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Early Life History of the Northern Pikeminnow in the Lower Columbia River Basin

DENA M. GADOMSKI,* CRAIG A. BARFOOT,[1] JENNIFER M. BAYER, AND THOMAS P. POE[2]

U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605, USA

Abstract.—The northern pikeminnow *Ptychocheilus oregonensis* is a large, native cyprinid in the Columbia River basin that has persisted in spite of substantial habitat alterations. During the months of June to September 1993–1996, we investigated the temporal and spatial patterns of northern pikeminnow spawning, along with describing larval drift and characterizing larval and early juvenile rearing habitats in the lower Columbia River (the John Day and Dalles reservoirs and the free-flowing section downstream of Bonneville Dam) as well as in the lower sections of two major tributaries (the John Day and Deschutes rivers). The density of newly emerged drifting larvae was higher in dam tailraces (a mean of 7.7 larvae/100 m^3 in surface tows) than in the lower reservoirs (0.3 larvae/100 m^3), indicating that tailraces were areas of more intense spawning. Density was particularly high in the Bonneville Dam tailrace (15.1 larvae/100 m^3), perhaps because adult northern pikeminnow are abundant below Bonneville Dam and this is the first tailrace and suitable main-stem spawning habitat encountered during upriver spawning migrations. Spawning also occurred in both of the tributaries sampled but not in a backwater. Spawning in the Columbia River primarily took place during the month of June in 1993 and 1994, when the water temperature rose from 14°C to 18°C, but occurred about 2 weeks later in 1995 and 1996, possibly because of cooler June water temperature (14–15°C) in these years. The period of drift was brief (about 1–3 d), with larvae recruiting to shallow, low-velocity shorelines of main-channel and backwater areas to rear. Larvae reared in greatest densities at sites with fine sediment or sand substrates and moderate- to high-density vegetation (a mean density of 92.1 larvae/10 m^3). The success of northern pikeminnow in the Columbia River basin may be partly attributable to their ability to locate adequate spawning and rearing conditions in a variety of main-stem and tributary locations.

The northern pikeminnow *Ptychocheilus oregonensis* is a large, native cyprinid in the Columbia River basin. This species has persisted and is widely distributed even though the basin has been extensively altered by hydroelectric development. Northern pikeminnow are important predators of juvenile salmonids, particularly in dam tailraces and in the lower Columbia River downstream from Bonneville Dam (Poe et al. 1991; Ward et al. 1995; Zimmerman 1999). Because of this predation, the management of northern pikeminnow in the basin is of particular concern. Control programs have been implemented to remove a portion of predaceous northern pikeminnow from the system and thereby reduce juvenile salmonid mortality (Rieman and Beamesderfer 1990; Beamesderfer et al. 1996; Zimmerman and Ward 1999). Additionally, there has been extensive research on various aspects of predator–prey dynamics for northern pikeminnow (e.g., Mesa 1994; Petersen et al. 1994; Petersen and Gadomski 1994) as well as on the ecological characteristics of older juvenile and adult northern pikeminnow (Beamesderfer and Rieman 1991; Parker et al. 1995).

Management efforts may be aided by knowledge of the ecology of all life stages of northern pikeminnow. However, little is known about the early life history of this species in the Columbia River basin. It may be particularly important to understand the processes during this stage because for many fish species year-class strength is determined by the survival of larvae or juveniles (Houde 1987). Available information suggests that spawning by northern pikeminnow occurs in a variety of habitats, including rivers, lakes, and reservoirs (Jeppson and Platts 1959; Hill 1962; Patten and Rodman 1969; Beamesderfer 1992). Spawning aggregations ranging from a few hundred to several thousand fish have been observed in other systems (Patten and Rodman 1969; Beamesderfer 1992)

* Corresponding author: dena_gadomski@usgs.gov

[1] Present address: Tribal Fisheries, Confederated Salish and Kootenai Tribes, Box 278, Pablo, Montana 59855, USA.

[2] Present address: BioAnalysts, Inc., Post Office Box 1537, White Salmon, Washington 98672, USA.

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but not in the Columbia River, perhaps because the greater depth of the latter makes observation more difficult (Beamesderfer et al. 1996). During spawning, benthic-adhesive eggs are broadcast in a range of water depths over substrates varying in size from gravel to rubble (Jeppson 1957; Patten and Rodman 1969; Beamesderfer 1992). Larvae and young juveniles have been observed rearing in shallow, low-velocity shoreline areas in the John Day Reservoir of the Columbia River (LaBolle et al. 1985) as well as in other systems (Hill 1962; Beamesderfer 1992).

Our goal was to conduct a broad survey of the early life stages of northern pikeminnow in a variety of locations and habitats of the lower Columbia River basin to aid in understanding the factors that might affect recruitment dynamics in this area. Specifically, our objectives were to determine the timing and location of spawning, to describe larval drift, and to characterize larval and early juvenile rearing habitats. The Columbia River encompasses a range of environments; although large reaches of semilentic habitat behind dams are dominant, free-flowing sections remain. Tributaries in the region vary from relatively unaltered systems to highly modified ones. To determine how the early life history of northern pikeminnow might vary among these environments, we sampled larvae and early juveniles in the limnetic and littoral zones of two impoundments, two major tributaries, and a segment of the more free-flowing, unimpounded lower Columbia River.

