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Physical and Biological Constraints on Summer Rearing of Juvenile Coho Salmon (*Oncorhynchus kisutch*) in Small Western Washington Streams

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Availability of suitable habitat and food resources both influenced the population dynamics of juvenile coho salmon rearing in small western Washington streams. During summer, depth and water velocity were the primary physical factors determining fish location. Underyearling coho were found where water was greater than 5 cm deep and velocities were less than 25 cm/s, roughly half of the total wetted area of the stream, but areas with depth greater than 8 cm and velocity less than 12 cm/s were occupied preferentially over shallower areas with swifter current. Densities of coho fry in pools and riffles were similar in microhabitat locations wherever suitable hydraulic conditions existed; therefore, habitat composition influenced fish density in summer only to the extent that depths and velocities preferred by coho salmon were present. Although large woody debris did not strongly influence early to mid-summer fish location relative to its potential use as cover habitat, there was a significant correlation between woody debris abundance and the area of the stream containing preferred depths and velocities. Compensatory growth and mortality occurred as food availability declined over summer, leading to end of summer biomasses that were fairly similar from year to year, i.e., populations contained relatively large numbers of small fish or fewer numbers of large fish. A weak negative association was observed between underyearling coho and age 1 and older trout, but in years when recruitment of coho salmon was low, underyearling cutthroat trout *O. clarki* increased dramatically. Overall, coho density was constrained chiefly by physical habitat (suitable depth and current velocity), while growth rate and apparent survival were constrained chiefly by biological factors (food availability and intraspecific competition). Population biomass reflected both physical and biological aspects of the environment, and tended to converge to a common range of values regardless of density at the beginning of summer. Density, biomass, and growth thus provided different information about the summer carrying capacity of a stream for juvenile coho salmon.

INTRODUCTION

Juvenile coho salmon rearing in small streams in the Pacific Northwest encounter physical and biological constraints that potentially limit survival and growth (Mason and Chapman 1965; Chapman 1966). Interactions between such factors as food availability, habitat quality, young-of-the-year recruitment, and a variety of other influences often make predictions of the capacity of a stream to produce coho salmon tenuous at best. Salmonid enhancement programs as well as provincial and state regulations governing land use usually contain goal statements that call for streams to contain habitat that is "optimum" for salmonid production. It is therefore important to understand how coho salmon respond to factors that may operate simultaneously to potentially limit their population size in streams or influence their ability to survive at some later life history stage. Otherwise, a working definition of what constitutes "optimum" habitat will likely incorporate many untested assumptions that may lead to substantial error (Fausch et al. 1988).

Measuring pool area or volume, for example, may provide an estimate of the availability of habitat for salmon and trout, as there is some evidence that certain salmonid species or age groups are positively associated with pool abundance (Bowlby and Roff 1986). Nickelson and Hafele (1978) found that pool volume explained 93.5% of the standing crop of juvenile coho in coastal streams in Oregon. However, salmonid populations may not be correlated with pool area (Figure 1) because pools vary considerably in hydraulic characteristics and can provide different rearing environments, depending on the predominant types of pools in the stream (Bisson et al. 1988). Grant and Kramer (1990) suggested that the maximum

density of territorial salmonids would be limited by territory size requirements in two dimensional habitats (riffles) but would probably not be limited by territory size requirements in three dimensional habitats (pools). If this hypothesis is true and a coho population is at or near a stream's carrying capacity, pool *area* will not limit density but pool *volume* might, depending upon the hydraulic characteristics of the pools. Additionally, coho salmon may be associated with certain substrates or with cover conditions provided by large woody debris (Dolloff and Reeves 1990). The quantity of suitable gravel and cover is generally not reflected in measurements of pool area or volume. Food availability also strongly influences summer populations of juvenile coho salmon in streams (Mason 1976; Dill et al. 1981; Fausch 1984), but the abundance of drifting invertebrates may be more closely associated with the area of riffles than with pools (Mundie 1969). These observations illustrate a few of the difficulties in indexing habitat quality to a single variable or even a small group of variables strictly associated with channel dimensions.

Since the early 1980s we have undertaken summer surveys of stream habitat and fish populations in several small streams in western Washington. Our objective has been to study the effects of various types of disturbance (e.g., clear-cut logging, debris flows, volcanic eruption) on streams and fish communities. Some sites have been monitored for up to 11 years. In the late 1980s we began a more intensive examination of a single site with the objective of determining how food availability and stream channel morphology interacted to regulate coho salmon production. The purpose of this paper is to review the physical and biological constraints on summer rearing of juvenile coho salmon in small streams based on the results of both the extensive and intensive studies, and to identify population statistics that yielded useful information about carrying capacities of the streams.

METHODS

Study Areas

Extensive Stream Surveys

A total of 14 reaches from 10 streams (Figure 2) was surveyed between 1981 and 1991. Reaches ranged in length from 0.1 to 1.1 km and included a wide variety of habitat types and channel disturbance histories. Most of the streams were 3rd-order, and exposed channel widths ranged from 3-15 m. Riparian conditions varied from completely open forest canopies, in the case of sites with recent debris flows or clear-cuts, to old-growth coniferous forest. Surveys of stream habitat following the classification system of Bisson et al. (1982) were conducted during the summer low flow period from June to late September.

A subset of channel units (different types of riffles and pools) representing all possible habitat types within the reach was selected for fish population censuses. Individual riffles and pools were isolated with blocking nets and electrofished three times. Populations were estimated using the removal method for small samples of Carle and Strub (1978). All individuals were identified to species and fork lengths measured to the nearest millimeter. Length-weight regressions permitted estimates of individual mass, and the sum of individual weights yielded estimates of biomass for each channel unit. Size-frequency distributions were used to estimate fish age for populations with multiple cohorts, but almost all coho salmon at our sites were determined to be age 0. Summing the products of the frequencies of each habitat type and the density and biomass of each species in that type produced overall population density and biomass estimates for the reach.

Salmonid populations in the streams typically included coho salmon, steelhead *O. mykiss*, and coastal cutthroat trout *O. clarki clarki*. In addition, most of the sites contained sculpins *Cottus spp.*, and some streams contained speckled dace *Rhinichthys osculus*. One site (Herrington Cr.) occasionally contained

a few longnose dace *R. cataractae*, but this species was very rare. A few of the streams also possessed populations of lamprey *Lampetra spp.* However, electrofishing proved ineffective at capturing lampreys that were buried in mud and lampreys were therefore omitted from the analyses. In our extensive surveys no attempt was made to distinguish sculpin species, but dominant taxa included torrent sculpin *C. rhotheus*, shorthead sculpin *C. confusus*, reticulate sculpin *C. perplexus*, and riffle sculpin *C. gulosus*.

