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TABLE 4. Hemoglobin-splitting activities of various fish tissues.

	Specific activity ($\mu\text{M tyrosine/mg protein per hr}$)
Cod spleen	2.8-3.4
Hake spleen	2.0-2.7
Cod kidney	0.96
Cod liver	0.42
Cod skin (soluble protein)	0.12
Cod white muscle	0.05
Salmon eggs	0.17-0.31
Hake eggs	0.18
Lobster eggs	0.40

autolytic process. The commercial species of crustaceans studied had levels of cathepsins in the muscle adequate to explain the rapid postmortem deterioration of this tissue.

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Habitat Selection and Spatial Interaction by Juvenile Chinook Salmon and Steelhead Trout in Two Idaho Streams

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During summer sympatric steelhead trout and summer chinook salmon segregated in Crooked Fork and Johnson creeks. In short-term allopatry, each species occupied the same types of habitat as in sympatry. Most age 0 steelhead lived over rubble substrate in water velocities and depths of less than 0.15 m/sec and 0.15 m, respectively; most age 0 chinook lived over silt substrate in water velocities of less than 0.15 m/sec and depths of 0.15-0.3 m; most age 1 steelhead resided over large rubble substrate in water velocities of 0.15-0.3 m/sec (near bottom) and 0.75-0.9 m/sec (near surface), and in depths of 0.6-0.75 m. As fish of each species became larger they moved into faster, deeper water. Juvenile chinook and steelhead of the same size used the same physical space. But steelhead spawn in spring and chinook spawn in early fall, and disparate times of spawning create discrete intra- and inter-specific size groups of pre-smolts. The size differences minimize potential for social interaction, both intra- and inter-specific.

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En été, les populations normalement sympatriques de truites steelhead et de saumons chinook vivent séparément dans les cours d'eau Crooked Fork et Johnson. Durant cette courte période allopatrique, chaque espèce occupe le même genre d'habitat que durant leur période sympatrique. La plupart des truites d'âge 0 vivent au-dessus de fonds caillouteux, dans des courants plus faibles que 0.15 m/sec et à des profondeurs inférieures à 0.15 m. La majorité des saumons d'âge 0 se rencontrent au-dessus de fonds vaseux, dans des courants inférieurs à 0.15 m/sec et à des profondeurs de moins de 0.15-0.3 m. La plupart des truites de la classe d'âge 1 fréquentent des fonds de gros cailloux, où les courants sont de 0.15-0.3 m/sec (près du fond) et 0.75-0.9 m/sec (près de la surface) et les profondeurs de 0.6 à 0.75 m. Avec la croissance, les poissons des deux espèces se déplacent vers des eaux plus rapides et plus profondes. Les jeunes saumons et truites de même taille occupent le même espace physique. Par contre, la truite fraie au printemps et le saumon au début de l'automne. Il en résulte, au stade pré-taçon, des groupes de longueur intra- et interspécifiques distincts, ce qui réduit d'autant la possibilité d'interaction sociale entre les groupes.

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JUVENILE spring and summer chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*) coexist in tributaries of the Clearwater and Salmon rivers in Idaho. Juveniles of the two species have similar sizes, morphology, and behavior, although steelhead spend two or three growing seasons in fresh water while chinook normally spend one. The young of both species feed mostly on drifting invertebrate organisms. The two species appear to draw broadly upon the same environmental re-

sources, making the potential for interspecific interaction high.

Interaction between similar stream fishes can result either in displacement of one species or coexistence through segregation. Two mechanisms may allow closely related, morphologically similar fishes to coexist. Interactive segregation (Nilsson 1967) occurs when severe interaction results in segregation. Secondly, more pronounced genetic differences may keep the species segregated in the environment (selective segregation). Obviously both phenomena may take place in concert.

Our research had three primary objectives: (1) To define quantitatively the physical habitats used

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by juvenile spring and summer chinook salmon and steelhead trout; (2) To assess probable degree of interaction between the species for physical habitat; and (3) To identify factors which may allow coexistence of such similar salmonids.

Study Areas

CROOKED FORK CREEK

Crooked Fork Creek originates in the Bitterroot Mountains of northeastern Idaho at an elevation of 2030 m and flows southward 35 km to its confluence with the Lochsa River at an elevation of 1070 m (Fig. 1). Flow varied from about 3.6 m³/sec in mid-August to 50+ m³/sec during the spring freshet in 1966-67. Flow variations of this magnitude keep the streambed nearly clear of vegetative cover and log jams. The stream drops about 14.0 m/km through the study area. As a result, during summer most of the shallow stream flows rapidly over large rock substrate. We observed maximal and minimal water temperatures of 18 and 0 C in August 1966 and February 1967, respectively. The diel temperature range in August averaged 9-17 C. During winter, shell, anchor, frazil, and drift ice formed in the stream.

We selected sampling stations which contained a spectrum of physical habitats. We also collected data at transects 0.16 km apart along the lower 8 km of this area. U.S. Highway 12 parallels the lower 9.6 km of the creek and provides year-round access.

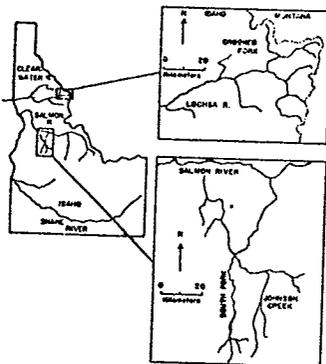


Fig. 1. Location of Crooked Fork and Johnson Creek.

