

SEAWARD MOVEMENTS OF KEOGH RIVER STEELHEAD PARR:  
DENSITY-DEPENDENT DISPERSAL AND PREMATURE MIGRATION

by  
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## Abstract

Steelhead (*Oncorhynchus mykiss*) parr captured at a full stream enumeration trap at the mouth of the Keogh River, northern Vancouver Island, British Columbia comprised 9–35% (mean = 20%) of seaward dispersing juvenile (smolts + parr) steelhead, 1977–1993. Total parr annually varied from 400–5000 (mean = 1600). I tested two competing hypotheses to explain this biologically significant phenomenon: parr seaward movement is (1) premature but directed migration homologous to smolt migration, and (2) downstream dispersal resulting from upstream, density-dependent interactions among juvenile steelhead. At the watershed scale, reconstruction of past stream population sizes of steelhead juveniles suggested exponentially increasing parr dispersal as estimated main stem population size increased. At the reach scale, steelhead parr dispersed from experimentally stocked reaches; high initial stocking densities revealed limits to reach carrying capacity. At the individual trout scale, observations of agonistic behaviour of non-dispersing and dispersing parr in artificial stream channels showed that parr size was more important than parr type in determining attack rate. Dispersing parr had both growth rates and body shape (indexed by condition factor) that were intermediate between smolts and non-dispersing parr of the same age. Finally, parr dispersal followed the same seasonal timing pattern that smolt migration followed in 14 years of daily downstream movement data. Experimental manipulation and observation of naturally occurring patterns produced data supporting each hypothesis. Therefore, parr seaward movement in the spring at the Keogh River seems to be a phenomenon blended from indirect density-dependent effects as well as premature migration.

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# Steelhead Parr Seaward Movements

## Steelhead Life History

Steelhead are anadromous rainbow trout *Oncorhynchus mykiss*, that remain in freshwater for 1–5 years and complete growth to mature adults for 1–3 years at sea. Biologists have thoroughly described their life history in populations originating in eastern Pacific coastal rivers (e.g. Pautzke and Meigs 1940, Shapovalov and Taft 1954, Maher and Larkin 1955, Chapman 1958, Withler 1966, Horncastle 1981, Ward and Slaney 1988, Peven 1990, Dambacher 1991, Winter 1992). Briefly, adult steelhead return from the ocean to natal streams in late spring to early fall (“summer steelhead”), or late winter to early spring (“winter steelhead”); they spawn in the spring, and fry emerge from redds in the late spring or early summer. As fry and then as parr (age 1+), steelhead juveniles inhabit streams, and like other species of stream dwelling, drift feeding salmonids, defend feeding territories (Chapman 1966) until they undergo smoltification and migrate to the ocean (Hoar 1976, Folmar and Dickhoff 1980). Smolts are “pre-adapted” to live in seawater, which is osmotically “dry” relative to freshwater. Concomitant with the internal physiological changes that occur during the process of smoltification and which prepare them to competently osmoregulate in seawater, smolts take on the external physical features that distinguish them from parr: parr marks submerged beneath the silvery sheen of guanine and hypoxanthine

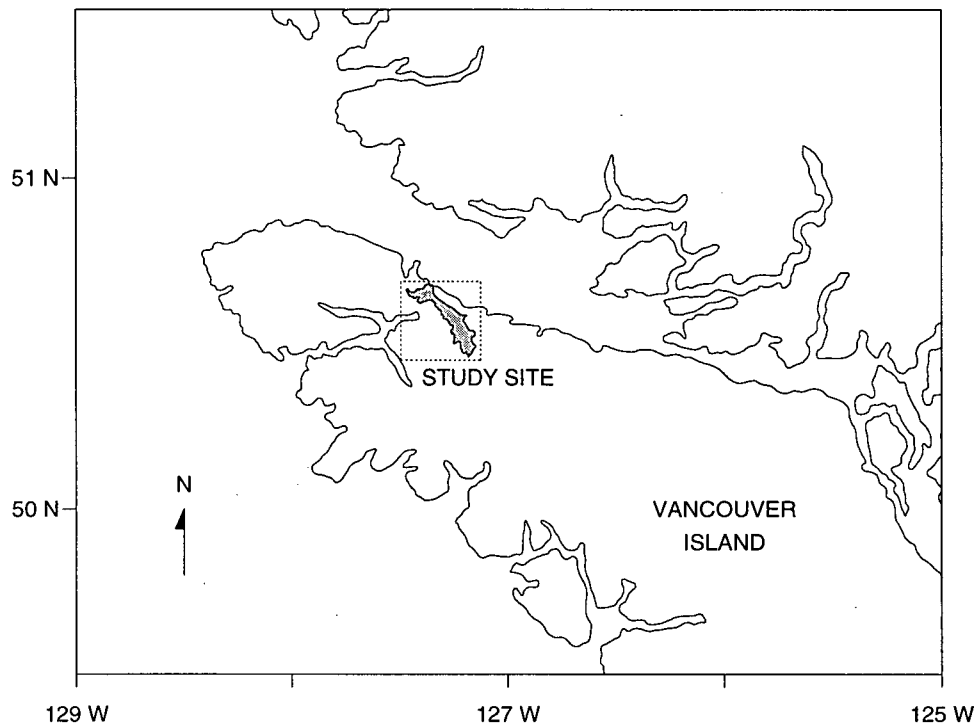


Figure 1: Keogh River watershed location on northern Vancouver Island

crystals deposited nearer the surface of the dermis, darkened fin margins, and the leaner appearance resulting from lower body lipid content (Wedemeyer et al. 1980, Hoar 1976).

Recently biologists have published detailed descriptions of juvenile steelhead migrations in Oregon and Washington (Dambacher 1991, Winter 1992, respectively) that consist not only of steelhead smolts, but also of parr. In fact, in a review of primary and agency literature, Dambacher (1991) discovered that the phenomenon of parr accompanying smolts during spring seaward movements is common (Beere 1993, Chrisp and Bjornn 1978, Leider et al. 1986, Peven 1990), although most frequently observed at some distance upstream from the sea.

Parr have likewise formed a portion of downstream juvenile steelhead movements from the Keogh River at the north end of Vancouver Island, British Columbia (Figure 1). The

mechanisms underlying downstream dispersal of steelhead parr in spring in the Keogh River form the subject of this thesis. The remainder of this introductory section reveals these springtime movements to be a biologically significant phenomenon, and proposes two hypotheses that might account for it.

## Juvenile Steelhead at the Keogh River

### Location and Description of the Keogh River

Several publications describe the Keogh River in detail: its location, attributes, and fish populations (e.g. Ward and Slaney 1979, Johnston et al. 1986, Irvine and Ward 1989).

The 33 km long, low gradient, fourth order river drains a 129 km<sup>2</sup> watershed on the northern end of Vancouver Island northward into Queen Charlotte Strait, at 127.34°W, 50.68°N (Figure 2). Rain dominates the hydrological regime: discharge (mean = 5.3 m<sup>3</sup>·s<sup>-1</sup>) is maximum (254 m<sup>3</sup>·s<sup>-1</sup>) in the winter months and minimum (0.1 m<sup>3</sup>·s<sup>-1</sup>) in summer. Climax forest cover consists of western hemlock and red cedar trees. At the upstream tidal limit of its small (1 ha) estuary (400 m from the sea at low tide) is a full-stream fish enumeration trap which the British Columbia Fisheries Branch has operated annually since 1976. The trap has contributed much towards documenting the watershed's migrant fish community which consists of not only steelhead trout, but also coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), Dolly Varden char (*Salvelinus malma*), cutthroat trout (*O. clarki*), coast range and prickly sculpin (*Cottus aleuticus* and *C. asper*), and Pacific lamprey (*Lampetra tridentata*).

### Seaward Dispersing Steelhead Parr Numerical Abundance

Ward et al. (1990) described the enumeration trap's installation, daily operation, and standard fish sampling. Trap crews extensively sampled migrating steelhead, both upstream (adult spawning migration), and downstream (juvenile steelhead and adult kelts).

Steelhead parr have contributed large numbers to the total production of steelhead

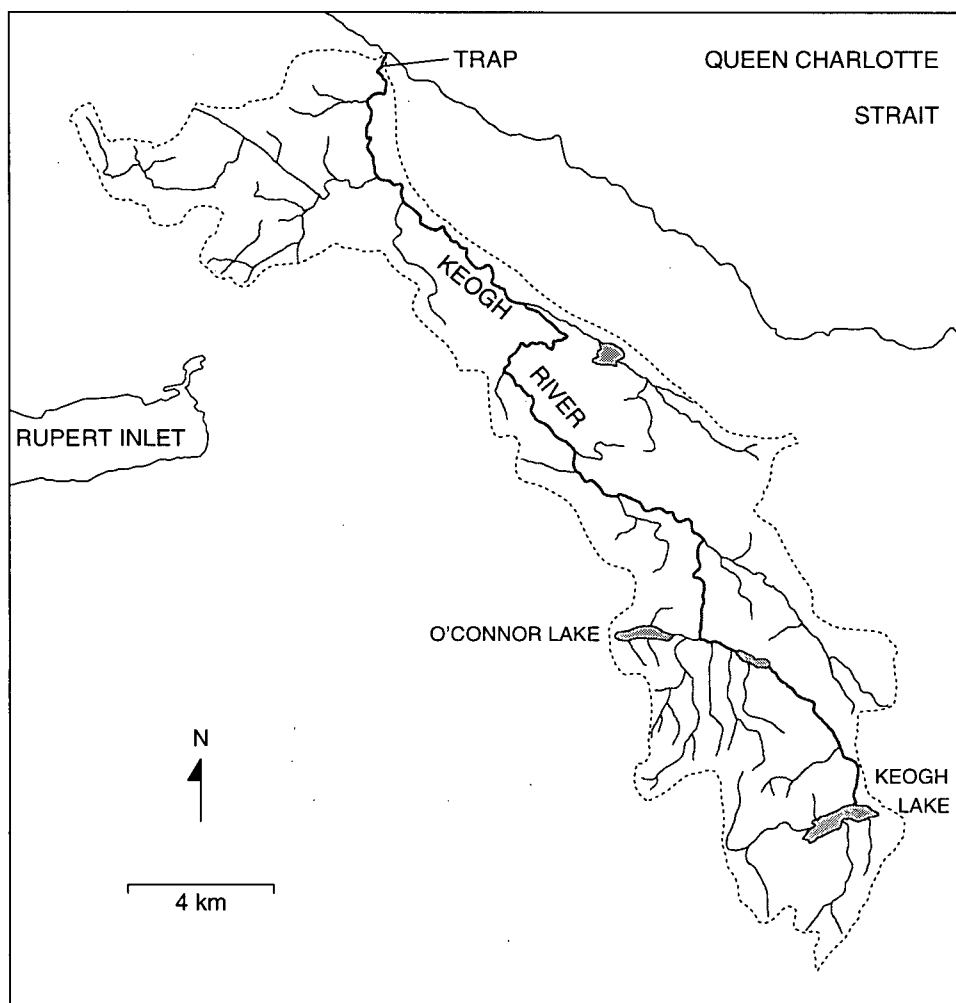


Figure 2: The Keogh River watershed, the river, and tributary streams and lakes.

tallied through the enumeration trap each spring (Figure 3). Annual smolt production has varied from approximately 2100–14000 individuals (mean = 6675), and annual parr production has varied from approximately 400–5000 individuals (mean = 1600). As a percentage of the total juvenile production recorded in the enumeration trap, steelhead parr have contributed 9–35% (mean = 20%). Clearly this phenomenon is a significant natural event at the Keogh River, as it is in other streams where biologists have observed

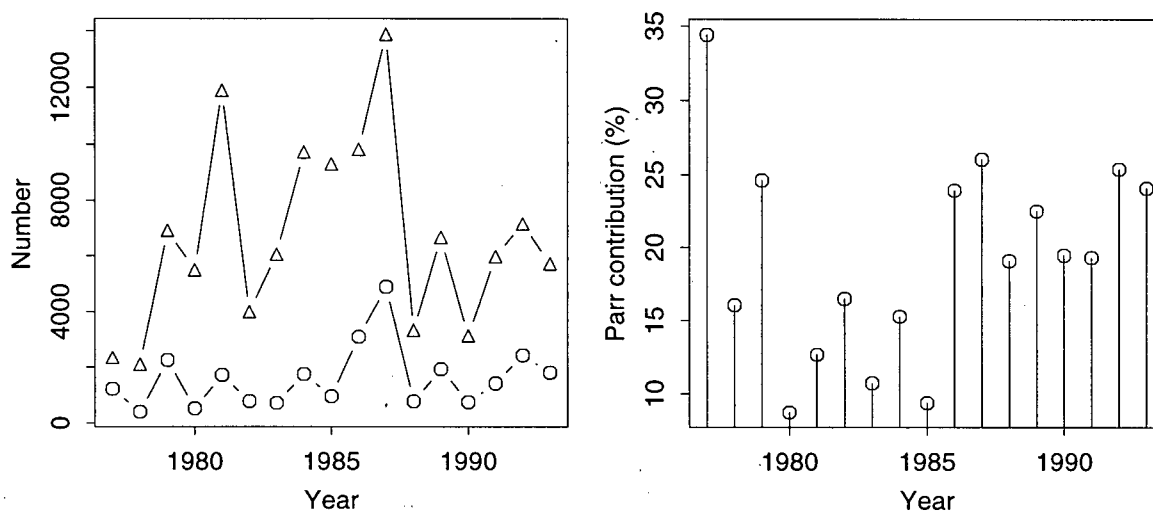


Figure 3: History of the Keogh River juvenile steelhead migration. Left panel shows the annual total number of smolts (top line) and parr (bottom line); right panel shows parr as a percentage of total juvenile dispersal (smolts + parr).

steelhead juvenile seaward movements in detail.

### Size related survival and pre-adaptation to salt water

Development of the ability to osmoregulate in seawater in juvenile steelhead takes place at minimum lengths of approximately 140 mm (Conte and Wagner 1965); yet virtually all parr observed at the Keogh enumeration fence have been < 155 mm fork length (Figure 4; 99th percentile = 154 mm. Figure A.1 in the appendix depicts length distributions by year).

