ESTUARINE USE BY JUVENILE COHO SALMON (ONCORHYNCHUS KISUTCH): IS IT A Viable LIFE HISTORY STRATEGY?

by

DANA YUTAKA ATAGI

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Department of Zoology

The University of British Columbia
Vancouver, Canada

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ABSTRACT

Across its geographic distribution in North America and Eurasia, juvenile coho salmon (*Oncorhynchus kisutch*) utilize an array of different freshwater habitats prior to moving seaward. These freshwater habitats include streams, lakes, beaver ponds, and off-channel sites. In recent years, pre-smolt juvenile coho salmon use of other habitats such as estuaries has been documented. This finding raises the question of whether or not estuarine use by pre-smolt coho salmon is a viable alternative life history?

Juvenile pre-smolt coho were present in the upper intertidal portion of the Salmon River estuary from May through November with peak abundance occurring in August. Coho salmon use of an experimental tidal channel was similar to that of a nearby natural channel. Coho densities were similar in the two habitats. Mean residence time in the upper estuary was estimated to be 13.4 and 7.1 days in 1989 and 1990, respectively. It is postulated that the presence of a low tide refuge in the experimental channel lengthened residence time and increased site fidelity. Both young-of-the-year and yearling pre-smolt coho were captured in the estuary. By late summer, high estuarine growth rates of young-of-the-year fish enabled them to grow to the size of yearling coho. The age structure of the estuarine coho population shifted from predominantly young-of-the-year coho in spring and early summer to yearling coho in late summer and fall.

Agonistic behaviour has been proposed as a potential cause for the emigration of stream resident coho to the estuary. Observations of juvenile coho in a stream and in an estuarine tidal channel indicated that stream coho defended territories and were highly aggressive while estuarine coho aggregated into small groups and were infrequently aggressive. In mirror image stimulation (MIS) experiments, stream resident forms were found to be more
aggressive than either estuarine resident or stream emigrant forms. These differences in social organization and agonistic behaviour were appropriate for an existence in a resource-limited, stream environment and a resource-rich, high predation risk, estuarine environment.

In field enclosures with paired groups of fish, estuarine coho were dominated by smaller stream resident and stream emigrant conspecifics. In the laboratory, a comparison showed that estuarine coho dominated both stream residents and stream emigrants. This was probably due to size advantages associated with high estuarine growth rates and occurred in spite of estuarine coho exhibiting lower levels of aggression in MIS experiments. These apparently conflicting results suggest that facultative switching of behavioural modes (i.e. non-aggressive to highly aggressive) in estuarine reared coho can occur.

Juvenile pre-smolt coho inhabit specific localities in the Salmon River estuary for several weeks. Physiologically, they are able to withstand the level of salinity encountered in estuaries and often exhibit high rates of growth. Behaviourally, they exhibit low levels of aggression but they can dominate smaller, more aggressive stream forms. These results increase a growing body of evidence suggesting that estuarine use by juvenile pre-smolt coho salmon may be a viable alternate life history.
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INTRODUCTION

The importance of estuaries to each of the five species of eastern Pacific salmon varies considerably. Chinook salmon (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) are considered to be heavily dependent upon estuaries whereas pink (*O. gorbuscha*), sockeye (*O. nerka*), and coho salmon (*O. kisutch*) are all considered to be less dependent upon estuaries (Dorcey et al. 1978; Healey 1982).

As the number of estuarine research programs increased, more and more information accumulated regarding the use of estuaries by salmonid species that were once considered to infrequently use this habitat. For example, sockeye fry were found to extensively use slough habitats of the Fraser River estuary (Birtwell et al. 1987). Results such as this have not only been limited to studies in British Columbia but also have been observed in Alaskan estuaries (Murphy et al. 1984). A similar pattern has been observed for coho salmon with studies both in British Columbia (Tschaplinski 1982, 1987, 1988) and Alaska (Crone and Bond 1976; Murphy et al. 1984; Thedinga and Koski 1984) showing that juvenile coho salmon can use estuaries.

The early life history of the coho salmon (*Oncorhynchus kisutch*) is assumed to be structurally very rigid. Following hatching and emergence from the spawning gravels, the typical juvenile coho fry usually requires an extended period of freshwater residence of at least one and up to two years prior to moving seaward (Crone and Bond 1976; Sandercock 1991). The freshwater habitat requirements of juvenile coho salmon are known to be diverse (i.e. they rear in lakes, rivers, and streams) for varying lengths of time before migrating to sea as smolts (Scott and Crossman 1973). It has previously been assumed that the all coho juveniles that moved seaward prior to this extended freshwater residence period perished. It now appears that this life history pattern may not
be as rigid as previously thought. There is an expanding body of literature
documenting the presence of juvenile coho salmon in estuaries (Crone and
Bond 1976; Tschaplinski 1982, 1987, 1988; Murphy et al. 1984; Thedinga and
Koski 1984; Ryall and Levings 1987), but detailed information regarding their
ecology and life history in estuarine rearing environments is currently
unavailable.

Given that coho juveniles are frequently found in estuaries (Stockner and
Levings 1982; Tschaplinski 1982, 1987, 1988; Murphy et al. 1984; Ryall and
Levings 1987) and they can successfully rear in estuaries (T.G. Brown,
Department of Fisheries and Oceans, Nanaimo, B.C., personal communication),
I examined what potential ecological benefits could be derived from a period of
estuarine residence. It has been hypothesized that the presence of pre-smolt
coho salmon in estuaries was simply a result of intraspecific behavioural
interactions causing coho fry to be displaced from stream habitats to estuary
habitats. It is these emigrants or "nomads" that take up residence in the
estuaries of their natal streams (Sandercock 1991). Chapman (1962) thought
that "nomad" coho fry had an innate tendency to migrate even if there was an
abundance of available stream rearing space. Northcote (1992) suggested that
these emigrants might not be simply "ecological losers" but possibly "explorers
or colonizers" of new unused habitats that could be of benefit to the population
in general. The question remains were these fish simply "ecological losers" as
suggested by Glova (1990) or could they be exhibiting an alternative life history
strategy? Additionally this scenario raises the question "what are the impacts
of rearing in these different environments on behavioural interactions?"

Juvenile coho salmon exhibit extensive innate agonistic behaviours (Hoar
1951) and stream dwelling coho juveniles use these behaviours to defend
territories against other salmonids (Hartman 1965; Lister and Genoe 1971;
Stein et al. 1972; Johnson 1981; Johnson and Ringler 1981) and conspecifics (Chapman 1962; Mason and Chapman 1965; Dill et al. 1981; Rosenau and McPhall 1987). Territoriality in stream dwelling coho is hypothesized to have evolved as a mechanism to disperse the population to reduce the incidence of disease, parasitism, and predation (Chapman 1962) and/or to ensure that adequate food resources are available in an environment where food may be limited (Chapman 1962; Dill 1978; Dill et al. 1981).

It is widely accepted that a strong genetic basis exists for inter-population differences in behaviour for a number of salmonid species (Brannon 1967; Raleigh 1967, 1971; Bowler 1975). In juvenile coho salmon agonistic behaviours (i.e. aggression and territoriality) has been shown to be genetically based and can be adaptations to local environments (Rosenau 1984; Rosenau and McPhall 1987). In contrast, Chapman (1962) found intra-population differences in levels of aggression exhibited by "resident" and "nomad" coho juveniles. Recently, Swain and Holtby (1989) documented behavioural differences between coho rearing in stream and lake habitats. These studies suggest that the rearing environment plays an important role in determining whether or not individuals within a population should exhibit high levels of aggression and defend territories. Consequently this territorial behaviour should be expressed through strong agonistic tendencies and through aggressive behavioural interactions.

It has become apparent that coho can successfully rear in estuaries and frequently return to stream habitats following this residence period (Murphy et al. 1984; Thedinga and Koski 1984; Ryall and Levings 1987; Tschaplinski 1987; T.G. Brown, Department of Fisheries and Oceans, Nanaimo, B.C., personal communication) but relatively little is known about the outcome of social interactions between these estuarine reared and stream reared forms of coho
salmon. Recent studies raise questions regarding the potential behavioural and ecological consequences of estuarine rearing.

The goal of this thesis was to first document the numbers of juvenile coho salmon utilizing two types of upper intertidal habitats (one man-made and the other naturally occurring) within the Salmon River estuary, Vancouver Island, British Columbia. Seasonal changes in coho abundances on both a tidal and as well as a seasonal basis were documented. Residence times of juvenile coho salmon in these estuarine habitats were estimated.

The second goal was to assess some of the effects of estuarine rearing on the behaviour of juvenile coho salmon. I compared the agonistic behavioural repertoires of three eco-types (stream resident, stream emigrant, and estuary resident) of coho salmon under both field and laboratory conditions. Field behavioural observations were undertaken in both natural stream and natural estuarine habitats. Field enclosures were used to compare levels of aggression between eco-types of coho. In the laboratory, mirror image stimulation experiments were conducted to examine levels of aggression of stream resident, stream emigrant, and estuary resident coho. Finally, pairwise comparisons were used to examine the outcome of agonistic encounters between eco-types.

The outcome of behavioural interactions in the stream environment may answer some questions regarding the fate of estuarine reared coho juveniles while also shedding light on the possible mechanism(s) which may cause coho juveniles to emigrate and subsequently rear in estuaries.
MATERIALS AND METHODS

I. STUDY AREA

Salmon River

The Salmon River watershed is located on northern Vancouver Island, British Columbia (Fig. 1). The Salmon River is a fifth order stream with a permanent stream course of 208 km and a watershed area of 1200 km², making it the fourth largest river system on Vancouver Island. The watershed lies primarily in the coastal Douglas fir biogeoclimatic zone (Ptolemy et al. 1977) and the Salmon River flows northwest into Johnstone Strait at Salmon Bay. The Salmon River has two major tributaries currently accessible to anadromous fish. The White River enters the Salmon 11.5 km above the estuary and has a watershed area of 370 km². The Memekay River enters the Salmon River 28.8 km above the estuary and has a watershed area of 223 km².

Adult coho salmon (*Oncorhynchus kisutch*) spawn in the Salmon River and its tributaries between July and December, with the peak occurring in late October and November. Besides coho salmon, chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*) on both even and odd numbered years, sockeye salmon (*O. nerka*), coastal cutthroat trout (*O. clarki*), steelhead trout (*O. mykiss*), and Dolly Varden char (*Salvelinus malma*) all spawn in the Salmon River and its tributary streams. Currently, the spawning escapements of all the enumerated salmonid species appear to be declining (Fig. 2).

As is common in many northern Vancouver Island watersheds, logging activities dominate the land use in the Salmon River watershed. Other impacts on the Salmon River include the British Columbia Hydro and Power Authority's 1957 construction of a diversion dam on the Salmon River 45 km upstream from the estuary. Water is diverted to the Campbell River system for
hydroelectric power generation at the John Hart power station.

Previous mitigation efforts have included the installation of a smolt
deflector screen to keep outmigrating Salmon River coho and steelhead smolts
from entering the Campbell River system. Boulders have been placed in the
mainstem of the Salmon River and Springer Creek to increase juvenile salmonid
rearing habitat (Ward and Slaney 1981).

Salmon River Estuary

The Salmon River estuary is located at longitude 50°24'N and latitude
125°57'W and is oriented along a north-south axis (Fig. 3). The estuary is
approximately 74 ha in size and totally dewatered on tides less than 2.0 m. The
intertidal zone substrates are predominantly mud-silt or mud-sand (Ptolemy et
al. 1977).

The fish fauna inhabiting the estuary is diverse. Along with juvenile coho
salmon, chinook salmon, chum salmon, Dolly Varden char, and many non-
salmonid fish species were captured in the Salmon River estuary. Threespine
stickleback, Pacific staghorn sculpin (Leptocottus armatus), starry flounder
(Platichthys stellatus), and shiner perch (Cymatogaster aggregata) were common
while Pacific herring (Clupea harengus pallasii), Pacific sandlance (Ammodytes
hexapterus), and surf smelt (Hypomesus pretiosus pretiosus) were less
frequently captured.
Figure 1. Map of the Salmon River watershed, Vancouver Island, British Columbia.
The estuary and lower river have been used for log handling and storage since the 1880s. Over the next one hundred years several major projects have encroached upon the Salmon River estuary. Channels were dredged and dykes were built to drain land for agricultural and saw-milling purposes. From 1937 to 1964 the northwest corner of the estuary was used for log booming and storage until MacMillan Bloedel constructed the current log dump area (Anon. 1987). The village of Sayward discharges its treated sewage effluent into the southwest portion of the estuary. Currently, the major industrial use of the estuary is the dry-land sort operation of MacMillan Bloedel Limited, Kelsey Bay Division (Fig. 3).
Figure 3. Map of the lower Salmon River and estuary.
In May 1988 the MacMillan Bloedel log dump site was converted into a dry land log sort operation. During construction a 5.5 ha portion of the estuary adjacent to the MacMillan Bloedel property was filled. Under the Department of Fisheries and Oceans management policy of "no net habitat loss", MacMillan Bloedel constructed an estuarine pond as compensation for lost fish habitat.

The mitigation project, completed in September 1987, consisted of the excavation of a large pond on the west side of the upper intertidal portion of the estuary. The rationale for the construction of the pond was to provide a low tide refuge for juvenile salmonids inhabiting the tidal channels of the upper estuary (Levings 1982). For the purpose of clarity the pond will be forthwith referred to as the experimental channel. It is hour-glass shaped, approximately 180 m in length and 70 m in width (Fig. 4). The maximum low tide water depth in the experimental channel is approximately 2.0 m. The channel morphology is dominated by three openings (inlet/outlets) which consist of rip-rap sills over which water passes when tidal levels are high enough. All water exchange occurs via these three inlet/outlets. Two inlets are located at the east end of the experimental channel (nearest the Salmon River mainstem) and the third inlet is located at the west end. All three inlet/outlets connect the experimental channel to adjacent tidal channels (Fig. 5). The estimated low and high tide wetted surface areas of the experimental channel are 4,557 m² and 7,760 m², respectively. The colonization of the experimental channel by aquatic vegetation occurred naturally and has continued since fall 1987.
Figure 4. Schematic diagram of the experimental channel showing shoreline gradients at low tide.
Figure 5. Map of the natural tidal channel and the experimental channel in the upper intertidal portion of the Salmon River estuary.
Juvenile coho salmon rearing densities, residence times, and movement patterns in the experimental channel were compared to an adjacent tidal channel located on west side of the upper intertidal portion of the estuary, near the experimental channel (Fig. 4 and 5). This natural tidal channel provides low tide pool habitats which appear in general similar to the experimental channel habitat. Again for clarity this channel will be referred to as the natural channel. At low tide, two pools are formed on either side of a 12.4 m long by 1.2 m diameter culvert which passes beneath the experimental channel access road (Fig. 5). The estimated low and high tide wetted surface areas of the pool at the west end of the culvert are 153 m$^2$ and 216 m$^2$, respectively. The estimated low and high tide wetted surface areas of the pool at the east end of the culvert are 795 m$^2$ and 1782 m$^2$, respectively. The functional area of the east pool during low tide is very much lower than the estimated 795 m$^2$ due to the fact that most of the wetted areas are very shallow (<15 cm deep) making them unsuitable for use by many species of fish. The functional low tide area is approximately 20% of the total area or about 160 m$^2$. On low tides these pools provide a naturally occurring refuge for fish to remain in until the area flooded. The predominant direction of flow in the natural tidal channel is from west to east on an ebbing tide (i.e. towards the mainstem of the Salmon River).