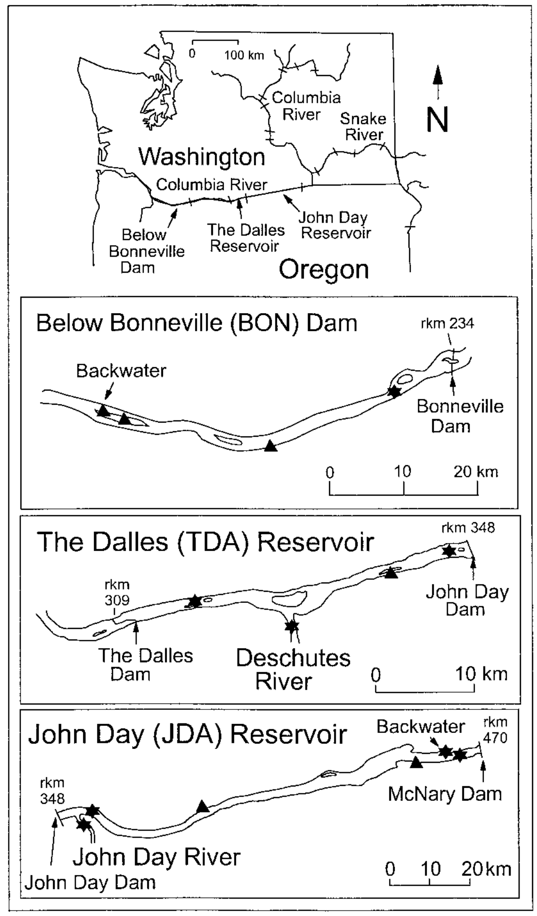

FIGURE 1.—Lower Columbia River basin study area. Locations at which both ichthyoplankton tows and shoreline sampling were conducted are indicated by stars; locations at which only shoreline sampling was conducted are indicated by triangles. The abbreviation rkm stands for river kilometer; rkm are measured from the mouth of the Columbia River.

Methods

Study Areas

Our primary objective was to compare the abundance of larval and juvenile northern pikeminnow in four major habitat types in the Columbia River: upper reservoirs (including dam tailraces), lower reservoirs, backwaters, and tributaries. To accomplish this, we sampled limnetic areas with ichthyoplankton nets in (1) the tailraces of Bonneville, John Day, and McNary dams, (2) the lower Dalles and John Day reservoirs, (3) Plymouth Slough, a backwater of the upper John Day Reservoir, and (4) lower sections of the Deschutes and John Day rivers (Figure 1). To determine larval and early juvenile rearing areas, shorelines were sampled at a variety of sites below Bonneville Dam, in the Dalles and John Day reservoirs, in two backwaters (Plymouth Slough and a backwater below Bonneville Dam), and lower sections of the Deschutes and John Day rivers (Figure 1). We primarily sampled during the months of June to August 1993–1996; each location was sampled consecutively for 2 years (1993–1994 or 1995–1996), except for the upper John Day Reservoir main channel (including the McNary Dam tailrace) and backwater, which were sampled in all 4 years to provide a baseline for interannual comparisons (Figure 2; Table 1).

The substrate composition and morphological characteristics of Columbia River sample locations differed considerably. Water velocity was highest at our tailrace sample sites (mean, 0.7 m/s; range, 0.2−1.3 m/s) and lowest in the lower reservoirs (range, 0.1−0.3 m/s) and backwaters (<0.1 m/s). Because Bonneville Dam is the most downstream dam on the Columbia River, the unimpounded

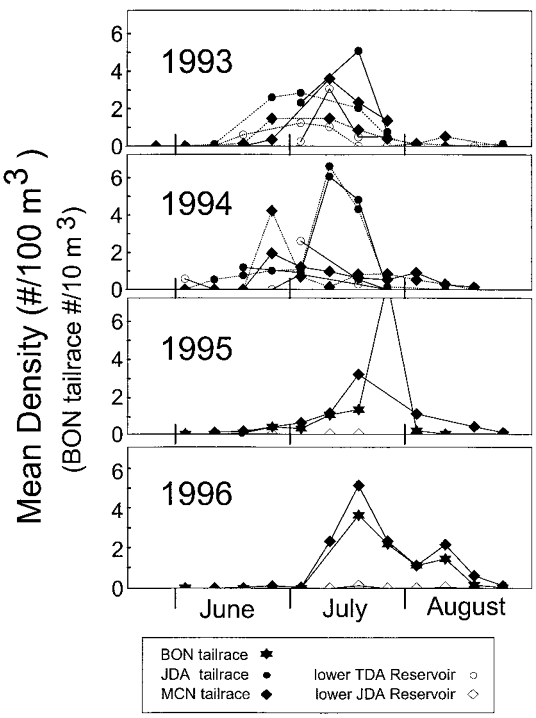

FIGURE 2.—Mean weekly densities of northern pikeminnow larvae in ichthyoplankton tows conducted from June to August 1993–1996 in the Bonneville (BON), John Day (JDA), and McNary (MCN) dam tailraces and the lower Dalles (TDA) and John Day reservoirs, Columbia River. Black lines indicate surface tows and dashed lines stepped−oblique tows (the latter only conducted in 1993–1994). Note the different scale of the vertical axis for the Bonneville Dam tailrace.

reach below it (river kilometers [rkm] 0–234, measuring from the river's mouth] is a largely riverine environment. Except in the tailrace, the substrate below Bonneville Dam is predominantly sand, and water depths are generally shallow (Parsley et al. 1993; Parsley and Beckman 1994). The substrate in the Dalles Reservoir (rkm 309–348) consists of sand, cobble, and bedrock, while that in John Day Reservoir (rkm 348–470) is mud, sand, gravel, and cobble (Parsley et al. 1993; Parsley and Beckman 1994).

We sampled the lower 1.1 km of the Deschutes River and the lower 6.5 km of the John Day River (Figure 1). Habitat conditions in these two tributaries differed considerably. The lower Deschutes River was more typical of a free-flowing stream, with a comparatively narrow channel, high water velocity (0.2–0.9 m/s at our sample sites), and large substrates. In contrast, the relatively wide, flooded mouth of the John Day River was characterized by low-velocity ($<$0.2 m/s) depositional habitats. The John Day River empties into John Day Reservoir at rkm 353, an area that is greatly influenced by water level management at John Day Dam 5 km downstream.

