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Implications of Floodplain Isolation and Connectivity on the Conservation of an Endangered Minnow, Oregon Chub, in the Willamette River, Oregon

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Abstract.—The objectives of this study were to determine the distribution and abundance of endangered Oregon chub *Oregonichthys crameri*, a small floodplain minnow endemic to the Willamette Valley of western Oregon; to describe the fish communities in current and historic chub habitats; and to establish new populations through introductions. Various sampling gears were used, including seines, minnow traps, dip nets, and a gill net. Oregon chub distribution was found to be restricted in comparison with their historical range, whereas nonnative fishes were widespread in the off-channel habitats preferred by Oregon chub. Oregon chub were absent, or low in abundance, when nonnative fishes were present, and several populations declined or were extirpated when their habitats were invaded by nonnative fishes. Isolated habitats with low connectivity supported larger populations of Oregon chub and were less likely to contain nonnative fish species than were habitats with high connectivity. In habitats that supported abundant Oregon chub populations, chub were often the numerically dominant fish species. Results suggest that increasing the connectivity of floodplain habitats in a system where nonnative fishes are widespread may be detrimental to the conservation and recovery of this species.

Channelization and the construction of flood control dams restricts or eliminates many of the linkages and interactions between the river and its floodplain (Gabriel 1993). Suppression of flooding alters the hydrologic cycle of riverine environments and impacts native fish that rely on floodplain habitats (Bayley 1991; Osmundson and Burnham 1998; Modde et al. 2001). The connectivity of off-channel habitats to the river can be important for persistence of local populations of fish, and when substantial habitat fragmentation occurs, metapopulations can undergo severe decline (Hanski and Gilpen 1997). In the past 150 years, the channel length of the Willamette River drainage has been drastically reduced by the construction of 13 major flood control dams; large-scale removal of snags for navigation, channelization, and revetments; and the drainage of wetlands to increase the land available for river bottomland agriculture (Sedell and Froggatt 1984; Benner and Sedell 1997). Floods in the winter and spring months were common before construction of the dams (1941–1969), averaging 14 floods above bank full per decade from about 1884 through 1969 (U.S. Corps of Engineers 1970). What would have been a 10-year flood event before construction of the dams now has a 100-year return interval (Benner and Sedell 1997).

The Oregon chub *Oregonichthys crameri* (Snyder 1908) is a small floodplain minnow endemic to the Willamette Valley of western Oregon (Markle et al. 1991). Historically, this species was widely distributed throughout the Willamette Valley (Markle et al. 1991). Oregon chub prefer off-channel habitats with minimal or no flow, an abundance of vegetation, and depositional substrate (Pearsons 1989; Scheerer and McDonald 2000). Studies conducted in the 1960s (Bond 1966), 1970s, and 1980s (Bond and Long 1984; Markle et al. 1991) revealed the distribution of Oregon chub to be restricted, estimated at approximately 2% of their historic range. The loss of habitat and the restricted range led to the species being listed as endangered in 1993 (U.S. Fish and Wildlife Service 1993).

Introduction of nonnative fishes into the Willamette River, starting in the late 1800s (Dimick and Merryfield 1945; Lampman 1946; McIntosh et al. 1989), has been a major factor affecting the distribution and abundance of Oregon chub. Markle et al. (1991) found nonnative fishes were common in historic Oregon chub habitats that no longer contained Oregon chub. Nonnative fishes, especially centrarchids and *Ameiurus* spp., have been widely implicated in the decline of native fish (Moyle 1976; Lemly 1985; Rinne and Minckley

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1991; Newman 1993; Simon and Markle 1999); common in the Willamette River basin, they are considered to be the greatest current threat to Oregon chub populations and to present the largest obstacle to the recovery of chub (U.S. Fish and Wildlife Service 1998).

The objectives of this study were to (1) describe the distribution and abundance of Oregon chub populations; (2) describe the fish communities in Oregon chub habitats; and (3) establish new populations of Oregon chub through introductions of the species. This paper describes the current knowledge of the distribution and status of Oregon chub populations and their habitats, the proliferation of nonnative fishes in these habitats, and the implications of isolation and connectivity on the conservation of this species.

Methods

Oregon chub distribution surveys were conducted by the Oregon Department of Fish and Wildlife throughout the Willamette Valley from 1991 to 2000. A total of 471 off-channel habitats and small tributaries were sampled in the basin, distributed over 14 subbasins and the main-stem Willamette River (Figure 1).