Intensive Stream Survey

Detailed ecological investigations of coho salmon rearing were undertaken in Huckleberry Creek, a small 3rd-order tributary of the Deschutes River, which flows into southern Puget Sound in western Washington. The Huckleberry Creek watershed was forested with second-growth Douglas-fir *Pseudotsuga menziesii*, and the riparian zone was dominated by 30-40 year-old red alder *Alnus rubra*. Considerable old-growth coniferous woody debris remained in Huckleberry Creek as a result of logging and subsequent debris flows in the early 1950s. Woody debris contributed to excellent rearing conditions for coho salmon, and this stream has had consistently high adult returns within the Deschutes River system over the past decade (unpublished data, Washington Department of Fisheries, Olympia, WA). Our study site included approximately 1200 m of the lower reaches of Huckleberry Creek, the area in which most coho salmon spawning and rearing took place.

On January 6, 1990, the upper 700 m of the study site was severely impacted by a very large debris flow that completely scoured the channel and a substantial portion of the riparian zone. No coho salmon were observed in the impacted section during the summer of 1990, but some recruitment did take place in 1991. Cutthroat trout, riffle sculpins, and torrent sculpins were observed in the impacted section of Huckleberry Creek in both 1990 and 1991.

Channel mapping, population estimates, and visual observations of fish location were initiated in 1986 and have continued to the present. Within the 1200 m study site, 14 segments 10-30 m long and each containing from one to three channel units were established (Figure 3). Segments were mapped at least once during early summer in 1987-1989 using surveying instruments. Mapping included topographic contours, wetted channel and upper streambank dimensions, and substrate characteristics. Location and dimensions of large woody debris were also mapped, and water depth and current velocity were measured at each point on a 0.25 m grid throughout the channel. Data were entered into a 3-dimensional plotting system (Surfer) that enabled us to produce computer-drawn maps of depth and velocity isopleths. The relative amount of large woody debris (LWD) in each segment was ranked from 1-5 based both on debris size (length and diameter of dominant pieces) and total number of pieces. Segments themselves included different types of habitat units and varied from predominantly riffles to deep pools, as our intent was to study fish populations in a variety of channel conditions.

Mid-day visual observations of the location and behavior of 557 individual coho salmon were made from the streambank and entered directly onto maps of each segment. Observers were careful not to disturb the fish and spent at least 15 min recording location and behavioral characteristics. The position of all salmonids, including those inhabiting riffles, was mapped. Observations were usually made twice during the summer when visibility permitted easy viewing.

Population censuses were performed at intervals of 1-2 months by isolating each segment with blocking nets and employing 3-pass removal electrofishing. In some instances electrofishing was continued until no more fish were present in the segment, as determined by at least 2 consecutive fishless passes. As many as 18 passes were required for complete removal at some sites. Where 3-pass removal was undertaken we used the Carle and Strub (1978) population estimation procedure; where electrofishing was continued until no more fish were captured, the population was considered to be the total number caught

in the segment. With the exception of lampreys, all species were enumerated.

Salmonids were marked with a combination of fin clips unique to each segment. Only the tips of median and paired fins were removed, and it was necessary to occasionally re-mark individuals. Marking assisted in documenting movement of fish from one segment to another, or in documenting the movement of new unmarked individuals into a site. All fishes were weighed and measured at each sampling, and stomach contents from a subsample of coho salmon were removed by flushing. While we attempted to minimize the use of anaesthetic and handling to reduce stress and mortality, some losses were recorded.

Invertebrate drift samples were taken every 3-5 week using three 200 μm mesh rectangular drift nets positioned adjacent to each other at the downstream end of a riffle. This arrangement of nets permitted us to sample most of the streamflow in summer. Drift nets were placed in Huckleberry Creek at sunset following the recommendation of Allan and Russek (1985), who felt that evening drift samples were appropriate for comparisons between different dates. One set of samples was taken in the lower half and one set was taken in the upper half of the 1200 m study reach. All material collected in each of the three nets was combined prior to preservation. Water velocity and water depth at net intakes was measured at the beginning and end of the interval so that sample volume could be calculated. Net openings extended above the water surface to capture adult aquatic and terrestrial invertebrates falling onto riffles but they failed to sample aerial invertebrates falling into pools. While these organisms were readily preyed upon by coho salmon, they were not well represented in drift samples.

Drift samples were preserved in the field and transported to the laboratory for enumeration. Large samples were split and a minimum of 200 organisms was identified to order, family, or genus. Stomach contents of juvenile coho in Huckleberry Creek contained nearly all taxa present in drift samples except for extremely small invertebrates, which were not efficiently sampled by the nets in any case. We therefore assumed that all organisms in drift samples represented potentially available food items, and food availability estimates were based on the average number of invertebrates passing a single point in the stream. Indexing food availability to the number of invertebrates passing a single point in the stream was preferred to estimates of drift density (no./m^3) because the latter did not reflect changes in the abundance of food caused by changes in stream discharge.

RESULTS

Physical Constraints

Depth and Current Velocity

By mid-June, over 95% of the juvenile coho salmon in Huckleberry Creek were located where depth was greater than 5 cm and current velocity was less than 25 cm/s (Figure 4). During the period of summer low streamflow this area corresponded to about half of the total wetted area of the stream. In spring, recently emerged coho fry were observed along the margins of the stream in water less than 5 cm deep, but by early summer most fry had grown to at least 50 mm and had abandoned shallow margin areas.

Based on data in Figure 4, we identified combinations of depth and velocity (Figure 5) that yielded preferred hydraulic conditions (greater than average coho density), tolerated conditions (less than average density), and avoided conditions (absence of coho). Coho fry preferentially occupied portions of the stream that where depth was greater than 8 cm and current velocity was less than 12 cm/s. In early summer the fry did not exhibit increased preference for deeper water; however, some areas with suitable depth were avoided completely because velocities were too great. Fish displaying aggressive behavior

toward other coho and holding a fixed position in the channel tended to select areas of the stream where velocity was greater than 6 cm/s, while fish not exhibiting agonistic behavior or defending a fixed feeding station foraged in areas with lower velocities. Resting coho were observed only in areas with very low or no current velocity, often in proximity to overhead cover.

