

Emigration of age-0 chinook salmon (*Oncorhynchus tshawytscha*) smolts from the upper South Umpqua River basin, Oregon, U.S.A.

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Abstract: Two rotating smolt traps were used through 4 consecutive years to monitor emigrations of age-0 chinook salmon (*Oncorhynchus tshawytscha*) from two watersheds of the upper South Umpqua River basin, Oregon, U.S.A. The number of wild smolts moving past the mainstem South Umpqua River trap ranged from 26 455 in 1991 to less than 5000 in 1993. The number of wild smolts passing the Jackson Creek trap ranged from 13 345 in 1991 to 0 in 1993. Higher numbers of wild smolts were significantly ($P = 0.003$) correlated with higher numbers of prespawning adults counted in index reaches the preceding year. Timing of emigration of smolts was found to be significantly related to stream temperature ($P < 0.05$) and phase of the lunar cycle ($P < 0.05$) but not related to changes in discharge ($P > 0.05$). Median emigration dates, which varied over 9 weeks, were earlier when spring water temperatures were higher. On average, two thirds of yearly smolt runs occurred when the moon was either waning or new, even though these moon phases were present only about half of the time. Significantly ($P < 0.05$) more fish than expected emigrated past both traps when day length was increasing.

Résumé : On a utilisé deux pièges à smolts rotatifs durant 4 années consécutives pour surveiller l'émigration des quinnats (*Oncorhynchus tshawytscha*) d'âge 0 depuis deux sous-bassins du cours supérieur de la South Umpqua, en Oregon (É.-U.). Le nombre de smolts sauvages qui ont été dénombrés dans le piège du cours principal de la South Umpqua se situait entre 26 455 en 1991 et moins de 5 000 en 1993, et le nombre de ceux qui ont été recensés dans le piège du ruisseau Jackson, entre 13 345 en 1991 et 0 en 1993. Les effectifs élevés de smolts sauvages étaient corrélés significativement ($P = 0,003$) avec les effectifs élevés d'adultes dénombrés avant la fraye dans des tronçons témoins l'année précédente. On a observé que le moment de l'émigration des smolts était relié à la température de l'eau ($P < 0,05$) et à la phase du cycle lunaire ($P < 0,05$), mais n'était pas relié aux variations du débit ($P > 0,05$). Les dates médianes d'émigration, qui ont varié sur 9 semaines, étaient plus hâtives quand les températures printanières de l'eau étaient plus élevées. En moyenne, les deux tiers des smolts d'une année étaient en dévalaison quand la lune était déclinante ou nouvelle, même si ces phases de la lune n'étaient présentes que la moitié du temps. Un nombre de poissons significativement ($P < 0,05$) plus important que prévu sont passés par les deux pièges quand le jour allongea.

[Traduit par la Rédaction]

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) smolts typically emigrate seaward from rivers in either their first or second spring following emergence (Gilbert 1913). The age at which seaward migration occurs is influenced by both genetic (Taylor 1990) and environmentally mediated developmental processes (Thorpe 1989). In general, smolts of stocks from more southern and coastal areas emigrate during their first spring, whereas smolts of stocks from more northern, inland areas emigrate at an older age (Carl and Healey 1983).

Although considerable research has focused on understanding the physiological and genetic aspects of chinook salmon smolt emigrations (Carl and Healey 1983; Taylor 1988, 1990), much less information exists on the factors affecting the timing of these migrations (Nicholas and Hankin 1989). Overall, the timing and variation of smolt movements probably reflect past selection processes that have minimized mortality risk while maximizing growth (Riddell and Leggett 1981; Holtby et al. 1989).

