ASPECTS OF THE POPULATION BIOLOGY OF ESTUARY-REARED AND STREAM-REARED JUVENILE COHO SALMON IN CARNATION CREEK: A SUMMARY OF CURRENT RESEARCH

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ABSTRACT

Juvenile coho salmon inhabit a large number of small coastal streams (e.g., ≤ 20 km long) in northwestern North America. Thousands of newly emerged coho fry emigrate from these streams in spring and early summer each year. In Carnation Creek (Vancouver Island), some of these emigrants inhabit the estuary from March to October-November. Coho inhabit main-channel and side-channel habitats in the uppermost 250 m of the estuary. Coho habitat requirements were identical to those of their stream-dwelling siblings. Most of the coho inhabited low-velocity sites, including deep pools. The largest number of fish in the main channel occurred in areas where midstream water velocities at low tide were ≤ 40 cm/s. Little or no water movement occurred in the side channels. Areas preferred by coho contained cover in the form of undercut banks, overhanging vegetation, and large debris (e.g., root masses, fallen trees). Coho occurred in waters ranging in salinity from 0 to 19 ‰ during periods of maximum high tide in summer.

The late-summer (September) populations of estuary coho totalled 1205 and 2453 fry respectively in 1979 and 1980. These numbers comprised respectively 9.1% and 12.1% of the numbers of coho enumerated in Carnation Creek for the 2 years. Coho emigrating to the estuary from the stream showed high rates of survival and growth. May to September survival rates of the spring (March to May) emigrants were respectively 33.9% and 26.0% for 1979 and 1980. These coho rapidly outgrew their stream-dwelling siblings and were 16.1 mm and 18.0 mm larger on the average by mid-to-late September respectively in the same 2 years. On the average, estuary coho grew from 1.8 to 2.3 times more rapidly than stream-dwelling fry on a monthly basis.

Stream fry emigrating into brackish estuaries gradually develop tolerance to waters of midrange salinities (e.g., 15 ‰) and increase their resistance to high-salinity water (e.g., 30 ‰) as they grow during summer. This long-term adaptation allows fry to inhabit brackish estuaries efficiently. By autumn, about 50% of the estuarine fry are at least as large as 1-year-old smolts which leave Carnation Creek in spring. Most of these estuary coho disperse seaward into Barkley Sound in autumn with the onset of the first seasonal freshets. These fry are physiologically able to withstand the midsalinity, near-store, surface waters of Barkley Sound in winter. Large numbers of these estuary-reared fry must be marked to investigate the numbers which can potentially return to Carnation Creek to spawn.

INTRODUCTION

Adult coho salmon (Oncorhynchus kisutch, Walbaum) are noted to spawn in small coastal streams such as Carnation Creek. For example, coho in British Columbia select approximately 970 of these relatively small streams (Scott and Crossman 1973). Spawning occurs usually from late September to November (but sometimes to March) in shallow, swift water (Hart 1973; Scott and Crossman 1973). Large numbers of eggs are deposited by each female. Egg number varies
with size of female, area, and year and has been reported in Washington State to be 5700 eggs/female in fish ≥ 72 cm long (Scott and Crossman 1973). The fecundity of coho in British Columbia waters varies on the average from 2100 to 2789 eggs/female (Scott and Crossman 1973). Despite the observation that egg-to-fry survival rates are highly variable (Crone and Bond 1976; Hartman et al. 1982; Koski 1966; Pritchard 1947) and may be low (e.g., 15% to 26%) (Crone and Bond 1976), thousands more fry emerge from the stream gravels than these small coastal systems can possibly support. Therefore, thousands of fry leave these streams and enter or pass through the estuaries when they "emigrate" each year in spring and early summer (Hartman et al. 1982; Mason 1974).

Movements of fry downstream occur during the period of fry emergence from the gravel and for variable periods of time afterward (Hartman et al. 1982; Mason 1974). In Carnation Creek, fry emerge generally from April to June. Peak numbers emerge during May (Hartman et al. 1982).

The fate of these "downstream emigrants" was completely unknown until recently. It has generally been assumed that emigrant fry are "in excess of the numbers of fish that streams can support" (Chapman 1962, 1965; Mason 1966, 1976; Mason and Chapman 1965); therefore, these fish have frequently been called "surplus" fry (Hartman et al. 1982). All coho fry were thought to perish soon after entering estuaries and other saltwater environments (Mason 1976; Wickett 1951), even though little evidence was obtained to support this notion. Scale analysis suggested that seaward emigrating fry did not contribute to the next generation of adult spawners (Mason 1976; Wickett 1951). However, a recent study in Alaska has shown that coho fry rearing in estuaries contribute substantially to the population of adult spawners and that these adults can be identified from their scales to have been estuarine-reared individuals (Koski 1982, pers. comm.).

Previous to the present work, estuary populations of coho fry have neither been widely recognized nor studied in detail. This work summarizes some of the salient aspects of an intensive study made from 1979 to 1981 of the biology of coho fry rearing in the Carnation Creek estuary. This summary stresses that:

1. Some of the fry which emigrate from coastal streams become established as a population of estuary-resident coho.

2. Estuaries of small coastal streams are sources of large, rapidly-growing juvenile coho.

3. Estuary-reared populations can contribute important numbers of new recruits to the ocean-dwelling, commercially-fished coho populations and can provide significant numbers of adult spawners.

THE STUDY SITE

The lowermost 3 km of Carnation Creek are available to adult coho for spawning and to juvenile coho (fry and yearlings) for rearing habitat (see Hartman et al. 1982 for descriptions of the stream and watershed). Each year, coho populations (juveniles) in Carnation Creek are enumerated (usually 3 times) during spring, summer, and autumn by the Seber-LeCren (1967) removal method as part of the ongoing research at this experimental watershed. Information from these studies is used to determine population numbers, growth rates, and rates of survival (Narver and Andersen 1974; Andersen and Narver 1975; Andersen 1978). In addition, all fry and smolts emigrating from Carnation Creek during spring and summer are enumerated using a permanent weir facility (Narver and Andersen 1974).