The number of fish present in a stream segment varied primarily with the relative amount of the channel that contained suitable depth and velocity. Although riffles were far less likely than pools to contain preferred hydraulic conditions (Figure 6), we found no obvious relationship between the type of pool or riffle (*sensu* Bisson et al. 1982) and coho salmon abundance. Various habitat types thus influenced summer coho density only insofar as they possessed differing combinations of suitable depth and velocity. For example, plunge pools tended to contain more suitable rearing space than backwater pools in summer because backwater pools had become too shallow in the small streams, not because the percentages of slow moving water varied greatly between these two habitat types.

We also found that coho density declined in an upstream direction, that is, segments close to the mouth of the stream tended to contain more fish than those further upstream from the mouth. It is possible that coho fry were able to freely move downstream but were constrained from moving upstream by physical blockages existing at low streamflows that would not have limited upstream passage at higher flows. Potential blockages in Huckleberry Creek included small log jams and a road culvert.

Large Woody Debris

The presence of LWD did not strongly influence the location of coho fry in a pool or riffle from early to mid-summer. In late summer or early autumn, fish were attracted to woody debris and undercut roots in streambanks regardless of the presence of suitable depth and velocity elsewhere in the habitat unit (Figure 7). Although the presence of LWD was not critical to the microhabitat location of fish in early summer, we found that debris abundance was a significant factor influencing the area of the stream containing preferred depth and velocity. Sites with a low combined debris ranking contained less than 30% preferred depth and velocity, while segments with high LWD ranking contained greater than 60% preferred depth and velocity (Figure 8). Our early and mid-summer results agreed with the conclusions of Shirvell (1990), who felt that LWD did not actually serve as cover habitat, but rather created cover habitat. Our late summer and early autumn results suggested that coho fry were preferentially utilizing rearing space near LWD even though suitable depth and velocity was available at nearby locations in the stream.

Biological Constraints

Food Availability

Total numbers of invertebrates drifting from riffles in Huckleberry Creek (Figure 9) peaked in early spring and declined steadily throughout summer and autumn. Figure 9 was taken from several years of drift sampling and was assumed to represent a general pattern of food availability to drift feeding salmonids in forested streams of the Coast Range and Cascade Mountains in western Washington. Consistent with this pattern of progressively declining food abundance throughout the summer, growth rate of fry was negatively correlated with density. In streams with early summer coho densities less than 1/m², growth was much faster than in streams having densities greater than 1/m² (Figure 10). Growth was negatively density-dependent in every stream examined, suggesting that intraspecific competition for food coupled with declining invertebrate drift always limited growth rates during summer. As a result, populations at the end of summer contained high densities of small coho or fewer but significantly larger fish (Figure 11).

Mortality and Emigration

Like growth rates, apparent mortality (true mortality plus emigration) showed a compensatory response to initial population density (Figure 12). A few streams with low recruitment of coho fry actually exhibited a net positive change in site density over the summer as a result of immigration of new individuals into the stream reaches, but this only occurred when initial densities were low. Sites with very high early summer densities usually had the greatest population declines.

Many of the streams with high early summer coho fry densities had been stocked with hatchery fish. These fry tended to be relatively large because they had been fed high ration levels at the hatchery prior to outplanting. Coho salmon biomasses in streams stocked late in the spring with large fry were extremely high relative to biomasses of wild populations in the Pacific Northwest, in some cases exceeding 25 g/m² (Figure 13a). However, these biomass levels were never carried through the summer, and declined rapidly to 3-7 g/m² by early August. In sites containing only wild coho populations, biomass generally remained constant or rose slightly throughout the summer and early autumn (Figure 13b) (i.e., biomass gained from growth offset biomass lost to mortality and emigration). By summer's end, biomass at all sites usually ranged from 2-6 g/m² regardless of whether the streams had been stocked with hatchery fish or contained only native populations (Figure 13). Where streams contained mixtures of wild and hatchery fry, we were unable to determine the survival rates of coho of different origin. The bimodal distribution of size frequencies in mixed coho populations observed in early summer disappeared by late summer.

Interspecific Interactions

We observed little apparent effect of other salmonid populations on juvenile coho salmon at our study sites. In most streams, coho fry densities far outnumbered fry of steelhead and cutthroat trout. Coho fry did appear to exert a strong negative effect on age 0 cutthroat trout density in both riffle and pool habitats in early summer (Figure 14). Further evidence of the negative impact of coho fry on underyearling cutthroat trout occurred in Huckleberry Creek before and after the debris flow (Figure 15). In the 3 years prior to the debris flow, cutthroat trout comprised only a small fraction of the salmonid assemblage. In 1990, when there was no recruitment of coho fry in the area of the stream impacted by the debris flow, age 0 cutthroat trout became much more abundant. The following year saw limited coho spawning in the debris flow impacted reach and a lower density of cutthroat trout, many of which were survivors of the 1990 brood year.

The presence of age one and older trout appeared to have a negative influence on coho fry density, but the association was not statistically significant (Figure 16). Coho were never abundant in stream reaches with relatively abundant large trout, however. Stomach samples of age one and older trout in late spring revealed that coho fry were frequently eaten, but once the fry attained sizes of 50-60 mm they apparently became too large to be taken. Visual observations of behavioral interactions between coho and trout indicated that large trout would occasionally displace coho fry from preferred feeding locations at the upstream end of pools, but microhabitat segregation of coho and trout often served to ameliorate direct behavioral interactions. Coho fry interacted with each other far more than with other species. Additionally, we saw no evidence that the abundance of non-salmonid fishes directly affected survival and growth of coho salmon in our study sites. Coho fry were occasionally seen protruding from the mouths of large torrent sculpins in spring, but incidences of predation by sculpins in summer were probably rare.

DISCUSSION

Small streams in the Pacific Northwest are prone to frequent disturbances and large annual variations in discharge. These rigorous and often unpredictable conditions would suggest that physical processes regulate the dynamics of stream-dwelling fish populations. Yet the period of low stream discharge that generally extends from June to late September does provide relatively stable conditions in terms of streamflow and water quality. We found that juvenile coho salmon were regulated during this interval by density-dependent survival and growth, mediated by the availability of suitable habitat and food resources. Chapman (1966) suggested that food availability would most likely limit coho salmon production in summer, and the experimental food supplementation study of Mason (1976) strongly supports this hypothesis. Our findings suggest that underyearling coho are limited in summer by *both* food and habitat resources, but that these limitations are expressed by populations in different ways.

