Transactions of the American Fisheries Society 117:262–273, 1988
© Copyright by the American Fisheries Society 1988

Channel Hydraulics, Habitat Use, and Body Form of Juvenile Coho Salmon, Steelhead, and Cutthroat Trout in Streams

PETER A. BISSON, KATHLEEN SULLIVAN, AND JENNIFER L. NIELSEN

Weyerhaeuser Company, Technology Center
Tacoma, Washington 98477, USA

Abstract.—Habitat use by juvenile coho salmon *Oncorhynchus kisutch,* steelhead *Salmo gairdneri,* and the coastal subspecies of cutthroat trout *Salmo clarki clarki* in small streams in western Washington was influenced by hydraulic characteristics of different types of channel units. Coho salmon preferred pools with average velocities less than 20 cm/s; very few fish were found in riffles with high current velocities. Steelhead occurred in riffles and also utilized deep pools with relatively high velocities along the center of the channel. Cutthroat trout were intermediate between coho salmon and steelhead in their use of swiftly flowing habitats. Variation in body shape and fin size among the three species generally fit the predicted morphologies that would be favored in different locations within the channel. Coho salmon possessed a deep, laterally compressed body with large median and paired fins. These features are believed to facilitate rapid turns and quick but transient burst swimming. Steelhead possessed a more cylindrical body shape with short median fins and relatively large paired fins, attributes that appear well adapted to holding a position in swift water. The cutthroat trout's lack of morphological adaptation to either fast or slow water may help to explain why this species is dominated by coho salmon and steelhead in areas of sympatry.

Salmon and trout growing in small streams along coastal drainages of western North America tend to be found only in certain types of habitat within the channel. Use of particular locations may be influenced by a wide variety of environmental factors that include water quality, substrate, cover, and hydraulic conditions, as well as intra- and interspecies interactions and food availability. The outcome of these influences, namely, the distributions of the populations, further reflects life history requirements that vary in both time and space (Northcote 1978; Miller and Brannon 1982). Attempts to predict population abundance based on stream habitat surveys often meet with only limited success or with failure (Annear and Conder 1984; Mathur et al. 1985) due to a multitude of possible consequences of physical and biological interactions and to an incomplete understanding of the behavioral responses of salmon and trout to the requirements of feeding and reproduction within the setting of a seasonally changing stream system.

We examined the use of different areas of the stream channel by three salmonid species during summer low streamflow in western Washington State. We tested the hypotheses that velocity and depth differentially influence selection of particular habitat types, and that patterns of habitat partitioning among species are, in part, reflected in body shapes that function well under certain flow conditions. Although the hydraulic regime represents only part of all environmental influences on habitat use, its importance has been studied less intensively than many other factors (Chapman 1966a; McFadden 1969).

Stimulus for this study came from three areas of research that have developed more-or-less independently and have yielded additional insight into the question, "Why are fish found where they are in streams?" These areas include studies of habitat classification, energetics of feeding behavior, and body form and the mechanics of locomotion. We have chosen to examine variation in species abundance because our focus is on factors affecting the distribution of fishes among different habitat types, where habitat types are recognized as discrete hydraulic units (riffles and pools) within the channel.

The foraging tactics of drift-feeding salmonids favor maximizing energy intake while minimizing the effort of maintaining a feeding position. In terms of channel hydraulics, an individual fish gains in fitness if it can occupy a site where current is slow but where there is ready access to drifting food, the abundance of which is believed to be proportional to water velocity (Elliott 1967; Wankowski and Thorpe 1979; Smith and Li 1983). Such tactics have been confirmed for several salmonid species and are used as the basis for explaining the defense of foraging stations and the development of dominance hierarchies (Dill et al. 1981; Fausch and White 1981; Bachman 1984; Fausch 1984; Puckett and Dill 1985).

Other studies have shown that multispecies as-

semblages of salmonids typically segregate within the channel, either by vertical stratification (Fraser 1969; Allee 1982) or by horizontal separation (Hartman 1965; Lister and Genoe 1970). Competition for feeding stations is usually invoked to explain this segregation (Kalleberg 1958; Chapman and Bjornn 1969; Glova 1984, 1986, 1987), with aggressive behavior being the means by which individuals of certain species displace others from preferred habitats. Aggressive encounters often involve fin displays, and fin morphology has been shown to influence dominance in several species (Chapman 1962; Keenleyside and Yamamoto 1962; Stein et al. 1972).

Webb (1984) and Webb and Weihs (1986) have summarized a large number of studies of body form, locomotion, and foraging behavior in aquatic vertebrates. Salmonid fishes fit the pattern of a locomotor generalist whose morphology represents a compromise among the maneuvering requirements for prey capture, predator avoidance, aggression, and station holding. Swimming is accomplished by body and caudal fin propulsion, with emphasis placed on the ability to accelerate rapidly and execute quick turns. Because hydraulic parameters such as current velocity vary according to habitat type but are predictable from stream to stream (Sullivan 1986), we postulate that different body shapes would be favored, depending upon whether a species tends to occupy riffles or pools. Such morphological variation might influence competitive ability and the way in which populations are distributed within the channel. For example, Taylor and McPhail (1985a, 1985b) have presented evidence that morphological variation among coastal and interior populations of coho salmon in British Columbia is related to life history responses to different hydrologic conditions.

According to a functional classification of locomotor propulsion mechanisms (Webb 1984), sustained swimming at moderate velocity—or, in the case of streams, occupation of a feeding station in or near a swiftly flowing riffle habitat—would favor a design that included a streamlined body with a low surface area to volume ratio. We predicted that salmonids in habitats with rapid flow should possess cylindrical bodies with stiff, shortened fins. Pool dwellers, in contrast, would be expected to rely more on transient propulsion by means of larger fins and a deep, laterally compressed body for improved turning and rapid angular acceleration.