Ichthyoplankton Sampling

Overview.—Ichthyoplankton samples were collected weekly from early June through late August at all locations except the John Day River. Because higher water temperatures in this river could result in earlier spawning than in the Columbia River, sampling (during 1995 and 1996) was initiated in mid-May, about 3 weeks earlier than at other locations. Occasionally, weekly samples could not be collected at a location owing to equipment failure or severe weather. At each of the five Columbia

TABLE 1.—Mean density (number/10 m^3) and standard deviation (SD) of northern pikeminnow larvae collected in sled tows at four main-channel, two backwater, and two tributary sampling locations during 1993–1996. Means are for periods when the majority of larvae were collected (June through mid-July for the John Day River and late June through August for all other locations). Only sites with fine sediment or sand substrate are included. The symbol *N* stands for the number of tows; 6,593 larvae were collected.

	1993		1994		1995		1996	
Location	Mean (SD)	*N*	Mean (SD)	*N*	Mean (SD)	*N*	Mean (SD)	*N*
Below Bonneville Dam								
Main channel					0.9 (3.0)	10	12.8 (17.4)	8
Backwater					117.9 (225.3)	5	1.8 (2.9)	8
Lower Dalles Reservoir	70.8 (109.7)	12	5.4 (8.9)	13	0.3 (0.6)			
Lower John Day Reservoir						5	0.0 (0.0)	7
Upper John Day Reservoir								
Main channel	45.7 (117.7)	14	123.8 (401.5)	26	1.1 (3.6)	11	64.0 (301.5)	28
Backwater	10.7 (22.5)	7	27.3 (30.1)	9	4.0 (6.1)	6	16.4 (40.3)	6
Deschutes River	29.6 (54.4)	15	88.9 (118.0)	16				
John Day River					3.5 (6.1)	17	0.4 (1.1)	24

River main-channel locations (Figure 1), we sampled ichthyoplankton with boat-towed nets at three fixed sites, one mid-river and one along each shoreline. Sample site depth varied greatly, with ranges of 1.9–88.5 m for mid-river sites and 0.4–37.5 m for nearshore sites. Additionally, we sampled at one site in the John Day Reservoir backwater that had depths of 0.3–5.0 m. At the Deschutes River, we collected ichthyoplankton samples at four fixed sites, two east and two west of a central island. In the John Day River, we sampled at six fixed sites, one mid-river and two near the shore at each of two transects that were 0.5–1.2 km and 4.0–6.0 km from the mouth. At each sample site on each sample date, we measured the surface water temperature at the start of an ichthyoplankton tow.

Ichthyoplankton samples were collected with two bridleless conical nets 0.5 m in diameter (2.5 m long with 500-μm mesh) (Nester 1987). Tows were conducted from about 2 h after sunset until 0100 hours because northern pikeminnow larvae drift almost exclusively at night (Gadomski and Barfoot 1998). Ichthyoplankton nets were suspended off the port and starboard sides of the boat and towed simultaneously, resulting in paired samples. In most instances, we immediately replicated the tows to obtain two sets of paired samples per site per night. A General Oceanics model 2030 flowmeter was attached inside each net to estimate the volume of water filtered. Nets were usually towed for 9 min, with the result that about 135 m^3 of water was filtered for each sample. Samples were preserved in a 10% solution of formalin buffered with sodium borate, except for a small number in 1996 that were preserved in a 95% solution of ethanol to allow laboratory examination of larval otoliths.

Surface versus stepped−oblique tows.—Because we did not know the vertical distribution of northern pikeminnow larvae, during 1993 and 1994 we conducted both surface and stepped−oblique ichthyoplankton tows in the Columbia River main channel (the lower Dalles Reservoir and John Day and McNary dam tailraces). In 1993, surface sampling was limited primarily to July, the peak period of larval northern pikeminnow drift; in 1994 we sampled using both tow types throughout the months June to August. Owing to shallow water, in all years only surface tows were conducted in the John Day Reservoir backwater and the Deschutes River. Stepped−oblique tows lasted 3 min each at three depths: one-half of start depth, one-quarter of start depth, and the surface. The maximum initial net depth was 10 m. Stepped−oblique tows were conducted with the starboard plankton net, and surface tows were conducted with the port plankton net. Tows were immediately replicated at a site to obtain paired surface and stepped−oblique tow samples.

To determine the best tow type for sampling northern pikeminnow larvae, we performed a paired-comparisons, two-tailed *t*-test to ascertain whether the mean difference between larval densities in surface and stepped−oblique tows was significantly different from zero ($P < 0.05$). In 1993, the density of northern pikeminnow in main-channel Columbia River surface ichthyoplankton tows (mean = 1.7 larvae/100 m^3; SD = 2.3; N = 34) was significantly higher than that in stepped−oblique ichthyoplankton tows (mean = 1.0 larva/100 m^3; SD = 1.5; N = 34). In comparison, in 1994 no significant difference was detected between surface (mean = 1.1 larvae/100 m^3; SD = 2.7; N = 63) and stepped−oblique (mean = 1.0 larva/100 m^3; SD = 2.8; N = 63) ichthyoplankton tows. Because density was as high or higher in surface tows and this tow type was easier and safer to conduct, all ichthyoplankton tows were done at the surface during 1995–1996.

Shoreline Sampling

Sled.—Shoreline locations were sampled weekly during daytime with a manually towed net attached to a sled (LaBolle et al. 1985). The conical net was 1.5 m long with 500-μm brown mesh and a mouth 1.5 m wide × 10 cm deep. Our gear type dictated that we sample shallow littoral areas with gentle gradients and relatively even terrain; thus, we chose sites with substrates ranging from fine sediment to cobble. Altogether, 32 sled sites were sampled, 7 below Bonneville Dam (including a backwater site), 4 in the lower Dalles Reservoir, 3 in the upper Dalles Reservoir, 5 in the lower John Day Reservoir, 6 in the upper John Day Reservoir (including 1 in the backwater), 2 in the mouth of the Deschutes River (where there were few feasible sites), and 5 in the John Day River.

