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BEHAVIOURAL INTERACTIONS BETWEEN JUVENILE COHO SALMON (*Oncorhynchus kisutch*), AND JUVENILE ATLANTIC SALMON (*Salmo salar*) AND BROOK TROUT (*Salvelinus fontinalis*)

by

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ABSTRACT

Behavioural interactions were studied, in a stream tank, between juvenile coho salmon (*Oncorhynchus kisutch*) and brook trout (*Salvelinus fontinalis*), and between coho and Atlantic salmon (*Salmo salar*). Coho distributions were different when observed alone than when with either brook trout or salmon parr, but coho had little effect on the distributions of either of the other two species. Inter-specific displacements of coho by brook trout and salmon parr were greater than inter-specific displacements by coho of either brook trout or salmon parr. Salmon parr appear better adapted to the fast water environment than coho, which are better adapted to the pool environment, so these two species would probably be ecologically compatible. More severe competition might be expected between coho and brook trout, but the latter appear the more aggressive of the two, and would probably not be displaced.

RESUME

Les interactions éthologiques du saumon coho avec la truite mouchetée d'une part et avec le saumon Atlantique d'autre part ont été étudiées dans un réservoir d'eau courante. La distribution des cohos s'est avérée différente lors de la présence de truites mouchetées ou de tacons tandis que celle de chacune de ces espèces fut peu affectée par la présence de cohos. Les déplacements inter-spécifiques des cohos faits par les truites mouchetées et les tacons étaient plus nombreux que les déplacements produits par les cohos sur les truites mouchetées ou les tacons. Les tacons apparaissent mieux adaptés à une eau plus rapide tandis que les cohos le sont davantage à une eau plus calme. Ces deux espèces seraient probablement écologiquement compatibles. Une compétition plus sévère est à prévoir entre coho et truite mouchetée mais cette dernière, semblant plus aggressive, ne serait probablement pas deplacée.

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INTRODUCTION

Coho salmon (Oncorhynchus kisutch), a Pacific salmonid (Scott and Crossman 1973), has in recent years been introduced to the Great Lakes and to the east coast of North America. Its life history and habitat requirements are very similar to those of Atlantic salmon (Salmo salar), so there is much concern that populations of the indigenous salmon might be adversely effected (e.g. Gruenfeld 1977). Coho salmon spawn later than Atlantic salmon, and might use some of the same spawning sites, and the coho fry emerge earlier than Atlantic salmon, so that they have an early growth advantage. The juvenile coho is primarily insectivorous but can be partly pisciverous, so that they might prey upon Atlantic salmon and brook trout . A further danger is that an exotic disease might be introduced.

The present study was undertaken to analyze behavioural interactions during the fluviatile period when juvenile coho would be most likely to interact with salmon parr and brook trout. 'Parr' is the term applied to juvenile Atlantic salmon between the fry stage, when they first emerge from the gravel, and the smolt stage, when they migrate to the sea.

Juvenile coho salmon naturally co-exist with juvenile steelheat trout (Salmo gairdneri) 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 (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). Juvenile coho salmon appear to have similar ecological requirements to brook trout.

Questions under consideration in this study were, whether salmon parr may compete successfully with coho, and what might be the possible effects of coho on brook trout.

MATERIAL AND METHODS

Observations were made in a stream tank at the Woods Hole Oceanographic Institution. The entire apparatus is 9 m long an d 3 m wide, and consists of a circular flume with recirculated water. A channel 1.2 m wide and another 0.6 m wide are 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 are screened to prevent fish from entering the section containing an electrically driven propellor which moves the water. In the observational section the lengths of the wide channel, pool and narrow channel are respectively 4.9 m, 3 m and 3.7 m. The total observation area measures 13.2 m^2. The water depths were 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. Water velocities at mid-depth were 6 - 8 cm/sec in the wide channel, 3.8 - 6 cm/sec in the pool, and 14 - 17 cm/sec in the narrow channel. 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 one cold water experiment 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 0.95×10^{-2} to 2.16×10^{-2} langleys/min. over the water surface. A photoperiod of 14 hours was made by means of a time switch. The lights came on gradually in the morning, intensifying over fifteen minutes, but went off suddenly for the night.

The inner walls of the tank are made of plexiglass, including the rounded observational window of the pool, and observations were made from this inner perimeter of the tank. As the fish were wary, the observational area was screened with black plastic and black cardboard, 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 .09 m^2 sections with inconspicuous stones. The wall opposite the observation windows was marked with lines at 0.3 m intervals to allow the observer to correct for visual distortion.

