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[Article]

Fish Use of Intermittent Watercourses Draining Agricultural Lands in the Upper Willamette River Valley, Oregon

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Abstract.—Historically, the upper Willamette River valley in western Oregon was characterized by seasonal floods and large expansions of its stream network. During the past century, human activities have altered or eliminated many intermittent stream and floodplain habitats in the valley. As a result, the remaining intermittent streams and ditches, referred to as watercourses, may still provide habitat that is critical for native fish. Our objectives were to determine (1) fish presence, (2) the spatial gradients of fish distribution (including species identity, native versus nonnative status, and numbers), (3) fish use of the intermittent streams as spawning and nursery habitats, and (4) the main factors that influence the numbers of fish and fish species. In the winter and spring of 2002–2003, we examined the distributions of fish species in five subbasins within the Willamette River valley. The sampling sites were in intermittent watercourses that drained grass seed–producing fields. We collected water samples and sampled fish from December to May with minnow traps and an electrofishing unit and collected data on the standard fish habitat variables at all sites in spring. Thirteen fish species were found and only three of them were exotic. The presence of recently hatched and juvenile fish shows that intermittent watercourses offer conditions suitable for spawning and juvenile rearing. The two watershed-scale variables with the most influence on fish species richness were the percentage of the watershed covered by forest and the distance to perennial water, the first of which had a direct relationship to species diversity and the second an inverse relationship. In turn, fish abundance had a negative, albeit modest, relationship with the distance to perennial water. Among local-scale variables, water velocity and conductivity were inversely related to species richness and fish numbers. Our results highlight the relevance of intermittent agricultural watercourses for native fish species in the Willamette River valley and call for the promotion of agricultural conservation practices that benefit farmers while maintaining aquatic biodiversity in floodplain habitats.

In the lowlands of the upper Willamette River valley, Oregon, winter flooding is an annual phenomenon driven by the seasonal precipitation regime of the Pacific Northwest (Greenberg and Welch 1988; Hamlet and Lettenmaier 1999). Predictable inundation of river floodplains and the expansion of stream networks like these are major processes influencing the diversity and production of aquatic vertebrates (Tockner et al. 2000; Tockner and Stanford 2002).

In many rivers, native fish species are adapted to having seasonal access to refuges where they can find shelter as well as spawning, nursery, and foraging habitats (Junk et al. 1989; Bayley 1991; Sommer et al. 2004). In tropical and temperate systems, flooding tends to signal the onset of favorable foraging and breeding conditions to many species of fish (Welcomme 1985; Junk et al. 1989). A contrasting pattern occurs in the Pacific Northwest, where most flooding and stream network expansion coincide with the onset of less favorable conditions, as fall transitions into winter and both temperature and photoperiod decrease. In this region, most off-channel habitat use studies have focused on salmonids in either forested or multiple-land-use watersheds. Juvenile salmon and trout *Oncorhynchus* spp. are thought to enter such habitats principally to escape high water velocities in the main stems of streams; however, they also benefit from off-channel foraging opportunities during winter, especially where there is groundwater input (Brown and Hartman 1988; Nickelson et al. 1992a, 1992b;

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Giannico and Healey 1998a; Giannico and Hinch 2007).

During the past 150 years, the cumulative effects of navigation improvement and flood control projects, agricultural activities, and urban development have altered the hydrology of the system, removed miles of side channels, and eliminated acres of active floodplain in the Willamette River valley (Boag 1992; Hulse et al. 2002). Flood control and improved drainage have been achieved through channel straightening, wetland filling, dike construction, and ditch development (Benner and Sedell 1997). Channel straightening alone has eliminated meanders and secondary channels in the Willamette River and reduced the length of its main stem. Along a portion of the Willamette River downstream of our study sites (between its confluence with the McKenzie River and the city of Albany), the main channel is approximately 45–50% shorter than it was in 1850 (Sedell and Froggatt 1984; Benner and Sedell 1997; Hulse et al. 2002). Also, lowland floodplains have been partly drained by ditches and underground tile systems for agriculture. These floodplains sustain 95% of Oregon's grass seed production and represent approximately 50% of the tillable land (some 2,000 km^2) in the entire Willamette River valley (Gohlke et al. 1999).

Flood control efforts are not effective everywhere in the Willamette River Valley, however; as a result, many grass seed–producing fields become partly submerged on an annual basis. Intermittent watercourses, which include both altered stream channels and dug-out drainage ditches, have replaced most natural channels (Hulse et al. 2002) and could be considered a vestige of the larger preexisting floodplain–river complex, one that encompassed the entire upper valley (Boag 1992).