I confirmed that Keogh River migrant steelhead parr had not yet developed the ability to osmoregulate in seawater in a seawater challenge test conducted in June, 1991. Smolts and migrant parr were captured at the enumeration trap. Over 48 hours, I monitored mortality in groups of parr placed in holding pens in freshwater (control; salinity= 0 ‰) and in the sea several hundred metres to the west of the mouth of the river (salinity= 27 ‰), as well as in groups of parr and of smolts placed in holding pens at a site in the outer estuary (sea salinity for 11–12 hr per 24 hr; otherwise fresh). In addition, I monitored mortality for 24

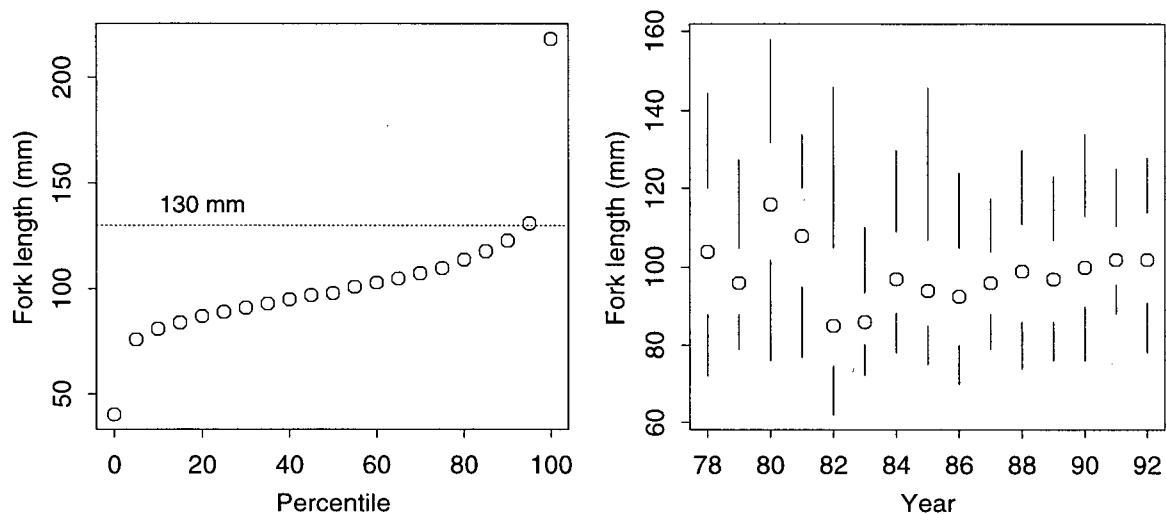


Figure 4: Parr lengths ( $n = 9047$ ) 1978–1992. Left panel plots length versus percentile. Virtually 95% of all parr were < 130mm (horizontal line). Right panel contrasts length distributions by year (points are the median, segments are 5th to 25th and 75th to 95th percentiles respectively).

Table 1: Seawater challenge tests: percentage mortality of juvenile steelhead exposed to ambient river, estuarine, and sea water (salinity = 27 ‰). Sea water was present at the inner and outer estuary sites for 6 and 11–12 hr per 24 hr respectively. “NA”= not available

Site	Exposure duration (hr)	% Mortality (n)		
		Parr $\leq 100$ mm	Parr $>100$ mm	Smolts
River	48	0 (30)	0 (30)	NA
Inner estuary	24	0 (10)	0 (10)	NA
Outer estuary	48	53 (30)	13 (30)	2.5 (40)
Sea	48	97 (31)	86 (29)	NA

hours in groups of parr placed in holding pens at a site in the inner estuary (sea salinity for 6 hr in 24 hr; otherwise fresh).

Although this small experiment had unbalanced and unreplicated treatments at any given combination of site and steelhead juvenile type, reasonably clear mortality patterns emerged (Table 1). Parr mortality was high (up to 97%) in sea water and outer estuarine



conditions, compared to smolt mortality (outer estuary site was the only possible comparison) and freshwater controls. In addition, parr mortality decreased as size increased, at both the outer estuary and sea sites. Most mortality occurred in the first 24 hours of the 48 hour challenge test. Thus the lack of mortality recorded at the inner estuary site, where challenges were for 24 hours instead of 48 hours, indicated that at least part of the estuary was not lethal to parr. The inner estuary site was shallower than the outer estuary site such that even at high tide, there was a thin lens of freshwater flowing through the upper several centimetres of the holding pen. I observed parr in this lens during the flow, peak, and ebb of the tide; thus the apparent higher survival at the inner estuary site may be due to the availability of low salinity or fresh water. Nevertheless, downstream dispersing steelhead parr at the Keogh River clearly did not have as full an osmoregulatory ability as steelhead smolts had in outer estuarine conditions, and in comparison with parr performance in fresh water.

Ward and Slaney (1988) demonstrated for Keogh River steelhead that smolt-to-adult survival was positively correlated with smolt size. Even more to the point, Ward et al. (1989) back-calculated size at sea entry from scales that trap crews had sampled from returning adults, and compared the resulting length distributions at ocean entry of steelhead that had survived to return to spawn, to the known length distributions of migrating juveniles. Back-calculated smolt lengths were larger than observed smolt lengths, and in fact of 800 back-calculated lengths, virtually none were less than 140 mm, suggesting that the majority of downstream dispersing parr (Figure 4) do not survive to return as adults.

Parr passage with smolts through the enumeration trap, only 400 m from full, ocean strength seawater, is clearly biologically significant and demands explanation.

## Hypotheses Potentially Explaining Parr Seaward Dispersal

### Density-dependent dispersal

Several biologists have hypothesized that territoriality in stream dwelling salmonids could limit population density, and several others have provided evidence for this hypothesis. For example, both Allen (1969) and Le Cren (1965) hypothesized that in the first three months of salmonid stream life, social interactions disperse fish until densities are tolerable. McFadden (1969) emphasized that fry-parr stages are critical in stream salmonid population dynamics because the operation of density-dependent processes during these stages determines the strength of each year class.

Supporting evidence comes primarily from investigations of underyearling salmonids. Chapman (1962) demonstrated that aggressive behaviour is a major factor causing downstream displacement of coho salmon fry in artificial stream channels. Elliott (1989) found that density-dependent survival during early life stages controlled population density of one stream population of wild brown trout, but not another in an unfavourable habitat with low 0+ fish density. On the same theme, Slaney and Northcote (1974) found territory size and frequency of aggression to decrease with increasing prey levels for 0+ rainbow trout in artificial stream channels, while densities of trout were highest at the highest prey level, i.e., where territoriality and aggressiveness were least.

Scepticism remains about the significance of the role territoriality plays in limiting density (Noakes and Grant, 1986). In an investigation of the ecology and interaction of 0+ coho and steelhead, Hartman (1965) observed that a downstream displacement of steelhead in laboratory stream channels did not occur although density and rate of aggression were "high" (displaced steelhead moved upstream and laterally more frequently than they moved downstream, within the stream channels). In a study of underyearling hatchery rainbow trout introduced into an artificial side channel of a stream, Jenkins (1971) concluded that the trout showed neither social density regulation nor socially induced dispersal; rather, he states that dispersal resulted from different individual responses to habitat. However, the

hatchery rearing environment may confound this result, because juvenile salmonids held in groups show reduced agonistic responses to other individuals (Keenleyside and Yamamoto 1962).

In spite of the scepticism, Grant and Kramer (1990) used a method suggested by Allen (1969) to test the hypothesis that territory size limits population density; the inverse slope of a territory size vs. body size regression for stream dwelling salmonids, or maximum density regression, should predict the maximum density of a population composed of a single size class. The method assumes that the fish have a minimum territory size. After comparing their regression to the results and observations of numerous studies, Grant and Kramer (1990) suggest that the regression has value in predicting the maximum density of salmonids in riffles (but not in pools), as well as in predicting the occurrence of density-dependent population responses. The regression has this value even though not all fish defend territories and when they do, territory size changes with prey availability ( e.g. Slaney and Northcote, 1974), visibility of the competitor (Kalleberg, 1958), and other factors.

Winter (1992) explicitly considered the hypothesis that steelhead parr downstream movements could be density-dependent, and concluded that parr migrations in the Queets River system in Washington were determinate and unrelated to changes in the quantity of parr habitat (inferred from discharge measurements), and therefore unrelated to parr density. However, there are numerous observational and experimental opportunities unexploited that could also shed light on the likelihood of this hypothesis, and they form the basis of the second section of this thesis.

### **Premature migration**

Dambacher (1991) argued convincingly that large scale parr migration (in 1988, 61,000 of 65,100 juvenile steelhead emigrants were parr) from Steamboat Creek in Oregon was deliberate movement to take advantage of higher quality habitat downstream, in the North Umpqua River. Steelhead parr passing through the Keogh enumeration trap may simply be dispersing to take advantage of potential riverine habitats downstream, since it is unlikely

that they would be able to predict the distance to the ocean from any particular point in the watershed, including a point at a mere dozen metres from the upper limit of tidewater.

However, premature migration might well go beyond mistaken entry into salt water environments. Atlantic salmon (*Salmo salar*) have a similar life history to steelhead trout (Scott and Crossman, 1973). In particular, they feed and live as parr for up to several years in streams, before migrating to the sea. Atlantic salmon parr exhibit downstream movements, similar to Keogh River steelhead parr downstream movements, into estuarine environments (Cunjak et al. 1989). But they appear to have elevated moisture levels and depressed plasma sodium concentrations similar to smolts (Birt et al. 1990) suggesting that these movements are associated with partial smoltification.

Thus the hypothesis is plausible that Keogh River parr dispersal in spring is premature migration (in the Webster dictionary sense: "happening, arriving, existing, or performed before the proper or usual time," since they are clearly unable to cope with Queen Charlotte Strait seawater). The third section of this thesis considers evidence available to evaluate this hypothesis.

## Data Analysis

Berger and Berry (1988) demonstrated the subjective nature of hypothesis testing, a nature that can lead, unfortunately, to equally valid but different values for  $p$ , for a single data set. Carver (1978) described the contradictions of attempting to infer the probability of a hypothesis given observations, by the opposite method of inferring the probability of observations given a (null) hypothesis. Edwards (1992) likewise cast doubt on the utility of classical hypothesis testing to determine the relative likelihood of several hypotheses competing to explain a natural phenomenon. Finally, statistically significant differences may arise from large sample sizes, rather than from biological significance. Krebs (1989) made the following his "eighth rule" of ecological data:

Never confuse statistical significance with biological significance.

I have therefore emphasized whether results agree or do not agree with my research hypothesis predictions of biological parameters and patterns, and use graphical analysis to informatively depict these patterns, a technique with a long (> 800 years) and productive history (Tufte 1983), and which has convincing modern proponents (e.g. Chambers et al. 1983, Tufte 1983, and Cleveland 1993).

# Density-Dependent Dispersal Hypothesis

## Introduction

The introductory section provided a background review of previously published material which suggested that downstream movements of parr are density-dependent. This idea in fact incorporates two hypotheses, not a single hypothesis. Density-dependent dispersal might be a result of (1) aggressive interactions which directly displace unsuccessful individuals downstream, or (2) a result of individual parr perceiving aggregate parr density (for example visually) and reacting with voluntary dispersal downstream.

## Evidence

### River population reconstruction

A direct method of determining the density dependence of parr downstream dispersal, whether it is due to aggressive interactions directly or due to voluntary dispersal as a function of density, is to inspect dispersal itself as a function of stream steelhead densities. Although other fish inhabit the Keogh watershed, in particular, coho salmon *O. kisutch* (Irvine and Ward 1989), Swales et al. (1988) reported that the predominant winter distribution of steelhead and coho was main stem Keogh River and tributary/lake respectively.

This segregation likely continues into the migration season, because during main stem sampling in 1991 I encountered steelhead:coho catch ratios of up to 30:1, in spite of the numerical dominance of coho in the Keogh watershed (e.g. 1990 enumeration trapping captured 57,238 juvenile coho and 3,890 juvenile steelhead; Ward et al. 1990). Therefore density-dependent population dynamics of steelhead juveniles are likely confined to intraspecific rather than interspecific interactions.

## Methods

Because the Keogh River trap provides catch-at-age data, that is, an estimate of river smolt production factored by smolt age and year, it is possible to reconstruct an estimate of the number of steelhead juveniles present in the river at the beginning of each spring, prior to migration. I used a method commonly employed in temperate fisheries stock assessment, virtual population analysis - VPA (Hilborn and Walters 1992), in simplified form (simplified mainly because there was no fishing mortality requiring estimation). The method in this case consists of recursively applying the following equation from the oldest smolts to the youngest, in any given cohort:

$$N_t = N_{t+1} + M_t \quad (1)$$

$N_t$  is number of fish in year  $t$ ,  $N_{t+1}$  is the number of fish the following year, and  $M_t$  is mortality in year  $t$ .

In order to estimate natural mortality I used fry-to-smolt survival data that Ward and Slaney (1993) provide (their Table 1). Given fry-to-smolt survival ( $S$ ) over a certain number of years ( $n$ ), annual survival ( $S_a$ ) is:

$$S_a = (S/.25)^{1/(n-1)} \quad (2)$$

Ward and Slaney (1993) also report 7% and 25% as the only two estimated mean values for fry-to-parr (1+) survival in the Keogh River. The former value as well as the mean

Table 2: Estimates of annual parr survival rates based on data in Ward and Slaney (1993)

Cohort	Years to final smolt observation	Fry-smolt Survival (%)	Annual Survival (%)
1977	5	12	82
1978	5	5	65
1979	4	20	92
1980	4	22	95
1981	4	11	76
1982	4	3	51

(16%) imply nearly 100% or even greater than 100% survival in subsequent years to give the measured fry-to-smolt survivals for some cohorts. Therefore I incorporated 25% into equation 2. Assuming that annual survival didn't vary much after age 1+, it would appear that a plausible range for mean annual survival of steelhead parr in the Keogh River was 50–95% (Table 2).