Atlantic salmon parr and brook trout were brought from the Matamek River, Quebec. Coho used in the first experiment came from the University of New Hampshire, and those used in the rest of this study were obtained locally, from a Massachusetts fish and game hatchery. The fish were kept in two holding tanks, each measuring 3 m in diameter, and water was kept 80 cm deep. In one tank were 20 coho, and in the other about 50 parr and 20 trout. A jet of well water at 11° - 12°C. created a current in the tanks. Some shelter was provided in these tanks with rocks and broken brick pipes.

Fish were anaesthetized with MS 222 and individually branded by the cold method (Fujihara and Nakatani 1967), and were also weighed and measured under anaesthetization at the beginning and end of each experiment. Following 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 (sometimes rather hard to differentiate from the 'charge' of the trout, as the trout 'charge' was not always as vigorous as that of the salmon parr). A fish biting another is called '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. 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 a 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.

The type and dates of the experiments are shown in Table 1; sizes of fish in Table 2.

RESULTS

When coho were alone at 15°C. they were seen mainly in the wide channel (experiment 6), and in the wide channel and pool (experiment 13). At 20°C. occurrences of coho in the fast flow increased. These distributions changed in the presence of both salmon parr and brook trout, and coho were then found more in the pool or fast flow. At 20°C. activity of all species increased, and displacements of the coho became even more marked (Table 3). Neither salmon parr nor trout distributions appeared to be changed markedly by the presence of coho (Tables 4 and 5). Most occurrences of salmon parr were in medium flow, except at 7°C., when half of the parr were in the pool. Trout were mainly in medium flow in experiments 1, 10, and 11, but were more often in the pool in experiment 12, and distributed throughout the tank in experiment 14.

Except in experiment 1, intra-specific displacements by coho were more common than inter-specific displacements (Table 6). In experiment 1, most inter-specific displacements of brook trout were made by one very aggressive coho, which was responsible for 75°/₀ of displacements recorded for coho. Intra-specific displacements among the coho increased when trout were present. In all experiments with salmon parr and coho, inter-specific displacements were made more frequently by salmon parr than by coho (Table 7). Except in experiment 1, inter-specific displacements of coho by brook trout were more frequent than inter-specific displacements of brook trout by coho (Table 8). Salmon parr generally were more territorial than either brook trout or coho, and this is indicated in the mean distances between neighbours, especially in fast

Table 1. The type of experiments conducted. C = coho salmon; S = Atlantic salmon; T = brook trout

Expt. No.	Species	Temp. (^{o}C.)	No. of Obsvns.	Duration
1	6 C; 6 T	15	20	May 7-25/1976
2	6 S	15	20	Nov. 17-21/1976
3	6 S; 6 C	15	20	Dec. 8-29/1976
4	6 S; 6 C	20	20	Jan. 24-Feb. 1/1977
5	5 S; 6 C	7	10	Feb. 7-9/1977
6	6 C	15	20	Feb. 19-25/1977
7	6 C	20	10	Mar. 4-7/1977
8	6 C; 5-6 S	15	10	Mar. 14-17/1977
9	6 C; 5 S	20	10	Mar. 21-27/1977
10	6 T	15	10	Apr. 4-11/1977
11	6 T; 6 C	15	10	Apr. 16-26/1977
12	6 T; 6 C	20	10	Apr. 29-May 6/1977
13	6 C	15	10	May 16-19/1977
14	6 C; 5 T	15	10	May 23-28/1977

Table 2. The mean sizes of fish used in the experiments, and their increase in length through the experiment. Ranges are given in brackets.