Streams that contained excellent habitat often had high densities of coho fry (especially those stocked with large numbers of hatchery fish), but compensatory growth led to corresponding individual weights that were relatively low. Conversely, streams with poor physical habitat had few fish, but individual growth rates were often quite high. This resulted in a convergence of biomass among streams at the end of summer. Our findings suggested that limits on biomass during this period were set by availability of food as well as by availability of suitable hydraulic conditions, while density was regulated primarily by the amount and quality of suitable rearing space and did not seem to be strongly influenced by food resources.

Although streams with abundant habitat supported more coho fry than streams where suitable habitat was rare, the larger average size of coho in streams with poor quality rearing conditions may confer improved ability to survive the following winter. At Carnation Creek, a coastal rainforest stream in British Columbia, habitat quality declined after logging but coho were larger at the end of summer, leading to increased overwinter survival (Holtby and Scrivener 1989; Hartman and Scrivener 1990). Thus, compensatory growth may influence smolt yield in streams with differing hydraulic and geomorphic characteristics. Numbers of coho smolts produced by a stream can be influenced by growth during the previous summer as well as by mortality and emigration prior to smolting.

The presence of large woody debris did not seem to influence fish location early in the summer. At this time, coho at high densities and with relatively abundant food appeared to select areas of the channel where food delivery would be maximized, rather than areas that provided proximity to cover from predators. Aggressive interactions were frequently observed among actively feeding coho fry in early summer. However, at the end of summer preferred locations often shifted to areas adjacent to LWD and other cover structures. It is possible that low food availability during this period resulted in a shift in feeding strategy from maximizing food intake to minimizing energy expenditure and predation risk. When food was scarce, aggressive behavior became much less frequent and resting behavior more common.

What, then, is the best measure of the carrying capacity of a stream? We suggest there is no single population parameter that reflects all aspects of the capacity of a stream to produce coho salmon. Carrying capacity is often taken to mean the maximum number of fish that can be supported by available resources, but biological factors (especially food availability) have too often been ignored in the Pacific Northwest (Gregory et al. 1987). In the case of coho salmon, the maximum number of stream-dwelling fry during summer may not always lead to the greatest number of smolts or to subsequently returning adults (Hartman and Scrivener 1990). Population density is probably the best overall indicator of physical habitat quality, particularly early in the year when ample food is present. Assuming there has been sufficient adult escapement and adequate egg survival to provide enough fry to colonize available

habitats, streams with high quality rearing conditions should support more fish than streams with poor habitat. Density, however, is partially regulated by mortality, emigration, or immigration, and these processes may be influenced by factors other than habitat quality (Bilby and Bisson 1987; Bilby and Bisson 1992). Additionally, density should not be used to compare carrying capacity among streams if samples have been taken at different times of the summer. Population biomass reflects food and habitat availability by integrating density and growth, but does not in itself reveal the relative influence of different physical and biological processes. Growth rate reflects both food availability and the opportunity to exploit food resources, but is generally not useful in establishing carrying capacity without knowing the density.

Ideally, production of the cohort(s) or the ratio of production to biomass (Waters 1992) provides the best overall indicator of the capacity of the stream to produce coho salmon. Production integrates survival and growth in such a way that compensatory adjustments to both food and rearing space can be considered (Chapman 1978). Yet production estimates are time consuming and costly because they require frequent sampling, accurate age determinations, and measurements of immigration and emigration. In their absence, we believe fishery workers should attempt to measure density, biomass, and weights of juvenile coho salmon at the beginning and end of summer. When combined with habitat survey data, these measurements will be very helpful in assessing how populations are making use of available resources. Reliance on single population parameters such as density or indices of habitat quality such as percent of the stream in pools may provide very limited and easily misinterpreted information on the carrying capacity of streams.

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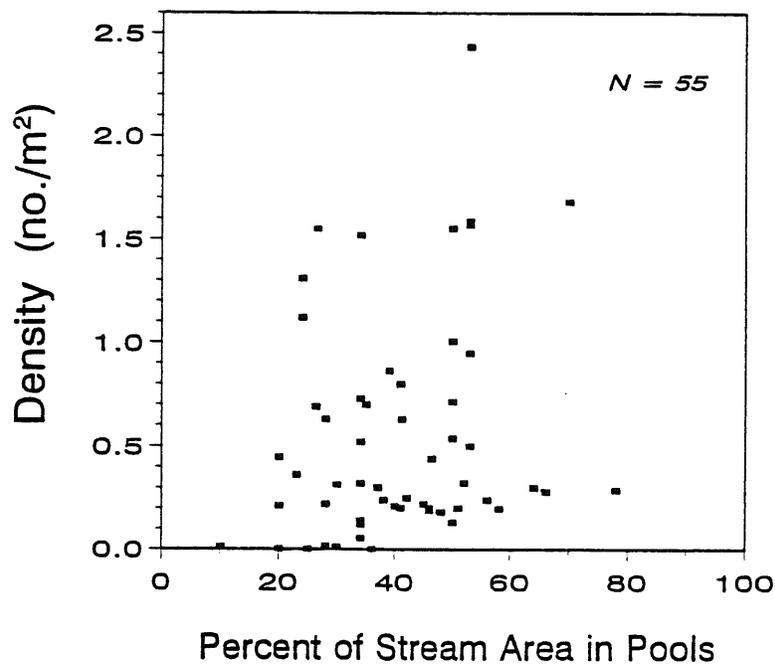


FIGURE 1. Density of juvenile coho salmon in western Washington streams having different percentages of pool area. See text for location of streams and sampling methods.

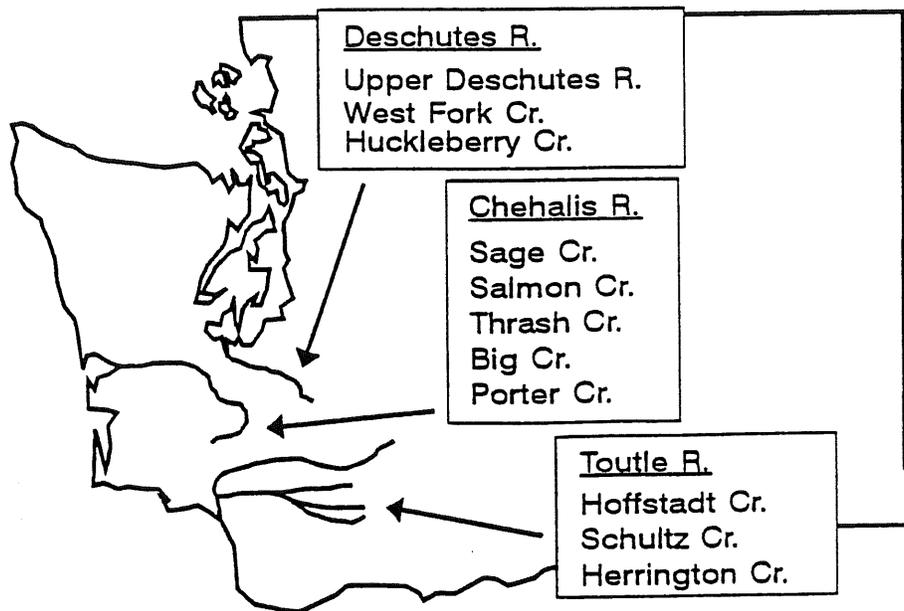


FIGURE 2. Location of study sites.

