Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population

Timothy Copeland and David A. Venditti

Abstract: The most productive juvenile life history in the Pahsimeroi River Chinook salmon (*Oncorhynchus tshawytscha*; Idaho, USA) population (in terms of smolt production) is being eliminated. Length at emigration and survival from spawning areas to Lower Granite Dam within each of three juvenile phenotypes (age-0 smolts, fall parr, age-1 smolts) were influenced by initial cohort abundance. The proportion of age-1 emigrants reaching Lower Granite Dam was dome-shaped with respect to initial cohort abundance. As initial abundance increased, higher proportions of juveniles adopted the age-1 smolt phenotype or emigrated as fall parr. The age-0 smolt phenotype had the highest relative survival, and the fall parr phenotype, the lowest. The contributions of each emigrant type to cohort smolt production varied with circumstances; hence, the full expression of phenotypic diversity is important to the study population. However, there were no records of tagged age-0 smolts surviving to return from the Pacific Ocean. Given the potential productivity of this life history, management and recovery efforts should be directed at the age-0 smolt phenotype.

Résumé : Le cycle biologique juvénile le plus productif (en ce qui a trait à la production de saumoneaux) de la population de saumons chinook (*Oncorhynchus tshawytscha*) de la rivière Pahsimeroi, Idaho, É.-U., est en train d'être éliminé. La longueur à l'émigration et la survie depuis les sites de fraie jusqu'au barrage Lower Granite chez chacun des trois phénotypes juvéniles (saumoneaux d'âge 0, tacons d'automne et saumoneaux d'âge 1) sont influencées par l'abondance initiale de la cohorte. La proportion d'émigrants d'âge 1 qui atteint le barrage Lower Granite se répartit en dôme par rapport à l'abondance initiale de la cohorte. À mesure que l'abondance initiale augmente, des proportions plus élevées de jeunes adoptent le phénotype de saumoneau d'âge 1 ou émigrent comme tacons d'automne. Le phénotype d'âge 0 possède la survie relative la plus élevée et le phénotype de tacon d'automne la plus basse. Les contributions de chaque type d'émigrant à la production de saumoneaux de la cohorte varient selon les circonstances; l'expression de l'entière diversité phénotypique est donc importante dans l'étude de la population. Cependant, il n'existe aucune information concernant des saumoneaux d'âge 0 marqués ayant survécu jusqu'à leur retour du Pacifique. Étant donné la productivité potentielle de ce type de cycle biologique, on devrait concentrer des efforts de gestion et de conservation sur le phénotype de saumoneau d'âge 0.

[Traduit par la Rédaction]

Introduction

Intrapopulation diversity is important to population resilience (McElhany et al. 2000; Kendall and Fox 2002; Gamfeldt and Källström 2007). Life history diversity is diversity in time; multiple phenotypes are a population-level insurance policy against extinction (Healey and Prince 1995). Wilbur (1996) demonstrated theoretically that additional life history complexity could increase population productivity via niche expansion in time and space. Diversity of geographic and life history components increases regional resilience of a species (Hilborn et al. 2003). Managers need to understand how population components contribute to overall production and fitness for effective conservation. Here we document a case in which a major life history type in a Chinook salmon (*Oncorhynchus tshawytscha*) population has been compromised. Conservation of this population will be more effective with an understanding of how various juvenile life history types contribute to population functioning.

In Pacific salmon (*Oncorhynchus* sp.), adult life history diversity is well known but juvenile diversity may be greater and more important than currently understood (Hilborn et al. 2003). Juvenile life history types, defined with respect to timing of habitat use, contribute differentially to population productivity (Reimers 1973; Mobrand et al. 1997). Snake River spring–summer (SRSS) Chinook salmon generally exhibit a stream-type life history, rearing for 1 year in freshwater before migrating to the ocean (Healey 1991). However, a percentage of SRSS Chinook salmon juveniles exhibit an ocean-type life history, smolting and migrating to the ocean during their first year (Healey 1991; see also Connor et al. 2001). Emigration phenotypes in juvenile salmon may result from links between growth and smoltification (Thorpe et al. 1998; Beckman et al. 2007) as modified by the tradeoff between size and survival (Zabel and Achord 2004; Scheuerell 2005), genetic control (Taylor 1990), or density-dependent emigration (Dunham and Vinyard 1997; Grant et al. 1998; Dunham et al. 2000). The literature is am-

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biguous as to whether migration types result from facultative responses or adaptive life history differences.

