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

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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

by

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Behavioural interactions were studied, in a stream tank, between coho salmon (*Oncorhynchus kisutch*), brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*), and between steelhead trout (*Salmo gairdneri*), Atlantic salmon and brook trout. Steelhead trout and Atlantic salmon were the most aggressive species. Steelhead were the most aggressive, and able to displace any of the other species of similar or slightly larger size, from preferred locations. Brook trout and coho were the least aggressive and least territorial of the four species. In pools they formed groups, with a dominant fish in the lead. Both species were more mobile than Atlantic salmon or steelhead. Dominance was based to a large extent on size. In all experiments the dominant species showed the best growth. Morphological and behavioural characteristics probably favour Atlantic salmon parr over the other three species in shallow fast water. Severe competition might be expected between Atlantic salmon parr and juvenile steelhead trout, both riffle dwellers, and between coho and small brook trout, both predominantly found in the pool environment. Introductions of these Pacific salmonids should be discouraged until adequate field studies have been undertaken.

Key words: juvenile salmonids, behavioural interactions

RÉSUMÉ

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. Can. Tech. Rep. Fish. Aquat. Sci. 1029: v + 116 p.

On a étudié, dans une fosse d'un cours d'eau, les relations éthologiques entre le saumon coho (*Oncorhynchus kisutch*), l'omble de fontaine (*Salvelinus fontinalis*) et le saumon de l'Atlantique (*Salmo salar*) ainsi qu'entre la truite arc-en-ciel (*Salmo gairdneri*), le saumon de l'Atlantique et l'omble de fontaine. La truite arc-en-ciel et le saumon de l'Atlantique furent les espèces les plus agressives. Les truites arc-en-ciel démontrèrent le plus d'agressivité et furent capables de déloger toute autre espèce, de taille égale ou légèrement plus grande, de meilleurs emplacements. Des quatre espèces, l'omble de fontaine et le saumon coho manifestèrent le moins d'agressivité et d'attachement à un territoire. Dans les bassins, ils formèrent des groupes, avec un dominant à leur tête. Les deux espèces étaient plus mobiles que le saumon de l'Atlantique ou la truite arc-en-ciel. La dominance dépendait en grande partie de la taille. Dans toutes les expériences, les espèces dominantes

connurent une meilleure croissance. Les caractères morphologiques et éthologiques favorisent probablement davantage la croissance, dans une eau rapide et peu profonde, des jeune saumons de l'Atlantique (tacons) que des trois autres espèces. On peut s'attendre à une forte compétition entre les tacons de saumon de l'Atlantique et les jeunes truites arc-en-ciel qui habitent les haut-fonds ainsi qu'entre les saumons coho et les petites ombles de fontaine, qui, pour leur part, s'il se trouvent surtout dans de même bassins. L'introduction de ces salmonidés du Pacifique est à déconseiller tant que l'on n'aura pas entrepris des études appropriées sur le terrain.

2. INTRODUCTION

Coho salmon (Oncorhynchus kisutch), a Pacific salmonid, has in recent years been introduced to the Great Lakes and to the east coast of North America and is being successfully maintained by fish culture. Early attempts at introduction were unsuccessful (Scott and Crossman 1973; Everhart 1966). However, increased efforts at introduction and natural stock selection may gradually allow ecological compatibility or competitive advantage over native salmonids. Its life history and habitat requirements both in the river and at sea are very similar to those of Atlantic salmon (Salmo salar), so there is much concern that populations of the indigenous salmon might be adversely affected (e.g. Gruenfeld 1977; Williams 1980). The coho salmon spawning time overlaps that of Atlantic salmon, with coho spawning later so that some of the same spawning sites might be used. Coho fry emerge earlier than Atlantic salmon, so that the earlier growth and therefore larger size might give a competitive advantage. Like the native salmonids juvenile coho are primarily insectivorous and therefore potential competitors but they can be partly pisciverous, so that also they might prey upon Atlantic salmon and brook trout. A further danger is that an exotic disease or parasite might be introduced. Rainbow trout and steelhead, the anadromous strain (Salmo gairdneri), is established on the East Coast (MacCrimmon 1971) and the range is being extended. As an exotic salmonid from the West, it also presents dangers to the native species.

Juvenile coho salmon naturally co-exist with juvenile steelhead trout in many streams of the west coast of North America. In spring and summer the steelhead are found mainly in the riffle areas and the coho in the pools. This interactive segregation is brought about by aggression (Hartman 1965). Trout were aggressive and defended areas in riffles but not in pools; coho were aggressive in pools but were less inclined to defend space in the riffles. In Atlantic salmon rivers of eastern North America, the fry and parr stages of Atlantic salmon usually co-exist with brook trout (Salvelinus fontinalis). These are frequently the two dominant fish species in the river. Parr are more abundant in riffle areas whereas brook trout are more common in the pools (Keenleyside 1962; Gibson 1966). In the absence of salmon parr, or when food is abundant, brook trout can inhabit fast water areas. The presence of parr reduces the biomass of brook trout, especially of yearlings. These interactions are brought about by both aggression and competition (Gibson 1973).

Questions under consideration in this study were, whether salmon parr and brook trout may compete successfully with coho and steelhead, and what might be the possible interactions between these species at the juvenile fluviatile stages.

3. MATERIALS AND METHODS

Observations were made in a stream tank. The entire apparatus was 9.1 m long and 3.0 m wide, and consisted of a circular wooden flume with recirculated water (Fig. 1). A channel 1.2 m wide and another 0.6 m wide were joined by a pool section 1.5 m wide and deeper by 30 cm than the two channels. The ends of the channels opposite the pool end had screens of 0.64 cm plastic mesh to prevent fish from entering the section containing an electrically driven propeller, which moved the water. A 2 h.p. electric motor was housed on a

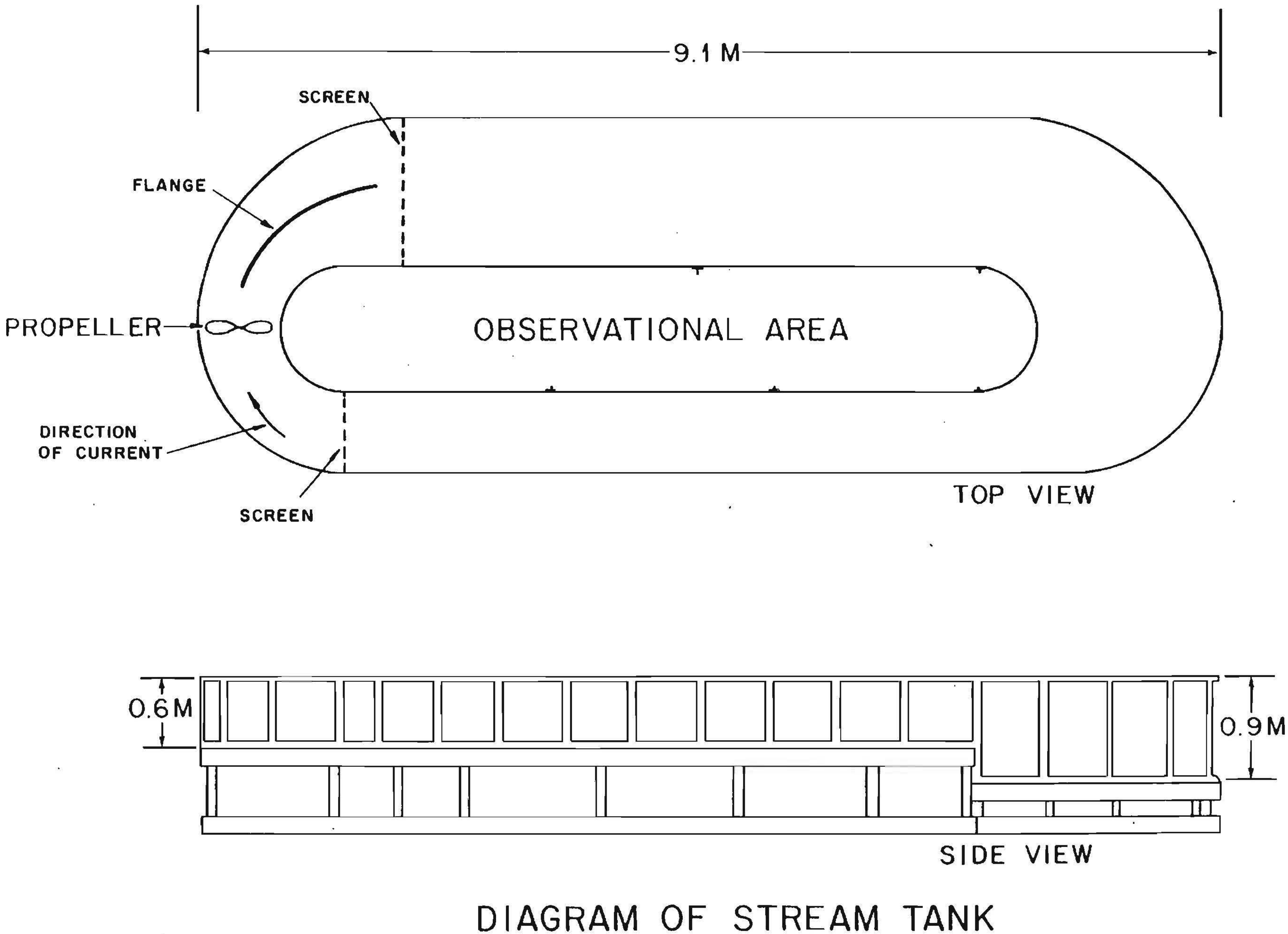


Fig. 1. A plan view of the stream tank.

concrete base constructed on the floor on the external (convex) side of the apparatus at the narrow end. This was connected by belts to the propulsion unit. In the observational section, the lengths of the wide channel, pool and narrow channel were respectively 4.9 m, 3.4 m and 5.5 m. In the first nine experiments the narrow channel was 3.7 m long. The total observation area measured 14.3 m^2. The water depths were maintained at 45 cm in the two channels and 75 cm in the pool. A current was created by driving water down the wide channel, around the pool and back up the narrow channel. An even flow down the wide channel was maintained in the last twelve experiments (13-24) by having a 1.5 m long wooden flange downstream from the propeller, but between the screens, out of the observation area. In the earlier twelve experiments three additional flanges were used, of 1.7 m, 1.4 m, and 1.3 m, in length. The four flanges were fixed parallel to each other. Judging by conditions in the latter experiments, one flange was sufficient to give a satisfactorily even velocity.

Water velocities could be varied by changing gears to the propeller. The inside of the flume and the flanges were painted with epoxy varnish, and the propeller and housing with non-toxic paint. A constant trickle of well water and an overflow were at the machinery end of the tank. Also at this end were a heater and a thermostat, and during cold water experiments 9 m of 1.27 cm diameter aluminum tubing was coiled here, through which was run sea water at 2°C.

Fluorescent and incandescent lights were suspended 85 cm above the water surface; three fluorescent and three incandescent lights over the wide channel, three incandescent and one fluorescent above the pool, and three fluorescent and two incandescent lights over the narrow channel. These produced radiant energy of 1.09×10^{-2} langleys/min over the water surface in the narrow channel, 1.73×10^{-3} langleys/min over the pool, and 1.18×10^{-2} langleys/min over the wide channel. These are average readings as radiant energy under the incandescent lights was slightly greater (mean 1.53×10^{-2}) than under the fluorescent lights (mean 1.11×10^{-2}). A time switch initiated the lights coming on gradually in the morning, intensifying over fifteen minutes, and going off suddenly for the night. In experiments 1-9, the fish were given a photoperiod of 14 hours. This was reduced to 8 hours in experiments 10-24, to deter possible smoltification.

The inner walls of the tank were made of acrylic (Plexiglass) 1.27 cm thick. There were two windows with a central support of angle iron for the wide channel, a single rounded sheet for the pool, and three windows for the narrow channel, with angle iron supports at the joins. Observations were made from this inner perimeter of the tank. As the fish were wary, the observational area was screened with black plastic, held on a frame away from the plexiglass, and observations were made through small slits in the screen.

The bottom of the tank was covered with a gravel substrate, marked out in 0.09 m^2 sections with white or differently coloured stones. The gravel was banked with a gradual incline from the channels to the pool. The wall opposite the observation windows was marked with lines at 0.3 m intervals to allow the observer to correct for visual distortion.

The type of experiments are shown in Table 1, and the size of the fish in Table 2. In experiments one to nine, water velocities, measured at mid-depth, were 6-8 cm/s in the wide channel, 14-17 cm/s in the narrow channel, and 3.8-6 cm/s in the pool. In experiments 10-12, water velocities were about 12 cm/s in the wide channel, 24 cm/s in the narrow channel, and up to about 10 cm/s in the pool. In experiments 13-24, water velocities were 17-24 cm/s in the wide channel, 40-42 cm/s in the narrow channel, and 0 to about 15 cm/s in the pool. The measurements were made with a Hiroi electric acoustic current meter, and by timing small pieces of drift, such as brine shrimp, over a measured distance, at approximately 0.6 x depth from the surface. The current pattern in the pool was more complicated than in the channels, as there was some upwelling, and areas of no flow. In the pool, fastest flows were at the outer parimeter and at the inlet of the narrow channel.

Automatic feeders were placed so that food as nearly as possible was provided equally for each section. One was placed at the head of the wide channel, another at the upstream end of the pool, and a third at the upstream end of the narrow channel. The feeders were made of Plexiglass discs, about 30 cm in diameter, mounted horizontally on the machinery from a time switch, so that the disc slowly revolved. 'Silver Cup' trout pellets were placed on the circumference, and as the disc turned, a flange knocked pellets off into the water. The feeders were plugged into the same electrical outlets as the lights, so that they did not function in the dark. Fresh food also was given, but after observation times. Frozen brine shrimp were frequently thrown into the machinery end of the tank, so that as the block melted upstream from the inlet screen, shrimps drifted through the tank. Chopped frozen squid was fairly frequently given, and occasionally chopped liver. These were thrown in from below the level of the tank, so as to disturb the fish as little as possible, and equally through the sections. Freshwater invertebrates from a nearby stream were occasionally added, and sometimes meal worms and garden earth worms. On some occasions fish were seen to take live freshwater invertebrates, and once fish were seen feeding on a hatch of chironomids, so that the stream tank was providing close to natural (although rich) conditions.

Atlantic salmon parr and brook trout were from the Matamek River in Quebec. In experiments 21, 22, and 23, Atlantic salmon fry were used from the Nashua National fish hatchery in New Hampshire. The eggs were taken from anadromous fish in the Penobscot River, Maine, but these originated from landlocked salmon at Cortland, N.Y. Coho salmon were from the Massachusetts hatchery in Sandwich, and were F_1 and F_2 generation fish from an anadromous run in the North River, Massachusetts. The west coast origin was from the Green River hatchery, state of Washington. Steelhead were from Perryville hatchery, Rhode Island, and originated as eggs taken from adult steelhead returning to the Washougal River, a tributary of the lower Columbia River, Washington. These adults were of hatchery origin from the Skamania Hatchery. The majority of these adults have been of hatchery origin since 1960.

The fish were kept in two hexagonal holding tanks with four glass walls and four fibre-glass walls. Each tank was 3 m in diameter, and 2.5 m high. Water was kept 80 cm deep. In one tank were kept coho, or steelhead, and in the other the Atlantic salmon parr and brook trout together. A jet of well water at 11°-12°C created a current in the tanks and an aerator was provided for each tank. Some shelter was provided on the bottom in these tanks with rocks and broken brick pipes. Fish were fed daily from automatic feeders with 'Silver Cup' trout pellets, and at intervals with chopped squid or chopped liver.

Fish were anaesthetized with MS 222 and individually branded. Atlantic salmon, coho and steelhead were branded by the cold method (Fujihara and Nakatani 1967). Brook trout were branded with a hot Nichrome wire. Fish were also weighed and measured under anaesthetization at the beginning and end of each experiment. Observations were begun at least five days after introduction of the fish. This gives time for the fish to set up territories (Symons 1971). Following a number of experiments, relative buoyancies were ascertained by placing anaesthetized fish into containers of water with various densities of dissolved common table salt. Water density was measured with a G-K Co. Squibb Urinometer. Six containers were set up, each differing in specific gravity by 0.010. The specific gravity at which a fish floated was recorded.

An experiment consisted of 10 or 20 observations. An observation was made by recording locations of each fish in the tank, and its estimated height above the substrate, on a diagram of the bottom of the stream tank. Each section of the tank (wide channel, pool, narrow channel) was observed for 15 minutes, and the behaviour of each fish was recorded verbally on a small portable tape recorder. Only acts used by an attacking fish which caused a displacement are analyzed in this paper.

The agonistic acts recorded were those suggested by Keenleyside and Yamamoto (1962), Gibson (1973), and Hartman (1965). 'Charge and chase' took place at high speed, causing displacement. 'Approach' refers to an attacking fish swimming at another fish without accelerating. A fish biting another is called a 'Nip'. 'Lateral display' refers to the maximal opening of all the fins with a slight concavity of the dorsal surface of the fish, and head and tail flexed upwards usually aligning laterally to the other fish. In 'Frontal display', the fish orients with its head pointed towards another fish, the dorsal surface of the fish is slightly convex with the head lower than the tail, the mouth is open, and the floor of the mouth is slightly depressed. 'Presence' describes the act causing a subordinate to flee at the mere sight of another fish, although the latter has made no obvious effort to displace the former. 'Drift' is used to describe a fish drifting downstream towards another but without display. In 'Supplant' one fish approaches another and takes its exact position without a contest. A fish doing a 'Wigwag' is at an angle to the horizontal, head usually down, sometimes up, with fins extended, and the fish swims with accentuated lateral movements. 'Threat nip' refers to a nip made in the direction of another fish but no contact is made. The last two acts were seen being performed only by coho salmon and steelhead trout.

4. RESULTS

The experiments and their dates are shown in Table 1, and size of the fish in Table 2.

4.1 DISTRIBUTION

The relative distribution of the four species is shown in Table 3 and in Fig. 2-5. The area of the pool was 5.0 m^2, the wide channel 6.0 m^2, and the narrow channel 2.2 m^2 in experiments 1-9, and 3.3 m^2 in experiments 10-24. Figure 2 shows the distribution of Atlantic salmon parr, brook trout and coho in the experiments with slowest flows (1-9). In these experiments at 15°C,

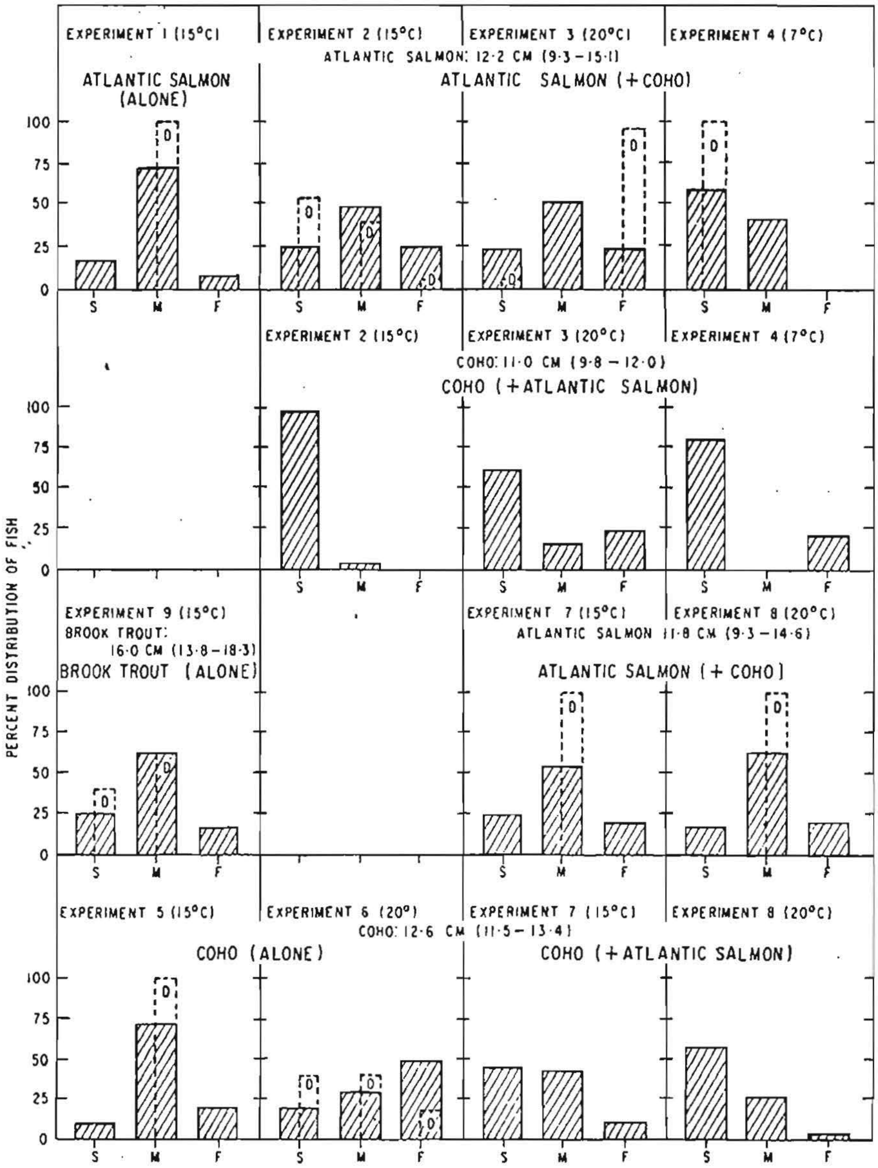


Fig. 2. The distribution of fish during experiments 1-9 in the three parts of the stream tank. S=Slow flow (pool), <6 cm/s; M=Medium flow (wide channel) 6-8 cm/s; F=Fast flow (narrow channel), 14-17 cm/s. D, in the dotted column, shows location of the dominant fish in each experiment. One group of coho was used in experiments 2, 3, and 4 (mean fork length, 11.0 cm) and another group in experiments 5, 6, 7, and 8 (mean fork length, 12.6 cm). The same Atlantic salmon were used in experiments 1, 2, 3, and 4 (mean fork length, 12.2 cm), and another group in experiments 7 and 8 (mean fork length, 11.8 cm). The relative areas were: pool (S) 5.0 m^2, wide channel (M) 6.0 m^2, and narrow channel (F) 2.2 m^2.

when either parr or coho were the sole species (experiments 1 and 5), the majority were found in the wide channel. At 20°C coho were more dispersed and were found through the narrow (50%) and wide channels (30%), and with 20% of the occurrences in the pool (experiment 6). Brook trout also at 15°C mainly occurred in the wide channel (60%) with 25% of the occurrences in the pool (experiment 9). At temperatures of 15°C and 20°C with parr and coho together, the distribution of parr was not changed (experiments 2, 3, 7, and 8). However, in experiments 2, 3 and 8, parr apparently displaced coho to the pool. In experiment 7, at 15°C coho were more numerous in the wide channel than in experiments 2 and 3, and parr did not displace coho to the same extent, possibly because the mean size of the parr was somewhat smaller than that of the coho in this experiment. However, neither were the parr displaced. At 20°C, in experiment 8, with the same fish, activity and aggression was higher, and coho were generally displaced to the pool.

In experiment 2 the coho in the pool formed a school. This school possibly attracted parr, as parr occurred more frequently in the pool (25%) than in the previous experiment (18%), and parr were sometimes seen to join the school. During the following experiment (experiment 3), at 20°C, with the same fish, the coho behaved quite differently, were dispersed, as opposed to being in a group in experiment 2, and were constantly active. They were higher in the water much of the time, and frequently rising to the surface. Coho ventured into the wide channel, but were chased out. Coho were considerably harassed by the parr, and their distribution was probably more the result of where they were chased to, rather than a preferred location. It is possible their change from a grouping behaviour, seen in experiment 2, was due in part to greater activity of the parr, tending to disperse the coho. Coho were harassed by the parr in all sections, and appeared to be mainly in unfavourable locations, such as the downstream end of the fast channel, next to the glass and at the surface, etc. The behaviour changed remarkedly for both species in the following experiment, at 7°C, when both species occurred mainly in the pool. Activity of both species was low. All the parr were motionless on the bottom, although they fed when fresh food was thrown in. Coho were more active than parr, were in a small school, and appeared to be feeding.

In experiments 10, 11, and 12, almost twice the water velocity was used than in the previous experiments. Also the narrow channel was extended an extra 1.2 m^2. Coho, parr and brook trout were tested together. The most frequent coho observations, and the dominant coho, which was the dominant fish, were in the pool. A fish was referred to as 'dominant' if it could displace all the others, and generally itself was not displaced, although it might not make the most agonistic acts. The other two species were mainly in the wide channel (Fig. 3). In experiment 11 all three species were mainly in the wide channel. More fish were able to occupy the wide channel than when a parr was the dominant fish there. A brook trout was the dominant fish in experiments 11 and 12, although a different dominant trout emerged in experiment 12. Both preferred the wide channel. Fish were more active at the higher temperature in experiment 12.