For security reasons, only generalized site location descriptions are presented in this paper, because many site names describe landmarks easily found on local maps. Between 1991 and 2000, Oregon chub were found in three major subbasins (Middle Fork Willamette River, Coast Fork Willamette River, Santiam River) and two small mid-Willamette River tributaries. For this paper, sites in the Middle Fork Willamette River drainage were coded beginning with the letter ''M,'' sites in the Coast Fork Willamette River basin with the letter ''C,'' sites in the Santiam River drainage with the letter ''S,'' and sites in the main-stem and mid-Willamette River tributaries with the letter ''W.'' Within each subbasin, site codes were assigned numbers in ascending order, based on the population estimate for 2000. For example, the largest chub population in the Santiam drainage in 2000 was coded S1, the second largest was S2, and so on.

Fish sampling was conducted with a combination of gear types. At least 20% of the surface area of each site was sampled, including the range of habitat types present at each location. Most habitats were sampled with a 1-m × 5-m seine (64-mm mesh). In deep sites (>1.5 m maximum depth) or sites where seining was inefficient because of large amounts of woody debris, baited minnow traps, dip nets (32-mm mesh), and a gill net (four panels measuring 7.6 m long × 1.8 m deep, with square mesh sizes of 127, 191, 254, and 381 mm) were used. Minnow traps were regularly spaced at a density of one trap per 100–250 m^2 of surface area, as many as 60 traps per site. Dipnetting was conducted in shallow shoreline areas and around woody debris. The gill net was set to extend from the shore into deeper water and was fished for a minimum of 2 h. All fish captured were identified, counted, and measured for length in 25-mm increment categories.

Population estimates were obtained for Oregon chub (>35 mm total length) at selected locations between 1992 and 2000. Population estimates for other fish species present at locations containing Oregon chub were obtained beginning in 1997. At that time, population estimates were attempted at all locations containing chub. When catch rates were very low, attempts to estimate abundance were abandoned. The numbers of centrarchid fishes captured during our sampling efforts were low compared with visual observations of their abundance. No population estimates were obtained for these species. Minnow traps measuring 23 cm × 46 cm with 64-mm mesh were used to capture fish for marking. The traps were baited with a half of a slice of bread and set for 3–18 h. Minnow traps were regularly spaced at a density of one trap per 100–250 m^2 of surface area, as many as 60 traps per site, to ensure that fish were marked from all locations within the pond or slough. When repeat estimates were obtained at a location in subsequent years, the length of time a trap was set was related to the expected fish abundance and to the catch rates of fish at each location.

All fish were given a partial upper caudal fin clip and then returned to the water. Marked fish were distributed throughout the pond to promote random mixing with the unmarked segment of the population. During the first 2 years of the study and when catch rates were particularly low, marking was done over a period of several days. Population size was estimated by using an adjusted Peterson mark–recapture procedure (Ricker 1975), based on the total number of marked fish and on the catch and recaptures from the last sample date. The last sample date was separated by at least 2 days from the last date of marking, to allow time for adequate mixing of the marked and unmarked segments of the population. Confidence intervals were calculated by using a Poisson approximation (Ricker 1975). No estimates were made for age-0 fish (<35 mm), which were too small to be cap-