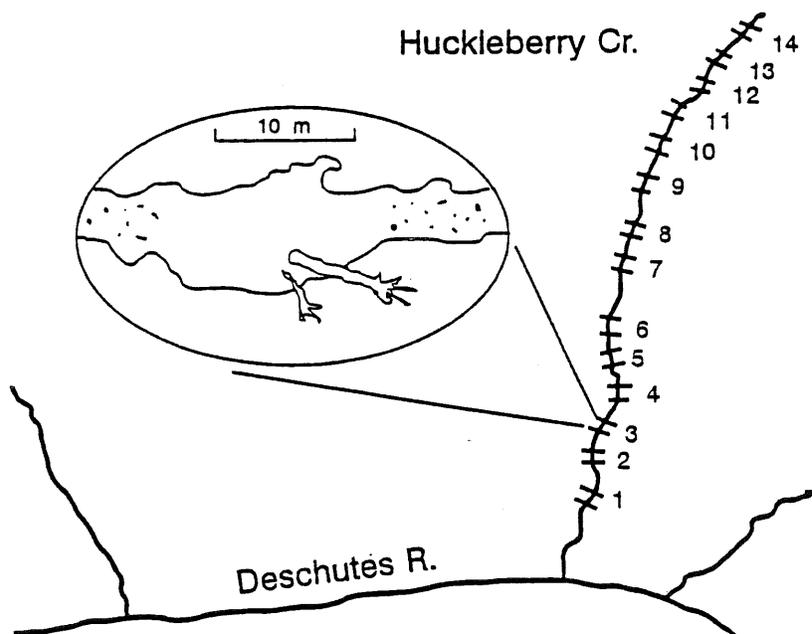


FIGURE 3. Diagram of the 14 segments of Huckleberry Creek in which detailed channel morphology and microhabitat distribution of coho salmon were studied.

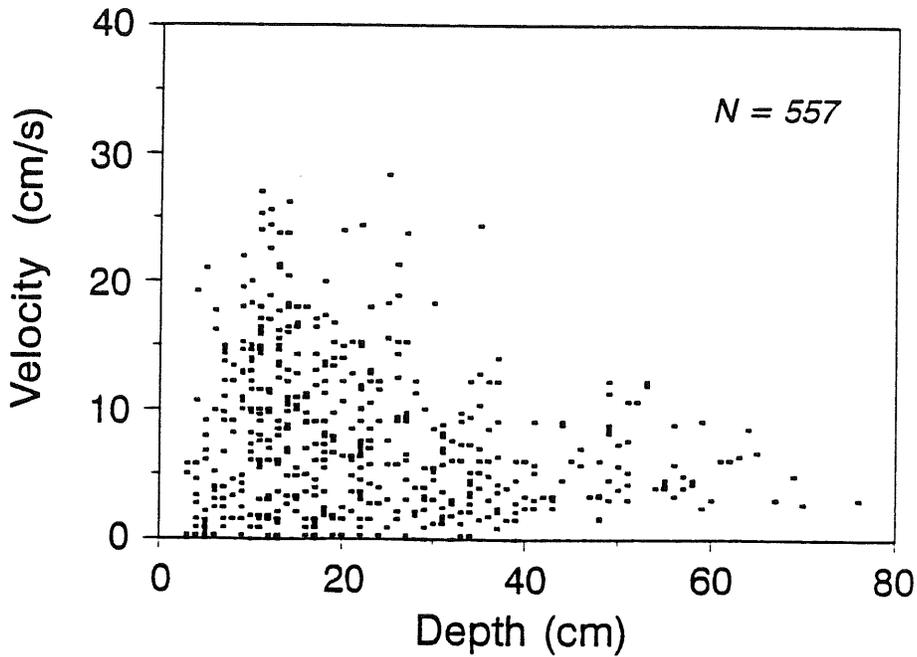


FIGURE 4. Location of age 0 coho salmon in Huckleberry Creek from early to mid-summer with respect to current velocity and stream depth. Each point represents one fish.

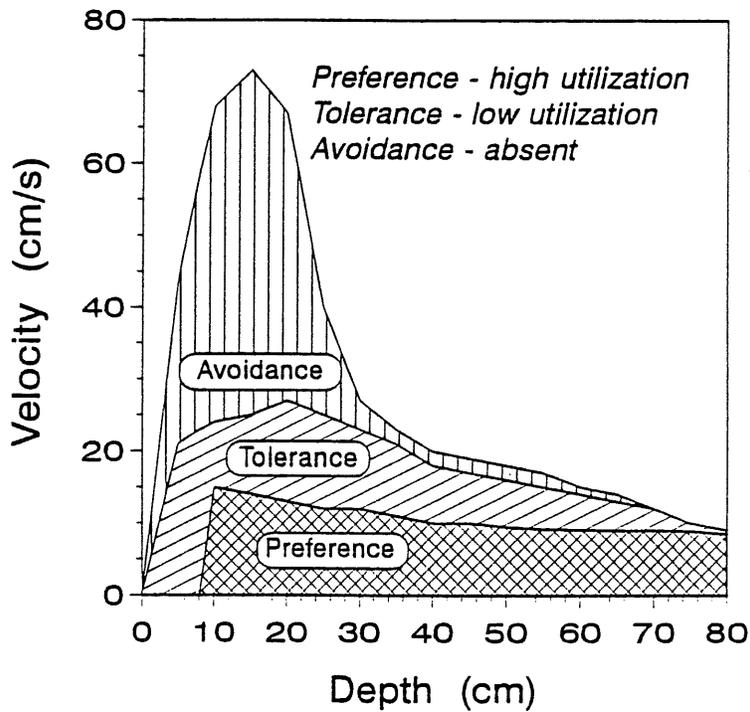


FIGURE 5. Combinations of current velocity and stream depth in Huckleberry Creek that were preferred, tolerated, or avoided by coho salmon fry in summer. Preferred conditions were those in which the density was greater than the average density of coho throughout the stream. Tolerated combinations of depth and velocity held fish, but at lower than average summer density. Avoided conditions were those in which coho fry were absent.