In experiments 13-24, water velocities were increased once more. In experiment 13 six parr at 15°C were observed. The majority of observations, and the dominant fish, were in the wide channel. In the following experiment six steelhead were added. A steelhead became dominant in each section, and all the parr were displaced. The dominant steelhead was in the wide channel,

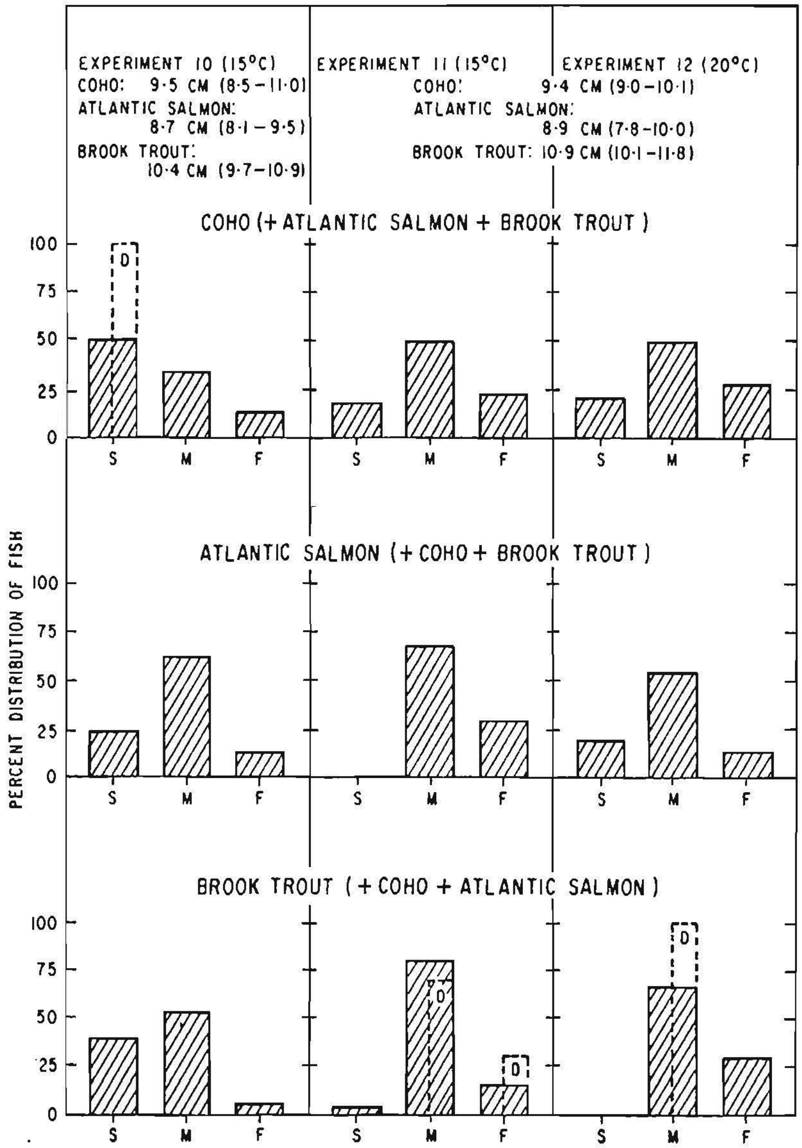


Fig. 3. The distribution of fish in the stream tank during experiments 10, 11, and 12. S=Slow flow (pool) <10 cm/s; M=Medium flow (wide channel) 12 cm/s; F=Fast flow (narrow channel) 24 cm/s. D=location of the dominant fish in each experiment. The same fish were used in experiments 11 and 12. Mean fork lengths for experiment 10 were: coho-9.5 cm; Atlantic salmon-8.7 cm; brook trout-10.4 cm. Mean fork lengths for experiments 11 and 12 were: coho-9.4 cm; Atlantic salmon-8.9 cm; and brook trout-10.9 cm. The relative areas were: pool (S) 5.0 m^2, wide channel (M) 6.0 m^2, and narrow channel (F) 3.3 m^2.

(and kept the upstream half to itself). None of the parr was in a good feeding position, except the dominant one, (and this secondary, as it had been displaced from its previous territory in the upper three-quarters of the wide channel to downstream of the dominant steelhead). Most of the parr were prevented from feeding. The distribution of the same fish changed in the following experiment, at 7°C, and both species were seen more frequently in the wide channel. The dominant steelhead, unlike its behaviour in the previous experiment, tolerated a group of fish behind it. The distribution of parr was rather different from experiment 4, at 7°C, without steelhead, when most parr were in the pool. Possibly in experiment 15 the difference was due to being kept active by aggression from the steelhead. Steelhead at this temperature held station in the fast channel (32%), whilst parr rarely occurred there (5%). Seven new steelhead were used for experiment 16. Most were seen in the narrow channel (Fig. 4). However this was due to the dominant fish occupying the upper half of the wide channel, and the next dominant occupying the lower half of the wide channel but usually chasing out all other fish from the pool. The remaining five steelhead were kept to the narrow channel. Much the same situation occurred in experiment 17, and the parr, which were introduced for this experiment, were also kept to the narrow channel. The following experiment was at 20°C, with the same fish. The main difference compared with the previous experiment was that, most of the fish occurred in the wide channel, and the dominant steelhead spent much of the time in the pool, where it was very aggressive. The next dominant at these times moved to the upper end of the wide channel. For some reason at the temperature of this experiment, most of the fish left the narrow channel, possibly related to the higher activity and greater aggression. In experiment 19 the same steelhead (minus one) were observed with six brook trout at 15°C. Two steelhead were dominant to all the other fish, and usually kept many of them in the narrow channel where there was much chivying. A group of four brook trout were sometimes at the upper end of the wide channel, but were usually not attacked by the dominant steelhead unless one became detached from the group. It was difficult to tell the hierarchy of the small steelhead with the small trout, as there was little displacement between them.

Ten unbranded coho fry were used for experiment 20. One fish became dominant and this usually kept others out of the wide channel. It could be recognized by a distinctive pink mark on its side, and appeared the largest. There was considerable movement, but most fish were in the pool. In experiment 21 ten Atlantic salmon fry were added. Generally they were ignored, but were occasionaly attacked by coho. The distribution of the two species was similar. The same coho from the previous experiment was dominant in the wide channel, and another about the same size became dominant in the pool. Their sizes at the end of the experiment were, respectively, 8.9 cm-9.0 g, 9.0 cm-9.5 g. The upper three-quarters of the wide channel had usually no Atlantic salmon, or other coho, but only the dominant coho. In experiment 22, with seven Atlantic salmon as the sole species, the wide channel appeared to support 4-5 fry (0.7-0.8 m^{-2}). Any more were chased out. In experiment 23, with the addition of coho, a coho was again dominant and it tended to concentrate most of the fish at the downstream end of the wide channel. It appeared to be the largest fish in the tank. The dominant fish in the pool was also a coho. Nevertheless, the majority of Atlantic salmon fry were in the wide channel, as when alone. The largest Atlantic salmon (7.4 cm-5.0 g), was always in the narrow (fast) channel.

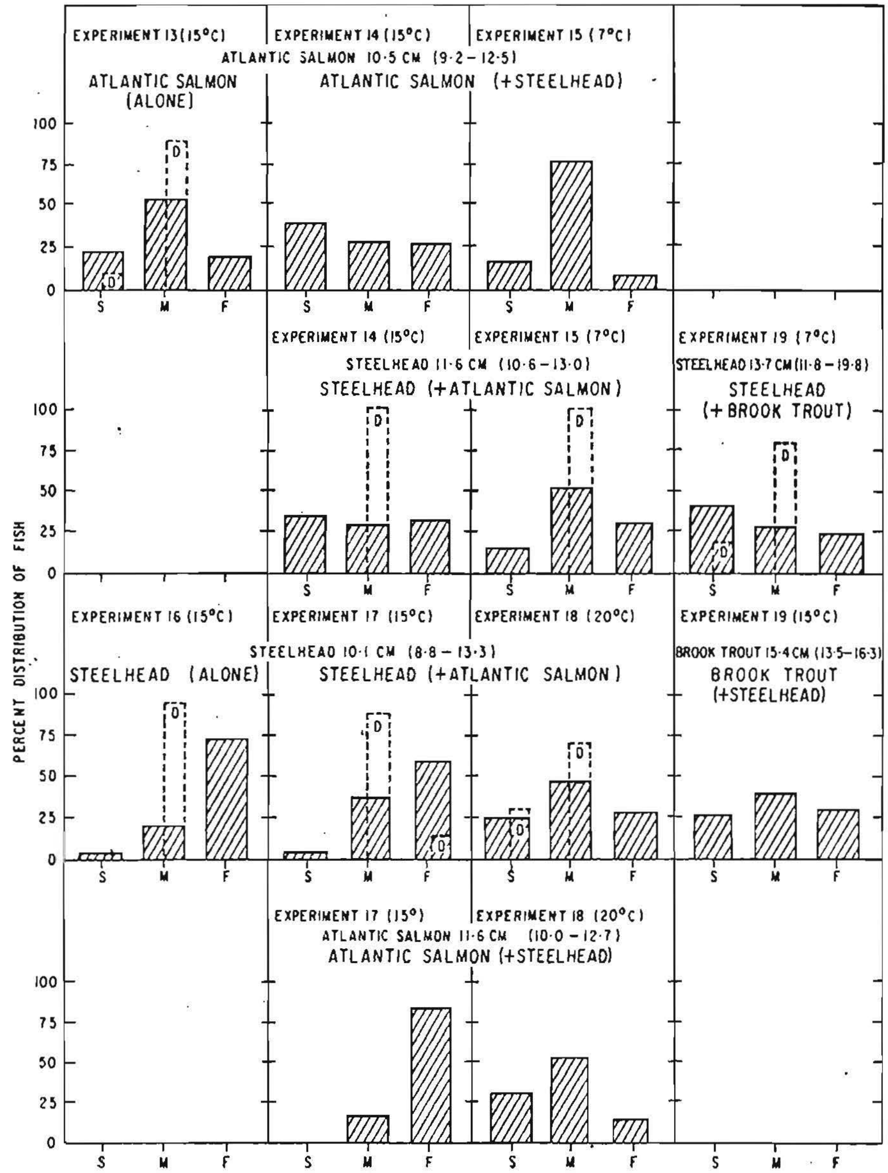


Fig. 4. The distributions of Atlantic salmon and steelhead trout in experiments 13-19. The same Atlantic salmon were used in experiments 13, 14, and 15 (mean fork length, 10.5 cm) and another group in experiments 17 and 18 (mean fork length, 11.6 cm). One group of steelhead was used in experiments 14 and 15 (mean fork length, 11.6 cm) and another group in experiments 16, 17, 18, and 19. The experiments 16, 17, and 18, mean forklength was 10.1 cm. For experiment 19 it was 15.4 cm. S=Slow flow (pool) <15 cm/s; M=Medium flow (wide channel) 17-24 cm/s; F=Fast flow (narrow channel) 40-42 cm/s. D=Locations of the dominant fish in each experiment. The relative areas were: pool (S) 5.0 m^2, wide channel (M) 6.0 m^2, and narrow channel (F) 3.3 m^2.

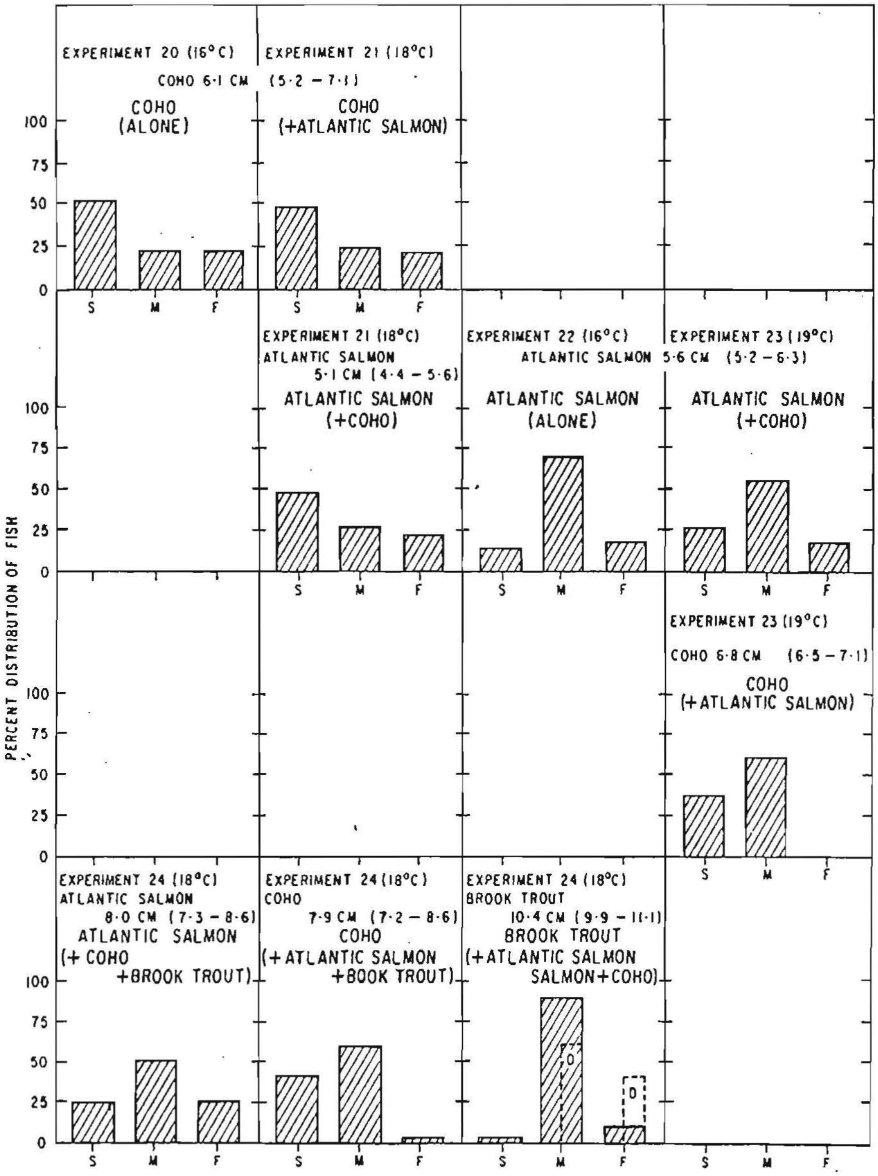


Fig. 5. Fish distributions for experiments 20-24. S=Slow flow (pool) <15 cm/s; M=Medium flow (wide channel) 17-24 cm/s; F=Fast flow (narrow channel) 40-42 cm/s. D=Dominant fish (a brook trout) in experiment 24. The same coho were used in experiments 20 and 21 (mean fork length, 6.1 cm). The mean fork length of coho in experiment 23 was 6.8 cm and in experiment 24, 7.9 cm. The mean fork length of Atlantic salmon was 5.1 cm in experiment 21, 5.6 cm in experiments 22 and 23, 8.0 cm in experiment 24. The mean fork length of brook trout in experiment 24 was 10.4 cm. The relative areas were: pool (S) 5.0 m^2, wide channel (M) 6.0 m^2, and narrow channel (F) 3.3 m^2.

The final experiment (24) was made with coho, brook trout, and Atlantic salmon. Most occurrences were in the wide channel. However, the dominant brook trout, and dominant fish (11.1 cm) was also frequently at the upper end of the narrow channel. The dominant coho (8.6 cm) was in the wide channel. The next dominant coho (7.8 cm) was usually at the lower end of the wide channel, and endeavoured to keep the other coho downstream, in the pool. The dominant Atlantic salmon (8.6 cm) was in the pool, but two Atlantic salmon remained in the wide channel (8.0 cm and 7.3 cm), and one (8.1 cm) remained in the narrow channel.

4.2 HEIGHT ABOVE THE SUBSTRATE

Mean height of holding positions above the substrate are shown in Table 4-6, and Fig. 6 and 7. Generally, stations closer to the bottom were held in faster flows than in slower water. Also parr usually held station closer to the bottom than any of the other three species, except at the higher temperature of 20°C. The change in level with temperature was not obvious with brook trout. Parr frequently were in contact with the substrate, which behaviour was seen occasionally with brook trout, but never with the other two species, except temporarily when a subordinate might be trying to escape. Neither coho nor steelhead ever normally held station in contact with the substrate. Dominant Atlantic salmon and steelhead frequently were higher off the bottom than subordinate fish (Table 7, Fig. 6 and 7). All four species fed throughout the water column, including the surface, and there was no evidence of stratification of species, although individuals within a species might show this type of feeding behaviour, especially in the pool.

4.3 DISTANCE TO THE NEAREST NEIGHBOUR

This was measured from the dominant fish (Table 7), as less aggressive fish would allow closer proximity of other fish and the greater variability of taking a general mean would mask specific differences and indications of real territory size. Distance from the dominant fish to the nearest neighbour was rather similar for Atlantic salmon and coho, but brook trout appeared to tolerate somewhat closer proximity. These distances were an average of 1.1 m at 15°C and 1.6 m at 20°C for Atlantic salmon; 1.2 m at 15°C and 1.0 m at 20°C for coho; 0.9 m at 15°C, 0.7 m at 18°C and 0.4 m at 20°C for brook trout. The distance was greater for steelhead: 1.9 m at 15°C and 2.3 m at 20°C. Distances decreased at 7°C for the species tested, and was only 0.3 m for Atlantic salmon, and 0.5 m for steelhead.

These distances were generally to fish in the rear of the dominant fish, as dominant fish rarely tolerated subordinates ahead.

4.4 AGONISTIC BEHAVIOUR

Data for individual experiments are summarized in Tables 14-31, which are presented in the appendix. The first nine experiments were reported in a previous publication (Gibson 1977a). These are given in summarized form in Tables 14-16. The remaining experiments are summarized individually for each experiment in Tables 17-31.

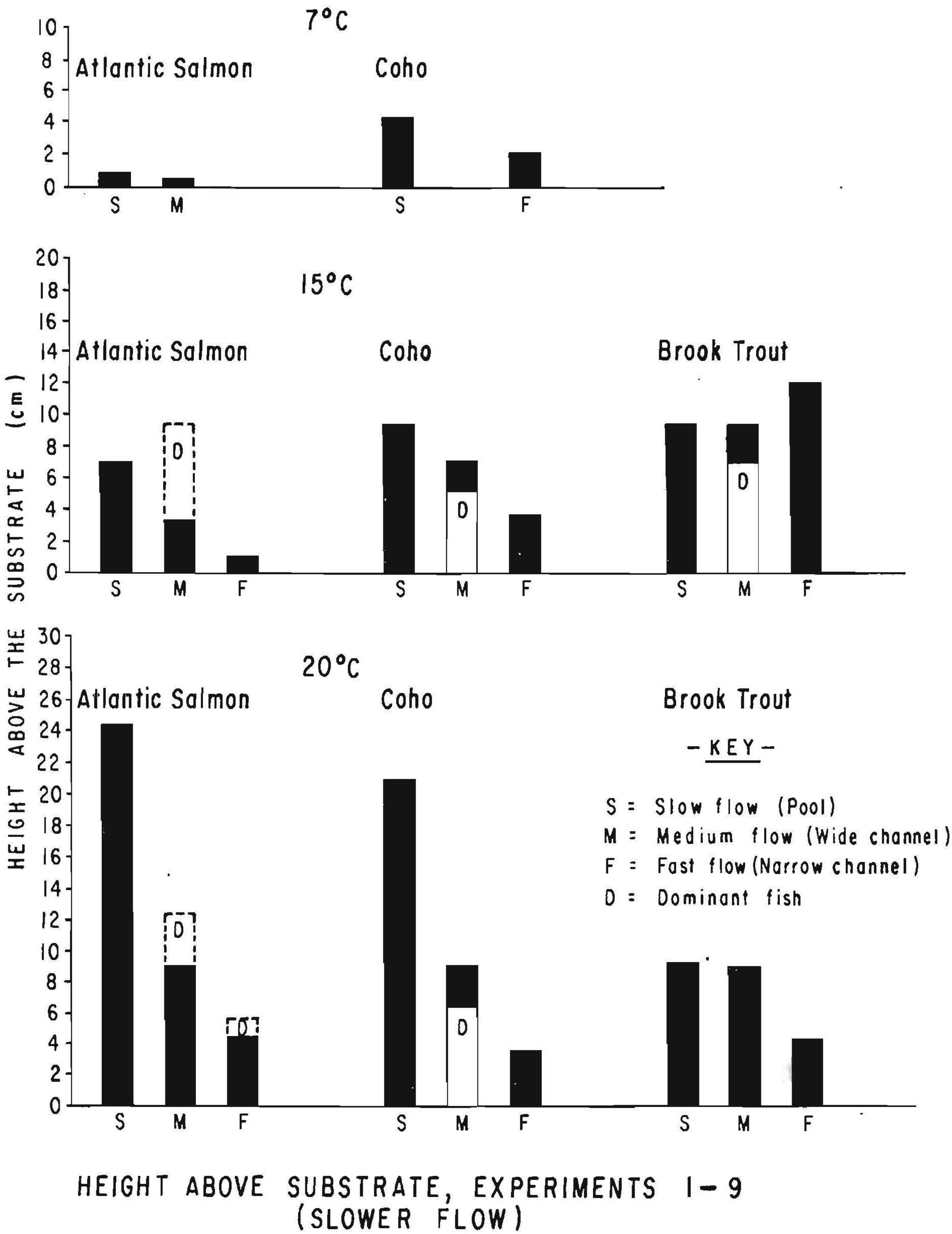


Fig. 6. An average of the means for Atlantic salmon, coho, and brook trout, of heights held above the substrate in experiment 1-9 (slower flow). Data for brook trout at 20^{0}C from Gibson 1977a.

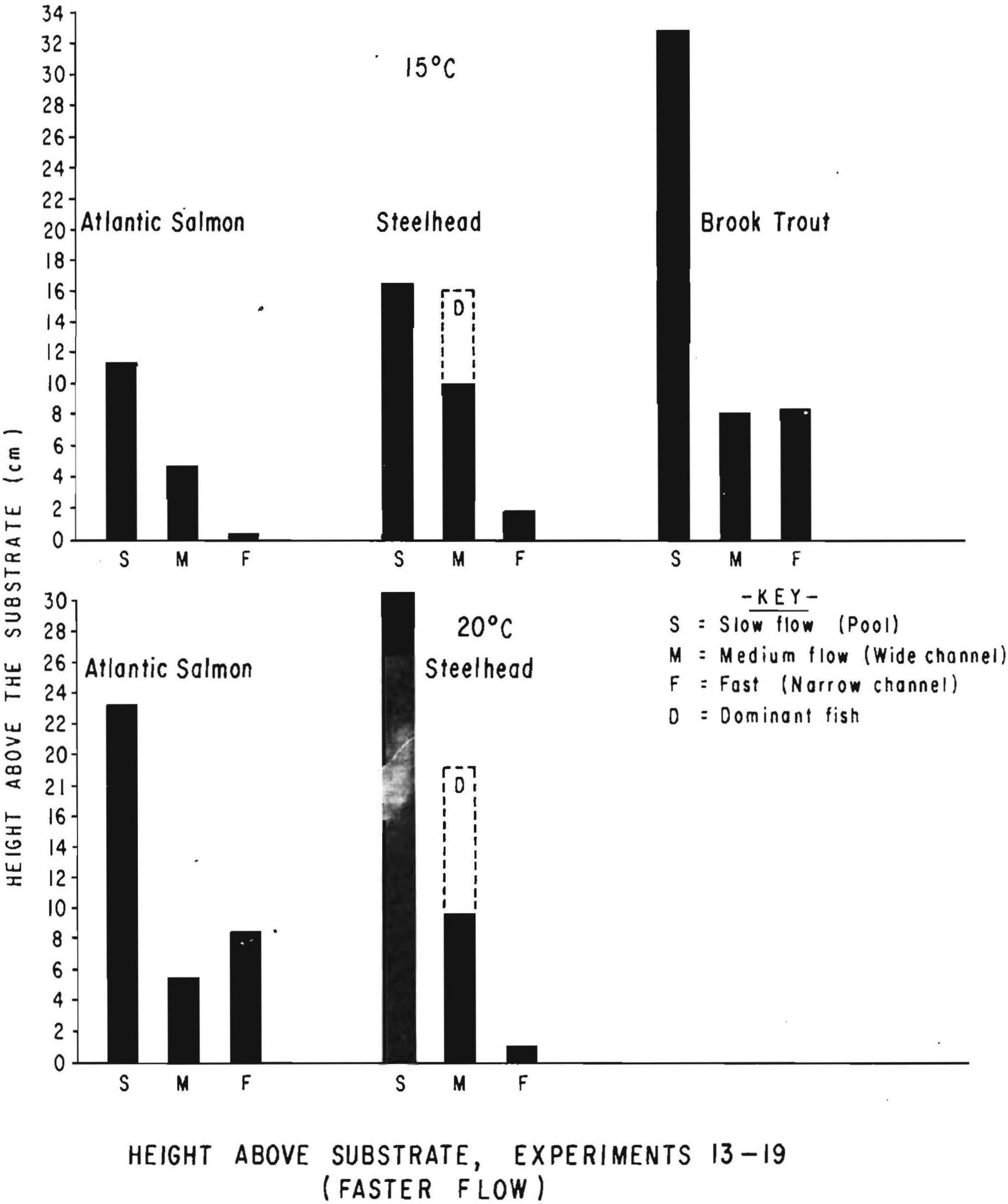


Fig. 7. An average of the means for Atlantic salmon, steelhead, and brook trout of heights held above the substrate in experiments 13-19 (faster flow).