The next step was to apply VPA to catch-at-age data (Table 3). I programmed the computer to reconstruct stream population sizes for four possible annual survival rates within the plausible range I described above: 60%, 70%, 80%, and 90%. The stream population size estimate, then, was the reconstructed population + the number of dispersing parr.

## Results and Discussion

Density dependence appears graphically as a positively or negatively changing specific rate (e.g. mortality or emigration per capita) versus population size and biologists often demonstrate it that way (Walters 1986). Therefore, plots of absolute rates (in this case total parr numbers dispersing) versus population size do not show density dependence when the relationship increases or decreases with constant slope (producing a per capita dispersal rate—the slope—that does not vary with population size). Instead such plots suggest density dependence when either (1) the x-intercept is positive (dispersal begins only after the population reaches a minimum size) or (2) the slope changes as population size changes



Table 3: Steelhead smolt abundance by year, for cohort analysis, with each year's production divided into age groups. 1977–1983 data from Ward and Slaney (1988); 1984–1992 data on file, B.C. Fisheries Branch. For an illustration, smolts and non-dispersing parr surviving to smolt age in the Keogh in 1979 are in **bold type**. Annual downstream dispersing parr not included. “NA” = not available.

Year	1+	2+	3+	4+	5+
1977	0	909	1207	227	0
1978	0	1117	789	198	0
1979	<b>0</b>	<b>835</b>	<b>4892</b>	<b>1173</b>	<b>0</b>
1980	0	<b>1546</b>	<b>3350</b>	<b>561</b>	<b>44</b>
1981	0	3474	<b>5592</b>	<b>2713</b>	<b>118</b>
1982	0	1504	2376	<b>104</b>	<b>16</b>
1983	0	1951	3701	401	<b>0</b>
1984	0	5291	3569	866	0
1985	0	6600	2504	205	0
1986	226	8300	1257	39	0
1987	1485	9786	2443	167	0
1988	0	3030	287	7	0
1989	23	2146	1969	108	0
1990	5	843	276	16	0
1991	0	818	3969	1095	0
1992	NA	NA	NA	NA	0

(producing a dispersal rate per capita that changes as population size changes).

I fitted both a local regression model (“loess” with span=2/3 and degree=1; Cleveland et al. 1993) and an exponential model (non-linear least squares fitting of parameters; Bates and Chambers 1993) of the form  $D = e^{aP+b}$  (where  $D$  is the number of parr dispersing,  $P$  is the estimate of stream population size, and  $a$  and  $b$  are parameters influencing the shape and rate of increase of the exponential curve) to the dispersing parr versus estimated stream population (Figure 5).

At the lowest hypothesized annual survival rate ( $S=60\%$ , Figure 5), there appears to be no evidence for density dependence because neither of the fitted models approaches a positive x-intercept or changes with changing population size. However, as the hypothesized

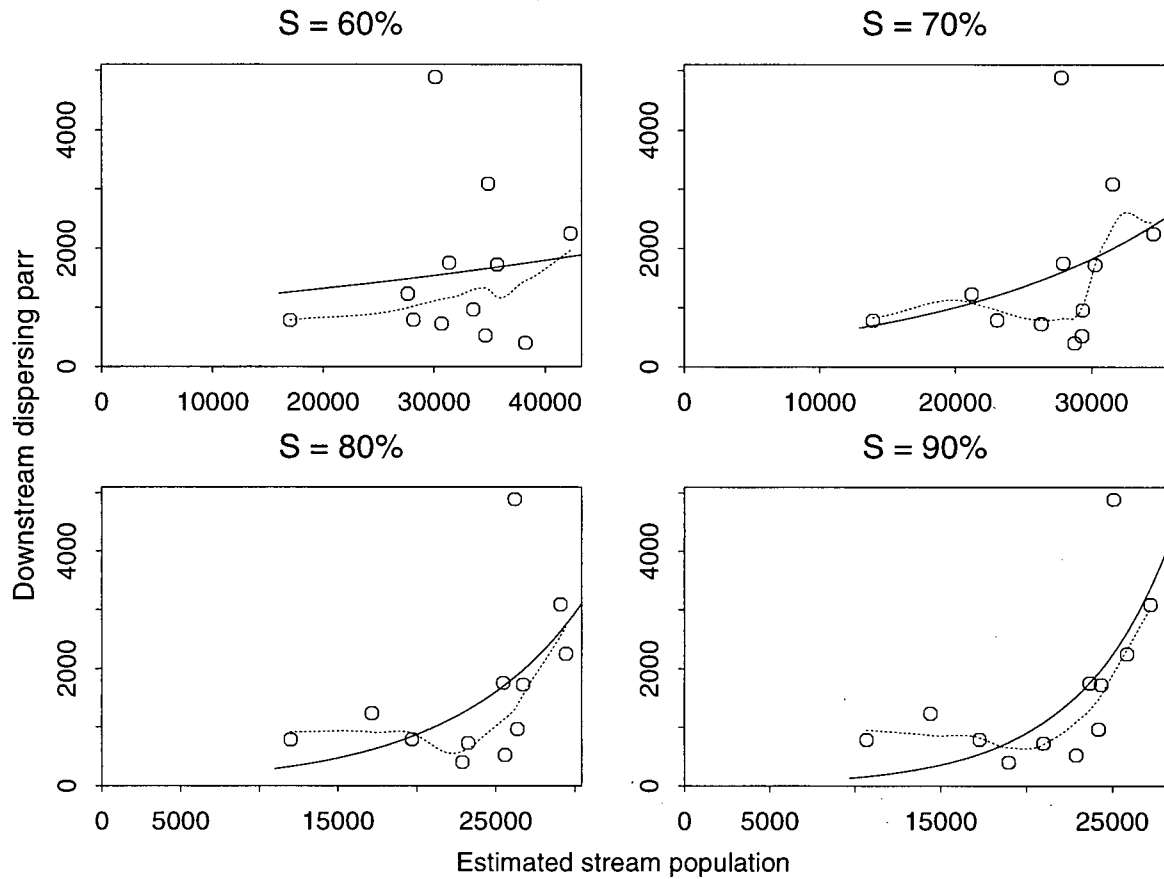


Figure 5: Downstream dispersing parr versus estimated stream population at four assumed annual survival rates (S). Dashed line fitted with an empirical local-regression model; solid line fitted with a logarithmic model.

annual survival rate increases through the range of plausible values from 70%–90% (Figure 5), we see increasing support for the hypothesis that parr dispersal is density-dependent. In each of these panels, dispersal increases in a non-linear fashion (changing slope) as population size increases.

In addition, at all four hypothesized annual survival rates, the empirically fitted model (loess) suggests that regardless of density, there is always some background parr migration

(the approximately horizontal section of the modeled fit, at lower estimated population sizes).

This reconstruction of past stream populations requires not only several assumptions about the values of important yet minimally known population parameters (mainly natural annual mortality rates of steelhead parr in the Keogh River, and their variation with age), but also requires an assumption that a given number of juvenile steelhead resident in the Keogh in one year produces the same density effect as the same number in another year. If less or more habitat were available in these different years, this assumption would clearly be incorrect.

If the cohort analysis is robust to departures from the assumptions, the results indicate a density-dependent downstream parr dispersal at higher stream population numbers, and a background level of parr dispersal that appears at lower population sizes, and may form part of dispersal at higher population sizes as well.

### **Stream Channel Behavioural Observations**

Biologists have successfully observed salmonid behaviour in artificial stream channels and tanks (Kalleberg 1958, Mason and Chapman 1965, Fraser 1969, Slaney and Northcote 1974, Chandler and Bjornn 1988, Mesick 1988). I set up such channels to observe what behavioural differences existed between dispersing parr captured at the enumeration trap and parr captured in the stream, examining in particular, differences in aggressive behaviour. If dispersing parr are the losing individuals of territorial interactions upstream and main stem resident (stream caught) parr are individuals that have successfully maintained a position, then the latter should, on average, continue this pattern and dominate dispersing parr in stream channels.

### **Methods**

**Channel construction** In the spring of 1991, I constructed two artificial stream channels at the site of the Keogh River enumeration trap, where partial impoundment of

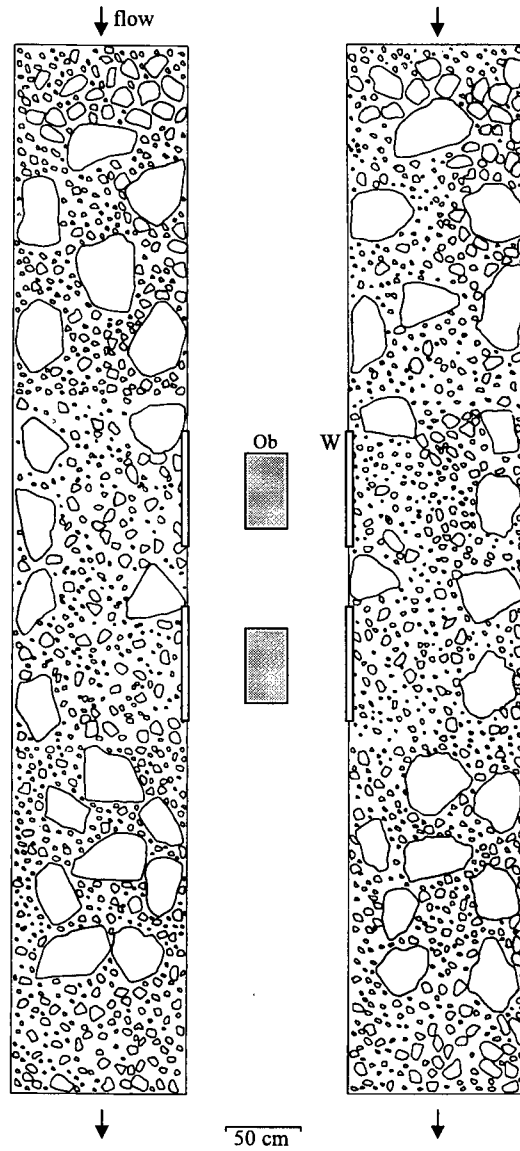


Figure 6: Overhead view of stream channels showing the outline of both cobbles and boulders, and their precise placement. I made behavioural observations through four windows (one labelled “W”) from two observation points (one labelled “Ob”).

Table 4: Artificial stream channel dimensions, flow, and habitat characteristics

Parameter	Value
Length	7.02 m
Width	1.18 m
Water depth	0.45 m
Mean flow (range)	$34 \text{ l} \cdot \text{s}^{-1} (\pm 8 \text{ l} \cdot \text{s}^{-1})$
Mean water velocity (range)	$6.4 \text{ cm} \cdot \text{s}^{-1} (0\text{--}55 \text{ cm} \cdot \text{s}^{-1})$
Median boulder dimension (range)	33 cm (19–55 cm)
Median gravel/cobble dimension (range)	2 cm (0.5–10 cm)

the river by the trap provided a ready source of river water at ambient temperatures and with some invertebrate drift (verified by placing a fine mesh net fitted over the downstream end of the intake pipe). Plywood sheeting on a wooden frame created the channel walls, bottom, and a header box to collect water and redirect it to spill into the upstream end of each channel in plunge pool fashion. Stream gravel and cobbles formed a natural substrate. Green seine netting draped over the channels and placement of 20 boulders per channel provided parr with cover. Two glass observation windows per channel permitted observation (Figure 6). Over the course of the observational period or afterwards, I measured salient physical features of the stream channels (Table 4).

**Parr observations** From late April through mid-June, 1991 I electrofished throughout the Keogh River main stem to capture a sample of stream resident parr, and during the same period sampled steelhead parr that passed through the enumeration trap (Figure 7).

I collected behavioural observations during the period 17–20 June, 1991. I added fifty (25 emigrant, 25 resident) parr to each channel and allowed them to acclimatize overnight, fed them with brine shrimp twice daily to supplement stream drift that entered with the channel water supply, and observed agonistic behaviour for 15 minute periods at each of the four windows for a total of eleven hours of observation (eight experimental groups of 50 parr, 44 subsampled observation periods). By marking emigrant parr with a lower caudal

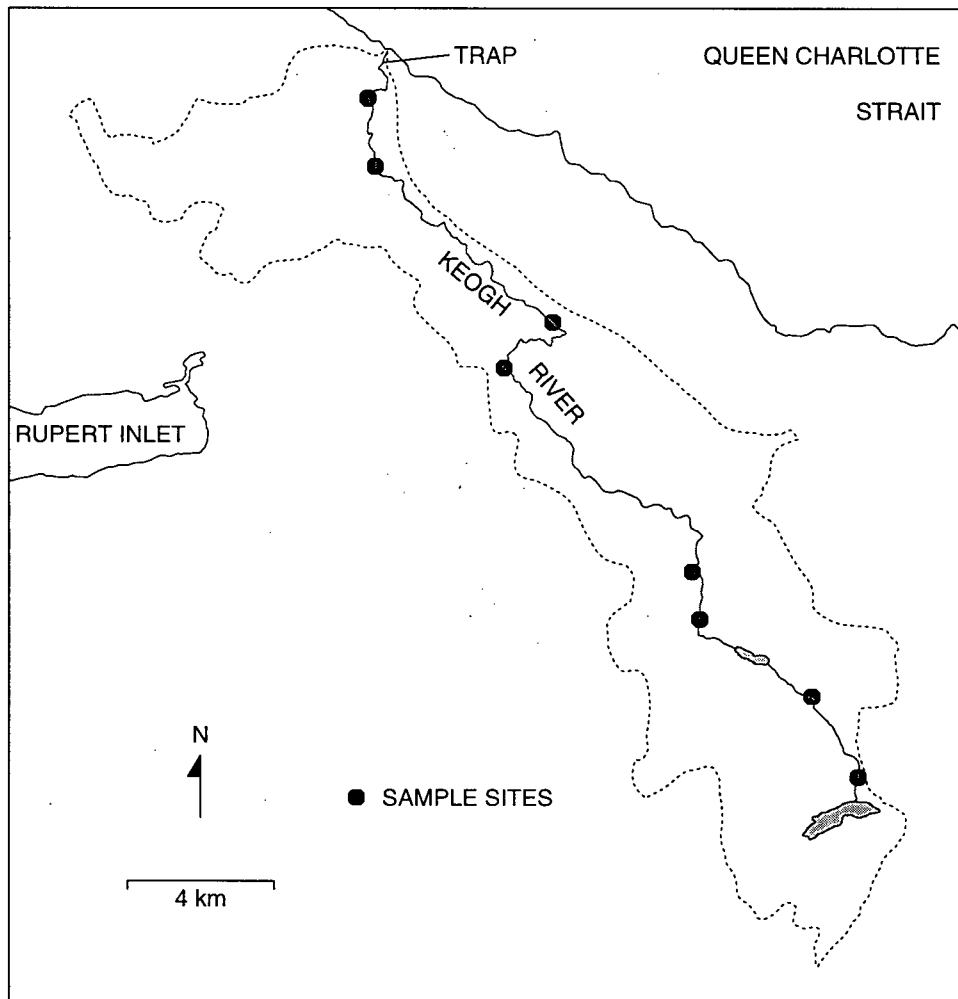


Figure 7: Steelhead parr sampling sites at the mouth (TRAP) and in the main stem of the Keogh River.

fin clip and resident parr with an upper caudal fin clip I enabled quick distinction between them during observation periods.

