EVIDENCE FOR ADAPTIVE DIFFERENCES IN THE ONTOGENY OF OSMOREGULATORY ABILITY, CURRENT RESPONSE AND SALINITY PREFERENCE OF COHO SALMON, ONCORHYNCHUS KISUTCH, FROM COASTAL AND INTERIOR POPULATIONS.

by

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ABSTRACT

This thesis examines the ontogeny of plasma sodium regulation (an indicator of osmoregulatory ability), current or rheotactic response (an indicator of emigration timing) and salinity preference in juvenile coho salmon (Oncorhynchus kisutch). The purpose of the study was to determine if there are inherited differences in the development of these traits between coastal and interior British Columbia populations of coho. An interior (Coldwater River) and a coastal (Rosewall Creek-Big Qualicum River) population were monitored for the above traits throughout the year. Both wild and laboratory groups were included in the study. The laboratory raised populations were divided into two incubation treatment groups: one incubated under a coastal temperature regime, and the other incubated under an interior temperature regime.

There were no differences in the development of sodium regulatory ability between wild populations when the data were sorted by coho weight. Coastal coho, however, physiologically smolted after one year in the natal streams, while interior coho smolted after at least two years of freshwater growth. No obvious differences were noted between wild resident populations in the timing of downstream movement or the shift in salinity preference from hypotonic to isotonic and hypertonic salinities. Both of these behavioural responses typically occurred in the spring (April-May) of each year. Fyke net catches, however, suggested that, in addition to the spring emigrations observed in both populations, a portion of the interior population migrated in the fall (November).

ABSTRACT (CONTINUED)

No differences in the development of sodium regulatory ability were observed either within or between laboratory raised populations. Ion regulatory ability increased to a plateau in the fall and winter following emergence, and increased to smolting levels during the following spring (April-May). There were differences between coastal and interior populations in the pattern of development of both nocturnal current responses and the preference for isotonic or hypertonic salinities. Interior laboratory raised coho developed negative nocturnal rheotaxis and a preference for isotonic salinities about three months earlier (November) than laboratory raised coastal coho (late February-March). Within populations, no differences were observed in the ontogeny of these traits in the groups reared under different temperature regimes.

Because these interpopulation ontogenetic behavioural differences persisted in fish reared under identical laboratory conditions, they probably have some genetic basis. Such an innate component in behaviour implies an adaptive role and in juvenile coho these behavioural traits may allow populations to use a variety of habitats at different distances from the sea, even though a major physiological schedule (in this case the development of ion regulatory capabilities) appears to be fixed within the species. Perhaps variations in migratory timing and salinity preference in juvenile coho evolved to assure survival in a relatively unstable and often severe environment by optimizing habitat use within the constraints of an overriding physiological schedule.

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INTRODUCTION

The tendency among salmonids for juveniles to imprint on their natal stream and for mature adults to return to this stream to spawn results in the formation of numerous genetically discrete populations or stocks (Simon and Larkin 1972, Ihssen 1977, Horrall 1981). These stocks are intraspecific population units that show temporal or spatial integrity, and that are maintained through recruitment and sustained through at least partial reproductive isolation (Booke 1981, Ihssen et al. 1981). Consequently, the identification and definition of the functional characteristics of stocks are of interest to fisheries managers, aquaculturists, geneticists and ecologists (Larkin 1972 and 1981, Altukhov 1981, Krueger et al. 1981, MacLean and Evans 1981). Additionally, the stock may be the population unit at which evolution occurs (Ehrlich and Raven 1969), and therefore stock variation and its adaptive significance are important in understanding the role of selection in the definition of population characteristics.

Stocks have been identified by a variety of population characteristics including biochemical, morphometric, meristic, calcareous, physiological and behavioural characters (Ihssen et al. 1981). Of these traits, only the biochemical or electrophoretic data (and possibly cytogenetic information) provide a phenotypic description that is relatively unaffected by environment. Electrophoretic evidence of genetic differentiation among salmon stocks is substantial and has been used to study relationships among stocks (Utter et al. 1973, Huzyk and Tsuyuki 1974, May 1975, Allendorf and Utter 1979). Electrophoretic descriptions, however, are of little value if there are no, or only small, differences in isozyme frequencies among stocks. Allendorf

and Utter (1979) indicate that electrophoretic analyses detect as little as 33% of possible amino acid substitutions and, in salmonids in particular, electrophoresis suggests generally low levels of heterozygosity (Utter et al. 1980). Indeed, in salmonids, stocks can be electrophoretically indistinguishable but still genetically differentiated and differentially adapted to their respective environments (Utter 1981).

In most characters used to define stocks, the observed variation is a result of the interaction of genetic and environmental factors that together determine phenotypic traits (Ricker 1972, Ihssen et al. 1981). Before the adaptive significance of such traits and their importance to stock discreteness and maintenance can be investigated, these environmental and genetic components must be recognized.

Morphometric and meristic characters, along with calcareous (scales and otoliths) zonation patterns often are useful and powerful means of estimating discreteness and relationships among stocks. The observed variation in such characters, however, is not easily related to direct genetic differences and such traits can be largely a result of environmental factors and physiological constraints (Martin 1949, Bock 1980). Environmental parameters such as temperature, salinity, pH, oxygen tension and latitude all contribute to variation in the phenotype (Fowler 1970, McGlade 1981), and occasionally character differences are even traceable to the parental environment (Dentry and Lindsey 1978). Until recently, morphological traits in salmonids were rarely examined for their adaptive significance, although the adaptiveness of body morphology and fin size has been inferred in Atlantic (Salmo salar) and coho salmon (Oncorhynchus kisutch) (Riddell and Leggett 1981, Taylor and McPhail 1985a and 1985b).

Intuitively, physiological and behavioural characters should be closely associated with the fitness of individuals and therefore should be particularly important to the functional application of the stock concept to fisheries management (Ihssen et al. 1981). Unless they are investigated under controlled conditions, the genetic and environmental contributions to physiological and behavioural phenotypes are often confounded. If, however, different stocks are raised under identical conditions, starting with the unfertilized gametes, then any environmental effects are common to both stocks and thus any observed differences in phenotype can be inferred to be innate. This experimental procedure has been used to examine genetically controlled physiological and behavioural differences in fish in characters such as sodium efflux in fresh and salt-water populations of medaka (Oryzias latipes) (Kado and Momo 1971), temperature preference in white perch (Morone americana) (Hall et al. 1978) and age at smolting in Atlantic salmon (Refstie et al. 1977). In particular, this method has proven useful in untangling stock specific migratory behaviour in sockeye salmon (Oncorhychus nerka), rainbow trout (Salmo gairdneri) and cutthroat trout (S. clarki) (Brannon 1967, Raleigh 1967, Raleigh and Chapman 1971, Kelso et al. 1981, Northcote 1981).

Stock differences in coho salmon (O. kisutch) have been investigated using electrophoresis (May 1975, Allendorf and Utter 1979, Hjort and Schreck 1982, Wehrhahn and Powell 1987), morphometric and meristic data (Hjort and Schreck 1982, Taylor and McPhail 1985a, Taylor 1986), swimming performance (Taylor and McPhail 1985b) and agonistic behaviour (Rosenau and McPhail 1987). Of these studies, Taylor and McPhail (1985a and 1985b) and Rosenau and McPhail (1987) attempted to look at the functional importance of the

characters studied and thus were able to comment on the adaptive significance of these characters. Taylor and McPhail (1985a and 1985b) suggested differences in morphology and swimming performance in juvenile coho were a consequence of the distance between spawning grounds and the sea. Rosenau and McPhail (1987) postulated differences in agonistic behaviour were related to either the presence of different predator species or differences in rearing habitat space and productivity. Associated physiological and behavioural characters, which may be equally important aspects of life history, have not been studied. This thesis attempts to examine physiological and behavioural characteristics that may be adaptive in the juvenile life history phases of spatially segregated stocks of coho salmon.

PHYSIOLOGICAL AND BEHAVIOURAL CHARACTERISTICS STUDIED

A literature review indicated two physiological and behavioural characteristics that are of primary importance to juvenile coho. These are the time of downstream migration and the process of smolt formation. Interpopulation differences in migratory characteristics and in the components of smolt formation, if inherited, could reflect important adaptations to different environments.

Timing and direction of migration are the means whereby juvenile salmonids either reach nursery areas (Northcote 1962 and 1981, Raleigh 1967 and 1971, Raleigh and Chapman 1971, Brannon 1972, Kelso and Northcote 1981) or successfully negotiate lake systems enroute to the sea (Groot 1965, Quinn and Brannon 1982). Such migratory activity is controlled by an interaction between the environment and genome of a specific stock (Raleigh 1971, Brannon 1972, Kelso and Northcote 1981, Northcote 1981).

Juvenile coho exhibit two main periods of downstream movement and both periods have nocturnal peaks during the first hours after dusk (MacDonald 1960, Hoar 1976). In the spring and summer immediately following emergence, coho fry are displaced downstream either as a result of increased current velocities (Hoar 1954) or biological interactions (Chapman 1962, Mason and Chapman 1965). From late April to early June of the following year, in some cases two years later, smolted coho actively migrate downstream (Hasler and Scholz 1983, Smith 1985). Between these two periods, coho exhibit both localized upstream and downstream feeding migrations (Gribanov 1948 cited by Smith 1985) and fall movements into overwintering habitat such as spring fed tributaries, sidechannels, beaver ponds and riverine ponds (Skeesick 1970, Dinneford and Elliot 1974, Bustard and Narver 1975, Cederholm and Scarlett 1982, Peterson 1982, Peterson and Reid 1984, Scarlett and Cederholm 1984). Some of these latter movements are for extensive distances downstream, and may have evolved as a redistribution behaviour that acts to buffer the impact of severe upriver overwintering conditions (Cederholm and Scarlett 1982). This behaviour assures increased survival by dispersing interior coho into accessible overwintering tributaries in the lower reaches of large Pacific coast river systems.

Smoltification is recognised as a dynamic process that transforms what have been freshwater animals into marine animals. This process involves numerous physiological, behavioural and morphological changes (Folmar and Dickhoff 1980, Wedemeyer et al. 1980). Through the smolting process, cryptic and territorial stream resident parr are transformed into the gregarious, streamlined and silvery migrant smolt (Hoar 1976). Genetic variation in the age of smoltification and in the relative sequence of component changes has

been demonstrated in both Atlantic and Pacific salmon (Ricker 1972, Refstie et al. 1977).

Of the many changes that take place during the smoltification process, the increase in osmoregulatory ability that allows marine survival and growth is of prime importance. Variation in the osmoregulatory ability of coho smolts has been suggested by Wedemeyer et al. (1980). These authors indicate that different salmon races may have inherently different smolt levels of the ATPase enzyme which is important in univalent ion regulation.

Seasonal changes that reflect ion and osmoregulatory capacity during juvenile coho development suggest a rapid increase in capacity in the first months following emergence (Conte et al. 1966, Otto 1971) with either limited or no reversion during fall and winter, and then a transition to smolting capabilities the following spring (Zaugg and McLain 1972, Clarke and Blackburn 1978, Scholz 1980, Folmar and Dickhoff 1981). The early increase in osmoregulatory capacity, as indicated by increased seawater tolerance or survival, is thought to be an "acclimative" phase (Folmar and Dickhoff 1980) after which survival in seawater may be high but growth and further development are restrained (Canagaratnam 1959, Otto 1971, Clarke et al. 1981). In situations where a reversion in osmoregulatory capacity has been observed during winter, it may be due to a decrease in the activity of enzymes controlling ion regulation (Giles and Vanstone 1976). The ion regulatory capabilities of coho smolts in the spring following emergence are a function of a preadaptive increase in hormonal activity and enzyme production (Hoar and Bell 1950, Baggerman 1960, Dickhoff et al. 1978, Scholz 1980). This apparently prepares the juvenile coho for the transition to seawater

(Zaugg and McLain 1972, Giles and Vanstone 1976, Folmar and Dickhoff 1979, Hasler and Scholz 1983).

Of the behavioural changes associated with smolting in coho, changes in salinity preference often are seen as an important orientation mechanism during migration (McInerney 1964) and salinity preference has been used as an index of migratory disposition or capacity (Baggerman 1960, Otto and McInerney 1970). There is also evidence for genetic variation in the timing of preference shifts, at least within a population. Otto (1971) alluded to the possibility of such genetic differences between presmolt and smolt emigrants within one stream. This observation might explain the apparent stage specific differences in seawater tolerance.

The development of a preference for hypertonic seawater in coho is correlated with the onset of seaward migration (Baggerman 1960, McInerney 1964, Otto and McInerney 1970). Coho subyearlings appear to prefer salinities up to a concentration corresponding to isotonicity (Houston 1957, McInerney 1964), whereas smolted coho prefer hypertonic seawater (Houston 1957, Baggerman 1960). McInerney (1964) suggested that the development of a preference for saline water is a biphasic process. Initially, a preference for slightly saline water, independent of exposure to seawater, acts as an orientation mechanism during migration (Baggerman 1960, McInerney 1964). Subsequently, exposure to increasing salinities, such as encountered in estuaries, results in an increasing preference for higher salinities and consequently a movement into full seawater (McInerney 1964, Otto and McInerney 1970). Thus, when coho fry in December and January were offered a gradient of 0-13 ppt seawater, Otto and McInerney (1970) observed

a shift in preference from 4-5 ppt to 6-7 ppt. When freshwater was not included in the gradient (4-19 ppt), preferences ranged from 4-8 ppt before January but shifted to 13-14 ppt in January and February.

This thesis investigates the ontogeny of three physiological and behavioural traits in juvenile coho salmon. These are osmoregulatory ability, current response and salinity preference. Seasonal changes in these traits were followed in wild and laboratory raised coho from both coastal and interior British Columbia streams to document any ontogenetic differences. Streams were chosen for their similarity in physico-chemical parameters and differences in the distance from the spawning grounds to the sea and the severity of overwintering habitat. At least the former parameter apparently contributes to adaptive variation in morphology and swimming performance in coho salmon (Taylor and McPhail 1985a and 1985b). The ontogeny of these three traits was monitored in populations reared under identical laboratory conditions to determine the genetic contribution to any observed stock differences. To examine possible effects of geographic variation in incubation rates on the ontogeny of the characters studied, the laboratory populations were divide into two treatment groups: one group was incubated under a coastal temperature regime, while the other group was incubated at interior temperatures. My hypothesis was that the physiological and behavioural characteristics mentioned above are adaptive and, therefore, any differences observed between coastal and interior populations should be inherited.

STUDY STREAMS

Two streams, one in the interior and one in coastal British Columbia (B.C.), were selected as sources for the experimental populations. The criteria used to select these streams were year-round road accessibility, available previous background studies, and similarities in the general biophysical and chemical parameters of rearing habitat. Interior streams were arbitrarily defined as those upstream of the Fraser River canyon, while coastal streams were viewed as those draining the coastal mountains into the Strait of Georgia.

The interior stream was the Coldwater River (Figure 1) and the coastal stream was Rosewall Creek on the east coast of Vancouver Island (Figure 2). Hatchery raised juvenile coho from an alternative coastal stream, the Big Qualicum River, were also used in the study. The Big Qualicum is located 15 km southwest of Rosewall Creek (Figure 2), and coho have been transplanted between the two systems (Bilton 1978, Bilton and Jenkinson 1980). Previously collected bio-reconnaissance data and survey reports are available for all three drainage systems (Smith 1969, Fraser et al. 1974, Wightman 1979, Whelen et al. 1983).

THE COLDWATER RIVER

The Coldwater River is part of the Fraser system and originates in the Cascade Mountains of southern B.C. It first flows east and then north to join the Nicola River near the town of Merritt (Figure 1). The headwaters flow through the interior Douglas fir biogeoclimatic zone but below Kingsvale

Figure 1.

The Coldwater River study area.

Sampling was confined to the area upstream of the canyon located between the confluence with Brook Creek and Brodie. This map details access roads at the time of the study (1980-83).

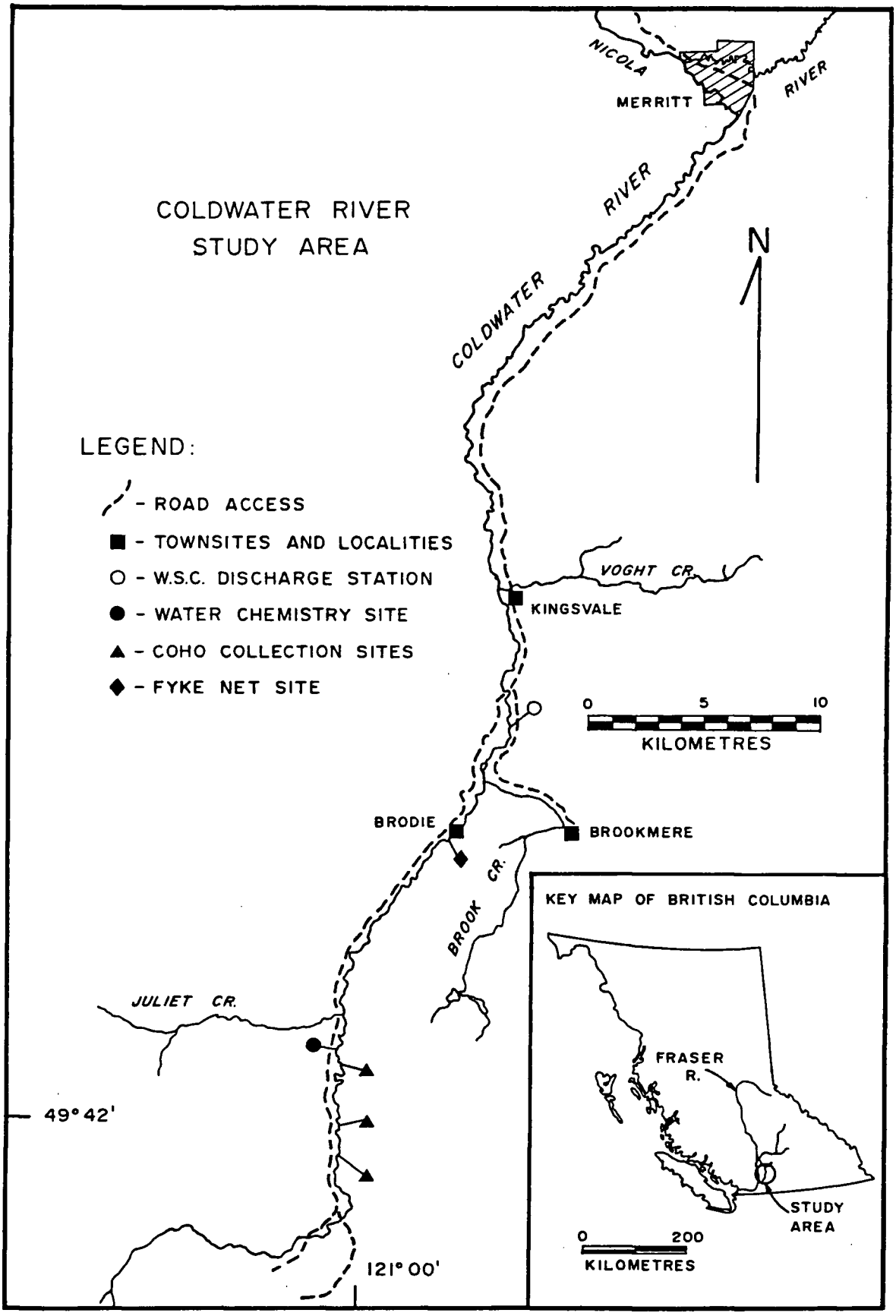
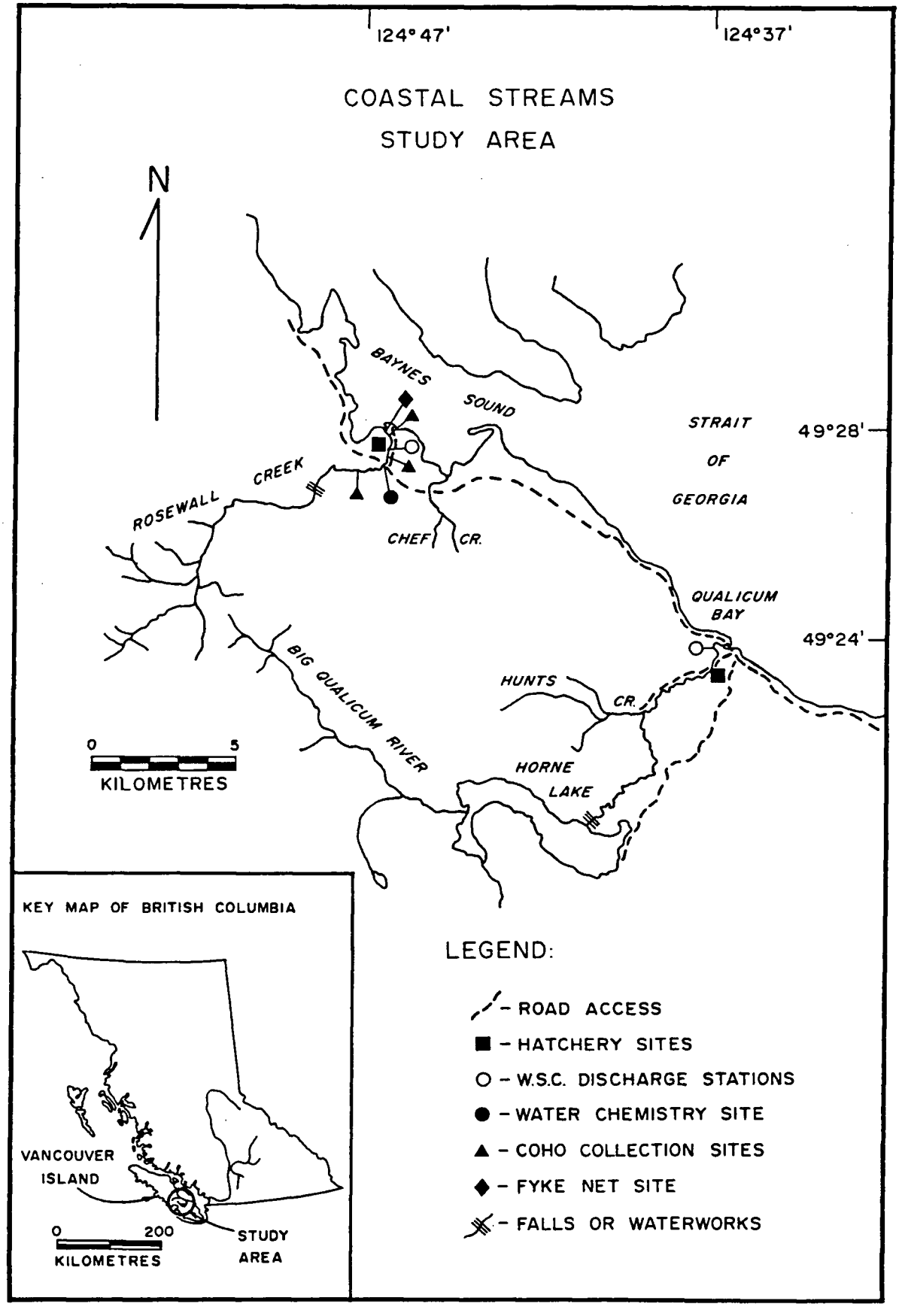

COLDWATER RIVER
STUDY AREA
NICOLA
RIVER
MERRITT
COLDWATER
RIVER
N
LEGEND:
- ROAD ACCESS
- TOWNSITES AND LOCALITIES
- W.S.C. DISCHARGE STATION
- WATER CHEMISTRY SITE
- COHO COLLECTION SITES
- FYKE NET SITE
VOGHT CR.
KINGSVALE
0 5 10
KILOMETRES
BRODIE
BROOKMERE
BROOK CR.
JULIET CR.
49°42'
121°00'
KEY MAP OF BRITISH COLUMBIA
FRASER R.
STUDY AREA
0 200
KILOMETRES

Figure 2.

The coastal streams study area.

Adult coho access is limited by fences associated with the hatcheries, and by a waterfall on Rosewall Creek and flow control facilities on the Big Qualicum River.


124°47'
124°37'
COASTAL STREAMS
STUDY AREA
N
BAYNES
SOUND
STRAIT
OF
GEORGIA
49°28'
ROSEWALL
CREEK
CHEF CR.
QUALICUM
BAY
49°24'
HUNTS
CR.
BIG QUALICUM RIVER
HORNE
LAKE
0
5
KILOMETRES
KEY MAP OF BRITISH COLUMBIA
VANCOUVER
ISLAND
0
200
KILOMETRES
STUDY
AREA
LEGEND:
- ROAD ACCESS
- HATCHERY SITES
- W.S.C. DISCHARGE STATIONS
- WATER CHEMISTRY SITE
- COHO COLLECTION SITES
- FYKE NET SITE
- FALLS OR WATERWORKS

the stream is surrounded by the Ponderosa pine-bunchgrass zone typical of the Thompson Plateau (Farley 1979). The Coldwater is characterized by cold winter temperatures, relatively low productivity and primarily spring (with lesser fall) freshets (Figure 3). For much of its length, the river is an aggrading, regularly meandering watercourse with back and sidechannels and other diverse habitat types (Wightman 1979).

Twelve fish species are known from the Coldwater River drainage, including coho and chinook salmon (Oncorhynchus tshawytscha), steelhead trout and bull trout (Salvelinus confluentus) (Table 1). Of these species, the salmon, trout and char, as well as whitefish (Prosopium williamsoni), sculpins (Cottus cognatus), suckers (Catostomus catostomus) and lamprey (Entosphenus tridentatus and/or Lampetra spp.) ascend into the headwaters, upstream of Brodie (Figure 1). The remaining species are confined to the lower river.

The Coldwater River supports the majority of coho spawners in the Nicola River drainage, with the area upstream of Brodie the most heavily used (Figure 1) (Kosakoski and Hamilton 1982, Whelen et al. 1983). Spawners enter the lower river in October and migrate upstream as the fall freshets begin. Peak spawning occurs in mid-November (Brown et al. 1979, Whelen et al. 1983). Coho eggs then incubate for up to 7 months before the fry emerge in late May, June and early July. The prolonged incubation period is a result of relatively low winter water temperatures (Table 2).

Coho rear throughout the Coldwater River, but are concentrated near the spawning areas upstream of Brodie (Kosakoski and Hamilton 1982). In this

Figure 3.

Seasonal discharge trends for study streams.

Error bars represent 95% confidence limits. These discharge data are from W.S.C. stations in the Coldwater River (08LG048), Rosewall Creek (08HB037) and the Big Qualicum River (08HB001).

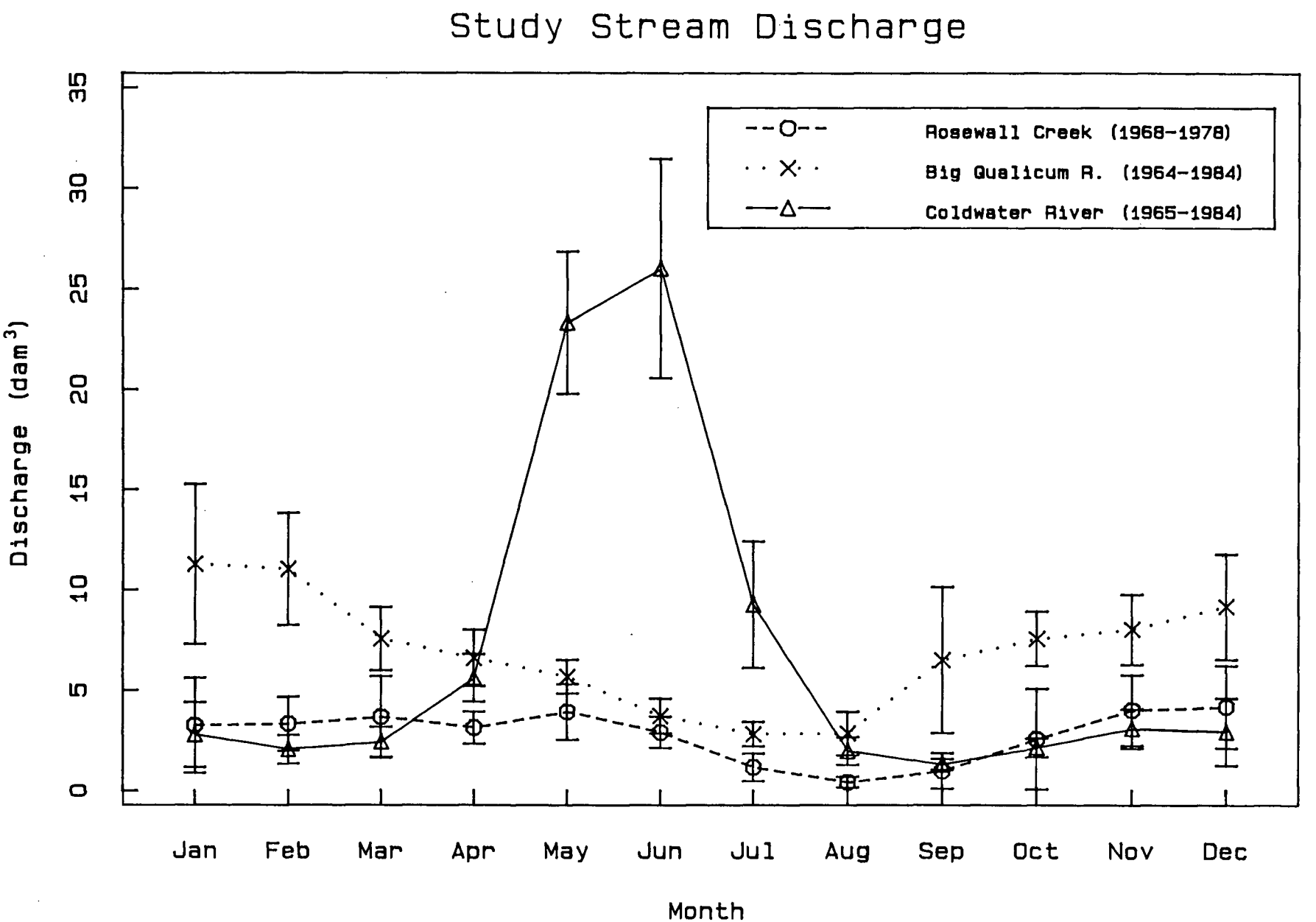

Study Stream Discharge
Rosewall Creek (1968-1978)
Big Qualicum R. (1964-1984)
Coldwater River (1965-1984)
Discharge (dam3)
0
5
10
15
20
25
30
35
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

TABLE 1
FISH SPECIES COMPOSITION AND AVERAGE COHO ESCAPEMENT (1970-1982) AND SPAWNING TIMES FOR THE STUDY STREAMS.[a]

Parameter	Study Streams		
	Rosewall Creek	Big Qualicum River	Coldwater River
Fish Species[b]			
coho salmon	X	X	X
chinook salmon	X	X	X
chum salmon	X	X	
pink salmon		X	
kokanee/sockeye salmon		X	
steelhead trout	X	X	X
cutthroat trout	X	X	
Dolly Varden char	?	?	
bull trout (char)			X
mountain whitefish			X
coastrange sculpin	X	?	
prickly sculpin	X	?	X
slimy sculpin			X
threespine stickleback	X	X	
redside shiner			X
longnose dace			X
leopard dace			X
finescale sucker			X
lamprey	X	X	X
Average Coho Escapement (1970-1982)	348 ± 105.0 (n=12 yr.)	30,362 ± 7,690.6 (n=13 yr.)	494 ± 137.5 (n=13 yr.)
Coho Spawning Times			
Arrival	mid-October	September	October
Start	late October	October	late October
Peak	mid- to late Nov.	late November	early to mid-Nov.
End	December	December	late November

X - Species reported.
? - Species reported but questionable, or not reported but expected.
[a] - Data sources - Lister and Walker 1966, Brown et al. 1977, Wightman 1979, Brown et al. 1979, and Hancock et al. 1985.
[b] - Scientific names are given in Appendix 1.

TABLE 2
PHYSICAL AND CHEMICAL DATA FROM THE STUDY STREAMS.

Parameter	Study Streams		
	Rosewall Creek	Big Qualicum River	Coldwater River
Longitude[c] Latitude[c]	124° 47' W 49° 27' N	124° 37' W 49° 24' N	121° 01' W 49° 42' N
Distance from the spawning grounds to the sea (km)[c]	<4	<10	420
Accessible stream length (km)[a]	3.8	9.6	94
Average width (m)[a]	14.5	18.0	12.0
Drainage area (km^2)[a]	45.3	150.2	914.3
Pool:Riffles:Run area ratio[b]	Lower-0.03:0.05:0.92 Upper- 0.2:0.3:0.5	0.11:0.24:0.65	0.22:0.26:0.52
Average gradient (%)[a,c]	1.0 - 1.6[c]	0.5 - 0.7[c]	0.5 - 1.0[a]
Mean annual precipitation (mm)[c] (1951-1980)	1,317.2 ± 219.9 (n=16)		307.5 ± 74.3 (n=12)
Mean annual discharge ($x10^3$ dam^3)[c] (1964-1984)	82.6 ± 5.79 (n=6)	223.4 ± 13.0 (n=11)	216.6 ± 15.15 (n=17)
Daily water temperature (1980-1982) (°C)[b,c] Mean Maximum Minimum	(1982)[c] (n=317) 6.39 ± 0.209 16.5 0.0	(1982)[c] (n=356) 8.85 ± 0.175 15.5 2.4	(1980-1981)[b] (n=353) 4.69 ± 0.220 17.5 0.0
Estimated Coho incubation temperature (°C)[b,c]	4.6 ± 0.13[c] (n=212)	6.8 ± 0.18[c] (n=212)	2.7 ± 0.17[b] (n=241)
pH range[b,c]	6.7 - 7.93[b]	7.4 - 7.8[c]	6.5 - 7.68[b]
Conductivity (umho/cm @ 25°C)[b,c]	44.7 ± 2.82[b] (n=6)	76.2 ± 1.20[c] (n=23)	48.9 ± 4.14[b] (n=16)

[a] - Data sources - Fraser et al. 1974, Mundie and Mounce 1978, Wightman 1979, Brown et al. 1979 and Hancock et al. 1985.

[b] - Data source - Field data collections.

[c] - Data source - Survey and Maps Branch, Department of Energy, Mines and Resources; Department of Fisheries and Oceans; and Water Survey of Canada.

area, juveniles live amongst cover along the stream margin and the periphery of pools (Wightman 1979), as well as in sidechannels, accessible beaver dams and off-channel pools (Rosenau et al. 1986, Swales et al. 1986). Sidechannels and beaver dams appear to be the most important overwintering habitats (Swales et al. 1986). Based on scales, most Coldwater coho juveniles appear to spend one year in freshwater. Seventy to 90% of returning adults are age 3_2*, and the remainder are age 4_3 (Kalnin 1982 cited by Kosakoski and Hamilton 1982, Whelen et al. 1983).

ROSEWALL CREEK

Rosewall Creek drains the Vancouver Island Beaufort Range northeast into Mud Bay on Baynes Sound (Figure 2). Most of the watercourse lies in the Coastal Douglas fir biogeoclimatic zone (Farley 1979). Rosewall Creek is bounded by valley and canyon slopes over much of its course, with an aggrading, irregular pattern followed on the lower coastal plain. Fish accessibility is limited by an impassable fall near the entrance to a canyon, located about 3.8 km upstream of the mouth (Hancock and Marshall 1985). A repetitive pool-riffle regime is found above the plain, while several long runs and sidechannels are incorporated into the stream character on the plain. Winter floods (Figure 3) commonly result in gravel displacement and redistribution in the lower reaches.

Nine fish species were captured in the system during field studies (Table 1). Most of these were numerous, but only a single stickleback

* The Gilbert-Rich system of age designation is used in this thesis (Koo 1962). Age 3_2 indicates a fish returning to spawn in its fourth year that migrated to sea in its second year.

(Gasterosteus aculeatus) and one chinook smolt were captured. The latter may have strayed into the lower river from Baynes Sound. Historically, coho spawned throughout the accessible portion of the creek, while chum (Oncorhynchus keta) were limited to the lower 1-2 kilometres. An electric fish fence was installed in 1968 as part of experimental hatchery operations (Hancock and Marshall 1985). The fence has restricted most fish species to the lower 0.75 km of the stream. Rainbow and possibly cutthroat trout, however, still manage to migrate upstream of the fence and coho are annually lifted over by hatchery personnel.

Coho spawners begin to move into Rosewall Creek in mid-October. Spawning peaks in late November, although ripe spawners are present earlier in the month. Coho incubate until early spring, emerging as early as March and early April. Some newly emerged coho are displaced downstream during the first spring, but the majority appeared to rear amongst cover in pools and along cutbanks bordering runs. Seaward migration appears to occur during May of the second spring of life. Most of the returning spawners from an experimental program conducted during 1972-77 were 3 years old (mostly aged 3_2) (93.3-96.2%), with fewer numbers of two year old "jacks" (aged 2_2) (Bilton 1978, Bilton and Jenkinson 1980).

THE BIG QUALICUM RIVER

Coho from the Big Qualicum River Hatchery were included in the study after rearing problems eliminated one of the Rosewall incubation treatment groups (6°C incubation group). Biophysical and chemical characteristics, and recognised coho life history patterns for the two streams are similar (Tables 1 and 2, Figure 3).

The Big Qualicum River drains the same mountain range and biogeoclimatic zones as Rosewall Creek. The river initially flows southeast into Horne Lake and then northeast into the Strait of Georgia, just south of Qualicum Bay (Figure 2). An impassable falls and waterworks are located just downstream of the lake outlet. The lower river flows along a static, irregular course, which benefits from the flow control implemented in 1963 (Lister and Walker 1966). A good portion of the lower river is comprised of runs with interspersed pool-riffle patterns.

All five species of northeast Pacific salmon have been recorded from the Big Qualicum River, and trout, cottids (Cottus asper and C. aleuticus), stickleback and lamprey are also present (Table 1). The Big Qualicum River Hatchery (built in 1968) actively enhances chinook, coho and chum salmon, as well as steelhead trout (Minaker et al. 1979). Most of the returning coho during 1975-83 were aged 3_2 (an average of 68.8%) with the remainder comprised of two year old jacks (30.6%) and 4 year old adults (<1%).

