of the study (Table 3). Likewise, taxa ranks were concordant among seasonal catches at individual main-channel locations except at the

TABLE 3. Seasonal comparisons (spring and summer) of fish assemblages in the John Day Reservoir, Columbia River, in 1984, 1985, and 1995. Agreement between seasonal assemblages was calculated with Spearman's rank correlation coefficient (r_s) on the rank ordered abundances of the 10 overall most abundant taxa for each comparison. Proportional similarity indices (PSI) were calculated on the catch of all taxa. * = $P < 0.05$.

Year and location	r_s	PSI
1984		
Forebay	0.86*	0.83
Lower pool	0.25	0.45
Upper pool	0.82*	0.77
Tailrace	0.80*	0.62
Paterson Slough	0.22	0.29
Plymouth Slough	0.33	0.76
Pooled data		
All main-channel locations	0.97*	0.82
All backwater locations	0.37	0.71
1985		
Forebay	0.80*	0.95
Lower pool	0.71*	0.73
Upper pool	0.87*	0.68
Tailrace	0.81*	0.36
Paterson Slough	-0.18	0.22
Plymouth Slough	-0.07	0.28
Pooled data		
All main-channel locations	0.85*	0.66
All backwater locations	-0.21	0.22
1995		
Forebay	0.54	0.70
Lower pool	0.91*	0.76
Upper pool	0.92*	0.56
Tailrace	0.77*	0.69
Paterson Slough	0.78*	0.77
Plymouth Slough	0.72*	0.71
Pooled data		
All main-channel locations	0.76*	0.73
All backwater locations	0.73*	0.79

lower pool in 1984 and the forebay in 1995. In contrast to the general pattern at main-channel locations, correlations between seasonal taxa ranks in backwaters (catches pooled across both backwater locations) were low and not significant except during 1995 (Table 3). Similarly, agreement between assemblages was low and not significant (r_s range = -0.18 - 0.33) at individual backwater locations between spring and summer in both 1984 and 1985, but seasonal assemblages were similar in 1995 (Table 3). In backwaters during 1984 and 1985, ranked abundances of some native taxa

(peamouth [*Mylocheilus caurinus*], northern pikeminnow, suckers, and sand rollers) consistently declined from spring to summer, and ranked abundances of introduced sunfishes increased.

Proportional similarity indices (PSI) exhibited moderate agreement with rank correlation measures of assemblage similarity at the seasonal level of comparison (Table 3). Only six of 16 significant rank correlations had PSI values of < 0.70, with only two of these < 0.62, indicating at least moderate similarity for nearly all seasonal comparisons. An additional three comparisons lacked significant concordance among ranks, but had relatively high (> 0.70) PSI values.

Annual Comparisons

Annual comparisons of main-channel fish faunal composition revealed few differences between 1984 and 1985. The correlation between rank orders (catches pooled across all main-channel locations) was significant ($P < 0.05$), indicating strong concordance between years (Table 4). Annual comparisons of assemblage structure at

TABLE 4. Annual (1984 compared to 1985) and long-term (pooled 1984-1985 compared to 1995) comparisons of fish assemblages in the John Day Reservoir, Columbia River. Agreement between assemblages was calculated with Spearman's rank correlation analysis (r_s). Analyses were conducted on the rank ordered abundances of the 10 overall most abundant taxa for each comparison. Proportional similarity indices (PSI) were calculated on the catch of all taxa. * = $P < 0.05$.

Time period and location	r_s	PSI
Annual		
Forebay	0.74*	0.70
Lower pool	0.85*	0.86
Upper pool	0.89*	0.86
Tailrace	0.84*	0.65
Paterson Slough	0.38	0.74
Plymouth Slough	0.43	0.61
Pooled data		
All main-channel locations	0.85*	0.73
All backwater locations	0.56*	0.63
Long term		
Forebay	0.29	0.21
Lower pool	-0.44	0.30
Upper pool	0.24	0.57
Tailrace	0.47	0.50
Pooled data		
All main-channel locations	0.07	0.44

individual main-channel locations also demonstrated strong agreement between 1984 and 1985. Backwater faunal composition, in contrast, was dissimilar between the 2 yrs at individual locations (Table 4). The rank correlation of annual catches pooled across all backwaters was low but significant ($P < 0.05$). In both years, suckers dominated backwater catches. Differences in catch composition (catches pooled across both backwaters) were largely due to changes in the rank abundances of introduced sunfishes and yellow perch.

Long-Term Comparisons

Long-term comparisons of fish taxa ranks indicated that main-channel shoreline fish faunal structure changed greatly between the earlier period (pooled 1984-85 catch) and 1995. Large changes in catch composition were indicated by low ($r_s \leq 0.47$) and nonsignificant correlations at all main-channel locations (Table 4). Major shifts in faunal composition between the two periods (catches pooled across all main-channel locations) resulted from declines in the rank abundance of native suckers and cyprinids (chiselmouth and northern pikeminnow) and increases in ranks of sculpins, and introduced sunfishes and yellow perch. Similar long-term changes in taxon contributions to assemblage structure occurred at individual main-channel locations.