## Results and Discussion

I observed in each type of parr the classic agonistic patterns that Kalleberg (1958), for example, identified in juvenile Atlantic salmon *Salmo salar* and brown trout *S. trutta*:

1. frontal and lateral threat displays;
2. displaced aggression (juveniles seizing algae or other debris in the mouth and spitting it out);
3. direct attacks, with or without nipping.

By far the most common and unambiguous parr-parr interaction was a direct attack. Therefore I tabulated the number of attacks, type of parr attacking (emigrant, resident), and the size of the aggressor relative to the parr it attacked (larger, same, or smaller). I observed that attacking parr were maintaining territories, and displacing other parr from their territory.

The mean attack rate for resident and migrant parr was virtually identical (2.79 and 2.74 per 15 minutes respectively; left panel, Figure 8). In contrast, the mean attack rates for larger, similar, and smaller parr as aggressor were 3.66, 1.34, and 0.65 per 15 minutes respectively (right panel; Figure 8). In relative terms, larger parr aggressors attacked 4.7× as often as smaller parr aggressors, whereas stream resident parr attacked 1.02× as often as emigrant parr.

There is virtually no difference in the attack rates that emigrant and stream resident parr display, particularly compared to the effect that size of parr has on attack rate. These observations provide no support for the hypothesis that dispersing parr are victims of direct, agonistic, displacement.

## Parr Length

Individual territorial interactions would cause direct displacement of parr that were smaller, on average (see above section). However, biologists have observed that territory size increases with body size in several stream dwelling, territorial salmonids: juvenile Atlantic

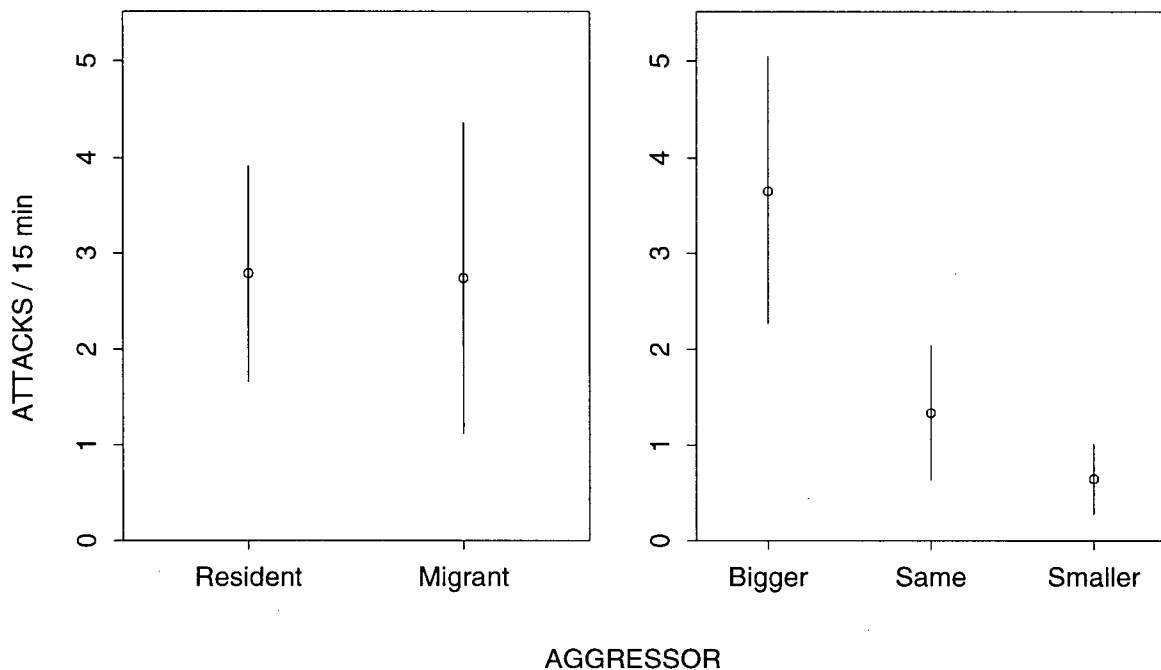


Figure 8: Mean attack rates ( $\pm$  standard error,  $n=8$ ) of steelhead parr factored by parr type and size. The left hand panel contrasts attack rates of emigrant and stream resident parr; the right hand panel contrasts attack rates factored by size of aggressor relative to the parr it attacked. Both panels use the same data set.

salmon (Keeley and Grant 1995), brook trout (Grant et al. 1989), and brown trout (Elliott 1990). Since steelhead parr are territorial, this is likely the case for them as well. If parr are abundant enough that Keogh main stem habitat is limited, then larger parr would find themselves under stronger territorial pressure than smaller parr, and may disperse to seek space elsewhere, including downstream.

## Methods

I described sampling of dispersing and stream resident parr in the previous section. Roughly uniform sampling of each type of parr over the migration period allowed a direct comparison of fork lengths without factoring out confounding effects of time (and therefore growth).



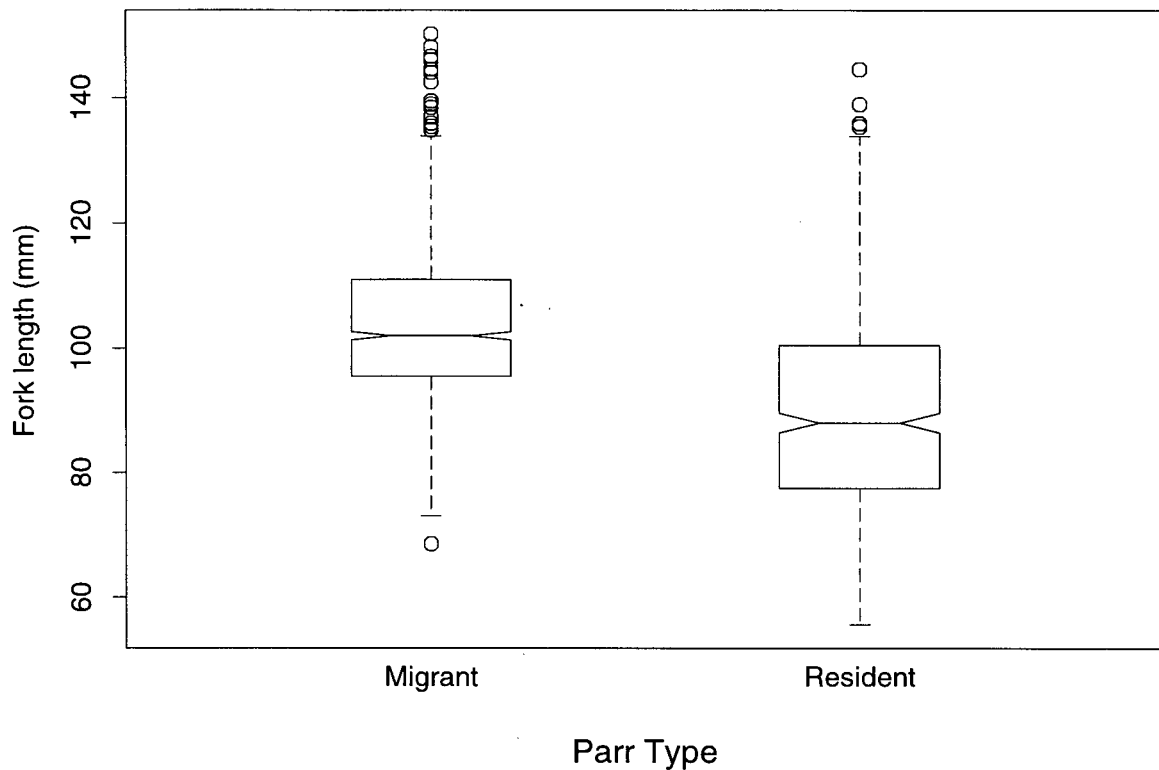


Figure 9: Boxplot comparison of fork lengths of migrant and stream resident parr.

### Results and Discussion

Because stream sampling occurred during the migration period, it was possible that dispersing parr “polluted” the stream sample of parr: I could have captured migrant parr either in temporary resting cover, or even in transit, when sampling in the Keogh main stem river. The effect on the data of a fraction of purported stream resident parr being in reality migrant or dispersing parr, is to shift comparisons in a conservative direction. In other words, whatever differences exist between stream resident and migrant parr are surely larger than portrayed.

Boxplots<sup>1</sup> depict several differences between the length distributions of each sample of parr (Figure 9). The migrant parr fork length distribution partially overlapped that of the stream resident parr; however, migrant parr were larger at all landmark points in the length distribution (minimum, maximum, quartiles, and median). The average migrant (trap caught) parr was fork length=104 mm, nearly 16% larger than the mean stream resident parr at 90 mm.

Smaller stream parr are unlikely to have displaced larger downstream dispersing parr through direct aggressive interactions (stream channel observations discussed in the previous section suggest this conclusion). However, increasing territorial requirements of growing parr could result in this observation of larger fish dispersing downstream. Dambacher (1991) argues that parr migrations from Steamboat Creek, Oregon are in fact an adaptation to take advantage of better rearing conditions downstream in the North Umpqua River.

### **Variable Density Stocking Experiment**

Though the stream channels that I built had an exit at the downstream end through which parr could leave (albeit into a collecting bucket), few parr did leave once placed in the channels. Thus the stream channels were not directly useful in examining dispersal as a function of density. However, I was able to investigate direct density-dependent dispersal. To measure the influence of density on dispersal rate I ran a small scale stocking experiment in a tributary stream in the upper Keogh watershed.

### **Methods**

**Site and experimental reach description** O'Connor Lake's outlet has a third order tributary that flows northward and joins the outlet a short distance upstream of the Keogh main stem (Figure 10). The stream was inaccessible to anadromous fish because of gradient

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<sup>1</sup>boxplot—first and third quartiles of sample data are the bottom and top border of each box; median is the horizontal line within the box; range is whiskers extending out from each box; outliers (points) are  $> 1.5 \times$  the interquartile distance from the quartile; notches indicate approximate 95% confidence intervals for the median.

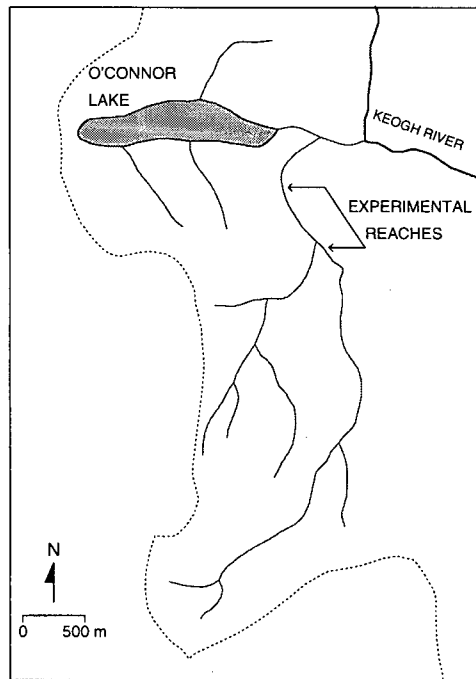


Figure 10: Variable density stocking experiment: experimentally stocked reaches located in the length of tributary the arrows indicate.

and several waterfalls; however, it was not barren because some steelhead fry stocked above the barriers over a decade earlier had colonized the stream instead of emigrating (Slaney et al. 1980).

In 1991 I surveyed a series of 15 reaches from 14 m to 100 m long, separated from each other by small waterfalls or cascades intended as upstream dispersal barriers. Average stream gradient in the section of the creek containing the experimental reaches was 6.2%. The dominant habitat type in each reach was various types of pool (plunge, scour, trench, and backwater; Bisson et al.'s 1982 terminology), and within a factor of two was similar among reaches (Figure 11).