The existence of less productive phenotypes is a central problem in evolutionary biology (Reeve and Sherman 1993). Our study took advantage of a 13-year data set (1992 through 2004 cohorts) on a Chinook salmon population with multiple juvenile emigration phenotypes (age-0 smolt, fall parr, and age-1 smolt) to gain insight on this question. We assumed that the observed phenotypes arose as a tradeoff of long-term expectations versus short-term stochasticity (Stearns 1992; Roff 2002) and further that observed phenotypes will contribute under some circumstances. We used survival to Lower Granite Dam (Fig. 1) as our measure of fitness to avoid the influence of anthropogenic changes to the migratory corridor in the Snake and Columbia rivers (Waples et al. 2008). Our objectives were (*i*) to compare survival by phenotype, (*ii*) to describe the influence of growth and density on proportions of each phenotype in successful emigrants, and (*iii*) to model relative survival among phenotypes. Using the latter information, we considered how the study population functioned historically and how it is functioning currently.

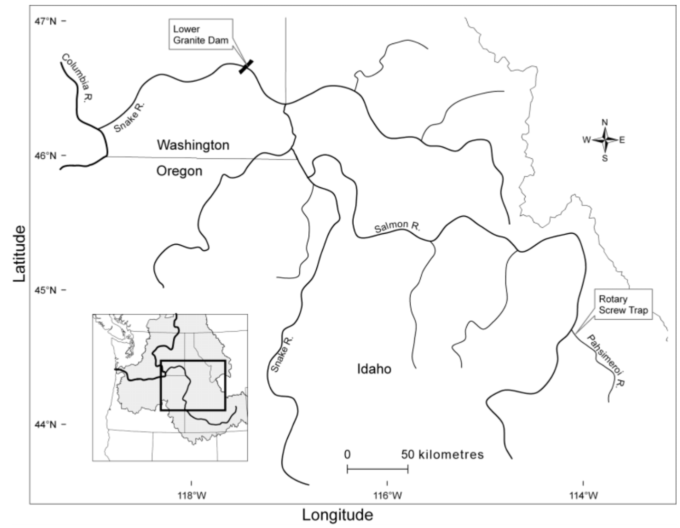
Materials and methods

Study population

The study population was the Chinook salmon spawning in the Pahsimeroi River of central Idaho, USA (Fig. 1). The population is classified as summer-run, based on timing of adult entry into freshwater. It is part of the SRSS Chinook salmon Evolutionarily Significant Unit, which is listed as threatened under the Endangered Species Act. This is considered a key population for the recovery of the upper Salmon River major population group (MPG), and this MPG cannot be considered recovered without a viable Chinook salmon population in the Pahsimeroi River (Interior Columbia Technical Recovery Team (ICTRT) 2007). All SRSS Chinook salmon are considered to have a stream-type life history (Good et al. 2005), that is, they have an extended freshwater rearing phase and enter the ocean as yearlings, whereas ocean-type Chinook salmon typically enter the ocean as subyearlings (Healey 1991). Juvenile emigrants pass a total of eight dams on the Snake and Columbia rivers before reaching the Pacific Ocean; the first is Lower Granite Dam and the last is Bonneville Dam. A hatchery operates on the Pahsimeroi River with a weir 1.5 km upstream from the mouth. All hatchery-produced juveniles were marked with an adipose fin clip and excluded from this study. During the spawning run, marked adults were removed from the river at the weir, whereas unmarked fish were allowed to continue upstream.

The Pahsimeroi River is a tributary to the Salmon River, within the Snake River basin (Fig. 1), and historically supported a substantial, relatively productive Chinook salmon run (Good et al. 2005). The river lies in a dry intermontane sagebrush valley, with the mouth at an elevation of approximately 1500 m. Most tributaries are disconnected by irrigation diversions and the flow is often intermittent in the upper parts of the basin. Diverted water returns to the river via large springs near the center of the valley, so the lower Pahsimeroi River has substantial flow year-round and high connectivity to the Salmon River. Chinook salmon currently

Fig. 1. Map showing the position of the Pahsimeroi River (Idaho, USA) in relation to the Snake and Columbia rivers. Locations of the rotary screw trap and Lower Granite Dam are marked. Inset map shows location within the US Pacific Northwest.



occupy the lower 20 km of the Pahsimeroi River. Within this reach, the river is a low-gradient stream dominated by groundwater flow, which moderates temperature (Trapani 2002). The channel is sinuous and well developed and has a large proportion of pool habitat. During the summer, submergent plants grow in a large proportion of the main channel, indicating a relatively high level of aquatic productivity, which sets the Pahsimeroi River apart from other tributaries in the Salmon River basin.