Variation in the magnitude and timing of salmonid emigrations is influenced by a variety of factors including species (Groot and Margolis 1991), adult escapement, rearing history (Bilby and Bisson 1987), and size of juvenile fish (Ewing et al. 1984; Irvine and Ward 1989) as well as environmental factors such as stream temperature (Morrill 1972; Holtby et al. 1989), stream discharge magnitude and changes (Bjornn 1971), lunar cycle (Grau et al. 1981), and photoperiod (Wagner 1974; Zaugg et al. 1986). The importance of these factors on emigration magnitude and timing may vary greatly among years. To compound the difficulty of understanding emigration and its causes, the shape of the emigration curve may be influenced by the location within the

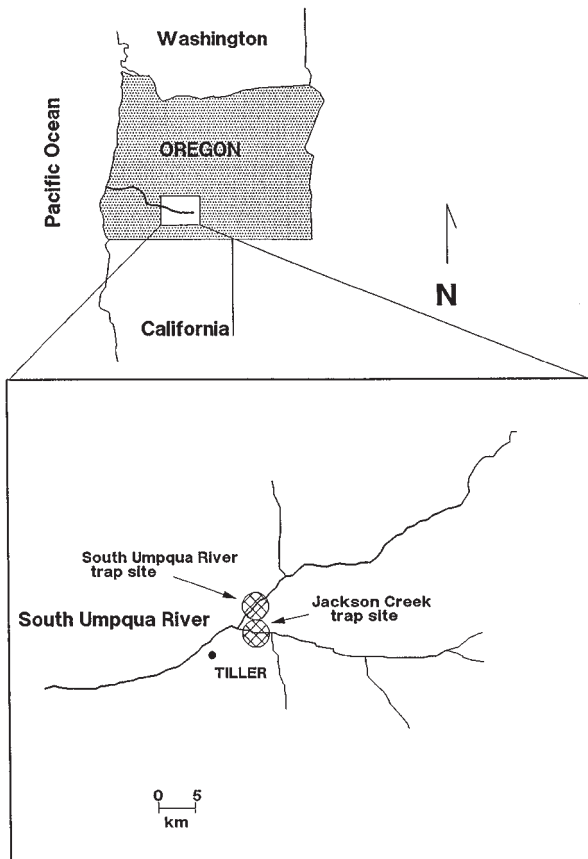
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Fig. 1. Location of the two smolt traps within the South Umpqua River basin.



watershed where smolts are enumerated (Irvine and Ward 1989).

Understanding factors affecting the magnitude and timing of smolt emigrations is important for stock restoration and management. The objectives of this paper were to (i) characterize the magnitude and timing of age-0 chinook salmon emigrations from two adjacent basins in a southwestern Oregon, U.S.A., river system and (ii) relate the timing of these emigrations to adult escapement and four environmental factors: stream temperature, changes in stream discharge, lunar cycle, and photoperiod. For adult escapement, our null hypothesis was that the magnitude of smolt emigrations was unrelated to the number of adult fish returning to spawn the previous year. For environmental factors, our null hypotheses were that percentages of the total smolt emigrations would occur in proportion to the frequencies of occurrence, during the emigration period, of specific stream temperatures, daily changes in discharge, phases of the lunar cycle, and photoperiod.

Materials and methods

Study site

The study was conducted in two large drainages of the upper South Umpqua River basin, Oregon, U.S.A. (Fig. 1): the mainstem South Umpqua River drainage basin (area 78 567 ha) and the Jackson Creek drainage basin (area 37 297 ha). Stream width at the study sites during low flows was 20 m in the mainstem and 15 m

Table 1. Percentage of age-0 chinook salmon populations emigrating between 15 April and 31 August estimated to have been missed due to trap malfunctions or traps not being deployed.

Year	Rearing history	Run missed due to trap malfunction, %	
		South Umpqua River	Jackson Creek
1991	Wild	2.9 (26 455)	4.2 (13 345)
	Hatchery	—	0.5 (47 453)
1992	Wild	14.8 (14 689)	0.0 (1635)
	Hatchery	0.0 (82 031)	—
1993	Wild	16.1 (4978)	0.0 (0)
	Hatchery	12.7 (85 537)	—
1994	Wild	0.1 (15 665)	0.0 (7394)
	Hatchery	—	—

Note: Run strength when traps were not operating was estimated using regression methods. Numbers in parentheses are the estimated total run size. Dashed indicate no hatchery fish released.

at Jackson Creek. Discharge, riparian zone vegetation, and land use practices are described in Roper (1995).

