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[Article]

Juvenile Salmonid Use of Freshwater Emergent Wetlands in the Floodplain and Its Implications for Conservation Management

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Abstract.—A recent trend of enhancing freshwater emergent wetlands for waterfowl and other wildlife has raised concern about the effects of such measures on juvenile salmonids. We undertook this study to quantify the degree and extent of juvenile Pacific salmon *Oncorhynchus* spp. utilization of enhanced and unenhanced emergent wetlands within the floodplain of the lower Chehalis River, Washington, and to determine the fate of the salmon using them. Enhanced emergent wetlands contained water control structures that provided an outlet for fish emigration and a longer hydroperiod for rearing than unenhanced wetlands. Age-0 and age-1 coho salmon *O. kisutch* were the most common salmonid at all sites, enhanced wetlands having significantly higher age-1 abundance than unenhanced wetlands that were a similar distance from the main-stem river. Yearling coho salmon benefited from rearing in two enhanced wetland habitats, where their specific growth rate and minimum estimates of survival (1.43%/d by weight and 30%; 1.37%/d and 57%) were comparable to those in other side-channel rearing studies. Dissolved oxygen concentrations decreased in emergent wetlands throughout the season and approached the limits lethal to juvenile salmon by May or June each year. Emigration patterns suggested that age-0 and age-1 coho salmon emigrated as habitat conditions declined. This observation was further supported by the results of an experimental release of coho salmon. Survival of fish utilizing emergent wetlands was dependent on movement to the river before water quality decreased or stranding occurred from wetland desiccation. Thus, our results suggest that enhancing freshwater wetlands via water control structures can benefit juvenile salmonids, at least in the short term, by providing conditions for greater growth, survival, and emigration.

Annual inundation of floodplains is the principal force determining productivity and biotic interactions in river–floodplain systems (Junk et al. 1989; Bayley 1995). Emergent wetlands are common features of such systems, which under normal surface water conditions have no surface inlet to provide access for riverine fishes. During periods of high water, however, rivers may overflow their banks onto the floodplain, rejuvenating the wetlands and establishing temporary connections between the two systems (Snodgrass et al. 1996). This periodic flooding, accompanied by the decomposition of organic matter and release of nutrients, increases primary production and can influence yields of fish (Bayley 1991, 1995). However, the role of these wetlands in the composition and functioning of native fish communities, particularly salmonid communities, has received little research attention.

Freshwater emergent wetlands in the floodplain are significant features of many river systems in the Pacific Northwest (Brown and Hartman 1988; Taft and Haig 2003). Although their role in the life history of salmonid fishes is poorly understood, studies in this region have shown that slow-water side pools and beaver ponds can be important overwintering habitat for juvenile coho salmon *Oncorhynchus kisutch* (e.g., Bustard and Narver 1975; Brown and Hartman 1988; Swales and Levings 1989). Most of these studies, however, have been limited to coastal watersheds having 10–300-km^2 river drainages, narrow floodplains, and low discharges. Their associated habitats

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have been described as off-channels, seasonal tributaries, side-channels, backwater ponds, riverine ponds, and beaver ponds (Bustard and Narver 1975; Peterson 1982; Scarlett and Cederholm 1984; Swales et al. 1986). The off-channel ponds are typically small (0.05–1.0 ha), offer good water quality (dissolved oxygen concentration, 6–8 mg/L; Swales et al. 1986), and are often directly connected to the main-stem river during fall and winter. Isolated emergent wetlands, although functionally similar to off-channel ponds, differ in critical ways, such as size, river connectivity, water quality, vegetation, and location within river systems. Thus, although emergent wetlands are often lumped with the off-channel fish literature (e.g., Beechie et al. 1994), such isolated wetlands differ considerably from oxbows, side-channels, and off-channel habitats that are continuously connected to the stream by a channel and have open water.

Juvenile salmon have only recently been documented in floodplain emergent wetlands during the spring (Sommer et al. 2001; Baker and Miranda 2002; Henning 2004), and the significance of this association is unclear. In part, this is related to the perception that floodplain freshwater emergent wetlands are atypical salmonid habitat; they become seasonally anaerobic, have intermittent connections with the river main stem, are shallow, vegetated, and lack woody cover. However, the shallow depths, increased water temperatures, and emergent vegetation support high invertebrate production (Eldridge 1990; Fredrickson and Reid 1998). Such conditions may enhance prey resources, providing opportunities for fish growth and survival that are superior to those found in the main river channel. Thus, during the spring, floodplain emergent wetlands may provide excellent habitat for juvenile salmonids, but these factors can be offset by the risk of stranding as the wetland desiccates and oxygen levels decline.