The emergent and intertidal vegetation communities established in the experimental channel differed from those in the natural tidal channel (Table I). The aquatic vegetation in the experimental channel changed between 1989 and 1990 which probably reflects the dynamic nature of the colonization process. The emergent vegetation surrounding the experimental channel consisted primarily of Kentucky blue grass (*Poa pratensis*), bentgrass (*Agrostis alba* var. *stolonifera*), and cinquefoil (*Potentilla pacifica*) while the emergent vegetation surrounding the tidal channel consisted mainly of Lyngbei's sedge (*Carex*
lyngbel) and tufted hair grass (*Deschampsia cespitosa*) (Kennedy 1979). The experimental channel was slowly being colonized by small eel grass beds (*Zostera spp.*) while rockweed (*Fucus spp.*) grew on the rocks at the sills of the inlets/outlets. The rocky portions of the tidal channel also supported small patches of rockweed but eel grass was uncommon in the tidal channel.

Table I. Emergent and intertidal vegetation communities in the study sites of the Salmon River estuary, Vancouver Island (Kennedy 1979).

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<tr>
<th>Natural Channel</th>
<th>Experimental Channel</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Poa pratensis-Agrostis alba var. stolonifera-Potentilla pacifica</em>  (Kentucky blue grass-Bentgrass-Cinquefoil)</td>
<td>X</td>
</tr>
<tr>
<td><em>Carex lyngbel</em>  (Lyngbel's sedge)</td>
<td>X</td>
</tr>
<tr>
<td><em>Deschampsia cespitosa-Carex lyngbel</em>  (Tufted hair grass-Lyngbel's sedge)</td>
<td>X</td>
</tr>
<tr>
<td><em>Zostera spp.</em>  (Eel grass)</td>
<td>X</td>
</tr>
<tr>
<td><em>Fucus spp.</em>  (Rockweed)</td>
<td>X</td>
</tr>
</tbody>
</table>

**Springer Creek**

Springer Creek is a small east slope tributary stream located 10 km upstream from the estuary (Fig. 1). It has a permanent stream course length of 6 km and supports a fish fauna representative of the Salmon River. Coho and pink salmon, steelhead trout, cutthroat trout, Dolly Varden char, threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), and
Western brook lamprey (*Lampetra richardsoni*) all reside in Springer Creek during some stage of their freshwater life history.

II. PHYSICAL-CHEMICAL OBSERVATIONS

Temperature and Salinity

Surface water temperatures were measured (to the nearest 0.5 °C) during low tide using a hand-held thermometer. Surface water salinity was measured (to the nearest 1 part per thousand) using a hand-held salinometer/refractometer. A Yellow Springs Instrument (YSI model 33) temperature and salinity meter was used to measure temperature and salinity profiles of the experimental channel and the natural tidal channel. Profiles were recorded on three dates July 24 (low and high tide), October 22, and October 30, 1990 (high tide only for the latter dates).

Water Circulation Patterns

The water flow and circulation patterns within the experimental channel were qualitatively described during both flooding and ebbing tides by observation of surface water movements during the periods of peak tidal flows.

III. ESTUARINE RESIDENCE OF JUVENILE COHO SALMON

1989 Field Studies

Preliminary field studies were undertaken during 1989. The experimental channel was sampled using a 10 m by 1.5 m and 0.7 cm stretched mesh beach seine set from a 3.6 m boat powered by a 9.9 hp outboard motor. Fish sampling started in June and continued until late August. Fish utilizing the experimental channel were captured during both low and high tides and at approximately biweekly intervals.
Low tide juvenile salmonid abundances in the experimental channel were estimated using a multiple mark and recapture technique (Ricker 1975; Krebs 1989). Fish were seined, anaesthetized (using a 0.1 percent solution of 2-phenoxyethanol), marked (adipose fin clipped or caudal fin dye injected) and measured to the nearest mm for fork length. A random sample of 25 specimens were kept and preserved until fixed in a 10% solution of buffered formalin. All other fish were released. The microcomputer program "Schnabel" was used to calculate the abundance estimate and 95% confidence limits (see Appendix 2.3 in Krebs (1989) for source code). The abundance of juvenile coho salmon was estimated using the Schumacher-Eschmeyer estimator (Schumacher and Eschmeyer 1943). The Schumacher-Eschmeyer estimator, which is considered to be more robust than alternatives such as the Schnabel estimator (Seber 1982), is described below.

Schumacher-Eschmeyer (1943) Estimator

Estimated Population Size

\[ \hat{N} = \frac{\sum C_t M_t^2}{\sum R_t M_t} \]

where:
- \( C_t \) = Total number of individuals caught in sample \( t \);
- \( R_t \) = Number of individuals already marked when caught in sample \( t \);
- \( M_t \) = Number of marked individuals in the population just before the \( t \)th sample is taken;
- \( s \) = Total number of samples (see Krebs 1989).

To increase the accuracy and the precision of the population estimate, the capture-mark-recapture procedure was repeated until the ratio of the number of marked individuals in the sample \( R_t \) to the total number of individuals caught in the sample \( C_t \) was equal to or greater than 0.1 (Seber 1982).
1990 Field Studies

A more intensive field study was initiated in 1990. The experimental channel and the natural tidal channel were sampled throughout the late spring (May 25) and fall (November 7) of 1990. The fish capture and sampling protocols were modified from those used in 1989 to examine both high and low tide fish use of the experimental channel and to compare these findings with a natural tidal channel. These changes are noted below.

Population and Density Estimates

Comparisons of population and density estimates were used to examine use of the experimental channel and the natural tidal channel by estuary populations of juvenile coho salmon. Juvenile coho abundances were estimated on a monthly basis between June and October. Abundances in the experimental and the natural tidal channels were estimated during both high and low tides. Since only a single census could be made per tidal cycle, each month's population estimates took a minimum of four sampling days to complete.

Low tide estimates for the experimental channel were obtained using the same method as described for 1989 (Schumacher-Eschmeyer abundance estimator). High tide population estimates were conducted using a stop seine net technique similar to that used by Levy and Northcote (1982). A 0.7 cm stretched mesh stop seine net was placed across each of the three experimental channel outlets. Stop nets were installed during the low tide prior to the high tide to be censused. The stop seine nets were anchored to reinforced angle iron posts and the lead line was secured using rebar anchors. The float line was weighted with rocks to keep it submerged until high slack tide when nets were set. Pulling on the float line removed the rocks and the nets began fishing when all the floats were freely floating. Nets were set at high slack tide as estimated
by the Department of Fisheries and Oceans tide guide. A multiple mark and recapture census was conducted when the experimental channel dewatered and all three sills were exposed. The losses of fish between the initial setting of the net (high slack tide) and the time of the census was considered to be low due to the gradually sloping banks of the experimental channel inlets which allowed a secure seal to be formed. However this does not include losses due to predation. The time between high slack tide and commencement of the population estimate was usually about four hours.

The initial method used to estimate coho abundances in the natural tidal channel was the Schumacher-Eschmeyer multiple mark and recapture method. The tidal channel itself was censused in two sections. The first section extended from the east end of the culvert to the confluence of the channel adjacent to the west outlet of experimental channel, a distance of approximately 135 m. The second section extended from the west end of the culvert to the end of the pool, a distance of approximately 20 m (Fig. 5). Fish populations were sampled using the same 0.7 cm stretched mesh 10 m x 1.5 m beach seine net. Initially, low tide juvenile salmonid abundances were estimated using a multiple mark and recapture method but following the first sampling period the method was subsequently changed to a four pass depletion estimator (Leslie and Davis 1939). The method was altered because it was possible to capture a large proportion of the fish in these small pools with a single sweep of the seine net.
The Leslie and Davis (1939) depletion estimator can be mathematically expressed as:

**Leslie and Davis (1939) Estimator**

\[
\hat{N} = \bar{K} + \left( \frac{\bar{Y}}{\bar{C}} \right)
\]

where:  
\( Y \) = mean catch per unit effort \((Y_i)\);  
\( K \) = mean value of accumulated catch \((K_i)\);  
\( s \) = total number of samples.

The microcomputer program "Catch" was used to calculate the abundance estimate and 95% confidence limits (see Appendix 4.5 in Krebs (1989) for source code). High tide abundance estimates for the tidal channel were obtained using a method similar to that for high tide estimates in the experimental channel. Stop seine nets were placed at the culvert and at the confluence of the study tidal channel and the channel adjacent to the experimental channel. Rocks and U-shaped rebar anchors were used to secure the nets. The number of fish remaining in the two pools was censused on the following low tide. In areas that could not be effectively sampled using a beach seine (because of shallow water depths), a two-man pole seine was used to collect and directly enumerate the salmonids trapped in the small pockets of standing water and trapped in the bunt of the stop seine net. The numbers of individuals captured in this way was generally low (usually < 10 individuals) and as a result they were not incorporated into the population estimate.
Juvenile coho salmon densities were calculated using the wetted surface areas previously described.

**Seasonal Change in Abundance**

Seasonal changes in juvenile coho salmon numbers were estimated using an index of abundance. The index used was simply the total number of juveniles captured in any monthly sampling period.

**Residence Time**

**Marking**

Juvenile coho salmon were marked for both population and residence time estimates by either clipping fins: adipose (ad), upper caudal (uk), and lower caudal (lk); or by marking fins with Alcian blue or Alcian green dyes injected with a Pan Jet inoculator (Kelly 1967; Hart and Pitcher 1969). Several fins were dyed during the course of the study: upper caudal lobe (uc blue/green), lower caudal lobe (lcb/g), middle portion of caudal fin (mcb/g), and anal fin (anb/g). Earlier work suggested that the longevity of the Alcian blue mark would supersede the length of this study (Pitcher and Kennedy 1977; Herbinger et al. 1990). Different marks were used for each subsequent sampling period and/or sampling site. In some instances, a combination of fin clips and a dyed fins were used to mark fish.

Residence times of the experimental channel were estimated in both 1989 and 1990, but the residence times of the natural channel were only estimated in 1990. In 1989, juvenile coho salmon were marked on six dates (June 14-August 24). In 1990, juvenile coho salmon were marked on 14 dates (June 6-October 23). The residence time of recaptured individuals was calculated from their marking codes which indicated the date of initial capture.
The residence time was calculated according to the following equation:

\[
\text{Mean Residence Time} = \frac{\sum \text{individual residence time estimates (days)}}{\text{number of individuals recaptured}}
\]

Movement Patterns

In 1990, separate marks were used to distinguish both the marking date and the release site. The movements of juvenile coho salmon between the experimental and natural tidal channel habitats were monitored. A fish was defined as exhibiting site fidelity if it was recaptured in the same location as it was originally captured. Alternatively, a recaptured fish exhibited no site fidelity if it was not recaptured at the same location where it was first captured.

General Sampling Regime

All fish were anaesthetized (using a 0.1 % solution of 2-phenoxyethanol) and measured for fork length prior to marking and release. A sample of 30 juvenile coho from both the Salmon River estuary and the Salmon River and its tributaries during both 1989 and 1990 were collected and preserved in 10% formalin solution for later analysis in the laboratory. Lengths and weights were obtained from these preserved samples.

Age Determination

Scale samples were taken from preserved coho salmon collected during the 1990 field season. These samples were aged by staff at the Canadian Department of Fisheries and Oceans Vancouver Scale and Morphology Laboratory according to the methods established by Clutter and Whitesel (1956). Additionally, all scales were examined for accessory or false checks and/or other scale anomalies which commonly result from temperature-related or other stresses (Clutter and Whitesel 1956).
IV. FIELD BEHAVIOUR EXPERIMENTS

Estuary and Stream Behaviour Observations

Between July 22-24, 1991, behavioural observations of wild juvenile coho salmon rearing in Springer Creek (stream resident) and the west pool of the natural tidal channel in the Salmon River estuary (estuary resident) were conducted. Observations were made using binoculars (8x magnification and 20 mm diameter objective lens) over 10 minute periods. Fish were observed in an area of 1 m² in 30 cm or less of water depth, with little overhead or instream cover and sand or pebble substrates. All of these sites were selected to optimize viewing ability. Only overt behaviours (approaches, charges, chases, and nips) were counted (Table II). The numbers of coho juveniles that could be reliably observed was approximately 10 individuals.

Stream Resident Observations

Observations were conducted in a large, slow-moving pool located approximately 1.4 km upstream of the confluence of Springer Creek and the Salmon River. This section of Springer Creek provided an excellent vantage point as well as high abundances of juvenile coho. A small wooden bridge 2.5 m above the stream surface provided an overhead viewing platform. Fish were observed for a total of eleven 10 minute periods.
Table II. A description of the types of behaviour observed for juvenile coho salmon during this study.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>Non-defined behaviour or no behaviour.</td>
</tr>
<tr>
<td>Swim Against Mirror</td>
<td>Any swimming motion with the nose of the fish touching the mirror (MIS experiment only).</td>
</tr>
<tr>
<td>Heads-Up Wig Wag</td>
<td>Erect dorsal and anal fins, accompanied by an opening of the mouth, a stiffening of the body, an exaggerated swimming motion, and head held higher than horizontal.</td>
</tr>
<tr>
<td>Heads-Down Wig Wag</td>
<td>Similar to heads-up wig wag but with head held lower than horizontal.</td>
</tr>
<tr>
<td>Horizontal Wig Wag</td>
<td>Similar to heads-up wig wag but with head and body in a horizontal position.</td>
</tr>
<tr>
<td>Dorsal Fin Erection</td>
<td>Extended dorsal and anal fins but no associated swimming activity.</td>
</tr>
<tr>
<td>Submission Display</td>
<td>Dorsal fin completely depressed.</td>
</tr>
<tr>
<td>Charge</td>
<td>Swimming directly towards a conspecific with an increased velocity.</td>
</tr>
<tr>
<td>Chase</td>
<td>Chasing and pursuing a fish past the point from where the fleeing fish was originally stationed (flow aquaria experiments only).</td>
</tr>
<tr>
<td>Nip</td>
<td>Bites or biting gestures which were aimed at another fish but may or may not have resulted in contact between the two fish (flow aquaria experiments only).</td>
</tr>
</tbody>
</table>
Estuary Resident Observations

Observations were conducted during low slack tide in the west pool of the natural tidal channel. The observations were conducted from an elevated vantage point approximately 3.0 m above the water surface. Fish were observed for a total of eleven 10 minute periods during low slack tide and continued until the tide change (from low slack to flood tide) when excessively high water flow limited visibility.

Statistical Analyses

Differences in behaviour exhibited by the two juvenile coho salmon populations, stream residents in Springer Creek and estuary residents in an upper Salmon River estuary tidal channel were compared using an independent sample t-test for each type of behaviour observed. Additionally qualitative differences in social organization and feeding were noted.

V. ENCLOSURE BEHAVIOUR EXPERIMENTS

Field Enclosure Observations

Enclosure experiments were conducted in Springer Creek between July 16 and August 24, 1991. Two 2.4 m by 2.4 m square enclosures were constructed and placed in Springer Creek approximately 1.5 km upstream of its confluence with the Salmon River. Each enclosure was divided to create two viewing arenas. Each enclosure was oriented in the stream so that flow through each compartment was approximately equal. A live box was attached to each enclosure so that fish could volitionally leave the enclosure and be captured (Fig. 6).

The enclosure was constructed from wood frame (5.1 cm x 10.2 cm) fence panels with dimensions of 0.7 m high and 2.4 m in length. Each panel was lined with 0.7 cm galvanized wire hardware cloth. It was further lined by 0.35
cm plastic Vexar mesh along the bottom 0.3 m of the fence panel to prevent the escape of small coho fry. Additionally, a 0.3 m strip of clear polypropylene plastic was attached to the bottom of each panel and covered with gravel in order to prevent the passage of small coho fry (Conlin and Tutty 1979). The live box was constructed of 0.95 cm plywood with dimensions 1.2 m long by 0.6 m wide by 0.6 m deep. Each live box included baffles to create reduce water velocities in an effort to minimize mortalities. Live boxes were attached to each enclosure by lengths (1.5 m to 3.0 m) of 10 cm diameter P.V.C. sewer pipe. Each of the two enclosures were placed in similar stretches of the stream and were located 100 m apart.