Coho fry inhabit the upper part of the Carnation Creek estuary from the beginning of the period of fry emergence in spring (e.g., March-April) to October-November. Their distribution comprises both the main channel of Carnation Creek which flows through the tidal surge zone and side channels which occur on either side of the main stream. The side channels have low-velocity water and frequently are isolated from the main channel at low tide, especially during summer when stream discharge volumes are lowest (e.g., 0.03 m³/s) (Stockner and Shortreed 1976). When the side channels are isolated, they occur as discrete pools with no water movement.

Including both the main channel and side channels, the total length of the estuary inhabited by coho fry is 400 m. The channels are 8 m wide on the average at low tide, giving a low-tide "total wetted" area that varies roughly between 3400 m² to 3900 m², depending on discharge volumes from Carnation Creek.

The estuary contains both vertical and horizontal salinity gradients. Coho inhabit the upper part of the
estuary where salinities may reach 19 o/oo near the channel bottoms at high tides of 3 m.

COHO POPULATIONS IN THE CARNATION CREEK ESTUARY

Downstream Emigration

Thousands of newly-emerged fry move downstream toward the sea from Carnation Creek each year (Hartman et al. 1982). Investigators have long attempted to determine the cause of this annual “emigration” that has been observed in many streams. Chapman (1962, 1966), Mason (1966, 1969), and Mason and Chapman (1965) maintained that young fry are displaced downstream as an outcome of in-specie competition for food and space. These authors and Dill (1978) claimed that coho in streams are territorial and aggressively defend space within which they feed. Those coho, unable to maintain feeding territories, were termed “competitively inferior” and must move downstream to find suitable habitat and food.

Au (1972) also thought that so-called “density-dependent” competition for food and space regulated coho numbers in streams, but not during spring and early summer when thousands of fry are moving downstream. He presented evidence that fry were displaced physically from streams by the action of rapid currents. He thus called these seasonal movements the “early dispersal and colonization phase” because physical dispersal by stochastic processes would place new fry in suitable habitats along the entire length of streams. Au (1972) believed that coho populations were competition-regulated only after these early movements of large numbers of fry were completed. Hartman et al. (1982) found that the relationship between floods and the rates of downstream emigration was complex. Peaks in numbers emigrating sometimes occurred before peak discharge volumes were recorded, thus, suggesting complex cause-effect relationships.

Observation in Carnation Creek in February to April (1981) provided no evidence for density-dependent causes for the early emigration of fry downstream. In 1981, fry began to emerge from the stream gravel during February. During the first week of emergence, coho in the estuary and in 6 selected sections of Carnation Creek were enumerated visually using snorkel techniques. Fry numbers in no section of Carnation Creek exceeded 0.01 fish/m²; however, >300 newly-emerged fry had already entered the estuary at the same time. Only 45 fry were counted in all 6 reaches of Carnation Creek which totalled 212 m in length. Despite these low numbers inhabiting Carnation Creek, coho fry already had moved downstream in large numbers.

Whatever processes cause these displacements, it is clear that not all of the downstream emigrants are lost from the rearing population of coho fry. Some of the fish displaced seaward at Carnation Creek inhabit the estuary during summer (Table 1).

Table 1 compares the numbers of fry emigrating downstream in spring and early summer for 1970 to 1980 with the numbers inhabiting the stream in late summer (late August-September) for the same time period and with the numbers inhabiting the estuary in late summer for 1979 and 1980.

The numbers of fry emigrating from Carnation Creek show extreme between-year variability (expressed by 95% confidence limits) which renders prelogging and during-logging mean movements to be statistically equal (p > 0.05). Much less between-year variation occurred in the late-summer populations inhabiting Carnation Creek. Eleven-year mean fry numbers of 12 400 ± 1 821 were recorded. Prelogging and during-logging means were statistically equal. The population of fry inhabiting Carnation Creek in 1980 was unusually high (20 293). This value is the only significant departure from the 11-year mean. The relative between-year constancy in coho population numbers likely reflects the total numbers of fry and yearlings that Carnation Creek can support in summer.

The data also show that significant numbers of downstream emigrants establish themselves in the estuary during summer. Estuary fry were enumerated accurately on a monthly basis using the Seber-LaCren (1967) removal method using both pole-seine nets and electrofishing equipment. From 5285 downstream emigrants in 1979, 1205 fry remained in the estuary in late September. This population comprised 9.1% of the numbers of fry rearing upstream in Carnation Creek. Despite the unusually high numbers of coho inhabiting the stream in 1980, the late-summer estuary population comprised 12.1% of the total numbers in Carnation Creek. Over 5 times more fry emigrated from Carnation Creek in 1980 than in the previous year. Accordingly, the late-summer estuary population more than doubled in size in 1980.
Table 1. Mean numbers of coho fry emigrating downstream from Carnation Creek compared with mean numbers of coho juveniles inhabiting the stream from 1970 to 1980. Annual (11-year), prelogging, and during-logging means are given. Fry numbers averaged over the same time periods are given in small numerals. For 1979 and 1980, numbers of emigrant fry are compared with the stream-resident populations and those emigrants which remained to inhabit the estuary in late summer. Mean values and stream and estuary population sizes for 1979 and 1980 are expressed with 95% confidence limits.

<table>
<thead>
<tr>
<th></th>
<th>Carnation Creek Stream Population Numbers (Late Summer)</th>
<th>No. of Fry Emigrating From Carnation Creek</th>
<th>Estuary Population Numbers (Late Summer)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Annual mean</strong></td>
<td>13 645 ± 1 983</td>
<td>30 006 ± 19 796</td>
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<tr>
<td></td>
<td>Fry 12 400 ± 1 821</td>
<td></td>
<td></td>
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<tr>
<td><strong>Prelogging mean</strong></td>
<td>12 469 ± 1 428</td>
<td>44 111 ± 34 652</td>
<td></td>
</tr>
<tr>
<td>(1970 to 1975)</td>
<td>Fry 11 393 ± 1 427</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>During-logging mean</strong></td>
<td>15 057 ± 3 647</td>
<td>15 900 ± 7 807</td>
<td></td>
</tr>
<tr>
<td>(1976 to 1980)</td>
<td>Fry 13 608 ± 3 325</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>1979</strong></td>
<td>14 776</td>
<td>5 285</td>
<td>1 205 ± 6.1</td>
</tr>
<tr>
<td></td>
<td>Fry 13 230 ± 93</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>1980</strong></td>
<td>23 095</td>
<td>27 654</td>
<td>2 453 ± 11.0</td>
</tr>
<tr>
<td></td>
<td>Fry 20 293 ± 141.5</td>
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compared to 1979. In September 1980, 2453 (± 11) fry were enumerated in the estuary.