Since 1982, we have been collecting information on the hydraulics of small stream channels, the distribution and abundance of juvenile coho salmon *Oncorhynchus kisutch,* juvenile steelhead *Salmo gairdneri,* and juveniles and adults of the coastal subspecies of cutthroat trout *Salmo clarki clarki,* and the morphological variation among these three species (unpublished observations). Although the data were not always obtained from identical sites, the patterns of channel hydraulics, habitat use, and body morphology were sufficiently similar over a range of streams to suggest that a relationship between them existed. The objectives of our paper are to (a) characterize the hydraulic conditions present in different types of channel units, (b) examine the distribution of coho salmon, steelhead, and cutthroat trout in light of the hydraulic properties of each habitat type, and (c) determine if morphological differences among these species fit the design features predicted by mechanical studies of fish locomotion to allow for efficient function in different hydraulic environments.

Methods

Study sites.—Measurement of channel hydraulics and fish populations took place in headwater tributaries of the Deschutes, Chehalis, Toutle, and Nisqually rivers in western Washington State. Watershed area, stream order, and average channel width and gradient (Table 1) were typical of coastal watersheds in the Pacific northwest where coho salmon, steelhead, and cutthroat trout occur in sympatry. Sites were selected in order to provide a wide array of available habitat types.

Habitat inventory followed the technique of Bisson et al. (1982) in which riffles and pools were classified into various types according to hydraulic characteristics. *Backwater pools* were positioned along channel margins and were caused by eddies behind large obstructions such as boulders or trees. *Lateral scour pools* were usually associated with the central axis of flow (thalweg) and occurred where the flow was directed toward one side of the stream by a partial channel obstruction. *Plunge pools* occurred where the stream passed over a complete or nearly complete channel obstruction and dropped vertically into the streambed below, scouring out a depression. *Trench pools* were elongated, generally deep slots in a stable substrate such as bedrock. *Secondary channel pools* were those that remained within the bank-full margins of the stream after freshets and were usually associated with gravel bars and meander bends. *Dammed pools* consisted of water impounded up-

TABLE 1.—Characteristics of the study locations where habitat use by salmonid populations was measured in Washington State. Habitat composition is expressed as percentage of total reach area for each habitat type. Habitat type designations are as follows: Bkw = backwater pool; Scr = lateral scour pool; Pln = plunge pool; Trn = trench pool; 2ch = secondary channel pool; Dam = dammed pool; Rif = low-gradient riffle; Rap = rapids; Cas = cascade; and Gli = glide.

Stream site	Water shed area (km^2)	Stream order (map scale, 1:24,000)	Average wetted width (m)	Average channel gradient (%)	Habitat type (% of total reach area)									
					Pools						Riffles			
					Bkw	Scr	Pln	Trn	2ch	Dam	Rif	Rap	Cas	Gli
Deschutes River (46.7°N, 122.4°W)														
West Fork Creek[a]	8.5	3	3.3	2	6	26	24		2	1	15	8	18	
Upper mainstem[a]	2.6	3	2.3	4	6	16	9		2		23	3	41	
Chehalis River (46.5°N, 123.4°W)														
Big Creek[a]	9.4	3	2.7	2	4	27	5		3		32	2	27	
Thrash Creek														
Site 1	17.0	4	4.9	3	6	13			3		59	3	17	
Site 2	12.8	3	4.0	2	4	30		4	1		52	2	3	3
Site 3	10.7	3	3.4	2	3	29		2	4	2	50	3	6	2
Site 4	7.9	3	3.4	2	2	20		9		2	33	11	19	
Site 5	2.7	3	3.5	4	5	20	8		2	36	14	9	7	
Site 6[a]	1.8	2	2.4	6		33	31				36			
Sage Creek	5.1	3	2.7	3	5	35	12		1		21	8	8	
Salmon Creek														
Site 1	9.0	3	3.5	3	6	35			2		34	17	5	2
Site 2[a]	5.7	3	3.2	3	5	31	37		3		21	4		
Toutle River (46.4°N, 122.4°W)														
Hoffstadt Creek	33.0	4	5.3	2	2	15	7	2			29	4	40	
Herrington Creek	8.1	3	4.3	1		46			1		54			
Nisqually River (46.7°N, 122.0°W)														
Beaver Creek[a]	28.8	4	4.8	2	5	24	19	27		11	2	13		

[a] Locations where detailed hydraulic measurements were made.

stream from a complete or nearly complete channel blockage. *Low-gradient riffles* were shallow and possessed moderate current velocity and turbulence; an upper limit of 4% gradient was set for this habitat type. *Rapids* possessed a gradient greater than 4%, with swiftly flowing water and considerable turbulence. *Cascades* also had a gradient steeper than 4% but, unlike rapids, they consisted of a stepped series of alternating small waterfalls and shallow pools. *Glides* were intermediate in many respects between pools and riffles and were characterized by moderately shallow water that lacked pronounced turbulence. Although they were most often located at the transition between a pool and the head of a riffle, glides were occasionally found in long, low-gradient stream reaches with stable banks and no major flow obstructions. Illustrations of each habitat type are found in Bisson et al. (1982) and Helm (1985).

Selected reaches of each stream were surveyed to determine the surface area of individual habitats. The frequencies of each type, expressed as a percentage of the total reach area, are given in Table 1. All surveys were conducted during summer from 1982 through 1984.