Attacks and retreats for all four species at 7°C, 15°C, and 20°C, are shown in Fig. 8-13, and in Tables 8-11. Level of activity increases with the higher temperatures, and this is shown by comparing displacements made/observation/fish at the three temperatures. The means, at 7°, 15°, and 20°C, are respectively (with standard error in parenthesis):

Atlantic salmon:	1.45 (0.71);	1.47 (0.55);	3.08 (0.89);
Coho:	0.03 (n=1);	1.35 (0.19);	1.98 (0.63);
Brook trout:	---;	2.35 (0.48);	4.28 (n=1);
Steelhead:	9.82 (n=1);	6.77 (0.64);	13.60 (n=1);

However, there is such variation between experiments, depending on factors other than tempreature, such as other species present, density of fish, size of the fish, water velocity, etc., that it is more meaningful to compare experiments which used the same fish at the same water velocity.

With Atlantic salmon parr (Table 8), in experiments 1, 2, 3, and 4, with the same fish, the displacements/observations/fish were: 0.35 at 15°C when the sole species; and with coho present it was, 0.44 at 7°C, 0.93 at 15°C, and 6.15 at 20°C. Attacks on coho accounted for most of the displacements at 20°C. Intra-specific attacks in the latter three experiments were, 0.27, 0.61, and 1.74, respectively. Interspecific attacks (against coho) were, 0.17, 0.32 and 4.41. The same trend is seen with the other experiments. In experiments 7 and 8, the figures were, for total displacements/observation/fish, 0.64 at 15°C, and 2.22 at 20°C. For experiments 11 and 12 it was, 0.82 at 15°C, and 2.06 at 20°C. With steelhead in experiments 14 and 15, displacements by Atlantic salmon parr were 2.45 at 7°C and 4.9 at 15°C. The figure at 7°C is higher than that for experiment 4, with coho present, and is probably due to harassment by the steelhead, which kept the parr more active. In experiment 17 at 15°C the figure is 0.83, and in experiment 18 at 20°C it is 1.90.

With coho (Table 9) there was a similar trend of increasing activity with temperature, although this was not shown in all experiments. In experiments 2, 3, and 4, with the same fish, displacements/observation/fish, were 0.03 at 7°C, 1.08 at 15°C and 1.55 at 20°C. With experiments 5-8 at 15°C as the sole species it was 0.83, at 20°C as the sole species it was 1.10, but with Atlantic salmon parr added it was 1.25 at 15°C, and 1.13 at 20°C.

In these latter two experiments the aggression of the parr increased considerably at the higher temperature (Table 8) and this probably had a subduing effect on aggression of the coho. In experiments 11 and 12 displacements were 2.1 at 15°C and 4.14 at 20°C.

Brook trout showed an increase in activity with increase in temperature for 15°C to 20°C in experiments 11 and 12 (Table 10). Displacements increased from 3.2 at 15°C to 4.28 at 20°C. A previous experiment (Gibson 1977a) showed a similar increase, from 8.77 at 15°C to 11.0 at 20°C. None was done with this species at 7°C.

Steelhead showed an increase in activity at 20°C, increasing from 7.14 displacements at 15°C in experiment 17 to 13.6 displacements at 20°C in experiment 18 (Table 11). However at 7°C in experiment 15 there were 9.82 displacements, as opposed to 8.56 at 15°C in experiment 14. This was caused by an increase in attacks on Atlantic salmon parr, apparently because at this temperature more

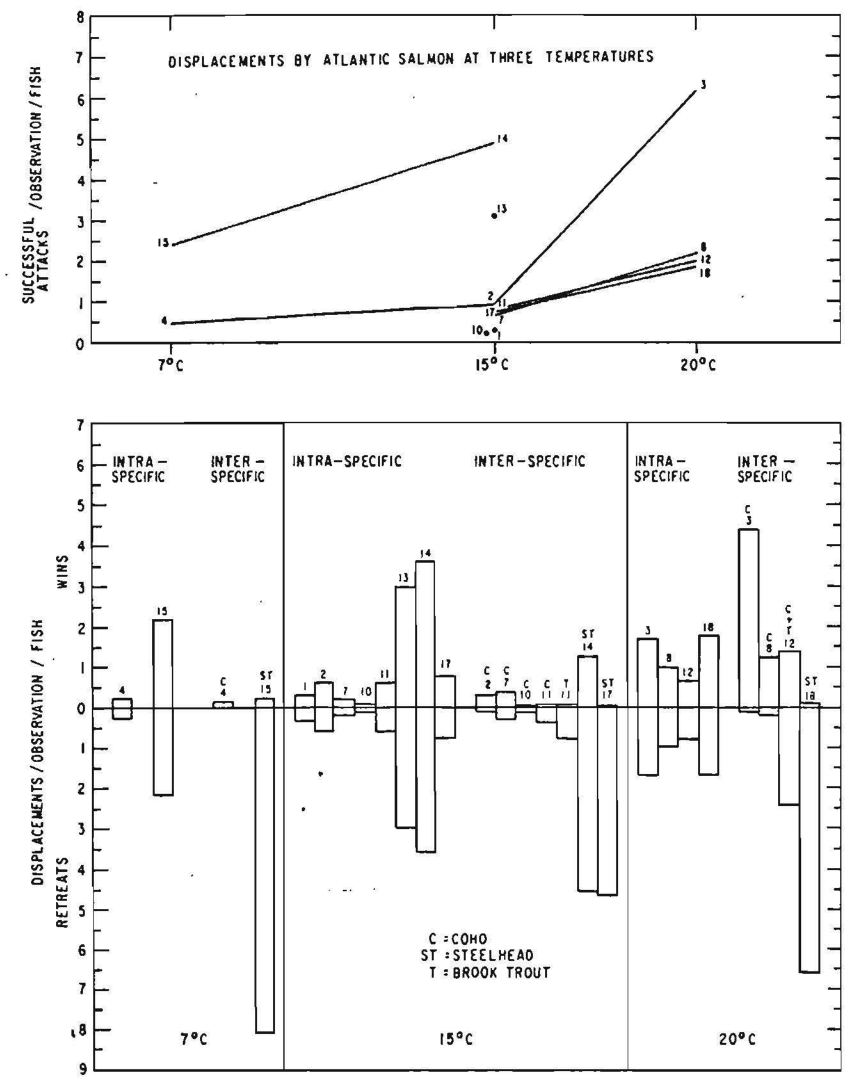


Fig. 8. The average successful attacks and the retreats of Atlantic salmon for observations at 7°C, 15°C, and 20°C. The upper figure shows successful attacks at the three temperatures. Points are marked by the experiment number and experiments containing the same fish are joined by a line. The lower figure shows intra-specific and inter-specific encounters. Wins are shown in the upper half, and retreats in the lower half.

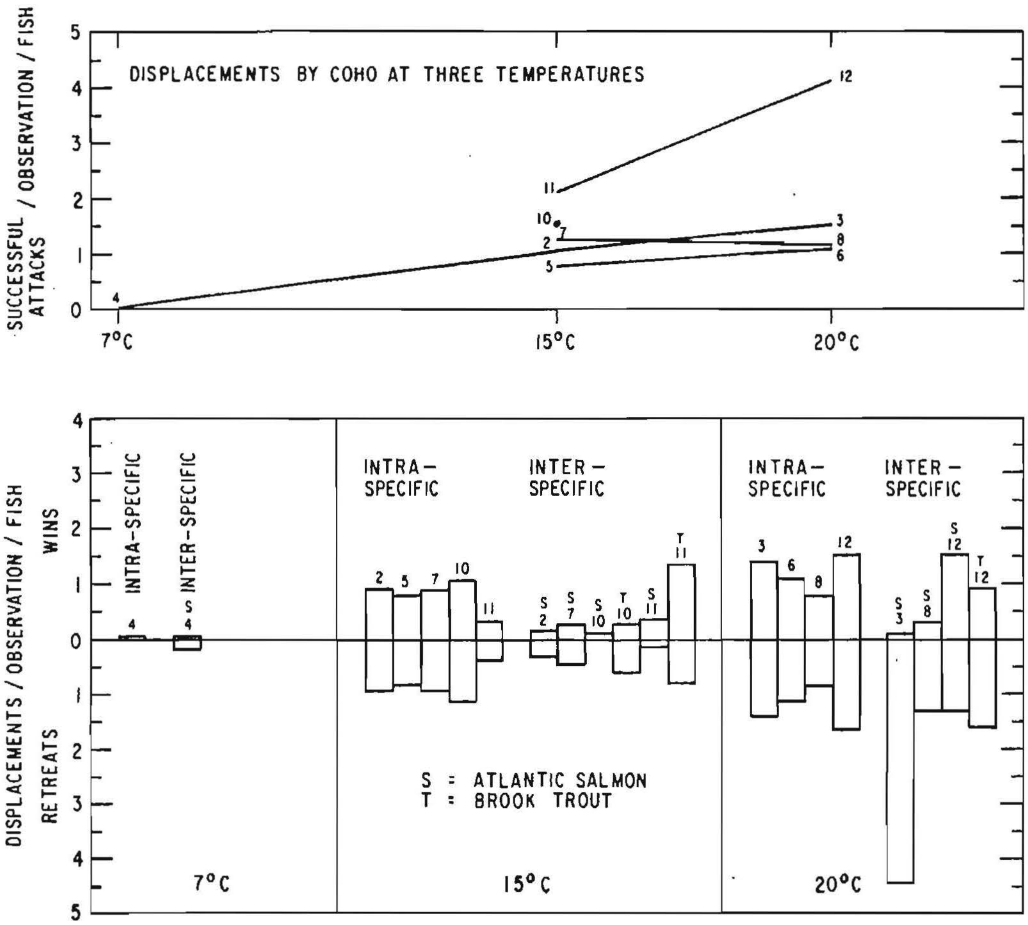


Fig. 9. The average successful attacks and inter-specific encounters, of coho, at 7^0C, 15^0C and 20^0. The upper figure shows the mean number of attacks at the three temperatures. The lower figure shows intra- and inter-specific encounters for each experiment.

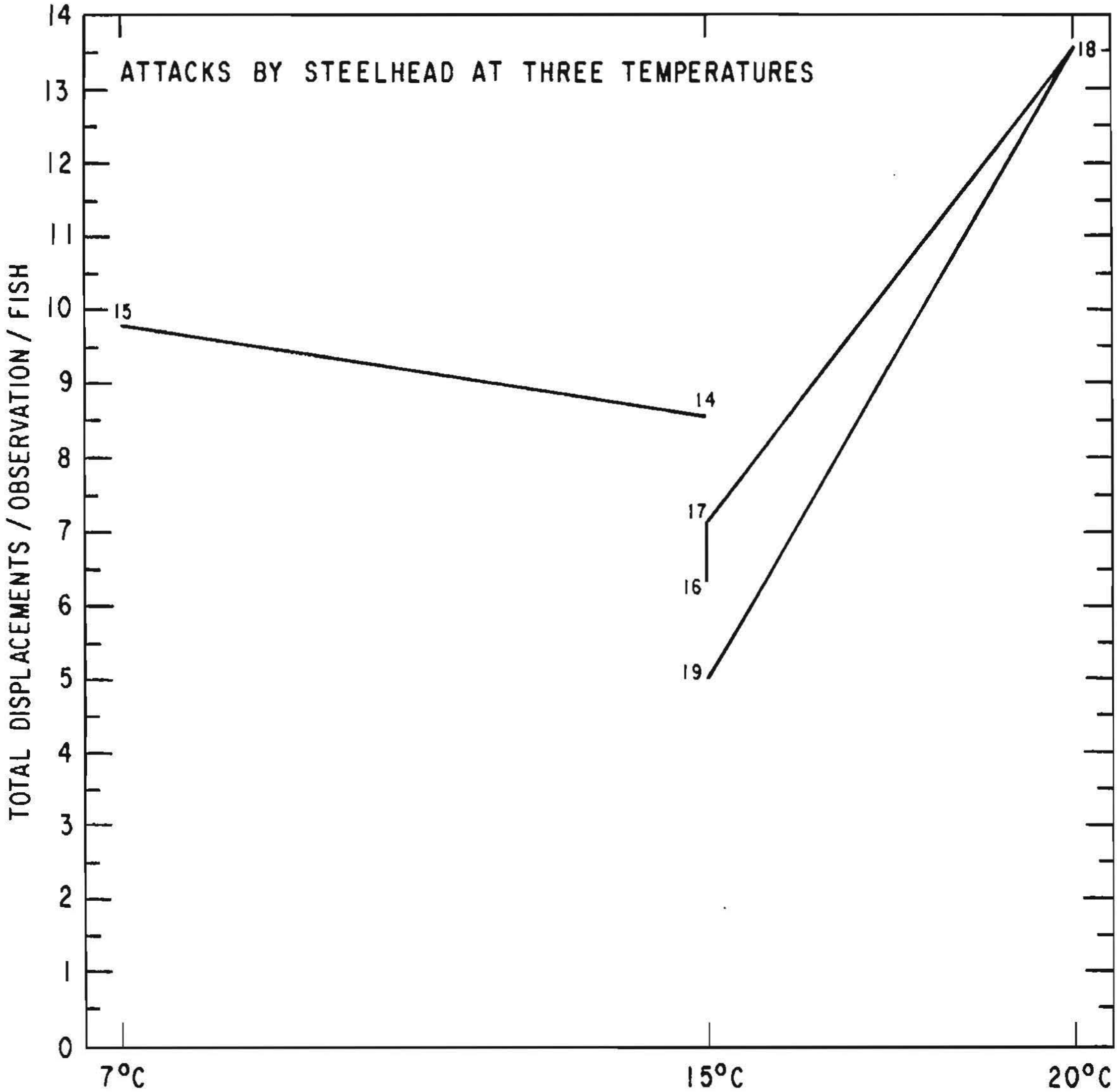


Fig. 10. The successful attacks by steelhead at 7°C, 15°C, and 20°C. Experiments with the same fish are joined by a line.

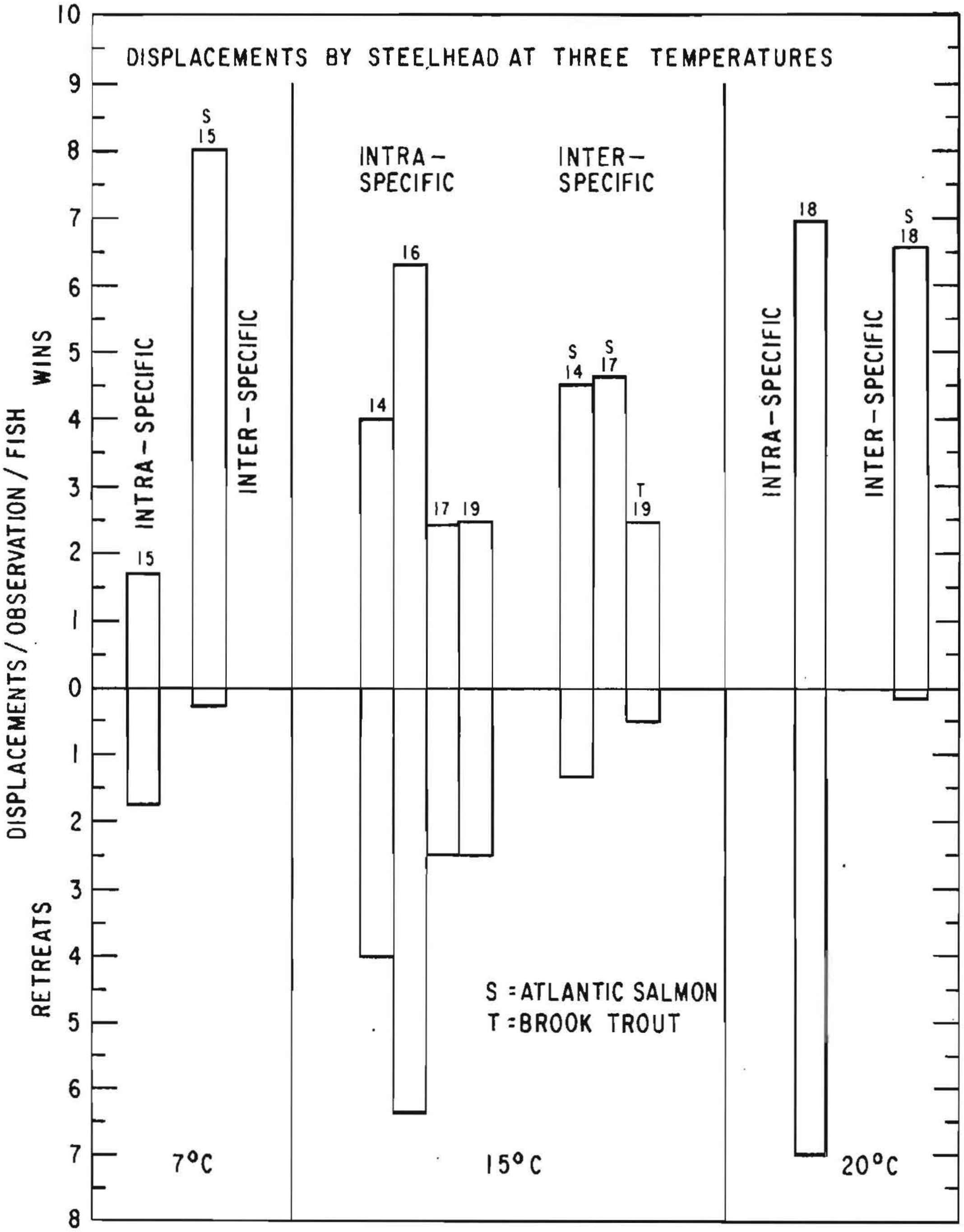


Fig. 11. The encounters of steelhead at 7°C, 15°C, and 20°C. The relative areas were: pool (S) 5.0 m², wide channel (M) 6.0 m², and narrow channel (F) 3.3 m².

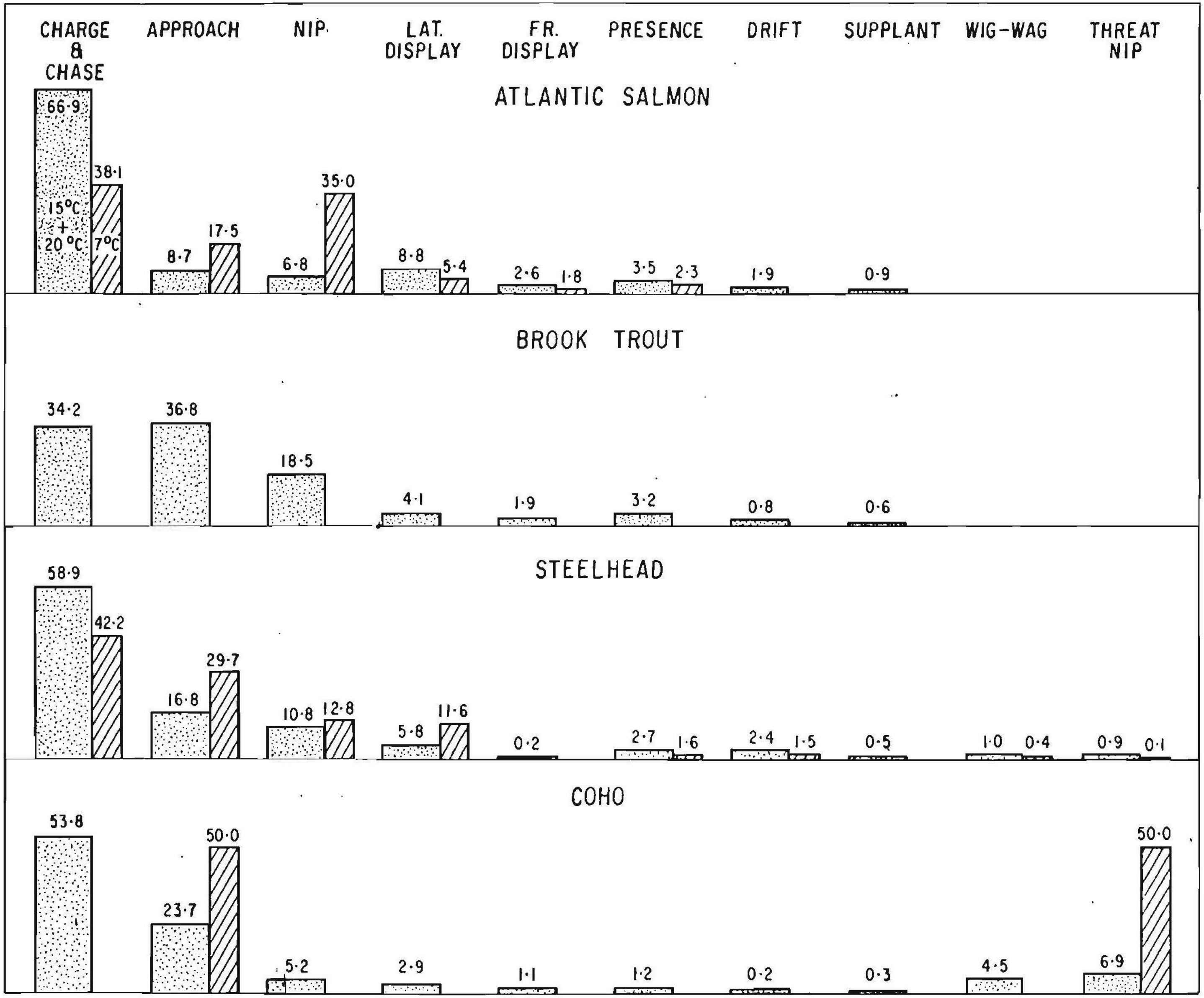


Fig. 12. Mean percentages of agonistic acts used in displacements, at 15°C and 20°C, and at 7°C.

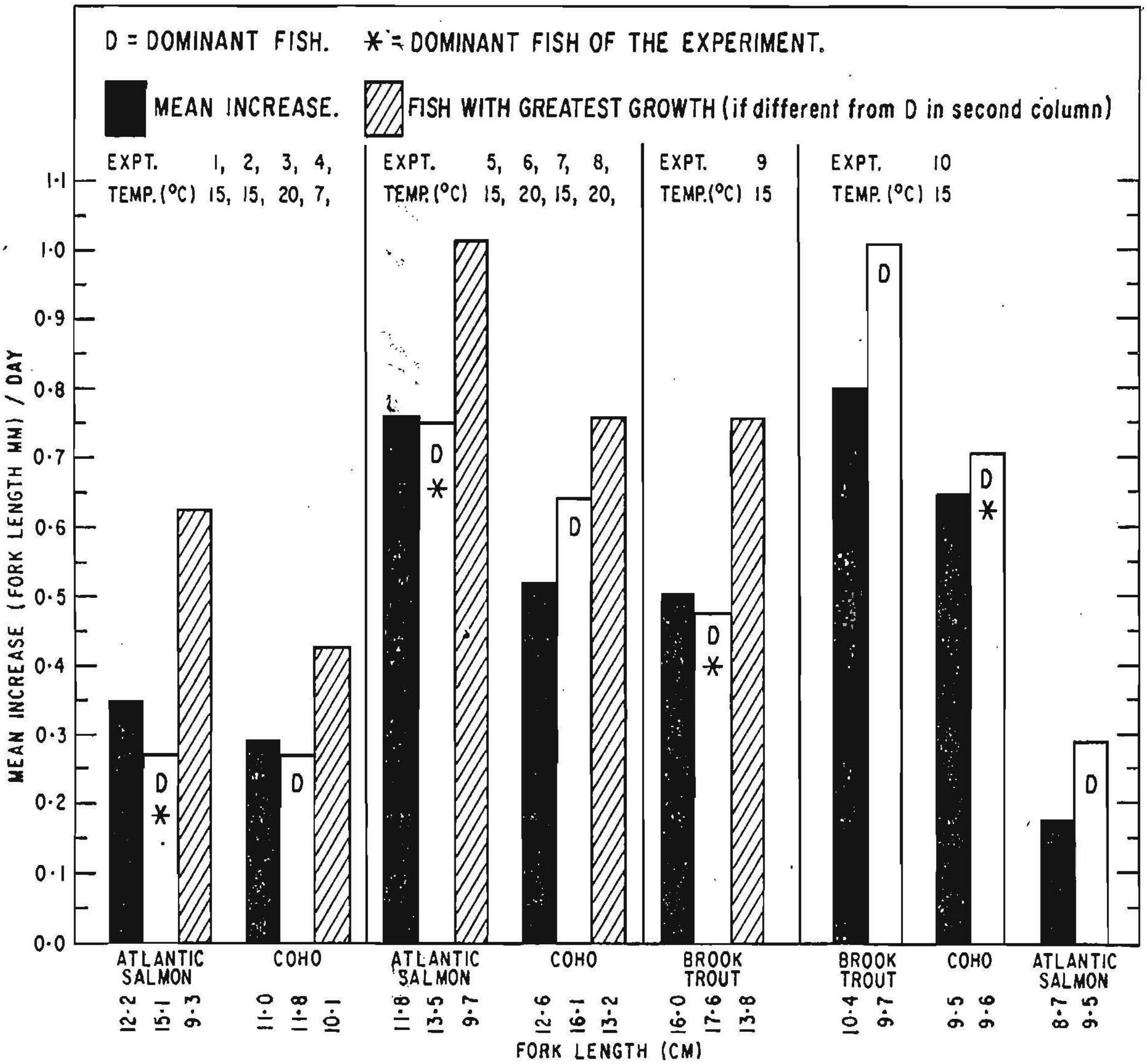


Fig. 13. Relative increases in fork length of fish in experiments 1–10.

parr moved into the wide channel, and were in closer association with the steelhead. An aggressive steelhead in the pool tended to displace parr from there. The total number of displacements was very much higher than with any of the other species, followed by brook trout, Atlantic salmon, and coho, in decreasing order. Steelhead made relatively more displacements, as follows: with Atlantic salmon, x 4.0 at 7°C (experiment 15), x 1.75, x 8.6, at 15°C (experiments 14 and 17), x 7.2 at 20°C (experiment 18); and with brook trout, x 2.2 at 15°C (experiment 19).