**Seasonal Population Dynamics**

Figure 1 illustrates the seasonal changes in the numbers of juvenile coho inhabiting the estuary from spring to late summer in 1979 and 1980. The major curves for each year were constructed from monthly enumerations of the estuary populations; therefore, the curves illustrate the seasonal survivorship of coho in the estuary. In all months, nearly 100% of the population was comprised of fry. In none of the monthly population estimates were more than 16 yearlings found.

The seasonal pattern of downstream emigration (Fig. 1, lower curve for 1979 and 1980) strongly affected the numbers and rates of survival of the estuary population. In May 1979, > 3960 coho occurred in the estuary. The main period of emigration occurred from late March to early May (Fig. 1, lower curve for 1979). Most of the 5285 emigrants in that year thus entered the estuary as a single-period, large influx of fry. This emigration resulted in an estuary population having a length-frequency distribution that was unimodal and normally distributed throughout the summer (not shown). The population decreased in size rapidly from 3964 to 1485 between May and July (Fig. 1). Numbers then stabilized after this period of adjustment which was caused either by mortality or by emigration of individuals from the estuary to the sea (Fig. 1).

The survival rates of coho in the estuary far exceed those of stream-resident coho in Carnation Creek (Holby and Hartman, these proceedings). Including the May-to-July period when coho numbers were declining rapidly, the seasonal survival from May to September was 30.4%. This rate becomes about 82% when the July-to-September period is considered. Population numbers were far more stable during the latter months.
Fig. 1. Seasonal changes in the numbers of coho fry inhabiting the Carnation Creek estuary in 1979 and 1980. The daily numbers of fry emigrating downstream from Carnation Creek are shown by the lower curves for the 2 years. Population numbers are shown by the heavy curves and were drawn from monthly population estimates made by the Seber-LeCren (1967) removal method. The entire populations were enumerated directly each month, except May and June 1979 when selected small sections were enumerated and values were extrapolated for the remaining area. In 1980, 2 major periods of fry emigration produced in July to September a bimodally-sized estuary population comprising (a) original ("Group 1") emigrants (dashed line) and (b) smaller-sized, midsummer emigrants ("Group 2" coho). The numbers of the latter group (July to September) are equal to the difference between the total population numbers (solid line) and the numbers of large-sized Group 1 fry. For all population estimates, 95% confidence limits were $< \pm 11$ fry.
In contrast to 1979, 2 periods of fry emigration from the stream to the estuary occurred in 1980 (Fig. 1). The typical early-spring influx occurred from March to May and resulted in 5451 fry, enumerated in the estuary in mid-May (Fig. 1). Population numbers declined rapidly as in the previous year and fell to 3337 fry in June. It is assumed that population numbers were determined by the available resources of space and food in the estuary.

However, a second major influx of emigrants from Carnation Creek occurred in midsummer (Fig. 1; late June and July). This additional emigration, not occurring the previous year, was due to a storm which produced very high discharge volumes in Carnation Creek. The population curve (Fig. 1, 1980) shows that the estuary was able to accommodate initially many of the > 5000 new emigrants that were displaced downstream. Thus, in mid-July, the fry population rose to 5898.

The new emigrants (called “Group II” fry) were much smaller in average size (length and weight) than the original emigrants from Carnation Creek (called “Group I” fry). The 2 groups of coho were readily separated, both numerically and by size, using the probability-distribution methods of length-frequency analysis (Cassie 1954; Harding 1949). Accordingly, 2 population survivorship curves are given for the estuarine coho from July to September in 1980 (Fig. 1). Both “Group I” and “Group II” (new fry) are distinguished in Fig. 1. The 1980 population was bimodal in size-frequency due to the presence of two temporally separated emigrations. The growth rates, numbers, and survival of each normally distributed size mode of fry were easily determined for the entire season.

The mean size (length) of the original (Group I) estuary residents was 58.3 mm ± 0.1 mm (95% confidence limits) in July, whereas that of the new (Group II) emigrants was only 42.2 mm ± 0.1 mm. This size difference suggests that fry inhabiting the estuary grow more rapidly than their stream-resident siblings. Given the observation that downstream emigrants may be slightly smaller in mean size (e.g., 1 mm to 3 mm shorter) than fish which remain upstream (Chapman, 1962; Mason 1966, 1969, and later discussion in this work), it is possible that differences in size between estuarine and stream fry may be thus biased towards showing increased differences in growth rate. However, the differences in average size between the “Group I” and “Group II” fry were large (16.1 mm) and suggest strongly that estuarine fry rapidly outgrow stream-resident coho.

The influx of additional fry in the midsummer of 1980 resulted in other changes in the dynamics of the estuary population. The period of numerical decline in the population as a whole was prolonged until after the input of new fish (Fig. 1). The “mortality” (“disappearance”) rate of the new emigrants was especially high. From July to September, only 33.9% of the Group II fry survived in the estuary; the survival rate of the Group I coho was significantly higher at 47.3% over the same period. Even though this July-to-September survival rate for the original residents was > 57% lower than that observed for estuary coho in 1979 (July to September), the seasonal survival rate (May to September) of 26.0% compares favorably with the seasonal rate of 30.4% achieved by estuary coho for 1979 (May to September).

Despite the facts that (1) the initial (May) population numbers were much higher in 1980 than in 1979 and (2) the midsummer (July) numbers were more than 4 times higher, the larger 1980 population did not markedly reduce the survival of Group I (original) estuary fry. These large-sized, prior-resident fry may have outcompeted many of the later, smaller emigrants for available food and space and thus achieved a higher survival rate than the latter coho. However, it is clear the estuary was still able to accommodate large numbers of new coho displaced from upstream habitats due to catastrophic events (e.g., floods). The estuary thus provided additional or “reserve” habitats to such displaced coho (individuals that might otherwise be lost to the rearing population of the Carnation Creek system).