Annual and long-term PSI values were consistent with rank concordance measures of assemblage similarity (Table 4). Annual comparisons of assemblage structure with significant Spearman's rank correlations always had PSI values of ≥ 0.65 , whereas most long-term comparisons of main-channel assemblage structure (all correlations were nonsignificant) had PSI values ≤ 0.5 . Proportional similarity index values, however, indicated higher similarities at individual backwater locations between 1984 and 1985 than did rank concordance measures of annual similarity.

Ordinations of Taxon Associations and Sample Location Relationships

A plot of fish taxa loadings on the first two principal component (PC) axes revealed three relatively well-defined, ecologically interpretable fish taxa associations (Figure 3). The first component explained 30% of the variance in the relative abundance data and separated native (negative or

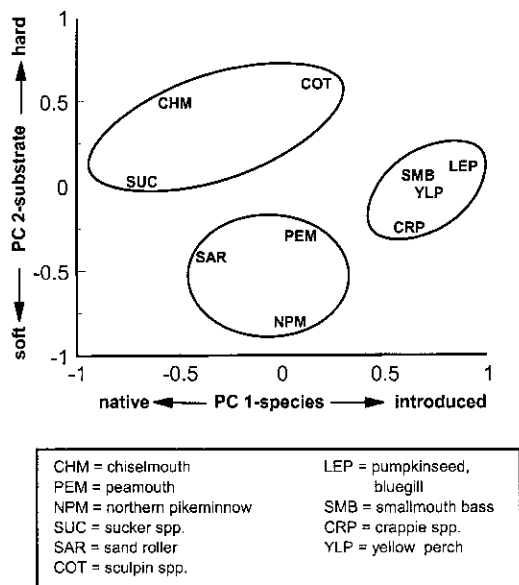


Figure 3. Taxa loadings on the first two axes of a principal components (PC) analysis of fish relative abundance. Fishes were collected by beach seining during May-September 1984, 1985, and 1995.

low positive loadings on PC 1) from introduced taxa (loadings ≥ 0.60 on PC 1). The second component accounted for 21% of the variation in the data set and separated taxa (high positive loadings on PC 2) that were generally associated with hard substrate (gravel-cobble) habitats from taxa associated with soft (fines-sand) sediments. The three major groups of taxa were a native association of chiselmouth, suckers, and sculpins, a native association of peamouth, northern pikeminnow, and sand rollers, and a third group of introduced fishes: pumpkinseed (*Lepomis gibbosus*), bluegill (*L. macrochirus*), smallmouth bass, white crappie (*Pomoxis annularis*), black crappie (*P. nigromaculatus*), and yellow perch.

An ordination of monthly (by year) location scores on the first two principal components exhibited both spatial and temporal (seasonal and annual) trends in clusters of sampling units. Temporal patterns in groupings of monthly samples concurred closely with the seasonal, annual, and long-term measures of concordance (Figure 4). There was generally little separation of monthly location scores from within a year at individual main-channel locations. Monthly scores at individual main-channel locations also did not differ

greatly between 1984 and 1985, however, 1984 and 1985 location scores typically differed substantially from 1995 scores. Monthly backwater scores showed an overall greater amount of variability than main-channel scores, both within a year and between years, which is consistent with the rank measures of assemblage similarity (Table 4).

The fish assemblages present at a location influenced the groupings of location scores (Figures 3, 4). For example, introduced taxa had comparatively high positive loadings on PC 1; thus, monthly samples with high relative abundances of introduced taxa have higher scores on PC 1. Samples from Paterson Slough generally had the highest positive scores on the first component, particularly during August 1984 and 1985, and May and June 1995 (we were unable to sample in this area after June 1995), indicating the importance of this habitat to introduced taxa (e.g., sunfishes and yellow perch). In Plymouth Slough, high relative abundances of young-age classes of peamouth and northern pikeminnow contributed to relatively large negative monthly scores on PC 2, regardless of year (Figure 4). An increased relative abundance of introduced taxa in Plymouth Slough during August 1985, and during July and August 1995, shifted location scores to the right of the ordination. Positive location scores on PC 1 in 1995 indicate the increasing importance of introduced taxa to assemblage structure at nearly all main-channel locations. The main-channel area with the highest average monthly PC 1 scores in 1995 was the lower pool location, where more than half of all fishes collected were introduced. The main-channel area with the lowest average scores on PC 1 in 1995 was the tailrace location, an area that harbored a mostly native fish species assemblage. Monthly tailrace location ordination scores also exhibited the least amount of separation from 1984-1985 ordination scores; this area additionally had the highest, but still low and nonsignificant, measure of concordance over the long-term sampling period (Table 4).