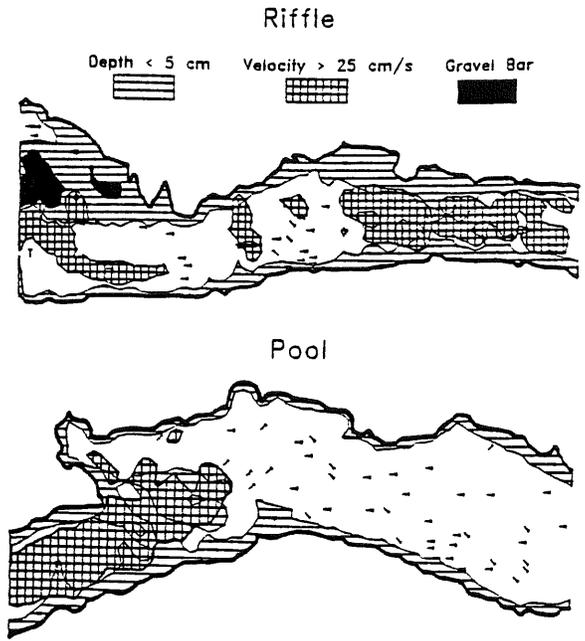


FIGURE 6. Microhabitat distribution of coho salmon (Y-shaped symbols) in two segments of Huckleberry Creek. One segment consisted of a low gradient riffle; the other was dominated by a lateral scour pool. Areas of the channel with depth < 5 cm and current velocities > 25 cm/s are differentially crosshatched.

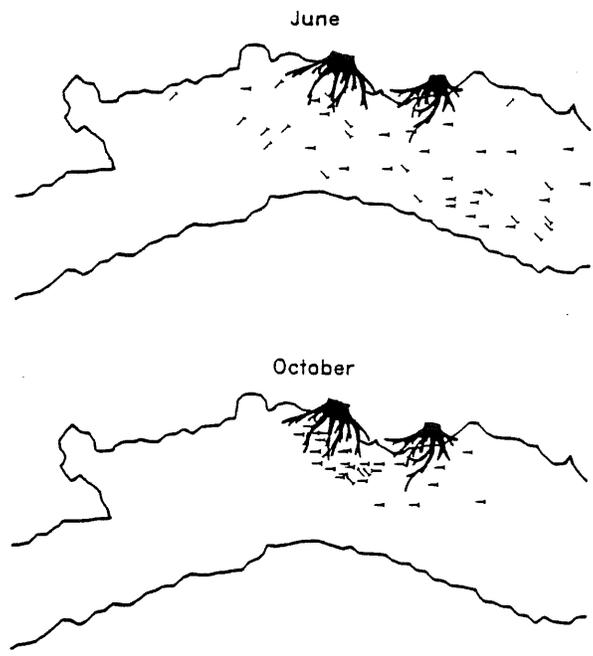


FIGURE 7. Location of coho salmon fry in June and early October in a lateral scour pool relative to rootwads on one streambank. The pool (Figure 6, bottom) was at low flow when the observations were made.

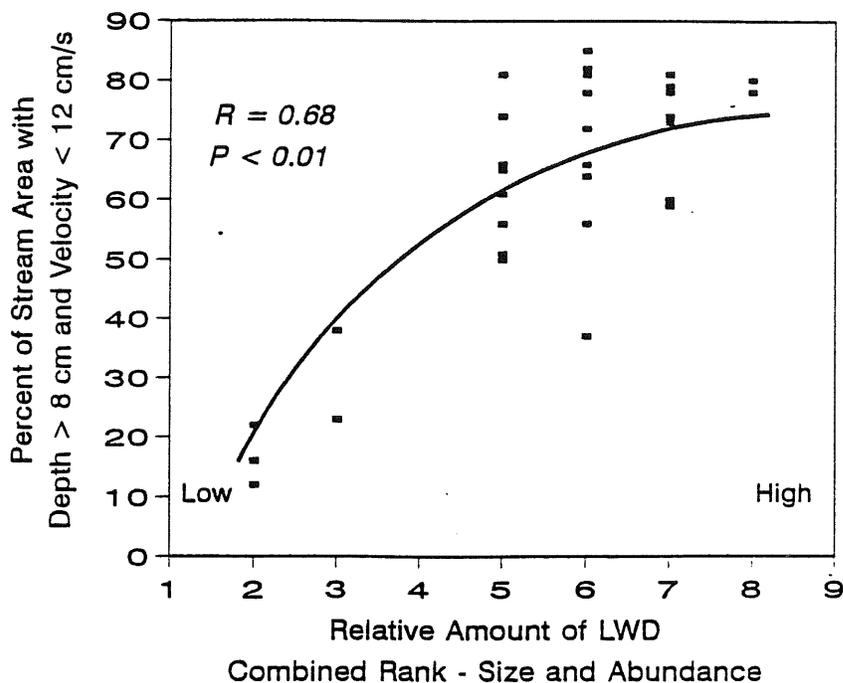


FIGURE 8. Relationship between the percent of stream area in Huckleberry Creek with depth > 8 cm and current velocity < 12 cm/s (preferred hydraulic conditions for coho fry in this study) and the relative amount of LWD in individual stream segments over a 3 year period.

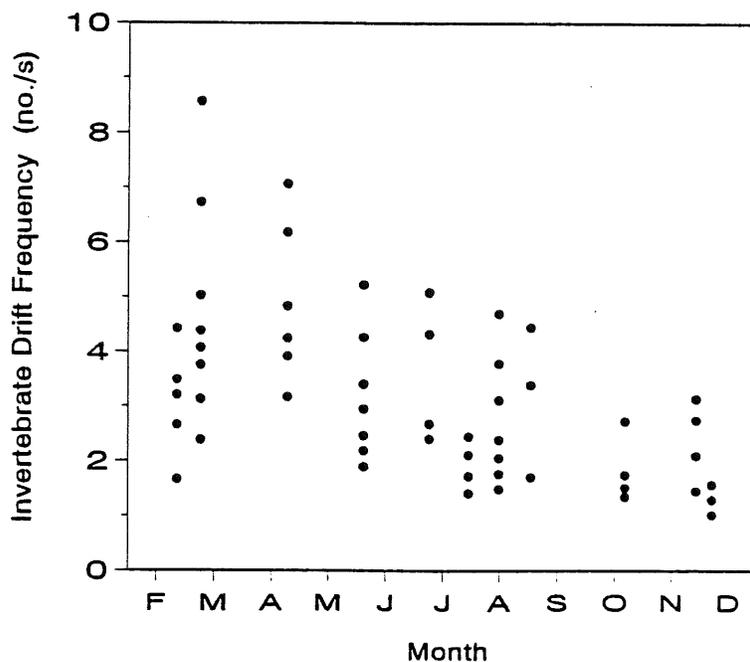


FIGURE 9. Evening drift of invertebrates in Huckleberry Creek from spring to early autumn over a 3 year period. Each point represents an estimate of the total number of invertebrates per second passing a single location in the stream.