**Distribution of Coho**

**In the Estuary**

The characteristics of the physical habitats in Carnation Creek and its estuary differ in several ways. Even for a small stream such as Carnation Creek, the total “wetted” area of the tidal portion can be large (varying between 3400 m² to 3900 m²). Much of this area is unsuitable for coho fry to inhabit; therefore, the overall coho numbers per square metre (“densities”) are lower on the average than those found in Carnation Creek (Table 2).

Table 2 illustrates the late-summer densities of coho in Carnation Creek and its estuary relative to total surface (“wetted”) area and to area of pool habitat.
Table 2. Late summer coho numbers per square metre in Carnation Creek and its estuary in 1979 and 1980. Values are given relative to total surface (“wetted”) area and area of pool habitat. The stream and the estuary were subdivided into separate sections to enumerate coho populations. The ranges about each overall “density” value reflect the maximum and minimum numbers per square metre determined among the study sections. Annual (11-year) mean densities and mean values for prelogging and during-logging periods are also included together with 95% confidence limits.

<table>
<thead>
<tr>
<th>Coho Fry Densities (Late Summer)</th>
<th>Numbers/m² Wetted Area</th>
<th>Numbers/m² Pool Area</th>
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</thead>
<tbody>
<tr>
<td>1979</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Estuary</td>
<td>0.31</td>
<td>0.45</td>
</tr>
<tr>
<td>- Stream</td>
<td>0.74</td>
<td>0.92</td>
</tr>
<tr>
<td>1980</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Estuary</td>
<td>0.75</td>
<td>1.05</td>
</tr>
<tr>
<td>- Stream</td>
<td>1.26</td>
<td>1.60</td>
</tr>
<tr>
<td>Stream</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- 11-year mean</td>
<td>0.81 ± 0.14</td>
<td>1.02 ± 0.31</td>
</tr>
<tr>
<td>- Prelogging</td>
<td>0.87 ± 0.12</td>
<td>1.09 ± 0.29</td>
</tr>
<tr>
<td>- During-logging</td>
<td>0.74 ± 0.24</td>
<td>0.95 ± 0.33</td>
</tr>
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</table>

Comparatively low numbers of coho inhabited the estuary in 1979 (Table 1); consequently, the mean overall numbers per square metre were less than one-half the numbers per square metre averaged for several sections in Carnation Creek (Table 2). Similarly, estuarine coho densities in 1980 were lower than those determined for the stream population. However, the 1980 coho population in Carnation Creek was unusually large (Table 1). When the coho numbers per square metre for the estuary in 1980 are compared to either the (a) 11-year, (b) prelogging, or (c) during-logging mean values for Carnation Creek, the estuary densities fall within these means (Table 2).

The estuary was divided lengthwise into 10 sections to capture and enumerate fry conveniently. Several sections differed in physical habitat characteristics. The numbers of coho per square metre were determined in each section and the highest and lowest values comprise the range about each value for overall coho density given in Table 2.

Table 2 shows clearly that the ranges about the mean fry densities are extreme and illustrate that coho are distributed irregularly in the estuary. In different estuary sections, densities ranged from 0.08 to 1.79 fry/m² (wetted area) and 0.11 to 1.89 fry/m² (pool area).

High concentrations of fry (e.g., 1.89/m² in late summer) were found in (1) main-channel reaches of low water velocity (≤ 40 cm/s) having ample cover provided by deep pools (e.g., ≥ 45 cm deep), undercut banks, and masses of large debris (logs, fallen trees) and (2) side channels with little or no water movement and having shelter in the form of undercut banks with overhanging vegetation (shrubs, grasses, sedges). In May when populations are large, such sites supported up to 4.08 coho/m² (pool area).

The spatial requirements for coho inhabiting estuaries are identical to those of their stream-rearing siblings (Hartman 1965). Low-velocity habitats
(e.g., pools), containing cover in the various forms described, are essential to coho occupying both
environments. Coho fry do not undergo shifts in their
habitat requirements when they move from streams to
estuaries in spring and summer.

Space thus seems to be the main factor limiting the
numbers of coho inhabiting the Carnation Creek es-
tuary. Very low numbers of fry (e.g., 0.08/m² pool
area) occur in reaches containing broad (8 m to
15 m), open areas of relatively shallow, rapidly-
flowing water (> 50 cm/s) having little cover pro-
vided by banks, overhanging vegetation, or large
debris.

About 200 m of estuary occurred downstream of the
part of the tidal region occupied by coho fry. Coho
did not occur in this lower (outer) portion of the
estuary which was characterized by a wide, shallow
channel containing no cover. This part of the estuary
contained no habitats suitable for coho. Salinities
during high tide in the outer estuary were somewhat
higher than the 19 to 20 °/oo values observed at the
channel bottom in the upper reaches occupied by
coho. However, high-tide salinities never exceeded
25 °/oo near the channel bottom in the outer estuary
during summer. The distribution of coho in the Car-
nation Creek estuary was thus concluded to be
limited mainly by available habitat space and to a
lesser degree by higher salinities (see later discussion
of salinity tolerance of coho fry).

Comparative Seasonal Growth
Between Estuary and Stream Coho

Figure 2 and Table 3 compare respectively the mean
monthly sizes and monthly growth increments of
coho fry inhabiting Carnation Creek and its estuary.
In early spring (April), stream and estuary siblings
are very close to the same size (Fig. 2). Accurate
determinations of mean fish size in early spring is
difficult in reference to true determinations of
growth because large numbers of new, small-size fry
emerge daily during April and May. True determina-
tions of growth rates are impossible, unless fish are
marked individually for identification. During early
spring (especially in 1979), mean fish sizes were cal-
culated from small samples (e.g., N < 200) collected
from the stream and estuary populations and from
downstream emigrants enumerated at the Carnation
Creek main weir.