STUDY STREAM COMPARISON

The study streams were chosen for similarities in the physico-chemical parameters of rearing habitat, associated with major differences in migratory distance and overwintering habitat severity. This study postulates that life history differences exist between coastal and interior coho populations as adaptive consequences of major environmental differences between resident streams.

The three streams studied are all located just north of the 49° N. latitude and, thus, experience similar photoperiod regimes. Field sampling during this study indicated that both the Coldwater and Rosewall are softwatered and seasonally vary from slightly acidic to slightly alkaline in pH. The Big Qualicum River appears to exhibit similar water chemistry (Table 2, Mundie and Mounce 1978). Although the Coldwater River drains a much larger area than Rosewall Creek (approximately 20 times larger), the drier interior climate (roughly 1/4 of the total coastal precipitation) results in a much smaller difference in mean annual discharge (only about 2.6 times)(Table 2). The Big Qualicum and Coldwater rivers share similar mean annual discharge levels. Despite different hydrographs (Figure 3), the streams are similar in habitat parameters such as wetted width and pool:riffle:run ratios (Table 2).

Fish populations in the study streams differed with the coastal populations composed of different and fewer species than the Coldwater River population. Many of the species encountered in the main rearing areas, however, were similar. In the Coldwater, juvenile coho rear in association with juvenile chinook, steelhead trout, char, whitefish and sculpins. In Rosewall Creek and the Big Qualicum River, juvenile coho rear along with steelhead (rainbow) trout, sculpins and possibly cutthroat trout. In the Big Qualicum, coho also rear with juvenile chinook. Peak coho spawning times are common to all study drainages and most of the spawning coho in each system are aged 3_2.

While similar in general rearing parameters, coho in the study streams encounter dramatically different migratory distances, severity of the overwintering environments and freshet timing. The coastal coho populations studied rear within 4-10 km of the sea and can delay emigration until they

are prepared for seawater. The Coldwater River study area, on the other hand, was approximately 400 km from the mouth of the Fraser River, which may result in early emigrations. The Coldwater River exhibits low flows and freezing temperatures during the winter months, which could affect not only incubation rates but also overwintering survival. Coastal coho emerge at least a month earlier than Coldwater juveniles and experience warmer and probably more productive winter habitat in the main watercourse. Coho juveniles in the Coldwater-Nicola system are believed to compensate for the severity of the habitat by overwintering in beaver ponds (Rosenau et al. 1986), sidechannels and off-channel pools fed by groundwater seepages (Swales et al. 1986). Freshet flows occur primarily in the spring in the Coldwater River, while winter freshets are common on the coast any Coldwater coho don't emerge until after the freshets and, therefore, only encounter the weaker fall floods during the first year of life. Coastal coho, however, must maintain position in the streams during both the winter and lower spring floods. Life history characteristics such as migratory and smoltification timing may, as a result, vary between coastal and interior coho populations.

METHODS

TERMINOLOGY

The terminology for juvenile life history stages used in this thesis generally follows that described by Allen and Ritter (1967). A juvenile coho refers to the stream resident period, or that time prior to transition to a saline environment. Alevins are juveniles with the yolk sac still showing. The term fry refers to the pre-smolt but post-alevin period. A smolt is a juvenile coho which is usually one or two years of age and is physiologically prepared for transition to the sea. Subyearling fry are age 0+, while yearling juveniles are aged 1+.

The stocks used in this study were from the Coldwater River (an interior stock), Rosewall Creek and Big Qualicum River (coastal stocks). Laboratory reared groups of these stocks were incubated under two different temperature regimes and are referred to throughout the thesis as stock treatments.

The terminology of current responses among fish was discussed by Arnold (1974). Rheotaxis refers to a volitional, directed reaction to a water current. The source of stimulation is along the long axis of the body which is then oriented in line with the source. Positive rheotaxis involves movement towards the source, whereas negative rheotaxis involves movement away from the source. Fish that maintain position in the current while oriented into the stimulus have been described as exhibiting positive rheotaxis (Keenleyside and Hoar 1954), but to allow a distinction between responses I described this as a holding response. Indirect reactions resulting in passive movement downstream are described as displacement.

FIELD METHODS

Several items of equipment were used consistently throughout the study. In most cases, temperatures were taken with a calibrated pocket thermometer (to the nearest 0.5°C) or a small digital thermister unit (to the nearest 0.1°C). A Fisher Model 119 pH meter was used to collect pH measurements (accuracy ±0.02 pH) and conductivity was measured with a Radiometer-Copenhagen Type CDM2d conductivity meter (accuracy ±2% of scale). Dissolved oxygen levels were monitored with a YSI Model 51B oxygen meter (accuracy ±0.2 $mg.L^{-1}$).

Chemical and Physical Measurements

Most chemical and physical data from the various stream systems were obtained from survey reports (Wightman 1979, Brown et al. 1979, Hancock and Marshall 1985) and publications of the Inland Waters Directorate of Canada (Anon. 1982, Anon. 1985). Included were gradient, wetted width, drainage area, annual precipitation and annual discharge. Longitude and latitude, distance from the sea and accessible stream length were taken from 1:50,000 and 1:250,000 scale maps. Pool:riffle:run ratios were measured in the field with a tape measure.

During each field trip, several water quality measurements were taken at standard sites and included water temperature and pH. In addition, a water sample was collected and later tested for conductivity at 25°C.

From November 1980 until November 1981, daily water temperature fluctuations were monitored in the Coldwater River and Chef Creek. Chef

Creek is a small stream located less than a kilometre south of Rosewall Creek (Figure 2) and was originally intended as the source of the coastal coho stock. Limited adult returns in 1981, however, necessitated turning attention to Rosewall Creek. Regular sampling with a pole seine for coho juveniles was conducted during 1980-81 in the Coldwater River and Chef Creek, and during 1981-82 in Rosewall Creek. These samples were used to roughly establish when emergence occurred and how long relative incubation periods extended. Incubation in the Coldwater appeared to occur from early November until mid- to late June, while in the coastal streams incubation ran from November to May. Mean incubation temperatures for coastal and interior streams were then calculated using the 1980-81 temperature data and similar temperatures were used in laboratory incubation treatments. For purposes of comparison, temperature data were obtained from Rosewall Creek and the Big Qualicum River for 1981-82.

Adult Coho Capture and Egg Handling

Adult coho were captured in the Coldwater River and Rosewall Creek during November 1981. Coho spawners were collected by positioning a marquesette pole seine downstream of a likely looking holding area and then electroshocking the area downstream towards the net using a Smith-Root Type VII electroshocker. Ripe adults were held in portable pens until they were artificially stripped. Sampling areas are shown in Figures 1 and 2.

To maximize genetic variability within experimental groups, as many ripe male and female spawners as possible were collected (Appendix 2). Each adult was sexed, weighed to the nearest 0.05 kg with a spring balance and

measured to the nearest 0.5 cm with a tape measure (standard length). Scale samples for later ageing were also collected (Appendix 2).

Spawners were stripped and the eggs fertilised using the "dry method" described by Murray (1980) and Piper et al. (1982). Eggs and milt from several males and females were mixed in a clean dry bucket, washed well with stream water and poured into a 2 L glass jar. The jar was filled with water and placed in the stream, out of direct light for at least two hours, to allow water hardening of the fertilized eggs. Jars of fertilized eggs were transported to the lab in coolers filled with stream water.

Wild Coho Fry Capture and Handling

Starting in May of 1982, wild coho fry were collected at two to three month intervals from several sites in each study stream (Figures 1 and 2). Resident juvenile coho were collected with baited Gee minnow traps and 10 m x 2 m and 3 m x 1.5 m marquesette mesh pole seines. The minnow traps were set overnight for periods of 16 to 20 hours. Downstream migrant coho were sampled with a marquesette mesh Fyke net. The Fyke net mouth measured 0.9 m x 0.6 m and the bag was equipped with a floating live box (Figure 4). Catches were identified, counted and the coho placed in holding pens until sampling was completed.

Juvenile coho were transported to the lab in 77 L garbage pails lined with heavy (3 ml) plastic bags. Coho were usually separated into size groupings to prevent predation. The bags were half filled with stream water and fish, inflated with oxygen, securely sealed, packed with ice and covered for the trip. On arrival at the laboratory, the size groupings were checked and the

Figure 4.

The Fyke net used for downstream sampling in the Coldwater River (Photo 1) and Rosewall Creek (Photo 2).

Photo 1 - Rosewall Creek just above tidal influence.

Photo 2 - The Coldwater River at Brodie.

juveniles were transferred to 65 L oval fiberglass tanks. An exchange rate of approximately 5 $L.min^{-1}$ was maintained through the tanks, which received a natural outdoor photoperiod. Each tank was covered with 2 cm stretch mesh green netting, and provided with submerged cover (plastic cylinders and pieces of brick). The wild fish were fed an equal mixture of Tetramin Tropical Fish food and Clarke's New Age Trout food twice a day, and available live food (gammarids, tubifex, mealworms, earthworms etc.) once a day while the experimental tests were being conducted.

EXPERIMENTAL GROUP MAINTENANCE

Temperature, pH, conductivity and dissolved oxygen measurements were monitored with the same equipment mentioned under Field Methods. Light intensities over rearing and experimental equipment were measured with a Li-Cor LI-185A Quantum/Radiometer photometer (accuracy 1% of full scale).

Incubation and Emergence

Incubation was carried out in temperature controlled incubators described by Murray (1980). About half of the eggs of each study population were incubated at 2°C (approximating interior stream conditions) and at 6°C (representing coastal conditions).

The egg containers used during incubation differed from those used by Murray (1980). Eggs were placed on a bed of 1-2 cm of "pea gravel" (6.3-9.5 mm diameter) in an aquarium filter box that served to drawn water down over the eggs and through the gravel. The gravel was small enough to prevent the alevins from burying themselves.

Since the eggs are particularly sensitive during the first 20 to 30 days of incubation or until after blastopore closure (C.B. Murray pers. comm.), they were not handled during this period except to remove dead eggs that started to develop fungal problems. After blastopore closure, dead, coagulated or fungus infected eggs were removed every few days until emergence. Individual egg volumes were determined for a sample of 30 eggs from each stream. These data together with laboratory incubation temperatures and incubation survival rates are listed in Appendix 3.

Emergence times were predicted using a graphic technique devised from data provided by Murray (1980). As predicted emergence dates approached, actual emergence was quantified using a modification of Mason's (1976) "choice box" technique. Several incubation boxes containing alevins were placed in a 12 L aquarium covered with black plastic and filled with incubation water. The aquarium was covered with a weighted black plexiglass lid and the whole apparatus was submerged in a larger aerated tank of the same water. After a period of 30 minutes, the lid was slid back 1 cm and alevins were allowed to escape into the surrounding tank for 40 minutes. Three to six replicates were tested for each experimental group and, if an average of more than 20% of the fish exhibited a photopositive response and escaped, the entire group was deemed to have emerged (Appendix 4). Boxes of emerged fry were transferred to rearing troughs and left for 24 hours to complete the emergence process.

Rearing of Experimental Fry

Laboratory incubated groups initially were reared in 95 L rectangular rearing troughs. Once the coho fry reached 1.0 to 1.5 g in weight, at about

3 months, they were transferred to oval 750 L plexiglass tanks where they were reared for the remainder of the study. Rearing densities were kept comparable between populations (Appendix 5).

The various rearing containers were supplied with constantly flowing dechlorinated water. In both types of rearing containers, a constant directional current was established by the orientation of the water inlets. Water was fed into the bottom of the head of each trough, and into the larger tanks at several depths down one side. During rearing, exchange flow rates were manipulated to maintain acceptable dissolved oxygen levels. Initially, water was supplied to each rearing trough at a rate of 3 $L.min^{-1}$. As the fry grew, the exchange rate was raised to 5 $L.min^{-1}$. The larger plexiglass tanks initially were supplied at a rate of 5 to 6 $L.min^{-1}$, but as the fish grew this was raised to 8 to 10 $L.min^{-1}$. During periods of high temperature and thus lower dissolved oxygen in late September and October (1982), the flow rates were increased to 10 to 12 $L.min^{-1}$.

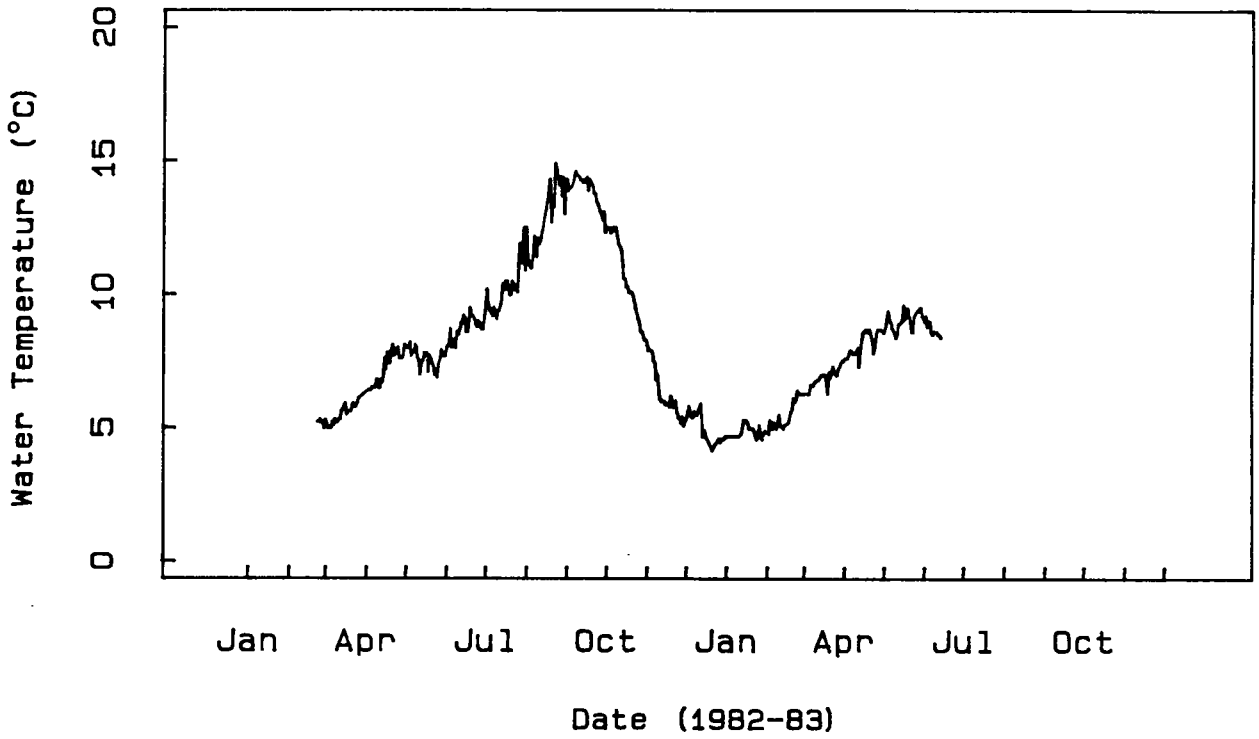
Rearing temperatures were not manipulated; thus they fluctuated seasonally and represented only coastal rearing temperatures. Temperature was monitored daily at a set time (12:00 hours). Water temperature ranged from 4.0°C on January 4, 1983 to 14.8°C on September 12, 1982 (Figure 5).

Dissolved oxygen levels, pH, total ammonia and flow were monitored weekly until July 1982 and then twice a month for the duration of the study (Appendix 5). Total ammonia nitrogen (NH_3-N) levels were measured with a Hach Model NI-8 kit (to the nearest 0.05 mg NH_3-$N.L^{-1}$). Dissolved oxygen levels during the study ranged from 6.2 $mg.L^{-1}$ at 14.4°C (61% saturation) to 11.4 $mg.L^{-1}$ at 8.2°C (96.8% saturation), while pH ranged from 6.0 to 7.0.

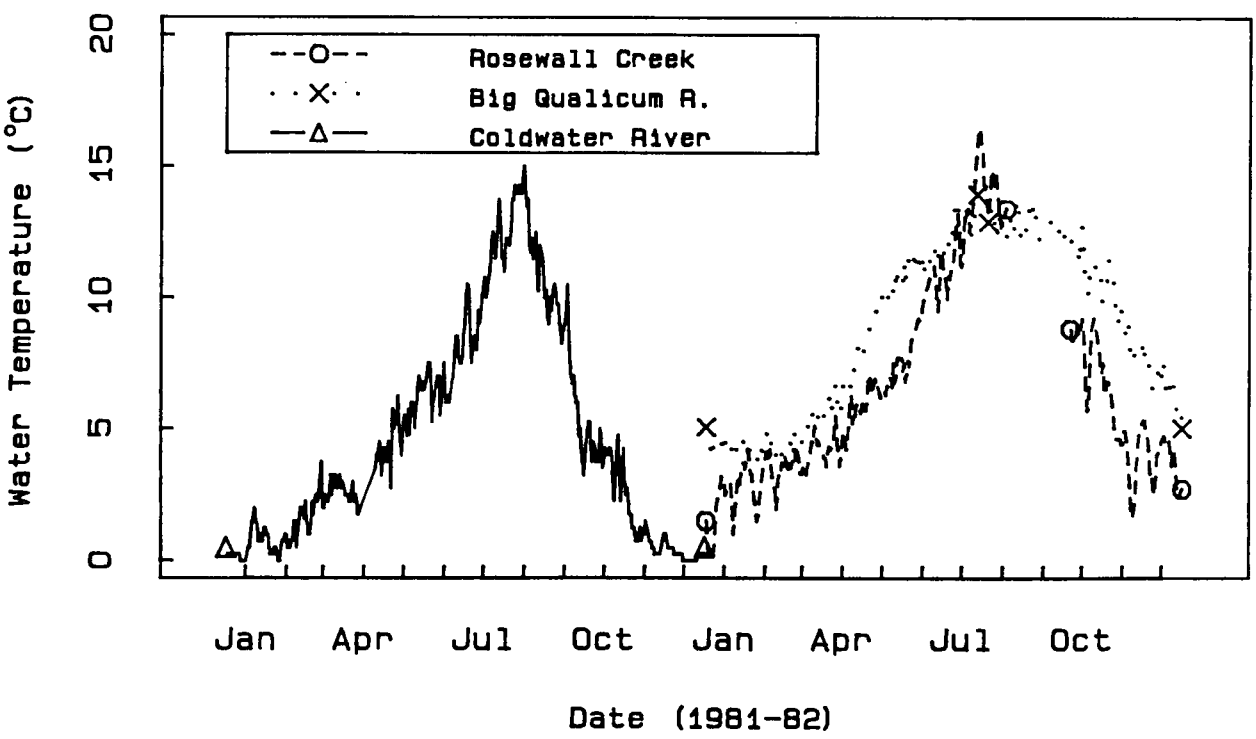
Figure 5.

Seasonal temperature changes in the laboratory and study streams.

Laboratory Temperatures



Study Stream Temperatures



Total ammonia nitrogen levels were rarely above 0.05 $mg.L^{-1}$, which was the lowest readable level of the kit, but on several occasions ammonia levels did rise as high as 0.25 $mg.L^{-1}$. Such increases resulted in an immediate thorough cleaning of the problem container. Buckley (1978) listed levels of 0.45 mg NH_3-$N.L^{-1}$ as toxic.

Observable problems with incoming rearing water were also monitored. The only problems recorded were suspensions of silt during December 5 to 19, 1982 and on October 2, 1982 and January 1 to 3, 1983.

Following emergence, fry were fed on ground Tetramin Tropical Fish food every half hour to hour during daylight for the first few days. Over the remainder of the first two weeks, an mixture of ground Clarke's New Age Trout food and Tetramin was dispensed 6 to 8 times a day using automatic feeders. Finally, the coho were fed 2 to 3 times daily on Trout food, with the pellet size roughly following the Oregon Moist Pellet feeding chart. Feeding was to satiation and no attempt was made to control growth rate through food rationing. Except when ammonia levels were high, tanks were cleaned weekly and troughs every few days.

All laboratory reared fry were exposed to a natural photoperiod, calculated for 50° N latitude. A system of timers, an automatic dimmer switch, and frosted incandescent (25 W) and fluorescent (40 W) lights were arranged (one set per trough or tank) to approximate dawn and dusk shifts in light intensity and timing, as well as a natural photoperiod. The inclusion of a dawn-dusk dimmer system was deemed necessary after observing that coho fry are stressed by a rapid shift between darkness and full illumination.

The automatic feeders were connected to the fluorescent light timer so that feedings occurred only during full illumination.

An interruption in the water flow on September 10, 1982 to the stock treatment of Rosewall Creek fish incubated at 6°C resulted in substantial mortality (>95%). To allow the experiments to continue, approximately 1,000 coho fry were obtained from the Big Qualicum River Hatchery on October 28, 1982. Since the two systems share biophysical features, and since Big Qualicum coho were transplanted to Rosewall Creek during experiments in the 1970's (Bilton 1978, Bilton and Jenkinson 1980), the genetic makeup and life histories of the two stocks were presumed to be similar.

WEIGHT AND LENGTH MEASUREMENTS, AND AGEING PROCEDURES

Starting one month after emergence, and at approximately monthly intervals thereafter, a sample of fry from each stock and incubation treatment was measured for weight and length. Ten fry from each experimental replicate were measured, for a total of 80 fry per a stock treatment. Wild fry brought back to the laboratory were also measured within a day or two of capture.

Coho were anaesthetised with 2-phenoxyethanol (0.25 $ml.L^{-1}$), weighed moist to the nearest 0.01 g on a Sartorius Model 1219MP balance and measured to the nearest 0.5 mm on a smolt board. While lengths are given as fork length in the study, samples were also measured for standard and total length, and conversion equations are given in Appendix 6. The length definitions given by Ricker and Meerman (1945) were used.

Coho scale samples were aged by fixing the separated scales between two microscope slides and reading them with a Nikon binocular compound microscope or a Leitz scale reader. Adult coho scales were imprinted on acrylic sheets and read using an overhead projector at the Department of Fisheries and Oceans.

Significant differences in size were tested for between stocks and treatments to examine the potential for size effects on the physiological and behavioural responses studied. Comparisons also were made to see if migrant fry differed in size significantly from resident fry.

EXPERIMENTAL TECHNIQUES

Three juvenile life history traits which might vary in response to environmental differences were monitored at approximately monthly intervals on each stock and incubation treatment, and at 2 to 3 month intervals on wild samples. Life history characters included plasma sodium regulatory ability, current response and salinity preference. Laboratory raised groups were monitored beginning one month after emergence.

Plasma Sodium Regulatory Ability

The osmoregulatory ability of coho juveniles was tested using the seawater challenge test described initially by Clarke and Blackburn (1977). The test measures the ability of coho to regulate the concentration of sodium in the blood plasma after 24 hours in seawater (salinity of 29 to 30 ppt). This test was chosen over survival, or tolerance of seawater, because coho are capable

of entering seawater some 6 to 7 months before actual migration to the sea (Conte et al. 1966), even though physiological stress will limit subsequent activity and growth (Canagaratnam 1959, Otto 1971). Plasma sodium concentration is a good index of osmoregulatory ability because sodium chloride (NaCl) is a major osmotic component in extracellular fluid (Clarke and Blackburn 1977). The relative simplicity of the methodology, combined with the sensitivity of sodium ion measurement using a flame photometer, were important advantages in selecting this method. Handling techniques were, however, modified to meet the requirements of the study.

Test containers consisted of 90 L rectangular plastic garbage pails lined with a 3 ml plastic bag. Water in these containers was kept to within 1°C of rearing water temperatures by running freshwater from the same source through cooling coils wrapped between the walls of the container and the liner bag. Each container was divided into 9 equal sections by suspended mesh bags. Suitable dissolved oxygen levels were maintained with air stones, and pH and dissolved oxygen were regularly monitored. Dissolved oxygen levels were kept above 90% saturation, while the pH in seawater was around 7.5 and in freshwater was comparable to rearing pH levels. Experiments were conducted under dawn-dusk and photoperiod conditions identical to those experienced by rearing groups.

For each test, 20 fish were exposed for 24 hours to 29 to 30 ppt seawater while 10 control fish were placed in freshwater for the same time period. Seawater challenge tests usually started around mid-afternoon (14:00 to 17:00 hours) and plasma samples were collected the following afternoon and measured for sodium content the following day. Each test began by gently dipnetting each fish out of the rearing tank, drying it with a soft damp

cloth, placing the fish in a preweighed container of water and recording the weight difference. The fish were then placed into the mesh baskets and suspended in either seawater or freshwater.

After 24 hours, the fish were removed, still in their mesh baskets, anaesthetized in 2-phenoxyethanol, weighed again, measured and sacrificed for a caudal blood sample (Clarke and Blackburn 1977). An IL443 Flame Photometer was used to measure the sodium concentration in 2 or 5 ul aliquots of plasma. Plasma handling procedures followed those outlined by Clarke and Blackburn (1977) and the photometer operating manual (Anon. 1977), except that samples were diluted by an extra factor of two (1:400) (see section on Design and Calibration of Experiments).

Only those fish that passed several criteria were sampled for plasma sodium levels and the data used in subsequent analyses. Test fish were required to be robust and healthy and, following 24 hours in seawater, only those fish which were swimming normally were sampled. In addition, replicates of plasma aliquots were collected for each fish and, if aliquot sodium concentrations differed by more than 5 $mM.L^{-1}$, the data were eliminated.

Mean sodium levels for seawater challenged and control fish were plotted over time to demonstrate the development of osmoregulatory ability. Developmental patterns were compared between incubation treatments within populations to determine incubation effects on plasma sodium regulation, and then compared between populations within incubation treatments to examine stock variation.

Current Response

The current response of different coho populations and groups was examined using a modification of the response channel design outlined by Kelso and Northcote (Kelso 1972, Kelso et al. 1981, Northcote and Kelso 1981).

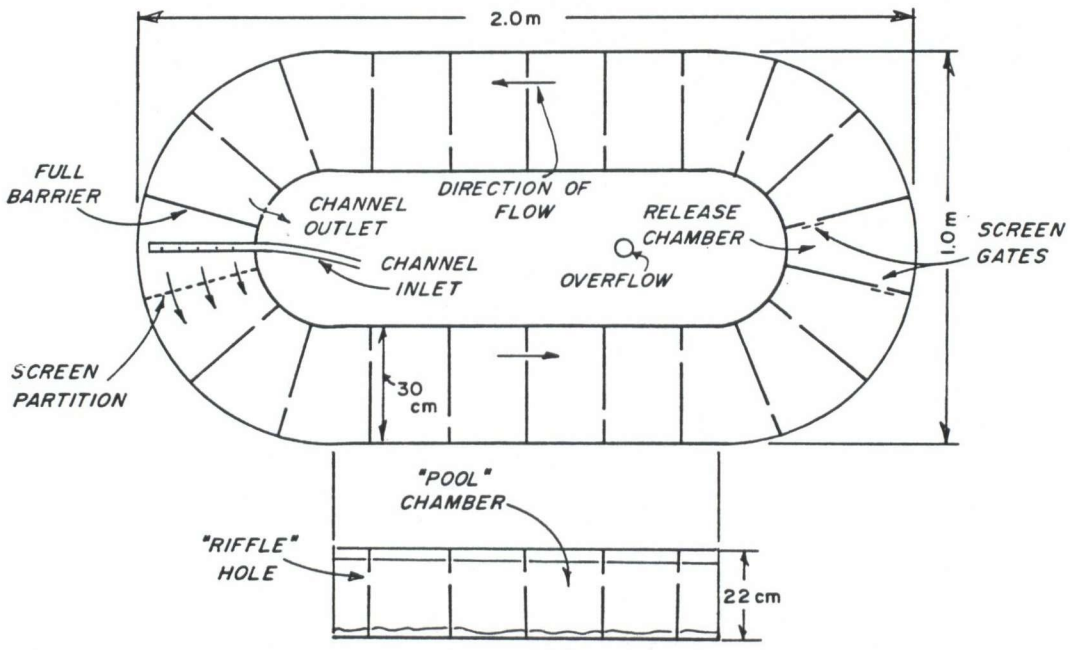
The channels used in this study were built from oval stream channels described by Rosenau (1984), and had a circumference of 5 m, a depth of 0.22 m and a volume of 0.26 m^3 (260 L) (Figure 6). Each channel was divided into 22 chambers with an individual volume of 0.012 m^3 (12 L).

One end of each channel was closed with a fiberglass resin coated plywood barrier. Water was fed into the channel from a central area through a tube on one side of the barrier. This set up a flow around the channel. The first, or inlet chamber, was separated from the second chamber by a screen partition both to prevent fish from reaching the inlet tube and also to partially diffused the inflow current. Each of the successive partitions were of plywood with a 2.5 cm hole positioned at least 2 cm below the channel water level. Water drained back into the central area through a submerged screen in the last downstream chamber. The partition holes were staggered from side to side down the channel to produce a series of 21 accessible "pools" (chambers) separated by "riffles" (holes). A release chamber was provided with mesh gates, which could be raised to allow fish to move through 10 chambers upstream or downstream.

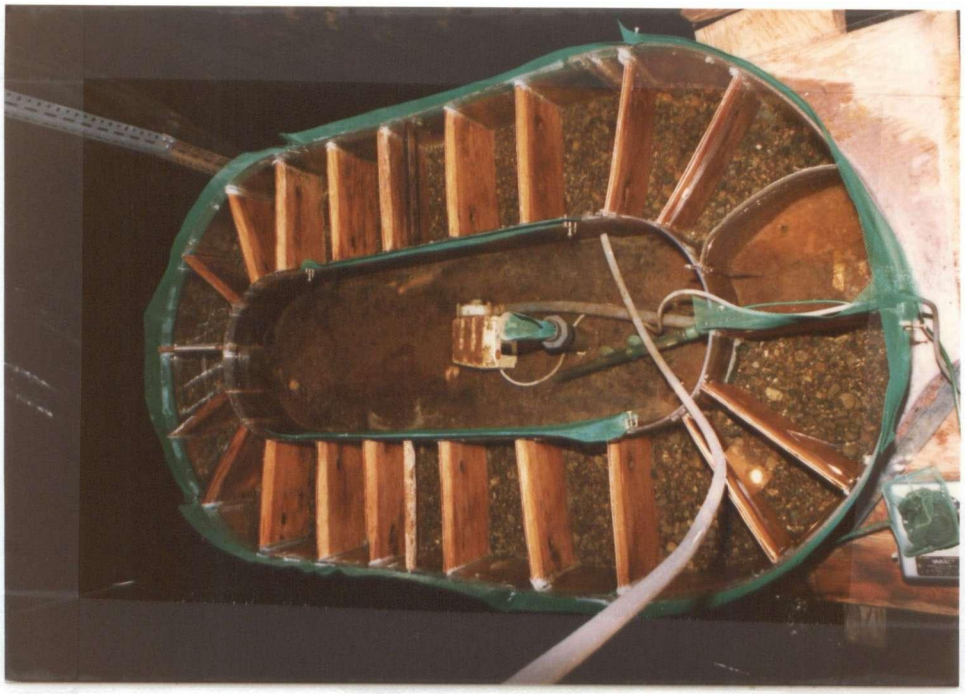
Figure 6.

Current response channel design.

SCHEMATIC TOP VIEW OF A CHANNEL



SCHEMATIC SIDE VIEW OF A PORTION OF A CHANNEL



Three channels, stacked one on top of the other, on an aluminium rack were used in the current response experiments. The rack was enclosed in a darkroom built of Dexion angle iron, plywood and black plastic. Each channel received illumination from two 40 W flourescent lights and 60 W frosted incandescent lights. The intensity of the incandescent lights was controlled by an external dimmer switch. The fluorescent lights were also controlled from outside the chamber. Light intensities at the center of each of the 21 chambers comprising each of the three channels averaged 11.5 ± 0.41 lux, 11.9 ± 0.43 lux and 11.5 ± 0.35 lux.

The starters for fluorescent lights produce a magnetic field and the importance of magnetic orientation during seaward migration of sockeye and chum salmon has been documented (Quinn and Brannon 1982, Quinn and Groot 1983). To check if the starters might cause a localized deviation in the magnetic orientation of the channel apparatus, a field compass (Silva Type 15T) was used to check the orientation at the top and bottom of each chamber. No deviation from the longitudinal NE-SW orientation of the channels was observed. Coho moving upstream and downstream in the channels would, therefore, move in the same general easterly direction.

A single gravity feed holding tank provided with a De Laval milk cooler unit fed water into the central area in each channel. Submerged Little Giant Model 3E-12NDVR pumps then fed water into each inlet chamber. Water from the gravity feed source to each channel was controlled by a valve which could be adjusted to vary the water flow and subsequently the temperature in each channel. An overflow pipe provided a drain for excess water. The exchange rate in each tank varied between 3 and 5 $L.min^{-1}$, and the temperature of each channel was kept to within 1°C of rearing temperatures.

Dissolved oxygen levels were occasionally checked at the most downstream chamber and were routinely greater than 95% saturation.

A second valve between each pump and channel inlet tube was used to adjust the flow rate. Current velocities were set at approximately 10 $cm.s^{-1}$ at each riffle and were monitored with a Nixon Instrumentation Limited Streamflo meter Type 403. On a monthly basis, a full flow regime along each channel was determined (Appendix 7). The velocity used was less than the minimal critical swimming speeds for coho fry (16 $cm.s^{-1}$) and smolts (40.1 $cm.s^{-1}$) (Glova and McInerney 1977), but was greater than the rheotactic threshold for coho (0.4 $cm.s^{-1}$) (Gregory and Fields 1962). Any movements observed, therefore, should have been responsive and not a product of current displacement. Finally, to better simulate stream conditions, the channels were provided with a substrate of sand and pea gravel to a depth of 2 cm.

The test procedure for laboratory reared stocks followed that of Kelso et al. (1981). Because current responses are strongly affected by illumination (Hoar 1958, Northcote 1962, Hartman et al. 1967, Brannon 1972, Kelso et al. 1981), tests were run under both light (diurnal) and dark (nocturnal) conditions. Prior to each test, temperatures were checked and flow levels were noted at the riffles immediately upstream and downstream of the release chamber. Adjustments were made if necessary.

Samples of 20 juvenile coho were used in each test. Test fish were isolated in the central release chamber of each channel by closing the screen gates. Diurnal tests began with a 30 minute acclimation period in the dark. The intensity of the incandescent lights was increased over a 30 minute period,

after which the fluorescent lights were switched on. Fifteen minutes after the test had begun, the gates were raised. Two and a half hours after the test started, the fluorescent lights were extinguished, the incandescent lights were dimmed to half intensity and the distribution of the test fish recorded. The central chamber gates were then closed, the fish returned to the release chamber and a nocturnal test conducted. Nocturnal tests began with an acclimation period (30 minutes) under full illumination, the fluorescent lights were then extinguished and the incandescent lights dimmed over 30 minutes. As with the diurnal test, the release chamber gates were raised after 15 minutes. Two and a half hours into the test, the incandescent lights were raised to half intensity and the distribution of the fish recorded.

A given sample of 20 coho was used for only one set of diurnal and nocturnal tests. In all, 12 replicates of each incubation treatment for each stock were conducted monthly using a total of 240 fry. Test coho were kept separate from the rearing stock until each month's testing was completed.

Wild fish from each population were handled in a similar fashion, although the sample sizes varied with the number of fish collected. Only 6 replicates of each stock per test period were run. Whenever possible, six separate samples were used. When this was not possible, the fish were mixed together after each test, left for at least 24 hours and a new sample taken. Equal sized samples were used during each test period.

A "net rank number" (NRN) scoring system described by Northcote (1981) was used to quantify the directional response of each sample. A rank number was given to each chamber, with the release chamber zero, upstream chambers +1 to +10 and downstream chambers -1 to -10 (Figure 6).

Following each test, the number of fry in each chamber was counted and the NRN score was calculated as:

$$NRN = \frac{\sum_{i=-10}^{10} (n_i i)}{\sum_{i=-10}^{10} n_i} + 10$$

where i = the chamber rank number and
n_i = the number of fish in chamber i.

The constant of 10 was added to maintain positive scores. Thus a score of more than 10 indicated on average an upstream response, while a score of less than 10 indicated a downstream response. A score of 10 indicated the sample maintained position.

NRN scores under light and dark conditions were plotted over time for each treatment and stock to portray the ontogeny of current responses. As with the seawater challenge data, the trends in NRN scores were compared between incubation treatments within stocks to determine incubation temperature effects and between stocks within incubation treatments to examine stock variation.

Salinity Preference

Salinity preference was tested using a modified Staaland device (Fivizzani and Spieler 1978). The modified Staaland device is a channel divided by a series of baffles which effectively provide a horizontal gradient of discontiuous salinities maintained by differential densities (Staaland 1969).

The device has been used to monitor the movements of eight Fundulus grandis, 6 cm in length, with no significant instability in the gradient (Spieler et al. 1976). Each channel used in this study was 1.8 m long, 0.18 m wide, 0.5 m deep and was divided into 6 chambers (salinities) by 11 baffles (Figure 7). The baffles separating chambers and salinities were 0.3 m deep and overlapped 0.15 m.

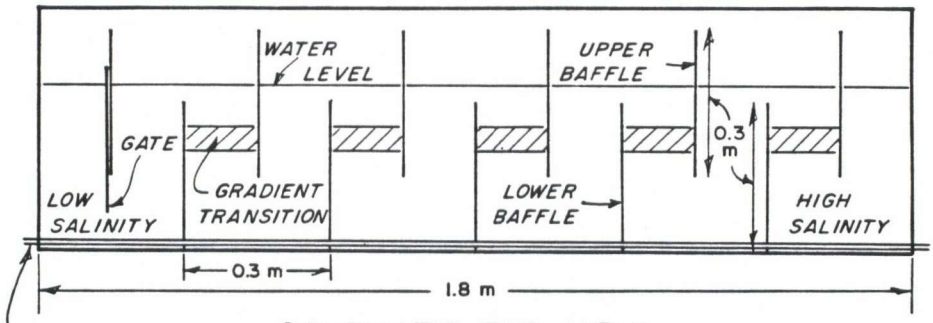
Four channels were attached longitudinally to provide a bank of test gradients. The sides, ends and bottom of the channels were made of white plexiglass (15 mm thick), while the baffles were made of black plexiglass (5 mm thick). Colouring the baffles black orients exploration by test fish along the longitudinal axis of the channel and thus reduces the "trial and error" time required to negotiate the channel (Fivizzani and Spieler 1978). All of the interior surfaces were roughened with steel wool to reduce reflection. A pulley operated plexiglass gate was used to allow isolation of one end chamber in each channel. The isolated chambers served as release sites, and were alternated end to end from channel to channel to reverse the direction of the incremental salinity gradients. This design served to lessen the effect on the results of outside stimuli such as variations in light intensity and magnetic field.

