

# Egg-to-Smolt Survival and Fry-to-Smolt Density Dependence of Keogh River Steelhead Trout

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The population dynamics of steelhead trout (*Oncorhynchus mykiss*) in a coastal stream on Vancouver Island, B.C., were studied since 1976. Estimates of numbers of spawners, fecundity, potential egg deposition ( $n = 12$  yrs), fry abundance ( $n = 7$  yrs) and parr abundance ( $n = 2$  yrs) provided information on survivorship when combined with smolt counts from brood years. The relationship between eggs and fry (1-month post-emergence) was linear with the exception of 1976, when flows during spring were exceptionally high. Mean egg-to-fry survival was 6.5% (min., 1.8%; max., 11.5%). Mean fry-to-smolt survival was 12.9% (min. 3.3%, max. 21.9%). The relationship between fry and smolts suggested an asymptotic yield of ca. 7,500 smolts, or 2.7 smolts per 100 m<sup>2</sup> of river, based on a Beverton-Holt recruitment relationship. Yield of smolts by brood year varied from 5,725 to 10,750 fish. Variation was larger in the annual yield of smolts, which was comprised of four age-classes; 2,104 (1978) to 11,897 fish (1981) were enumerated. Fry size (g) in mid-summer was a significant correlate of mean smolt age and percent composition of age-2 smolts. We conclude that variation in smolt number and size, and thereby in adult returns, is mainly determined at the fry-to-1+ parr stage and thus the production of steelhead trout smolts is highly density dependent.

La dynamique de la population de truites arc-en-ciel (*Oncorhynchus mykiss*) dans un cours d'eau côtier de l'île de Vancouver (C.-B.) est à l'étude depuis 1976. Les estimations sur le nombre de géniteurs, la fécondité, le potentiel de ponte ( $n = 12$  ans), l'abondance des alevins ( $n = 7$  ans) et l'abondance des tacons ( $n = 2$  ans) ont donné de l'information sur le taux de survie lorsqu'on les combine au dénombrement des smolts par année d'éclosion. La relation entre les oeufs et les alevins (un mois après l'émergence) était linéaire, à l'exception de 1976, année où les débits printaniers étaient exceptionnellement forts. Le taux moyen de survie de l'oeuf à l'alevin était de 6,5 % (min., 1,8 %; max., 11,5 %). Le taux moyen de survie de l'alevin au smolt était de 12,9 % (min., 3,3 %, max., 21,9 %). La relation entre les alevins et les smolts semblait indiquer un rendement asymptotique d'environ 7 500 smolts, soit 2,7 smolts pour 100 m<sup>2</sup> de rivière, selon le modèle du recrutement de Beverton-Holt. La production de smolts par année variait de 5 725 à 10 750. La variation était plus forte dans la production annuelle de smolts, qui se composait de quatre classes d'âge; on a dénombré de 2 104 (1978) à 11 897 poissons (1981). La taille des alevins (g) au milieu de l'été déterminait de façon significative l'âge moyen des smolts et la part en pourcentage de smolts d'âge 2. Nous concluons que la variation dans le nombre et la taille des smolts, et donc dans les remontes d'adultes, est déterminée principalement au stade alevin-tacon 1+, et donc que la production de smolts de truite arc-en-ciel dépend fortement de la densité.

## Introduction

Wild steelhead trout are a highly-prized sports fish distributed throughout most streams of the western coast of North America. They are iteroparous and return as both summer-run and winter-run migrants which spawn in the spring. Fry emerge several weeks later, and rear through the parr stage in rivers before migration as smolts at ages of usually from 2 to 4 years (Withler 1966). Adult steelhead return after one to three years in the ocean and enter the sport fishery. To sustain this valued fishery under the pressures of commercial fishery interceptions (Hilborn and Walters 1977), habitat degradation (Larkin 1974; Hartman et al. 1983), and increasing angler effort (Billings 1988), steelhead management in British Columbia has necessarily become more intensive.

Until recently, steelhead management has not been complemented by intensive research on wild populations, and thus it has lacked supportive information on population dynamics. Most reported studies of steelhead trout have emphasized evaluations of hatchery fry and smolts (e.g., Wagner 1969; Slaney and Harrower 1981; Wentworth and LaBar 1984; Hume and Parkinson 1987; Seelbach 1987; Ward and Slaney 1990), or life history data obtained from anglers' catches (Maher and Larkin 1954; Narver 1969; Narver and Withler 1971; Hooton et al. 1987), or examined age and survival (smolt-to-adult) with a fish fence (Ward and Slaney 1988; Ward et al. 1989). Aside from an earlier study of a small stream in northern California (Shapovalov and Taft 1954) and comparisons of wild and hatchery migrants in Washington Rivers (Leider et al. 1986; Pevin and Hays 1989),

little published information is available on the population dynamics of wild steelhead during the freshwater rearing stage.