Juvenile Chinook salmon emigrating from the Pahsimeroi River display four distinct phenotypes. A group of fry exits the river soon after emergence in March. Because these fish were too small to be tagged with passive integrated transponder (PIT) tags, they were excluded from our study. From April to June, another group of subyearlings (age-0 smolts) leave the Pahsimeroi River, move through the Salmon River into the Snake River, and pass Lower Granite Dam, 619 km downstream (Fig. 1). Juvenile emigration from the Pahsimeroi River then essentially ceases until late August when a third group, fall parr, begins to emigrate. Fall parr spend the winter in the Salmon River and reach Lower Granite Dam the following spring. Lastly, yearling (age-1 smolts) leave the Pahsimeroi River during March and April, travel quickly to the Snake River, and pass Lower Granite Dam.

Data collection

Emigrating juveniles were collected by a rotary screw trap located 1.5 km upstream from the river mouth (Fig. 1). The trap was deployed as early as possible in the spring, usually in the last week of February or the first week of March, and operated until ice-up (usually the first week of December). For the first few years of the study (1992–1995), the trap was not operated in the summer (June–August).

Fish were processed at least once daily and were counted and measured, and a subsample was PIT-tagged. The transponder in these tags emits a unique code that can be read by a detector when the tag passes through a magnetic field (Prentice et al. 1990). All fish were anesthetized before processing with a buffered solution of tricaine methanesulfonate (MS-222). All fish were measured to the nearest 1 mm from the tip of the nose to the fork of the caudal fin (fork length, FL) and scanned for the presence of PIT tags. Fish ≥60 mm FL were eligible for tagging (see procedures below). After processing, all PIT-tagged fish were placed in a live box (a perforated container through which water could flow freely) 0.4 km upstream from the trap and released at dusk. Efficiency of the trap was calculated from recaptures of these fish. Recaptured fish and any individuals not tagged were placed in a second live box immediately below the trap and released at dusk.

Tagging procedures followed recommendations of the PIT Tag Steering Committee (1999). Tags were injected into the body cavity using a hypodermic needle. Needles and tags were sterilized in 70% ethanol for 10 min prior to and between uses. All age-1 smolts were tagged. All other groups (except fry) were tagged at a rate determined by the expected number of emigrants and the number of tags available for the year. Tagging data were recorded into a computer file each day and were uploaded to the central repository for all PIT-tagging activities in the Columbia basin (PTAGIS, www.ptagis.org) within 48 h.

Abundance of each emigrant type was estimated with a mark–recapture program specific to rotary screw trap data developed by Steinhorst et al. (2004). Each calendar year was partitioned into periods defined by changes in flow, subject to the constraint that at least seven recaptures occurred during the period. Population abundance of all emigrants from a cohort was estimated using a summation of Bailey's modified estimator (Ricker 1975):

$$N = \sum_{i=1}^{n} c_i(m_i + 1)/(r_i + 1)$$

where N is number of emigrants, n is the number of periods designated, c_i is the number of fish captured, m_i is the number of tagged fish released, and r_i is number of recaptures in period i. The estimator was computed using an iterative maximization of the log-likelihood, assuming that fish are captured independently with probability p_i (equivalent to trap efficiency) and tagged fish mix thoroughly with untagged fish.

Initial abundance of each cohort was indexed by multiple-pass redd counts. Redds are nests constructed in the stream gravel by spawning females and are a surrogate for the number of eggs spawned. The stream was surveyed three times annually between early September and early October. Trained observers walked the bank, scanning the stream substrate using polarized sunglasses to identify redds. To avoid double counting, each redd was marked by flagging a nearby bush or tree.

Emigrant survival was estimated from the detection of PIT-tagged individuals in the lower Snake and Columbia rivers. For this study, emigrants were considered successful if they passed Lower Granite Dam. Daily detection records were obtained by querying the PTAGIS database (www.ptagis.org) for all observations of fish tagged at the Pahsimeroi River trap by calendar year.

Data analyses

We categorized emigrant types by a combination of FL and day of tagging (Fig. 2*a*). Age-1 smolts were always distinct from age-0 smolts based on size and emigration date, but a subsample of ages was verified by scale examination (Lutch et al. 2003). After exclusion of the age-1 smolts, we separated age-0 smolt and fall parr types by constructing discriminant functions for each year using data from fish detected at downriver dams. Date and length at tagging were used to predict group membership. Individuals detected in the year of tagging were age-0 smolts, whereas individuals detected in the spring after tagging were fall parr. We applied the discriminant functions to all tagged fish. Abundance estimates were parsed into emigrant type for each estimation period by proportions of the tagged population.