Water Temperature and Discharge Patterns

Temperature and discharge conditions in 1995 were generally intermediate between 1984 and 1985 (Figure 5). Discharge was lowest in 1985, and highest in 1984, with peaks in the hydrograph occurring in all years during late May or early

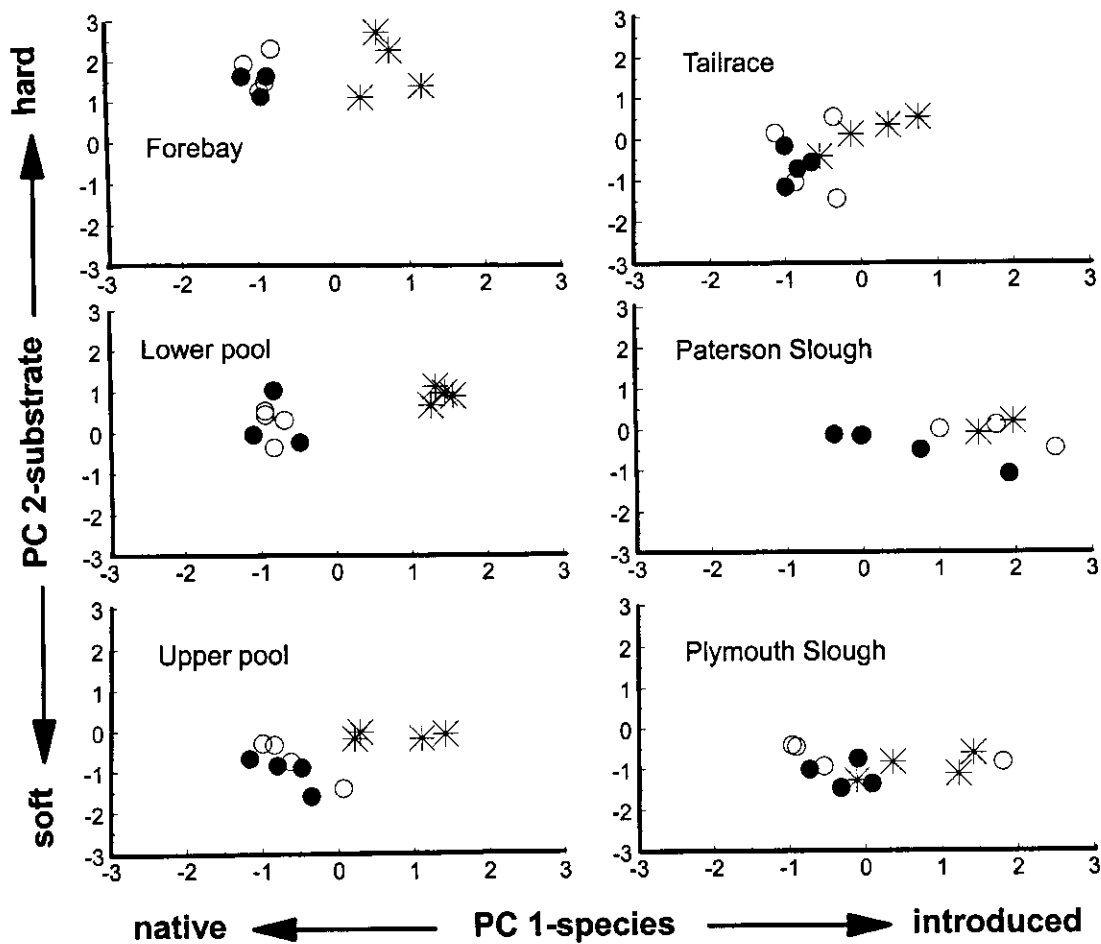


Figure 4. Principal components (PC) ordination of monthly location scores for six major beach seine sampling locations. The PC analysis was conducted on a correlation matrix of the monthly catch of the 10 overall most abundant fish taxa in beach seine samples collected during spring and summer 1984, 1985, and 1995. Black circles represent scores for 1984 monthly samples, white circles represent 1985, and stars represent 1995.

June. Annual water temperature and discharge patterns were inversely related. Temperatures were highest in 1985 and lowest in 1984. Water temperatures early in 1995 were slightly higher (typically $\leq 1.5^\circ\text{C}$) than temperatures in 1985 until early June, and then were intermediate. Within a year, main-channel temperatures were highest in late July or early August, with peaks ranging from 21.7 to 23.3 $^\circ\text{C}$.

Discussion

We detected both seasonal and long-term variations in the makeup of shallow water fish assemblages within the John Day Reservoir. Season-

ally, the proportion of introduced sunfishes in backwaters increased from spring to summer during 1984 and 1985. This increase is likely related to environmental conditions in these areas. Both slough locations are shallow, well vegetated, and have low water exchange rates resulting in summer water temperatures often several degrees higher than nearby main-channel habitats with greater water exchange (Gadomski and Barfoot 1998). These higher temperatures are nearer to optimal for some introduced species such as bluegill and smallmouth bass (Hornig and Pearson 1973, Lemke 1977). Temperature is associated with seasonal movements and distributions of fishes