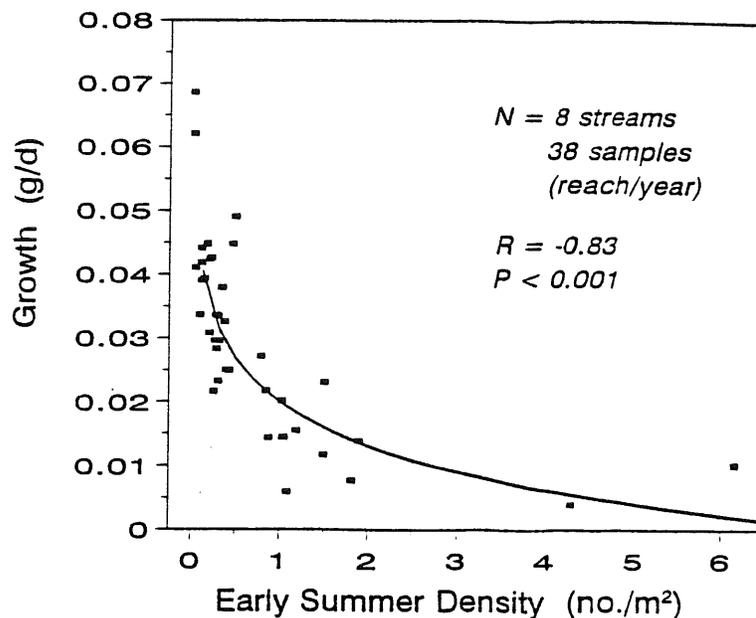


FIGURE 10. Relationship between growth of coho fry from June to September and the density of fry in early summer in eight western Washington streams. Each point represents samples from an individual stream reach for one summer. Some streams are represented by samples from several reaches and/or several years.

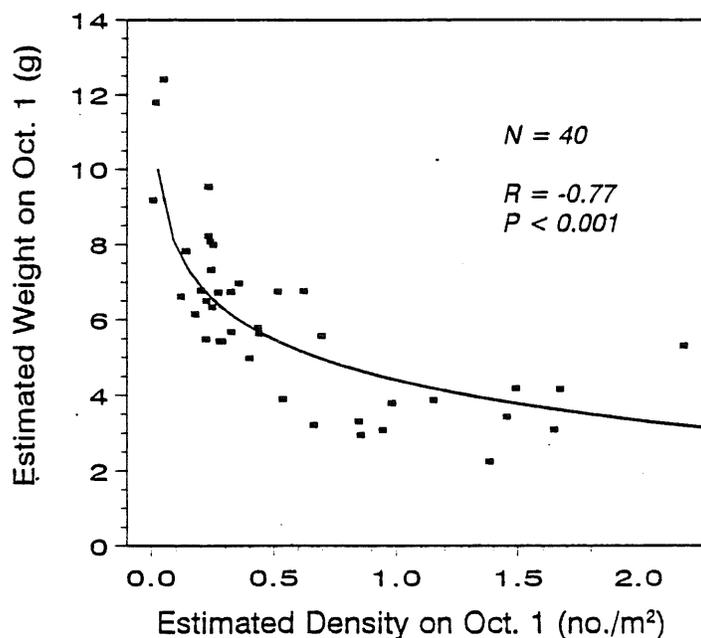


FIGURE 11. Relationship between the weight of juvenile coho salmon and average population density on October 1 in western Washington streams, based on extrapolations of summer growth and mortality rates. Each point represents an estimate from an individual stream reach for one summer. Some streams are represented by samples from several reaches and/or several years.

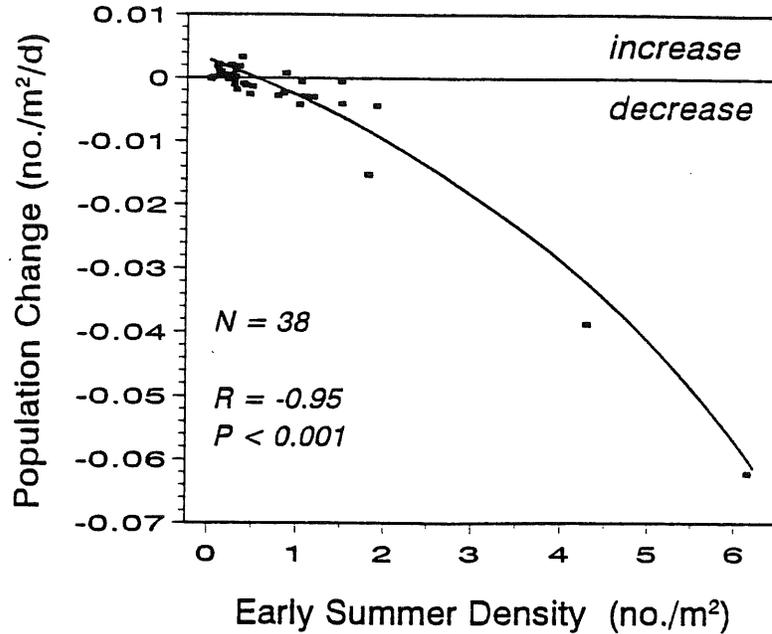


FIGURE 12. Relationship between the change in density of coho fry from June through September and early summer population density. Each point represents an estimate from an individual stream reach for one summer. Some streams are represented by samples from several reaches and/or several years. Increased density reflects a net immigration of fry; decreased density indicates that mortality and emigration exceeded immigration.