We estimated survival to Lower Granite Dam by emigrant type within each cohort using a Cormack–Jolly–Seber model implemented by SURPH software (Lady et al. 2001). Model inputs were records of the PIT tags released at the Pahsimeroi River trap and their subsequent detection at downstream dams. Model outputs were the probability of being detected at Lower Granite Dam (based on detections there and downstream) and the probability of survival to Lower Granite Dam. The number of each emigrant type surviving to Lower Granite Dam was computed by multiplying abundance estimates at the Pahsimeroi River trap by survival probability.

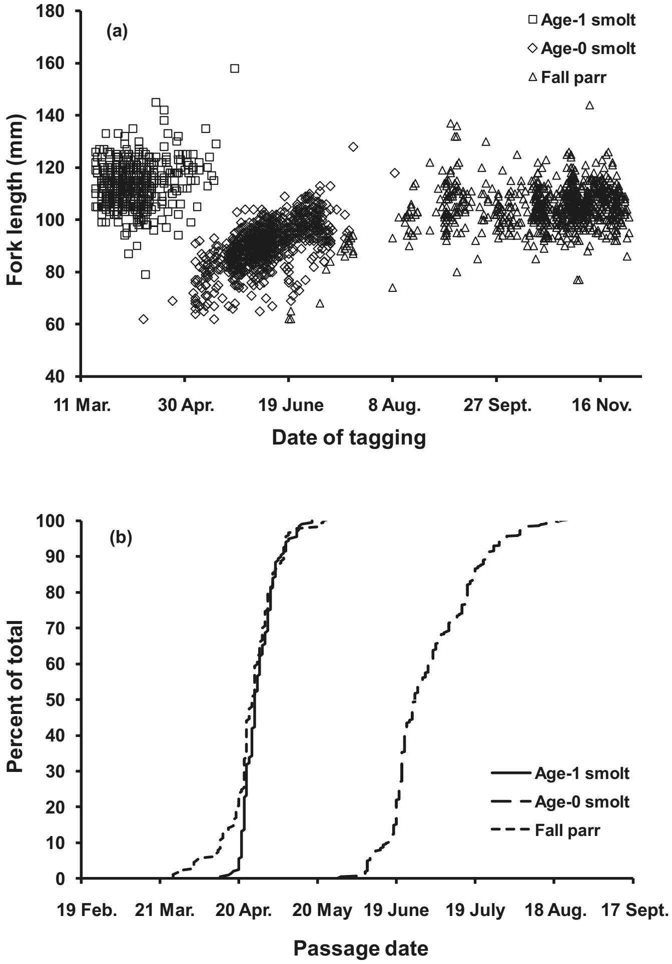
We hypothesized that the expression of migratory phenotype is influenced by growth and abundance. The effect of abundance on growth was examined by plotting a growth index for each emigrant type versus the redd count for the year they were spawned. Power functions were used to describe the relationships (Grant and Imre 2005). These models were fit using a Gauss–Newton algorithm in SYSTAT (Systat Software Corporation 2004). Regressions were considered significant if their 95% Wald confidence interval (CI) did not contain zero, and the slopes of the functions differed if their CIs did not overlap. To index growth, we used mean FL of PIT-tagged emigrants in June for age-0 smolts, in November and December for fall parr, and all age-1 smolts collected. Mean lengths for age-0 smolts from the 1992 and 1993 cohorts were not calculated because the trap was not operated in June in those years. We also compared annual proportions of age-1 smolts surviving to Lower Granite Dam with initial cohort abundance, indexed by redd counts.

We examined the implications for population regulation with a deterministic model of relative survival contrasting age-0 smolts and fall parr to age-1 smolts. For prereproductive life stages, survival is equivalent to fitness (Roff 2002). The relevant question is how likely is a juvenile salmon to survive to Lower Granite Dam if it adopts a particular strategy? To understand fitness, a measure of survival prior to passing the trap is necessary. Therefore, we estimated two survival rates for each emigrant type to determine its relative survival: from the end of the cohort's first spring to emigration from the Pahsimeroi River ($S_{\mathrm{pah},k}$) and from the trap to Lower Granite Dam ($S_{\mathrm{lgd},k}$) for each emigrant type k. Relative survival (RS) was computed as

$$\mathrm{RS}_k = \frac{S_{\mathrm{pah},k} \times S_{\mathrm{lgd},k}}{\sum (S_{\mathrm{pah,age\text{-}1}} \times S_{\mathrm{lgd,age\text{-}1}})}$$

