

ADAPTIVE DIVERSIFICATION OF JUVENILE LIFE HISTORIES IN
THE CHINOOK SALMON, ONCORHYNCHUS TSHAWYTSCHA (WALBAUM)

by

ERIC BURKE TAYLOR

B.Sc.(Hon.), University of British Columbia, 1981
M.Sc., University of British Columbia, 1984

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
May 1989

© Eric Burke Taylor, 1989

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date June 19, 1989

ABSTRACT

Over its native range in the north Pacific, the chinook salmon (Oncorhynchus tshawytscha (Walbaum)) exhibits two life history patterns distinguished by the age at which juveniles migrate from their natal streams to the sea. Those that migrate seaward during their first 3 months of stream residence are "ocean-type" chinook, while those that migrate after 1 or more years in freshwater are "stream-type" salmon. Both types may be found within populations but they also distinguish populations dominated by one type or the other.

Stream-type salmon were found to be more aggressive, had a stronger seasonal rheotactic response, grew more slowly, and were less tolerant of saline water than ocean-type chinook. These differences were present in both wild- and laboratory-reared juveniles and were concluded to be, at least in part, genetically determined. Consistent differences in behavioural and physiological traits were found in comparisons among chinook populations from different river systems, between populations within a river system, and among families with different freshwater life histories from a single population. These phenotypic differences were in directions appropriate for different durations of freshwater residence which is consistent with the idea that they represent adaptive diversification and components of functionally important "strategies" for alternative juvenile life histories.

A geographic survey indicated that stream-type chinook predominate in interior streams south of 56°N , and in both coastal and interior streams north of this latitude. Although ocean-type salmon predominate in coastal streams south of 56°N , there are also many rivers with both stream- and ocean-type populations. Ocean-type populations are characterized by earlier emergence in areas of warmer air temperature and longer growing season, in streams close to the sea.

In laboratory stream environments, juvenile coho salmon socially dominated juvenile chinook salmon from a number of populations. In nature, sympatric coho and chinook used different stream microhabitats, but allopatric chinook used microhabitats more similar to those of coho. Manipulative field experiments demonstrated that coho and chinook preferred different habitat types ("pools" and "riffles" respectively), but that coho may be able to displace chinook from "pool" habitats. While genetic differences in habitat preference between coho and chinook probably minimize the influence of coho on freshwater residence behaviour of chinook, aggressive interaction with coho may promote early downstream migration of chinook when alternative stream habitats preferred by chinook are lacking.

It is concluded that: (i) stream- and ocean-type juvenile life histories are, at least in part, genetically based, (ii)

stream- and ocean-type chinook represent functional diversification of juvenile phenotype resulting in alternative life history patterns, (iii) selection for size at migration and time of migration are major factors driving divergence in juvenile life history among chinook populations; environmental control via "growth opportunity" or behavioural exclusion from stream habitats by coho salmon is of secondary importance, and (iv) the sympatric occurrence of stream- and ocean-type chinook in many river systems is probably the result of repeated, independent episodes of divergence. Thus, stream- and ocean-type salmon probably do not represent distinct evolutionary lineages.

TABLE OF CONTENTS

ABSTRACT	ii
LIST OF TABLES	ix
LIST OF FIGURES	xii
ACKNOWLEDGEMENTS	xvi
GENERAL INTRODUCTION	1
CHAPTER 1: Phenotypic correlates of life history variation	
in juvenile chinook salmon	6
Introduction	6
1. Behavioural and morphological variation among	
populations of newly-emerged chinook salmon fry	10
Methods	10
Study populations	10
Collection and maintenance of wild fry	13
Gamete collection and incubation	13
A. Response of newly-emerged chinook fry to water	
current	15
B. Aggressive behaviour of newly-emerged chinook fry	17
C. Chinook fry morphology	21
Results	22
A. Response of newly-emerged fry to water current	22
B. Aggressive behaviour of newly-emerged chinook	
salmon fry	26
C. Morphology and colouration	43
2. Inter-, intrapopulation, and temporal variation in	

behaviour and growth of juvenile chinook salmon	48
Methods	48
Experimental animals	48
A. Inter-, intrapopulation, and temporal variation in rheotactic behaviour	50
B. Inter-, intrapopulation, and temporal variation in aggressive behaviour	51
C. Variation in growth rate	55
D. Statistical analysis	55
Results	57
A. Inter-, intrapopulation, and temporal variation in rheotactic behaviour	57
B. Inter-, intrapopulation, and temporal variation in aggressive behaviour	60
C. Variation in growth rate	67
3. Variation in aggressive behaviour and salinity tolerance among families of juvenile chinook salmon	72
Methods	72
Experimental crosses	72
A. Variation in aggressive behaviour	76
B. Variation in salinity tolerance	78
C. Statistical analysis	79
Results	80
A. Adult freshwater rearing life history	80
B. Variation in aggressive behaviour	84
C. Variation in salinity tolerance	89
1. Effects of size on salinity tolerance	89

2. Variation in weight loss and survival	92
D. Correlations among variables	98
Discussion	100
CHAPTER 2: Geographic variation in, and environmental correlates of, juvenile chinook salmon life history	115
Introduction	115
1. Geographic distribution of chinook salmon and variation in life history	118
Methods	118
Geographic distribution of chinook salmon	120
Geographic variation in juvenile life history	124
2. Environmental correlates of variation in juvenile chinook life history	149
Methods	149
Results	156
Discussion	160
CHAPTER 3: Behavioural interaction between juvenile coho and chinook salmon and chinook life history	172
Introduction	172
1. Social interaction between juvenile chinook and coho salmon	176
Methods	176
Behavioural observations	176
Statistical analysis	177
Results	177
2. Microhabitat use by juvenile chinook salmon in allopatry and sympatry with coho salmon	181

Methods	181
Statistical analysis	184
Results	185
3. Experimental introductions of juvenile coho and chinook salmon	197
Methods	197
Experimental animals	197
Experimental facility	197
Experimental design and protocol	201
Statistical analysis	209
Results	210
Initial behaviour	210
Emigration from the channel	210
Habitat use	213
Discussion	223
CHAPTER 4: GENERAL DISCUSSION	233
LITERATURE CITED	245

LIST OF TABLES

Table 1. Aggressive behaviours recorded for chinook salmon in the study	19
Table 2. Net movement scores for newly-emerged wild chinook salmon fry	23
Table 3. Net movement scores for newly-emerged, laboratory- reared chinook salmon fry	25
Table 4. Principal component coefficients derived from MIS behavioural data	27
Table 5. Component coefficients derived from principal components analysis of stream tank behavioural data	31
Table 6. Component coefficients derived from principal components analysis of MIS behavioural data of laboratory-reared chinook fry	35
Table 7. Component coefficients derived from principal components analysis of stream tank behavioural data for laboratory-reared chinook fry	39
Table 8. Morphological comparison of wild-reared, newly- emerged chinook salmon fry	44
Table 9. Morphological comparison of laboratory-reared, newly-emerged chinook salmon fry	46
Table 10. Number of male and female parents used in experimental crosses of chinook salmon from stream- and ocean-type populations	49
Table 11. Net movement scores for juvenile chinook salmon	

in nocturnal current response tests	61
Table 12. Net movement scores for juvenile chinook salmon in diurnal current response tests	62
Table 13. Behaviour coefficients from principal components analysis of stream tank behavioural interactions among juvenile chinook salmon	64
Table 14. Covariance analysis summary of specific growth rate data for stream- and ocean-type chinook salmon	71
Table 15. Body length and freshwater scale counts for adult salmon and wet weights of newly-emerged fry from Nanaimo River crosses	81
Table 16. Behaviour coefficients from principal components analysis of juvenile chinook salmon interaction	85
Table 17. Mean (\pm SE) aggression scores for juvenile chinook from the Nanaimo and Squamish rivers	88
Table 18. Percentage weight loss after 24 h in 20‰ seawater for juvenile chinook salmon	95
Table 19. Percentage survival after 24 h in 30‰ seawater for juvenile chinook salmon	97
Table 20. Correlations between parental freshwater life history, from scale circulus counts, and progeny aggression and salinity tolerance	99
Table 21. Juvenile chinook life history patterns in the Kamchatka River (Soviet Union) and several New Zealand rivers	147
Table 22. Principal components analysis of environmental variables characteristic of populations of chinook	

salmon	157
Table 23. Physical measurements recorded at fish microhabitats	183
Table 24. Principal components analysis of microhabitat use by juvenile chinook and coho salmon	186
Table 25. Matrix of Mahalanobis distances among microhabitat centroids for juvenile chinook and coho salmon, 1985	191
Table 26. Matrix of Mahalanobis distances among microhabitat centroids for juvenile chinook and coho salmon, 1986	195
Table 27. Average water velocities and water depths in subsections of Jones Creek experimental stream sections	204
Table 28. Number (mean \pm SE) of chinook found in pool habitats in Jones Creek	221
Table 29. Number (\pm SE) of chinook found in riffle habitats in Jones Creek	222

LIST OF FIGURES

Figure 1. Geographic location of various study populations of chinook salmon	11
Figure 2. Mean aggression scores for newly-emerged, wild-reared chinook salmon fry in MIS tests	29
Figure 3. Mean aggression scores for newly-emerged, wild-reared chinook salmon fry in stream tank tests	33
Figure 4. Mean aggression scores for newly-emerged, laboratory-reared chinook salmon fry in MIS tests	36
Figure 5. Mean stream tank aggression scores for laboratory-reared chinook fry	40
Figure 6. Major features of the Nanaimo River including spawning areas (stippling) of "Lower Nanaimo" (A) and "1st Lake" (B) populations of chinook salmon in the river	52
Figure 7. Net movement scores for stream- and ocean-type juvenile chinook salmon in current response tests	58
Figure 8. Mean (\pm SE) aggression scores for juvenile chinook salmon for Nanaimo River and Slim Creek populations at several ages	65
Figure 9. Specific growth rate for stream- and ocean-type chinook salmon from emergence to 12 months of age	69
Figure 10. Photomicrograph of adult chinook salmon scale illustrating key features used to determine juvenile life history pattern	74

Figure 11. Relationship between female standard length and fry wet weight at emergence for Nanaimo River chinook salmon	82
Figure 12. Mean (\pm SE) aggression scores for juvenile chinook salmon from the Nanaimo River families and Squamish River over 3 months of age	86
Figure 13. Relationship between body size and measures of salinity tolerance in juvenile chinook salmon over 3 months of age	90
Figure 14. Changes in percentage survival after exposure to 30‰ seawater with time in Nanaimo and Squamish rivers chinook over their first 3 months of age	93
Figure 15. Trivariate plot of the relative ranks of mean parental freshwater circuli count and the ranks of aggressive behaviour and salinity tolerance of their progeny	101
Figure 16. Geographic distribution of chinook salmon in the North Pacific Ocean	121
Figure 17. Distribution of juvenile life histories for chinook salmon spawning populations in the Sacramento and Klamath rivers, California	126
Figure 18. Distribution of juvenile life history patterns for chinook salmon spawning populations in Oregon coastal streams	129
Figure 19. Distribution of juvenile life history patterns for chinook salmon spawning populations of the Columbia River	132

Figure 20. Distribution of juvenile life history patterns for chinook salmon spawning populations of coastal Washington and Puget Sound	137
Figure 21. Distribution of juvenile life history patterns in chinook salmon spawning populations in southern British Columbia	139
Figure 22. Distribution of juvenile life history patterns in chinook spawning populations in northern B.C. and Alaska	144
Figure 23. Relationship between mean annual air temperature and mean annual water temperature for study streams	152
Figure 24. Plot of principal component scores of stream- and ocean-type populations along component axes 1 and 2	158
Figure 25. Interspecific aggression indices between coho and chinook salmon fry	178
Figure 26. Plots of mean (\pm SE) principal component scores summarizing microhabitat use by juvenile coho and chinook salmon, 1985	188
Figure 27. Plots of mean (\pm SE) principal component scores summarizing microhabitat use by juvenile coho and chinook salmon, 1986	193
Figure 28. The Jones Creek spawning channel facility.	198
Figure 29. Relationship between fish size and water velocity of microhabitats occupied	207
Figure 30. Temporal changes in mean (\pm SE) proportion of total emigration by juvenile salmon in the experimental stream sections	211

Figure 31. Mean (\pm SE) sizes of initial and emigrant salmon juveniles	214
Figure 32. Mean (\pm SE) proportion emigration from experimental channel sections by chinook when introduced alone and with coho salmon	216
Figure 33. Relative use of pool and riffle habitats in Jones Creek experimental stream sections by coho and chinook salmon	219

ACKNOWLEDGEMENTS

This thesis was completed under the supervision of Dr. P.A. Larkin. I thank him sincerely for the guidance, advice, and support that he has provided so freely over the last five years. More generally, I will always appreciate, and be grateful for, the confidence that he has displayed in me since our first meeting.

I also am grateful to Drs. M.C. Healey, D. Schluter, C.C. Lindsey, and J.D. McPhail for their enthusiastic support while serving on my research committee. Additional thanks are due Drs. Healey, Schluter, Lindsey, and C.F. Wehrhahn who read, and provided constructive criticisms of, an earlier draft of this thesis. I have benefited substantially from the friendship and advice from numerous colleagues, most notably C.J. Foote, G. Pogson, S. Courtenay, and M. Labelle. For assistance in the field and in the laboratory I thank W. Gibson, C.J. Foote, A. Tompkins, M. Labelle, and R. Gregory. I also am indebted to Ms. H. Hahn who provided administrative support and to Messers A. Blachford and J. Messer of the Biological Data Center for assistance with computing facilities.

Research funding was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant awarded to P.A. Larkin. I appreciate personal support from NSERC in the form of research assistantships, and graduate fellowships awarded by the University of B.C.

The Canadian Department of Fisheries and Oceans (DFO) is acknowledged for providing assistance during collection of adult chinook salmon. Specifically, I thank P. Preston (Nanaimo River Hatchery), D. Harvey and C. Harrison (Eagle River Hatchery), L. Kahl (Chehalis River Hatchery), D. Celli (Tenderfoot Hatchery), B. Huber (DFO, Prince George), R. Harrison (DFO, Fraser River-Yukon), and the staffs of the Little Qualicum, and Quesnel rivers hatcheries. The co-operation of B.C. Hydro and D. Buxton (Chilliwack River Hatchery) in providing access to, and accommodation at, the Jones Creek Spawning Channel Facility is gratefully acknowledged.

For providing data or access to data bases of adult chinook salmon scale ages I thank F. Fisher and T.J. Mills (Calif. Dept. of Fish and Game), J. Wilcock (Alaska Dept. of Fish and Game), M.J. Unwin (New Zealand Dept. of Agriculture and Fisheries), and Camille Goslin (DFO Scale Morphology Lab).

I thank my wife, Nini, for her support, enthusiasm, and encouragement.

GENERAL INTRODUCTION

One of the major goals of evolutionary biology is to promote an understanding of the causes and significance of biological diversity. Historically, efforts focussed on explaining the origin and patterns of variability at or above the species level (Mayr 1963; Futuyma 1988). In more recent times, the recognition of extensive phenotypic variability among individuals within populations, and among populations of single species has received intensive study and provided the foundation for modern evolutionary theory operating at the population level (Mayr 1963; Lewontin 1974; Wright 1978). One aspect of studies of intra- and interpopulation variability that is controversial concerns the debate over the relative importance of natural selection to the maintenance of variability in morphological, behavioural, physiological, and, most recently, biochemical traits (Mayr 1963; Nei and Koehn 1983; Endler 1986; Futuyma 1986).

If the form of selection of traits important to survival or mating success in a population is "disruptive", then two or more distinct phenotypes may be favoured and such populations are referred to as polymorphic. Frequency dependent selection and environmental heterogeneity are thought to be important in maintaining polymorphisms (Mather 1955; Mayr 1963; Endler 1986). Across the range of a species, different selective environments associated with local populations may result in alternative

phenotypes being favoured among populations. Taxonomically, such species are polytypic, while ecologically, their component populations are ecotypes or ecological races (Mayr 1963).

The life history of an organism is a pathway or series of events leading to successful reproduction. The study of natural selection of life history traits or pathways may focus on non-sexual selection during non-reproductive life history stages and/or sexual selection during the reproductive stage. Discrete intra- and interpopulation variability in reproductive life history are exemplified in many plant and animal groups (van Rhijn 1973; Howard 1978; Anon 1984; Chiarello and Roughgarden 1984; Lott 1984; Taborsky et al. 1987). In addition to alternative breeding systems and behaviours, discrete variability may be present in life history patterns during non-reproductive periods. Examples include social organization in vertebrates (Lott 1984), extent and mechanism of dispersal and duration of diapause in insects (Harrison 1980; Tauber and Tauber 1981), trophic morphology and behaviour, and habitat use in insects and vertebrates (Kornfield et al. 1982; Caro and Bateson 1986; Smith 1987; Gardner et al. 1988).

The Salmonidae are teleost fishes that exhibit alternative life history patterns within and between populations, both during reproductive (Berg 1959; Gross 1985; Myers et al. 1986) and non-reproductive life history stages (Campbell 1977; Hindar and Jonsson 1982; Wood et al. 1987; Metcalfe et al. 1988).

Extensive interpopulation variability (see Ricker 1972) is promoted by the diverse selective environments occupied by populations over each species' range and by the tendency of adults to return to natal areas to spawn and, hence, to be reproductively isolated from other populations.

The life history of anadromous salmonids includes periods of freshwater spawning by adults, incubation of eggs and larvae, and freshwater rearing by young fish, followed by migration to the sea where individuals feed and grow to maturity before returning to freshwater to spawn. The duration of freshwater rearing may vary among species from less than 1 day to several years (Hoar 1976). Similarly, the duration of the marine phase is highly variable (about 1-6 years) among species (Miller and Brannon 1982; Healey 1986).

The chinook salmon, Oncorhynchus tshawytscha, is an anadromous species native to the north Pacific. Over its geographic range, the chinook commonly exhibits two life history patterns distinguished by the age at which juveniles migrate from natal streams to the sea. Gilbert (1913) first detailed these alternative behavioural types and referred to those juveniles that migrate seaward as underyearlings, usually during their first three months of life, as "sea-" or "ocean-type" chinook and designated yearling or later migrants as "stream-type". These alternative life histories may be found within a single population, but they also differentiate populations

dominated by one type or the other. Stream- and ocean-type migratory behaviours appear to be genetically based (Rich and Holmes 1928) and are associated with genetic differences in morphology and enzyme frequency (Carl and Healey 1984). The juvenile life history types also show genetic differences in seasonal migration timing as adults (Rich and Holmes 1928).

In this thesis, I explore the phenomenon of stream- and ocean-type life histories in chinook and its variability both within and among populations. Two principal questions are addressed. First, do stream- and ocean-type chinook differ genetically in aspects of juvenile phenotype appropriate for their different durations of freshwater residence before smoltification? Stated another way, do stream- and ocean-type life histories represent adaptive diversification within a single species? In Chapter 1, I address this general question by assessing predictions concerning relative performance of stream- and ocean-type juveniles in behavioural, morphological, and physiological attributes associated with alternative rearing patterns in fishes. Both wild-reared juveniles and salmon reared in the laboratory are tested to assess the degree of genetic differentiation between life history types. The second question asked is, what factors in the abiotic and biotic environment of juvenile salmon may promote differentiation in life history? Chapter 2 presents a summary of geographic variability in juvenile life history pattern and addresses abiotic factors which vary among the habitats of chinook

populations and which might promote variation in juvenile life history. Chapter 3 addresses variability among populations in the extent of interaction with other species as a biotic factor which might influence juvenile life history. Lastly, I consider my findings in light of the phenomenon of functional diversity within species, the genetic versus environmental control of the expression of alternative life histories, and the possible sympatric origin of alternative life history types in salmon.

CHAPTER 1: PHENOTYPIC CORRELATES OF LIFE HISTORY VARIATION IN JUVENILE CHINOOK SALMON

Introduction

Stearns (1976) defined a life history "strategy" as a set of co-adapted reproductive traits resulting from selection in a specific environment. While reproductive traits may provide measures most closely linked to fitness, characteristics of other stages of an organism's life history that influence growth and/or survival can be important components of a life history pattern. Selection during particular life history stages, often in specific environments, may be different from selective factors operating during other life history stages in other environments.

Within major taxa, life history patterns vary widely and physiological, behavioural, and morphological aspects of a phenotype are often interpreted as adaptive characteristics of a particular life history stage (e.g. gills of amphibian larvae, structural and behavioural adaptations to prevent downstream displacement in benthic aquatic invertebrates). The more spectacular life history variations may incorporate a rapid transformation or metamorphosis associated with a distinct habitat shift (e.g. metamorphosis in holometabolous insects and anurans). Certainly the timing of both the metamorphosis and the accompanying habitat shift are aspects of a life history

that may be subject to selection (Werner 1986).

Wilbur (1980) termed such variation in life cycles "complex life-histories"; a term most often applied to insect and amphibian life cycles. A less striking but still impressive complex life history is that involving a "parr-smolt transformation", or smoltification, in anadromous Salmonidae (Hoar 1988). During this transformation, several species of juvenile salmon and trout change from stream-resident, territorial individuals that live in a hypotonic environment, and have parr markings and brightly coloured fins, to downstream migrating, "silvery" and countershaded, schooling animals known as "smolts" that soon enter pelagic, hypertonic near-shore marine habitats. Therefore, smoltification initiates a series of behavioural, morphological, and physiological changes accompanied by a habitat shift (Folmar and Dickhoff 1980; McCormick and Saunders 1987; Hoar 1988). As with other animal metamorphoses and habitat shifts, the timing of smoltification is subject to change by natural selection. Such changes in the timing of development, or heterochrony (Gould 1977), have been implicated in the evolutionary radiation within the Salmonidae (Balon 1980; McCormick and Saunders 1987).

Indeed, in salmonids the timing of smoltification, and its associated phenotypic changes, varies widely both between and within species (Randall et al. 1987). In the Pacific salmon Oncorhynchus, pink salmon (O. gorbuscha) appear to lack a smolt

transformation and migrate seaward very soon after the fry emerge from their gravel nests (< 1 g in weight). They are schooling, non-territorial, "silvery", and are able to osmoregulate in, and develop an early preference for, seawater as newly-emerged fry (Weisbart 1968; McInerney 1964; Hoar 1988). By contrast, coho salmon (O. kisutch) are intolerant of seawater as fry, prefer fresh or low salinity water, have parr markings and brightly coloured fins, and are territorial and highly aggressive (Chapman 1962; McInerney 1964; Weisbart 1968; Otto and McInerney 1970). In coho salmon, smoltification most commonly occurs after 1 or 2 years in freshwater at 10 g or more in weight (Clarke 1982; McCormick and Saunders 1987). Similar phenotypic contrasts between closely related species with different juvenile life histories have been documented in Salvelinus (Ferguson and Noakes 1982, 1983a,b) and Gasterosteus (Gasterosteidae, Bakker and Feuth-de Bruijn (1988)).

The chinook salmon, O. tshawytscha, is highly variable in the duration of freshwater residence before smoltification. It is the only species of Pacific salmon widely characterized by populations of individuals that (i) smolt and migrate seaward as underyearlings (i.e. ocean-type), (ii) smolt and migrate seaward as yearling or older juveniles (stream-type), or (iii) contain mixtures of (i) and (ii) (Randall et al. 1987).

In this chapter I examine variation within the chinook salmon in aspects of juvenile phenotype thought to be

appropriate for different durations of freshwater residence. I studied aggressive behaviour, response to water current (rheotaxis), growth rate, morphology, and salinity tolerance in wild and laboratory reared juvenile chinook salmon from as many as eight populations with different freshwater life histories. The specific goals were to: (1) assess the degree of differentiation among populations in traits thought to be related to the duration of freshwater residence before smoltification, (2) determine if any observed phenotypic variability has a genetic basis, and (3) to assess, by examining variation both between and within populations, the closeness of the linkage between aspects of juvenile phenotype and duration of freshwater residence. The essential hypothesis of this chapter was that stream-type chinook would be behaviourally, morphologically, and physiologically specialized for extended stream residence while ocean-type chinook would be phenotypically specialized for early seaward migration. Specifically, stream-type salmon were expected to be more aggressive, show stronger positive rheotaxis until age 1 year, be less tolerant of saline water as fry, and possess morphological traits thought to be important in social interaction during territorial stream residence (e.g. deeper bodies, larger and more pigmented median fins) compared to ocean-type chinook.

1. BEHAVIOURAL AND MORPHOLOGICAL VARIATION AMONG POPULATIONS OF NEWLY-EMERGED CHINOOK SALMON FRY

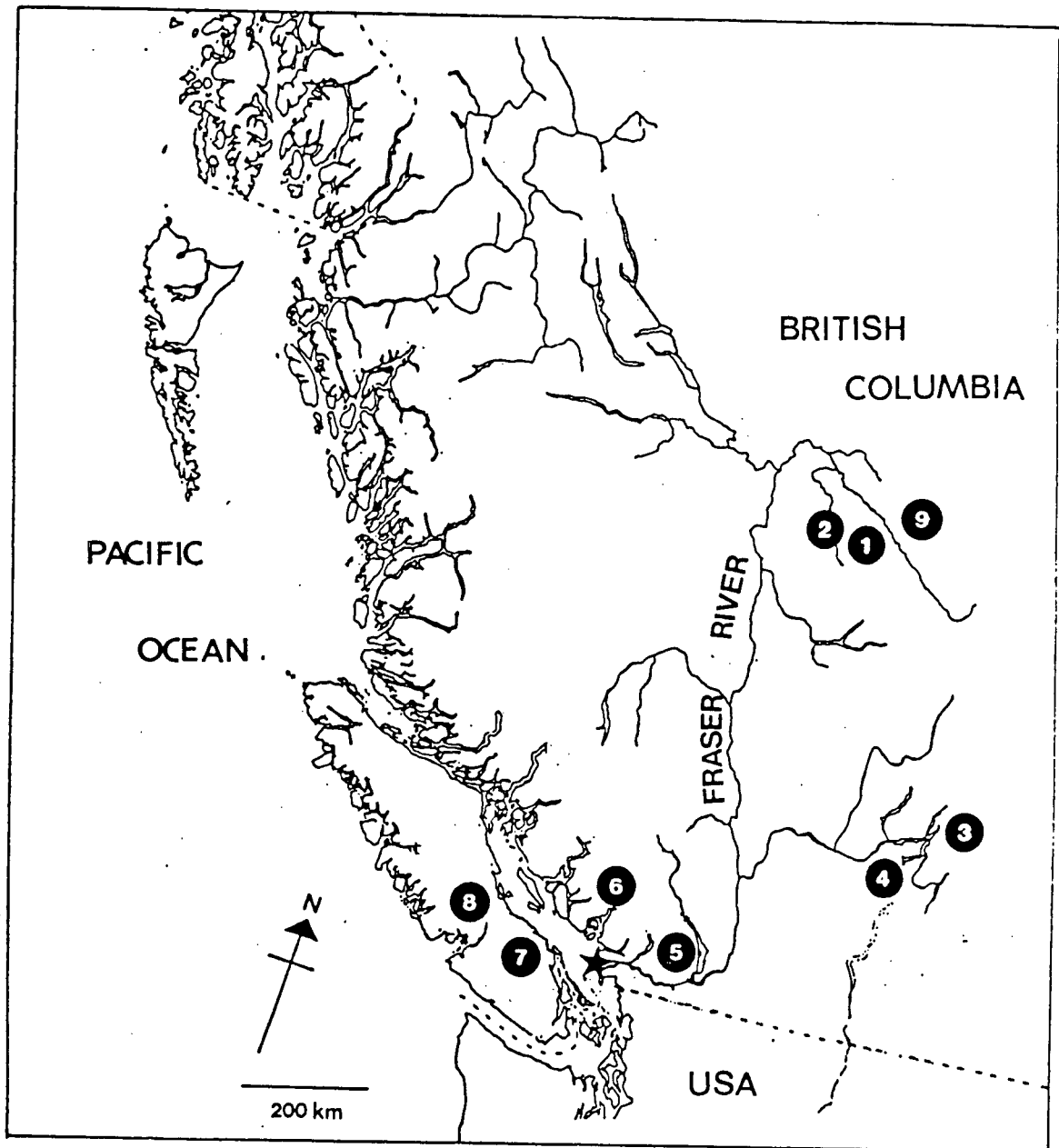
Methods

Study populations

The first set of experiments concerned wild and laboratory-reared chinook fry from four populations (Fig. 1): Slim Creek, Eagle River, Harrison River, and Nanaimo River. Fry collected from Slim Creek and Harrison River were studied in 1985. Because these wild fry had experienced different incubation and rearing environments that might have influenced subsequent juvenile behaviour and morphology, fry from these two populations as well as from the Eagle and Nanaimo rivers were raised from eggs in the laboratory under identical conditions during 1986. From scale analysis of adults and from field surveys, Slim Creek and Eagle River chinook are predominately (>95%) stream-type and juveniles overwinter in freshwater (Shepherd et al. 1986a). By contrast, chinook from Harrison and Nanaimo rivers are predominately ocean-type (Shepherd et al. 1986a). The Nanaimo River eggs came from the "fall run" population that spawns in the lower Nanaimo River; its fry move downstream to the Nanaimo estuary soon after emerging from their gravel nests (Healey 1980; Carl and Healey 1984).

Information concerning the salmonid populations and

Figure 1. Geographic location of various study populations of chinook salmon. (1) Slim Creek, (2) Bowron River, (3) Eagle River, (4) Salmon River, (5) Harrison River, (6) Squamish River, (7) Nanaimo River, (8) Little Qualicum River, (9) Walker Creek, Star=Vancouver.



biophysical features of the study rivers can be found in Brown and Musgrave (1979), Healey (1980), Marshall and Manzon (1980), Whelan et al. (1981), Healey and Jordan (1982), and Shepherd et al. (1986a,b).

Collection and maintenance of wild fry

Recently emerged chinook salmon fry were collected from Harrison River on April 10, 1985 using a beach seine and from Slim Creek using a 1.25 X 0.6 m fyke net on the spawning grounds on May 11-12. All fry were transported to the laboratory within 12 h of capture. Fry were recognized as newly-emerged by their small size (32-36 mm standard length (SL)), developmental state (i.e. degree of yolk-sac absorption), and by monitoring the collection sites for first appearance of fry. In the laboratory, fry were maintained in 94 L aquaria in a controlled environment chamber (10°C) on a 12 h light: 12 h dark photoperiod. Fish were fed a diet of crushed Tetramin fish food thrice daily.

Gamete collection and incubation

Eggs and milt were collected from ripe, wild chinook salmon during September (Slim Creek and Eagle River), October (Nanaimo River), and November (Harrison River) of 1985. Slim Creek adults were collected on the spawning grounds by electroshocking while adults from the Eagle, Harrison, and Nanaimo rivers were

collected at fences or by seining in conjunction with enhancement operations. Eggs from each female were kept separate and were fertilized with the milt of individual males in the field (Slim Cr., 4 females X 7 males; Eagle R., 6 females X 4 males; Nanaimo R., 3 females X 4 males; Harrison R., 3 females X 2 males). Facilities for transportation and subsequent incubation and rearing of salmon were limited, so zygotes were pooled after fertilization. Zygotes were transported (5°C) to the laboratory at the University of British Columbia. Elapsed time from fertilization to placement in the incubator ranged from 2 h (Harrison River) to 24 h (Slim Creek).

The incubation apparatus consisted of a large (1.8 m x 0.6 m x 0.9 m) cooling unit described by Murray and McPhail (1988). Within the cooling unit, zygotes were incubated in "corner type" aquarium filters with about 3-4 cm of pea gravel. Water flow through the incubator was set to 2 L/min and the embryos and larvae were kept in darkness at 5°C during the approximately 7 months of incubation.

Upon emergence, fry were placed in 94 L fiberglass rearing troughs where they were left for 24 h. The water flow through the troughs was maintained at 4 L/min and fry were fed Oregon Moist Pellet (OMP) food thrice daily on a schedule of increasing pellet sizes. The light schedule followed the natural photoperiod and was provided by a single 40 W fluorescent bulb per trough. A single 25 W light bulb controlled by a rheostat-

timer simulated "dawn-dusk" each day.

A. Response of newly-emerged chinook fry to water current

In an attempt to assess migratory "restlessness" in newly-emerged wild fry (1985) and laboratory-reared fry (1986), I studied rheotactic behaviour during current response tests. Current response tests of various designs have been effective in detecting differences in rheotaxis among populations that correlate well with migratory behaviour differences observed in nature (e.g. Raleigh 1971; Brannon 1972; Kelso et al. 1981; Lundqvist and Eriksson 1985; Thorpe et al. 1988).

The tests were run in two artificial, oval-shaped stream channels (3.8 m stretched length). Each of two current channels was subdivided into 21 compartments (0.15 X 0.20 X 0.25 m) ranked from -10 (most downstream) through 0 (central compartment) to +10 (most upstream). In wild salmonid populations most downstream migration is nocturnal, but diurnal downstream movement is often observed (Folmar and Dickhoff 1980; Godin 1982; Shepherd et al. 1986a). Therefore, each trial assessed the movements of 20 chinook fry through the channel compartments during successive light ("diurnal") and dark ("nocturnal") tests.

Fry were placed in the central compartment with the entrance and exit holes blocked. After 0.5 h the lights were

either dimmed (nocturnal tests) or raised (diurnal tests) in intensity over a 0.5 hr period. After 15 min, the screens blocking the holes in the compartment walls were removed and the fish were free to move through the compartment holes. After 2.25 h (i.e. 2 hr after complete dark or light conditions were reached), the distribution of fry among the compartments was recorded. After a diurnal or nocturnal test, fry were returned to the central compartment and left for 0.5 h. A second test was then repeated under opposite light conditions (i.e. if the first test was diurnal, the second was nocturnal or vice versa).

For each test, a "movement score" was calculated by summing the products of the number of fish in each compartment and the rank of that compartment and then dividing by 20, the number of fish in each test. To provide a net movement score the downstream score was subtracted from the upstream score; a constant of 10 was added to eliminate negative scores. For each population twelve trials, each consisting of a nocturnal and a diurnal test, were run in 1985 and twenty in 1986. Fry size averaged (SE) 32.6 (0.1) and 36.3 (0.1) mm SL respectively for Slim and Harrison fish in 1985. During the tests on laboratory-reared fry, salmon averaged (SE) 33.1 (0.3), 31.6 (0.4), 34.3 (0.3), and 33.9 (0.2) mm SL for Slim, Eagle, Nanaimo, and Harrison populations respectively. Water temperature was maintained between 10-10.5°C for all tests and water velocity through the compartment openings averaged about 10 cm/s. Analysis of variance, with population as the main effect,

followed by Tukey's a posteriori means test (Zar 1984) were used to test statistical hypotheses.