Expt. No.	Species	Mean fork length (cm)	Mean weight (g)	Mean increase in length/day (mm)
1	Brook trout	14.5 (13.8 - 15.7)	33.1 (26.3 - 45.5)	0.41 (0.19 - 0.62)
1	Coho	14.3 (11.9 - 15.4)	30.1 (16.0 - 37.0)	0.33 (0.22 - 0.48)
2,3,4,5	Atl. salmon	12.2 (9.3 - 15.1)	18.4 (6.4 - 35.7)	0.35 (0.19 - 0.63)
3,4,5	Coho	11.0 (9.8 - 12.0)	14.1 (9.2 - 19.2)	0.29 (0.10 - 0.43)
6,7,8,9	Coho	12.6 (11.5 - 13.4)	19.5 (14.9 - 25.9)	0.52 (0.31 - 0.76)
8,9	Atl. salmon	11.8 (9.3 - 14.6)	18.5 (9.4 - 33.2)	0.76 (0.37 - 1.08)
10,11,12	Brook trout	16.0 (13.8 - 18.3)	40.5 (20.3 - 63.3)	0.51 (0.37 - 0.76)
11,12	Coho	16.0 (13.7 - 16.8)	50.5 (32.5 - 59.7)	0.23 (0.04 - 0.40)
13,14	Coho	16.2 (14.5 - 17.4)	52.5 (35.5 - 69.4)	0.25 (0.17 - 0.41)
14	Brook trout	16.4 (14.2 - 17.8)	46.4 (28.3 - 64.0)	0.60 (0.25 - 0.88)

Table 3. The distributions of coho salmon in the stream tank. Associated species are indicated under the 'Species' column. The means are given of distances and heights with the ranges in brackets. C = coho; S = Atlantic salmon; T = brook trout. A dash (-) indicates insufficient or no data.

Expt. No.	Temp. (°C.)	Species	Location (°/o Distributions)			Distance to Nearest Neighbour (m)			Height Above Substrate (cm)		
			Fast	Medium	Pool	Fast	Medium	Pool	Fast	Medium	Pool
1	15	5C;6T	78.4	14.7	6.9	0.3 (.1-2.8)	0.7 (.2-1.1)	1.3 (.2-2.6)	-	-	-
3	15	6C;6S	0.9	3.3	95.8	-	0.6 (.5-.8)	0.2 (.1-.8)	-	10 (10-10)	10 (3-25)
4	20	6C;6S	23.8	16.2	60.0	0.4 (.1-1.3)	0.8 (.3-2.0)	0.5 (.1-1.1)	11.2 (1 - 40)	9.7 (3-20)	21.9 (1-70)
5	7	6C;6S	25.0	0	75.0	0.4 (.1-2.0)	-	0.1 (.05-1.4)	1.8 (1 - 5)	-	4.5 (2-10)
6	15	6C	19.0	72.0	9.0	1.6 (.3-3.7)	0.8 (.3-2.0)	0.7 (.5-1.4)	14.4 (5 - 20)	6.0 (2-10)	7.8 (5-10)
7	20	6C	51.7	30.0	18.3	0.7 (.1-2.1)	1.2 (.5-2.1)	1.0 (.2-1.7)	9.6 (2 - 30)	5.3 (5-10)	8.2 (5-10)
8	15	6C;5-6S	10.0	42.0	48.0	0.7 (.4-.7)	0.7 (.2-2.3)	0.5 (.1-1.7)	3.0 (1 - 10)	5.9 (2-20)	10.7 (5-30)
9	20	6C;5S	3.0	40.0	57.0	1.2 (.9-1.5)	0.6 (.3-1.3)	0.7 (.3-2.0)	7.5 (5 - 10)	9.1 (1-20)	13.7 (5-40)
11	15	6C;6T	72.0	10.0	18.0	0.5 (.2-1.5)	0.9 (.5-1.2)	0.8 (.4-1.2)	5.3 (1 - 40)	16.0 (5-40)	12.9 (5-30)
12	20	6C;6T	30.0	11.7	58.3	0.6 (.2-1.4)	1.5 (.5-2.8)	0.5 (.1-1.1)	2.6 (1 - 5)	5.0 (5- 5)	8.0 (2-20)
13	15	6C	0	38.3	61.7	-	1.1 (.1-2.6)	0.6 (.1-1.5)	-	2.8 (1 -5)	4.8 (1-10)
14	15	6C;5T	34.0	30.0	36.0	1.5 (.2-3.1)	1.9 (.7-3.8)	0.5 (.3-.6)	5.7 (1 - 10)	4.5 (1-10)	14.7 (1-30)

Table 4. The distributions of Atlantic salmon in the stream tank. Associated species are shown under the 'Species' column. S = Atlantic salmon; C = coho. The means are given of distances and heights, with ranges in brackets.