Wetland restoration and enhancement activities have focused on improving habitat characteristics, including aquatic connectivity, productivity, and native emergent vegetation that are critical for migratory wildlife and threatened and endangered aquatic and semiaquatic animal and plant species. These techniques (e.g., water control structures and water drawdowns) have focused on benefits for wildlife (Fredrickson and Taylor 1982; Fredrickson and Reid 1988), and our knowledge of the effects of such enhancement measures on fish remains rudimentary.

The purpose of this study was to quantify the use of floodplain freshwater emergent wetlands by juvenile coho salmon in a large river system. Initially, we sought to determine if patterns of fish use are similar in enhanced wetlands (with water control structures), unenhanced wetlands (without water control structures), and oxbows. Subsequently, we evaluated the influence of water temperature and dissolved oxygen concentrations on the use of enhanced wetlands by juvenile coho salmon. Patterns of growth, survival, and emigration were assessed for naturally produced coho salmon yearlings that were resident in the wetlands, as well as individuals introduced experimentally.

Methods

Study area.—The study was conducted from January to June in 2003 and 2004 on the floodplain of the Chehalis River, southwestern Washington (Figure 1). The Chehalis River Basin, the third largest river basin in the Washington State, drains an area of approximately 6,900 km^2 and has a mean annual discharge of 116 m^3/s (Washington Department of Ecology 1980). The study sites were located in the lower portion of the basin (below river kilometer [rkm] 60), where the river is unconstrained and moves sinuously through the floodplain in a broad flat valley floor. The basin was chosen for sampling because of the large size and minimally degraded floodplain. Although ditching and draining for conversion to cropland or pasture has occurred in the Chehalis River valley, there are few levees and no main-stem dams to affect the hydrograph. Generally, flood events are triggered by heavy winter rainfall during most years in the Chehalis River basin.

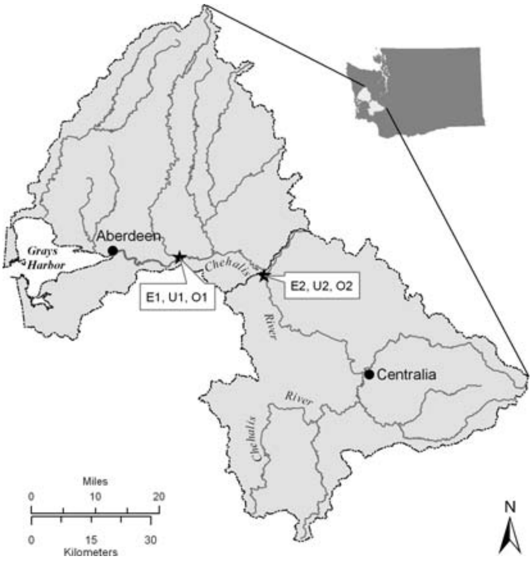

FIGURE 1.—Location of study sites within the Chehalis River basin, Washington, where age-0 and age-1 coho salmon use of enhanced wetlands (E1 and E2), unenhanced wetlands (U1 and U2), and oxbow habitats (O1 and O2) was examined.

TABLE 1.—Characteristics of the six study sites—two enhanced wetlands (E1 and E2), two unenhanced wetlands (U1 and U2), and two oxbow habitats (O1 and O2)—in the lower Chehalis River, Washington. The months in parentheses represent the dates when sites U1, U2, and O2 became dry.

Study site	River kilometer	Surface area (ha)		Winter depth (m)	Water sources (order of dominance)	Water input	Predominant vegetation at wetland edge
		Winter	Summer				
E1	27.4	14.5	0.5	1.0	Rain, river	Seasonal	Reed canarygrass *Phalaris arundinacea*
U1	27.4	3	0 (May)	0.5	Rain, river	Seasonal	Reed canarygrass
O1	30.6	4	4	3.0	Spring, rain, river	Permanent	Woody species
E2	57.9	7.3	1	1.5	Rain, runoff, river	Seasonal	Reed canarygrass
U2	59.5	1	0 (Jul)	1.0	Rain, runoff, river	Seasonal	Reed canarygrass
O2	53.1	3	0 (May)	1.0–3.0	River, rain, runoff	Seasonal	Reed canarygrass

Four seasonal emergent wetlands and two oxbow habitats between rkm 27 and 58 were selected for sampling (Figure 1; Table 1). The freshwater emergent wetlands included two enhanced sites with water control structures (E1 and E2) and two unenhanced wetlands (U1 and U2). The enhanced wetlands E1 and E2 were similar: shallow depths, low currents, abundant emergent vegetation, and large surface areas during winter that declined in size during summer due to desiccation. The wetlands were drained previously as part of a county drainage district project to facilitate farming. Soils are predominantly rennie and salzer clays that are deep, poorly drained, hydric soils (USDA, Soil Conservation Service 1986), and the area experiences frequent periods of flooding from November to April. Wetland enhancement occurred in 1997–1998 to primarily improve conditions for wildlife and vegetation; the effects on fish were given only a secondary consideration. Drainage ditches were blocked, levees were constructed to retain water and protect adjacent lands, and water control structures were installed to create a defined outlet connecting each wetland to an adjacent tributary stream of the Chehalis River and, thus, provide for fish emigration. As a consequence of this enhancement, dense, monotypic stands of invasive reed canarygrass that once predominated the vegetation before restoration were slowly replaced by native emergent vegetation.