B. Aggressive behaviour of newly-emerged chinook fry

Aggressive behaviour of chinook was observed in tests both with individual fry and groups of fry. In the single fry tests, 25 fry from each population were isolated in individual 9 L aquaria in the controlled environment chamber (10°C). Fry were left to acclimate in the aquaria for 1 wk. During this time they were fed crushed Tetramin thrice daily. Each aquarium was covered on three sides by black plastic to prevent fry in adjacent aquaria from observing one another. The aquaria were placed on racks the fronts of which were draped with plastic sheeting with observation holes. To provide aeration, each aquarium had a subgravel filter. Fry were observed daily for signs of feeding which usually commenced within 2-4 d after they were isolated in the aquaria. For the tests on wild fry, photoperiod was maintained at 12 h light:12 h dark while the tests on laboratory-reared fry were conducted under a natural photoperiod regime.

Mirror-image-stimulation (MIS, Gallup 1968) tests were conducted after fry had been in their aquaria for 7 d. Rosenau and McPhail (1987) used the MIS technique to study newly-emerged coho salmon fry and found that fry aggression increased for up to 7 d after which aggression stabilized.

To minimize the influence of daily volatility of behaviour of individuals, I used repeated measurements when testing juvenile salmon (Martin and Kraemer 1987). This is especially appropriate for testing newly-emerged salmon because their behaviour is unstable as they refine behaviours with experience (e.g. Cole and Noakes 1980; Martin and Bateson 1986). During the MIS tests, a mirror was placed in an aquarium (selected in random order) and after a 1 min period, the behavioural responses of the fry (Table 1) were recorded for 3 min using an OS-3 Observational Systems Inc. event recorder.

Fry size averaged (SE) 32.8 (0.1) and 34.7 (0.2) SL mm respectively for Slim and Harrison wild fish, and 31.9 (0.2), 30.3 (0.3), 34.9 (0.4), and 34.1 (0.3) mm SL for Slim, Eagle, Nanaimo, and Harrison laboratory-reared salmon respectively. Fish fed vigorously and gained an average of almost 10% of their original body weight over the 7 d tests.

In group fry tests, behavioural reactions (Table 1) were observed among sixteen newly emerged chinook by scan sampling in replicate stream tank sections. The Plexiglas stream channel sections measured 1.0 X 0.30 X 0.25 m and water level was maintained at 0.22 m by an overflow pipe. The bottom of each channel section was covered with sand and gravel (<1.0 cm diameter) to a depth of 4.0 cm. Inflowing dechlorinated water (2.5 L/min) maintained water temperature at between 10 and 11°C.

Table 1. Aggressive behaviours recorded for chinook salmon in the study. (*MIS only, **stream tank tests only, ***both MIS and stream tanks tests).

Behaviour	Definition
Swim-against-mirror*	Any swimming motion by a fish with its snout up touching the mirror. (Rosenau and McPhail 1987)
Approach***	Any movement by one fish towards another (or its mirror image) by swimming or drifting; this behaviour usually initiates contests and is often followed by a nip or lateral display (Kratt and Smith 1979).
Nip**	Any biting motion made by one fish towards another; contact does not necessarily occur and thus includes the "threat nip" of Chapman (1962).
Charge**	Any rapid, direct movement by an aggressor towards another fish; this behaviour is distinguished from approach by rapid acceleration (Kratt and Smith 1979).
Chase**	Any prolonged approach by one fish towards another followed by fleeing of the chased fish from the point where it was originally stationed.
Lateral display***	Erection of the dorsal and anal fins while motionless, often accompanied by erection of the pelvic and pectoral fins, lowering of the lower jaw, and "quivering" of the body; corresponds to the "lateral threat" of Chapman (1962) and Hartman (1965).
Wigwag***	Lateral displays while swimming in an exaggerated motion with the mouth open and lowering of the pectoral and pelvic fins; may be performed while body is horizontal, or inclined upwards (head-up wigwag) or downwards (head-down wigwag). (North 1979)

Photoperiod was maintained at 12 h light:12 h dark (wild fry tests) or followed the natural light:dark schedule (laboratory-reared fry tests). Sizes of newly-emerged fry were slightly larger than those reported for MIS tests, about 33-36 mm SL. In each test, 16 fry from the population being tested were placed in the stream tank sections and left for 48 h during which time they were fed thrice daily with crushed Tetramin. For 5 consecutive days thereafter, the number and duration of aggressive behaviours among fry over 10 min were recorded thrice daily for each stream tank section. Fish were fed after each observation period and at least 2 h elapsed between observation periods.

Data on the duration of aggressive behaviours were summarized by principal components analysis (PCA) using MIDAS (Fox and Guire 1976). Principal components analysis produced summaries of aggressive behaviour consisting of one or more independent behavioural vectors as an efficient alternative to examining behavioural variation character-by-character (cf. Huntingford 1976; Nishikawa 1985). For each observation period, principal component scores along those component axes that accounted for 5% or more of the total variance were calculated and subjected to repeated measures analysis of variance with population as the main effect. A posteriori means tests were conducted using Tukey's test.

C. Chinook fry morphology

During freshwater stream residence, juvenile salmonids have deep bodies with parr marks, and large, often falcate and brightly coloured fins. These body form and colouration traits are thought to function, in part, in social interaction (Hartman 1965; Maeda and Hidaka 1979; Keenleyside 1979). As part of the smolt transformation, juveniles become more streamlined, they lose their parr markings and become "silvery" and countershaded. Also, colouration in the fins fades and the fins become smaller in relation to body size (Fessler and Wagner 1969; Hoar 1976, 1988; Winans and Nishioka 1984; Taylor unpub. data). These morphological traits are not only features of the life history transition within an individual, but also characterize species and populations within species with variable migration timing (Hikita 1962; Hoar 1976; Carl and Healey 1984). Stream-type chinook should thus possess deeper bodies, more parr marks, and larger and more brightly coloured median fins than earlier migrating ocean-type chinook salmon.

Morphological analysis on preserved (10% buffered formalin) newly-emerged chinook fry scored the following body measurements: standard length, maximum body depth, head depth, head length, dorsal and anal fin heights, dorsal and anal fin lengths, and caudal fin depth (Hubbs and Lagler 1967). I also counted the number of major parr marks (i.e. those bisecting the lateral line), and total parr marks and took measurements of

maximum parr mark length and width. All measures except standard length and counts were made on the left side under a dissecting microscope fitted with a micrometer eyepiece. Standard length was measured with Vernier calipers. A general evaluation of colouration of the body and fins of fry was made on anaesthetised specimens after the stream tank tests. To minimize size-related differences in body shape, body measurements were adjusted to the overall sample mean standard length by covariance analysis on \log_{10} transformed data. To assess differences in adjusted means among populations, pairwise, t -tests were used and α was set $0.05/k$, where k is the number of pairwise tests.

Results

A. Response of newly-emerged fry to water current

Wild fry

During diurnal tests, newly-emerged wild ocean- and stream-type fry responded with slight but significant (t -tests for $\mu=10$, Harrison $P < 0.01$; Slim $P < 0.05$, $df=11$) upstream movement (Table 2). The mean number of fry making an upstream choice tended to be higher for stream-type, Slim Creek fish than for Harrison River ocean-type fish (eight and six fry respectively). The downstream response of fry from both populations under nocturnal test conditions was pronounced (both $P < 0.0001$,

Table 2. Net movement scores for newly-emerged wild chinook salmon fry. Values are means, \pm SE (range). Net movement score 0=maximum downstream movement, 10=no net movement upstream or downstream and 20=maximum upstream movement. For tests of equality of means *** $P < 0.001$. N=12 for each population.

	Slim Creek (Stream-type)	Harrison River (Ocean-type)
Diurnal tests	10.9 \pm 0.57 (8.5-14.1)	10.9 \pm 0.35 (8.7-13.1)
Nocturnal tests***	4.1 \pm 0.63 (1.2-7.1)	0.4 \pm 0.17 (0.0-1.6)

df=11). Harrison River, ocean-type chinook fry, however, showed more pronounced downstream movement than stream-type fry from Slim Creek (Table 2, $P < 0.0001$, df=1,22). During the nocturnal tests, an average of 92% of Harrison River chinook fry moved to the most downstream compartment. By contrast, while Slim Creek chinook also moved downstream, an average of only 40% moved to the most downstream compartment and, hence, they tended to be more evenly distributed among the compartments. Whereas in three nocturnal tests at least 1 Slim Creek fry moved upstream, no Harrison River chinook moved upstream.

Laboratory-reared fry

In the stream channels, the laboratory-reared chinook fry from all populations responded by "holding" or swimming slightly upstream during diurnal tests while moving downstream during nocturnal tests (Table 3). In order of increasing downstream movement during nocturnal tests the populations ranked Nanaimo, Slim, Eagle, and Harrison. In order of increasing upstream movement during diurnal tests, the populations ranked: Harrison, Eagle, Slim, and Nanaimo. Fry movement tended to be more pronounced during nocturnal tests. All populations showed significant downstream movement (t -tests for $\mu=10$, all $P < 0.001$, df=19), but during diurnal tests all populations, except Harrison River, showed slight, but significant, upstream movement ($P < 0.05$, Table 3). Ocean-type fry from the Harrison River had a significantly lower net movement score ($P < 0.0001$,

Table 3. Net movement scores for newly-emerged, laboratory-reared chinook salmon fry. Values are mean (SE) and in all cases N=20. Underlining indicates those mean scores which are not significantly different by Tukey's test ($P > 0.05$). A score of 0=maximum downstream movement, 10=no net movement upstream or down

	Stream-type		Ocean-type	
	Slim Creek	Eagle River	Nanaimo River	Harrison River
Diurnal tests	11.74 (0.43)	10.90 (0.47)	12.28 (0.41)	10.44 (0.44)
Nocturnal tests	6.37 (0.44)	6.14 (0.44)	7.48 (0.42)	3.02 (0.43)
Overall	8.99 (0.31)	8.51 (0.35)	9.98 (0.38)	6.64 (0.31)

df=3,76) during nocturnal tests than fry from the three other populations.

B. Aggressive behaviour of newly-emerged chinook salmon fry

Wild fry

In MIS tests, most fry adjusted quickly to the presence of the mirror. Fry typically oriented towards their mirror image, then gradually approached the mirror and followed with bouts of "swim-against-mirror" and "lateral display". Both the time it took fry to show some overt reaction to their mirror image and to approach it decreased over the 7 d tests. Fry were occasionally observed to "charge" and even "nip" their mirror images but these behaviours were observed so infrequently that they were not included in the analysis.

Principal components analysis of the data from the MIS tests summarized 94% of the behavioural variation in two component axes (Table 4). As indicated by their large component coefficients "swim-against-mirror" dominated the first axis while "wigwag" dominated the second axis. Over all days combined, Slim Creek, stream-type chinook fry were more aggressive than ocean-type fry from the Harrison River (Fig. 2a, $P = 0.001$, $df=1,48$). Along this first component, fry from the two populations showed different behavioural trends with time. Slim Creek fry were highly responsive to their mirror

Table 4. Principal component coefficients derived from MIS behavioural data.

Behaviour	Coefficient from PCA	
	Component 1	Component 2
Approach	-0.023	0.005
Swim-against-mirror	-0.996	0.001
Lateral display	0.009	-0.469
Wigwag	-0.006	-0.883
Cumulative % total variance	81.3	93.5

images from observation day 1, but declined somewhat in "swim-against-mirror" behaviour through to observation day 7. By contrast, Harrison River fry showed little response at the start of testing but steadily increased up to observation day 6 (day X population $P = 0.002$, $df=6,234$).

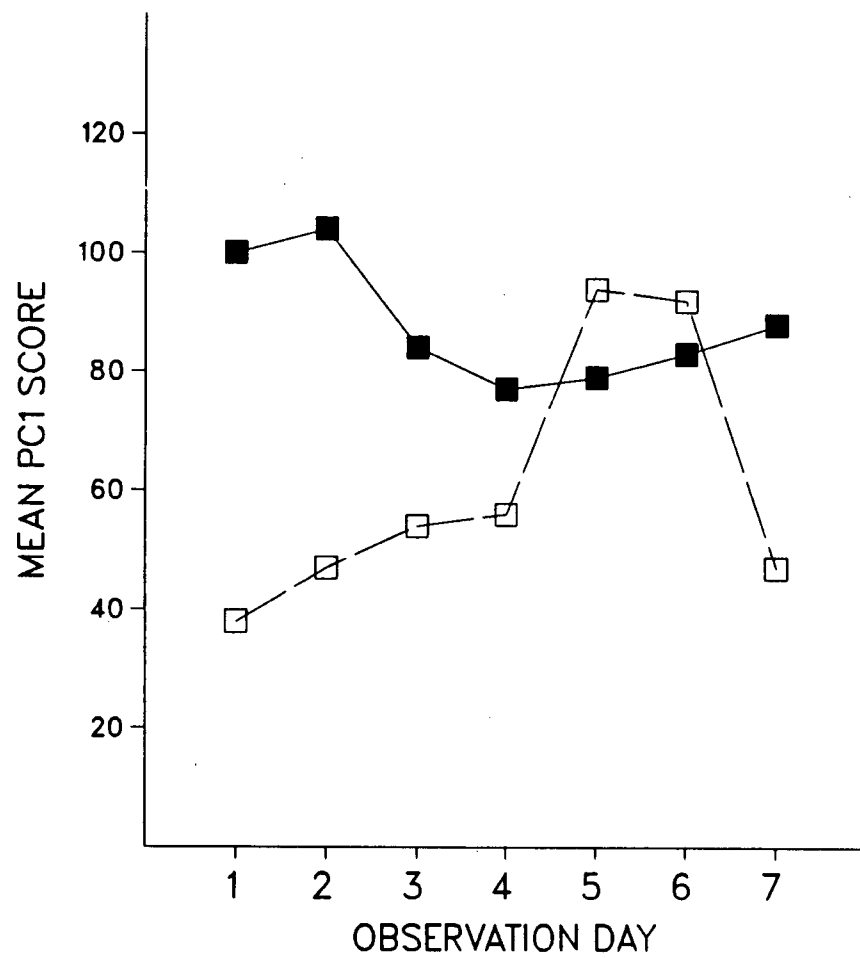
Along the second component axis ("wigwag") Slim Creek, stream-type fry were also more aggressive than the Harrison River newly-emerged fry (Fig. 2b, $P=0.006$). Fry spent more time performing aggressive displays as time progressed (Fig 2b).

In the stream tanks, the juvenile chinook salmon defended exclusive areas and actively drove away intruders by overt aggression ("nipping" and "charging") or by advertisement ("lateral displays" and "wigwags") and appeared to form territorial "mosaics" (Keenleyside 1979). Individuals tended to remain in specific areas while making brief aggressive and feeding forays to other locations in the stream tanks. Certain fish (1-4 per section) usually accounted for most of the interaction. These "dominant" fish usually maintained a territory at the most upstream end of the stream tank sections.

Two component axes were produced by PCA which summarized 89% of the total behavioural variation; "lateral display" and "wigwag" behaviours dominated the first and second component axes respectively (Table 5). The stream-type fry from Slim

Figure 2. Mean aggression scores for newly-emerged, wild-reared chinook salmon fry in MIS tests. 2a=principal component axis 1, 2b=principal component axis 2. N=25 for each population.

2a



2b

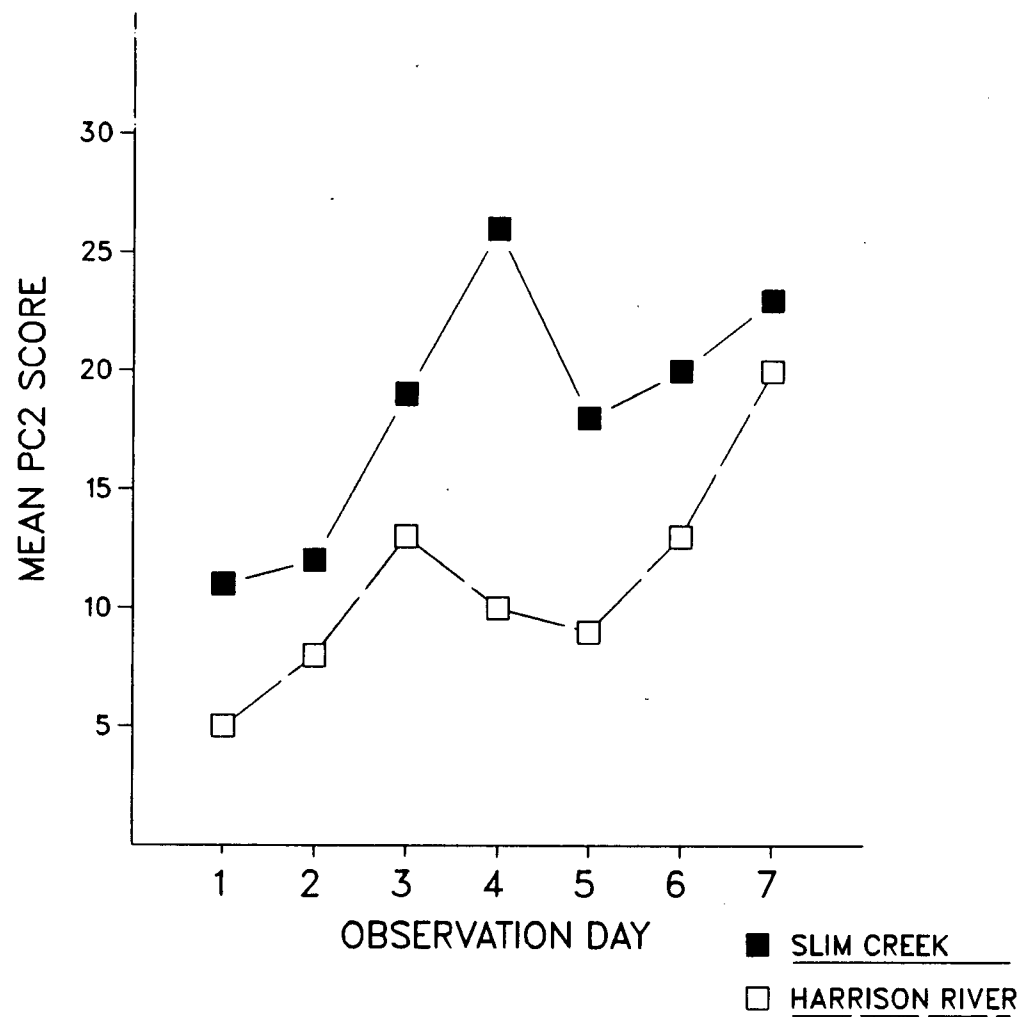


Table 5. Component coefficients derived from principal components analysis of stream tank behavioural data.

Behaviour	Coefficient from PCA	
	Component 1	Component 2
Approach	0.496	0.127
Lateral display	0.850	-0.259
Wigwag	0.163	0.956
Charge	0.068	0.019
Nip	0.010	0.031
Chase	-0.010	0.016
Cumulative % total variance	52.7	89.7

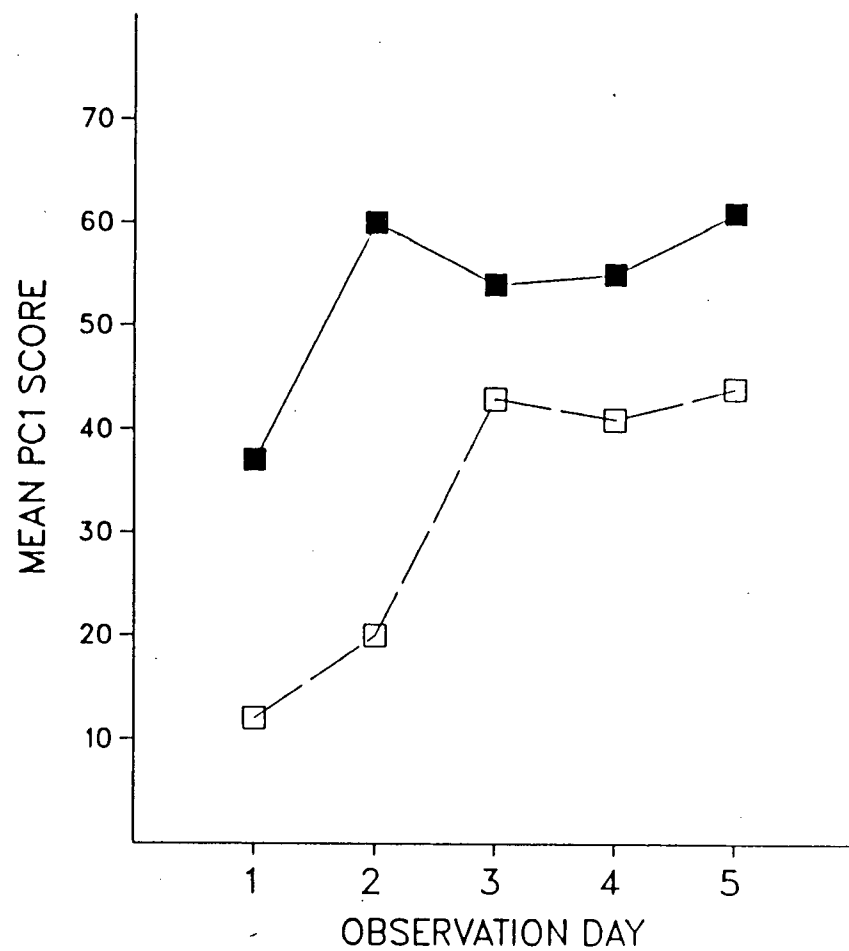
Creek were more aggressive along the first axis (55% of total variation, Fig. 3a, $P = 0.01$, $df=1,4$) and both Slim and Harrison fry became more aggressive with time ($P=0.05$, $df=4,16$). There was, however, no difference in aggression levels between stream- and ocean-type fry along the second component axis (34% total variation, Fig. 3b, $P = 0.1$). An increase in "wigwag" (PC2) display behaviour both by Slim and Harrison chinook fry by observation day four suggests an increase in complexity of behavioural displays with time (within factor "day", $P=0.0003$, $df=4,16$).

Laboratory-reared fry

When subjected to PCA, 97% of the behavioural variation from the MIS tests involving laboratory-reared fry was summarized by two component axes (Table 6). As was the case for the wild-reared fry, "swim-against-mirror" dominated the first axis whereas "lateral display" behaviour dominated the second (Table 6). Along component axis 1, Slim Creek fry were more aggressive than Eagle River fry, but fry of both these stream-type populations were more aggressive than the ocean-type fry from the Nanaimo and Harrison rivers (Fig. 4a, $P=0.0001$, $df=3,96$). Although the trend was less marked than in the wild fry MIS tests, a slight trend towards increasing responsiveness with time was evident in the laboratory-reared fry (day factor, $P=0.02$, $df=6,450$). Along component axis 2 Slim Creek fry were the most aggressive (i.e. highest mean PC scores), Nanaimo

Figure 3. Mean aggression scores for newly-emerged, wild-reared chinook salmon fry in stream tank tests.
3a=principal component axis 1, 3b=principal component axis 2. N=3 groups of 16 fry per population.

3a



3b

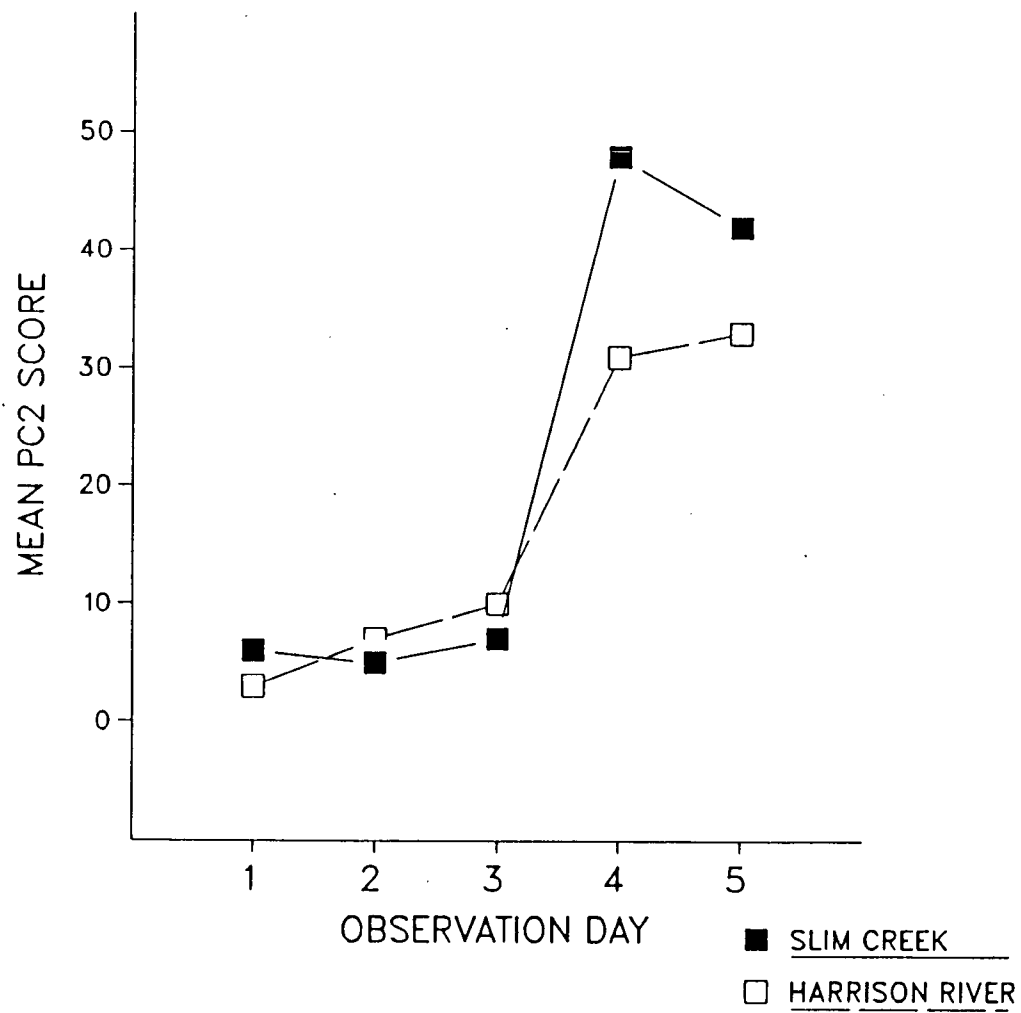
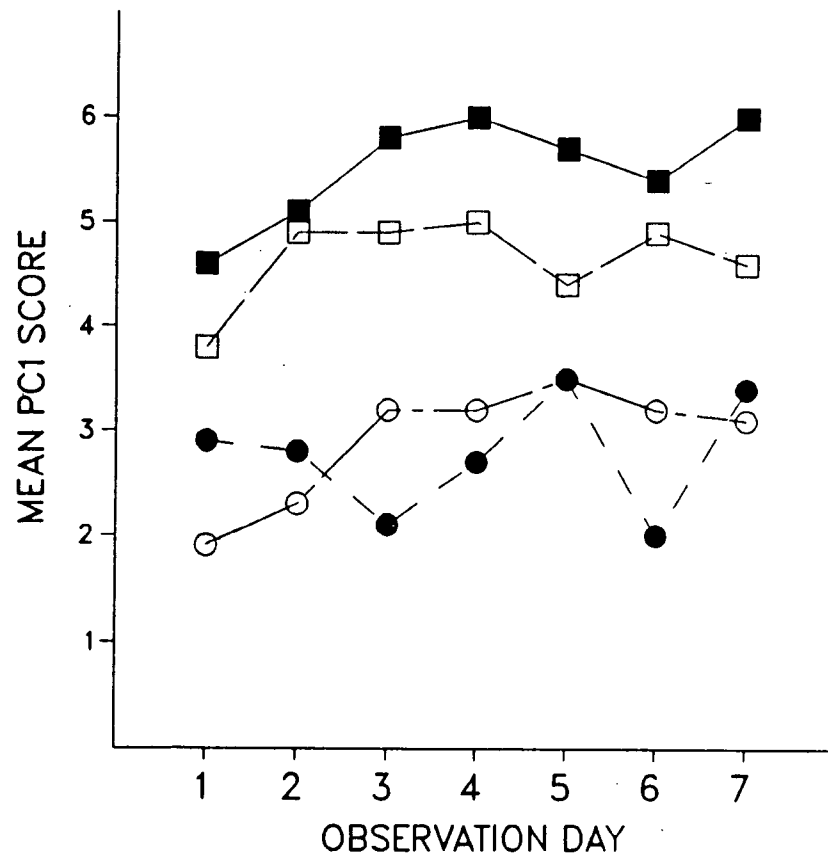


Table 6. Component coefficients derived from principal components analysis of MIS behavioural data of laboratory-reared chinook fry.

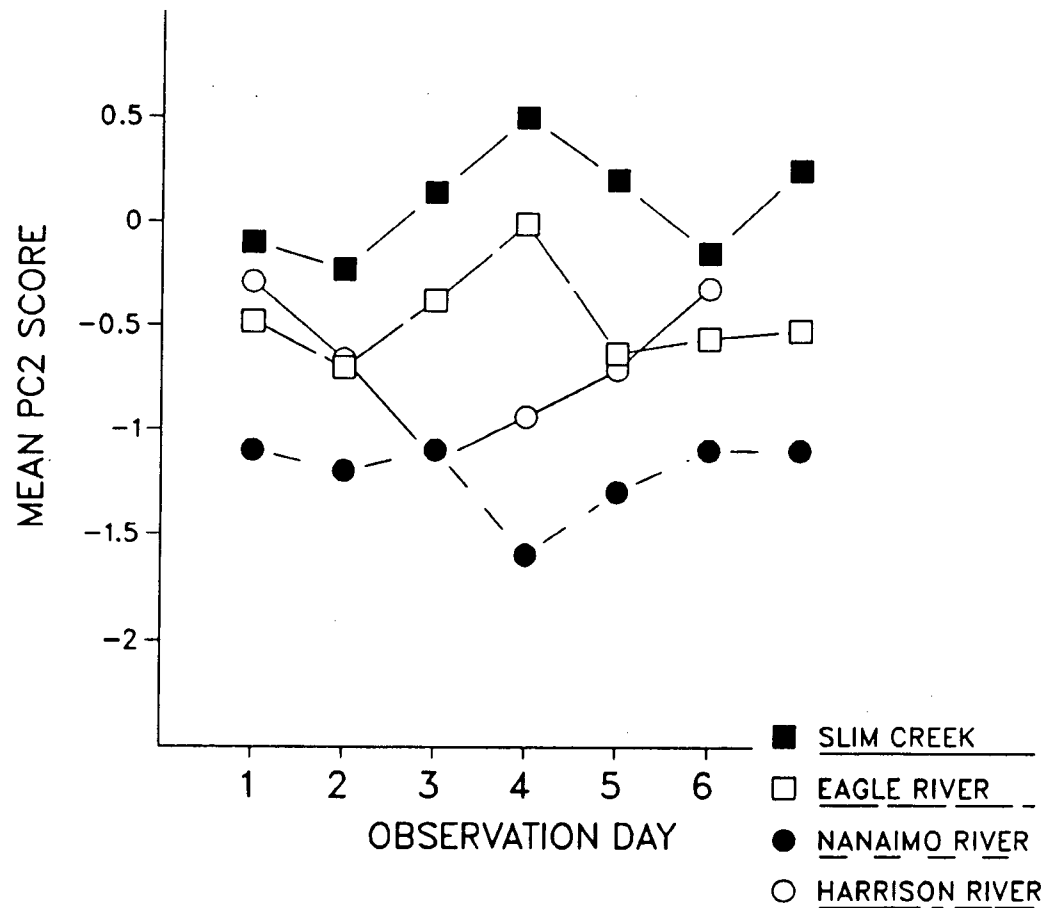
Behaviour	Coefficient from PCA	
	Component 1	Component 2
Approach	-0.004	0.019
Swim-against-mirror	0.999	-0.043
Lateral display	0.039	0.952
Wigwag	0.022	0.299
Cumulative % total variance	89.1	97.3

Figure 4. Mean aggression scores for newly-emerged,
laboratory-reared chinook salmon fry in MIS tests.
4a=principal component axis 1, 4b=principal component axis
2. N=25 fry per population.

4a



4b



River, ocean-type fry were the least aggressive, and Harrison and Eagle rivers fry were intermediate (Fig. 4b, $P=0.0001$).

Stream tank interaction data summarized by PCA produced three component axes (97% of total variation) dominated by "wigwag", "lateral display", and "approach" behaviours respectively (Table 7). Along component axis 1 (58% of total variance) stream-type fry from Slim Creek and Eagle River were clearly more aggressive than the ocean-type fry from Harrison and Nanaimo rivers (Fig. 5a, $P=0.0001$, $df=3,8$) with little consistent change with time (day factor, $P=0.9$, $df=4,32$).

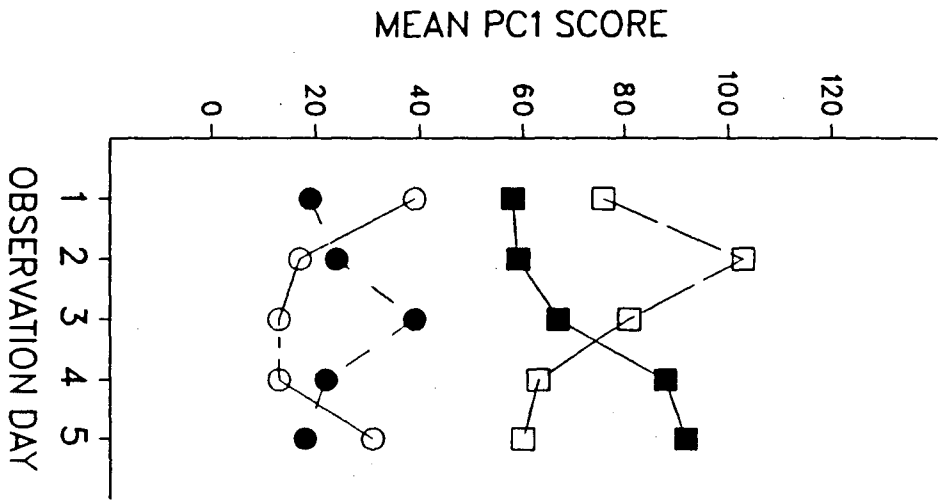
Component axis 2, contrasted "lateral display" with the more elaborate "wigwag" display (Table 7). Along component axis 2 (Fig. 5b), the populations fell into three groups based on their mean PC scores. Slim Creek fry had the highest mean score indicating high levels of "lateral display" behaviour, ocean-type fry from Harrison and Nanaimo rivers had intermediate scores, and Eagle River, stream-type fry had the lowest mean score. The low mean PC score of Eagle River chinook fry resulted from high levels of "wigwag" display behaviours on observation days 2 and 3 (Fig. 5b). The component coefficient for "wigwag" on component axis 2 is reasonably high and opposite in sign to that for "lateral display" (-0.47 , Table 7) and Eagle River fry had high negative PC scores early during the test period (Fig. 5b) which declined as the tests proceeded. Therefore, at least early in the test period, both Slim and

Table 7. Component coefficients derived from principal components analysis of stream tank behavioural data for laboratory-reared chinook fry.