Agonistic acts are summarized in Table 12 and Fig. 12. At temperatures when all species were active charge and chase was the commonest agonistic act with Atlantic salmon (70%) steelhead (59%), and coho (54%), but not with brook trout (34%). This difference was significant at the 1% level comparing brook trout with Atlantic salmon and steelhead, and at the 5% level comparing brook trout with coho. Brook trout made relatively more approaches and nips. At 7°C charge and chase was reduced with the three species tested.

The wide channel appeared to be the preferred area generally, and usually had the dominant fish, perhaps because it was the 'upstream' section, even though there was ample food in all sections. To provide some idea of territory size the number of fish in the section have been tabulated under dominant fish in the experiment (Table 13).

If the experiments at 7°C and 20°C are not included, the area was about 0.7 fish/m^2 when an Atlantic salmon or coho was the dominant fish (1 fish/1.4m^2), about 0.5 fish/m^2 when a steelhead was the dominant fish (1 fish/2 m^2), and about 1.3 fish/m^2 when a brook trout was the dominant fish (1 fish/0.77 m^2). The range is from 1.6 fish in the channel (0.3 fish/m^2) in experiment 16, with seven steelhead, to 12.0 (2 fish/m^2) in experiment 11, with 6 coho, 6 Atlantic salmon, and 6 brook trout, when a brook trout was the dominant fish.

Summarizing general observations that were made for each species, Atlantic salmon were the least mobile of the four species tested, and the only species commonly in contact with the substrate. Brook trout sometimes were in direct contact with the bottom, but neither coho nor steelhead were seen in contact with the bottom, except temporarily. Atlantic salmon frequently oriented to a stone, and sometimes appeared to rest the inferior part of the head on a pebble. Subordinate Atlantic salmon usually remained on the bottom and were less active than dominant Atlantic salmon, which were frequenctly off the bottom, rising for food, and frequently changed station within their general area. There was usually less aggression amongst Atlantic salmon than amongst coho, probably because Atlantic salmon generally remained individually more segregated. Close proximity did not always lead to an agonistic encounter, especially at 7°C. Fidelity to a territory, as reported in some of the literature, may be a result of artificial crowding, or of a heterogenous food supply, but in these experiments, with all species, the locations of the territories changed. The charges by Atlantic salmon were more vigorous than either coho or brook trout. In charges it was sometimes difficult to see if contact were made, but with Atlantic salmon sometimes a shower of tiny scales was seen to float downstream, which was not noticed with the other species. Scales were more easily displaced from Atlantic salmon than the other species, and fights were serious resulting in white marks and loose deranged scales, and pieces missing from fins, especially the tail.

Coho were more mobile than Atlantic salmon, and frequently changed position. Coho also spent more time (and therefore energy) in aggressive behaviour than Altantic salmon. For their length, they were more robust (and less streamlined) than Atlantic salmon. They often changed position with long (3 m or so) fast dashes. Territories were undefined and they were somewhat more tolerant of the presence of a neighbour. Although dominant coho remained in certain areas, they defended a territory in a different way from Atlantic salmon, and were always on the move, only holding station briefly. It was difficuly assigning a territory to subordinate coho in the pool, as there was constant movement and bickering amongst them. Aggression with this species may be more important for spacing individuals, rather than to defend territories. If attacked by a subordinate fish sometimes the dominant made a wig-wag. The wig-wag was sometimes the precursor of chasing. If a subordinate fish were attacked the subordinate sometimes made a wig-wag before fleeing. The coho appeared to be more of a 'nervous' fish than Atlantic salmon because it could be displaced sometimes by a subordinate. Also its movements from place to place, and faster tail beat (Gibson 1977a) gave the same impression. A subordinate coho sometimes sank to the bottom when approached by a dominant, but only temporarily, and none was seen to remain in contact with the substrate, as was common with Atlantic salmon.

Brook trout were more roaming than Atlantic salmon, and their charges less vigorous than Atlantic salmon. None seemed to defend an area in the same way as Atlantic salmon, and there was indiscriminate roaming and chasing. Their stations generally were temporary and it was difficult to assign territories. Schooling was not apparent in these experiments, as opposed to others (Gibson 1973) possibly because pockets of slow water adjacent to faster water were not available in this tank. The greater movement of brook trout, allowing for more encounters, and higher experimental water velocities may also account for the relatively more numerous agonistic acts than were found in the previous study. Subordinate trout being displaced often turn and raise the anterior part of the body, with the dorsal fin down, as it leaves downstream, with the head slightly higher than the rest of the body, possibly an appeasment gesture. Coho were occasionally seen to behave in the same manner, but this method of retreating was not noticed in either of the other two species.

Steelhead were the most aggressive of the four species tested, in both number of agonistic acts and in intensity of aggression. Steelhead were dominant in all the experiments in which they were tested, and were able to displace fish larger than themselves, e.g., in experiment 17 all steelhead were dominant over Atlantic salmon, although mean size of the Atlantic salmon was the greater. As with Atlantic salmon the steelhead charge was very vigorous, and more so than that of coho or brook trout. Steelhead were more mobile than Atlantic salmon and it was common for them to change station during an observation. None was seen to hold contact with the substrate. Some very vigorous and vicious fights were seen, especially after initial introductions. In two fights seen with the steelhead of experiment 14, although not during regular observations, sustained lateral displays interspersed with charges and biting at the flanks and caudal peduncle, lasted in one bout for 1 min. 19 sec., and another for 15 min. White marks were left over the lateral surface of each fish after the bites and nips, indicating the severity of the encounters. As an incidental observation, some of the dorsal fins of the steelhead were badly eroded when we first got them from the hatchery. This is a common condition with salmonids in hatcheries. We were told this may have been due to nipping in the close confines of the hatchery trough. However, in the stream tank and uncrowded holding tank, these fins grew back. The dorsal fin appears less likely to be nipped than the tail, which was intact in the hatchery fish, and as crowding decreases aggression, it is more likely that the damaged dorsal fins were attacked by some pathogen in the crowded conditions of the hatchery troughs. In experiment 15 at 7°C steelhead appeared to remain aggressive, but not to show territorially, so that a group was formed, with the dominant steelhead in the lead. In this, and other experiments, when the water flow was stopped at the end of the experiment all the fish in the tank (12) formed a school and swam up and down the tank. It appears both schooling and territorial behaviour can be performed by all four species when the occasion warrants the response of the appropriate type of behaviour.

4.5 COLOUR CHANGES ASSOCIATED WITH AGONISTIC BEHAVIOUR

All species except brook trout showed obvious differences in colouration related to the dominance hierarchy. These were transient colours related to aggression, so were not due to individual variation. Although colour changes were not consistently tabulated, they were noted on a qualitative basis in conjunction with each experiment. Detailed description of colouration is not given, but the more obvious changes in colouration and pattern for dominant and submissive fish are described below.

Brook trout varied somewhat in colour, but the differences were not as marked with the other three species, so were not recorded, although they may have been related to dominance. In other studies it has been noted that male brook trout, in addition to their brilliant colouration at spawning time, become temporarily lighter coloured on the dorsal surface during courting and during the spawning act, so at this time anyway they are capable of transient colour changes. However, such obvious changes were not seen in the present experiments, although in some experiments it was noted that the dominant fish was lighter coloured than subordinate brook trout.

Colour changes of juvenile coho and steelhead were rather similar between the two species, but were somewhat different to those shown by Atlantic salmon parr. However, with all three species submissive fish were pale above the lateral line, with a darker pigmented area along the lateral line, which tended to blur the outlines of the parr marks. Dominant fish of all three species were generally lighter coloured than submissive fish. It is possible the white flashes and fin colouration were more marked in dominant fish than subordinates, but this was not such an obvious feature.

Dominant coho were lighter coloured than the subordinates, and the whole lateral surface appeared a light brown or sandy colouration, possibly partly through reflection, with prominent parr marks.

Surbordinate coho had a dark line through the parr marks from the eye to the mid-caudal peduncle, and were darker dorsally. They also had a light stripe from the dorsal part of the eye to the dorsal end of the caudal peduncle. The light line at the top of the parr marks, a dark dorsal surface, and the darker area through the parr marks gave a definite striped appearance to the subordinates. The light stripe from the upper part of the eye to the top of the caudal peduncle was present in some dominant coho, but was more obvious in subordinates because of the darker dorsal area and darker area through the parr marks. There appeared also to be intermediate subordinate colours.

Dominant steelhead were lighter coloured than the subordinates, with usually the dominant fish being the lightest. Dominant steelhead were more evenly coloured over the whole body, but lighter coloured down the mid-lateral surface. They were an even grey green above and below the lateral line with a pink stripe down the mid-lateral region, and with the blue bars, or parr marks.

Subordinate steelhead had the opposite colouration to dominant fish. They had a "stripey" look, a darker dorsal surface, were darker in the mid-lateral region, but lighter above this. They were coloured similarily to subordinate coho, with the light stripe above the lateral line, and a dark line below the lateral line. The light and dark stripes began behind the eye, on the gill cover, and extended to the end of the caudal peduncle. There appeared to be intermediate colours, and the most subordinate steelhead usually had the lightest and darkest stripes above and below the lateral line. In experiment 18, at 20°C, the two subordinate steelhead were darker than the more dominant fish, but did not have the "stripey" colouration which was seen in the cooler experiments.

As with steelhead and coho dominant Atlantic salmon were more evenly coloured over the whole body than subordinates. Generally, this was a light greenish colour, but this may depend on the background. They were generally lighter coloured than the subordinates. Subordinate salmon parr were mottled with light and dark mottling on the dorsal surface, and had a horizontal light pigmented line just above the lateral line going from the eye to the top of the caudal peduncle. The light longitudinal line was not as obvious as seen with subordinate coho or steelhead. Frequently the whole eye including the iris was black. This was not noticed with coho or steelhead. Subordinate Atlantic salmon usually remained motionless on the bottom and their colouration made them difficult to see, as they blended in with the substrate. On light coloured gravel subordinate fish sometimes appeared overall lighter coloured than dominant fish but were mottled and harder to see. A subordinate colouration was seen in some instances to develop temporarily in some fish after agonistic encounters, and could change quite rapidly. This reversal in subordinate and dominant colouration was also noted with coho and steelhead.

The subordinate type of colouration may also be associated with activity. In the first cold temperature experiment (4) the majority of the parr remained motionless on the bottom and became dark and mottled. However, one Atlantic salmon parr remained fairly active and it retained its previous light colours. In a cold water experiment with steelhead (15), aggression of the salmon parr was less, but they were kept active by the steelhead, and showed no colour change.

Detailed colouration differences for dominant and subordinate salmon parr are described and illustrated by Keenleyside and Yamamoto (1962).

The behaviour, colour and pattern of submissive salmon parr may be useful in protecting them from harassment. These subordinate fish were still chased by dominant fish, so that the colouration does not appear to act as a signal, but these fish are more cryptically coloured and probably not attacked as often as more dominant fish, which are more active and overall lighter coloured. Movement and feeding in the water column and at the surface frequently initiates attack, so that the inactivity of submissive fish would decrease the number of attacks. To the human eye submissive parr are better camouflaged, and much more difficult to see than dominant parr. The colouration of dominant parr may be a compromise between signalling the defence of a feeding territory to other parr by brighter colours and patterns and protective colouration against predators. The colouration of inactive parr in cold water experiments suggests that, on the bottom anyway, the dark and mottled colouration is more protective. It is possible that above the substrate a silvery reflective surface has better protection than a darker colouration.

The colouration of submissive coho and steelhead is more difficult to interpret. Again thse submissive fish were still chased by dominant fish, so that the colours do not appear useful in discouraging attacks. Also, from the lateral surface anyway, these fish are not less well seen, so the colours are probably not cryptic. To a human observer these stripey coloured fish look remarkably like many of the schooling minnows which have similar light and dark stripes. Several of these species live in the same streams as young coho and steelhead, and it is possible that in the natural environment subordinate coho or steelhead would be confused with minnows and be less liable to attack. An alternative explanation is that the longitudinal stripes provide some form of disruptive colouration (e.g. Hailman 1977), and this is used for the same reason by submissive coho, submissive steelhead, and some minnows, similar to the mid dorsal stripe on the head of certain fishes which Barlow (1967) suggests is disruptive colouration.

Neither coho nor steelhead were seen to rest on the bottom, except temporarily, so that a cryptic colouration for them would be less valuable than for salmon parr. Brown trout when inactive or submissive have a colour pattern very similar to that of submissive parr. Also frequently when inactive or submissive they are in contact with the substrate (unpub. data), so that such colouration is effective for camouflage. This lends support to the theory that a cryptic colouration is useful for submissive fish which are in contact with the substrate, but for submissive fish above the bottom some other sort of protective colouration is more useful.

4.6 RELATIVE LENGTH OF PECTORAL FIN

Salmon parr have a relatively greater length of pectoral fin than the other salmonids used in these experiments, and they use these fins in a special way to keep the fish in contact with the substrate in running water (Kalleberg 1958). The fins are also used to help stabilize the fish when off the bottom. The relative fin lengths were measured to see if there were some relation between pectoral fin length and the fish's habitat. As there was a difference in amount of fork in the caudal fin of each species, the ratio of pectoral fin length: standard length in mm was determined. In a previous study (Gibson 1973) this ratio for Atlantic salmon was 1:4.6, and for brook trout 1:5.9. In the present study 25 coho, of S.L. 79-154 mm and 43 steelhead, of S.L. 87-144 mm were measured. These have given the following results:

	Atlantic salmon	Brook trout	Coho	Steelhead
Mean pectoral fin lengths: S.L.	1:4.6	1:5.9	1:6.6	1:7.1
(S.E.)	(0.05)	(0.02)	(0.07)	(0.08)

Steelhead, which normally occupy faster water than coho (Hartman 1965), apparently do not have longer pectoral fins than coho. This lends support to the hypothesis that the larger pectoral fins of Atlantic salmon parr are mainly for use in holding the fish in contact with the substrate, as it is the only one of the four species that behaves in this manner.

4.7 BUOYANCY

Buoyancy experiments to measure specific gravity gave the following means (standard errors in parenthesis):

Atlantic salmon	Steelhead	Coho	Brook trout
1.038	1.028	1.020	1.015
(0.0030)	(0.0040)	(0.0015)	(0.0010)

The differences between Atlantic salmon and steelhead, and between steelhead and coho were insignificant ($P > .05$), but there was a significant difference between Atlantic salmon and coho ($P < .01$), between Atlantic salmon and brook trout ($P < .01$), between steelhead and brook trout ($P < .01$), and between coho and brook trout ($P < .05$).

The fish could choose parts of the tank of differing water velocity and no doubt adjusted their buoyancy accordingly (Saunders 1965). Also, being physostomous, buoyancy may have changed somewhat as they were removed from the tank. However, as all species were treated alike, the results do indicate relative differences in buoyancy.

4.8 GROWTH

Size of fish and their increase during the experiments are shown in Tables 2-1 to 2-8. Mean increases in length are shown in Fig. 14-19. Atlantic salmon showed a greater increase in length (0.35 mm/day) than coho (0.29 mm/day) in the first four experiments, in which Atlantic salmon were dominant over coho. In experiments 5-8, growth of coho was better, at 0.52 mm/day, possibly related to the fact that the mean size of coho was larger, and coho were alone in the first two experiments. However, again Atlantic salmon grew better, at 0.76 mm/day. Brook trout growth, in experiment 9, was 0.51 mm/day.

In experiment 10 coho were larger, were the dominant fish, and had a mean increase of 0.65 mm/day. The dominant coho had the best growth of the species, at 0.71 mm/day. Brook trout were actually better, with 0.8 mm/day, and the dominant trout growing at 1.06 mm/day. In this experiment Atlantic salmon were the smallest of the three species, and grew only 0.18 mm/day, with the dominant salmon growing 0.29 mm/day.

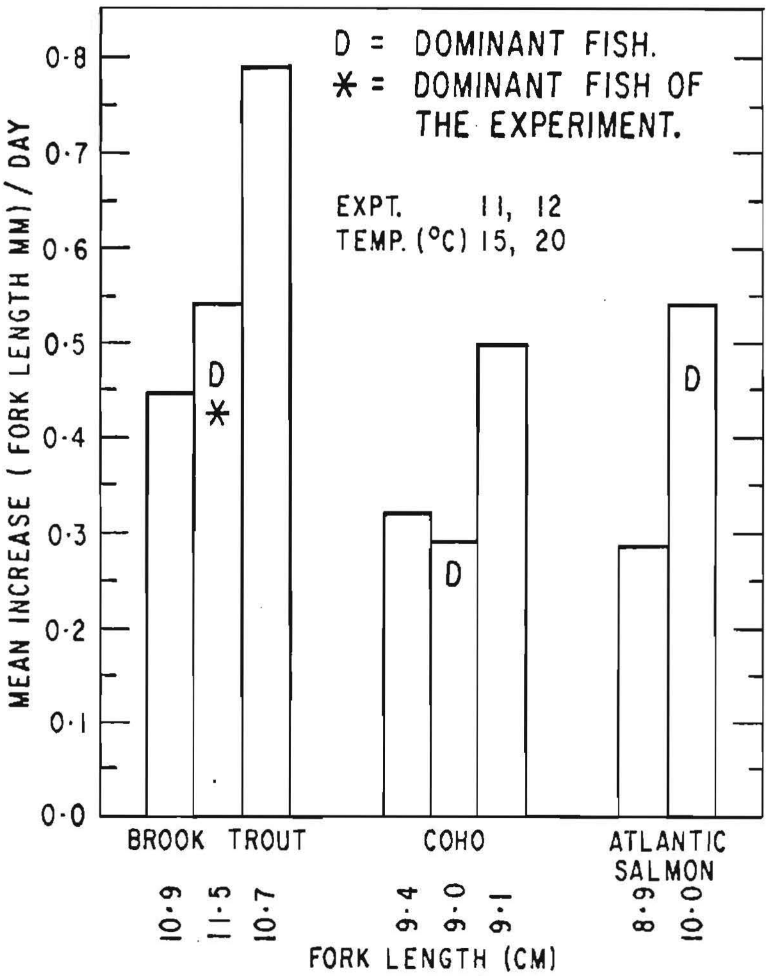


Fig. 14. Relative increases in fork length of fish in experiments 11 and 12.

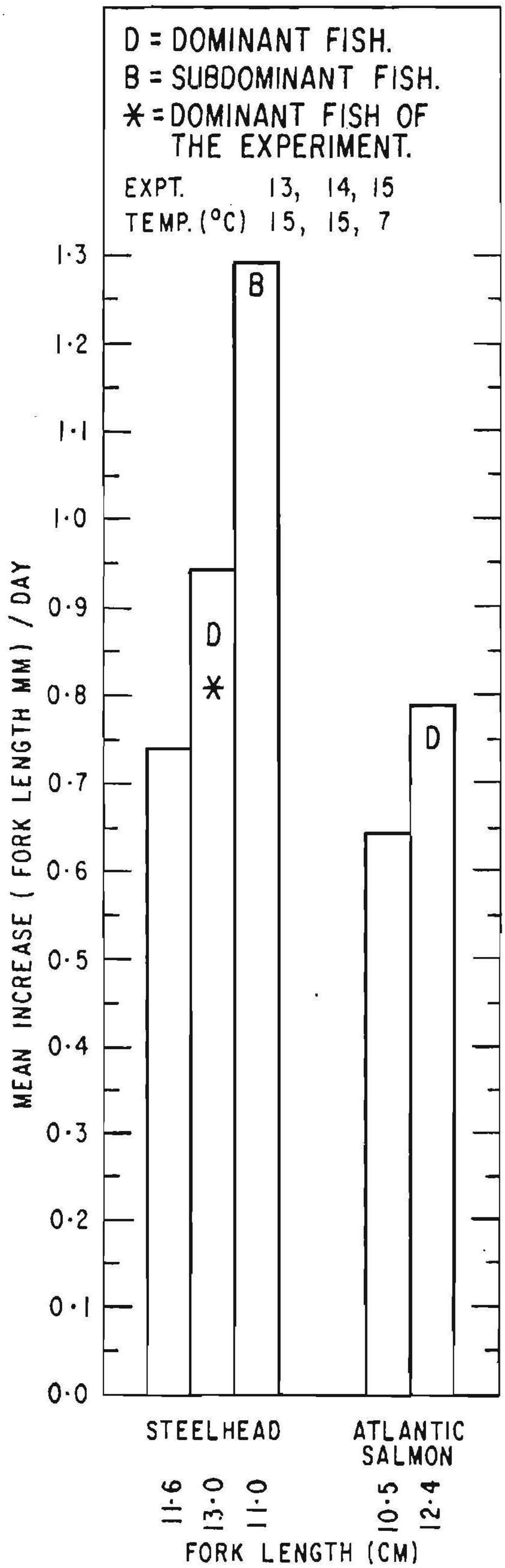


Fig. 15. Relative increases in fork length of fish in experiments 13, 14 and 15.

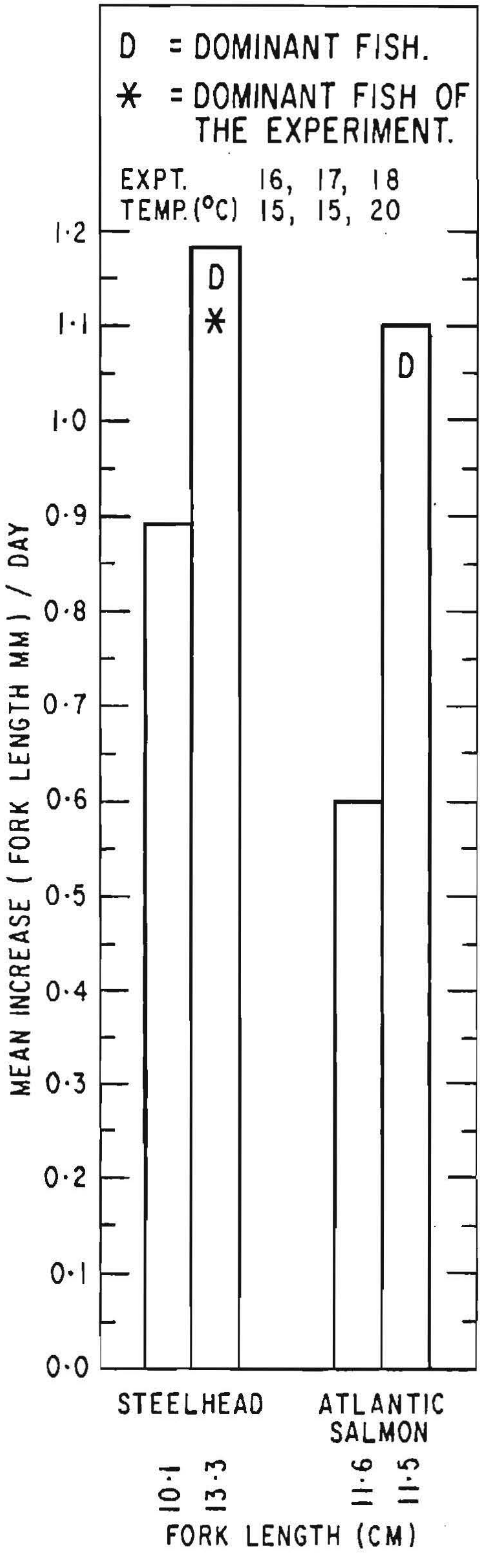


Fig. 16. Relative increases in fork length of fish in experiments 16, 17 and 18.