We examined the survival from egg to smolt of seven broods of wild winter-run steelhead of the Keogh River on northern Vancouver Island (1976 to 1982). We estimated survivals from data including estimates of the adult population size, the size and fecundity of females, estimates of fry and parr abundance, and counts and ages of smolts migrating into the ocean. Here, we report on rates and variation in the egg-to-fry survival and fry-to-smolt survival, relating the latter to fry size and density.

## Methods

The Keogh River is a coastal stream located in southwest British Columbia on northern Vancouver Island. It is 33 km in length and with a mean annual discharge of  $5.62 \text{ m}^3\text{s}^{-1}$ , and is more fully described in Ward and Slaney (1979), Johnston et al. (1986), and Irvine and Ward (1989).

The procedure for deriving the population estimates and ages of adult steelhead and methods of enumerating and sampling smolts at the Keogh River are described elsewhere (Irvine and Ward 1989; Slaney et al. 1990; Ward and Slaney 1988, 1990; Ward et al. 1989; 1990). Briefly, smolts were enumerated through a counting fence near the mouth of the river during their downstream migration each spring; they were sub-sampled for age from scales from 1977 to 1979, then stratified random sampled for scales by 10-mm size intervals after 1980 (Ricker 1975; Ward and Slaney 1988). Adult numbers were based on Petersen mark-recapture estimates (Ricker 1975). Adult steelhead were marked (small hole on the edge of the operculum) as they migrated upstream, kelts were examined for marks when they left the river, and a Petersen population estimate was derived separately for each sex (Ward and Slaney 1988, 1990). Most of the females in the population were handled, either as upstream migrant adults, or unmarked kelts (mean, 77% from 1976 to 1982; Ward and Slaney 1988). The recapture rate of females marked in their upstream migration averaged 45%, and the rate of marking of the estimated number of females averaged 51% (Ward and Slaney 1988). Survival estimates from smolt to adult and variation in age structure of smolts and adults have been reported earlier (Ward 1988, 1989; Ward and Slaney 1988; Ward et al. 1989).

Total fecundity of an adult run of steelhead was determined from the population estimates of females and female lengths (Ward and Slaney 1988), and the log-linear relationship between female length and fecundity ( $n = 27$ ; Bagenal 1967; Ricker 1968). Egg counts were performed on mature females which were sacrificed as they migrated through the fish fence near the mouth of the Keogh River. Atresia of eggs from the time of sampling to the time of spawning (1–3 months) was not likely a factor for this winter-run

population, although this was untested. The fecundity of females sampled for length in each run was determined, and the geometric mean fecundity was calculated from length samples. Total fecundity for the run was the total fecundity of length-sampled females plus the average fecundity times the estimated number of unsampled females.

Potential egg deposition (PED) was calculated after subtracting mortalities or losses resulting from handling, sampling, broodstock collection for hatchery purposes (Slaney and Harrower 1981), and estimates of fish removed by anglers. Numbers of females removed by anglers were determined by requesting anglers to complete a questionnaire on cards at access points to the river from 1976 to 1980 (Ward and Wightman 1989). Agreement on number of fish killed with the annual steelhead harvest analysis (e.g., Anon. 1979) was within 5%. After 1980, fishery regulations were changed to catch-and-release. Estimates of PED were not corrected for egg retention because Shapovalov and Taft (1954) reported that steelhead were completely spent, having few, if any, eggs remaining in kelts. Thus, PED was equal to total fecundity less mortalities. For those years which included returns of hatchery adults (1981, 1982), PED was based on wild and hatchery females.