The first clear differences in growth rates between
stream-reared and estuarine coho are discernible in
May (Fig. 2 and Table 3). From June to September,
the estuary coho rapidly outgrew stream-dwelling
fry. The mean size (length) of estuary juveniles in-
creased until the fry became 16.1 mm and 18.0 mm
larger than stream coho by mid-to-late September in
1979 and 1980 respectively. Growth rates of down-
stream emigrant coho therefore increase and exceed
the rates of stream-dwelling coho after these emi-
grants enter estuaries, regardless of the initial size
of the emigrant fry in spring. By autumn, about 50%
of the fry which inhabited the estuary from April-
May to September are at least as large as the 1-year-old
smolts leaving Carnation Creek for the sea
in spring.

In 1980, coho fry grew at rates identical to those
occurring in 1979, even though the estuary
population had more than doubled in size. Coho were
clearly not food-limited in the estuary, even at these
higher numbers (which occurred in the same total
area as in 1979).

Table 3 illustrates and compares monthly growth
increments between stream and estuary coho. In
1979 and 1980, estuary fry grew respectively 1.8
and 2.3 times faster than their stream-dwelling
siblings on a mean monthly basis. These trends
are consistent when the growth rates of estuary
fry are compared to mean monthly growth incre-
ments of coho in Carnation Creek that were averaged
over 10 years (Table 3).

The growth of estuary coho illustrated in Figure 2
and Table 3 for 1980 includes only the original
(Group I) emigrants which entered the estuary in
the spring. The later (midsummer) emigrants were
not included in those calculations. The population
curves in Figure 1 show that these Group II coho
survived in lower numbers (about 34%) than the
original group; however, those midsummer emigrants
which were able to find suitable habitat survived and
grew as rapidly as the larger Group I individuals.
Between July and September, the smaller Group II
coho increased their mean length from 42.2 mm
(± 0.1 mm, 95% cl) to 54.4 mm (± 0.1 mm), a total
change in length of 12.2 mm.

In July 1980, the late-emigrating fry were > 16 mm
smaller on the average than the spring emigrants.
Because of the great differences in body size between
the two groups of coho in the estuary, the population
was heterogeneous and covered a broad range in
sizes. For example, fry in August ranged in body
length from 39 mm to 84 mm.
Fig. 2. Comparative seasonal growth in stream-dwelling and estuarine coho fry. Growth is illustrated by monthly mean lengths (mm) of coho collected from the two environments. For 1980, growth in estuary coho is shown only for "Group I" fry (see text). All values are given with 95% confidence limits, except for stream fry in August 1979 and 1980 when no data were available. Values for the latter period were interpolated between those of July and September. Mean sizes for stream fry for April-May 1979 and April to June 1980 were determined from small samples collected randomly from Carnation Creek (N < 200 for each month). All other mean values were determined from large samples of coho measured when populations were enumerated.
Table 3. Comparative monthly growth increments between stream-dwelling and estuarine fry. Mean monthly growth increments and total seasonal growth for stream and estuary fry are included for 1979 and 1980 and are compared to annual (10-year) mean values for coho populations in Carnation Creek. For 1980, growth is shown only for the “Group I” (original) estuary residents (see text). Mean monthly growth and annual mean values for Carnation Creek are given with ranges. Interpolated values are given for July-August and August-September intervals for stream coho (see explanation, Fig. 2). All growth values between stream and estuary coho were significantly different (P < 0.05, Wilcoxon paired-sample test).

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<tbody>
<tr>
<td>April</td>
<td>3.5</td>
<td>6.3</td>
<td>0.5</td>
<td>4.6</td>
</tr>
<tr>
<td>May</td>
<td>4.2</td>
<td>8.8</td>
<td>1.9</td>
<td>7.6</td>
</tr>
<tr>
<td>June</td>
<td>5.8</td>
<td>9.2</td>
<td>7.2</td>
<td>8.5</td>
</tr>
<tr>
<td>July</td>
<td>3.1</td>
<td>6.2</td>
<td>2.3</td>
<td>6.0</td>
</tr>
<tr>
<td>August</td>
<td>3.2</td>
<td>5.4</td>
<td>2.2</td>
<td>5.4</td>
</tr>
<tr>
<td>Mean</td>
<td>4.0</td>
<td>7.2</td>
<td>2.8</td>
<td>6.4</td>
</tr>
<tr>
<td>Total Growth</td>
<td>19.8</td>
<td>35.9</td>
<td>14.1</td>
<td>32.1</td>
</tr>
</tbody>
</table>

Carnation Creek (1971 to 1980):  
- Mean monthly summer growth = 2.9 (0.3 to 8.3)  
- Mean total season growth = 16.0 (8.0 to 21.7)

△ interpolated value
This broad size-frequency distribution minimizes intraspecific competition among estuary coho, for example, for the same food resources. Efficient food-resource partitioning among different size-classes of coho can occur through size-selective predation. Such mechanisms result in rapid growth in all size-classes of coho (discussed in a later work).

Physiological Adaptation of Coho Fry to Estuarine Environments

Introduction

Typically, fry must remain at least 1 year in streams before emigrating (usually during spring and early summer) seaward as smolts. The transformation of freshwater fry into smolts is a complex process involving morphological, behavioral, and physiological changes (Hoor 1976; Vanstone and Markert 1968).

Prior to this work, one of the main arguments against the notion that coho fry inhabit estuaries successfully involved the question of the physiological ability of coho fry to survive and grow in saline waters. Laboratory tests have shown that coho juveniles (alevins and fry) survive poorly in high salinity water (e.g., about 32 °/oo) before they achieve the smolt life stage (Weisbart 1968). Clarke et al. (1978), Clarke and Nagahama (1977), and Kennedy et al. (1976) observed that coho fry which survived in seawater grew poorly. Poor growth was correlated with the inability of fry to osmoregulate in high-salinity water. Unlike smolts, fry could not maintain their plasma sodium (Na⁺) concentrations at or below 170 mM (Clarke and Blackburn 1978; Clarke et al. 1978; Clarke and Nagahama 1977). Within 24 h, the plasma sodium ion concentrations of the intercellular fluid increased and exceeded 200 mM and became lethal in many fry.