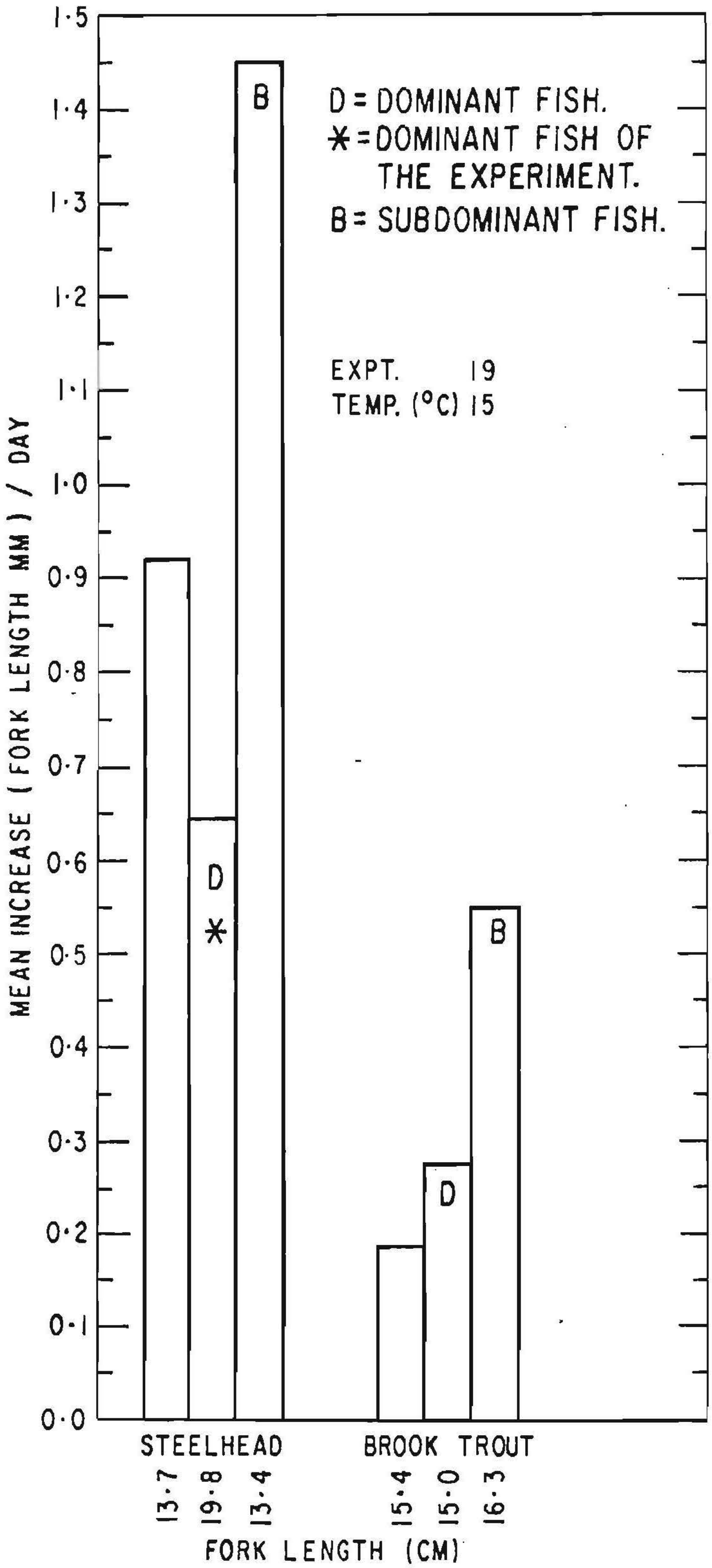


Fig. 17. Relative increases in fork length of fish in experiment 19.

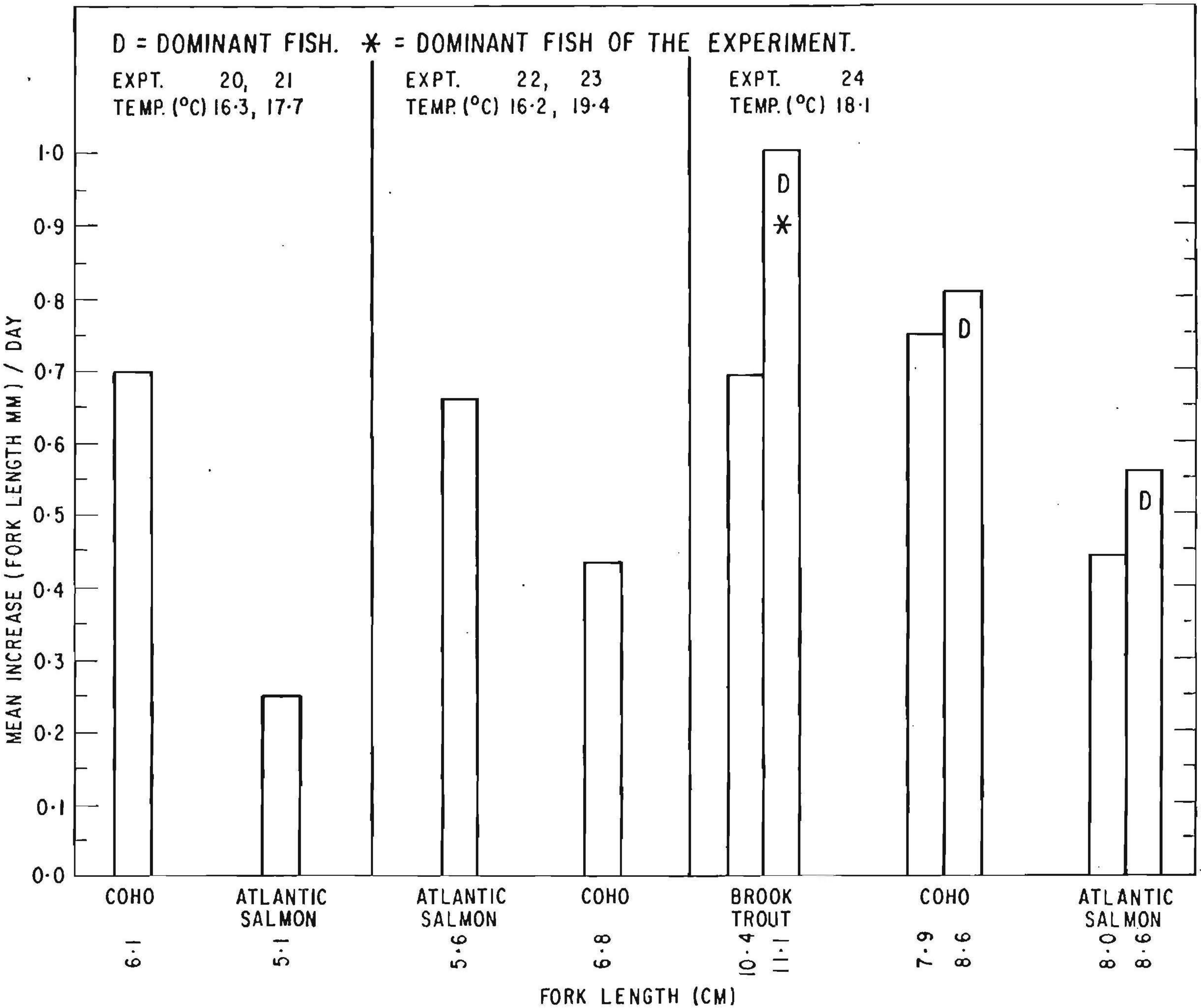


Fig. 18. Relative increases in fork length of fish in experiments 20–24.

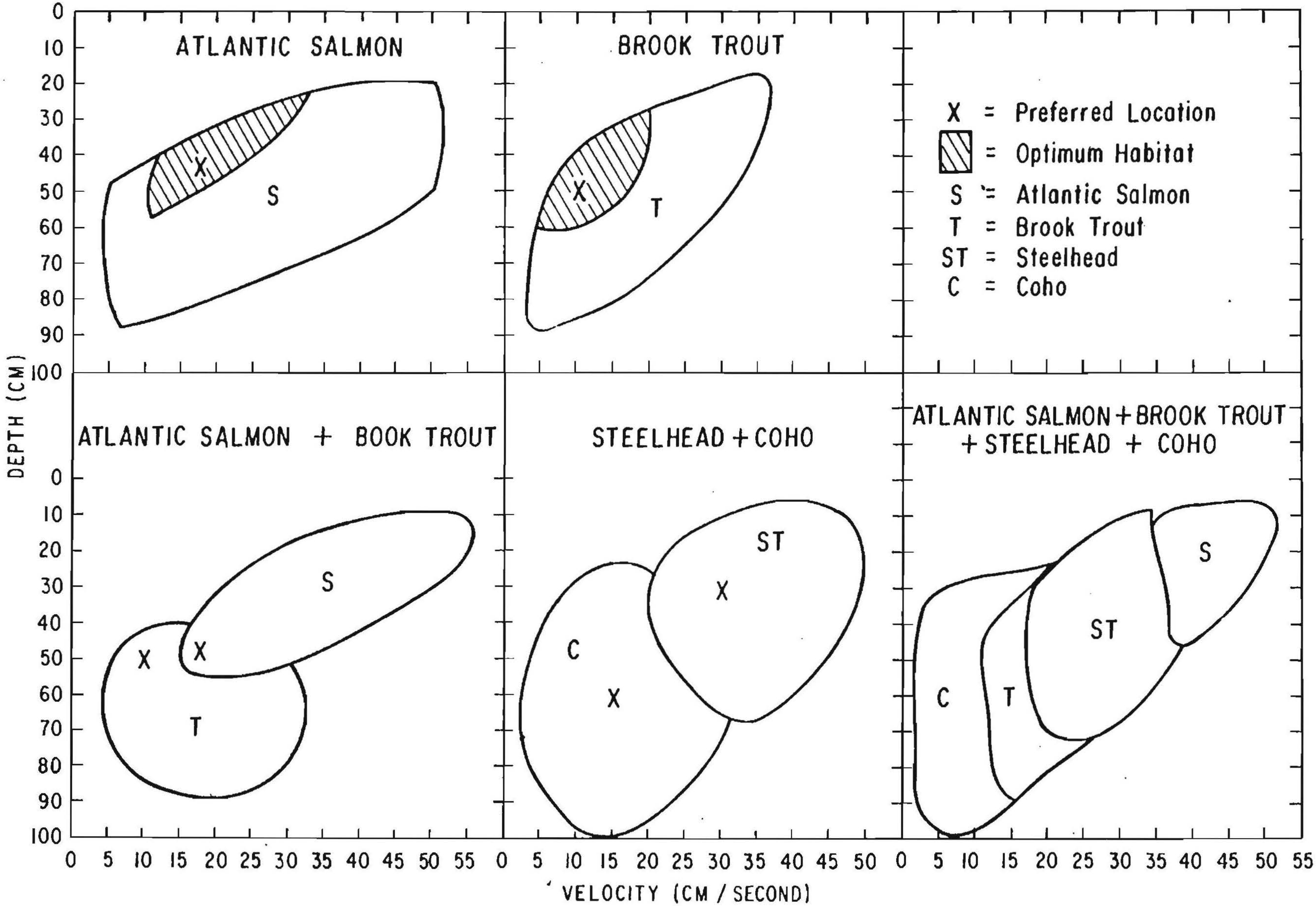


Fig. 19. General stream distribution of juvenile Atlantic salmon, brook trout, coho and steelhead.

In experiments 11 and 12 brook trout were the dominant fish and had the best growth, 0.45 mm/day. The best growth for the species, 0.79 mm/day, was not by the dominant brook trout which had an increase on 0.54 mm/day. Coho and Atlantic salmon had a similar mean increase of 0.32 mm/day for coho and 0.29 mm/day for Atlantic salmon. The dominant Atlantic salmon had the best growth of the species of 0.54 mm/day but not the dominant coho, which had a growth of 0.29 mm/day. Greatest increase of coho was with the most subordinate, and was 0.50 mm/day.

In experiments between steelhead and Atlantic salmon, Atlantic salmon had fairly good growth, of 0.64 mm/day in the first series of experiments and 0.60 mm/day in the second series of experiments, but steelhead, which were dominant, had better growth, of 0.74 mm/day in experiments 14 and 15, and 0.89 mm/day in experiments 16-18. The dominant Atlantic salmon had the best growth of the species, at 0.78 mm/day and 1.10 mm/day in the two series respectively, but in experiment 14 and 15 the sub-dominant steelhead showed the best growth (1.29 mm/day). The dominant steelhead had the best growth in the second series, at 1.20 mm/day.

In experiment 19, steelhead were dominant and had a growth of 0.90 mm/day. Brook trout grew only 0.18 mm/day. In both species the sub-dominant grew better, the sub-dominant steelhead growing 1.50 mm/day, and the sub-dominant brook trout growing at 0.55 mm/day.

With coho and Atlantic salmon fry in experiments 20 and 21 coho were larger, and dominant, and showed the better growth of 0.70 mm/day. Atlantic salmon grew only 0.25 mm/day.

In the following two experiments, (22 and 23), the Atlantic salmon fry were a little larger, were observed over one experiment without coho, and grew 0.66 mm/day. Prior residence, or their larger size had given them some advantage although still subordinate to the coho. The growth of the coho was 0.43 mm/day. As they were unbranded it was not possible to show relative growth of the dominant fish.

In experiment 24, a brook trout was the dominant fish, and it had the best growth, of 1.00 mm/day. Mean increase was 0.69 mm/day. The dominant coho had the best growth of the species, at 0.81 mm/day. Mean increase of coho was 0.75 mm/day.

The dominant Atlantic salmon, which was subordinate to the dominant coho, was 0.56 mm/day. Mean increase was 0.44 mm/day.

These experiments were made at different temperatures and in different seasons, both of which parameters probably affected the growth. However, food itself was not limiting, and the results show besides specific differences in growth rates, that agression has some effect on growth rate, psychologically, physiologically or by prevention of subordinates from feeding, with the dominant species usually showing the best growth. This effect may be more severe with Atlantic salmon, as the dominant fish usually showed the best growth, and the most subordinate fish sometimes showed no growth at all. With the other three species the dominant fish did not always have the best growth. In a natural stream a dominant would take the best feeding position, but in the present experiments food was available throughout the tank, so that subordinates could feed if they were not prevented from doing so.

5. DISCUSSION

The distribution of the fish in these experiments indicates that the wide channel was the preferred section in most experiments, and except for an Atlantic salmon parr which chose the fast narrow channel in experiment 2, a coho which chose the pool in experiment 10, and an Atlantic salmon which chose the pool at 7°C in experiment 4, the dominant fish spent most of the time in the upper part of the wide channel at all three water speeds. This may be because this section represented the 'upstream' section, and therefore the source of food, rather than an attraction to a preferred water velocity. Nevertheless the fish appeared to behave in a natural way, and as east coast salmonids have been observed to do in the river. Prior residence has been shown in other experiments to give advantage (Payne 1975; Miller 1958), but in the present experiments species and size appeared to be of overriding importance.

Some problem may be associated with the source of the fish. There may be racial differences in behaviour, and hatchery fish have been shown to have different behaviour from native fish with at least brook trout (Vincent 1960) and Atlantic salmon (Fenderson and Carpenter 1971). Nevertheless, tentative predictions can be made on the results, in association with pertinent reports in the literature on salmonid ecology.

When coho co-exist with juvenile steelhead in spring and summer the coho are found in pools and the steelhead in riffles, whereas with only one species present both types of environment are used by each (Hartman 1965). A similar situation exists with Atlantic salmon parr and brook trout, where in summer parr usually are more abundant in riffles and brook trout in pools, (Keenleyside 1962; Gibson 1966) but in the absence of one species, or when the second species is sparse, or when the food is abundant, either species occupies both habitats (Gibson 1973, 1978). Riffles are the preferred location, probably related to the amount of suitable food, which is more plentiful in riffle areas than in slow, deep sections. The mechanisms of the former interactive segregation with coho and steelhead was aggression, and in the latter with parr and brook trout both aggression and exploitation.

The young steelhead in the present experiments were more aggressive than the Atlantic salmon parr, which would suggest that Atlantic salmon parr would be displaced from riffles if both species were present. Coho were less aggressive that parr, but could displace smaller parr then themselves. However, parr in pool areas are usually the larger ones, so these would probably not be displaced by aggression from young coho, although the aggression of Atlantic salmon parr has been shown to be less in slow water than in fast (Gibson 1978). Hearn (1978) found in a pool environment that with similarly sized parr, juvenile coho dominanted juvenile Atlantic salmon. Usually larger fish of a species occupy deeper water than small fish of the species (Huntsman 1948). The distribution of small parr in rapids and larger ones in deeper water is partly the result of aggression (Symons and Heland 1978). It appears however that the morphological characteristics and more stationary character of parr in holding a territory may give parr an advantage in fast water, enabling them to displace other species from this type of habitat by exploitation (Nilsson 1967). The ability to hold station on the bottom without swimming, and the low mobility of the species, would allow less energy to be spent swimming against the current, which would be beneficial in fast water to Atlantic salmon parr, hence giving it a competitive advantage. Similarly Solomon (1979) believes that competition between coho and Atlantic salmon would not be severe in European rivers. A hypothetical distribution of these salmonids, related to depth and water velocity is shown in Fig. 19. Probability-of-use curves for Atlantic salmon, as derived by the methods of Bovee and Cochnauer (1977), and which have been derived for steelhead, coho and brook trout, may be useful in predicting possible competition.

Atlantic salmon parr did not show complete fidelity to a territory, the location of which could change, and movements of their station within an area were common. Probably limited movements are valuable in adapting to changing conditions within a river. Nevertheless Atlantic salmon parr tend to remain over the summer within a fairly limited area (Gibson 1973). Similarly steelhead trout generally show limited movement within the season (Edmundson et al. 1968).

Ruggles (1966) reported that coho change their behaviour with water velocity, and that at low velocities they spent much time in extensive cruising and agonistic behaviour, whereas in the riffle-like environment coho tended to remain fixed to a given location in the channel, usually in close proximity to the gravel bottom. Both Atlantic salmon parr and brook trout similarly appear to change their behaviour with differing water velocity (Gibson 1978). All four species took food at the water surface and in the water column. No vertical spatial segregation was noticed between species, although some individuals of all species concentrated on surface food, usually near a feeder, whereas others fed mainly near the bottom.

It is likely that coho would compete severely with small brook trout, as both species appear to be adapted to the pool environment. However, as coho emigrate at the smolt stage, none large enough would remain to displace large brook trout by aggression. Brook trout fry and yearlings might be displaced by aggression, but immigration from areas above obstructions to coho, if such exist, would provide recruitment for larger brook trout. It might be argued that a replacement of brook trout by coho would be beneficial, as coho emigrate to sea, with the resulting return of a large biomass derived from resources far away, and brook trout are numerous in areas where coho could not colonize, such as above impassable falls and in inland waters, so would not become rare.

Coho evidently will feed on smaller fish, if available, (Hunter 1959) so this presents a danger to salmonid fry from predation. However, in rivers with a diverse fish fauna, perhaps coho could use this resource without preying on salmonids. In some Atlantic salmon rivers, such as in insular Newfoundland and along the North Shore of the Gulf of St. Lawrence, competing and predatory species are scarce, and Atlantic salmon parr are abundant in pools and deep slow flowing areas. In these rivers, especially where typical parr rearing habitat is restricted, the introduction of a competing pool dweller would have a deleterious effect on the natural Atlantic salmon production. Juvenile coho were found in a New Brunswick stream in 1976 by Symons (1978). These were found in the pool-like habitat, co-habiting with brook trout. However, their numbers were sparse, so that it is unlikely noticable interactions would occur. Similarly young coho captured in a Nova Scotia stream were in the pool environment (D. J. Cox, pers. comm.).

As fish become larger they move to deeper water, may become less aggressive, (Chiszar et al. 1975) and take larger food items, such as small fish. Large rainbow trout are usually in pools (Lewis 1969), and will become partly pisciverous. Hence, they will occupy a similar niche to large brook trout or brown trout and they have displaced brook trout in some waters. There appears to be an effect of temperature in determining the relative success of the genera Salmo or Salvelinus (Fry 1947). Ayers et al. (1964) state that when water temperatures are over 18°C the environment usually favours rainbow trout over brook trout. In some rivers brook trout occupy the cooler headwaters, but rainbow trout have the competitive advantage in the lower warmer waters (Powers 1929; Burton and Odum 1945). Similarly climatic factors may favour rainbow trout in the warmer environment (Allen 1956; Gibson 1972). Rainbow trout are the most resistant species to high temperatures and low oxygen, (Mills 1971) but the least resistent to acidic conditions. The lower tolerance limit may be as high as pH 5.5-6.0 in some natural waters (Grande et al. 1978). These factors may limit the extension of rainbow trout and steelhead trout in such areas as the North Shore of the Gulf of St. Lawrence, Labrador and Newfoundland where waters are acid and temperatures cool for much of the year. Occasional rainbow trout are caught in some rivers along the North shore of the Gulf of St. Lawrence (Gibson 1977b; Ouellet and Côté 1977) but do not appear to be common there, although they thrive further west in the St. Lawrence River and in the Great Lakes. Similarly, they appear to be rare around Newfoundland, although they were introduced in 1887 (Scott and Crossman 1964). They are known to be anadromous in Shoal Harbour River at Clarenville and in some adjacent streams (A. Jamieson, pers. comm.), Occasional mature anadromous steelhead are caught at three other locations around the island, and interestingly enough the rivers at all four sites lie on allkaline rocks (Chadwick and Bruce, submitted). A few anadromous rainbow trout have been caught at St. Pierre and Miquelon, but they may have come from nearby cage rearing projects (A. Champigneulle, pers. comm.). However, rainbow trout apparently have displaced brook trout in some waters near St. John's, such as Picco's Brook and adjacent lakes.

Territory size for several species of juvenile salmonids appears to be similar with the average area of stream bed per fish being proportional to the cube of the length of the fish (Allen 1969). He noted that the density of salmonids in streams is usually about 1.7 g/m^2, and that territories of one particular size comprise only 2-20% of the total stream bed.

In the present experiments at temperatures above 7°C the distance tolerated by a dominant fish was between 0.4 m for brook trout at 20°C (experiment 12) to 2.4 m at 15°C for steelhead (experiment 19). Territories for all species tested broke down at 7°C, and the average distance from its neighbour was 0.3 m for Atlantic salmon and 0.5 m for the dominant steelhead (Table 7). If requirements at 7°C and 20°C are not included the range of density in the wide channel was 0.3 $fish/m^2$ in experiment 16 with a steelhead dominant, to 2 $fish/m^2$ in experiment 11 with a brook trout dominant. With Atlantic salmon or coho dominant the mean density was $0.7/m^2$ (Table 13). Presumably this can be interpreted as with abundant food a greater biomass could be expected if brook trout were dominant than with the other species, and the least amount with juvenile steelhead. However, apparently aggression changes with size, amount of food, and water velocity, so further experiments are needed. Dill (1978) found with juvenile coho that both approach and lateral display distances tend to increase with increasing intruder size. Stringer and Hoar (1955) found with both Kamloops trout and coho that larger fish defended larger territories.

They also found that the presence of an aggressive fish reduced the attacking tendencies of other members. In the present experiments a dominant fish, but of a less aggressive species, such as brook trout, may have reduced aggression amongst subordinates, allowing more fish to use the wide channel. As the wide channel was the preferred section, and the one occupied by dominant and territorial fish, territory size can be estimated from the number of fish occupying this area (6 m^2). As shown in Table 13 at 15°C this ranges from 3.8 m^2 when a steelhead was dominant in experiment 16, to 0.5 m^2, with a brook trout dominant in experiment 11. Means for experiments at 15°C were 1.4 m^2 for coho, 1.8 m^2 for steelhead, 1.4 m^2 for Atlantic salmon, and 0.8 m^2 for brook trout. The sizes of these territories are in accord with the general conclusions of Allen (1969), and similar to territorial sizes of dominant Atlantic salmon parr (1.1 m^2) in experiments of Symons (1971). However, that of the brook trout was least, suggesting that it is the species most tolerant to the presence of neighbours. The size of the territory is proportional to the weight of the fish, but decreases or is abandoned with low temperatures and with low water velocity. In lentic conditions salmon parr have been seen to aggregate or to school. They are common in slow water areas or pools where competing species are sparse. At these times they may be feeding, in which case they will be actively searching for food. If conditions are adverse in neighbouring riffle areas, due to high temperatures or sparse food, a territory is no longer economically defendable, and schooling in pools or hiding in the substrate will result. Examples of the latter are, attraction to cool spring water when the main river temperature rose above 22°C (Gibson 1966), when water velocities are experimentally decreased (Gibson 1978), or when high water temperature and low food presumably make the metabolic cost of holding territory in fast water unprofitable, and scholing results in adjacent pools. These latters conditions have been observed in a Newfoundland stream (unpublished data). When food is abundant, aggression decreases, and higher numbers of fish can occur, presumably as food supply is adequate for metabolism and maximum growth, and greater territorial defense would result in less energy benefit.