Fishes present in the study area (in order of decreasing abundance) in 1966 included: juvenile steelhead trout, juvenile chinook salmon, mountain whitefish (*Prosopium williamsoni*), hatchery-produced rainbow trout, longnose dace (*Rhinichthys cataractae*), cutthroat trout (*Salmo clarki*), and dolly varden (*Salvelinus malma*), sculpins, (*Cottus rhotheus* and *C. bairdi*), lived throughout the study area but we did not record their abundance. A small adult chinook run in 1966 produced very low numbers of age 0 chinook in the creek in 1967.

JOHNSON CREEK

Johnson Creek heads at an elevation of 2400 m in the Salmon River Mountains of central Idaho and flows through a little-disturbed watershed 56 km north to its confluence with the East Fork of the Salmon River (Fig. 1). Flow ranged in 1966-67 from late-summer minima of about 4.2 m³/sec to spring-freshet maxima of about 70 m³/sec. The gradient of the stream changes rapidly in the 8-km study area. In the upper 2.4 km the stream drops at 5.1 m/km as it flows through a broad valley, where the stream has quiet runs and occasional riffles and pools to 3 m in depth. In the lower 5.6 km the stream drops at 13.3 m/km. We sampled in both steep and moderate gradients. Water temperatures ranged from 9 to 17 C from July through September.

Age 0 chinook made up most of total fish numbers, with juvenile steelhead trout, whitefish, dolly varden, hatchery-produced rainbow, cutthroat, and eastern brook trout (*Salvelinus fontinalis*) present (in decreasing order). As in Crooked Fork Creek, we did not estimate abundance of sculpins.

Materials and Methods

In summer we collected data in large units of habitat and in microhabitat. Quantitative description of microhabitat was facilitated by the fact that during the summer juvenile summer chinook and steelhead in both creeks remain in a small home area (Edmundson et al. 1968). In these streams over 60% of all observed daily movements of steelhead extended less than 3 m, and in stream aquarium studies (Edmundson et al. 1968) 67% of all observed daily movements of juvenile chinook covered less than 0.6 m. The two species generally held the same stations in the morning, midday, and late afternoon. But when mortalities create vacancies in habitat the space vacated is quickly occupied by immigrant young steelhead (Pollard MS 1969).

HABITAT ANALYSIS

We quantitatively defined the physical characteristics of habitat used in June, July, and August by sympatric and allopatric populations of pre-smolt summer chinook

and steelhead. Stations measured 25 and 45 m long and included as much variety of habitat as the stream offered. We gridded each station in 4.5-m squares, marked grid corners with green plastic flagging, then assessed physical characteristics at 1.5-m intervals on the grid (or at more frequent intervals along environmental clones).

We measured bottom and surface velocities, depth, and substrate size. Current speed was measured 5 cm above the substrate and 5 cm below the surface with a midget Bentzel current speed tube (Everest 1967) to the nearest 0.03 m/sec over a range of 0.03-1.2 m/sec. We mapped silt, sand, 2-5-cm gravel, 5-10-cm gravel, 10-20-cm rubble, 20-40-cm rubble, and rock > 40 cm.

Divers also recorded species, age, and density of fish in each station between 1000 and 1400 hr, the period of maximum underwater visibility. We easily identified chinook and steelhead in their first growing season (age 0), but could not separate steelhead in their second and third growing seasons by sight, and therefore designated them as age 1+. We collected juveniles with "Primacord" detonating fuse for age-length analysis.

At each station we followed a strict chronological order for collecting data, completing the grid on the first day and then delaying work within the station to allow the fish to redistribute. On the second day we counted fish, starting at the downstream end of the station and working slowly upstream, and on subsequent days recorded physical parameters.

Later we summarized these data by mapping substrate size, fish positions, and the shoreline contours of each station, then superimposed clear acetate overlays of depth contours (stratified into 0.15-m intervals) and velocity contours (stratified into 0.15-m/sec intervals) on the base map. We calculated the area of each combination of habitat conditions (termed a "set") and recorded the number, age, and species of fish within that set. This produced a measure of fish density per unit area for all freshwater age-groups of each species over a wide variety of habitat conditions.

We calculated multiple correlations of fish density and certain physical habitat statistics. We used a minimum sample size in multivariate analysis of 4.5 m² of homogeneous habitat, an area which exceeded the territory size of the largest fish (age II steelhead). We also examined overall density of fish independently in relation to each single habitat parameter (univariate analysis). We analyzed data separately from low-gradient and steep-gradient stations on Johnson Creek, and pooled the data from all sampling stations on Crooked Fork.

In 1967 we repeated habitat analysis on Johnson Creek at two stations after removing steelhead from them and at two stations in Crooked Fork after removing the few chinook present. We used these sections because we could kill and remove the undesired species most conveniently there. Then we compared distribution of fish in induced allopatry to the sympatric distribution of the previous year by multiple regression analysis and a modified chi-square test of independence. We removed fish of the unwanted species from these areas 2 weeks before sampling, with a speargun and a diver-operated gun which fires an electric blasting cap under water. The latter device collected individual fish with

minimum disturbance. We cleared unwanted immigrants a second time 1 or 2 days before sampling. Pollard (MS 1969) observed that habitat emptied by mortalities was filled again by immigrants in less than 2 weeks. We assumed that space vacated by one species would quickly fill.