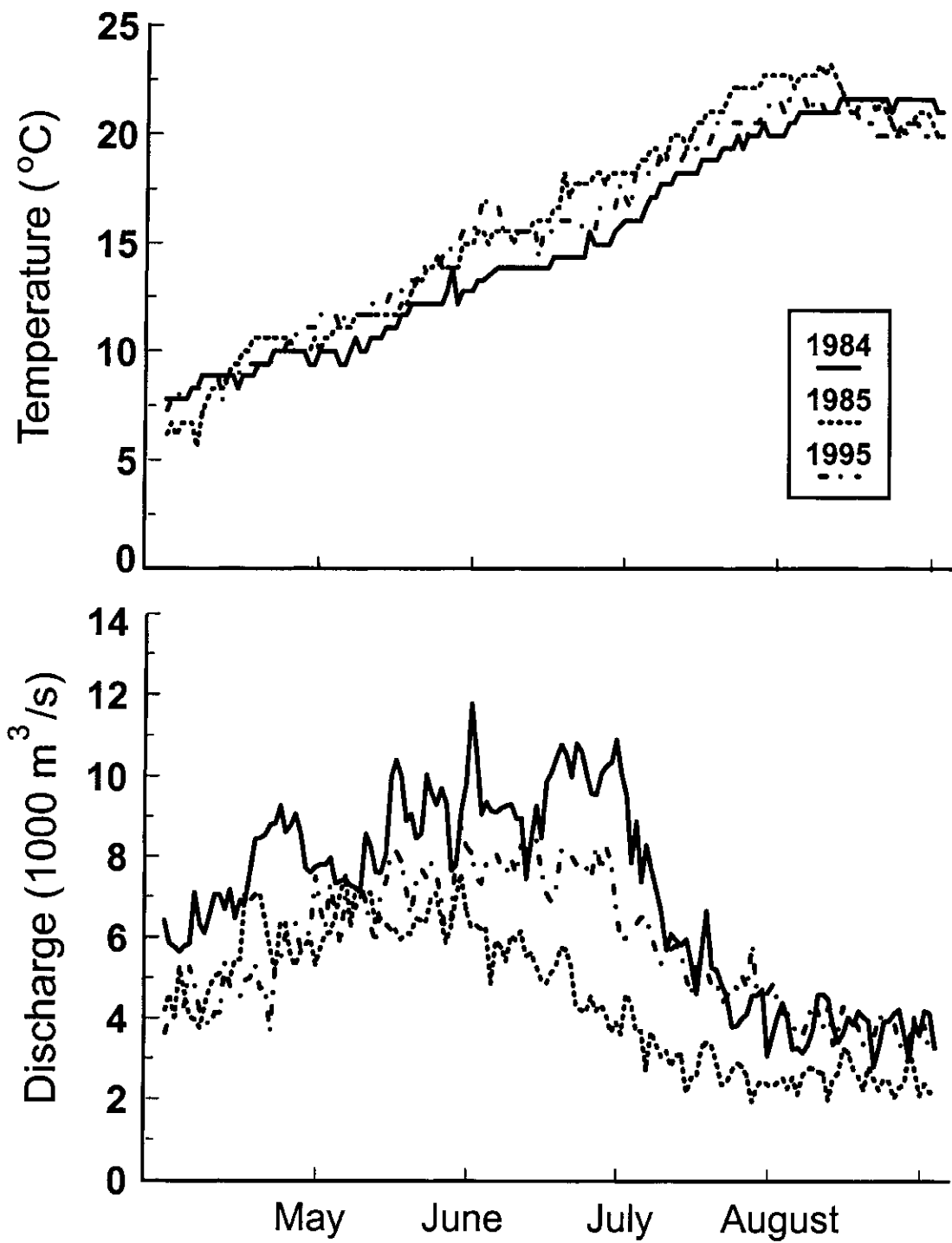


Figure 5. Columbia River temperature and discharge regimes at McNary Dam during spring and summer 1984, 1985, and 1995. Data were obtained from StreamNet 2001.

in lentic habitats (Hall and Werner 1977, Hubert and Lackey 1980, Tufescu 1994, Garret and Bennett 1995). Thus, higher late summer temperatures may have caused native taxa to shift habitat use out of backwaters, while introduced warmwater taxa may have moved into or remained in these areas.

We also observed substantial long-term changes in shallow-water fish assemblages of the John Day Reservoir. At our scale of examination, fish catch composition between 1984 and 1985 was similar, but was different from 1995 catches. Two native taxa assemblages dominated the catch in the earlier 1984-1985 sampling period and appeared to be generally separated along a habitat gradient of hard (gravel and cobble) versus soft (silt and sand) substrate types. The hard substrate assemblage comprised chiselmouth, suckers, and sculpins. The chiselmouth is a native herbivorous cyprinid that is strongly associated with hard substrates from which it scrapes plant material (Moodie and Lindsey 1972), and sculpins as a group are generally lithophilic. Chiselmouth and sculpins were typically most abundant in low-velocity cobble habitats of the forebay sample location.