However, such laboratory tests of salinity tolerance using high-salinity water are not relevant to coho fry inhabiting brackish estuaries where salinities vary widely. For example, Clarke and Blackburn (1978) found that coho fry survive and grow well in the laboratory in 20 °/oo brackish water. Conte et al. (1966) demonstrated clearly that coho fry in the laboratory could survive and grow in water of intermediate-range salinity. Furthermore, Otto (1971) showed that the tolerance of juvenile coho to high-salinity water was increased by a 35-day exposure to water of relatively low salinity. His fry achieved their highest growth rates, food consumption, and growth efficiencies when they were kept in water of 5 to 10 °/oo throughout the fry-to-smolt period. Otto (1971) thus demonstrated that tolerance to saline water in coho fry can occur before the smolt transformation and is partly independent of that process. His results suggest that coho fry may adapt gradually to waters of progressively higher salinities after they enter estuaries.

Fry in the Carnation Creek estuary were sampled on a monthly basis from July to October-November to determine (1) if fry were seasonally developing increased salinity resistance (e.g., to high-salinity water), (2) if fry were able to osmoregulate in middle-range salinities during their summer period of rapid growth, and (3) if estuary and stream-dwelling siblings collected at the same time showed differences in tolerance to waters of different salinities.

Methods

Samples of coho fry of the same mean body length were collected monthly from Carnation Creek and the estuary (see Fig. 3 for sizes of fish used). Fry were transported immediately to the laboratory and allowed to acclimate in fresh water in 189-litre tanks at 15°C for 24 h before experiments were conducted. Fry from the Goldstream River estuary (Vancouver Island) were used in October-November due to the low numbers inhabiting the Carnation Creek system at that time of year.

In order to regulate their ionic composition, coho juveniles in saline water must activate the so-called "chloride cells" of the gill tissues (Hoor 1976; Vanstone and Markert 1968). These cells effect ion movements actively with the external environment (Hoor 1976). To determine if such regulation is occurring, short-term exposure (for example, for 24 h) of coho to high-salinity water is sufficient (Clarke and Blackburn 1977, 1978). Longer tests (e.g., 72 h) are convenient when fry are examined in water of midrange salinity in order to achieve consistent, reproducible values for plasma ion concentrations.

To examine both long-term (in reference to monthly collection fry) and short-term (e.g., acute, 24-hour tests) salinity adaptation, groups of estuary and stream fry were then placed into different 189-litre tanks containing (a) freshwater, (b) 15 °/oo (midrange) brackish water, and (c) 30 °/oo (high-salinity) seawater respectively for 24, 72, and 24 h at 15°C. Ten fry from both the stream and the estuary were used for each of the 3 tests each month. The temperature chosen approximates closely the mean diurnal maximum temperatures in both Carnation
Creek and its estuary in summer and is also a temperature at which coho growth efficiencies are maximum (Averett 1969).

After the appropriate time period, each fish was removed from the experimental tanks and anesthetized with a 1:4000 aqueous solution of 2-phenoxyethanol. An aliquot of blood was taken from the caudal artery using heparinized microcapillary tubes. A 2-μL aliquot of pooled plasma was eventually prepared for analysis. The degree of osmoregulation was determined by measuring the plasma concentrations of the sodium ion (Na\(^+\)) by flame-emission spectrophotometry (Clark and Blackburn 1977, 1978). Techniques and methods of analysis employed followed those of Clarke and Blackburn (1977, 1978). Fish in fresh water served as “controls” to determine baseline values for solutes in the intercellular body fluids (blood).

Results and Discussion

Control fry (freshwater test) from both the stream and the estuary maintained their plasma sodium concentrations below 170 mM throughout the summer growing period (Fig. 3). These concentrations are the same as those of osmoregulating smolts living in high-salinity seawater. In no month did the stream and estuary fry differ significantly (p < 0.05) in their plasma sodium concentrations. Both groups of fry osmoregulated consistently at the same levels in the hypoosmotic medium. However, estuary and stream fry showed marked seasonal differences in their ability to control their plasma Na\(^+\) concentrations in both brackish and high-salinity water (Fig. 3).

In midsummer (July), stream and estuary fry kept for 72 h in 15 \(\text{‰}\) brackish water did not differ significantly (p > 0.05) in their plasma Na\(^+\) concentrations. Nevertheless, the estuary fry did show a trend toward lower concentrations. Even though both groups of fry maintained their plasma Na\(^+\) levels above 170 mM, the concentrations of sodium ion in their plasma was only slightly higher on the average (Fig. 3). These plasma ion concentrations were not lethal and did not impair in any way the feeding frequency or activity levels (swimming ability) of the fry.

From August to October-November, estuary-dwelling fry maintained their plasma Na\(^+\) concentrations at or below the 170 mM level (Fig. 3) and thus were able to osmoregulate completely in the mid-salinity water of the estuary for most of the summer and during autumn. In contrast, stream fry not previously exposed to saline water were unable to achieve similarly low plasma Na\(^+\) levels. The plasma Na\(^+\) concentrations of stream coho remained nearly the same as the July value throughout the experimental period (Fig. 3).

These results demonstrate that: (1) regardless of the size of the fish, complete adaptation to brackish water in presmolt estuary coho is a long-term (gradual) process occurring midway during the first summer of growth; (2) short-term adaptation is not possible as shown for stream fry immersed for 72 h in 15 \(\text{‰}\) water from July to early November; and (3) stream fry displaced into estuaries at any time in summer are able to withstand brackish water without lethal effects (no mortality was observed) but then require a long-term period (e.g., > 30 d; Otto 1971) to adapt fully to the salinity regime of the upper estuary.

Similar differences were demonstrated by stream and estuarine coho immersed in acute tests for 24 h in 30 \(\text{‰}\) (high-salinity) water (Fig. 3). Regardless of body size, stream fry were unable to osmoregulate and demonstrated plasma Na\(^+\) concentrations > 200 mM throughout the season. Therefore, no short-term adaptation to high-salinity water occurred. Mortality occasionally occurred among these stream fish. Estuarine fry were able to maintain significantly lower plasma Na\(^+\) levels from August to October-November; however, concentrations of Na\(^+\) were always > 180 mM (Fig. 3). At no time during the experimental period were the estuary fry able to osmoregulate fully in 30 \(\text{‰}\) seawater. Despite the fact that their plasma Na\(^+\) concentrations were > 180 mM, swimming and feeding activity in estuary-reared fry appeared unchanged from the controls, and lethal plasma Na\(^+\) concentrations were never reached.