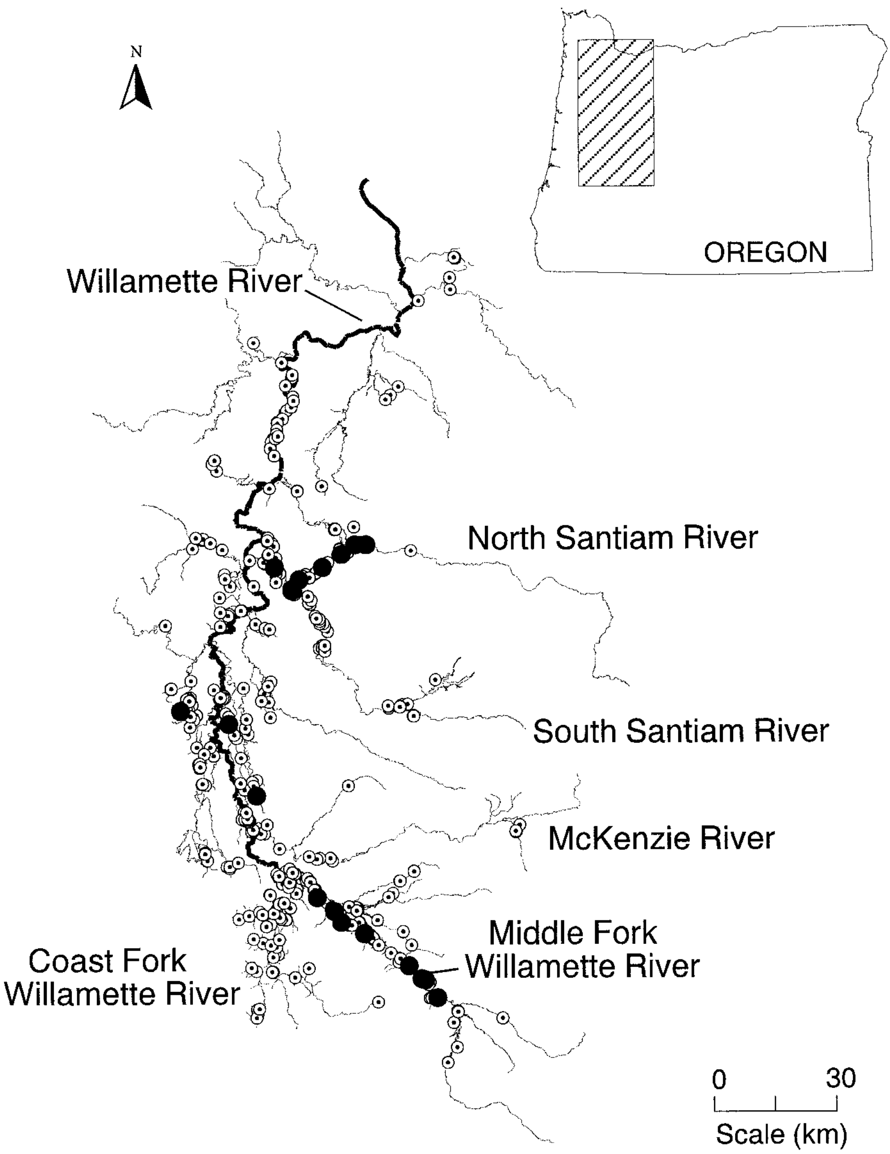

FIGURE 1.—Distribution of sampling effort during 1991–2000 surveys. Circles with center dots indicate sites where sampling occurred; solid circles indicate the current distribution of Oregon chub.

tured in the minnow traps (author's unpublished data). Regeneration of caudal fins was rapid after marking, substantial regeneration being noted as early as 3–4 weeks postmarking. In subsequent years, caudal fin clips from the previous years' marking were almost completely regenerated and easily distinguished from new fin clips.

In 1994, 50 marked fish were placed in a live box in the pond and held for 48 h after marking. No mortality of marked fish was observed over this period (Scheerer et al. 1995). Also in 1994, recapture rates for marked chub were compared by using both minnow traps and seines to test the assumption that there was an equal probability of capturing marked and unmarked fish (no trap avoidance or attraction to traps). No consistent differences were observed between these gear types (author's unpublished data).

The connectivity of a habitat to the river or reservoir, described for sites containing Oregon chub, was based on the degree of isolation of the off-channel habitat from the adjacent water body. Sites with high connectivity had year-round connection, yearly influx of water during the spring months, or a culvert connection to the adjacent river or reservoir. Sites with low connectivity were isolated from the adjacent river by impassable culverts, beaver dams, regulated flows, or some combination of these. All sites characterized with low connectivity remained isolated during two 1996 flood events (approximate 10- to 20-year recurrence interval after construction of the dams).

Abundance estimates were used to determine the status of Oregon chub in relation to recovery criteria set forth in the Oregon Chub Recovery Plan (U.S. Fish and Wildlife Service 1998). The Recovery Plan adopted the following criteria for downgrading the species from endangered to threatened: (1) Establish and manage 10 populations of at least 500 adults each; (2) maintain stable or increasing trends in all populations for 5 years; and (3) ensure that at least three populations are located in each of the three major subbasins (Middle Fork Willamette, Santiam, and main-stem Willamette). Delisting, or removal from the endangered species list, will occur when 20 populations totaling 500 or more adults maintain a stable or increasing trend for 7 years. At least four populations must be located in each of the three subbasins. Management of these 20 populations must be guaranteed in perpetuity.

Abundance trends were defined quantitatively as increasing, declining, stable, not declining, or unknown. A linear regression of abundance over time was calculated for each population for the past 5 years (1996–2000). When the slope of this regression was negative and significantly different from zero ($P < 0.05$), the population was defined as exhibiting a declining trend in abundance. When the slope was positive and significantly different from zero ($P < 0.05$), the population was defined as exhibiting an increasing trend in abundance. When the slope was not significantly different from zero ($P > 0.05$), then I calculated the coefficient of variation of the abundance estimates for the past 5 years. When this coefficient of variation was less than 0.5, the population was defined as stable; otherwise, the population was defined as not declining in abundance. At locations where no abundance estimates were obtained because of low catch rates, the abundance trend was defined as unknown.