We used median S_{lgd} for the study period in the model as a measure of the central tendency in survival to reduce the ef-

Fig. 2. Patterns in Chinook salmon emigration from the Pahsimeroi River during 1999. (*a*) Fork length versus date of tagging by emigrant type for juvenile Chinook salmon tagged at the Pahsimeroi River trap. Age-1 smolts were spawned in 1997. Age-0 smolts and fall parr were spawned in 1998. Note that only a subsample of each type was tagged. (*b*) Cumulative percentage by emigrant type versus passage date at Lower Granite Dam. Age-1 smolts and fall parr were spawned in 1997. Age-0 smolts were spawned in 1998.



fect of extreme values. We assumed that daily survival was equivalent among all juveniles within the Pahsimeroi River and considered three scenarios about when mortality occurred: summer only, summer and fall only, or summer through winter. We further assumed that survival did not change appreciably with the seasons because flows were relatively stable and temperature was moderate throughout the year. Because age-0 smolts emigrate at the end of their first spring, $S_{\text{pah,age-0}} = 1$. We iteratively solved for S_{pah} for fall parr and age-1 smolts while constraining model output such that

$$\frac{S_{\text{pah,age-1}} \times S_{\text{lgd,age-1}}}{\sum (S_{\text{pah},k} \times S_{\text{lgd},k})}$$

equaled the median ratio of age-1 smolts at Lower Granite Dam to total cohort production.

Results

The three life history types were present in every cohort studied and emigration followed a consistent pattern. Age-0 smolts were the first emigrants from each cohort, leaving the Pahsimeroi River in the spring after hatching (Fig. 2*a*) and continuing past Lower Granite Dam in the same year. Fall parr began emigrating during August (Fig. 2*a*) but did not pass Lower Granite Dam that year. In the following spring, age-1 smolts began emigrating in early March and usually were gone by mid-May. The first emigrant type from a cohort to reach Lower Granite Dam was the age-0 smolts, but when viewed from a calendar-year perspective, this emigrant type consistently passed the dam two months later than the other two types (Fig. 2*b*).

The discriminant functions were effective for distinguishing between age-0 smolts and fall parr. Classification accuracy of individuals with known life history averaged 97.5%. However, a small number of fish classified as age-0 smolts arrived at the dam in the year after tagging, i.e., they were actually fall parr. Classification of these fish as age-0 smolts did not alter survival estimates greatly (≤0.03). No juveniles classed as fall parr were detected as age-0 smolts. Age-1 smolts were quite distinct from age-0 smolts (Fig. 2*a*); hence, there was no need to use statistical techniques to classify them.

There were consistent differences in survival to Lower Granite Dam among emigrant types and FL at emigration (Table 1). Median survival to Lower Granite Dam of age-0 and age-1 smolts was similar. Age-0 smolt survival fluctuated more and was more similar to fall parr survival for 4 of 13 cohorts. Survival of fall parr was usually lower than that of age-1 smolts but was more stable. The lowest survival (0.13) was experienced by the age-0 smolts from the 2000 cohort, which emigrated during the extreme drought of 2001. Very high survivals (0.73–0.74) were experienced by age-1 and age-0 smolts in the 1997 cohort and age-1 smolts in the 1998 cohort. Length followed order of age; age-1 smolts were largest and age-0 smolts were smallest (Table 1). However, there was a wide range among annual means within each type. Mean FL for fall parr varied by up to 21.1 mm, but the range for age-0 smolts was only 14.1 mm.

Initial cohort abundance affected survival to Lower Granite Dam. Redd counts varied over an order of magnitude, from 11 in 1995 to 354 in 2003. The calculated slope of initial abundance on survival was steepest for age-0 smolts (Fig. 3), but because survival was highly variable, the slope was not significantly different from zero (b = –0.20; 95% Wald CI –0.44 to 0.03, mean corrected r^2 = 0.27). For fall parr, the slope of the relationship was significantly different from zero, although less steep than for age-0 smolts (b = –0.16, 95% Wald CI –0.25 to –0.06, mean corrected r^2 = 0.55). However, for age-1 smolts, survival was not related to cohort abundance (b = 0.07, 95% Wald CI –0.22 to 0.08, mean corrected r^2 = 0.09).

The relationship between initial cohort abundance and length at migration from the Pahsimeroi River was also well described by descending power functions (Fig. 4). The slopes for each type were similar and were significantly different from zero. The slope estimate was –0.04 (95% Wald

Table 1. Median probability of survival from the Pahimeroi River to Lower Granite Dam and mean fork length at emigration (mm) for each emigrant type.