**Juvenile Coho Capture**

Stream resident coho were captured by pole seining in Springer Creek. Fish were held in live boxes for 24-48 hours prior to initiation of an experiment.

Stream emigrant coho were captured using a downstream fry fence installed and operated between June 1 and October 22, 1991. Emigrants were temporarily held in holding boxes for 24-48 hours prior to initiation of an experiment.

Estuary residents were captured using a beach seine in either the experimental channel or the natural tidal channel sites in the upper intertidal area of the Salmon River estuary. Fish were carefully transferred from brackish waters (salinity range: 7-12 °/oo) in insulated coolers. Large buckets were used to acclimate these fish to freshwater. Water salinity was slowly reduced to 0 °/oo over a 48 hour period and fish were monitored for symptoms of stress prior to initiation of an experiment. Individuals showing indications of stress were not used as experimental animals.
Figure 6. Diagram of enclosure used for behaviour observations.
Experimental Protocol

Each enclosure was stocked with 14 juvenile coho salmon yielding densities of approximately 5 fish per m$^2$. All fish were anaesthetized, weighed (to the nearest 0.01 gram), and then measured (fork length to the nearest 0.5 mm). All three eco-types of coho (stream residents, stream emigrants, and estuary residents) were tested alone in the enclosures to establish behavioural repertoires and emigration rates. Coho used in the behavioural observations averaged (SE) 48.8 (1.1), 44.1 (0.6), and 57.0 (0.9) FL mm for stream resident, stream emigrant, and estuary resident coho respectively. The eco-type, weight and fork length of fish that emigrated were recorded. Following the conclusion of each trial run, individuals remaining in the enclosure were removed by electroshocking and their fork lengths and weights were recorded.

Coho eco-types were paired up (7 fish of each type, 14 fish total per enclosure) and placed in the enclosures. Stream residents and estuary residents, stream residents and stream emigrants, stream emigrants and estuary residents were placed in the enclosures and emigration rates and behavioural interactions were monitored. Size of paired eco-types averaged (SE) 46.3 (1.1) and 47.6 (1.3) FL mm for emigrant and stream resident pairings and they were not significantly different (independent sample t test, $p = 0.43$). Size of the stream resident and estuary resident pairings averaged (SE) 57.6 (1.0) and 62.5 (1.2) FL mm and they were significantly (independent sample t test, $p = 0.003$). The size of the stream emigrant and estuary resident pairings averaged (SE) 46.6 (1.2) and 58.3 (1.0) respectively and they were also significantly different (independent sample t test, $p < 0.001$). The variation in size between the eco-types reflected the differences in size of individuals rearing in those respective environments. I selected experimental animals to be as close in body size as was possible given the large differences encountered. For
these paired experiments each eco-type of coho was marked using a Pan Jet dye inoculator and either Alcian blue or Alcian green dye. Marks were placed on either the upper lobe or the lower lobe of the caudal fin. These fin marks could be easily seen during behavioural observations and aided in distinguishing between the types of coho.

Behavioural observations were conducted from a 1.6 m high viewing platform situated 1.0 m downstream from the enclosure. Each observation period was 10 minutes in duration. The number and type of agonistic behaviours were recorded. When two types of coho were placed in the enclosure together, the aggressor eco-type was also noted. Observation periods were repeated 10 to 14 times per enclosure per day. Duration of each experiment was 2 to 4 days. After several pilot observation experiments only the downstream enclosures were used for behavioural observations due to the poor viewing conditions (canopy cover and light conditions) in the upper enclosures.

Statistical Analyses

The number of individual behaviours (i.e. approaches, charges, chases, and nips) were summed for all observation days and log (X+1) transformed to improve normality (Zar 1984) prior to testing using a one way analysis of variance (ANOVA). When appropriate the data were then subjected to Tukey's Honestly Significant Difference (HSD) test. The daily emigration rate of each eco-type and the size (FL) of migrants were compared using independent sample t tests.

VI. LABORATORY BEHAVIOUR EXPERIMENTS

Juvenile Coho Capture and Laboratory Rearing

On September 3, 1991, 50 stream resident coho salmon fry were collected from Springer Creek using a Coffelt backpack 12 volt DC
electroshocker. They were collected from a variety of stream habitats (pools, riffles, and glides) and transported live to laboratory facilities at the University of British Columbia.

On September 3, 1991, 27 stream emigrant coho salmon fry were collected using a downstream fry migration fence that had been installed on Springer Creek. These fry were transported live to the University of British Columbia. A further 10 stream emigrant coho were collected on October 22, 1991.

On September 15, 1991, 74 estuary resident coho salmon were collected using a 10 m by 1.5 m beach seine from the reference tidal channel of the Salmon River estuary. They were transported live back to the laboratory at the University of British Columbia.

Upon arrival at the laboratory, stream resident and emigrant coho juveniles were transferred directly to separate 85 L holding aquaria equipped with a water exchange system. Estuary fish were gradually acclimatized to freshwater by replacing saline water with de-chlorinated freshwater until a reduction in salinity of 2 °/oo per day was achieved. Estuary coho were transferred from 11 °/oo to freshwater over a four day period and then they were transferred to 85 L flow-through holding aquaria. Water temperature was not controlled and thus reflected naturally occurring temperature regimes (7-16 °C). The light schedule followed a natural photoperiod. Each day at 1400 h they were fed a mixture of frozen brine shrimp and blood worms.

**Data Recording**

All behaviours were recorded on a TRS 80, model 100, personal computer using an event recorder program. Data were entered through the keyboard and then transferred to an IBM compatible personal computer. The raw data were then converted into a useable format using a spreadsheet program.
VII. MIRROR IMAGE STIMULATION (MIS) EXPERIMENTS

Since many species of fish react to mirror images as if they were conspecifics of equal size and demeanor (Gallup 1968), mirror image stimulation (MIS) experiments were used to compare agonistic behaviour between the three eco-types of coho. MIS experiments were used to determine a baseline level of aggression for each of the three eco-types of juvenile coho salmon.

**Experimental Protocol**

A single fish was placed in a 13.2 L aquarium and allowed to acclimate for approximately 24 h before being tested. Each aquarium was lined with black plastic to keep fish isolated from surrounding aquaria and external distractions. One side of the aquarium was left open for observations (Fig. 7). Eight observation aquaria were used. The water temperature was measured following each day of observations. A natural photoperiod was maintained throughout the duration of the experiment. Aquaria were cleaned and disinfected between trial groups.

Fish from all three populations were observed for at least four consecutive days to minimize daily volatility of individual behaviour. During MIS tests a mirror was placed in an aquarium and after one minute, the responses/type and duration of behaviour (Table II) were recorded for a five minute period.

Coho size averaged (SE) 60.0 (2.5), 57.8 (2.9), and 89.3 (6.0) FL mm for stream resident, stream emigrant, and estuary resident coho respectively. Emigrant coho were observed between October 25-28, 1991 on a daily basis. Estuary coho were observed between October 31-November 3, 1991 and resident coho were observed between November 14-18, 1991.
Figure 7. Diagram of mirror image stimulation (MIS) aquarium. Diagram from Rosenau (1984).
**Statistical Analyses**

Principal components analysis (PCA) was used to summarize the duration of agonistic behaviours. Principal components analysis summarizes agonistic behaviours as one or more behavioural vectors. PCA can describe complex behavioural differences and is an efficient alternative to examining behavioural variation character-by-character (Huntingford 1976; Nishikawa 1985). For this analysis all wig wag displays (heads-up, heads-down, and horizontal) were summed and termed "lateral displays". Behavioural characters used in the PCA were swim against mirror, lateral display, dorsal fin erection, and submission displays.

PCA was performed on a total correlation matrix of the untransformed behavioural data set. The probability or quantile plot of the untransformed behavioural data matrix resulted in a linear relationship which suggested multivariate normality existed in the data set (Ryan and Joiner 1971; Filliben 1975). Log (X+1) transformations of the data did not improve normality and as a result the untransformed data set was used in the analysis.

A total correlation matrix method was used because of the variable response that the mirror image elicited from some experimental animals. This variability in response to their mirror image resulted in unequal variances among the behavioural characters (lateral display, dorsal fin erection, submission displays etc.). When unequal character variances exists it is recommended that PCA on a correlation rather than a covariance matrix should be employed (Haas 1988). The correlation matrix standardizes the data to mean zero and unit standard deviation such that the character contributions are more equal (Davis and Baker 1974; Thorpe 1976, 1980, 1983; Pimentel 1981; Reyment et al. 1984). Similar results were nonetheless obtained using a total covariance matrix. The similarity between these two PCA techniques
suggests that my results are realistic.

Principal component scores for the first three component axes (PC1, PC2, and PC3) were subjected to a two way repeated measures analysis of variance with eco-type, observation day, and the interaction between eco-type and day as the main effects. *A posteriori* means tests were conducted using Tukey's "Honestly Significant Difference" (HSD) test where applicable.

VIII. FLOW AQUARIA ECO-TYPE COMPARISON EXPERIMENTS

Experimental flow aquaria were used to test dominance among the three eco-types of juvenile coho salmon under lotic conditions. Flow aquaria were constructed from 13.2 L glass aquaria as described by Gee and Bartnik (1969) (Fig. 8). The volume of these flow aquaria was 6.75 L. Each aquarium provided a single viewing arena for pairwise comparisons of dominance among the three eco-types of coho salmon.

**Experimental Protocol**

Two fish, each a different eco-type, were placed in a flow aquarium and allowed to acclimate for a 24 hour period. Prior to placement in the aquarium each individual was marked using a Pan Jet dye inoculator and either Alcian blue or Alcian green (Hart and Pitcher 1969) to ensure eco-types were distinguishable. Behavioural observations were conducted for 10 minute periods on the first two days of the four day experiment duration. The number and type of aggressive acts as well as the aggressor were recorded. At the end of the 10 minute observation period the "winner" of the agonistic encounter was scored. In some instances neither individual was clearly dominant and the agonistic encounter was scored a draw. On the last two days of each experiment (observation days three and four) only the dominance hierarchy within each aquarium was determined and the levels of agonistic behaviour
were not documented. Four criteria were used to determine the winner of the encounter. Three criteria (colour, nipping, and dorsal fin position) were the same as those of Rosenau (1984) and the fourth (position within the aquaria) was ranked by me after several observations (Table III). The water temperature was recorded following each observation period.

Figure 8. Diagram of flow aquaria used in pairwise eco-type behavioural experiments. 1 = deflector plate; 2 = air source; 3 = false bottom; 4 = screen.
Observations occurred between December 4-20, 1991. On December 4, individuals from the stream resident and the stream emigrant populations were paired with similar sized fish. Coho size averaged (SE) 52.4 (1.2) and 52.1 (1.5) FL mm for stream resident and stream emigrant coho respectively. Paired individuals were not significantly different in size (independent sample t test; p = 0.39). On December 10, individuals from the stream resident and the estuary resident populations were paired. Unfortunately, the largest of the stream residents was still much smaller than the smallest of the estuary resident population.

Table III. Four criteria used to determine the winner of an agonistic encounter.

<table>
<thead>
<tr>
<th>Criterion</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colour</td>
<td>Dominant salmonids are lighter along sides of body whereas submissive individuals are much darker (Newman 1956, Keenleyside and Yamamoto 1962).</td>
</tr>
<tr>
<td>Nipping</td>
<td>Dominant individuals will more often nip submissives than vice versa (Newman 1956).</td>
</tr>
<tr>
<td>Dorsal Fin Position</td>
<td>Submissive individuals usually drop their dorsal fin lower than dominant individuals.</td>
</tr>
<tr>
<td>Submission</td>
<td>Usually includes the depression of the anal fin and folding of the caudal fin (Newman 1956).</td>
</tr>
<tr>
<td>Position in Aquaria</td>
<td>Personal observations suggest that dominant coho prefer to hold a position near the air stone end of aquaria and force submissive fish to remain in the areas of faster moving water.</td>
</tr>
</tbody>
</table>
Estuary coho were significantly larger than their stream resident con-specs, mean (SE) 75.4 (2.0) and 64.1 (1.9) FL mm (independent sample $t$ test; $p = 0.01$). On December 15, individuals from the stream emigrant and the estuary resident populations were paired. Again, matching fish of equal size was very difficult due to the large size of the estuary coho. Estuary coho were significantly larger than their stream emigrant con-specs, mean (SE) 73.5 (4.5) and 65.0 (5.0) FL mm (independent sample $t$ test; $p = 0.03$).

In the instances when larger estuary reared coho were paired with stream coho, I assumed that the size differences did not limit the behavioural comparisons. Such differences are very likely to occur in the wild as it is common for estuary reared coho to return to stream habitats in late summer to overwinter (Murphy et al. 1984; Tom G. Brown, Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

**Statistical Analyses**

Due to small sample sizes, low levels of observed aggression in each paired trial, and relatively constant levels of aggression between observation day 1 and 2, the behaviour data from these two days were pooled. For similar reasons all agonistic behaviours were summed and only the total agonistic display was analyzed. To improve normality the data were log $(X+1)$ transformed (Zar 1984). The levels of aggression exhibited by each eco-type were compared using an independent sample $t$ test.

The chi square goodness of fit test was used to determine whether or not one eco-type was clearly dominant during each observation day of a paired experiment. The proportion of decided comparisons were compared to the null hypothesis that each eco-type should win 50% of the encounters. Chi square tests were conducted on data for each observation day.
RESULTS

I. TEMPERATURE AND SALINITY MEASUREMENTS

Seasonal Changes in Temperature and Salinity

In both 1989 and 1990, the daily peak surface water temperature in the experimental channel was recorded in early August. The water temperature ranged from $16.5$ to $8.0 \, ^\circ C$ (August-December) during 1989. In 1990, the water temperature ranged from $21.0$ to $8.0 \, ^\circ C$ (August-November) (Fig. 9).

Surface salinity varied considerably during the study. Lower surface salinities coincided with freshet events, but also fluctuated with the tidal cycle. In 1989, surface salinities ranged from $2.5$ to $12.0 \, ^\circ/00$ and in 1990, from $7.5$ to $33.5 \, ^\circ/00$ (Fig. 9). Surface salinities were lowest during freshet and highest following periods of low river discharge.

Comparison of Experimental and Natural Channels

In 1990, surface temperatures and surface salinities of the experimental channel and the natural channel were compared. The observed temperatures were very similar in the two habitats except during early August when there were higher water temperatures in the natural tidal channel habitat (Fig. 10). This was probably due to solar heating of the shallow water (< 1 m) in the pools during low tide.

The surface salinities recorded in the two habitats exhibited a similar pattern but the salinity of the experimental channel appeared to be much more variable than the natural tidal channel habitat (Fig. 10). This was probably due to nearly complete flushing of the natural tidal channel during ebbing tides.
Figure 9. Seasonal changes in experimental channel surface water temperature and surface salinity, 1989 (upper) and 1990 (lower).