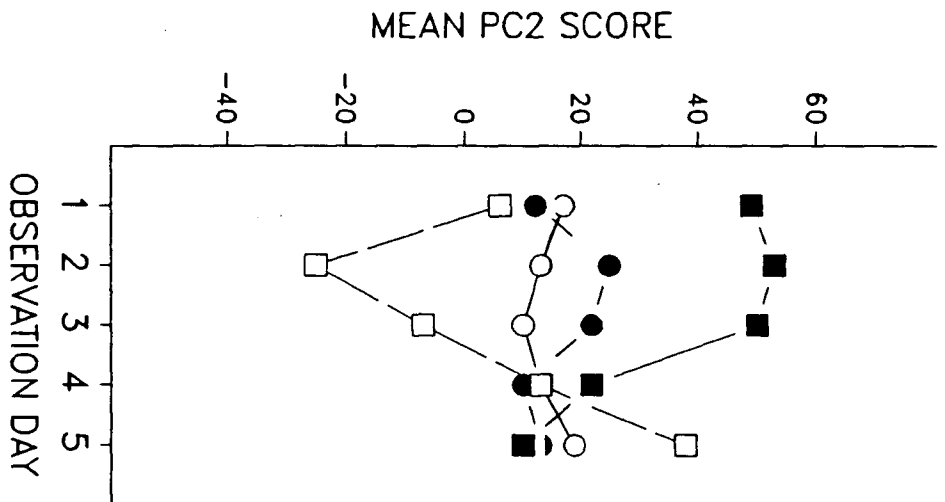
Behaviour	Coefficient from PCA		
	Component 1	Component 2	Component 3
Approach	0.500	0.231	-0.831
Lateral display	0.307	0.837	0.398
Wigwag	0.807	-0.473	0.351
Charge	0.064	0.115	0.137
Nip	0.016	0.097	0.092
Chase	0.002	0.004	-0.009
Cumulative % total variance	58.5	87.9	96.7

Figure 5. Mean stream tank aggression scores for laboratory-reared chinook fry. 5a=principal component axis 1, 5b=principal component axis 2, 5c=principal component axis 3. N=3 groups of 16 fry per population.

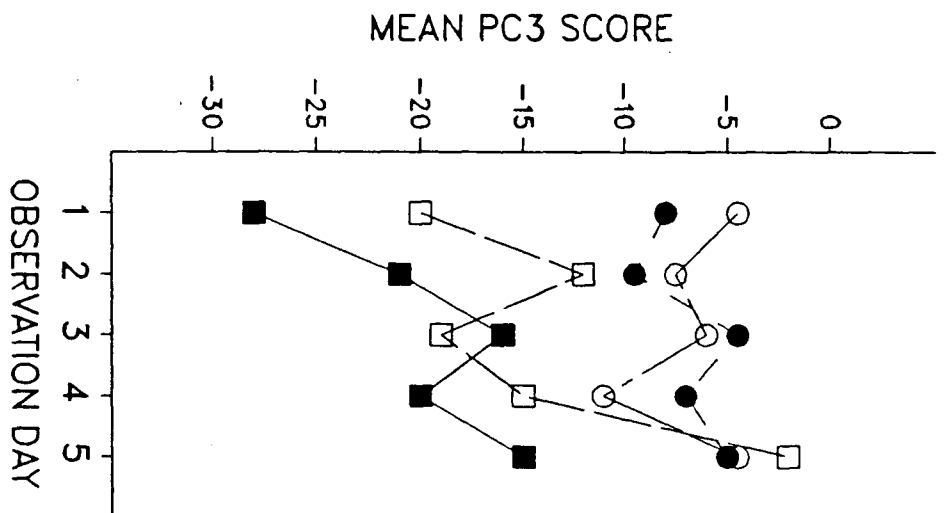
5a



5b



5c



■ SLIM CREEK
 □ EAGLE RIVER
 ● NANAIMO RIVER
 ○ HARRISON RIVER

Eagle, stream-type chinooks were the most aggressive fry, but in terms of different behaviours - lateral display for Slim Creek chinook and wigwag for Eagle fry. By contrast, no trend was apparent in display behaviours for Harrison or Nanaimo river chinook fry; both had similar intermediate positive PC scores throughout the 5 day test period.

Component axis 3 was dominated by "approach", but also served to contrast this overt behaviour with aggression expressed through display behaviours (Table 7). The populations again tended to diverge into two groups based on mean PC scores; Slim Creek and Eagle River stream-type fry had higher negative scores (i.e. they were more aggressive in terms of "approach") than Harrison and Nanaimo fry. The only significant differences, however, were between Slim Creek fry and fry from the ocean-type populations, Harrison and Nanaimo rivers (Fig. 5c, $P < 0.001$).

To summarize, both wild and laboratory-reared stream-type chinook salmon fry were consistently more aggressive than the earlier migrating, ocean-type chinook fry. Within these broad juvenile life history categories, Slim Creek stream-type fry were the most aggressive while Harrison River, ocean-type chinook were usually the least aggressive.

C. Morphology and colouration

Wild fry

Slim Creek, stream-type chinook fry had larger body parts and median fins than ocean-type fry of the same size from the Harrison River. Body depth, head depth, dorsal fin height, caudal fin depth, and maximum parr mark length showed significant differences (Table 8). Slim Creek fry also had more parr markings and more elaborate body colouration (an orange stripe along the lower jaw and bright orange-black colouration on the caudal fin). This colouration was apparent when fry were first collected and persisted during rearing in the laboratory (about 2 months). Slim Creek chinook were prominently pigmented at the beginning of the stream tank behaviour tests. By contrast, Harrison River, ocean-type fry initially had transparent median fins. By the end of the stream tank experiments, however, some Harrison River fry had developed prominent markings on their median fins consisting of black leading edges with white tips and some yellow/black colouration on the caudal fin.

Table 8. Morphological comparison of wild-reared, newly-emerged chinook salmon fry. Body proportions are means (SE) adjusted to a standard length of 34 mm by covariance analysis; N=30 for each population, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ for $df=1,57$.

Character	Slim Creek	Harrison River
Standard length	31.2 (0.18)	34.9 (0.32)
Body proportions		
Body depth*	5.8 (0.07)	5.4 (0.05)
Head depth*	5.5 (0.05)	5.3 (0.05)
Head length	9.5 (0.08)	9.4 (0.08)
Dorsal fin height*	4.2 (0.06)	3.8 (0.09)
Dorsal fin length	6.7 (0.08)	6.5 (0.09)
Anal fin height	3.7 (0.08)	3.6 (0.08)
Anal fin length	5.3 (0.04)	5.1 (0.04)
Caudal fin depth* ¹	9.0 (0.10)	7.8 (0.12)
Maximum parr mark length*	3.5 (0.10)	3.1 (0.10)
Maximum parr mark width	1.7 (0.06)	1.8 (0.06)
Counts		
No. major parr marks**	10.7 (0.25)	9.6 (0.25)
No. total parr marks***	23.8 (0.84)	15.2 (0.84)

¹-heterogenous standard length-character regression slopes ($P < 0.05$, $df=1,56$).

Laboratory-reared fry

Morphological analysis suggested no consistent stream/ocean-type dichotomy with respect to body form or colouration among the laboratory-reared fry from the four populations (Table 9). Although stream-type chinook from Slim Creek and the Eagle River had the deepest bodies and heads, it was Slim Creek fry and ocean-type, Nanaimo River fry that had the largest median fins. In fact, although Slim Creek fry consistently had the largest fins, in all but one fin measurement (afl) Eagle River, stream-type fry had the smallest fins. The populations also differed in the number of parr marks, but again there was no distinction between stream- and ocean-type salmon; Nanaimo and Eagle river fry had the most major and total parr marks (Table 9).

All fry possessed black and white leading edges on the dorsal fin and white tips on their anal fins. As was the case for the wild-reared fry, the greatest distinction with respect to fin colouration was in the degree of orange pigment in the median and paired fins. Slim Creek fry were the most elaborately coloured, they had prominent orange colouration on all median and paired fins. Nanaimo River fry were also well coloured, but they lacked the bright orange-black colour on the caudal fin and orange colouration on the paired fins shown by Slim fry. Stream-type fry from the Eagle River tended to be

Table 9. Mean (SE) standard length, body proportions in mm, and parr mark counts for newly-emerged, laboratory chinook salmon fry from the study populations. N=30 in all cases and measurements were adjusted to an overall sample mean standard length of 30.6 mm by covariance analysis. The indicated probability is that all adjusted means are the same (df=3,115).

Character	Slim Cr.	Eagle R.	Nanaimo R.	Harrison R.	P
Standard length	30.5 (0.22)	28.6 (0.20)	32.7 (0.29)	31.2 (0.16)	-
Body proportions					
Body depth	6.3 (0.06)	6.4 (0.08)	5.7 (0.08)	5.9 (0.06)	< 0.001
Head depth*	5.8 (0.05)	5.5 (0.05)	5.4 (0.06)	5.4 (0.05)	< 0.001
Head length*	8.6 (0.05)	8.2 (0.07)	8.5 (0.07)	8.6 (0.05)	< 0.001
Dorsal fin height	3.7 (0.07)	2.8 (0.09)	3.1 (0.09)	2.9 (0.07)	< 0.001
Dorsal fin length	6.3 (0.07)	5.2 (0.09)	5.7 (0.09)	5.8 (0.07)	< 0.001
Anal fin height	3.5 (0.05)	2.8 (0.07)	3.0 (0.07)	2.9 (0.05)	< 0.001
Anal fin length	4.8 (0.09)	4.2 (0.12)	4.2 (0.11)	4.4 (0.09)	< 0.001
Caudal fin depth*	7.7 (0.14)	7.5 (0.18)	7.6 (0.18)	7.5 (0.14)	> 0.05
Parr mark length	3.1 (0.11)	2.6 (0.14)	2.5 (0.13)	2.8 (0.10)	< 0.005
Parr mark width	1.8 (0.04)	1.4 (0.05)	1.3 (0.05)	1.3 (0.04)	< 0.001
Counts					
No. major parr marks	9.2 (0.21)	10.6 (0.29)	11.4 (0.28)	10.1 (0.22)	< 0.001
No. total parr marks	16.7 (0.73)	18.4 (0.97)	21.1 (0.93)	15.1 (0.74)	< 0.001

*heterogenous standard length-character regression slopes ($p < 0.05$, $df=3,112$)

lighter in colour than fry from either Slim Creek or the Nanaimo River. Although Eagle River chinook fry had orange pigment on their median fins it was not universal, especially on the caudal fin. In addition, many Eagle fry lacked the orange mandible stripe characteristic of the Slim Creek and Nanaimo River fry. The Harrison River, ocean-type fry were the least brightly coloured; they lacked any trace of orange pigment in their fins, although some faint yellow colour was present on the caudal fin.

2. INTER-, INTRAPOPULATION, AND TEMPORAL VARIATION IN BEHAVIOUR AND GROWTH OF JUVENILE CHINOOK SALMON

Methods

Experimental animals

The experimental fish were progeny of adult salmon from eight populations in British Columbia collected during the autumn of 1986 (Table 10), four were stream-type and four ocean-type. They were classified using field observations of juvenile downstream migration timing and the presence of a freshwater annulus on adult scales (Healey and Jordan 1982; Carl and Healey 1984; Shepherd et al. 1986a).

Adult salmon were collected by seining, driftnetting, or from fences associated with enhancement facilities. In all cases, gametes from a number of males and females (Table 10) were obtained and fertilization was completed in the field as outlined previously (pp. 13-14). Zygotes were transported to the laboratory at the University and incubated at 8°C. The embryos and larvae were incubated in darkness for approximately 6 months at a water flow of 2 L/min.

At emergence, approximately 1,500 fry from each population were randomly assigned to one of eight 94 L fiberglass rearing troughs. Rearing conditions were as described earlier (1.1).

Table 10. Number of male and female parents used in experimental crosses of chinook salmon from stream- and ocean-type populations.

Population	No. males x no. females
Stream-type	
Bowron River	10 X 10
Slim Creek	6 X 7
Eagle River	5 X 5
Salmon River	5 X 3
Ocean-type	
Little Qualicum River	4 X 5
Harrison River	5 X 5
Nanaimo River (lower)	10 X 10
Nanaimo River (1st lake)	8 X 6

The growing salmon were transferred to 900 L, oval rearing tanks at 3 months of age where photoperiod and water flow conditions were identical to those in the rearing troughs.

A. Inter-, intrapopulation, and temporal variation in rheotactic behaviour

Current response was tested for juvenile salmon at "spring" through "late summer" (emergence, 1, 2, 3 and 4 months), "fall" (6 months), "winter" (9 months), and 1 year following emergence (12 months). These tests were run over a full year to detect differences among populations that might correspond to major periods of juvenile seaward migration other than at emergence (i.e. 2-4 months in ocean-type chinook or 1 year in stream-type chinook).

The tests were run in the two oval-shaped stream channels described earlier (1.1). The channel structure and test protocol were modified slightly to account for the increasing size of fish with age. Both channels were subdivided into 13 compartments ranked from -6 (most downstream) through 0 (central compartment) to +6 (most upstream). Each compartment (30 x 30 x 25 cm) was connected to adjacent compartments by holes (4.5 cm diameter) in the compartment walls. The holes in successive compartment walls were staggered "side-to-side" so that the salmon had to "search" for the openings as they moved upstream or downstream. Each test assessed the movements of 15 fish

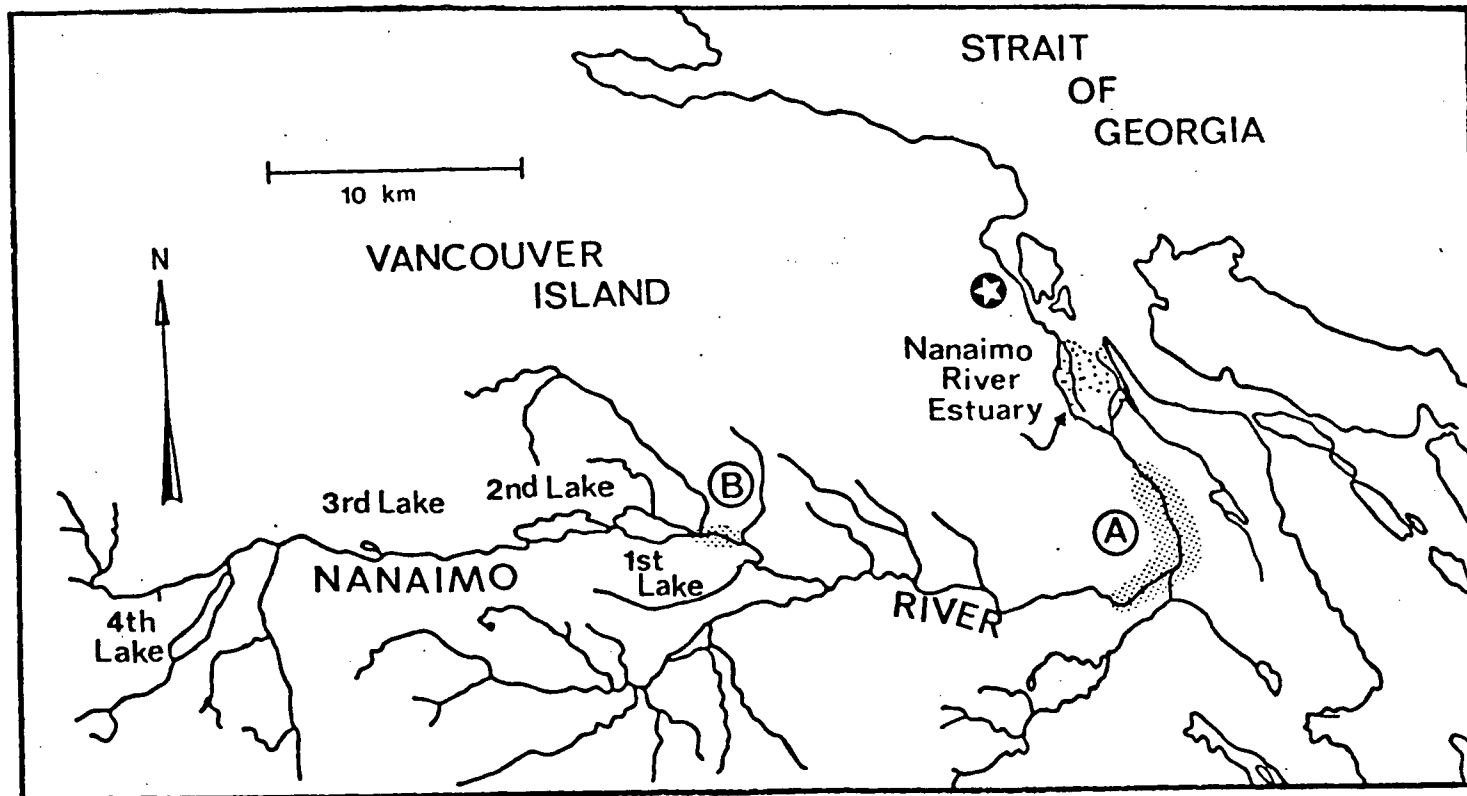
through the compartments during a 3 h period under simulated nocturnal and diurnal conditions. The evening before a test, 15 fry were placed in the central compartment with the exit and entrance holes closed. Commencing at about mid-day the following day the tests were initiated as described earlier (1.1). At each age, eight diurnal and eight nocturnal tests were run on each population.

For each test, a "movement score" was calculated by summing the products of the number of fish in each compartment and the rank of that compartment then dividing by 15, the number of fish in each test. A constant of 6 was added to eliminate negative scores. Water temperature was maintained between 10-10.5°C for all tests and water velocity through the compartment openings averaged about 10 cm/s.

B. Inter-, intrapopulation, and temporal variation in aggressive behaviour

Test fish at 5 ages: emergence, 1, 2, 3, and 6 months of age were from Slim Creek (stream-type) and two Nanaimo River populations. One population ("1st Lake, Fig. 6) spawns about 20 km upstream of the estuary at the outlet of 1st Lake and most of its juveniles migrate seaward after 2-3 months in freshwater (Carl and Healey 1984). The second population ("lower river") spawns about 5-10 km upstream of the estuary and its fry migrate to the estuary within a few days of emergence (Carl and Healey

Figure 6. Major features of the Nanaimo River including spawning areas (stippling) of "Lower Nanaimo" (A) and "1st Lake" (B) populations of chinook salmon in the river. Location of Nanaimo townsite is indicated by the open star. Redrawn from Healey and Jordan (1982).



1984).

The number and duration of aggressive behaviours during multiple fry, stream tank tests (10°C) were recorded using methodology modified slightly from that described earlier (1.1). The bottoms of stream tank sections were covered with gravel to a depth of about 4 cm. Eight small stones, about 5 cm diameter, formed a zig-zag pattern along the bottom to serve as reference points for the fish. Inflowing dechlorinated water was set to 2.5 L/min and water velocity to 6-7 cm/s for tests run at emergence and 1 month of age. Thereafter, a water velocity of 10 cm/s ensured upstream orientation in the older (and larger) test fish. The stream tanks were enclosed within black plastic sheeting with observation holes, and photoperiod followed the seasonal cycle. For each population at each age, ten fish were allowed to adjust in each of three stream tank sections for 48 h. Thereafter, the number and duration of aggressive behaviours were recorded in each section for 10 min at 09:00 and 17:00 for five consecutive days. The behaviours recorded were: "null", "approach", "lateral display", "wigwag", "charge", and "nip" (Table 1). Fish were fed after each observation period, and at mid-day, at about 5% bw/d. At emergence and 1 month of age they were fed live brine shrimp (Artemia salina) nauplii, and at older ages they were fed live, adult shrimp.

C. Variation in growth rate

Growth of chinook was monitored by standard length (SL), fork length (FL, Ricker (1979)), and weight measurements of a random sample of 30 individuals from each population at monthly intervals. Individuals were lightly anaesthetized with 2-phenoxyethanol, blotted on a moist paper towel, measured and weighed to the nearest 0.5 mm and 0.01 g respectively. Specific growth rates (SGR) were calculated as:

$$SGR = \ln(W_f/W_i) \cdot 100 \cdot d^{-1},$$

where W_f and W_i are the final and initial mean wet weights over the time period d , in days, for each population (Clarke and Shelbourn 1986). To promote maximum growth rates with changing temperature and biomass, fish were fed three times per day on a schedule of pellet sizes and ration levels recommended by the manufacturer (Moore-Clarke Ltd., LaConner, Washington).

D. Statistical analysis

Data from the current response tests run under diurnal and nocturnal conditions were analyzed separately by factorial, nested analysis of variance. Age and life history type (ocean- or stream-type) were the fixed, main effects and population was considered as a random effect nested within life history type. To determine if the mean movement scores for each population at

each age were significantly different from 6 (i.e. a score of 6 = no significant upstream or downstream movement), t-tests were used with the level of significance adjusted through division by the number of tests.

Data on the duration of aggressive behaviours were summarized by principal components analysis (PCA) as described earlier. Subsequently, I analyzed the PC scores using factorial, repeated measures analysis of variance; age and population were the main effects.

Growth rate was analyzed by regressing SGR on age and comparing growth rates among populations and life history types at a common age by nested, analysis of covariance. Again, life history type was the main, fixed effect and population considered as the random effect nested within life history type, and age was the covariate. In all statistical tests, differences among group means were assessed using Tukey's test and variance homogeneity was verified by Bartlett's test.

No behavioural or growth rate data were available from Little Qualicum and lower Nanaimo populations after four months due to >80% losses from chlorine in the municipal water supply.

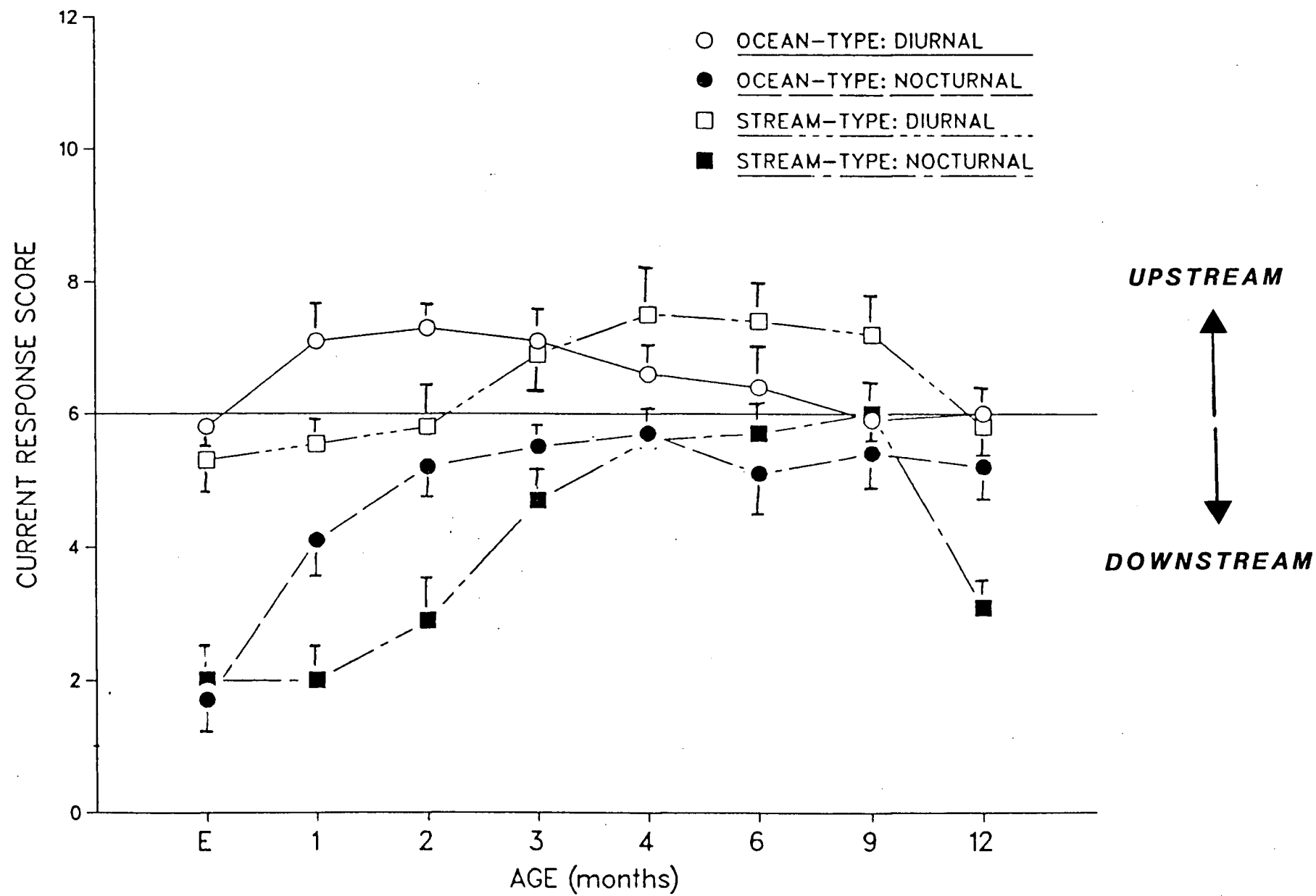
Results

A. Inter-, intrapopulation, and temporal variation in rheotactic behaviour

Under simulated nocturnal conditions, stream-type chinook had a lower mean net movement score (i.e. they moved downstream more) over the 1 year period than ocean-type chinook (Fig. 7, $P < 0.05$, $df=1,6$). As well, populations varied significantly within stream- and ocean-type life history groupings ($P < 0.001$, $df=6,412$, Table 11). Most of the variation in movement scores was attributable to age (50%, $P < 0.0001$, $df=7,36$, Fig. 7). Downstream movement occurred primarily at emergence, 1, 2, and 12 months; little movement was evident between 3 and 9 months.

The effect of age on downstream movement scores was, however, influenced by life history type (age X life history interaction $P < 0.0001$, $df=7,36$, Fig. 7). Stream-type chinook moved downstream to a greater extent up to 2 months ($P < 0.05$), but movement scores were most similar between stream- and ocean-type chinook between 4 and 9 months (Fig. 7). By 12 months, however, stream-type chinook again showed significantly greater downstream movement than ocean-type ($P < 0.05$, Fig. 7). Although ocean-type chinooks showed no significant change in their degree of downstream movement at 12 months from that at 9 months ($P > 0.05$), stream-type chinooks shifted from "holding" behaviour at 6 and 9 months to pronounced downstream movement at

Figure 7. Net movement scores for stream- and ocean-type juvenile chinook salmon in current response tests. Values are means (\pm SE), N=4 populations per life history type at each age except for ocean-type at 6, 9, and 12 months were N=2. E=emergence, 1-6, 9, and 12=month of age at testing.



12 months ($P < 0.05$).

Under simulated diurnal conditions, no differences were apparent between stream- and ocean-type chinooks over all ages combined, (Fig. 7, $P > 0.1$, $df=1,6$), but populations differed significantly within life history type ($P < 0.0001$, $df=6,412$, Table 12). Age variation in diurnal movement scores was also significant ($P < 0.0001$, $df=7,36$). As for nocturnal movement, changes in diurnal movement with age interacted with life history type (age X life history $P < 0.0001$, $df=7,36$). Stream-type chinooks "held position" until 3 months, then showed significant upstream movement at 4 (peak), 6 and 9 months after which there was an abrupt reduction in upstream movement at 12 months (Fig. 7). By contrast, ocean-type chinooks held position at emergence then showed significant upstream movement at 1 through 4 months with peak movement upstream at 2 months (Fig. 7). By contrast to the abrupt reduction in upstream movement by stream-type chinooks between 9 and 12 months, ocean-type chinooks showed no such change; they maintained position or moved slightly upstream at 6, 9 and 12 months ($P > 0.05$, Fig. 7).

B. Inter-, intrapopulation, and temporal variation in aggressive behaviour

Principal components analysis summarized 92% of the total behavioural variance in two components (Table 13). The first

Table 11. Mean (SE) net movement scores during nocturnal current response tests for juvenile chinook salmon from the eight study populations. In each case N=8. For t-tests of $\mu=6$, * $P<0.006$ for tests up to 6 months and $P<0.008$ thereafter (df=7). Mean scores greater or less than 6 represent significant upstream or downstream movement respectively. E=emergence, 1-6, 9 and 12 indicate age (in months) at testing. NT=not tested.

Age	Population								
	Stream-type				Ocean-type				
	Bowron R.	Slim Cr.	Eagle R.	Salmon R.	L. Qualicum R.	Nanaimo 1st L.	Nanaimo lower	Harrison R.	Mean
E	1.32* (0.43)	1.21* (0.52)	2.48* (0.52)	3.13* (0.56)	2.05* (0.47)	1.08* (0.42)	0.98* (0.44)	2.81* (0.41)	1.86 (0.19)
1 m	1.25* (0.22)	1.60* (0.32)	2.27* (0.39)	2.91* (0.56)	5.44* (0.22)	3.53* (0.52)	3.92* (0.21)	3.47* (0.44)	3.00 (0.21)
2 m	3.33* (0.27)	1.10* (0.16)	4.33* (0.32)	2.93* (0.41)	5.76* (0.21)	3.92* (0.42)	5.40* (0.21)	5.24 (0.32)	4.03 (0.21)
3 m	4.87* (0.21)	3.72* (0.30)	4.72 (0.37)	5.46 (0.20)	5.86 (0.41)	5.61* (0.45)	5.28 (0.43)	5.20 (0.33)	5.08 (0.14)
4 m	6.41 (0.25)	5.47* (0.20)	5.42 (0.23)	5.27 (0.31)	5.70 (0.19)	5.56 (0.29)	5.71 (0.19)	5.71 (0.15)	5.65 (0.10)
6 m	5.26* (0.14)	5.78 (0.41)	6.39 (0.54)	6.08 (0.54)	NT	5.68 (0.20)	NT	5.67 (0.18)	5.52 (0.13)
9 m	5.87 (0.40)	6.08 (0.41)	5.90 (0.54)	6.06 (0.54)	NT	5.74 (0.28)	NT	5.68* (0.18)	5.78 (0.17)
12 m	3.01* (0.40)	2.51* (0.51)	3.17* (0.20)	3.71* (0.40)	NT	5.29 (0.40)	NT	5.01 (0.26)	4.00 (0.20)
Mean	3.76 (0.25)	3.27 (0.27)	4.20 (0.23)	4.45 (0.22)	4.96 (0.26)	3.88 (0.31)	4.73 (0.22)	4.70 (0.19)	4.22 (0.09)

Table 12. Mean (SE) net movement scores during diurnal current response tests for juvenile chinook salmon from the eight study populations. All N=8. For t-tests of $\mu=6$, *P<0.006 for tests up to 4 months and *P<0.008 thereafter (df=7). Mean scores greater or less than 6 represent significant upstream or downstream movement respectively. E=emergence, 1-6, 9 and 12 indicate age (in months) at testing. NT=not tested.

Age	Population								Mean
	Stream-type				Ocean-type				
	Bowron R.	Slim Cr.	Eagle R.	Salmon R.	L. Qualicum R.	Nanaimo 1st L.	Nanaimo lower	Harrison R.	
E	4.75 (0.68)	5.48 (0.51)	5.59 (0.27)	5.57* (0.12)	5.86 (0.29)	5.63 (0.22)	5.63 (0.17)	6.10 (0.17)	5.57 (0.14)
1 m	5.60 (0.66)	4.38 (0.51)	5.99 (0.27)	5.78 (0.37)	7.89* (0.35)	5.90 (0.49)	7.97* (0.33)	6.72 (0.27)	6.25 (0.21)
2 m	7.53* (0.44)	3.57* (0.52)	6.14 (0.36)	4.96 (0.45)	7.50* (0.33)	7.29* (0.36)	7.48* (0.35)	6.44 (0.36)	6.40 (0.22)
3 m	7.72* (0.51)	6.51 (0.30)	7.33 (0.63)	5.71 (0.44)	7.06 (0.40)	7.01 (0.34)	7.47 (0.34)	6.82 (0.44)	6.95 (0.16)
4 m	9.68* (0.39)	6.40 (0.20)	7.32* (0.60)	6.60* (0.20)	7.50* (0.33)	6.37 (0.32)	6.24 (0.27)	6.33 (0.19)	7.08 (0.18)
6 m	7.84* (0.62)	7.01 (0.36)	7.92* (0.45)	6.97* (0.26)	NT	7.01 (0.34)	NT	6.80 (0.31)	7.10 (0.20)
9 m	8.51* (0.79)	7.72* (0.35)	5.92 (0.16)	6.40* (0.63)	NT	6.11 (0.37)	NT	5.72 (0.32)	6.73 (0.24)
12 m	5.26 (0.52)	6.05 (0.57)	5.96 (0.20)	5.99 (0.21)	NT	6.04 (0.23)	NT	5.87 (0.22)	5.89 (0.17)
Mean	6.99 (0.27)	5.88 (0.22)	6.48 (0.16)	6.00 (0.15)	7.16 (0.19)	7.00 (0.20)	6.37 (0.15)	6.24 (0.14)	6.46 (0.07)

component accounted for 77% of the variance and was dominated by "wigwag" displays, but most behaviours loaded positively on this component (Table 13). The second component, which accounted for 15% of the total variance, was dominated by "lateral display", but, "nip" also loaded highly (Table 13). All subsequent components accounted for less than 5% of the total variance.

Analysis of variance of mean PC1 scores suggested that over all ages combined, the Slim Creek, stream-type juveniles and the 1st Lake Nanaimo (ocean-type) chinook, which reside in freshwater for about 2 months before seaward migration, were significantly more aggressive than the lower Nanaimo ocean-type juveniles which emigrate to the estuary soon after emergence (population $P < 0.0001$, $df=2,24$, Fig. 8a). Slim Creek salmon were the most aggressive salmon ($P < 0.05$) over all ages combined. Juvenile chinook from all three populations were most aggressive at emergence, 1, and 2 months with significant declines at older ages (age $P < 0.0001$, $df=4,24$, Fig. 8a).