Native fish species in this basin are adapted to a flood-pulse-driven environment and respond to annual changes in discharge by moving into seasonally inundated habitats. Migratory behavior may be critical to their survival, sheltering them from high water velocities during the coldest months (Giannico and Healey 1998a) while increasing the foraging and reproductive opportunities of some species in early spring (Sommer et al. 2004). In addition to the human-made habitat alterations, fish in the Willamette River Valley must cope with a host of exotic fish and the exotic American bullfrog *Rana catesbeiana*. The introduction of these species began in the late 1800s, and the current list of most common exotic species includes the bullfrog and bluegill *Lepomis macrochirus*, largemouth bass *Micropterus salmoides*, mosquitofish *Gambusia affinis*, smallmouth bass *Micropterus dolomieu*, warmouth *Lepomis gulosus*, and yellow bullhead *Ameiurus natalis* (Lampman 1946; Hulse et al. 2002; Waite and Carpenter 2000). Although several of these species have been implicated in changes in the general distribution and abundance of some native aquatic species (McIntosh et al. 1989; Scheerer 2002), their influence on the use of intermittent watercourses by native fish is unknown. Among the native species expected to use seasonally flooded habitats are three listed as threatened or endangered under the U.S. Endangered Species Act. They are the upper Willamette spring Chinook salmon *Oncorhynchus tshawytscha*, upper Willamette steelhead *Oncorhynchus mykiss* (anadromous rainbow trout), and Oregon chub *Oregonichthys crameri* (USFWS 1993, 1999).

In the upper Willamette River valley, fish use of intermittent watercourses has not been verified; therefore, our first objective was (1) to document fish presence. Subsequently, we aimed to (2) determine the spatial gradients of fish distribution (including species identity, native versus nonnative status, and numbers); (3) document fish use of the intermittent streams as spawning and nursery habitats; and (4) identify the main factors that influence both the numbers of fish (all species combined) and fish species (species richness). The information provided by this study would be valuable to managers responsible for the design and implementation of agricultural conservation practices in the region.

Methods

Fish and habitat assessment.—The following five subbasins of the upper Willamette River basin were used in this study: the Luckiamute, Marys, and Long Tom Rivers (which are on the west side of the valley) and the Calapooia River and Muddy Creek (which are on the east side) (Figure 1). These subbasins cover three ecoregions: the high-elevation western Cascades, the Coast Range mountains, and the lowlands on the Willamette River valley floor (Hulse et al. 2002). The Muddy Creek subbasin is unique because it is found entirely within the lowland ecoregion. Most of its tributaries and those of the Calapooia River run through the relatively flat agricultural lands that extend east of the main-stem Willamette River. The west side subbasins have steep slopes that limit the extension of grass seed agriculture and thus favor woodland development. The data for this study were collected between December 2002 and May 2003.

We selected 22 sites (Figure 1B) based on landowners' grant of access and geographical information systems (GIS [based on 10-m digital elevation maps]) and PC-ORD analysis (McCune and Mefford 1999) of the following watershed-scale variables:

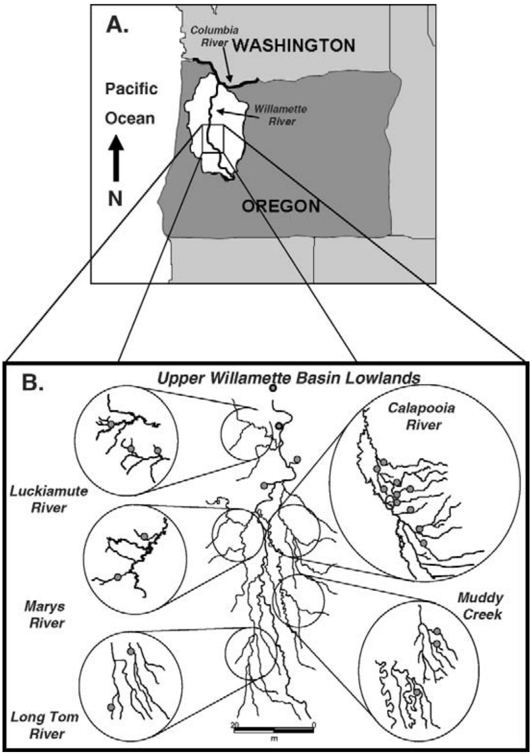

FIGURE 1.—Maps showing the locations of **(A)** the upper Willamette River valley and **(B)** the five subbasins used in the study. The small circles indicate the 22 sampling sites.

stream slope (% gradient), watershed area (>1 km^2 [estimated to the nearest square kilometer]), land use (≥70% grass seed agriculture), and stream intermittency. Two criteria were used to confirm intermittency: (1) the stream reach was completely dry at the road crossing during August and (2) there was no water in the stream directly upstream and downstream of site. At each site, a 100-m-long reach was randomly chosen based on GIS analysis and on-the-ground scouting to be sampled during repeated visits. Considering the overall habitat uniformity of these glide-like reaches, a length of 100 m was deemed adequate to capture all of the variability at each site.

Fish collection started in late December and ended in late May and was done with minnow traps (He and Lodge 1990) and a backpack electrofishing unit. The latter was used to ensure detection of both large-size fish and recently hatched fish that would not be caught in traps as well as to calibrate trap efficiency across sites in late spring. We considered the presence of adult fish as indicative that intermittent watercourses offered winter refuge to some fish species. The presence of recently hatched fish was regarded as evidence of upstream spawning because fish at such an early stage would be unable to swim upstream against the currents. In addition, the presence of both recently hatched and juvenile fish (including both young of the year and age-1 individuals) was taken as confirmation that these intermittent systems were being used as nursery habitats. At each sampling site, nine minnow traps baited with salmon roe were randomly placed within the 100-m study reach for 24 h. All of the fish caught were identified to species, counted, measured (total length and fork length to the nearest 0.1 cm) and weighed (to the nearest 0.1 g) (He and Lodge 1990). All 22 sampling sites were visited within a 10-d period each month. Minnow traps were set once each month from late December through April. Electrofishing involved one pass through each 100-m reach, first in February and again in late May.