**Temperature and Salinity Profiles**

In July 1990, the waters of the experimental channel exhibited only a slight temperature gradient during both high (Fig. 11, panel A) and low tides (Fig. 11, panel B). During the same low tide period the Salmon River mainstem was isothermal and exhibited no salinity gradient (Fig. 11, panel C). Salinities in the experimental channel were much higher than those in the Salmon River mainstem. At high tide, salinities in the experimental channel ranged from 21-25 o/00 (panel A). At low tide, the channel had a pronounced freshwater lens approximately 15-20 cm deep, resulting in a strong vertical salinity gradient (panel B).
Temperature and salinity gradients in the experimental and natural tidal channels were also measured on October 22, 1990 (Fig. 12, panels A and B). The salinity and temperature profiles of the experimental channel (panel A) differed from those of the natural channel (panel B). The experimental channel exhibited a strong salinity gradient and a weak thermal gradient (panel A). At the same time the natural tidal channel was essentially isothermal and isohaline (Fig. 12, panel B).
Figure 11. Water temperature and salinity profiles of the experimental channel and the Salmon River mainstem. Experimental channel high tide (A), experimental channel low tide (B) and Salmon River mainstem low tide (C).

This probably reflected differences in the physical characteristics of the experimental and the natural tidal channels. Since the experimental channel never completely dewatered, saline water probably became entrained in the basin of the experimental channel creating a strong and relatively stable salinity gradient. The depth of the freshwater lens in the experimental channel was much deeper (1.4 m) than the earlier in the summer (0.2 m).
Following the first fall freshet on October 30, 1990 the strong salinity and weak temperature gradients in the experimental channel were disturbed and the temperature and salinity profiles resembled those in the natural tidal channel (Fig. 12, panels C and D). The strong flushing effects of the freshet probably combined with cooler water temperatures to break down both the salinity and temperature gradients until complete mixing and flushing of the experimental channel waters occurred.

**Water Circulation Patterns**

Since the experimental channel had three inlet/outlets, the water circulation pattern was complex. The flow pattern was determined by the elevation of the three sills. The west inlet had the lowest sill elevation (-2.0 m) and when the experimental channel flooded the water first entered through the west inlet. The two eastern inlets were slightly higher (-1.5 m) and resulted in water first breaching the southeast inlet followed by the northeast inlet. Initially, the water flowed from west to east until the water level breached the two eastern sills at which time the direction of flow reversed.

On a falling tide dewatering of the experimental channel resulted in the northeast sill being exposed first followed by the southeast sill and finally the west sill. Initially, the water exited the experimental channel via all three outlets with no clear pattern of flow developing. When the two eastern sills became exposed the direction of flow was predominantly from east to west with all the remaining water exiting through the west outlet. At tidal heights less than approximately 2.0 m all three sills were exposed and the experimental channel was an isolated body of water.

**II. ESTUARINE RESIDENCE OF JUVENILE COHO SALMON**

**Seasonal Changes in Juvenile Coho Salmon Abundance**

In both 1989 and 1990 the trends in juvenile coho salmon abundance in the upper intertidal portion of the estuary were similar (Fig. 13). The index of coho abundance was lowest during May and June but increased through the summer until it peaked in August in 1989 and in late July in 1990 (Fig. 13, panel B). The difference in the maximum abundance estimate between years was probably due to differences in sampling effort as sampling intensity was greater in 1990 than in 1989, but the seasonal changes in abundance should be independent.
**Estuary Coho Salmon Population and Density Estimates**

Juvenile coho salmon densities were low for the experimental channel in 1989 and 1990, rarely exceeding 0.6 fish per m$^2$. The maximum densities observed were nearly identical in both years of the study (Fig. 13, panel A). The density estimates ranged from 0.05 - 0.69 fish per m$^2$ of wetted surface area in 1989. In 1990, coho densities were similar and ranged from 0.03 - 0.68 fish per m$^2$ of wetted surface area. In both years the maximum recorded coho densities occurred at similar times (early August in 1989 and late July in 1990) (Fig. 13, panel A).

There were marked differences in the abundance of coho and chinook salmon inhabiting the experimental channel during the course of the study. The maximum observed density of juvenile coho salmon was almost threefold greater than the maximum observed chinook densities in both years (Atagi 1992 MS).

**High Tide and Low Tide Density Estimates**

Juvenile coho salmon densities were estimated in both the experimental and natural tidal channel habitats between June and October, 1990. A comparison of high and low tide density estimates indicated that coho numbers often (6 out of 10 cases) were greater during high tides than during low tides (Fig. 14), but 95% confidence limits of the population estimates frequently overlapped suggesting that the differences were not statistically significant. These comparisons are limited by the precision of the mark-recapture and depletion methods used. None-the-less this suggested that fish moved into both tidal channel habitats during flooding tides. The one exception to this finding occurred in the natural channel during the July 25-August 1 sampling period.
Figure 13. 1989 and 1990 low tide coho density estimates (number per m$^2$) (panel A) and abundance indices (panel B) for the experimental channel. The bars represent 95% confidence limits and asterisks indicate coho present but too few to estimate (panel A).
Figure 14. Seasonal changes in high and low tide coho density estimates (number per m²) for the experimental and two sections of the natural tidal channels (June to October 1990). Bars represent the upper half of the 95% confidence limits. Asterisk (*) indicates that coho were present but too few to estimate and plus (+) indicates that populations were not censused.

Experimental and Natural Channel Density Estimates

Early in the season (June 26-July 6, 1990), densities of coho juveniles were considerably greater in the natural channel than in the experimental channel habitat. However, by the July 25-August 1 sampling period the pattern of habitat use had shifted from the natural channel to the experimental channel habitat (Fig. 14). High water temperatures (near lethal) in the natural channel habitat during the dewatered periods may have contributed to the shift in habitat use. During this period, low tide natural channel water temperatures as high as 26.0 °C were recorded while low tide experimental channel...
temperatures were only 13.0 °C. By late August the densities of coho salmon in the experimental channel and the natural tidal channel dropped to levels observed earlier in the summer (Fig. 14). Late September density estimates indicated that coho salmon numbers in both habitats continued to decline. This decline corresponded to the onset of the annual fall freshets. Following these freshet events juvenile coho were rarely found in the upper intertidal habitats.

In most instances the natural channel habitat supported higher densities of juvenile coho salmon than did the experimental channel. However, this does not accurately represent the absolute number of fish rearing in the experimental channel as it was almost four times larger, by area, than the natural tidal channel. Although the experimental channel reared lower densities of fish, the absolute number of fish residing there at times was very high. For example, on July 25, 1990, some 8,888 coho juveniles were estimated to be rearing in the experimental channel while the highest estimated number of coho juveniles rearing in the natural channel was only 1,106 individuals on June 24, 1990 (Table IV). Although the experimental channel rearing densities may be low relative to the natural channel, the absolute contribution of this man-made habitat to the estuary coho population may be much higher.
Table IV. Summary of 1990 juvenile coho salmon population estimates for the experimental and natural tidal channel habitats of the Salmon River estuary, Vancouver Island.

<table>
<thead>
<tr>
<th>Date</th>
<th>Tide</th>
<th>Population Estimate</th>
<th>Water Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Experimental Channel</td>
<td>Natural Channel</td>
</tr>
<tr>
<td>Jun 24</td>
<td>high</td>
<td>1,388</td>
<td>1,106</td>
</tr>
<tr>
<td>Jun 26</td>
<td>low</td>
<td>*</td>
<td>404</td>
</tr>
<tr>
<td>Jul 25</td>
<td>high</td>
<td>8,888</td>
<td>65</td>
</tr>
<tr>
<td>Jul 26</td>
<td>low</td>
<td>3,100</td>
<td>64</td>
</tr>
<tr>
<td>Aug 24</td>
<td>high</td>
<td>2,835</td>
<td>--</td>
</tr>
<tr>
<td>Aug 25</td>
<td>low</td>
<td>1,461</td>
<td>198</td>
</tr>
<tr>
<td>Oct 2</td>
<td>high</td>
<td>491</td>
<td>35</td>
</tr>
<tr>
<td>Sep 27</td>
<td>low</td>
<td>114</td>
<td>34</td>
</tr>
</tbody>
</table>

* coho present but too few to estimate.

**Estuary Coho Salmon Residence Time**

In 1989, recaptured juvenile coho salmon had a mean (SE) residence time of 13.4 (0.97) days (Table V). In 1990, coho recaptured in the experimental channel had a mean (SE) residence time of 9.3 (1.22) days (Table VI). The 1990 estimate of residence time of the experimental channel was significantly lower than the 1989 estimate (p < 0.001, Mann-Whitney U Test). In 1990, the mean residence time of all 325 recaptured coho juveniles regardless of capture site was significantly lower (7.1 days, SE 0.74 days, p < 0.001, Mann-Whitney U test; Table VII) than the 1989 estimate for coho captured in the experimental channel (13.4 days, SE 0.97 days; Table V).
Table V. Summary of 1989 juvenile coho salmon releases, recaptures, and residence times of the experimental channel.

<table>
<thead>
<tr>
<th>Release Month (Number)</th>
<th>Number Released</th>
<th>Number Recaptured</th>
<th>Mean Residence Time (d) and (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June (3)</td>
<td>78</td>
<td>4</td>
<td>10.5 (5-16)</td>
</tr>
<tr>
<td>July (5)</td>
<td>742</td>
<td>80</td>
<td>13.5 (1-44)</td>
</tr>
<tr>
<td>August (2)</td>
<td>635</td>
<td>6</td>
<td>14.0 (14)</td>
</tr>
<tr>
<td>Overall 1989</td>
<td>1,455</td>
<td>90</td>
<td>13.4 (1-44)</td>
</tr>
</tbody>
</table>

Table VI. Summary of 1990 juvenile coho salmon releases, recaptures, and residence times of the experimental channel.

<table>
<thead>
<tr>
<th>Release Period (Number)</th>
<th>Number Released</th>
<th>Number Recaptured Experimental Channel</th>
<th>Mean Residence Time (d) and (Range)</th>
<th>Number Recaptured Natural Channel</th>
<th>Mean Residence Time (d) and (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June (1)</td>
<td>7</td>
<td>0</td>
<td>--</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td>July (4)</td>
<td>938</td>
<td>79</td>
<td>11.4 (1-70)</td>
<td>11</td>
<td>25.5 (3-90)</td>
</tr>
<tr>
<td>August (3)</td>
<td>806</td>
<td>32</td>
<td>6.2 (1-30)</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td>September (1)</td>
<td>68</td>
<td>16</td>
<td>5.0 (5)</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td>October (2)</td>
<td>349</td>
<td>1</td>
<td>2.0 (2)</td>
<td>6</td>
<td>3.7 (2-7)</td>
</tr>
<tr>
<td>Overall 1990</td>
<td>2,168</td>
<td>128</td>
<td>9.3 (1-70)</td>
<td>17</td>
<td>17.8 (2-90)</td>
</tr>
</tbody>
</table>
Table VII. Summary of 1990 juvenile coho salmon releases, recaptures, and residence times of the natural channel.

<table>
<thead>
<tr>
<th>Release Period (Number)</th>
<th>Number Released</th>
<th>Number Recaptured Natural Channel</th>
<th>Mean Residence Time (d) (Range)</th>
<th>Number Recaptured Experimental Channel</th>
<th>Mean Residence Time (d) (Range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June (3)</td>
<td>391</td>
<td>154</td>
<td>1.0 (1)</td>
<td>7</td>
<td>20.9 (11-59)</td>
</tr>
<tr>
<td>July (0)</td>
<td>0</td>
<td>0</td>
<td>--</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td>August (1)</td>
<td>135</td>
<td>10</td>
<td>34.1 (32-39)</td>
<td>2</td>
<td>37.0 (37)</td>
</tr>
<tr>
<td>September (1)</td>
<td>31</td>
<td>3</td>
<td>7.0 (7)</td>
<td>2</td>
<td>26.0 (26)</td>
</tr>
<tr>
<td>October (2)</td>
<td>92</td>
<td>1</td>
<td>18.0 (18)</td>
<td>1</td>
<td>1.0 (1)</td>
</tr>
<tr>
<td>Overall 1990</td>
<td>649</td>
<td>168</td>
<td>3.2 (1-39)</td>
<td>12</td>
<td>22.8 (1-59)</td>
</tr>
<tr>
<td>Overall for both</td>
<td>2,817</td>
<td>325</td>
<td>7.1 (1-90)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Experimental and</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natural Channels</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

When the 1990 data were separated into the two habitats (experimental and natural tidal channels) significant differences in the estimated residence times were found. Coho spent a longer residence period in the experimental channel (9.3 days, SE 1.22 days) than they spent in the natural tidal channel (3.2 days, SE 0.61 days; p < 0.001, Mann-Whitney U test; Table VIII).
Table VIII. Mean residence time of juvenile coho salmon exhibiting site fidelity and exhibiting no site fidelity from two sample sites (experimental and natural tidal channel) from the Salmon River estuary, Vancouver Island (1990).

<table>
<thead>
<tr>
<th>Site Fidelity</th>
<th>No Site Fidelity</th>
<th>Difference in Fidelity (Mann-Whitney U test)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experimental Channel</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9.3 d (1.22)</td>
<td>17.8 d (6.58)</td>
<td>p = 0.054 NS</td>
</tr>
<tr>
<td><strong>Natural Channel</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.2 d (0.61)</td>
<td>22.8 d (4.50)</td>
<td>p &lt; 0.001 SIGN</td>
</tr>
<tr>
<td><strong>Difference Between Habitats</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p &lt; 0.001 SIGN</td>
<td>p = 0.050 NS</td>
<td></td>
</tr>
</tbody>
</table>

**Estuary Coho Site Fidelity**

In 1990, movement patterns were determined for juvenile coho salmon. Marked individuals were frequently recaptured at the same site as they were initially captured and marked in (experimental channel 88.3% and natural channel 93.3%; Table IX). Juvenile coho salmon exhibited a high degree of site fidelity regardless of capture site.

When individuals were recaptured at a site other than their initial capture site they usually exhibited a longer period of residency in the sampling area (Table IX). Coho initially captured in the experimental channel and subsequently recaptured in the experimental channel (i.e. individuals exhibiting site fidelity) had a mean residence time of 9.3 days whereas individuals that were recaptured in the natural channel (i.e. exhibiting no site fidelity) had a longer mean residence time (17.8 days), but this difference was not statistically significant (p = 0.054, Mann-Whitney U test; Table VIII) because of small sample size.
sizes and high individual variability. Coho juveniles marked in the natural channel exhibited a similar trend in residence times. Individuals exhibiting site fidelity there had a significantly shorter residence period (3.2 days) than individuals which did not exhibit fidelity to that site (22.8 days; p < 0.001, Mann-Whitney U test; Table VIII). The residence times of fish exhibiting no site fidelity to either the experimental channel (17.8 days) or the natural channel (22.8 days) were not significantly different (p = 0.050, Mann-Whitney U test; Table VIII) although the differences were nearly significant, suggesting that individuals which remained in the area for an extended period of time moved more freely between the two habitats.

Table IX. Summary of recaptured juvenile coho salmon from the experimental and natural tidal channels of the Salmon River estuary, Vancouver Island (1990).

<table>
<thead>
<tr>
<th></th>
<th>Experimental Channel</th>
<th>Natural Channel</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total Number Marked</strong></td>
<td>2,168</td>
<td>649</td>
</tr>
<tr>
<td><strong>Total Number Recaptured</strong></td>
<td>145</td>
<td>180</td>
</tr>
<tr>
<td><strong>Percentage Recaptured</strong></td>
<td>6.7 %</td>
<td>27.7 %</td>
</tr>
<tr>
<td><strong>Percentage of Recaptures Exhibiting Site Fidelity</strong></td>
<td>88.3 %</td>
<td>93.3 %</td>
</tr>
<tr>
<td><strong>Mean Residence Time (SE)</strong></td>
<td>9.3 d (1.22)</td>
<td>3.2 d (0.61)</td>
</tr>
<tr>
<td><strong>Percentage of Recaptures Exhibiting No Site Fidelity</strong></td>
<td>11.7 %</td>
<td>6.7 %</td>
</tr>
<tr>
<td><strong>Mean Residence Time (SE)</strong></td>
<td>17.8 d (6.58)</td>
<td>22.8 d (4.50)</td>
</tr>
</tbody>
</table>
Length Frequency Distributions

In both years, coho smolts (1+ and older juveniles) were present from the first sampling date (late May) until early July (Figs. 15, 16). Seasonally extended sampling in 1990 (Fig. 16) indicated the upper intertidal habitats were predominantly inhabited by young-of-the-year (0+ year old) coho fry up until the time of the first fall freshets which began in October of that year.