The four chambers were submerged, up to the gradient water level, in a elongated fiberglass trough through which water from the same source as the rearing water was passed to regulated gradient temperatures to within 1°C of rearing temperatures. A line of silastic medical grade tubing (3.35 mm ID x 4.65 mm OD; Dow-Corning catalogue number 601-335) was run down the middle of each channel about 2 cm from the bottom. Each tube was connected at both ends to an oxygen cylinder. Oxygen was fed into the tubes at about

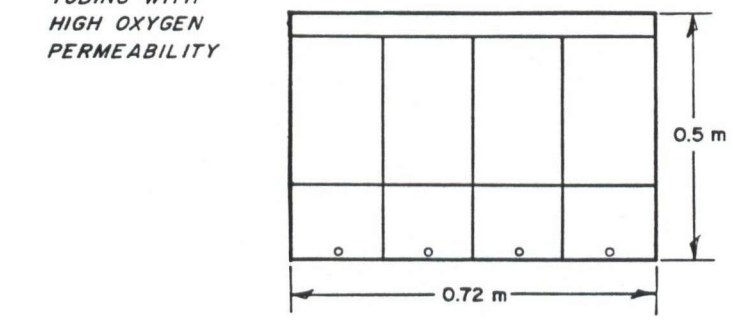
Figure 7

Salinity preference channel design.

SCHEMATIC SIDE VIEW OF A SINGLE CHANNEL



SCHEMATIC END VIEW



5.8 $kg.cm^{-2}$ (100 psi) pressure, and diffused evenly into each chamber along the length of each channel. Dissolved oxygen levels were checked following a number of tests involving a variety of different sized test fry. Dissolved oxygen levels ranged from 7.6 $mg.L^{-1}$ at 12°C to 11.1 $mg.L^{-1}$ at 11.2°C (71-100% saturation). As noted by Otto and McInerney (1970), dissolved oxygen gradients are unavoidable because of differences in oxygen solubility at different salinities.

Salinities were mixed by volumetrically combining freshwater and 30 ppt seawater and checking the resulting solution with a hydrometer and density-salinity tables (Jorgensen 1979). To establish a gradient, each channel was filled with the appropriate salinity, and then water of the lowest salinity in the gradient was added slowly until the water level was 4-5 cm over the tops of the lower baffles. Towards the end of filling the channel, water of the highest salinity in the gradient was added at the opposite end to ensure shifts in salinity were sharp. Salinity gradients were usually established the day before a test and allowed to stabilise in temperature.

Following each test, the maintenance of the gradient in one randomly selected channel was checked by withdrawing 10-20 ml of water at four set depths (surface, 6 cm, 12 cm, and the bottom), measuring sample conductivity and determining the corresponding salinity. Temperatures were measured at the same depth. Salinity gradients were well maintained throughout the tests, although temperatures occasionally varied as much as 1.5°C along a channel.

The salinity preference apparatus was surrounded by a plywood, black plastic and angle iron enclosure extending approximately 2 m above the top of

the channels. The enclosure was open to natural light and provided with the added illumination of two centrally located 40 W fluorescent lights positioned 1 m above the channels. Light intensities averaged (n=12) 5.4 ± 0.09 lux, 5.5 ± 0.09 lux, 5.4 ± 0.14 lux and 5.4 ± 0.15 lux along each of the four channels. Because previous studies noted no diel shifts in preference (Baggerman 1960, Otto and McInerney 1970), tests were conducted during both the morning and afternoon.

Distributions of fry in the four channels were viewed through two mirrors, located at the top of the enclosure and at about a 45° angle to the channels. The observer sat to one side of the enclosure and could watch fish movements in each of the channels.

Salinity preferences were tested in two seawater gradients, 0 to 20 ppt and 4 to 24 ppt. These gradients were chosen because acclimation to a slightly saline solution, as might occur in estuarine conditions, can subtly shift salinity preferences (Otto and McInerney 1970). Salinities in the 20 to 24 ppt range are below normal coastal salinities, but reflect the range encountered by coho migrating into the southern Strait of Georgia in late spring and early summer when the area is affected by the Fraser River freshet discharge (Waldichuk 1952, Thomson 1981). For each test, 0 to 20 ppt and 4 to 24 ppt salinity gradients, and freshwater and 4 ppt salinity controls were established in separate, randomly selected channels. Four replicates of each gradient and control for each stock treatment were run each month.

The test procedure began by placing 5 juvenile coho in each closed release chamber. Test fry were left for an acclimation period of at least 30 minutes,

after which the gates were raised and the fry allowed to explore the channels for two hours. The distribution of fish in each channel was observed at one minute intervals for four 20 minute periods over the next two hours. As a result, 400 observations were collected for each replicate.

Each channel, when viewed from above, had 12 sections. In a gradient, every second section represented a pure salinity while the intervening sections represented gradient shifts. Since the vertical position of coho in the gradient shift sections was unknown, the number of observations in these sections were divided proportionately between the adjoining pure salinities. This resulted in a distribution over six salinities. Control distributions were treated in a similar manner.

Control and test replicate distributions were pooled and compared. When the distributions were not significantly different, slight deviations in frequency peaks could unrealistically change modal preferences. Therefore, when not different, the data were eliminated from further analyses. Previous workers have noted an "end on" effect or a tendency for test fish to orient towards the release chamber (Houston 1957, Hurley and Woodall 1968, Williams 1969, Otto and McInerney 1970). To avoid such a problem, the control distribution was subtracted from the related test distribution. Modal preferences were then plotted against time for each stock and incubation treatment, and discussed as to incubation treatment effects and stock variation.

STATISTICAL METHODS

Standard parametric and nonparametric techniques (Sokal and Rohlf 1981) available in several software statistical packages were used throughout the thesis. Data sets were routinely checked for normality using a graphic method (Sokal and Rohlf 1981) or a Shapiro-Wilk test (Minitab Release 5.1 (MTB51); Ryan et al. 1985). When necessary, continuous data were $\log_{10}$ transformed, counts were square root transformed and proportions were angular transformed to improve normality and reduce variance.

Comparisons between normal data sets were conducted with appropriate t-tests or analyses of variance (ANOVA) (UBC GENLIN; Greig and Bjerring 1980) after equality of variance was tested using an F-max or Bartlett's test. Unplanned multiple comparisons of means were carried out using a T-method, Tukey-Kramer's test or T'-test (Sokal and Rohlf 1981) or a pairwise comparison, Dunnett's test (Steel and Torrie 1980). When sample variances were heteroscedastic, a t'-test or the Games and Howell method were used to approximately test for equality of means (Sokal and Rohlf 1981). Nonparametric data sets were compared using the Mann-Whitney U test (MTB51). Unplanned multiple comparison by nonparametric STP test was then used to group data sets (Sokal and Rohlf 1981).

To test for differences between growth trends for wild and experimental groups, regression analyses were carried out on $\log_{10}$ transformed weight and time data. Consecutively numbered days, over a two year period (1-730 days), were used as time units. Regression lines were then compared using analyses of covariance (ANCOVAR) (BMPD P-IV; Dixon 1981).

Salinity preference data were plotted as the mode of net gradient distributions over time. In general, preference data has been describe as the mode of a preference distribution (Hurley and Woodall 1968, Otto and McInerney 1970). Prior to determining the net distribution, however, control and test distributions were compared with a Mann-Whitney U test and the data omitted from the plots if no significant difference was observed. Best fitted lines were applied to the plots of modal preference points using "lowess", a smoothing program in S (Becker and Chambers 1984). Program parameters were standardized at default which comprised the fraction of data used in smoothing each point f=2/3, the number of iterations iter=3, and the interval size delta=1% of the range of x=log(time).

Tabulated data are generally listed as a mean and one standard error of the mean. When plotted, data are shown as the mean with 95% confidence limits.

DESIGN AND CALIBRATION OF EXPERIMENTS

The following tests and analyses were carried out to establish the design of the experiments and particularly to calibrate the behavioural experiments. Calibration of the various apparatus under nonexperimental conditions was essential to the interpretation of responses observed under experimental conditions. The tests are discussed only briefly here; additional descriptions and full results are given in the appendices (Appendix 8).

Plasma Sodium Regulatory Ability

Timing of Sample Collection

Clarke and Blackburn (1977 and 1978) observed that when plasma sodium concentrations approach 170 $mM.L^{-1}$ after 24 hours in seawater, coho are capable of growing in salt water and have apparently physiologically smolted. Other workers, however, have suggested migratory or smolted coho require 30 hours to initiate osmoregulation (Conte et al. 1966) or 36 hours to adapt to seawater (Miles and Smith 1968). Presmolt coho, on the other hand, appear to require 4 to 7 days of acclimation to develop an operational sodium pump (Folmar and Dickhoff 1979). To reaffirm that a 24 hour sampling period was acceptable for separating smolted and non-smolted coho, particularly considering the handling and confinement procedures used in this thesis, a time series of sampling was conducted on both coho fry and smolts.

Plasma sodium levels for fry and smolts appeared to peak after 6 to 8 hours in seawater (Appendix 8, Figure 1). This is somewhat earlier than the 16 hours observed by Clarke and Blackburn (1977) or the 24 to 48 hours reported by Folmar and Dickhoff (1981). Within both the fry and smolt groups, mean sodium concentrations were not different between 24 and 48 hour periods (t-test, $p > 0.05$) (Appendix 8, Table 1). This indicates that adaptation was generally complete. Thus, plasma sodium levels measured after 24 hours in seawater appear to be a good measure of the preacclimation osmoregulatory capacity of coho juveniles.

Dilution and Range Setting Effects on Photometric Readings

Under normal circumstances, the IL443 Flame Photometer uses a 140 Na^+/5 K^+ calibration standard diluted 1:200 in a 15 mEq $Li^+.L^{-1}$ "blank" solution (Anon. 1977). Plasma samples receive the same dilution treatment and sodium concentrations are read directly from a digital readout. This photometer, however, is a clinical instrument designed to measure sodium concentrations in human fluids. These fluids give measurements of 3.5 mM $Na^+.L^{-1}$ (saliva) to 180 mM $Na^+.L^{-1}$ (urine) (Anon. 1977). Consequently, the machine is limited to a 0 to 199.9 mM $Na^+.L^{-1}$ range. Because, in coho, plasma sodium levels often exceed 200 mM $Na^+.L^{-1}$, certain modifications in measurement techniques were necessary to reach the actual sodium concentration. Such modifications could include changes in calibration standard and sample dilution and adjustment of the range settings on the photometer.

To examine how several alternative modifications affected the plasma sodium values measured by the photometer, plasma samples from fish held in fresh and salt water were divided between four different treatments (Appendix 8). One of these was equivalent to the recommended techniques and served as a control. Plasma sodium values under the four treatments were not different among fish held in fresh or salt water (ANOVA, $p >> 0.05$) (Appendix 8, Table 2). Mean sodium values, however, were highest in the control treatment. A treatment in which samples were diluted 1:400 and the resulting readings increased by a factor of two was selected for use in this study.

Handling and Confinement Effects

For non-smolted coho exposed to seawater for 24 hours, mean plasma sodium levels in this study were generally higher than expected (Conte et al. 1966, Clarke and Blackburn 1978, Clarke et al. 1981). Coho involved in the seawater challenge tests first were weighed and confined in mesh bags during the tests. Perhaps this handling and confinement produced the higher than expected plasma sodium levels through a stress induced hydromineral and osmotic imbalance (Schreck 1981). Pretest weighing, however, was considered necessary since hypertonic tissue water loss during saltwater adaptation can result in weight loss (Miles and Smith 1969). Confinement was required to allow later analysis of weight versus plasma sodium relationships.

To test the effects of handling and confinement, samples of coho smolts received three different treatments while exposed to either fresh or salt water. As a control treatment, coho were not weighed prior to salt water exposure and were not confined. Two other treatments involved various levels of handling and confinement (Appendix 8). Care was taken to eliminate fish size as a factor in plasma sodium values (Appendix 8, Table 3).

Handling and confinement produced significant differences between treatment sodium plasma means in both fresh (Games and Howell method) and salt water (ANOVA, $p < 0.01$) samples (Appendix 8, Table 3). Mean values were highest, however, under the control treatment. Consequently, the results of this test do not explain the higher than expected sodium levels observed among seawater adapted coho. Confinement, however, appeared to partially compensate for the effects of pretest weighing (treatment 2 compared with treatment 3; Appendix 8, Table 3). Recent work suggests that both test

container dimensions and the time the fish are in anaesthetic following a test contribute to raised plasma sodium levels (Blackburn and Clarke 1987). These same conditions probably contributed to the higher than expected sodium values observed here. Although plasma sodium levels were high with pretest weighing and confinement, they were consistently high and thus the seasonal patterns examined in this study should not have been differentially affected.

Current Response

Timing of Distribution Collection

The technique for measuring current response followed Kelso (1972) and Northcote (1981) including their schedule of observations. This schedule starts collecting distributional data 2.5 hours after the test begins. Other current response studies use a variety of periods (16-30 minutes to 24-48 hours), often variable within a study, before data collection (McKinnon and Hoar 1953, Brannon 1967 and 1972, Raleigh 1967 and 1971, Raleigh and Chapman 1971). In these studies, the time fish were allowed to show a response appeared to be partially dependent on the design of the response device. Since the channels used in this study differed from those used by Kelso (1972), the effects of exploration time and the time of data collection were investigated (Appendix 8).

To examine such effects, movements of several samples of coho were observed over a 4.0 hour period under light and dark conditions. The data suggest that movement away from the central release chamber was stable after 3.0 hours, but movement to the ends of the channels continued throughout

the 4.0 hour experimental period and probably would have continued until all fish had explored the channel to its ends (Appendix 8, Figures 2 and 3). Since the main movement out of the release chamber occurred before 2.0 hours, 2.5 hours appeared to be a reasonable time for collecting observations providing the distribution attained by that time was relatively comparable to later values. Under light conditions, distributions were not significantly different over the entire observation period (0.5 to 4.0 hours), but under dark conditions distributions changed significantly for the first 1.0 to 1.5 hours and then remained relatively stable (Appendix 8, Table 5). These observations suggest that the data collection schedule used by Kelso (1972) and Northcote (1981) was acceptable under the modified test conditions.

Salinity Preference

Test Sample Size, Exploration Time and Gradient Stability

In past salinity preference experiments on Oncorhynchus, responses to a gradient were examined for single fish (Otto and McInerney 1970) or schools of 5-12 fish (Houston 1957, Baggerman 1960, McInerney 1964, Hurley and Woodall 1968, Williams 1969) using exploration periods of 1.0 to 2.0 hours. In vertical gradient tanks, groups of pink (O. gorbuscha) and sockeye (O. nerka) juveniles were used to take advantage of the narrow distributions that result from schooling (Hurley and Woodal 1968, Williams 1969). Coho, however, are aggressive until after they smolt (Chapman 1962) and this may explain why Otto and McInerney (1970) used single fish. Fivizzani and Spieler (1978) observed that, in a Staaland channel, test fish (Fundulus grandis) explore each partition before moving to the next and that this "trial and error" behaviour increases the time needed to search the channel.

Perhaps the intraspecific aggression displayed by coho could reduce search time by interrupting this tendency to explore each chamber.

To determine an adequate sample size and exploration period for this experiment, groups of 1 to 5 coho were observed as they explored the channels in freshwater over a 4.0 hour period (Appendix 8). Generally, the number of coho that reached the opposite end of a channel from the release section increased with group size. This suggests that interactions within the group may reduce exploration time. The time required to reach the end of the channels ranged from 0.5 to 4.0 hours, but as group size increased the majority of fish explored the channels within 1.0 to 2.0 hours (Appendix 8, Table 6). From these observations, a standard exploration period of 2.0 hours for a group of 5 coho was established.

To check gradient stability, salinity gradients were examined before and after 5 large coho juveniles were allowed to explore separate gradients of 0 to 20 ppt and 4 to 24 ppt for 24 hours. The results indicate that, even after 24 hours, their activity was not sufficient to alter the gradient significantly (Appendix 8, Table 7).

Timing of Distribution Observations

With test groups of 5 coho in 4 channels, only 20 observations could be taken at any one time. To arrive at a distribution within a salinity gradient sufficient to indicate salinity preference, observations were collected over a period of time and then pooled. Qualitative observations suggested that once coho explored an entire channel, they continued to explore but over a narrower range of sections. Shifts in salinity preference over short term

observation periods, however, have been observed for both sockeye (Williams 1969) and coho (Houston 1957, McInerney 1964). Consequently, tests were conducted to determine how variable distributions were after the 2.0 hour exploration period (Appendix 8).

The standard test procedure was used and the position of two stocks of fish documented every 15 minutes for 4 hours. The distributions of Rosewall coho fry were not significantly different after 0.5 hour, whereas Coldwater fry distributions were comparable only after 1.5 hours (STP method) (Appendix 8, Table 8). It was concluded that such observations could provide a salinity preference distribution if collected from 2 to 4 hours after the sample was released to search a channel.

Possible Biases Caused by Preference Channel Design

After several months of collection and analysis of salinity preference data, it became obvious that the design of the modified Staaland channel tended to bias fish distributions within the channel. This problem is probably not confined to my methods, but it should be kept in mind when examining the results. Salinity preference data is affected by a tendency for test fish to limit their movements to the vicinity of the release chamber or to concentrate explorations near the confined ends of the various test devices. The latter effect is known as an "end on" effect (Houston 1957, Hurley and Woodall 1968, Williams 1969, Otto and McInerney 1970). In my tests in freshwater or in 4 ppt seawater, coho tended to prefer the release site or far end of each channel. The end on effect, however, was further modified by other design aspects. As described previously, counts were pooled according to the salinity present in a given section of the channel. In most cases, this meant

that the number of observations at any salinity was made up of the count for that salinity section plus a proportion of the observations from the two adjoining sections where gradient shifts occurred. At the release end of each channel, however, the count included the observations in two sections containing either fresh or 4 ppt salt water plus a portion of the observations from the first gradient shift section. Because of this additional area, the counts for the release salinity were even higher than expected. In contrast, at the high end of each gradient (20 or 24 ppt), the opposite occurred. Here counts included the observations from the last pure salinity section plus a proportion of the count for the single adjoining gradient shift section. Consequently, channel area was reduced and this tended to reduce the end on effect and accentuate the counts in the adjacent chamber (Appendix 8, Figure 4).

Design experiments on the salinity preference channels were carried out in April and May. During this period, test fish explored the channels throughout the observation periods and seldom held position for long. By the fall and winter, however, coho were more likely to explore to a certain point and then remain in one section for the entire observation period. This increased the variability in replicate distributions. At this time, the salinity gradients were stable and temperature varied by less than 1°C. Thus, gradient changes did not produce this effect and it was probably a result of low winter temperatures reducing fish activity. In other studies, gradients have been maintained throughout the year at a standard temperature (10°C) (Otto and McInerney 1970), possibly to standardize test fish response rates. In my study, however, seasonal temperature shifts may be important in the development of behavioural responses and so they were incorporated into the study design.

Some of the biases uncovered when calibrating my channel design were compensated for by subtracting control distributions from test distributions, and deleting data sets in which control and test distributions were not significantly different (Appendix 9). The modal preferences observed, however, probably were still at least partially the result of design biases.

Potential Effects of Size and Growth

Seasonal differences in weight can affect each of the traits studied either directly (Folmar and Dickhoff 1981) or indirectly through threshold sizes reached at a given age (Conte et al. 1966). Size is important in seawater adaptation (Houston 1960), seawater survival (Parry 1960, Conte et al. 1966), and time of smolting (Donaldson and Brannon 1976, Clarke and Shelbourn 1982). Size influences swimming performance in young coho (Glova and McInerney 1977) and has been suggested as a possible trigger initiating behavioural changes associated with seaward movement (Bjornn 1971). Size also affects inter- and intraspecific interactions (Chapman 1962, Lister and Genoe 1970) and thus can contribute to fry displacement. Finally, age and/or size are/is correlated with transition in salinity preference (Hurley and Woodall 1968).

To examine variability in growth of the groups used in this study, $\log_{10}$(weight) versus $\log_{10}$(time) were regressed for each experimental group (Appendix 8, Table 9 and Figures 5, 6 and 7) and compared among groups with analyses of covariance. The growth trends in the two wild stocks sampled were significantly different ($p < 0.001$) (Appendix 8, Table 10). Rosewall coho fry appeared to grow faster and were heavier overall than Coldwater River fry. Within incubation treatments, laboratory raised groups

of Coldwater and Rosewall-Big Qualicum coho used in each of the experimental tests also showed differences in growth. These observed differences were usually the result of differences in regression slopes but were not as substantial as those found in the wild stocks. Growth trends were also compared for experimental series within stock and incubation treatment. Growth trends within wild coho and the 2°C incubated fry groups were significantly different (at most $p < 0.001$), while those of 6°C incubated groups were similar ($p > 0.05$) (Appendix 8, Table 11). The differences, however, probably are not sufficient to cause serious variations in the ontogeny of the traits studied.

Since size may contribute to migratory tendencies, the weight of wild captured migratory coho was compared to resident fry of the same stock caught at approximately the same time. Samples included fall and spring migrant fry caught in the Coldwater River, and spring migrants caught in Rosewall Creek. Migrant and resident fry did not differ in size within season in the Coldwater River (t-test or Mann-Whitney U, $p > 0.05$) (Appendix 8, Table 12). Resident fry, however, were heavier than the corresponding migrants in Rosewall Creek (Mann-Whitney U, $p < 0.05$). Size, therefore, may contribute to the spring displacement of post-emergent coho in Rosewall Creek, but not apparently in the Coldwater system.

RESULTS

Plasma Sodium Regulatory Ability

Seawater challenge tests for wild Rosewall (Figure 8) and Coldwater (Figure 9) coho showed a general plateau in sodium regulation until smolting begins during the first or second spring following emergence. Both Rosewall and Coldwater coho exhibited a tendency for lower regulatory capabilities and thus higher plasma sodium levels during the winter months.

Rosewall fry showed a slow decrease in plasma sodium levels, indicating a slow increase in osmoregulatory ability, throughout the year. Rosewall coho physiologically smolted as early as April 7 (aged 1). In contrast, Coldwater fry required at least 2 years to smolt and occasional 3 year olds were caught. No coho smolted at one year in collections from the Coldwater River; however, two smolted, wild, 2 year old fish were caught and tested (May 10 and June 7).

Fall (November 17) subyearlings and a single spring (April 10) migrant (aged 1) from the Coldwater River were tested in the seawater challenge (Figure 9). Fall migrants displayed less ability to regulate sodium levels in seawater than corresponding resident coho (t-test, $p < 0.05$), whereas the spring migrant showed a lower, but not statistically different, plasma sodium value than corresponding resident coho (t-test, $p > 0.05$) (Table 3). No migrant coho from Rosewall Creek and no migrant age 1+ coho from the Coldwater River were tested.

Figure 8.

Seawater challenge test results for
wild Rosewall Creek coho.

The horizontal line at 170 mM $Na^{+}.L^{-1}$ represents the plasma sodium level for physiologically smolted coho (Blackburn and Clarke 1977). Error bars represent 95% confidence limits.

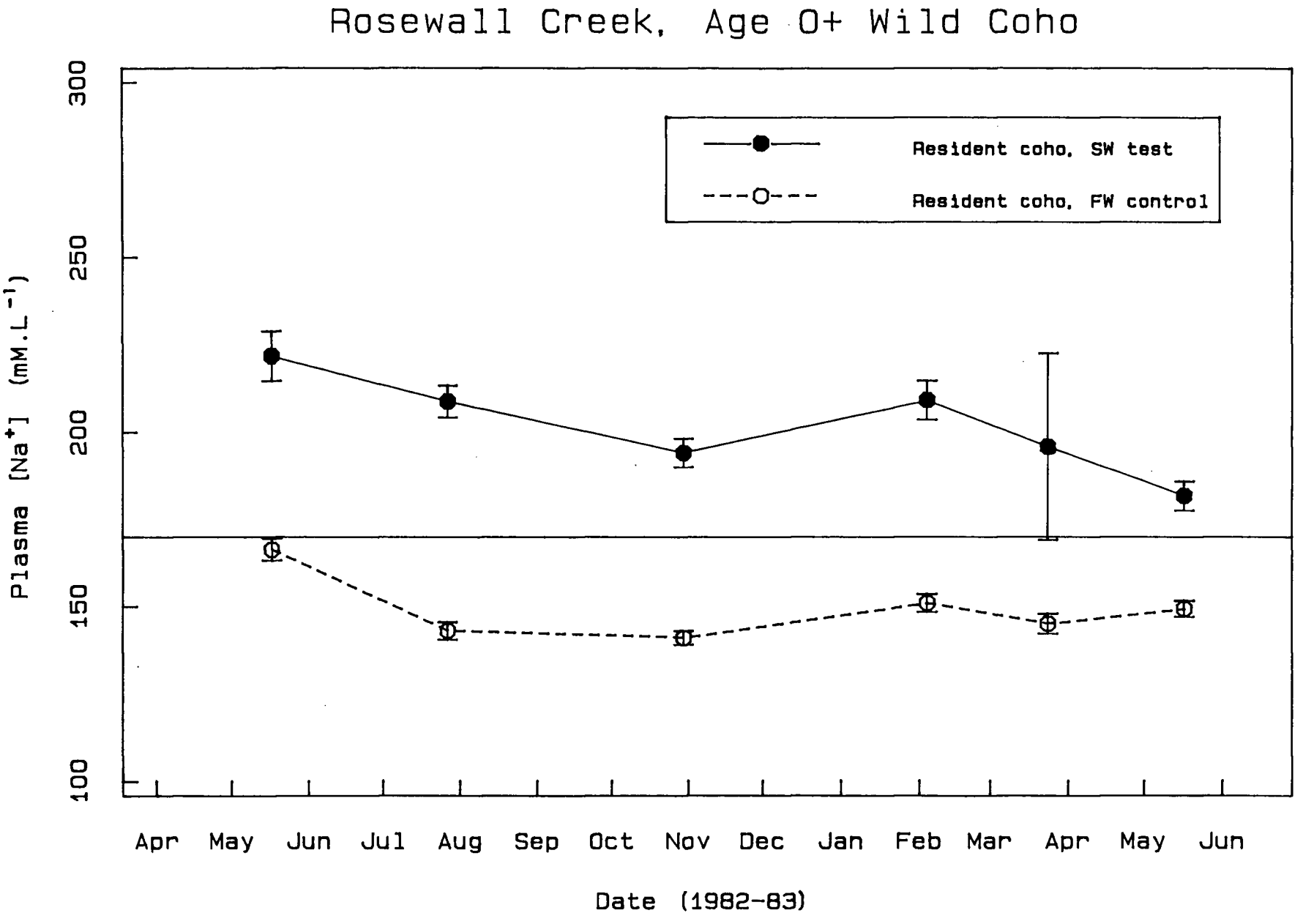
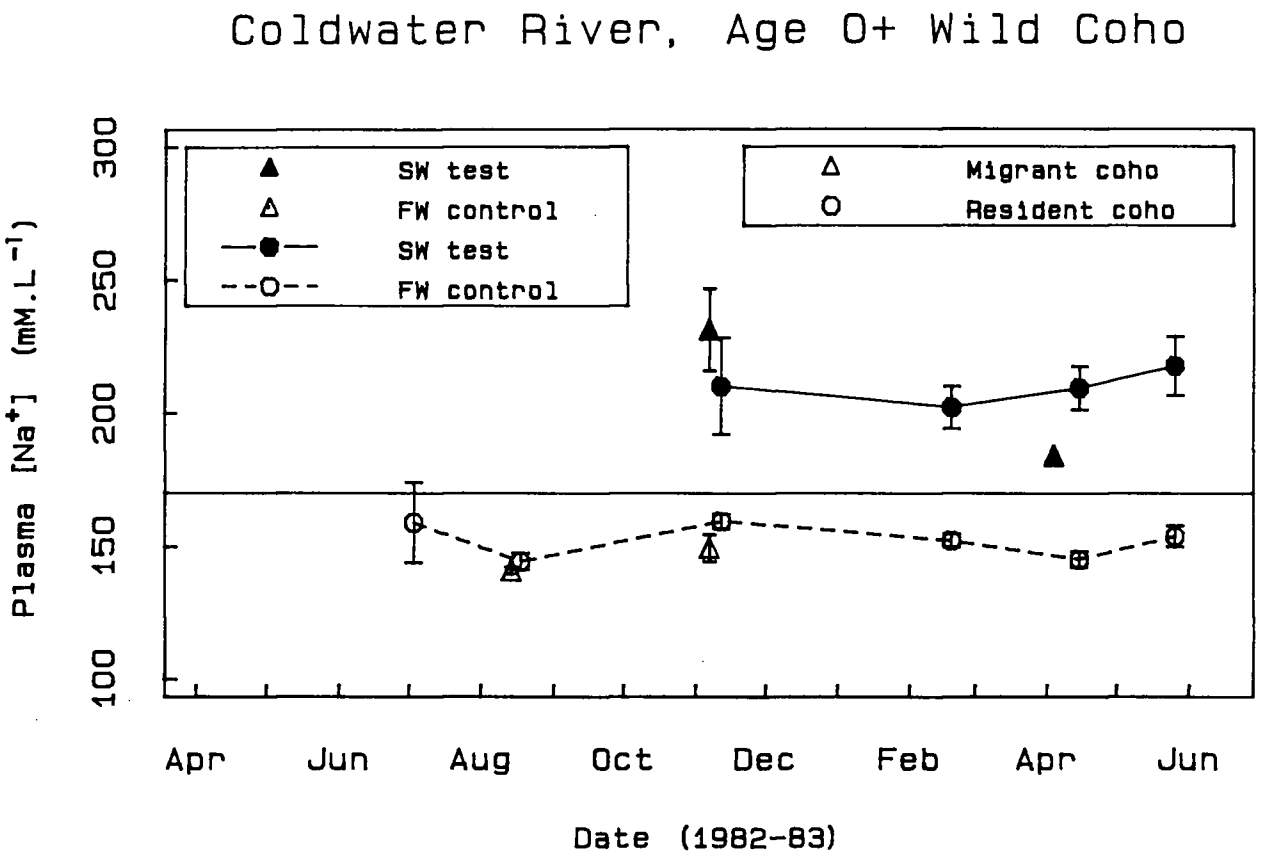

Rosewall Creek, Age 0+ Wild Coho
Resident coho, SW test
Resident coho, FW control
Plasma [Na+] (mM.L-1)
300
250
200
150
100
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Date (1982-83)

Figure 9.

Seawater challenge test results for
wild Coldwater River coho.

The horizontal line at 170 mM $Na^{+}.L^{-1}$ represents the plasma sodium level for physiologically smolted coho (Blackburn and Clarke 1977). Migrant results have been slightly offset from resident results to avoid confusion. Error bars represent 95% confidence limits.


Coldwater River, Age 0+ Wild Coho
SW test
FW control
SW test
FW control
Migrant coho
Resident coho
Plasma [Na+] (mM.L-1)
300
250
200
150
100
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

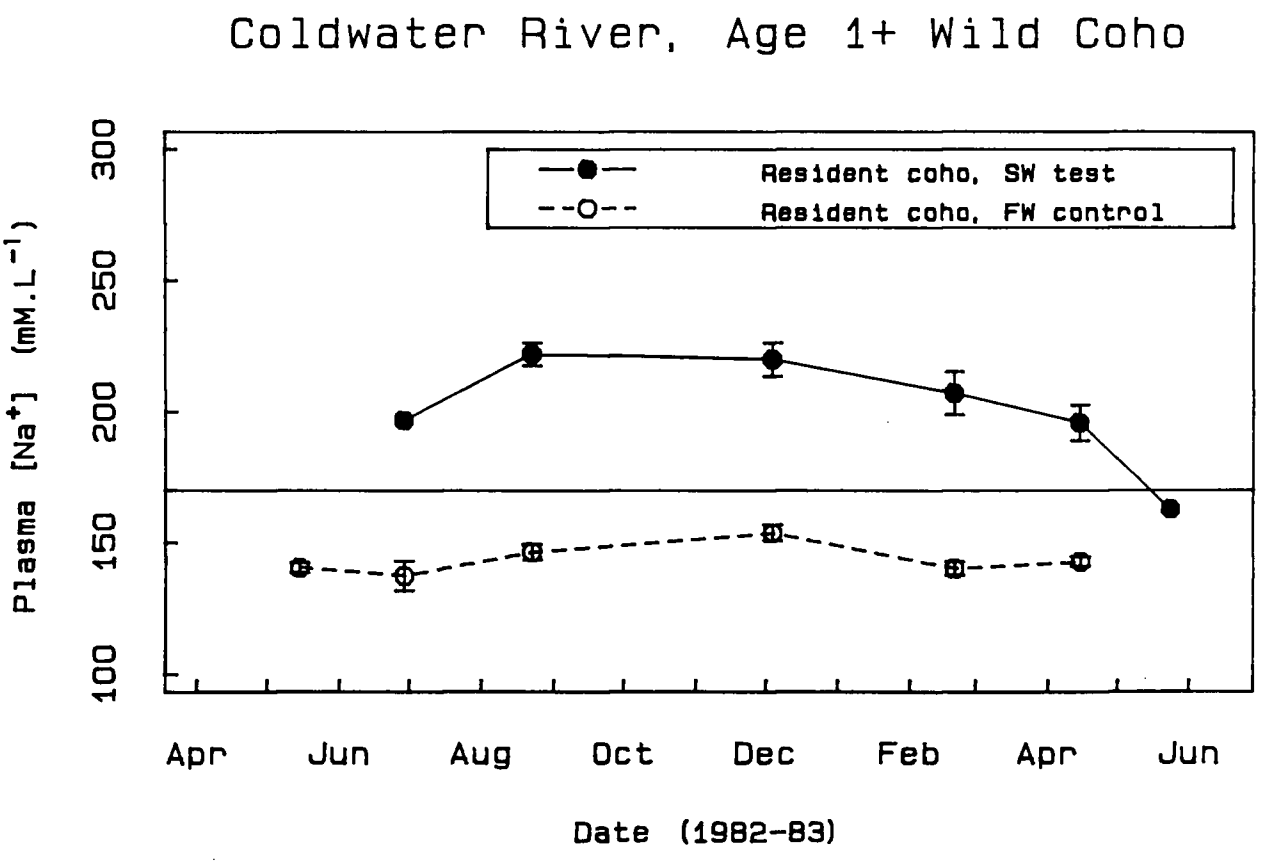

Coldwater River, Age 1+ Wild Coho
Resident coho, SW test
Resident coho, FW control
Plasma [Na+] (mM.L-1)
300
250
200
150
100
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

TABLE 3
COMPARISONS BETWEEN RESIDENT AND MIGRANT COLDWATER RIVER COHO SUBYEARLING PLASMA SODIUM CONCENTRATIONS.

Date (1982-1983)	Fry Capture Status	Sample Size	Plasma Na^+ ($mM.L^{-1}$)	t-test Statistic
April 30	Resident	9	213.6 ± 4.13	t_s=2.242 $p > 0.05$
April 21	Migrant	1	184.2	
November 17	Resident	6	210.2 ± 7.03	t'_s=3.03 $p < 0.05$
	Migrant	2	231.3 ± 1.20	

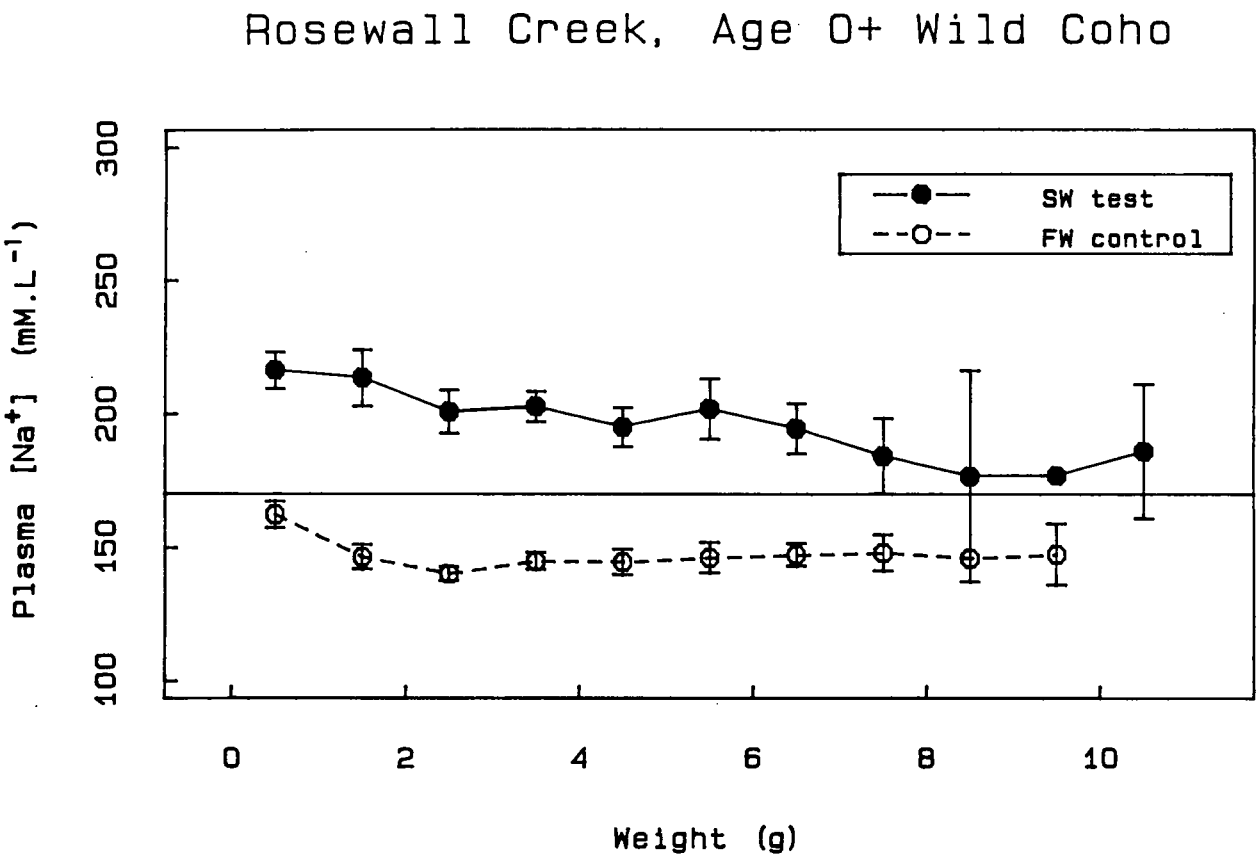
Wild Rosewall coho reached a weight of 7-11 g within one year, whereas Coldwater coho took two years to attained a similar size range. Since size may be a variable influencing ion regulatory capability, sodium regulatory changes with weight were compared between stocks. Coho of < 11 g were sorted and the mean plasma sodium values for one gram divisions were calculated and plotted (Figure 10). Coho larger than 11 g were mostly from Rosewall Creek and were too few to attempt comparisons. The values for each population show considerable overlap in confidence limits throughout the size range, but average plasma sodium values were consistently lower in Rosewall coho in the 7 to 11 g weight range.