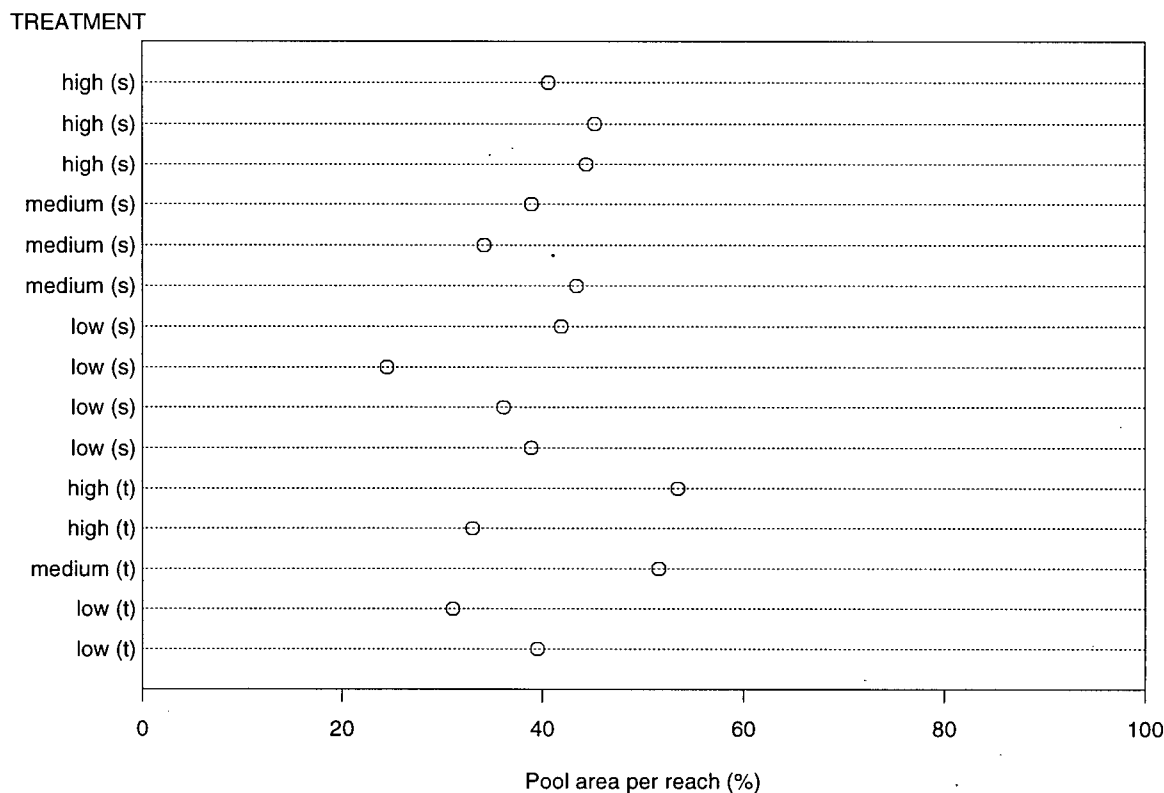


Figure 11: Percentage pool area in each experimental reach. TREATMENTS were high, medium, and low stocking densities of migrant (t: trap caught) and resident (s: stream caught) steelhead parr.

**Experimental design** Into each reach I introduced either main stem resident or migrant parr at one of three (stocking) densities (high = 0.45, medium = 0.15, low = 0.05 parr · m<sup>-2</sup>) (Table 5). Main stem captured parr were introduced prior to the beginning of the migration (and therefore could have included some potentially dispersing type parr) on 27 April 1991, and migrant parr were introduced after a sufficient number had accumulated at the enumeration fence, on 1 June 1991.

Treatment assignment to each reach was not random: I stocked the originally main stem resident parr in the 10 downstream reaches, and originally migrant parr in the 5 upstream

Table 5: Variable density stocking treatments in O'Connor outlet tributary

Reach	Parr type	Number stocked	Reach area (m <sup>2</sup> )	Density	Fins marked subdermally
1	stream resident	37	80	high	upper, lower caudal
2		18	42	high	upper caudal, right pectoral
3		53	114	high	upper caudal, left pectoral
4		8	49	medium	lower caudal, anal
5		23	158	medium	lower caudal, right pectoral
6		30	205	medium	lower caudal, left pectoral
7		6	101	low	upper caudal, lower caudal, anal
8		24	471	low	upper caudal, anal
9		7	142	low	anal, left pectoral
10		14	274	low	anal, right pectoral
11	migrant	43	92	high	upper caudal
12		15	31	high	lower caudal
13		18	103	medium	anal
14		8	105	low	right pectoral
15		15	229	low	left pectoral

reaches, with high, medium, and low stocking densities grouped together in a down- to upstream pattern. Migrant parr reaches were separated from downstream resident parr reaches by a buffer reach 90 m long; otherwise parr were free to remain in the original reach, or move downstream any distance including through downstream experimental reaches, or entirely out of the experimental section into O'Connor outlet, or the Keogh main stem. Parr could not move upstream due to impassable waterfalls that fell into pools (1–2 m high, one was 8 m high into a pool depth > 1 m).

I used a subdermally injected dye mark (Alcian blue) to batch identify parr by source (trap or main stem) and by reach (and therefore stocking density) (see Hart and Pitcher, 1969 for method). After marking but before stocking, I held the fish overnight in tanks supplied with fresh river water; there were no mortalities. Stop seines closed each section to emigration for the first 24 hours after stocking, in order to prevent disorientation as a

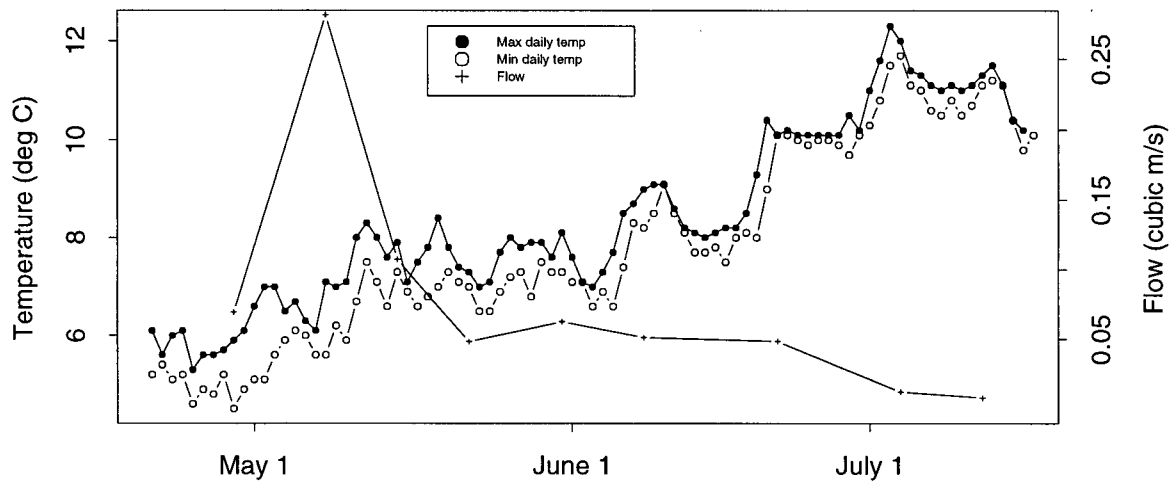


Figure 12: Stream discharge and daily water temperatures through the duration of the variable density stocking experiment

source of emigration.

During the course of the experiment, a Ryan thermograph continuously recorded stream temperature, and I periodically recorded stream flows (Figure 12) using methods in Linsley et al. (1982). A freshet occurred after I stocked main stem resident parr, but before I stocked migrant parr.

From July 1–6 for the resident parr treatments (stocked April 27) and from July 7–10 for the migrant parr treatments (stocked June 1) I used four pass electrofishing depletions, separated by a minimum of 1 hour, to estimate final experimental reach parr densities, and recapture and identify the original stocking site of marked parr. Several days were additionally expended to sample the tributary and O'Connor outlet downstream of the experimental reaches.

Since depletions were linear (appendix), I used the Leslie and Davis (1939) method to compute a total parr (including residualized steelhead) population estimate for each reach.

Table 6: Final observed parr population numbers in experimental reaches

Reach	Stocked	Stocked remaining	Stocked upstream	Native	Total	Depletion estimate	Final density (parr/m <sup>2</sup> )
1	37	7	1	5	13	13	.16
2	18	1	7	3	11	11	.26
3	53	3	4	7	14	15	.13
4	8	2	5	7	14	14	.29
5	23	8	1	13	22	23	.15
6	30	7	7	26	40	39	.20
7	6	1	4	7	12	12	.12
8	24	4	2	42	48	48	.10
9	7	1	3	22	26	25	.18
10	14	5	2	27	33	33	.12
11	43	4	0	28	32	32	.35
12	15	2	0	9	11	11	.36
13	18	2	0	38	40	39	.39
14	8	0	0	33	33	32	.31
15	15	5	-	83	88	86	.38

## Results and Discussion

Recapture locations consisted of the original stocking site, experimental stocking sites downstream of the original stocking site, locations in the tributary to O'Connor Lake's outlet downstream of the experimental reaches, and the outlet itself. In addition, some experimentally stocked parr were never recaptured. Overall, 16% of stocked parr stayed at their stocking site, 14% moved into other experimental reaches (or a buffer reach in between the resident parr and emigrant parr sections) downstream of their stocking sites, and 10% were found in the tributary downstream of the experimental reaches, or in O'Connor Lake outlet. The trap at the mouth of the main stem Keogh captured no experimentally stocked parr. To compute final densities for each experimental reach, including the unmarked native residual steelhead population, I used the larger of the depletion estimate or the total number of parr captured (Table 6).

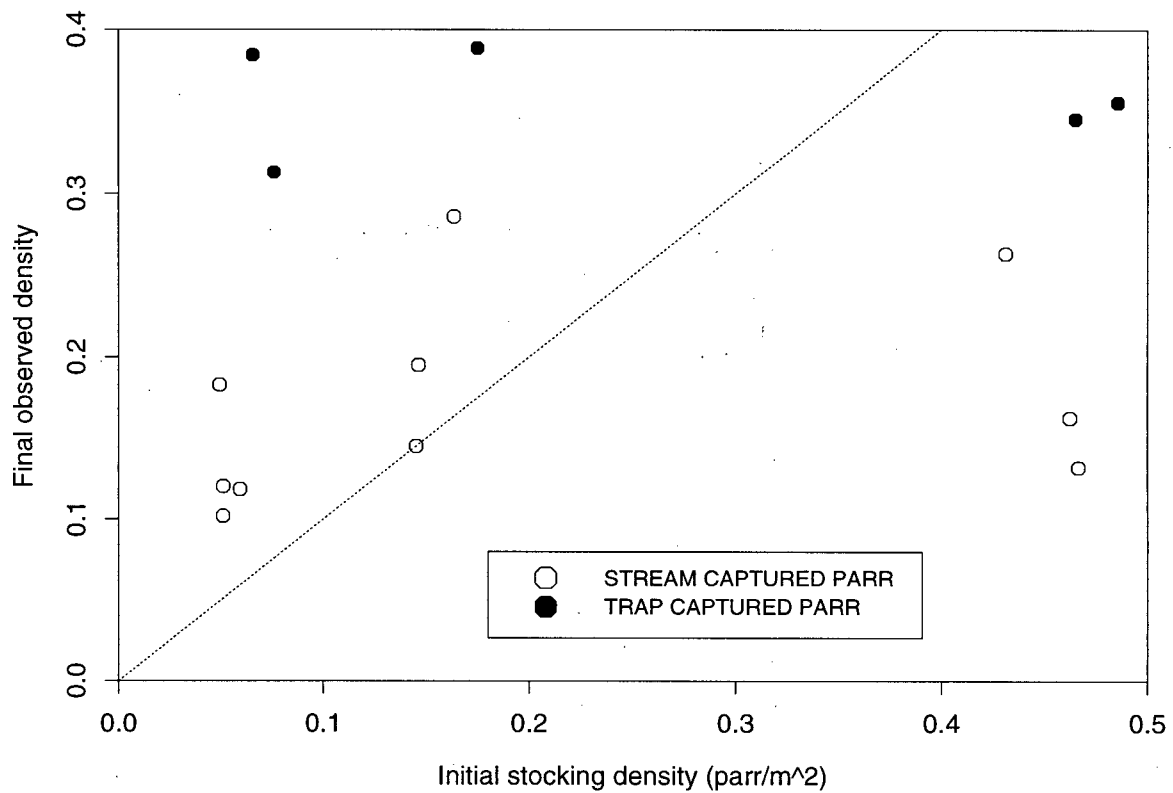


Figure 13: Final observed parr density versus initial stocking density. The diagonal line is the replacement line (final observed density equal to initial stocking density).

Because the initial ambient density of residual steelhead on top of which I added experimental parr was unknown, whereas the final total density was actually observed, I evaluate density effects using initial stocking densities and final observed absolute densities (Figure 13).

These data show a density effect in the contrast between high density and medium or low density treatments. The high density treatment of both types of parr resulted in final observed densities lower than the initial stocking density, in contrast to low and medium stocking density treatments. Low and medium stocking densities, for both types of parr, did



not cause steelhead to disperse at a high enough rate to result in final observed densities the same (except in one medium density, resident parr treatment) or lower than initial stocking density.

Final sampling caught stocked parr in experimental reaches downstream of the initial stocking site (Table 6), as well as downstream of the experimental section entirely. In addition to mortality unobserved as a cause for high density treatments to have resulted in steelhead numbers lower than that initially stocked, dispersal as a response to density clearly contributed to the observed result. In short, this experiment, in spite of real but unavoidable design flaws (imposed by field conditions), demonstrated density-dependent dispersal of steelhead parr at the stream reach scale.

The second major pattern in the data (Figure 13) are final densities in migrant parr reaches that were all higher than final densities in stream resident parr reaches. Given otherwise similar habitat, one possible cause of this anomaly is the freshet that occurred prior to stocking main stem resident parr, which may have caused a density-independent reduction of steelhead numbers in the resident parr reaches.

# Premature Migration Hypothesis

## Introduction

If downstream dispersal of parr is a directed but premature migration, then it is likely that the same mechanisms that cause most parr in subsequent years to migrate as smolts, cause these dispersing parr to migrate prematurely. In the case of the hypothesized migrant parr, these mechanisms simply have not advanced completely enough to result in fish with the outward appearance of true smolts and fully competent osmoregulatory ability.

Although I did not collect any physiological data common to evaluations of smolting status of juvenile salmonids (Folmar and Dickhoff 1980, Beeman et al. 1995), scales that I sampled in 1991 provided an opportunity to examine parr growth. Increased thyroid activity during smoltification, leads to increased levels of growth hormone, and thus increased growth rates (Folmar and Dickhoff 1980, Wedemeyer et al. 1980).

If parr movements are in fact migratory (and due to the same proximate causes for which smolts migrate), then migrant parr should have growth patterns similar to smolt growth patterns, and should respond to the same environmental cues to which smolts respond, such as photoperiod (Wagner 1974). If, on the other hand, parr downstream dispersal is simply density-dependent, the two types of parr should respond similarly when experiencing similar habitat and density conditions.