Expt. No.	Temp. (°C.)	Species	Location (°/o Distributions) Fast	Medium	Pool	Distance to Nearest Neighbour (m) Fast	Medium	Pool	Height Above Substrate (cm) Fast	Medium	Pool
2	15	6 S	8.7	73.0	18.3	2.3 (.6-3.5)	1.0 (.2-4.2)	1.6 (.8-3.0)	7.0 (0-15)	3.3 (0-20)	3.5 (0-10)
3	15	6S;6C	22.0	50.0	28.0	1.4 (.3-3.0)	1.3 (.3-4.0)	0.4 (.1-1.8)	2.6 (0-10)	3.7 (0-15)	4.3 (0-20)
4	20	6S;6C	22.6	51.3	26.1	1.2 (.2-2.4)	1.3 (.3-3.4)	0.8 (.2-1.2)	8.5 (0-30)	8.4 (1-15)	17.0 (5-30)
5	7	5S;6C	0	48.3	51.7	-	1.4 (.4-3.7)	0.4 (.1-0.8)	-	1.4 (0-10)	1.25 (0-10)
8	15	5-6S;6C	19.0	55.0	26.0	1.4 (.3-1.7)	0.8 (.2-2.7)	0.8 (.2-2.0)	2.0 (0-10)	7.4 (0-20)	15.5 (5-40)
9	20	5S;6C	20.0	62.0	18.0	2.0 (.5-4.4)	1.1 (.3-1.7)	0.7 (.4-1.2)	4.8 (1-10)	10.5 (5-20)	35.5 (5-55)

Table 5. The distributions of brook trout in the stream tank. Associated species are shown under the 'Species' column. T = brook trout; C = coho salmon. The means of distances and heights are given, with the ranges in brackets.

Expt. No.	Temp. (°C.)	Species	Location (°/o Distributions) Fast	Medium	Pool	Distance to Nearest Neighbour (m) Fast	Medium	Pool	Height Above Substrate (cm) Fast	Medium	Pool
1	15	6T;6C	25.7	57.5	16.8	0.6 (.1-2.7)	0.6 (.1-2.1)	1.0 (.1-2.1)	- Insufficient data -		
10	15	6T	15.0	60.0	25.0	2.5 (1.2-3.5)	1.2 (.3-1.8)	1.2 (.4-2.1)	10.8 (2-30)	12.2 (5-40)	8.8 (0-30)
11	15	6T;6C	22.0	42.0	37.0	0.5 (.2-.9)	1.8 (.5-4.0)	1.0 (.3-2.3)	8.3 (0-15)	10.0 (5-20)	19.8 (0-40)
12	20	6T;6C	33.3	20.0	46.7	0.5 (.1-1.9)	1.8 (.5-2.8)	0.3 (.1-0.6)	4.1 (1-10)	8.8 (5-10)	9.3 (2-20)
14	14	5T;6C	34.0	30.0	36.0	1.5 (.2-3.1)	1.9 (.7-3.8)	0.5 (.3-0.6)	5.7 (1-10)	4.5 (1-10)	14.7 (1-30)

Table 6. 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.
1 (C;T)	69.6	4.5	8.0	1.8	0	1.8	3.6	0.9	8.0	1.8	0.67	1.28
3 (C;S)	48.0	18.0	8.0	1.0	1.0	0	1.0	0	8.0	14.0	0.96	0.12
4 (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
5 (C;S)	0	50.0	0	0	0	0	0	0	0	50.0	0.03	0
6 (C)	52.0	16.8	4.8	1.6	3.2	1.6	0	0	10.4	9.6	0.83	-
7 (C)	43.2	34.6	1.2	0	1.2	1.2	0	1.2	6.2	11.1	1.1	-
8 (C;S)	52.9	20.0	5.9	1.2	0	2.4	0	1.2	3.5	12.9	0.92	0.33
9 (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
11 (C;T)	56.2	20.2	5.6	2.8	1.7	0.6	0.6	0	8.4	3.9	2.28	0.12
12 (C;T)	88.4	9.1	2.1	0.4	0	0	0	0	0	0	3.9	0.17
13 (C)	54.9	33.6	0	3.3	0.8	0.8	0.8	0	2.5	3.3	1.82	-
14 (C;T)	69.5	22.1	3.1	0.8	0	0	0	0	1.8	2.8	5.7	0.33

Table 7. 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.

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

Table 8. Agonistic acts used in intra- and inter-specific displacements (successful attacks) by brook trout. Species are listed with the experiment numbers. T = brook trout; C = coho.