MICROHABITAT ANALYSIS

While habitat analysis related distribution and abundance of fish to characteristics of the physical environment it did not reveal the microhabitat that individual fish occupied. To define microhabitats we employed a different approach. On each study stream we established transects 9 m long at 0.16-km intervals over 8 km of stream, then sampled these transects at predetermined distances of 0.3-9.0 m from shore to ensure that fish were collected in all habitats from margin to mid-stream.

We collected individual fish from their territorial focal points (the location at which the fish spends the most time; Wickam 1967) with a blasting-cap gun, then measured several environmental characteristics at the focal point: substrate size, velocity faced by the fish, surface velocity, depth, distance of fish from substrate, maximum water velocity within 0.6 m, and distance from other steelhead or chinook. In sampling a transect the diver entered the water 15 m downstream and slowly crawled along the bottom up to the transect line looking for fish at the specified distance from shore. When the diver sighted a fish he observed it from downstream for 3-5 min before collecting it so that he could estimate focal point, distance from bottom, and distance from other fish visible to the diver. Immediately after stunning the fish, the diver marked the focal point with a red flag. To minimize errors in marking locations of focal points, we initially observed fish from distances of 4-8 m and then approached them with extreme caution. If a fish showed any indication of alarm or displacement, we did not collect it.

To ensure microhabitat sampling for all sizes of chinook, from post-emergence to pre-smolt, we collected fish (as noted above) at 3-week intervals on Johnson Creek from May 13 to mid-August 1967, and collected steelhead in Crooked Fork in August 1967.

We calculated multiple correlations of fish lengths and physical features of the environment.

INVERTEBRATE DRIFT SAMPLING

Stream salmonids consume mostly invertebrate drift, and may select a habitat which provides maximum drift (Chapman 1966), so we collected drifting invertebrate organisms from each stream with drift nets in 1967 to determine if current speed affected food availability. The sampling net had 1-mm mesh and a mouth 15 x 30 cm and we fished it with the shortest side upright in different current speeds for 15 min at 4-hr intervals, affixing the net to steel fenceposts driven into the substrate.

TIMING OF LIFE HISTORY EVENTS AND SEASONAL GROWTH

Chinook spawn in August and September in both creeks. Fry emerge primarily in March of the following

year and migrate to sea in the spring about 14-15 months after emergence. A few precocious male chinook remain for a second growing season in fresh water, then die. Summer steelhead spawn in May and most fry emerge in July. Most steelhead spend three growing seasons in fresh water before migrating to sea.

These differences in time of spawning, emergence, and seaward migration of the two species create intra- and inter-specific size groupings (Fig. 2). For example, by August 1 in Crooked Fork Creek age 0 steelhead reach a mean size of about 32 mm, age 0 chinook 62 mm, age 1 steelhead 95 mm, and age 11 steelhead 143 mm.

In these streams juveniles of both species either move downstream in the fall (but not to sea) or burrow into the substrate for the winter (Edmundson et al. 1968). Most large juvenile steelhead that will undergo smolt transformation the following spring move downstream in the fall (Chapman and Bjornn 1969). Many age 0 chinook and age 0 and age 1 steelhead enter the substrate in late October and do not begin growing again until the following May.

Juvenile chinook actually grow during about 8 of the 15 months they spend in fresh water; they spend the remaining 7 months overwintering in the substrate. At the end of the first growing season the cohort has a mean length of about 77 mm. The following year the fish resume feeding in May and become smolts in late May or early June at a mean length of about 85 mm.

Steelhead usually spend about 35 months in these tributaries, 14 growing and 21 overwintering. Their mean length reaches 60 mm when they enter the substrate in late October. In the second summer mean length increases about 12 mm/month and they attain mean lengths of 125 and 165 mm at the end of the second and third growing seasons respectively. The fish usually become smolts in late May and early June prior to their fourth summer at an average length of about 170 mm. Steelhead appear to increase in mean length slightly faster than chinook so the interspecific size discrepancy between age 0 fish decreases slowly (Fig. 2). But at no time were the mean lengths of steelhead and chinook of given age-classes equal.

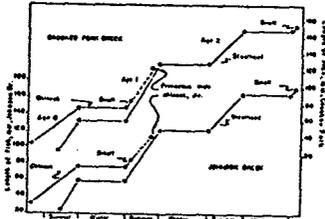


FIG. 2. Comparative growth of juvenile summer chinook salmon and steelhead trout in Crooked Fork Creek (above) and Johnson Creek (below). (Mean lengths for 1966-68 presented in simplified linear form.)