The stock of chinook salmon is small, averaging less than 300 returning adults annually (Oregon Department of Fish and Wildlife, Roseburg, Oreg.) and has a low probability of remaining viable through the next 100 years (Ratner et al. 1999). Surveys conducted for adult chinook salmon indicated that spawning occurred upstream from the confluence of the mainstem and Jackson Creek. For the entire distance between the ocean and the confluence of these rivers (314 km), no dams impede salmon migration.

Smolt trapping and population estimation

Traps

Age-0 chinook salmon were sampled and enumerated in the spring and summer, from 1991 to 1994, with two rotating smolt traps. The larger trap (2.44-m orifice) was located in the mainstem South Umpqua River 2 km upstream from its confluence with Jackson Creek; the smaller trap (1.52-m orifice) was located in Jackson Creek 1 km upstream from its mouth (Fig. 1). Cabling systems on both traps permitted operation in the area of greatest water velocity. Thedinga et al. (1994) described operation of traps of this design.

Traps were deployed in April or early May and removed in mid-October. Both traps were fished continuously, barring malfunctions, until the end of July. From August until mid-October, they were operated intermittently, typically 5 days out of 7. This April–October time period encompassed the period during which most of the age-0 smolts emigrated from the South Umpqua River watershed (Table 1). All captured fish were measured for fork length or randomly sampled for lengths if catches were large.

Population estimation

Trap efficiencies were determined by marking captured fish with one of four caudal fin marks and then transporting the marked fish 400 m above the trap site and releasing them into the stream so that they were available for recapture as they moved past the trap a second time. Four unique caudal marks were used because 99% of the recaptures from bimonthly releases at the Jackson Creek trap site in 1990 were subsequently recaptured within 4 days. The percentage of the marked fish recaptured was used to estimate trap efficiency (Seelbach et al. 1985). Trap efficiencies were determined independently at each trap site. Confidence intervals (CI) for trap efficiencies were calculated directly from the binomial distribution (Seber 1973; Dowdy and Wearden 1983). Trap efficiency averaged about 15% at both traps throughout the study.

Population estimates were determined by multiplying the number of unmarked fish captured in the trap by the inverse of the trap efficiency (Ricker 1975; Seelbach et al. 1985). For example, if trap efficiency was 20% and 100 unmarked fish were captured, then the estimate of that day's emigration was 500 fish ($(1/0.2) \times 100$).

Daily population estimates were based on daily estimates of trap efficiency when the total number of recaptures from a daily release group exceeded seven. Because mark-recapture estimates are biased when recaptures are few (Robson and Regier 1964; Seber 1973; Jensen 1981), we combined several days' data (between 2 and 30 days) to estimate smolt populations over those days when the number of recaptures from a release group was less than seven.

On the few days when a trap either malfunctioned or was not operated, we used regression methods and the number of smolts emigrating before and after to estimate the number of smolts leaving when the trap was inactive (Seelbach 1993). For a more complete description of the methods used to estimate smolt populations, see Roper (1995) and Roper and Scarnecchia (1996).

In addition to wild fish, estimates of recently released hatchery-reared age-0 chinook salmon were made during those periods when hatchery fish were present. Hatchery fish were released into Jackson Creek during the spring of 1991 and into the mainstem during the springs of 1992 and 1993. In both rivers the releases occurred 20–30 km above the trap sites during the last week of May. Hatchery-reared fish were identifiable by the absence of an adipose fin. In 1992 and 1993, more than 98% of these fish were marked, whereas in 1991, only 52% were marked. Estimates of hatchery-reared smolts leaving Jackson Creek in 1991 were based on a near doubling of the counts of marked fish. The number of wild fish was then estimated as the total catch minus the estimated number of hatchery-reared fish. All future discussions and analyses in this paper refer strictly to wild fish unless stated otherwise.