During winter, elevated water discharge and turbidity combined with low recapture rates of fin-clipped fish precluded reliable estimation of fish numbers. Hence, the catch per unit effort (CPUE) with the minnow traps (i.e., the number of fish caught/the number of traps set) was used as the indicator of relative abundance among sites. It was not until May of each year that we could deplete fish numbers effectively with an electrofishing unit and thus calibrate trap efficiency. To do this, we blocked each 100-m sampling reach at both ends with stop nets to prevent fish from entering or leaving and set nine minnow traps overnight, as described above. The following morning, before captured fish were released back into the stream, multiple-pass electrofishing was used to remove as many of the remaining fish as possible. Electrofishing passes were repeated from three to seven times per reach until they did not yield any fish. Subsequently, trap efficiency was calculated as the percentage of fish caught with minnow traps relative to the total number of fish captured with both gears combined.

A stream habitat assessment method developed by Kaufmann et al. (1999) and based on the Environmental Protection Agency's Environmental Monitoring and Assessment Program protocol was used. We selected habitat variables that were common to agricultural systems and had been reported to influence fish presence and assemblage composition (Maret et al. 1997). Some of these variables were indicators of natural watershed conditions and others could reflect the impacts of land use activities. In March 2003, 17 habitat variables were recorded along five transects 20 m apart within each of the 100-m-long reaches (Table 1). Five watershed-scale variables that could be readily estimated with GIS were selected: upstream slope, watershed area, percentage of the watershed covered by forest, percentage of the watershed covered by grass

TABLE 1.—Values of the local- and watershed-scale habitat variables at the 22 sampling sites in intermittent watercourses of the upper Willamette River valley.

Variable	Range	Average	SD
Local scale			
Depth (cm)	0.10–1.0	0.33	0.21
Water velocity at 0.6 depth (nearest 0.01 m^3/s)	0.01–0.50	0.16	0.09
% Vegetated substrate	0.00–83.30	25.9	21.70
Wetted width (cm)	1.23–13.00	3.58	2.58
Bankfull width (cm)	2.12–13.50	5.22	3.20
Maximum daily temperature (nearest 0.1°C)	20.31–33.00	27.79	4.38
Minimum daily temperature (nearest 0.1°C)	6.06–10.53	7.76	1.41
% Change in depth at bankfull width	543.75–22.15	184.15	131.66
Suspended sediment concentration (nearest 0.1 mg/L)	72.14–129.67	85.65	15.83
NO_3 concentration (nearest 0.1 mg/L)	67.90–108.80	4.13	2.29
PO_4^{3-} concentration (nearest 0.1 mg/L)	0.01–0.11	0.05	0.03
Conductivity (μS)	54.50–220.89	163.36	41.50
Watershed scale			
Upstream slope (%)	0.10–3.30	1.18	1.12
Watershed area (km^2)	0.85–26.95	9.00	7.10
% Watershed covered by forest	0–27	5.30	7.60
% Watershed covered by grass agriculture	70–99	87.60	8.80
Distance to perennial water (m)	202–12,018	3,180.80	3,026.40

agriculture, and distance to perennial water (Table 1). Three equidistant sampling points were set on each transect, for a total of 15 sampling points per reach, and the multiple values for each variable were averaged for the reach. We measured velocity at these points with a Marsh-McBirney flowmeter using standard methods (Bain and Stevenson 1999). Mean site depth was estimated (to the nearest 0.01 m) from the 15 depth measurements taken along the five transects. Mean wetted width, bankfull width, and bankfull depth were estimated at each transect to the nearest 0.01 m. Suspended sediment, nitrate, and phosphate concentrations were collected by taking three "grab" water samples monthly (December–May) at each of the sampling sites. To determine the suspended sediment concentrations, water samples were filtered and dried; the dry filter weight was subtracted from the total dry weight to obtain the weight of total suspended solids per volume of water (SMEWW 1992). The nitrate concentration was determined by flow injection analysis, which determines nitrate in the sample within a range of 0.20–20 mg N/L (Wendt 1999). The orthophosphate concentration (PO_4^{3-}) was also determined by flow injection analysis colorimetry, which is sensitive in the range of 0.01–2 mg P/L (Prokopy 1994). We used USEPA (1987) procedures to measure the conductivity of unfiltered water samples. In addition, the water temperatures at our sites were continuously recorded by HOBO stowaway temperature loggers with a software-correctible precision of ±0.5°C.

Statistical analyses.—The first three of our objectives did not require statistical data analyses. However, to address the final one—identifying the main factors that influence the numbers of fish and species richness—data were first analyzed by means of nonmetric multidimensional scaling (NMS) ordination. This nonparametric method, combined with Sorensen distance, more effectively represents the gradients in assemblage composition than other, more popular ordination methods (McCune and Grace 2002). This technique assumes no underlying distribution of the data and is robust to departures from normality, so it is recommended for use with ecological data (McCune and Mefford 1999). The NMS ordination was performed using the "medium" autopilot setting of PC-ORD, applied Sorenson (Bray–Curtis) distance measure, and involved a minimum of 200 iterations. This setting executes multiple runs of both real and randomized data, each with a random starting configuration, and selects the best solution by comparing the lowest final stress for each dimensionality (McCune and Mefford 1999; McCune and Grace 2002). In this analysis, the ordination plot was rotated to maximize the variance explained by the most strongly correlated environmental variables. Monte Carlo tests were used to determine the significance of the NMS axes; ordinations were then evaluated by examining the stress values. They were considered stable if the stress value was below 20 with more than 200 iterations and the instability was less than 0.001 (McCune and Grace 2002). Pearson's correlation coefficients (r) were used to quantify the relationships between fish numbers or habitat variables and ordination axis scores. A value of 0.50 was chosen as a cutoff for ecologically meaningful correlations (McCune and Grace 2002). These