Criteria for selection of Oregon chub introduction sites included the following: (1) Sites must be secure from imminent or future threats of habitat destruction and invasion by warmwater fish, (2) sites must fulfill all life history requirements (adequate vegetation and temperatures), and (3) sites must contain sufficient habitat to support a population of 500 or more adult fish. Sites included ponds that were at least 0.5 ha in size with silt and/or organic substrate, varied and abundant aquatic vegetation, little or no water velocity, water depth mostly less than 2 m, limited use or access by the public, an absence of nonnative fish species, and summer water temperatures exceeding 16°C. Sites with low connectivity were preferred because of the lessened risk of invasion by nonnative fishes. Site modifications were permitted for sites to meet these criteria.

Habitat and aquatic community variables at locations supporting Oregon chub populations were evaluated by using correlation and multiple regression models with SAS statistical software. A multiple regression model was developed with Oregon chub population abundance as the dependent variable. Because mark–recapture abundance estimates were unavailable at some chub locations due to low catch rates, a catch-per-unit-effort estimate was devised, 1 unit of effort being defined as 12 minnow traps fished for 3 h. Fourteen independent variables were used in the model: wetted surface area, vegetated area, minimum (late summer) wetted surface area, site connectivity, species richness, number of species of native fish, total fish abundance (all species summed), presence/absence of nonnative fishes, number of days when maximum temperature exceeded 16°C (the minimum temperature required for chub to spawn; author's unpublished data), number of species of native amphibians observed, presence/absence of nonnative bullfrogs *Rana catesbeiana* (potential predators), presence/absence of native redlegged frogs *R. aurora* (species using similar habitats), presence/absence of native western pond turtles *Clemmys marmorata* (species using similar habitats), and presence/absence of beavers *Castor canadensis*. The surface area and vegetated area of each site was estimated from cross-sectional transects run every 15 m; distances were measured with a laser range finder. Water temperatures were monitored by using Hobo data loggers that recorded temperatures at 5-h intervals. Variables were added to the model in a stepwise fashion (adding a variable required $r^2 = 0.15$). Introduced populations were excluded from the model.

Results

In 2000, 23 locations were identified that contained Oregon chub in the Willamette basin. Eight

TABLE 1.—Oregon chub population abundance, status, and trends. Mark–recapture population estimates were obtained at locations where totals exceed 39 fish. Totals less than 40 fish (bold) are the numbers of fish captured. Numbers in parentheses are the numbers of fish introduced at the sites. See text for an explanation of site codes.

Site	Year 1992	1993	1994	1995	1996	1997	1998	1999	2000	5-year trend	Connectivity
W1[a]						(500)	460	4,860	14,090	Increasing	Low
M1		8,770	7,540	7,130	4,470	4,020	4,440	4,780	5,050	Stable	Low
M2[a]					(500)	475	1,420	6,310	5,030	Increasing	Low
M3[a]	**3**			**0**	**1**	**9**	**25**	160	4,580	Increasing	Low
M4		1,640	4,780	3,830	4,220	3,790	3,650	2,860	3,830	Stable	Low
M5								3,010	3,570	Stable	Low
M6		690		780		3,160	3,030	3,020	2,980	Stable	Low
M7		4,010		1,910		2,010	5,350	3,780	2,360	Stable	Low
M8	780			140	40	2,250	1,280	1,180	2,320	Not declining	High
W2[a]							(105)	360	1,750	Increasing	Low
W3		340	600	460	470	520	620	510	730	Stable	Low
S1					8,340	8,700	1,830	860	360	Declining	High
M9			**4**	**8**		**2**	**21**	480	140	Unknown	High
S2[a]								(85)	80	Stable	High
S3						**5**	**2**	**3**	**13**	Unknown	High
S4			1,250		830	320	250	**13**	**4**	Declining	High
S5				**2**	**3**	**2**	**0**	**13**	**4**	Unknown	High
M10	**0**								**3**	Unknown	High
M11	**7**			**6**				**1**	**2**	Unknown	High
S6						**2**	**0**	**0**	**2**	Unknown	High
W4[b]			**26**			**2**				Unknown	High
W5[b]		**5**			**2**					Unknown	High
S7							**3**	**4**	**1**	Unknown	High
S8		**5**			**2**	**5**	**0**	**2**	**0**	Unknown	High
S9						**2**			**0**	Unknown	High
M12[a]			(525)	3,500	5,610	7,160	3,490	**0**	**0**	Extinct?	High
M13						**3**	**0**	**0**	**0**	Extinct?	High
M14			**3**		**0**		**0**	**0**	**0**	Extinct?	High
C1	**1**	**2**	**0**		**0**			**0**	**0**	Extinct?	High

[a] Oregon chub reintroduction sites.
[b] Access was denied 1997–2000.

of these were from the list of 29 historic sites in museum records, 5 were locations where populations were introduced between 1988 and 2000, and 10 were new populations discovered since 1991. Distribution (Figure 1) included the Santiam River (7 sites), three small tributaries to the mid-Willamette River (5 sites), and the Middle Fork Willamette River (11 sites). The known distribution in 2000 was broader than that reported in the early 1990s, when only three populations, restricted to about 30 km of the Middle Fork Willamette River, were known to exist (Markle et al. 1991). The current expanded known distribution of Oregon chub is probably the result of increased sampling effort rather than range expansion.