Steelhead fry and parr abundances were estimated for seven years and three years respectively, using similar techniques as those to determine Dolly Varden (*Salvelinus malma*) fry, as described in Smith and Slaney (1980). Briefly, densities were determined within habitat-stratified reaches of the Keogh River by electrofishing. Generally, a 3–4 step removal method was utilized (Seber and LeCren 1967) except within complex habitat where a Petersen mark-recapture method was employed (Ricker 1975). In 1978 and 1982, only the fry populations were sampled within 100-m sections in each reach, using the latter method. Total numbers were calculated based on average densities within five habitat strata, multiplied by the area for that strata, similar to the method of Hankin and Reeves (1988). Habitat strata and area were determined by visual classification and measurements, respectively, with the latter from calibrated range finders, over the entire river length (Ward and Slaney 1979). Fish ages were determined using length frequency to separate fry and parr, and ages of the latter were determined using the methods for smolts described in Ward and Slaney (1988). Differences in stream area were measured among years, and thus corrections to area-based population methods were based on the relationship between stream flow and width (e.g., Hogan and Church 1989). Although estimates of fry abundance were available for 1976 to 1982, sampling intensity in parr habitat was adequate only in 1976, 1977, and 1979. Owing to the more sporadic nature of parr distribution, greater area must be sampled to adequately estimate parr abundance (Hankin and Reeves 1988); thus, years where parr habitat was inadequately sampled were excluded from this analysis.

Fry weights were determined in late July to early August from 1976 to 1985 in representative reaches, and geometric mean fry weight for the main river was determined, as reported by Johnston et al. (1990). Mean weights used in this study were from km 28 to the river mouth, where the majority of fry rearing occurs, which excludes the short "control" section (3 km) reported in Johnston et al. (1990). However, since no data were available for the main river for 1981, their upstream "control" site was used to represent the river for that year. No whole-river fertilizer treatment occurred in 1981; mean fry size in their control section was not statistically different from the main river sites during untreated years (Johnston et al. 1990).

The relationships between annual mean fry weight and mean smolt age of a brood, and annual mean fry weight and the percent composition of age-2 smolts (arcsine-squareroot transformed) were determined by linear regression. Similarly, we regressed fry density on fry size (Sokal and Rohlf 1981).

The survival from egg to smolt was examined. Egg-to-fry survival was determined from PED and fry estimates. The relationship was examined by linear regression. Because egg-to-smolt and fry-to-smolt relationships were curvilinear, the Beverton-Holt curve was fitted in both relationships (Ricker 1975). The relationships between fry size and both fry density and fry-to-smolt survival rate were tested with linear regression techniques where survivals were transformed to the reciprocal of the natural logarithm of survival.

## Results

The fecundity of adult females was positively and significantly related to fork length ( $n = 27$ ):

$$\ln[\text{Eggs}] = 3.053 \ln[\text{Length}_{\text{mm}}] - 11.89, r^2 = 0.51, p < 0.05$$

Using this relationship, measurements of female lengths from fish migrating upstream, and the population estimates of females, we determined the total fecundity of individual runs of steelhead from 1976 to 1982 (Table 1). PED (corrected for fish removals) was estimated to be highest in 1982, at ca.  $2.6 \cdot 10^6$  eggs, and lowest in 1980, at only 466,000 eggs, representing a 5.6-fold difference in egg density. On average, ca.  $6 \text{ eggs} \cdot \text{m}^{-2}$  (S.D. 3.4) were deposited annually in the main river (Table 1). Earlier investigations confirmed that few if any steelhead spawn in the main tributaries from which smolt production was insignificant ( $0\text{-}30 \text{ smolts} \cdot \text{yr}^{-1} \cdot \text{tributary}^{-1}$ ; data on file).

Population estimates of wild females and their fecundities suggested an average fecundity per female of 3,740 eggs during the study period. Hatchery females from net-pen reared smolts returned in 1981 and 1982, for an estimated 24,270 and 815,506 eggs from hatchery fish, respectively. The average length of wild adult females of the Keogh River (714 mm; Ward and Slaney 1988) suggested a slightly lower fecun-

dity per female of 3,537 eggs, based on the length and fecundity relationship. Because wild adult numbers and ages varied biennially (Ward and Slaney 1988), annual PED also varied; even-numbered years (1976, 1978, 1980, 1982) averaged approx. 4,000 eggs per female whereas odd-numbered years (1977, 1979, 1981) averaged 3,300 eggs per female.

Fry density varied from 11 to  $92 \text{ fish} \cdot 100 \text{m}^{-2}$  and averaged  $34 \text{ fry} \cdot 100 \text{m}^{-2}$  over seven years (Table 1). When adjusted for small differences in stream width between years, estimates of total fry abundance averaged 85,860, with a high variation (SD, 77,821; Table 1). Mean fry weight was also variable annually, ranging from 0.4 to 2.03 g from 1976 to 1985 (Table 1).