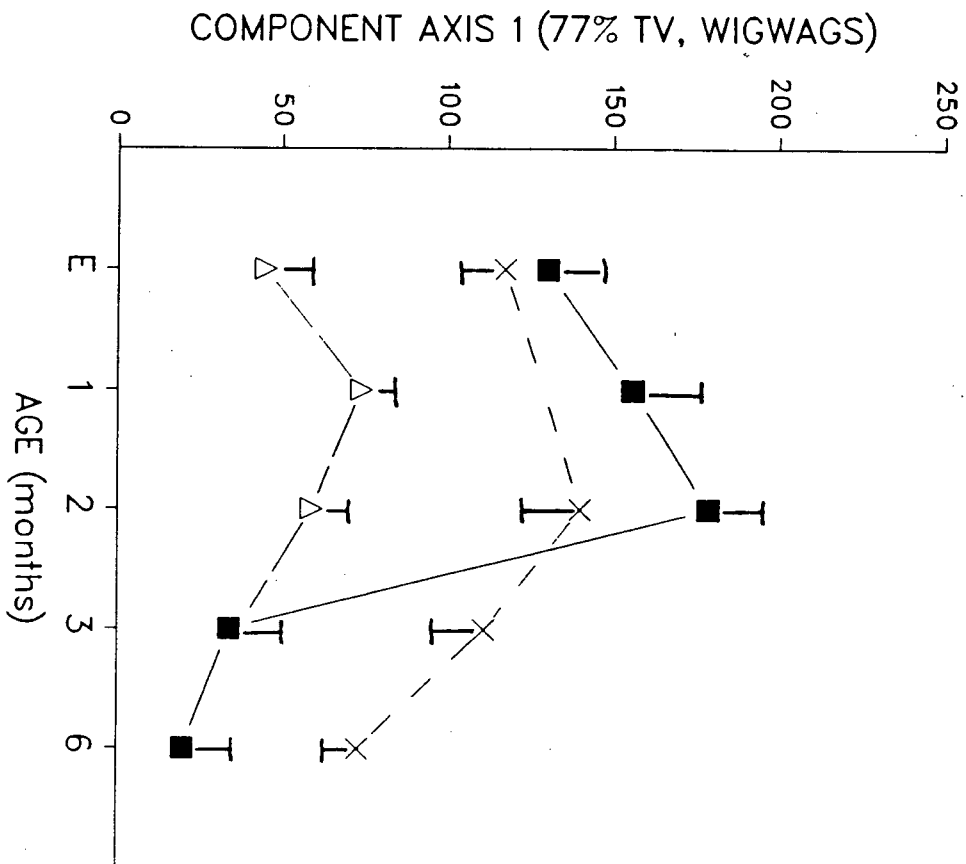
Changes in aggressive behaviour with time also differed significantly among the three populations (population \times age $P < 0.001$, $df=5,24$). Aggressive behaviour intensity increased relatively steeply in the 1st Lake Nanaimo juveniles with a peak at 2 months followed by a sharp decline at 3 months ($P < 0.05$) and a further decline at 6 months (Fig. 8a). The earliest smolting lower Nanaimo fish, however, had a more gradual rise in aggressive behaviour with a peak at 1 month followed by declines

Table 13. Behaviour coefficients from principal components analysis of stream tank behavioural interactions among juvenile chinook salmon.

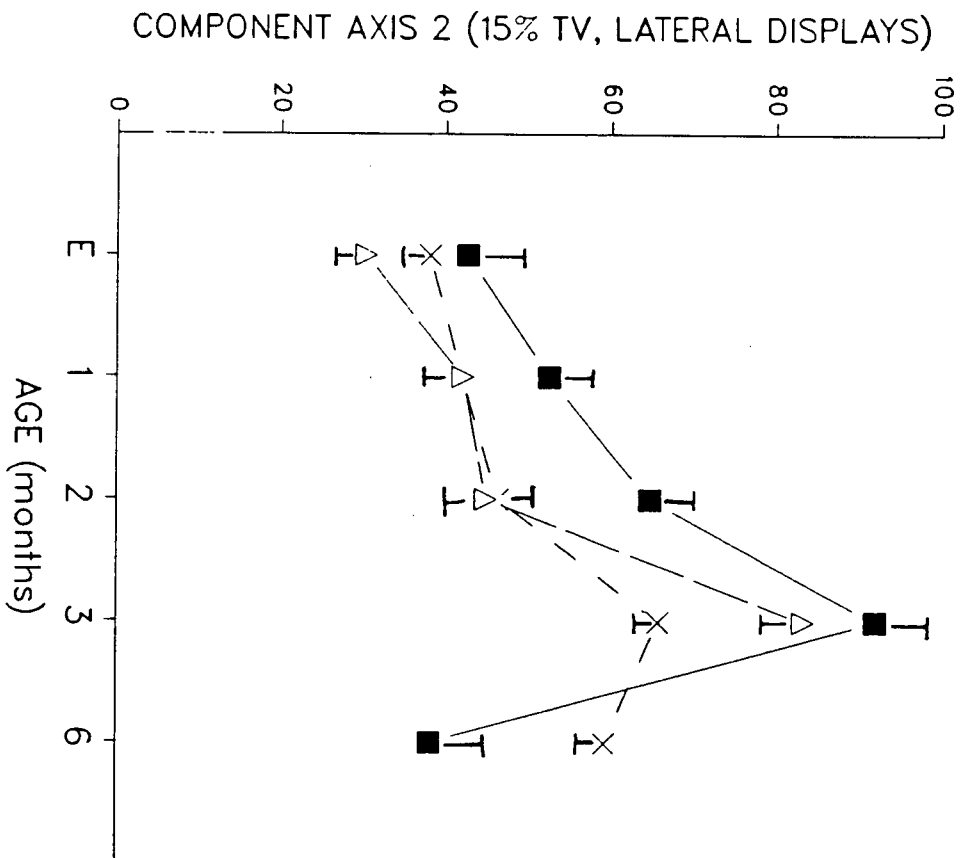
Behaviour	Coefficient from PCA	
	Component 1	Component 2
Approach	0.075	0.247
Lateral display	-0.056	0.859
Wigwag	0.985	-0.034
Charge	0.089	0.250
Nip	0.109	0.369
Chase	0.021	0.043
Cumulative % total variance	77.2	92.3

Figure 8. Mean (\pm SE) aggression scores for juvenile chinook salmon for Nanaimo River and Slim Creek populations at several ages. 8a=principal component axis 1, 8b=principal component axis 2. N=3 groups of 10 fry per population at each age. 1st Lake Nanaimo (■), lower Nanaimo (Δ), Slim Creek (x).

8a



8b



at 2 and 3 months. No data were collected from the Slim Creek fish at 1 month, but these fish were less extreme in their changes in aggressive behaviour with time and maintained significantly higher levels of aggression at 3 and 6 months ($P < 0.05$, Fig. 8a) than the two populations of Nanaimo River, ocean-type salmon.

Along the second component axis, the 1st Lake Nanaimo chinook and the stream-type salmon from Slim Creek again were more aggressive than the lower Nanaimo fish at emergence, but at 1, 2, and 3 months 1st Lake salmon were most aggressive (Fig. 8b, population $P < 0.01$). As was the case for aggressive behaviour along PC 1, chinook from all three populations increased in aggressiveness from emergence to 3 months (age $P < 0.0001$) but with a distinct decline by 6 months ($P < 0.05$). Slim Creek juveniles again were the least extreme in their changes in aggressiveness with time. Aggressive behaviour in these stream-type fish declined less dramatically between 3 and 6 months ($P > 0.05$) and they were more aggressive than the 1st Lake Nanaimo River chinook by 6 months (population \times age $P < 0.001$).

C. Variation in growth rate

Specific growth rate (SGR) declined with increasing age of juvenile salmon (Fig. 9). No significant difference was apparent in the slopes for stream- and ocean-type regressions

(Table 14, $P > 0.1$) and the pooled regression slope was significantly less than zero ($P < 0.0001$). There were no significant differences among populations within life history type in adjusted SGR ($P > 0.1$). Ocean-type chinook, however, grew at a greater rate than did stream-type fish ($P < 0.01$, Table 14).

Figure 9. Specific growth rate for stream- and ocean-type chinook salmon from emergence to 12 months of age. Each point is the calculated SGR for a single population at each age.

GROWTH RATE: LAB-REARED CHINOOK

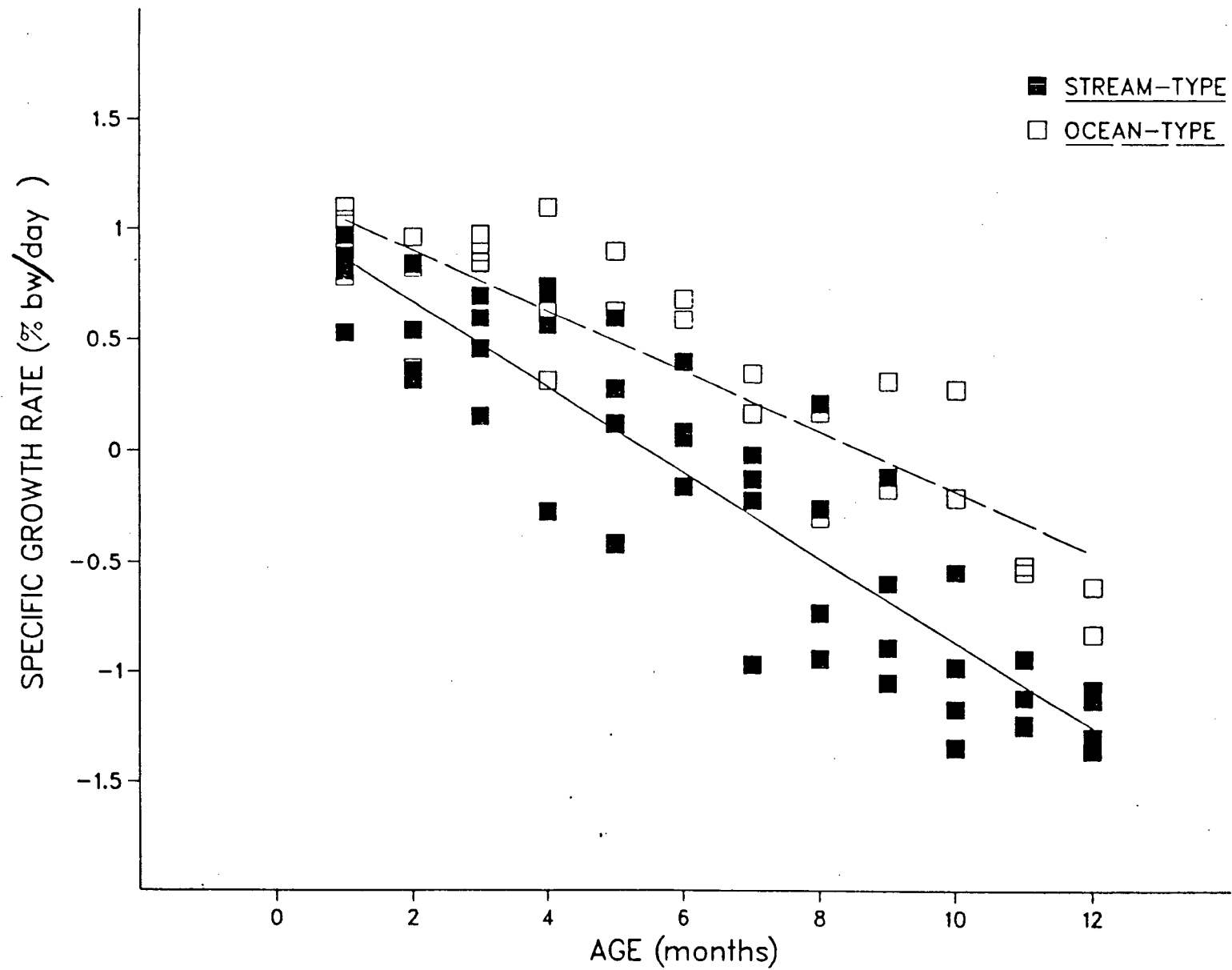


Table 14. Covariance analysis summary of specific growth rate data for stream- and ocean-type chinook salmon. Means (SE) are values adjusted to 6 months of age. For all populations N=12 except for L. Qualicum River and Nanaimo lower where N=4.

Population	Adjusted specific growth rate (% bw/day)
Stream-type	
Bowron River	1.12 (0.12)
Slim Creek	1.03 (0.13)
Eagle River	0.83 (0.14)
Salmon River	1.04 (0.13)
Mean	1.01 (0.06)
Ocean-type	
L. Qualicum River	1.45 (0.21)
Nanaimo lower	1.26 (0.21)
Nanaimo 1st Lake	1.56 (0.12)
Harrison River	1.26 (0.24)
Mean	1.40 (0.07)
Covariance summary by life-history type:	
Equality of slopes within: $P > 0.05$, $df=6,63$	
Equality of slopes between: $P > 0.05$, $df=1,63$	
Equality of adjusted means within: $P > 0.10$, $df=6,63$	
Equality of adjusted means between: $P < 0.01$, $df=1,6$	
Pooled slope (SE): $-0.17 (0.01)$, $P < 0.0001$, $r^2 = 0.61$	

3. VARIATION IN AGGRESSIVE BEHAVIOUR AND SALINITY TOLERANCE AMONG FAMILIES OF JUVENILE CHINOOK SALMON

Methods

To assess further phenotypic variation between 1st Lake Nanaimo and lower Nanaimo River chinook salmon, which differ in their duration of freshwater residence, I studied behaviour and physiology of the progeny of individual family crosses maintained separately under identical environmental conditions. By making crosses with parents of known freshwater life history I hoped to: (1) obtain a better understanding of how closely linked phenotypic variation in behaviour and physiology are with life history variation, and (2) compare variation among families within populations with variation between populations.

Experimental crosses

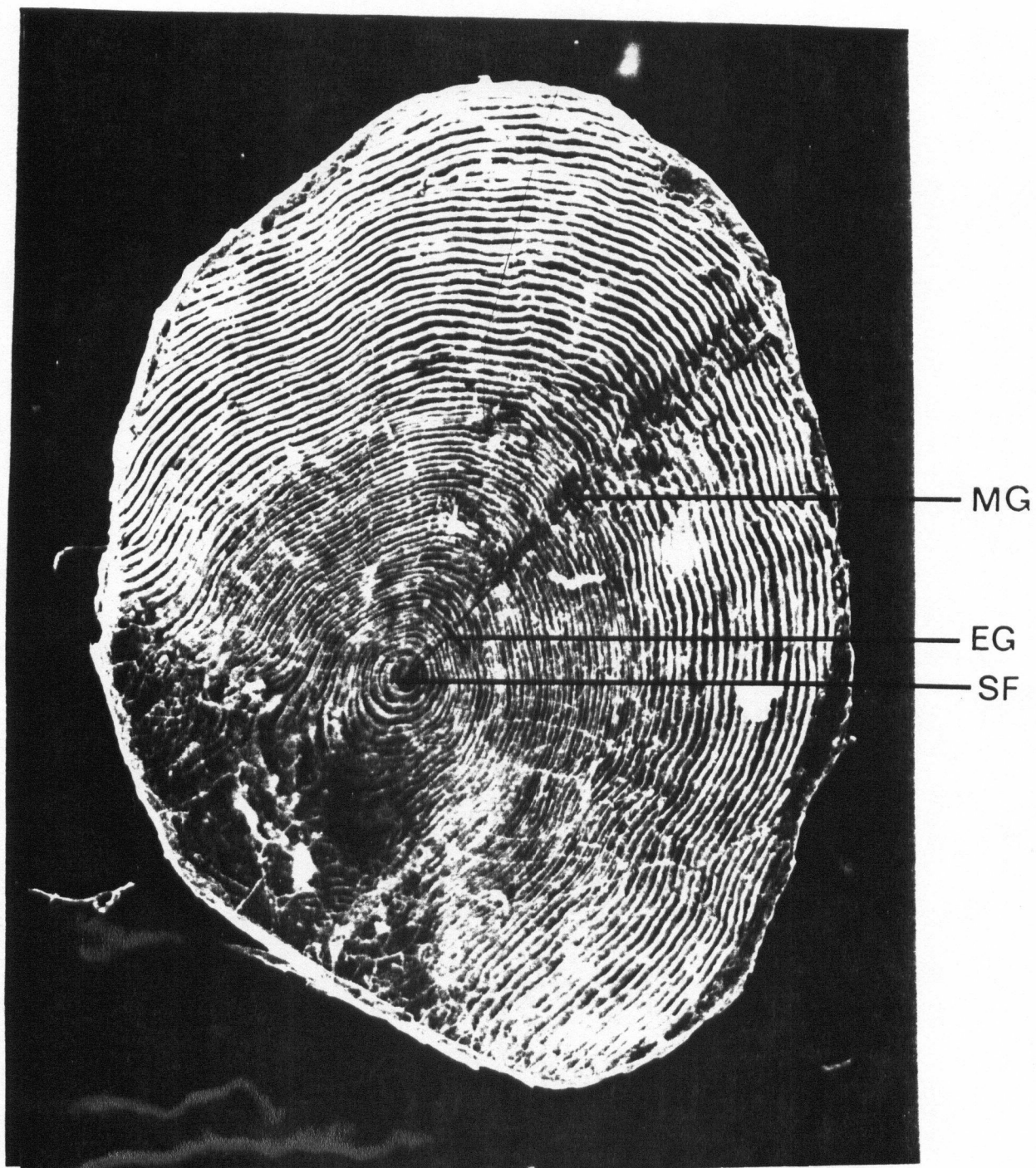
Juveniles were progeny from single male X female crosses made from the "lower" (migrate to estuary as fry) and "1st Lake" (migrate to estuary at 2-3 months) spawning populations of the Nanaimo River (Fig 6). Mature adults were collected at the outlet of 1st Lake or in the lower spawning area by staff from the Nanaimo River Community Salmon Hatchery during October 1987. Eight full-sib family matings were completed; 3 families from 1st Lake population and 5 from the lower Nanaimo. Zygotes (about 500-700 per cross) were disinfected with Ovadine and then

placed, by family, in adjacent sections of a single incubation tray ($11-12^{\circ}\text{C}$) at the Nanaimo Hatchery until the "eyed" stage (about 1 month). At the eyed stage the embryos were transported to UBC to complete incubation at 6°C .

The freshwater life history of the parents in the crosses was assessed from 5 scales sampled from both sides of each parent. Scales were removed from an area between the posterior margin of the dorsal fin and the lateral line and standard length was determined for each parent. Scale impressions were made following the methodology of Clutter and Whitesel (1956). Photographic prints were made of each scale impression at 34X magnification under a 3M microfiche reader-printer. Freshwater circuli counts were made from the projected scale impressions (100X) with the assistance of a technician from the Department of Fisheries and Oceans Scale Morphology Laboratory (555 West Hastings Street, Vancouver, BC). Freshwater circuli were identified as the relatively thin, tightly-spaced circuli near the scale focus (Fig. 10). Estuarine and/or ocean circuli were identified by looking for an abrupt increase in the width and/or spacing of circuli (Fig. 10). A measure of duration of freshwater residence of the parents was obtained by counting the number of tightly-spaced, thin freshwater circuli; fish with more freshwater circuli were assumed to have spent more time in freshwater.

In addition to the Nanaimo River crosses, progeny resulting

Figure 10. Photomicrograph of adult chinook salmon scale illustrating key features used to determine juvenile life history pattern. SF=scale focus from where freshwater circuli begin, EG=beginning of estuarine growth, MG=beginning of marine growth.



from matings of 15 female and 10 male Squamish River (Fig. 1) chinook salmon were obtained in late September 1987. The zygotes from these crosses were mixed and incubated at 11°C for 1 month at the Squamish River Hatchery and then transported to UBC to complete incubation at 6°C . Squamish River chinook are a coastal spawning population which are predominately stream-type (unpubl. data, Chapter 2). Upon emergence, each of the eight families of Nanaimo chinook and fry from the Squamish River (hereafter referred to as the experimental groups) were assigned randomly to one of nine, 94 L rearing troughs, where they were maintained under conditions of water flow, water temperature, diet, and a natural photoperiod regime as described earlier (1.1). Size-at-emergence (standard length, fork length, and wet weight) were determined for each experimental group and growth was monitored at monthly intervals as described previously (1.1).

A. Variation in aggressive behaviour

Studies of aggressive behaviour of juvenile chinook from the nine experimental groups took place in three stream tanks. Each stream tank (1.4 X 0.9 X 0.30 m) was divided into two parallel stream channels (1.0 X 0.35 X 0.30 m) which were separated from each other by a central compartment (1.0 X 0.25 X 0.30 m). One side of each stream channel was formed by 0.5 cm thick Plexiglass for viewing. Each stream channel was isolated from the surrounding area by stainless steel wire mesh barriers

(0.30 cm mesh at emergence and 1 month, 0.65 cm mesh at 2 and 3 months of age) at the upstream and downstream ends. Environmental conditions within each stream channel (n=6, 2 channels for each of the three stream tanks) were as described earlier; gravel and stone substrate, 10^o C, natural photoperiod with 0.5 h "dawn" and "dusk" periods daily). The observer was visually isolated from each stream channel by black plastic sheeting with observation holes.

To encompass the various ages-at-migration for Nanaimo River chinook, salmon behaviour was observed at emergence and at 1, 2, and 3 months of age. At each age, I obtained two or three samples of ten juveniles from each experimental group and assigned them randomly to a separate stream channel 48 h before the start of observations. For 5 min, twice daily for 5 consecutive days, I recorded the frequency and duration of "null", "approach", "nip", "charge", and "display" behaviours (both "lateral" and "wigwag" displays, see Table 1 for definitions) as well as two non-aggressive behaviours: "forage" and "yawn". "Forage" was defined as any swimming movement covering at least 2 bodylengths followed by attempted ingestion, and "yawn" consisted of an exaggerated opening of the mouth accompanied by pronounced gill flaring and terminated with rapid closing of the mouth.

Juveniles were fed through tubes located at the upstream ends of each stream channel after each observation period, and

at mid-day, at a rate of 5-6% bw/d. Live Artemia nauplii were fed to newly-emerged and 1 month old chinook, thereafter frozen Chironomus larvae were used as food.

B. Variation in salinity tolerance

Variation among experimental groups of juvenile chinook in ability to tolerate hypersaline water was investigated using "seawater challenge" tests (Clarke and Blackburn 1977, Blackburn and Clarke 1987). When freshwater acclimated fishes are placed in hypersaline water, osmotic stress occurs and is reflected in changes in blood chemistry (plasma sodium levels, osmolality), moisture content and survival, all of which are intercorrelated (Blackburn and Clarke 1987). Weight loss (dehydration) and mortality, due to hypersaline transfer, were recorded at 20‰ seawater, which is representative of the Nanaimo River estuary (Healey 1980) and at 30‰ which is representative of nearshore marine salinities and is the most common salinity used in seawater challenge tests. Filtered seawater from Burrard Inlet was standardized to 30‰ by addition of salt and 20‰ seawater was prepared by dilution with dechlorinated tap water. Salinities were determined with the aid of a hydrometer.

"Static" 24 h seawater challenge tests (Blackburn and Clarke 1987) were run in five, 75 L plastic garbage pails in a controlled environment chamber (10°C). For each test, three pails were randomly assigned as experimental (containing saline

water) and the other two as freshwater controls.

Tests were run on the progeny from each experimental group at emergence, and at 1, 2, and 3 months of age. Twenty-four h before a test, 50 fish were isolated and deprived of food for 24 h, then separated into five groups of 10, blotted on moist paper towel, and weighed individually to the nearest 0.001 g. Each group of 10 was then returned to freshwater to recover from handling. After 1 h, each group of fish was placed in one of the five pails and left for 24 h. Air bubblers in each pail provided aeration. After 24 h, the survivors in each pail were enumerated, collected, and individually weighed to the nearest 0.001 g and preserved in 10% buffered formalin. Subsequently, percentage weight loss for each group was adjusted by subtraction of the percentage weight loss of the freshwater controls.

C. Statistical analysis

Data on the aggressive behaviour of juvenile chinook were summarized into principal component scores for each observation. Subsequently, a mean PC score was calculated over all repeated measures (observation periods and observation days). The mean PC scores were analysed by factorial, nested analysis of variance; age and population were the main effects and family was nested within population. Data on percentage survival and weight loss in seawater were arcsine square-root transformed

prior to analysis and subjected to factorial, nested analysis of covariance with \ln standard length as the covariate. In all tests, homogeneity of variance tests were run using Bartlett's test and a posteriori means tests followed Tukey's procedure. Since the families of Squamish River salmon were not kept separate after fertilization, their data were not compared statistically with those data of Nanaimo River families.

Results

A. Adult freshwater rearing life history

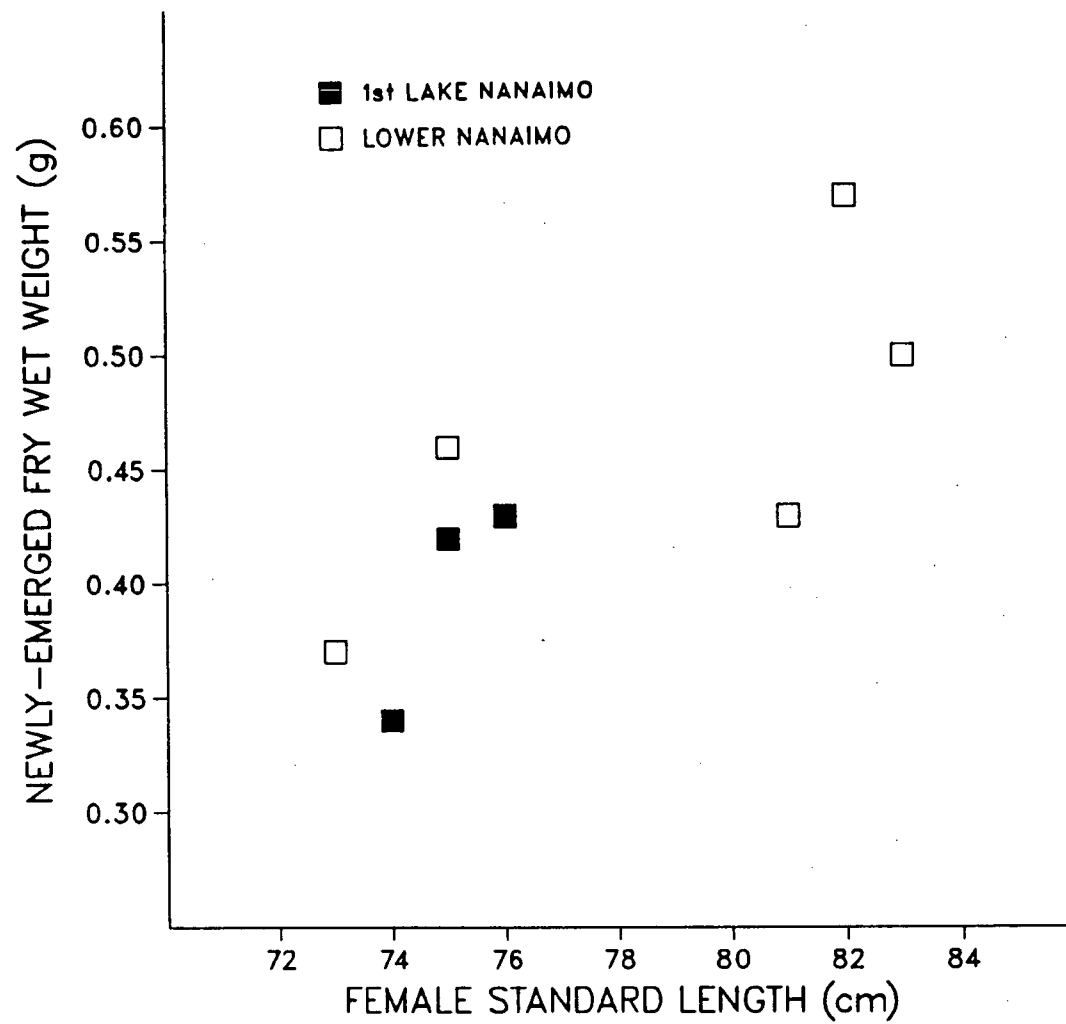
Duration of freshwater residence among the adult chinook used for experimental crosses (as inferred from freshwater circuli counts) ranged from 7 to 21 circuli (Table 15). First Lake family 3 had parents with the highest mean freshwater circuli count (17.5); the female had a freshwater annulus and 21 circuli, the male had 14 circuli. Lower Nanaimo family 5 had the fewest freshwater circuli (mean=7.5). Squamish River adults' freshwater circuli counts ranged between 10 and 21 (Table 15).

Adults, especially females, tended to be larger in the lower Nanaimo population and tended to produce larger fry at emergence (0.46 ± 0.07 vs 0.39 ± 0.05 g, $P > 0.05$, $df=1,6$), but interfamilial differences were more notable ($P < 0.0001$, $df=6,232$, Fig. 11).

Table 15. Parental standard length (cm), number of freshwater circuli (FWC) and mean (SE, N=30) wet weights (g) of newly emerged fry from the Nanaimo and Squamish rivers. Among families within the Nanaimo River populations, those mean fry weights not annotated by the same letter are significantly different (Tukey's $P < 0.05$).

Trait	1st Lake families			Lower Nanaimo families					Squamish River
	1	2	3	1	2	3	4	5	
Female SL	75	76	74	73	75	81	82	83	62-86
Male SL	62	77	70	72	80	84	83	63	54-86
Female FWC	12	10	21	10	9	8	7	8	12-20
Male FWC	8	8	14	10	10	11	9	7	10-21
Mean FWC	10	9	17.5	10	9.5	9.5	8	7.5	-
Fry weight	0.42a (0.02)	0.43a (0.03)	0.34b (0.03)	0.37a (0.03)	0.46b (0.03)	0.43c (0.03)	0.57d (0.02)	0.50e (0.03)	0.34 (0.03)

Figure 11. Relationship between female standard length and fry wet weight at emergence for Nanaimo River chinook salmon.



B. Variation in aggressive behaviour

Variation in behaviour among the nine experimental groups was summarized in 2 principal components (97% of the total variation, Table 16). Aggressive behaviours ("lateral display" PC1, "approach" PC2) dominated both axes while non-aggressive behaviours had consistently low loadings. Along the first principal component, 1st Lake juvenile chinook were strikingly more aggressive than chinook from the lower Nanaimo River population (Fig. 12a, $P=0.0002$, $df=1,6$). Marginally statistically significant differences were also evident among families within populations (Table 17, $P=0.04$, $df=6,45$). Age was also a significant factor ($P=0.05$, $df=3,18$); juvenile chinook from all groups reached maximal aggressiveness at 2 months with a significant decline at 3 months (Fig. 12a). No significant interactions were evident among the main factors ($P > 0.1$).

Stream-type chinook from the Squamish River had similarly high aggression scores to those of 1st Lake salmon along the first PC axis, but were more aggressive than chinook from both populations of the Nanaimo River by 3 months (Fig. 12a).

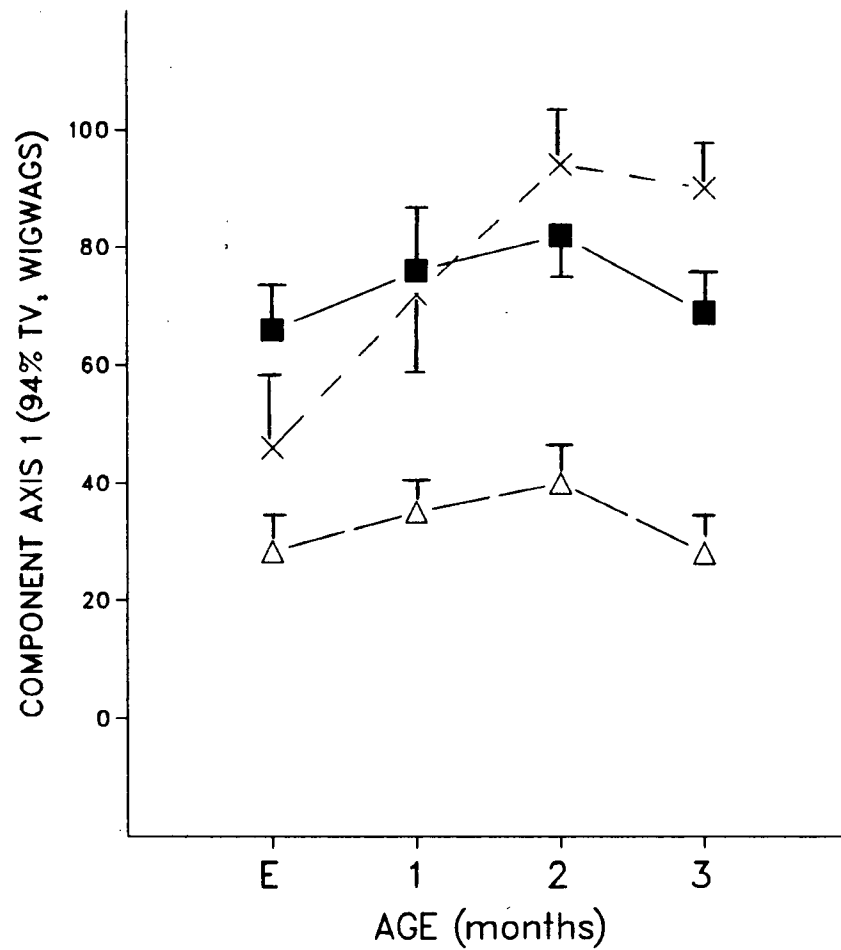
There was a significant difference between the Nanaimo River populations along the second component axis ("approach", Table 17, Fig. 12b, $P=0.05$, $df=1,6$); again the 1st Lake chinook

Table 16. Behaviour coefficients from principal components analysis of juvenile chinook salmon interaction.

Behaviour	Coefficient from PCA	
	Component 1	Component 2
Approach	0.065	0.867
Lateral display	0.987	-0.123
Charge	0.094	0.221
Nip	0.106	0.425
Forage	-0.001	0.004
Yawn	-0.002	0.055
Cumulative % total variance	94.1	97.3

Figure 12. Mean (\pm SE) aggression scores for juvenile chinook salmon from the Nanaimo River families and Squamish River over 3 months of age. 12a=principal component axis 1, 12b=principal component axis 2. For 1st Lake N=7, 6, 6, 7, for lower Nanaimo N=11, 12, 13, 15 and for Squamish N=2, 2, 2, and 3 at emergence, 1, 2 and 3 months of age respectively.

12a



12b

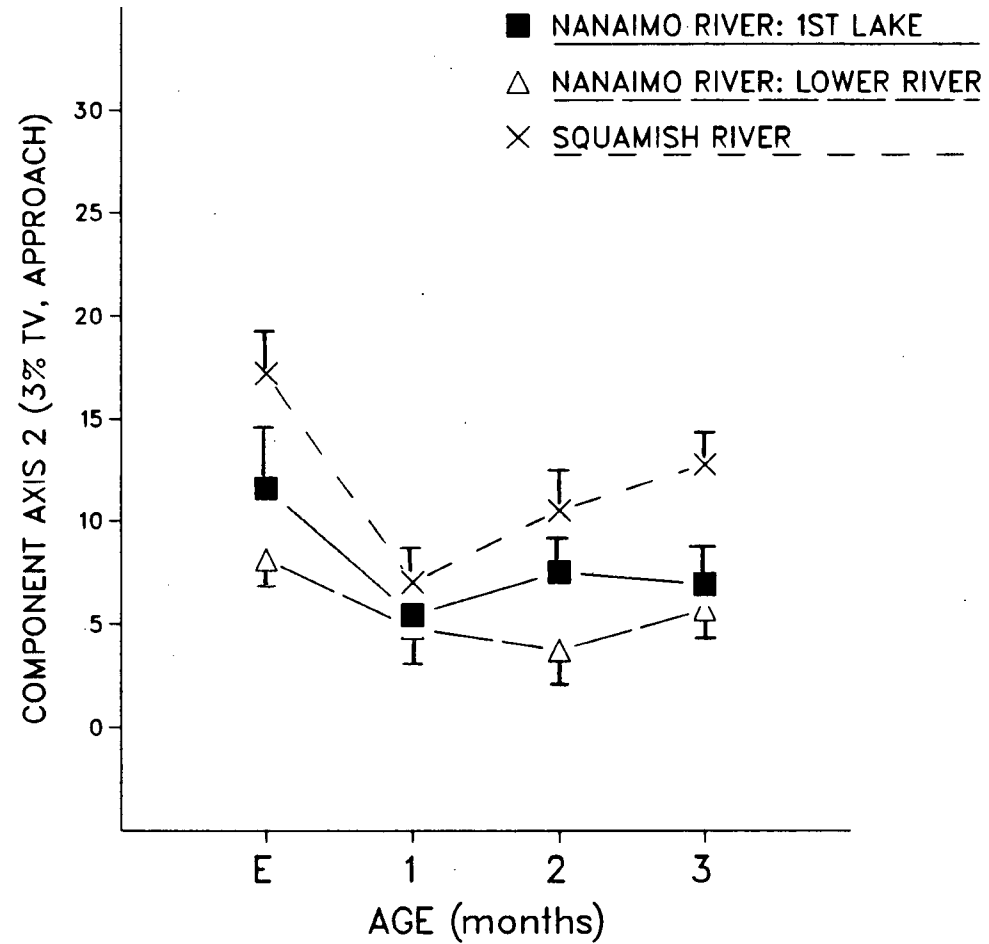


Table 17. Mean (\pm SE) aggression scores for juvenile chinook from the Nanaimo and Squamish rivers.