To conduct a tow, the sled was positioned offshore at a water depth that just covered the mouth of the net (about 25 cm). We waited approximately 1 min for fish to adjust to the disturbance and then manually towed the sled upstream parallel to the shore at about 0.75 m/s. Tow distance was normally 50 m. The volume of water filtered was calculated by multiplying the mouth area by the distance towed (volume was 7.5 m^3 when the tow distance was 50 m). All samples were preserved in a 10% solution of formalin buffered with sodium borate. At each site, we categorized substrate composition as (1) fine sediment or sand, (2) gravel or cobble, or (3) a mixture of the previous two sediment types. The vegetation density was indexed as (1) absent or trace or (2) moderate or high. At each sample site on each sample date, we measured the surface water temperature at the start of a sled tow.

Beach seine.—Because the sled did not effectively sample juvenile fish, during June–September 1994 we initiated weekly sampling with a small beach seine (15.2 m × 1.2 m, with 2.0-mm mesh and a 1.2-m^2 bag with 0.8-mm mesh) at five main-channel sites and one backwater site in the upper John Day Reservoir. Sampling was done during daytime; sites were shallow, with sand or sand and gravel substrate and low or zero water velocity. In 1995 and 1996, seining was conducted every 1–2 weeks, primarily during July–September, at three main-channel sites in each of the following locations: the lower John Day Reservoir, the upper John Day Reservoir, and the John Day River (the latter of which was only sampled during 1996). Additionally, four sites in the main channel and one site in a backwater below Bonneville Dam were sampled.

Sample Processing

In the laboratory, fish larvae and juveniles were sorted and identified to the lowest possible taxon. We defined larvae as fish from the hatching stage through that of complete fin fold absorption. A maximum of 50 northern pikeminnow from each ichthyoplankton and sled sample were measured to the nearest 0.1 mm standard length (SL) with either a binocular microscope equipped with an ocular micrometer or calipers, depending on the size of the fish.

In the Columbia River, some specimens of early yolk-sac larvae ($< \approx 9$ mm SL) of northern pikeminnow and another cyprinid, peamouth *Mylocheilus caurinus,* did not have fully developed diagnostic pigment and were thus not considered in analyses of northern pikeminnow distributions and abundance (these larvae represented only 2.5% of the total larval northern pikeminnow catch). Additionally, the larvae of chiselmouths *Acrocheilus alutaceus* that are less than approximately 12 mm SL (i.e., prior to pelvic fin formation) have not been adequately described, so that one cannot separate them from northern pikeminnow. However, only nine juvenile chiselmouths were collected in the Columbia River with all sampling gears during the 4 years of our study, so we assumed that chiselmouth spawning was negligible in the Columbia River areas we sampled. In the Deschutes River, several cyprinid species (dace *Rhinichthys* spp., redside shiner *Richardsonius balteatus*, chiselmouth, and northern pikeminnow) with similar meristic attributes could not always be separated when less than approximately 11 mm SL and thus were grouped into a single undetermined-cyprinid category.

To determine the age of northern pikeminnow larvae in the drift, we examined the sagittal otoliths of 107 larvae from ichthyoplankton samples that had been preserved in 95% ethanol. These otoliths were from larvae collected during July–August 1996 from the Bonneville and McNary dam tailraces and the John Day Reservoir backwater. Sagittae were removed from larvae with a fine probe and processed as described by Wertheimer and Barfoot (1998). The number of increments in the left or right sagittal otolith of each larva was counted twice. Wertheimer and Barfoot (1998) validated daily increment deposition in northern pikeminnow larvae, so the mean of the two counts was used as an estimate of age in days after hatching. Regression analysis was used to determine the relationship between estimated age and standard length.

Results

Ichthyoplankton Sampling

Overview.—In all, 6,446 northern pikeminnow larvae were collected during 4 years of ichthyoplankton sampling in the Columbia and John Day rivers. Only 53 juvenile northern pikeminnow were collected in these locations during the ichthyoplankton tows, of which 64% were from the John Day River. In the Deschutes River, we were only able to identify three larvae and one juvenile in ichthyoplankton samples as northern pikeminnow, while 1,604 larvae were in the undetermined-cyprinid category. The mean size of northern pikeminnow larvae collected each year in main-channel Columbia and John Day river locations ranged from 9.2 mm SL (Bonneville Dam tailrace, 1996; N = 1,261; SD = 0.5) to 9.9 mm SL (lower Dalles Reservoir, 1993; N = 30; SD = 1.4). A high percentage (79–99%) of northern pikeminnow in the Columbia River main channel were yolk sac larvae; the one exception was the lower Dalles Reservoir in 1994, where only 40% of larvae retained yolk. In contrast, only 11–46% of the larvae in the backwater and in the John Day River had yolk.

The mean ages (days after hatching) of larvae in the Bonneville Dam tailrace, the McNary Dam tailrace, and the John Day Reservoir backwater were 12 d (N = 59; SD = 4), 13 d (N = 34; SD = 4), and 15 d (N = 14; SD = 4), respectively. The 95% confidence limits for the mean ages of larvae collected in the Bonneville and McNary dam tailraces were 11–13 d and 11–14 d, respectively. The relationship between age and standard length for the range of fish examined (4–24 d old and 7.9–10.5 mm SL; N = 107) was best modeled by the exponential function (R^2 = 0.78)

$$\log_e(\text{age}) = -3.47 + 0.63 \cdot \text{SL}.$$

Main-channel Columbia River.—During 1993–1994, northern pikeminnow larvae were first collected in ichthyoplankton tows in the main-channel Columbia River during early June and were abundant from mid-June through late July (Figure 2). In contrast, during 1995–1996, low numbers of larvae were first collected in late June, and larvae were most abundant from early July through early to mid-August.

Northern pikeminnow larvae in the drift were most abundant in dam tailraces (Figure 2). From late June through August, the mean density in tailrace surface tows was 7.7 larvae/100 m^2 (N = 232; SD = 18.8). Density was particularly high in the Bonneville Dam tailrace, 15.1 larvae/100 m^2 (N = 104; SD = 26.2) versus 0.3/100 m^2 in the lower reservoirs (N = 79; SD = 0.9).