TABLE 2.—Fish species sampled, number of specimens caught (*N*), CPUE (number of fish caught/trap or number electrofished/s), and number of sites where species were sampled in intermittent watercourses during winter–spring surveys (22 sites), by gear type. Single asterisks denote exotic species, double asterisks federal- or state-listed threatened or endangered species.

Fish species	*N*	CPUE		Number of sites where sampled
		Minnow traps	Electrofishing	
Threespine stickleback *Gasterosteus aculeatus*	347	0.2729	0.0029	17
Redside shiner *Richardsonius balteatus*	524	0.1978	0.0094	15
Reticulate sculpin *Cottus perplexus*	301	0.1067	0.0047	10
Speckled dace *Rhinichthys osculus*	228	0.1254	0.0032	7
Largescale sucker *Catostomus macrocheilus*	20	0.0063	0.0004	6
Northern pikeminnow *Ptychocheilus oregonensis*	51	0.0113	0.0011	4
Cutthroat trout *Oncorhynchus clarkii*	28	0.0128	0.0005	4
Chinook salmon *Oncorhynchus tshawytscha***	5	0.0022	0.0001	5
Rainbow trout *Oncorhynchus mykiss*	6	0.0011	0.0001	3
Riffle sculpin *Cottus gulosus*	2	0.0011	0.0001	2
Mosquitofish *Gambusia affinis**	9	0	0.0003	4
Goldfish *Carassius auratus**	3	0	0.0001	1
Bluegill *Lepomis macrochirus**	2	0	0.0011	2

analyses were not intended to define species groups that could be used as environmental disturbance indicators. Instead, sites were spatially arranged by their similarities in terms of selected biotic and abiotic variables. Although species numbers and the presence of common species are used in examining the differences among sites, species compositions are not explicitly considered.

To determine whether the absence of fish from some samples could be attributed to a particular combination of factors, the first NMS analysis was performed with only the local-habitat and watershed-scale variables (i.e., no fish data) for all 22 sites. Because the variables were expressed in different metrics and scales, we used a "relativization" method to lower the variation between them and give them similar weight in the ordination (McCune and Grace 2002). Subsequent ordinations included both fish numbers and species in addition to the environmental variables. Owing to seasonal hydrologic changes in the study systems, the analyses that included fish samples were performed two different ways: (1) by individual season and (2) pooled for the entire study period. Samples collected with minnow traps in December–February were used to estimate mean winter values, and samples obtained in March–April were used to calculate mean spring values. A total of 31 samples (i.e., 22 sites $\times$ 2 seasons less 13 fishless samples) were analyzed first. The final ordination used the entire data set and included 17 samples (i.e., 22 sites less 5 fishless sites). There were large differences in CPUE among samples owing to the numbers of juvenile fish in spring and rare species; this affected normality, so the data were $\log_e(x + 1)$ transformed.

Subsequently, we examined the relationships between the environmental variables and fish species richness and CPUE using regression and correlation analyses. Following the rule of thumb of 1 regression variable per 10 observations, we looked at only one- or two-variable regression models. We first checked to see whether the fish species richness or CPUE data were strongly related to natural variables (e.g., watershed area and distance to perennial water). If a natural variable was significantly correlated with a fish variable, we chose the variable with the highest Pearson correlation coefficient. We then looked at the correlation between the residuals of the fish–natural variable regression and the disturbance-related environmental variables (e.g., water chemistry and percent forest cover). The variable most correlated with the residuals was selected for a final two-variable (one natural, one disturbance) multiple-regression model. If no natural variable was related to the fish data, we used an all-subsets multiple-regression approach examining all possible one- and two-variable models and selected the one with the highest r^2. The distance to perennial water and watershed area data were skewed, so they were log transformed before analysis. Fish CPUE was log transformed as described earlier for the NMS analysis.

Results

The abundance and diversity of the 13 fish species found during our survey testify to the substantial presence of fish in the upper Willamette River valley winter floodplain (objectives 1 and 2; Table 2). Not only was the proportion of native to exotic species very high (10:3), natives also dominated the samples numerically. Of the 1,526 fish captured, almost all (99%) belonged to species native to the Willamette

TABLE 3.—Number (N) and CPUE of recently hatched (RH) and juvenile individuals of fish species found in intermittent watercourses during winter–spring surveys (22 sites), by gear type. See Table 2 for additional details.