Emigrant type	Median survival	Mean fork length
Age-0 smolt	0.51 (0.13–0.73)	90.8 (83.7–97.8)
Fall parr	0.27 (0.20–0.38)	105.2 (95.8–116.9)
Age-1 smolt	0.56 (0.33–0.74)	112.1 (104.0–124.0)

Note: Ranges of annual values are given in parentheses.

Fig. 3. Survival to Lower Granite Dam by type versus redd count, an index of initial cohort abundance. Lines are fitted power functions. Equations: for age-1 smolts (open squares), survival = 0.72(redds)$^{-0.07}$, mean corrected r^2 = 0.09; for age-0 smolts (solid diamonds), survival = 1.06(redds)$^{-0.20}$, mean corrected r^2 = 0.27; for fall parr (open triangles), survival = 0.52(redds)$^{-0.16}$, mean corrected r^2 = 0.55.

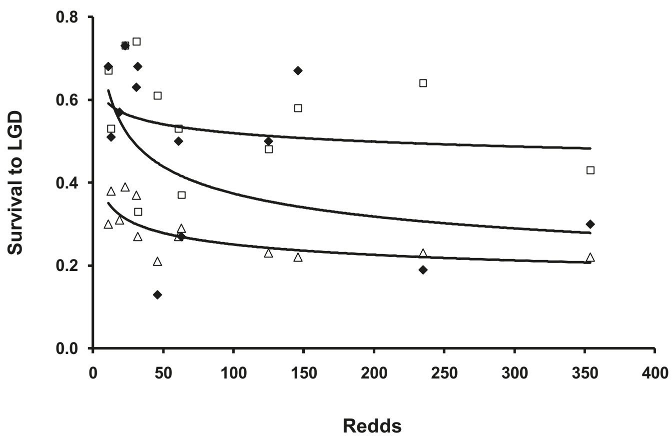
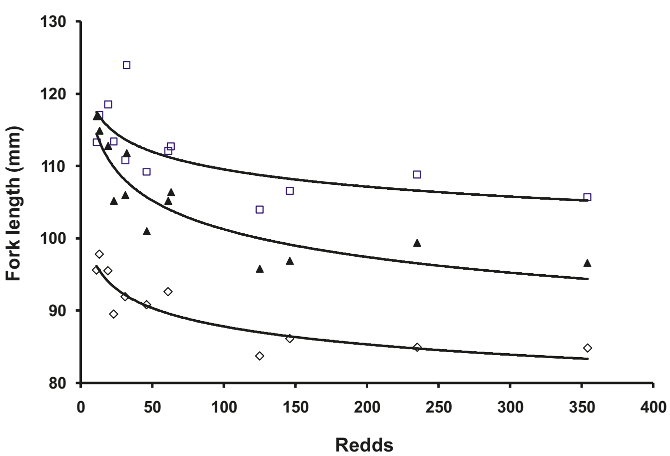


Fig. 4. Mean fork length at emigration by type versus redd count, an index of initial cohort abundance. Lines are fitted power functions. Equations: for age-1 smolts (open squares), length = 126.84(redds)$^{-0.03}$, mean corrected r^2 = 0.49; for age-0 smolts (open diamonds), length = 106.36(redds)$^{-0.04}$, mean corrected r^2 = 0.82; for fall parr (solid triangles), length = 131.43(redds)$^{-0.06}$, mean corrected r^2 = 0.81.



CI –0.06 to –0.03, mean corrected r^2 = 0.82) for age-0 smolts, –0.06 (95% Wald CI –0.08 to –0.04, mean corrected r^2 = 0.81) for fall parr, and –0.03 (95% Wald CI –0.05 to –0.01, mean corrected r^2 = 0.49) for age-1 smolts.

Fig. 5. Percentage of cohort surviving to Lower Granite Dam that emigrated as age-1 smolts versus initial cohort abundance as indexed by redd counts.