The second native species association dominant in 1984-1985 was most abundant over soft substrates and contained two cyprinids (peamouth and northern pikeminnow) and sand rollers. Younger age classes of peamouth and northern pikeminnow rear in sandy low-gradient habitats (Beamesderfer 1992, Gadomski et al. 2001), while sand rollers are particularly abundant over sandy bottoms at nighttime (Gray and Dauble 1976). The highest abundances of these three species were at Plymouth Slough sites and some upper pool sample locations with soft substrates.

The third species assemblage we identified was generally not abundant in 1984-1985, except in the Paterson Slough, but in 1995 became increasingly more important to fish assemblage composition at nearly all main-channel locations. This assemblage comprised bluegill, pumpkinseed, smallmouth bass, white and black crappies, and yellow perch. All of these taxa are introduced and typical of lake-like habitats, with the exception of smallmouth bass, which occurs in both still and moving waters (Edwards et al. 1983).

The long-term differences in fish assemblages we observed may be due to simple year-to-year variation, decadal environmental differences, or

to persistent habitat changes related to reservoir aging. The three years of sampling did not allow us to assess year-to-year variation in any detail, however. Similar studies in the basin are unavailable for comparison with ours, and information is minimal on the temporal variability and structure of shallow-water fish assemblages in impoundments (Hubert and O'Shea 1991).

General environmental conditions in the John Day Reservoir differed between the early 1980's and 1990's, which could be responsible for observed changes in fish fauna. Discharge regimes in the Columbia River associated with the two sample periods were dissimilar (Figure 6). Discharge has been shown to covary with spring and summer water temperatures (Quinn and Adams 1996), turbidities, and reservoir water-retention rates. Conditions leading up to and encompassing the earlier 1984-1985 sampling period were primarily characterized by above average annual discharge, while average annual discharge for the later period was generally below the long-term average (Figure 6). Additionally, in 1983 a water budget was adopted by the Columbia Basin hydrosystem. The goal has been to augment river flows during spring to increase down-river migration rates of juvenile salmonids, but this also has resulted in lower than average summer flows (Berggren and Filardo 1993).

Discharge and temperature regimes, in particular, can influence annual variations in reservoir fish assemblages by differentially influencing year-class strengths of individual species or groups of species with similar life histories. For example, Kallemeyn (1987) found a positive relationship between percid year-class strengths and thermal regimes, with the strongest year classes being produced in years with comparatively high, stable water temperatures. Elevated turbidities (Mitzner 1991) and high reservoir flushing rates (Walburg 1971, Beam 1983, Maccina and Stimpert 1998), both correlates of high reservoir inflows, can be negatively related to crappie recruitment success. Thus, the high discharge regime during the early 1980's may have favored the reproductive success of native taxa in the John Day Reservoir, while several successive years of low precipitation and runoff in the early 1990's might have favored introduced taxa.

Alternatively, the long-term changes that we observed in fish assemblages may be more persistent and less related to short-term, climatically