Numbers of age-1+ and age-2+ parr were estimated during mid-summer for the three years 1976, 1977, and 1979. Respective age-1+ and age-2+ parr ( $\pm$ SE) were 6,063 ( $\pm 1,929$ ) and 3,969 ( $\pm 2,036$ ) in 1976, 10,869 ( $\pm 1,585$ ) and 5,433 ( $\pm 1,233$ ) in 1977, and 11,207 ( $\pm 1,325$ ) and 7,193 ( $\pm 1,281$ ) in 1979. Standard errors from habitat stratified sampling were larger for the estimates of age-2+ parr due to their lower abundance.

The number of smolts produced from each brood year varied from 6,071 to 10,750 fish (Table 1). Numbers of fish in each age-class were variable; e.g., composition of age-2 smolts averaged 33.2% and ranged between 12.1 to 82.3% (Table 1). Average yield from the river was ca.  $2.6 \text{ smolts} \cdot 100 \text{ m}^{-2}$ , or, expressed as weight,  $127 \text{ g} \cdot 100 \text{ m}^{-2}$ , for an average biomass yield of 336 kg (ca.  $13.3 \text{ kg} \cdot \text{ha}^{-1}$ ).

The relationship between PED and fry abundance was linear (Fig. 1), based on limited data ( $n = 6$ ). Excluding the 1976 outlier, when flow during incubation and rearing was three times higher ( $5.1 \text{ m}^3 \cdot \text{s}^{-1}$ ) than the 10-yr average ( $1.6 \text{ m}^3 \cdot \text{s}^{-1}$ ), mid-summer fry abundance (F) and PED were positively correlated ( $r = 0.97$ ) and described by:

$$\text{PED} = 0.102F - 23550.78, r^2 = 0.93, p < 0.05.$$

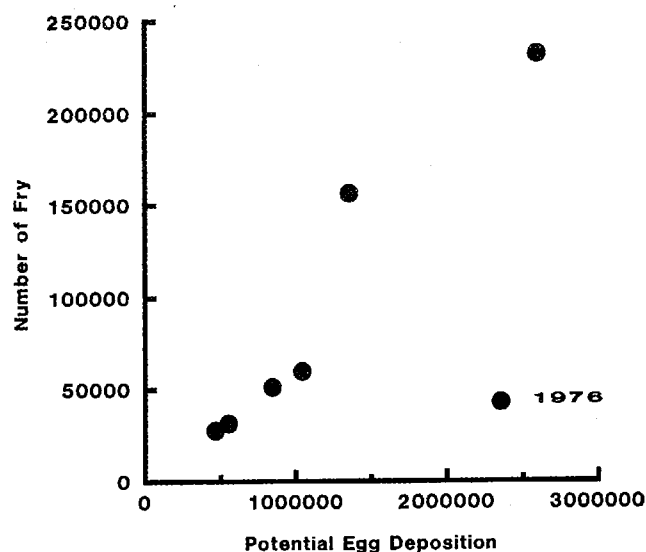


FIG. 1. The abundance of fry during mid-summer from 1976 to 1982 in relation to the potential egg deposition of adult steelhead of the Keogh River, B.C.

TABLE 1. Steelhead trout potential egg deposition, numbers of fry, fry weights, survival to the fry and smolt stage, and smolt yield by brood year in the Keogh River, 1976 to 1985.