Hydraulic measurements.—Thirteen plots on 6 of the streams (Table 1) were picked for detailed measurements of flow in relation to fish habitat characteristics. Plots varied in length from 8 to 22 m and in width from 6 to 14 m, and usually included a sequence of channel units in which riffles formed the upstream and downstream boundaries and pools occupied the center of the plot. Some plots had several riffle–pool sequences, whereas 3 of the 13 were composed almost entirely of riffles. Sites were intentionally selected to sample a range of channel units associated with various kinds of channel obstructions, including single logs, root wads, debris jams, boulders, and channel meanders.

Hydraulic measurements were taken during summer flow conditions but excluded extreme low-flow periods (those occurring less than 10% of the time). A rectangular grid was established at each

site, the coordinates of which were placed at 0.5-m intervals across the channel (x-coordinate) and at 1.0-m intervals along the length of the channel (y-coordinate). Points on the grid were marked in the channel bed with painted nails that could be seen easily. Water velocity was measured at each point with an electromagnetic current meter that was accurate to 1 cm/s. The current measuring probe was oriented into the flow to give the maximum velocity reading at each point. Velocity was measured at 60% of the total depth relative to the surface; this depth approximated the average velocity of the water column, if a logarithmic velocity profile from streambed to surface is assumed (Leopold et al. 1964). Total water depth was measured to the nearest 1 cm. Depth and velocity were measured wherever grid points fell, including beneath logs, cutbanks, or waterfalls, and were believed to represent conditions typical of streams in this area.

Fish population census.—Within each reach, individual habitats were isolated from adjoining areas of the stream with blocking nets. Care was taken not to frighten the residents of selected habitats prior to placing the blocking nets, which might cause the fish to move to a different location. Once the nets were in place, the habitat was electrofished three times and all fishes were retained separately for each pass. Habitat-specific density was estimated by the removal summation method of Carle and Strub (1978). Average reach density was figured as the sum of the products of the habitat-specific densities and habitat frequencies (from Table 1). In order to compare the use of habitat types among streams with different overall population levels (almost always the case), we employed an index of habitat use based on the formula:

$$\text{habitat use} = (D_h - D_r)/D_r;$$

D_h = habitat-specific density;
D_r = average reach density.

The index of habitat use provided a density-independent means of comparing habitat partitioning by fish populations in different streams. Scores greater than zero indicated that a species used a particular type of habitat to a greater extent than average for all habitats in the stream; scores less than zero indicated below-average habitat use. However, the values of this quotient range theoretically from -1 to $+\infty$, and the scores for a particular habitat type among all sites were not distributed normally. Therefore, a nonparametric measure of central tendency, the Wilcoxon point estimate of center (Hollander and Wolfe 1973), was used to compute the mean use index for each habitat type over all sites combined. Association between habitat utilization and velocity or depth was calculated as the first- or second-order correlation between the Wilcoxon mean index of habitat use and the arithmetic mean velocity or depth of channel units that were mapped for hydraulics.

Most of the fish populations were wild (i.e., not the result of hatchery plantings). However, coho salmon populations at all sites were either mixtures of wild and hatchery stocks or pure hatchery stocks. We were unable to distinguish wild from hatchery coho salmon on the basis of size or habitat preference, and we assumed that patterns of habitat use were not influenced by the brief period of hatchery conditioning before outplanting. Although this assumption was untested, we observed that many young hatchery coho salmon emigrated from the study sites within a few days of planting (Bilby and Bisson 1987) and the remaining fish took up feeding stations similar to those occupied by wild fish. In all cases, hatchery stocks were derived from the same river systems as the study streams or from ones nearby.

Body morphology.—Because our scientific study permit prohibited retention of fishes captured during population censuses, we obtained museum specimens (Department of Fisheries and Wildlife, Oregon State University) of coho salmon, steelhead, and cutthroat trout collected from streams in the Pacific northwest. Specimens were selected based on overall condition, absence of obvious changes in body proportions due to preservation, and the probability that they came from wild populations rather than populations of hatchery origin (the latter specimens often showed signs of fin erosion). Thirty specimens of each age-group of each species were obtained from coastal drainages in Oregon and Washington and from tributaries to the lower Columbia River (30 river systems in total), in order to provide broad geographical representation for each species. Some morphological variation among the stocks from different river systems (Taylor and McPhail 1985a) probably was obscured as a result of sample pooling. However, because samples for studying body morphology and habitat use were drawn from different streams, we felt that detection of broadly based patterns of morphology and habitat use required that samples be combined.

All body proportions and fin lengths were ex-

TABLE 2.—Average velocities (mean ± SE) and depths (mean ± SE) for different habitat types in small streams in Washington State during summers of 1982–1984.

Habitat type	*N*	Velocity (cm/s)	Depth (cm)
Pools			
Backwater	9	6.3±1.3	19.4±2.2
Lateral scour	8	15.3±1.8	24.3±2.1
Plunge	3	16.8±7.4	37.8±7.6
Trench	1	18.0	35.4
Secondary channel	5	6.3±2.7	10.3±2.5
Dammed	6	6.1±1.4	25.0±3.6
Riffles			
Low-gradient	8	35.1±4.9	13.4±1.1
Rapids	7	74.0±5.5	20.5±1.8
Cascades	9	24.8±3.2	10.0±1.4
Glides	1	20.3	11.1

pressed as fractions of standard length. Ages of specimens were determined from scale samples. As far as possible, individuals of approximately similar size ranges were selected for comparisons between given age-groups of different species. No significant differences in any of the measured body proportions were found between age-1+ and age-2+ cutthroat trout; therefore, samples of these two age-classes were combined.

Results

Channel Hydraulics

Considerable variation in velocity and depth existed among different stream habitats during summer flow conditions (Table 2). Velocity was greatest in riffle habitats (low-gradient riffles, rapids, and cascades), intermediate in glides and pools located along the thalweg (lateral scour, plunge, and trench), and least in dammed pools and pools along the channel margin (backwater and secondary channel). There was about a 12-fold difference in average velocity (6–74 cm/s) between the lowest and highest ranking habitat types, whereas there was only a four-fold difference in average depth (10–38 cm) between the shallowest and deepest habitats. Because trench pools and glides were represented by single samples only, velocities and depths reported for these channel units in Table 2 must be viewed as preliminary.