	Minnow traps			Electrofishing		
Fish species	N	Juveniles	RH	N	Juveniles	RH
Threespine stickleback	0	0	0	64	0	0.0019
Redside shiner	2	0.0021	0	165	0.0051	0
Reticulate sculpin	8	0.0082	0	86	0.0009	0.0018
Speckled dace	14	0.0144	0	54	0.0017	0
Largescale sucker	5	0.0053	0	5	0.0002	0
Northern pikeminnow	9	0.0092	0	25	0.0008	0
Cutthroat trout	3	0.0031	0	0	0	0
Chinook salmon	2	0.0022	0	2	0.0001	0
Mosquitofish	0	0	0	9	0.0003	0
Bluegill	1	0.0011	0	0	0	0

River basin. Redside shiner (524 specimens caught) and threespine stickleback (347) were the most common fish species, found at 77% and 68% of sampling sites, respectively (Table 2). The late-spring trap efficiency for all species combined ranged from 50% to 79%. Although no strong spatial patterns were detected, trap efficiency was negatively affected by both the percentage of vegetated substrate and water velocity.

The presence of recently hatched and juvenile fish showed that a relatively large proportion of the native fish species found in these intermittent watercourses used them as spawning or nursery habitats (objective 3; Table 3). We found recently hatched and juvenile threespine stickleback and reticulate sculpin and juvenile (either young-of-the-year or age-1+) largescale sucker, northern pikeminnow, redside shiner, speckled dace, Chinook salmon, cutthroat trout, and rainbow trout. Minnow traps were much more effective than electrofishing in collecting these young fish (Table 3).

The NMS ordinations used to explain fish distributions (objective 4) revealed some interesting patterns. First, the ordination analysis of all sites based exclusively on local-habitat and watershed-scale variables (independently of fish presence) did not group "fishless" sites in any clear manner; rather, they were widely spread along the two main axes of the NMS plot (stress value = 12.5; instability = 0.001; Figure 2). This suggests that the absence of fish from some of our samples cannot be easily attributed to individual environmental variables or some combination of them. Axis 1 (which explained 54% of the observed variation) was correlated with the percentage of the watershed covered by forest and upstream slope at one end and with the distance to perennial water and the percentage of the watershed covered by grass agriculture at the other end. Axis 2 (which explained only 23% of the observed variation) indicated that water velocity and wetted width played some lesser role in explaining habitat variation.

The NMS ordination that included fish-related variables as well as local-habitat and watershed-scale variables produced a two-dimensional solution in which 95% of the variation among sites was explained by the first two axes (stress value = 8.2; instability = 0.00001). Axis 1 accounted for 69% of the variation and was correlated with two watershed-scale variables (at $r > 0.5$): the distance to perennial water and the percentage of watershed covered by forest as well as fish species richness; axis 2, by contrast, did not show a strong correlation with any variables and only explained the remaining 26% of the variation (Figure 3). Most of the sites in the west side subbasins (the Long Tom, Luckiamute, and Marys rivers) were toward the left end of axis 1 (i.e., with higher percentages of the watershed area covered by forest).

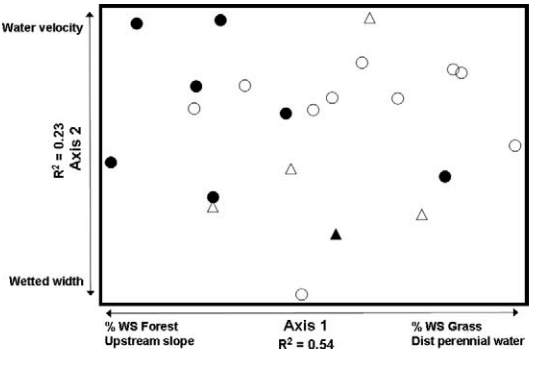

FIGURE 2.—Nonmetric multidimensional scaling ordination plot of physical habitat and watershed-scale (WS) variables. Black symbols indicate sites in subbasins west of the Willamette River main stem, white symbols sites in subbasins east of it; circles indicate sites with fish, triangles sites without fish. See the text for a more detailed explanation of the variables.

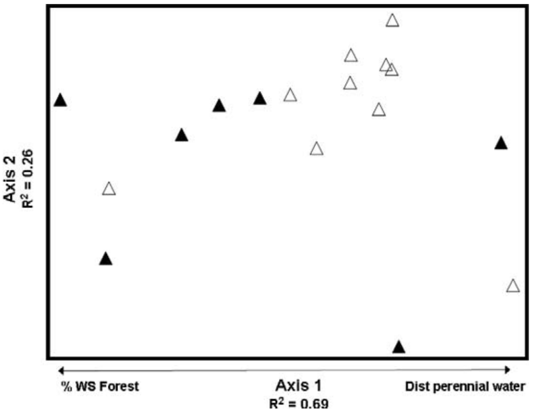

FIGURE 3.—Nonmetric multidimensional scaling ordination plot of physical habitat and watershed-scale variables and fish species sampled with minnow traps (regional discrimination). Black symbols indicate sites in subbasins west of the Willamette River main stem, white symbols sites in subbasins east of it. See the text for a more detailed explanation of the variables.

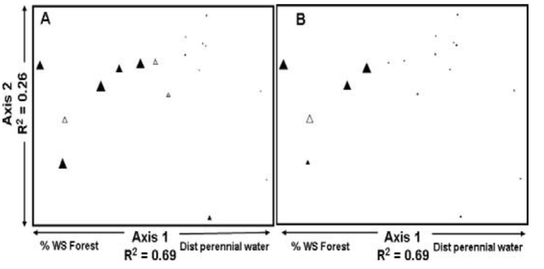

FIGURE 4.—Nonmetric multidimensional scaling ordination plot of the number of **(A)** reticulate sculpin and **(B)** speckled dace sampled with minnow traps. The sizes of the symbols denote the relative abundances of the two species in various samples relative to those in all samples. Black symbols indicate sites in subbasins west of the Willamette River main stem, white symbols sites in subbasins east of it. See the text for a more detailed explanation of the variables.