Within any year, weekly water temperatures varied little between main-channel Columbia River locations (a maximum difference of 1–2°C). Mean temperatures during early June were similar in all years. However, in 1993 and 1994 the temperature increased steadily in June (from 14°C to 18°C), while in 1995 and 1996 it remained low (14–15°C) until late June. Mean temperature rose steadily in all years in July, reaching highs of 21–22°C in August.

Columbia River backwater.—In the upper John Day Reservoir backwater, the density of northern pikeminnow larvae in ichthyoplankton tows was low in 1993–1995, with a mean of 0.3/100 m^2 (N = 32; SD = 0.4). In contrast, in 1996 there were abundance peaks in late July (7.8 larvae/100 m^2) and mid-August (17.4 larvae/100 m^2). Water temperature in the backwater was generally 2–3°C higher than in the main-channel Columbia River, ranging from about 16°C in early June to 20–25°C in July and August.

John Day River.—In the John Day River, larvae were first collected in ichthyoplankton tows during May and early June, with no larvae being collected in August. During both 1995 and 1996, the highest density of northern pikeminnow larvae occurred at upper-river sample sites (0.9/100 m^2 during May−July; N = 59; SD = 2.6), with few larvae being collected at lower-river sample sites (0.03/100 m^2; N = 62; SD = 0.1). In 1995, the abundance of larvae at upper-river sites peaked in mid-July at 9.4/100 m^2. Fewer larvae were collected in 1996, with small abundance peaks of 0.5–0.8/100 m^2 in late June and early July.

Water temperatures in the John Day River were very similar at the lower- and upper-river sample sites, but they were more variable and often as much as 5°C warmer than in the main-channel Columbia River. The temperature in the John Day River increased from about 15°C in May to a maximum of about 25°C in late July.

Shoreline Sampling

Sled.—In all, 7,185 northern pikeminnow larvae and 898 juveniles were collected with the sled during 4 years of sampling in the Columbia, Deschutes, and John Day rivers. However, juveniles were observed avoiding the sled, and length-frequency distributions indicated that larvae (juvenile transformation usually occurs at about 18–20 mm SL) were most effectively collected (Figure 3). Therefore, only larvae were considered in the following comparisons. Larvae collected in the sled ranged from 7.2 mm to 22.6 mm SL, with a mean length of 13.9 mm (N = 2,228; SD = 2.8). Yolk material was present in 3% of the larvae collected.

In both main-channel and backwater Columbia River locations, northern pikeminnow larvae first appeared in shoreline samples in late June or early July in all 4 years, with the highest density generally occurring in late July and early August. In the Deschutes River, in which water temperature was similar to that in the main-channel Columbia River, larvae were also first collected in shoreline areas in late June and early July. In contrast, in the warmer John Day River larvae were only collected from early June through mid-July.

The highest abundance of northern pikeminnow larvae occurred in sled tows over fine sediment or sand substrate with moderate-density to high-density vegetation. From late June through August, the mean density of larvae in sled tows over areas characterized by these environmental conditions was 92.1 larvae/10 m^3 (N = 64 samples; SD = 270.7) for all years and locations combined. The mean density of larvae was intermediate in