Experimental group	N	Component axis	
		PC1	PC2
1st Lake			
Family 1	9	73.5 (6.1)	10.3 (1.5)
Family 2	9	66.1 (4.7)	8.3 (0.5)
Family 3	9	78.9 (7.0)	5.4 (1.0)
Lower Nanaimo			
Family 1	12	30.3 (2.8)	5.6 (0.7)
Family 2	9	27.8 (3.0)	5.9 (0.9)
Family 3	11	42.5 (4.1)	5.4 (1.0)
Family 4	9	26.4 (2.7)	5.8 (0.8)
Family 5	10	36.2 (4.5)	4.9 (0.8)
Squamish River	9	77.7 (7.5)	12.1 (1.4)

were more aggressive than the lower river population. No differences in aggressive behaviour along the "approach" axis were found among families nested within population (Table 17, $P=0.1$, $df=6,45$). Along this second axis, juvenile chinook tended to be most aggressive at emergence while being less aggressive at 1, 2, and 3 months (Fig. 12b, age $P=0.006$). Both populations and all families within populations showed no significant differences in trends in aggression with time (all interactions $P > 0.1$).

Squamish River fry tended to have higher scores along the second component axis than the Nanaimo River populations (Fig. 12b).

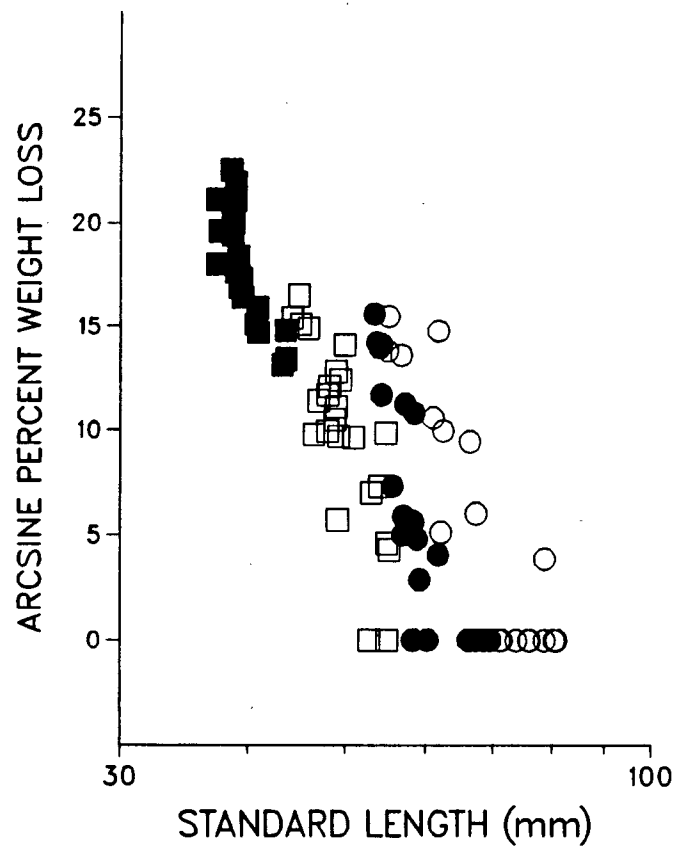
C. Variation in salinity tolerance

1. Effects of size on salinity tolerance

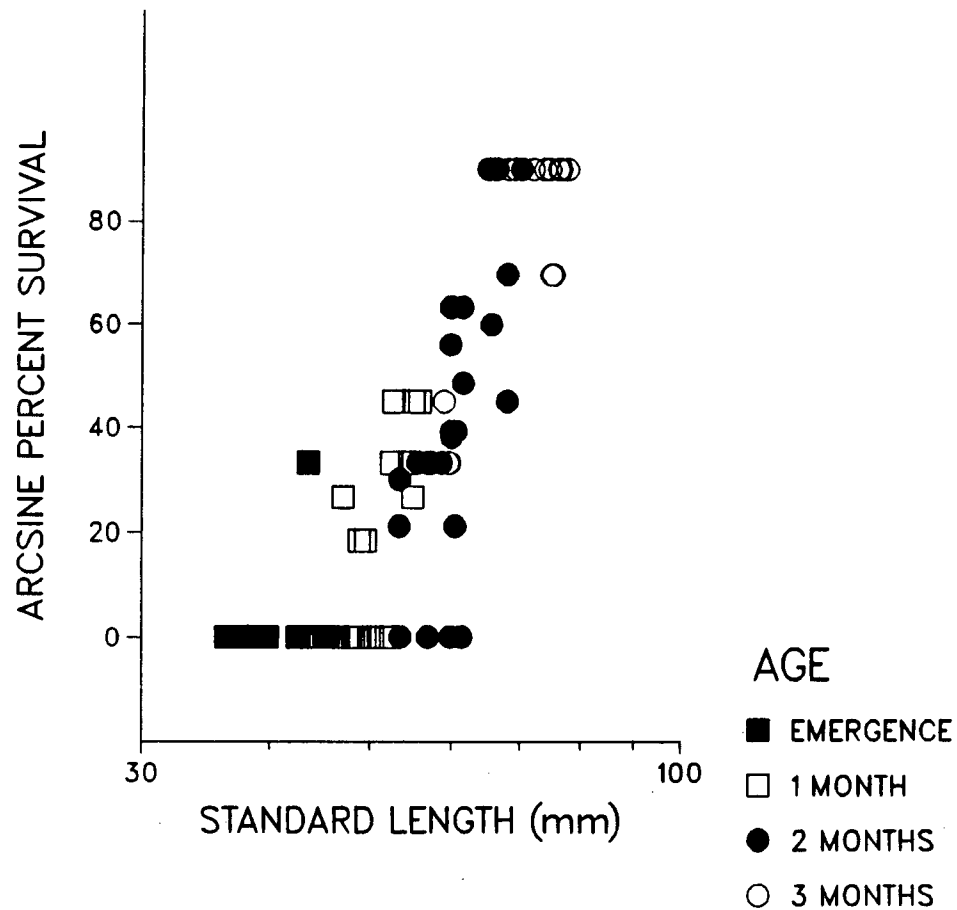
At emergence, most juvenile chinook survived 24 h exposure to 20‰ seawater; only three families experienced mortality: 1st Lake families 2 and 3 (30 and 37%), and lower Nanaimo family 1 (17%). At older ages there was no mortality in any experimental group in 20‰ seawater. At emergence and until testing at 3 months, percentage weight loss after 24 h in 20‰ seawater was strongly size-dependent in the juvenile salmon (Fig. 13a); smaller juveniles, both within and between families, lost proportionally more weight. Survival after 24 h exposure to

Figure 13. Relationship between body size and measures of salinity tolerance in juvenile chinook salmon over 3 months of age. 13a = weight loss in 20‰ seawater as a function of fish size, 13b = percentage survival in 30‰ seawater as a function of fish size.

13a



13b



30‰ seawater was much lower than for 20‰ and was also size-dependent (Fig. 13b); again, larger fish were better able to survive. There was no survival in eight of nine groups of salmon when exposed to 30‰ seawater at emergence, but survival was substantial in some families at 1 month and reached 100% in lower Nanaimo families 4 and 5 at 2 months (Fig. 14). While linear models explained variation in weight loss ($r^2=0.80$) and survival ($r^2=0.73$) in terms of size variation, there is some suggestion that both measures of salinity tolerance increased abruptly at 55-65 mm (SL) or 2.0-3.5 g. (Fig. 13a,b, cf. Clarke and Shelbourn 1985).

2. Variation in weight loss and survival

From emergence to 3 months, the smaller 1st Lake chinook lost a greater percentage of their weight when exposed to 20‰ seawater than chinook from the lower Nanaimo population (4.5% vs 1.8%). When adjusted to a common standard length (53 mm), fish from both populations lost a similar percentage of weight (1st Lake: 3.2% vs lower Nanaimo: 2.3%, $P=0.3$, $df=1,6$). Significant variation, however, was apparent among families within populations at a common size ($P=0.0002$, $df=6,49$, Table 18). All chinook lost less weight with increasing age (and increasing size, Fig. 14), but interpretation of age variation in weight loss independent of differences in standard length was compromised by heterogeneity among age group variances and weight loss on SL regression slopes (both $P < 0.01$).

Figure 14. Changes in percentage survival after exposure to 30% seawater with time in Nanaimo and Squamish rivers chinook over their first 3 months of age. Each point is the mean of 3 groups of 10 fish per group at each age.

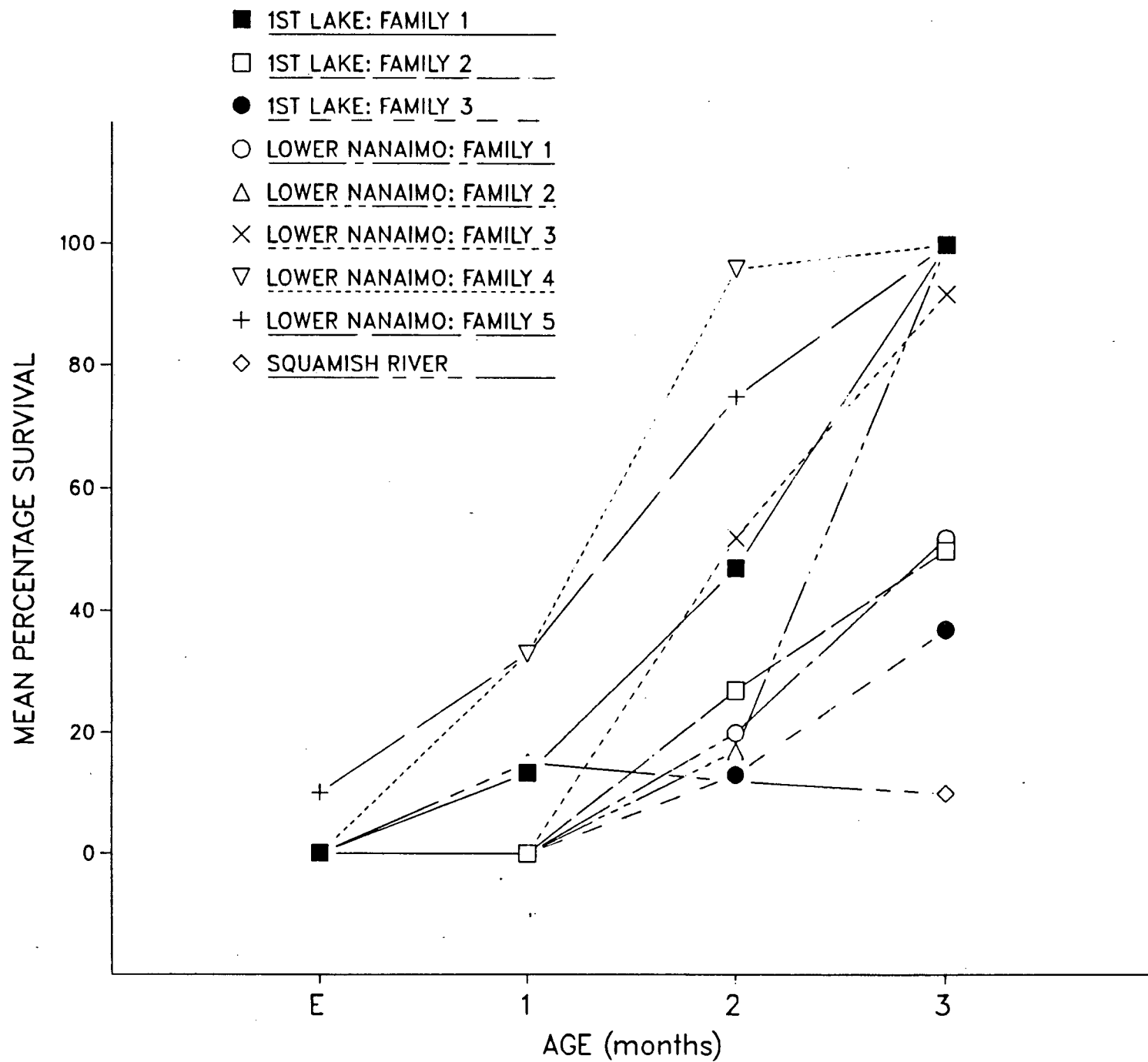


Table 18. Percentage weight loss after 24 h in 20‰ seawater for juvenile chinook salmon. Values (mean±SE) are averaged over 3 months and are adjusted to an overall size of 53 mm SL. For comparison among families within populations.

Experimental group	N	Percentage weight loss
1st Lake		
Family 1	12	1.95 (0.72)
Family 2	12	3.55 (0.75)
Family 3	12	4.10 (0.84)
Lower Nanaimo		
Family 1	12	3.15 (1.09)
Family 2	12	1.31 (0.63)
Family 3	12	1.98 (0.63)
Family 4	12	2.20 (0.98)
Family 5	12	3.85 (1.18)
Squamish River	12	5.50 (0.89)

Over the 3 month test period, lower Nanaimo chinook had a higher mean survival rate after 24 h exposure to 30‰ seawater ($34.2 \pm 1.5\%$ vs $13.2 \pm 1.9\%$), but after adjustment to a common standard length (54 mm) survival rates were similar between the two populations of Nanaimo chinook (both 25-26%). There was, however, significant variation among families within populations ($P = 0.0001$, $df=6,49$, Table 19) after adjustment for size differences. Within the 1st Lake population, family 3 had the lowest overall survival while family 1 had the highest (and third highest survival among all eight families). Among the lower Nanaimo families family 4 had the highest survival while family 1 had the lowest. Survival increased with increasing age, but heterogeneous error variances among the age classes compromised statistical analysis. Where variances were similar, however, (i.e. emergence and 3 months) size-independent survival was much higher at the older age. Both populations and all families within populations increased survival in 30‰ seawater with increasing age in similar fashion (all interactions $P > 0.3$, Fig. 14).

Salmon from the Squamish River (stream-type) performed poorly in saline water relative to both populations of Nanaimo River ocean-type chinook (Tables 18-19, Fig. 14). Over the 3 month test period, Squamish River chinook averaged about 5.5% weight loss in 20‰ seawater and 13% survival in 30‰ seawater compared to averages of 2.0-3.0% and 25% both for 1st Lake and

Table 19. Percentage survival after 24 h in 30‰ seawater for juvenile chinook salmon. Values (mean±SE) are averaged over 3 months and are adjusted to an overall size of 54 mm SL.

Experimental group	N	Percentage survival
1st Lake		
Family 1	12	37.0 (3.22)
Family 2	12	26.0 (3.46)
Family 3	12	22.1 (5.11)
Lower Nanaimo		
Family 1	12	25.8 (5.14)
Family 2	12	30.0 (2.93)
Family 3	12	32.6 (2.96)
Family 4	12	43.7 (5.91)
Family 5	12	43.3 (4.66)
Squamish River	12	13.1 (4.58)

lower Nanaimo River chinook of the same size.

Percentage weight loss in 20‰ seawater and survival in 30‰, as two measures of salinity tolerance, were well correlated ($r=0.92$, $P < 0.01$, 7 df) among the experimental groups of salmon. Juveniles from groups that lost the most weight in 20‰ seawater experienced the highest mortality in 30‰ seawater.

D. Correlations among variables

Freshwater life history of the parents of the Nanaimo River families and the Squamish River tended to be related to the behavioural and physiological performance measures of their progeny (Table 20). Freshwater circuli counts of both male and female parents were positively correlated with mean aggression score of their progeny, at least until 3 months, with correlations involving the female parent circuli count usually higher (Table 20). Similarly, the longer both male and female parents spent in freshwater as juveniles (increasing freshwater circuli number) the greater the weight loss in 20‰ seawater and the lower the survival in 30‰ of their progeny (Table 20). In sum, parents with prolonged freshwater residence tended to produce young with high aggression levels and poor salinity tolerance up to 3 months. These relationships, however, were strongly influenced by the data for 1st Lake family 3 and Squamish River, both of which had at least one stream-type

Table 20. Correlations between parental freshwater life history, from scale circulus counts, and progeny aggression and salinity tolerance. * $P < 0.05$, ** $P < 0.01$, $df = 7$.

	Female FWC	Male FWC	Mean PC1 Score	Mean % Weight loss
Male FWC	0.82**	-		
Mean PC1 Score	0.81**	0.50	-	
Mean % weight loss	0.73*	0.64	0.60	-
Mean % survival	-0.78*	-0.76*	-0.55	-0.92*

parent (Fig. 15).

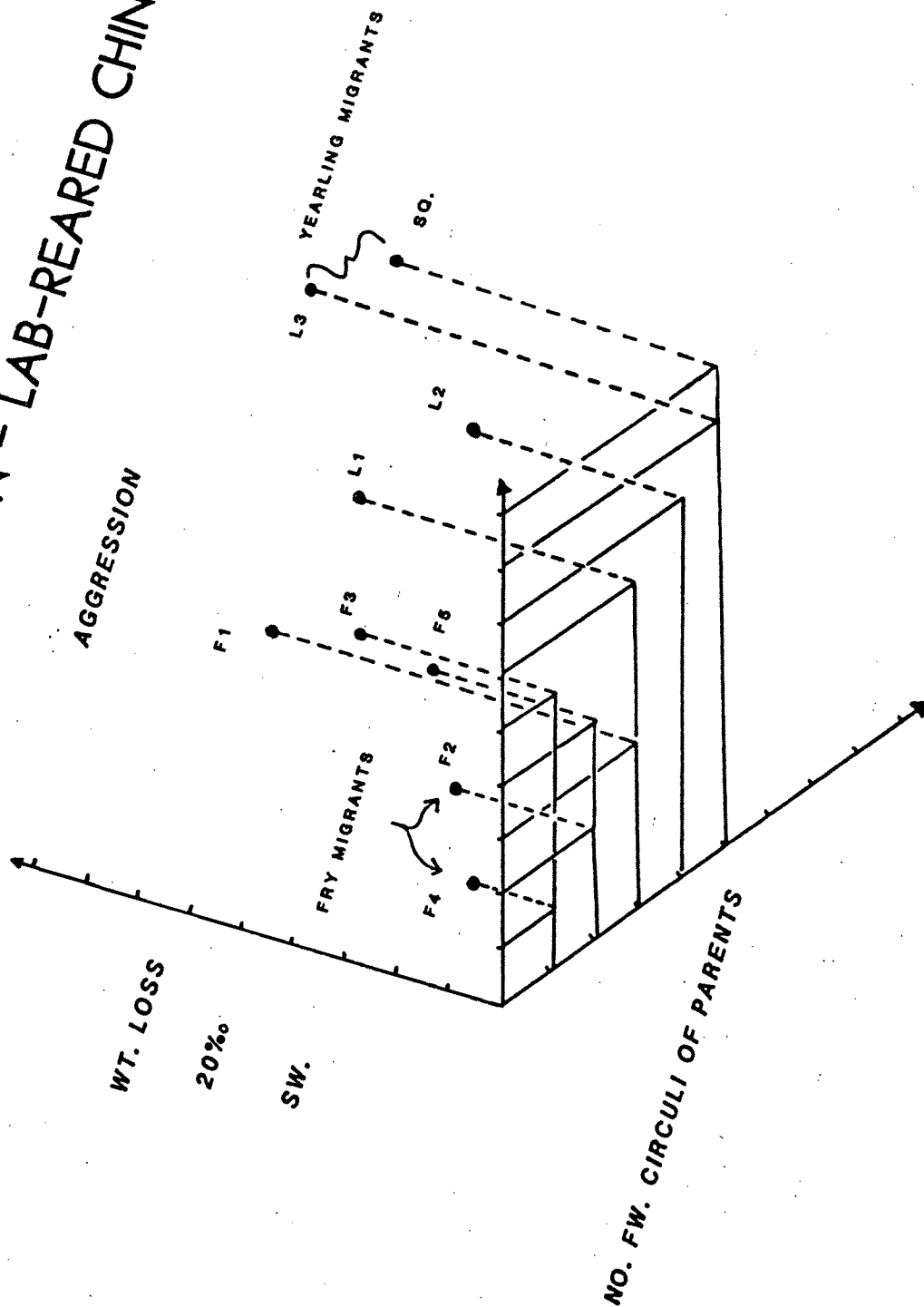
Discussion

Rheotactic behaviour

Considerable variation in response to water current (rheotaxis) by juvenile chinook salmon is evident from my experiments. Not only did populations vary in rheotaxis, but juveniles showed significant changes in rheotaxis with increasing age. At least a portion of this variability among experimental groups appears to be related to differences in juvenile freshwater life history. Differences in rheotaxis between wild-reared, newly-emerged chinook fry from Slim Creek and the Harrison River were consistent with reported differences in juvenile migration timing. Slim Creek chinook summer and overwinter in freshwater before seaward migration as yearlings and they showed less pronounced downstream movement than Harrison River fry. By contrast, greater nocturnal downstream movement of Harrison River chinook fry in the laboratory channels is consistent with their movement downstream to the Fraser River estuary when newly-emerged (Fraser et al. 1982; Levy and Northcote 1982). Very similar results were obtained when newly-emerged fry were incubated in the laboratory under identical conditions and tested in the rheotaxis apparatus. The maintenance of these phenotypic differences in fry incubated in identical environments suggests that this variation is, at least

Figure 15. Trivariate plot of the relative ranks of mean parental freshwater circuli count and the ranks of aggressive behaviour and salinity tolerance of their progeny. Aggression scores and percentage weight loss are averaged over 3 months of age for each group. F1 through F5 are lower Nanaimo families, L1 through L3 are 1st Lake families, SQ is Squamish River.

AMONG FAMILY VARIATION - LAB-REARED CHINOOK



in part, genetically controlled.

The inclusion of data from laboratory-incubated fry from Eagle and Nanaimo rivers did not support the hypothesis that freshwater life history acts to promote divergence in rheotaxis. For instance, Carl and Healey (1984) suggested that lower Nanaimo River chinook fry migrate to the estuary soon after emergence, but Nanaimo River fry exhibited rheotactic behaviour similar to stream-type fry. The explanation may lie in local conditions unrelated to and more influential than the duration of freshwater residence. For instance, the Nanaimo River estuary is within 5 km of the lower spawning area. To reach the estuary soon after emergence, chinook fry from the lower Nanaimo river population probably do not require as strong a downstream response as those from other ocean-type populations with longer migration distances. For instance, Harrison River fry must migrate about 100 km to the Fraser River estuary. For Nanaimo River fry a more gradual downstream drift, similar to the behaviour of Slim Creek and Eagle River fry, would accomplish migration in a short time.

Hoar (1976) reported that newly-emerged chinook fry require some acclimation time for survival at salinities above 15‰. Since salinities in the Nanaimo River estuary are commonly above 20‰ (Healey 1980) a more gradual movement into the estuary by Nanaimo fry may be necessary to prevent osmoregulatory shock. Healey (1980) also reported that mean weights of chinook fry

entering the Nanaimo estuary were about 0.57 g. The laboratory-incubated, newly-emerged salmon used in my tests were about 20% lighter (0.30-0.53 g) and Nanaimo River chinook lost up to 15% body weight when exposed to 20‰ seawater (Fig. 13a). Thus, as a consequence of the different migration distances to their respective estuaries, ocean-type chinook from the Nanaimo and Harrison rivers appear to be genetically distinct in their manner of downstream migration as newly-emerged fry.

Alternatively, nocturnal downstream dispersal to freshwater rearing areas is commonly observed in newly emerged fry of various stream resident salmonids (e.g. Reimers 1973; Randall 1982; Elliot 1986; Naesje et al. 1986; Shepherd et al. 1986b). Consequently, current response tests may not have been able to distinguish between a gradual "drift migration" downstream at night by estuary bound Nanaimo River chinook fry and a gradual downstream "dispersal" following emergence by stream-type chinooks.

Whereas tests with newly-emerged fry yielded no clear distinction in rheotaxis based on juvenile life history, differences in rheotaxis were observed between stream- and ocean-type chinook when tested over a full year. Stream-type chinooks showed pronounced reduction in positive rheotaxis during nocturnal tests at 1 year, when, in nature, they smolt and migrate seaward (Carl and Healey 1984; Shepherd et al. 1986a,b). By contrast, laboratory-reared, ocean-type

chinook appeared to be sensitive to water current only during their first 2-3 months or about 2-5 g in weight when, in nature, they too would migrate to estuarine areas (Reimers 1973; Fraser et al. 1982; Carl and Healey 1984). The correspondence between their laboratory "migration" behaviour and their migration timing in the wild suggests that the inherited differences in rheotaxis are adaptive and a function of divergence between chinook populations in freshwater rearing life history (i.e. stream- vs ocean-type life histories).

Aggressive behaviour

Levels of aggressive behaviour were also closely related to freshwater life history in chinook salmon. Fish from populations or families that reside for extended periods in freshwater were more aggressive than those that abandon it at an early age. The relationship between life history pattern and aggressive behaviour was consistent among populations from different rivers, between populations within a single river, and among families within a population, although the latter differences were minor relative to interpopulation differences. The greater aggressiveness of stream-type chinook was apparent both in wild fish and those incubated and reared in a common laboratory environment. Therefore, the variation in behaviour is, in part, based upon genetic differences among populations. Even within a population, changes in aggressive behaviour with age correlate well with temporal shifts in rearing habitat

(Fig. 8a,b); the pronounced decline in aggressive behaviour in 1st Lake chinooks at 3 months (3.9 g) corresponds with their migration to the estuary at this time (3.5-4.1 g) and the shift to a more pelagic existence (Healey 1980; Healey and Jordan 1982; Carl and Healey 1984). By 3 months and at 6 months, the Slim Creek, stream-type juveniles were more aggressive than ocean-type fish from the Nanaimo River. In sum, aggressive behaviour correlates well with the differences in smoltification and migration timing among the groups of chinook salmon investigated. Earliest migrating juveniles were least aggressive and showed the earliest declines in aggressive behaviour whereas salmon that migrate later maintained the highest aggression levels.

Salmonids with extended residence in streams have well defined territories (Keenleyside 1979), which confer advantages in feeding efficiency (Allen 1969; Keenleyside 1979; Fausch 1984) and protection from predation (Allen 1969; Symons 1974). Territory formation and maintenance involve site fidelity and defence by expulsion of intruders with overt aggression, displays, or both (Keenleyside 1979). Aggressive behaviour must, therefore, be an important component of extended stream residence. By contrast, migrating fish often school, which probably involves greater social tolerance. I suggest, therefore, that the genetic differences in aggressive behaviour among chinook salmon populations results, in part, from selection acting through the functional associations among

duration of stream residence, territoriality, and aggression. Divergence between chinook salmon life history-types may result from high aggression being favoured in territorial, stream-type populations whereas low aggression is favoured in early migrating, ocean-type populations. Reimers (1968) noted that ocean-type chinook fry in the Sixes River (Oregon) estuary switched from aggregative, passive behaviour on flood tide to territorial, aggressive behaviour on ebb tide. Under more constant conditions of river flow, however, natural selection might favour high levels of aggressive behaviour in stream-type chinook.

The association between freshwater life history and aggressive behaviour in chinook salmon is supported by work on other fish. For instance, Ferguson and Noakes (1982, 1983a,b) demonstrated that brook charr (Salvelinus fontinalis), a territorial stream-dweller, is more aggressive than the lake charr (S. namaycusch), a more widely-roaming lacustrine species, and that these behavioural differences were inherited. Also, for threespine stickleback, Gasterosteus aculeatus, Bakker and Feuth-de Bruijn (1988) found that permanent residents of freshwater were more aggressive than their anadromous counterparts. More generally, aggressive behaviour often appears to be correlated with differences in life history in several taxa (e.g. mating system variation in birds (Wingfield et al. 1987), variation in intensity of interspecific competition in salamanders (Nishikawa 1985), and habitat

variation in fishes (Parzefall 1986)).

Morphology

With the exception of major parr mark number, morphological differences between wild chinook fry from the Harrison River and Slim Creek were maintained in the laboratory-reared fry; Slim fry had larger body parts and median fins and were more brightly coloured (Table 9). A significant environmental component to parr mark number is suggested since Slim and Harrison fry had similar counts when both were incubated and reared in the same laboratory environment. Incubation water temperature regime can alter parr mark counts in chinook fry; lower water temperatures produce higher counts (C.C. Lindsey and E.B. Taylor, unpubl. data). Therefore, water temperature differences in the incubation environments of the Harrison River and Slim Creek (colder) probably account for the greater differences in parr mark number in wild fry.

Despite the inherited differences in morphology between chinook fry from Slim Creek and the Harrison River, the inclusion of data for Eagle and Nanaimo chinooks did not support a general morphological distinction within chinook salmon based on juvenile life history pattern. Whereas Slim Creek fry had the largest body parts and median fins and were the most colourful fry, those from both ocean-type populations tended to have larger fins than Eagle River chinook fry. Furthermore,

Nanaimo River fry were as brightly coloured as were those from the Eagle River. Again, local population factors unrelated to duration of freshwater rearing may account for the morphological differences among the populations of newly-emerged chinook fry. Selection associated with migration distance, water flow levels, and predation have been associated with interpopulation differences in morphology and colouration in stream fishes (Liley and Seghers 1975; Endler 1980; Riddell and Leggett 1981; Taylor and McPhail 1985a,b).

Growth rate

In the laboratory, ocean-type chinook grew faster than stream-type. Withler et al. (1987) also detected significant genetic variation in growth rate among chinook salmon populations and in their study ocean-type salmon grew faster than chinook from stream-type populations.

Among anadromous salmonids, larger individuals regulate electrolytes better and have higher survival rates during seawater "challenge" tests (Parry 1960; Conte and Wagner 1965; Conte et al. 1966; McCormick and Naiman 1984b; Clarke and Shelbourn 1985), and smaller ones are more susceptible to predation in nearshore marine habitats (Parker 1971; Martin et al. 1981; Healey 1982; Hargreaves and Lebrasseur 1986). These observations suggest that, as underyearlings, the earlier migrating, ocean-type chinook salmon may be under strong

selection for fast growth which might explain their higher growth rates compared to stream-type fish.

Salinity tolerance

Once size variation among the experimental groups of chinook salmon was accounted for, significant interfamily variation was detected in both weight loss in 20‰ seawater and survival in 30‰ seawater. Juvenile chinook from the lower Nanaimo River spawning population ranked better than 1st Lake chinooks in terms of salinity tolerance, but variability among families within populations was greater such that no significant differences in salinity tolerance attributable to spawning population were detected. The low salinity tolerance of Squamish River chinook relative to Nanaimo river chinooks, however, suggests that differences between populations from different river systems may exist.

Variability in size-adjusted salinity tolerance was broadly related to juvenile life history pattern. Both stream-type juveniles from Squamish River and 1st Lake family 3 were salinity intolerant up until 3 months which is consistent with the extended freshwater residence of their parents (Table 15). By contrast, progeny from lower Nanaimo families 4 and 5 (whose parents had the shortest freshwater residence) performed best in seawater at emergence and increased their performance most

rapidly with age.

Size variation is suspected to be a primary factor influencing survival, reproductive success and, hence, fitness in fish populations (Schaffer and Elson 1975; Oliver et al. 1979; Reisenbichler et al. 1982; Healey and Heard 1984; Miller et al. 1988). In salmonids, larger females tend to produce larger eggs and larger newly-emerged fry (Brown 1946; Fowler 1972; Gall 1974; Beacham et al. 1985; Fig. 11), and the larger fry maintain their size advantage for variable time periods (Brown 1946; Fowler 1972; Gall 1974; Taylor unpubl.). Maternal effects (through female size/egg size and egg size/fry size relationships) probably influence size-dependent fry survival. Size at maturity in fish is known to be at least partially under genetic control (Ricker 1972; Allendorf et al. 1983; Stearns 1983). Therefore, biochemical adaptations for survival in high salinity water may be secondary to selection for large size-at-emergence in early downstream migrating fry. The larger size of lower Nanaimo females and of their newly-emerged fry (Healey and Jordan 1982; Fig. 11) may be adaptive responses to the closeness of the lower spawning area to the estuary. Whether driven largely by selection for fry size-at-emergence or by biochemical adaptations, the variability in seawater performance among the groups of chinook salmon is consistent with their differences in duration of freshwater residence and, hence, probably reflects adaptive diversification.

Interrelationships among variables

In salmonids, growth rate may influence timing of developmental processes such as smoltification (Thorpe 1986), perhaps through its relationship with hormones thought to synchronize components of smoltification (see reviews by Folmar and Dickhoff 1980; Dickhoff and Sullivan 1987; Hoar 1988). Increased growth rate, elevated thyroid or other hormone levels, decreased aggressive behaviour, and increased migratory restlessness occur concurrently during smoltification (Folmar and Dickhoff 1980; Dickhoff and Sullivan 1987; McCormick and Saunders 1987; Hoar 1988). In addition, McCormick and Naiman (1984a) reported a positive correlation between growth rate and plasma thyroxine levels in brook charr, Salvelinus fontinalis. Godin et al. (1974) demonstrated that juvenile Atlantic salmon injected with thyroxine showed reduced aggressiveness and increased downstream orientation.

The higher growth rates of ocean-type chinooks may be associated with elevated hormone levels during their first few months. Therefore, growth rate related differences in hormone dynamics may also contribute to differences in aggressive behaviour between life history types. Less aggressive, early migrating chinook from the lower Nanaimo River grew faster than the more aggressive, later migrating chinook from 1st Lake over the first 3 months in the laboratory. The abrupt decline in

aggressive behaviour between 2 and 3 months of age by the 1st Lake Nanaimo chinook juveniles was accompanied by an increase in specific growth rate.

The juvenile life history types investigated in this study differed genetically in rheotaxis, aggressive behaviour, and in growth rate. Ferguson and Noakes (1982, 1983a,b) demonstrated genetic differences in aggressive behaviour and mobility patterns between the highly aggressive and territorial brook charr and the less aggressive, more mobile lake charr. Based on these studies, Noakes (1986) suggested that, for Salvelinus, natural selection may have favored the inheritance of suites of characters; one set for a life history involving defence of fixed territories in stream environments (brook charr) and another set for a more free-ranging, pelagic lifestyle in lacustrine environments (lake charr).

Also, Eriksson and Lundqvist (1985) showed that seasonal changes in rheotaxis and salinity tolerance in yearling Atlantic salmon tended to coincide. During the normal period of seaward migration in the wild, salmon yearlings tended to swim downstream in a laboratory apparatus and showed annual peaks in tolerance to 20‰ seawater. As the seasonal peak in downstream migration in wild populations tailed off, laboratory-reared fish showed an increasing tendency to swim upstream and they became increasingly intolerant of seawater (Eriksson and Lundqvist 1985).