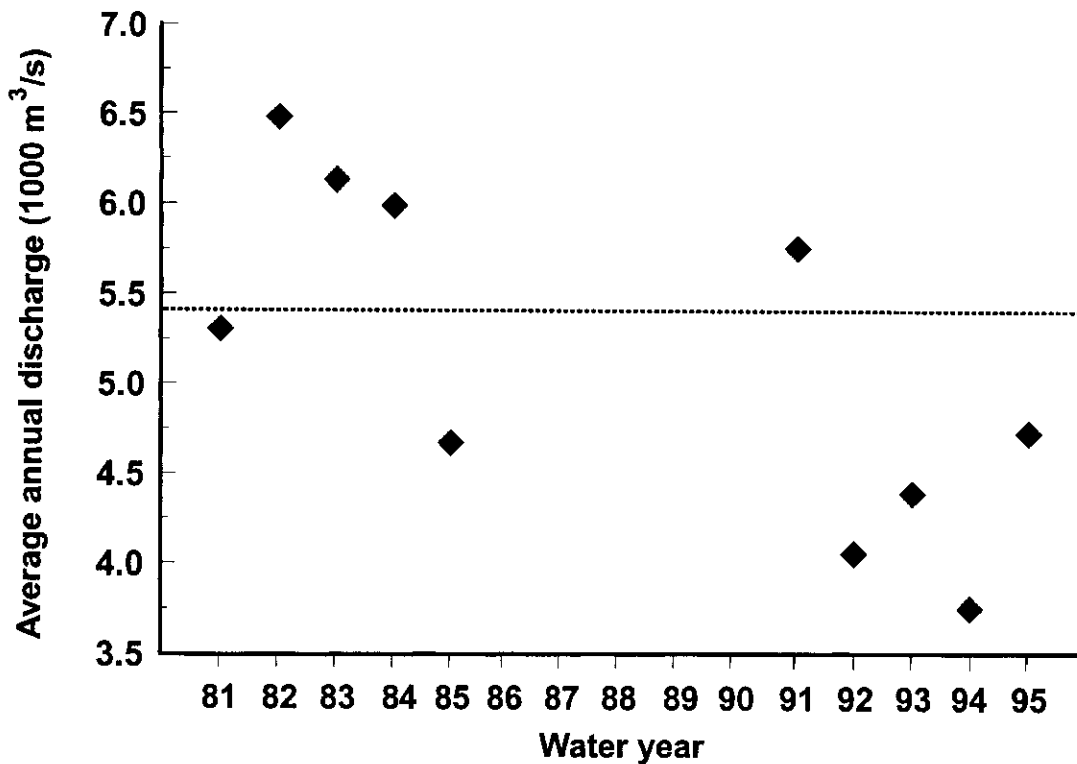


Figure 6. Mean annual discharge at The Dalles Dam, Columbia River, during five-year intervals before and during each of the two fish sampling periods (1984-1985; 1995). The dashed horizontal line indicates the long-term average annual discharge at The Dalles Dam. Data were obtained from the USGS (2001).

influenced variations in distribution and reproductive success. The trends we observed in 1995 (i.e., an increasing relative abundance of introduced species more typically associated with lake-like habitats) are consistent with long-term, post-impoundment patterns of assemblage change described by Li et al. (1987) for the Snake and Columbia rivers, suggesting that such changes can be expected in John Day Reservoir near-shore fish assemblages. Similar large-scale persistent shifts in post-impoundment fish assemblage composition have also been described elsewhere. For example, in a Colorado Reservoir, species composition changed substantially over a 6-yr period from an assemblage dominated by native riverine species to one primarily of introduced taxa adapted to lentic conditions (Martinez et al. 1994).

The abundance of aquatic macrophytes in John Day Reservoir, a habitat feature associated with reservoir aging, is one mechanism that likely influenced fish assemblage composition over the long

term. An increase in the abundance of aquatic macrophytes in impoundments over time is a predictable outcome of siltation due to both anthropogenic induced and natural reservoir aging processes (Kimmel and Groeger 1986). We observed an abundance of aquatic macrophytes in many shallow areas of John Day Reservoir during 1995, whereas investigators who conducted the earlier sampling (1984-1985) reported some beds of macrophytes, primarily pondweed (*Potamogeton* spp.), but at lower densities (Michael J. Parsley, USGS, personal communication). In Paterson Slough, for example, macrophyte abundance (primarily milfoil) prevented us from sampling with a beach seine after mid-summer in 1995. Rooted aquatic vegetation can play a key role in altering the ecology of shallow habitats by changing water circulation patterns, dissolved oxygen, pH, and the temperature of localized areas (Carter et al. 1991). In Columbia River impoundments, these changes may favor non-native lentic taxa over

native riverine species. Macrophyte beds also create structurally complex spawning, rearing, and foraging habitats (Kilgore et al. 1989, Weaver et al. 1997), which are well-suited to many of the introduced fish species (e.g., bluegill, pumpkinseed, black crappie, and yellow perch) present in John Day Reservoir.

Since shallow littoral reservoir habitats are rearing areas for anadromous salmonids, particularly fall chinook salmon (*Oncorhynchus tshawytscha*) post-impoundment shoreline habitat and fish assemblage changes could be affecting the suitability of reservoirs for salmonid production. However, relatively little is known about the complex relationship between reservoir food webs, habitat conditions, introduced fish taxa, and juvenile salmonids. Many introduced fish species now abundant in shoreline and backwater areas of the John Day Reservoir could directly prey upon or compete with juvenile salmonids, although these relationships have generally not been studied. Earlier predation studies (Poe et al. 1991, Vigg et al. 1991) in John Day Reservoir did not identify sunfishes or yellow perch as important predators of juvenile salmonids, although crappie and yellow

perch diets in some locations of the impounded lower Snake River comprised 20-25% juvenile salmonids (Bennett 1999).

More information on how short- and long-term changes in near-shore habitats and fish assemblages affect anadromous salmonids would aid ongoing recovery efforts in the highly regulated Snake and Columbia Rivers. The last major population of main-stem Columbia River fall chinook salmon is in the unimpounded Hanford Reach, an area where introduced taxa represent only a minor component of the fish assemblage (Li et al. 1987). This suggests that management actions that may partially restore riverine conditions and natural fish assemblages to impounded reaches of the Snake and Columbia rivers may ultimately benefit salmonid production.

Acknowledgements

We thank Jennifer Kelly for field assistance, and Samuel C. Lohr and two anonymous readers for reviewing the manuscript. This work was funded by the Army Corps of Engineers.