Although comparisons of plasma sodium levels between wild populations over time potentially were confounded by the effects of differential growth and size, such problems were less evident among laboratory reared stocks, at least within incubation treatments. When experimental groups were sorted for those fish that were physiologically smolted (arbitrarily set as < 175 mM $Na^{+}.L^{-1}$, taking into account the slightly higher than expected plasma sodium levels), the coastal and interior smolt samples within incubation treatments were comparable in weight and length (Table 4). Mean lengths among smolt groups were different (ANOVA, F_S=18.373, df=(5,57), $p < 0.5$), but pairwise comparison tests demonstrated homogeneity within incubation treatments. Weight data were heteroscedastic but the Games and Howell approximate test for equality of means again suggested homogeneity within incubation groups. All of the laboratory reared smolts reached sizes slightly larger than observed in the wild (greater than or equal to 7.3 g in weight and 84.5 mm in length). These sizes were also larger than the critical smolting size of 70 to 80 mm suggested for coho by Conte et al. (1966).

Figure 10.

Wild coho seawater challenge test results
sorted by size classes

The horizontal line at 170 mM $Na^{+}.L^{-1}$ represents the plasma sodium level for physiologically smolted coho (Blackburn and Clarke 1977). The upper graph represents data from Rosewall Creek, while the lower graph is from Coldwater River coho. Error bars represent 95% confidence limits.


Rosewall Creek, Age 0+ Wild Coho
Plasma [Na+] (mM.L-1)
100
150
200
250
300
0
2
4
6
8
10
Weight (g)
SW test
FW control

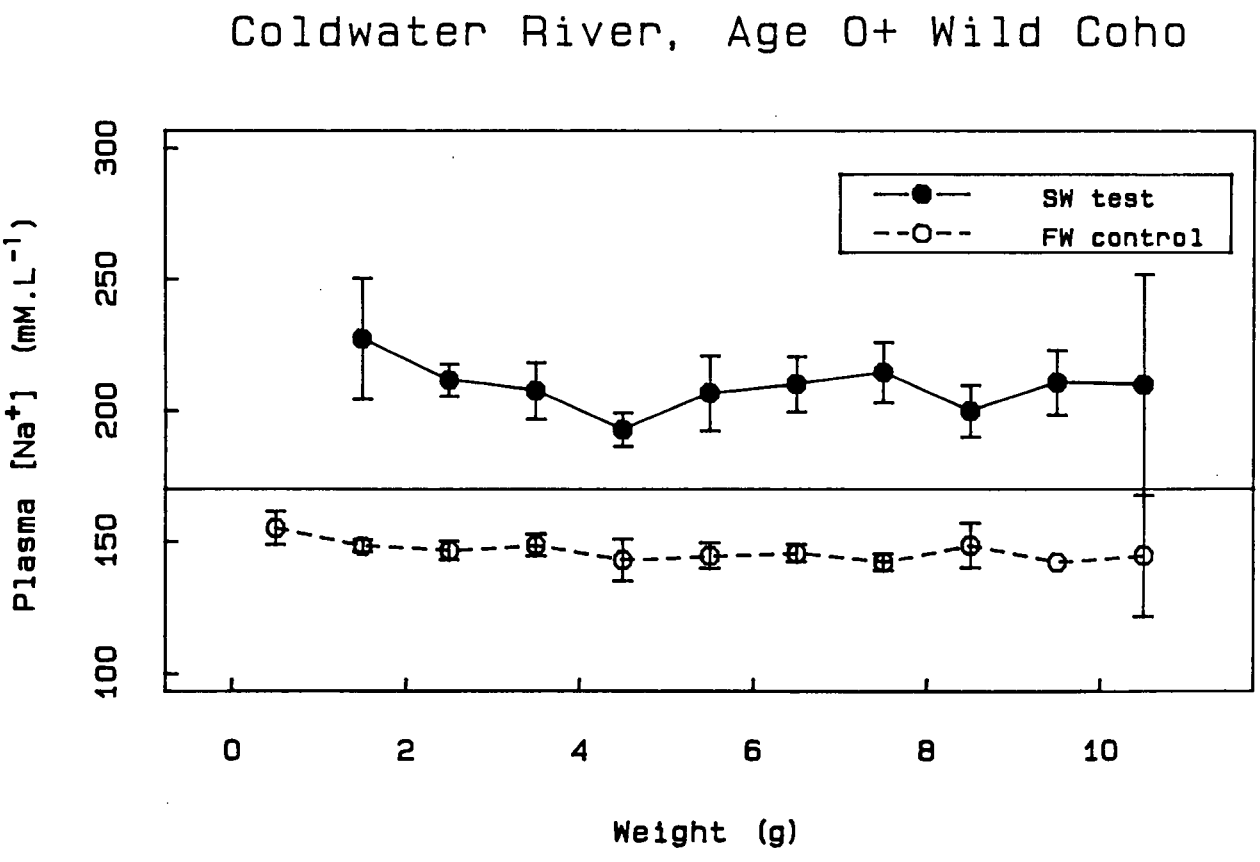

Coldwater River, Age 0+ Wild Coho
Plasma [Na+] (mM.L-1)
100
150
200
250
300
0
2
4
6
8
10
Weight (g)
SW test
FW control

TABLE 4
COMPARISONS OF WEIGHT AND LENGTH MEASUREMENTS
AMONG GROUPS OF PHYSIOLOGICALLY SMOLTED COHO.[a]

Smolt Group	Sample Size	Weight (g)	Multiple Range Comparison[b]	Folk Length (mm)	Multiple Range Comparison[c]
Rosewall Creek, Lab Raised, 6°C Incubation.	11	19.27 ± 1.358		122.5 ± 2.92	
Coldwater River, Lab Raised, 6°C Incubation.	13	21.22 ± 0.863		127.3 ± 1.79	
Rosewall Creek, Lab Raised, 2°C Incubation.	19	11.14 ± 0.716		103.5 ± 2.37	
Coldwater River, Lab Raised, 2°C Incubation.	13	11.13 ± 0.497		101.2 ± 1.45	
Rosewall Creek, Wild Coho.	5	10.38 ± 2.309	-d-	98.1 ± 7.26	-d-
Coldwater River, Wild Coho.	2	10.33 ± 4.010	-d-	101.5 ± 13.50	-d-

a - Smolted coho were arbitrarily determined as those with $\leq$175 mM $Na^{+}.L^{-1}$ in the plasma after being tested in the seawater challenge.
b - Games and Howell approximate test for equality of means.
c - Tukey-Kramers method.
d - Samples not included in comparisons, samples too small.

The seawater challenge results for laboratory raised coho are given in Figures 11 and 12. Generally the tested fish followed trends similar to those in the literature. Among the 6°C incubation groups, there was a dramatic early increase in May and June in ion regulatory capabilities, followed by a plateau that lasted until early April when plasma sodium levels decreased towards the fully smolted condition. Once testing started in September and October, the trend in plasma sodium levels in test fish of the 2°C incubation groups (Figure 12) closely followed the pattern displayed by the corresponding 6°C incubation group (Figure 11).

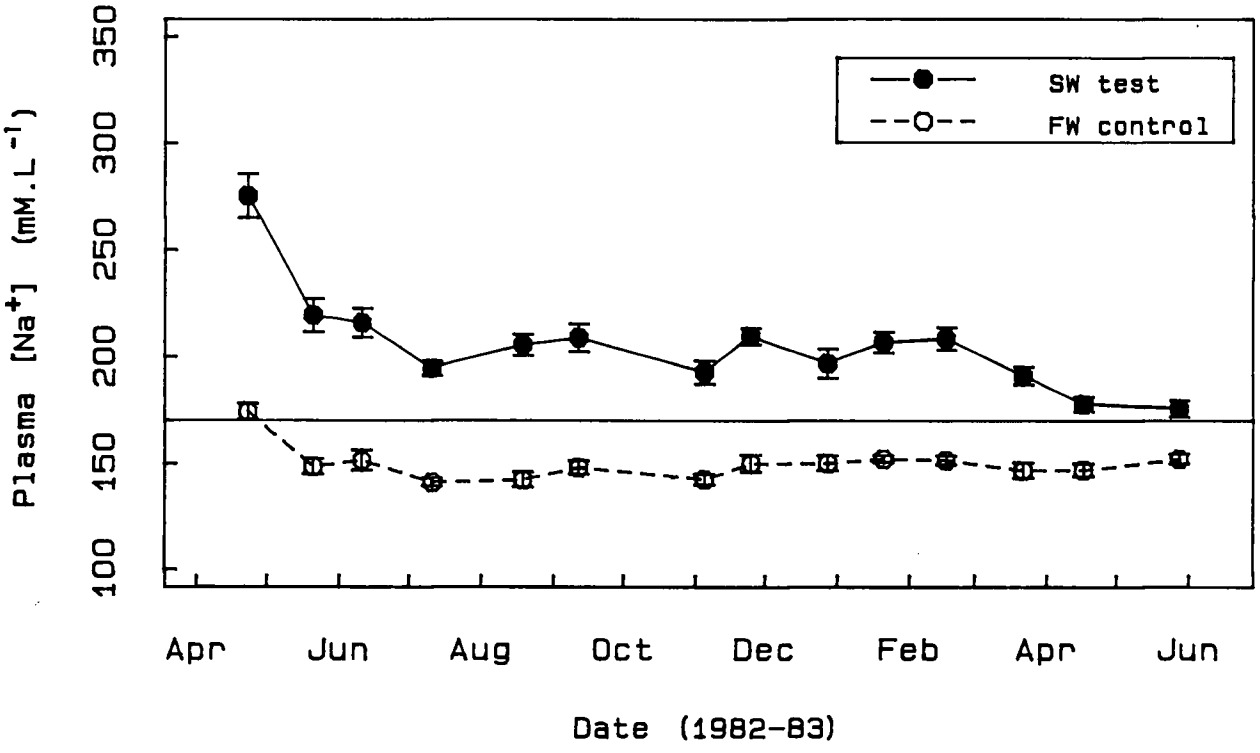
Mean plasma sodium values for control samples for each stock, under each treatment, were usually within the 140 to 155 mM $Na^{+}.L^{-1}$ range. During the initial experiments for each group, however, mean levels reached 187.0 ± 2.54 mM $Na^{+}.L^{-1}$ (Coldwater River, 6°C incubation group on May 4). Such high values are not reported in the literature (Conte et al. 1966, Miles and Smith 1968). The samples with these high values usually were less than 1.0 g in weight and less than 50 mm in length. Some dexterity is required to sample blood from coho juveniles, and it is possible that contamination occurred when handling the smaller fry and contributed to the raised early sodium levels. If such an error existed, it probably also contributed to the high, early test values for the 6°C incubation groups (Figure 11). Except for these early measurements, which may have been partially contaminated during sampling, there were no differences within stocks in seasonal trends in plasma sodium levels. Similarly, the trends between stocks both within and among treatments were not different. Thus, the physiological development of sodium regulatory ability appears to be fixed within the species and shows no differences between interior and coastal populations.

Figure 11.

Seawater challenge test results for 6°C incubation, laboratory reared coho.

The horizontal line at 170 mM $Na^{+}.L^{-1}$ represents the plasma sodium level for physiologically smolted coho (Blackburn and Clarke 1977). In the upper graph, data collected up until September were for Rosewall Creek coho. Data collected starting in November were for Big Qualicum River coho incubated and initially reared at the hatchery. Error bars represent 95% confidence limits.

Rosewall Cr.-Big Qualicum R., 6°C Incub.



Coldwater River, 6°C Incubation

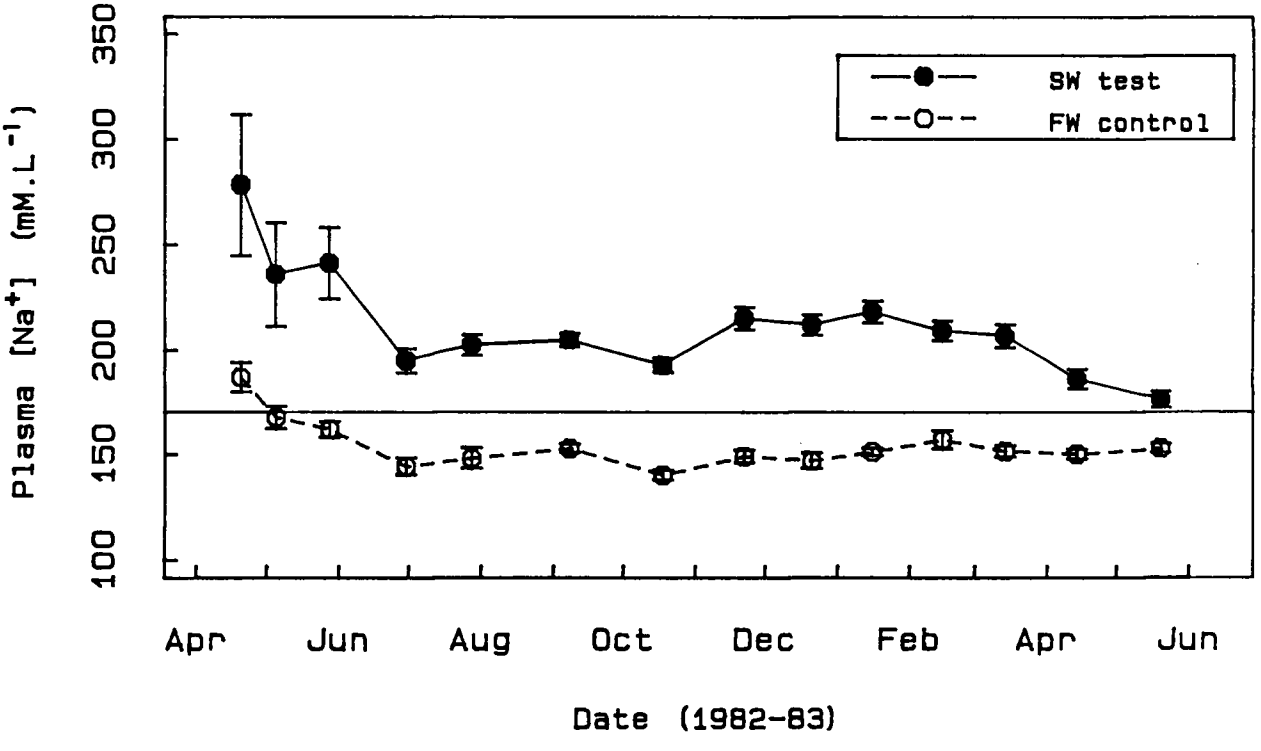
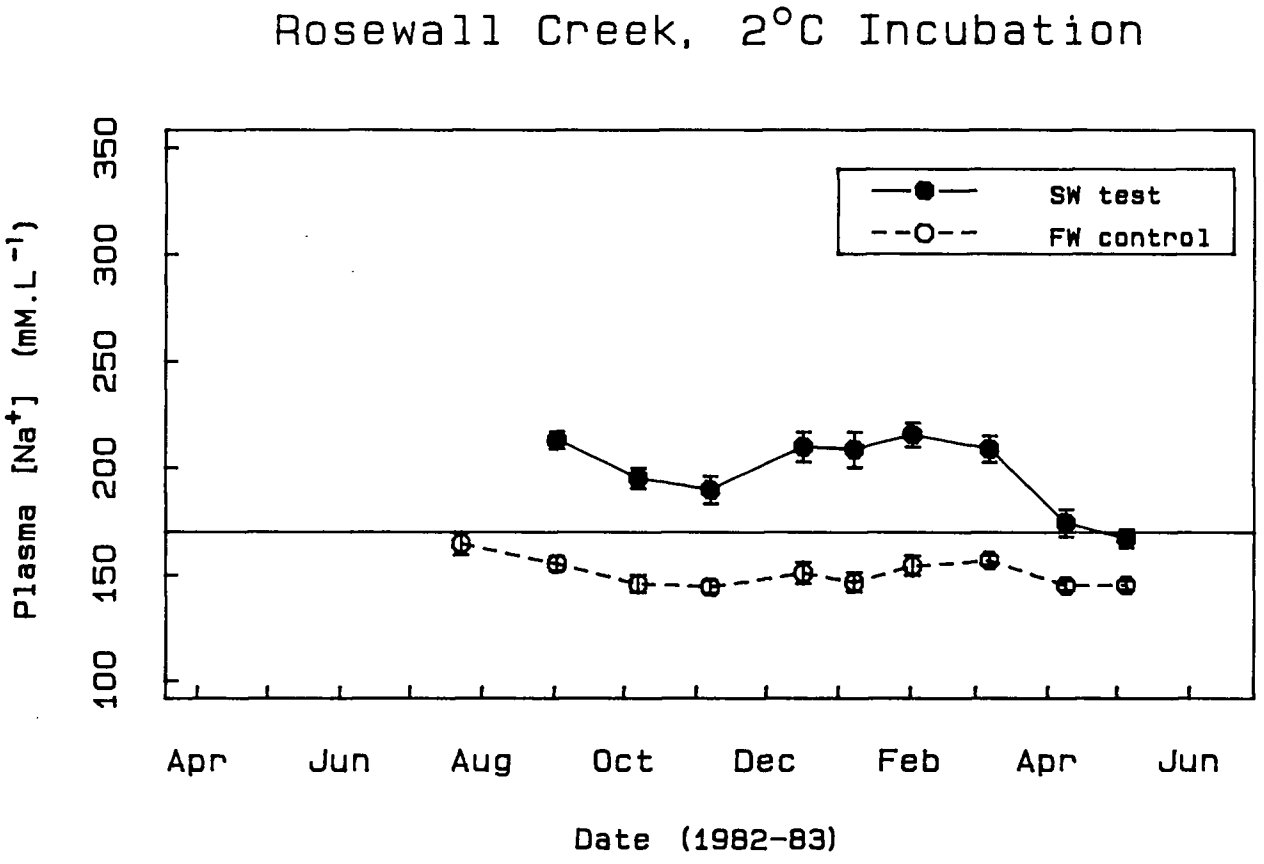
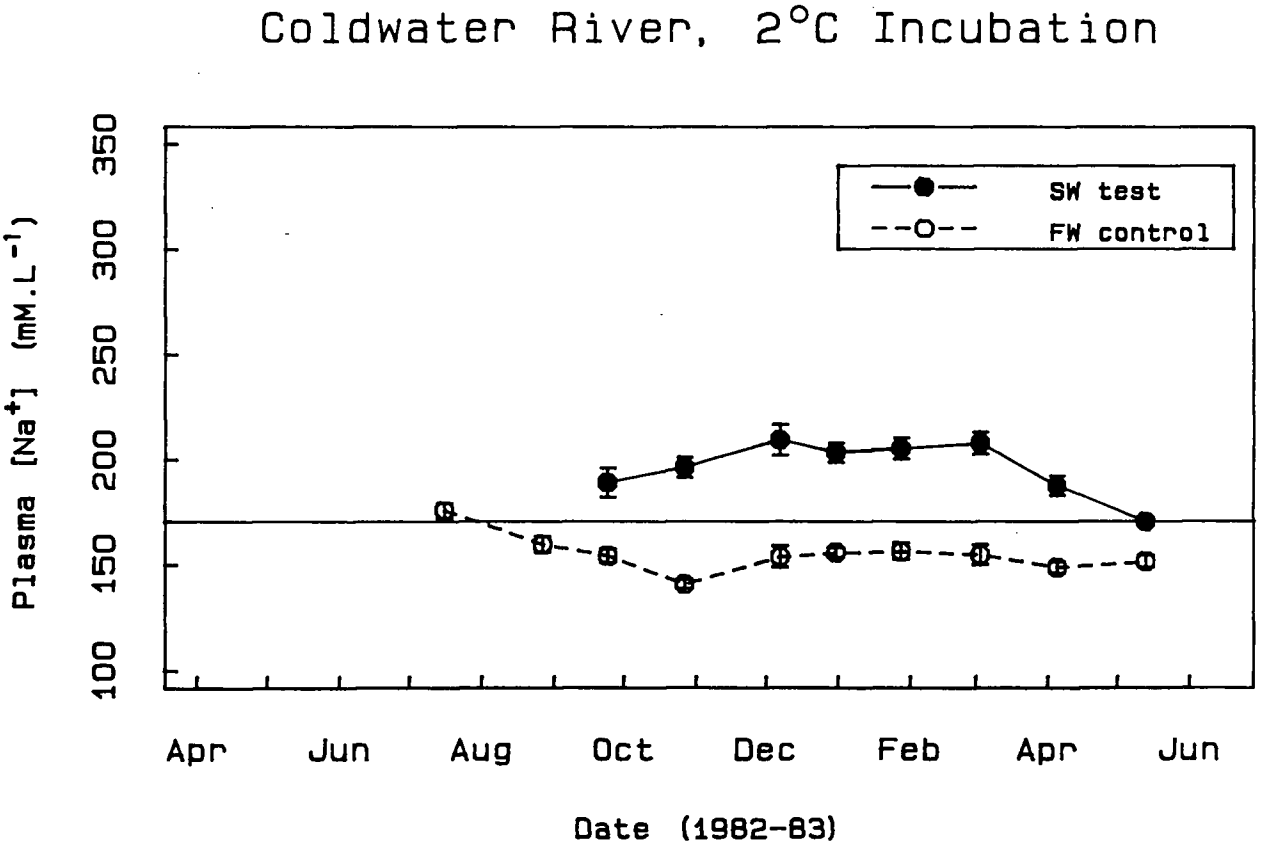


Figure 12.

Seawater challenge test results for
2°C incubation, laboratory reared coho.

The horizontal line at 170 mM $Na^{+}.L^{-1}$ represents the plasma sodium level for physiologically smolted coho (Blackburn and Clarke 1977). Error bars represent 95% confidence limits.


Rosewall Creek, 2°C Incubation
Plasma [Na+] (mM.L-1)
100
150
200
250
300
350
SW test
FW control
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)


Coldwater River, 2°C Incubation
Plasma [Na+] (mM.L-1)
100
150
200
250
300
350
SW test
FW control
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

Current Response

Differences in seasonal Fyke net catches between the Coldwater River and Rosewall Creek suggest differences in migration timing may exist between these two coho stocks (Table 5). Rosewall Creek coho appeared to migrate seaward only in the spring (May), whereas Coldwater River coho migrated downstream in both the spring (April) and fall (November). These differences may have result from passive downstream displacement due to increased flow velocities; however, the Coldwater system was not in freshet during either of the observed migratory periods.

When tested in the current response channels, resident wild coho from both Rosewall Creek and the Coldwater River showed both diel and seasonal variations in response (Figures 13 and 14). Current response scores under daylight conditions were usually greater than 10, indicating that the fish were either holding position or moving upstream. During darkness, the response scores were usually less than 10 indicating a net downstream movement. Seasonally, each year, subyearling coho from both streams showed the strongest downstream responses during April and May. Notably, subyearling coho from both stocks showed similar responses despite significant differences in their size. Yearling coho from the Coldwater system also showed a downstream response during the spring of their third year.

Current responses of spring migrant fry, under both diurnal and nocturnal conditions, were usually different from the responses of resident fry from the same drainage collected at the same time (Table 6). Migrant fry were those caught in the Fyke net trap, whereas resident fry were usually caught with minnow traps. This distinction is probably more valid in Rosewall Creek

TABLE 5
SEASONAL FYKE NET CATCHES OF COHO IN THE
ROSEWALL CREEK AND COLDWATER RIVER.

Drainage System	Date (1980-1983)	Coho Catch[a]	
		Subyearlings	>1 Year Old
Rosewall Creek.	January 15-16	0	0
	March 11-12	2	0
	March 28-29	1	0
	May 11-12	44	83
	July 20-21	0	0
	October 2- 3	0	0
	November 16-17	0	0
Coldwater River.	February 5- 6	0	0
	March 4- 5	0	0
	April 9-10	43	1
	May 9-10	-b-	-b-
	June 19-20	-b-	-b-
	August 21-22	7	0
	November 6- 7	37	0
	November 27-28	18	0

a - Coho subyearlings and older juveniles were arbitrarily separated on the basis of size, with size groupings determined from wild subsample agelngs.

b - The catch was omitted because the trap sank and probably biased the catch results.

Figure 13.

Current response trends for wild
Rosewall Creek coho.

Only subyearling fry were tested. Resident fry and migrant fry were tested separately. Migrant fry responses are slightly offset from resident responses to avoid confusion. A mean response of more than 10 indicates an upstream response, while a score of less than 10 indicates downstream movement. Error bars represent 95% confidence limits.

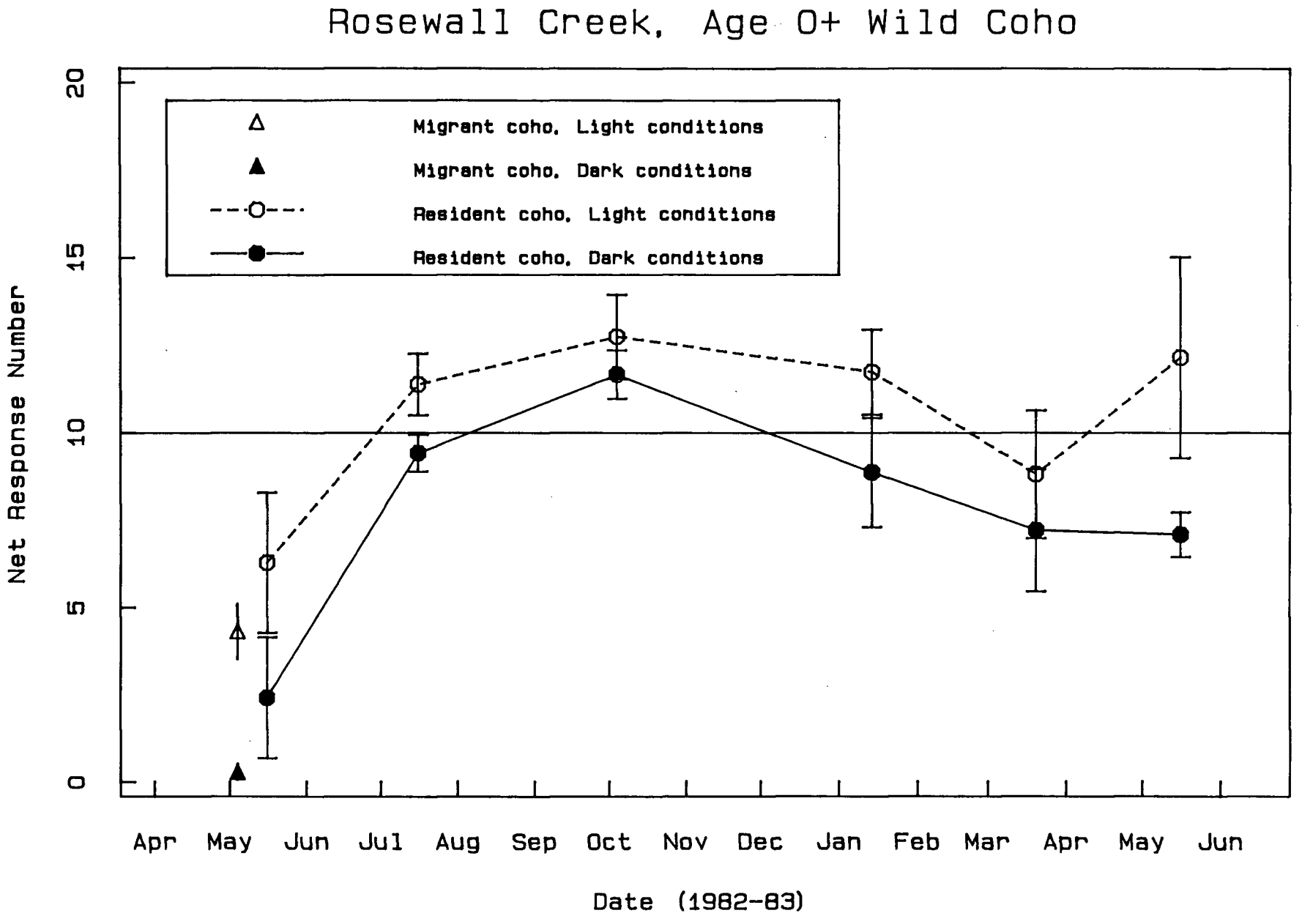
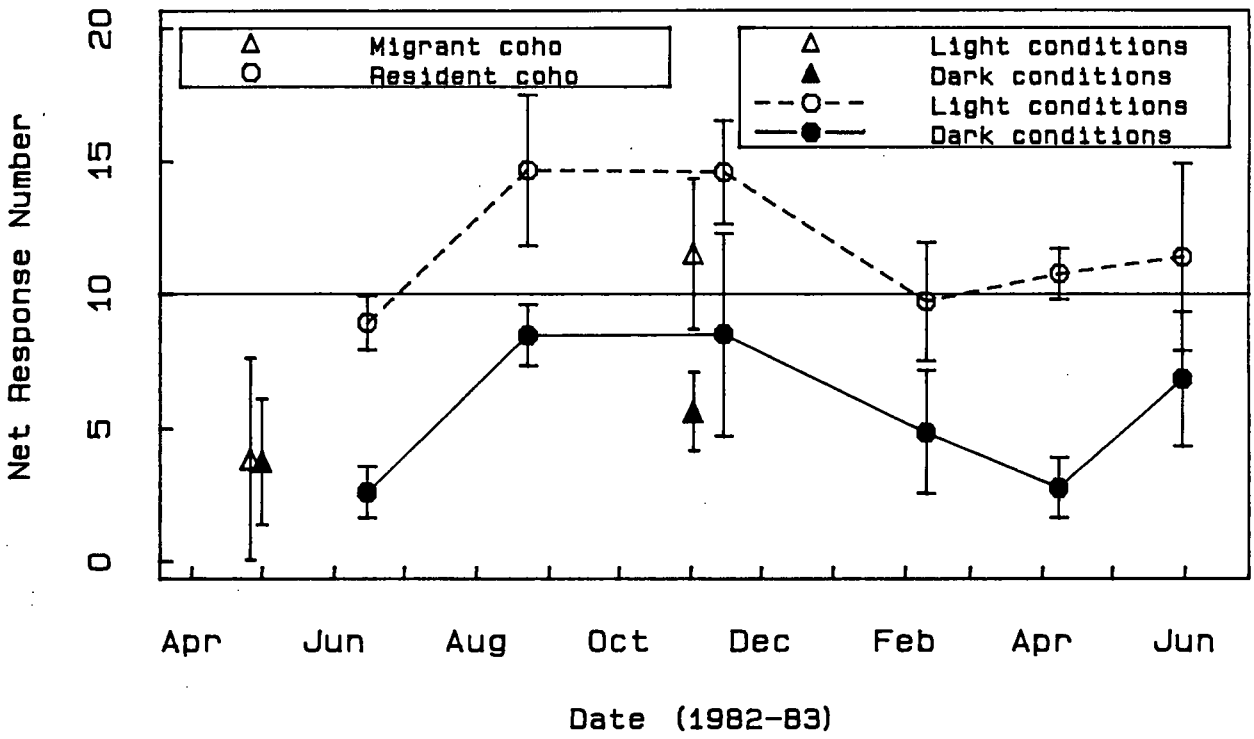

Rosewall Creek, Age 0+ Wild Coho
Migrant coho, Light conditions
Migrant coho, Dark conditions
Resident coho, Light conditions
Resident coho, Dark conditions
Net Response Number
0
5
10
15
20
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Date (1982-83)

Figure 14.

Current response trends for wild
Coldwater River coho.

The upper graph depicts the net current reponse of subyearling fry, while the lower graph depicts the responses of age 1+ fry. Resident fry and migrant fry were tested separately. Migrant fry responses were slightly offset from resident responses to avoid confusion. A mean response score of more than 10 indicates an upstream response, while a score of less than 10 indicates downstream movement. Error bars represent 95% confidence limits.

Coldwater River, Age 0+ Wild Coho



Coldwater River, Age 1+ Wild Coho

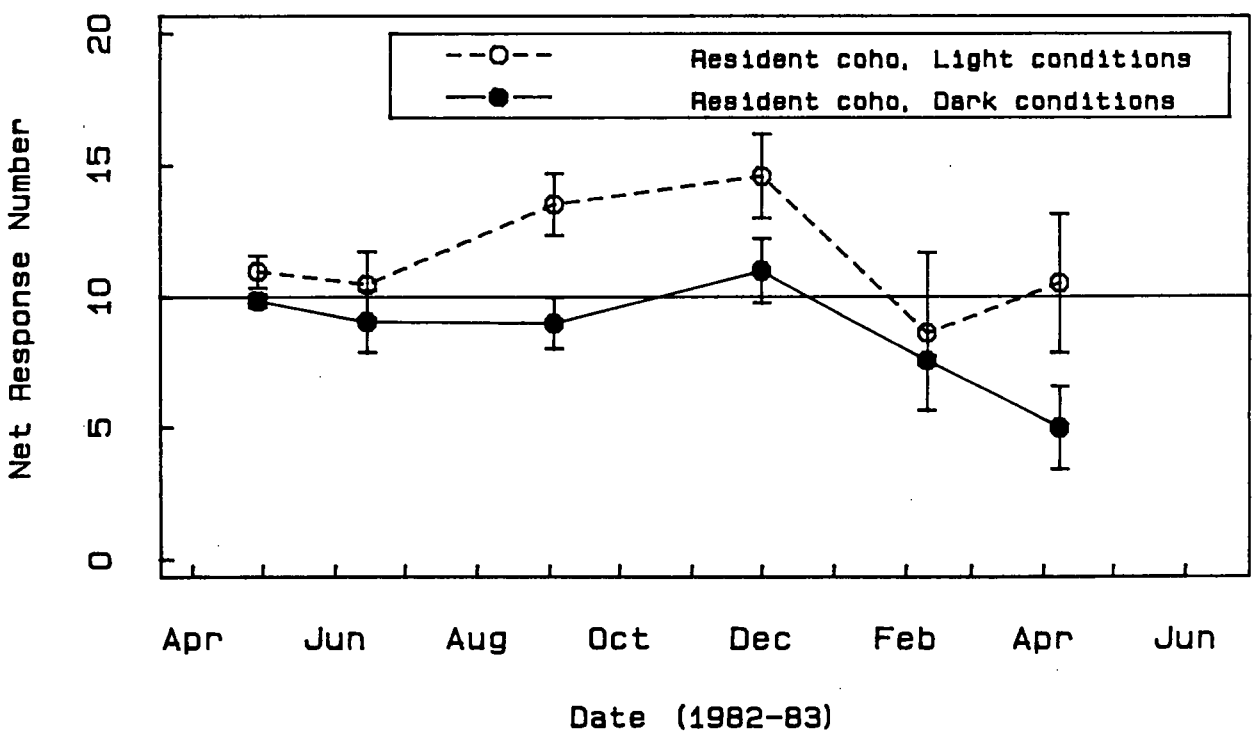


TABLE 6
COMPARISONS OF CURRENT RESPONSES BETWEEN RESIDENT AND MIGRANT COHO SUBYEARLINGS WITHIN ILLUMINATION CONDITIONS AND POPULATION.

Illumination Condition	Population Type and Capture Status	Date (1982-1983)	Sample Size	Current Response (NRN)[a]	t_s	U_s
Diurnal	Rosewall Cr., Resident.	May 30	6	6.28 ± 0.783	2.538 $p < 0.05$	
	Rosewall Cr., Migrant.		6	4.32 ± 0.302		
Nocturnal	Rosewall Cr., Resident.	May 30	6	2.42 ± 0.672		32.5 $p < 0.05$
	Rosewall Cr., Migrant.		6	0.28 ± 0.088		
Diurnal	Coldwater R., Resident.	June 29	12	8.92 ± 0.663		65 $p < 0.01$
	Coldwater R., Migrant.	April 22	6	3.83 ± 1.470		
Nocturnal	Coldwater R., Resident.	June 29	12	2.60 ± 0.615	2.597 $p < 0.05$	
	Coldwater R., Migrant.	April 22	6	3.75 ± 0.911		
Diurnal	Coldwater R., Resident.	November 29	6	14.60 ± 0.751	2.295 $p < 0.05$	
	Coldwater R., Migrant.		6	11.53 ± 1.104		
Nocturnal	Coldwater R., Resident.	November 29	6	8.56 ± 1.496	1.850 $p > 0.05$	
	Coldwater R., Migrant.		6	5.62 ± 0.567		

a - Net Response Number.

where the Fyke net was set just above tidal influence. Coho caught in the Fyke net in the Coldwater River, while moving downstream at that locality, may only have been redistributing themselves. Spring migrant Coldwater fry exhibited a greater downstream response than resident fry under diurnal conditions, whereas the resident coho exhibited a greater downstream response than spring migrant fry under nocturnal conditions. Spring migrant Rosewall fry showed greater downstream responses, compared to resident fry, under both light and dark conditions. Fall migrant Coldwater fry showed greater downstream responses than residents under diurnal conditions but comparable responses under nocturnal conditions. Generally, in both drainages, it appears that migrant fry show stronger downstream responses under both diurnal and nocturnal conditions.