Smolt emigrations

Magnitude

The total annual emigration was estimated as the sum of daily estimates between 15 April and 31 August. Differences in magnitude among years were examined with pairwise comparisons. Variations in the magnitude of annual smolt emigrations from the mainstem and Jackson Creek were assessed using the coefficient of variation.

Adult escapement

Indexes of adult salmon abundance in both the mainstem and Jackson Creek were based on the number of adults counted in selected large pools just prior to spawning (Oregon Department of Fish and Wildlife, Roseburg, Oreg.). Counts in index pools accounted for about 50% of the total number of adults within the basin (B.B. Roper, personal observation). Regression methods were used to relate an index of numbers of adults the previous fall in each of the two rivers to the number of smolts emigrating the following spring.

Timing

The timing of the smolt emigrations (both wild and hatchery reared) was characterized by the date of peak emigration (mode) and the date when half of the estimated total smolt emigration had occurred (median emigration date).

Environmental factors

For stream temperatures, we recorded daily values at midmorning (08:30–10:30) at both trap sites. We calculated the percentages of the observed emigration that occurred in six temperature ranges: <10, 10 to <12.5, 12.5 to <15, 15 to <17.5, 17.5 to <20, and $\geq 20^\circ\text{C}$. Under the null hypothesis, the percentage of the total emigration within each temperature range would not differ from

the percentage of the trapping season within that temperature range. For example, if stream temperatures of less than 10°C were encountered during 10% of the trapping season, one would expect 10% of the total smolt run to have occurred within this temperature range. Deviations from the null hypothesis were evaluated using the χ^2 goodness-of-fit test. Because the large number of smolts leaving the basin would have resulted in extremely high statistical power (i.e., significant differences in cases when deviations from the null hypothesis were small), we standardized the total number of smolts (yearly) to 100 when making all goodness-of-fit comparisons (Gorman 1988; Roper et al. 1994). Linear regression methods were used to compare the day of year of median emigration (dependent variable) with average midmorning water temperatures from 1 May to 15 June.

For changes in discharge, we obtained daily mean discharges of the South Umpqua River basin from a permanent gauging station located at Tiller, Oreg. (United States Geological Survey gauge 1430800). Its location 8 km downstream from the confluence of the mainstem and Jackson Creek represented the summed discharge of the two rivers. We characterized changes in discharge as (i) rapidly decreasing: discharge was more than 10% lower than that of the previous day, (ii) slowly decreasing: discharge was >1 to 10% lower than that of the previous day, (iii) no perceptible change: discharge was within 1% of the previous day's discharge, (iv) slowly increasing: discharge was from >1 to 10% higher than that of the previous day, and (v) rapidly increasing: discharge was more than 10% higher than that of the previous day. Under the null hypothesis, if flow was slowly increasing 25% of the time that the traps were operating, we would have expected 25% of the fish to have emigrated under these conditions. Departure from the null hypothesis was assessed with a χ^2 goodness-of-fit test.

For lunar cycle, we calculated the percentage of fish emigrating at each of four moon phases: new moon, waxing towards a full moon, full moon, and waning toward a new moon (Moore 1990). For fish to have been considered to be emigrating during either the new or full moon phase, they had to have been captured during the 7 days nearest either the new or full moon. Fish captured on the days between the new and full moon were considered to be emigrating as the moon was waxing towards full; those fish captured in the days between a full and new moon were considered to be emigrating as the moon was waxing towards new. Under the null hypothesis, we expected about 25% of the fish to leave at each moon phase. Departure from the null hypothesis was tested with a χ^2 goodness-of-fit test.

For photoperiod, we assessed what portion of the total emigration was completed during the period of increasing day length (i.e., prior to 21 June). If a majority of the fish emigrated as day length increased, and timing of emigration was consistent among years, the hypothesis of emigration timing being related to photoperiod was supported.