## Evidence

### Scale Measurements

#### Methods

**Scale features and sampling** Salmonid scales have two features that are useful for measuring past growth of an individual fish: annuli and circuli. Measurement of scale radius at each annulus and of total scale radius allow back-calculation of length at age (Ricker 1992). In addition, circuli spacing increases with growth rate (Bhatia 1931, Gray and Setna 1931), and therefore measurement of intercirculus distances provides an index of growth rate.

Back-calculation of length at age, and measurement of circulus spacing, required a sample of scales from each of smolts, stream resident, and migrant parr. Accordingly I randomly sampled scales from April to June 1991, over the full length range of each type of steelhead, choosing several scales from a consistent and preferred (Maher and Larkin 1955) location on each individual (left side, above the lateral line, and somewhat behind the posterior edge of the dorsal fin). I rejected all regenerated scales, obvious under magnification because of a very large placode. These result from the loss of a scale and its rapid replacement—leading to missing annuli and circuli, shape distortions, and concomitant measurement bias.

After mounting several scales from each fish between two microscope slides, I used a video camera mounted on a microscope to capture a digital image of a suitable scale at a suitable magnification ( $240\times$  for all but the largest smolt scales, which I examined at  $95\times$ ) for ageing and measurement.

Using custom software I digitized the anterior radius, intercirculi widths, and anterior radius to each annulus, of each scale (Figure 14) on a high resolution computer monitor ( $1280\times 1024$  pixels). Measurements of a calibration slide indicated zero bias and high precision using this method (the standard deviation of 56 calibration slide measurements was 1.1 micrometres; the minimum intercirculus width measured was 6.2 micrometres and the first quartile of all scale measurements—including radii to both the anterior scale edge and

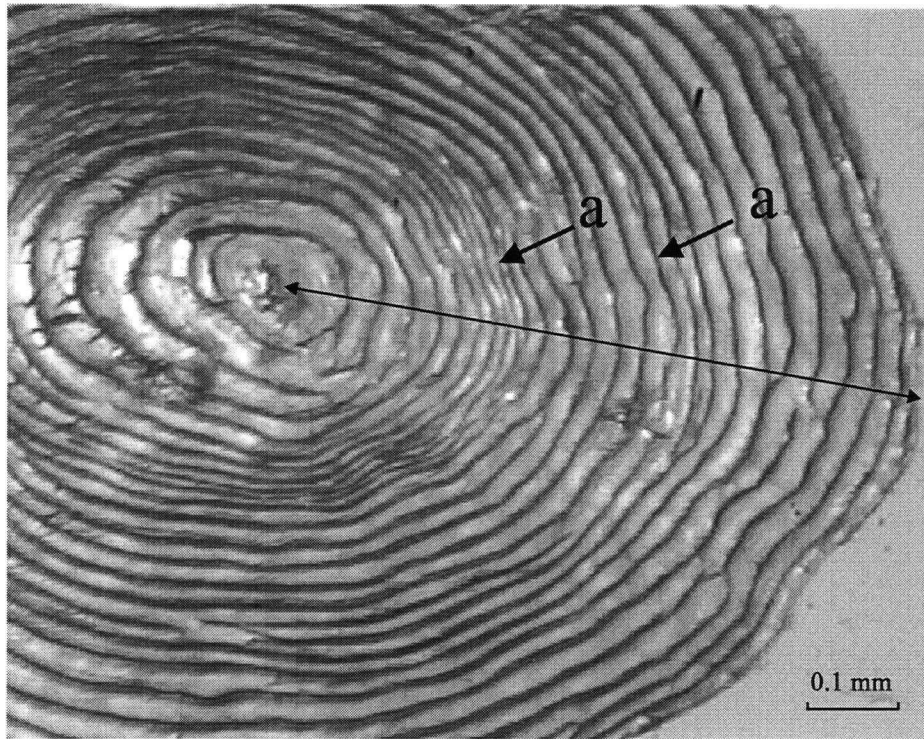


Figure 14: A Keogh River steelhead parr scale from a migrant parr, captured 14 June 1991, fork length 133 mm. Numerous circuli are clear, “a” marks two annuli, and the arrowed line traces the anterior radius of the scale, from focus (center) to anterior edge.

Table 7: Steelhead scale sampling intensity for back-calculation, by steelhead type and age (number of winters)

Steelhead type	Number	Age			
		1+	2+	3+	4+
Smolt	108	0	21	52	35
Migrant	183	45	133	5	0
Stream	152	51	91	10	0

to annuli in addition to intercirculi widths—was 16.8 micrometres).

Table 7 summarizes the numbers of scales I sampled from each type of steelhead, and also tabulates the age distribution which I interpreted from the scales. An experienced salmonid

scale reader<sup>2</sup> had previously aged all of the smolt scales, and after I had done the same I compared our results to find that in 97 of 106 cases our ages agreed, with the remainder roughly evenly split between being younger or older. Thus my scale interpretation was probably in the majority of cases, correct. Alternatively, we were both wrong in similar ways; however, without belabouring validation procedures the remainder of this section assumes accurate and unbiased interpretation.

**Back-calculation** Ricker (1992) describes the methods I followed to back-calculate size at age. First I computed  $C$ , the intercept of the geometric regression of all of the steelhead lengths and their corresponding scale radii. To compute length at age  $i$ ,  $L_i$ , given length at the time of sampling,  $L$ , scale radius at the time of sampling  $S$ , and scale radius at age  $i$ ,  $S_i$ , the equation that incorporates the Fraser-Lee adjustment for variation in scale radius at length is

$$L_i = (L - C) \times S_i/S + C. \quad (3)$$

Figure 15 demonstrates this geometrically.

For the sample of steelhead I calculated  $C$  to be 11.8 mm (Figure 16).

## Results and Discussion

Using equation 3 and  $C = 11.8$  mm I back-calculated the length at all ages for all of the steelhead sampled (Table 7 lists sample sizes).

Plots of mean fork length at age for the 1988 and 1989 cohorts (ages 3+ and 2+ respectively, when sampled in 1991) show for each cohort a similar pattern of growth: the fish smolting in 1991 were larger and had clearly grown faster than individuals in the cohort that remained parr (Figure 17). And the migrant (downstream dispersing) parr were likewise larger and had grown faster than parr remaining in the river, for each cohort. Thorpe (1977, 1980) has described similar growth rate differences for Atlantic salmon cohorts in

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<sup>2</sup>Bob Land, B.C. Fisheries Branch, Abbotsford Research Hatchery

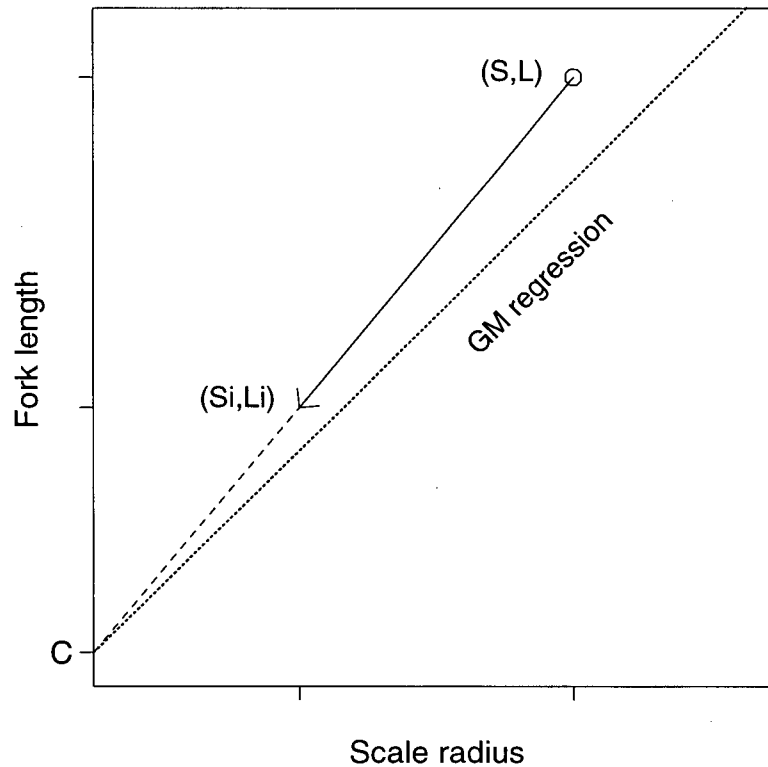


Figure 15: Geometry of fork length back-calculation based on the method that Ricker (1992) recommends: see text for details.

which parr had bimodal growth differences such that each growing mode smolted in a different year (the slower mode at 2+, the faster at 1+). Apparently Keogh River steelhead parr have trimodal growth resulting in some of a cohort becoming large enough to smoltify, some growing slowly enough to remain parr until they smolt after a subsequent year or more of growth, and the remainder growing at an intermediate rate, resulting in an ambiguous parr-smolt: growing too slowly to be a smolt, and growing too fast to be a parr.

Standard errors of mean fork length at age for the different types of steelhead are relatively small compared with the differences between the means (Table 8).

Although these apparent growth rate differences are support for the premature migration hypothesis, we can also examine an index of growth rate since the last winter check: circuli

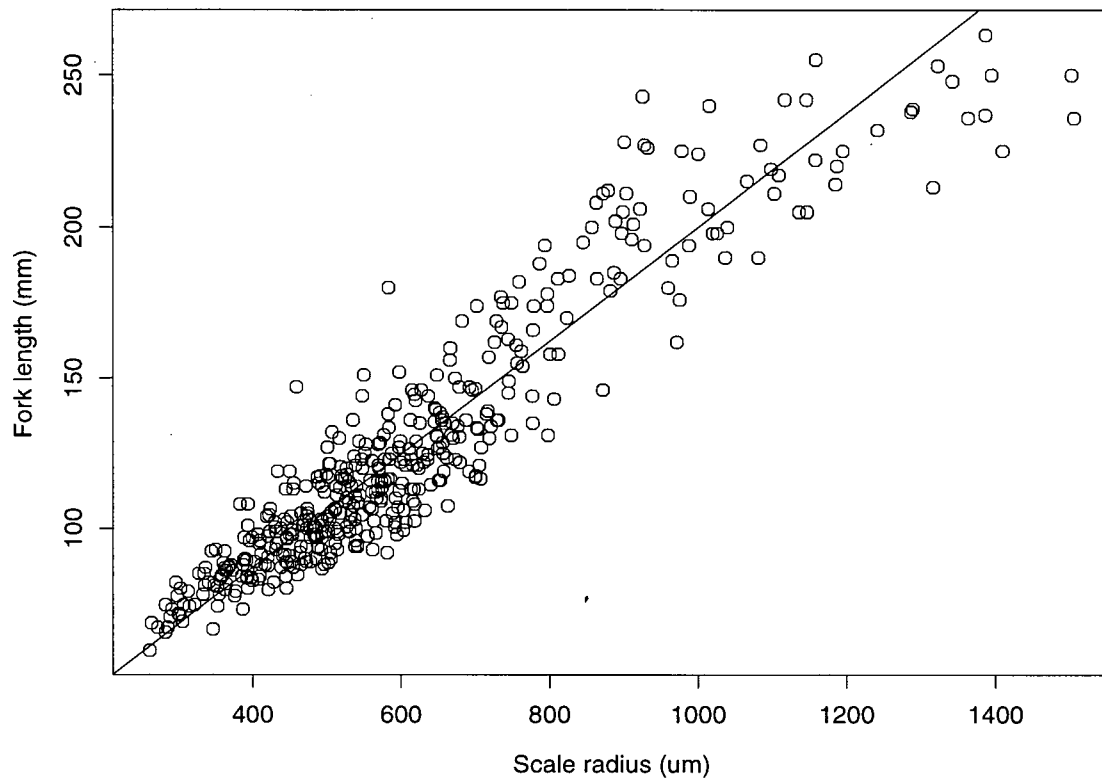


Figure 16: Steelhead fork length versus scale radius. Y-intercept (not shown) of geometric regression  $C = 11.8$  mm.

spacing. Exploratory data analysis suggested that although mean intercirculi width since the most recent winter check in growth did not change as the sampling date increased, it did increase with steelhead age, therefore I separated the data once again by cohort for comparisons.

Clearly, for any given age, smolts have the largest intercirculi widths, followed by migrant parr, with stream resident parr having the smallest (Figure 18). Although the sample sizes are not large for parr at age 3+ (1988 cohort) the trend in circulus spacing is consistent with younger cohorts and therefore probably not an artifact. The previous analysis of back-



Figure 17: Growth comparison of two steelhead cohorts based on lengths back-calculated from scale features, factored by type of steelhead.

calculated lengths at each winter check demonstrated differing growth rates up to the most recent winter check. In this data set of intercirculi widths, we have corroboration with the results of back-calculating length at age up until the last winter check in growth, but now extending the inference of faster growth rates beyond the last winter check, up until the very day of capture and sampling.

In short, migrant parr are intermediate in growth between stream resident parr and smolts.

## Condition Factor Contrast

### Methods

The previous section describes in detail the sampling of downstream dispersing parr and main stem resident parr. In addition, I subsampled smolts at the enumeration trap during the same time period in 1991. I measured fork length to the nearest mm and weight to



Table 8: Length at age comparison for two steelhead cohorts, from lengths back-calculated based on scale features. The mean values are depicted in Figure 17.