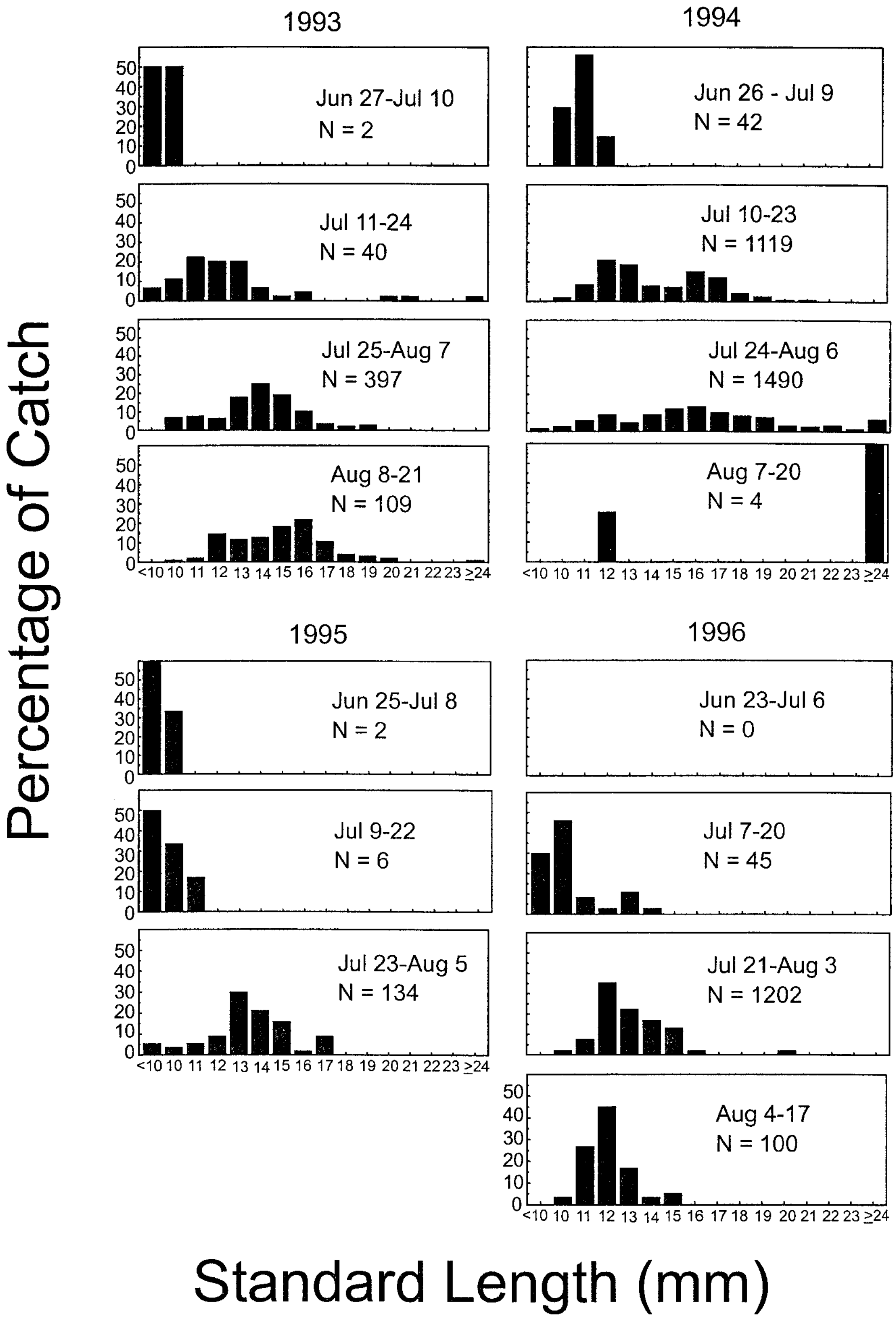

FIGURE 3.—Biweekly length-frequency distributions of age-0 northern pikeminnow collected at three sled sites in the main-channel upper John Day Reservoir, Columbia River, from June to August 1993–1996. In 1995, samples were not collected after early August.

TABLE 2.—Mean catch per unit effort (number of pikeminnow collected per haul), standard deviation (SD), and percent larvae for northern pikeminnow larvae and juveniles collected in beach seine hauls at three main-channel, two backwater, and one tributary sampling location during 1994–1996. Hauls during July–September are presented for all locations except the lower John Day Reservoir, which was only sampled during August–September. The upper John Day Reservoir was sampled during June in 1994–1996 (27 hauls) and the John Day River in June 1996 (5 hauls), but no northern pikeminnow were collected. The symbol *N* stands for the number of hauls; altogether, 12,183 larvae and 11,857 juveniles were collected.

	1994			1995			1996		
Location	Mean (SD)	*N*	Larvae (%)	Mean (SD)	*N*	Larvae (%)	Mean (SD)	*N*	Larvae (%)
Below Bonneville Dam									
Main channel				0.9 (2.2)	25	22	6.9 (26.6)	29	65
Backwater				8.1 (8.5)	8	92	1.2 (1.8)	11	85
Lower John Day Reservoir				0.8 (2.7)	11	0	0.1 (0.3)	10	0
Upper John Day Reservoir									
Main channel	344.8 (541.0)	30	39	231.2 (690.2)	26	58	200.8 (445.7)	33	61
Backwater	41.7 (109.5)	10	86						
John Day River							11.0 (27.0)	30	12

tows over fine sediment or sand substrate with absent or trace vegetation as well as in those over mixed sand−cobble substrate with moderate to high amounts of vegetation; density at these sites was 20.8 larvae/10 m^3 (N = 182; SD = 125.6) and 30.9 larvae/10 m^3 (N = 5; SD = 67.7), respectively. Tows over cobble substrate and mixed substrate with absent or trace vegetation collected few fish (means of 0.8–4.3 larvae/10 m^3; N = 210).

Because differences in density among substrate types might bias comparisons of catch from locations with different substrates, we only included the fine sediment or sand sites in further analyses. The density of northern pikeminnow larvae in sled tows over fine sediment or sand varied greatly among years and locations (Table 1). Density was high during some years in backwater sampling sites, the lower Dalles Reservoir, the upper John Day Reservoir main channel, and in a tributary, the Deschutes River. In all sampling years, catches were low in the main channel below Bonneville Dam, in the lower John Day Reservoir, and in the John Day River. In 1995, sled catches at all Columbia River sites were very low except in the backwater below Bonneville Dam. However, shoreline catches in 1995 may have been low because the highest abundances occurred after we terminated sled sampling in early August.

Catch data from the upper John Day Reservoir main channel show that larvae appeared in shoreline areas about 2 weeks earlier in 1993–1994 than in 1995–1996 (Figure 3), which reflects the abundance patterns of larvae in ichthyoplankton tows during these years (Figure 2). In 1993 and 1994, few larvae less than 11 mm SL were collected from shorelines by mid-July, whereas in 1995 and 1996 most larvae in shorelines were less than 11 mm SL until late July.

Shoreline temperatures were generally higher than those in the main channel, usually ranging from about 18°C to 25°C in July and August. The highest shoreline temperatures, which neared 30°C in some instances, were observed in backwaters and the John Day River during 1993–1995.

Beach seine.—The highest beach seine catches in all sample years (1994–1996) were in the upper John Day Reservoir main channel, with mean catch per unit effort of more than 200 larvae and juveniles (Table 2). In 1994, northern pikeminnow abundance in the upper John Day Reservoir was highest in late July and early August, whereas in 1995 and 1996, fish abundance peaks were about 2 weeks later. The results conform to those of the ichthyoplankton and sled tows (Figures 2 and 3).

Intermediate numbers of northern pikeminnow were collected at the John Day Reservoir backwater and the John Day River. In the John Day River during 1996, larvae were first collected at shorelines in early July, about 3 weeks earlier than in the Columbia River. Catches were low (mean catch per unit effort < 10 fish) at all other sample sites (the main channel and backwater below Bonneville Dam and the lower John Day Reservoir; Table 2).