The unenhanced emergent wetlands in this study lacked water control structures and were chosen based on their proximity and similarity to the enhanced wetlands (Table 1). The comparable pairs (E1 and U1, E2 and U2) have free-flowing hydrologic connections to the main stem when river flows exceed the riverbanks and overflow onto the floodplain. However, unlike the enhanced wetlands, the lack of a surface water outlet and desiccation in the unenhanced wetlands during the late spring and summer precludes the ability of aquatic species to emigrate once flood flows have declined.

The oxbow habitats O1 and O2 did not contain water control structures. They were chosen for this study because of their proximity to the other study sites and because these sites had free-flowing hydrologic connections to the river during most of the sampling season (Table 1). In addition, physical characteristics of the oxbow sites seemed to be typical salmon off-channel rearing habitat. Oxbow O1 was connected to the same drainage as U1 and E1, but upstream. It was a remnant oxbow channel with spring inputs and a beaver dam. This beaver dam oxbow was characterized by steep channel slopes, minimal emergent vegetation, and an abundance of large wood. Oxbow O2 was a seasonal oxbow side-channel directly connected to the river in winter (Table 1). The depth and discharge at the side-channel oxbow O2 were dependent on river stage, and it became desiccated by mid-May.

Water quality.—Water temperature and dissolved oxygen concentrations were measured approximately once a week in March–June 2003 and in January–June 2004. Measurements were taken via a YSI 85 probe (Yellow Springs, Ohio) at approximately 0.5 m below the water surface near the outlet (E1, E2, O1, O2) or middle of the wetland (U1, U2) during similar times of the day at each site. Differences in dissolved oxygen concentrations among habitats were analyzed using an unbalanced one-way analysis of variance (ANOVA) model with wetland type as a fixed factor (Zar 1974). In addition, a Welch's *t*-test was used to compare dissolved oxygen concentration between years at the enhanced wetlands.

Fish sampling.—Fish were sampled in late winter and spring of 2003 and 2004 via fyke nets, which are often used in shoreline habitat similar to that of the shallow emergent wetlands in our study (Nielsen and Johnson 1983). Moreover, presampling in 2002 showed fyke nets to be more effective at capturing fish, both in terms of abundance and diversity of species, than electrofishing, seining, and minnow traps. Each fyke net consisted of a five-ringed steel hoop net with two trapping throats that were 4.5 m long, 1.2 m wide, and covered with 4.8-mm stretch-mesh netting. The box trap of each net consisted of a polyvinyl chloride pipe frame that was 1.2 m long, 0.6 m wide, and covered with 3.2-mm stretch-mesh netting. A lead (1.2×15 m) was attached to each fyke net to guide fish into the net. Within the wetland, nets were set perpendicular to its shoreline, and usually separated by a minimum of 100 m to maintain independence during each 24-h sample. To increase comparability among sites, the number of nets set per site was proportional to wetland surface area. Nets were set not to exceed a maximum density of 1 net/ha in each wetland.

One-way emigrant traps were installed downstream of study sites that contained a defined outlet (E1, E2, O1, and O2). Each emigrant trap consisted of a holding box (0.6×1.2 m) attached to wing nets that channeled fish into the box for identification and counting. These traps were operated continuously, except during floods when most of the floodplain was inundated or when the site desiccated and lost hydrologic connection to the river and the trap became dry. Traps were checked every 48 h, and captured yearling coho salmon were measured (fork length) and weighed.

The purpose of the study in 2003 was to compare fish use among wetland sites. This was measured using relative fish abundance obtained by fyke nets during January–May. Relative fish abundance was calculated as the number of fish captured in a fyke net over 24 h and expressed as catch per unit effort (CPUE). Emigrant traps were used to examine fish abundance and emigration patterns of coho salmon from 4 March to 5 June 2003 and 7 January to 4 June 2004.