Inter- and Intra-Specific Differences in Habitat Occupied

Crooked Fork Creek — In August 1966 in 924 m² of habitat on Crooked Fork Creek, the two species used some of the same velocities or depths or substrata, but had different modal densities (Fig. 3). Age 0 chinook and age 0 steelhead were found together on 17 sets out of the 24 and 30 respectively on which they occurred. Age 0 chinook and age 1+ steelhead were found together on 17 sets of the 24 and 28 respectively. Age 0 steelhead and 1+ steelhead occurred together on 16 sets. The species were found together in sets where density of one or both species was low (less than 0.1 fish/m²) and never where the density of both species was high (0.5 fish/m² or more). Age 0 and age 1+ steelhead overlapped in the same manner. In other words, chinook and steelhead tended to differ both intra- and inter-specifically by age or size, with respect to physical habitat used. We compared patterns of habitat occupancy with a modified chi-square test; for example, we tested the numbers of age 0 chinook against the numbers of age 1+ steelhead on all occupied habitat sets to assess significant differences in distribution. We tested all species and age-group combinations. The pattern of habitat occupancy for each age-group of steelhead differed significantly from that of chinook (P<0.01). Age 0 and age 1+ steelhead also differed in habitat occupancy (P<0.01).

We observed greatest densities of underyearling chinook some distance from shore in pools or eddies 0.6-1.0 m deep (Fig. 3) and velocities under

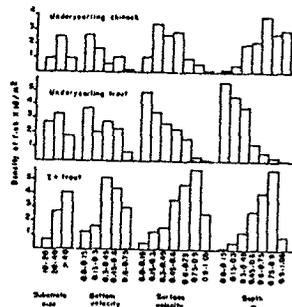


FIG. 3. Distributions of juvenile chinook and steelhead according to habitat characteristics in 924 m² of habitat in Crooked Fork Creek in August 1966.

0.5 m/sec. We found lower densities of chinook in shallower, faster (over 0.6 m/sec) water where the fish behaved territorially.

Underyearling steelhead lived in highest density in water of less than 0.5 m depth and less than 0.3 m/sec velocity. They lived as territorial bottom dwellers and associated with large rubble. Despite the high densities of steelhead fry in water of low velocity, we saw few fish in still water.

We observed the greatest densities of age 1+ steelhead in deeper, (>0.6 m), faster (>0.5 m/sec) water. Under all observed circumstances age 1+ steelhead lived territorially in association with the substrate.

We calculated stepwise multiple linear regressions with density of underyearling chinook or steelhead, or age 1+ steelhead, as the dependent variable, and substrate size, bottom velocity, surface velocity, depth, and density of the remaining two species or age-groups as the independent variables. Depth correlated significantly with the distribution of chinook and it accounted for 31% of the observed variation in density. The other five variables accounted for only an additional 18% of the variability. Depth correlated significantly with the distribution of 0 steelhead and 1+ steelhead and "explained" 34 and 41% respectively of the observed variation in their densities. The other five variables accounted for an additional 12% and 11% of variability respectively. While depth alone correlated significantly with distribution of all three groups of fish, we noted a negative correlation (-0.59) for age 0 steelhead and a positive correlation for age 0 chinook and age 1+ steelhead (0.56 and 0.64 respectively). We also related density of fish individually to the four parameters of physical habitat and concluded that chinook and steelhead segregate, albeit incompletely. For example, we calculated the density of fish within each 0.15-m depth stratum independently of the other three variables. This artificial separation of habitat features of course does not represent the actual pattern of habitat occupancy since the four parameters were inseparably interrelated.

Johnson Creek — Sympatric populations of juvenile chinook salmon and steelhead trout in Johnson Creek tended to segregate with respect to depth, velocity, and substrate. We sampled habitat in Johnson Creek during July 1966 examining 1914 m² of habitat; 1253 m² in the upstream low-gradient portion of the study area and 561 m² in the steep-

gradient area downstream. The low-gradient area, sampled early in July before emergence of age 0 steelhead, contained over 1.8 m² age 0 chinook and 0.1 m² age 1+ steelhead (Fig. 4). We also sampled the steep-gradient area later in the month and found densities of age 0 steelhead, age 0 chinook, and age 1+ steelhead in this habitat of 0.2, 0.5, and 0.1/m², respectively.

Low gradient — In the low-gradient area we found 30 habitat sets of area greater than 4.5 m². Age 1+ steelhead and age 0 chinook lived together on 9 out of the 10 and 49, respectively, on which they occurred. No 1+ steelhead resided in the habitat most densely occupied by chinook and we saw only 0.1 age 0 chinook/m² in the habitat most densely occupied by steelhead. Chi-square tests of independence demonstrate highly significant differences of habitat occupancy for both species. A negative correlation of -0.63 between densities of age 0 chinook and age 1+ steelhead also suggests interspecific segregation. We saw most age 0 chinook in water of less than 0.6 m/sec velocity over a sand or silt substrate. A density of 6.5 fish/m² in this type of habitat was four times greater than the highest densities recorded on Crooked Fork Creek (1.6 fish/m²) and in the steep-gradient area of Johnson Creek (1.4 fish/m²). We also found a mean of 2.8 fish/m² in quiet water over sand bottom at a depth 1.6 m. In water of higher velocities the fish lived territorially and closely associated with the substrate. Few age 1+ steelhead lived in the low-gradient area. We saw greatest densities in fast water between pools. In this latter environment

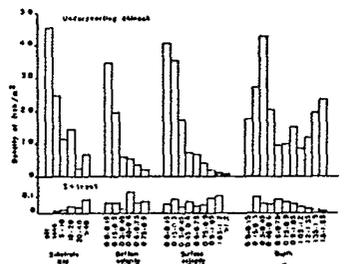


FIG. 4. Distributions of juvenile chinook and steelhead according to habitat characteristics in low-gradient area of Johnson Creek 1966.