Density would necessarily be greater in the present experiments than would occur naturally, but were below densities that would induce schooling (Keenleyside and Yamamoto 1962; Fenderson and Carpenter 1971). The present results, and previous studies (Gibson 1973, 1978), suggest that brook trout are somewhat more tolerant of the proximity of other species. Brook trout in the present study had a relatively high number of agonistic encounters. However, this may have been related to their more mobile behaviour, resulting in more frequent encounters, rather than to a high level of aggression. The high intensity aggressive act of charge and chase was less frequent in this species than in the other three species. Lateral displays were less frequent amongst coho and steelhead than was found by Hartman (1965). However, in the present experiments only acts by a fish causing a displacement are presented. Also, density of fish was lower here and the fish were allowed at least five days to be conditioned to the tanks, whereas Hartman began his observations a day after introducing the fish. A longer residence gives time for the fish to form a hierarchy, and probably individual recognition would decrease prolonged combats involving displays. Giving time to form a hierarchy allowed a subordinate fish to appear, which illustrated the interesting phenomenon of submissive colours. Other than brook trout, which did not show striking colour and pattern differences between dominant and subordinate fish, the most obvious features were the contrasting vertical parr marks against a light background with dominant fish, and the striped pattern of the subordinate coho and steelhead, which remained mobile, and the cryptic colouration of subordinate Atlantic salmon, which remained stationary in contact with the substrate. In streams vertical parr marks are characteristics of aggressive juvenile salmonids, whereas fish with longitudinal stripes are usually schooling or unaggressive fish, as is seen in some minnows. The latter is probably a form of disruptive colouration, and may be more difficult to distinguish then vertical bars. The lighter colouration of a dominant fish may reduce attacks. Stringer and Hoar (1955), found that underyearling Kamloops trout attacked fish with dark colouration more frequently than ones with light colouration. Subordinate fish were usually less mobile than dominant fish. In other experiments (Fabricius 1952; Stringer and Hoar 1955) mobile fish have been seen to elicit more attacks than stationary fish.

Chapman (1966) points out that in streams habitat differentiation is usually on the basis of velocity, turbulance, and cover, and that conventional competition for space seems to have been substituted for direct competition for food, Keenleyside (1979) states that territoriality among stream living salmonids was probably related to the securing of food resources and of shelters in which to avoid predators, but that there was surprisingly little experimental evidence bearing directly on the function of stream territories.

However, if the resource is to be shared to achieve some optimum growth for the individuals present, holding territories when in fast water appears to be the most efficient method. The food consisting of organic drift is brought to the individual in moving water, so active searching and swimming is both unnecessary and inefficient in this type of habitat. Young Atlantic salmon appear especially well adapted for the fast water habitat and can apply themselves to the substrate using their pectoral and pelvic fins rather like suckers (Kalleberg 1958) so can hold station using little energy, occassionally darting out for food or defense of the territory. It seems reasonable therefore, in this type of habitat, to defend a defined area rather than search for food. Kalleberg (1958) showed that the presence of large boulders or turbidity allowed more visual isolation and therefore smaller territories among Atlantic salmon underyearlings, and that faster water flows also brought about smaller territories by bringing the under yearlings closer to the substrate and reducing visual contact with neighbours. In the present study dominant Atlantic salmon and steelhead held position higher above the substrate than subordinate fish and had larger territories. The species more commonly found in pools (brook trout and coho salmon) did not show this change in height off the substrate related to dominance status. Fish were less likely to be attacked if they were close to the bottom and stationary, but apparently a more favourable position for holding large territories for seeing and catching the food, including surface items if the water is sufficiently shallow, is off the bottom, the preferred water velocity affecting the height. The dominant fish can be mobile with impunity, whereas it is to the dominant fish's advantage to prevent a subordinate from feeding and to the subordinate's advantage to be immobile to deter attack.

Ebersole (1980) defines the optimum territory size as that at which the per-area benefit of increased food most greatly exceeds the per-area (or per-perimeter) costs of travel time, territorial defense, and increased exposure to predators. Brown (1964) postulated that the form of territoriality evolved in a species, is determined primarily by competition and economic defendability. His thesis can be applied to salmonids. Although the dominant fish did not always have the best growth in the present experiments, in conditions where food is limiting, the selective advantage of defending an area can be seen if it is economically worthwhile. If food density is high, presumably higher than in these experiments, high levels of aggression would be a waste of energy. There is evidence that with abundant food some territorial salmonids allow an increase in neighbours by a reduction in aggression and smaller territories, as with Salmo gairdneri (Slaney and Northcote 1974) or by allowing subordinates within the territory, as with Atlantic salmon (Symons 1968, 1971). Hixon (1980) has developed an energy-time budget model in which he predicts for food energy maximizers that feeding territory size should vary inversely with both food production and competitor density. On the other hand Ebersole (1980) proposes that no critical maintenance level exists for the majority of territorial animals and gave examples to show that many food maximizers will expand their territories when food becomes abundant.

In the pool environment food is more dispersed and settles to the bottom (McLay 1970). Territoriality appears not to be economically worthwhile, probably because food must be hunted beyond the visual field in all directions, so that territoriality gives way to schooling (for protection or hydro-dynamic reasons), or to aggression limited simply to dispersion of individuals. Aggression may be directed to fish upstream of a dominant, but not behind so that a hierarchy is formed in the school. In pools a more roaming type of behaviour is prevalent, with more feeding at the water surface, or from the bottom, rather than in the water column.

This is the situation with brook trout, brown trout and juvenile coho salmon, when occupying pools. It appears from the literature that salmonids can change their behaviour to be aggressive in rapid water, but less aggressive and frequently schooling in pools, e.g. this applies with Atlantic salmon (Gibson 1978); brook trout (Elson 1939; Keenleyside 1962); coho (Ruggles 1966; Hartman 1965; Mason and Chapman 1965); steelhead trout (Hartman 1965; Jenkins 1969); brown trout (Hartman 1965), and chinook salmon (Reimers 1968). A salmon like fish in Japan, Plecoglossus altivelis is territorial in rapids, but schooling in pools (Kawanabe 1957). Even Atlantic salmon smolt, generally a schooling stage (Kalleberg 1958; Keenleyside and Yamamoto 1962), become territorial when obliged to hold station in a current (Kalleberg 1958; Gibson 1977). Probably Atlantic salmon smolt are usually seen in slow water, schooling, because they have become more buoyant than parr (Saunders 1965) and therefore find it more efficient to feed in pools, where the schooling type of response appears. This change of behaviour in response to water current provides evidence towards the advantage of territorial behaviour for sharing the food resource in fast water.

All four species showed an increase in activity with increased temperature, as would be expected, with greatest activity at 20°C; the highest temperature used. Above this temperature the activity of brook trout decreases, whereas the activity of species in the genus Salmo increases up to the lethal temperature (Fry 1947, 1948, 1951). Salmo fry have higher temperature preferences than Salvelinus fry (Peterson et al. 1979). Mason and Chapman (1965) found a positive relation between level of aggression and temperature among underyearling coho. Glova and McInerney (1977) found that critical swimming speeds of coho varied directly with temperature, with maxima occurring between 20 and 23°C. In the present experiments steelhead were aggressive at 7°C, but were less territorial. Hartman (1966) found that steelhead aggression fell from May to

January, in spite of water temperature, whereas coho aggression levels tended to follow water temperature. Levels of aggressive behaviour among steelhead were affected by, but were not entirely dependent on temperature. Among steelhead, aggressiveness underwent a significant decrease with age independent of temperature. Contest rates for steelhead were lower in June than in May, even though the May water temperature was lower. Similarly in controlled temperatures, he found that contest rates were lower in September than in July, even though the September controlled temperature was higher than that of July. Seasonal effects were not taken into account in the present series of experiments, although the photoperiod was controlled, which may have mitigated behavioural changes. Keenleyside and Hoar (1954), using experimental tubs, discovered a change in rheotactic behaviour with temperature with some salmonids, and the rheotactic behaviour of coho fry and smolt changed from a positive response at 4.5°C and 9°C to a negative one at 13-14°C. This behaviour was not observed in the present experiments, possibly because the stream tank provided more natural conditions for the fish to hold station.

The breakdown of territoriality found at 7°C may be related to the movement of salmonids to pools and cover in the winter (Allen 1941; Hartman 1965; Bustard and Narver 1975; Gibson 1978). Bjorn (1971), working in two Idaho streams, studied the movements of rainbow trout, brook trout, Dolly Varden, chinook salmon, sculpin and dace. He found many juvenile salmon and trout migrated from the Lenhi River drainage each fall-winter-spring period. Fish emigrated before the abundance of drift insects declined in the winter and emigration occurred in spite of the relatively stable flows in both streams. The movements of non-smolt trout and salmon correlated best with the amount of cover provided by large rubble substrate. Saunders and Gee (1964) found in a small stream in New Brunswick that Atlantic salmon parr and fry in winter left riffle areas and were found under cover in pools. In a tributary of the Miramichi River, salmon parr in winter did not move from their summer habitat, but took cover in crevices of the substrate (Rimmer 1980). Suitable winter habitat appears to be necessary for survival over this period, and is probably provided by either nearby pool areas or crevices in the substrate. The available habitat probably determines whether fish remain or move from the area.

Newman (1956), observing larger rainbow trout than in the present experiments, found that brook trout dominated slightly larger rainbow. It appears that the behaviour of rainbow trout changes with size from a highly aggressive and territorial riffle dwelling juvenile, to a less aggressive and more pool dwelling larger fish.

In a study of interactions between juvenile coho and steelhead trout, Allee (1974) came to the conclusion that in agonistic encounters juvenile coho were dominant over steelhead trout, regardless of size. In his experiments, he found that steelhead did not nip coho at all in any microhabitats, and steelhead nipped steelhead very frequently in the riffle microhabitat. He thought that species specific habitat preferences and intraspecifc effects seemed to play a greater role in the final species composition of experimental populations then did the direct interactions between species. He observed that coho fed significantly more at the surface than the bottom, and that steelhead fed significantly more on the bottom substrate than on the surface. He concluded that coho and steelhead did not appear to have a negative impact on each other. The relative aggression of the two species in his study conflict with the findings in mine, and illustrate the need for further experiments.

Relative growth has important bearings on interactions, as size may be the deciding factor in many aggressive encounters. In several situations with co-existing salmonids the pool dweller is larger for a certain age than the riffle dweller, e.g. in Europe brown trout tend to occupy the pools, and are faster growing than the Atlantic salmon, which occupy the riffles. Egglishaw and Shackley (1973) suggest the main causitive factor in maintaining this size differential is the earlier emergence of the brown trout, which gives them an advantage which they maintain through the juvenile stages. Similarly brook trout emerge a month earlier than Atlantic salmon (White 1940), and in most waters maintain this growth advantage through the juvenile stages. Dickson (1980) from experiments in Quebec, believes that, like brown trout, it is the earlier emergence of the brook trout that allows it to maintain a growth advantage. Coho also emerge earlier then steelhead, and are larger than steelhead through the summer, but by winter sizes are alike (Hartman 1965). It is possible that the pool dweller has evolved to be larger so that it is not displaced from both the riffle and the pool by the more aggressive riffle dweller. However, both steelhead and coho may be faster growing than the east coast salmonids, and experiments should be conducted with the species concerned in sympatry. If they are at a competitive disadvantage, their growth rate may be reduced below that of the native salmonids. However, the underyearling coho caught in the New Brunswick stream by Symons and Martin (1978) had an average fork length of 89 mm (range 75-100) compared with 60-70 mm for underyearling Atlantic salmon, and 40-60 mm for underyearling brook trout captured at the same time. In this situation the Atlantic salmon were larger than the brook trout, which is rather unusual, but may reflect the presence of the coho which were occupying the same habitat as the brook trout.

In most situations the dominant fish has the best growth. Yamagishi (1962) reported that in the earlier part of his experiments, dominant rainbow trout fry did not always grow faster than the subordinate ones, but in the latter part of his experiments, the dominant fish grew most rapidly and ranked first in size. There were therefore, some periods in which the size hierarchy is not directly effective to growth. This may explain why in the time interval of the present experiments the dominant fish was not always the fastest in growth. Li and Brocksen (1977) found that dominant rainbow trout as a group grew faster, grew more efficiency, and contained greater lipid content than the rest of the population. However, certain subordinate individuals were noted to grow faster and more efficiently than the alpha trout, which they thought might reflect greater energy expenditure in territorial defense by the alpha trout. Ejike and Schreck (1980), working with coho salmon, found that plasma cortisol concentration, interrenal nuclear diameter, and tail beat frequency were lowest in the dominant fish and highest in the subordinate fish, and that hepatic glycogen varied directly with social position. They suggested that dominance status was inversely related to a low-level, chronic state of stress in the fish, the dominant individuals being the least stressed.

Fecundity and age at first maturity may be significant factors affecting competition. Lee (1971), in a study of rainbow trout, brown trout, landlocked salmon, and brook trout on the Avalon Peninsula, Newfoundland, found that female brook trout matured a year earlier, at 2+, than the other three species, giving the advantage of a shorter generation cycle. However, fecundity of rainbow trout and brown trout was higher than brook trout. Landlocked salmon had the least number of ova/fish weight compared with the other species.

It is unlikely that the marine phase would cause negative interactions, as the fish would be so dispersed that interactions would be unlikely. Numbers of adult Atlantic salmon are unlikely to regain their original numbers, so suitable prey should be abundant, and mortality in the sea is most likely density independent. These factors however are unknown. Steelhead return to spawn in the spring. If this coincides with the smolt run, would steelhead, or large rainbows in the estuary, prey on migratory Atlantic salmon smolt? If steelhead spawn before Atlantic salmon fry emerge, there could be disturbance of the gravel over the redds and mortality of the fry. Coho in North America spawn from November to January (Scott and Crossman 1974) and this, overlaps or is later than Atlantic salmon. If the same spawning sites were used, considerable damage could be done to Atlantic salmon eggs, if spawning sites were limiting, or if escapement of Atlantic salmon were sparse. Coho adults have high straying rates, between 15-27% in native streams (Shapovalov and Taft 1954) and higher where they have been released as smolts (Allen et al. 1978). This makes it difficult to confine experimental releases to a single stream.

In recent years a number of adult coho have been caught in the St. Lawrence in the waters encircling Montreal (Laberge 1980; C. Pomerleau, pers. comm.). Besides the young coho caught in New Brunswick in 1976 (Symons and Martin 1978), four juvenile coho have been caught in Nova Scotia by D.J. Cox in October 1979 (D.J. Cox, pers. comm.). They were found in a tributary of the Cornwallis River, Kings Country, N.S.; they were caught in a pool area. Also captured were brook trout, brown trout, and threespine sticklebacks. The adult coho parents may have originated from aquaculture projects in New England or from the Great Lakes.

Other problems which must also be considered with introductions of exotic salmonids are the possibilities of introducing disease and parasites, increasing predator pressure, increasing fishing pressure by introducing new methods of capture, such as trolling in the estuaries, or snagging in rivers, and sociological problems related to increased angling pressure. Additional pressures would adversely affect already depleted Atlantic salmon stocks.

Their good growth rates and relatively good resistance to disease have encouraged the pen-rearing of coho and rainbow trout, and these species have been very successful in the Great Lakes where over exploitation, habitat changes, pollution and introduction of non-indigenous species have virtually eliminated the original large salmonids. However, where Atlantic salmon stocks still thrive, much caution must be taken in introducing exotic fish. Some possible interactions have been indicated in the present exposition, but field experiments over all phases of the life cycle should be made and all aspects of the ecological requirements tested before introduction are made. This should be possible in areas where coho and rainbow trout already have been introduced and are thriving.

6. CONCLUSIONS AND RECOMMENDATIONS

Steelhead trout appear to be a close ecological equivalent to Atlantic salmon parr, and coho to brook trout. Steelhead trout and Atlantic salmon were more aggressive than coho or brook trout, with steelhead being the most aggressive of the four species. Atlantic salmon and steelhead were the least buoyant, and brook trout the most buoyant, hence were better adapted to fast water and slow water environments respectively. Atlantic salmon parr were able to displace coho when the two species were about the same size, or even if parr were somewhat smaller, both when parr had prior residence (experiments 2, 3, and 4), and when coho had prior residence (experiments 7 and 8). However if coho were considerably larger, the coho were dominant over Atlantic salmon (experiments 10, 21, 23, and 24). Brook trout, if larger, could dominate parr or coho (experiments 11, 12, and 24). Steelhead were dominant over parr in all experiments, whether parr had prior residence or not, and even over larger parr than themselves (experiments 14, 15, and 17). Steelhead also could dominate larger brook trout (experiment 19).

Interactions other than aggression are likely to affect distribution in the natural situation, and Atlantic salmon parr can probably co-exist in the presence of the other species if fast riffle areas are present. Their morphological adaptions and territorial behaviour are the best developed of the four species to give it the competitive advantage in shallow fast water. However parr have a wider range of habitat if predators or competing species are sparse, as on the North Shore of the Gulf of St. Lawrence, or in insular Newfoundland. In these situations it is very likely that the biomass of parr would be reduced by the introduction of either steelhead or coho. In systems where competing species in the lentic environment confine parr to rapids, juvenile coho may not cause the numbers of parr to decrease. However, juvenile steelhead, as riffle dwellers, would be likely to compete with parr. Also rainbow trout have been shown to have the competitive advantage over brook trout in warmer and in eutrophic waters. Coho would be expected to compete with brook trout, but would not be able to displace large trout. Recruitment of brook trout would probably be sustained from small tributaries and areas above obstructions, which coho could not colonize. These theoretical interactions should be tested in the natural situation, and preferably where coho and steelhead have already been introduced.

7. SUMMARY

7.1 ECOLOGICAL RELATIONSHIPS

Juvenile salmonids at the fluvatile stage were studied in an experimental steam tank. These were: Atlantic salmon parr, brook trout, steelhead trout and coho salmon. Juvenile steelhead and juvenile coho are native to Pacific drainages, but have been introduced to the East. Where they naturally co-exist, in the spring and summer, steelhead occupy the riffles of streams, and coho occupy the pools, although in experimental conditions both species will occupy both environments in the absence of the other. In the winter both species occur together in pools.

Juvenile Atlantic salmon, or parr, and brook trout, naturally co-exist in many rivers and streams of the East coast. In the summer parr are most common in the riffles, and brook trout in the pools. Brook trout also occur in riffles if food is abundant or parr are few or absent. In the winter parr hide under rocks, or leave the riffles and occur with brook trout in pools.

All four species live at the same trophic level, and are primarily insectiverous, taking their food from the water column, at the surface, and on the bottom, if exposed. Riffles are the preferred location, probably related to the amount of suitable food, which is more plentiful in riffle areas than in slow, deep sections. In pools, probably related to both depth and to suspended food items settling out, fish apparently take more food at the surface, or on the bottom.

Salmonids in general appear to defend territories when feeding in running water. These feeding territories appear to be defended in accord with the economic defendability hypothesis. They tend to break down in slow water, where food must be acquired by searching, in cold water when metabolism is slowed below some acceptable level, and probably in warm water when food is sparse, and metabolic costs too high. Other studies have shown that aggression decreases with abundant food.

7.2 COMPARATIVE BEHAVIOUR

Steelhead and Atlantic salmon parr were more aggressive than coho or brook trout, with steelhead being the most aggressive of the four species. Generally, with fish of the same size, or slightly larger, steelhead could displace any of the other species from preferred areas by aggression, and parr could displace coho or brook trout. Both coho and brook trout are known to group in pools, with a dominant fish in the lead. Both rainbow trout and coho are reported to have a faster growth rate than Atlantic salmon parr and brook trout. If they were able to sustain this greater growth in sympatry with parr and brook trout, they would have a competitive advantage, as larger fish are usually dominant over smaller fish in agonistic encounters. In the present experiments the dominant species had the better growth rate.

7.3 THE BIOLOGICAL ADVANTAGES OF INTRODUCING EXOTIC SALMONIDS

Rainbow trout, or steelhead the anadromous form, and coho, are the most popular salmonids for commercial aquaculture, both for pen-rearing and for release, as they are relatively hardy and have faster growth than the East coast salmonids. Smolts of these species can therefore be released a year earlier than Atlantic salmon because of this growth differential. Sea ranching of coho and steelhead has proved to be successful on the West coast and in the Great Lakes. Rainbow trout are more tolerant of warm temperatures, low oxygen, and eutrophic conditions, so might successfully replace Atlantic salmon where conditions are now too degraded or marginal for that species. This is the case in many rivers draining into the Great Lakes, where rainbow trout and more recently coho are now providing excellent sports fishing. Atlantic salmon in Lake Ontario have been extinct there since 1898. The pen-raising of coho might be economically more worthwhile then raising the presently used strains of Altantic salmon. The pen-raising and sea ranching of brook trout are still in the experimental stages, and so far have not been shown to be economically worthwhile.

It might be argued that a replacement of brook trout by coho would be beneficial, as coho emigrate to sea, with the resulting return of a large biomass derived from resources far away, and brook trout are numerous in areas where coho could not colonize so would not become rare. It is unlikely that the marine phase would cause negative interactions, as the fish would be so dispersed that interactions would be unlikely.

7.4 PREDICTIONS ON THE EFFECTS OF INTRODUCING EXOTIC SALMONIDS

There are still fish diseases confined to certain areas, some to watersheds, and these should not be spread by indiscriminate stocking. Other dangers of introductions are that the new species might prey on indigenous species. Numbers may be adversely affected by competition, by interference, such as digging up the eggs or by aggression, or by exploitation such as more efficiently taking the food in the habitat. A further danger is that the species may be destroyed by hybridization, as was the case with the Pyramid lake cutthroat, which used to be the largest North American trout.

The main concerns with steelhead and coho are probably, the introduction of an exotic disease or parasite, displacement of indigenous salmonids by competition, and predation of Atlantic salmon smolt by large rainbows or steelhead. There is some danger that the redds of Atlantic salmon may be disturbed by spawning coho and steelhead.

Atlantic salmon parr and juvenile steelhead appear to have a similar niche, as do coho and brook trout. Atlantic salmon parr have morphological adaptations that may give them the advantage in fast shallow water riffles, but they have a wide tolerance of habitat which they exploit with lack of competition, so that production of parr would be adversely affected by the presence of steelhead and probably by coho. Coho may adversely affect the numbers of small brook trout, but as coho at the smolt size migrate from the stream, older brook trout of larger size would remain, which would not be displaced by aggression. Rainbow trout displace brook trout at temperatures of 18°C and higher, and are more successful in eutrophic waters. Large rainbow trout may prey on parr and migrating smolt.

7.5 RECOMMENDATIONS

With these considerations in mind it would be very unwise to proceed with the stocking of steelhead or coho in Atlantic salmon rivers, or as both species tend to stray, anywhere close to Atlantic salmon rivers. Some possible interactions have been indicated in the present exposition, but field experiments over all phases of the life cycle should be made and all aspects of the ecological requirements tested before introductions are made. This should be possible in areas where coho and rainbow trout already have been introduced and are thriving.

The cultivation of these species in pens where there is access to the sea should also be discouraged, as loss of nets and escapes are inevitable. It is possible these Pacific salmonids present no danger. Rainbow trout are less tolerant of acid waters than Atlantic salmon or brook trout. This plus chemical and climatic factors may prevent rainbow trout from extending their range on the east coast. Occasional captures are made, but numbers do not appear to be increasing. In Newfoundland rainbow trout have been present since 1887, and yet still have a restricted distribution. Coho have been deliberately released in Massachusetts, New Hampshire and Maine for several years, but have apparently strayed to only one New Brunswick and one Nova Scotia stream, yet were unsuccessful there. However, greater numbers of spawners might have greater success. If there is demand for culture of these Pacific salmonids on the East coast, field work should be undertaken to more thoroughly test the hypotheses presented in this manuscript with regard to competitive interactions, before aquaculture and stocking is allowed to proceed in the region of Atlantic salmon waters.

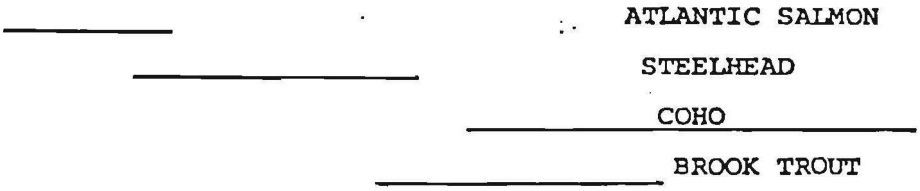
SUMMARY TABLE

Adaptations to water velocity as applied to Atlantic salmon, coho, steelhead, and brook trout. Factors suitable for fast water are in the left hand column, and for slower water in the right hand column.

WATER FLOW			TYPE OF PARAMETER
FAST	——	SLOW	Water velocity
	Suitable food		
Invertebrate food of aquatic origin in the drift	——	Surface & benthic invertebrates. Fish (minnows, etc.)	Feeding
	Morphology		
Streamlined	Length:Body Depth	Robust	
decrease	Buoyancy	increase	
	Special adaptations (e.g. use of fins as suckers by At. salmon parr)		Adaptations to water velocity
	Behaviour		
Territoriality (including high level of aggression & reduced mobility in holding station)	——	Schooling (including reduced level of aggression, increased mobility, & roaming type of behaviour)	
Holding station close to substrate	——	Holding station in mid-water	

HYPOTHETICAL DISTRIBUTIONS

Hypothetical distribution of the species in allopatry (occupying mutually exclusive geographical areas).



Hypothetical distribution of the 4 species in sympatry (occurring in the same area).