Literature Cited

- Bass, D. G. 1990. Stability and persistence of fish assemblages in the Escambia River, Florida. *Rivers* 1:296-306.
- Beam, J. H. 1983. The effect of annual water level management on population trends of white crappie in Elk City Reservoir, Kansas. *North American Journal of Fisheries Management* 3:34-40.
- Beamesderfer, R. C. 1992. Reproduction and early life history of northern squawfish, *Ptychocheilus oregonensis*, in Idaho's St. Joe River. *Environmental Biology of Fishes* 35:231-241.
- Bennett, D. H. 1999. So many predatory resident fishes—what needs to be done? Pages 197-202 *In Oregon Department of Fish and Wildlife and National Marine Fisheries Service (editor), Management Implications of Co-occurring Native and Introduced Fishes: Proceedings of a Workshop 27-28 October, 1999 Portland, Oregon.*
- Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River Basin. *North American Journal of Fisheries Management* 13:48-63.
- Carpenter, A. L., W. N. Jessee, and D. A. Rundstrom. 1981. Evaluating community similarity: an exploratory multivariate analysis. Pages 369-375 *In N. B. Armantrout (editor), Acquisition and Utilization of Aquatic Habitat Inventory Information, Proceedings of a symposium 28-30 October, 1981 Portland, Oregon.*
- Carter, V., N. B. Rybicki, and R. Hammerschlag. 1991. Effects of submersed macrophytes on dissolved oxygen, pH, and temperature under different conditions of wind, tide, and bed structure. *Journal of Freshwater Ecology* 6:121-133.
- Ebel, W. J., C. D. Becker, J. W. Mullan, and H. L. Raymond. 1989. The Columbia River — toward a holistic understanding. Pages 205-219 *In D. P. Dodge (editor), Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences 106.*
- Edwards, E. A., G. Gebhart, and O. E. Maughan. 1983. Habitat suitability information: Smallmouth bass. U.S. Department of the Interior, Fish and Wildlife Service FWS/OBS-82/10.36. Washington, D.C.
- Finger, T. R., and E. M. Stewart. 1987. Response of fishes to flooding regime in lowland hardwood wetlands. Pages 86-92 *In W. J. Matthews and D. C. Heins (editors), Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman, Oklahoma.*
- Gadomski, D. M., and C. A. Barfoot. 1998. Diel and distributional abundance patterns of fish embryos and larvae in the lower Columbia and Deschutes rivers. *Environmental Biology of Fishes* 51:353-368.
- Gadomski, D. M., C. A. Barfoot, J. M. Bayer, and T. P. Poe. 2001. Early life history of the northern pikeminnow in the lower Columbia River Basin. *Transactions of the American Fisheries Society* 130:250-262.