*"Accounted for" or "explained" variation means the proportional reduction in total sum of squares owing to regression.

age 1+ steelhead occupied the same habitat as in Crooked Fork Creek, seeking areas of large substrate (greater than 20 cm in diameter), depths of 0.6-0.9 m, and velocities up to 0.6-0.9 m/sec.

Multiple regressions calculated for fish density on all habitat sets in the low-gradient area indicated that only surface velocity correlated significantly with distribution of both species and accounted for 54% of the variability of chinook density and 57% of the variation in age 1+ steelhead density. But chinook density correlated negatively with surface velocity (-0.74) while steelhead density correlated positively with this parameter.

All variables accounted for 55 and 80% of variation in density of age 0 chinook and 1+ steelhead, respectively. The overall regression (F) for age 0 chinook was highly significant ($P, 0.1$). For age 1+ steelhead the overall regression was significant at about $P, 15$, which indicates a 15% probability that chance may have reduced the total sum of squares. This relatively higher probability results from a few observations and many independent variables.

High gradient — In the steep-gradient area the fish tended to segregate inter- and intra-specifically in respect to habitat (Fig. 5). We identified 27 habitat sets of area greater than 4.5 m²; age 0 chinook occupied 19, age 0 steelhead 11, and age 1+ steelhead 18. Habitat occupation overlapped only in areas of low density of one or both species. Age 0 chinook and age 1+ steelhead occurred together on 12 habitat sets of 19 and 18, respectively, on which they were observed. Age 0 chinook and age 0

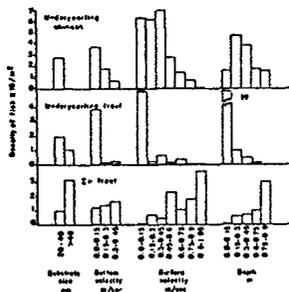


FIG. 5. Distributions of juvenile chinook and steelhead according to habitat characteristics in steep-gradient area of Johnson Creek 1966.

steelhead were observed together on 9 sets of 19 and 11, respectively, and age 0 steelhead and 1+ steelhead on 5 habitat sets. The habitat sets most densely occupied by the two groups of fish overlapped very little, and overall patterns of habitat occupancy of age 0 chinook, age 0 steelhead, and age 1+ steelhead significantly differed. Age 0 steelhead lived in water of velocity less than 0.15 m/sec and depths less than 0.15 m; age 0 chinook resided in greatest abundance in deeper (over 0.15 m) water of up to 0.5 m/sec farther offshore, and age 1+ steelhead lived in the midstream environment. The smallest fish of either species lived close to the stream margin and the largest fish faced more rapid velocities (0.5-1.0 m/sec) in the main flow.

In multiple regression analysis of data from the steep-gradient area, we found that surface velocity and density of age 0 steelhead correlated significantly (negatively) with distribution of age 0 chinook and accounted for 71% of observed variability. All parameters accounted for 73% of observed variability. Depth and substrate correlated significantly with distribution of age 0 steelhead. Three variables (depth, substrate, and density of 0 chinook) accounted for 79% of observed variation in distribution of 0 steelhead; all variables explained 80% of variability. Distribution of 1+ steelhead significantly correlated with substrate size which accounted for 69% of observed variation in density.

For all areas studied, it appears that distributions of the species and age-classes do overlap, but as response surfaces in several variables overlap in space. The loci of maximum response (modal sets) are discrete, even though parts of the surfaces may intersect.

Effects of Sympatry on Local Distribution

Steelhead — Nilsson (1967) notes that the interactive segregation results from competition between closely related species with similar ecological demands. If the distributions of fish in sympatric populations of two species equal those in allopatric populations, environmental preferences probably differ genetically and interspecific spatial interaction should not occur.

We found no evidence that steelhead changed preferred habitat in the presence of chinook. During the summer of 1967 we examined the distribution of steelhead on Crooked Fork Creek after we removed all juvenile chinook from two stations, then compared data from the 677 m² area with data collected in the same area in 1966 when chinook lived there (Fig. 6). In multivariate analysis of the data we learned that the most densely occupied habitat set for each age-group of steelhead remained the same in 1967 as in 1966. Across years

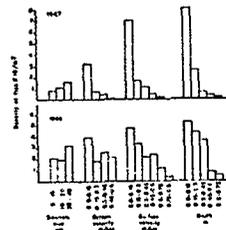


FIG. 6. Distributions of age 0 steelhead according to habitat characteristics in sympatry (1966) and in allopatry (1967) in Crooked Fork Creek.

the age-groups did not differ significantly ($P, .05$) in mean length or densities. The numbers of each age-group of steelhead on all occupied habitat sets in both years did not differ statistically ($P, .05$). In both 1966 and 1967 most age 0 steelhead lived in inshore waters while in both years age 1+ steelhead usually occupied the deeper, faster water of the mid-stream environment.