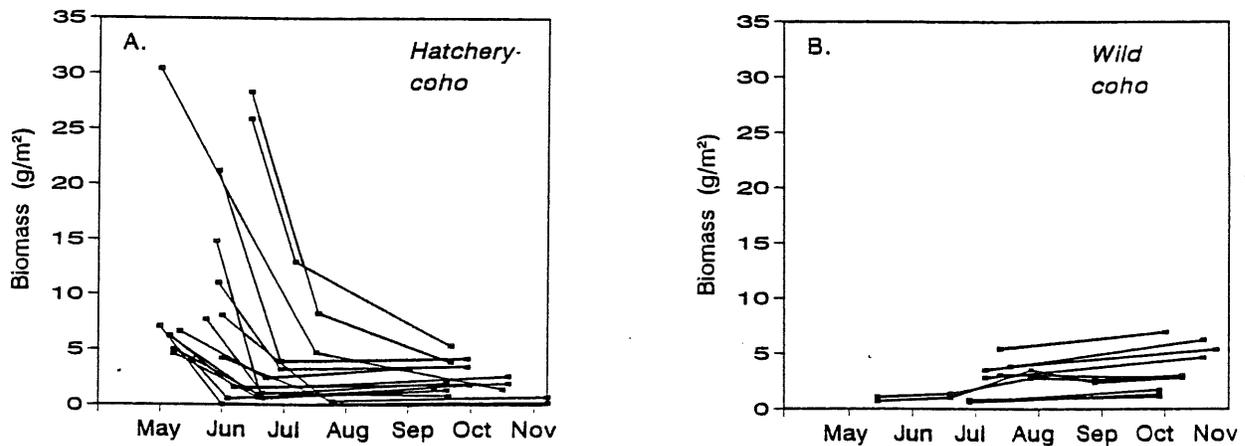


FIGURE 13. Change in the biomass of coho fry of (A) hatchery origin and (B) naturally-spawned origin from late spring to early autumn. Each line represents a single cohort.

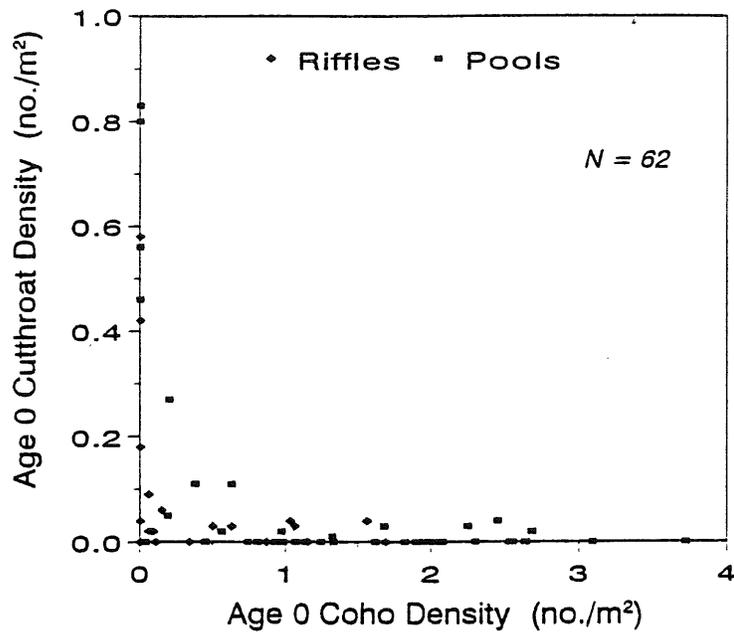


FIGURE 14. Relationship between the early to mid-summer density of age 0 cutthroat trout and age 0 coho salmon in pools and riffles.

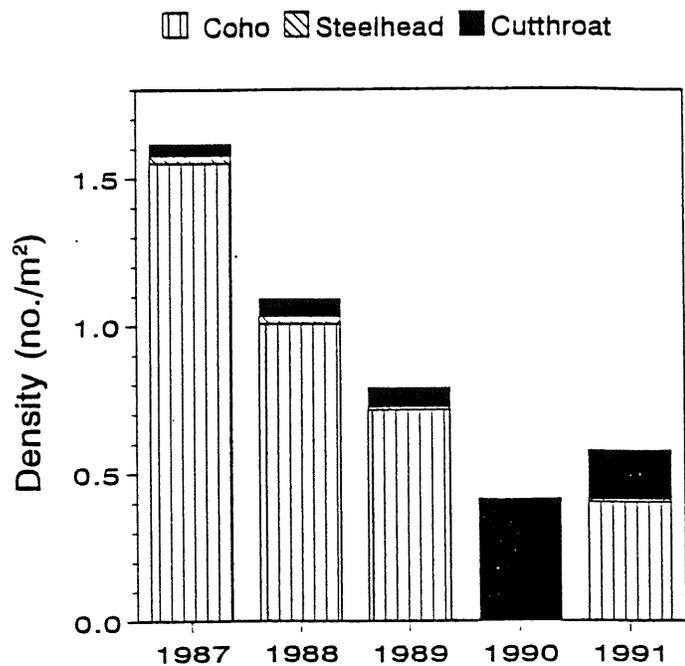


FIGURE 15. Mid-summer population estimates of coho salmon, steelhead, and cutthroat trout in the upper study section of Huckleberry Creek before and after the January 6, 1990, debris flow.

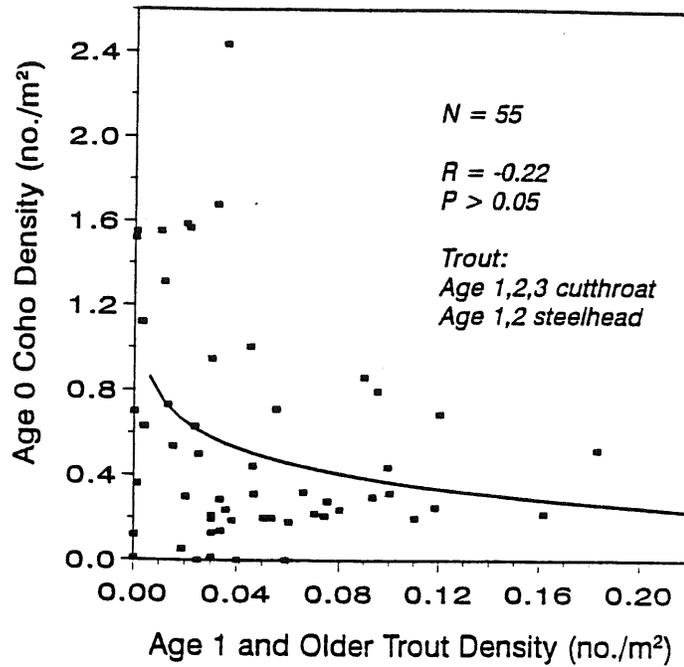


FIGURE 16. Relationship between the mid-summer density of coho fry and the density of yearling and older trout in stream reaches.