Discussion

The mean size of the northern pikeminnow larvae that we collected in ichthyoplankton tows in main-channel locations of the Columbia and John Day rivers (9–10 mm SL) was the same as that of

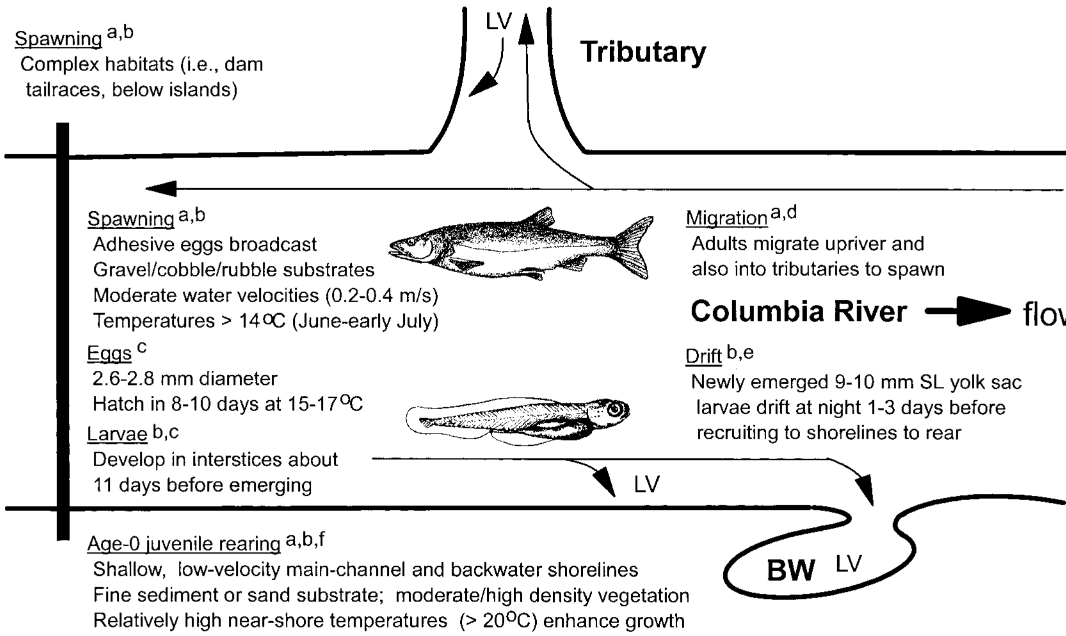

FIGURE 4.—Conceptual model of the early life history of the northern pikeminnow in the Columbia River based on the current and past studies. Studies are indicated by lower-case letters as follows: a = Jeppson 1957, Patten and Rodman 1969, and Beamesderfer 1992; b = this study; c = Gadomski, unpublished laboratory data; d = Martinelli and Shively 1997; e = Gadomski and Barfoot 1998; and f = Barfoot et al. 1999. The abbreviation LV stands for larvae, BW for backwater.

larvae at emergence in the laboratory (Gadomski, unpublished data; Figure 4). Thus, the larvae we collected were probably drifting passively downriver, since fish in early stages of development are unable to swim against strong currents (Pavlov et al. 1972). Childs and Clarkson (1996) found that the larvae of Colorado pikeminnow *Ptychocheilus lucius* 10 mm in length had a swimming ability of about 0.1 m/s, which is less than the water velocity in our tailrace and tributary locations.

The limited size and age ranges (for age, the 95% confidence interval was 11–14 d) of the northern pikeminnow collected in our ichthyoplankton tows, along with the high percentage of larvae with yolk, suggests that the period of drift was brief, particularly considering that part of the variation in age is probably due to differences in the timing of larval emergence (Figure 4). Thus, it is unlikely that larvae would drift the entire length of most Columbia River reservoirs before recruiting to shoreline rearing areas, especially as northern pikeminnow larvae have been shown to drift almost exclusively at night (Gadomski and Barfoot 1998). The average water transit time through John Day Reservoir for flows commonly observed in June–July is estimated as 4–12 d (Berggren and Filardo 1993). In areas of higher velocity, larval drift speed might be somewhat greater than that of ‘‘average particles’’; for example, at a mean velocity of 0.5 m/s, a larva would be transported 10.8 km during a 6-h nighttime period.

Because the northern pikeminnow in the drift were newly emerged, a higher density of larvae in an area probably indicates that spawning sites were relatively near. In the Columbia River main channel, the density of larvae was higher in upper-reservoir than in lower-reservoir locations, which suggests that dam tailraces were areas of more intense spawning. This is corroborated by Martinelli and Shively (1997), who reported that radio-tagged adult northern pikeminnow in the lower Columbia River moved upriver in June and tended to end their movements at tailraces over cobble substrate, which they attributed to the movements being spawning migrations. The three tailrace locations in our study contained environmental conditions reported by other researchers to be optimal for northern pikeminnow spawning, that is, substrate consisting of gravel, cobble, or rubble with enough water velocity to keep spawning areas clean of sediment but also with some protection so that spawning fish can maintain position (Jeppson and Platts 1959; Patten and Rodman 1969; Beamesderfer 1992; Figure 4).

We found the density of larvae to be particularly high in the Bonneville Dam tailrace, perhaps because adult northern pikeminnow are much more abundant downstream from that dam than in the reservoirs (Ward et al. 1995) and this is the first tailrace encountered during upriver spawning migrations. Intense spawning activity in this area may also stem from the availability of larger substrate immediately below the dam; although the Columbia River below Bonneville Dam is free-flowing, with higher velocities that may be optimal for spawning, much of the lower river is predominantly sand, which is an unsuitable spawning substrate.

Larvae collected in lower-reservoir areas and the John Day Reservoir backwater were generally larger than those in tailrace areas and a lower percentage had yolk sacs, suggesting that they had been in the drift for a longer period and had been spawned elsewhere. Although in 1996 we observed abundance peaks for northern pikeminnow larvae in the John Day backwater in late July and mid-August, these peaks corresponded to the abundance peaks in the McNary Dam tailrace (Figure 2). Because 1996 was a year with high discharge (U.S. Army Corps of Engineers, http://www.cbr.washington.edu/dart/river.html), more larvae may have been transported from the main channel into the backwater than during other years.

It is probable that northern pikeminnow spawned in both of the tributaries studied, although results were somewhat confounded by our inability to assign the early stages of some cyprinid larvae to definite species in the Deschutes River. However, high densities of older larvae were collected in the shoreline areas of the Deschutes River, and it is unlikely that these larvae migrated into this system from the Columbia River. In addition, the Deschutes River contains substrate and water velocities characteristic of spawning locations. In contrast, the mouth of the John Day River is characterized by low-velocity depositional habitats, and consistent with this, almost no larvae were collected in lower-river ichthyoplankton tows. At our upriver sample sites, however, the presence of larvae indicated that spawning was occurring, in all probability upstream of our sample locations where the backwater influence of the impoundment of the Columbia River by John Day Dam (Figure 1) is diminished and the John Day River is more of a free-flowing stream. It is unknown whether the northern pikeminnow that spawned in tributaries represented resident tributary populations or had migrated from the Columbia River. Northern pikeminnow have been reported to ascend tributaries to spawn (Beamesderfer 1992), and radiotelemetry studies have documented the movement of northern pikeminnow from the Columbia River into both the Deschutes and John Day rivers (Martinelli and Shively 1997; Martinelli, unpublished data).