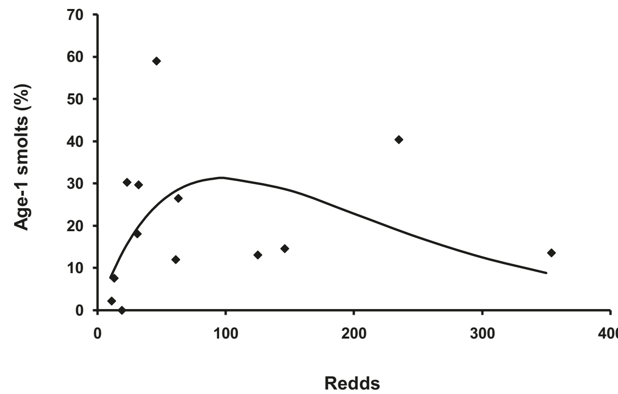
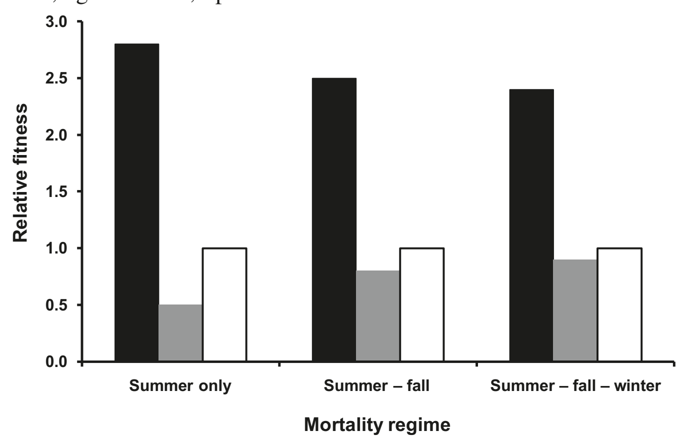


Fig. 6. Output of the relative survival model under three scenarios regarding in which season mortality occurs in Chinook salmon parr in the Pahsimeroi River: age-0 smolts, solid bars; fall parr, shaded bars; age-1 smolts, open bars.



The relative importance of emigrant type changed with initial cohort abundance. The contribution of the age-1 smolt type, the group with highest survival from the trap to Lower Granite Dam, to the number of emigrants reaching Lower Granite Dam was dome-shaped with respect to redd counts (Fig. 5). The proportion of successful emigrants that left the Pahsimeroi River as age-1 smolts was above 33% of total smolt production only twice out of 13 cohorts. Relative survival, our surrogate for relative fitness, differed among the emigrant types and followed a consistent pattern. When scaled to age-1 egg-to-smolt survival, the age-0 smolt type consistently had the highest relative survival (2.4–2.8), and the fall parr type, the lowest (0.5–0.9) (Fig. 6). Results were robust to the exact timing of mortality within the Pahsimeroi River. Given the values of S_{lgd} observed, any mortality above the trap caused the relative survival of the age-0 smolts to become greater than that of the other types. We verified the model by replacing the median S_{lgd} values with survivals measured for cohorts with the worst and best survivals (2000 and 1997, respectively) and allowed the proportion of age-1 smolts at Lower Granite Dam to vary. The proportions predicted were close to proportions observed (50% predicted versus 54% observed for 2000 and 22% predicted versus 28% observed for 1997). Given this corroboration, we believe our simple model is a useful tool with which to gauge relative fitness.

Discussion

Population functioning in Pahsimeroi River Chinook salmon

The proportions of smolt production by each life history type varied with circumstances; hence, the full expression of phenotypic diversity is important to this population. Relative fitness patterns (as measured by egg-to-smolt survival) explained the dome-shaped relation of proportion of successful emigrants from juveniles tagged as age-1 smolts. In most years, if a young Chinook salmon can grow fast enough, it should emigrate immediately to maximize its chances of reaching the Snake River and the migration corridor to the ocean. If growth opportunity is not sufficient, then a salmon parr in the Pahsimeroi River should delay smoltification until becoming a yearling and then emigrate. At extreme low densities, few parr stay in the Pahsimeroi River to spend the winter. This framework is consistent with Lichatowich and Mobrand's (1995) hypothesis that sufficient growth opportunity and habitat connectivity lead to emergence of an age-0 emigrant life history as an important part of population productivity in stream-type Chinook salmon. In fact, stream-type Chinook salmon are able to smolt as subyearlings (Connor et al. 2001) given sufficient growth and an increasing photoperiod (Clarke et al. 1992).

We had no data on survival within the Pahsimeroi River. Instead, we modeled a survival regime (summer survival = 32.5%) that was reasonable given the data observed. Healey (1991) described Chinook salmon fry–smolt survival >30% as high but cited survivals up to 34%. The survival rate that we derived may be high, but the Pahsimeroi River is a relatively benign environment for young salmonids. The ground-water-dominated flow moderates temperatures and maintains flow throughout the year. The water is fertile and summer growth of aquatic vegetation provides shelter and food. The model results agreed well with the observed proportions of age-1 smolts; therefore, high and consistent survival in the Pahsimeroi River after the parr stage begins is reasonable.