- Garret, J. W., and D. H. Bennett. 1995. Seasonal movements of adult brown trout relative to temperature in a coolwater reservoir. *North American Journal of Fisheries Management* 15:480-487.
- Gray, G. C., Palmer, D. E., B. L. Hilton, P. J. Connolly, H. C. Hansel, and J. M. Beyer. 1984. Feeding activity, rate of consumption, daily ration, and prey selection of major predators in John Day Reservoir. Unpublished Annual Report to Bonneville Power Administration, Portland, Oregon.
- Gray, R. H., and D. D. Dauble. 1976. New distribution records and notes on life-history and behaviour of the sand roller, *Percopsis transmontana* (Eigenmann and Eigenmann). *Syesis* 9:369-370.
- Gray, R. H., and D. D. Dauble. 1977. Checklist and relative abundance of fish species from the Hanford Reach of the Columbia River. *Northwest Science* 51:208-215.
- Grossman, G. D., P. B. Moyle, and J. O. Whitaker. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *American Naturalist* 120:423-454.
- Hall, D. J., and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* 106:545-555.
- Hoff, M. H., and C. R. Bronte. 1999. Structure and stability of the midsummer fish communities in Chequamegon Bay, Lake Superior, 1973-1996. *Transactions of the American Fisheries Society* 128:362-373.
- Horning, W. B., II, and R. E. Pearson. 1973. Growth temperature requirements and lower lethal temperatures for juvenile smallmouth bass (*Micropterus dolomieu*). *Journal of the Fisheries Research Board of Canada* 30:1226-1230.
- Hubert, W. A., and R. T. Lackey. 1980. Habitat of adult smallmouth bass in a Tennessee River reservoir. *Transactions of the American Fisheries Society* 109:364-370.
- Hubert, W. A., and D. T. O'Shea. 1991. Temporal patterns of the small fishes in the littoral zone of Grayrocks Reservoir, Wyoming. *Journal of Freshwater Ecology* 6:107-113.
- Kallemeyn, L. W. 1987. Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year walleye and yellow perch in four lakes in Voyageurs National Park. *North American Journal of Fisheries Management* 7:513-521.
- Kilgore, K. J., R. P. Morgan, II, and N. B. Rybicki. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River. *North American Journal of Fisheries Management* 9:101-111.
- Kimmel, B. L., and A. W. Groeger. 1986. Limnological and ecological changes associated with reservoir aging. Pages 103-109 *In* G. E. Hall and M. J. Van Den Avyle (editors). *Reservoir Fisheries Management: Strategies for the 80's*, Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.
- Lemke, A. E. 1977. Optimum temperature for growth of juvenile bluegills. *The Progressive Fish Culturist* 39:55-57.
- Li, H. W., C. B. Shreck, C. E. Bond, and E. Rexstad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. Pages 193-202 *In* W. J. Matthews and D. C. Heins (editors). *Community and Evolutionary Ecology of North American Stream Fishes*, University of Oklahoma Press, Norman, Oklahoma.
- Lichatowich, J. A. 1999. *Salmon without rivers: a history of the Pacific salmon crisis*. Island Press, Washington, D.C..
- Maceina, M. J., and M. R. Stimpert. 1998. Relations between reservoir hydrology and crappie recruitment in Alabama. *North American Journal of Fisheries Management* 18:104-113.
- Mahon, R., S. K. Brown, K. C. T. Zwanenburg, D. B. Atkinson, K. R. Buja, L. Claffin, G. D. Howell, M. E. Monaco, R. N. O'Boyle, and M. Sinclair. 1998. Assemblages and biogeography of demersal fishes of the east coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1704-1738.
- Martinez, P. J., T. E. Chart, M. A. Trammell, J. G. Wullschleger, and E. P. Bergersen. 1994. Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. *Environmental Biology of Fishes* 40:227-239.
- Matthews, W. J., R. C. Cashner, and F. P. Getwick. 1988. Stability and persistence of fish faunas and assemblages in three midwestern streams. *Copeia* 4:945-955.
- Meffe, G. K., and A. L. Sheldon. 1990. Post-defaunation recovery of fish assemblages in southeastern blackwater streams. *Ecology* 71:657-667.
- Meng, L., P. B. Moyle, and B. Herbold. 1994. Changes in abundance and distribution of native and introduced fishes of Suisun Marsh. *Transactions of the American Fisheries Society* 123:498-507.
- Mitzner, L. 1991. Effects of environmental variables upon crappie young, year-class strength, and the sport fishery. *North American Journal of Fisheries Management* 11:534-542.
- Moodie, G. E. E., and C. C. Lindsey. 1972. Life-history of a unique cyprinid fish, the chiselmouth (*Acrocheilus alutaceus*), in British Columbia. *Syesis* 5:55-61.
- Moyle, P. B., R. A. Daniels, B. Herbold, and D. M. Baltz. 1986. Patterns in distribution and abundance of a noncoevolved assemblage of estuarine fishes in California. *Fishery Bulletin* 84:105-117.
- Nigro, A. A. (Editor) 1988. Status and habitat requirements of white sturgeon populations in the Columbia River downstream from McNary Dam. Unpublished Annual Report to the Bonneville Power Administration, Portland, Oregon.
- Palmer, D. E., H. C. Hansel, J. M. Beyer, S. C. Vigg, W. T. Yasutake, P. T. Lofy, S. D. Duke, M. J. Parsley, M. G. Mesa, L. A. Prendergast, R. Burkhardt, C. Burley, D. W. Eib, and T. P. Poe. 1986. Feeding activity, rate of consumption, daily ration, and prey selection of major predators in John Day Reservoir. 1985. Unpublished Annual Report to the Bonneville Power Administration, Portland, Oregon.
- Parsley, M. J., L. G. Beckman, and G. T. McCabe. 1993. Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. *Transactions of the American Fisheries Society* 122:217-227.

- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405-420.
- Poe, T. P., R. S. Shively, and R. A. Tabor. 1994. Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake rivers. Pages 347-360 *In* D. J. Stouder, K. L. Fresh, and R. J. Feller (editors), *Theory and Application in Fish Feeding Ecology*, University of South Carolina Press, Columbia, South Carolina.
- Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77:1151-1162.
- Rose, D. R., and A. A. Echelle. 1981. Factor analysis of associations of fishes in Little River, central Texas, with and interdrainage comparison. *American Midland Naturalist* 106:379-391.
- Ross, S. T., J. A. Baker, and K. E. Clark. 1987. Microhabitat partitioning of southeastern stream fishes: temporal and spatial predictability. Pages 42-51 *In* W. J. Matthews and D. C. Heins (editors), *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman, Oklahoma.
- Ross, S. T., W. J. Matthews, and A. A. Echelle. 1985. Persistence of stream fish assemblages: effects of environmental change. *The American Naturalist* 126: 24-40.
- Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704-726.
- StreamNet. 2001. StreamNet Fish Data. Available online at http://www.streamnet.org/online_data.html.
- Tufescu, M. V. A. 1994. Seasonal variation patterns of the fish community in the littoral waters of northern Lake Ontario, the Pickering-Darlington area. *Hydrobiologia* 281:141-154.
- USGS. 2001. U.S. Geological Survey calendar year streamflow statistics for Oregon. Available online at <http://water.usgs.gov/or/nwis/annual>.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:421-438.
- Walburg, C. H. 1971. Loss of young fish in reservoir discharge and year-class survival, Lewis and Clark Lake, Missouri River. Pages 441-448 *In* G. Hall (editor), *Reservoir Fisheries and Limnology*, American Fisheries Society, Special Publication 8, Bethesda, Maryland.
- Weaver, M. J., J. J. Magnuson, and M. K. Clayton. 1997. Distribution of littoral fishes in structurally complex macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2277-2289.

Received 14 May 2001

Accepted for publication 23 December 2001