Brood Year	Total Fecundity	Potential Egg Deposition	Fry/100 m <sup>2</sup> (1 SE)	Number of Fry (1 SE)	Mean Fry Weight (g)	Egg to Fry Survival (%)	Number of Smolts by Age					Total Smolts	Percent Age Composition					Egg to Smolt Survival (%)	Fry to Smolt Survival (%)
							age 2	age 3	age 4	age 5	age 1		age 2	age 3	age 4	age 5			
1976	2,529,039	2,356,227	17 (0.025)	42,840 (6,300)	0.40	1.82	1117	4892	561	118	6688	0	16.7	73.1	8.4	1.8	0.28	15.61	
1977	1,110,000	1,043,623	24 (0.021)	59,724 (5,226)	0.70	5.72	835	3350	2713	16	6914	0	12.1	48.5	39.2	0.2	0.66	11.58	
1978	1,424,000	1,355,242	62 (0.014)	156,240 (35,280)	0.75	11.53	1546	5592	104	0	7242	0	21.3	77.2	1.4	0	.53	4.64	
1979	585,000	553,154	12 (0.020)	31,500 (5,250)	0.57	5.69	3474	2376	401		6251	0	55.6	38	6.4	0	1.13	19.84	
1980	466,000	466,000	11 (0.007)	27,720 (1,764)	0.85	5.95	1504	3701	866		6071	0	24.8	61	14.3	0	1.30	21.90	
1981	851,000	845,845	20 (0.045)	51,156 (11,510)	1.47	6.05	1951	3569	205		5725	0	34.1	62.3	3.6	0	0.68	11.19	
1982	2,657,000	2,589,526	92 (0.206)	231,840 (51,912)	0.66	8.95	5291	2504	39		7834	0	67.5	32	0.5	0	0.30	3.38	
1983					2.03		6600	1257	167		8024	0	82.3	15.7	2.1	0			
1984					1.65		8300	2443	7		10750	0	77.2	22.7	0.1	0			
1985					1.71		9786	287	108		10407	2.2	94	2.8	0	0			
Average	1,374,577	1,315,660	18	51,258	0.77	6.53	2245	3712	698	45	6675	0.0	33.2	56.0	10.5	0.3			
SD	891,900	847,068	28	67,860	0.34	3.03	1590	1178	933	64	727	0.0	20.9	17.1	13.5	0.7			

Thus, the ratio of eggs to fry was approx 10:1, except in the year of abnormal spring flow.

The egg-to-smolt relationship (Fig. 2) indicated density dependence (Ricker's  $\alpha$  and  $\beta$ ,  $1.303 \times 10^{-4}$ , and 18.64, respectively). Smolt yield reached an asymptote at ca. 7,500 fish, when egg deposition was  $2.2 \times 10^6$  (Fig. 2), which corresponded to approx. 1,080 adults. Accordingly, only ca. 235 adults, or  $4.4 \times 10^5$  eggs, would yield ca. 5,800 smolts, after which density-dependent mortality would reduce smolt output from the river. The fry-to-smolt relationship demonstrated density dependence (Fig. 3). Beverton-Holt parameters  $\alpha$  and  $\beta$  were  $1.284 \times 10^{-4}$  and 1.137, respectively. Alternatively, the fry-to-smolt survival relationship may be based on fry density:

$$Y = 0.268 + 0.006D, r^2 = 0.995, p < 0.05.$$

where  $Y$  = the reciprocal of the natural logarithm of fry-to-smolt survival (%), and  $D$  = the number of fry per 100 m<sup>2</sup> of stream. Fry-to-smolt survival averaged 12.9% (min. 3.3%; max. 21.9% - Table 1). The above relation suggests that fry-to-smolt survival may achieve a maximum of ca. 40% at very low fry densities, and ca. 3.4% at carrying capacity, defined as the point where the replacement line meets the asymptote of the Beverton-Holt curve for fry and smolts.

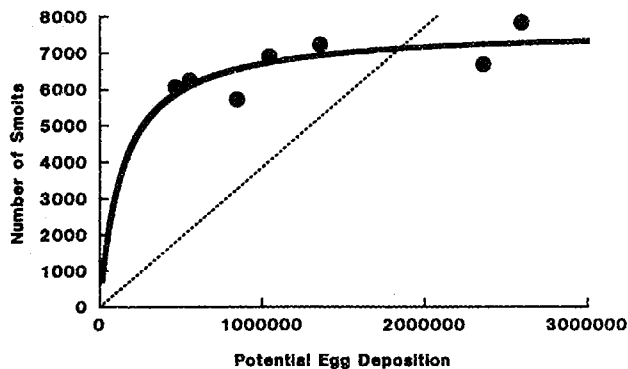


FIG. 2. Smolt yield within brood years and the potential egg deposition of steelhead of the Keogh River spawning in 1976 to 1982. The dashed line is the line of replacement assuming average smolt-to-adult survival and fecundity.