Expt. No. (Species)	Agonistic Acts (°/o) Charge + Chase	Approach	Nip	Lateral display	Frontal display	Presence	Drift	Supplant	Displacements made/ Observation/Fish INTRA-SP.	INTER-SP.
1 (T;C)	34.6	14.4	30.1	6.5	5.2	2.6	5.2	1.3	1.83	0.46
10 (T)	63.4	19.6	9.4	3.6	0.5	2.7	0	0.9	3.1	-
11 (T;C)	45.6	34.8	14.2	1.5	0.7	2.1	0.2	1.0	3.0	5.77
12 (T;C)	47.5	36.6	12.7	0.7	0	2.0	0.1	0.4	4.72	6.28
14 (T;C)	47.5	29.5	19.5	0.9	2.7	0	0	0	1.28	3.98

and medium flows (Tables 3, 4, and 5). Salmon parr usually held station closer to the substrate than coho, and frequently were in contact with the bottom, whereas coho were never seen in contact with the substrate (Tables 3 and 4). At 20°C., salmon parr were generally higher off the bottom than at cooler temperatures. Brook trout appeared to hold stations above the substrate at heights similar to those of coho, but sometimes were seen in contact with the bottom (Table 5). At 7°C., the salmon parr were usually motionless on the bottom. They became darker and more mottled, except for one parr which was the most active. Parr activity was low, but some nipping went on among them in the pool. The parr remained separated from one another, but the coho generally remained in a small school. At this temperature the coho did not change colour. They held position 1 - 10 cm above the bottom, and fed actively, but their aggression was low.

Of the agonistic acts, 'charge and chase' was the most common method of displacement used by all three species (Tables 6, 7, and 8). Raising the temperature to 20°C. increased the relative frequency of this act with coho and salmon parr, but not with brook trout. 'Approach' was used by coho and brook trout more often than by salmon parr, and 'nip' was seen more often in brook trout than in the other two species. Only coho demonstrated 'wigwag' and 'threat nip'.

Salmon parr had the greatest overall mean growth increment (0.52 mm/day), followed closely by brook trout (0.50 mm/day); the least was recorded for coho (0.32 mm/day) (Table 2). Fastest coho growth was during experiments 6, 7, 8, and 9 (0.52 mm/day), in which the coho were not mixed with another species from February 14 to March 8, in experiments 6 and 7. Generally the dominant fish in each species grew fastest.

Buoyancy experiments to measure specific gravity showed a mean of 1.046 for salmon parr (range 1.020 - 1.060), a mean of 1.023 for coho (range 1.010 - 1.040), and a mean of 1.015 for brook trout (range 1.010 - 1.020). Analysis of variance and LSD tests (Snedecor and Cochran 1967) showed that the specific gravity of salmon parr vs brook trout, and salmon parr vs coho, were different from each other ($P < .01$), but that there was no significant difference between brook trout and coho ($P > .05$).

DISCUSSION

Both salmon parr and brook trout were considerably more aggressive than coho. Surprisingly, the coho were more often displaced by brook trout than by salmon parr. In a previous study, salmon parr were found to be more aggressive than brook trout (Gibson 1973). Probably coho were more often attacked by brook trout because they were in closer association, and because brook trout frequently changed station, and therefore had a greater opportunity for contacts. Coho and salmon parr were spatially more segregated. Salmon parr generally had more permanent territories than either coho or brook trout. Brook trout appeared to harass and keep the coho more active than when the coho were with salmon parr.

Hartman (1965) describes the tendency of coho to school, and this was seen in some of the experiments discussed in this paper. In experiment 3, at 15°C., the coho were usually in a school in the pool, where the velocity of the water was about 3.5 cm/sec, with a coho of 11.8 cm in the lead. This coho attacked the coho which had left the school, and they rejoined it. However, in the next experiment, which was number 4, at 20°C., these coho were dispersed and constantly active. Territories were not as rigid as those of salmon parr, and the aggressiveness of the coho appears to be used to disperse rather than to hold a territory. Coho gave the impression of being a more nervous fish than either salmon parr or brook trout. They appeared to flee more readily when attacked, and when holding station, even without attempts to displace them, they frequently made dashes to new positions. With another species present, coho less often held station in the middle of the wide channel, and entered the channel in a nervous way along the sides. Although not necessarily due to nervousness, this impression seemed to be conveyed by an apparent lower amplitude of tail beats, with a higher rate than for the other two species; e.g., 50 tail beats were timed for each of the three species in the medium flow, and 2.20 tail beats/sec ($S_{\bar{x}}$ = 0.07) were recorded for coho, 1.74 ($S_{\bar{x}}$ = 0.09) for salmon parr, and 1.29 ($S_{\bar{x}}$ = 0.05) for brook trout.