The seasonal change in mean fork length of coho juveniles was unclear (Fig. 17) due to the confounding effects caused by the presence of two or more age classes in the population (Fig. 15 and Fig. 16). Scale aging data was used to examine changes in fork lengths of both 0+ and 1+ year olds.
Figure 15. Length frequency distributions of juvenile coho salmon captured in the upper intertidal portion of the Salmon River estuary (June 8, 1989 to August 24, 1989).
Figure 16. Length frequency distributions of juvenile coho salmon captured in the upper intertidal portion of the Salmon River estuary (May 23, 1990 to October 23, 1990).
Figure 17. Seasonal change in mean juvenile coho salmon nose to fork length from the Salmon River estuary in 1989 and 1990. Bars represent two standard errors.

Estuary Coho Salmon Size and Age

Age determination of coho juveniles in the Salmon River estuary showed that not all individuals were 0+ years old. All sampling periods (June-October 1990) contained some 1+ year old fish in the random sample even though some of the length frequency distributions indicated the presence of only a single age class (Fig. 16). In June, the catch consisted mainly of 0+ year old fish with only a few 1+ year olds being captured. The proportion of 0+ year old fish in the catch declined throughout the summer months until the fall when the catch consisted predominantly of 1+ year old fish (Fig. 18, upper).

Of the 97 readable 1+ year old scales examined, only two scales were noted as having obscure annuli. Scales from the remaining 95 individuals had well defined annuli and exhibited growth following the first winter as indicated by the presence of circuli following the winter check (first annulus).
Furthermore no accessory or false checks were found in any of the scale samples so reliability of aging was probably high.

The mean fork length of the individuals in these two age classes indicated that 0+ year old fish were significantly smaller than 1+ year olds in June, July, and August, 1990 (p < 0.001, p < 0.002, p < 0.002, two-sample t test, respectively). However, the differences in body size diminished as the season progressed until September and October when the size differences between 0+ and 1+ year old fish were not statistically significant (p = 0.750 and p = 0.307, two-sample t test, respectively) (Fig. 18, lower).

Figure 18. Seasonal changes in proportion (upper) and mean fork length (lower) of 0+ and 1+ year old coho salmon captured in the Salmon River estuary in 1990. Sample sizes (n) are given (upper) and bars (lower) represent one standard error.
III. ESTUARY AND STREAM RESIDENT BEHAVIOUR OBSERVATIONS

The level of aggression (approaches, chases, and total aggressive acts) was significantly higher in the stream coho population than in the estuary population (Table X). Although the number of nips was not statistically tested, the data suggested that nips occurred more frequently under stream conditions than under estuarine conditions (Table X). Since no charges were observed during any of the observation periods it was not tested.

Table X. Comparison of mean number of aggressive acts (ten minute observation periods) exhibited by a Salmon River estuary and an upriver stream population (Springer Creek) of juvenile coho salmon (*Oncorhynchus kisutch*).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Salmon River Estuary Population (SE)</th>
<th>Springer Creek Population (SE)</th>
<th>Independent Sample t-Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approach</td>
<td>0.55 (0.25)</td>
<td>2.25 (0.62)</td>
<td>p = 0.020 SIGN</td>
</tr>
<tr>
<td>Chase</td>
<td>0.55 (0.21)</td>
<td>6.08 (1.11)</td>
<td>p &lt; 0.001 SIGN</td>
</tr>
<tr>
<td>Nip</td>
<td>0 (-- )</td>
<td>1.42 (0.37)</td>
<td>NOT TESTED</td>
</tr>
<tr>
<td>Charge</td>
<td>0 (-- )</td>
<td>0 (-- )</td>
<td>NOT TESTED</td>
</tr>
<tr>
<td>Total Number of Aggressive Acts</td>
<td>1.09 (0.28)</td>
<td>9.75 (1.59)</td>
<td>p &lt; 0.001 SIGN</td>
</tr>
<tr>
<td>Feeding Attempts</td>
<td>18.18 (6.45)</td>
<td>76.75 (15.39)</td>
<td>p = 0.003 SIGN</td>
</tr>
</tbody>
</table>
Throughout the study several qualitative differences in the behaviour of coho rearing in the estuary channel (natural) and the stream (Springer Creek) were observed. As already shown, coho juveniles rearing in Springer Creek were far more aggressive than conspecifics rearing in the estuary. But other differences were also observed in the social organization of individuals within the two habitats (Table XI). In the natural tidal channel, juvenile coho were often observed in small groups of 10-20 individuals, which appeared to be organized into "loose" aggregations. In contrast, coho in Springer Creek defended and maintained individual territories as they commonly returned to their holding station following a feeding attempt or a display towards a conspecific. In both habitats coho consistently oriented themselves to face directly into the current except in the tidal channel when water flow was absent. In this instance, juvenile coho oriented themselves in a less organized manner where individuals generally swam parallel to the shoreline but not in a consistent direction (Table XI). Differences in foraging were also observed between the two coho populations. Stream residents examined or investigated nearly all drifting food or non-food items that entered the observation quadrat and apparently had higher feeding rates than their estuary counterparts (Table X). Estuary residents made significantly fewer feeding attempts than stream coho possibly in response to the limited water flow in the tidal channel. However, when the tide changed and the water began to flow the number of feeding attempts increased sharply.
Table XI. Qualitative differences in the behaviour of juvenile coho rearing in the Salmon River estuary and a tributary of the Salmon River (Springer Creek).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Estuary Coho (Salmon River Estuary)</th>
<th>Stream Coho (Springer Creek)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Number of Aggressive Acts</td>
<td>few</td>
<td>many</td>
</tr>
<tr>
<td>Social Organization</td>
<td>&quot;loose&quot; aggregations</td>
<td>territorial</td>
</tr>
<tr>
<td>Maintenance of Position</td>
<td>when flow is absent, orient in random direction but when flow commences, coho orient themselves facing towards current</td>
<td>hold position and always orient facing towards current</td>
</tr>
<tr>
<td>Foraging</td>
<td>when flow is absent, feed at low levels but as flow increases, feed at elevated levels (e.g. during the tide change)</td>
<td>feed constantly</td>
</tr>
</tbody>
</table>

IV. ENCLOSURE BEHAVIOUR EXPERIMENTS

Behavioural Observations

The results of the field enclosure experiments (Fig. 19) clearly indicated that there were differences in the levels of aggression exhibited by the three eco-types (resident, emigrant, estuary) and their corresponding pairwise comparisons. When all agonistic behaviours and all observation periods were summed the mean number of total agonistic displays exhibited by the six trial groups were significantly different (one way ANOVA, p < 0.001). Tukey's Post Hoc Honestly Significant Difference (HSD) test indicated that estuary and emigrant coho exhibited higher levels of aggression than resident coho but they did not significantly differ from each other. The resident-emigrant and the
resident only trials exhibited intermediate levels of aggression. The final two trials, the emigrant-estuary and the estuary-resident trials, showed lower levels of agonistic behaviour than the previous trials and they were also significantly different from each other. A summary of the Tukey HSD test results is given as follows:

\text{estuary only} = \text{emigrant only} > \text{resident only} = \text{emigrant-resident} > \text{emigrant-estuary} > \text{estuary-resident}

Figure 19. Mean number of agonistic displays exhibited by stream resident (Resident), stream emigrant (Emigrant), and estuary resident (Estuary) ecotypes of coho salmon during stream enclosure experiments. Paired comparisons stream emigrant and estuary resident (Emi-Est), stream resident and stream emigrant (Res-Emi), and estuary resident and stream resident (Est-Res) are also shown. Bars represent 2 standard errors (SE).
In three of the six trials there were significant increases in the number of aggressive displays with each observation day (Fig. 20). The estuary only, emigrant-estuary, and the estuary-resident trials all exhibited increasing levels of aggression (one way ANOVA, p = 0.02, p = 0.01, and p = 0.01 respectively). The emigrant only and resident-emigrant trials showed no apparent trend however results from the resident only trial suggests a slight increase in aggression with time (one way ANOVA, p = 0.31, p = 0.19, and p = 0.08 respectively).

In most instances, estuary coho appeared to exhibit all the behavioural attributes that their stream rearing counterparts did. Surprisingly, they exhibited higher levels of aggression than their stream conspecifics and the levels of aggression in enclosures with estuary coho increased significantly with observation day. This pattern of increasing aggression with observation day was not observed in the stream resident only or the stream emigrant only enclosures.

**Paired Comparison of Eco-types**

An examination of the paired eco-type comparisons indicated that there were differences in the levels of aggression exhibited by each eco-type (Fig. 21). The level of aggression exhibited by the stream residents and stream emigrants in the resident-emigrant trial (RES1 versus EMG1) was not statistically different (Fig. 21; independent sample t test, p = 0.49). However, the trials involving estuary coho (EST2 versus EMG2 and EST3 versus RES3) indicated that estuary coho were significantly less aggressive than either emigrants (EMG2) or residents (RES3) (independent sample t test, p = 0.002 and p = 0.001 respectively).
These experiments suggest that both resident and emigrant coho were much more aggressive than estuary coho and were able to behaviourally subordinate their larger estuary counterparts. When similarly sized stream resident and stream emigrant coho were grouped together neither eco-type was able to dominate the other.
Figure 21. Comparison of the mean total number of agonistic displays per observation period for the mixed eco-type enclosure experiments. Experiment 1, stream resident and stream emigrant pair (RES1 vs. EMG1); experiment 2, estuary resident and stream emigrant pair (EST2 vs. EMG2); and experiment 3, estuary resident and stream resident pair (EST3 vs. RES3). Bars represent the standard error of the mean value.

Emigration Rates

Throughout the duration of each experiment, coho juveniles volitionally leaving the enclosures were defined as "migrants" and upon capture they were identified to eco-type of origin and measured. These migrant individuals should not be confused with the experimental eco-type designated as "stream emigrants".

The emigration rate appeared to vary with eco-type but it was not statistically significant due to the small migrant sample sizes (one way ANOVA.
p = 0.66; Fig. 22). Stream resident (Resident), stream emigrant (Emigrant), and resident-emigrant (Res-Emi) pairs had lower mean emigration rates than the estuary only (Estuary), the emigrant-estuary (Emi-Est), or the resident-estuary (Res-Est) pairs but variability was high. It is interesting to note that enclosures with estuary reared coho appeared to have higher rates of emigration (Fig. 22).

**Paired Comparison of Eco-types**

The comparison of the number of migrants of each eco-type in the paired eco-type experiments also was limited by small sample sizes and as a result pairwise comparisons using an independent sample t test were not statistically significant for any of the experiments. Nevertheless some trends were evident in the data (Fig. 23). When paired, stream emigrants (EMG1) seemed more likely to emigrate than stream residents (RES1). When estuary resident coho (EST2) and stream emigrant coho (EMG2) were paired it appeared that estuary coho were more likely to emigrate than stream emigrant coho (Fig. 23). This result is not surprising given the fact that estuary coho were significantly less aggressive than emigrants during these experiments (Fig. 21). Trials in which stream resident (RES3) and estuary resident (EST3) coho were grouped together were less conclusive (Fig. 23).
Figure 22. Comparison of the mean number of migrants per observation day for the stream enclosure experiments. Stream resident only (Resident), stream emigrant only (Emigrant), estuary resident only (Estuary), emigrant-estuary pair (Emi-Est), resident-emigrant pair (Res-Emi), and estuary-resident pair (Est-Res). Bars represent standard errors of the mean value.
Figure 23. Comparison of the mean number of migrants per observation day in the paired eco-type enclosure experiments. Experiment 1, stream resident and stream emigrant pair (RES1 vs. EMG1); experiment 2, estuary resident and stream emigrant pair (EST2 vs. EMG2); and experiment 3, estuary resident and stream resident pair (EST3 vs. RES3). Bars represent the standard error of the mean value.

Size of "Migrants"

The mean size (FL) of migrants was compared with that of individuals stocked in the enclosures. However rates of emigration were low in all experiments (0.4-0.8 migrants per day) which limited the power of the statistical analyses (Table XII). In four of the five replicates, the migrants from the resident only enclosures were equal to or smaller than the mean size of the individuals initially stocked in the enclosure. Replicate 1 had a large enough sample size to conduct a t test on mean size and it suggested that migrant coho tended to be smaller than their stocked counterparts (p = 0.08; Table XII). In two of the three replicates, migrants from the emigrant only enclosures were similar in size or smaller than their stocked counterparts (Table XII). This pattern was less apparent in the estuary only enclosures.
Table XII. Comparison of the mean size FL (SE) of individuals stocked into stream enclosures and the mean size FL (SE) of migrants from the enclosure (resident only, emigrant only, and estuary only trials). Standard errors were calculated and an independent sample $t$ test was attempted when the number of migrants was greater than 2.

<table>
<thead>
<tr>
<th>ECO-TYPE</th>
<th>REPlicate</th>
<th>MEAN FORK LENGTH STOCKED FL (SE) (mm)</th>
<th>MEAN FORK LENGTH MIGRANTS FL (SE) (mm)</th>
<th>INDEPENDENT SAMPLE $t$ TEST (one tailed) P VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resident</td>
<td>1</td>
<td>46.0 (1.1)</td>
<td>43.5 (1.4)</td>
<td>0.08</td>
</tr>
<tr>
<td>Resident</td>
<td>2</td>
<td>50.0 (1.8)</td>
<td>50.5 (--)</td>
<td>not tested</td>
</tr>
<tr>
<td>Resident</td>
<td>3</td>
<td>47.7 (1.1)</td>
<td>44.5 (--)</td>
<td>not tested</td>
</tr>
<tr>
<td>Resident</td>
<td>4</td>
<td>47.7 (1.5)</td>
<td>49.3 (2.1)</td>
<td>0.22</td>
</tr>
<tr>
<td>Resident</td>
<td>5</td>
<td>45.0 (0.9)</td>
<td>42.0 (--)</td>
<td>not tested</td>
</tr>
<tr>
<td>Emigrant</td>
<td>1</td>
<td>43.8 (0.8)</td>
<td>none</td>
<td>not tested</td>
</tr>
<tr>
<td>Emigrant</td>
<td>2</td>
<td>44.3 (0.8)</td>
<td>39.0 (--)</td>
<td>not tested</td>
</tr>
<tr>
<td>Emigrant</td>
<td>3</td>
<td>43.4 (1.0)</td>
<td>42.5 (1.7)</td>
<td>0.39</td>
</tr>
<tr>
<td>Emigrant</td>
<td>4</td>
<td>44.6 (1.0)</td>
<td>44.3 (3.7)</td>
<td>0.48</td>
</tr>
<tr>
<td>Estuary</td>
<td>1</td>
<td>54.8 (0.9)</td>
<td>52.6 (1.1)</td>
<td>0.08</td>
</tr>
<tr>
<td>Estuary</td>
<td>2</td>
<td>59.2 (1.2)</td>
<td>59.8 (1.9)</td>
<td>0.39</td>
</tr>
<tr>
<td>Estuary</td>
<td>3</td>
<td>61.2 (0.7)</td>
<td>61.0 (0.4)</td>
<td>0.42</td>
</tr>
</tbody>
</table>

**Paired Comparisons of Eco-types**

Comparison of the size of migrant body size relative to the size of individuals initially stocked in the enclosure (paired eco-type experiments) indicated (though not conclusively) that migrants tended to be smaller than their stocked counterparts. Results from the resident-emigrant trials also suggested that both emigrant and resident coho migrants usually were smaller than their stocked counterparts although again the results were not statistically significant (Table XIII). The emigrant-estuary trial was less clear as estuary coho migrants were larger than their stocked counterparts in two of the three
replicates. In contrast, emigrant coho which migrated from the enclosure tended to be smaller than their stocked counterparts and in one instance the result was statistically significant (replicate 3, p = 0.03; Table XIII). Likewise, estuary-resident trials suggested that migrants of both eco-types were usually smaller than their stocked counterparts (Table XIII).