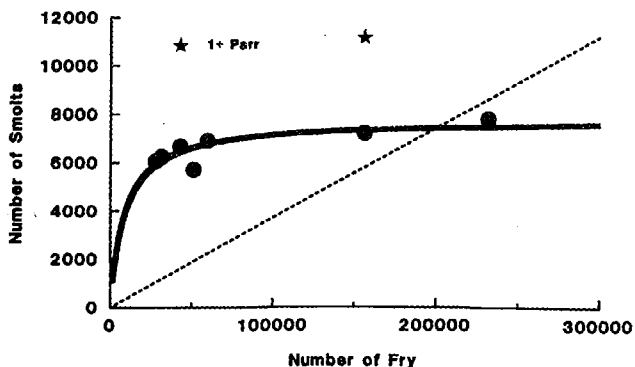


FIG. 3. Parr yield (star-shaped points,  $n = 2$  yr) and smolt yield (circles,  $n = 7$  yr) from fry abundance in the Keogh River, B.C. The continuous line is the Beverton-Holt curve fitted to the data. The dashed line is the line of replacement based on average smolt-to-adult survival, average fecundity, and egg-to-fry survival of 10%.

Fry-to-smolt survival at maximum sustainable yield was estimated as 13.4%.

Fry-to-parr (1+) survival was estimated at 25.4% and 7.2% for 1976 and 1978 fry, respectively. Fry-to-parr survival, although based on only two data points, appeared to be density-dependent (Fig. 3). Parr-to-smolt survival for 1+ parr only was estimated at 61.5% and 64.6% for 1976 and 1978 broods, respectively. Of the age 2+ fish from the 1977 brood which were sampled in 1979, 835 had already left as age-2 smolts (Table 1) and 7,193 were estimated to have remained in the river by that summer. Thus, the survival from 2+ parr to age-3 smolts and older was 84.5%.

Mean smolt age was positively correlated ( $n = 10$ ,  $r = 0.67$ ) with mean fry weight in mid-summer (Fig. 4b), but there was no relationship with fry density ( $n = 7$ ,  $r = 0.52$ ,  $p > 0.05$ ). The relationship between mean smolt age and mid-summer fry weight expressed linearly was:

$$y = 3.112 - 0.484x, r^2 = 0.446, p < 0.05,$$

where  $y$  = mean age of smolts from a brood year, and  $x$  = the mean weight of steelhead fry in the brood year (mid-summer). Similarly:

$$y = 18.609 + 23.867x, r^2 = 0.501, p < 0.05,$$

where  $y$  is the arcsine-squareroot transformation of percent composition of age-2 smolts from a brood year (Fig. 4a). Fry density and fry size were not correlated ( $r = 0.12$ ,  $p > 0.05$ ).

## Discussion

The egg-to-smolt and fry-to-smolt survivals of steelhead from the Keogh River were found to be dependent on fish density. Mid-summer fry abundance appears to be positively and linearly related to the number of eggs deposited by adult steelhead, as found by Bjornn (1987), but it was suggested that flow is a major factor. High flows have been suggested as a major cause of egg mortality in other salmonids (pink and chum, McNeil 1969; Atlantic salmon, Frenette et al. 1984; sockeye salmon, Thorne and Ames 1987). In the density-dependent relation between fry and smolts, fry size was a correlate of smolt age, whereas density was not, nor were density and size correlated. Because smolt age is related to smolt size, which ultimately affects adult returns from the sea (Ward and Slaney 1988; Ward et al. 1989), the importance of fry size cannot be underestimated. The egg-to-smolt and fry-to-smolt survivals determined in this study for steelhead trout at maximum smolt yield (or carrying capacity) and at maximum sustainable yield (Ricker 1975) are in close agreement with low and medium survivals, respectively, determined by Symons (1979) for Atlantic salmon of similar age (mean 2.8 yr; Ward and Slaney 1988).