Oregon chub population abundance trends during this study ranged from relatively stable to quite variable (Table 1). Abundance estimates ranged from 40 fish to more than 14,000 fish per population. The lower 95% confidence limits for the estimates were fairly tight, averaging 76% of the estimate (95% confidence interval, 73–78%; range, 50–94%). Three of the four largest Oregon chub populations in 2000 were introduced populations. Oregon chub were more widespread and abundant in the Middle Fork Willamette River drainage than in the other Willamette River subbasins. Eight of the 11 largest populations (>500 fish) were found in the Middle Fork Willamette River drainage. Small drainages of the mid-Willamette River contained five populations of Oregon chub in 2000. Three of these populations totaled 500 or more individuals; the two largest populations were introduced. Oregon chub were found at seven locations in the Santiam River drainage in 2000, yet none of these populations totaled more than 500 fish. Two of the largest populations in the Santiam River drainage declined substantially in abundance during this study. In 2000, six populations met the U.S. Fish and Wildlife Service's recovery criteria (>500 fish with a stable or increasing abundance trend).

Oregon chub abundance was low at locations where nonnative fishes were present (Table 2). In

TABLE 2.—Fish communities and species richness at locations containing Oregon chub in the Willamette River, Oregon, in 2000. Oregon chub abundance estimates were obtained using mark–recapture protocols except those shown in bold, which are the numbers of fish captured. Fish codes are as follows: CHUB = Oregon chub, RSS = redside shiner *Richardsonius balteatus,* COT = sculpins *Cottus* spp., D = speckled dace *Rhinichtys osculus,* NPM = northern pikeminnnow *Ptychocheilus oregonensis,* SKB = threespine stickleback *Gasterosteus aculeatus,* SU = largescale sucker *Catostomus macrocheilus,* SR = sandroller *Percopsis transmontana,* SAL = salmonids (i.e., cutthroat trout *Oncorhynchus clarki,* rainbow trout *O. mykiss,* and chinook salmon *O. tshawytscha*), LAM = Pacific lamprey *Lampetra tridentata,* WF = mountain whitefish *Prosopium williamsoni,* CENT = centrarchids (i.e., bluegill *Lepomis macrochirus,* largemouth bass *Micropterus salmoides,* and pumpkinseed *L. gibbosus*), MF = western mosquitofish *Gambusia affinis,* and B = brown bullhead *Ameiurus nebulosus* or yellow bullhead *A. natalis.*

		Native fish											Nonnative fish			Species richness		
Site	2000 abundance	CHUB	RSS	COT	D	NPM	SKB	SU	SR	SAL	LAM	WF	CENT	MF	B	Native	Nonnative	Total
W1[a]	14,090	X														1	0	1
M1	5,050	X	X		X											3	0	3
M2[a]	5,030	X			X											2	0	2
M3[a]	4,580	X			X					X						3	0	3
M4	3,830	X	X	X	X	X		X		X						7	0	7
M5	3,570	X	X	X	X	X		X		X						7	0	7
M6	2,980	X	X	X	X			X								5	0	5
M7	2,360	X	X	X	X	X	X			X						7	0	7
M8	2,320	X	X	X		X										4	0	4
W2[a]	1,750	X														1	0	1
W3	730	X	X	X	X		X			X					X	6	1	7
S1	360	X	X	X	X	X	X	X			X	X	X		X	9	2	11
M9	140	X	X		X											3	0	3
S2[a]	80	X														1	0	1
S3	**13**	X	X	X	X	X	X	X	X				X			8	1	9
S4	**4**	X	X	X	X	X	X	X	X		X		X	X		9	2	11
S5	**4**	X	X	X	X	X	X	X								7	0	7
M10	**3**	X	X	X	X					X						5	0	5
M11	**2**	X	X	X	X		X	X							X	6	1	7
S6	**2**	X	X	X	X	X		X								6	0	6
W4	**2**[b]	X	X	X	X		X	X	X							7	0	7
W5	**2**[b]	X	X			X							X	X	X	3	3	6
S7	**1**	X	X	X			X						X	X		4	2	6
S8	**0**	X	X	X	X	X	X						X			6	1	7
S9	**0**	X	X	X	X	X	X	X	X							8	0	8
M12[a]	**0**	X											X	X		1	2	3
M13	**0**	X	X	X		X	X						X			5	1	6
M14	**0**	X											X	X		1	2	3
C1	**0**	X	X			X			X				X	X		4	2	6

[a] Oregon chub reintroduction sites.
[b] Site access was denied in 2000. Abundances listed are the number of Oregon chub captured the last time the site was sampled.