Salmon parr and brook trout attack each other without species discrimination (Gibson 1973), but coho showed much higher intra-specific aggression than inter-specific aggression. Both salmon parr and brook trout have distinctive red spots along their sides, with brook trout being more colourful than either of the other two species, so that species recognition would be easily possible. The relatively high proportion of displays, especially lateral displays, that

Hartman (1965) recorded for coho were not evident in the present study. This may be partly explained by the fact that only acts which displaced fish were recorded here. Hartman also used a greater density of fish than used in these experiments, which might induce more displays than chases. The coho used in experiment 1 were becoming smolts, so their aggression could be expected to be lower. They were brought to the holding tanks on March 12th. They had been kept in an outdoor pond in New Hampshire with a natural photoperiod, and were to have been released that spring. This may explain why the majority of the coho in that experiment were in the fast channel, as they were mainly at the downstream end for much of the time, possibly attempting to emigrate. However, all the fish in the later experiments were kept in a 14 hour photoperiod throughout the winter. A scientist familiar with juvenile coho salmon on the west coast of North America observed the coho used in the final experiments of this study, and confirmed that they did not have smolt colouration. Aggression of coho has been shown to be related to temperature. However, aggression changes with the season, and is in part related to age or time period as well as water temperature (Hartman 1966). In the present study, the seasonal effects were minimized by keeping the fish under a regular long photoperid, and the changes observed in activity and aggression could be related mainly to temperature. At 7°C., coho showed greater affinity for the pool, which can be expected from their behaviour observed in the field (Hartman 1965). Some occurrences were at the downstream end of the fast channel, which possibly indicated an attempt to emigrate rather than a preference for the higher water velocity. The increase in numbers of salmon parr in the pool, at 7°C., their reduced aggression, and their affinity for the substrate was to be expected, as this behaviour has previously been observed at water temperatures below 9°C. (Gibson 1976).

Salmon parr were more aggressive than coho, and naturally occupy riffle habitat, so that parr might be expected ecologically to resemble juvenile steelhead trout, and so successfully compete with coho in the fast water environment. Parr usually do not displace brook trout larger than themselves by aggression, but apparently can do so by competition. Salmon parr are more streamlined than brook trout, but also have other attributes which make them more efficient than brook trout in fast water. They are less buoyant than brook trout (Saunders 1964), and they have larger pectoral fins. These fins can be used like ailerons when the fish hold station above the bottom, but in fast currents parr can apply themselves to the substrate and use their pectoral and pelvic fins like suckers, by applying the leading edges of the pectoral fins to the substrate, and curving the posterior part of the fins backwards and slightly upwards. Neither brook trout nor coho were observed to use their fins in this way. Brook trout and coho swim actively above the bottom in fast water to hold position. The pectoral fin length was compared with the standard length, of 13 coho, range 11.8 to 15.4 cm. The mean ratio was found to be 1:6.7 ($S_{\bar{x}}$ = .09). This compares with 1:4.6 for salmon parr and 1:5.9 for small brook trout (Gibson 1973). The buoyancy of coho is also more similar to that of brook trout than of parr. Like the brook trout, coho look more 'chunky' than parr. Coho therefore, like brook trout, are not as well adapted to fast water conditions as parr, so that parr could be expected to outcompete coho that are too big to be displaced by aggression. Coho have ecological requirements closer to those of brook trout than parr, so that more severe competition should be expected between coho and brook trout. From this study it appears that brook trout can displace coho of similar size by aggression. Small brook trout might be displaced by larger coho, but as the majority of brook trout do not go to sea, there would be be brook trout present larger than coho. However, field studies should complement the present findings, so that all phases of the life history of the three species can be taken into account and different aspects of ecological requirements tested.

Concern that coho salmon may threaten Atlantic salmon probably arises from its common name, but despite being called a salmon, it is a different genus. More severe competition might be expected from other species within the same genus. In fact, brown trout (<u>Salmo</u> <u>trutta</u>) have been shown to be severe competitors of salmon parr (Le Cren 1965). Juvenile steelhead appear to occupy a niche very similar to that of salmon parr, and yet this species is being introduced to the east coast of North America with relatively little public concern. Behavioural interactions of brown trout and steelhead trout with salmon parr and brook trout will be studied during the coming winter.

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