Table XIII. Comparison of the mean size FL (SE) of individuals stocked into stream enclosures and the mean size FL (SE) of migrants from the enclosure (resident-emigrant, emigrant-estuary, and estuary-resident pairs). Standard errors were calculated and an independent sample t test was attempted when the number of migrants was greater than 2.

<table>
<thead>
<tr>
<th>EXPERIMENT</th>
<th>REPLICATE</th>
<th>ECO-TYPE</th>
<th>MEAN FORK LENGTH STOCKED FL (SE) (mm)</th>
<th>MEAN FORK LENGTH MIGRANTS FL (SE) (mm)</th>
<th>INDEPENDENT SAMPLE t TEST (one tailed)</th>
<th>P VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resident-Emigrant</td>
<td>1</td>
<td>Emigrant</td>
<td>46.3 (2.2)</td>
<td>38.0 (-)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>48.0 (2.4)</td>
<td>54.0 (-)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td>Resident-Emigrant</td>
<td>2</td>
<td>Emigrant</td>
<td>45.6 (0.9)</td>
<td>46.5 (3.5)</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>48.2 (2.3)</td>
<td>none</td>
<td>not tested</td>
<td>0.38</td>
</tr>
<tr>
<td>Resident-Emigrant</td>
<td>3</td>
<td>Emigrant</td>
<td>47.0 (1.0)</td>
<td>45.6 (3.4)</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>46.7 (1.5)</td>
<td>43.5 (1.8)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td>Resident-Emigrant</td>
<td>4</td>
<td>Emigrant</td>
<td>44.4 (0.9)</td>
<td>none</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>43.6 (0.9)</td>
<td>41.3 (1.8)</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>Resident-Emigrant</td>
<td>5</td>
<td>Emigrant</td>
<td>42.7 (1.3)</td>
<td>42.5 (0.5)</td>
<td>0.36</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>44.8 (0.9)</td>
<td>none</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td>Emigrant-Estuary</td>
<td>1</td>
<td>Emigrant</td>
<td>49.8 (2.5)</td>
<td>46.0 (-)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Estuary</td>
<td>54.8 (1.6)</td>
<td>53.8 (2.0)</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>Emigrant-Estuary</td>
<td>2</td>
<td>Emigrant</td>
<td>47.2 (1.2)</td>
<td>48.0 (--)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Estuary</td>
<td>58.3 (1.3)</td>
<td>60.0 (---)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td>Emigrant-Estuary</td>
<td>3</td>
<td>Emigrant</td>
<td>42.9 (0.9)</td>
<td>40.5 (0.5)</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Estuary</td>
<td>61.9 (0.8)</td>
<td>63.3 (0.8)</td>
<td>0.15</td>
<td></td>
</tr>
<tr>
<td>Estuary-Resident</td>
<td>1</td>
<td>Estuary</td>
<td>61.1 (1.1)</td>
<td>none</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>59.8 (1.9)</td>
<td>61.0 (---)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td>Estuary-Resident</td>
<td>2</td>
<td>Estuary</td>
<td>61.1 (3.0)</td>
<td>none</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>58.6 (1.1)</td>
<td>53.5 (---)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td>Estuary-Resident</td>
<td>3</td>
<td>Estuary</td>
<td>65.1 (0.4)</td>
<td>64.0 (---)</td>
<td>not tested</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Resident</td>
<td>54.3 (0.6)</td>
<td>54.8 (0.3)</td>
<td>0.26</td>
<td></td>
</tr>
</tbody>
</table>
V. MIRROR IMAGE STIMULATION (MIS) EXPERIMENTS

During MIS tests, most juveniles adjusted to the presence of the mirror. Juveniles oriented themselves towards the image in the mirror and the time to first response decreased over the four testing days. Fish often responded to their image with "dorsal fin erection", "swim against mirror", and "lateral display" behaviours. Occasionally, fish "charged" or "nipped" their images but these behaviours were observed so infrequently that they were not included in the analysis.

Three principal component axes were used to describe the behaviour of the three eco-types during the MIS experiments. The first axis of the principal components analysis (PCA) summarized 35.0% of the behavioural variation in the MIS data (Table XIV). Lateral display and swim against mirror (SAM) behaviours dominated although they loaded in opposite directions as indicated by high positive and high negative coefficients. Positive first component axis (PC1) scores were associated with long lateral display durations and high negative scores were associated with long SAM durations. Coho either exhibited long lateral display durations or long SAM durations and rarely both types of behaviours. This resulted in the respective positive and negative dominance of later display and SAM behaviours in the first eigenvector. Since lateral display and SAM behaviours have been positively correlated with aggression (Taylor and Larkin 1986; Rosenau and McPhail 1987; Swain and Holtby 1989; Riddell and Swain 1991), the first axis was used to represent such agonistic or aggressive behaviour.

The second axis summarized 26.3% of the total behavioural variation and was dominated by submissive displays as indicated by its high loading (Table XIV). In general, the second axis represents the overall degree of submissiveness among the three eco-types.
The third axis summarized 24.4% of the behavioural variation in the observations and was dominated by dorsal fin erections as indicated by its high loading (Table XIV). This axis represented dorsal fin erections which are less overt analogs of lateral display behaviours (i.e. lateral displays without the exaggerated swimming movements), and therefore a less overt form of aggressiveness. Cumulatively, these three axes summarized 85.7% of the total behavioural variation. The remaining eigenvectors did not each account for significant or readily interpretable variation.

Table XIV. Loadings derived from principal components analysis (PCA) of mirror image stimulation behaviour data for three coho eco-types (stream resident, stream emigrant, estuary resident).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Principal Component Analysis Loadings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Eigenvector (EV1)</td>
</tr>
<tr>
<td>Swim Against Mirror</td>
<td>-0.679</td>
</tr>
<tr>
<td>Lateral Display</td>
<td>0.690</td>
</tr>
<tr>
<td>Dorsal Fin Erection</td>
<td>0.229</td>
</tr>
<tr>
<td>Submission Display</td>
<td>-0.106</td>
</tr>
<tr>
<td>Percent of Total Variation (eigenvalues)</td>
<td>35.0</td>
</tr>
</tbody>
</table>

Tests for the effect of observation day on PC1, PC2, and PC3 using analyses of variance (ANOVA) indicated that the variability in the response of all three types of coho to their mirror images was very high and no statistical differences were detected (two way ANOVA; PC1, p = 0.19; PC2, p = 0.22; PC3, p = 0.72; Table XV).
Table XV. ANOVA comparison of the principal components scores for the first three principal components (PCs) (PC1, PC2, and PC3) from mirror image stimulation (MIS) behaviour data.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum of Squares</th>
<th>DF</th>
<th>Mean Square</th>
<th>F-Ratio</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observation Day</td>
<td>5.835</td>
<td>3</td>
<td>1.944</td>
<td>1.616</td>
<td>0.19</td>
</tr>
<tr>
<td>Eco-type</td>
<td>9.599</td>
<td>2</td>
<td>4.780</td>
<td>4.139</td>
<td>0.02**</td>
</tr>
<tr>
<td>Eco-type*Day</td>
<td>8.204</td>
<td>6</td>
<td>1.367</td>
<td>1.137</td>
<td>0.35</td>
</tr>
<tr>
<td>Error</td>
<td>91.436</td>
<td>76</td>
<td>1.203</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum of Squares</th>
<th>DF</th>
<th>Mean Square</th>
<th>F-Ratio</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observation Day</td>
<td>4.845</td>
<td>3</td>
<td>1.615</td>
<td>1.518</td>
<td>0.22</td>
</tr>
<tr>
<td>Eco-type</td>
<td>6.825</td>
<td>2</td>
<td>3.143</td>
<td>2.953</td>
<td>0.06*</td>
</tr>
<tr>
<td>Eco-type*Day</td>
<td>6.840</td>
<td>6</td>
<td>1.140</td>
<td>1.071</td>
<td>0.39</td>
</tr>
<tr>
<td>Error</td>
<td>80.870</td>
<td>76</td>
<td>1.046</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum of Squares</th>
<th>DF</th>
<th>Mean Square</th>
<th>F-Ratio</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observation Day</td>
<td>1.349</td>
<td>3</td>
<td>0.450</td>
<td>0.453</td>
<td>0.72</td>
</tr>
<tr>
<td>Eco-type</td>
<td>0.131</td>
<td>2</td>
<td>0.065</td>
<td>0.066</td>
<td>0.94</td>
</tr>
<tr>
<td>Eco-type*Day</td>
<td>10.609</td>
<td>6</td>
<td>1.768</td>
<td>1.780</td>
<td>0.12</td>
</tr>
<tr>
<td>Error</td>
<td>75.507</td>
<td>76</td>
<td>0.994</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: ** significant p < 0.05
* suggestive 0.05 < p < 0.10

Over all observation days combined, analysis of variance indicated that the level of aggression, as represented by PC1, was significantly different between the three eco-types stream resident, stream emigrant, and estuary resident (two way ANOVA, p = 0.02; Table XV). Tukey's HSD test indicated that significant differences between stream residents and estuary residents (p = 0.014) existed. However, the analysis could not show conclusively how stream emigrant aggression levels were related to those for either resident or estuary coho. The total mean PC1 score for the emigrant population was intermediate between stream residents and estuary residents (Fig. 24). Zar (1984) stated that the inability of the Tukey test to determine from which group the emigrants
came from suggests that at least one type II error has been committed and that the power of the analysis of variance is greater than the power of the multiple comparison test. Graphically, the emigrant population appears to be intermediate between the two populations (Fig. 24).

Figure 24. Comparison of total mean PC1 (aggression) scores for stream resident, stream emigrant, and estuary resident coho juveniles in mirror image stimulation (MIS) experiments. Bars represent standard errors (SE).

The mean daily PC1 score for stream resident coho increased with observation day whereas stream emigrants' scores fluctuated dramatically from day to day (Fig. 25). This latter pattern resembled that exhibited by estuary residents although their level of aggression was lower (Fig. 25). This suggests that stream emigrants may be more similar to estuary coho than to stream residents with respect to changes in aggression with over time.
Figure 25. Comparison of daily mean PC1 (aggression) scores and observation day for stream resident, stream emigrant, and estuary resident coho juveniles in mirror image stimulation (MIS) experiments. Standard error (SE) bars have been omitted for clarity.

PC2 (submissiveness) scores differed weakly but not significantly between the three eco-types of coho salmon (two way ANOVA, $p = 0.06$; Table XV). PC2 scores revealed that stream residents were much less likely to exhibit submission displays than either stream emigrants or estuary residents (Fig. 26).

Analysis of variance on PC3 (dorsal fin erection) scores indicated that neither eco-type, observation day, nor the interaction between eco-type and day were statistically different (two way ANOVA, $p = 0.94$, $p = 0.72$, $p = 0.12$ respectively; Table XV). The plot of total mean PC3 score shows the similarity between the stream residents, stream emigrants, and estuary residents (Fig. 27). This result could imply that dorsal fin erections or less overt aggression does not vary between the eco-types or that it may have arisen spuriously simply due to the PCA method.
Figure 26. Comparison of total mean PC2 (submission) scores for stream resident, stream emigrant, and estuary resident coho juveniles in mirror image stimulation (MIS) experiments. Bars represent standard error (SE).

Figure 27. Comparison of total mean PC3 (dorsal fin erection) scores for stream resident, stream emigrant, and estuary resident coho juveniles in mirror image stimulation (MIS) experiments. Bars represent standard error (SE).
VI. FLOW AQUARIA EXPERIMENTS

A comparison of the level of aggression exhibited by the stream residents (RES1) and the stream emigrants (EMG1) suggested that residents were more aggressive than emigrants (Fig. 28). Although the difference was not statistically significant, at the \( p = 0.05 \) level, it was highly suggestive (independent sample \( t \) test, \( p = 0.07 \)) given the relatively small sample size (\( n = 15 \)). In trials involving estuary residents (EST2 versus EMG2 and EST3 versus RES3), the larger estuary coho were more aggressive than their stream emigrant and stream resident counterparts (Fig. 28). The mean level of aggression exhibited by estuary coho (EST2) was significantly greater than the emigrant coho (EMG2) (independent sample \( t \) test, \( p < 0.01 \)), while the difference was not significant between estuary coho (EST3) and stream resident coho (RES3) (independent sample \( t \) test, \( p = 0.08 \)), again probably a result of the small sample size (\( n = 12 \)).

![Figure 28](image)

Figure 28. Comparison of mean total number of agonistic displays during paired eco-type flow aquaria experiments. Experiment 1, stream resident and stream emigrant pair (RES1 vs. EMG1); experiment 2, estuary resident and stream emigrant pair (EST2 vs. EMG2); and experiment 3 pair (EST3 vs. RES3). Bars represent the standard error (SE) of the mean value.
A pattern was evident in the dominance hierarchy in the paired flow aquaria experiments. In all three trials the level of domination by one of the eco-types increased with observation day. This was evident as the number of draws declined with each passing day until one eco-type was clearly dominant (Fig. 29). The dominant-subordinate relationship was commonly determined by the third observation day which suggests that dominance is established within the first 72 hours. In the estuary resident and stream resident trial (middle panel, Fig. 29), the level of observed aggression was so intense that the experiment was terminated following the third day.

The degree of behavioural domination as indicated by the level of significance (probability value) in chi square goodness of fit tests varied between the three trials (Fig. 30). At no time did the stream residents behaviourally dominate their emigrant conspecifics, although by the fourth day they dominated most comparisons with the chi square probability value approaching significance (p = 0.06, top panel, Fig. 30). In contrast, estuary coho dominated both freshwater eco-types (residents and emigrants) in almost all of the pairings and their degree of domination was significant from the onset of the experiments (middle and bottom panels, Fig. 30). The degree of domination apparently increased with observation day as probability values decreased to below 0.01 (Fig. 30).
Figure 29. Comparison of the dominance hierarchy by eco-type in the paired eco-type flow aquaria experiments for each observation day. The three bars in each panel correspond to the legend at the top left of each panel. The three panels represent the stream RESIDENT and stream EMIGRANT pair (top), the ESTUARY resident and stream RESIDENT pair (middle), and the ESTUARY resident and stream EMIGRANT pair (bottom).
Figure 30. Comparison of p-values from chi square goodness of fit tests for the paired eco-type flow aquaria experiments for each observation day. The three panels represent the stream RESIDENT and stream EMIGRANT pair (top), the ESTUARY resident and stream RESIDENT pair (middle), and the ESTUARY resident and stream EMIGRANT pair (bottom). * represents significance at $0.05 > p > 0.01$ and ** represents significance at $p < 0.01$. 

DISCUSSION

Use of Estuarine Habitat

The use of estuarine tidal channels by juvenile coho salmon has only recently been observed (Tschaplinski 1982, 1987, 1988; Murphy et al. 1984; Ryall and Levings 1987) and few details have been reported. Most of the past and current coho research was concentrated on the freshwater rearing phase (i.e. in streams, flooded back-water channels, and lakes). However, there is a growing literature describing the potential importance of estuarine rearing to coho production (Tschaplinski 1982, 1987, 1988; Murphy et al. 1984; Ryall and Levings 1987).