2000, only one location that supported an abundant population (>500 fish) of Oregon chub (site W3) contained nonnative fishes. Oregon chub was the most abundant fish species at 9 of the 11 locations where their abundance exceeded 500 fish and was one of the least abundant species at locations where nonnative fish were present (Figure 2).

The fish species found most frequently at locations containing Oregon chub, excluding those sites where chub were reintroduced, were redside shiners (96%), sculpins (78%), speckled dace (74%), northern pikeminnow (61%), threespine sticklebacks (52%), and largescale suckers (48%; Table 2). Fish communities containing Oregon chub, redside shiners, speckled dace, and sculpins were found at 65% of these locations.

More than half (58%) of the locations sampled in the Willamette River drainage contained nonnative fishes (205 of 356 sites), excluding locations where no fish were collected ($N = 115$). Centrarchids and *Ameiurus* spp., the nonnative species considered to pose the greatest threat to Oregon chub, were common in off-channel habitats (Table 3). The subbasins with the greatest concentration of nonnative fishes—the main-stem Willamette River (48 of 70 sites; 69%), the Coast Fork Willamette River drainage (27 of 51 sites; 53%), mid-Willamette River tributaries (50 of 107 sites;

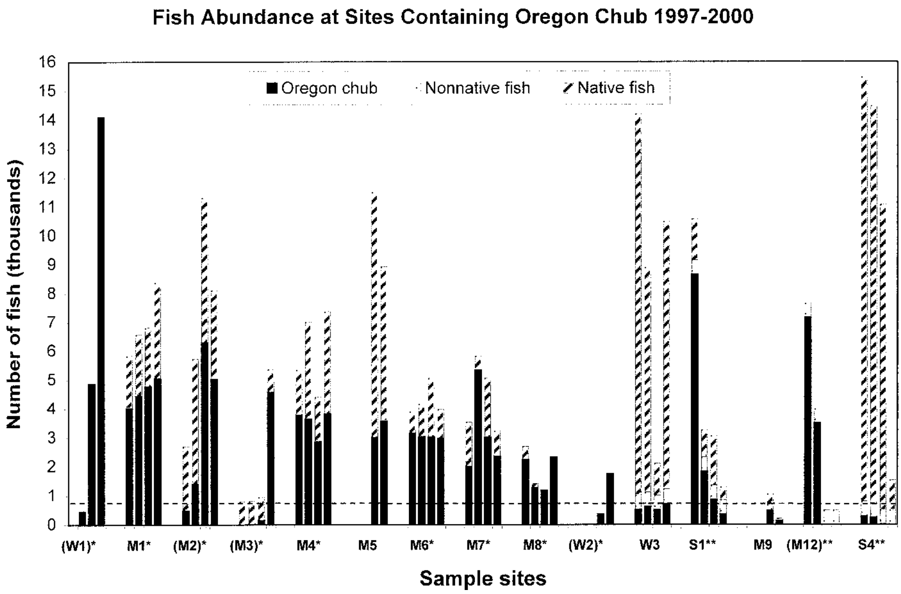

FIGURE 2.—Abundance estimates for Oregon chub and other native fishes at locations containing Oregon chub. Nonnative fish abundance was not estimated. When nonnative fishes were present, an abundance of 500 fish was used. Sites were ordered, on the basis of chub abundance in 2000, from the largest population on the left to the smallest population on the right. The four bars per site represent abundance estimates for 1997–2000 (left to right). The horizontal dotted line denotes the recovery goal for minimum chub population size (N = 500). Sites in parentheses contained introduced populations of chub. Single asterisks denote sites where chub were the numerically dominant species. Double asterisks denote sites where chub abundance declined in the presence of nonnative fishes. See text for an explanation of site codes.

47%), and the Santiam River drainage (49 of 105 sites; 47%)—were also subbasins where chub were less common or in decline. The Middle Fork Willamette River drainage, which supports the greatest concentration of abundant chub populations, had the lowest occurrence of nonnative fishes in off-channel habitats (31 of 127 sites; 24%).