In contrast, most of the sites in the Calapooia River and Muddy Creek subbasins were toward the right end (with less forest cover and greater distance to perennial water; Figure 3). Axis 1 was also negatively correlated with species richness (with higher species richness toward the left end). Only two of the four most common species showed some spatial segregation in our ordination. Reticulate sculpin ($r = -0.848$; Figure 4A) and speckled dace ($r = -0.786$; Figure 4B) seemed to prefer west side sites (with shorter distances to perennial water and more forest cover). The other two most common species, threespine stickleback and redside shiner, showed more homogeneous distributions among all sampling sites.

Regression analyses showed that among the natural environmental variables, fish species richness was most strongly related to the distance to perennial water ($r = 0.42$, $P = 0.049$; Figure 5A). The best-fit regression line had an intercept of 8.49 and a slope of −1.89, yielding an expected richness of 4.7 species at a distance of 100 m from perennial water. At 5,000 m the expected fish richness declines to 1.5 (Figure 5A). The residuals of this regression were most strongly related to the percentage of watershed covered by forest ($r = 0.57$, $P = 0.006$; Figure 5B). They were also strongly related to conductivity ($r = -0.56$, $P = 0.005$) and, to a lesser degree, mean water velocity ($r = 0.50$, $P = 0.032$). In Figure 5B, the positive residuals are those associated with higher species richness than expected given the distance from perennial water. Negative residuals indicate fewer species than expected for their distance. Thus, after adjusting for the natural gradient of distance from perennial water, higher species richness was related to higher percentages of forest cover, lower conductivity, and higher velocity. The two-variable multiple-regression model that best predicted species richness included the distance to perennial water and the percentage of watershed covered by forest ($r^2 = 0.60$, $P < 0.0001$).

Fish CPUE was not significantly related to any of the natural variables. In all of the single-variable regression models, CPUE was most correlated to the percentage of watershed covered by forest ($r = 0.50$, $P = 0.017$) and mean water velocity ($r = 0.46$, $P = 0.031$). The all-subsets multiple regression produced a two-variable model in which conductivity and nitrate were most related to CPUE ($r^2 = 0.61$, $P < 0.0001$). The next best multiple-regression model related to CPUE included nitrate and the percentage of watershed covered by forest ($r^2 = 0.52$, $P = 0.0009$).

Discussion

Numerous fish species, most of them native, inhabit the network of intermittent watercourses flowing through upper Willamette River valley agricultural fields in winter and spring. The seasonal habitats provided by these watercourses offer not only winter refuge but also conditions appropriate for fish spawning and juvenile rearing. The environmental factors that had some influence on the numbers of fish and species richness were few and included both natural variables (e.g., the distance to perennial water) and disturbance indicators (e.g., the percentage of watershed covered by forest and water conductivity).

The NMS ordination analysis excluding fish data, which clearly showed that fishless sites were not greatly influenced by single or multiple environmental variables, presented a west-to-east trend in relation to