Depth was relatively uniform in riffles. Velocities in riffles were greater on average than in pools (Table 2), and there was a much sharper gradient from high to low velocity near the stream's edge. Cobbles and boulders protruding from the bed in low-gradient riffles, rapids, and cascades added roughness to the substrate, creating small, discrete pockets of slow water (eddies) interspersed among areas of swiftly flowing water. Thus, a wide range of velocities occurred within riffle habitat types, but often on a scale too small to appear on the 0.5 × 1.0-m-grid reach maps. Low water velocities also existed in the boundary layer near riffle substrates. For example, boundary layer velocities in low-gradient riffles ranged from 0 cm/s at the surface of the bed to an average of 20 cm/s at a height of 4 cm above the bed. Depth of the low-velocity boundary layer increased with the abundance of roughness elements (cobbles and boulders). Difference in bed roughness accounted for average velocity in cascades being less than in low-gradient riffles (Table 2), despite the steeper gradient in cascades.

Habitat Use

Each salmonid species and age-group used habitat types differently (Figures 1, 2). Age-0+ coho salmon occupied nearly all pool types and avoided low-gradient riffles, rapids, cascades, and glides. Underyearling steelhead showed neither extensive use nor strong avoidance of most habitats, except backwater pools, where they were relatively abundant. Age-1+ steelhead preferentially occupied lateral scour and plunge pools, but they were scarce in secondary channel and dammed pools, low-gradient riffles, and glides. Underyearling cutthroat trout used backwater pools and glides; however, they tended to avoid all riffle types as well as dammed and trench pools. Age-1+ and age-2+ cutthroat trout used similar habitats; both age-groups preferred lateral scour and plunge pools and tended to avoid backwater and secondary channel pools, low-gradient riffles, rapids, cascades, and glides.

Although a close correspondence between habitat use and individual hydraulic parameters was not expected due to the confounding effects of other environmental variables (particularly the relative abundance of cover), depth and velocity did influence habitat selection in some instances. There was a strong negative association between average velocity and habitat use by age-0+ coho salmon (Figure 1). These fish avoided habitat types where average velocities exceeded 20 cm/s; however, the association between depth and habitat selection by coho salmon was much weaker (Figure 2).

Age-0+ steelhead were found in a wide variety of hydraulic conditions (Figures 1, 2). There were no significant correlations between their habitat use and velocity or depth. Age-1+ steelhead also occupied habitats with a wide range of velocities, but they tended to favor deeper pools with relatively high velocities associated with the thalweg.