The data in Figure 3 show clearly that coho fry are able to enter estuaries, survive, and adapt gradually to brackish water as they grow. It is known that salinity adaptation during the smolt transformation is correlated strongly with growth rate and is stimulated by pituitary growth hormone (Clarke et al. 1977; Clarke and Nagahama 1977; Komourdian et al. 1976). Clarke and Blackburn (1978) documented that the ability of coho fry to osmoregulate increases markedly as the fish grow to smolt size. In fact, Garrison (1965, 1971) raised coho fry in brackish ponds and found that the fish grew rapidly and became smolts in their first year (in about 90 d). Similarly, Heard (1976) reared fry from Sashin Creek (Alaska) in estuarine pens and discovered that (1) coho fry grew rapidly, (2) fry transformed into
Fig. 3. Seasonal salinity tolerance in stream-dwelling and estuarine coho fry. Ten fry each from the stream and the estuary were used each month for each of the 3 experimental groups noted. The degree of salinity tolerance is measured by the sodium ion concentration of the blood plasma. Estuary fry from the Goldstream River (Vancouver Island) were used for the October-November sample.
smolts normally, and (3) 2 groups of released smolts completed a normal oceanic life and returned as spawning adults in numbers proportional to the sizes of the released groups. Heard (1976) speculated that the higher growth rates of fry in estuaries might be due partly to warm temperatures and to decreased metabolic costs of osmoregulation in brackish waters compared to fresh water. The rapid growth of estuary coho is a positive stimulus for these fish to increase their salinity tolerance through physiological adaptation (see Hoar 1976).

During summer, rapidly growing fry in the Carnation Creek estuary gradually shift their distribution to increasingly saline waters at high tide (e.g., water of 19 to 20 °/oo). This shift allows fry to occur lower in the water column at high tide as the season progresses (since saline water is more dense than fresh water). Benthic feeding on prey temporally abundant at high tide can then occur (discussed in a later work).

In autumn (e.g., October-November), coho fry disperse from the Carnation Creek estuary. Few fish remain and few return to the lower reaches of Carnation Creek and its tributary Dick Creek. Most leave the estuary by emigrating seaward with the onset of the first seasonal freshets. In Porcupine Creek, Alaska, roughly 60% of estuary-reared fry return upstream to overwinter before leaving for the open ocean in the following spring (Koski 1982, pers. comm.). The remaining 40% leave Porcupine Creek for the sea in autumn. Both fractions contribute to the population of spawning adults which eventually return to the system (Koski 1982, pers. comm.).

Although the smolt-sized fry leaving Carnation Creek in autumn are shown not to fully osmoregulate at 30 °/oo, other tests demonstrated that coho fry were able to maintain plasma Na⁺ concentrations in water at 26 °/oo (not shown in Fig. 3) that were statistically equal to levels of Na⁺ measured in fish kept in 15 °/oo water. It is therefore concluded that coho fry leaving the estuary in autumn are readily able to physiologically tolerate the brackish conditions of near-shore surface waters of, for example, Barkley Sound in winter.

GENERAL SUMMARY
AND DISCUSSION

About 300 large estuarine fry were “nose-tagged” with coded wire in late autumn 1981 to investigate the numbers which might return as adult spawners. In the future, much larger numbers must be tagged to ensure better chances of recapture. Returns are awaited.

There are several biological and management implications of the use of estuaries as rearing habitat for coho fry. In terms of habitat protection and enhancement, the spatial requirements of coho fry are clear. Fry prefer channels with cover provided by large debris (e.g., fallen trees), undercut banks, and overhanging vegetation. Young coho require low-velocity microhabitats. For example, midchannel water velocities ≤ 40 cm/s are sufficient. Deep pools comprise preferred habitat, but slow-moving water varying from 5 cm to 200 cm deep at low tide is sufficient.

Estuary coho are able to prey efficiently on the abundant invertebrate food organisms in estuaries, especially “marine” benthic species (e.g., Corophium, Eogammarus, Neomyysis, and several others in the Carnation Creek estuary). Coho prefer small estuaries (e.g., Carnation Creek, Goldstream River, Porcupine Creek) because the sheltered habitats they require are usually present in small systems. Given the fact that numerous sites occur along the northwest coast of North America, small estuaries may provide important numbers of coho smolts to the entire population. Obviously, practices which may destroy or alter estuarine habitats such as log booming and the input of large amounts of small-sized, logging-caused debris (e.g., wood chips) or gravel from streams should be avoided or minimized.

Coho population processes in estuaries are relatively unaffected by events occurring upstream. This work has shown that estuary fry have rates of growth and survival that are independent of those of stream fry. Neither the numbers nor the biomass of estuary coho are affected directly by processes occurring upstream. Regardless of any catastrophic event occurring upstream which causes fish to be displaced into estuaries, the tidal areas of such streams can thus function to provide large, fast-growing fry which can conserve the spawning run of adults, despite low numbers of smolts occasionally produced upstream.

Therefore, in a heavily exploited commercial population such as coho salmon, the recruitment of large numbers of large-sized, rapidly-growing fry from estuaries is important to:
1. Maintain the commercially-fished stock through "recruitment" (Ricker 1975) and thus contribute to the "stock density" of the fishery (Ricker 1975).

2. Conservation of the ocean-dwelling populations (by recruitment which provides new adults to the population regardless of habitat destruction in streams which causes coho to be displaced into estuaries).

3. Contribute individuals to the population of adult spawners (large, fast-growing fish of supposed high ecological "fitness").

4. Increase the effective reproductive potential of spawning females—not all young coho displaced from streams (e.g., by intraspecific competition, floods, or other causes) are lost to the rearing population.

REFERENCES


Clarke, W.C., S.W. Farmer, and K.M. Hartwell. 1977. Effect of teleost pituitary growth hormone on growth of Tilapia mossambica and on growth

Clarke, W.C., J.E. Shelbourne, and J.R. Brett. 1978. Growth and adaptation to sea water in "under-yearling" sockeye salmon (Oncorhynchus nerka) and coho (O. kisutch) salmon subjected to regimes of constant or changing temperature and day length. Can. J. Zool. 56:2413-2421.