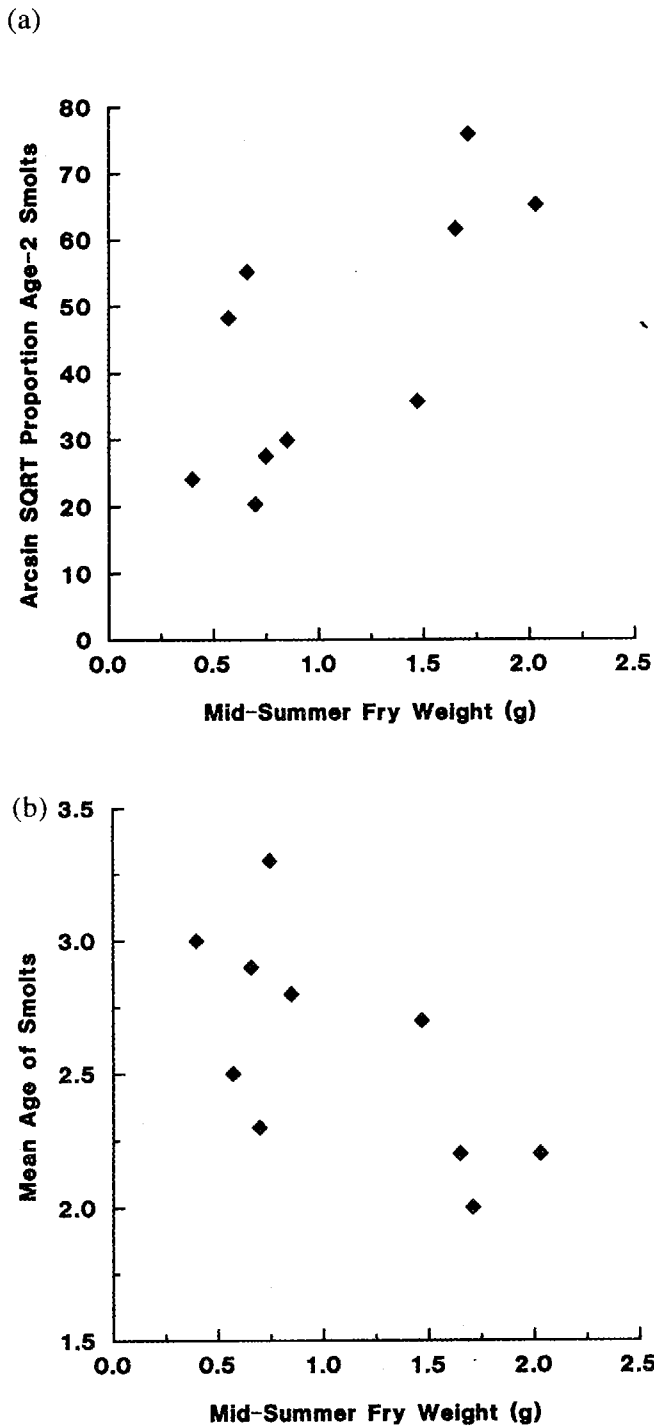


FIG. 4.(a) The proportion of age-2 steelhead smolts (arcsine square-root transformation) in relation to the size fry attained by mid-summer in the Keogh River, and (b) mean age of steelhead smolts in relation to mid-summer fry weight in the Keogh River, from 1976 to 1985 broods.

Some of the variation in fry weight in this study was induced by whole-river fertilizer additions (Slaney et al. 1986; Johnston et al. 1990). The data suggested that age of smolts was correlated with mid-summer fry weight, the former expressed as either mean age or as composition of age 2-smolts. However, it is unclear what influence additional growth (induced by nutrient additions) at the age-1+ parr to the age-2 smolt stage may have had on the relationship between fry size and smolt age. Until this impact is clarified, caution

must be utilized in interpretation of these results. Furthermore, the investigation of the relationship between fry size and density would have been confounded by the altered nutrient conditions of the river, but complete density data were not available during enriched conditions. Also, the relation of fry-to-smolt survival and steelhead fry size, as well as smolt age and fry size would likely have been different if based on late-summer fry size rather than mid-summer fry size. Scottish researchers have found that the smolt age of Atlantic salmon fry in the laboratory can be predicted from the size fry attained by late summer (Thorpe 1977; Metcalfe et al. 1988; Metcalfe 1991). Our results provide field evidence confirming their results, based on mid-summer fry size, but only three data points on late-summer fry sizes were available (Johnston et al. 1990), where fry size was large and smolts were predominantly age-2. Field studies are needed on the relationship of late-summer fry size and subsequent smolt yield.

In steelhead trout, density-dependent mortality occurs at the fry-to-parr stage based on both releases of hatchery fry (Bjornn 1978) and our results with wild fish, thus recruitment curves are asymptotic. Peven and Hays (1989) altered survival rates in a life history model of steelhead to determine which variables in the natural production equation would have the greatest effects on the population. Manipulation of survivals at the egg-to-smolt stage changed the estimates of adult abundance to the greatest degree. Our study agrees with that result, and further indicated that the most sensitive life stage controlling recruitment is from fry to parr.

A limited amount of data ( $n = 7$ ) from the Keogh River demonstrated apparently asymptotic relations between eggs and smolts or fry and smolts. Additional data at high egg or fry densities probably would not significantly alter estimation of the asymptote, but more data at low densities, near the ascending portion of the Beverton-Holt curve, are required to more accurately define the parameters of Ricker (1975). Although our findings are preliminary in terms of actual curve shape until more years are examined, the results indicate that density dependence is an important factor controlling smolt production and adult returns of steelhead trout, and that variation in number likely occurs mainly at the fry to parr stage (i.e., ca. 30–110 mm). Ultimately, further research will lead to an optimum escapement model.