There is a common pattern in the seasonal abundance of estuarine rearing coho populations. The number of coho present in the Salmon River estuary gradually increased until their numbers peaked in late July and early August. These coho were present in the upper intertidal portion of the estuary until late fall when the fall freshets began. This same pattern in estuarine coho abundance and residency was first noted by Tschaplinski (1982) in Carnation Creek, British Columbia. The seasonal changes in the abundance of coho juveniles in the Salmon River estuary reflected the immigration of juvenile coho into the estuary, the emigration of juveniles out of the inner estuary, and the losses due to mortality (predation and/or disease). Current dogma suggests that a density dependent mechanism such as competition for space or food in the stream environment forces surplus fry to emigrate from their natal streams (Chapman 1962; Mason and Chapman 1965) and it is believed that these individuals probably become resident in the estuary.

In contrast, Murphy et al. (1984) noted that coho fry rearing in the "stream/estuary ecotone" of Porcupine Creek, Alaska migrated back to the mainstem to overwinter. Recently, a small number of coho juveniles marked in
the estuary of Carnation Creek were found to overwinter in a small tributary, Dick's Creek (Tom G. Brown, pers. comm., Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia). The Salmon River is considerably larger than either Carnation or Porcupine creeks, making it very difficult to determine whether any estuarine coho returned to an upstream freshwater overwintering site. It seems plausible that some of these coho could have emigrated to some suitable overwintering habitat in the Salmon River. In Porcupine Creek a significant portion of these upstream migrants smolted the following year and successfully returned as adults two years later (Thedinga and Koski 1984).

The observed densities of juvenile coho salmon were consistent with levels observed in other studies. Late summer coho fry rearing densities in the estuary of Carnation Creek were estimated at 0.31 coho per m$^2$ and 0.75 coho per m$^2$ in 1979 and 1980, respectively (Tschaplinski 1982). Estuary coho densities in Porcupine Creek were estimated at 1.60-1.97 coho/m$^2$ (Murphy et al. 1984). Late summer low tide coho densities for the Salmon River estuary (0.69 coho/m$^2$ and 1.15 coho/m$^2$ in 1989 and 1990, respectively) were intermediate to those observed in the two previous studies. Overall, the rearing densities observed in the Salmon River experimental channel were similar to levels observed in two other estuaries.

The experimental channel provided a unique opportunity to determine both high tide and low tide coho densities. Coho densities were marginally greater during high tides than during low tides. This probably reflected the immigration of large numbers of fish into the tidal channel during the incoming tide. As many as 5,700 coho were estimated to have entered the experimental channel on a single tide change (Table IV). In most instances, the use of tidal channels by juvenile salmonids was limited to times when tidal inundation was
sufficient to flood the tidal channels to inhabitable levels (Levy and Northcote 1982). Even though the experimental channel provided a low tide refuge, all of the individuals inhabiting the channel at high tide did not necessarily remain there. Large numbers of fish emigrated from the experimental channel during the ebbing tides as was typically observed in the natural tidal channel. As a result, the density of coho salmon in the upper intertidal habitats of the Salmon River estuary varied both with the season and with the tidal cycle.

Temporary residence of estuarine habitats by juvenile salmonids has been well documented (Healey 1980; Levy and Northcote 1982; Ryall and Levings 1987; Pearcy et al. 1990; Shreffler et al. 1990). Dorcey et al. (1978) described the dependence of juvenile coho salmon upon the Fraser River estuary as low but recent studies have shown that smaller systems (such as Carnation Creek, British Columbia, Porcupine Creek, Alaska, Sashin Creek, Alaska, Salmon River (Kelsey Bay), British Columbia, and the Squamish River, British Columbia) can rear substantial estuary coho populations (Crone and Bond 1976; Tschaplnski 1982; Murphy et al. 1984; Ryall and Levings 1987).

Estimates of coho residence time in a tidal channel of the Squamish River estuary (3.1 days and 10.1 days; Ryall and Levings 1987) were comparable to the estimates of residence time in the Salmon River estuary (7.1 days and 13.4 days). Both of these estimates were derived for specific tidal channels and/or similar habitats and do not represent the residency period for the entire estuary (inner and outer areas). They probably are only minimum residence times for tidal channel habitats. The previously accepted low level of dependence of coho juveniles on estuaries was in part derived from the use of estuaries by coho smolts during their seaward migration. Dorcey et al. (1978) rated coho use of the Fraser River estuary as low whereas for the Salmon (Kelsey Bay) and the Squamish estuarine use by juvenile coho may be much
higher, particularly in the estuaries of smaller watersheds.

The longer residence time of the experimental channel relative to the natural tidal channel of the Salmon River estuary could be due to a number of factors. The most probable explanation was simply that young coho did not have to physically leave the pond portion of the experimental channel during low tides. Using factor and multiple regression analyses, Levy and Northcote (1981) determined that low elevation refuges (i.e. tide pool habitats) were the most important variable affecting juvenile chinook and chum fry abundances in the tidal channels of the Fraser River estuary. Since the experimental channel never fully dewatered it provided a habitat with a larger low tide refuge area than did the natural tidal channel. This may have enabled juvenile coho to remain in the experimental channel for extended periods of time.

Water temperature also probably played an important role in the use of upper intertidal habitats, especially during the months of July and August when low tide surface water temperatures reached 26.0 °C in the pools of the natural tidal channel. Coho salmon densities under extremely high water temperatures were much lower than in the experimental channel where water temperatures were much lower. Brett (1952) determined that juvenile coho salmon suffered high mortality at temperatures in excess of 25 °C, so although no mortalities were observed it was likely that coho juveniles in the natural channel were stressed from the sub-lethal effects of high water temperatures. Lower densities in the natural channel during these periods probably represented an avoidance response to near lethal water temperatures. Ryall and Levings (1987) noted a similar problem with high water temperatures in a rejuvenated tidal channel in the Squamish River estuary, British Columbia. During summer the low tide water temperatures recorded in the experimental channel were much cooler (13.0 °C versus 26.0 °C) and the rearing densities
were much higher than those measured in the natural channel. Coincidentally, Brett (1952) found that the preferred temperature range of juvenile coho was 12-14 °C which was considered to be close to optimum for maximum growth efficiency (Sandercock 1991). At most times of the year the surface water temperatures of the experimental channel and the natural channel were similar except during the period of low summer water flows and high ambient air temperatures (see Table IV). It was only during this period that the experimental channel may have provided a more favourable habitat than that of the natural tidal channel. The low tide refuge and lower water temperatures of the experimental channel may have contributed to the longer residency of coho juveniles there.

The salinities observed in the natural tidal channel and in the experimental channel appeared to pose few osmotic problems to juvenile coho salmon as they were captured under a wide range of salinities from almost freshwater to full strength seawater (1-32 ppt). Pre-smolt coho salmon can adapt to a wide range of water salinities, though they have been shown to prefer waters of intermediate salinities (Otto and McInerney 1970; Otto 1971; Tschaplinski 1982). Studies have shown that the salinity tolerances of juvenile coho salmon increased with exposure to dilute salinities (Otto 1971; Crone and Bond 1976) until pre-smolt fish could withstand full strength seawater (Tschaplinski 1982). Additionally, Glova and McInerney (1977) showed that pre-smolt underyearling coho were capable swimmers in a range of estuarine salinity and temperature conditions. The temporary residency in the brackish waters of the upper intertidal habitats may better enable juvenile coho salmon to physiologically adapt to the rigours of ocean life (Brauner et al. 1992). Osmoregulatory dysfunction in coho pre-smolts has been linked to stunting in both domestic (Bern 1978) and wild (Varnavsky et al. 1992) coho salmon
However this phenomenon was not observed in the Salmon River estuary.

The age structure of the juvenile coho salmon captured in the upper intertidal portion of the Salmon River estuary and the apparent size differences between the two age classes raised two interesting questions. Firstly, why did the differences in body size between 0+ year old fish and 1+ year old fish decrease by late summer? Secondly, why did the proportion of 0+ year old to 1+ year old coho juveniles in the catch also decrease throughout the summer?

The reduction in the differences in body size between 0+ year old and 1+ year old coho juveniles may be attributable to a combination of either high 0+ year old growth rates and/or the immigration or recruitment of small 1+ year old stream fish into the estuary population. The growth rates of estuary coho from Carnation Creek were twice that of their stream-reared counterparts (Tschaplinski 1982), and similar growth patterns may partially account for the decrease in size differences observed in the Salmon River estuary. Several studies have documented the emigration of pre-smolt coho juveniles from their natal streams during the summer months (Chapman 1962; Mason and Chapman 1965; Mason 1975; Hartman et al. 1982; Scrivener and Anderson 1984; Bilby and Bisson 1987), but very few have documented the final destination of these migrants. The presence of 1+ year old coho juveniles in the upper intertidal portion of the estuary may be a result of downstream emigration of yearling coho salmon. When slow-growing, stream-reared, yearling coho and fast-growing, estuary-reared, underyearling coho co-occurred in the estuary it was almost impossible to distinguish the two age classes based on body size alone, especially later in the summer.

Several mechanisms could explain the reduced proportion of 0+ year old fish in the catch as summer advanced. Young-of-the-year coho fry could be leaving the upper intertidal portion of the estuary once they attained a
threshold size (Healey 1980; Levy and Northcote 1982). Since the outer estuary was not sampled during the study, it was possible that once the juveniles became large enough they moved offshore where they could not be sampled. An alternative hypothesis is that 0+ year old coho could have suffered disproportionately higher mortalities (via predation, physiological stress, disease, etc.) than 1+ year old fish. It is also possible that 1+ year old fish could be recruiting into the upper estuary resident coho population from tributary streams in greater numbers than 0+ year old fry especially later in the season. I have anecdotal evidence suggesting that this could be the case. Between October 22-30, 1990, coho were sampled in the natural channel shortly after the first fall freshet. These fish looked like stream resident coho parr rather than estuary resident coho, as they retained their prominent parr markings and brightly coloured fins. They also exhibited little or no sign of silvering considered to be a key indicator of the smoltification process (McMahon and Hartman 1988). Observations from the Salmon River estuary suggested that the degree of silvering of juvenile coho salmon increased during their period of estuarine residence. It may be common to have both 0+ and 1+ year old coho rearing in estuaries, rather than just 0+ fish, as previously thought.

One implication of this finding is that the claim by previous studies (i.e. Mason 1975) that a lack of diversity in the scale patterns of returning adults indicates a high mortality of emigrant coho and implicitly estuary reared coho could be incorrect. These previous studies assumed that since returning adults always exhibited at least one year of freshwater growth, those fish that were displaced to or volitionally emigrated to the estuary and reared there eventually perished (Mason 1975). Data from the Salmon River estuary suggested that large numbers of 1+ year old coho emigrated to the estuary throughout the summer months and were virtually indistinguishable from 0+ year old
conspecifics based upon body size. These individuals would appear to be stream reared based upon scale pattern characteristics when they returned to their spawning streams as adults and there would be little or no indication of an estuarine residence period. If the presence or absence of at least one year of freshwater growth was the only criterion used to determine the importance of estuarine residency, then it is possible that the importance of estuarine rearing to juvenile coho salmon may be underestimated.

This study was limited by the fact that none of the estuary reared coho salmon were marked with nose-implanted coded wire tags to determine if any of these fish survived to contribute to either the sport and/or commercial fisheries, or if any of these fish returned as adults to spawn in the Salmon River watershed. Without quantitative estimates of the actual contributions to the adult population, the only firm conclusions that can be drawn regarding estuary rearing are that juvenile coho salmon commonly spend 1-2 weeks in the upper intertidal portion of the estuary and that they rear there in high densities.

Field Behavioural Observations

The behavioural observations of juvenile coho salmon in Springer Creek and the Salmon River estuary indicated that the level of aggression was significantly lower in the estuary coho population than in the stream coho population. Significant differences were observed in several types of agonistic behaviour (approaches, chases, and nips) with the exception of charges which were not observed in either population. Along with these measured differences in behaviour, several qualitative differences were also observed. Coho residing in the estuary were less aggressive and often formed "loose" aggregations or schools whereas coho residing in Springer Creek were highly aggressive,
solitary, and defended territories. Stream coho also investigated most drifting food and non-food items as they passed by their feeding station throughout the daylight hours. Estuary coho foraged at lower levels during the slack tide period but increased foraging rates during the tide change.

The social organization of juvenile coho rearing in these two habitats differed substantially, however such differences are not uncommon for juvenile salmonids. Swain and Holtby (1989) found similar differences between juvenile coho rearing in a lake (schooling) and coho rearing in a stream (territorial). They also documented that the levels of aggression were appropriate for these types of social organizations (i.e. stream coho were more aggressive than lake coho).

The effects of water flow or velocity on juvenile salmonid behaviour has been previously documented (Kalleberg 1958; Hartman 1965). In both studies, stream dwelling salmonids were more likely to defend and hold territories in currents than in still waters. A similar situation exists between the current regimes in the estuary tidal channel (often with still water) and Springer Creek (moving water). The levels of aggression exhibited by coho in the estuary tidal channel and in Springer Creek were consistent with the observations of both Kalleberg (1958) and Hartman (1965), however the effect of current velocity on behaviour is still poorly understood.

Several hypotheses could potentially explain these large differences in agonism, social organization, and foraging between coho rearing in estuaries and coho rearing in streams. Rosenau and McPhail (1987) found heritable differences in levels of aggression between two populations of juvenile coho salmon and proposed that this was an adaptive response to higher predation rates in one of the populations. It is possible that a similar situation exists in the estuary of the Salmon River. Several juvenile salmonid predators were
commonly captured (Dolly Varden charr, staghorn sculpin, and chinook and coho smolts) or commonly observed (kingfishers and common mergansers) in the estuary of the Salmon River. The hypothesized mechanism is that, in the presence of predators, highly aggressive individuals would attract attention to themselves and suffer higher rates of predator induced mortality than their less aggressive counterparts. In these populations aggressive individuals would be at a selective disadvantage and disproportionately removed from the population.

An alternative to such an argument is that juvenile coho salmon facultatively switch behavioural modes or social systems in response to their ecological circumstances (Lott 1984; Grant and Noakes 1988; Swain and Holtby 1989). Swain and Holtby (1989) anecdotally described differences in the social systems of lake and stream resident coho populations. Lake populations schooled while stream populations defended territories. The observed differences in the behaviour of coho rearing in estuaries and coho rearing in streams could have arisen as a result of behavioural plasticity where the exhibited level of aggression is merely a response to different environments (Lindsey and Arnason 1981; Caswell 1983; Meyer 1987).

Several authors hypothesized that phenotypic or behavioural plasticity could be a result of adaptation to a highly variable environment (Wright 1931; Via and Lande 1985). Coastal British Columbia streams such as the Salmon River could reasonably be described as an unstable environment given the variability in stream discharge, erosion, and sedimentation associated with fall and winter freshet events. Under environmental conditions such as these, similar coastal British Columbia coho streams have suffered spawning mortalities as high as 80-100% (Hancock and Marshall 1985). It has been hypothesized that plastic behavioural or migrational responses would be favoured under such unstable environmental conditions (Quinn 1984).
Schooling or aggregational behaviour can provide ecological benefits to members of the group such as reduced risks of predation (Treisman 1975; Pulliam and Caraco 1984) which, in turn, may allow more time to be allocated to feeding and less time to vigilance (Seghers 1981). Behavioural plasticity has been observed in other species of wild Pacific salmon where juvenile chum salmon (O. keta) have been observed to facultatively switch from a schooling to a solitary agonistic organization in a small B.C. estuary (Mason 1974). Facultative switching has also been experimentally induced in laboratory reared chum salmon juveniles (Ryer and Ola 1991). They determined that a defensible point source of food was a key factor when inducing a switching of behavioural modes in juvenile chum salmon. When broadcast food sources were used, switching to a solitary agonistic social organization was not always observed. The large feeding areas of the Salmon River estuary may provide such a productive and widespread food source that defense of it would be unnecessary as well as impossible so the social behaviour of juvenile coho rearing there could reflect this.