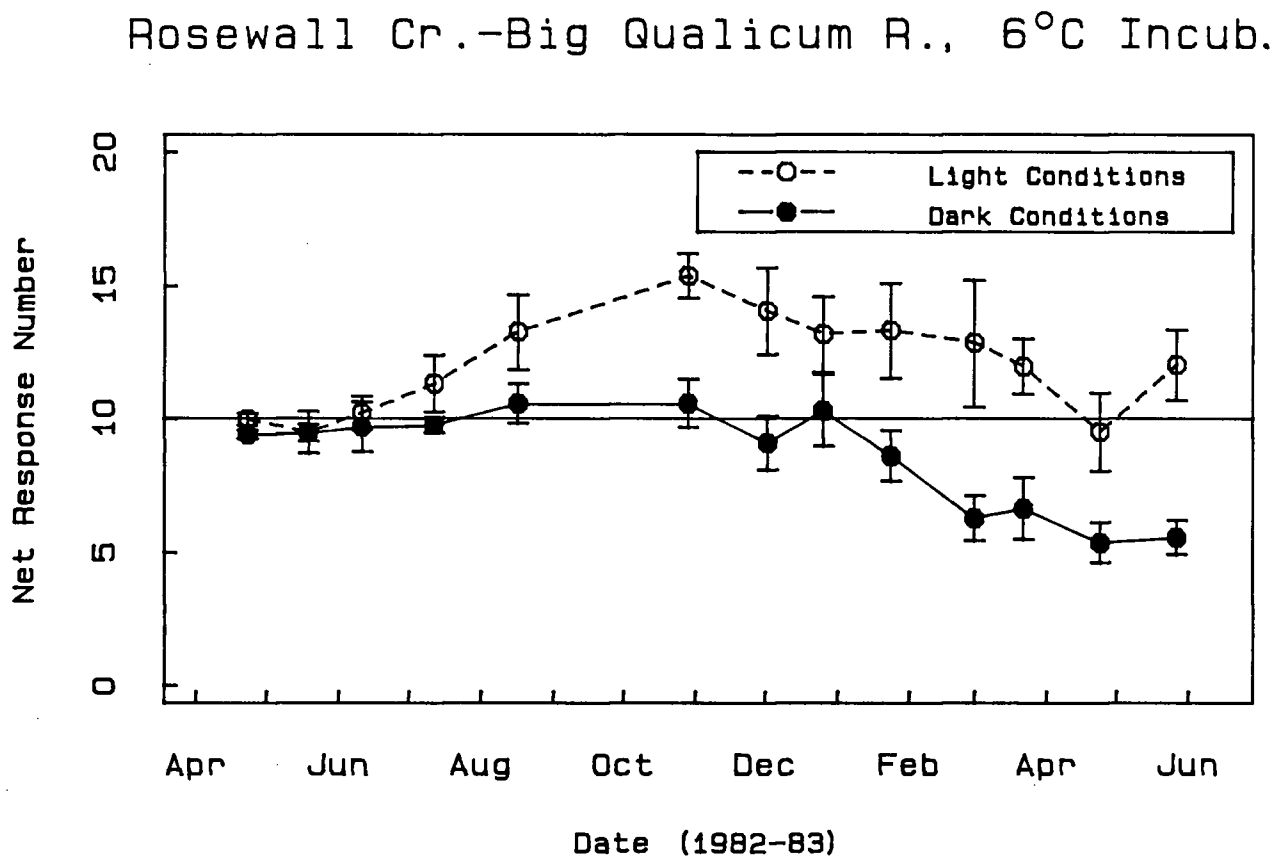
Because the net current responses of wild fry, under conditions of relatively low flows, corresponded to their capture status (resident or migrant), these responses probably were not a function of passive displacement. Perhaps they reflect innate differences. This seems especially likely in the Coldwater River where there was no difference in size between resident and migrant fry (Appendix 8, Table 12). The presence of fall migrant fry in the Coldwater River, but not in Rosewall Creek, suggests a difference in the pattern and timing of migration between these two stocks.

Seasonal patterns of current response among laboratory raised coho are depicted in Figures 15 and 16. Different seasonal trends in current response were evident between illumination conditions in each stock and treatment. Under diurnal conditions, trends were usually similar among stocks and treatments. First, a slight downstream response among the youngest fry was observed, then a net increase in response score that progressively became

Figure 15.

Current response trends for
6°C incubation, laboratory reared coho.

A mean response number of more than 10 indicates an upstream response, while a score of less than 10 indicates downstream movement. In the upper graph data collected up until September are from Rosewall Creek coho. Data collected starting in November are from Big Qualicum River coho incubated initially reared at the hatchery. Error bars represent 95% confidence limits.


Rosewall Cr.-Big Qualicum R., 6°C Incub.
Light Conditions
Dark Conditions
Net Response Number
0
5
10
15
20
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

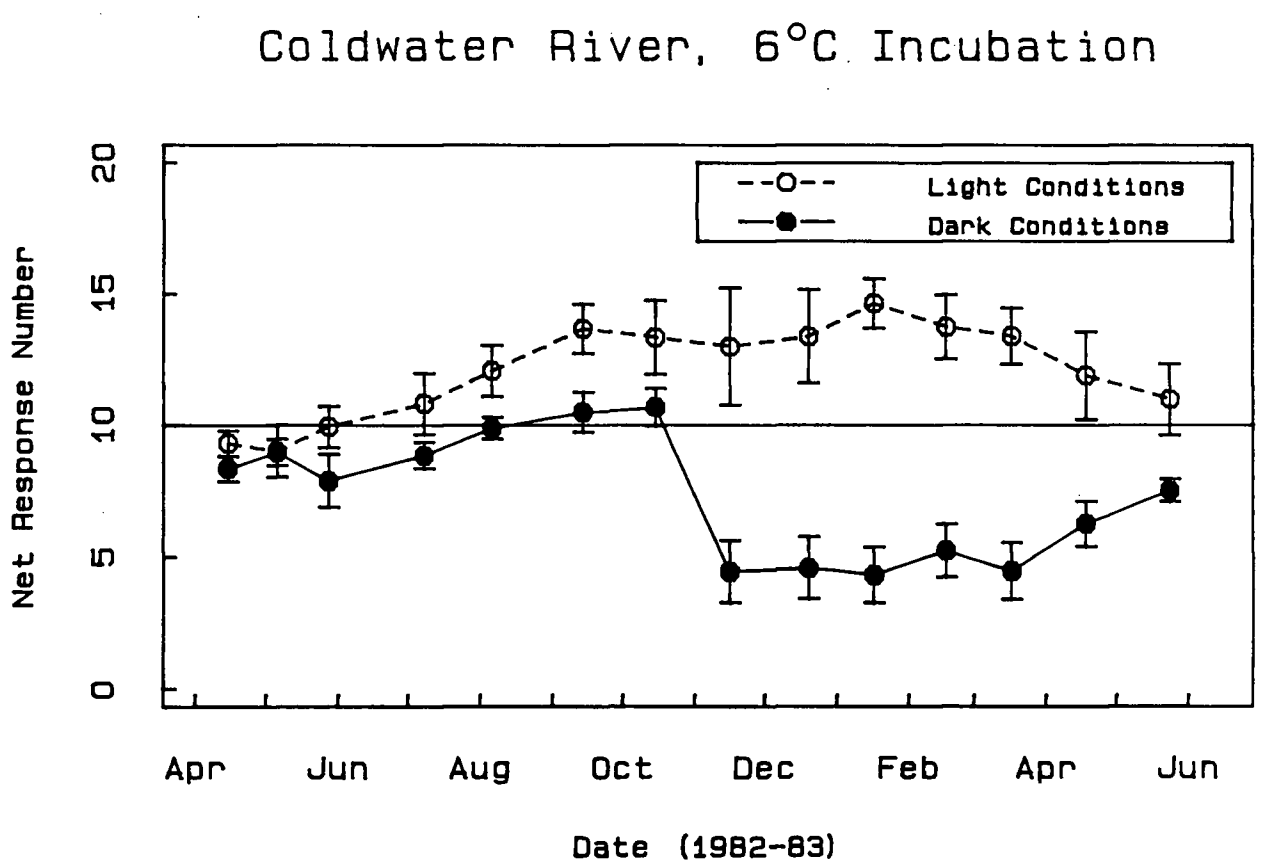
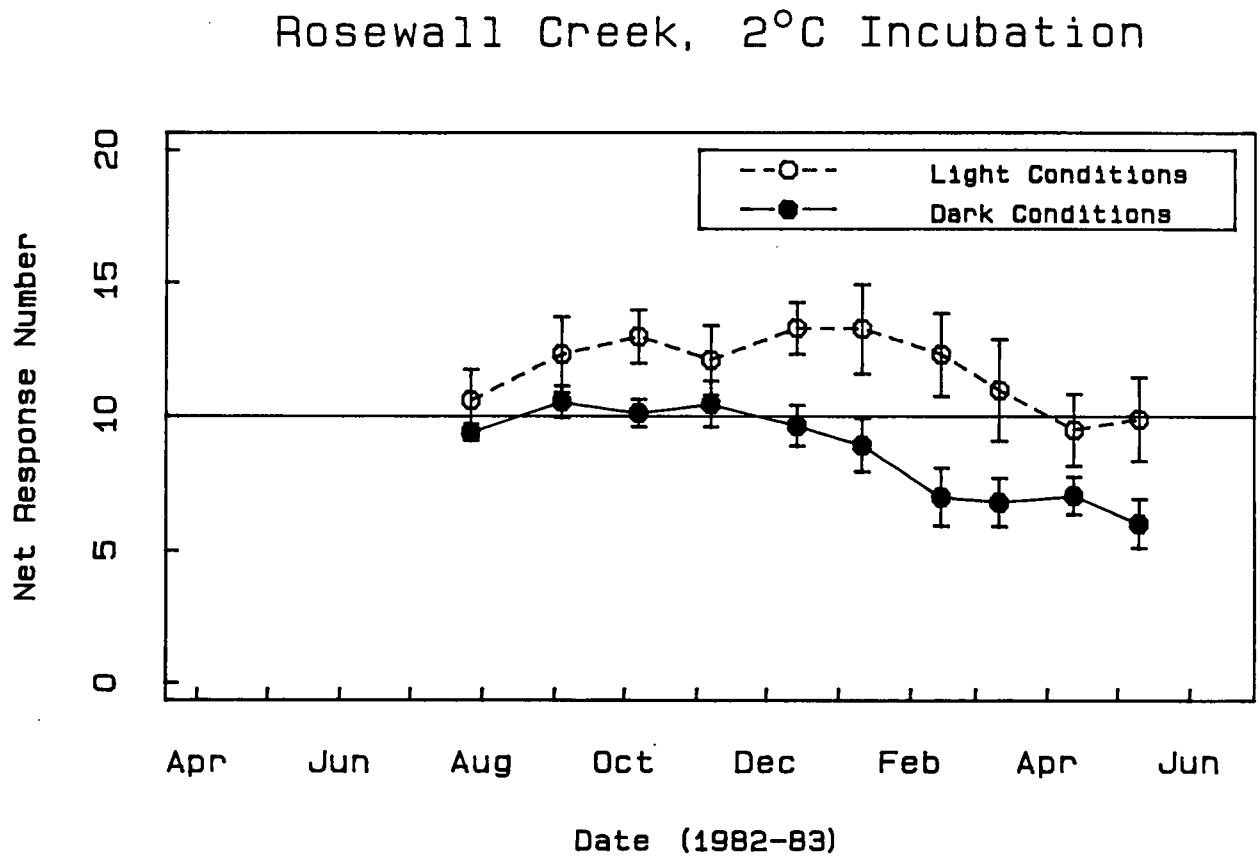
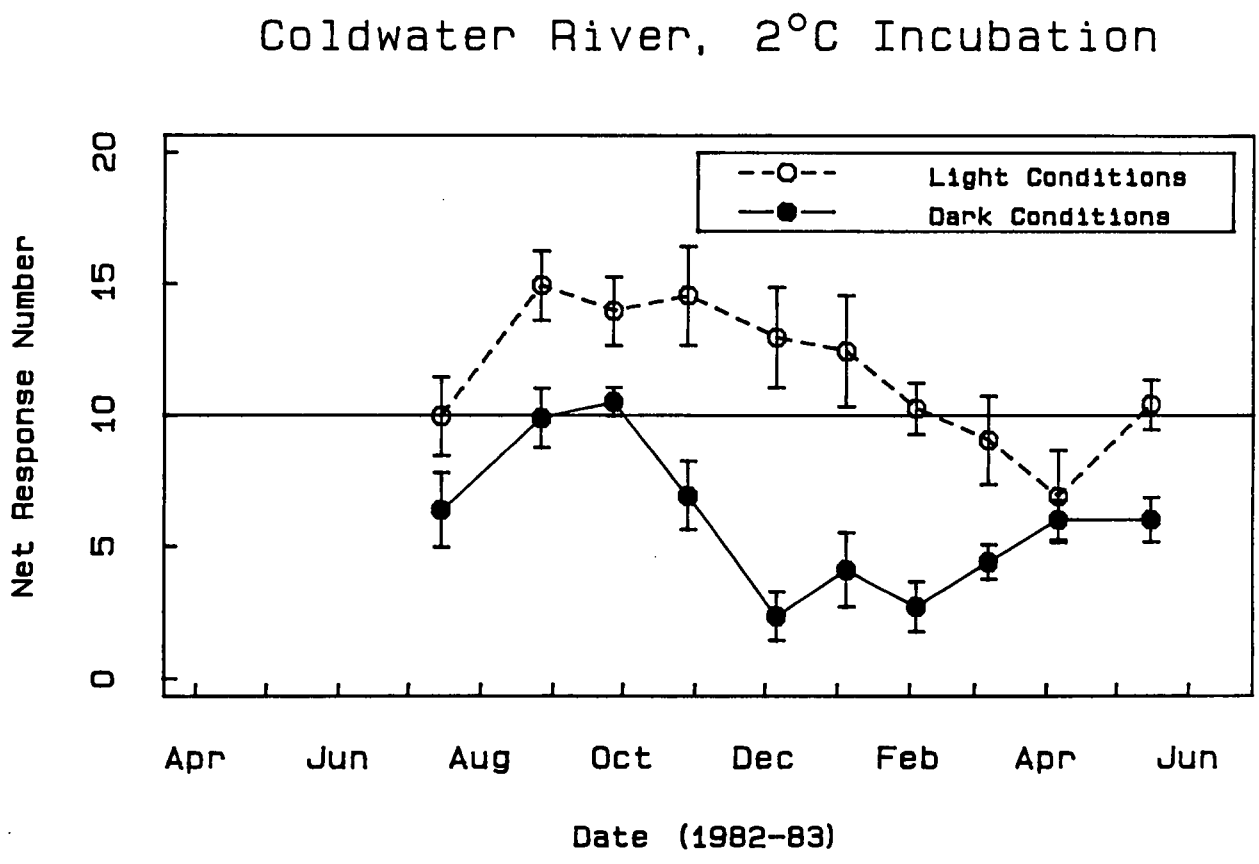

Coldwater River, 6°C Incubation
Light Conditions
Dark Conditions
Net Response Number
0
5
10
15
20
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

Figure 16.

Current response trends for
2°C incubation, laboratory reared coho.

A mean response number of more than 10 indicates an upstream response, while a score of less than 10 indicates downstream movement. Error bars represent 95% confidence limits.


Rosewall Creek, 2°C Incubation
Net Response Number
0
5
10
15
20
Light Conditions
Dark Conditions
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)


Coldwater River, 2°C Incubation
Net Response Number
0
5
10
15
20
Light Conditions
Dark Conditions
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

larger from the initial tests until September-October. The response score then remained high during the winter months. During February-March, the response scores progressively decreased and by April-May a downstream response was evident. The only exception to this daytime trend was in the Coldwater River, 6°C incubation treatment. These animals showed a decreasing response score under diurnal conditions as early as January (Figure 15); however, the mean net response score for this group never shifted to a downstream response (<10) during the second spring.

Under nocturnal conditions, the seasonal trend in response scores for Rosewall Creek-Big Qualicum River coho was similar to the diurnal trend described above, except that scores were lower throughout the year (Figures 15 and 16). The mean net score started at slightly under 10, indicating a slight downstream response among early post-emergent fry. The scores then increase gradually through to November-December as more of the fry began to successfully hold position. Starting in February, response scores progressively decreased and reached a maximum negative rheotaxis in May.

Seasonal trends in nocturnal current response in Coldwater River coho, for both incubation treatments (Figures 15 and 16), differed from the corresponding Rosewall Creek-Big Qualicum River trends. Up to October, the nocturnal response scores of the interior stock were similar to those of the coastal stocks. They started with a slight downstream response but, as the fry became more successful at holding position, the scores gradually increased. During November, however, a sharp drop in the mean response score occurred in both incubation treatment groups. This drop in response score suggests a switch from a positive to a strong negative rheotactic

response. The downstream response continued throughout the winter and early spring and became more moderate only as the corresponding upstream positive response under diurnal conditions decreased.

The laboratory results demonstrate that the effects of the two incubation treatments (i.e. coastal vs. interior temperature regimes) within stocks were not significantly different. Thus, trends in current response under diurnal conditions were generally the same for each stock and treatment group. Throughout the year, coho fry hold position or move upstream during the day. The two exceptions are recently emerged fry and juvenile fish in the second spring (April-May). In contrast to diurnal conditions, trends in current response under nocturnal conditions differ dramatically between stocks. Coldwater coho showed a shift to negative rheotaxis in November or about 3 months earlier than observed among coastal coho. Again, because the stocks were raised under identical environmental conditions, these observed differences in current responses between stocks are presumed to be innate.

Salinity Preference

Wild coho fry prefer salinities in the 0-8 ppt range throughout most of the year but shift in late winter and spring towards isotonic and hypertonic levels (Figures 17 and 18). Subyearling Rosewall Creek coho (Figure 17), and subyearling and yearling Coldwater coho (Figure 18) preferred 0-8 ppt seawater in a 0-20 ppt gradient. The only exception was a preference for 12 ppt seawater displayed by a Rosewall Creek coho sample on February 10. When presented with a gradient of 4-24 ppt seawater, however, both wild stocks showed preferences for salinities of 4-8 ppt until late April and May. At this time preferences shifted up to 12-16 ppt. Generally, migrant fry

Figure 17.

Salinity preference trends for wild Rosewall Creek coho.

Only subyearling fry were tested. Resident fry and migrant fry were tested separately. Migrant fry responses were slightly offset from from resident responses to avoid confusion. The horizontal line at 12 ppt seawater is the upper limit of the isotonicity range. A smoothing program (lowess in S) was used to draw the best fit lines.

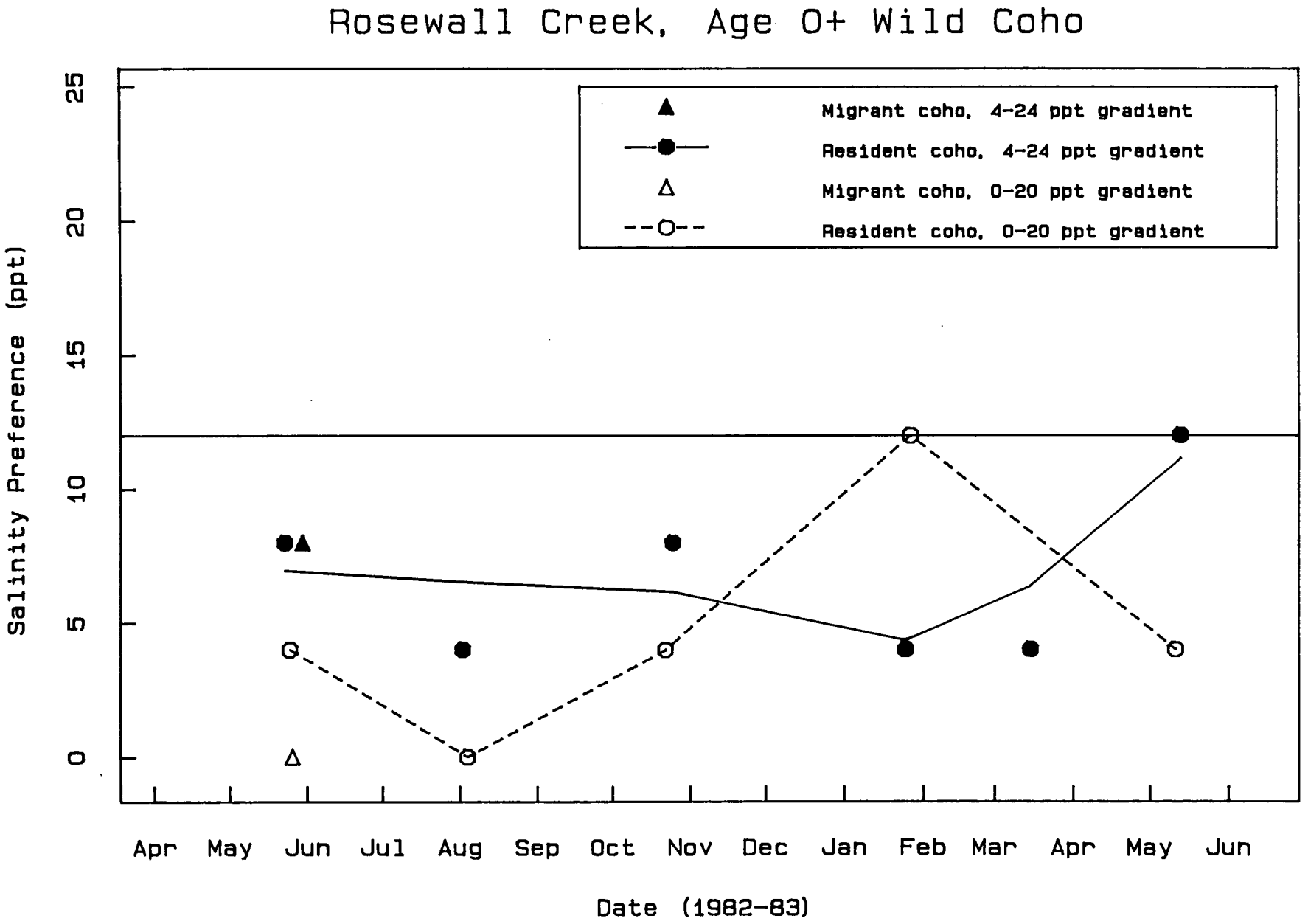
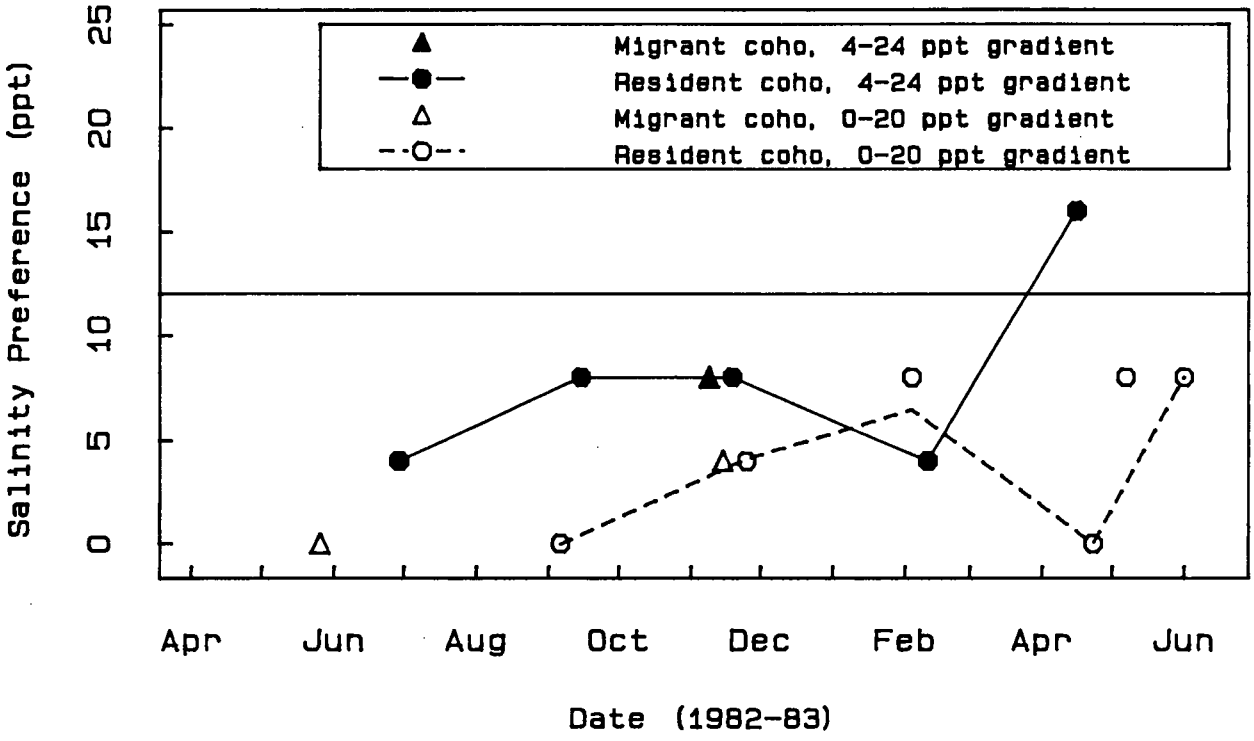

Rosewall Creek, Age 0+ Wild Coho
Migrant coho, 4-24 ppt gradient
Resident coho, 4-24 ppt gradient
Migrant coho, 0-20 ppt gradient
Resident coho, 0-20 ppt gradient
Salinity Preference (ppt)
0
5
10
15
20
25
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Date (1982-83)

Figure 18.

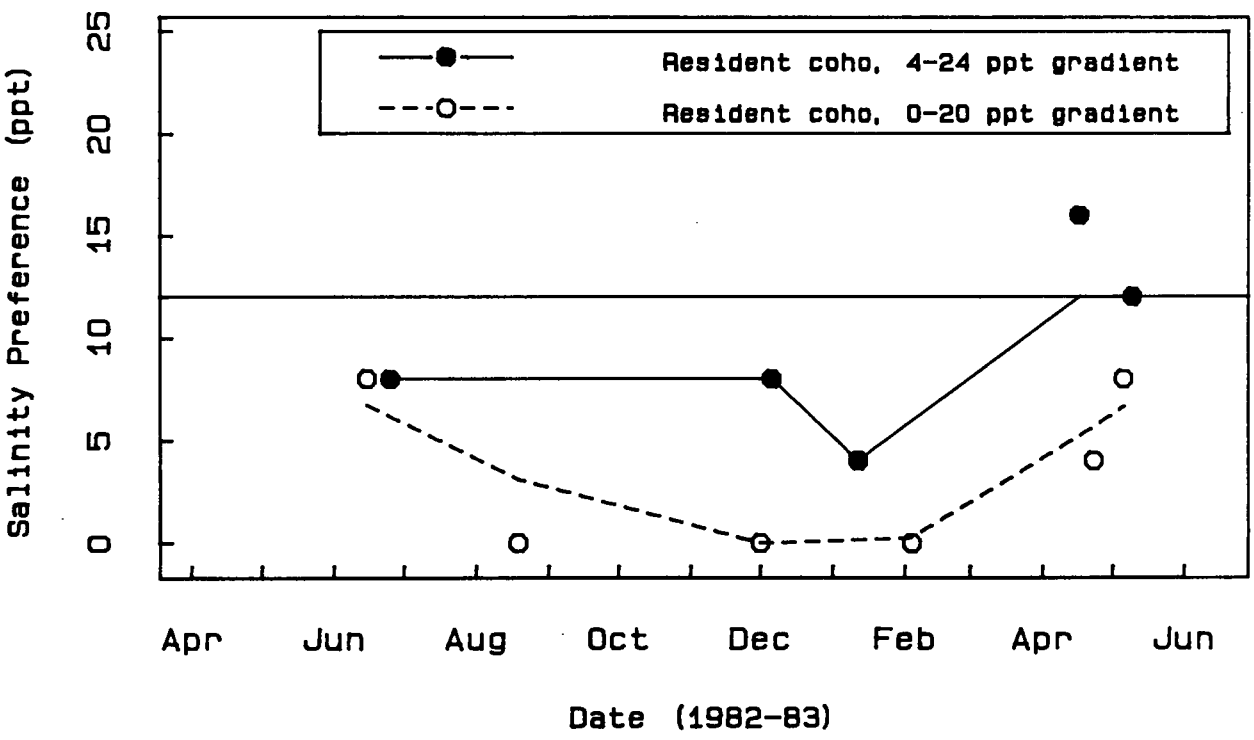
Salinity preference trends for wild
Coldwater River coho.

The upper graph depicts the net salinity preference of subyearling fry, while the lower graph depicts the responses of age 1+ fry. Resident fry and migrant fry were tested separately. Where necessary responses were slightly offset from each other in order to avoid confusion. The horizontal line at 12 ppt seawater is the upper limit of the isotonicity range. A smoothing program (lowess in S) was used to draw the best fit lines.

Coldwater River, Age 0+ Wild Coho



Coldwater River, Age 1+ Wild Coho



from both populations preferred hypotonic salinities (0-8 ppt) in both test gradients.

Salinity preference trends over time among laboratory raised coho are shown in Figures 19 and 20. No significant differences in salinity preference trends were observed between incubation treatments in either stock, although the data from the 2°C incubated coho were more variable for both populations (Figure 20). Significant variation between stocks, however, was observed.

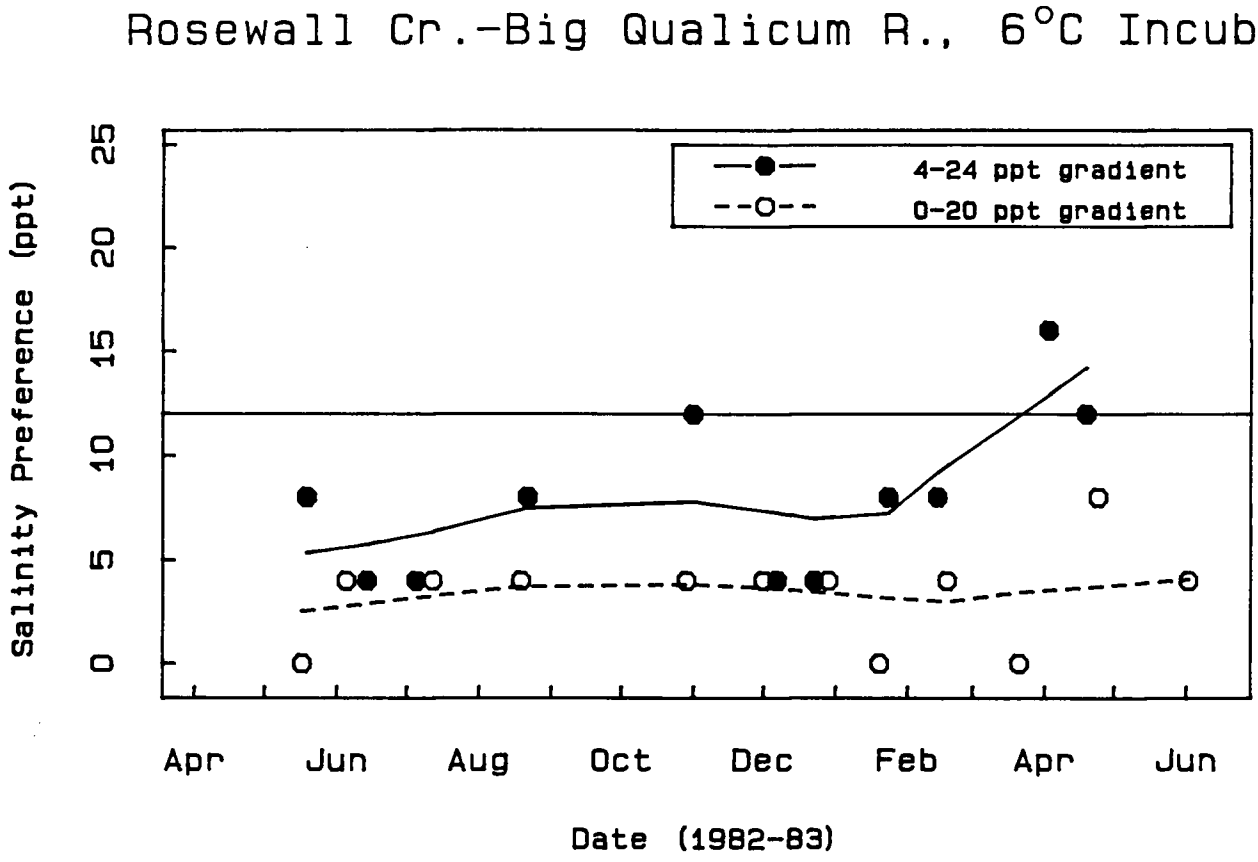
Generally, the data for laboratory raised Rosewall Creek-Big Qualicum River coho are similar to both my wild fish data and literature data. For most of the study, Rosewall Creek-Big Qualicum River coho juveniles, when presented with a 0-20 ppt gradient, preferred 0-4 ppt seawater. There was an increase in preferred salinities to 8-12 ppt on April 21 for the 2°C incubated group (Figure 20) and on May 8 for the 6°C incubated group (Figure 19). Salinity preferences in the 4-24 ppt gradient were higher during the spring, summer, fall and winter at 4-12 ppt, with an increase during the second spring to 8-16 ppt. The increase in salinity preferences during the second spring occurred on March 9 for the 6°C incubation treatment (Figure 20) and on April 17 for the 2°C incubation treatment (Figure 19).

Laboratory raised Coldwater coho also preferred hypotonic salinities during the spring and summer following emergence, but preferred higher salinities after November-December. From May until October or early November (October 31 in 0-20 ppt, November 5 in 4-24 ppt) coho incubated at 6°C preferred 0-8 ppt seawater in a 0-20 ppt gradient and 4-8 ppt seawater in a 4-24 ppt gradient (Figure 19). With a few exceptions, salinity preferences then increased to 12-16 ppt in both gradients.

Figure 19.

Salinity preference trends for
6°C incubation, laboratory reared coho.

The horizontal line at 12 ppt seawater is the upper limit of the isotonicity range. A smoothing program (lowess in S) was used to draw the best fit lines. In the upper graph, data collected up until September are from Rosewall Creek. Data collected starting in November are from Big Qualicum River coho incubated and initially reared at the hatchery.