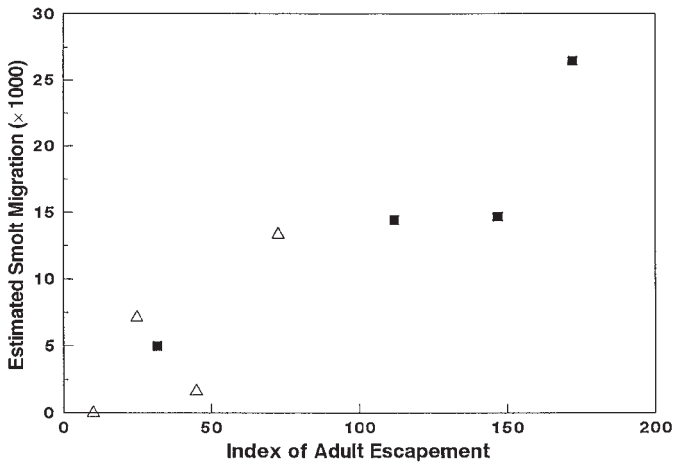
Results

Smolt migrations

Magnitude

The number of wild age-0 spring chinook salmon emigrating varied significantly among years and between the two sites. For the South Umpqua River the number of smolts ranged from a high of 26 455 (95% CI = 19 073 – 50 658) in 1991 to a low of 4978 (95% CI = 3137 – 13 975) in 1993. The number of smolts leaving the Jackson Creek basin ranged from a high of 13 345 (95% CI = 8616 – 33 243) in 1991 to a low of 0 in 1993. In both rivers the number of

Fig. 2. Relationship between index of adult escapement (1990–1993) and smolt emigration the following spring (1991–1994) for the mainstem South Umpqua River (■) and Jackson Creek (Δ).



smolts decreased from 1991 to 1993 and then increased slightly in 1994.

The number of smolts leaving the mainstem was larger and more stable than in Jackson Creek. Although annual emigration from the mainstem averaged 15 456 fish, roughly three times that of Jackson Creek (5593), the coefficient of variation in the mainstem (57) was essentially half that of Jackson Creek (108).

During the period 1991–1993 the number of hatchery-reared age-0 chinook salmon emigrating from the upper South Umpqua River basin ranged from 47 453 to 85 537 (mean = 71 674). Hatchery-reared smolts constituted a progressively larger portion of the total emigration from 1991 to 1993: 75% in Jackson Creek in 1991, 80% in the mainstem run in 1992, and 93% in the mainstem run in 1993. Hatchery-reared fish accounted for more than 50% of the total age-0 chinook salmon emigration from the basin in all years that they were present. Because no fish, wild or hatchery reared, emigrated from Jackson Creek in 1993, hatchery-reared fish constituted more than 90% of the juvenile chinook salmon emigrating from the entire upper basin that year. Because the fraction of smolts that were hatchery reared was high from 1991 to 1993, discernment of emigration patterns of wild fish was dependent on hatchery-reared fish being marked.

Adult escapement

The number of wild smolts leaving each river was positively related to higher numbers of spawning adults the previous fall (South Umpqua, $r^2 = 0.67$, $P > 0.05$; Jackson Creek, $r^2 = 0.61$, $P > 0.05$; combined, $r^2 = 0.80$, $P = 0.003$) (Fig. 2). Counts of adult fish in the mainstem (112) were nearly three times higher than in Jackson Creek (38), whereas the coefficient of variation of adult counts was lower in the mainstem (50) than in Jackson Creek (71). Both the magnitude and variation in the number of adults were thus closely related to the magnitude and variation in the number of smolts.

Timing

Peak (modal) times of emigration varied up to 2.5 months among years of this study. In the mainstem, emigration

peaked on 11 June in 1991, 29 April in 1992, 23 June in 1993, and 1 June in 1994. In Jackson Creek, emigration peaked on 11 July in 1991, 24 May in 1992, and 25 May in 1994.

The median emigration date of wild smolts (i.e., date by which half had emigrated) also differed between rivers and among years. In most cases, median emigration date occurred from 22 May to 11 June (Table 2) but occurred on 11 July in Jackson Creek in 1991 and on 8 May in the mainstem in 1992. In every case, peak emigration occurred within 2 weeks of, and usually within days of, the median emigration date (Table 2).