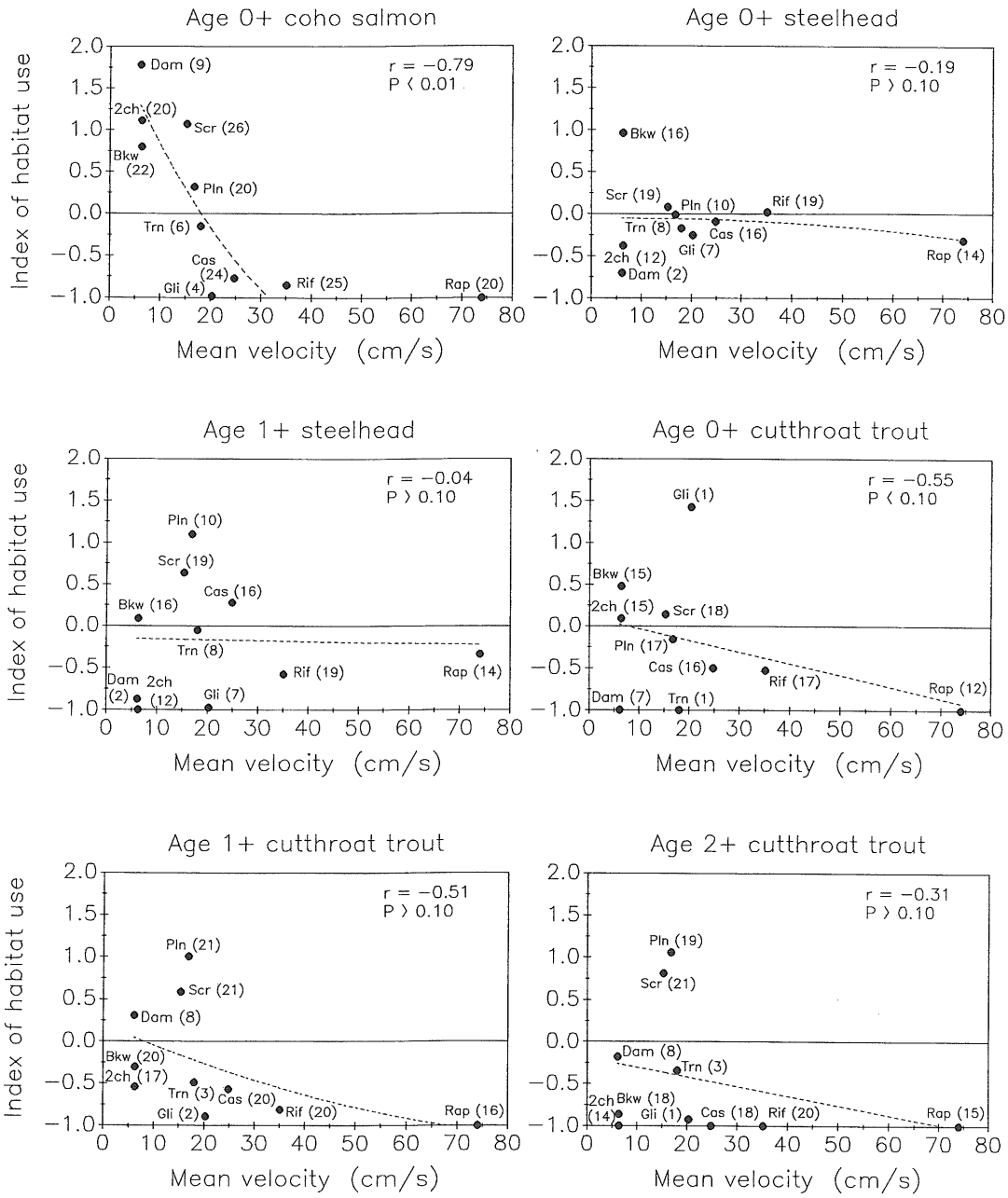

FIGURE 1.—Influence of mean habitat velocity on the index of habitat use by coho salmon, steelhead, and cutthroat trout in Washington State. Habitat type designations: Bkw = backwater pool; Scr = lateral scour pool; Pln = plunge pool; Trn = trench pool; 2ch = secondary channel pool; Dam = dammed pool; Rif = low-gradient riffle; Rap = rapids; Cas = cascade; and Gli = glide. Dashed lines indicate either first- or second-order regressions. Numbers in parentheses are the numbers of habitats sampled.

Overall, steelhead in both age-groups demonstrated an ability to live in habitats with moderate to swiftly flowing water and variable depths.

Cutthroat trout were intermediate between coho salmon and steelhead in their use of habitats with high velocities. The negative relationship between habitat use and average velocity for all three age-groups (Figure 1) became progressively less pronounced with increased age but, in all cases, it was weaker than the relationship observed for age-0+

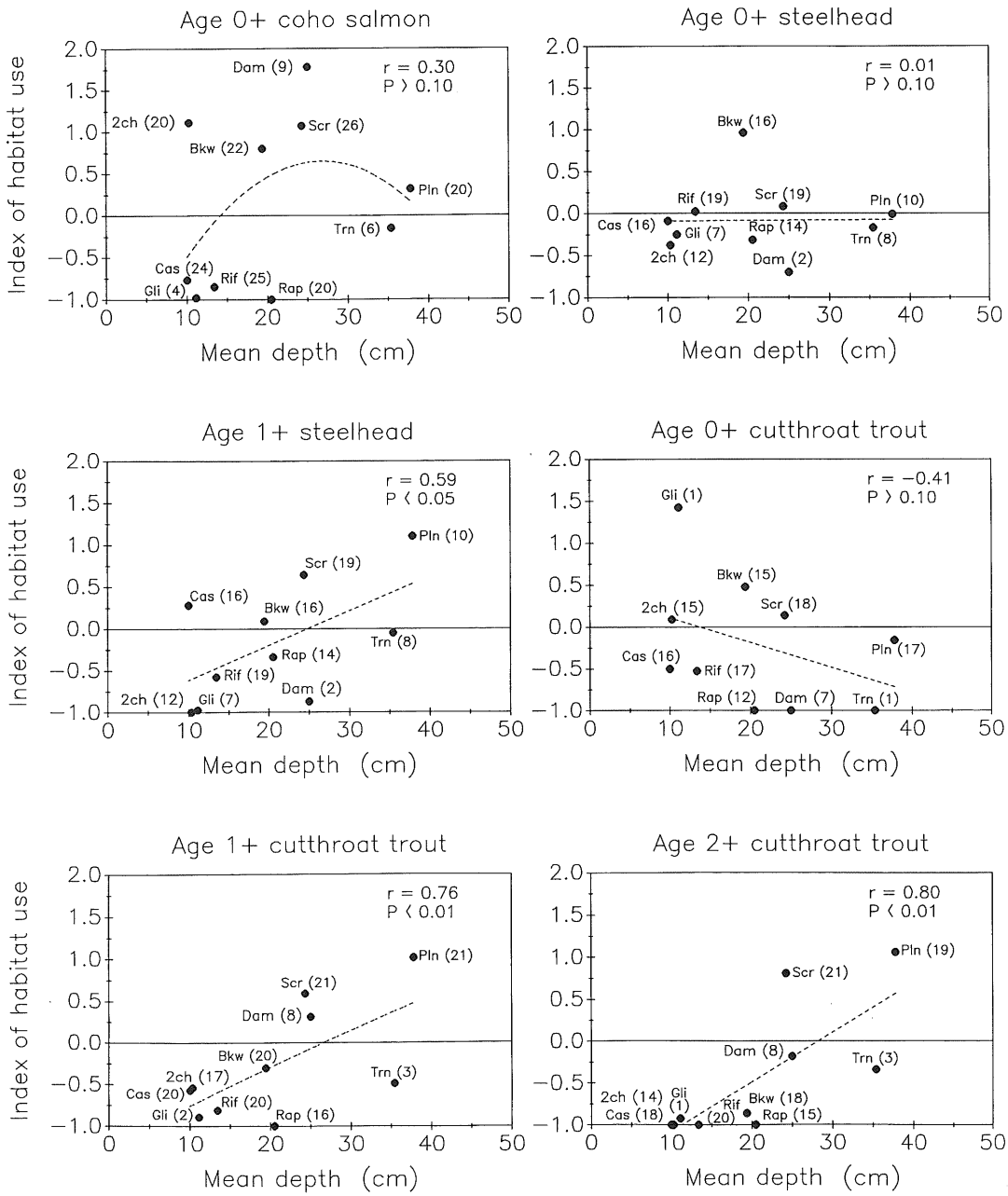

FIGURE 2.—Influence of mean habitat depth on the index of habitat use by coho salmon, steelhead, and cutthroat trout in Washington State. Habitat type designations: Bkw = backwater pool; Scr = lateral scour pool; Pln = plunge pool; Trn = trench pool; 2ch = secondary channel pool; Dam = dammed pool; Rif = low-gradient riffle; Rap = rapids; Cas = cascade; and Gli = glide. Dashed lines indicate either first- or second-order regressions. Numbers in parentheses are the numbers of habitats sampled.

coho salmon. Both age-1+ and age-2+ cutthroat trout were most abundant in deep pools (Figure 2), although they favored lateral scour and plunge pools, which usually possessed abundant cover, over trench pools, in which cover was infrequent.