Rosewall Cr.-Big Qualicum R., 6°C Incub.
4-24 ppt gradient
0-20 ppt gradient
Salinity Preference (ppt)
0
5
10
15
20
25
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

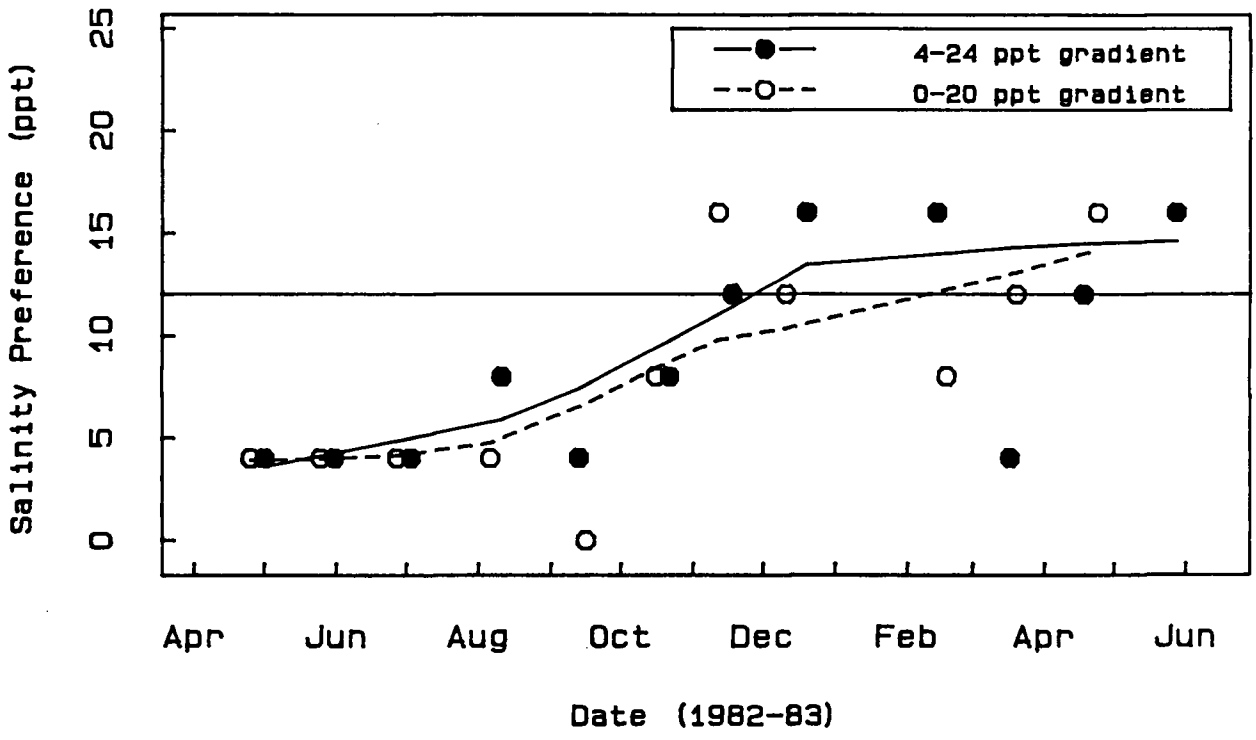
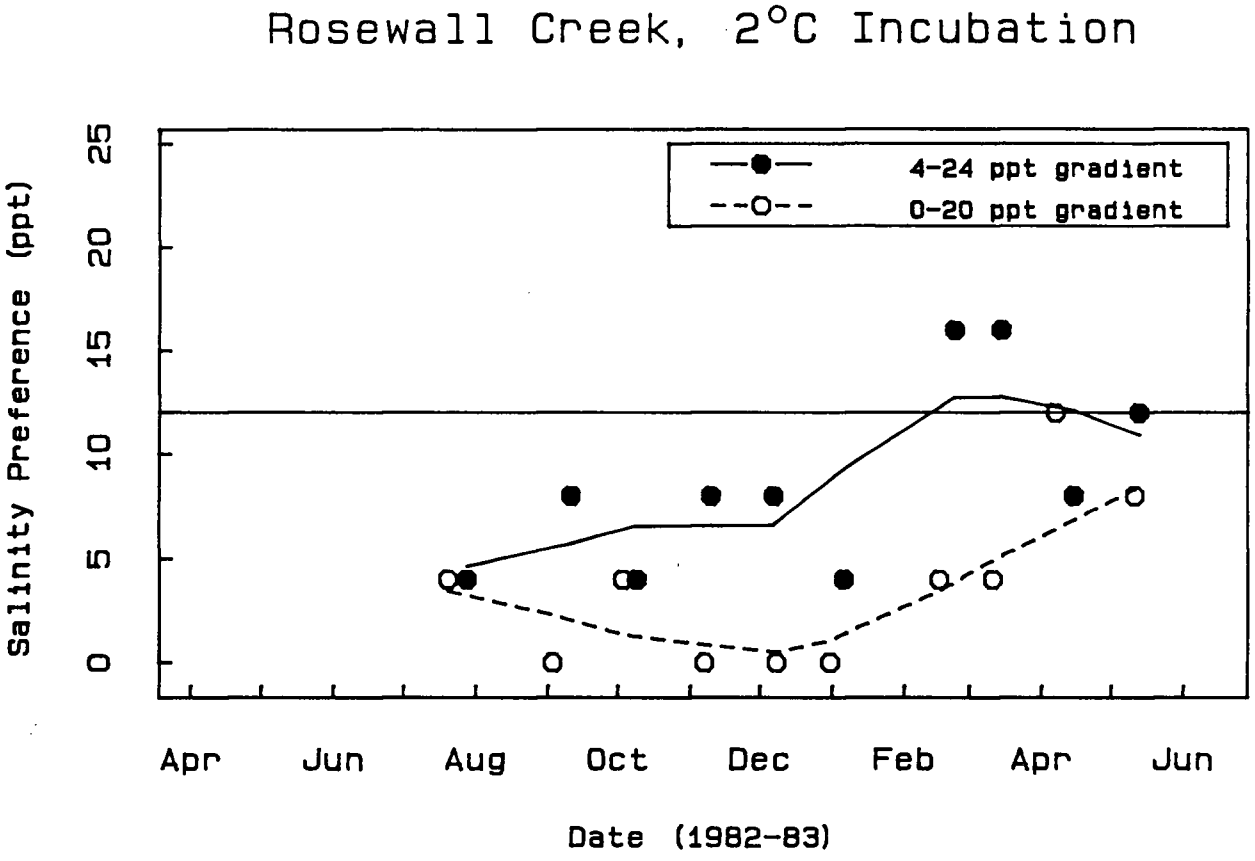
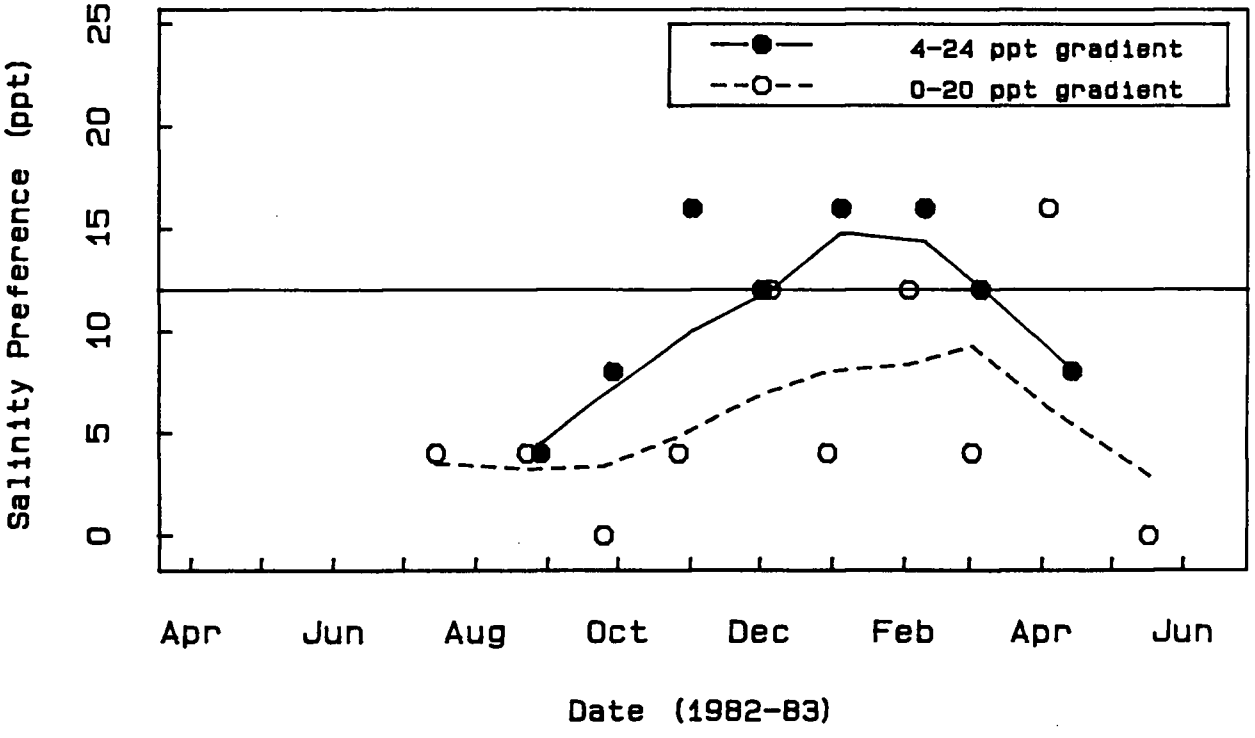

Coldwater River, 6°C Incubation
4-24 ppt gradient
0-20 ppt gradient
Salinity Preference (ppt)
0
5
10
15
20
25
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

Figure 20.

Salinity preference trends for
2°C incubation, laboratory reared coho.

The horizontal line at 12 ppt is the upper limit of the isotonicity range. A smoothing program (lowess in S) was used to draw the best fit lines.


Rosewall Creek, 2°C Incubation
4-24 ppt gradient
0-20 ppt gradient
Salinity Preference (ppt)
0
5
10
15
20
25
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)


Coldwater River, 2°C Incubation
4-24 ppt gradient
0-20 ppt gradient
Salinity Preference (ppt)
0
5
10
15
20
25
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date (1982-83)

Coldwater coho incubated at 2°C also shifted to higher salinity preferences after mid-October (Figure 20). These fish, tested in a 0-20 ppt gradient, preferred 0-4 ppt salinities from July to November and a wide range of preferences (0-16 ppt) beginning December 22. Those coho tested in a 4-24 ppt gradient preferred 4-8 ppt seawater during August and September, but after October 16 they preferred 8-16 ppt seawater. The drop in preference exhibited by the best fit lines in the lower graph in Figure 20 are a response to low salinity, final preference points. In the 4-24 ppt gradient, the drop occurred as a result of the elimination of a final preference of 20 ppt seawater observed on May 30. This point was omitted because test and control distributions were not significantly different (t_S=1.93, $p > 0.05$, Appendix 9). In the 0-20 ppt gradient, the final preference distribution was bimodal with a second, and not substantially different, peak at 20 ppt.

Generally, Rosewall Creek-Big Qualicum River coho salinity preference data indicate that coastal subyearling coho prefer salinities up to isotonicity throughout most of the rearing period. In their second spring, however, preferences increase from hypotonic to isotonic or even hypertonic salinities, particularly if freshwater is eliminated from the available gradient. The stronger hypertonic preferences in the spring observed in the 4-24 ppt gradient support McInerney's (1964) suggestion that the development of a preference for seawater is a biphasic process involving acclimation to increasing salinities.

Interior coho, represent by the Coldwater stock, exhibit a shift in salinity preferences to isotonic and hypertonic levels at least three months earlier than observed in coastal populations. The earliest shift in preference

occurred in Coldwater coho incubated under interior conditions (2°C, Figure 20). These coho showed an increase in preferred salinity from 4-8 ppt to 12-16 ppt in a 4-24 ppt seawater gradient as early as November 16.

DISCUSSION

The results suggest there is little difference in the development of the three characters monitored between the wild populations studied, except for downstream timing. Both Rosewall and Coldwater coho physiologically smolted in the spring (Figures 8 and 9) at a mean weight of about 10 g (Table 4). Rosewall Creek coho, however, smolted as yearlings, while Coldwater River coho smolted after two years in freshwater. This geographic variation agrees with previous observations for coho (Ricker 1972), but is somewhat in contrast to the predominance of sub-2 fish among returning adults to both streams. There were no significant differences between wild resident populations in the ontogeny of current response and salinity preference. As described by the literature (Shapavolov and Taft 1954, Mason 1975, Hasler and Scholz 1983), wild coho juveniles from both populations exhibited net downstream responses during the spring (April-June) as post-emergent fry and yearlings (Figures 13 and 14). Wild coho from both study streams preferred salinities in the 0-8 ppt seawater range during most of the year, but showed shifts to isotonic and hypertonic levels (12-16 ppt seawater) in April-May, if provided with a 4-24 ppt gradient (Figures 17 and 18). Again, these data agree with trends described in the literature (Houston 1957, Baggerman 1960, McInerney 1964, Otto and McInerney 1970). Fyke net catches, however, differed between the two study streams. In Rosewall Creek, emigrant fry and yearlings were caught only during May (Table 5). Coldwater fry were caught moving downstream in April and November, and these migrant fry generally showed stronger downstream responses than resident fry in laboratory tests (Table 6). These laboratory data suggest that the observed downstream responses were not due to passive displacement and may have been due to inherited differences between the two populations.

Under laboratory rearing conditions, there were no differences between coastal and interior coho stocks in either the ontogeny of plasma sodium regulation or diurnal current responses. There were, however, differences in the pattern of development of both nocturnal current responses and the shift in preference from hypotonic to isotonic and hypertonic salinities.

Throughout the fall and winter following emergence, coastal (Rosewall Creek-Big Qualicum River) coho held position at night and moved upstream during the daytime (Figures 15 and 16). These fry also exhibited a continuing preference for hypotonic salinities (Figures 19 and 20). These responses may provide a means of maintaining or re-establishing freshwater residence in the face of winter freshet conditions. Coastal coho delay downstream migratory activity and a shift to hypertonic salinity preferences until the spring following emergence. Starting in late February, there was a slow, but progressive, shift to a net downstream movement during the night accompanied by a preference for higher salinities. At first this current response is offset by continuing diurnal upstream movement, but ultimately an overall downstream movement occurs in late April and May. At this time, the coastal yearling coho are also physiologically capable of ion regulation in seawater (Figures 11 and 12). This scenario is compatible with both my wild data and the literature.

Laboratory raised Coldwater River coho exhibited strong nocturnal downstream responses beginning in the November following emergence and continuing throughout the following winter and spring (Figures 15 and 16). Daytime current responses shifted downstream in the spring (April-June). The nocturnal negative rheotaxis observed was accompanied by a November shift in salinity preference to isotonic and hypertonic levels (Figures 19

and 20). Again downstream responses occurred during both day and night during the period when interior coho have established smolt osmoregulatory capabilities (Figures 11 and 12) and, therefore, are prepared to move into salt water.

The differences between the results for wild and laboratory raised Coldwater coho are probably a result of laboratory rearing conditions, which differed from natural conditions, and may also be due to sequencing of component changes in the smolting process. The few physiologically smolted coho caught in the Coldwater River may have been due to a delay in the development of ion regulatory capabilities until overwintering residents are migrating seaward (Zaugg and McLain 1970, Chrisp and Bjornn 1978). Given the potential stress involved in overwinter survival at relatively high densities, low temperatures and low food availability (Rosenau et al. 1986, Swales et al. 1986), as well as the long migration distance, a delay in the physiological transition to the smolt condition might conserve energy. In contrast, Rosewall Creek coho have a much shorter migratory distance and so must be fully prepared to enter the sea during the spring when the usual yearling emigration occurs. Hence the more frequent smolt plasma sodium levels among the 7 to 11 g coho sampled in Rosewall Creek (Figure 10).

The strong negative nocturnal current response and preference for higher salinities observed among laboratory raised Coldwater River coho during the fall and winter suggests that, provided the appropriate stimulus is present, Coldwater fry will show a continual shift in behavioural responses once these are initiated. Wild fry also exhibited downstream movement, but only in a portion of the population during November. Wild migrant fry, however, did

not show higher salinity preferences at this time which suggests that the behavioural responses may not be strongly developed at the locality these fry were caught.

Interior coho, at least those in the Coldwater River, either overwinter in peripheral habitats, such as sidechannels and off-channel ponds that are both areally restricted and probably transitory (Swales et al. 1986, Rosenau et al. 1986), or migrate downstream in the fall. The limited survey data available for the upper Fraser drainage appear to support the above described variations in interior coho life history. During my field work, I caught emigrant Coldwater River coho in November (Table 5) and noticed that by December coho could only be captured in sidechannels and beaver ponds. Fall emigrants from the Coldwater River do not simply shift downstream to the Nicola system (M. Sheng pers. comm.). And coho generally do not overwinter in the mainstem Thompson River or the central and upper Fraser River (Beniston et al. 1985, Whelen and Slaney 1986). Consequently, fall Coldwater emigrants must either find alternative overwintering habitat peripheral to the main rivers enroute or continue downstream as far as the lower Fraser River where overwintering habitat is probably more extensive and coho would be better positioned for a seaward migration in the spring. In the latter locality, however, there has been no evidence that coho rearing densities increase during the winter (Northcote et al. 1978).

Similar migrations have been observed in the Clearwater River system in Washington (Cederholm and Scarlett 1982, Peterson 1982, Peterson and Reid 1984, Scarlett and Cederholm 1984). The frequency of accessible tributaries and alternative rearing habitat in the lower reaches of large Pacific coast

rivers, such as the Fraser River, may act to buffer the impact of severe interior overwintering conditions. The severity of the overwintering conditions in the upper reaches may be amplified by the transitory nature of the available overwintering habitats. Sidechannels and beaver ponds fill in over time and groundwater flows were observed to be discontinuous in the Coldwater River. Cederholm and Scarlett (1982) suggest that coho salmon have evolved such variable migration behaviour to assure survival in just such a relatively unstable environment.

The existence of such variable downstream migration behaviour raises questions regarding the environmental and physiological mechanisms that control such genetically based behavioural responses. Whatever the environmental cues that trigger fall downstream responses among interior coho are, they appear to have occurred under the laboratory rearing conditions which I used. It is known that environmental-genetic interactions often control migratory activity in salmonids (Groot 1965, Brannon 1967 and 1972, Raleigh 1967 and 1971, Raleigh and Chapman 1971, Kelso and Northcote 1981, Kelso et al. 1981, Northcote 1981). Generally, however, downstream migration in coho is considered to be the passive outcome of territorial aggression (Chapman 1962, Mason and Chapman 1965) or a component of the process of smolt formation (Hoar 1976, Folmar and Dickhoff 1980, Scholz 1980, Wedemeyer et al. 1980). Active migration in coho is associated with smolting and may be endogenous (Scholz 1980, Hasler and Scholz 1983). Smolting and downstream migratory timing are, however, fine-tuned by such cues as daylength and temperature (Hasler and Scholz 1983). Perhaps these same environmental cues also trigger the fall emigration of coho from interior streams such as the Coldwater River.

In coho, the development of the characteristics of smolts, including downstream movement, are closely synchronized with an increase in photoperiod (Baggerman 1960, Conte et al. 1966, Clarke et al. 1978, Ewing et al. 1979, Scholz 1980). Fall migrant coho from the Coldwater River, however, were experiencing a decreasing photoperiod, as were the laboratory raised stocks which showed a fall shift in behavioural responses. But if a decreasing photoperiod serves as a cue, then residents in the peripheral habitats should also have emigrated in the fall but didn't. It is unlikely, therefore, that photoperiod shifts act to initiate fall emigrations.

Northcote (1962) and Raleigh (1967) demonstrated the importance of temperature in explaining the variable migratory patterns found in rainbow trout and sockeye salmon. Keenleyside and Hoar (1954) suggested a rise in temperature of 4-5°C could induce a negative response to current in coho salmon; however, Zaugg and McLain (1976) showed that in coho temperature serves more to delay and prolong smolting activities than to initiate them. Yet Bardach and Bjorklund (1957 cited by Raleigh 1967) suggested that salmonids, in general, move downstream in the early winter into deeper water to avoid extremely low temperatures. It is possible, then, that in the Coldwater River coho leave the mainstem river during the winter to avoid the extremely cold winter temperatures in the main river (Table 2, Figure 5). During winter collection trips, I observed that habitats peripheral to the main Coldwater River were a often a few degrees warmer, probably because of either groundwater seepage or vegetation decomposition. This may explain why overwintering coho in the Coldwater River were only found in the off-channel habitats.

The problem with temperature as the environmental cue that triggers downstream migration is just how such a cue might work. If a decreasing temperature regime is the cue, then coho residing in both peripheral habitats and the main river should emigrate together. Both environments undergo the same seasonal temperature fluctuations (Figure 5), although the peripheral habitat may always be slightly warmer. If a low threshold temperature is critical to downstream movement, as shown by Northcote (1962) and Raleigh and Chapman (1971) for trout species, then the laboratory raised coho, which were reared at warmer temperatures than observed in both the peripheral Coldwater overwintering areas and the main river, should not have shown negative rheotaxis in the fall. Since the observed migrant timing of the various interior coho groups doesn't fit any of these descriptions, temperature cues do not appear to trigger emigration.

Other possible cues which may be instrumental in initiating emigration include size, rearing density and current velocity. Size, particularly critical or threshold size, has been shown to be important to salmon smoltification, including seaward migration (Folmar and Dickhoff 1980). If threshold size is important to fall movements, then the coho that were caught moving downstream should have been significantly larger than those that remained as residents. Certainly laboratory raised coho, from both incubation treatments, were significantly larger than wild Coldwater coho of the same age (Appendix 8, Figures 5, 6 and 7). Fall migrants caught in the Coldwater River, however, were not significantly different in size from residents caught on the same field trip (Appendix 8, Table 12). Size, therefore, does not appear to contribute to the initiation of fall emigration.

Coho are territorial during freshwater residence and increased densities can result in aggression and fry displacement (Chapman 1962). Since densities were high in laboratory rearing tanks (up to 1.5 to 2.6 fish.L^{-1}, Appendix 5), aggressive interactions may explain the downstream responses observed in the experiments. Natural densities recorded by Swales et al. (1986) in overwintering ponds peripheral to the main Coldwater River during the fall of 1984 were as high as 1.53 fish.m^{-3} (assuming the ponds averaged 1.0 m in depth). The laboratory rearing densities were, therefore, about two magnitudes higher than observed in the wild. These off-channel ponds serve as major overwintering areas in the Coldwater system and it is conceivable that, once a critical density has been reached, excess fry begin to emigrate. Swales (pers. comm.), however, has observed that most juvenile coho move into the overwintering areas in the Coldwater River during high waters in the early summer rather than in the late summer and fall. If critical densities occur, emigration should then take place earlier in the year as densities increase, not during the fall.

Brannon (1967 and 1972) demonstrated that stock specific current velocity thresholds are important in directing sockeye fry to nursery areas. Each sockeye stock responds to a different velocity threshold and fry move downstream unless that threshold is encountered. When they encounter velocities above the threshold, they show positive rheotaxis. Perhaps a similar mechanism is at work during the fall in coho stocks. In the Coldwater River, discharge levels decrease after the May-June freshet period (Figure 3) to less than 1 m.s^{-1} in August and September (Anon. 1982). Discharge levels then increase again and peak in early November before dropping off for the winter. If we assume that discharge levels are directly related to

changes in current velocity and if Coldwater coho emigration is triggered by water velocities falling below some threshold, then mainstem residents should migrate during August and September or in December to February (the two low discharge periods). At the same time, coho residing in peripheral areas where currents are generally lower than in the main river should also be prepared to emigrate. Since neither situation is observed in the Coldwater system, velocity threshold cues acting in a manner similar to that reported by Brannon (1967 and 1972) are unlikely amongst coho.

Velocity increases, however, may act as a cue since both wild and laboratory migrants experienced increased flows in the fall at about the time shifts in rheotaxis were observed. In the laboratory, flow rates in rearing tanks were increased from 5-6 $L.min^{-1}$ to 8-10 $L.min^{-1}$ during October, just prior to the change to downstream nocturnal current responses among Coldwater coho.

Another question the data pose is why salinity preferences should shift in the fall among coho that at that time are located over 400 km from the sea (Figures 15 and 16). McInerney's (1964) suggestion that salinity preference acts as a migrational orientation mechanism can only operate once the estuary is reached. The answer may lie in the hormonal regulation of behavioural characteristics normally associated with smolting. The administration of thyroid extract or TSH to juvenile coho causes an increase in downstream movement, a reduction in aggression and an increase in schooling behaviour (Hasler and Scholz 1983). All of these behavioural responses are necessary for abandoning stream residence and moving seaward. Baggerman (1960) showed that an increase in thyroid activity was correlated with a shift from a

preference for freshwater to a preference for 18-24 ppt seawater in yearling coho. The administration of TSH resulted in a similar shift in subyearling coho (Baggerman 1963). Perhaps then, the early shifts in salinity preference observed in laboratory raised Coldwater coho were a side effect of the hormonal regulation of migratory responses. Salinity preference shifts in laboratory raised coho also may have occurred slightly later than changes in rheotactic responses (compare Figure 16 with Figure 20). This could explain the lack of differences in preference observed between fall migrant and resident wild fry (Figure 18).

Finally, the question arises as to whether fall migrant coho are sufficiently imprinted on the Coldwater River to home as adults and thus contribute to continuing recruitment. This is a necessary prerequisite to the development and maintenance of the genetic discreteness of the population. Coho are believed to imprint on their natal stream during smoltification (Jensen and Duncan 1971, Mighell 1975). Scholz (1980), however, suggests that thyroid activity is not only responsible for a downstream current response in smolting coho, but also may be instrumental in olfactory imprinting. If this is so, then increased thyroid activity could explain not only the observed shifts in nocturnal current response and salinity preference in Coldwater coho, but also act to assure juveniles imprint on the stream prior to emigration.

The results of this study not only demonstrate differences between coho salmon populations in the ontogeny of behavioural characteristics but also suggest that the development of ion regulatory capabilities are fixed within the species. The behavioural data are particularly important in pointing to functional variations that could affect stock fitness. The observed

differences in the development of behavioural responses clearly have an inherited component and this implies an adaptive significance. Such differences deserve further study and two promising areas are comparisons of thyroid activity in fall migrant and resident interior coho fry, and investigations of the mechanisms responsible for initiating and maintaining behavioural responses in different stocks. Ultimately, it would be interesting to determine the proportionate contribution to production by fall migrant and winter resident interior coho groups.

This study also points to the importance of investigating life history variations within species and of not studying life history stages in isolation. While smolting has been recognised as a dynamic, metamorphic process (Hoar 1976) involving a series of morphological, physiological and behavioural changes (Wedemeyer et al. 1980), most of the research on the process has been limited to the 3-4 month period preceding and coincident with smolt production (eg. Scholz 1980). Since most of the work has been conducted on coastal populations, this approach has lead to conclusions on the timing of imprinting and emigration that are not necessarily representative of the entire species. Indeed, even with the recent considerations of variable life history forms within coho stocks (Peterson 1980 and 1982, Cederholm and Scarlett 1981), it generally has been concluded that stock production is determined by spawning numbers and some habitat limiting factor. If, however, coho have the capacity to imprint on a stream prior to the smolting phase, they can vary their responses to environmental stimuli in such a way as to optimize survival while still meeting an endogenous physiological schedule (in this case the development of ion regulation). Other Pacific salmon species also appear to exhibit stock specific life history variations. Because chinook salmon

emigrate as fry or smolts (Healey 1983), they probably also imprint at variable times. Again, these differences in migratory timing appear to be at least partially genetic (E.B. Taylor pers. comm.). Recent work suggests population differences also may occur in the development of osmoregulatory ability between ocean- and stream-type chinook (Wagner et al. 1969, W.C. Clarke pers. comm.).

The results of this study serve to support Raleigh's (1971) suggestion that populations of fish of the same species should not be viewed as "genetic and behavioural equivalents". Instead, unless there is evidence to the contrary, it should be assumed that each population is adapted to the requirements of its specific habitat. Population differences in the ontogeny of migratory and salinity preference responses also may be important for habitat selection in other diadromous fishes. For example, swimming stamina varies between Fraser River steelhead populations and this could affect directional components of current response behaviour (Huzyk and Tsuyuki 1974, Tsuyuki and Williscroft 1977, Northcote and Kelso 1981). In grunion (Leuresthes sardina) populations, Reynolds and Thomson (1974) observed that different ontogenetic changes in salinity preferences influence habitat use. Perhaps the variable life histories observed in Pacific fishes as diverse as the Pacific lamprey (Entosphenus tridentatus) and the longfin smelt (Spirinchus thaleichthys) are at least partially due to population differences in the ontogeny of behaviour that allow these species to exploit a variety of habitats.

CONCLUSIONS

1) There is no evidence for differences in the development of ion regulatory ability between wild, resident coastal and interior coho populations when the data are analysed by weight. In the spring, both populations develop sodium regulatory ability in the 7-11 g weight range.

2) There are differences in the age of smolting between wild populations. Rosewall Creek coho smolt after one year in freshwater, whereas Coldwater River coho may require 2 years of stream residence to reach smolt size. Smolts in both populations average about 10 g in weight and 100 mm in fork length.

3) In laboratory raised coho groups, there are no differences in the development of sodium regulatory ability between coastal and interior stocks, or between incubation treatments within stocks. All groups show an acclimative phase in the summer and early fall following emergence, an overwintering plateau and reach smolt capabilities in the following April-June.

4) There are differences in the timing of downstream movements between coastal and interior coho stocks. As indicated by Fyke net catches, Rosewall Creek coho migrate downstream in the spring (May) as post-emergents and yearlings, whereas Coldwater River coho fry move downstream in both the spring (April) and fall (November). Laboratory tested wild migrant coho display stronger downstream current responses

than similar sized resident fry. This argues that the downstream movement observed is not solely due to displacement.

5) There are no differences in the ontogeny of current response in resident subyearling, wild coho from Rosewall Creek and the Coldwater River. Both populations exhibit downstream responses as recently emerged fry during May and June and as yearlings in April. Two year old Coldwater River coho also show downstream responses in the spring.

6) Under diurnal illumination conditions, seasonal current responses are similar among laboratory reared coho stocks and incubation treatments. Rheotaxis becomes progressively more positive from post-emergence until fall. Daytime current responses then remain relatively constant until January-February, after which there is a decrease in response which reaches negative rheotaxis in April-May.

7) There are significant differences in the ontogeny of nocturnal current responses between coastal and interior laboratory reared coho, but not between incubation treatments within stocks. Rosewall Creek-Big Qualicum River coho generally display a holding response under dark conditions until February. Progressively stronger negative rheotaxis then occurs, and reaches a maximum in April-May. Coldwater River coho shift to a strong negative rheotaxis in November and maintain this response until spring.

8) There are no differences in the ontogeny of salinity preference between resident subyearling, wild coho stocks. Generally, resident and migrant

coho from both Rosewall Creek and the Coldwater River prefer hypotonic (0-8 ppt seawater) salinities throughout the year. During April-May, however, when subjected to a 4-24 ppt gradient, subyearling coho from both stocks and Coldwater River yearlings prefer isotonic to hypertonic salinities (12-16 ppt).

9) There are differences in the ontogeny of salinity preference between coastal and interior laboratory reared coho stocks, but not between incubation treatments within stocks. In a 0-20 ppt seawater gradient Rosewall Creek coho generally prefer salinities up to isotonic throughout the year. When placed in a 4-24 ppt gradient, however, Rosewall Creek coho shift to a preference for 8-16 ppt seawater in March-April. Coldwater River coho from both incubation treatments exhibit a shift in salinity preference from hypotonic to isotonic or hypertonic salinities in both gradients in November-December.

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APPENDIX 1
COMMON AND SCIENTIFIC NAMES OF FISH SPECIES
FOUND IN THE STUDY STREAMS.

Common Name	Scientific Name
coho salmon	*Oncorhynchus kisutch* (Walbaum)
chinook salmon	*O. tshawytscha* (Walbaum)
chum salmon	*O. keta* (Walbaum)
kokanee/sockeye salmon	*O. nerka* (Walbaum)
steelhead/rainbow trout	*Salmo gairdneri* Rischardson
cutthroat trout	*S. clarki* Richardson
Dolly Varden char	*Salvelinus malma* (Walbaum)
bull trout (char)	*S. confluentus* (Suckley)
mountain whitefish	*Prosopium williamsoni* (Girard)
coastrange sculpin	*Cottus aleuticus* Gilbert
prickly sculpin	*C. asper* Richardson
slimy sculpin	*C. cognatus* Richardson
threespine stickleback	*Gasterosteus aculeatus* Linnaeus
redside shiner	*Richardsonius balteatus* (Richardson)
longnose dace	*Rhinichthys cataractae* (Valenciennes)
leopard dace	*R. falcatus* (Eigenmann and Eigenmann)
longnose sucker	*Catostomus catostomus* (Forster)
lamprey	*Entosphenus tridentatus* (Gairdneri) *Lampetra* spp.

APPENDIX 2
ADULT COHO BROOD STOCK DATA FROM
ROSEWALL CREEK AND THE COLDWATER RIVER.

Population	Sex	Sample	Standard Length (cm)	Weight (kg)	Number at Age[a]	
					3_2	4_3
Rosewall Creek	Male	2	59.8 ± 3.25	3.05 ± 0.550	2	0
	Female	3	55.7 ± 0.33	2.07 ± 0.067	3	0
	Total	5	57.3 ± 1.45	2.46 ± 0.299	5	0
Coldwater River	Male	4	46.3 ± 1.70	1.13 ± 0.111	1	0
	Female	8	50.2 ± 1.48	1.34 ± 0.127	4	1
	Total	12	48.9 ± 1.23	1.27 ± 0.095	5	1

a - The age sample sizes for the Coldwater River stock are small due to resorption and regeneration problems.

APPENDIX 3
EGG SIZE, INCUBATION TEMPERATURE
AND INCUBATION SURVIVAL RATE BY POPULATION.

Population	Egg Volume (ml) (n=30)	Natural Incubation Temperature (°C)	Laboratory Incubation Temperature (°C)	Incubation Survival Rate (%)
Rosewall Creek	0.33 ± 0.007	4.6 ± 0.13 (n=212)	2.9 ± 0.15 (n=183)	76.3
			6.6 ± 0.06 (n=94)	68.0
Coldwater River	0.15 ± 0.003	2.7 ± 0.17 (n=241)	2.9 ± 0.19 (n=183)	82.3
			5.9 ± 0.02 (n=95)	82.9

APPENDIX 4
FRY EMERGENCE DATES, EMERGENT RATES,
EMERGENT NUMBERS AND LENGTH AND WEIGHT DATA.

Population	Incubation Treatment (°C)	Emergent Date (1982)	Emergence Rate (%) (Mean & range)	Total Emergent Number	Fork Length (mm) (n=30)	Weight (g) (n=30)
Rosewall Creek	2	July 1	92.5 (n=3) 91.4 - 94.0	851	34.4 ± 0.18	0.30 ± 0.006
	6	March 19	54.1 (n=6) 38.2 - 65.2	1,703	33.1 ± 0.21	0.28 ± 0.007
Coldwater River	2	June 23	66.1 (n=3) 43.1 - 78.1	1,184	30.4 ± 0.22	0.18 ± 0.006
	6	March 10	23.4 (n=6) 11.9 - 40.6	2,287	30.0 ± 1.05	0.22 ± 0.006

APPENDIX 5
LABORATORY REARING CONDITIONS.

Population	Incubation Treatment (°C)	Dissolved Oxygen Range ($mg.L^{-1}$ @ °C & % saturation)	pH	Rearing Container	Rearing Densities Range ($no.L^{-1}$)
Rosewall Creek (Big Qualicum River)	2	7.6 @ 14.4 - 11.4 @ 6.5 (75%-94%)	6.27 ± 0.053 (n=17)	Trough	7.9 - 9.0
				Tank	0.7 - 1.1
	6	8.3 @ 9.2 - 11.6 @ 6.6 (73%-96%)	6.30 ± 0.031 (n=28)	Trough	16.0-17.9
				Tank	1.0 - 2.2
Coldwater River	2	7.8 @ 14.4 - 11.4 @ 8.2 (76.5%-96.8%)	6.30 ± 0.048 (n=17)	Trough	10.9-12.5
				Tank	0.9 - 1.5
	6	6.2 @ 14.4 - 11.8 @ 6.6 (61%-96%)	6.27 ± 0.033 (n=30)	Trough	21.9-24.0
				Tank	1.0 - 2.6

APPENDIX 6

GEOMETRIC FUNCTIONAL REGRESSIONS OF STANDARD LENGTH ON FORK LENGTH AND TOTAL LENGTH ON FORK LENGTH FOR WILD AND LABORATORY RAISED COHO JUVENILES.

Total Length on Fork Length.

Population	Sample Size (n)	Slope (v)	Y-Intercept (a')	Correlation Coefficient (r)
Rosewall Cr., Wild coho.	409	0.930	-2.09	0.99961
Rosewall Cr.,[a] 6°C incubation.	640	0.934	-2.176	0.99987
Rosewall Cr., 2°C incubation.	530	0.924	-1.822	0.9998
Coldwater R., Wild coho.	725	0.930	-1.987	0.99915
Coldwater R., 6°C incubation.	700	0.933	-1.881	0.99989
Coldwater R., 2°C incubation.	534	0.927	-1.689	0.99983

Standard Length on Fork Length.

Population	Sample Size (n)	Slope (v)	Y-Intercept (a')	Correlation Coefficient (r)
Rosewall Cr., Wild coho.	409	1.128	-2.241	0.99956
Rosewall Cr.,[a] 6°C incubation.	640	1.099	-1.241	0.99981
Rosewall Cr., 2°C incubation.	530	1.101	-1.429	0.9977
Coldwater R., Wild coho.	617	1.118	-1.674	0.99963
Coldwater R., 6°C incubation.	670	1.099	-1.043	0.9998
Coldwater R., 2°C incubation.	534	1.103	-1.402	0.9998

a - Includes Big Qualicum River coho.

APPENDIX 7
THE OBSERVED FLOW REGIME IN THE CURRENT RESPONSE CHANNELS OVER THE 12 MONTH STUDY PERIOD.

Riffle	Flow Velocity ($cm.s^{-1}$) by Channel Number (n=12).		
	1	2	3
Upstream 1	10.7 ± 8.38	12.2 ± 0.68	11.0 ± 0.49
2	10.7 ± 0.34	11.3 ± 0.26	10.8 ± 0.27
3	10.4 ± 0.30	11.5 ± 0.34	11.1 ± 0.30
4	10.3 ± 0.25	10.8 ± 0.21	10.7 ± 0.29
5	10.6 ± 0.09	11.4 ± 0.37	11.0 ± 0.39
6	10.4 ± 0.24	10.9 ± 0.26	10.6 ± 0.33
7	10.5 ± 0.21	11.0 ± 0.27	10.3 ± 0.25
8	10.4 ± 0.23	10.9 ± 0.24	10.6 ± 0.26
9	10.2 ± 0.22	10.1 ± 0.27	10.3 ± 0.21
10[a]	9.7 ± 0.17	10.1 ± 0.26	10.2 ± 0.23
11[a]	10.0 ± 0.24	9.9 ± 0.19	9.7 ± 0.16
12	10.2 ± 0.22	9.6 ± 0.14	10.4 ± 0.32
13	9.5 ± 0.14	10.3 ± 0.29	10.1 ± 0.29
14	10.1 ± 0.23	10.8 ± 0.38	10.1 ± 0.25
15	9.5 ± 0.22	11.4 ± 0.51	9.7 ± 0.20
16	10.1 ± 0.15	10.0 ± 0.26	9.7 ± 0.29
17	10.2 ± 0.24	11.3 ± 0.40	10.1 ± 0.19
18	9.8 ± 0.20	11.0 ± 0.33	10.0 ± 0.21
19	10.0 ± 0.28	11.4 ± 0.45	10.3 ± 0.31
20 Downstream	10.0 ± 0.17	11.2 ± 0.59	10.0 ± 0.35

a - The location of the riffles immediately upstream and downstream of the release chamber.

APPENDIX 8

DESIGN AND CALIBRATION OF EXPERIMENTS

In most of the experiments discussed below, the preparatory procedures followed those described in this thesis under similar headings in Methods, Experimental Techniques. The general results and disccussion of these experiments are given in the main text of the thesis (Methods, Design and Calibration of Experiments). The full results for these experiments are given here, along with descriptions of specific treatments and variations in handling procedures.