Natural selection operating on sets of traits with close functional relationships to increase the fitness of a phenotype (Gould and Lewontin 1979; Arnold 1983; Mayr 1983) has been suggested in studies on foraging behaviour and trophic morphology (Echelle and Kornfield 1984; Lavin and McPhail 1986, 1987), and reproductive characters (Stearns 1983; Healey 1987) in fishes. Differential expression of suites of behaviours is also characteristic of individual Atlantic salmon adopting alternative life histories (Metcalf et al. 1988; Metcalfe 1989; Metcalfe et al. 1989). Similar integration of juvenile phenotype probably occurs in chinook salmon where selection favours low aggressiveness, a weak seasonal rheotactic response, high growth rate, and high salinity tolerance in early migrating, ocean-type chinook while favoring high aggressiveness, a pronounced seasonal rheotactic response, slower growth rate, and delayed saltwater tolerance ability in stream-type chinooks.

CHAPTER 2: GEOGRAPHIC VARIATION IN, AND ENVIRONMENTAL CORRELATES OF, JUVENILE CHINOOK SALMON LIFE HISTORY

Introduction

The geographic distribution of species, and phenotypic differences among populations of species, have been important sources for inferences about evolutionary change and the process of speciation (Mayr 1963; Gould and Johnson 1972; Wright 1978). Geographic variation is one of the most fundamental biological observations for it prompts the observer to ask how such variability could have arisen or could be maintained. Attempts to answer such questions have laid the foundation for current concepts and understanding of evolutionary and ecological theory (Gould and Johnson 1972; Lewontin 1974; Endler 1977; Arthur 1982; Futuyma 1986). The study of geographic variation is also central to the study of adaptation as an evolutionary consequence of natural selection (e.g. Johnson and Selander 1971; Endler 1986; Etter 1988).

In salmonid fishes, the study of geographic variation has been extensive because of the wide array of environments in the geographic range of the various species and the tendency of adults to return to their natal streams to spawn. Studies of intraspecific geographic variation have focussed on a variety of traits including allozyme frequencies (Thorpe and Mitchell 1981; Wehrhahn and Powell 1986), mitochondrial DNA (Birt et al. 1986),

developmental rate (Beacham and Murray 1986), scale growth characters (Lear and Misra 1978), morphology and meristics (Cavender 1978; Svardson 1979; Claytor and MacCrimmon 1988), and life history traits (Schaffer and Elson 1975; Healey and Heard 1984; Myers 1986). A major goal of many such studies has been not just to describe the range of variability, but to explain the variation in the context of current evolutionary and life history theory (e.g. Aspinwall 1974; Schaffer and Elson 1975; Altukhov 1982; Healey and Heard 1984). While general appreciation of geographic variability in juvenile life histories, both between and within species, has a long history it is only recently that systematic studies have been initiated (Withler 1966; Power 1981; Randall et al. 1987; Metcalfe and Thorpe 1989).

In Chapter 1 of this thesis, the range of variability in freshwater life history of chinook salmon was introduced and evidence was presented that this variability represents intraspecific adaptive divergence. This chapter deals with two further aspects of variability in juvenile life history. First, it discusses variability in juvenile life history in context with the geographic distribution of chinook salmon. Second, it presents results of association analyses between variation in juvenile life history and abiotic environmental factors in an attempt to determine the causes of variation in juvenile phenotype. Biotic factors, primarily in the context of competitive interactions with other species, are the subject of

investigation in Chapter 3.

1. GEOGRAPHIC DISTRIBUTION OF CHINOOK SALMON AND VARIATION IN LIFE HISTORY

Methods

Data concerning geographic variation in juvenile chinook freshwater life history pattern were derived from three sources: (i) surveys of the literature, (ii) personal communications or unpublished data from Canadian and U.S. Government fisheries biologists, and (iii) for B.C. and Yukon populations, a survey of the scale data base at the Scale Morphology Lab.

During the surveys of the scale data, an effort was made to note potential biases in the mode of collection of scales. For instance, most scale samples were taken from adult salmon holding in pools before spawning, from adults enumerated at counting fences, or from adult carcasses sampled after spawning. Collection methodology could bias the sexual composition of samples with a potential influence on subsequent freshwater age distributions. However, this does not seem to have been a serious source of error. For example, Snyder (1931) examined the scales of male and female chinook salmon returning to spawn in the Klamath River, California, over four years between 1919 and 1930. Snyder's data indicate roughly equal proportions of stream- and ocean-type life histories between the sexes (approximately 13 and 11% stream-type respectively). Clark's (1929) data for Sacramento River chinook salmon were similar

with perhaps a slightly greater proportion of stream-type life histories in females (12 vs 8%). A similar trend was evident for Monterey Bay fishery samples; males=17.3% stream-type, females=19.3% stream-type (Clark 1929). Scale samples from male and female chinook salmon spawning in tributaries of the Fraser River, and in streams in south coastal B.C., also suggest no major bias in freshwater life history between the sexes (Shepherd et al. 1986b).

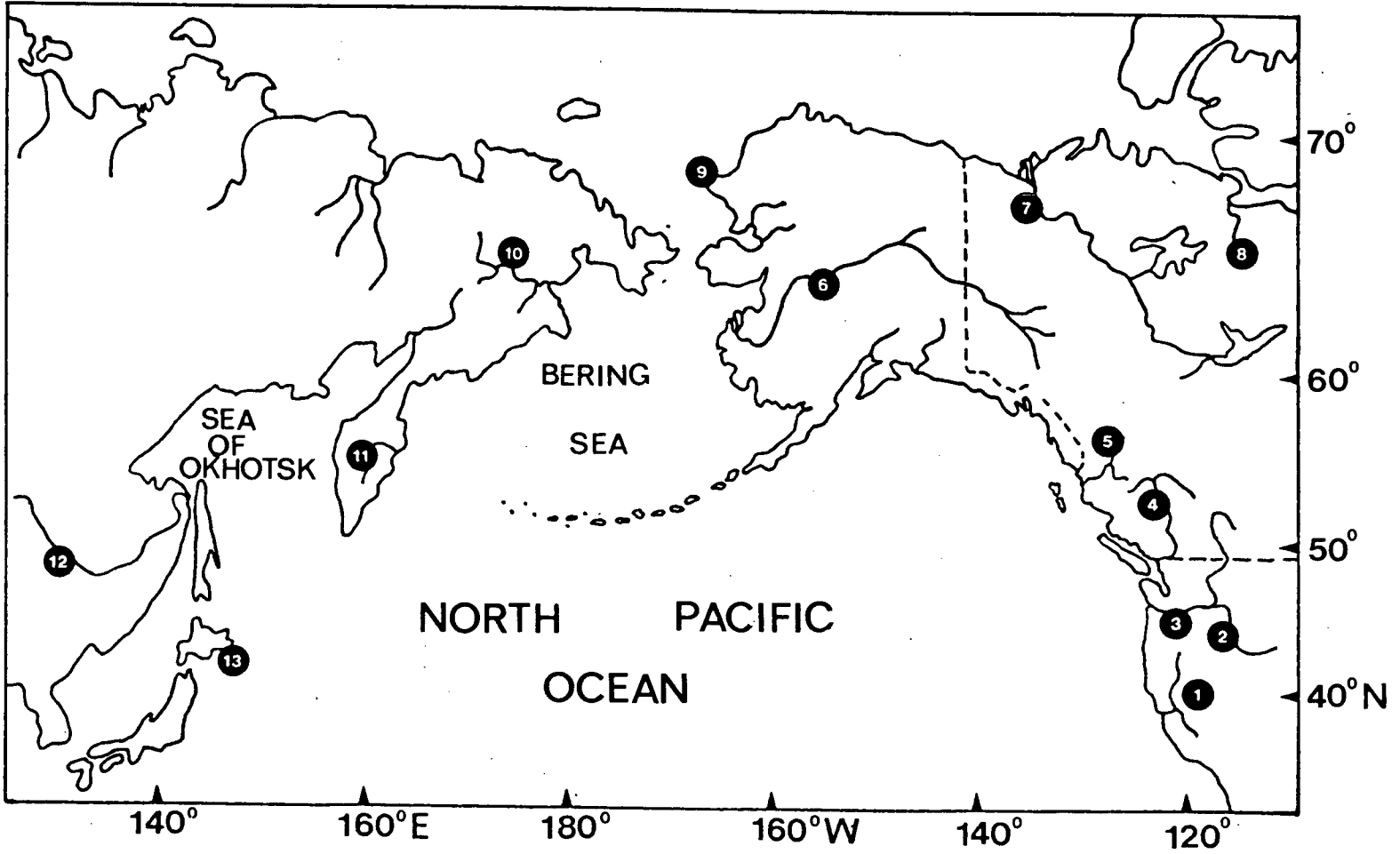
From the scale data base, the number of individuals occurring in each age class from 0.2 to 3.6 was enumerated from a minimum sample of 50 adults per population. The European system of age designation was used; the number to the left of the decimal represents the number of scale annuli formed in freshwater and the number right of the decimal represents the number of marine annuli. The mean percentages of "stream-type" (1 or more freshwater annuli) and "ocean-type" (no freshwater annulus) life histories were calculated for populations for which multiple year samples were available. These indicators of juvenile life history were checked when possible against field data on migration timing and seasonal abundance of juveniles in freshwater.

Geographic distribution of chinook salmon

Spawning populations of chinook salmon have been recorded in the eastern Pacific (Fig. 16) from as far south as the Ventura River (34 degrees N latitude) in south-central California, to Point Hope, Alaska, and perhaps east to the MacKenzie and Coppermine rivers (Hallock and Fry 1967; McPhail and Lindsey 1970; Scott and Crossman 1973; Lee et al. 1980; McLeod and McNeil 1983). Information on the distribution of chinook populations in the western Pacific is fragmentary but populations appear to be less abundant and less widespread (Major et al. 1978). Chinook salmon occur in the Anadyr River (tributary to the Bering Sea), the Kamchatka, Bol'shaya and Avacha rivers of the Kamchatkan Peninsula, the Amur River, and in a few streams tributary to the Sea of Okhotsk and on northern Hokkaido (Berg 1948; Shmidt 1950; Hikita 1956; Vronskiy 1972).

Within this broad geographic range chinook salmon are distributed among at least 1,000 separate spawning populations in North America (Aro and Shepard 1967; Atkinson et al. 1967). Spawning by adults and freshwater residence by young salmon occurs in a wide range of different types of rivers, from small coastal streams only a few kilometers from the ocean to large river systems such as the Sacramento-San Joaquin, Columbia, Fraser, and Yukon rivers in which headwater populations may spawn up to 3,200 km from the sea. Historically, the Columbia River, with its tributaries in Oregon, Washington, Idaho, and

Figure 16. Geographic distribution of chinook salmon in the North Pacific Ocean. (1) Sacramento-San Joaquin R., (2) Snake R., (3) Columbia R., (4) Fraser R., (5) Skeena R., (6) Yukon R., (7) Mackenzie R., (8) Coppermine R., (9) Point Hope, (10) Anadyr R., (11) Kamchatka R., (12) Amur R., (13) Hokkaido.



British Columbia, was probably the single largest producer of chinook salmon with total spawning runs of over 4,000,000 adults (Chapman 1986). Recently, however, overexploitation, dam construction, water abstraction, and other forms of habitat alteration have greatly reduced the dominance of the Columbia as a producer of wild chinook (Van Hyning 1973; Chapman 1986).

Chinook salmon have been introduced to several areas outside their native range. Introductions to New Zealand streams, starting in the late 1800's, have been the most important and successful (Stokell 1962; Ricker 1972). After initially sporadic results, self-sustaining populations of variable size have become established in many New Zealand streams on both the east and west coasts (Flain 1972, 1981). Other notable introductions include transplants of chinook to several tributaries of the Great Lakes in eastern North America and to Southern Chile (Lee et al. 1980; Carl 1982; Flain 1983).

Geographic variation in juvenile life history

Sacramento-San Joaquin River and Klamath River

Historically, spawning populations of chinook salmon were present up to the headwaters of both the Sacramento and San Joaquin rivers in California's Central Valley (Clark 1929). At least 80% of the natural spawning and rearing area in these systems has been eliminated by dam construction and water abstraction. The Shasta and Keswick dams near Redding, California, (Fig. 17) were perhaps the most damaging; all salmon runs upstream of these barriers were eliminated (Needham et al. 1940; Moffett 1949). Most of these dams were constructed before any detailed studies of juvenile life histories were completed for specific tributary populations of the Sacramento-San Joaquin river system. Nevertheless, much of our present appreciation of the degree of variability in juvenile freshwater life histories is derived from the early work of Scofield (1900), Rutter (1903), Rich (1920), and Clark (1929) on Sacramento River chinook salmon. What is clear from these early studies is that both stream- and ocean-type juvenile life histories were present (Rich 1920), but the proportions of ocean-or stream-type life histories in specific tributaries is unknown.

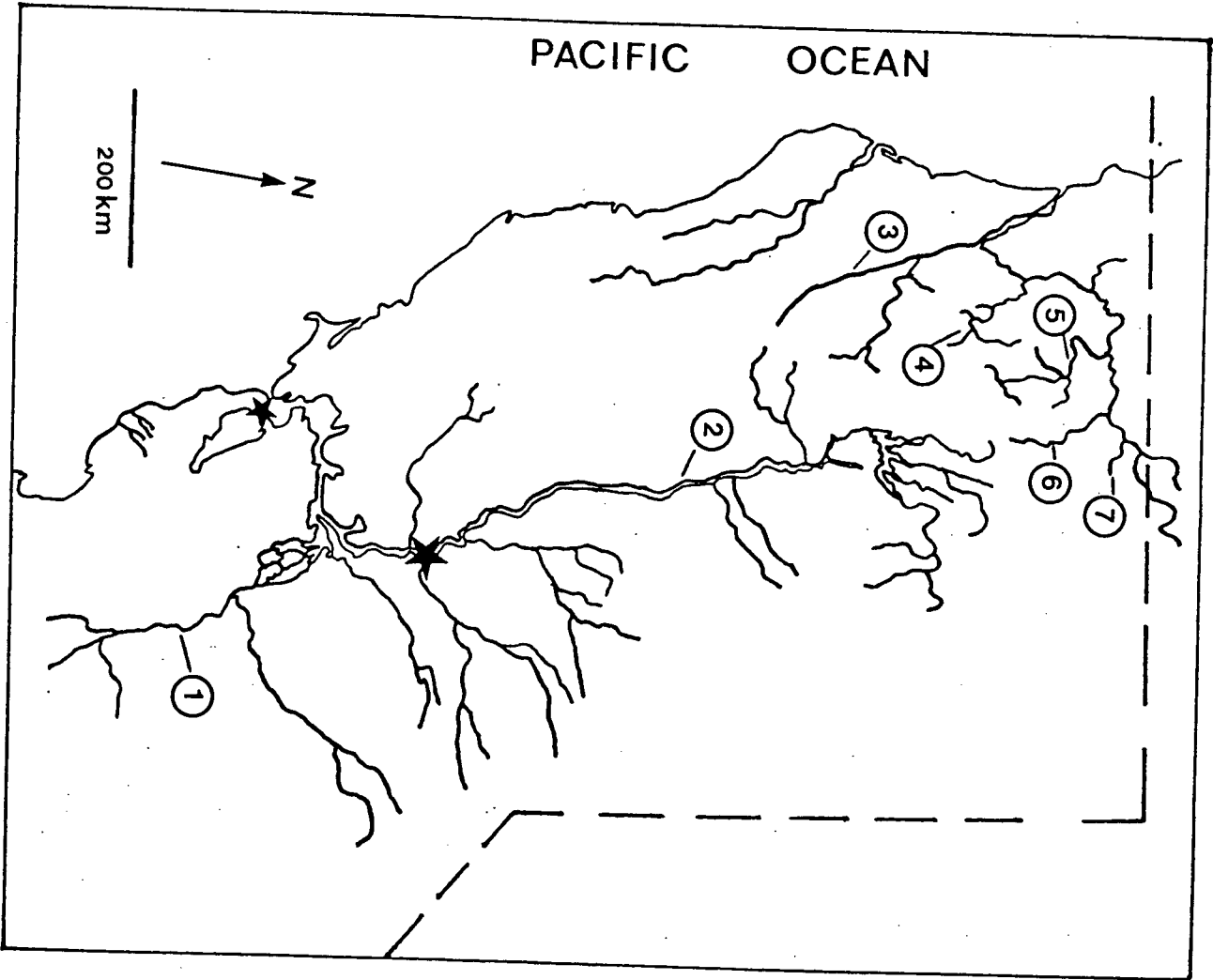
Clark (1929) examined scales from adult chinook collected near the confluence of the Sacramento and San Joaquin rivers for

1919 and 1921; the percentage of stream-type life histories in the scale samples was between 9 and 13%. Apparently, most stream-type fish were from the headwater tributaries (Rich 1920; Clark 1929; Major et al. 1978). Because dam construction has been concentrated in upstream reaches of the Sacramento, stream-type populations have probably been reduced more than ocean-type.

At present, the Sacramento contains remnant populations of four seasonal spawning runs of adult chinook salmon: fall, late-fall, winter, and spring (Ricker 1972; Kjelson et al. 1982). As their names suggest, these runs are distinguished by the season during which adult salmon migrate upstream. The fall run is dominant in both the Sacramento and San Joaquin rivers, constituting about 80 and 100% of their respective spawning runs. Within the Sacramento, most fall run chinook spawn in mainstem areas downstream from Keswick Dam. These salmon produce predominately ocean-type juveniles that begin entering the delta area as early as December-January after the adults have spawned in October-December (Frank Fisher, California Dept. Fish and Game, Stockton, CA, pers. comm.; Kjelson et al. 1982). Fry are abundant in the delta from January to March and marked fry remain in the estuary for roughly 2 months before migrating offshore (Kjelson et al. 1982).

The Klamath River in northern California (Fig. 17) is also a major producer of chinook salmon and spawning populations are

Figure 17. Distribution of juvenile life histories for chinook salmon spawning populations in the Sacramento and Klamath rivers, California. Open circles: ocean-type ($\geq 75\%$). (1) San Joaquin R., (2) Sacramento River, (3) South Fork Trinity R. (Klamath R.), (4) Salmon R., (5) Scott R., (6) Shasta R., (7) Bogus Cr. Large star=Sacramento, small star=San Francisco.

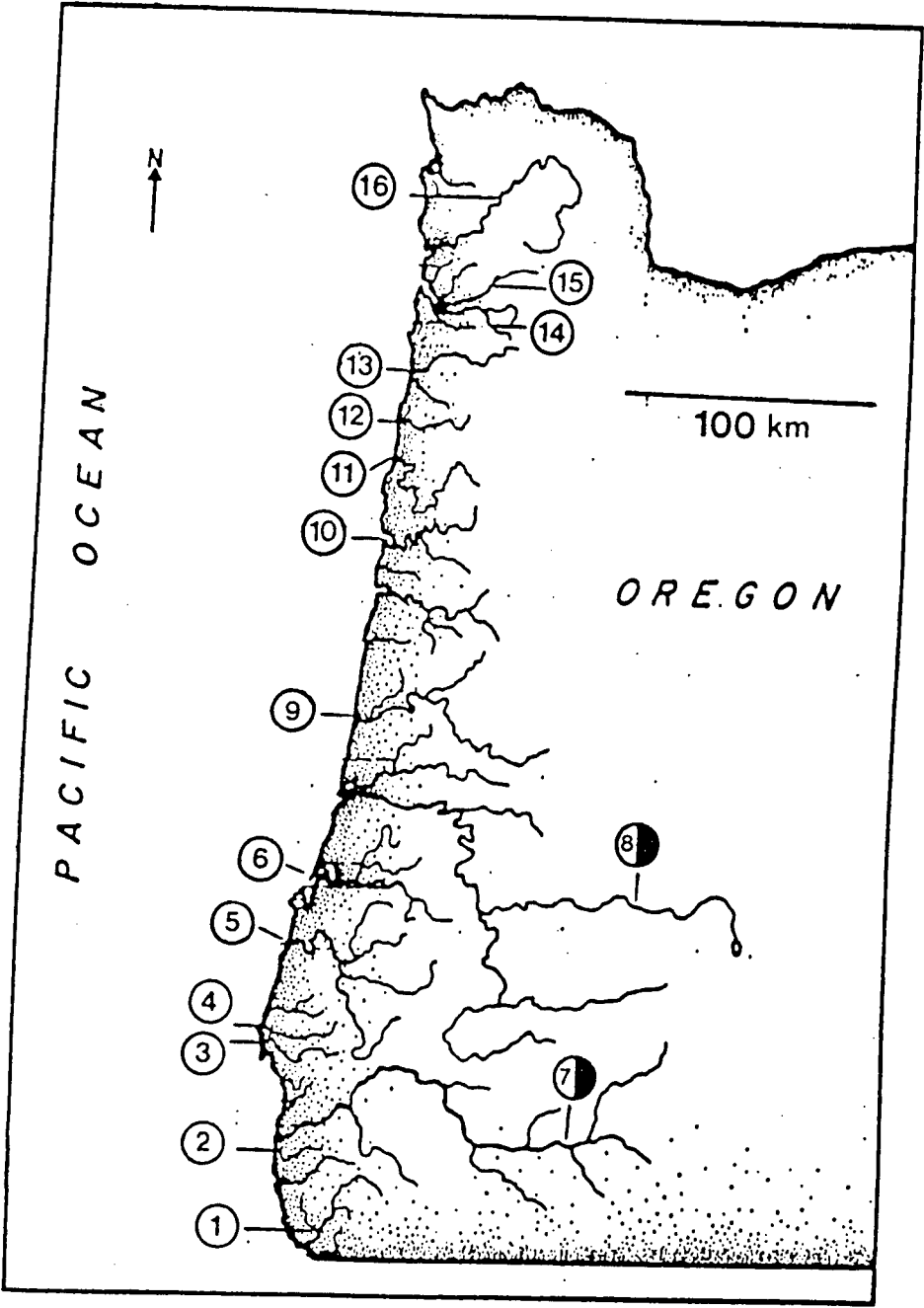


either spring or mid-late summer run (Snyder 1931; Ricker 1972). Most juvenile salmon in the Klamath system are ocean-type; only about 13% of spawning adults have stream-type scales (Snyder 1931). More recent evidence, from scales of adults spawning in tributaries of the Klamath, suggest that the relative contribution of stream-type life histories is between 0 and 7% (Fig 18, Calif. Dept. of Fish and Game, unpubl. data). Apparently, migrant chinook enter the Klamath estuary after a few months of stream residence because juveniles were detected there only during "late summer" (Snyder 1931).

Oregon coastal systems

Spawning populations of chinook salmon occur throughout Pacific coastal Oregon and have been the subject of numerous studies of juvenile life history (Reimers 1968, 1973, 1979; Schluchter and Lichatowich 1977; Neilson et al. 1985; Neilson and Geen 1986; Nicholas and Hankin 1988). Recently, Nicholas and Hankin (1988) summarized the present knowledge of variation in juvenile life history for most major streams of the Oregon coast except the Columbia River and its tributaries (see below). Both from stream surveys for juveniles and from scale analysis of adults, in some cases over a number of years, it is clear that ocean-type chinook predominate in coastal Oregon streams (Fig. 18, Nicholas and Hankin 1988). The percentage of stream-type life histories exceeded 10% in only one of 13 streams for which data were available (North Umpqua). For at least one

Figure 18. Distribution of juvenile life history patterns for chinook salmon spawning populations in Oregon coastal streams. Open circles: ocean-type ($\geq 75\%$); half-circles: intermediate ($<75\%$ ocean- or stream-type). (1) Chetco Cr., (2) Hunter Cr., (3) Elk R., (4) Sixes R., (5) Coquille R., (6) Coos R., (7) Rogue R., (8) North Umpqua R., (9) Siuslaw R., (10) Yaquina R., (11) Siletz R., (12) Salmon R., (13) Nestucca R., (14) Trask R., (15) Wilson R., (16) Nehalem R.



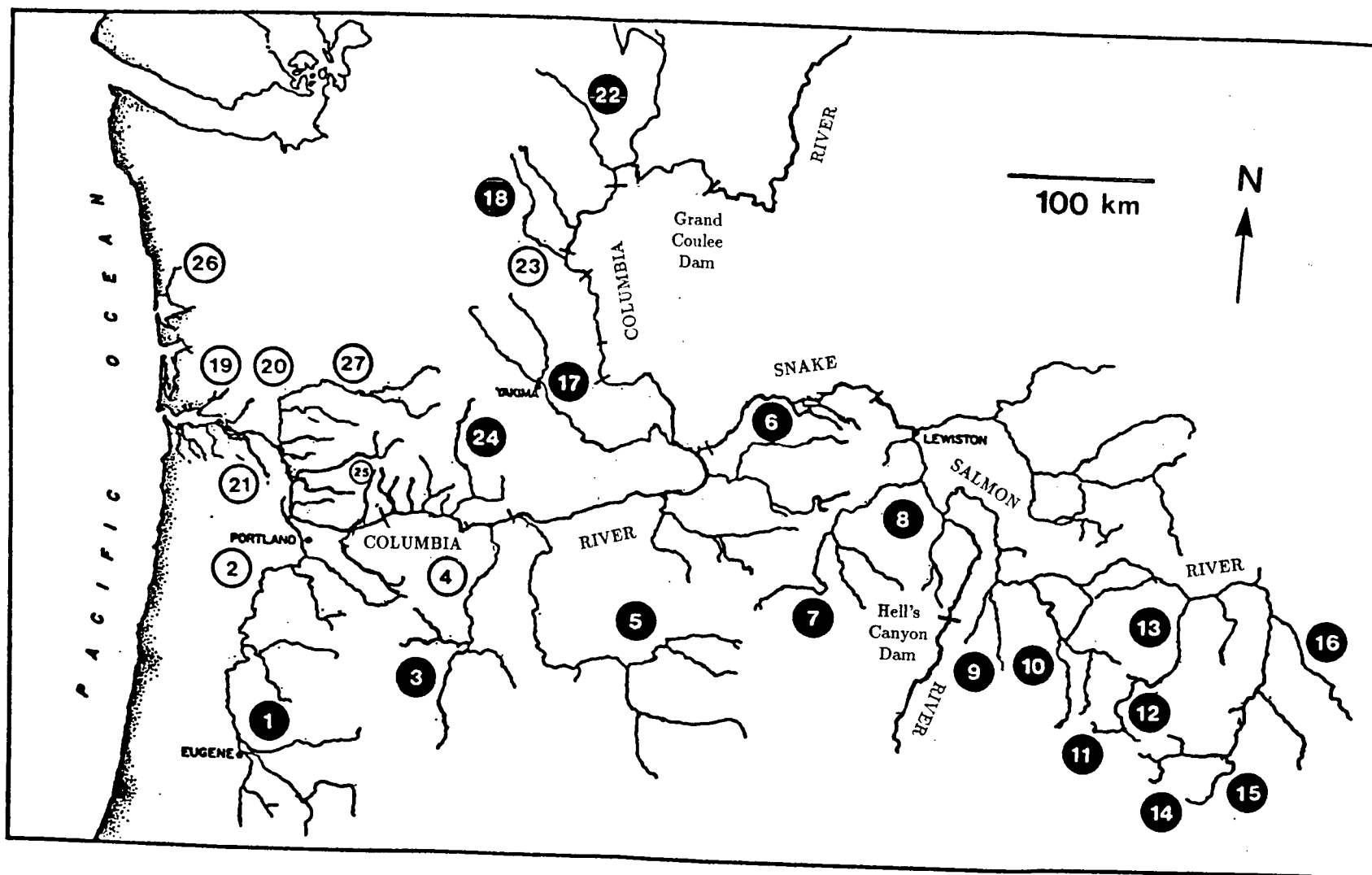
stream (Elk River) there may have been a decline in the relative occurrence of stream-type life history patterns in the scales of adults over the 17 year period from 1968 to 1985 (Nicholas and Hankin 1988).

Throughout coastal Oregon, juvenile chinook appear in estuarine areas in late spring (May-June), which is somewhat later than in the Sacramento-San Joaquin, and reside there for periods of up to 5 months before migrating to waters of higher salinity (Nicholas and Hankin 1988). The trend, then, is for stream residence during the early spring followed by estuarine residence during the late spring and summer. Most ocean-type chinook have entered medium to high salinity estuarine areas by September-October (Nicholas and Hankin 1988). More detailed scale studies are consistent with these generalities. Both Reimers (1973) and Schluchter and Lichatowich (1973) concluded that of 5 to 7 scale patterns observed in adults returning to the Sixes and Rogue rivers, the majority were fish that, as juveniles, had initially resided in the river, but as underyearlings had spent an extended period in estuaries.

Columbia River

The Columbia River system, covering a drainage area of about 671,000 sq km (McPhail and Lindsey 1986, Fig. 19), constitutes numerous large and small tributaries which support local spawning and juvenile populations of chinook salmon

Figure 19. Distribution of juvenile life history patterns for chinook salmon spawning populations of the Columbia River. Open circles: ocean-type ($\geq 75\%$); closed circles; stream-type ($\geq 75\%$). (1) Upper Willamette R., (2) lower Willamette R., (3) upper Deschutes R., (4) lower Deschutes R., (5) John Day R., (6) Tucannon R., (7) Grande Ronde R., (8) Imnaha R., (9) Little Salmon R., (10) South Fork Salmon R., (11) Bear Valley Cr., (12) Marsh Cr., (13) Middle Fork Salmon R., (14) Upper Salmon R., (15) East Fork Salmon R., (16) Lemhi R., (17) Yakima R., (18) Wenatchee R., (19) Gray's R., (20) Elochoman R., (21) Klatskanie R., (22) Methow R., (23) lower Wenatchee R., (24) Klickitat R., (25) Washougal R., (26) Gray's Harbour, (27) Cowlitz R.



(Fulton 1968). Proceeding upstream from the mouth of the Columbia the major tributaries are: the Willamette, Deschutes, John Day, Yakima, and Wenatchee rivers, and the Clearwater and Salmon river systems of the Snake River subdrainage.

Historically, chinook salmon were present in the headwater areas of the Columbia system in southeastern B.C., and to about Shoshone Falls in southcentral Idaho (Bryant and Parkhurst 1950; Fulton 1968). Dam construction at Grand Coulee on the mainstem Columbia (Grand Coulee Dam) and at Hell's Canyon on the Snake River has extirpated populations above these obstructions (Fig. 19), but wild spawning populations persist in several tributaries of the upper Salmon River drainage in central and southcentral Idaho. Historical treatments of the juvenile life history patterns of chinook salmon include the work of Rich (1920), Rich and Holmes (1928), and Reimers and Loeffel (1967). Juvenile life histories (Fig. 19) extend from migration downstream as newly-emerged fry or young parr (e.g. the Klaskanie River (Reimers and Loeffel 1967)) to yearling migrants (e.g. Toutle River, Yakima River, Salmon River tributaries, (Major and Mighell 1969; Reimers and Loeffel 1967; Howell et al. 1985)).

Many tributaries of the Columbia River illustrate within-stream variability in chinook life history. Alternative juvenile life histories within streams are usually associated with adult salmon runs that enter freshwater during different

times and spawn in different areas. For example, the Willamette River in the lower Columbia, has both spring and fall chinook runs. The spring run salmon typically spawn in the upper tributaries such as the MacKenzie River (river km 180) and have a stream-type juvenile life history (Howell et al. 1985). In contrast, most fall run adults spawn in streams tributary to the lower Willamette (lower 40 km) and their progeny emigrate from freshwater as fry (Howell et al. 1985). The presence of both life history types within single tributaries appears to be common in the lower Columbia River (below its confluence with the Snake River) (Fulton 1968). Therefore, the Columbia, both historically and to the present day, exhibits a range of juvenile life histories both among and within component tributary streams.

Ocean-type migrants enter the Columbia estuary as early as December of the year of spawning but are most abundant in the early spring (March-April). Some juveniles emigrate from coastal tributaries after residing in their natal streams through spring and summer and appear as a secondary peak movement into the estuary in the late fall (e.g. Reimers and Loeffel 1967). Stream-type chinook usually migrate in April through June (Major and Mighell 1969; Howell et al. 1985) although they have been found in the estuary from March through May (Rich 1920; McCabe et al. 1983). Once in the Columbia estuary, stream-type chinook appear to spend little time there before migrating offshore compared to ocean-type chinooks

(McCabe et al. 1983).

Washington coastal and Puget Sound chinook

Chinook salmon populations in Puget Sound and coastal Washington are dominated by ocean-type juvenile life history patterns (Fig. 20). Most systems, particularly those on the west coast, are characterized by $\geq 95\%$ ocean-type chinook. In a few of the larger systems that have tributaries extending into the Cascade Mountains, stream-type chinook are more abundant (e.g. Skagit and Snohomish rivers are about 70% stream-type).

Both juvenile ocean- and stream-type chinook enter Washington estuaries from March through June, but ocean-type migrants predominate during the early spring. A secondary peak of migration may occur in August and September (Simenstad et al. 1982). Individual residence times average 3-6 weeks in Washington estuaries, but in some salt marshes residence may be only a few days (Congleton et al. 1982; Simenstad et al. 1982).

British Columbia

Southern British Columbia (Vancouver Island, Southwestern Mainland, and Fraser River) exhibits the full range of juvenile chinook life history patterns present in more southern areas (Fig. 21). Vancouver Island populations are dominated by ocean-type salmon, but certain populations illustrate variability that

Figure 20. Distribution of juvenile life history patterns for chinook salmon spawning populations of coastal Washington and Puget Sound. Open circles: ocean-type ($\geq 75\%$); half-circles: intermediate ($<75\%$ stream- or ocean-type). (1) North Fork Nooksack R., (2) South Fork Nooksack R., (3) lower Nooksack R., (4) lower Skagit R., (5) lower Sauk R., (6) upper Skagit R., (7) North Fork Stilliguamish R., (8) South Fork Stilliguamish R., (9) Cedar R., (10) Green R., (11) Skykomish R., (12) Snoqualmie R., (13) Puyallup R., (14) Nisqually R., (15) Skokomish R., (16) Hamma Hamma R., (17) Duckabush R., (18) Dosewallips R., (19) Dungeness R., (21) Elwha R., (22) Hoko R., (23) Quillayute R., (24) Hoh R., (25) Clearwater R., (26) Queets R., (27) Quinault R., (28) Humptulips R., (29) Chehalis R., (30) Willapa R., (31) upper Sauk R. Star=Seattle.