In summary, coho salmon were generally not found in habitats with relatively high current velocities (low-gradient riffles, rapids, cascades, and glides), while steelhead were most tolerant of these habitat types and cutthroat trout tended to be in-

TABLE 3.—Variations in body form among age-0+ coho salmon (CO-0+; $N = 30$, mean standard length, SL = 66 mm), age-0+ steelhead (SH-0+; $N = 30$, mean SL = 53 mm), age-1+ steelhead (SH-1+; $N = 30$, mean SL = 95 mm), age-0+ cutthroat trout (CT-0+; $N = 30$, mean SL = 49 mm), and age-1+ and -2+ cutthroat trout (CT-1+; $N = 30$, mean SL = 104 mm). Values are means of the character measurement expressed as a fraction of SL. Within a row, means with a letter in common are not significantly different at $P < 0.05$, as determined by t-tests among all possible pairings.

Morphological character	Ranking				
	Lowest				Highest
Body depth	CT-1+ 0.227	SH-0+ 0.236	CT-0+ z 0.246	SH-1+ z 0.247	CO-0+ 0.259
Body width	CO-0+ z 0.125	CT-0+ z 0.128	CT-1+ z 0.128	SH-1+ y 0.142	SH-0+ y 0.147
Dorsal fin height	CT-1+ 0.157	SH-1+ z 0.164	CT-0+ z 0.172	SH-0+ z 0.174	CO-0+ 0.222
Anal fin height	CT-1+ z 0.146	SH-1+ z 0.147	SH-0+ 0.156	CT-0+ 0.166	CO-0+ 0.195
Caudal fin length	CT-1+ z 0.174	SH-1+ zy 0.179	SH-0+ zy 0.179	CT-0+ y 0.186	CO-0+ 0.226
Pectoral fin length	CT-1+ z 0.159	CT-0+ z 0.163	SH-0+ zy 0.165	SH-1+ zy 0.171	CO-0+ y 0.174
Pelvic fin length	CT-1+ z 0.132	SH-0+ z 0.133	CT-0+ z 0.135	SH-1+ z 0.136	CO-0+ z 0.138

termediate. Average depth did not strongly affect habitat use by underyearlings of any species, but age-1+ steelhead and age-1+ and age-2+ cutthroat trout preferentially used deep pools with ample cover.

Morphological Variation

Coho salmon possessed deeper and more laterally compressed bodies than either steelhead or cutthroat trout (Table 3). Steelhead had the widest bodies of the three species and were more cylindrically shaped. Cutthroat trout possessed the elongate profile of steelhead and the narrow width of coho salmon.

Coho salmon had longer fins (especially the median fins) than either of the trout species (Table 3). Average lengths of paired fins were slightly greater in coho salmon than in the two trout species, but differences in paired fin lengths between coho salmon and yearling steelhead were not significant. All underyearling cutthroat trout and steelhead possessed proportionately longer median fins than yearling and older fish. There were few significant differences in fin lengths between steelhead and cutthroat trout, although older cutthroat trout consistently had the shortest fins.

Discussion

Overall, the body forms of two of the three salmonid species fit the characteristics that were predicted to be adaptive under specific hydraulic conditions. The deep, laterally compressed body and large median fins of coho salmon would likely confer increased maneuverability in pools, whereas the added drag caused by large fin surfaces and the high surface-area to body-volume ratio would be a disadvantage for sustained swimming in riffles. The more cylindrical body shape and short median fins of steelhead would lessen the drag of sustained swimming in swift turbulent riffle habitats, but at the cost of maneuvering ability. The intermediate body shape of cutthroat trout suggests that they are not as well adapted to pools as coho salmon or to riffles as steelhead. In southwestern Washington State, Bisson and Sedell (1984) found juvenile steelhead and coho salmon weighed almost the same for a given length, whereas both species weighed approximately 10% more than cutthroat trout. Field studies of interspecific competition in British Columbia streams have shown that coho salmon displace juvenile cutthroat trout from pools (Glova 1984, 1986, 1987) and steelhead dominate cutthroat trout in riffles (Hartman and Gill 1968).

The leading fin ray in both the dorsal and anal fins of coho salmon is elongated for use in lateral displays (Mason and Chapman 1965; Stein et al. 1972), and it serves to exaggerate the differences in measured fin height between coho salmon and cutthroat trout and steelhead. However, there is additional evidence that the surface areas of the dorsal and anal fins are greatest for coho salmon.

Carl et al. (1967) gave the ranges of the number of fin rays for the dorsal and anal fins of coho salmon as 9–13 and 12–17, respectively. The same authors gave the ranges for steelhead as 10–12 and 8–12 and for coastal cutthroat trout as 8–11 and 8–12 (dorsal and anal fins, respectively); thus both of these species have fewer median fin rays than coho salmon.