Despite minor differences across years, distinct similarities in the importance of the habitat variables for each age-group in each year led us to conclude that fish of each species tend to distribute themselves similarly in allopatry and sympatry. In multiple-regression analyses we found similarities in the importance of the four habitat variables to fish distribution in both years. In 1966 both substrate size and water depth correlated significantly with density of age 0 steelhead. In 1967 substrate alone correlated significantly with fish distribution although depth approached significance ($P, .09$). Substrate size, surface velocity, and depth each correlated significantly with distribution of 1+ steelhead in 1966 while all four variables correlated significantly with distribution of 1+ steelhead in 1967.

In univariate analysis of these data we also noted no change in habitat selection by fish between 1966 and 1967. In 1966, steelhead lived more often in deeper, faster water and over smaller substrate than they did in 1967. Intraspecific agonistic behavior resulting from high steelhead numbers in 1966 could have caused this difference. In 1966 density of age 0 steelhead equalled 0.3 fish/m² (1.3 fish/m² in preferred habitat). In 1967 density reached only 0.1 fish/m² (1.5 fish/m² in preferred habitat) in spite of the absence of chinook. Overall densities in the 2 years differed significantly ($P, .05$) while density on preferred habitat did not.

In univariate analyses of the distribution of age 1+ steelhead in 1966 and 1967 we found small differences in the most densely occupied strata. The presence of chinook in 1966 had no effect on habitat selection of age 1+ steelhead (Fig. 7).

Chinook — The distribution of chinook in two stations on Johnson Creek in 1967 was examined after we removed as many steelhead as we could from these areas. In one station we sampled before emergence of age 0 steelhead and successfully removed age 1+ steelhead. In the other station, we sampled in August after age 0 steelhead had emerged and after the fall downstream movement of age 1+ steelhead apparently had begun. Attempts to remove all steelhead of either age-group failed. In addition, the mean size of chinook was significantly larger in 1967 than it was in 1966 and distributions differed significantly across years. For these reasons we could not make a direct comparison of intra- and inter-specific distribution in August of age 0 chinook and steelhead.

In the station examined in June across years we observed juvenile chinook on 49 habitat sets in 1966 and on 45 habitat sets in 1967. The overall pattern of habitat occupancy differed little between years (Fig. 8). In both years most age 0 chinook usually lived in water of less than 0.6 m/sec, in all depths, and over silt, sand, and rock of less than 10 cm diameter.

Multiple regression analyses indicated that in 1966 and 1967 surface velocity correlated significantly with distribution of age 0 chinook and accounted for 52 and 57% of variation in density, respectively. In addition, distribution significantly correlated with substrate in 1966 and with depth in 1967. All variables accounted for 58 and 65% of observed variation in distribution in 1966 and 1967, respectively.

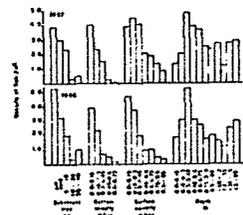


FIG. 7. Distributions of age 1+ steelhead according to habitat characteristics in sympatry (1967) and in allopatry (1966) in Crooked Fork Creek.

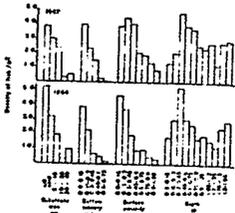


Fig. 8. Distributions of age 0 chinook according to habitat characteristics in sympatry (1966) and in allopatry (1967) in Johnson Creek.

Preferred strata remained the same in both years, except that in 1966 greatest densities were found in the surface velocity stratum of 0.0-0.15 m/sec, and in 1967 in 0.15-0.3 m/sec. But the numbers present on preferred strata did not differ significantly ($P > .05$) between years.

Influence of Fish Size on Habitat Occupancy

Because mean lengths of steelhead and chinook of given age-classes were not equal, we examined microhabitats selected by individuals of each species at a given body length. We included only fish that we collected farther than 3 m from members of the other species; the data therefore represent as nearly as possible intraspecific microhabitat selection.

In August 1967 a diver collected 77 steelhead (28-171 mm) from the focal points of their territories in Crooked Fork Creek. We then related length of each fish to selected physical characteristics of the focal point (Fig. 9). Steelhead of all sizes most often chose territories over large rubble substrate and rarely more than 15 cm off the bottom. They apparently shifted from shallow slow water at the stream margin to deeper faster water as they increased in length. We calculated respective simple correlations of 0.75, 0.59, 0.60, and 0.63 for the relationship between steelhead length and water velocity at the focal point, surface velocity, depth, and maximum velocity 0.6 m laterally.

In stepwise multiple regression analysis six independent variables accounted for 76% of total variability in microhabitat selection related to fish length. Velocity at focal point, distance from bottom, and maximum velocity 0.6 m laterally were all correlated significantly ($P < .01$) with fish length and in combination accounted for 74% of total variability.

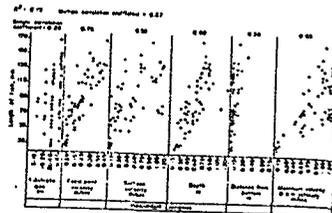


Fig. 9. Correlations between steelhead length and habitat variables in Crooked Fork Creek 1967.

A diver collected data on microhabitat selection of juvenile chinook (Fig. 10) from May 15 to August 15, 1967, on Johnson Creek. During this period we collected 58 fish (32-117 mm) from the focal points of their territories. We rarely took chinook larger than 100 mm, but sampled a few precocious males in their second growing season.