The emigration timing of hatchery-reared and wild smolts differed in the upper basin. In all three years, emigration of hatchery-reared fish peaked within 2 days of their release, and at least 10% of the total emigration occurred on a single day. In 1992, almost half of the hatchery fish emigrated on a single day. The date of median emigration for hatchery-reared fish occurred within 8 days of release in 1991, within 3 days of release in 1992, and within 20 days of release in 1993.

Smolt length

Although the dates when wild smolts first reached 50 mm in length varied among years by nearly a month (Table 3), lengths at emigration showed an interannual consistency. Nearly half (44%) of the annual emigrants from the mainstem from 1991 to 1994 were between 50 and 59.9 mm in length (Table 4). Less than 10% of the fish emigrated before they reached 50 mm or after they had reached 80 mm. A similar tendency for emigration at these lengths (50–59 mm) was found in Jackson Creek, but inadequate length data in 1991–1993 precluded firmer conclusions.

Environmental factors

Stream temperature

Higher average spring temperatures at the trap sites were associated with an earlier median emigration date of wild smolts ($r^2 = 0.78$, $P = 0.01$) (Fig. 3). Smolt emigrations past both traps began once stream temperature exceeded 10°C, were greatest when temperatures were between 12.5 and 15°C, and were nearly complete by the time stream temperatures exceeded 20°C (Table 5). Although stream temperatures in the mainstem ranged between 12.5 and 15°C on only 74 (13%) of the 556 days from 15 April to 31 August 1991–1994, on average, 50% of the annual emigration of wild age-0 chinook salmon occurred between these temperatures. In contrast, when temperatures were below 10°C (on 106, or 19%, of 556 days) and above 20°C (on 137, or 25%, of 556 days), less than 10% of the total wild smolt emigration occurred.

Movement of smolts through the Jackson Creek trap occurred at higher temperatures than the emigration through the mainstem trap. The largest percentage (43%) of the Jackson Creek fish left when stream temperatures were between 12.5 and 15°C, even though these temperatures were encountered only 9% of the time the traps were in operation. The year 1993 was excluded because no fish were captured that year. Deviations from the null hypothesis that emigration of smolts was equally likely at all stream temperatures

Table 2. Peak emigration dates and first emigration quartile (25%), median emigration quartile (50%), and third emigration quartile (75%) of age-0 chinook salmon emigrating from the South Umpqua River and Jackson Creek.

	Peak emigration	Emigration quartile		
		25%	50%	75%
South Umpqua River				
1991	11 June	8 June	11 June	22 June
1992	29 April	29 April	8 May	26 May
1993	23 June	4 June	19 June	2 July
1994	1 June	19 May	4 June	22 June
Jackson Creek				
1991	11 July	22 June	10 July	12 July
1992	24 May	21 May	25 May	28 May
1994	25 May	19 May	28 May	8 June

Table 3. Dates when age-0 chinook salmon smolt sizes (lower tail of a 95% CI) first exceeded 50, 60, and 70 mm.

	Fish size		
	50 mm	60 mm	70 mm
South Umpqua River			
1991	16 May	14 June	27 June
1992	29 April	15 June	14 June
1993	23 May	17 June	30 June
1994	14 May	5 June	16 June
Jackson Creek			
1994	16 May	7 June	21 June

were large and significant ($P < 0.01$) in both rivers and for all years.

Changes in discharge

For more than 60% of the days when traps were in operation, discharges were slowly decreasing, i.e., from >0 to 10% less below the previous day's flow. Nearly 70% of the smolts emigrated during these days. Deviations from the null hypothesis that emigration was proportional to the number of days in each of the five discharge categories were small and nonsignificant ($P > 0.05$). Wild smolts were evidently not relying on changes in discharge as an emigration cue.