TABLE 1. TYPE OF EXPERIMENTS AND THEIR DATES
S = ATLANTIC SALMON; T = BROOK TROUT;
C = COHO SALMON; ST = STEELHEAD TROUT

NO.	DURATION	SPECIES	WATER TEMPERATURE (°C.)	NO. OF OBSERVATIONS
1	Nov. 17 - 21/76	6S	15	20
2	Dec. 8 - 29/76	6S; 6C	15	20
3	Jan. 24 - Feb. 2/77	6S; 6C	20	20
4	Feb. 4 - 9/77	5S; 6C	7	10
5	Feb. 19 - 25/77	6C	15	20
6	March 4 - 7/77	6C	20	10
7	March 14 - 17/77	6C; 5 - 6S	15	10
8	March 21 - 27/77	6C; 5S	20	10
9	April 4 - 11/77	6T	15	10
10	Sept. 22 - Oct. 17/77	6C; 3S; 3T	15	10
11	Oct. 24 - 31/77	6C; 6S; 6T	15	10
12	Nov. 7 - 16/77	6T; 6C; 6S	20	10
13	Jan. 28 - Feb. 2/78	6S	15	10
14	Feb. 13 - 24/78	6S; 6St	15	10
15	March 3 - 10/78	6S; 6ST	7.3	10
16	March 27 - April 9/78	7ST	15	10
17	April 17 - 25/78	7ST: 6S	15	10
18	May 2 - 8/78	3S; 7ST	20	10
19	May 14 - 21/78	6ST; 6T	15	10
20	July 7 - 11/78	10C	16.3	10
21	July 18 - 21/78	10S; 10C	17.7	10
22	July 28 - Aug. 4/78	7S	16.2	10
23	Aug. 8 - 12/78	7S; 7C	19.4	10
24	Aug. 29 - Sept. 9/78	4S; 4T; 5C	18.1	10

TABLE 2-1

SIZES AND INCREASES IN EXPERIMENTS 1-9.

EXPT. # (C.)	MEAN SIZE (RANGE) F.L.(cm)	MEAN SIZE (RANGE) WT.(g)	MEAN INCREASE/DAY LENGTH (mm)	MEAN INCREASE/DAY WEIGHT (g)		Dominant fish (and fish with greatest increase in length) F.L.(cm)	WT.(g)	mm	g
1, 2, 3, 4	ATLANTIC SALMON								
15° 15° 20° 7°	12.2	18.4	0.35	0.28		15.1	35.7	0.27	0.16
	(9.3-15.1)	(6.4-35.7)			(greatest growth,	9.3	6.9	0.63	0.41)
2, 3, 4	COHO								
	11.0	14.1	0.29	0.13		11.8	17.8	0.27	0.13
	(9.8-12.0)	(9.2-19.2)			(greatest growth,	10.1	10.2	0.43	0.19)
5, 6, 7, 8	COHO								
15° 20° 15° 20°	12.6	19.5	0.52	0.48		13.4	25.9	0.64	0.87
	(11.5-13.4)	(14.9-25.9)			(greatest growth,	13.2	25.0	0.76	0.71)
7, 8	ATLANTIC SALMON								
	11.8	18.5	0.76	0.31		13.6	28.1	0.75	0.58
	(9.3-14.6)	(9.4-33.2)			(greatest growth,	9.7	9.4	1.08	0.32)
9	BROOK TROUT								
15°	16.0	40.5	0.51	0.56		17.6	53.9	0.47	0.77
	(13.8-18.3)	(20.3-63.3)			(greatest growth,	13.8	20.3	0.76	0.62)

TABLE 2-2

SIZES AND INCREASES IN EXPERIMENTS 10 - 12.

EXPT. # (C.)	MEAN SIZE (RANGE) F.L. (cm)	WT. (g)	MEAN INCREASE/DAY LENGTH (mm)	WEIGHT (g)	DOMINANT FISH (SIZE)			SIZE INCREASE/DAY	
10	COHO								
15°	9.5	9.0							
	(8.5-11.0)	(6.3-13.8)	0.65	0.28	DOM. C.	9.6 cm	9.4 g	0.71 mm	0.33 g)
	ATLANTIC SALMON								
	8.7	5.2							
	(8.1- 9.5)	(4.5- 6.5)	0.18	0.08	(DOM. S.	9.5 cm -	6.5 g	0.29 mm	0.14 g)
	BROOK TROUT								
	10.4	10.2							
	(9.7-10.9)	(9.8-10.5)	0.80	0.25	(DOM. T.	9.7 cm -	9.8 g	1.06 mm	0.23 g)
11 & 12	BROOK TROUT								
15° 20°	10.9	10.5			DOM. T.	11.5 cm	11.6 g	0.54 mm	0.50 g)
	(10.1-11.8)	(8.5-13.9)	0.45	0.33	(greatest growth	10.7 cm -	9.4 g	0.79 mm	0.52 g)
	COHO								
	9.4	9.5							
	(9.0-10.1)	(7.8-11.8)	0.32	0.16	(DOM. C.	9.0 cm	7.8 g	0.29 mm	0.14 g)
					(greatest growth	9.1 cm -	8.6 g	0.50 mm	0.26 g)
	ATLANTIC SALMON								
	8.9	6.0							
	(7.8-10.0)	(3.9- 8.7)	0.29	0.15	(DOM. S.	10.0 cm -	8.1 g	0.54 mm	0.34 g)

TABLE 2-3

SIZES AND INCREASES IN EXPERIMENTS 13, 14, 15

EXPT. # (C.)	SPECIES	MEAN SIZE (RANGE) F.L. (cm)	MEAN SIZE (RANGE) WT. (g)	MEAN INCREASE/DAY F.L. (mm)	MEAN INCREASE/DAY WT. (g)	DOMINANT FISH	INCREASE/DAY F.L. (mm)	INCREASE/DAY WT. (g)
13 - 15° 14 - 15° 15 - 7°	ATL. SALMON	10.5 (9.2-12.5)	11.87 (7.58-18.96)	0.64	0.39	Dom. 12.4 cm-18.34 g	0.78	0.66
14 - 15° 15 - 7°	STEELHEAD	11.6 (10.6-13.0)	15.39 (12.19-21.03)	0.74	0.53	STEELHEAD 13.0 cm-21.03 g	0.94	0.82
						(Greatest growth 11.0 cm-13.2 the 'B' fish	1.29	0.87

<u>TABLE 2-4</u>

EXPT. # - T°(C.)	SPECIES	MEAN SIZE (RANGE)		INCREASE/DAY F.L. (cm)	INCREASE/DAY WT. (g)	DOMINANT FISH	INCREASE/DAY BY DOMINANT F.L. (mm)	INCREASE/DAY BY DOMINANT WT. (g)
16 - 15° 17 - 15° 18 - 20°	STEELHEAD	10.1 cm (8.8-13.3)	11.01 g (6.61-23.56)	0.89	0.60	DOM. (13.3 cm-23.56 g)	1.18	1.28
						STEELHEAD DOMINANT		
17 - 15° 18 - 20°	ATL. SALMON	11.6 cm (10.0-12.7)	15.23 g (9.27-20.26)	0.60	0.32	(DOM. 11.5 cm-15.05	1.10	0.90

TABLE 2-5

EXPT. # (C.)	SPECIES	MEAN SIZE (RANGE) F.L. (cm)	WT. (g)	MEAN DAILY INCREASE F.L. (mm)	WT. (g)	DOMINANT FISH	INCREASE/DAY F.L. (mm)	WT. (g)
19 - 15°	STEELHEAD	13.7	34.25	0.92	0.54	DOM. 19.8 cm-93.86 g	0.64	0.0
		(11.8-19.8)	(18.04-93.86)			'B' FISH 13.4 cm-35.98 g	1.45	0.99
19 - 15°	BROOK TROUT	15.4	33.37	0.18	0.22	(DOM. T. 15.0 cm-29.67 g)	0.27	0.62
		(13.5-16.3)	(21.25-38.96)			'B' FISH 16.3 cm-35.68 g	0.55	1.15

TABLE 2-6

EXPT. # (C.)	SPECIES	MEAN SIZE (RANGE) F.L. (cm)	MEAN SIZE (RANGE) WT. (g)	SIZE INCREASE/DAY F.L. (mm)	SIZE INCREASE/DAY WT. (g)
20 - 16.3° 21 - 17.7°	COHO	6.1 (5.2-7.1)	2.5 (1.4-4.1)	0.7	0.15
21 - 17.7°	ATL. SALMON	5.1 (4.4-5.6)	1.6 (1.0-2.9)	0.25	0.0

TABLE 2-7

		MEAN SIZE (RANGE)		MEAN INCREASE/DAY	
EXPT. # (C.)	SPECIES	F.L. (cm)	WT. (g)	F.L. (mm)	WT. (g)
22 - 16.2° 23 - 19.4°	ATL. SALMON	5.6 (5.2-6.3)	1.6 (1.3-2.2)	0.66	0.11
23 - 19.4°	COHO	6.8 (6.5-7.1)	3.3 (2.7-3.8)	0.43	0.13

TABLE 2-8

EXPT. # 24. THE DOMINANT FISH WAS THE LARGEST BROOK TROUT.
DOMINANCE HIERARCHY T(11.1), T(10.2), C(8.6), S(8.6), T(9.9),
S(8.0) T(10.2), S(8.1), C(7.8), S(7.3), C(8.5), C(7.2), C(7.6). (F.L. in cm).

EXPT. # (C.)	SPECIES	MEAN SIZE (RANGE) F.L. (cm)	WT. (g)	MEAN INCREASE/DAY F. L. (mm)	WT. (g)	DOMINANT FISH	INCREASE/DAY F.L. (mm)	WT. (g)
24 -18.1°	BROOK TROUT	10.4 (9.9-11.1)	9.6 (8.1-12.5)	0.69	0.38	11.1 cm-12.5 g	1.0	0.59
	COHO	7.9 (7.2- 8.6)	6.1 (4.2- 9.0)	0.75	0.23	(DOM. C. 8.6 cm- 9.0 g	0.81	0.20)
	ATL. SALMON	8.0 (7.3- 8.6)	5.1 (3.1- 6.3)	0.44	0.15	(DOM. S. 8.6 cm-6.3 g	0.56	0.23)

TABLE 3. THE DISTRIBUTION OF FISH IN THE EXPERIMENTS (°/o OF OBSERVATIONS).
TEMPERATURE IS GIVEN IN BRACKETS AFTER THE EXPERIMENT NUMBER.
EXPERIMENTS IN WHICH THE SAME FISH WERE USED ARE CONTAINED WITHIN HORIZONTAL LINES.

EXPT. # (T C.)	ATL. SALMON (S)			COHO (C)			BROOK TROUT (T)			STEELHEAD (ST)			DOMINANT FISH				SPECIES
	SLOW	MED.	FAST	SLOW	MED.	FAST	SLOW	MED.	FAST	SLOW	MED.	FAST	SPECIES	SLOW	MED.	FAST	
1(15)	18.3	73	8.7										S		100		6S
2(15)	25	49.2	25.8	95.8	3.3	0.9							S	55	40	5	6S; 6C
3(20)	24	53	24	60	16.2	23.8							S	4.5	0	95.5	5S; 6C
4(7)	58	42	0	77	0	23							S	100			5S; 6C
5(15)				9	72	19							C		100		6C
6(20)				20	30	50							C	40	40	20	6C
7(15)	26	55	19	48	42	10							S		100		6C; 5-6S
8(20)	18	62	20	57	40	3							S		100		6C; 5S
9(15)							25	60	15				T	40	60		6T
10(15)	23.3	63.3	13.3	51.7	35	13.3	40	53.3	6.7				C	100			6C; 3S; 3T
11(15)		68.3	31.7	18.3	51.7	23.3	3.3	80	16.7				T		70	30	6C; 6S; 6T
12(20)	20	55	15	21.7	50	28.3	0	68.3	31.7				T		100		6C; 6S; 6T
13(15)	23.3	55	21.7										S	10	90		6S
14(15)	40.9	30.3	28.8							39.4	28.8	31.8	ST		100		6S; 6ST
15(7.3)	17.2	77.6	5.2							16.7	51.7	31.7	ST		100		6S; 6ST
16(15)										4.1	22.6	73.3	ST	3.3	93.3	3.3	7ST
17(15)		16.7	83.3							4.6	37.1	58.6	ST		87.5	12.5	7ST; 6S
18(20)	30	53.3	16.7							25.7	47.1	27.1	ST	30	70		7ST; 3S
19(15)							28.3	40	31.7	43.3	30	26.7	ST	20	80		6ST; 6T
20(16.3)				53	23	24							*				10C
21(17.7)	48.8	27.4	23.8	50	26	24							*				10C; 10S
22(16.2)	13.6	68.2	18.2										*				7S
23(19.4)	27.1	55.9	17.0	38.8	61.2	0							*				7S; 7C
24(18.1)	25	50	25	40	58	2	2.5	87.5	10				T		60	40	4S; 4T; 4C

*Fry without distincitve brands were used in experiments 20 - 23.

Table 4. Mean heights of holding positions above the substrate (cm) in the three sections of the tank for experiments 1 - 9 (slowest velocities). (Standard errors in parenthesis).

Experiment No. (T°C)	Species	Pool (Slow)	Wide Channel (Medium)	Narrow Channel (Fast)
1 (15°)	At. salmon	3.5 (0.7)	1.2 (0.3)	0.7 (0.5)
2 (15°)	At. salmon	4.7 (0.09)	3.5 (0.5)	1.4 (0.9)
7 (15°)	At. salmon	13.2 (2.5)	5.5 (0.7)	1.1 (0.5)
2 (15°)	Coho	9.8 (0.3)	8.8 (1.1)	5.0 (0)
5 (15°)	Coho	8.2 (0.7)	6.3 (0.3)	5.0 (0)
7 (15°)	Coho	10.1 (0.9)	5.7 (0.5)	1.0 (0)
9 (15°)	Brook trout	9.4 (2.2)	9.6 (0.9)	12.0 (3.7)
3 (20°)	At. salmon	16.0 (1.5)	8.4 (0.4)	5.5 (1.2)
8 (20°)	At. salmon	32.9 (6.1)	10.4 (1.1)	3.6 (0.5)
3 (20°)	Coho	21.0 (2.2)	9.3 (1.0)	3.8 (0.7)
4 (7°)	At. salmon	1.1 (0.5)	0.4 (0.4)	(-)
4 (7°)	Coho	4.3 (0.3)	(-)	2.0 (0.4)

Table 5. Mean heights of holding positions above the substrate (cm) in the three sections of the tank for experiments 10 - 12 (intermediate flows). (Standard errors in parenthesis).

Experiment No. (T°C)	Species	Pool (Slow)	Wide Channel (Medium)	Narrow Channel (Fast)
10 (15°)	At. salmon	0.1 (0.1)	0 (0)	0 (0)
11 (15°)	At. salmon	-	0.5 (0.2)	0 (0)
10 (15°)	Coho	5.6 (0.5)	4.8 (0.1)	5.0 (0)
11 (15°)	Coho	6.8 (0.7)	4.2 (0.3)	4.7 (0.3)
10 (15°)	Brook trout	4.5 (0.5)	1.6 (0.3)	1.0 (0.2)
11 (15°)	Brook trout	6.5 (1.1)	4.5 (0.4)	3.0 (0.6)
12 (20°)	At. salmon	8.3 (1.6)	5.2 (0.5)	0 (0)
12 (20°)	Coho	-	5.0 (0.4)	4.1 (0.3)
12 (20°)	Brook trout	-	8.5 (0.6)	4.8 (0.2)

Table 6. Mean heights of holding positions above the substrate (cm) in the three sections of the tank for experiments 13 - 24 (fastest flows). (Standard error about the mean in parenthesis).

Experiment No. (T°C)	Species	Pool (Slow)	Wide Channel (Medium)	Narrow Channel (Fast)
13 (15°)	At. salmon	7.0 (1.9)	1.4 (0.1)	0.4 (0.1)
14 (15°)	At. salmon	15.8 (3.0)	8.2 (1.3)	0.2 (0.1)
17 (15°)	At. salmon	-	0.3 (0.2)	1.1 (0.6)
21 (17.7°)	At. salmon	5.1 (2.6)	0.3 (0.1)	0.1 (0.1)
22 (16.2°)	At. salmon fry	2.5 (1.2)	0.8 (0.2)	0.1 (0.1)
23 (19.4°)	At. salmon fry	6.7 (2.4)	1.0 (0.3)	0 (0)
24 (18.1°)	At. salmon fry	0.5 (0.3)	0.3 (0.3)	0.8 (0.1)
18 (20°)	At. salmon	23.3 (3.5)	5.4 (0.6)	8.4 (3.5)
15 (7.3°)	At. salmon	18.8 (3.6)	3.6 (0.6)	0 (0)
20 (16.3°)	Coho fry	21.3 (3.1)	5.6 (1.1)	1.0 (0)
21 (17.7°)	Coho fry	17.1 (2.2)	3.3 (0.4)	1.0 (0.1)
23 (19.4°)	Coho	41.3 (2.7)	5.3 (0.6)	-
24 (18.1°)	Coho	19.9 (3.7)	7.3 (1.6)	-
14 (15°)	Steelhead	33.4 (3.1)	8.8 (1.1)	1.5 (0.3)
16 (15°)	Steelhead	-	9.5 (2.2)	1.4 (0.2)
17 (15°)	Steelhead	5.0 (0)	7.9 (1.3)	1.6 (0.4)
19 (15°)	Steelhead	27.9 (4.0)	12.0 (1.9)	2.0 (0.5)
18 (20°)	Steelhead	30.6 (6.4)	9.7 (1.4)	1.0 (0)
15 (7.3°)	Steelhead	27.5 (2.2)	9.6 (1.0)	1.4 (0.2)
19 (15°)	Brook trout	31.6 (6.2)	8.0 (1.9)	8.2 (3.5)
24 (18.1°)	Brook trout	1.5 (0.2)	1.9 (0.2)	1.2 (0.2)

Table 7. Height held above the substrate, and distance from its nearest neighbour, by the dominant fish in each of the experiments. (Standard deviation is given in parenthesis). Slowest flows were in experiments 1 - 9. Water velocities were approximately doubled in experiments 10 - 13, and were increased again from experiments 13 - 24.

Experiment No. (T°C)	Species	Location	Height above substrate (cm)	Distance from nearest neighbour (m)
1 (15°)	Salmon	Wide Channel	8.1 (8.9)	0.8 (0.6)
2 (15°)	Salmon	Narrow Channel	0 (0)	1.0 (0.9)
3 (20°)	Salmon	Narrow Channel	5.8 (5.7)	1.5 (0.8)
4 (7°)	Salmon	Pool	0.4 (1.4)	0.3 (0.1)
5 (15°)	Coho	Wide Channel	5.1 (1.3)	0.7 (0.4)
6 (20°)	Coho	Wide Channel	6.3 (2.2)	1.1 (0.4)
7 (15°)	Salmon	Wide Channel	10.6 (5.8)	0.9 (0.5)
8 (20°)	Salmon	Wide Channel	12.5 (5.6)	1.6 (0.6)
9 (15°)	Brook trout	Wide Channel	7.0 (2.5)	0.9 (0.3)
10 (15°)	Coho	Pool	6.0 (2.0)	1.3 (0.6)
11 (15°)	Coho	Pool	7.0 (2.5)	1.5 (0.3)
12 (20°)	Coho	Pool	15 (7.8)	0.9 (0.2)
13 (15°)	Salmon	Wide Channel	3.1 (1.2)	1.8 (0.6)
14 (15°)	Steelhead	Wide Channel	10.9 (5.1)	1.9 (0.8)
15 (7°)	Steelhead	Wide Channel	15.5 (4.2)	0.5 (0.2)
16 (15°)	Steelhead	Wide Channel	13.1 (6.5)	1.7 (0.8)
17 (15°)	Steelhead	Wide Channel	15.1 (6.8)	1.5 (0.8)
18 (20°)	Steelhead	Wide Channel	19.3 (1.8)	2.3 (0.6)
19 (15°)	Steelhead	Wide Channel	20 (0)	2.4 (1.1)
21 (17.7°)	Coho fry	Wide Channel	4.6 (0.8)	1.3 (0.5)
24 (18.1°)	Brook trout	Wide Channel	1.2 (0.4)	0.7 (0.2)

Table 8. Displacements (successful attacks) by Atlantic salmon during experiments 1 - 18. The following experiments had the same fish used in the group of experiments: 1, 2, 3 and 4; 7 and 8; 11 and 12; 13, 14 and 15; 17 and 18. C = Coho; T = Brook trout; and ST = Steelhead.

Displacements/Observation/At. salmon (Intra-specific & Inter-specific)											
Temperature 7°C				Temperature 15°C				Temperature 20°C			
Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ
				1	0.35	--	0.35				
4	0.27	0.17 (C)	0.44	2	0.61	0.32 (C)	0.93	3	1.74	4.41 (C)	6.15
				7	0.21	0.43 (C)	0.64	8	0.97	1.25 (C)	2.22
				10	0.10	0.03 (C)	0.13				
				11	0.63	0.12 (C) 0.07 (T)	0.82	12	0.68	1.25 (C) 0.13 (T)	2.06
				13	3.05	--	3.05				
15	2.20	0.25 (ST)	2.45	14	3.60	1.3 (ST)	4.90				
				17	0.79	0.04 (ST)	0.83	18	1.77	0.13 (ST)	1.90

Table 9. Displacements by coho during experiments 2 - 12. The following experiments had the same coho used in the group of experiments: 2, 3 and 4; 5; 6, 7 and 8; 11 and 12. S = Atlantic salmon; T = Brook Trout.

Displacements/Observation/Coho
(Intra-specific & Inter-specific)

Temperature 7°C				Temperature 15°C				Temperature 20°C			
Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ
4	0.03	0	0.03	2	0.96	0.12 (S)	1.08	3	1.43	0.12 (S)	1.55
				5	0.83	--	0.83	6	1.10	--	1.10
				7	0.92	0.33 (S)	1.25	8	0.81	0.32 (S)	1.13
				10	1.12	0.10 (S) 0.28 (T)	1.50				
				11	0.35	0.40 (S) 1.35 (T)	2.1	12	1.62	1.57 (S) 0.95 (T)	4.14

Table 10. Displacements made by brook trout during experiments 9 - 19, and in a previous study (Gibson 1977a). The same fish were used in experiments 11 and 12, and in B, C and D. S = Atlantic Salmon; C = Coho.

Displacements/Observation/Brook Trout
(Intra-specific & Inter-specific)

Temperature 15°C				Temperature 15°C			
Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ
9	3.10	--	3.10				
10	0.03	0.20 (S) 0.57 (C)	0.80				
11	1.60	0.80 (S) 0.78 (C)	3.2	12	1.88	0.85 (S) 1.55 (C)	4.28
19	1.78	0.50 (ST)	2.28				
B	3.10	--	3.10				
C	3.0	5.77 (C)	8.77	D	4.72	6.28 (C)	11.0

Table 11. Displacements made by steelhead during experiments 14 - 19. Experiments 14 and 15 had the same fish, as also did experiments 16, 17, 18 and 19. S = Atlantic Salmon; T = Brook Trout.

Displacements/Observation/Steelhead (Intra-specific & Inter-specific)

Temperature 7°C				Temperature 15°C				Temperature 20°C			
Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ	Expt.	Intra-sp.	Inter-sp.	Σ
15	1.77	8.05 (S)	9.82	14	4.0	4.55 (S)	8.56				
				16	6.37	--	6.37				
				17	2.47	4.67 (S)	7.14	18	6.94	6.63 (S)	13.6
				19	2.50	2.50 (T)	5.0				

Table 12. Mean % of agonistic acts used by the four species in displacements at 15° C. - 20° C. and at 7° C. (Standard error is given in brackets for figures at the higher temperatures).

SPECIES	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP
15°C. - 20°C.										
At. salmon	66.9 (5.29)	8.7 (1.59)	6.8 (1.42)	8.8 (1.52)	2.6 (0.59)	3.5 (1.30)	1.9 (1.18)	0.9 (0.62)	--	--
Brook trout	34.2 (5.10)	36.8 (4.07)	18.5 (1.86)	4.1 (1.08)	1.9 (0.44)	3.2 (0.86)	0.8 (0.48)	0.6 (0.15)	--	--
Steelhead	58.9 (4.26)	16.8 (1.81)	10.8 (1.24)	5.8 (0.9)	0.2 (0.05)	2.7 (0.73)	2.4 (1.03)	0.5 (0.29)	1.0 (0.16)	0.9 (0.11)
Coho	53.8 (3.41)	23.7 (2.74)	5.2 (0.72)	2.9 (0.84)	1.1 (0.37)	1.2 (0.36)	0.2 (0.10)	0.3 (0.17)	4.5 (0.95)	6.9 (1.57)
7°C.										
At. salmon (Range, expts. 4 & 15)	38.1 (27.3-48.9)	17.5 (9.1-25.8)	35 (54.6-15.4)	5.4 (3.0-7.7)	1.8 (3.0-0.6)	2.3 (3.0-1.6)	0	0	--	--
Steelhead	42.2	29.7	12.8	11.6	0	1.6	1.5	0	0.4	0.1
Coho	0	50	0	0	0	0	0	0	0	50

Table 13. The average number of fish occupying the wide channel ($6\ m^2$) in each experiment (usually the preferred section), grouped under the species which was the dominant fish at the time. C = Coho; T = Brook trout; ST = Steelhead; S = At. salmon. *20°C; **7°C. The mean size of the territories is derived from the number of fish in the wide channel at the time that species was the dominant fish.