Cohort	Steelhead type	Age	Fork length mean (mm)	Fork length s.e. (mm)	n
1989	Migrant	1	57.3	0.77	133
		2	83.3	1.12	133
	Stream	1	53.9	0.94	91
		2	76.4	1.24	91
	Smolt	1	69.3	2.99	21
		2	110.8	3.41	21
1988	Migrant	1	48.0	2.74	5
		2	86.3	4.33	5
		3	109.5	3.52	5
	Stream	1	44.5	2.47	10
		2	71.2	5.77	10
		3	97.1	5.24	10
	Smolt	1	55.8	1.44	52
		2	105.2	2.14	52
		3	143.4	2.75	52

the nearest tenth of a gram of all captured parr. From these data I was able to compute condition factor  $CF$  as

$$CF = 100000 \times \frac{weight}{length^3} \quad (4)$$

## Results and Discussion

The distribution of condition factors of migrant parr lies in between that of smolts and stream resident parr (Figure 19). Because of the changing body shape of growing and smolting steelhead (Beeman et al. 1995) these computations of condition factor are less an index of juvenile steelhead condition, and more an index of transition to smolt body shape. Ewing et al. (1994) compared condition factors of rainbow trout permitted voluntary emigration from a hatchery raceway and found the migrants to consistently have a lower condition factor; at the same time, those migrating out of the raceway had higher gill  $Na^+-K^+-ATPase$  activity than those remaining behind. In spite of the lack of physiological

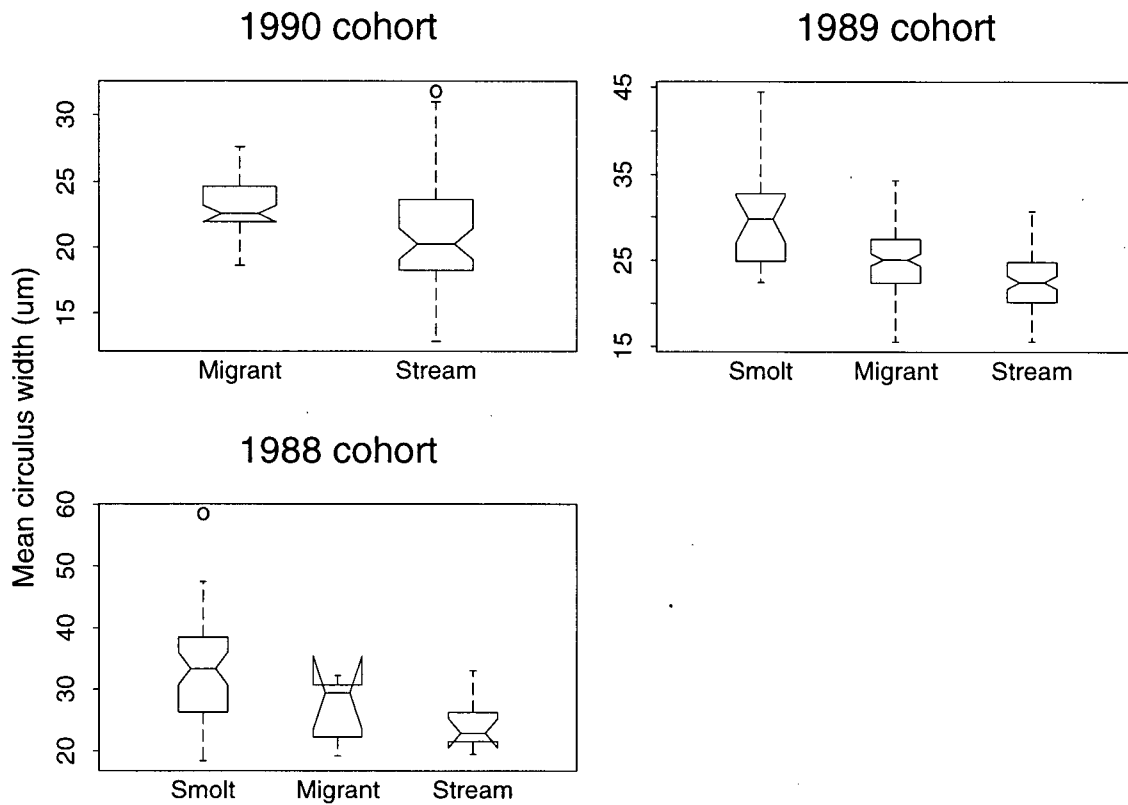


Figure 18: Mean inter-circulus width since most recent winter growth check for 3 juvenile steelhead cohorts sampled in 1991, factored by type of juvenile.

measurements similar to Ewing et al.'s (1994) study, Keogh River juvenile steelhead condition factors suggest that parr captured at the enumeration trap are true migrant steelhead, like smolts.

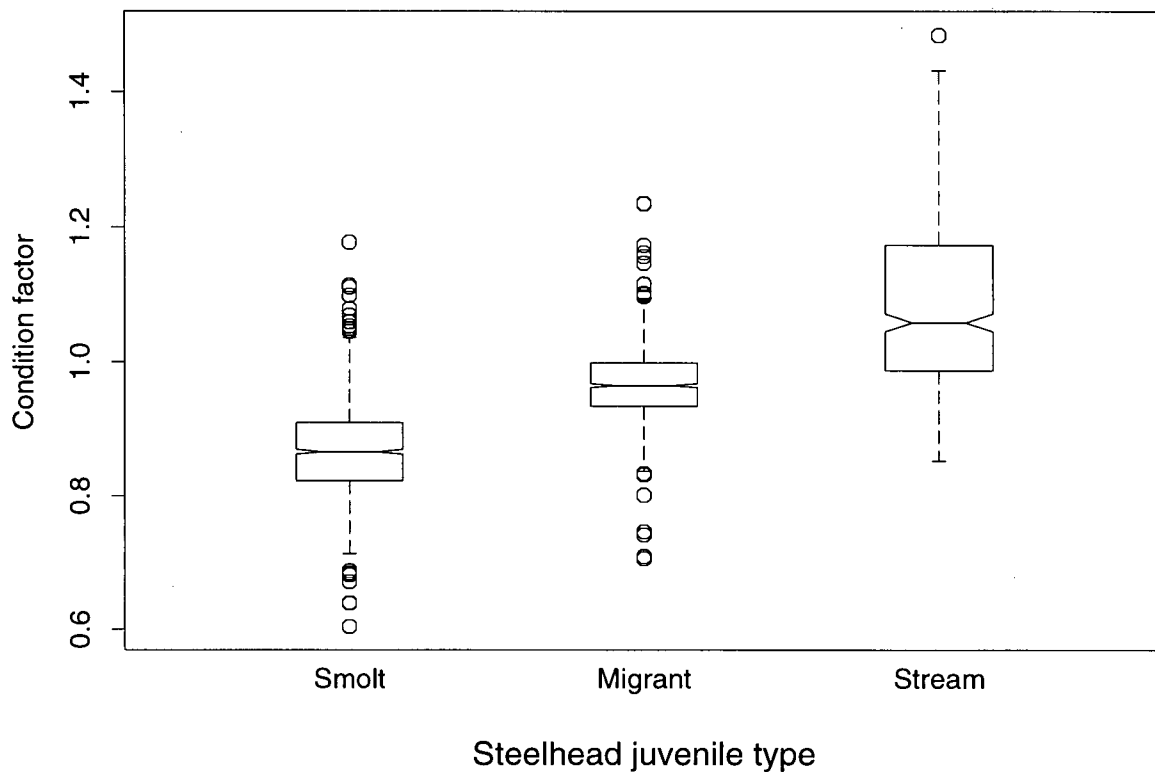


Figure 19: Condition factors of juvenile steelhead: smolts, potentially migrant, and stream resident parr

## Run Timing

### Methods

The Keogh River enumeration trap records include daily counts of smolts and parr captured in the downstream trap for most of the years of operation. I computed daily cumulative migration for smolts and parr, for the years 1976–1981, 1984, 1985, and 1987–1992, in order to compare downstream run timing of the two types of juvenile steelhead.

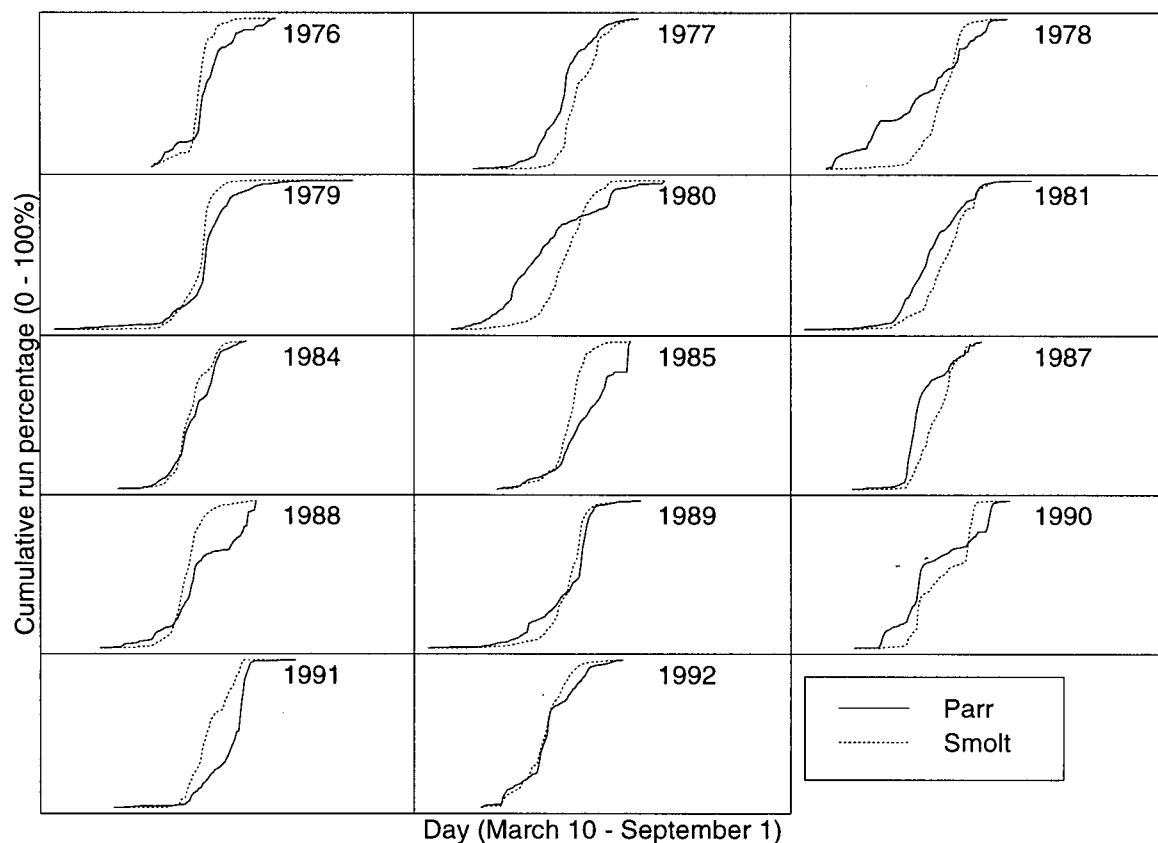


Figure 20: Run timing of migrant steelhead parr and smolts

## Results and Discussion

Parr and smolts share similar run timing curves (Figure 20). Parr start migrating neither before nor after smolts start migrating in any consistent pattern. Steeper slopes on these cumulative run curves indicate shorter duration peaks in run timing whereas shallower slopes indicate longer duration runs with shallower peaks in daily numbers. Again, parr mimic quickly peaking and diminishing smolt runs as well as longer drawn out runs.

Steelhead smolts respond to photoperiod as the main factor influencing smoltification and migratory behaviour (Wagner, 1974). Photoperiod is clearly unrelated to density of

steelhead juveniles; if steelhead parr downstream dispersal is primarily density-dependent, then these data suggest uncanny coincidence of density-dependent effects with photoperiod. Although this analysis establishes no causal links between environmental cues such as photoperiod and parr migration, it is more likely that parr too are responding to environmental cues such as photoperiod to migrate, given the closely matching migration timing of steelhead parr with that of smolts, and the known predilection of steelhead smolts to use photoperiod as a cue for migration.

## **Variable Density Stocking Experiment**

### **Methods**

The previous section outlined in detail the design and execution of these experiments in a tributary to O'Connor Lake's outlet. After identifying the subdermal dye mark on the fins of a recaptured parr, it was possible to measure how far downstream it had traveled from the original stocking site.

### **Results and Discussion**

A total of 36 and 39 originally migrant and originally stream resident parr were recaptured downstream of their original stocking site. On average, the former had moved roughly three times as far downstream after stocking than the latter (migrant mean distance = 360 m; stream resident mean distance = 124 m). Overall, migrant parr had moved a minimum, median, and maximum distance downstream that was farther than the distances that stream resident parr had moved (Figure 21).

In spite of the shorter time available in which to move downstream after stocking, and in spite of the similar habitat available in the experimental reaches, apparently migrant parr have a greater tendency to disperse than the stream resident parr.

Although experimental design flaws exist (stocking time differences, unknown ambient residual steelhead densities, and experimental units that were not independent of each other—all unavoidable due to the logistical limitations of field conditions), this is never-

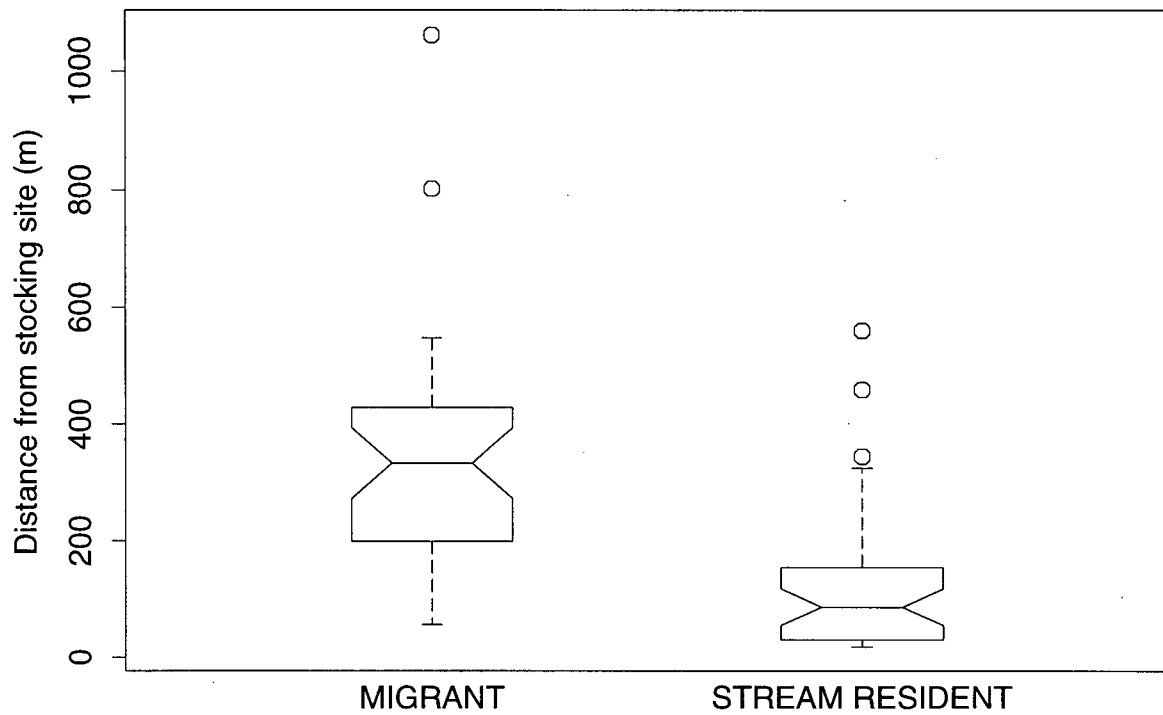


Figure 21: Distance downstream of original stocking site that recaptured parr had dispersed since original stocking.

theless another piece of evidence supporting the notion that dispersing parr are premature migrants.