Nonnative fishes invaded several Oregon chub locations during the course of this study. Three Santiam River locations (sites S1, S4, S7) were invaded during flooding in 1996 and one Middle Fork Willamette River location (site M12) was illegally stocked with largemouth bass in 1997. The Oregon chub populations subsequently declined at three of these locations. I suspect that nonnative fishes may have caused the extirpation of Oregon chub from three locations where I had found the species coexisting in the early 1990s. Oregon chub have not been collected from site C1 in the Coast Fork Willamette drainage since 1993 nor from sites M14 and M13 in the Middle Fork Willamette drainage since 1994 and 1997, respectively. Nonnative fishes were also collected from six historical Oregon chub locations that no longer contain Oregon chub.

Sites with low connectivity to the adjacent river or reservoir supported larger Oregon chub populations (P = 0.0476) and contained fewer species of nonnative fish (P = 0.0103) than did sites with high connectivity (Table 4). Compared with sites in the Santiam and mid-Willamette River basins, sites in the Middle Fork Willamette River basin, which tended to be more isolated, supported larger Oregon chub populations (P = 0.0419 and 0.0490, respectively) and had lower species richness (P = 0.0050 and 0.0348, respectively; Table 4).

A multiple regression model found that site connectivity, vegetated area, number of species of native amphibians, and fish species richness accounted for 71% of the variation in Oregon chub population abundance (F = 13.89, df = 22, $P < 0.0001$). The estimates for model parameters were as follows: intercept (350.1343, $P < 0.0001$), connectivity (–142.8554, P = 0.0003), number of species of native amphibians (42.5198, P = 0.0151), species richness (–13.3902, P = 0.0374), and vegetated area (–0.0044, P = 0.0914). The variables showing a strong positive correlation with Oregon chub abundance included number of days when maximum pond temperatures exceeded 16°C (r =

TABLE 3.—Native and nonnative fish species collected in off-channel habitats sampled between 1991 and 2000 in the Willamette River basin, Oregon. Only the locations that contained fish are included ($N = 356$).

Species	Number of sites	Percentage of sites
Native fishes		
Redside shiner	170	48
Speckled dace	135	38
Threespine stickleback	122	34
Sculpins	114	32
Northern pikeminnow	109	31
Largescale sucker	67	19
Oregon chub	23	6
Cutthroat trout	15	4
Sandroller	8	2
Chinook salmon	5	1
Peamouth *Mylocheilus caurinus*	2	<1
Chiselmouth *Acrocheilus alutaceus*	2	<1
Rainbow trout	2	<1
Coho salmon *Oncorhynchus kisutch*	1	<1
Mountain whitefish	1	<1
Nonnative fishes		
Western mosquitofish	150	42
Bluegill	137	38
Largemouth bass	63	18
Common carp *Cyprinus carpio*	35	10
Brown bullhead	30	8
White crappie *Pomoxis annularis*	14	4
Pumpkinseed	10	3
Yellow bullhead	10	3
Black crappie *Pomoxis nigromaculatus*	3	1
Golden shiner *Notemigonus crysoleucas*	3	1
Banded killifish *Fundulus diaphanus*	3	1
Goldfish *Carassius auratus*	1	<1
Smallmouth bass *Micropterus dolomieu*	1	<1
Redear sunfish *Lepomis microlophus*	1	<1

0.5687, $P = 0.0425$), number of species of native amphibians observed ($r = 0.4708$, $P = 0.0115$), and presence of western pond turtles ($r = 0.3909$, $P = 0.0397$). Variables with a strong negative correlation included site connectivity ($r = -0.7255$, $P < 0.0001$), number of species of nonnative fish ($r = -0.4878$, $P = 0.0085$), and species richness ($r = -0.5140$, $P = 0.0051$).

Discussion

Habitat degradation and introduced species have been implicated in the decline of native minnows throughout the western United States (Cross 1976; Kaeding et al. 1990; Blinn et al. 1993; Scoppettone 1993; Meng and Moyle 1995; Marsh and Douglas 1997; Sommer et al. 1997; Osmundson and Burnham 1998; Simon and Markle 1999). In large alluvial rivers, decreases in populations of native floodplain fishes have been attributed to altered river–floodplain connectivity and function and the impacts of nonnative fishes (Moyle 1976; Minckley 1982; Tyus 1987; Marsh and Brooks 1989; Mueller 1995; Modde et al. 2001). Floodplain habitats increase the productivity and diversity of riverine communities (Junk et al. 1989; Bayley 1995; Gutreuter et al. 1999) and provide survival and growth advantages to fish (Starrett 1951; Peterson 1982; Tyus 1987; Kwak 1988; Matheney and Rabeni 1995; Osmundson and Burnham 1998; Modde et al. 2001; Sommer et al. 2001).