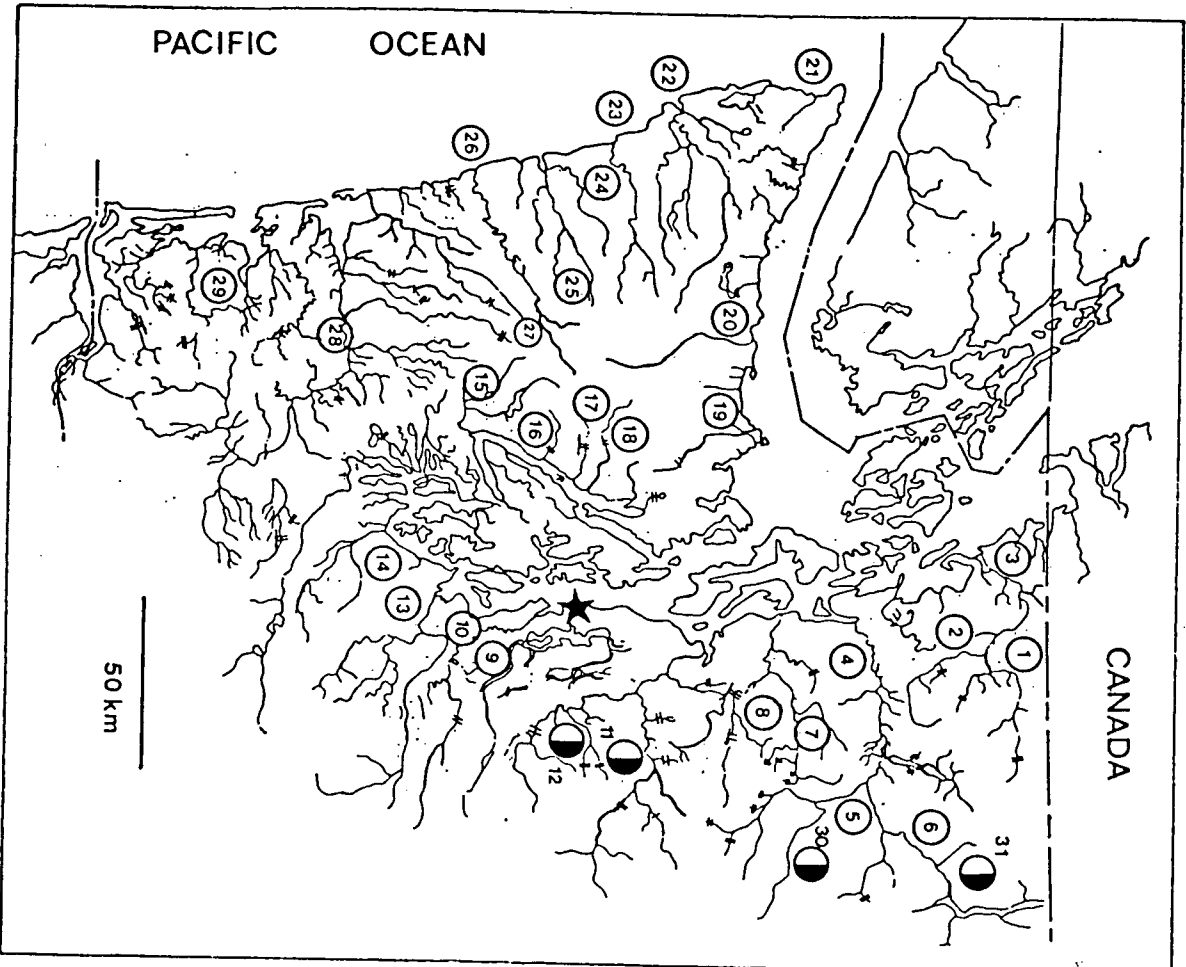
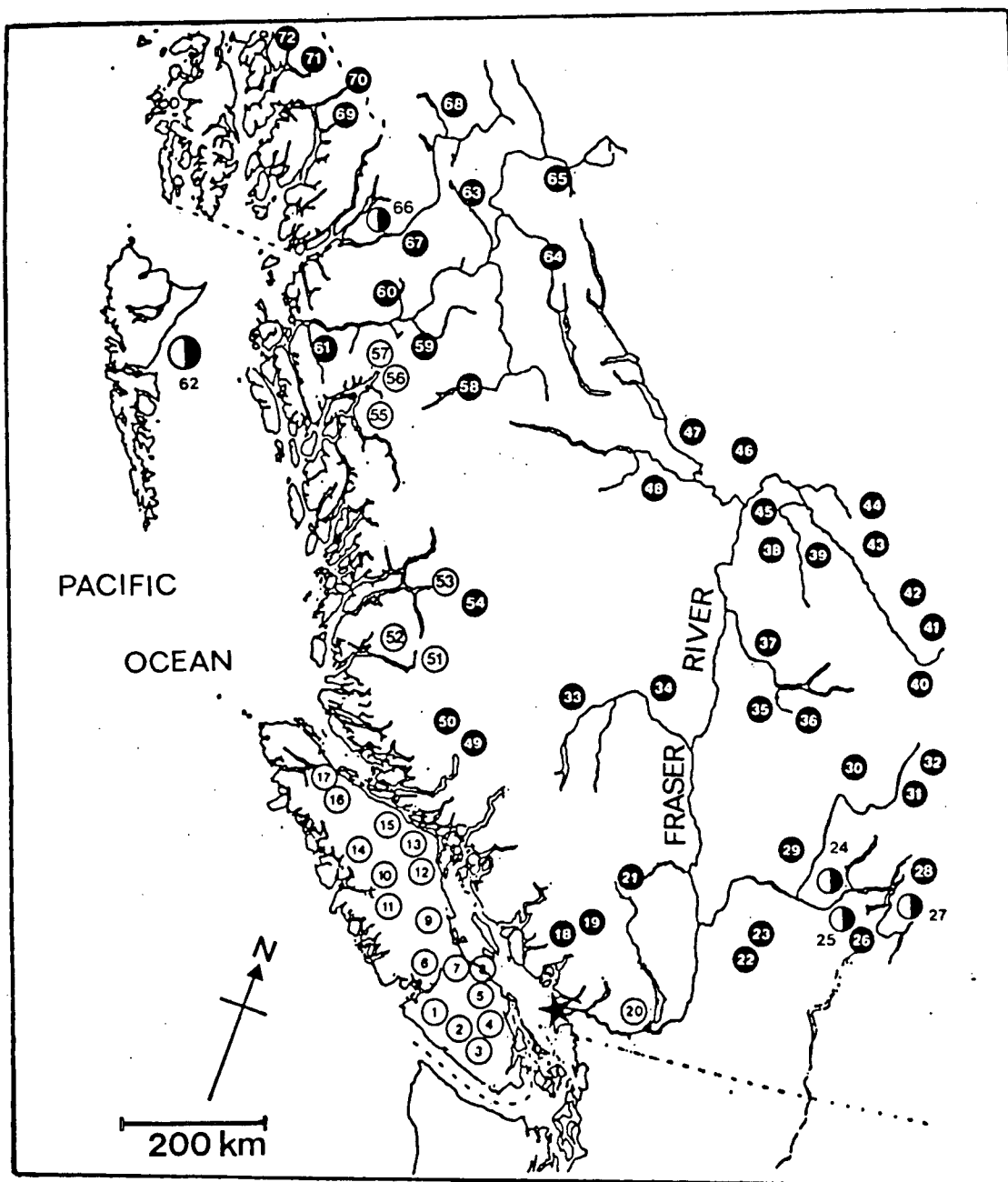


Figure 21. Distribution of juvenile life history patterns in chinook salmon spawning populations in southern British Columbia. Open circles: ocean-type ($\geq 75\%$); closed circles: stream-type ($\geq 75\%$); half-circles: intermediate.

(1) Nitinat R., (2) Gordon R., (3) San Juan R., (4) Cowichan R., (5) Nanaimo R., (6) Alberni Inlet, (7) Big Qualicum R., (8) Little Qualicum R., (9) Puntledge R., (10) Gold R., (11) Burman R., (12) Quinsam R., (13) Campbell R., (14) Conuma R., (15) Salmon R., (16) Woss R., (17) Marble R., (18) Ashlu R., (19) Squamish R., (20) Harrison R., (21) Birkenhead R., (22) Coldwater R., (23) Nicola R., (24) Adams R., (25) South Thompson R., (26) Salmon R., (27) Shuswap R., (28) Eagle R., (29) Deadman R., (30) Clearwater R., (31) Blue R., (32) North Thompson R., (33) Chilko R., (34) Chilcotin R., (35) Horsefly R., (36) McKinley Cr., (37) Quesnel R., (38) Bowron R., (39) Slim Cr., (40) Swift Cr., (41) Tete Jean (Fraser R.), (42) Holmes R., (43) Walker Cr., (44) McGregor R., (45) Willow R., (46) Salmon R., (47) Stuart R., (48) Nechako R., (49) Ahnuhati R., (50) Mussel Cr., (51) Wannock R., (52) Kilbella R., (53) Bella Coola R., (54) Atnarko R., (55) Hirsch Cr., (56) Kildata R., (57) Kitimat R., (58) Morice R., (59) Zymoetz R., (60) Kitsumkalum R., (61) Eckstall R., (62) Yakoun R., (63) Kispiox R., (64) Babine R., (65) Bear R., (67) Kincolith R., (68) Cranberry R., (69) Meziadin R., (70) Chickamin R., (71) Unuk R., (72) Bradfield Canal. Star=Vancouver.



may exist within single, reasonably small river systems. For example, the chinook in the Nanaimo River on southeastern Vancouver Island are predominately ($\geq 95\%$) ocean-type, but there is a small population of up to 50% stream-type individuals in the headwaters (Carl and Healey 1984). In addition, the ocean-type chinook migrate to the estuary either as fry (lower river spawning population) or after 2-3 months of stream residence (middle river spawning population) (Carl and Healey 1984). Similarly, the Big Qualicum River appears to have distinct newly-emerged and 2-3 month old ocean-type migrants (Lister and Walker 1966; Lister and Geno 1970).

The Fraser River shows a predominance of the stream-type life history in terms of the number of populations. The Harrison River, however, is the single largest spawning population within the Fraser system (about 25% of mean annual Fraser escapement 1976-80, Fraser et al. 1982) and is ocean-type; fry emigrate to the Fraser estuary during March and April (Fraser et al. 1982; Levy and Northcote 1982). North of about 50 degrees N latitude, the Fraser is dominated by stream-type populations except for some apparently intermediate populations in the South Thompson sub-drainage (Fig. 21).

Areas north to the Nass River exhibit an increasing tendency towards domination by stream-type populations with notable exceptions being the Whonnock, Bella Coola, and Kitimat Rivers on the coast. North of the Nass River, the Canadian

portions of the Stikine and Taku rivers, and their tributaries, appear to have exclusively stream-type populations (Fig. 22). By contrast to southern areas, even small streams close to the coast have stream-type chinook (e.g. Harding River, streams tributary to Unuk River, Fig. 21).

In southern B.C., ocean-type chinook enter estuarine areas as newly-emerged fry as early as March and on through May (Lister and Genoe 1970; Levy and Northcote 1982; Healey 1980, 1982; Levings et al. 1986). For some populations, peaks in downstream movement may differ up to 1 month from year to year (Lister and Walker 1966; Fraser et al. 1982). Fry reside in estuarine areas for between 4 and 8 weeks until they reach a size of between 2 and 4 g, after which they migrate farther offshore (Healey 1980, 1982; Levy and Northcote 1982; Levings et al. 1986). Juvenile chinook that reside in their natal streams for 2-3 months after emergence begin entering estuarine areas from May to June where they may remain until July-August (Lister and Walker 1966; Healey 1980, 1982; Fraser et al. 1982; Carl and Healey 1984; Shepherd et al. 1986a).

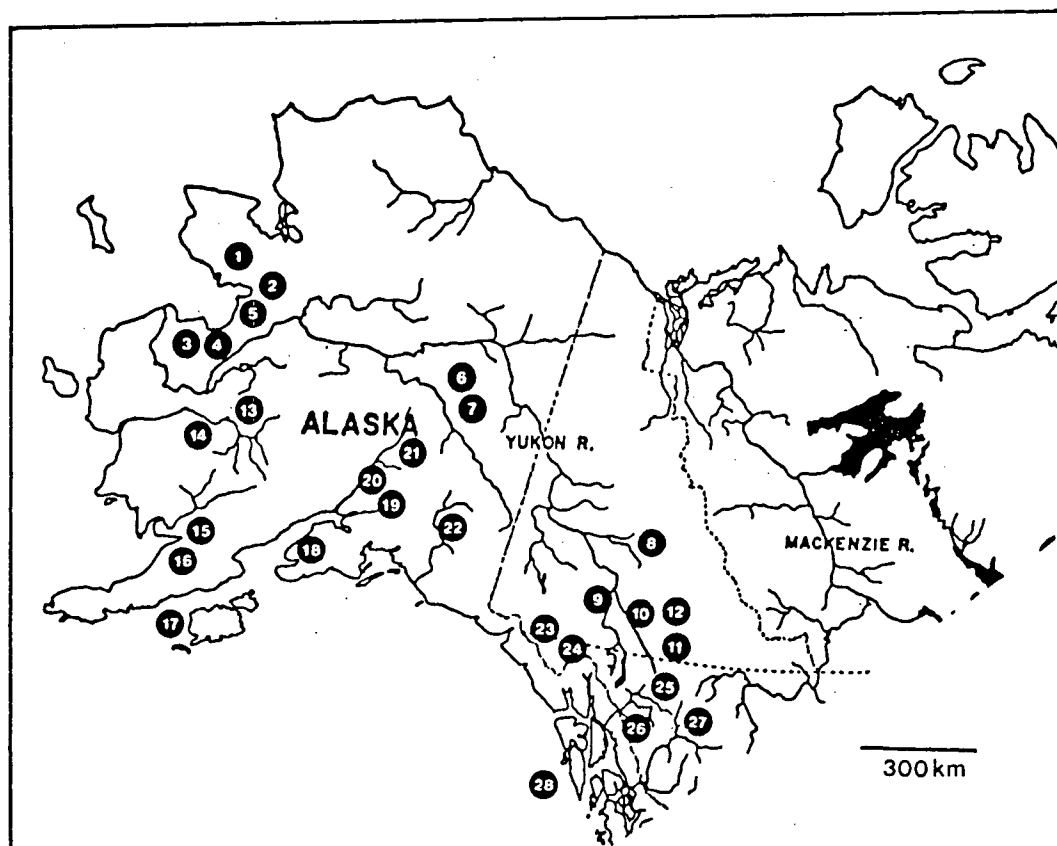
Stream-type chinook migrate downstream primarily in April and May in south and central B.C., with peaks near the end of April, and enter estuarine areas from May through June (Levy and Levings 1978; Shepherd et al. 1986b). Seaward migration appears to be later farther north where peak movement occurs in mid-May in the Taku and Stikine rivers (Meehan and Sniff 1962;

P. Kissner, Alaska Dept. of Fish and Game, pers. comm.). Once in estuarine areas, stream-type chinook apparently seek the outer margins of these habitats and spend little time there, compared to ocean-type chinooks, before migrating towards the open ocean (Levy and Levings 1978; Healey 1983).

Alaska and Yukon populations

The distribution of juvenile chinook life history patterns is perhaps least variable in coastal and inland areas in Alaska, and in Yukon portions of the Yukon River, where all populations sampled to date are stream-type (Fig. 22). Alaskan and Yukon River stream-type chinook may spend up to 2 years in freshwater before migrating seaward (McBride and Wilcock 1983; Milligan et al. 1985). Only very occasionally do ocean-type life histories appear in scale samples of adults returning to spawn in certain coastal populations in southeastern and southwestern Alaska (Alaska Dept. Fish and Game, unpubl. data). Seaward migration of Alaskan and Yukon River chinook salmon is generally later than in more southern portions of the chinook's range, extending from May to late July (Walker 1976; Loftus and Lenon 1977; Raymond 1981; Martin et al. 1987). As is consistent with estuarine residence distribution of stream-type salmon in more southern latitudes, Yukon River chinook utilize the deeper habitats in the prodelta before moving offshore (Martin et al. 1987).

Figure 22. Distribution of juvenile life history patterns in chinook spawning populations in northern B.C. and Alaska. Closed circles: stream-type ($\geq 75\%$). (1) Kwiniuk R., (2) Unalakleet R., (3) Andreafsky R., (4) Anvik R., (5) Nulato R., (6) Chena R., (7) Salcha R., (8) Big Salmon R., (9) Yukon R. (Whitehorse), (10) Teslin R., (11) Swift R., (12) Nisutlin R., (13) Kuskokwim R., (14) Holitna R., (15) Naknek R., (16) King Salmon R., (17) Karluk R., (18) Anchor R., (19) Little Susitna R., (20) Montana Cr. (Susitna R.), (21) Chulitna R., (22) Copper R., (23) Alsek R., (24) Tahini R., (25) Nakina R. (Taku R.), (26) Nahlin R. (Taku R.), (27) Tahltan and Little Tahltan R. (Stikine R.), (28) Harding R.



Western Pacific and New Zealand populations

Information on the distribution of juvenile chinook life histories is limited in areas other than the eastern Pacific. Scale analysis of salmon caught in the western Pacific near the Kamchatka peninsula and in the Sea of Okhotsk, and presumably of Asian origin, were all stream-type (Mason 1965). Vronskiy (1972) sampled scales from adult chinook returning to spawn in the upper Kamchatka River (Fig. 16) during 1965-70; all were stream-type and about 12% spent 2 years in freshwater (Table 21).

In New Zealand, the Rakaia River, and its component tributaries, is the most studied system (Flain 1982a; Unwin 1986). In this system, ocean-type chinook predominate (Table 21); most adults that survive to spawn spend 2-3 months residing in freshwater as juveniles before migrating seaward (Flain 1982a; Unwin 1986). As in the northern hemisphere, stream-type chinook tend to become more numerous with increasing latitude in New Zealand (Table 21). Whereas up to 30% of sampled adult chinook were stream-type in the Rangitata River (Davis et al. 1986), about 50% of adults sampled in the Waitaki River were stream-type (James and Deverall 1987). More limited sampling suggests that about 50% of the adults caught in sea fisheries near the Moeraki Peninsula were stream-type fish (Flain 1981). In a few systems, chinook may reside permanently in freshwater

Table 21. Juvenile chinook life history patterns in the Kamchatka River (Soviet Union) and several New Zealand rivers Kamchatkan data is from Vronskiy (1972); New Zealand data from Flain (1972), Unwin (1986), Davies et al. (1986), and James and Deverall (1987).

River	Latitude	Years	Percent Stream-type
Kamchatka River	55'10" N	1965-70	100
Glenariffe Stream (Rakaia River)	43'28" S	1967-76	8-34
Rangitata River	43'35" S	1972-83	28
Waitaki River	44'40" S	1976-83	26-66
Moeraki Peninsula	45'20" S	1976	58

despite access to the sea (Flain 1972). Some individuals in the anadromous components of these populations may spend 2 or 3 years in freshwater before seaward migration (Flain 1980). In the Rakaia River, seaward migration by ocean-type fish occurs primarily in November through January following emergence in September (Unwin 1986). The adults that migrated to sea as yearling smolts (about 23%) did so from August through November (Unwin 1986).

In summary, there is extensive variation in juvenile life history both within and among tributary populations of chinook, but a few generalities can be drawn. First, stream-type chinook tend to predominate with increasing latitude, although the transition is not a smooth one. Second, in river systems with large numbers of populations, stream-type chinooks predominate in interior areas and ocean-types in coastal areas. Lastly, alternative juvenile life histories can be found in single tributaries. Such sub-populations are usually associated with seasonal adult spawning runs and stream-type chinooks tend to predominate in the headwaters of single tributaries.

2. ENVIRONMENTAL CORRELATES OF VARIATION IN JUVENILE CHINOOK LIFE HISTORY

Methods

Four environmental variables characteristic of chinook spawning streams were examined for their covariation with juvenile life history: mean annual air temperature, hours of daylight at first feeding, total daylight hours during the growing season, and freshwater migration distance.

Temperature and photoperiod are major abiotic factors regulating growth and growth rate-dependent processes in fishes (Brett 1979; Thorpe 1987; Hoar 1988). Not only is growth expected to increase rapidly with increasing temperature within limits (e.g. Brett et al. 1969), but feeding and growth commence earlier in development as temperature increases (Heming et al. 1982). Thorpe et al. (1989) demonstrated that temperature and photoperiod were good indices of "growth opportunity" in laboratory populations of juvenile Atlantic salmon. A combination of these variables (the "thermal sum index") was an excellent predictor of the percentage of fish within sibling populations that would smolt at 1 rather than 2 years of age (Thorpe et al. 1989). Temperature and photoperiod also appear to be major determinants of freshwater life history variation among wild populations of Atlantic salmon (Metcalf and Thorpe 1989).

Photoperiod conditions experienced during early rearing influence the growth trajectories of stream-type chinook and juvenile coho salmon (Clarke and Shelbourne 1986; Clarke 1987; Clarke and Withler 1987; Thorarensen and Clarke 1989). Salmon that experience "low" daylight (< 12 hr) at first feeding grow faster and display physiological correlates of smolting earlier than slower growing juveniles that experience "long" daylight periods at first feeding. The data of Zaugg et al. (1986) also suggest that photoperiod conditions at first feeding may, in part, influence the rate at which size and physiological correlates of smolting are achieved in chinook salmon. Since wild populations of juvenile chinook experience different photoperiod regimes at first feeding due to variation in latitude and emergence timing, photoperiod at first feeding may explain some of the variability in duration of freshwater residence among populations.

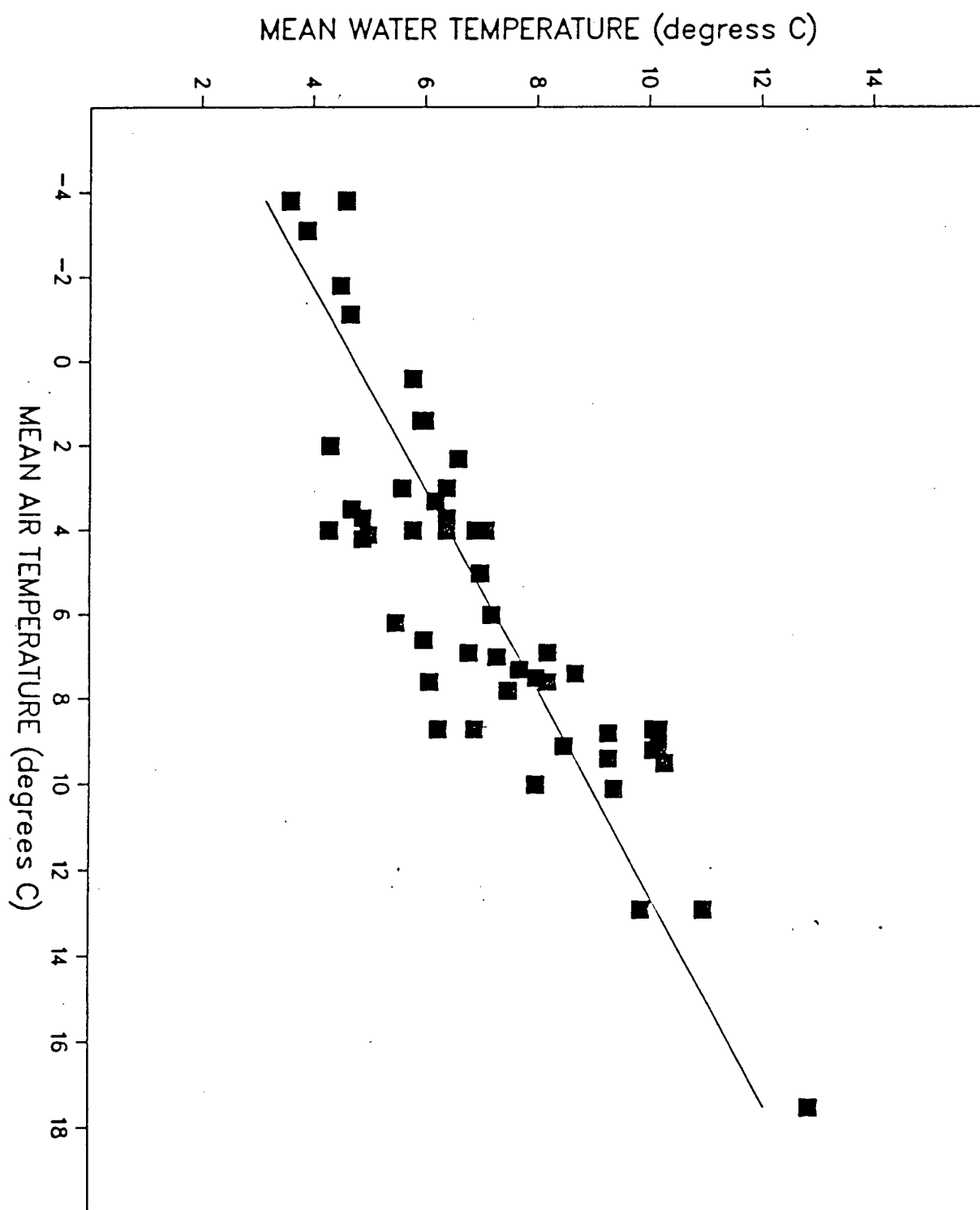
Lastly, longer smolt migrations are probably more costly in terms of energy expenditure and exposure to freshwater predators. Increasing migration distance might, therefore, select for increasing size at migration. Size at migration and growth opportunity could interact to influence age at migration.

Freshwater age distribution data for chinook populations were collected over as wide a geographic range as possible such that variability in both juvenile life history and environmental

variables was maximized. Limited data, however, were available for average stream water temperatures across a wide geographic range. Whereas most of the B.C. and Yukon chinook populations had reasonable time series data on water temperatures of their spawning streams, similar data were not generally available for spawning streams in other parts of the range. Therefore, air temperature at climatic stations in close proximity to the study streams, for which more complete data were available, was used as an indicator of water temperature. The implicit assumption that air temperatures are reasonable predictors of stream temperatures was tested by comparing these temperatures for 50 streams for which both station air temperatures and water temperatures were available. Air temperature data were from Anon (1982), Wernstedt (1972), and Ruffner (1985) while water temperatures were taken from Anon (1977), Unwin (1986), and from unpublished data of the California Department of Fish and Game (F. Fisher, Stockton, CA, pers. comm.). Both air and water temperature data were from streams representative of most of the chinook's range (California to Alaska), although the majority of data were from B.C. and Yukon streams.

Approximately 70% of the among stream variation in mean annual water temperature could be accounted for by variation in mean annual air temperature (Fig. 23, $df=1,49$; $P < 0.0001$). Mean annual air temperature was, therefore, used as a reasonable correlate of mean annual water temperature. Power (1981), L'Abée-Lund et al. (1989), Metcalfe and Thorpe (1989). All

Figure 23. Relationship between mean annual air temperature and mean annual water temperature for study streams.



found air temperature, as a measure of growing season length, to be a good predictor of smolting ages for Atlantic salmon and brown trout (Salmo trutta) populations. Even given perfect correlation between air and water temperatures, perhaps the more critical assumption is that measures of mean water temperature for a stream are related to thermal microhabitats occupied by juveniles. There are certainly cases in which water temperature monitoring stations are remote from the main juvenile salmon habitat in a stream. Temperature stations and juvenile habitat may, thus, have different water temperature regimes owing to the influence of local conditions such as lake outlets or sources of groundwater. Unfortunately, data on thermal microhabitats for a wide range of streams are not presently available.

Latitudes of study streams were determined from topographic maps (1:500,000) and were taken at the mid-length point of each stream unless information on the spawning distribution of adult salmon indicated a more restricted distribution. From latitudes, mean monthly hours of daylight were determined for each stream using the methods outlined in Duffett-Smith (1985).

Hours of daylight on the mid day of the month that mean monthly air temperature exceeded 4°C was used as a measure of photoperiod during early growth of juvenile salmon. A temperature of 4°C was chosen because growth of juvenile chinook is temperature dependent and juvenile salmonids exhibit reduced activity and "hiding" behaviour at temperatures below about 4°C .

5°C (Chapman and Bjornn 1969; Taylor 1988). Feeding activity is probably greatly reduced at temperatures below 4-5°C (Allen 1969). Also, Brett et al. (1969) reported that growth of sockeye salmon (O. nerka), during their first year of life, peaked between 5 and 17°C and chinook are probably characterized by similar thermal limits to growth efficiency.

Total hours of daylight during the growing season (i.e. air temperatures $\geq 4^{\circ}\text{C}$) was the final environmental variable used as an indicator of growth opportunity. Distance to the sea measurements were determined from topographic maps using a Derby map-unit counter.

The data on variation among populations in juvenile life history and environmental factors were summarized by principal component analysis (PCA) of the correlation matrix using MIDAS (Fox and Guire 1976). Distances to the sea were \log_{10} transformed before PCA to reduce skewness of the data. Populations over the geographic range were then grouped into two classes: (i) predominantly ($\geq 75\%$) stream-type or (ii) predominantly ocean-type. Mann-Whitney U-tests were used to test for equality of the average principal component scores for each group using SYSTAT (Wilkinson 1988). Spearman rank correlation coefficients were calculated between percentage stream-type life history and the principal component scores using SYSTAT.

Results

Information on juvenile life history variation and environmental variation was collected from a total of 160 populations ranging from California to Alaska, Kamchatka, and New Zealand. Principal components analysis of the environmental variables associated with the geographic locations of these spawning and rearing streams summarized 96% of the total variance in 2 component axes (Table 22).

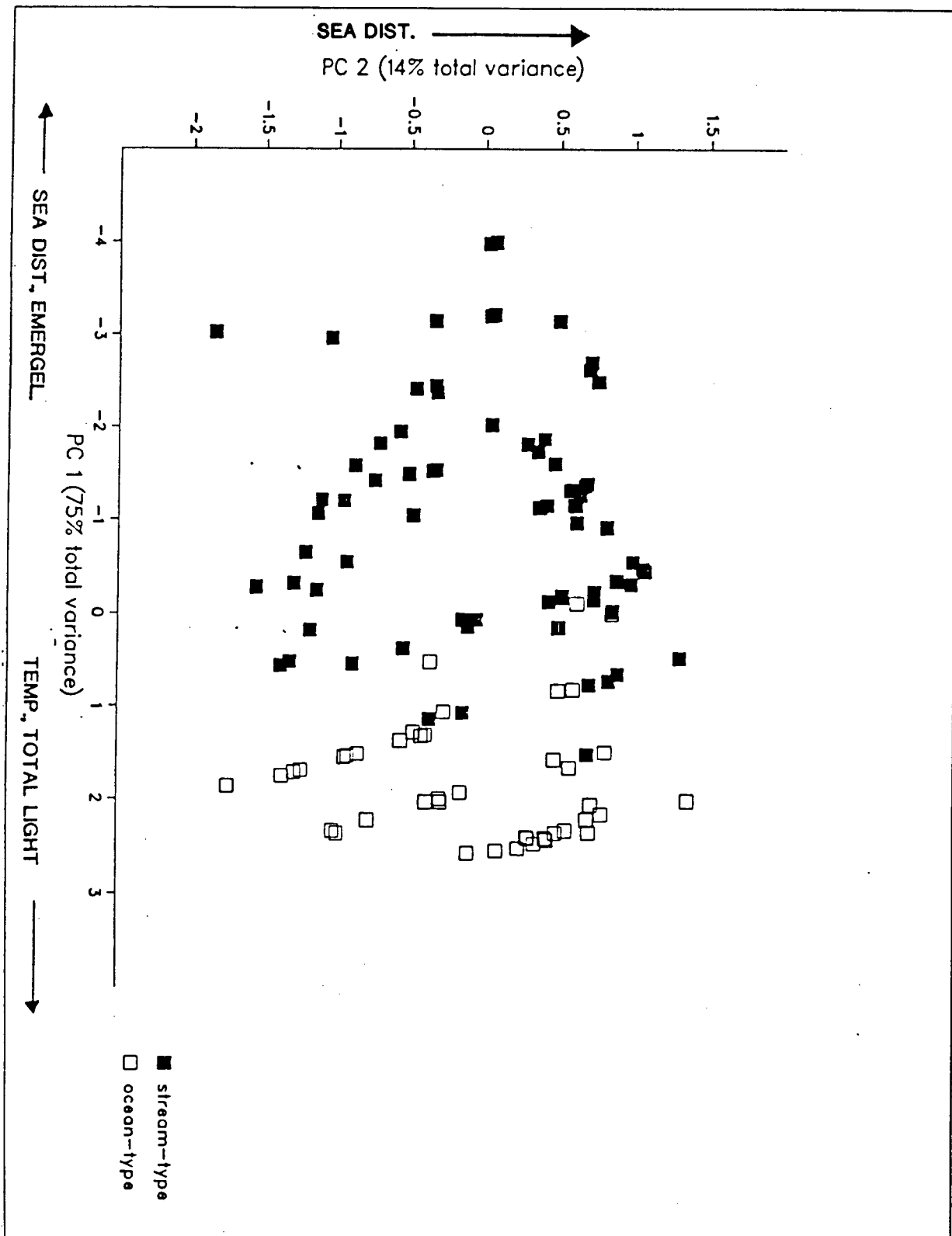
The first axis (79% total variance) was interpreted as contrasting streams in terms of distance from the sea and daylight hours at fry emergence (negative coefficients) with stream temperature and daylight hours over the growing season (positive coefficients). The second component axis (17% total variance) was interpreted as a "migration distance" component. Plots of PC scores for stream- and ocean-type populations suggested considerable separation between the life history types along PC1, but little along PC2 (Fig. 24). Mean PC scores between stream- and ocean-type chinook were, in fact, significantly different along PC1 (Mann-Whitney U-test, $P < 0.001$), but only barely along PC2 ($P = 0.05$). In addition, percentage of the stream-type life history was negatively correlated with scores along PC1 ($r_s = -0.84$, $P < 0.01$), but was uncorrelated with PC2 scores ($P > 0.05$).

Populations that tend to be stream-type in juvenile life

Table 22. Principal components analysis of environmental variables characteristic of populations of chinook salmon.

Environmental variable	Coefficient	
	PC1	PC2
Air temperature	0.531	0.222
Distance to sea	-0.366	0.928
Daylight hr at >4°C	-0.536	-0.260
Total daylight hr	0.545	0.151
Cumulative variance accounted for (%)	79.2	95.9

Figure 24. Plot of principal component scores of stream- and ocean-type populations along component axes 1 and 2. Distance to sea, mean annual air temperature, hours of daylight at fry emergence, and total annual daylight hours have been abbreviated as sea dist., temp., emergel., and total light respectively.



history tend also to be located in areas with a relatively short growing season (cold climates with low total daylight hours) and to be distant from the sea. By contrast, ocean-type chinook populations tend to be found in warmer areas with long growing seasons and closer to the sea (Fig. 24). In certain areas, however, (Northern B. C., Alaska, Yukon River) variation among populations in distance to the sea is not reflected in variability in juvenile life history pattern (PC2).

Discussion

Chinook salmon exhibit considerable variability in juvenile life history over a wide geographic range, but there is also much variability among nearby populations and even between populations within single tributaries. Broadly speaking there are two dichotomies where variation in juvenile life histories appears to change abruptly (see also Healey 1983). First, both ocean- and stream-type salmon are present south of about 56°N latitude, but only stream-type chinooks are found north of this point. Second, south of 56°N a "coastal-interior" dichotomy is apparent; stream-type chinook predominate in interior areas (e.g. upstream of Hell's Gate on the Fraser River and upstream of the Columbia-Snake confluence on the Columbia River), but ocean-type chinooks predominate in coastal streams. Perhaps more complete sampling would reveal a more continuous transition from ocean- to stream-type populations with latitude and with increasing distance from the sea. Many of the streams in the

transitional areas are remote and have only recently been the subject of investigation (Shepherd et al. 1986b). Sampling along coastal-interior transects is perhaps more complete, but there are still comparatively few "intermediate-type" populations.