In our study, the timing of northern pikeminnow spawning varied among years and may have been regulated by annual temperature regimes, as has been reported for northern pikeminnow in Idaho's St. Joe River (Beamesderfer 1992). Spawning probably occurred about 3 weeks before larval emergence because larvae in the drift were about 11–14 d old and laboratory-reared eggs have been reported to hatch in 8–10 d at 15–17°C (Gadomski, unpublished data; Figure 4). In the Columbia River in 1993 and 1994, the highest densities of larvae were collected in late June and July, so spawning probably occurred primarily in June, when temperatures were rising rapidly from 14°C to 18°C. In contrast, in 1995 and 1996 larvae were abundant in the drift about 2 weeks later, indicating a similar delay in spawning. In these 2 years, temperatures remained cool (14–15°C) until late June, perhaps suppressing spawning activity. In the John Day River in 1995–1996, however, larvae were collected in the drift much earlier (May), probably because higher water temperatures in this system stimulated earlier spawning.

The temporal abundance patterns of larvae at the shorelines of the upper John Day Reservoir reflect annual differences in the timing of spawning. Both sled and beach seine collections showed that shoreline recruitment in 1995 and 1996 was about 2 weeks later than in 1993 and 1994. The timing of spawning may affect juvenile fish growth and survival, and perhaps ultimately year-class strength, by controlling the length of the summer rearing season. Barfoot et al. (1999) found that age-0 northern pikeminnow collected at John Day Reservoir shorelines in early September were significantly ($P < 0.05$) larger in 1994 than in 1995 and 1996, which could be partly the result of a longer growing season in 1994. Larger age-0 fish have been shown to have lower overwinter mortality and to be in better condition the following spring (Miranda and Hubbard 1994; Cargnelli and Gross 1997).

Larvae reared in greatest densities at shoreline sites with fine sediment or sand substrates and moderate-density to high-density vegetation (Figure 4). Beamesderfer (1992) also found age-0 northern pikeminnow at shorelines with at least 90% sand substrate in the St. Joe River, Idaho. It is likely that larval northern pikeminnow densities were highest at sites with fine-grained substrate because these sites are usually areas with low current velocities. Calm conditions result in lower turbidity and higher temperatures (owing to solar heating and reduced mixing), which in turn lead to the increased growth of instream vegetation and enhanced food availability (Hall and Werner 1977). Studies in other locations have also reported that cyprinid larvae prefer shallow, low-velocity vegetated habitats (Copp 1992; Scheidegger and Bain 1995) because such habitats offer both better feeding conditions and protection from predation. If food is not limiting, higher temperatures in shallow nursery areas may also directly benefit fish by affecting their metabolic rate, resulting in enhanced growth and survival (Bestgen 1996; Barfoot et al. 1999).

Although age-0 northern pikeminnow were collected at the shorelines of all locations with adequate habitat conditions, catches were highly variable, with few consistent patterns of abundance at a location or during a year. This is probably partly the result of the patchy distribution of northern pikeminnow larvae, which have been observed to occur in schools of variable size both in the current study and in others (LaBolle et al. 1985). However, the use of a site for rearing may be related to its distance from spawning locations as well as its habitat characteristics. Consistently high shoreline densities of age-0 northern pikeminnow occurred at only one location, the upper John Day Reservoir main channel. This site was only about 10 km downstream from a spawning location, the McNary Dam tailrace (Figure 1), which is approximately the distance a larva might drift in one night.

In many systems, backwater areas are highly productive nursery sites with higher temperatures and enhanced food availability (Sheaffer and Nickum 1986; Scott and Nielsen 1989; Brown and Coon 1994). Age-0 Colorado pikeminnow rear in greatest abundance in the backwaters of the Colorado River basin (Tyus 1991; Tyus and Haines 1991). At our two backwater sampling sites, we collected large quantities of age-0 northern pikeminnow at shorelines on some occasions (Table 1). As with the main channel, however, catches in backwaters were highly variable, and thus our data do not indicate that northern pikeminnow were selectively rearing in backwaters. Use of both main-channel and backwater locations as nursery habitats is advantageous in an altered system such as the Columbia River that has few backwater areas.

Our study was a broad survey of northern pikeminnow early life history in a variety of locations and habitats of the lower Columbia River basin (Figure 4). Although this area has been drastically altered from a natural river system into a series of impoundments, the northern pikeminnow is still abundant in the basin. Impoundment may have decreased the amount of optimal spawning habitat in the Columbia River by reducing water velocity in many areas. However, we found that northern pikeminnow were still able to locate suitable spawning conditions (moderate water velocity and rubble or cobble substrate) in Columbia River dam tailraces and in tributaries. Additionally, although impoundment has decreased the number of complex side-channel habitats and backwater nursery locations, it has increased the proportion of potential low-velocity, main-channel shoreline rearing habitat. Other researchers have found the littoral zones of reservoirs to be productive nursery habitats (Gelwick and Matthews 1990; Hubert and O'Shea 1991; Scheidegger and Bain 1995). The use of a site as nursery habitat in the Columbia River, however, appeared to be a complex matter dependent on a combination of factors, including substrate type, vegetation, and proximity to spawning sites. In conclusion, although this study and others (Beamesderfer 1992; Figure 4) have shown that northern pikeminnow exploit only a fairly narrow range of spawning and rearing conditions, the success of this species in the Columbia River basin can perhaps be attributed in part to the occurrence of these conditions in a variety of mainstem and tributary locations.

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