Restoration guidelines for dammed rivers have focused on increasing the area and connectivity of the floodplain and restoring periodic flood flows to improve ecosystem function and aid in the recovery of native floodplain fishes (Bayley 1991; Gutreuter et al. 1999; Sommer et al. 2001). Many

TABLE 4.—Comparisons of species richness, number of species of nonnative fish, and 2000 Oregon chub population abundance (catch per unit effort; 1 unit = 12 minnow traps fished for 3 h) between locations with high and low connectivity and among Willamette River subbasins. Introduced populations were excluded from the comparisons. Comparisons of species richness between the Santiam and Middle Fork Willamette subbasins were significant ($P = 0.0050$), as were those between the mid-Willamette and Middle Fork Willamette subbasins ($P = 0.0348$). Comparisons of Oregon chub abundance between the Santiam and Middle Fork Willamette subbasins were significant ($P = 0.0419$), as were those between the mid-Willamette and Middle Fork Willamette subbasins ($P = 0.0490$).

Basis of comparison	N	Species richness		Nonnative fish		Chub abundance	
		Mean	SD	Mean	SD	Mean	SD
Connectivity							
Low	6	6.0	1.7	0.17	0.41	141.3	125.9
High	17	6.7	2.3	1.00	1.00	6.6	18.8
P-value		0.5169		0.0103		0.0476	
Subbasin							
Santiam	8	8.1	2.0	1.00	0.93	3.23	6.25
Mid-Willamette	3	6.7	0.6	1.33	1.53	6.30	10.39
Middle Fork Willamette	12	5.2	1.7	0.36	0.67	83.16	113.47

native fishes have adapted physical and behavioral adaptations that provide advantages over nonnative fishes during periodic flooding (Minckley 1981; Meffe 1984; Minckley and Meffe 1987; Osmundson and Kaeding 1991; Gido et al. 1997). In certain situations, however, flooding has resulted in invasion of habitats by nonnative fishes with subsequent decreases in native fish (Meffe 1983; Lafferty et al. 1999; this study). The risk of invasion of off-channel habitats by nonnative fishes should be considered when restoration includes increasing floodplain connectivity.

Proliferation of nonnative fishes in the Willamette Valley appears to pose a substantial threat to Oregon chub recovery. Nonnative fishes were collected from 58% of the off-channel habitats sampled, yet were conspicuously absent from most of the locations that supported large populations of Oregon chub. Seven of the 23 locations that supported Oregon chub in 2000 also contained nonnative fishes, but only 1 of these 7 locations supported an Oregon chub population exceeding 500 fish. Populations of Oregon chub were more abundant at locations that were isolated from the main river channel, habitats less likely to contain nonnative fishes. Conversely, sites with high connectivity supported mostly small, often declining, chub populations and frequently contained nonnative fishes. The concentration of abundant Oregon chub populations in the Middle Fork Willamette subbasin is probably related to the greater degree of isolation of these habitats. Oregon chub sites in this subbasin are proximate to four large flood control dams, and a larger portion of the Middle Fork Willamette subbasin is under flood control than are the other subbasins. These data suggest that the persistence of abundant Oregon chub populations in the Willamette River results largely from their isolation.

Historically, Oregon chub thrived in an unconstrained Willamette River under a hydrologic regime that featured frequent flood events (Benner and Sedell 1997), where off-channel habitats were continually being created and others lost (Lewin 1978; Dykaar and Wigington 2000). Floods provided the mechanism of dispersal and genetic exchange for Oregon chub populations. Hence, chub populations would have expanded in some locations and declined in others. Indeed, recent introductions of Oregon chub illustrate the ability of this species to rapidly colonize suitable habitats. In my opinion, however, floods now pose a substantial risk to chub populations through the dispersal of nonnative fishes. In the Santiam River basin, the two largest natural populations of Oregon chub declined substantially after nonnative fishes invaded these habitats during the 1996 floods. In addition, no new populations of Oregon chub were discovered in habitats located downstream of existing chub populations during thorough sampling in 1997–2000, suggesting that no successful colonization occurred as a result of this flooding.

Whereas natural perturbations like floods often favor native species over nonnative species, human perturbations typically favor the nonnative species. The severe human alteration of the Willamette drainage has relegated us to managing populations of Oregon chub in isolation. This strategy is contrary to their evolutionary life history and may have potentially severe genetic implications. Historically, Oregon chub thrived in a dynamic riverine environment with frequent connectivity between off-channel habitats and the main river channel. Currently, however, Oregon chub are most abundant in isolated habitats.

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