Dominant Fish	Coho		Steelhead			Atlantic salmon			Brook trout		
Expt.		Σ	Expt.		Σ	Expt.		Σ	Expt.		Σ
5	4.5C	4.5	14	1.9ST; 2.0S	3.9	1	4.5S	4.5	9	3.6T	3.6
6*	1.8C	1.8	15**	3.1ST; 4.5S	7.6	2	3S; 0.2C	3.2	11	3.1C; 4.1S; 4.8T	12.0
10	2.1C; 1.6T; 1.9S	5.6	16	1.6ST	1.6	3*	3.1S; 1.1C	4.2	12*	3.0C; 3.3S; 4.1T	10.4
20	2.3C	2.3	17	2.6ST; 0.8S	3.4	4**	2.1S	2.1	24	2.0S; 3.5T; 2.9C	8.4
21	2.6C; 2.3S	4.9	18*	3.3ST; 1.6S	4.9	7	3.2S; 2.5C	5.7			
23	3.3S; 4.1C	7.4	19	1.8ST; 2.4T	4.2	8*	3.7S; 2.9C	6.6			
						13	3.3S	3.3			
						22	4.3S	4.3			

The mean size of the territories in the wide channel (m^2)

Coho		Steelhead			Atlantic salmon			Brook trout	
15°C	20°C	15°C	20°C	7°C	15°C	20°C	7°C	15°C	20°C
1.4	3.3	1.8	1.2	0.8	1.4	1.1	2.9[a]	0.8	0.6

[a]Nevertheless, territories were reduced in size but most fish were in the pool.

Range: $3.8\ m^2$ (steelhead in expt. 16 at 15°C) to $0.5\ m^2$ (brook trout in expt. 11 at 15°C).

In the meanwhile aquaculture and enhancement of the native salmonids should be encouraged.

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APPENDIX 1

TABLES 14 - 35

TABLE 14

Agonistic behaviour used in intra- and inter-specific displacements (successful attacks) by Atlantic salmon. Species are listed with experiment numbers. C = coho; S = Atlantic salmon.

Expt. No. (Species)	Agonistic Acts (°/o)								Displacements made/ Observation/Fish	
	Charge + Chase	Approach	Nip	Lateral display	Frontal display	Presence	Drift	Supplant	INTRA-SP.	INTER-SP.
1 (S)	22.5	10	10	15	5	15	7.5	7.5	0.35	-
2 (S;C)	48	11	16	3	4	11	3	3	0.61	0.32
3 (S;C)	83.7	3.3	4.4	4.6	1.3	2.2	0.4	0	1.74	4.41
4 (S;C)	27.3	9.1	54.6	3	3	3	0	0	0.27	0.17
7 (S;C)	60	5	5	17.5	7.5	2.5	2.5	0	0.21	0.43
8 (S;C)	85	6.4	2.1	2.9	0.7	2.9	0	0	0.97	1.25

TABLE 15

Agonistic acts used in intra- and inter-specific displacements by coho salmon. Species are listed in the same column as the experiment numbers. C = coho; S = Atlantic salmon; T = brook trout.

Expt. No. (Species)	Agonistic Acts (°/o) Charge + Chase	Approach	Nip	Lateral display	Frontal display	Presence	Drift	Supplant	Wigwag	Threat Nip	Displacements made/ Observation/Fish INTRA-SP.	INTER-SP.
2 (C;S)	48.0	18.0	8.0	1.0	1.0	0	1.0	0	8.0	14.0	0.96	0.12
3 (C;S)	71.4	8.5	4.7	3.3	1.9	0.5	0.5	0	3.3	6.1	1.43	0.12
4 (C;S)	0	50.0	0	0	0	0	0	0	0	50.0	0.03	0
5 (C)	52.0	16.8	4.8	1.6	3.2	1.6	0	0	10.4	9.6	0.83	-
6 (C)	43.2	34.6	1.2	0	1.2	1.2	0	1.2	6.2	11.1	1.1	-
7 (C;S)	52.9	20.0	5.9	1.2	0	2.4	0	1.2	3.5	12.9	0.92	0.33
8 (C;S)	35.3	37.3	5.9	3.9	1.0	3.9	0	1.0	2.0	9.8	0.81	0.32

TABLE 16

Agonistic acts used in intra-specific displacements (successful attacks) by brook trout. T = brook trout.

Expt. No. (Species)	Agonistic Acts ($^{o}/o$) Charge + Chase	Approach	Nip	Lateral display	Frontal display	Presence	Drift	Supplant	Displacements made/ Observation/Fish INTRA-SP.	INTER-SP.
9 (T)	63.4	19.6	9.4	3.6	0.5	2.7	0	0.9	3.1	-

Tables 17 - 31 . Summary of agonistic acts for experiments 10 - 24, and the displacements (successful attacks) made/ observation/fish. C = Coho; S = Atlantic salmon; T = Brook trout; ST = Steelhead. Alphabetical suffixes denote the hierarchy, with a being the dominant fish.

TABLE 17-1 - EXPERIMENT 10

BROOK TROUT	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED
Ta	2	1		1					S 1 C 1
Tb	1	19	10	1	1	1			T 1 S 5 C 16
Tc									
Total	3	20	10	2	1	1			
°/o	8.1	54.1	27	5.4	2.7	2.7			WINS/T/OBVN INTRA-SP. 0.03 INTER-SP. S 0.2 INTER-SP. C 0.5 (bracketed total: 0.8)

TABLE 17-2 - EXPERIMENT 10

COHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS
Ca	47	15	1	1					1	2	C 45 S 5 T 12
Cb		4			1						C 3 S 1
Cc											0
Cd	10	3			1				2		C 9 T 4
Ce		1									T 1
Cf	1	5			1				4	1	C 10
Total Acts	56	28	1	1	3				7	3	
°/o	56.6	28.3	1	1	3				7.1	3	

WINS/C/OBVN

INTRA-SP. 1.12
INTER-SP. S 0.1 } -1.5
INTER-SP. T 0.28

TABLE 17-3 - EXPERIMENT 10

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa									0
Sb									0
Sc		4	1	2					S3
Total	0	4	1	2					C 1
°/o		57.1	14.3	28.6					WINS/S/OBVN INTRA-SP. 0.1 } 0.13 INTER-SP. C 0.03 }

TABLE 18-1 - EXPERIMENT 11

COHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED
Ca	2	1							1		T 4
Cb	1			1							C 1 T 1
Cc	7	2	1						1		C 2 T 4 S 3
Cd		2									T 2
Ce	3			1							T 1 S 3
Cf	85	22	9			1					C 18 T 69 S 18
Total Acts	98	27	10	2		1			2		
°/o	70	19.3	7.1	1.4		0.7			1.4		WINS/C/OBVN INTRA-SP. 0.35 INTER-SP. T 1.35 INTER-SP. S 0.4 } 2.1

TABLE 18-2 - EXPERIMENT 11

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	20	1		2					S 15 C 5 T 2
Sb	11	2		4	1				S 11 C 1 T 2
Sc	7	1		4		1			S 10 C 1
Sd		1							S 1
Se	1								S 1
Sf									0
Total Acts	39	5		10	1	1			
%	69.6	8.9		17.9	1.8	1.8			WINS/S/OBVN INTRA-SP. 0.63 INTER-SP. C 0.12 INTER-SP. T 0.07 } 0.82

TABLE 18-3 - EXPERIMENT 11

BROOK TROUT	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Ta	1	19	6	6	1	6			T 11 C 10 S 9
Tb	50	57	26	12		7	1	2	T 75 C 24 S 25
Tc	3	9	3	2		1			T 5 C 4 S 5
Td	2	7	2	1	1	6	1		T 4 C 6 S 7
Te			1	1	1				T 1 C 1
Tf		3				1			C 2 S 2
Total Acts	56	95	38	4	3	21	2	2	
°/o	25.3	43	17.2	1.8	1.4	9.5	0.9	0.9	

WINS/T/OBVN

INTRA-SP. 1.6
INTER-SP. C 0.78
INTER-SP. S 0.8
} 3.2

TABLE 19-1 - EXPERIMENT 12

BROOK TROUT	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Ta	52	60	34	4		7		1	T 49 C 45 S 28
Tb	19	45	12	2	1	7	1		T 42 C 22 S 8
Tc	3	6	2		1	1	1		T 6 C 5 S 0
Td	11	16	8	1		4			T 11 C 12 S 8
Te	5	4	3		4	2			T 3 C 5 S 3
Tf	6	1	3		1	1	1		T 2 C 4 S 4
Total Acts	96	132	62	7	7	22	3	1	
°/o	29.1	40	18.8	2.1	2.1	6.7	0.9	0.3	WINS/T/OBVN INTRA-SP. 1.88 INTER-SP. C 1.55 INTER-SP. S 0.85 } 4.28

TABLE 19-2 - EXPERIMENT 12

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	66	3	1	3	3	2			S 15 T 2 C 52
Sb	20	5		8	1				S 15 T 4 C 8
Sc	22	2	1	2					S 10 T 2 C 14
Sd									0
Se									0
Sf	2								S 1 C 1
Total Acts	110	10	2	13	4	2			
%	78	7.1	1.4	9.2	2.8	1.4			WINS/S/OBVN INTRA-SP. 0.68 INTER-SP. T 0.13 INTER-SP. C 1.25 } 2.07

TABLE 19-3 - EXPERIMENT 12

COHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
Ca	31	20	3	12		1			3		C 13 T 7 S 32
Cb	6	7	1	2					3	1	C 7 T 3 S 6
Cc	70	19	5	3		2					C 20 T 42 S 28
Cd											0
Ce	1										S 1
Cf	70	18	8	1		1				4	C 57 T 5 S 27
Total Acts	178	64	17	18		4			6	5	
°/o	61	21.9	5.8	6.2		1.4			2.0	1.7	WINS/C/OBVN INTRA-SP. 1.62 INTER-SP. T 0.95 INTER-SP. S 1.57 (total 4.14)

TABLE 20 - EXPERIMENT 13

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	34	10	4	4	2	4	2		52
Sb	76	6	3	5	3	3			87
Sc	29	2	2	2		1			33
Sd		1							1
Se	7	2	1		1				9
Sf	1								1
Total Acts	147	21	10	11	6	8	2		
°/o	71.7	10.2	4.9	5.4	2.9	3.9	1.0		WINS/S/OBVN INTRA-SP. 3.05

TABLE 21-1 - EXPERIMENT 14

STEELHEAD	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
ST a	45	18		5		3	10		1		ST 34 S 41
ST b	106	29	25	5		2	1	1		4	ST 71 S 71
ST c	50	18	9	3		1				1	ST 41 S 27
ST d	73	8	18	3	2						ST 21 S 60
ST e	77	45	19	2		1	3		4	3	ST 72 S 54
ST f	14	6	9	5		1					ST 2 S 20
Total Acts	365	124	80	23	2	8	14	1	5	8	
°/o	57.9	19.7	12.7	3.7	0.3	1.3	2.2	0.2	0.8	1.3	WINS/S /OBVN INTRA-SP. 4.0 } INTER-SP. S 4.55 } 8.56

TABLE 21-2 - EXPERIMENT 14

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	83	6	4	1					S 66 ST 23
Sb	135	9	4	10	1	1	1		S 127 ST 25
Sc	32	3	4	1					S 17 ST 18
Sd		1							S 1
Se	7	4	2			1			S 3 ST 9
Sf									0
Total Acts	257	23	14	12	1	2	1		
°/o	82.9	7.4	4.5	3.9	0.3	0.7	0.3		WINS/S/OBVN INTRA-SP. 3.6 } 4.82 INTER-SP. ST 1.3 }

TABLE 22-1 - EXPERIMENT 15

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	37	18	5	4		1			S 47 ST 10
Sb	34	16	8	8					S 53 ST 4
Sc	8	9	9	1	1	1			S 17 ST 1
Sd									
Se	10	4	6	1		1			S 15 ST 0
Sf									
Total Acts	89	47	28	14	1	3			
$^{o}/o$	48.9	25.8	15.4	7.7	0.6	1.6			WINS/S/OBVN INTRA-SP. 2.20 } 2.45 INTER-SP. ST 0.25 }

TABLE 22-2 - EXPERIMENT 15

STEELHEAD	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
ST a	20	49	19	21		3	5				ST 26 S 65
ST b	56	25	19	1		2	1		1		ST 17 S 67
ST c	107	82	27	52		3	4				ST 20 S 196
ST d	28	15	16	6		4				1	ST 8 S 44
ST e	97	44	12	3			1		2		ST 35 S 108
ST f	1	2	1	2							ST 0 S 4
Total Acts	309	217	94	85		12	11		3	1	
°/o	42.2	29.7	12.8	11.6		1.6	1.5		0.4	0.1	WINS/S /OBVN INTRA-SP. 1.77 } INTER-SP. S 8.05 } 9.82

TABLE 23 - EXPERIMENT 16

STEELHEAD	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
ST a	31	12	2	2		5					50
ST b	132	5	25	14		2	21	1	3		167
ST c	92	31	21	18		1	12		1	3	144
ST d	38	12	5	4			3	1		1	55
ST e	18	10	13	6	1					1	25
ST f	0	1									1
ST g	2			1							1
Total Acts	313	73	67	46	1	8	36	2	5	5	
°/o	56.3	13.1	12.1	8.3	0.2	1.4	6.5	0.4	0.9	0.9	WINS/ST/OBVN INTRA-SP. 6.37

TABLE 24-1 - EXPERIMENT 17

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa (6 Observns)	7	3	2						S 10 ST 0
Sb (7 Observns)	4	5	1	4	1				S 9 ST 1
Sc (5 Observns)	1	2	1	1					S 3 ST 1
Sd (10 Observns)	12	3	4	1					S 15 ST 0
Se (10 Observns)	1								S 1 ST 0
Sf (10 Observns)									
Total Acts	25	13	8	6	1				
%	47.2	24.5	15.1	11.3	1.9				WINS/S/OBVN INTRA-SP. 0.79 } 0.83 INTER-SP. ST. 0.04 }

TABLE 24-2 - EXPERIMENT 17

STEELHEAD	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
STa	6	19	3	3		13		2			ST 29 S 15
STb	76	3	2	14		10	5		2		ST 74 S 32
STc	31	21	12	5	1	1	1		2	2	ST 11 S 47
STd	82	24	30	7		6	4	9			ST 38 S 96
STe	41	53	30	16	1	4	4			2	ST 19 S 91
STf	17	4	4			1			1		ST 1 S 19
STg	8	15	3	4			3				ST 1 S 27
Total acts	261	139	84	49	2	35	17	11	5	4	
°/o	43	22.9	13.8	8.1	0.3	5.8	2.8	1.8	0.8	0.7	WINS/ST/OBVN INTRA-SP. 2.47 } INTER-SP. S 4.67 } 7.14

TABLE 25-1 - EXPERIMENT 18

STEELHEAD	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
STa	108	6	6	0		11				1	ST 74 S 49
STb	217	21	35	10		5	3			3	ST 146 S 108
STc	93	21	8	4		2	1		1		ST 51 S 66
STd	109	28	9	16		4			4	2	ST 44 S 102
STe	129	33	20	10		1	1		2	2	ST 81 S 88
STf	41	6	3	3	1	2			1	1	ST 44 S 25
STg	58	13	21	7						1	ST 46 S 26
Total	755	130	102	50	1	25	5		8	10	
°/o	69.5	12.0	9.4	4.6	0.1	2.3	0.5		0.7	0.9	WINS/ST/OBVN INTRA-SP. 6.94 } 13.6 INTER-SP. S 6.63 }

TABLE 25-2 - EXPERIMENT 18

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	19	1	1	1					S 16 ST 4
Sb	17		3	1	2				S 16
Sc	21		2	2					S 21
Total Acts	57	1	6	4	2				
%	81.4	1.4	8.6	5.7	2.9				WINS/S/OBVN INTRA-SP. 1.77 } 1.9 INTER-SP. 0.13 }

TABLE 26-1 - EXPERIMENT 19

STEELHEAD	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
STa	66	14	7			3					ST 24 T 60
STb	120	17	9	7		6		1	3	2	ST 73 T 66
STc	20	12	3	5					2		ST 26 T 5
STd	8	3									ST 7 T 4
STe	16	8	2	3					1		ST 15 T 11
STf	6	3									ST 5 T 4
Total acts	236	57	21	15		9		1	6	2	
°/o	68.0	16.4	6.1	4.3		2.6		0.3	1.7	0.6	WINS/ST/OBVN INTRA-SP. 2.5 } 5.0 INTER-SP. T 2.5 }

TABLE 26-2 - EXPERIMENT 19

BROOK TROUT	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Ta	33	43	27	18	3	1	1		T 72 ST 15
Tb	17	17	7	2				1	T 28 ST 7
Tc	1	2	1	1					T 1 ST 1
Td	1	6		2					T 4 ST 4
Te		1	2						T 2 ST 1
Tf		2							T 0 ST 2
Total Acts	52	71	37	23	3	1	1	1	
°/o	27.5	37.6	19.6	12.2	1.6	0.5	0.5	0.5	WINS/T/OBVN INTRA 1.78 } INTER ST 0.5 } 2.28

TABLE 27 - EXPERIMENT 20

OHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS
Total	291	136	93	58		6	6		27	16	463
%	46	21.5	14.7	9.2		0.9	0.9		4.3	2.5	WINS/C/OBVN 4.6

TABLE 28-1 - EXPERIMENT 21

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Total	27	5	4	9					S 27 C 5
%	60.0	11.1	8.9	20.0					WINS/S/OBVN INTRA 0.32 INTER C 0.06 (INTRA + INTER C) 0.38

TABLE 28-2 - EXPERIMENT 21

COHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS
Total	392	169	105	63		13	7	1	20	7	C 567 S 39
°/o	50.5	21.8	13.5	8.1		1.7	0.9	0.1	2.6	0.9	WINS/C/OBVN INTRA 5.7 } 6.1 INTER S 6.1 }

TABLE 29 - EXPERIMENT 22

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Total	107	15	39	33		1		1	94
°/o	54.6	7.7	19.9	16.8		0.5		0.5	WINS/S/OBVN 1.59

TABLE 30-1 - EXPERIMENT 23

COHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS
Total	340	154	89	99	4	2	2		41	9	C 354 S 165
°/o	46.0	20.8	12.0	13.4	0.5	0.3	0.3		5.5	1.2	WINS/C/OBVN INTRA 5.28 } 7.75 INTER S 2.46 }

TABLE 30-2 - EXPERIMENT 23

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Total	51	2	10	26					S 29 C 27
°/o	51.5	12.1	10.1	26.3					WINS/S/OBVN INTRA 0.49 } 0.95 INTER C 0.46 }

TABLE 31-1 - EXPERIMENT 24

BROOK TROUT	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Ta	10	23	10			2			T 22 C 8 S 5
Tb	1	28	7	3	1	1			T 22 C 5 S 4
Tc		1		1					C 1 S 1
Td	4	13	3	3	1				T 4 C 9 S 6
Total	15	65	20	7	2	3			
°/o	13.4	58.0	17.9	6.3	1.8	2.7			WINS/T/OBVN INTRA 1.2 INTER C 0.58 INTER S 0.4 } 2.18

TABLE 31-2 - EXPERIMENT 24

ATLANTIC SALMON	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	OTHER FISH ATTACKED (WINS)
Sa	38	3	4	5					T 6 C 34
Sb	18	1	3	2					S 9 C 9
Sc	3	1	1						C 2
Sd		2							C 2
Total	59	7	8	7					
°/o	72.8	8.6	9.9	8.6					WINS/S/OBVN INTRA 0.23 INTER T 0.15 INTER C 1.18 (total) 1.55

TABLE 31-3 - EXPERIMENT 24

OHO	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP	OTHER FISH ATTACKED (WINS)
Ca	131	76	12	17		2	1		1	3	C 137 T 5 S 54
Cb	58	44	19	13					3	1	C 96 T 1 S 10
Cc	3	7		1							C 5 T 1 S 4
Cd	1	1		3					2		C 3 S 1
Ce		2		1							C 2 S 1
Total Acts	193	131	31	36		2	1		6	4	
°/o	47.8	32.4	7.7	8.9		0.5	0.2		1.5	1.0	WINS/C/OBVN INTRA 4.86 INTER T 0.14 INTER S 1.4 } 6.42

TABLE 32. COHO. AGONISTIC ACTS USED IN INTRA- AND INTER-SPECIFIC DISPLACEMENTS (SUCCESSFUL ATTACKS). ($^{o}/_{o}$).

T (°C.)	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP
15	48.0	18.0	8.0	1.0	1.0	0	1.0	0	8.0	14.0
	52.0	16.8	4.8	1.6	3.2	1.6	0	0	10.4	9.6
	52.9	20.0	5.9	1.2	0	2.4	0	1.2	3.5	12.9
	56.6	28.3	1.0	1.0	3.0	0	0	0	7.1	3.0
	70.0	19.3	7.1	1.4	0	0.7	0	0	1.4	0
18	47.8	32.4	7.7	8.9	0	0.5	0.2	0	1.5	1.0
20	71.4	8.5	4.7	3.3	1.9	0.5	0.5	0	3.3	6.1
	43.2	34.6	1.2	0	1.2	1.2	0	1.2	6.2	11.1
	35.3	37.3	5.9	3.9	1.0	3.9	0	1.0	2.0	9.8
	61.0	21.9	5.8	6.2	0	1.4	0	0	2.0	1.7
	$\bar{x}$= 53.8	23.7	5.2	2.9	1.1	1.2	0.2	0.3	4.5	6.9
7	0	50.0	0	0	0	0	0	0	0	50.0

TABLE 33. STEELHEAD. AGONISTIC ACTS USED IN INTRA- AND INTER-SPECIFIC DISPLACEMENTS. (SUCCESSFUL ATTACKS). (°/o).

T (°C.)	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT	WIG-WAG	THREAT NIP
15	57.9	19.7	12.7	3.7	0.3	1.3	2.2	0.2	0.8	1.3
	68.0	16.4	6.1	4.3	0	2.6	0	0.3	1.7	0.6
	56.3	13.1	12.1	8.3	0.2	1.4	6.5	0.4	0.9	0.9
	43.0	22.9	13.8	8.1	0.3	5.8	2.8	1.8	0.8	0.7
20	69.5	12.0	9.4	4.6	0.1	2.3	0.5	0	0.7	0.9
	$\bar{x}$= 58.9	16.8	10.8	5.8	0.2	2.7	2.4	0.5	1.0	0.9
7	42.2	29.7	12.8	11.6	0	1.6	1.5	0	0.4	0.1

TABLE 34. ATLANTIC SALMON. AGONISTIC ACTS USED IN INTRA- AND INTER-SPECIFIC DISPLACEMENTS (SUCCESSFUL ATTACKS). (°/o).

T (°C.)	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT
15	22.5	10	10	15	5	15	15	7.5
	48	11	16	3	4	11	3	3
	60	5	5	17.5	7.5	2.5	2.5	0
	69.6	8.9	0	17.9	1.8	1.8	0	0
	71.7	10.2	4.9	5.4	2.9	3.9	1.0	0
	82.9	7.4	4.5	3.9	0.3	0.7	0.3	0
	47.2	24.5	15.1	11.3	1.9	0	0	0
	81.4	1.4	8.6	5.7	2.9	0	0	0
18	72.8	8.6	9.9	8.6	0	0	0	0
20	83.7	3.3	4.4	4.6	1.3	2.2	0.4	0
	85	6.4	2.1	2.9	0.7	2.9	0	0
	78	7.1	1.4	9.2	2.8	1.4	0	0
	$\bar{x}$= 66.9	8.7	6.8	8.8	2.6	3.5	1.9	0.9
7	27.3	9.1	54.6	3	3	3	0	0
	48.9	25.8	15.4	7.7	0.6	1.6	0	0
	$\bar{x}$= 38.1 (7°C.)	17.5	35	5.4	1.8	2.3	0	0

TABLE 35. BROOK TROUT. AGONISTIC ACTS USED IN INTRA- AND INTER-SPECIFIC DISPLACEMENTS (SUCCESSFUL ATTACKS). (°/o).

T (°C.)	CHARGE AND CHASE	APPROACH	NIP	LATERAL DISPLAY	FRONTAL DISPLAY	PRESENCE	DRIFT	SUPPLANT
15	34.6	14.4	30.1	6.5	5.2	2.6	5.2	1.5
	63.4	19.6	9.4	3.6	0.5	2.7	0	0.9
	45.6	34.8	14.2	1.5	0.7	2.1	0.2	1.0
	47.5	29.5	19.5	0.9	2.7	0	0	0
	25.3	43	17.2	1.8	1.4	9.5	0.9	0.9
	27.5	37.6	19.6	12.2	1.6	0.5	0.5	0.5
	8.1	54.1	27.0	5.4	2.7	2.7	0	0
18	13.4	58.0	17.9	6.3	1.8	2.7	0	0
20	47.5	36.6	12.7	0.7	0	2.0	0.1	0.4
	29.1	40	18.8	2.1	2.1	6.7	0.9	
	$\bar{x}$= 34.2	36.8	18.5	4.1	1.9	3.2	0.8	0.6