Although there were major differences in the hydraulic properties of various habitat types (Table 2), virtually none of the habitats were unoccupied during summer flow conditions. Even the habitats with swiftest flows (rapids) contained eddies behind boulders where velocity and turbulence were reduced to levels that were acceptable to some fish. With relatively few exceptions, each species could exist in almost all habitat types. We also noted that the presence of cover, such as large woody debris, boulders, and undercut banks, appeared to strongly influence the preference for some of the pool types. Nevertheless, it was obvious that use of channel units with different hydraulic patterns varied consistently according to species and age-group.

Some differences among age-groups were probably related to increasing fish size. Everest and Chapman (1972) observed that steelhead and chinook salmon *Oncorhynchus tshawytscha* moved into swifter water as their size increased, and Sheppard and Johnson (1985) found that both steelhead and coho salmon entered deeper water as they grew. Our study found no evidence that larger fish used habitats with faster water during summer, within the range of stream size and flow levels that were examined, although our study streams were smaller than those of Everest and Chapman (1972). However, a trend toward preference for deeper water with increased age was observed in cutthroat trout and steelhead (Figure 2). Dolloff (1983) found that age-1+ coho salmon preferred deeper water than underyearlings did in small streams in southeastern Alaska. Size alone, however, could not account for differences in habitat use between species. For example, age-0+ coho salmon were usually larger than both age-0+ steelhead and age-0+ cutthroat trout during the summer, owing to their earlier emergence from spawning redds, yet they were less frequent in habitats with higher water velocity than either of the trouts.

The preference of coho salmon for pools with low velocities has been well established (Hartman 1965; Mundie 1969; Lister and Genoe 1970; Bustard and Narver 1975a, 1975b). Dolloff (1983) found that approximately 85% of the coho salmon in a small stream occurred where current velocities ranged from 0 to 9 cm/s. In such an environment, the drift rate of aquatic invertebrates is expected to be low. Coho salmon juveniles are known to feed heavily on surface drift (Mundie 1969), much of which can originate from terrestrial sources (Chapman 1966b). Aerial insects can fall anywhere on the water surface, and an ability to perform quick turns and rapid acceleration in pursuit of surface-drifting prey would likely be advantageous for pool dwellers. Dunbrack and Dill (1983) demonstrated that juvenile coho salmon can react to prey at distances of up to 100 cm (>10 times their body length), and in a subsequent study (Dunbrack and Dill 1984) found that the three-dimensional reaction field was greater above the fish than below it. In addition to being useful in feeding, increased maneuverability in pools would aid in the defense of foraging stations. Burst swimming is an important component of both foraging and aggression in coho salmon (Puckett and Dill 1984), which are physiologically capable of many charges per hour at intruders. Puckett and Dill (1985) have also shown that a significant portion of the population may be composed of nonterritorial or "floater" individuals that rely heavily on free swimming, as opposed to station holding. We suggest that all of these behavioral characteristics require the ability to maneuver quickly and accelerate, and that the laterally compressed body and large median fins of coho salmon appear to be better adapted to making rapid turns and to burst swimming than do the morphologies of either steelhead or cutthroat trout.

The distribution of steelhead in riffles and in large pools along the thalweg (Figure 1) indicates that this species prefers foraging sites similar to those observed for brown trout *Salmo trutta* by Bachman (1984) and Atlantic salmon *Salmo salar* by Keenleyside and Yamamoto (1962). Juvenile steelhead often feed directly off the bottom and are usually located close to the substrate in both pools and riffles (Allee 1982). Their relatively large pectoral and pelvic fins (Table 3) may aid in holding them against the substrate, an energy-conserving behavior observed in both brown trout (Fausch 1984) and Atlantic salmon (Kalleberg 1958; Gibson 1981). Large paired fins may also be used for steering up and down against a swift current. A cylindrical body and small median fins would decrease downstream movement when turning in fast water by presenting a reduced surface area against the flow. The frequency of lateral chases has been

seen to decline in salmonids as current velocity increases (Dill 1978; McNicol and Noakes 1984), presumably to prevent displacement from a preferred feeding station. On the scale of a stream reach (as opposed to an individual riffle or pool), steelhead exhibit limited movement in summer (Edmundson et al. 1968), while coho salmon are much more mobile (Gibson 1981). Combined with a relatively large muscle mass, the elongated body and relatively small median fin area of steelhead confer improved continuous propulsion performance, whereas the deeper body and relatively large median fin area of coho salmon confer improved transient performance. These morphologies appear well suited to the types of small-stream habitats in which juveniles of the two species are found, and they also suggest an explanation for the dominance of both species over cutthroat trout in streams with pool–riffle sequences.

Acknowledgments

We thank James Ward and John Heffner for technical assistance. The Washington Department of Fisheries supplied coho salmon fry for some of the study sites. Partial support for K. Sullivan was provided by a graduate fellowship from the G. C. Whiting School of Engineering, The Johns Hopkins University. R. E. Bilby, L. M. Dill, J. D. Hall, G. H. Reeves, and several reviewers offered helpful comments on an earlier version of the manuscript.

References

Allee, B. A. 1982. The role of interspecific competition in the distribution of salmonids in streams. Pages 111–122 *in* E. L. Brannon and E. O. Salo, editors. Proceedings of the salmon and trout migratory behavior symposium. University of Washington, School of Fisheries, Seattle.

Annear, T. C., and A. L. Conder. 1984. Relative bias of several instream flow methods. North American Journal of Fisheries Management 4:531–539.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113: 1–32.

Bilby, R. E., and P. A. Bisson. 1987. Emigration and production of hatchery coho salmon (*Oncorhynchus kisutch*) stocked in streams draining an old-growth and a clear-cut watershed. Canadian Journal of Fisheries and Aquatic Sciences 44:1397–1407.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62–73 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of eastern Washington. Pages 121–129 *in* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests. Institute of Fisheries Research Biologists. (Available from J. W. Reintjes, Morehead City, North Carolina.)