In 2004, mark–recapture was undertaken to provide a more detailed evaluation of emigration patterns, residence duration, growth, and survival of coho salmon in the enhanced wetlands, E1 and E2. Fyke nets were used to capture and uniquely mark age-1 coho salmon for subsequent determination of growth rate. Salmon were anesthetized with tricaine methanesulfonate (MS-222), examined for visible implant fluorescent elastomer dye (VIE) marks, measured (fork length), and weighed. All yearlings without marks were marked with a VIE dye in a unique location and color combination. Yearling coho salmon were allowed to recover following marking and returned to their original habitat. Recapture of marked coho salmon was by fyke nets and emigrant traps. Specific growth rates (Ricker 1979) were calculated for recaptured juveniles (>1 week after initial capture) as

$$G = (\log_e W_{t2} - \log_e W_{t1}/t_2 - t_1) \cdot 100,$$

where G is the specific growth rate, W_{t1} is the initial weight, W_{t2} is the weight at recapture, t_1 is the initial date, and t_2 is the date of recapture. Specific growth rate differences among months and emergent wetlands were compared using a two-way ANOVA model with month and wetland type as fixed factors. Statistical significance in all tests was set at $\alpha = 0.05$.

In 2004, differences in emigration patterns between enhanced wetlands were assessed experimentally to determine whether they related to habitat characteristics (particularly dissolved oxygen concentrations) or the physiological state of the fish (e.g., smoltification). An experimental release of hatchery age-1 coho salmon was thus undertaken: 157 fish in E1 (22 March) and 176 in E2 (26 March). Fish were obtained from the Washington Department of Fish and Wildlife Aberdeen Hatchery, where they had been reared commonly and marked with VIE before release. Timing of emigration through the traps was compared between the enhanced wetlands. In addition, the median date of emigration was compared with that of naturally produced coho salmon yearlings during the same period (i.e., the day after release until the end of trapping) to determine whether the relative pattern of emigration from the two wetlands was similar for released and resident (naturally produced) fish.

Results

Fish Access

The number of days fish had access to the floodplain habitats was estimated with discharge data from a Chehalis River gauge station at rkm 30 (U.S. Geological Survey 2004). At approximately 480 m^3/s the river was connected to the floodplain at all study sites (Figure 2). At the enhanced and unenhanced sites, this occurred for approximately 8 d in February and at the end of March in 2003, and for about 5 d in both mid-November 2003 and early February 2004. By contrast, the oxbow habitats had about 63 d of hydrologic connection to the river between November and July 2003, and 75 d of connection to the river between November and July of 2004. The O1 site was connected all year, and the O2 site was connected until the river flows decreased to approximately 110 m^3/s.

Salmon Wetland Use

Coho salmon were the most abundant salmonid captured in the wetlands, and two age-groups were collected: ages 0 and 1. All of the salmonids captured had intact adipose fins and, thus, were presumed to be naturally produced because the adipose fin is removed from all hatchery fish in the Chehalis River system. Age-0 coho salmon were captured in all wetlands via fyke nets; their CPUE peaked in April at the unenhanced and enhanced wetlands and in May at

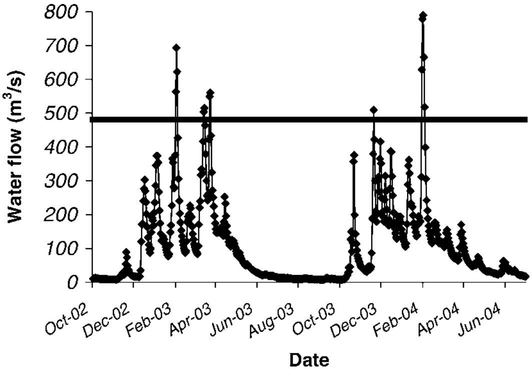

FIGURE 2.—Average daily discharge in the Chehalis River, Washington, at Porter gauge (12031000) from October 2002 to July 2004. The horizontal line at 481 m^3/s represents the approximate discharge at and above which the riverbanks were flooded and the river was connected to the study locations.

the oxbow habitats. The increase in CPUE age-0 coho salmon in the unenhanced wetlands during April was associated with the concentration of fish due to wetland desiccation. The relative abundance (CPUE) of age-1 coho salmon in fyke nets was highest at O2 in all months except January, when E1 had greater abundances (Table 2). In contrast, no age-1 coho salmon were captured in the U1 and U2.

In 2003, emigrant traps captured 117,255 fish representing 18 species (including four salmonid species: coho salmon, Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, and coastal cutthroat trout *O. clarkii clarkii*) emigrating E1, E2, O1, and O2 (Table 3) (Henning 2005). In 2004, emigrant traps captured 36,751 fish representing 17 species (including two salmonid species, coho salmon and coastal cutthroat trout) emigrating from E1 and E2 (Table 3; Henning 2005). Catches of age-0 and age-1 coho salmon in 2003 were 2 times greater at E1 and 12 times greater at E2 than in 2004.