Lunar cycle

Although smolts emigrated during all four lunar phases, in five of the seven monitored emigrations (mainstem, 1991, 1992, and 1994; Jackson Creek, 1991 and 1992), smolts were significantly ($P < 0.05$) more likely to have moved during the waning and new moon phases rather than during the waxing and full moon phases. On average, for all seven smolt runs, 66% of the smolts emigrated during the waxing and new moon phases, even though these phases constituted only half the emigration period.

Photoperiod

Significantly more fish than expected ($P < 0.05$) emigrated past both traps when day length was increasing. In six of the monitored emigrations (mainstem, 1991–1994; Jackson Creek, 1992 and 1994), at least 75% of the total spring emigration was completed prior to the summer solstice, whereas slightly less than 50% of the capture season oc-

Table 4. Percentage of total spring emigrations of age-0 chinook salmon within six length categories.

	Length category				
	<50 mm	50 to <60 mm	60 to <70 mm	70 to <80 mm	≥80 mm
South Umpqua River					
1991	2	58	20	16	4
1992	15	44	35	6	0
1993	8	37	21	26	8
1994	14	37	14	34	1
Average	10	44	22	21	3
Jackson Creek					
1994	13	52	19	16	0

curred prior to this day. In only one case (Jackson Creek, 1991) did a majority of fish leave when day length was decreasing. The variation in annual emigration timing provides evidence that photoperiod (or a correlated variable) was a migratory cue.

Discussion

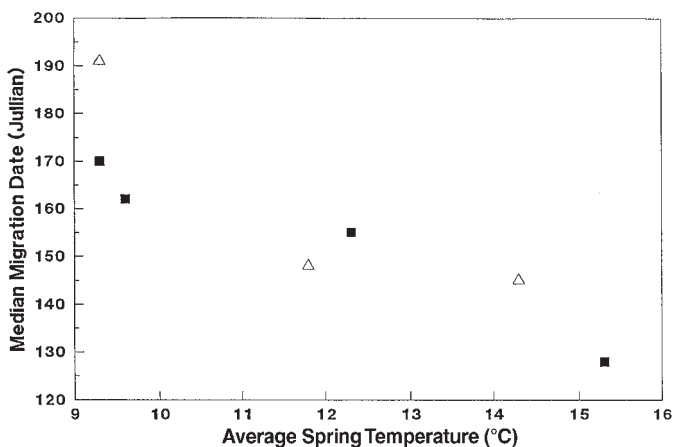
The strongly positive relationship between the number of adult chinook salmon in the upper South Umpqua River basin and the number of emigrating smolts the following year indicates the importance of adult escapement to smolt production, especially when adult escapement is low (Ricker 1975). The mere presence of adult salmon, however, did not guarantee smolt production the next year. Jackson Creek produced no juvenile chinook salmon in 1993, even though adults were seen in this creek the previous fall. It is thus important to estimate both juvenile and adult numbers, especially when populations are small.

Whereas the magnitude of annual smolt emigrations was consistently explained with just one variable, adult escapement, the timing of annual spring emigrations was more difficult to attribute to one environmental factor. Of the four environmental factors considered, stream temperature, changes in discharge, lunar cycle, and photoperiod, three, stream temperature, lunar cycle, and photoperiod, were significantly related to emigration timing. A central problem in interpreting this result is the confounding effect resulting from correlation among environmental variables.

Table 5. Percentage of total spring age-0 chinook salmon emigrations within six temperature categories.

	Temperature category					
	<10°C	10 to <12.5°C	12.5 to <15°C	15 to <17.5°C	17.5 to <20°C	>20°C
South Umpqua River						
1991	5 (33)	19 (9)	53 (11)	2 (5)	8 (13)	13 (29)
1992	<1 (1)	1 (9)	67 (19)	18 (22)	7 (18)	7 (31)
1993	6 (26)	42 (20)	18 (8)	21 (21)	14 (22)	1 (3)
1994	3 (17)	4 (12)	59 (15)	17 (9)	16 (12)	3 (35)
Average	3 (19)	17 (13)	49 (13)	15 (14)	11 (16)	6 (25)
Jackson Creek						
1991	5 (35)	3 (11)	11 (8)	18 (11)	54 (21)	9 (14)
1992	<1 (1)	<1 (9)	47 (19)	37 (23)	12 (34)	3 (14)
1994	<1 (17)	5 (16)	72 (12)	17 (11)	4 (18)	2 (26)
Average	2 (18)	3 (12)	43 (13)	24 (15)	23 (24)	5 (18)

Note: Numbers in parentheses are the percentage of the total trap season (15 April to 30 August) within each temperature category.