The density dependence detected in this study confirms similar results of fry releases and yearling migrant steelhead in the Lemhi River, Idaho (Bjornn 1978). Mortality rates were highest there in the first summer, but were independent of steelhead densities below 700 fry·100 m<sup>-2</sup> which is much higher than densities in the Keogh River. However, there was only one data point in the density-dependent stage and several for the density-independent stage (Bjornn 1978). Density-independent mortality also plays a significant role, particularly in relation to storm events,

as documented on stocked steelhead fry (Hume and Parkinson 1987) and wild sea trout fry (Elliott 1989). The relatively low survival from egg to fry in 1976 on the Keogh River was related to high flows.

Chadwick (1985) demonstrated that Atlantic salmon (*Salmo salar*) populations were below optimum escapement levels by examining the relationships between eggs deposited and smolts produced, or eggs deposited and adults produced in seven east coast Canadian streams where fish fences were operated. All relationships were linear, and further analysis in one of the streams (Western Arm Brook) confirmed that 8 out of 10 year classes showed near-constant survival in freshwater, with variations in year-class strength explained by egg deposition (Chadwick 1987). Chadwick and Randall (1986) demonstrated a linear relationship between Atlantic salmon kelts caught by anglers and 1+ parr captured in electrofishing surveys on the Miramichi River, New Brunswick. They argued that this suggests that the escapement was below optimum, since an asymptotic or domed-shaped relationship would have resulted otherwise. Also, Randall and Chadwick (1986) detected a positive correlation between age-0+ density and smolt production, again, based on intensive electrofishing over a 10-yr period. Such a linear relation would not be expected if density was sufficiently high to reduce production. The asymptotic levels of smolt yield by brood year in the Keogh River suggest escapement has been adequate under the current conditions of low harvest.

In contrast, Gee et al. (1978) developed dome-shaped recruitment curves between fry and pre-smolt Atlantic salmon parr, but at high fry densities (0.2–4.0 fry·m<sup>-2</sup>). However, in a later study near Aberdeen, Scotland, Buck and Hay (1984) developed an asymptotic relationship between eggs deposited and numbers of migrant parr, where about 300,000 eggs (2.6 eggs·m<sup>-2</sup>) were required to reach a level of 5,000 parr. Their results were based on capturing upstream migrant adults, habitat-stratified juvenile sampling and tagging, and downstream capture of juvenile migrants, during an 11-yr period.

From an extensive analysis of 18 years of data on a population of sea trout (*Salmo trutta*), Elliott (1989) showed that survival at different stages in the life cycle was strongly dependent on egg density. The relationship between eggs and emergent fry was found to approximate a Ricker curve (Ricker 1975) during the critical early stages of the life cycle. Evidence was strong for a critical period with high mortality in the first few weeks after fry emergence, after which density-dependent survival changed to proportionate survival, and the recruitment curve appeared nearly asymptotic (Elliott 1989). This work has led to a modified stock-recruitment model, with a time component that suggests maximum survivor density occurs at different egg densities as time progresses. Our fry samples were taken ca. 30 days after fry emergence; it's possible that a relationship between steelhead and

smolts is a dome-shaped curve when based on newly-emerged fry.

Variation in age-specific survivals is important information for the management of fish populations (Clark et al. 1980; Taylor 1981). For example, increased food abundance and fry size (e.g., Johnston et al. 1990) may reduce early mortality at what Elliott (1989) refers to as the critical stage. Subsequent improvement to size-biased over-winter survival and increased growth could ultimately decrease residence time and lead to earlier age at smolting (Slaney et al. 1986). Similarly, increased cover could increase fry-to-smolt survival by adding space for rearing parr (Ward and Slaney 1979). Elucidation of the life stage experiencing the greatest mortality and the amount of variation in that mortality will provide further direction for management (Bjornn 1987). Based on a limited amount of data, our results indicate that mortality is highest for emergent fry as a function of density, as in Elliott (1989). During the first summer and through to the next spring, mortality continues to affect the majority of fish. Mortality rates decrease nearer to smoltification but more detailed research on age-specific mortality rates is required over the range in environmental conditions to describe the life history more fully.

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