Fish emigration was considerably higher at the enhanced wetlands (3,015 fish/trap-night at E1, 346 fish/trap-night at E2) than the oxbow habitats (13 fish/trap-night at O1, 112 fish/trap-night at O2; Table 3) in 2003. Overall, salmon constituted 2.6% of the fish assemblage at the enhanced wetlands E1 and 34.6% at E2 in 2003 and 2.1% at E1 and 2.8% at E2 in 2004 (Table 3). The predominant fish emigrating from these sites was the threespine stickleback *Gasterosteus aculeatus* (Henning 2005). At the oxbow habitats, however, salmon were a far more prominent component of the emigrant assemblage (95.3% at O2 and 15.0% at O1). Yet, in absolute terms (total salmon), emigrating salmon were most abundant at the E2 wetland (119 salmon/trap-night) compared with O2 (107 salmon/trap-night) and E1 (79 salmon/trap-night; Table 3) in 2003. The lowest number of emigrating salmon occurred at O1 (2 salmon/trap-night; Table 3). Capture of emigrants increased in May at all sites, and emigration of age-0 fishes peaked at this time. Although fish abundance was greater in the enhanced wetlands, O2 had comparable numbers of coho salmon. In addition, coho salmon emigrants were similar in the enhanced sites and O2 when wetland size was accounted for (emigrant densities as salmon/ha: E1 = 0.02, E2 = 0.06, O1 = 0.002, O2 = 0.04).

There were temporal differences in the utilization of wetlands by age-0 and age-1 coho salmon. Age-1 coho salmon emigrated from the wetlands earlier than age-0 emigrants (Figure 3), and their emigration decreased considerably by the end of May. Age-0 emigrants were not captured until mid-March and increased until June. The median date of emigration of age-1 coho salmon was noticeably earlier at the enhanced wetlands than at O2 (31 March for E1, 17 April for E2, 30 April for O2), but the pattern for age-0 coho salmon was similar among sites. The O1 site was not included in the analysis because too few emigrating salmon were captured. The differences in median dates of emigration between ages 0 and 1 varied between years at all

TABLE 2.—Catch per unit effort (fish/net) of age-0 and age-1 coho salmon in fyke nets at two enhanced wetlands (E1 and E2), two unenhanced wetlands (U1 and U2), and two oxbow wetlands (O1 and O2) in the Chehalis River, Washington, floodplain 2003.

	Jan		Mar		Apr		May	
Site	Age 1	Age 0	Age 1	Age 0	Age 1	Age 0	Age 1	Age 0
E1	8.0	0	0.3	0	0.5	0.2	0	0
E2	0	0	0.5	0	0.9	0.3	0.5	0.3
U1	0	0	0	0.7	0	9.0	[a]	[a]
U2	0	0	0	0	0	0.5	0	0
O1	0	0	0	0	0	0	1.0	1.3
O2	2.3	0	0.5	0	12.2	3.8	17.0	61.0

[a] No sampling occurred due to wetland desiccation.

TABLE 3.—Total catches in one-way emigrant traps in oxbow habitats (O1 and O2) and enhanced wetlands (E1 and E2) in the Chehalis River, Washington, floodplain during the 2003 and 2004 sampling periods. The number of trap-nights is in parentheses.

	2003				2004	
Species	O1 (64)	O2 (32[a])	E1 (68)	E2 (70)	E1 (55)	E2 (64)
Age-1 coho salmon	9	179	619	485	290	282
Age-0 coho salmon	51	1,416	1,802	3,680	150	168
Age-0 Chinook salmon	0	111	1	14	0	0
Age-0 chum salmon	0	6	276	0	0	0
Cutthroat trout	0	1	1	9	0	2
Total fish	401	1,798	102,513	12,094	20,735	16,016

[a] Site O2 experienced flooding and was the earliest site to desiccate, thus reducing trap-nights.