Until recently coho have been considered an obligate solitary agonistic species during its' entire early life history up to the smoltification stage (Hoar 1958). Hoar (1958) first documented the facultative switching of social organization (from territorial to schooling) amongst juvenile coho salmon during fluctuating water flows. Data from the Salmon River estuary and Mesachie Lake (Swain and Holtby 1989) suggests that coho rearing in estuaries and lakes also may have the ability to abandon the solitary agonistic lifestyle and facultatively switch to a group oriented social organization.

A fourth possibility is that estuary coho were simply emigrant coho that were displaced from their natal streams. Chapman (1962) demonstrated that "nomad" coho were behaviourally subordinate to "resident" coho and in doing so
he implied that "nomads" were less aggressive than their "resident" counterparts, suggesting that this difference might have a genetic basis although he lacked data to support the latter statement. If Chapman's (1962) hypothesis that competition causes the emigration of juvenile coho from their natal streams and ultimately results in the displacement of these individuals to the estuary is true, then it may be that estuary coho are simply the segment of the stream population which did not gain or maintain a territory. Under this scenario, estuary rearing coho should exhibit lower levels of aggression than their stream rearing counterparts. This hypothesis suggests that estuary coho are not genetically distinct from their stream resident conspecifics and that some process such as late emergence date or poor early growth rate (Mason and Chapman 1965) might determine whether or not an individual can gain a territory and secure residence within the stream. Similarly, stochastic events such as a freshet or changing water temperature may affect whether an individual can gain a territory or must emigrate and take up residence in the estuary (Hartman et al. 1982; Rodgers et al. 1987).

The predator mediated hypothesis proposed by Rosenau and McPhail (1987) assumes that the two populations are reproductively isolated and genetically distinct. In the Salmon River the assumption that coho rearing in the estuary and coho rearing in streams are genetically distinct has not been proven nor refuted. Without a genetic study little can be concluded about the mechanism by which the differences in behaviour were established in the coho populations of the Salmon River estuary and Springer Creek. At present the mechanism which causes juvenile coho to migrate to the estuary is unresolved.
**Enclosure Behavioural Observations and Emigration Experiments**

The level of aggression exhibited by the three eco-types and their corresponding paired comparisons varied considerably and sometimes inconsistently. The results from the enclosure behaviour observations differed from the findings of other studies, specifically Chapman (1962) and Glova (1990). My enclosure behaviour observations suggested that estuary and emigrant coho exhibited the highest levels of aggression and that resident only and resident-emigrant coho enclosures exhibited intermediate levels of aggression. Emigrant-estuary trials exhibited still lower levels of aggression while estuary-resident trials exhibited the lowest levels of aggression. These findings are more easily interpreted when several studies are taken into consideration.

The finding that estuary only, emigrant only, stream only, and resident-emigrant enclosures exhibited higher levels of aggression than the emigrant-estuary and estuary-resident enclosures were probably influenced by the disparate variations in body size of the experimental animals (Newman 1956; Chapman 1962). Chapman (1962) demonstrated that aggression was greater among groups of coho of uniform size than among groups of coho of disparate size. This unequal size pairing scenario was common in the mixed eco-type enclosures as estuary coho were always significantly larger than their stream reared counterparts.

When stream resident and stream emigrant eco-types were paired in the enclosures, the two eco-types exhibited equal levels of aggression. This result was consistent with Chapman's (1962) findings, as the eco-types were about equal in body size. However, when stream resident and emigrant coho were paired with larger estuary coho, both of the freshwater eco-types were much more aggressive than their estuary counterparts. This contradicted the findings
of Chapman (1962) who observed that size differences as small as 1 mm FL could influence the outcome of an agonistic encounter. Dill (1978) showed that larger coho elicited an aggressive response at greater distances than smaller or equal sized conspecifics. This increase in reactive distance may have promoted aggression by the smaller freshwater eco-types towards the larger estuary eco-type. Rearing density, prey abundance and hunger have been shown to affect aggression and territory size in stream dwelling salmonids (Slaney and Northcote 1974; Mason 1976; Dill 1978; Dill et al. 1981) however, these factors were not examined during these experiments, although they may have unknowingly influenced the results.

The discussion of emigration and volitional migration from the enclosures is based solely upon trends observed in a small data set and should be viewed with caution. Chapman (1962) proposed that aggressiveness caused the emigration of "nomad" coho from his observation troughs. The emigration of coho from the enclosures, regardless of eco-type, was speculated to be related to increased levels of aggression observed in those enclosures (Fig. 19 and 22). My results are consistent with Chapman's hypothesis that aggression may influence emigration. The relationship was weaker in the paired eco-type comparison due to small sample sizes. Emigrants appeared to be more likely to emigrate than residents given approximately equal levels of aggression expressed by each eco-type (Fig. 21 and 23). This suggests that factors other than aggression may influence the out-migration of emigrant or "nomad" coho. In the emigrant-estuary enclosures, estuary coho were much more likely to migrate than emigrants and they were also significantly less aggressive than the emigrants. These findings are consistent with Chapman's hypothesis, however the estuary-resident enclosure data appeared to contradict his hypothesis, though the number of migrants was very low (seven individuals). These
relationships are speculative as only the number of aggressive acts exhibited by the aggressor were enumerated and the "recipient" of the aggression was not documented.

It has been previously observed that stream residents behaviourally dominated stream emigrant conspecifics (Chapman 1962; Mason 1969; Glova 1990). These differences in hierarchy were commonly attributed to small differences in body size with larger individuals dominating smaller ones (Chapman 1962; Glova 1990). Several studies have cited the importance of size in determining dominance among juvenile Pacific salmon (Chapman 1962; Mason 1969; Glova 1990) and my data are consistent with these findings. The influence of body size on emigration is better demonstrated when the confounding effects of eco-type are removed. When the size of migrants was compared with the size of the individuals stocked in the enclosure a consistent pattern was observed. In general, migrants were smaller than the mean size of the individuals stocked in the enclosure and this relationship held across all eco-types and paired eco-type comparisons (Table XII and XIII). These results were consistent with a number of studies (Chapman 1962; Mason 1969; Glova 1990), however Slaney and Northcote (1974) found no relationship between emigration and size in small rainbow trout fry.

**Mirror Image Stimulation Experiments**

MIS experiment results suggested that stream resident coho juveniles were significantly more aggressive than either stream emigrants and/or estuary resident coho. Additionally, the data also suggest that both the stream emigrants and estuary residents were more likely to display submissive behaviours than stream residents. The result that agonism did not vary with observation day differed from recent MIS studies of agonistic behaviour in coho
salmon where agonistic behaviour increased with observation day (Rosenau and McPhail 1987; Swain and Holtby 1989; Swain and Riddell 1990; Riddell and Swain 1991). In all of these studies, fish were reared from hatching in isolation so that learned behaviour could only occur during the initial days of the experiment which resulted in increased agonism with each passing observation day. Since only socially experienced individuals were used in my MIS experiments such an increase would not be expected and was not observed. Holtby et al. (1993) found a similar nonsignificant effect of observation day on the agonistic behaviour of juvenile coho which had been exposed to conspecifics for a 48 day period prior to use in their experiments.

These MIS results further corroborate the results of the behavioural observations of juvenile coho in Springer Creek (stream residents) and the natural tidal channel (estuary residents). However, these findings are consistent with both Chapmans' (1962) hypothesis that competitive interactions result in the displacement of individuals from tributary streams to downstream habitats and Rosenau and McPhails' (1987) hypothesis that high levels of predation thought to be present in the estuarine environment induces or favours less aggressive individuals. The results from my MIS behaviour experiments were not able to conclusively differentiate which of these two hypotheses was the probable mechanism through which the observed behaviour of coho in the Salmon River estuary could have arisen.

**Flow Aquaria Experiments**

In the pairwise comparison of stream resident and stream emigrant coho, the results suggested that residents dominated equal sized emigrants. However, the pairwise comparisons, involving estuary reared coho juveniles, conflicted with the results of the MIS experiments. In these trials (estuary
versus residents and estuary versus emigrants), estuary coho were significantly larger than their stream reared conspecifics which may explain their ability to dominate the more aggressive stream resident and emigrant eco-types. This suggests that levels of agonism determined from MIS experiments do not consistently predict dominance hierarchies (Ruzzante 1992) but such results suggest that any advantage conferred through higher levels of aggressiveness can be overcome by increased body size.

**Implications To Coho Life History Dogma**

It is currently not clear whether juvenile coho salmon rearing in the Salmon River estuary have altered their behaviour (agonism and social organization) in response to the estuarine environment or whether this shift was a genetically pre-determined adaptation to an unstable, freshet-prone coastal British Columbia stream. This is an example of the "nurture" versus "nature" argument. In either case, this shift in behaviour enables them to exploit a highly productive but risky habitat which potentially maximizes coho production within the system.

The results from the enclosure behaviour observations suggested that estuary coho can exhibit behaviours appropriate for a stream existence (i.e. territorial behaviours). However when estuary coho interacted with stream coho, both resident and emigrant, (in group situations) they were socially subordinate in spite of a significant size advantage. Other laboratory behaviour experiments where individuals were paired with an individual of a different eco-type, suggested that estuary coho were able to behaviourally dominate their smaller, more aggressive stream resident and stream emigrant counterparts. This indicates that estuary coho may be able to facultatively switch behavioural modes from a schooling existence to a territorial existence.
The ecology of stream dwelling juvenile coho salmon differs significantly between summer and winter. During winter young coho salmon move to pool habitats in streams (Hartman 1965; Mason 1965; Bustard and Narver 1975; Dolloff 1986; Glova 1986; McMahon and Hartman 1989), to lakes (Swales et al. 1988), to beaver ponds (Leidholt-Bruner et al. 1992), and to off-channel sites (Peterson 1982a; 1982b; Brown and Hartman 1988; Swales and Levings 1989) with an associated reduction in aggressive interactions (Hartman 1965). This shift in behaviour and habitat use may minimize the behavioural interactions between estuary reared coho and stream reared coho. Since estuary coho often re-enter streams in late fall and early winter it is possible that the importance of these behavioural interactions may be overestimated and the applicability of the results from my behaviour experiments may be limited. In spite of this, the application of my findings are relevant to the period prior to the movement of juvenile coho to their over-wintering habitats when a territorial social organization is still employed by coho salmon. Regardless, it appears that under certain conditions estuary reared coho can exhibit behaviours appropriate for a stream existence and they can dominate stream reared coho. This is probably due to size advantages associated with higher estuarine growth rates.

This study raises important questions regarding which mechanism phenotypic plasticity or genetic isolation is responsible for the observed differences in the behaviour of estuary and stream reared coho. The answer to this question has important implications to the way fisheries managers view the stock concept for coho salmon. If the estuary coho population consists simply of the displaced segment of the stream population and differ because of a "plastic" response to a different rearing environment then they can be treated as a single stock or genotype. On the other hand, if these differences in behaviour
are a result of an adaptation to life in an estuarine environment then these eco-
types should be treated as separate stocks which would significantly alter the
stock concept for coho salmon. Further study is required to resolve this
question.

Habitat use and biological sampling studies from the Salmon River
estuary suggest that current coho life history dogma should be re-evaluated. It
has generally been believed that the pre-smolt emigration of juvenile coho
salmon from their juvenile rearing streams was a direct result of intraspecific
competition for food and space (Chapman 1962; Mason and Chapman 1965). It
was also believed that these displaced individuals make up the majority of coho
that reside in the estuaries of many coastal streams. These individuals have
been described as "ecological losers" (Glova 1990). It was assumed that most of
these non-smolting fish do not contribute to the adult spawning population
even though they may greatly outnumber those juveniles that emigrate as
smolts (Foerster 1955; Chapman 1962; Mason 1975).

Several studies cited a lack of scale pattern diversity among the scales of
returning adults (i.e. the absence of scales showing no freshwater overwinter
growth period) as indirect evidence for this. The scales from most returning
adults usually exhibit at least one to three years of freshwater growth before
moving to sea as smolts (Otto 1971; Mason 1975; Crone and Bond 1976;
Sandercock 1991) however evidence from Carnation Creek, British Columbia
indicated that pre-smolt emigrants, which rear in the estuary, can and do
survive to adulthood and can contribute to the spawning population
(Tschaplinski 1987, 1988). Crone and Bond (1976) reared coho fry in saltwater
pens and found the scale patterns of these fish to be indistinguishable from
stream reared coho. Even though the Carnation Creek data suffered from small
sample sizes it nonetheless shows that estuary reared coho survive to
adulthood. A study of coho salmon in Porcupine Creek, Alaska found that as many as 50% of the approximately 11,500 adults returning to spawn were estuary reared as juveniles (Thedinga and Koski 1984).

Data from the Salmon River estuary suggested that a significant proportion of juvenile coho rearing in upper intertidal habitats were 1+ year old, pre-smolt fish. These fish were almost indistinguishable from 0+ year old fish based on size. This result was surprising, as most studies describe the co-occurrence of yearlings with fry only in the spring and early summer months when the yearlings were smolting in preparation for moving seaward (Tschaplinski 1988). This suggests that the lack of scale pattern diversity in spawning adult coho salmon does not necessarily provide good evidence against the survival of estuarine reared coho juveniles.

Pre-smolt emigrants that become resident in the estuary can exhibit high estuarine survival rates (26.0-33.9% from May to September in the Carnation Creek estuary) and they can gradually adapt to elevated water salinities (Tschaplinski 1982, 1987). By late summer (August), juvenile coho were able to fully osmoregulate in the brackish waters of Carnation Creek. These fish also grew at rates approximately twice that of their stream reared counterparts (Tschaplinski 1987). Most of these estuary coho moved seaward following the first freshet in the fall of their first year (Tschaplinski 1987). Some of these pre-smolt coho migrated back into a small tributary of Carnation Creek (Dick's Creek) to overwinter (Tom G. Brown, pers. comm., Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia). Evidence from physiological studies examining the osmoregulatory ability (Otto and McInerney 1970; Crone and Bond 1976; Tschaplinski 1982, 1987; Birch 1987), swimming ability (Glova and McInerney 1977; Brauner et al. 1992), and growth (Otto 1971; Tschaplinski 1982) suggest that pre-smolt coho salmon can adapt to and
thrive under estuarine salinity conditions.

The accumulating data regarding estuarine rearing of juvenile coho salmon are highly suggestive of a possible alternative coho life history pattern. Glova (1990) found that displaced chinook salmon fry, his "ecological losers", established feeding territories downstream from their natal rearing sites in New Zealand rivers and could contribute to the spawning population. Murray and Rosenau (1989) documented the rearing of chinook salmon fry in nonnatal tributaries of the lower Fraser River, but very little is known regarding their streams of origin or their ultimate fate. Chapman (1962) suggested that "nomad" coho fry had an innate tendency to migrate even if there was an abundance of available stream rearing habitat. Northcote (1992) suggested these emigrants were not simply "ecological losers" but possibly "explorers or colonizers" of new unused habitats that could be of benefit to the population.

There is an increasing data base accumulating which suggests that juvenile coho salmon appear to thrive in estuaries. Currently, it is not known whether this is a viable alternative life history strategy with a genetic basis or simply a case of behaviourally subordinate individuals being competitively displaced from stream habitats to an unused estuary habitat. Quantitative studies following the survival of estuary reared coho juveniles to adulthood are necessary to determine the viability of this life history.
REFERENCES