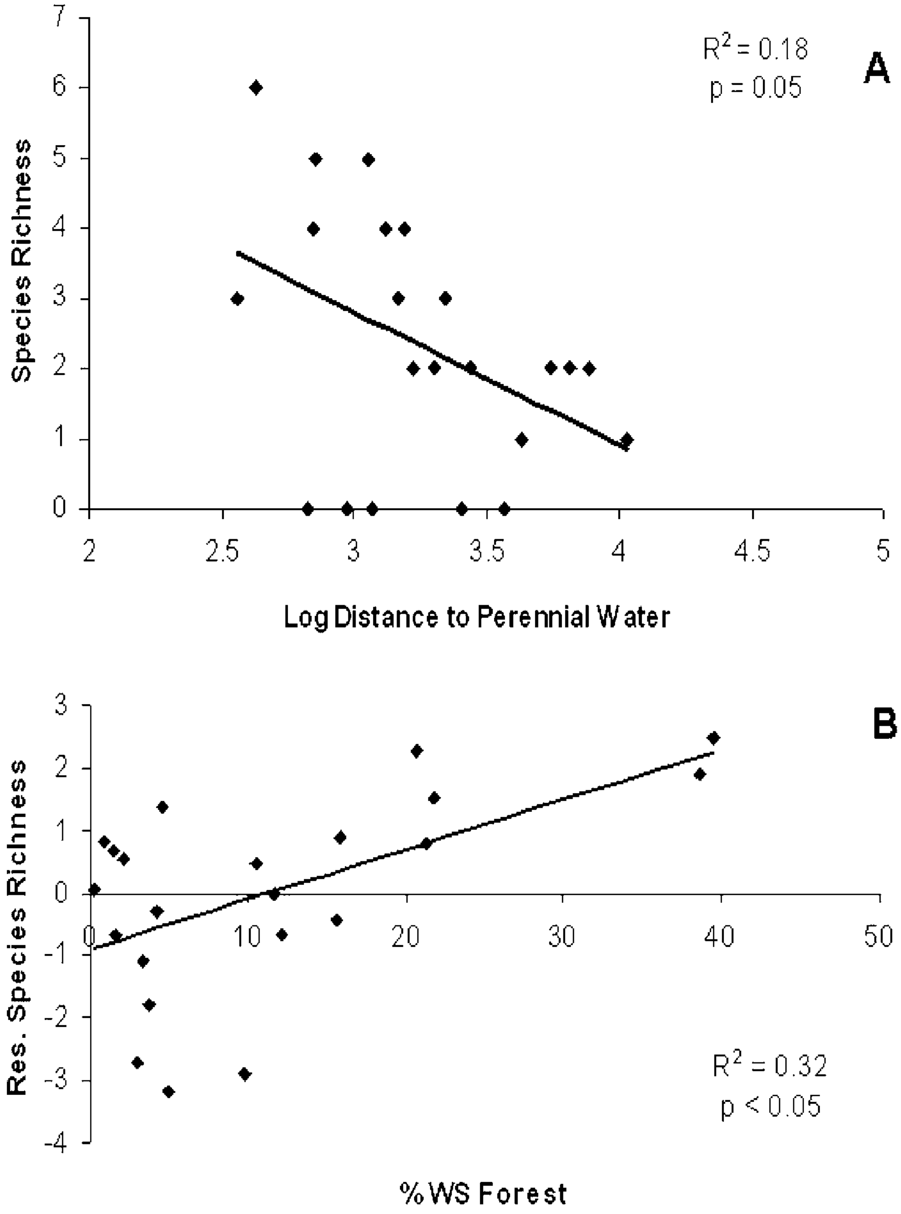

FIGURE 5.—Regressions of (**A**) fish species richness on the log-transformed distance to perennial water and (**B**) the residuals of fish species richness on the percentage of the watershed covered by forest.

those watershed- and local-scale variables that were identified as the most relevant in the classification of sites. West side sites were associated with subbasins that had more watershed area covered by forest and steeper slopes, which in turn correlated with high water velocities. The east side sampling sites were in more expansive floodplains, with greater distances to perennial water and within subbasins that had more of their total area under agricultural use. None of these differences should be unexpected because, though all of our sites are within visually similar grass seed–producing fields in seasonal floodplains, the sites in the western subbasins fall within the Cascade and Coast Range ecoregions and those in the eastern subbasins within the Willamette River valley ecoregion. As Waite and Carpenter (2000) reported, these ecoregions are characterized by different elevations, stream gradients, plant communities, and water chemistry.

East and west side streams also showed marked water quality differences in early winter, probably owing to soil type differences. The levels of water conductivity and suspended sediments and the concentrations of nitrates and phosphates tended to be higher in the east side streams. The east side spike in water nutrient concentrations and conductivity could be attributed to soil mineralization and fertilizer build-up during the dry summer months and their subsequent leaching from impervious clay soils with the first rains in late fall and early winter (Sattell et al. 1999).

The ordination analyses that included the biotic variables fish species richness and CPUE showed that the former was influenced by two watershed-scale variables: the distance to perennial water and the percentage of watershed covered by forest. The distance to perennial water was negatively correlated with the number of species, while the percentage of land under forest cover had a positive relationship. The negative relationship between species richness and the distance to perennial water is easily understood when dispersal options are considered. Stream networks only allow for bidirectional but linear fish migrations, and except during large flood events, fish can only access habitats within intermittent watercourses by moving upstream from reaches with perennial water. Hence, the distance traveled by fish is proportional to the number and range of upstream barriers (culverts, jumps in channel elevation, etc.) they encounter, which progressively restrict upstream species richness.

Regression analyses revealed that at the local-habitat scale, the number of fish species present was inversely related to water conductivity (potentially a disturbance indicator) and directly related to water velocity (a function of channel morphology but also of stream gradient). These relationships indicate that intermittent watercourses within subbasins that are more heavily forested and, because of their topography, less impacted by land use activities such as agriculture and residential development, sustained a relatively richer array of native fish species (Figure 5). In contrast, seasonal systems in more expansive floodplain networks that can be at relatively greater distances from perennial waters and within predominantly agricultural subbasins attracted fewer fish species. The combined effects of regional and local variables created a mosaic of physical and chemical habitat conditions with varying suitability to fish. Fish species did not distribute evenly through intermittent streams and ditches, and regional differences in their distributions were evident. For example, reticulate sculpin and speckled dace, two of the most common species in our samples, were rare and even absent in many east side sites. The reticulate sculpin is considered relatively tolerant to poor water quality (Hughes et al. 1998) and was reported to be a dominant species in both heavily altered and forested sites in the Willamette River valley during summer (Waite and Carpenter 2000). However, our study, like those of Bond et al. (1988) and Bateman and Li (2001), showed that during winter and spring this species was most often found in sites with relatively fast water and higher-gradient channels that drained subbasins with forested headwaters. Although threespine stickleback were present in almost all sites, they were the dominant species in most of the east side systems. Sticklebacks were found the furthest away from perennial water, as far as 12 km from the nearest perennial stream. This species is considered a species complex characterized by multiple life history strategies and subspecies, which helps explain their ability to effectively colonize remote temporary habitats as they become available (Bell and Foster 1994).