An implicit assumption for this analysis was that smolt-to-adult return (SAR) rates were comparable for the three types, historically. Unfortunately, there are insufficient data (28 adult detections from 30 895 juveniles tagged during the study period; D. Venditti, unpublished data) to validate this assumption for this population. However, it is not necessary to assume that SARs were equal. For lifetime survival of age-0 and age-1 smolts to be equal, historic age-0 smolt survival through the migration corridor and ocean would have needed to be approximately one-third that of the age-1 smolts. Even with greatly reduced SARs, adult contribution from age-0 smolts would have been substantial.

Fitness implications should be inferred beyond the observed life stage to the entire life span to understand variability in performance (Zabel and Achord 2004). Although our study focused on juvenile life history, we obtained adult detections from juveniles tagged at the Pahsimeroi River trap at Snake and Columbia river dams from the PTAGIS database. No fish tagged as age-0 smolts were detected returning from the Pacific Ocean. However, a few adults that emigrated as age-0 smolts were observed at Bonneville Dam (Whiteaker and Fryer 2007) during the time when adults from Pahsimeroi were returning to freshwater.

We concluded that the age-0 smolt life history trajectory could no longer be completed. But why might this strategy be maintained? Length at emigration was influenced by initial cohort abundance. Survival was also influenced by initial abundance. The expression of life history type was influenced by density and thus growth conditions. The Pahsimeroi River population produces the largest age-1 smolts in Idaho and the age-0 smolts are similar in size to age-1 smolts in most other SRSS Chinook salmon populations (Lutch et al. 2003). However, age-0 smolts pass through the hydrosystem two months later and encounter a different set of hazards (discussed below). Enough of the other types survive to support the population, even though their fastest-growing progeny will become age-0 smolts. Thus, the unique growth potential present in the Pahsimeroi River allows a greater range of juvenile Chinook salmon life histories than typical for central Idaho.

Waples et al. (2004) argued that the age-0 emigrant life history is not viable for stream-type Chinook salmon populations in the interior Columbia River basin because they reach the ocean when conditions are not conducive for survival and growth for the migratory path that such populations follow. Why then does this life history persist if it was never viable? The Situk River in Alaska produces age-0 Chinook salmon smolts despite being in an area dominated by stream-type populations (Johnson et al. 1992). Similarly, in inland British Columbia, Canada, substantial numbers of both stream- and ocean-type juveniles are produced in the South Thompson River (Beacham et al. 2003). The alternative hypothesis is that the phenotype is recently evolved, which is unlikely given the lack of surviving adults. We argue that the age-0 life history in the Pahsimeroi River population is not an aberration but once was a viable alternative.

Importance of juvenile life history diversity to salmon conservation

Conservation of life history diversity is important to recovery of endangered species. Life history components may change in importance over time; small stocks today may be major producers tomorrow (Hilborn et al. 2003). Managers need to understand the fitness value of the population components to identify important elements of diversity for conservation and management. Management should address the full suite of phenotypes, not just the most common or obvious ones (Watters et al. 2003). This should include passage alternatives for young salmon emigrating through the main stem rivers late in the season.

Salmon conservation requires an understanding of what the fish need to complete their life history. It is important that all options remain viable. The current recovery plan emphasizes adult return timing without addressing juvenile life history types. Arguably, in this case, the juvenile phase is more constrained than the adult phase. Given that age-1 smolts from the Pahsimeroi River are very large, one might expect this population to be healthier than others in central Idaho. None of the SRSS Chinook salmon populations has met regional objectives for survival and recovery (Good et al. 2005; ICTRT 2007). Reliance on measures aimed at age-1 smolts may not raise this population's productivity because the most productive portion of the population is using a life history trajectory that cannot be completed.

In conclusion, we believe that potential opportunities for conservation of Pahsimeroi River Chinook salmon are greatest for age-0 smolts. Historically, improvements to the hydrosystem were aimed at age-1 smolts and did not benefit age-0 smolts (Raymond 1988). More recently, actions such as summer flow augmentation and temperature moderation from release of cool water from storage reservoirs has been used to improve migration conditions for subyearling migrants (Connor et al. 2003; National Oceanic and Atmospheric Adminstration Fisheries (NOAAF) 2008). A current line of applied research in the Columbia River basin is the use of new technologies to aid emigration through the main stem corridor (NOAAF 2008). Small increases in the survival of age-0 smolts to adulthood would have large impacts on the productivity of this population.

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