Plasma Sodium Regulatory Ability

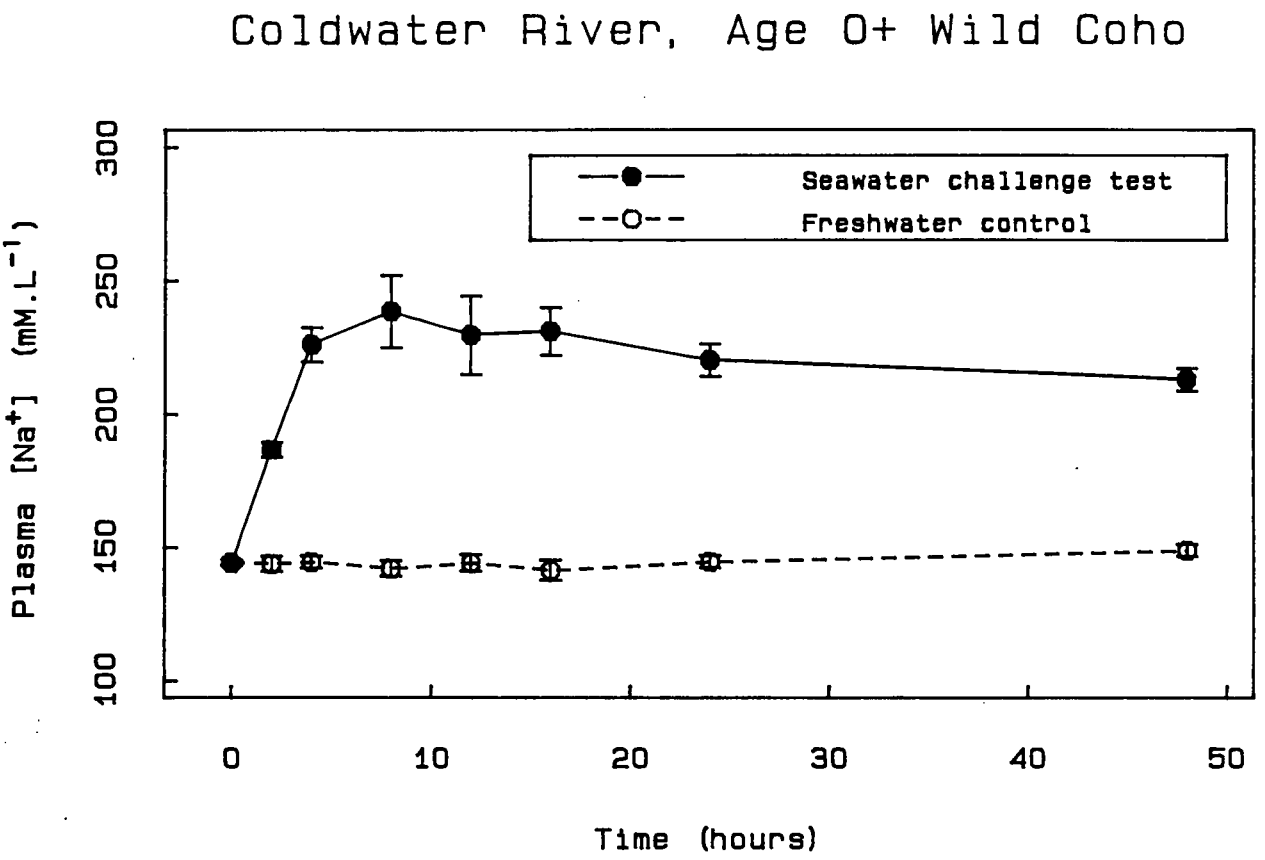
Timing of Sample Collection

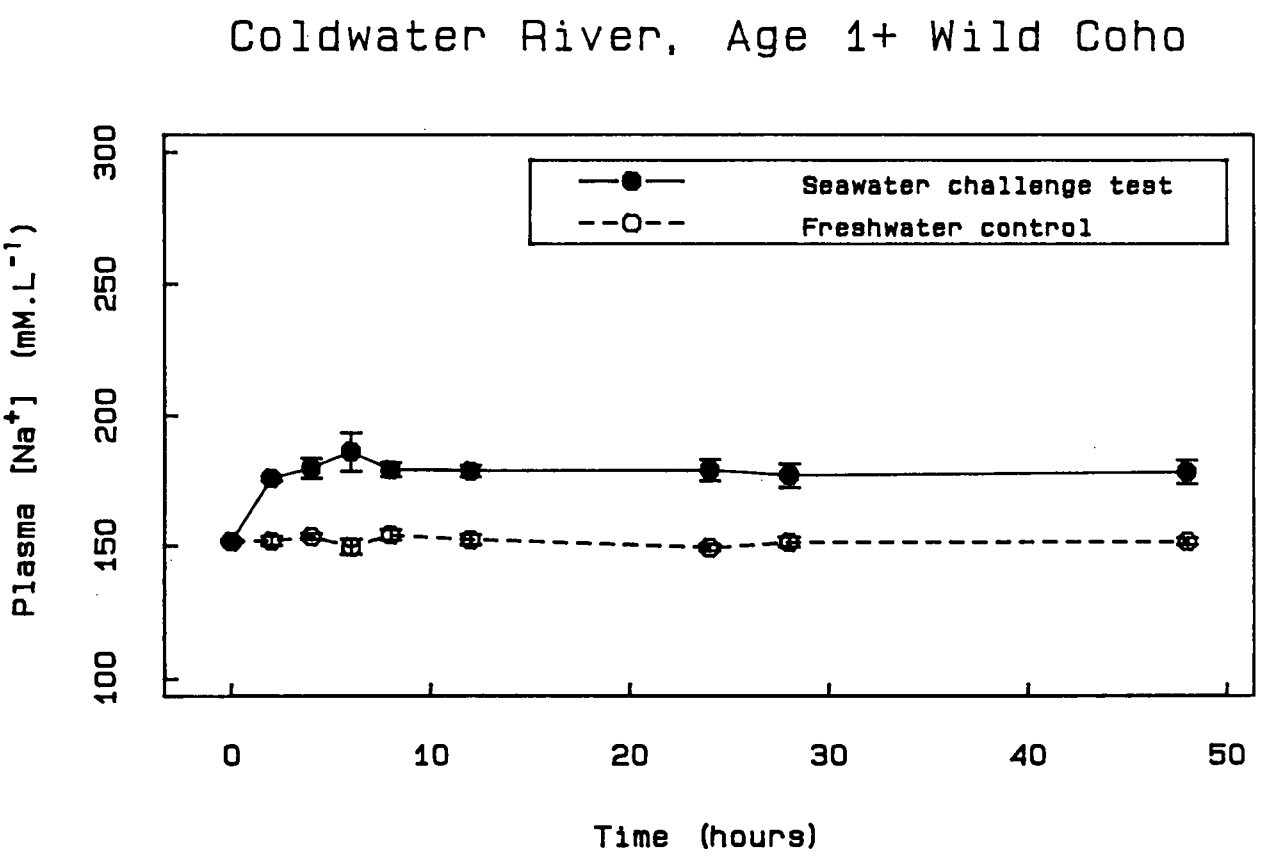
To examine the trend in plasma sodium levels in fish undergoing the seawater challenge test, as well as possible variations in sodium regulatory ability after 24 hours of treatment, subsamples of 5 coho were taken from both seawater and freshwater solutions at 0, 2, 4, 8, 12, 24, and 48 hours. These samples were anaesthetised and a caudal blood sample collected for plasma sodium analyses. Coldwater River subyearlings and Big Qualicum River yearlings were tested separately. The results of these collections are depicted in Figure 1. Comparisons between sodium levels at 24 and 48 hours (Table 1) indicate that 24 hours is an acceptable preacclimation interval for sample collection.

Appendix 8, Figure 1.

Seawater challenge tests exposure time experiments

Error bars represent 95% confidence limits.


Coldwater River, Age 0+ Wild Coho
Seawater challenge test
Freshwater control
Plasma [Na+] (mM.L-1)
100
150
200
250
300
0
10
20
30
40
50
Time (hours)


Coldwater River, Age 1+ Wild Coho
Seawater challenge test
Freshwater control
Plasma [Na+] (mM.L-1)
100
150
200
250
300
0
10
20
30
40
50
Time (hours)

APPENDIX 8: TABLE 1
SEAWATER CHALLENGE TEST TIMING EXPERIMENTS;
COMPARISONS BETWEEN PLASMA SODIUM CONCENTRATIONS COLLECTED
24 AND 48 HOURS AFTER EXPERIMENT INITIATION.

Population and Stage	Fork Length (mm)	Test or Control	Time (hr)	Plasma $[Na^+]$ ($mM.L^{-1}$)	t_s value
Big Qualicum River, yearlings (smolt size).	129.5 ± 0.99 (n=86)	Control (0 ppt)	24	149.1 ± 1.20 (n=5)	1.282 p>0.05
			48	151.4 ± 1.28 (n=5)	
		Test (30 ppt)	24	179.2 ± 4.06 (n=5)	0.125 p>>0.05
			48	178.4 ± 4.50 (n=5)	
Coldwater River, subyearling fry.	60.6 ± 1.13 (n=67)	Control (0 ppt)	24	144.7 ± 2.30 (n=5)	1.327 p>0.05
			48	148.9 ± 2.24 (n=5)	
		Test (30 ppt)	24	220.3 ± 5.99 (n=5)	0.844 p>>0.05
			48	213.1 ± 4.19 (n=5)	

Dilution and Range Setting Effects on Photometric Readings

Only large, smolt size, yearling coho, collected from the Big Qualicum River Hatchery, were used in this experiment. To examine the effects of changes in standard and sample dilutions, and in photometer range settings, plasma samples were collected from fish held in seawater or freshwater for 24 hours and were divided between four treatments. The treatments were:

1) calibration standard dilution - 1:200,
   sample dilution - 1:200,
   photometer range setting - 0-140,
   multiplicative factor - none.

2) calibration standard dilution - 1:200,
   sample dilution - 1:400,
   photometer range setting - 0-140,
   multiplicative factor - 2X.

3) calibration standard dilution - 1:400,
   sample dilution - 1:400,
   photometer range setting - 0-70,
   multiplicative factor - 2X.

4) calibration standard dilution - 1:400,
   sample dilution - 1:400,
   photometer range setting - 0-140,
   multiplicative factor - none.

Treatment 1 was the combination recommended by the operations manual (Anon. 1977) and served as a control. Mean sodium values were compared within freshwater and seawater groups using one-way ANOVA (Table 2). Treatments were grouped using the T-method multiple range test. Dunnett's pairwise comparison test was also used to group the data sets with the control (Table 2). Treatment means were homogenous, indicating that any of the above treatments would be acceptable.

APPENDIX 8: TABLE 2
SEAWATER CHALLENGE TEST DILUTION EFFECTS;
COMPARISONS BETWEEN PLASMA SODIUM CONCENTRATIONS IN SAMPLES TREATED
TO DIFFERENT DILUTIONS AND PHOTOMETER RANGE SETTINGS.

Test Conditions	Sample Size (n)	Weight (g)	Fork Length (mm)	Trtmt Type[a]	Plasma $[Na^+]$ ($mM.L^{-1}$)	F_s value	Multiple Range Comparison[b]
Control (0 ppt seawater)	34	23.26 ± 0.735	131.2 ± 1.54	1	160.5 ± 0.83	1.083 p>0.05	(1,2,3,4)
				2	158.3 ± 1.04		
				3	159.0 ± 0.94		
				4	158.7 ± 0.92		
Test (29 ppt seawater)	34	24.03 ± 1.191	133.2 ± 9.70	1	184.2 ± 1.49	0.715 p>0.05	(1,2,3,4)
				2	181.8 ± 1.61		
				3	181.3 ± 1.57		
				4	181.6 ± 1.53		

All coho used in this experiment were from the Big Qualicum River.
a - Treatment (Trtmt) types. For a description, see the text.
b - Both the T-method and Dunnett's pairwise comparison test (using treatment type 1 as the control) gave the same results.

Handling and Confinement Effects

Big Qualicum River yearlings were used in this experiment. To test for handling and confnement effects, samples of coho received three different treatments:

1) coho were not weighed prior to the test and were not confined during the test,

2) coho were weighed before the test but were not confined during the tests, and

3) coho were weighed before the test and were confined during the test.

These treatments were carried out in both fresh and salt water. Treatment 1 served as a control and the coho were weighed after the test. The other two treatments involved pretest weighing. Sample sizes varied, with 20 coho used in treatments 1 and 2, and 30 yearlings used in treatment 3. More fish were included in treatment 3 because it was possible that the extra handling might result in mortality.

Because different samples were used in each treatment, differences between mean weights and lengths were examined within fresh and salt water groups with one-way ANOVA (Table 3). Multiple comparisons confirmed the homogeneity in weight and length of sample fish (Table 3). Given this homogeneity, fish size was not considered further as a factor in the plasma sodium values.

APPENDIX 8: TABLE 3
SEAWATER CHALLENGE TEST HANDLING EFFECTS;
COMPARISONS OF WEIGHT, LENGTH AND PLASMA SODIUM CONCENTRATIONS IN SAMPLES TREATED TO DIFFERENT DEGREES OF HANDLING AND CONFINEMENT.

Test Conditions	Measurement	Treatment Type[a]			F_s value	Multiple Range Comparison[b]
		1	2	3		
Control (0 ppt seawater)	Weight (g)	16.33 ± 0.901 (n=20)	16.68 ± 0.868 (n=19)	18.5 ± 0.904 (n=30)	1.781 p>0.05	(1,2,3)
	Fork Length (mm)	117.3 ± 2.44 (n=20)	118.1 ± 1.78 (n=19)	120.3 ± 1.79 (n=30)	0.608 p>0.05	(1,2,3)
	Plasma ($mM\ Na^+.L^{-1}$)	155.6 ± 0.99 (n=20)	146.4 ± 2.06 (n=19)	147.1 ± 0.99 (n=30)	-c-	(1) (2,3)
Test (29 ppt seawater)	Weight (g)	15.24 ± 0.944 (n=20)	17.98 ± 0.870 (n=20)	16.27 ± 1.008 (n=18)	2.255 p>0.05	(1,2,3)
	Fork Length (mm)	115.4 ± 2.36 (n=20)	120.7 ± 2.04 (n=20)	116.4 ± 2.33 (n=18)	9.601 p>0.05	(1,2,3)
	Plasma ($mM\ Na^+.L^{-1}$)	177.1 ± 0.93 (n=20)	172.2 ± 1.14 (n=20)	176.9 ± 1.54 (n=18)	5.437 p<0.01	(1,3) (2)

All coho used in this experiment were from the Big Qualicum River.

a - Treatment types are described in the text.

b - Tukey-Kramer's test was used among homoscedastic freshwater control samples. The T'-test was used for homoscedastic test samples. The Games and Howell method was used for heteroscedastic control plasma sodium concentrations.

c - Sample variances heteroscedastic.

Differences in plasma sodium values in seawater treated coho were tested with a one-way ANOVA and a T' comparison test (Table 3). Since fresh water plasma sodium sample variances were heteroscedastic, the homogeneity of treatment means was examined using the Games and Howell method (Table 3). Handling and confinement produced significant differences between treatment means, with control mean values the highest.

Current Response

Timing of Distribution Collection

Three test groups were used in this experiment; wild Coldwater River, wild Rosewall Creek and laboratory raised Chef Creek yearling coho. Standard test procedures were used except that distribution observations were taken at 0.5 hour intervals over a 4 hour period to examine possible variation in response distributions over time. Distributions under light were observed from behind a black plastic screen, while distributions in the dark were checked with a penlight. The flow rate at the release points during this experiment averaged 9.03 ± 0.230 $cm.s^{-1}$ (n=18). Temperatures ranged from 8.8°C to 9.6°C, and deviated no more than 0.9°C from the rearing temperatures. Dissolved oxygen levels were relatively stable at 10.8 $mg.L^{-1}$ at 10°C to 11.2 $mg.L^{-1}$ at 10.2°C (95-96% saturation).

Three replicates of each group were tested under light and dark conditions. The resulting distributions were pooled within illumination treatments for each time interval. The proportion of fish in each group at the point of release and the ends of the channels at each observation interval

were then angular transformed, and the mean inverse was plotted to depict movement timing (Figures 2 and 3).

As discussed in the Methods section of this thesis, most of the movement occurred during the first 2.0 hours. Among groups, the larger Chef Creek coho (Table 4) responded more quickly under light conditions, whereas the interior Coldwater River fish showed a faster and greater response in the dark. Homogeneity in responses over time were examined by grouping distributions within populations and illumination conditions using a nonparametric multiple comparison by STP test (Table 5). Distributions were homogeneous after the first hour of movement.

Salinity Preference

Test Sample Size, Exploration Time and Gradient Stability

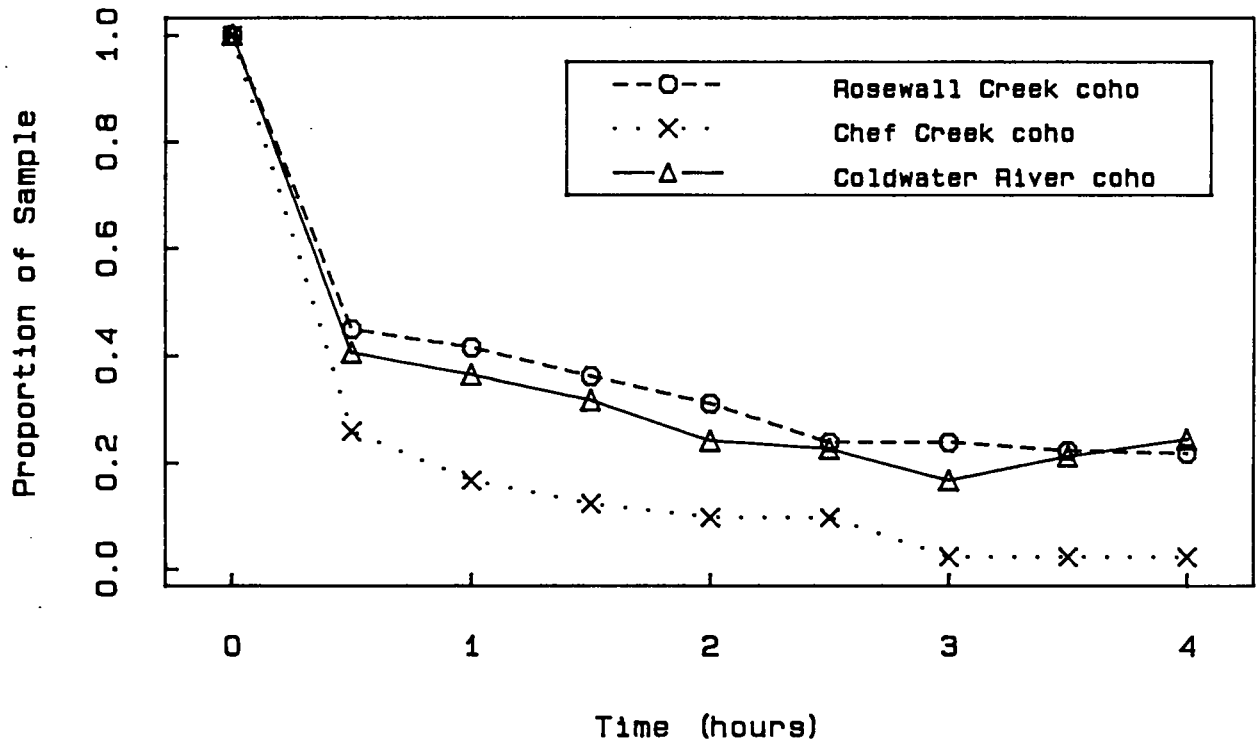
To determine an adequate sample size and exploration period, groups of 1 to 5 coho were observed as they explored the gradient channels. These tests were carried out in freshwater. Groups were released in the channels after a 0.5 hour acclimation period, and over a 4 hour period the position of each individual was noted and explorations to the end of each channel documented for each 0.5 hour interval. For each group size, three replicates from each of three different populations (Rosewall Creek, Chef Creek and Coldwater River) were completed and the results pooled (Table 6). Based on these results, a standard exploration period of 2.0 hours for a group of 5 coho was selected.

Appendix 8, Figure 2.

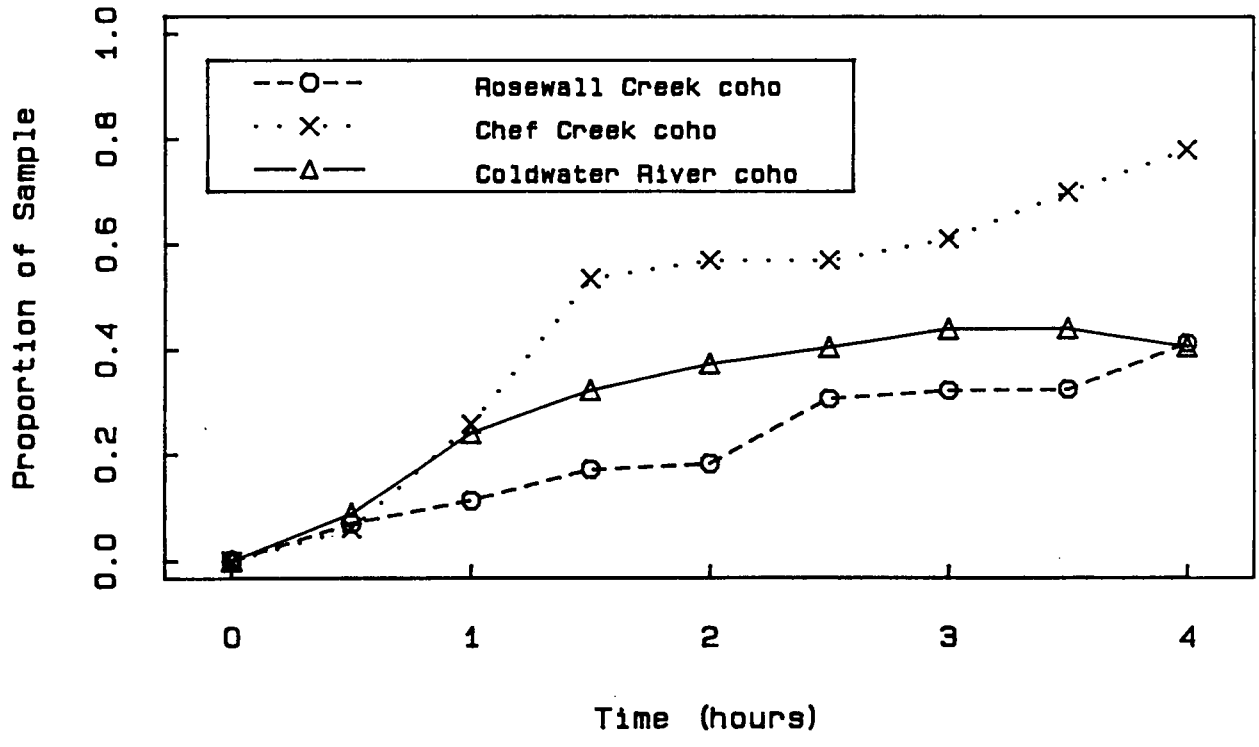
Current response test timing experiment; light conditions.

Each point represents the mean inverse of the angular transformed proportion observed (n=3).

Coho Remaining at Release Point



Coho Moving to Channel Ends

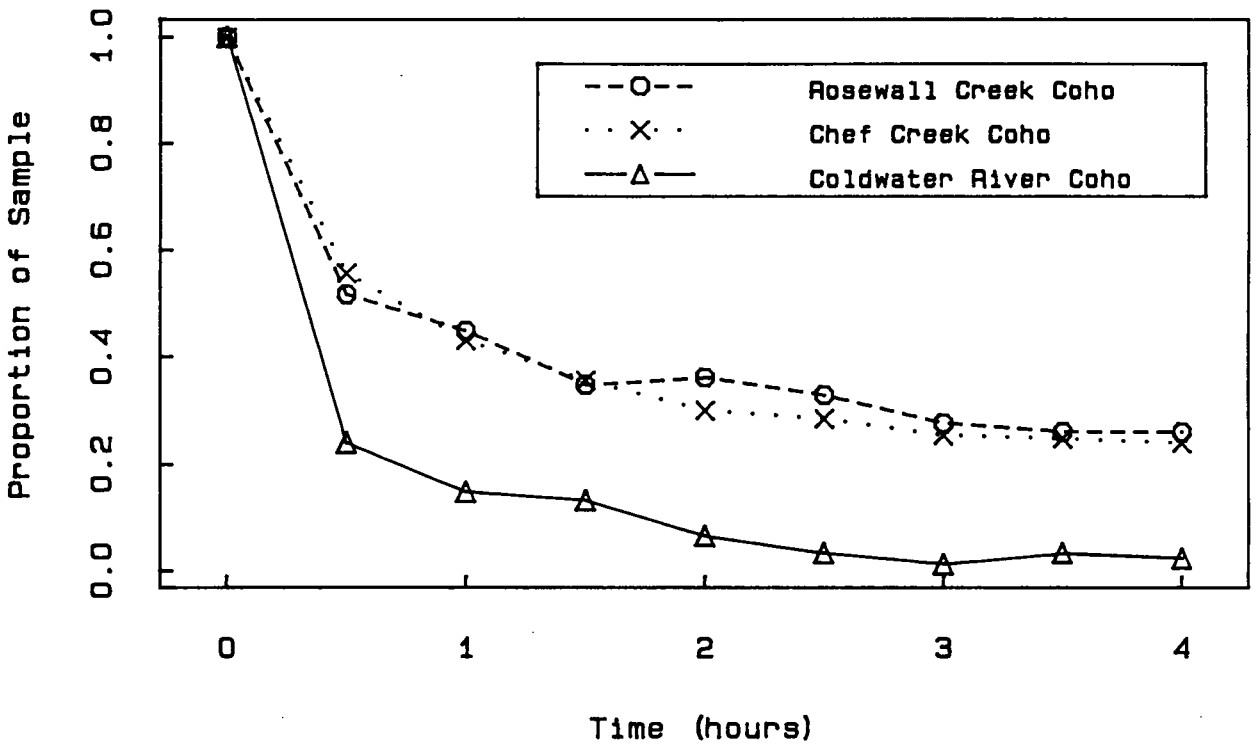


Appendix 8, Figure 3.

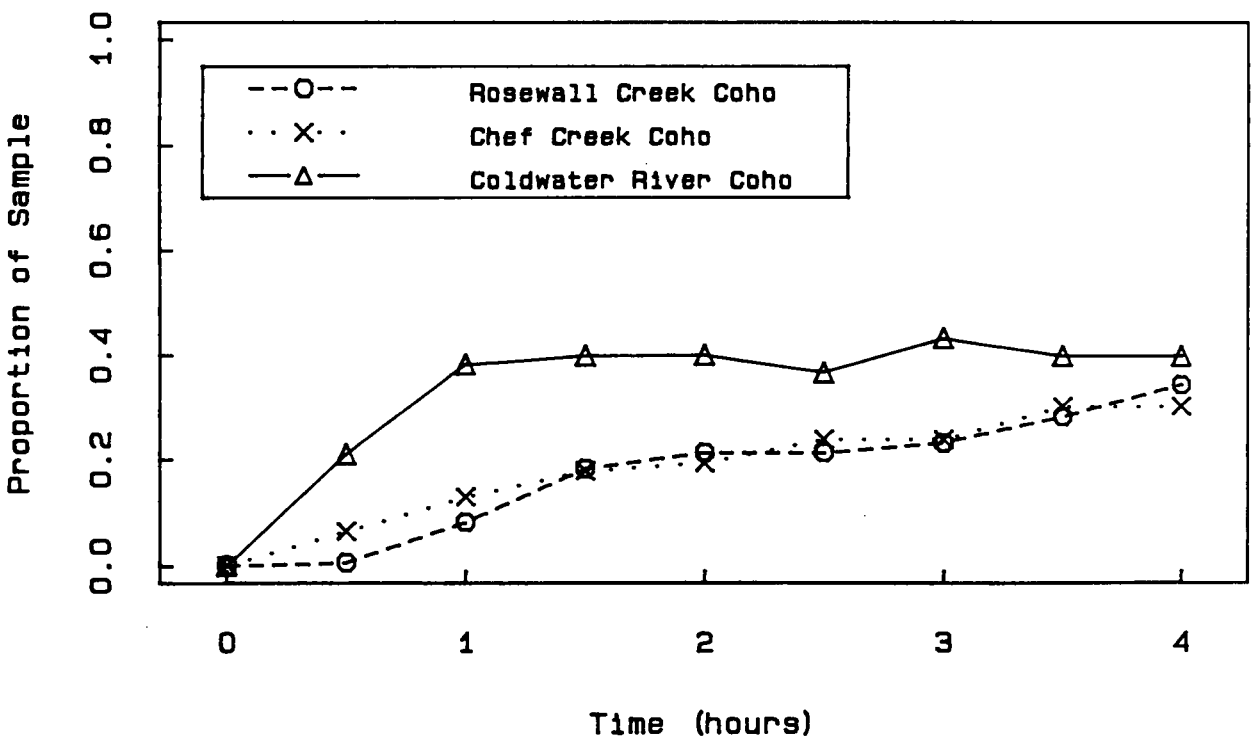
Current response test timing experiment; dark conditions.

Each point represents the mean inverse of the angular transformed proportion observed (n=3).

Coho Remaining at Release Point



Coho Moving to Channel Ends



APPENDIX 8: TABLE 4
CURRENT RESPONSE TESTS - TIMING OF DISTRIBUTION COLLECTION
COMPARISONS OF WEIGHT AND LENGTH OF TEST GROUPS.

Population	Sample Size (n)	Weight (g)	Fork Length (mm)	Multiple Range Comparison[a]
Rosewall Creek, Wild coho	60	12.27 ± 0.361	107.8 ± 1.05	Weight (1) (2) (3) Length (1) (2) (3)
Chef Creek, Laboratory reared coho	60	20.36 ± 0.526	125.4 ± 0.96	
Coldwater River, Wild coho	120	2.07 ± 0.070	59.5 ± 0.61	

a - Games and Howell method for heteroscedastic group comparisons used

APPENDIX 8: TABLE 5
CURRENT RESPONSE TESTS - TIMING OF DISTRIBUTION COLLECTION
MULTIPLE COMPARISON GROUPINGS OVER TIME.

Illumination Conditions	Population	Multiple Comparison Groupings of Half Hourly Distributions[a]
Light (Day time)	Rosewall Creek	(0.5,1.0,1.5,2.0,2.5,3.0,3.5,4.0)
	Chef Creek	(0.5,1.0,1.5,2.0,2.5,3.0,3.5,4.0)
	Coldwater River	(0.5,1.0,1.5,2.0,2.5,3.0,3.5,4.0)
Dark (Night time)	Rosewall Creek	(0.5,1.0,1.5,2.0) (1.0,1.5,2.0,2.5,3.0,3.5) (1.5,2.0,2.5,3.0,3.5,4.0)
	Chef Creek	(0.5,1.0,1.5,2.0,2.5,3.0,3.5) (1.0,1.5,2.0,2.5,3.0,3.5,4.0)
	Coldwater River	(0.5,1.0,1.5,2.0,2.5,3.0,3.5,4.0)

a - Multiple comparison groupings completed using the nonparametric STP method.

APPENDIX 8: TABLE 6
SALINITY PREFERENCE TESTS; TIME REQUIRED FOR COHO OF DIFFERENT GROUP SIZES TO EXPLORE A MODIFIED STAALAND CHANNEL.

Test Group Size	Proportion Reaching the Channel End	Time Required to Reach the End of the Channel (hr)	
		Mode	Range
1	0.333	2.0	2.0 - 2.0
2	0.167	4.0	4.0 - 4.0
3	0.61	2.0	1.0 - 3.5
4	0.792	1.0	0.5 - 3.5
5	0.61	2.0	0.5 - 4.0

Three replicates of three populations of each group size were combined to give the results. Weights and Fork lengths of the population samples used were:

- Rosewall Creek - n=40, Weight - 8.53 ± 0.241 g,
  Fork Length - 91.8 ± 0.94 mm.
- Chef Creek - n=30, Weight - 8.74 ± 0.433 g,
  Fork Length - 92.9 ± 1.55 mm.
- Coldwater River - n=42, Weight - 7.51 ± 0.364 g,
  Fork Length - 91.6 ± 1.25 mm.

To check gradient stability, separate gradients of 0 to 20 ppt and 4 to 24 ppt seawater were established in the four channels. The channels were left over night and then groups of 5 large Coldwater River coho were released into each channel. Size data for these fish are given in Table 6. The fish were left for 24 hours, and then water samples were collected and tested for salinity. The results indicate that little gradient change had occurred (Table 7).

Timing of Distribution Observations

These experiments were conducted to determine the period during which salinity preference observations could be collected and pooled without acclimation biasing the results. The experiments were carried out in freshwater. Coho groups of 5 fish were released into each channel after a standard holding period and distribution observations were collected every 15 minutes for 4 hours. Four replicates, or 16 observation sets for each population, were collected for Coldwater River wild fry and Rosewall fry. The data were then pooled and distributions over time compared and grouped using nonparametric comparisons by STP analyses (Table 8). Distributions between 2.0 and 4.0 hours were deemed to be homogeneous and suitable for pooling.

Possible Biases Caused by Preference Channel Design

Figure 4 shows the tendency for coho searching control gradients (fresh water or 4 ppt seawater) to localize their movements at the release site or the end of each channel.

APPENDIX 8: TABLE 7
SALINITY PREFERENCE TESTS; SALINITY GRADIENT STABILITY.

0-20 ppt Seawater Gradient		4-24 ppt Seawater Gradient	
Salinity before the Test (ppt)[a]	Salinity after the Test (ppt) (n=4)[b]	Salinity before the Test (ppt)[a]	Salinity after the Test (ppt) (n=4)[b]
0	0	4.6	4.2 ± 0.041
4.5	4.0 ± 0.041	8.6	8.2 ± 0.063
7.8	8.1 ± 0.041	12.3	12.1 ± 0.065
12.0	12.0 ± 0.085	16.9	16.1 ± 0.108
15.7	15.9 ± 0.065	20.6	20.4 ± 0.091
20.1	20.1 ± 0.058	24.6	24.5 ± 0.096

All coho used in this experiment were from the Coldwater River. For size data, see Appendix 8, Table 6.
a - Salinity measured by hydrometer.
b - Salinity measured by conductivity meter.

APPENDIX 8: TABLE 8
SALINITY PREFERENCE TEST - TIMING OF DISTRIBUTION COLLECTION;
MULTIPLE COMPARISON GROUPINGS OVER TIME.

Population	Multiple Comparison Groupings of Quarter Hourly Distributions[a]
Rosewall Creek, Wild coho.	(0.25,0.5) (0.75,1.0,1.25,1.5,1.75,2.0,2.25,2.5,2.75,3.0, 3.25,3.5,3.75,4.0)
Coldwater River, Wild coho.	(0.25,0.5) (0.5,0.75) (0.75,1.0,1.25,3.75,4.0) (1.0,1.25,1.5,1.75,2.0,2.25,2.5,3.25,3.5,3.75,4.0) (1.25,1.5,1.75,2.0,2.25,2.5,3.0,3.25,3.5,3.75,4.0) (1.5,1.75,2.0,2.25,2.5,2.75,3.0,3.25,3.5,3.75,4.0)

a - Multiple comparison groupings completed using the nonparametric STP method.

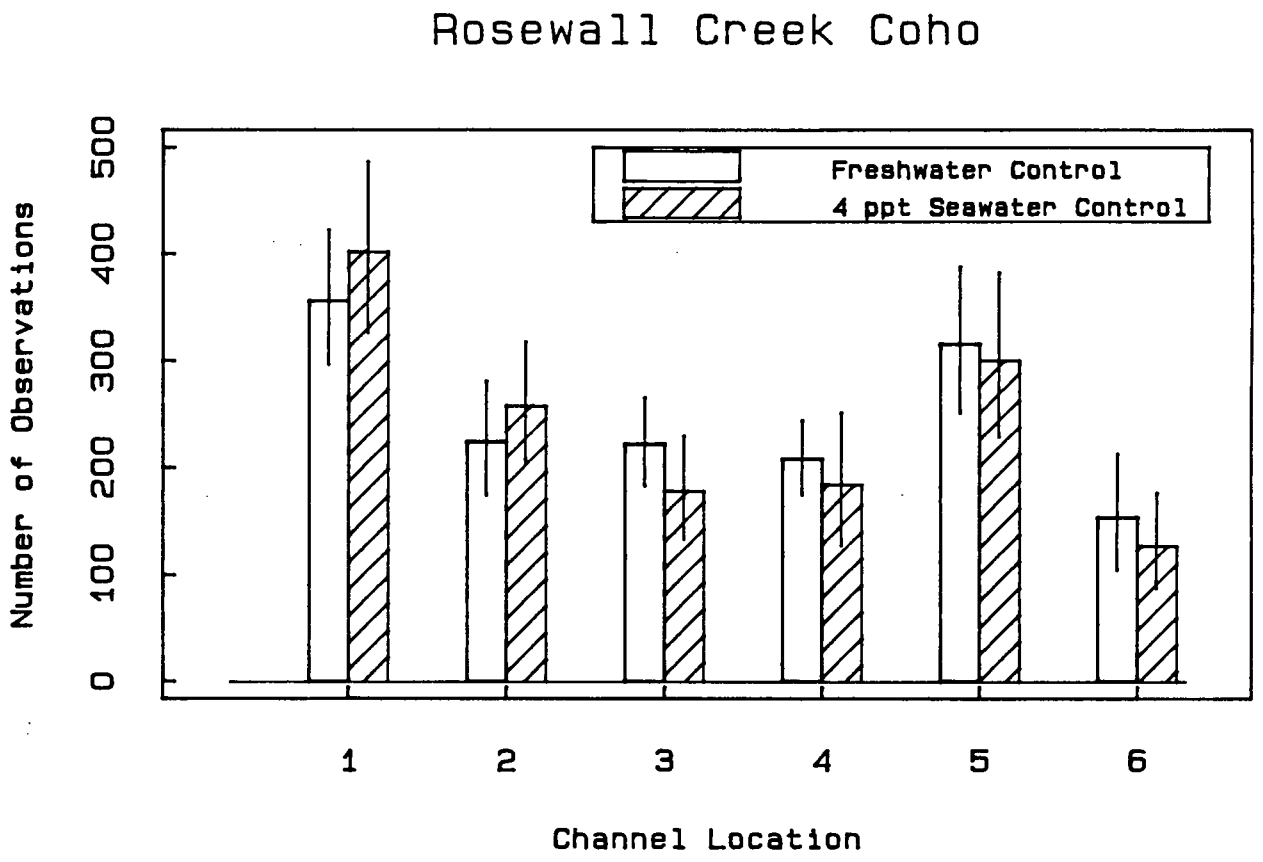
Weight and fork lengths of the population samples used were:

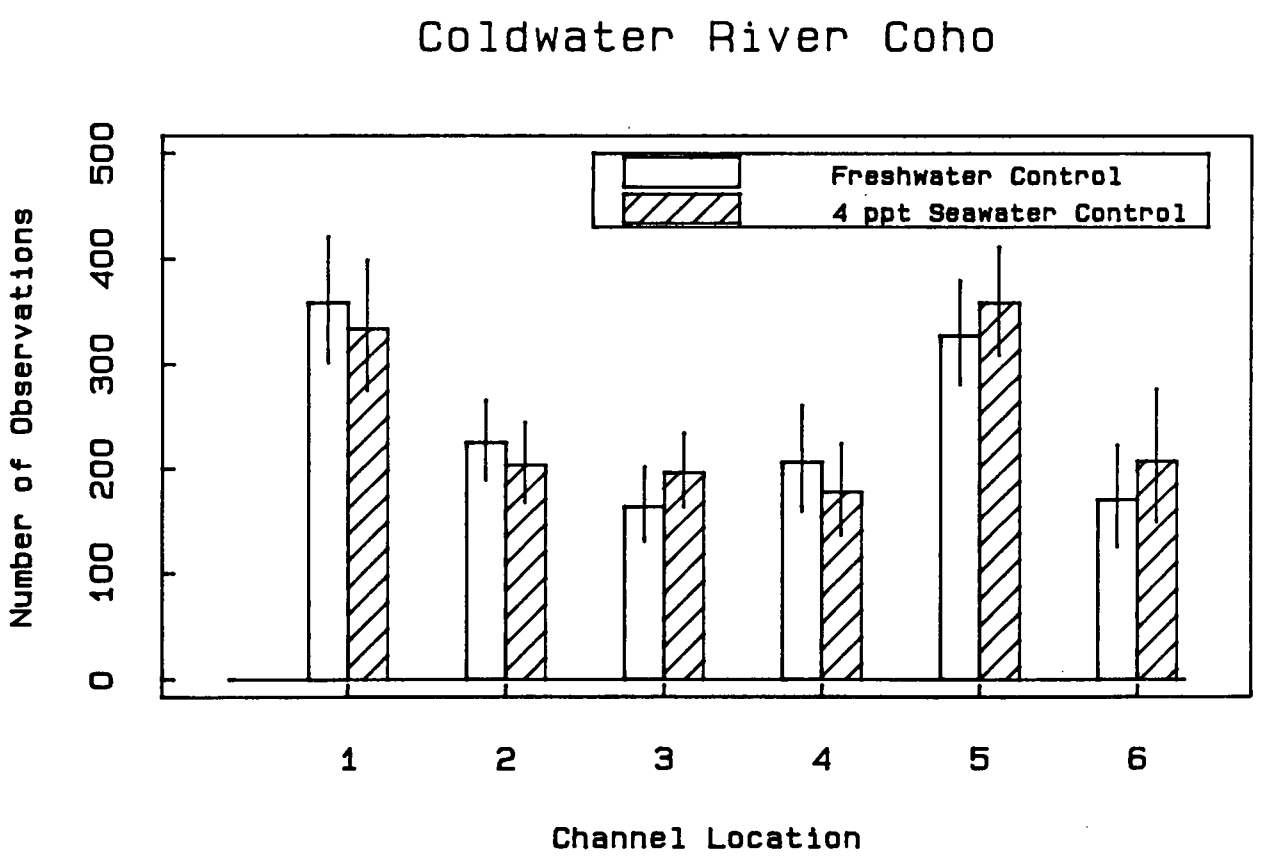
- Rosewall Creek - n=42, Weight - 12.26 ± 0.432 g.
  Fork Length - 107.8 ± 1.28 mm.
- Coldwater River - n=54, Weight - 9.42 ± 0.311 g.
  Fork Length - 96.4 ± 1.07 mm.