The number of native fish species was much greater than that of exotics (10:3) in the intermittent watercourses than has been reported for the Willamette River main stem (27:14; Hulse et al. 2002). These fish communities also differed markedly from those observed by Waite and Carpenter (2000), who reported proportions of native to exotic species (13:8) in other low-gradient Willamette River valley streams more similar to that of Hulse et al. (2002). These differences can probably be explained by dissimilarities not only in the types of habitats sampled but also in the timing of the surveys. Whereas we sampled intermittent watercourses from early winter to mid-spring, Waite and Carpenter (2000) sampled perennial urban and agricultural streams during the summer. Still, they found an average 90% relative abundance of native fish even in these heavily impacted sites. So regardless of these differences, the Willamette River valley still has a relatively higher ratio of native to exotic fish species than the greater Central Valley in California, where May and Brown (2000) found 13 native and 23 introduced species.

All of our study sites are dry in the summer. The few exotic species we captured (<1% of the total catch in our surveys), including bluegill, mosquitofish, and goldfish, are known to inhabit warm waters and were found exclusively in the spring at sites not far from perennial water. For exotic fish species in the Willamette River valley, winter use of intermittent watercourses is probably limited by physiological constraints resulting from the low water temperatures that prevail in these channels or developmental requirements for spawning in spring and summer. Not until the daily maximum water temperature exceeded 20°C in the spring did we find exotic fish in our samples. Because exotic species do not seem to respond to the seasonal availability of flooded habitat during the winter, these intermittent habitats might represent critical refuge for some of the most vulnerable native fishes. As the flooding period coincides with low water temperatures and the migratory response of exotic species does not occur until spring, the patterns observed in the current climate of the Willamette River valley tend to support the prediction that hydrologic regimes function as an effective barrier to invasive warmwater fish species, as has been suggested for California fish assemblages (Moyle and Light 1996).

The other fish-related variable we examined, fish abundance (expressed as CPUE), was not clearly associated with any of the variables included in the ordination analysis. Only two multiple-regression models, one with water conductivity and nitrate concentration and the other with conductivity and the percentage of watershed covered by forest (all of which are land disturbance indicators), accounted for a significant amount of the variation in fish numbers. The distance to perennial water was expected to have a clear effect on fish CPUE, but the presence of large schools of sticklebacks in different locations weakened the relationship between these two variables.

The intermittent watercourses of the upper Willamette River valley provide habitats that are suitable for spawning and juvenile rearing by several native fish species. Early life stages of the largescale sucker, northern pikeminnow, speckled dace, reticulate sculpin, threespine stickleback, and redside shiner were observed in our late-winter and early-spring samples. The indirect evidence of fish reproduction (i.e., the presence of recently hatched fish) in these intermittent watercourses agrees with the findings of Sommer et al. (2004) in California, who observed native suckers and minnows spawning and rearing in seasonally inundated habitats (Sacramento sucker *Catostomus occidentalis* and Sacramento splittail *Pogonichthys macrolepidotus*). As in other studies in which juvenile salmonids were located in agricultural channels and ditches during winter and early spring (Giannico 1996; Giannico and Healey 1998b; Sommer et al. 2001), we found juvenile Chinook salmon, cutthroat trout, and steelhead or rainbow trout in intermittent agricultural watercourses.

The high proportion of native species found in the intermittent watercourses we evaluated emphasizes the ecological significance of flooding and stream network expansion in the Willamette River valley. The upper valley was flooded extensively and much more often before the construction of dams and the creation of ditches and revetments (Boag 1992; Benner and Sedell 1997). The annual inundation of the floodplains and expansion of stream networks represents a remnant of the much broader floodplain–river complex that was present before Euro-American settlement of the valley (Hulse et al. 2002). According to the flood pulse concept (Junk et al. 1989) and its subsequent extension by Tockner et al. (2000), inundation of floodplains and the expansion and contraction of stream networks are the principal forces controlling productivity and shaping biotic communities in river–floodplain systems. Many of the species found in these communities are adapted to exploit the cyclically accessible resources of the floodplain. The river–floodplain connections help to explain the presence of native fish in the expanded stream network of the upper Willamette River valley during winter and spring.

Improved understanding of river–floodplain connections and their physical and biological processes can help us identify the potential impacts of land use activities in these lowland systems. In the upper Willamette River valley, many acres of low-lying swales and dry channels are tilled and cleaned annually during the summer. Often, these areas are seasonally flooded and not the best seed production sites (Steiner et al. 2000), rendering them potentially more valuable for preserving river and floodplain functions. Federal conservation programs currently compensate participating farmers for implementing practices that contribute to the conservation of aquatic resources. Traditionally, the intermittent watercourses we surveyed have not been considered fish habitat because they are essentially dry half the year. However, based on the diversity of native fish species and the abundance of fish we found in these winter- and early-spring-running "streams," we believe that these agricultural watercourses are important seasonal habitats with valuable floodplain functions. Furthermore, these agricultural watercourses are appropriate for the conservation practices such as wetland restoration, stream habitat improvement, the creation of fish passages and riparian buffers, and others that contribute to conservation of native aquatic species in managed landscapes. With funds available through the U.S. Department of Agriculture and other sources, farmers could be compensated for contributing to the long-term protection of native fish species and their winter habitats in the Willamette River valley.

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