QUESTIONS TO P.J. TSCAPLINSKI

Question (R. Murray): I have a question for Peter Tchapliniski. Regarding coho in the estuary, What proportion of the juvenile productivity would these fish comprise?

Answer (P. Tchapliniski): I haven’t gotten to productivity calculations yet. And in terms of numbers, roughly 9% to 12% of the numbers that are rearing upstream are found in the estuary. Proportionately, they should be reflected in the biomass as well. And you know it’s a figure that can be very easily derived, but I have just not determined the production figures as yet.

Comment (R. Murray): I was thinking that, given the larger size of those fish, if they were a significant part of it, any change in coho production from the stream would be partially masked by the productivity in the estuary.

Comment (P. Tchapliniski): That’s a fair assumption and it underlies one of the properties that the estuary population does possess: that is, what goes on in the estuary (as shown by graphs on the actual population statistics throughout the summer) are those events that are relatively unaffected by those events upstream. The estuary population is very important in the management aspect because, no matter what happens upstream, you may still have a number of fish in the estuary that could very rapidly reach a large size and would enter the sea many months in advance of those fish which are reared in the stream. However, it is not known in what form those fish return to the stream. Many people tell me they don’t
think they come back at all; so this is another thing we have to look at.

Question (T. Northcote): I want to know, is there any evidence from the adult scale characteristic, chemically, or the analysis of otoliths, that indicates the early estuary life stage?

Answer (P. Tschapliniski): There's no evidence for that whatsoever. The big question about the significance of the estuary population, and the biggest criticism I get, is that we just don't see evidence of estuary rearing in the scales of the fish that return to the stream. However, we must determine what the scale of the estuary fish is going to look like compared to the scale of the stream fish. Throughout the whole summer period of rearing, I can't tell the difference between the scales of the estuary fish and the stream fish, other than noting that the circuli of the estuary fish are set wider apart. We have to make some assumptions about where these fish go in the autumn, what they feed on, and what their total growth is during this period to be able to set a standard for measuring what their scales would look like if or when they come back as adults.

Comment (T. Northcote): But there are other ways of checking this than just looking at the scales. You could do chemical analysis of the central part of the scale. You could also check the early growth as shown by daily rings.

Answer (P. Tschapliniski): I certainly haven't done that and I know of no field investigations that did it.

Question (D. Narver): Peter, you just said you expected that these fish, these so-called nomad migrants, moved into the estuary and actually entered the ocean months ahead of the stream-resident type. So you're assuming that they don't overwinter in that area and go on as true smolts the next spring. They, in fact, go out some time that first year?

Answer (P. Tschapliniski): You certainly don't see them in the estuary in late autumn, and the time of their disappearance depends on the distribution of freshets in a system. They sort of respond to freshets much as do the stream fish. They just are not found in the main channels; they're not even found in side channels of the estuaries. Small numbers of fish can be seen throughout the early winter months, but certainly the numbers are very low. And there's no real return to the lowermost portions of Carnation Creek or even Dick Creek. I've looked through those sections quite thoroughly in winter and the fish are just not there. So I assume they are either in near-shore waters or the surface waters of Barkley Sound during that period.

Question (D. Narver): But nonetheless, whatever happened to the tens of thousands of fry that were marked by hand in 1972 or 1973 or near that time? Did any of these come back?

Answer (R. Ptolemy): In 1972, I was out there from May 1 onward through to late July. I marked 16,000 coho fry which were classed as nomadic fry passing downstream at the main fence. The subsequent low recovery of those marked fish the following year and second year would indicate that the percent of marked fish was rather small. However, I am not too sure that there was a lot of effort made to look for these fish as adults. The results are not really conclusive.

Comment (P. Tschapliniski): I think it's very important to consider the time of year that you do mark fish that go through the system. If, in fact, you mark many thousands of fry that go through the downstream counting fence in spring, only a very small proportion of those fish may actually take up residence in the estuary. I think perhaps it would be more productive to work with fish that have been in the estuary during the summer to mark them in the autumn and to look at returns from such marks because, in early spring, coho fry are somewhere around 36 mm to 40 mm long. Once these fish are introduced directly to the waters of Barkley Sound, I'm very pessimistic about their survival because there is plenty of information that suggests that, at this very small size, fish that don't manage to establish in the estuary fare very poorly in saline waters. Not only are they unable to osmoregulate but also they are very poor swimmers at this stage and the predation on these fish in a system like Barkley Sound must be fairly high. After all, they are very heavily parr-marked, and it's kind of like wearing a billboard saying "shoot me".

Comment (K. Koski): My name is K. Koski. I'm with the Auke Bay Laboratory and I'd just like to comment on Peter's work. We had a similar situation in southeastern Alaska. Our stream has an area comparable to your estuary which we call the stream estuary ecotone, for lack of a better word. It extends about 1500 m and it makes up about 20% of our entire rearing area. The stream in this area is also very similar in that a large number of fry move to
the estuary in the spring and summer and live at
probably twice the rearing density with an exception-
ally high growth rate. The food production there is
tremendously high; amphipod and isopod communi-
ties are up to 100,000 organisms per square metre.
The fish leaving that area leave it in the fall, and
we think a lot of them go back upstream over winter.
However, we have evidence that there are a large
number of these fish leaving and going out into the
actual estuary, perhaps as smolts, in the fall. Now
we have a real discrepancy in our smolt count. We’re
off about 50% on our smolt count for the spring,
indicating there could be a fairly significant fall
smolt movement out of our system. And there is
some evidence in Alaska that there are some systems
where fall smolts have returned. We have looked at
scales and there is a definite scale pattern on these
stream ecotone fish. And I have a graduate working
for me who is finishing a master’s thesis and his sole
purpose is looking at scale characteristics. Those
scales do have a different pattern, the circuli are
wider. He has been able to look at some of our adult
returns and he believes that a few of these fish are
ecotone-produced fish. Our stream-ecotone area is
a big area and it makes a big contribution to the
total rearing production of the stream.