In a multiple regression analysis all six independent variables accounted for 92% of variability in microhabitat selection due to length. Velocity at focal point, surface velocity, and depth all correlated significantly with fish length ($P < .01$).

After emergence chinook generally selected very quiet shallow water over a variety of substrata ranging from silt to 20-cm rubble. As the fish grew they continually shifted their distribution to deeper faster water. Territorial chinook associated closely with the substrate while hierarchical social groups occurred in quiet water up to 0.8 m above the substrate. We calculated strong simple correlations between fish length and focal point velocity (0.92), surface velocity (0.87), depth (0.65), and maximum velocity of 0.6 m laterally (0.77).

In comparing the microhabitats selected by equal-sized fish of the two species we found that age 0

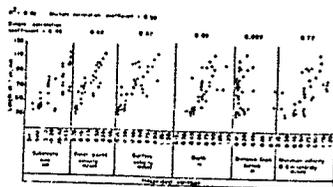


Fig. 10. Correlations between chinook length and habitat variables in Johnson Creek 1967.

chinook and steelhead 35 mm long select similar velocities and depth. We found 35-mm chinook over sandy or silty substrate while 35-mm steelhead selected 20-40-cm rubble. But we collected small postemergence chinook in May and early June during the spring freshet. Under these conditions, the quiet waters and shallow depths these fish seek lie almost exclusively in backwater areas with sand or silt substrate. If postemergence steelhead lived in the stream at this time of year they would also have to occupy areas of sandy or silty substrate. If steelhead and chinook of this size occurred simultaneously they would seek nearly identical habitat conditions and severe interaction for habitat would probably occur. But this potentially competitive situation does not occur because the species emerge at different times.

Precocious male chinook select microhabitat very similar to that selected by age II steelhead (Fig. 9 and 10). If all chinook remained in the stream for a second growing season they would probably compete directly for habitat with larger steelhead. Since size usually determines the outcome of aggressive encounters, chinook which stayed for a second growing season would probably suffer a disadvantage in attempting to occupy the habitat they desire. Age I steelhead and chinook do not compete because nearly all chinook migrate to sea after one growing season.

Invertebrate Drift and Microhabitat Selection

Both species consistently occupied microhabitat, as individual fish nearly always lay close to fast water and faced moderate current speeds. In 1967 we investigated the idea that food availability was correlated with this behavior. On both study streams water at high speed delivers more drift food to a given point than does water at lesser speed. We sampled on Crooked Fork Creek on July 11-12, 1967. Samples of 15 min duration were collected simultaneously from velocities of 0.4 and 0.8 m/sec every 4 hr for 24 hr (Fig. 11). The nets captured 382 invertebrate drift organisms at 0.8 m/sec and 205 organisms at 0.4 m/sec, a highly significant difference ($P < .01$). During daylight the nets took an average of 23 organisms/15-min sample at 0.8 m/sec and 10 at 0.4 m/sec. At night the nets captured an average of 144 organisms per sample at 0.8 m/sec and 83 at 0.4 m/sec.

When we compared the sizes (body length) of drifting insects delivered by the two current speeds we found that organisms captured during the day (mean length 2.4 mm) were significantly smaller ($P < .01$) than organisms drifting at night (mean length 4.1 mm). But the sizes of organisms captured at the two current speeds during the day

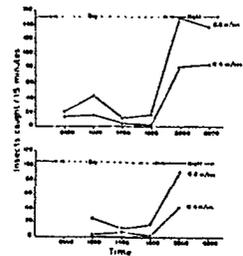


Fig. 11. Diel variation in quantity of drift insects captured during 15-min samples at two current speeds. Top graph for Crooked Fork Creek, July 11-12, 1967. Lower graph for Johnson Creek, August 22, 1967.

($\bar{x} = 2.8$ mm at 0.4 m/sec and 3.0 mm at 0.8 m/sec) and those at night ($\bar{x} = 3.8$ mm at 0.4 m/sec and 4.3 mm at 0.8 m/sec), did not differ significantly ($P > .05$).

Subsequent sampling on Johnson Creek on August 22 at current speeds of 0.4 and 0.8 m/sec yielded similar results (Fig. 11). Fifteen-minute samples were collected at 4-hr intervals between 1000 and 2200 hr; the nets took 62 organisms at 0.4 m/sec and 134 at 0.8 m/sec (difference significant at $P < .01$). Insect sizes at the two current speeds ($\bar{x} = 3.18$ mm at 0.4 m/sec and 3.45 at 0.8 m/sec), and between day ($\bar{x} = 3.40$ mm) and night ($\bar{x} = 3.69$ mm), did not differ significantly ($P > .05$).

Discussion

Sympatric chinook and steelhead trout segregated in summer. In short-term allopatry each species occupied the same types of habitat as in sympatry. In analysis of microhabitat we found strong positive correlations between individual fish size and depth and the water velocities that fish faced and lived near.

In samples of macrohabitat we noted considerable overlap in habitat sets occupied by chinook and steelhead. But such overlap occurred only where density of one species was low. Macrohabitat set classes probably glossed over more precise microhabitat sets and unduly emphasized overlaps.