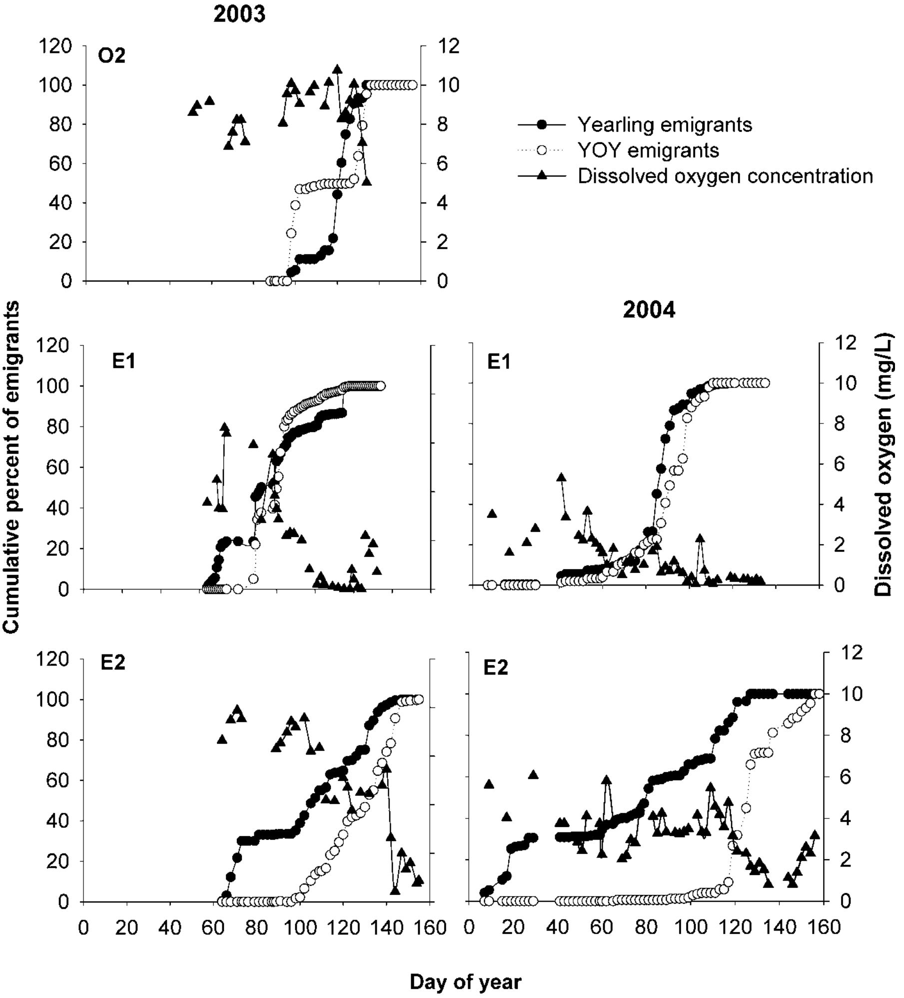

FIGURE 3.—Emigration patterns by day of year for age-0 and age-1 coho salmon departing enhanced wetlands (E1 and E2) of the Chehalis River, Washington, during the 2003 and 2004 sampling seasons and for oxbow O2 during 2003 compared with dissolved oxygen concentrations.

sites, but differences at E2 (25 d in 2003, 44 d in 2004) were greater than at E1 (11 d in 2003, 5 d in 2004). At O2, the median date of emigration of age 1 coho salmon in 2003 was 6 d earlier than that of age-0 emigrants. Coho salmon yearlings remained in E2 significantly longer than in E1 ($t = 6.45$, df = 291, $P < 0.01$). Residence duration averaged 51 d in E1 and 66 d in E2, the longest residence of a marked salmon was of 104 d in E1.

Coho Salmon Growth

In 2004, yearling coho salmon had an average specific growth rate of 1.37%/d by weight (SE = 0.06, $N = 107$) at E1 and 1.43%/d (SE = 0.05, $N = 134$) at E2. Although there was no difference in specific growth rate between the two wetlands ($F_{1,\,125} = 3.17$, $P = 0.07$), there were significant differences in growth among months ($F_{3,\,125} = 6.79$, $P < 0.01$). Specific growth rates were higher for fish recaptured in March and April than for fish recaptured in February or May.

Water Quality and Related Emigration Patterns

In 2003, water temperatures at all sites increased throughout the sample season, ranging from 6°C to 22°C. On 1 June, the E1 and E2 wetlands were 16°C and 19°C and O1 was 17.5°C; U1, U2, and O2 were desiccated and fish were stranded. Dissolved oxygen (DO) concentrations decreased throughout the sampling season (range, 0–10 mg/L) reaching lethal or near lethal levels for fish in June (<0.8 mg/L). Oxygen was probably a more significant limiting factor than temperature in the wetlands. Enhanced and unenhanced wetlands had significantly lower DO concentrations than oxbow habitats ($F_{5,\,182} = 62.12$, $P < 0.01$). The oxbows O1 and O2 had water quality suitable for fishes throughout the sampling season, but minimum DO levels in the unenhanced and enhanced wetlands were less than 1.0 mg/L. Although DO in O2 did not approach critical levels for fish survival, fish were stranded when the outlet channel desiccated. At wetlands, DO was significantly higher in 2003 than 2004 ($P < 0.01$ for E1, $P < 0.01$ for E2). In 2003, low DO did not occur until the end of April, but in 2004 substantial declines (to <2 mg/L) occurred by the end of February in E1 and by May in E2.

Dissolved oxygen concentrations appeared to influence the emigration patterns of age-0 and age-1 coho salmon in the enhanced wetlands (Figure 3). In 2003, dissolved oxygen concentrations decreased to less than 1.0 mg/L at the end of April at E1, and both age-groups continued to emigrate until 18 May (Figure 3). At E2, age-0 emigrants increased until 2 June when dissolved oxygen concentrations fell below 1.5 mg/L (Figure 3). At O2, the outlet channel desiccated before DO declined (5.0 mg/L), so fish were stranded because low DO did not hasten emigration. In 2004, DO at E1 decreased below 2.0 mg/L at the end of February, and age-0 and age-1 coho salmon continued to emigrate until mid-April when dissolved oxygen levels were less than 0.5 mg/L. At E2, age-1 fish emigrated until 22 May when dissolved oxygen levels decreased below 1.5 mg/L, but age-0 fish continued to emigrate until 6 June when the trap was removed.