Bustard, D. R., and D. W. Narver. 1975a. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32:667–680.

Bustard, D. R., and D. W. Narver. 1975b. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. Journal of the Fisheries Research Board of Canada 32:681–687.

Carl, G. C., W. A. Clemens, and C. C. Lindsey. 1967. The fresh-water fishes of British Columbia. British Columbia Provincial Museum, Handbook 5, Victoria, Canada.

Carle, F. L., and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34:621–630.

Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board of Canada 19:1047–1080.

Chapman, D. W. 1966a. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345–357.

Chapman, D. W. 1966b. The relative contributions of aquatic and terrestrial primary producers to the trophic relations of stream organisms. Pages 116–130 *in* K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman, editors. University of Pittsburg, Special Publications of the Pymatuning Laboratory of Ecology, volume 4. Pittsburg, Pennsylvania.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153–176 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, Institute of Fisheries, Vancouver, Canada.

Dill, L. M. 1978. Aggressive distance in juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 56:1441–1446.

Dill, L. M., R. C. Ydenberg, and A. H. G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 59:1801–1809.

Dolloff, C. A. 1983. The relationships of wood debris to juvenile salmonid production and microhabitat selection in small southeast Alaska streams. Doctoral dissertation. Montana State University, Bozeman.

Dunbrack, R. L., and L. M. Dill. 1983. A model of size dependent surface feeding in a stream dwelling

salmonid. Environmental Biology of Fishes 8:203–216.

Dunbrack, R. L., and L. M. Dill. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 41:1176–1182.

Edmundson, E. H., F. H. Everest, and D. W. Chapman. 1968. Permanence of station of juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 25:1453–1469.

Elliott, J. M. 1967. Invertebrate drift in a Dartmoor stream. Archiv fuer Hydrobiologie 63:202–237.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91–100.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

Fraser, F. J. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. Pages 253–266 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, Institute of Fisheries, Vancouver, Canada.

Gibson, R. J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and steelhead trout (*Salmo gairdneri*) at the juvenile fluviatile stages. Canadian Technical Report of Fisheries and Aquatic Sciences 1029.

Glova, G. J. 1984. Management implications of the distribution and diet of sympatric populations of juvenile coho salmon and coastal cutthroat trout in small streams in British Columbia, Canada. Progressive Fish-Culturist 46:269–277.

Glova, G. J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki clarki*) in a laboratory stream. Hydrobiologia 132:155–168.

Glova, G. J. 1987. Comparison of allopatric cutthroat trout stocks with those sympatric with coho salmon and sculpins in small streams. Environmental Biology of Fishes 20:275–284.

Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22:1035–1081.

Hartman, G. F., and C. A. Gill. 1968. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. Journal of the Fisheries Research Board of Canada 25:33–48.

Helm, W. T., editor. 1985. Glossary of stream habitat terms. American Fisheries Society, Western Division, Habitat Inventory Committee. (Available from Utah State University, Department of Fisheries and Wildlife, Logan.)

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. Wiley, New York.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta*). Institute of Freshwater Research Drottningholm Report 39:55–98.

Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour 19:138–169.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco.

Lister, D. B., and H. S. Genoe. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. Journal of the Fisheries Research Board of Canada 27:1215–1224.

Mason, J. C., and D. W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. Journal of the Fisheries Research Board of Canada 22:173–190.

Mathur, D., W. H. Bason, E. J. Purdy, Jr., and C. A. Silver. 1985. A critique of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825–831.

McFadden, J. T. 1969. Dynamics and regulation of salmonid populations in streams. Pages 313–329 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, Institute of Fisheries, Vancouver, Canada.

McNicol, R. E., and D. L. G. Noakes. 1984. Environmental influences on territoriality of juvenile brook char, *Salvelinus fontinalis*, in a stream environment. Environmental Biology of Fishes 10:29–42.

Miller, R. J., and E. L. Brannon. 1982. The origin and development of life history patterns in Pacific salmonids. Pages 296–309 *in* E. L. Brannon and E. O. Salo, editors. Proceedings of the salmon and trout migratory behavior symposium. University of Washington, School of Fisheries, Seattle.

Mundie, J. H. 1969. Ecological implications of the diet of juvenile coho in streams. Pages 135–152 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, Institute of Fisheries, Vancouver, Canada.

Northcote, T. G. 1978. Migratory strategies and production in freshwater fishes. Pages 326–359 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, England.

Puckett, K. J., and L. M. Dill. 1984. Cost of sustained and burst swimming to juvenile coho salmon (*On-*

corhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 41:1546–1551.

Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 42:97–111.

Sheppard, J. D., and J. H. Johnson. 1985. Probability-of-use for depth, velocity, and substrate by subyearling coho salmon and steelhead in Lake Ontario tributary streams. North American Journal of Fisheries Management 5:277–282.

Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173–180 *in* D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward, editors. Predators and prey in fishes. Dr. W. Junk, The Hague.

Stein, R. A., P. E. Reimers, and J. D. Hall. 1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. Journal of the Fisheries Research Board of Canada 29:1737–1748.

Sullivan, K. 1986. Hydraulics and fish habitat in relation to channel morphology. Doctoral dissertation. Johns Hopkins University, Baltimore, Maryland.

Taylor, E. B., and J. D. McPhail. 1985a. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2020–2028.

Taylor, E. B., and J. D. McPhail. 1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2029–2033.

Wankowski, J. W. J., and J. E. Thorpe. 1979. Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L. juveniles. Journal of Fish Biology 14:239–247.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist 24: 107–120.

Webb, P. W., and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. Transactions of the American Fisheries Society 115:115–127.

Received February 5, 1988
Accepted July 10, 1988