As juvenile steelhead and chinook become larger, they move into faster, deeper water, and, at any given size in summer steelhead and chinook use water of similar physical character. But steelhead

spawn in spring and chinook spawn in early fall, creating intra- and inter-specific size groupings of pre-smolts which minimize interaction for space. Mean lengths of chinook and steelhead begin to converge in their second growing season but severe interaction apparently does not occur because all chinooks but a few precocious males become smolts at the beginning of their second growing season. The growth of steelhead quickly moves each cohort away from the stream margin, minimizing interaction between the three year-classes of pre-smolts.

Studies of habitat utilization by underyearling coho and chinook (Lister and Genoe 1970) also revealed progressive movement from areas of low velocity at the stream margin to habitat of higher velocity as the fish grew. Lister and Genoe related segregation of juvenile coho and chinook to differences in life history patterns and growth rate, and concluded that small differences in life history patterns could effectively minimize interspecific interaction for space. Hartman (1965) related discrete microhabitat utilization of juvenile coho and steelhead to differences in behavior.

The positive correlation between water velocity and quantity of insect drift could suggest a key factor stimulating movement of juvenile salmonids into water of progressively higher velocity as the fish grow. Our studies of microhabitats occupied by steelhead and chinook indicate that even large pre-smolts living in swift mid-stream waters remain near the bottom in low velocity areas except when defending territories or pursuing food items. This behavior should maximize the quantity of drift food available to an individual fish while minimizing energy expenditures needed to remain at a feeding station.

Faster, deeper water also provides more overhead cover and protection from avian or terrestrial predators than does quiet shallow water, so movement of fish to deep, fast water could also be explained as cover-related. Distribution of chinook underyearlings in stream channels can be strikingly altered by moving points of food input (Chapman and Bjorn 1969). The fish adjust quickly to food sources. But proof or rejection of a food or cover-related shift to faster, deeper water would require extensive experimentation.

Development of different emergence times and different temporal demands for physical habitat typifies selective segregation (Nilsson 1967), which occurs when differences in behavior, morphology, or physiology become genetically encoded. Hartman (1965), Saunders and Gee (1964), Kalleberg (1958), and Lindroth (1955) all noted segregation of competing species through interaction. Nilsson (1967) termed this interactive segregation and speculated that it typifies young faunas in, e.g., recently de-

glaciated areas. Our studies indicate that spatial segregation between steelhead and chinook is probably based on genetic differences rather than inter-specific interaction, and in the continuum between interactive and selective segregation falls closer to the latter.

Evidence that chinook and steelhead can coexist leads us to state that sympatric populations of the two species would use available habitat more fully and produce more tissue in a given area than would allopatric populations of either species.

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OBITUARY

Andrea Kyle Pritchard

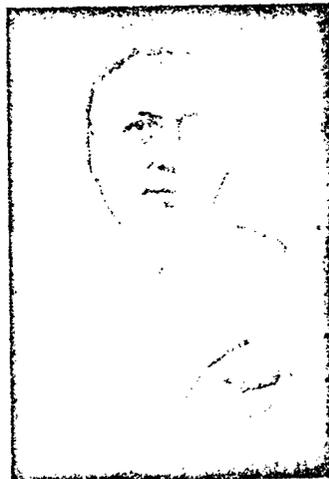
1905-1971

Dr A. L. (Andy) Pritchard died at the age of 66 in Ottawa on June 28, 1971, after several years of retirement from a distinguished career in fisheries research and management.

Dr Pritchard's career fell into two almost equal parts: first, as a fisheries research scientist and, second, as a fisheries manager. From 1928 to 1948 he served with the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., where he conducted pioneering research on pink salmon biology and published many outstanding papers. As a foretaste of things to come, he later headed an investigation of salmon problems on the Skeena River, from which developed the concept of total management of all the salmon runs in that river and later in others.

His second period, 1948 to 1966, was quite naturally in fisheries management, again in something of a pioneering role. Senior officials of the Federal Department of Fisheries recognized Dr Pritchard's management qualities as demonstrated by the success of his Skeena River project, and in 1948 offered him a senior post at Ottawa to develop an applied fisheries group of technical specialists. The branch, established by Dr Pritchard, initially known as Fish Culture Development and later Resource Development, was staffed by a group of biologists, engineers, and support staff, many of whom were associated with Dr Pritchard on the Skeena River and other Research Board projects. Dr Pritchard built a strong technical branch in the Department of Fisheries that was later merged with the enforcement branch to become Conservation and Development Service.

Dr Pritchard's devotion to the service continued as a senior administrator in Ottawa where he remained until his retirement in 1966. As well as building and organizing a strong technical and enforcement service, he served on a great many departmental and interdepartmental committees. He was active on the planning group responsible for formation of the Great Lakes Fishery Commission and continued as a Commissioner with that group until his death. Outside of the service, but still concerned with fisheries, he had a close association for



many years with the American Fisheries Society, and served as President of this international organization in 1954-55.

Andy Pritchard will be remembered for many achievements. He was a first-class research scientist. He was also a first-class fisheries manager on both the national and international scene. Most importantly, he was a dedicated, aggressive, warm-hearted, loyal, and inspirational leader. It was these qualities that placed his stamp on a generation of fisheries biologists, engineers, and administrators, who have carried the Pritchard touch into leading positions of authority in Canadian fisheries biology and management today.

E. W. BURRIDGE
R. R. LOGIE