Fig. 3. Relationship between average spring temperature and median emigration date of age-0 chinook salmon from the South Umpqua River (■) and Jackson Creek (Δ).

Of these three environmental factors, stream temperature explained the most variation in timing. An earlier median emigration date was consistently associated with higher average spring stream temperatures, and smolts emigrated within a narrow temperature range of 12.5–15°C. Timing of age-0 chinook salmon migrations was also related to temperature in a stream in British Columbia (Holtby et al. 1989). These authors and Rombough (1985) have suggested that the timing of emigration in age-0 smolts is influenced by stream temperature through controls on the rate of juvenile development. Cooler stream temperatures during winter and spring slow growth so that fish emerge and migrate later. In contrast, warmer stream temperatures accelerate juvenile development and hasten emigration in the spring. The idea that warmer water temperatures in spring could increase growth rates is supported by our data. Higher stream temperature were positively related to fish length within the South Umpqua River basin ($r^2 = 0.54$, $P \leq 0.001$; Roper 1995).

Although the positive relationship between stream temperature, fish size, and photoperiod (prior to 21 June) makes it difficult to distinguish their roles in controlling the emigration timing of wild smolts, water temperature rather than fish size or photoperiod evidently cued hatchery-reared fish. In 1992 and 1993 in the mainstem, when sizes of released

hatchery fish were similar (85.1 and 83.3 mm) and releases occurred at nearly the same day length (30 May versus 26 May), the number of days after release when median emigration occurred was substantially different (3 versus 20 days). In 1992, when average spring water temperatures were 15.3°C, the median emigration occurred 17 days sooner than in 1993, when average stream temperatures were 9.9°C. This difference suggests that even large fish may emigrate later when water temperatures are low (Ewing et al. 1984).

The greater tendency for smolts to emigrate during the new and waning moon phases in this study is consistent with other research relating moon phase to smolt emigrations (Grau et al. 1981). Because wild smolts in the South Umpqua River basin emigrate primarily at night (Roper and Scarnecchia 1996), movements during dark moon phases may be an adaptation to minimize predation risk.

We found little evidence that changes in discharge cued smolt emigrations, even though this factor has been shown to be important in other salmonid stocks in different basins (Folmar and Dickoff 1980).

Our conclusion is that these factors, temperature, lunar cycle, and photoperiod, interacted to influence emigration timing. The exact nature of their interaction is probably influenced by other factors as well.

For example, the trapping location may also affect the observed relationship between smolt emigrations and abiotic variables (Irvine and Ward 1989). Both traps within the South Umpqua River basin were more than 300 km from the ocean. If the traps had been closer to the ocean, the relationships between stream temperature or moon phase and smolt emigrations may not have been evident as a result of the increased travel time or the addition of smolts from other streams within the basin. Relationships between the magnitude and timing of smolt emigrations and other biotic and abiotic factors must therefore be investigated with reference to the location and scale of monitoring (McArdle et al. 1990).

Inasmuch as our research supports the idea that the timing of age-0 smolt emigrations is temperature dependent (Hartman et al. 1982; Rombough 1985; Holtby et al. 1989), land management activities that warm stream temperatures (Brown and Krygier 1970; Hostetler 1991) will probably affect emigration timing (Holtby et al. 1989) and alter life his-

tory characteristics (Lichatowich et al. 1995) as well as affect the ultimate survival of smolts (Bilton et al. 1982). Because land management activities have already simplified many of the streams within the upper South Umpqua River basin (Dose and Roper 1994), future land use within this basin must be undertaken with regard to potential effects on smolt emigration and survival.

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