Release Experiment and Survival

Patterns of emigration of released coho salmon differed significantly between E1 and E2 (median = 1 d versus 51 d after release, respectively). The DO at E1 was low (about 1.0 mg/L) when the coho salmon were released, and 70% emigrated within the first week. In contrast, DO at E2 remained higher (3.0–5.0 mg/L), and only 14% of the released coho salmon emigrated during the first month following release. However, the patterns of emigration of released coho salmon were similar to that of the naturally produced yearlings at both enhanced wetlands. The median date of emigration of released coho salmon at E1 was within 1 d of those naturally produced; at E2 the median followed the naturally produced age-1 fish by 2 weeks.

Survival rates for the age-1 releases were 38% at E1 and 22% at E2. Because estimates were calculated by dividing the number of released yearlings that emigrated by the total number released in the wetland, survival rates were considered minimum estimates. It is unlikely that emigration occurred after the traps were removed at E1 because low dissolved oxygen levels (<1.0 mg/L) probably reduced their survival. However, coho salmon in E2 could have continued to emigrate for a short time because DO was greater (1.4–3.1 mg/L). Minimum survival rates for naturally produced age-1 coho salmon (determined in 2004 from the uniquely marked individuals) were 57% at E1 and 30% at E2. Actual survival rates were probably higher for the reasons given above and because floods earlier in the season may have allowed fish to emigrate without passing through the trap. Survival estimates for naturally produced yearlings marked before the flood and recaptured after the flood were 65% and 67%, suggesting minimal emigration during the floods. Capture efficiencies were estimated with both naturally produced and the experimentally release fish; however, these estimates were affected by fish that did not emigrate from the wetlands, and thus, trap efficiency was probably underestimated.

Discussion

Enhanced wetlands on the floodplain of the Chehalis River appear to be important habitats for juvenile coho salmon. Coho salmon were the most abundant salmonid species rearing in the study sites and their densities in the enhanced wetlands frequently surpassed those recorded in the unenhanced wetlands and oxbow habitats. However, they were rarely the predominant fish species, except in the oxbow side-channel (O2). This was particularly true in the enhanced wetlands where native nonsalmonid species, such as threespine stickleback and Olympic mudminnow *Novumbra hubbsi* were far more common (Henning 2005). Growth and survival of age-1 coho salmon suggest that juvenile coho salmon benefited from the enhanced wetlands sampled in this study. Age-1 growth was higher than estimates from off-channel ponds in the Clearwater River, Washington (Cederholm et al. 1988). Moreover, minimum survival rates (30–57%) observed in our study are comparable to overwinter survival estimates in other off-channel ponds: 49–79% (Peterson 1982), 54–87% (Swales et al. 1986), and 56%; (Cederholm et al. 1988). These survival estimates suggest that coho salmon in the enhanced wetlands can emigrate successfully before water quality declines. By contrast, age-0 coho salmon captured and released after the last flood in the unenhanced wetlands (1 April 2003) suffered 100% mortality. Similarly, the coho salmon captured and released in O2 were stranded in the pond after the outlet desiccated in mid-May and presumably died.

Ponds created by beavers *Castor canadensis* have been shown to be productive habitats for juvenile coho salmon (Sanner 1987; Leidholt-Bruner et al. 1992; Nickelson et al. 1992). Although the oxbow beaver pond appeared to have habitat features that would attract juvenile coho salmon (i.e., low water velocity, abundant cover and large wood, adequate water quality and depth [3 m], and year-around connection to the river system), few salmon were captured there. Despite these similarities, several factors may explain the observed paucity of fish. One major distinction is that beaver dams built in the stream channel tend to be ephemeral and are often destroyed by high winter flows, requiring rebuilding each summer (Leidholt-Bruner et al. 1992). In the lower Chehalis River, however, beaver dams are frequently imbedded in the floodplain of agricultural ditches and remnant oxbows and are more permanent than instream beaver dams. In addition, nonnative fishes are abundant in oxbow lakes of the Chehalis River drainage, and they can often affect the presence of native species (Beecher and Fernau 1982). For example, piscivorous largemouth bass *Micropterus salmoides* and brown bullhead *Ameiurus nebulosus* that inhabit the oxbow beaver pond we studied may prey on juvenile salmon. Finally, floodplain ponds are less likely to experience the immigration of juvenile salmon by downstream drift than beaver ponds located in stream channels where salmon spawning may occur immediately upstream.