# Density-Dependent Dispersal or Premature Migration?

## Synthesis of Research Results

In the introductory section of this thesis, I argued that downstream dispersal of steelhead parr at the Keogh River is a biologically significant natural event for several reasons. Its existence at the Keogh River represents a geographic extension of the apparently general observation that parr form a part of juvenile steelhead springtime migrations, since the majority of available, published information is from the states of Washington, Oregon, California, and Idaho (Dambacher, 1991). More importantly, Keogh River steelhead parr annually comprise a large fraction of the total juvenile steelhead migration, and although sampling of this migration occurs virtually at tidewater, the migrant parr did not display evidence of osmoregulatory competence when challenged in outer estuarine and sea environments.

Review of primary literature revealed two plausible hypotheses that could account for such downstream dispersal. Premature migration homologous to smolt migration, and previously observed in Atlantic salmon, was one alternative. Density-dependent interactions upstream resulting in dispersal was the other alternative.

Winter (1992) explicitly considered the density-dependent dispersal hypothesis by inferring habitat abundance from stream discharge in a Washington state river, and found that steelhead parr emigrations were not related to density-dependent factors. However,

this Keogh River research describes the first investigation to consider several independent data sources, from both experimental manipulation and observation of naturally occurring events, to consider the likelihood of either of the proposed causes for parr migration.

In order to evaluate the hypothesis that seaward parr dispersal is density-dependent, the second section of this thesis considered several sets of data that I collected or compiled at three spatial scales: individual trout, reach, and watershed.

At the scale of individual trout, both migrant and main stem resident parr exhibited classic agonistic and territorial behaviour. Stream channel observations suggested that migrant and main stem resident parr were equally aggressive and that the important factor in determining which trout attacked and which trout was victim of an attack was the generally larger size of attacker. Since main stem and enumeration trap sampling in 1991 revealed that dispersing parr were larger than main stem resident parr, it seems unlikely that agonistic interactions upstream are directly displacing the migrants.

Because larger parr require a larger food ration than smaller parr to maintain growth, it is possible that indirect density-dependent dispersal is the cause of the phenomenon. To move downstream as it grows larger could be a survival strategy for steelhead in general, since downstream environments typically have more space (as tributaries add to a stream's flow), and therefore more substrate to produce drifting invertebrate forage. Hynes (1970) suggested that, in general in streams, there is a minimum in the seasonal fluctuation of insect abundance in late spring, which corresponds well with the actual timing of parr (and smolt) downstream dispersal. In a stream in the interior of British Columbia, Slaney (1972) measured a 50% decrease in numbers and an 80% decrease in biomass of drift starting in early June and reaching a minimum in mid-July. If this fluctuation occurs in the Keogh River, with a timing to match parr dispersal, then the fact that dispersing parr are larger than main stem resident parr may be a result of voluntary and directed movement in search of additional space and therefore food.

At the reach scale, parr demonstrated density-dependent dispersal from experimentally stocked reaches. Stocking at variable density demonstrated limited carrying capacity at



this spatial scale, because final densities were lower than stocking densities in the highest stocking-density treatments.

At the main stem river or watershed scale, reconstruction of past stream populations of juvenile steelhead suggested, at three of four hypothesized survival rates, that exponentially increasing dispersal occurs at higher stream population densities, but that there may be an additional background dispersal rate that was unrelated to density.

Although this research has resulted in data supporting the hypothesis that indirect density-dependent dispersal has played a real role in parr migration, the latter hint in the reconstructed stream population data of some background parr migration being density-independent leads us to consider support for the premature migration hypothesis, which I discussed in the third section of the thesis.

Dispersing parr exhibited several smolt-like traits. First, in a single cohort dispersing parr had higher growth rates than stream resident parr, though not as high as smolts. Second, dispersing parr body shape (condition factor as an index) was intermediate between smolts and stream resident parr. Third, dispersing parr had conspicuously similar timing in their downstream movements to smolt migration timing. And fourth, stocked migrant parr appeared to have a tendency to move farther downstream after stocking than stocked main stem resident parr.

Because the hypotheses are not mutually exclusive, I will not hesitate to conclude that downstream parr dispersal at the Keogh River has been and likely continues to be a result of both premature migration homologous to smolt migration, and indirect density-dependent interactions upstream. The data support each hypothesis.

Ultimately, natural selection could automatically solve the so-called puzzle of parr movement, and may have done so in the millennia preceding 1976–present: either premature migrants would perish prior to spawning and the behaviour die out, or traits would evolve to adapt parr to environments encountered downstream, whether they are encountered involuntarily or not. For example, Atlantic salmon parr partake freely of the resources in Newfoundland estuaries (Cunjak 1992, Cunjak et al. 1989). Perhaps the same occurs at the

Keogh River. Anecdotal observations of abundant parr in the Keogh River estuary suggest that parr may have solved the "problem" themselves.

## Conclusions

1. Downstream dispersing steelhead parr are as aggressive as stream resident parr, and are larger.
2. Reconstruction of past stream population sizes of juvenile Keogh River steelhead suggests low background dispersal rates at lower population sizes and exponentially increasing dispersal rates at high population sizes, at the watershed spatial scale.
3. Steelhead parr reach carrying capacity at the reach spatial scale, given sufficiently high density.
4. Downstream dispersing steelhead parr time annual migrations similarly with or identical to annual smolt migrations.
5. Downstream dispersing steelhead parr have growth rates and body shape intermediate between smolts and main stem resident parr of the same age.
6. Evidence supporting both research hypotheses exists. Seaward movements of steelhead parr at the Keogh River are a blended phenomenon with two causes: upstream density interactions and internal smolt-like changes in individual parr resulting in premature migration.

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# Appendix A

This appendix contains two figures supplying additional information

- on parr length distributions, which the introductory section summarizes, here expanded (Figure A.1);
- demonstrating the satisfaction of the assumption of linear depletion in Leslie and Davis (1939) depletion estimation in final recapture sampling in the O'Connor Lake outlet tributary experiment (Figure A.2).

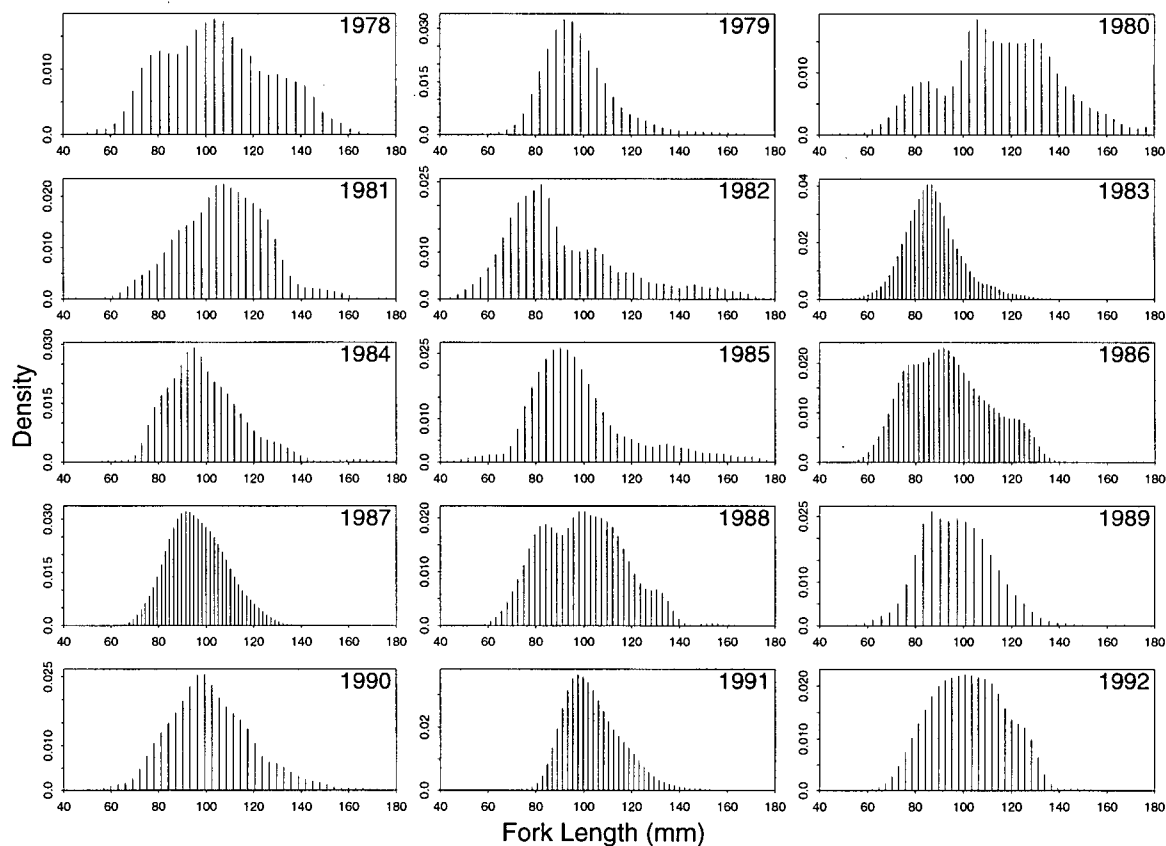


Figure A.1: Parr length distribution by year. Density value at each of 50 points computed based on a Gaussian weighting window with standard error = 15 mm. In some years 3 or 4 age modes are apparent (1978, 1980, 1982, 1986, 1988). 99.9% of all year's lengths were less than 180 mm (maximum length shown).

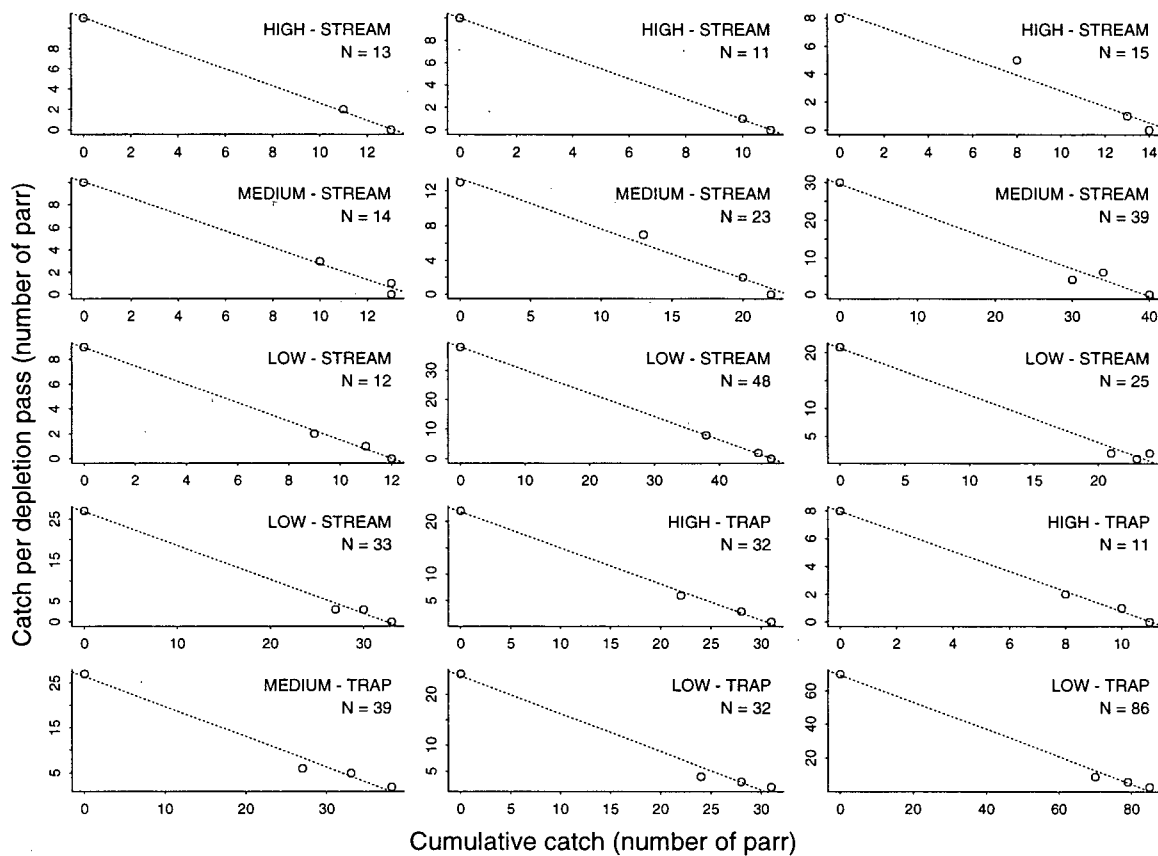


Figure A.2: Catch depletion pattern for final sampling in each treatment reach of the variable density stocking experiment in O'Connor Lake outlet tributary. Each site received four passes (two final passes of zero catch superimpose as one plotting character). Depletion was apparently linear (line is the least squares fit) and therefore the Leslie and Davis (1939) method to determine the x-intercept was justified. HIGH, MEDIUM and LOW refer to initial stocking densities; STREAM and TRAP refer to capture location of stocked fish. "N" is the x-intercept (estimated population).