Appendix 8, Figure 4.

Control distributions in salinity preference channels.

Histogram bars represent the mean inverse of square root tranformed counts. 95% confidence limits are also given.


Rosewall Creek Coho
Freshwater Control
4 ppt Seawater Control
Number of Observations
0
100
200
300
400
500
1
2
3
4
5
6
Channel Location


Coldwater River Coho
Freshwater Control
4 ppt Seawater Control
Number of Observations
0
100
200
300
400
500
1
2
3
4
5
6
Channel Location

Potential Effects of Size and Growth

To determine the degree of differences in size and growth among experimental groups, linear regressions of $\log_{10}$(weight) against $\log_{10}$(time) (Table 9, Figures 5, 6 and 7) were compared using analyses of covariance (Tables 10 and 11). In addition, to examine whether size differences could contribute to migratory tendencies, the weight of wild capture migratory coho was compared to the weight of resident fry from the same population collected at approximately the same time (Table 12). Wild population and laboratory group growth trends differed significantly within experimental series, however the trends among laboratory raised groups were much more similar than between wild populations (Table 10). Comparisons of growth trends within stocks and treatments showed that experimental series samples were significantly different over time for wild and 2°C incubation groups but similar for 6°C incubation groups (Table 11). Migrant and resident Coldwater coho fry did not differ in size within season, however Rosewall Creek spring, resident fry were significantly larger than corresponding migrant fry (Table 12).

APPENDIX 8: TABLE 9
REGRESSION SLOPES AND Y-INTERCEPTS FOR STUDY GROUP GROWTH TRENDS; (Log_{10}(weight) = a + b Log_{10}(time))

Population	Incubation Treatment	Study Test[a]	Sample Size (n)	Regression		Correlation Coefficient (r)
				Slope (b)	Y-intercept (a)	
Rosewall Creek - Big Qualicum River.	Wild coho	1	269	1.704	-3.782	0.864
		4	409	1.871	-4.162	0.877
	Lab raised 2°C incub.	1	300	3.171	-7.507	0.940
		2	400	3.328	-7.925	0.947
		3	400	3.024	-7.140	0.940
	Lab raised 6°C incub.	1	413	2.186	-4.695	0.975
		2	460	2.147	-4.600	0.968
		3	450	2.137	-4.572	0.969
Coldwater River.	Wild coho	1	395	1.880	-4.599	0.865
		4	660	1.765	-4.336	0.834
	Lab raised 6°C incub.	1	300	3.183	-7.673	0.935
		2	424	3.740	-9.105	0.964
		3	424	3.701	-8.997	0.961
	Lab raised 2°C incub.	1	420	2.647	-2.647	0.981
		2	530	2.616	-2.616	0.980
		3	519	2.651	-5.889	0.976

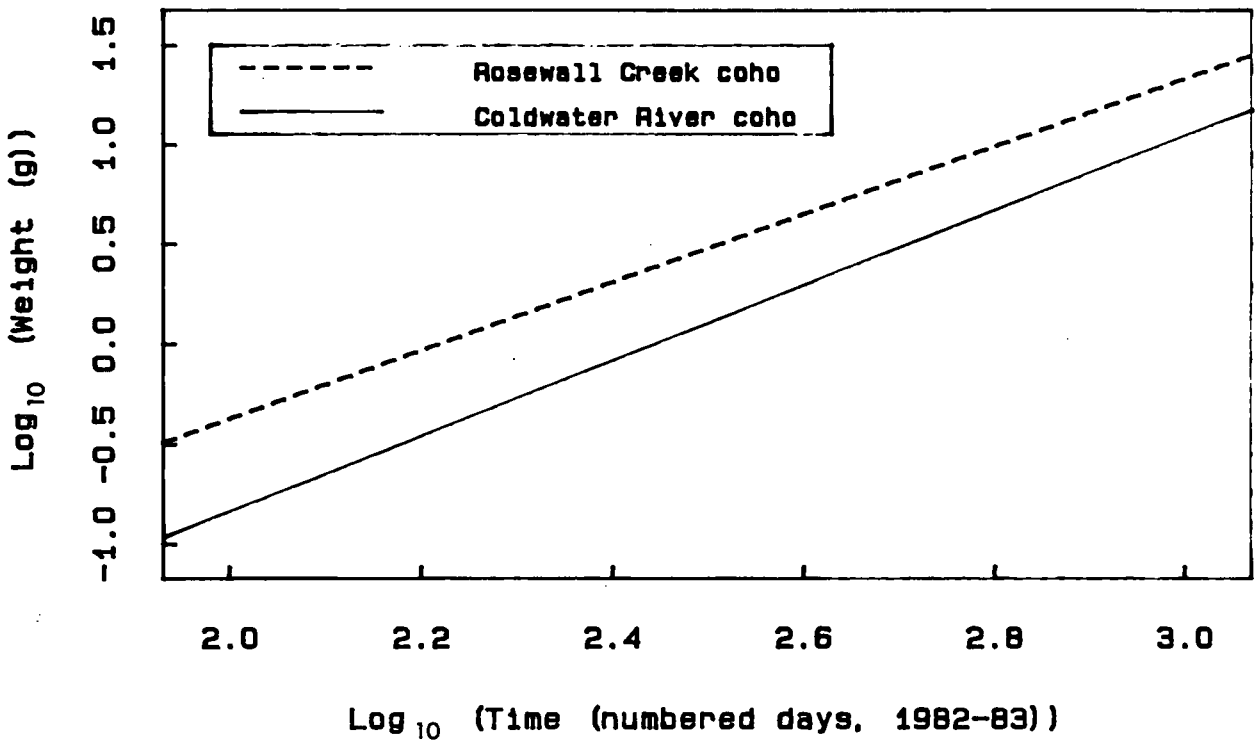
a - Study test - 1. Seawater Challenge Test.
2. Current Response Test.
3. Salinity Preference Test.
4. Both Behavioural Response Tests Combined (2 & 3).

Appendix 8, Figure 5.

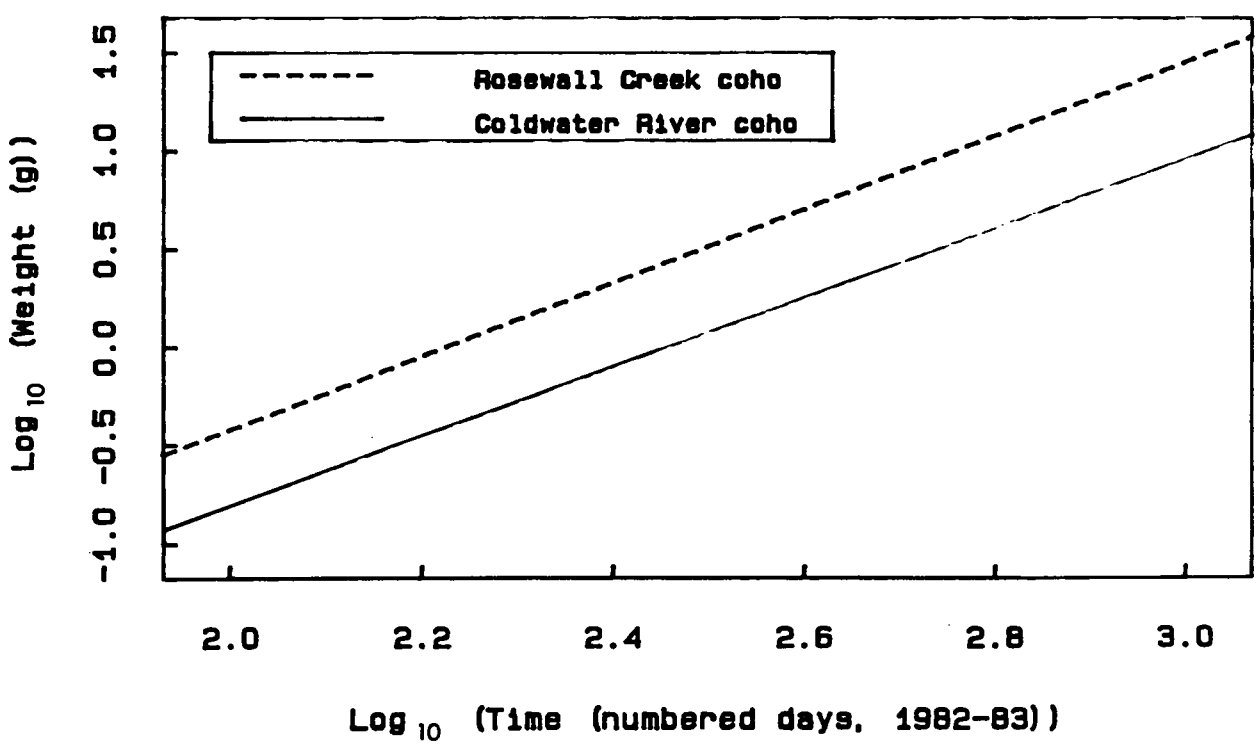
Growth regressions for wild stocks;
$\log_{10}$(weight) vs $\log_{10}$(time)

Units of time are consecutively numbered days (1-730) during 1982-83.

Seawater Challenge Test Sample



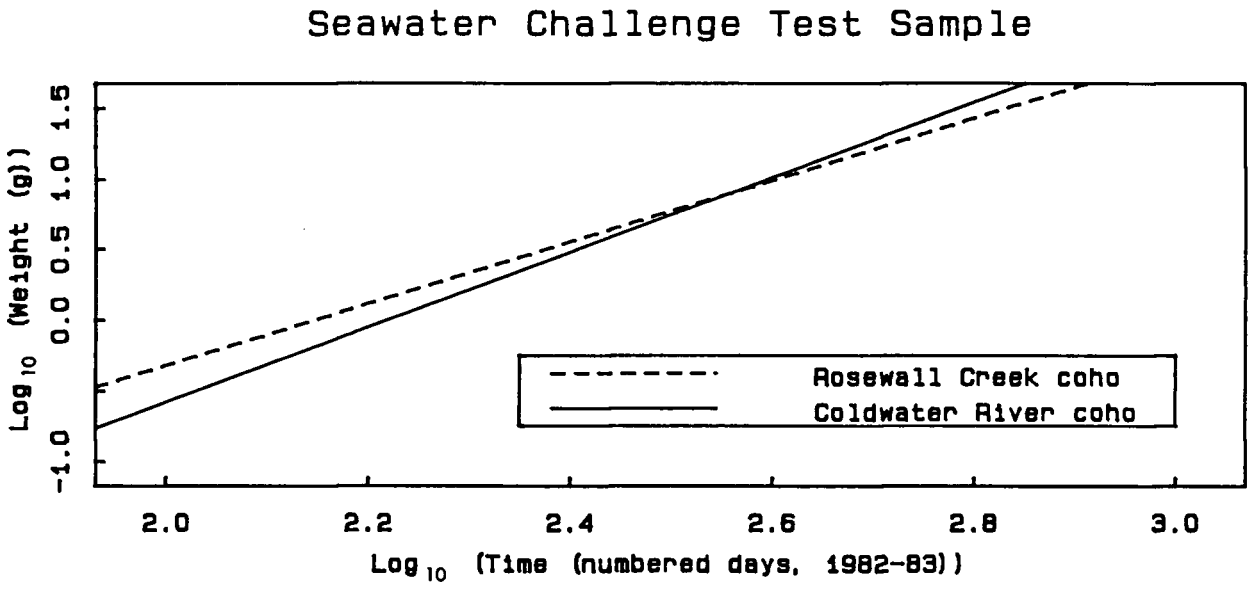
Total Wild Coho Sample

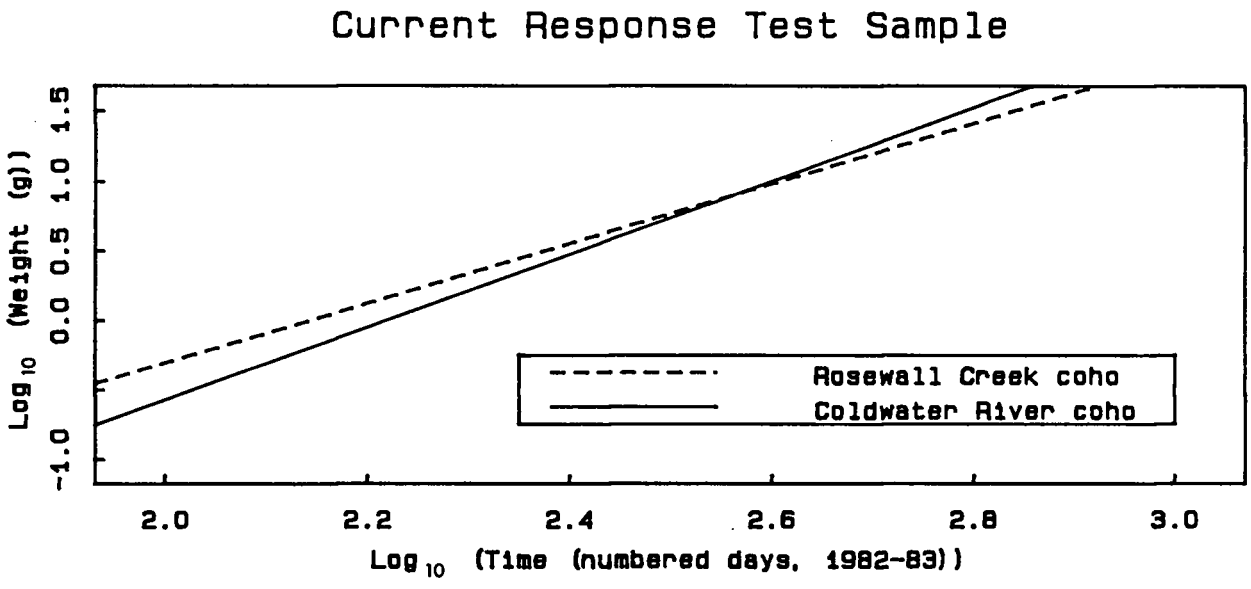


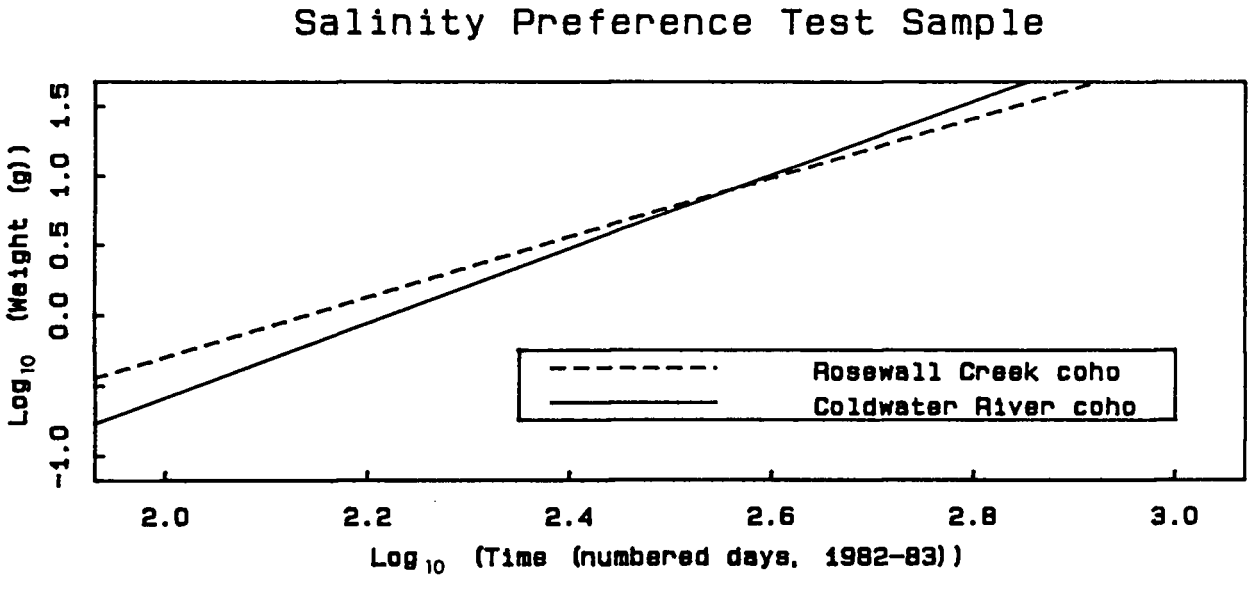
Appendix 8, Figure 6.

Growth regressions for 6°C incubated laboratory coho stocks; $\log_{10}$(weight) vs $\log_{10}$(time)

Units of time are consecutively numbered days (1-730) during 1982-83.


Seawater Challenge Test Sample
Log10 (Weight (g))
-1.0
0.0
0.5
1.0
1.5
2.0
2.2
2.4
2.6
2.8
3.0
Log10 (Time (numbered days, 1982-83))
Rosewall Creek coho
Coldwater River coho


Current Response Test Sample
Log10 (Weight (g))
-1.0
0.0
0.5
1.0
1.5
2.0
2.2
2.4
2.6
2.8
3.0
Log10 (Time (numbered days, 1982-83))
Rosewall Creek coho
Coldwater River coho

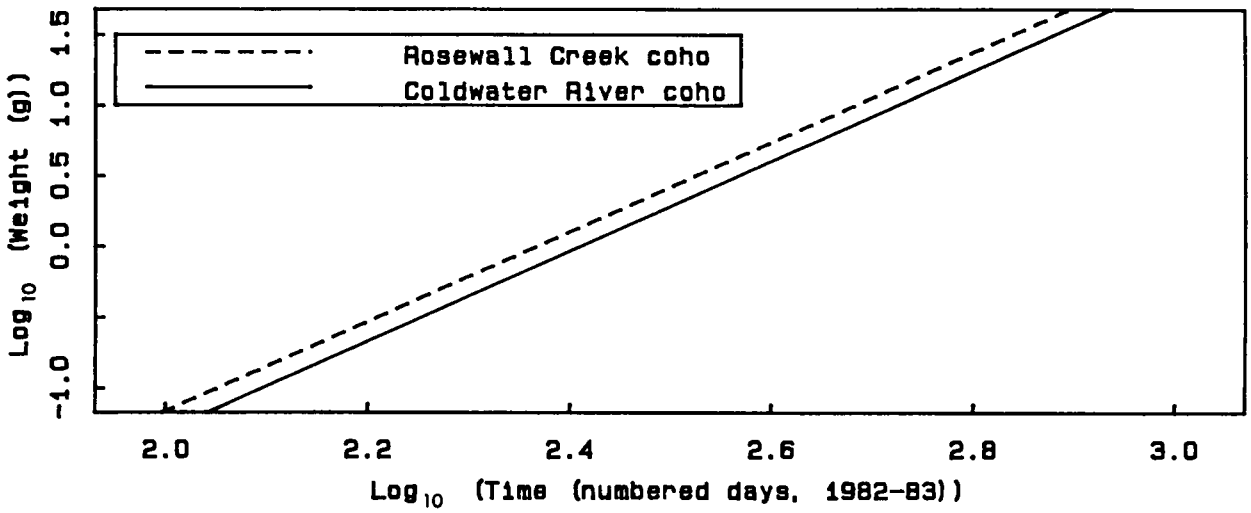

Salinity Preference Test Sample
Log10 (Weight (g))
-1.0
0.0
0.5
1.0
1.5
2.0
2.2
2.4
2.6
2.8
3.0
Log10 (Time (numbered days, 1982-83))
Rosewall Creek coho
Coldwater River coho

Appendix 8, Figure 7.

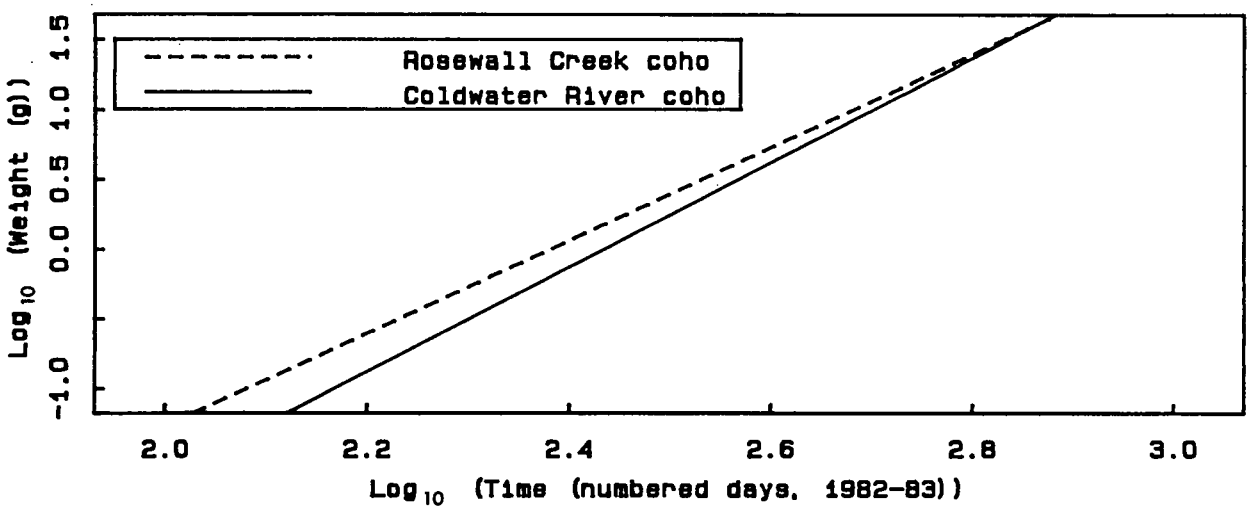
Growth regressions for 2°C incubated laboratory coho stocks; $\log_{10}$(weight) vs $\log_{10}$(time)

Units of time are consecutively numbered days (1-730) during 1982-83.

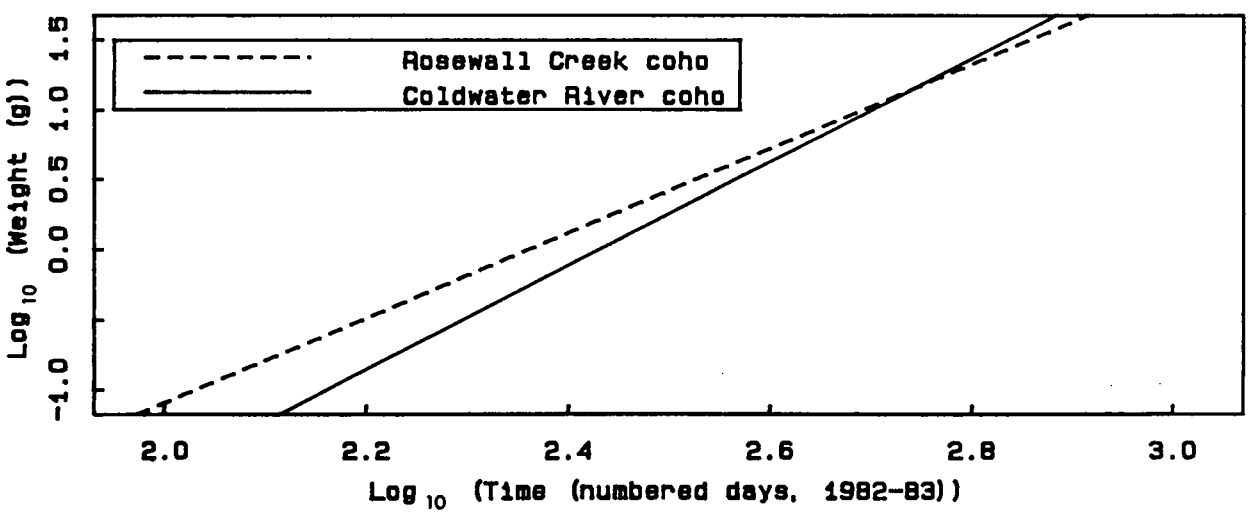
Seawater Challenge Test Sample



Current Response Test Sample



Salinity Preference Test Sample



APPENDIX 8: TABLE 10
ANALYSIS OF COVARIANCE COMPARISONS OF GROWTH REGRESSIONS FOR STUDY GROUPS.

Study Test	Incubation Treatment	Equality of Slopes (F_s)	Equality of Adjusted Means (F_s)
Seawater Challenge Test	Wild coho	4.517 p=0.034	
	Lab raised 6°C incub.	167.85 p<0.001	
	Lab raised 2°C incub.	0.017 p>0.05	148.011 p<0.001
Current Response Test	Lab raised 6°C incub.	187.76 p<0.001	
	Lab raised 2°C incub.	29.832 p<0.001	
Salinity Preference Test	Lab raised 6°C incub.	193.872 p<0.001	
	Lab raised 2°C incub.	79.206 p<0.001	
Both Behavioural Response Tests	Wild coho	2.508 p>0.05	895.947 p<0.001

APPENDIX 8: TABLE 11
ANALYSIS OF COVARIANCE COMPARISONS OF GROWTH REGRESSIONS WITHIN STOCKS AND TREATMENTS.

Population	Incubation Treatment	Equality of Slopes (F_s)	Equality of Adjusted Means (F_s)
Rosewall Creek (Big Qualicum River)	Wild coho	4.079 p=0.044	
	Lab raised 6°C incub.[a]	0.989 p>0.05	0.168 p>0.05
	Lab raised 2°C incub.	7.339 p<0.001	
Coldwater River	Wild coho	2.595 p>0.05	11.214 p<0.001
	Lab raised 6°C incub.	0.603 p>0.05	0.629 p>0.05
	Lab raised 2°C incub.	25.791 p<0.001	

a - Includes Big Qualicum River coho.

APPENDIX 8: TABLE 12
COMPARISONS OF SIZE BETWEEN
RESIDENT AND MIGRANT COHO SUBYEARLINGS.

Study Test	Date (1982-83)	Population, Capture Type	Sample Size (n)	Weight (g)	t_s value	U_s value
Seawater Challenge Test	Dec. 3	Coldwater R., Resident coho	11	2.33 ± 0.335	0.407 p>0.05	
		Coldwater R., Migrant coho	17	2.14 ± 0.255		
Both Behavioural Response Tests	May 19	Rosewall Cr., Resident coho	21	1.04 ± 0.085		966 p<0.05
		Rosewall Cr., Migrant coho	46	0.34 ± 0.001		
	May 9	Coldwater R., Resident coho	12	0.24 ± 0.001	1.30 p>0.05	
	May 4	Coldwater R., Migrant coho	11	0.28 ± 0.001		
	Nov. 20	Coldwater R., Resident coho	62	1.78 ± 1.148		724 p>0.05
		Coldwater R., Migrant coho	33	1.96 ± 0.493		

APPENDIX 9

SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Rosewall Cr., Wild coho, 0-20 ppt. gradient, Age 0+ Residents,	June 8	159	4	5.96 *
	Aug. 18	230	0	15.356 *
	Nov. 5	309	4	16.703 *
	Feb. 10	406	12	9.858 *
	Mar. 26	450	8	1.014 ns
	May 25	510	4	40.962 *
Age 0+ Migrants.	June 9	160	0	17.666 *
Rosewall Cr., Wild coho, 4-24 ppt. gradient, Age 0+ Residents,	June 6	157	8	17.679 *
	Aug. 16	228	4	4.359 *
	Nov. 8	312	8	17.28 *
	Feb. 8	404	4	17.563 *
	Mar. 29	453	4	30.239 *
	May 27	512	12	2.853 *
Age 0+ Migrants.	June 13	164	8	6.798 *
Rosewall Cr., 6°C incubation, 0-20 ppt. gradient.	May 7	127	4	1.164 ns
	May 31	151	0	12.07 *
	June 25	176	4	2.167 *
	July 25	206	4	13.70 *
	Sept. 2	245	4	27.299 *
	Nov. 12	316	4	14.831 *
	Dec. 15	349	4	14.726 *
	Jan. 10	375	4	26.011 *

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.

b - * - $p<0.05$, ns - $p>0.05$.

APPENDIX 9 (CONTINUED)
SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Rosewall Cr., 6°C incubation, 0-20 ppt. gradient, (continued).	Feb. 3	399	0	54.585 *
	Mar. 4	428	4	17.395 *
	Apr. 4	459	0	61.384 *
	May 8	493	8	4.758 *
	June 16	532	4	10.051 *
Rosewall Cr., 6°C incubation, 4-24 ppt. gradient.	June 2	153	8[c]	-c-
	June 28	179	4[c]	-c-
	July 24	207	4	14.652 *
	Sept. 5	248	8	42.606 *
	Nov. 15	319	12	6.831 *
	Dec. 21	355	4	25.410 *
	Jan. 6	371	4	23.109 *
	Feb. 7	403	8	41.804 *
	Feb. 28	424	8	9.996 *
	Apr. 17	472	16	4.946 *
	May 3	488	12	13.576 *
	June 22	538	4	0.342 ns
Rosewall Cr., 2°C incubation, 0-20 ppt. gradient.	Aug. 9	221	4	5.887 *
	Sept. 17	260	0	47.6 *
	Oct. 20	293	4	36.238 *
	Nov. 21	325	0	27.657 *

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.
b - * - $p<0.05$, ns - $p>0.05$.
c - No control distributions were collected. The modes given are for the test distribution.

APPENDIX 9 (CONTINUED)
SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Rosewall Cr., 2°C incubation, 0-20 ppt. gradient, (continued).	Dec. 22	356	0	11.25 *
	Jan. 14	379	0	27.968 *
	Mar. 2	426	4	28.238 *
	Mar. 25	449	4	4.313 *
	Apr. 21	476	12	12.778 *
	May 25	510	8	40.435 *
Rosewall Cr., 2°C incubation, 4-24 ppt. gradient.	Aug. 11	223	4	17.195 *
	Sept. 25	268	8	4.765 *
	Oct. 23	296	4	54.882 *
	Nov. 24	328	8	36.181 *
	Dec. 21	355	8	7.498 *
	Jan. 20	385	4	8.604 *
	Mar. 9	433	16	33.3 *
	Mar. 29	453	16	32.973 *
	Apr. 29	484	8	18.22 *
	May 27	512	12	5.675 *
Coldwater R., Wild coho, 0-20 ppt. gradient, Age 0+ Residents,	July 8	189	12	1.399 ns
	Sept. 20	263	0	15.357 *
	Dec. 9	343	4	40.977 *
	Feb. 18	414	8	25.310 *
	May 7	492	0	8.976 *

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.
b - * - $p<0.05$, ns - $p>0.05$.

APPENDIX 9 (CONTINUED)
SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Coldwater R., Age 0+ Residents, (continued),	May 21	506	8	9.775 *
	June 15	531	8	1.988 *
Coldwater R., Wild coho, 0-20 ppt. gradient, Age 1+ Residents,	July 7	188	8	25.546 *
	Sept. 2	245	0	6.706 *
	Dec. 15	349	0	2.903 *
	Feb. 18	414	0	103.02 *
	May 7	492	4	24.123 *
	May 22	505	8	5.670 *
Age 0+ Migrants.	June 9	160	0	24.131 *
	Dec. 6	340	4	5.770 *
Coldwater R., Wild coho, 4-24 ppt. gradient, Age 0+ Residents,	July 13	194	4[c]	-c-
	Sept. 29	272	8	5.413 *
	Dec. 3	337	8	43.02 *
	Feb. 25	421	4	10.137 *
	Apr. 30	485	16	15.543 *
	May 23	508	16	0.551 ns
	June 21	537	12	1.502 ns
Age 1+ Residents,	July 9	190	8[c]	-c-
	Sept. 8	251	8	0.221 ns
	Dec. 20	354	8	12.059 *

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.
b - * - $p<0.05$, ns - $p>0.05$.
c - No control distributions were collected. The modes given are for the test distribution.

APPENDIX 9 (CONTINUED)
SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Coldwater R., Wild coho, 4-24 ppt. gradient Age 1+ Residents, (continued), Age 0+ Migrants.	Feb. 26	391	4	14.019 *
	May 1	486	16	8.558 *
	May 24	509	12	2.01 *
	June 6	157	16	1.30 ns
	Dec. 3	337	8	3.569 *
Coldwater R., 6°C incubation, 0-20 ppt. gradient,	May 14	134	4	26.994 *
	June 10	161	4	9.118 *
	July 17	198	4	40.577 *
	Aug. 20	232	4	10.914 *
	Sept. 30	273	0	41.306 *
	Oct. 31	304	8	30.473 *
	Nov. 26	330	16	16.345 *
	Dec. 25	359	12	11.028 *
	Feb. 2	398	12	0.648 ns
	Mar. 4	428	8	20.824 *
	Apr. 3	458	12	9.283 *
	May 8	493	16	9.433 *
	June 8	524	16	0.243 ns
Coldwater R., 6°C incubation, 4-24 ppt. gradient	May 15	135	4[c]	-c-
	June 14	165	4[c]	-c-

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.
b - * - $p<0.05$, ns - $p>0.05$.
c - No control distributions were collected. The modes given are for the test distribution.

APPENDIX 9 (CONTINUED)
SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Coldwater R., 6°C incubation, 4-24 ppt. gradient, (continued).	July 17	198	4	18.202 *
	Aug. 25	237	8	19.298 *
	Sept. 27	270	4	23.892 *
	Nov. 5	309	8	27.974 *
	Dec. 2	336	12	16.564 *
	Jan. 3	368	16	21.463 *
	Feb. 4	400	20	1.255 ns
	Mar. 1	424	16	23.689 *
	Apr. 1	455	4	5.035 *
	May 2	487	12	10.172 *
	June 11	527	16	4.361 *
Coldwater R., 2°C incubation, 0-20 ppt. gradient.	July 29	210	4	21.528 *
	Sept. 13	256	4	30.289 *
	Oct. 9	282	0	31.527 *
	Nov. 10	314	4	49.808 *
	Dec. 22	356	12	1.982 *
	Jan. 13	378	4	10.516 *
	Feb. 17	413	12	27.388 *
	Mar. 16	440	4	5.284 *
	Apr. 18	473	16	7.016 *
	May 31	516	0	4.699 *

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.
b - * - $p<0.05$, ns - $p>0.05$.

APPENDIX 9 (CONTINUED)
SALINITY PREFERENCE DISTRIBUTION MODES AND MANN-WHITNEY U TEST COMPARISONS BETWEEN TEST AND CONTROL DISTRIBUTIONS.

Population & Treatment	Date (1982-83)	Time (day)[a]	Mode (ppt)	t_s Value[b]
Coldwater R., 2°C incubation, 4-24 ppt. gradient.	Aug. 5	217	16	0.344 ns
	Sept. 12	255	4	40.78 *
	Oct. 13	286	8	23.177 *
	Nov. 16	320	16	18.251 *
	Dec. 20	354	12	13.785 *
	Jan. 19	384	16	34.133 *
	Feb. 24	420	16	2.641 *
	Mar. 20	444	12	16.177 *
	Apr. 28	483	8	16.265 *
	May 31	515	20	1.93 ns

a - Time ranges from 1-730 days which are equivalent to the calender dates January 1, 1982 to December 31, 1983.
b - * - $p<0.05$, ns - $p>0.05$.