We observed temporal variation in emigration across the floodplain between age-groups of coho salmon and between sample years. Lengthy inundation of floodplains and associated emergent wetland habitats often results in low DO (i.e., anoxia; Mitsch and Gosselink 1993; McKinnon 1997), and the seasonal pattern of juvenile salmon emigration in our study appeared to reflect changing oxygen levels. Emigration was earlier in 2004 than 2003, paralleling the earlier decline in DO. Moreover, differences in the patterns of emigration between the two enhanced wetlands reflected the patterns of DO. Results of the experimental release exhibited similar patterns, indicating that the stimulus for emigration was related to the environmental conditions rather than the physiological state of the fish (i.e., smoltification). Low DO in wetlands may also limit spring residency of juvenile coho salmon. Average residence of naturally produced age-1 coho salmon and the released cohorts were greater in the enhanced wetlands, which had higher DO.

There were also temporal differences in the utilization of the wetlands between age-classes of coho salmon. Age-1 fish can often access floodplain habitat before the emergence of age-0 fish in late February. Compared with age-1 fish, age-0 fish emigrated from the enhanced wetlands later and appeared more tolerant of low DO. Although the onset of smoltification may have influenced the age-1 emigration timing, it was probably of secondary importance to environmental conditions (e.g., DO), as indicated by the results of the release experiment. Resident and experimentally released age-1 coho salmon from the two enhanced wetlands showed distinct differences in timing that paralleled the differences in environmental quality. Lower DO thresholds depend on fish size, age, and physiological state; temperature; and acclimation period to lower DO (Herrmann 1958; Colt et al. 1979). Although DO was below lethal limits for coho salmon parr (<1.0 mg/L; Colt et al. 1979), continued emigration from the enhanced wetlands suggests that numerous individuals survived these conditions. Concomitant with declines in dissolved oxygen, increases in ammonia, urea, and nitrites (Brett 1979) may also have contributed to the observed emigration patterns.

Not surprisingly, there was temporal variation in coho salmon abundance between years of the study. Salmon abundance in the enhanced wetlands was 5–9 times higher in 2003 than 2004. The smolt production forecast for the Chehalis River was 30% higher in 2003 than in 2004 (Washington Department of Fish and Wildlife, unpublished data), which could account partly for the higher age-1 abundance in wetlands in 2003. In contrast, the number of spawners that contribute to the estimated number of age-0 fish in the Chehalis system was similar between 2003 and 2004 and, thus, could not explain the difference in age-0 abundances (K. Holt, Washington Department of Fish and Wildlife, unpublished data). The frequency and timing of flooding each year probably determines accessibility to and use of off-channel emergent wetlands by riverine species (Brown and Hartman 1988). Floods occurred more often and later in 2003 (late March) than 2004 (early February), increasing and prolonging wetland access for fish, especially age-0 coho salmon.

Although our sample size of wetland types was small, the study suggests that heterogeneity in habitat and its use by salmon exists across the floodplain. Salmon abundances varied among emergent wetlands, and not all off-channel sites supported salmon. Although natural wetlands are generally considered atypical rearing habitat, our results show that under certain circumstances floodplain emergent wetlands, particularly those that are enhanced with water control structures, can offer important rearing opportunities for salmon. Thus, generalizing about the quality of habitat types for salmon across the floodplain should not be undertaken without classifying the habitat and determining fish presence (see Brown 1987). Wetland characteristics such as continuous connectivity to the river system, the length of the hydroperiod, the distance from the main river channel, and adequate DO and temperature during the rearing season are critical factors that affect the likelihood of use by juvenile salmon.

There can also be considerable temporal variation in the structure and function of off-channel habitats in an individual floodplain, as related to factors that affect fish access and residency in floodplain habitats (e.g., flooding). Habitats that have an abundance of fish one year may be inaccessible in another year. In addition, fish rearing in ephemeral habitats risk stranding and anoxia, but these risks may be mitigated by faster growth and higher survival that result in continued use of these habitats. It is also important to recognize the variable nature of habitats across a floodplain and their suitability to salmon. Agricultural landscapes with rehabilitated emergent wetlands, even when the habitat is only accessible to fish during floods, can offer valuable rearing habitat to riverine species. Although wetland enhancement and restoration are often initiated for purposes other than salmon conservation (e.g., wetland mitigation, waterfowl habitat, and amphibian breeding sites), our research shows that juvenile salmon can benefit from such activity, at least in the short term, if outlet structures are included that allow fish emigration and sites are seasonally drawn down so that nonnative fishes are discouraged. These projects are most beneficial when incorporated with large-scale restoration programs that ultimately restore ecosystem processes. Finally, emergent wetlands and side-channels in large coastal river systems may be important for sustaining a unique aspect of the life history of naturally produced juvenile coho salmon.

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