What factors may explain the origin and maintenance of the distribution of juvenile life histories in the North Pacific? Possible factors include: (i) historical patterns of postglacial dispersal, (ii) environmental variability among populations in "growth opportunity", and (iii) selective factors driving divergence in juvenile freshwater life histories. Of the latter factor, changes in fishing mortality may influence selection of life history traits in salmonids since fishing is size-selective and size is correlated with many life history traits (Ricker 1981; Healey 1983, 1986). Therefore, in some cases fishing mortality may have influenced the relative proportions of stream- and ocean-type life histories, between years or populations, since the development of commercial fisheries for chinook. Since, however, the focus of this study was concerned with broad geographic patterns, changes in fishing mortality are not considered as a serious source of error or mechanism of divergence.

Fish species distributions and patterns of intraspecific variability along the north Pacific coast have been dominated by glaciation and access routes from various refugia (Lindsey and

McPhail 1986; McPhail and Lindsey 1986). Chinook salmon probably survived the last (Wisconsinan) glaciation in two major refugia: (i) "Beringia", defined as the lower Yukon River and exposed portions of the Bering Sea and Siberia, and "Cascadia", defined as areas south of glaciation west of the Continental Divide (Lindsey and McPhail 1986, McPhail and Lindsey 1986).

During deglaciation (beginning about 13,500 years ago), chinook dispersed from these northern and southern refugia along the Pacific coast (Lindsey and McPhail 1986). South of the Taku River (about 58° N) the majority of extant populations were probably colonized from Cascadia whereas Beringia provided source populations for rivers north of the Taku. Rivers such as the Taku, Copper, and Alsek in southeastern Alaska were probably colonized by chinook that persisted both in Cascadia and Beringia (Lindsey and McPhail 1986); in fact, southeastern Alaskan chinook are intermediate electrophoretically between western Alaskan/Yukon River populations and chinook in Cascadia (Gharret et al. 1987). Therefore, if chinook that survived glaciation in Beringia were primarily stream-type while both stream- and ocean-type chinooks persisted in Cascadia, the latitudinal distribution of life history types in the North Pacific may, in large part, reflect patterns of postglacial dispersal. The rather abrupt discontinuity in life history distribution at about $54-56^{\circ}$ N is suggestive of a pattern resulting from survival in, and dispersal from, isolated refugia and is similar to distributional peculiarities in some other

species (Withler 1985; Lindsey and McPhail 1986). Rivers such as the Alsek, Taku, and Copper in southeastern Alaska, and the Stikine through to the Skeena River in northern B.C. were probably colonized, in part, from Cascadian chinook (i.e. both stream- and ocean-type) yet they now have only stream-type chinook. This suggests, therefore, that some factors operating after postglacial dispersal probably also explain some of the variation in juvenile life history.

In fishes, growth rate and/or differentiation rate are important determinants of the timing of developmental transitions such as larval metamorphosis, maturation, and smoltification (Thorpe and Morgan 1978; Policansky 1983; Thorpe 1986; Clarke 1987; Chambers and Leggett 1988). Environmental factors that influence growth rate, in particular water temperature, have long been considered as direct causes of variability in duration of freshwater residence before smoltification (Rich 1925; White and Huntsman 1938; Randall et al. 1987). The studies by Clarke et al. (1988), Clarke (1987), Clarke and Withler (1987), and Thorpe et al. (1989) have shown that increased growth rate is accompanied by earlier attainment of smoltification within populations. In these studies, temperature and photoperiod were environmental factors manipulated to accelerate growth rate and smoltification timing in young chinook and Atlantic salmon. Over the geographic range of chinook, average temperatures decrease both with increasing latitude and distance from the sea. Along the coast and

particularly at lower latitudes, the number of days at which average temperatures exceed 4°C is greater than at inland or high latitude areas. In sum, growing season length, as a measure of "growth opportunity", is greater in low latitude coastal areas where ocean-type chinook predominate.

Clarke (1987) and Clarke and Withler (1987) showed that low daylight hours at first feeding increased growth and smolting rates in young stream-type chinook. Inland and higher latitude populations of chinook generally emerge and begin feeding later, under longer daylight hours, than coastal or lower latitude populations due to the combined effects of increasing latitude and lower incubation temperatures (Walker 1976; Raymond 1981; Shepherd et al. 1986b). Association between the distribution of chinook life histories and environmental variability, coupled with the results from studies addressing the links among water temperature, photoperiod, growth, and smolting rate (Clarke 1987; Clarke and Withler 1987; Thorpe et al. 1989), suggest that variation in environmental factors that influence "growth opportunity" is causally related to the distribution of juvenile life histories.

The importance of "growth opportunity" is also suggested in the study by Holtby (1988) who documented an increase in the proportion of coho salmon smolting at 1 year of age, rather than at 2 years, over an 8 year period in a small coastal B.C. stream. The decline in the average duration of freshwater

residence by coho was associated with increased stream temperatures and increased growth rates over the same time period (Holtby 1988). Similar inverse relationships between "growth opportunity" and smolting age are observed in other salmonids in both the north Pacific and Atlantic (Randall et al. 1987; Thorpe et al. 1989; Metcalfe and Thorpe 1989) and for latitudinal clines in metamorphosis timing in urodeles and anurans (Sexton and Bizer 1978; Smith-Gill and Berven 1979).

Anuran metamorphosis and salmonid smoltification are similar developmental transitions because both are dependent on growth rate, both are influenced by thyroxine, and both encompass wide variation in the size and timing of metamorphic climax (Smith-Gill and Berven 1979; Thorpe 1987). Smith-Gill and Berven (1979) illustrated how the duration of anuran larval periods was determined largely by environmentally induced variation in differentiation rate ($r^2 > 90\%$) whereas variation in growth rate was a much weaker determinant of timing of metamorphosis ($r^2 = 51\%$). Differentiation rate is influenced more strongly than growth rate by temperature in anurans; at low temperatures differentiation rate is more strongly retarded than growth rate such that metamorphosis occurs at larger sizes than at higher temperatures (Smith-Gill and Berven 1979). Therefore, warmer climates accelerate differentiation rate faster than growth rate, and attainment of metamorphic climax at smaller sizes (and younger ages) is increasingly probable (Sexton and Bizer 1978; Smith-Gill and Berven 1979).

A parallel observation is the predominance of generally smaller, ocean-type chinook smolts in warmer, low latitude, coastal climates. If smoltification is also differentiation rate dependent, then colder climates (higher latitudes, interior areas) might require longer periods of freshwater residence before the developmental transition of smoltification can be completed. Consideration of anuran metamorphosis and differentiation rate might explain the often poor correlations observed between growth rate and smoltification rate in some salmonid populations (Randall et al. 1987), i.e. perhaps differentiation rate would be a better predictor of smoltification rate.

As noted by Randall et al. (1987), there are a few problems with concluding that variation in the duration of freshwater residence is largely environmentally determined. First, there are numerous cases of both stream- and ocean-type chinook in populations geographically close to one another, sometimes occupying the same river (e.g. Fulton 1968; Carl and Healey 1984). At least some of these populations appear to experience similar environmental conditions yet they exhibit different juvenile life histories. Second, growth rate and age at smolting are not always negatively correlated especially in comparisons among populations (Ricker 1972; Randall et al. 1987).

Third, there is mounting evidence that stream- and ocean-type chinook are genetically distinct from one another. For instance, Healey (1983), Carl and Healey (1984), and Taylor (1989) summarized and presented data that suggested that stream- and ocean-type chinook are divergent in several traits, e.g. oceanic migration behaviour, morphology, allozyme frequencies, and rate of male precocial maturation. Many of these traits, and others (Chapter 1), appear to be functionally important for different durations of stream residence before seaward migration. Genetic variation in traits correlated with freshwater life history is to be expected if variability in duration of freshwater residence is itself inherited. Rich and Holmes (1928) found positive correlations between parent and progeny age, and size, at seaward migration in several Columbia River chinook populations. These correlations were observed even when juveniles were released into streams where the native salmon migrated seaward at a different time than the transplants. In addition, stream-type chinook are usually the progeny of "spring-run" adult salmon whereas ocean-type chinook are typically produced by "fall-run" adults (Rich and Holmes 1928; Ricker 1972; Carl and Healey 1984). Since adult chinook migration timing is inherited (Rich and Holmes 1928; Ricker 1972) the associated juvenile migration behaviours might also be genetically controlled. Finally, studies on species other than chinook salmon have also implicated genotype as a determinant of freshwater life history (Ricker 1972; 1978; Refstie et al. 1977; Thorpe and Morgan 1978; Thorpe et al. 1983).

It is, therefore, strongly suggested that variability in juvenile life history pattern is, at least in part, inherited. What factors, then, might drive and maintain divergence in duration of freshwater residence among populations?

Migration distance, as a measure of migration difficulty, has repeatedly been implicated as a major selective factor driving divergence in morphological, behavioural, physiological, and life history traits among anadromous fish populations (Robertson 1957; Ricker 1972; Schaffer and Elson 1975; Glebe and Leggett 1976; Yevsin 1977; Taylor and McPhail 1985a,b; Taylor 1989). Increased migration distance is associated with greater energy reserves, energy expenditure, and larger body size in adult salmonids (Rich and Holmes 1928; Gilhousen 1980; Schaffer and Elson 1975; Thorpe and Mitchell 1981), and increased prolonged swimming capabilities in juveniles (Tsuyuki and Williscroft 1977; Taylor and McPhail 1985b). These studies taken together suggest that increased migration distance imposes greater energetic demands on migrants and, given increased prolonged swimming capability with increasing fish size (Brett and Glass 1973; Webb 1978), larger individuals are probably better able to complete longer, arduous migrations.

Predation on freshwater migrants can be substantial (Hunter 1959; Wood 1985) and longer smolt migrations may impose greater freshwater predation risk (e.g. Larsson 1985; Ruggertone 1986).

Since smaller salmon are more susceptible to predation (e.g. Hargreaves and LeBrasseur 1987), larger smolts might experience lower mortality rates from predation during migration. In addition, osmoregulatory ability increases with fish size (e.g. McCormick and Naiman 1984b) and larger size at ocean entry probably enhances physiological adjustment to high salinities after energetically demanding migrations.

These potential size-related determinants of "migration success" all suggest that increasing migration distance might select for increased size at migration in anadromous populations. Interestingly, Clarke (1987) found that he could manipulate photoperiod to increase the rate of growth and smolting in stream-type chinook, but these salmon, from a population 600 km upstream from the sea, weighed 10 g at smoltification. By contrast, the ocean-type chinook studied by Clarke were from a coastal stream and they smolted at 5 g.

Prolonged swimming ability and osmoregulatory ability may also be reduced at low water temperatures (Brett 1967; Beamish 1978; Virtanen and Oikari 1984). Therefore, large size at ocean entry might be favoured by selection in chinook populations located in cold climates.

In sum, there is considerable potential for selection on size at migration in chinook populations. Consequently, environmental variability among populations probably results in

selection for optimal smolt sizes that vary among populations (Ricker 1972). Except in situations where populations have similar smolt sizes, control of smoltification timing from differences in environmental "growth opportunity" may not be the ultimate cause of variability among populations in duration of freshwater residence. Growth opportunity may be a proximate factor, controlling the rate at which population-specific size thresholds are achieved.

Selection for size at migration coupled with selection for migration during seasonal migration "windows" (Walters et al. 1978; Lannan 1980; Bilton et al. 1982; Godin 1982; Miller and Brannon 1982; Holtby 1988) might promote divergence in alternative juvenile life histories. In populations where individuals achieve smolt size early, owing to favourable growth conditions and/or small size thresholds, selection may favour an ocean-type life history given favourable growth conditions in estuaries relative to freshwater habitats (Reimers 1973; Bachman 1982; Congleton et al. 1982; Kjelson et al. 1982). By contrast, in areas where larger smolt size is associated with higher survival, and/or growth conditions are limited such that threshold sizes are not reached by the spring/summer migration window, natural selection may favour extended stream residence rather than seaward migration at unfavourable times.

In conclusion, covariation between geographic distribution of stream- and ocean-type chinook and environmental factors

influencing "growth opportunity", coupled with experimental results demonstrating effects of environmental variables on smolting rate, are consistent with environmental modulation (Smith-Gill 1983) contributing to variability in duration of freshwater residence among chinook populations. Variation in juvenile freshwater life histories is, however, at least partially inherited, and a dominant role for modulation of smoltification rate by environment is probably constrained by selection for both size at migration and for seasonal optima in the timing of downstream migration and ocean entry.

CHAPTER 3: BEHAVIOURAL INTERACTION BETWEEN JUVENILE COHO AND CHINOOK SALMON AND CHINOOK LIFE HISTORY

Introduction

This chapter is concerned with evaluating the hypothesis that behavioural interaction with juvenile coho salmon (Oncorhynchus kisutch) influences duration of freshwater residence by chinook. Given the proximity of coastal streams to productive estuarine areas and the ability of chinook to acclimate rapidly to saline waters (Weisbart 1968), coastal chinook might undertake early migrations to reside in estuarine areas to reduce the costs of behavioural interaction with coho. More generally, variability in biotic (i.e. competitive) environments could explain some of the variation in duration of freshwater residence among chinook populations.

Over their geographic range, juvenile chinook salmon may coexist in freshwater habitats with at least four other species of Oncorhynchus, as well as steelhead and cutthroat trouts (Salmo gairdneri and S. clarkii), charr (Salvelinus malma and S. alpinus), and various whitefish (Coregoninae). Chinook may also occur sympatrically with several cypriniform fishes (minnows and suckers), at least one of which may interact behaviourally with chinook (i.e. redbside shiner, Richardsonius balteatus (Hillman et al. 1988)). For several reasons, however, interaction with coho salmon has the greatest potential to

influence freshwater residence behaviour of chinook. Coho have a natural distribution that is broadly similar to that of chinook in the north Pacific. Also, like chinook salmon, coho are anadromous and reside primarily in rivers and streams, but generally for a longer time (at least 1 year). Given their prolonged period of freshwater residence and their territorial and aggressive nature, coho appear be the most "stream-type" of eastern Pacific Oncorhynchus (Hoar 1976; Miller and Brannon 1982).

Comparative studies of morphology, physiology, behaviour, and biochemical genetics have indicated that coho and chinook are probably more closely related to each other than to the other species of Oncorhynchus (Brett 1952; Hikita 1962; Tsuyuki and Roberts 1966; Utter et al. 1973; McCormick and Saunders 1987; Thomas et al. 1986). Studies of behaviour and general ecology also suggest many similarities between coho and chinook (Rousenfell 1958; Reimers 1968; Stein et al. 1972; Johnson 1981; Johnson and Ringler 1981). Given their sympatric occurrence in many areas and their similarities in behaviour and ecology, behavioural interactions between coho and chinook might well influence aspects of their freshwater life histories.

Coho and chinook are found together in many streams in southern British Columbia, Washington, and Oregon. Coastal streams commonly support both coho and ocean-type chinook, but in interior streams, where stream-type chinook predominate, coho

populations are smaller and less abundant (Aro and Shepard 1967; Atkinson et al. 1967). Stein et al. (1972) documented behavioural domination of chinook by coho in a small, coastal Oregon stream. These authors concluded that interaction with coho impacted negatively on chinook.

In many species, including fishes, a behaviourally dominant species has been shown to influence the habitat use and dispersal tendencies of a subordinate (Orians and Willson 1964; Brown 1971; Jaeger 1971; Werner and Hall 1977; Gaines et al. 1979; Hixon 1980; Fausch and White 1981; Linzey 1984). Evidence for such "asymmetric" relationships (Morse 1974) is widespread in salmonid fishes. In several instances it has been suggested that behavioural domination of one species by another was responsible for differences in resource use (Kalleberg 1958; Hartman 1965; Northcote and Nilsson 1981; Cunjack and Green 1984; Glova 1986; Hindar et al. 1988).

If the hypothesis that coho influence the freshwater residence behaviour of chinook is correct, then it is expected that: (i) coho should be dominant during behavioural interaction with chinook, and (ii) coho should influence both the use of microhabitats and the residence tendency of chinook in stream environments. These expectations were evaluated by: (i) examining behavioural interaction and dominance relationships between chinook and coho juveniles under controlled conditions and (ii) assessing the influence of coho on habitat use and

emigration tendency of chinook in undisturbed and experimentally manipulated populations.

1. SOCIAL INTERACTION BETWEEN JUVENILE CHINOOK AND COHO SALMON

Methods

Behavioural observations

To study behavioural interaction and relative dominance between the species, juvenile chinook and coho salmon were observed together in stream tanks. Behavioural tests were conducted in 1985 using wild chinook fry from Slim Creek (stream-type) and Harrison River (ocean-type) and coho fry from Tin Can Creek, a small stream draining into the Strait of Georgia near the north arm of the Fraser River estuary. During 1986, laboratory-reared chinook from Slim Creek, Eagle, Harrison, and Nanaimo (fall run) rivers were studied with coho from Black Creek, a small stream draining into the Strait of Georgia near Courtenay, B.C. on east-central Vancouver Island.

Behavioural observations ($10-11^{\circ}\text{C}$) were conducted on each population using eight chinook and eight coho fry placed together in stream tanks. The tests were identical to the single species tests described in Chapter 1 and consisted of recording behaviours twice daily for five consecutive days. Behavioural observations were in two categories for each species towards the other: (1) overt behaviours (approach, nip, charge, and chase) and (2) display behaviours (lateral and wigwag displays). In each test mean sizes of coho and chinook fry were

within 1 mm of each other and ranged between 34 and 37 mm (SL).

Statistical analysis

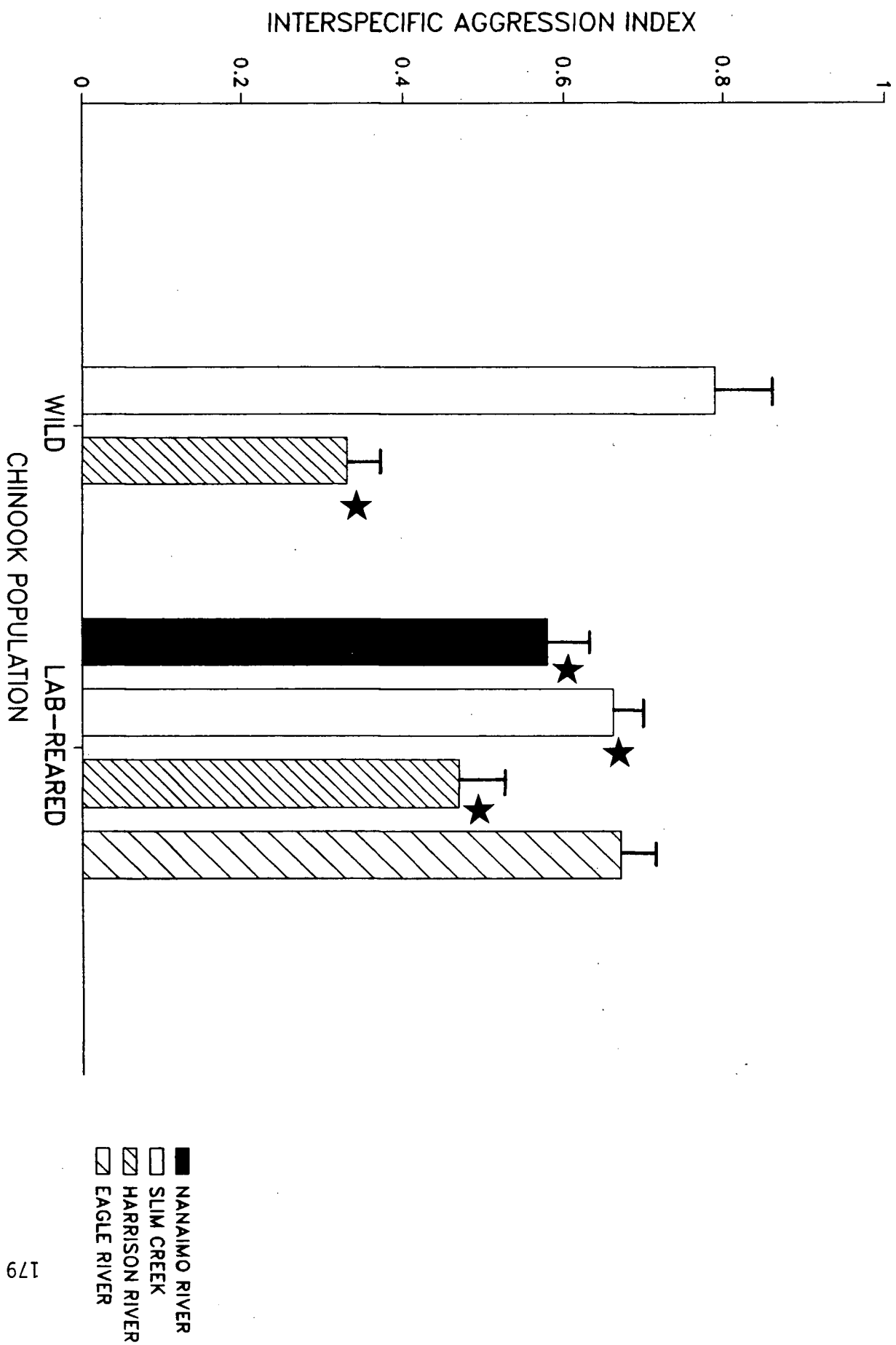
Data analysis consisted of summing the overt and display behaviour durations by species and calculating an "interspecific aggression index" for each observation period. This index was the ratio of all aggression by chinook directed towards coho to that of coho directed towards chinook. Any index of value less than 1, therefore, indicates greater aggression directed towards chinook by coho than vice versa and suggests domination of chinook by coho. Aggression indices were calculated for each chinook population and compared to the value 1 by t-tests.

Results

In the stream tanks, coho fry tended to dominate chinook fry (Fig. 25). Interspecific aggression indices in all trials were below 1, indicating coho spent more time directing aggression towards chinook than vice versa. Coho fry tended to initiate most aggressive encounters by charging and nipping chinook that entered "territories" of individual coho. By contrast, most chinook aggression appeared to be retaliatory; they responded to direct attacks by coho with brief displays, approaches, and then fled.

During behavioural observations, a dominant individual

Figure 25. Interspecific aggression indices between coho and chinook salmon fry. Values (mean \pm SE, n=3 for each population) significantly less than 1 (denoted by a star) indicate domination by coho salmon. Slim Creek and Eagle River chinook are stream-type, Nanaimo and Harrison river salmon are ocean-type.



could usually be identified as that which "patrolled" the upstream portion of the tank section (where food was introduced) and initiated most aggression. In trials with wild and laboratory-reared salmon this individual was always a coho. In a few cases where a single dominant could not be identified, the choice was usually between 1-3 coho fry. A chinook was never the dominant individual in the stream tanks. Chinook fry (and subdominant coho) were more restricted in their stream tank distribution; they were usually found along the tank margins or in the downstream two-thirds of each tank.

While coho tended to dominate chinook, there appeared to be differences among the four chinook populations in the degree of "domination" by coho. Slim Creek chinook did best against coho while both wild and laboratory-reared fish from Harrison River had the lowest interspecific aggression indices (Fig. 25).

2. MICROHABITAT USE BY JUVENILE CHINOOK SALMON IN ALLOPATRY AND SYMPATRY WITH COHO SALMON

Methods

Snorkelling surveys to identify microhabitats occupied by juvenile salmon were conducted in four study streams during two summers. During 1985, microhabitat use by allopatric chinook from Slim Creek and by chinook sympatric with coho salmon in the Eagle River was recorded. Microhabitat surveys were expanded in 1986 to include juvenile salmon in Eagle River, Slim Creek, allopatric chinook in Walker Creek (see Fig. 1, p. 11), and coho and chinook in the Salmon River. Chinook in all streams have a stream-type life history. Microhabitats were recorded during August when stream flows, and hence habitat area, were approaching annual minima in the study streams, and thus boundaries between habitat types were distinct.

Transect sites were selected in sections of each river such that a similar range of habitats was sampled in each. Transects were 10 m in length and located in "sidechannel", "pool", "run", and "riffle" habitats 24 h prior to observation. The habitat types were distinguished by water velocity: sidechannels (0-5 cm/s), pools (5-15 cm/s), runs (15-25 cm/s), and riffles (> 30 cm/s), but in the same sequence habitats also varied in decreasing average depth, amount of cover, and increasing average substrate sizes. Starting about 10 m downstream of a

transect, I swam upstream and marked, with flagged spikes, the "holding" or "focal" position (Wickham 1967, cited in Everest and Chapman 1972) of each fish encountered within 1.5 m of either side of the transect. Physical characteristics (Table 23) of each "spiked" microhabitat were recorded after swimming transects. The variables measured were those that have been found to be important determinants of microhabitat use by stream fishes (Everest and Chapman 1972; Moyle and Baltz 1985; DeGraaf and Bain 1986; Grossman and Freeman 1987). All water velocities were determined with Betzel flow meters (Everest 1967). Substrate was quantified by visually estimating the relative proportions of two dominant categories (Table 23) within a 15 cm radius of each focal position. A summary substrate score was expressed as the code for the most dominant category followed by a decimal and the code of the next most dominant substrate category. For example, a code of 5.2 indicates a microhabitat characterized primarily by gravel and secondarily by mud.

To determine if fish were using microhabitats which differed from those generally available, ten positions along the length of each transect were chosen from a random number table (distance along transect, lateral direction and distance from transect, distance above substrate). The characteristics of these "random" positions were recorded to compare with those occupied by fish.

Microhabitats were recorded for those fish of approximately

Table 23. Physical measurements recorded at fish microhabitats.

Variable	Definition
Focal velocity (V)	Water velocity
Maximum velocity (Vmax)	Maximum water velocity within 0.3 m of focal point
Water depth (Z)	Water depth
Distance to bottom (Zb)	Distance of fish to stream bottom
Distance to cover (Zcov)	Straight line distance between focal point and nearest cover under which fish is invisible from above
Distance to shore (Zsh)	Straight line distance to nearest shoreline
Substate: 1	Detritus
2	Mud
3	Silt
4	Sand
5	Gravel (2-5 cm)
6	Gravel (6-10 cm)
7	Rubble (11-20 cm)
8	Rubble (21-40 cm)
9	Rock (> 40 cm)

the same size to avoid possible complications from differences in microhabitat use due to variation in fish size. A size range of 60-75 mm was chosen because within this range size-dependent microhabitat variation is minor (Everest and Chapman 1972). Fish sizes were estimated while snorkelling by comparison with a reference rule. Water temperatures in all streams were between 16-18⁰ C during microhabitat surveys.

Statistical analysis

Because stream fishes probably do not select habitats on the basis of single attributes and many factors appear to be related to fish distribution (Moyle and Baltz 1985; Grossman and Freeman 1987), principal components analysis of the data correlation matrix was used to summarize variation in habitat use. A component score was then calculated for each fish position. Subsequent analyses of mean scores involved analysis of variance for each habitat axis and multivariate analysis of variance for combined axes. Pairwise comparisons of mean scores between species and populations were conducted with Bonferroni tests (Dixon 1986). Multivariable relationships among the various groups were summarized by the Mahalanobis D^2 . All computations follow Fox and Glure (1976), Pimentel (1979), and Dixon (1986).

Results

Principal components analysis of the microhabitat data for both 1985 and 1986 surveys accounted for about 75% of the total variability in three axes (Table 24). For both years, focal water velocity, maximum water velocity, and substrate size contributed most to differences in microhabitats along the first component axis (35 and 37% of total variance respectively). During both years, coefficients along the first axis were all positive indicating increasing magnitude for all variables.

The second axis for both years suggested the importance of water depth and fish depth as factors contributing to habitat variability. Water depth and fish depth measures (negative signs) appeared to contrast with all other variables (positive signs, except for distance to shore-1986). Thus, the second component axis suggests a gradient of microhabitats from deep, low velocity water areas close to cover and shore with small particle substrates to areas of shallower, faster water distant from shore and cover objects with predominantly larger particle substrates.

The third axis was different in the two years. In 1985, maximum water velocity contrasted with distance to cover, but in 1986 distances to cover and to shore contrasted with substrate size and contributed most to microhabitat variation.

Table 24. Principal components analysis of microhabitat use by juvenile chinook and coho salmon. Also indicated are the total variances contributed by each variable over the three axes.

	Variable coefficient			Total Variance
	Component axis			
	1	2	3	
<hr/>				
1985				
<hr/>				
Z	0.26	-0.64	0.10	83.8
Zb	0.06	-0.70	0.21	82.4
V	0.47	0.08	-0.12	75.9
Vmax	0.48	-0.03	-0.50	86.5
Zsh	0.40	0.24	0.39	70.2
Zcov	0.32	0.21	0.68	59.1
Substr	0.46	0.12	-0.25	52.7
Percent of variance	35	23	15	73
<hr/>				
1986				
<hr/>				
Z	0.28	-0.63	0.01	81.1
Zb	0.23	-0.67	0.11	81.3
V	0.52	0.27	0.12	82.6
Vmax	0.52	0.28	0.14	83.2
Zsh	0.32	-0.04	-0.48	48.0
Zcov	0.26	0.07	-0.73	69.7
Substr	0.39	0.08	0.44	58.2
Percent of variance	37	22	15	74

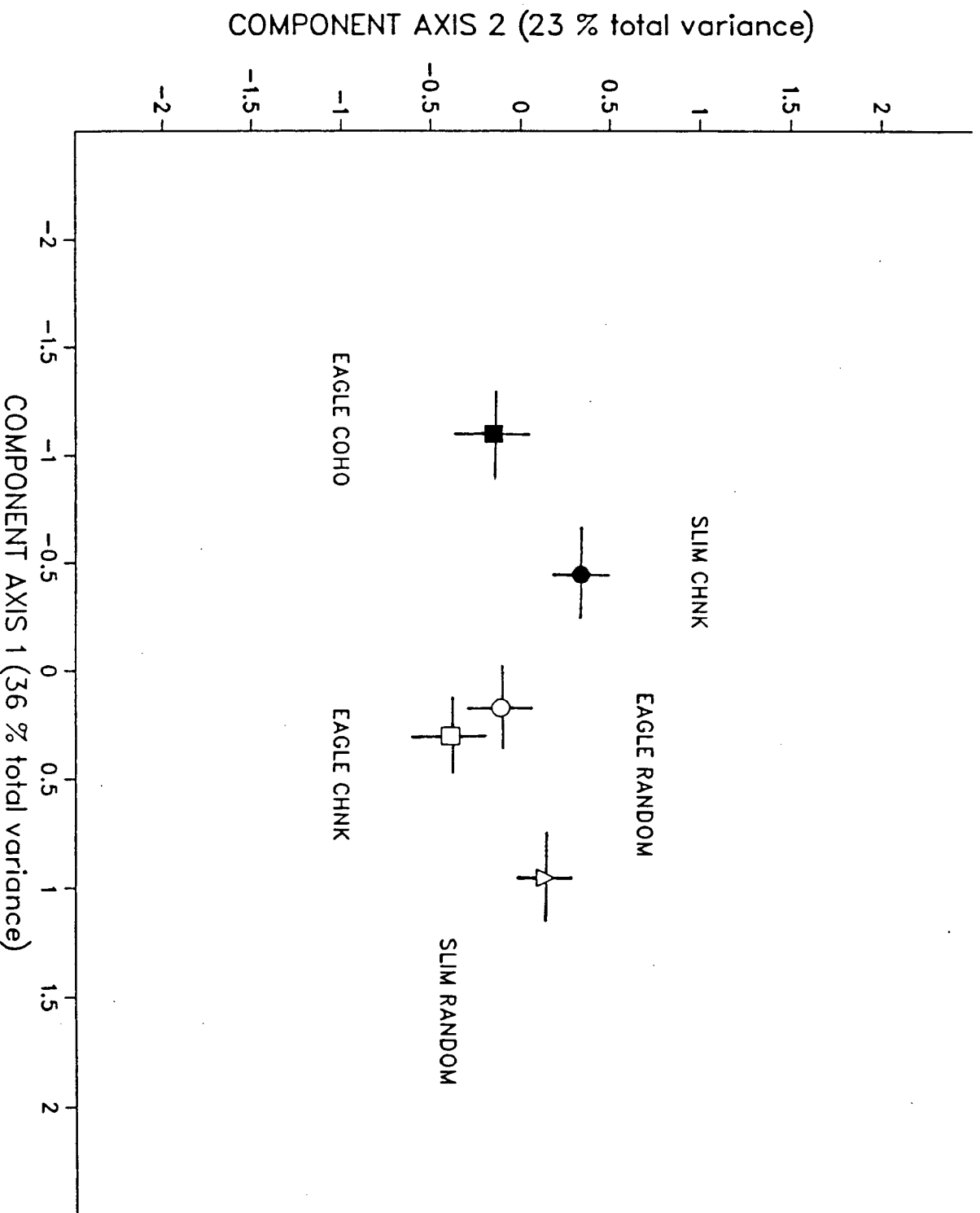
Following the methodology of Pimentel (1979, p. 67), the variables which contributed most to microhabitat variability over the first three axes are summarized by the sum of the variances accounted for by each. This analysis (Table 24) indicates that overall, the various water velocity and water depth measures were the most important determinants of microhabitat variability during 1985 and 1986 (cf. Moyle and Vondracek 1985).

In 1985, Slim Creek chinook were found in microhabitats of slower water velocity, shallower water, closer to shore and cover objects, and over smaller particle substrates than "random" positions (Fig. 26, PC 1, $P < 0.001$). Eagle River chinook were found at microhabitats similar to random positions along the first axis ($P > 0.05$). By contrast, Eagle coho microhabitats were characterized by slower water velocities, shallower water, greater proximity to cover and shore, and smaller particle substrate classes than at random focal points (Fig. 26, $P < 0.001$).

In the Eagle River, chinook salmon were found at greater values for all variables than coho along the first component axis ($P < 0.001$, Fig. 26). The "microhabitat separation", however, between Eagle coho and Slim chinook was less than between coho and chinook in sympatry in the Eagle River (0.85 vs 1.35, Fig. 26).

Figure 26. Plots of mean (\pm SE) principal component scores summarizing microhabitat use by juvenile coho and chinook salmon, 1985.

MICROHABITAT USE: 1985



Along PC axis 2, there were no differences in the microhabitat features of random focal points and those occupied by juveniles (all $P > 0.05$) nor was there evidence of significant microhabitat differences between sympatric coho and chinook in both streams ($P > 0.1$). Juvenile chinook in sympatry, however, had lower values along PC2 (i.e. greater water depths) than Slim Creek fish ($P < 0.001$, Fig. 26). Along the third component axis, no significant microhabitat differences between sympatric coho and chinook were detected ($P > 0.05$). Eagle coho had higher PC3 values (higher maximum water velocities, larger substrates) than at random positions ($P < 0.005$), but no differences existed between Eagle chinook and random positions ($P > 0.05$). Slim Creek chinook had a similar distribution to random positions along PC3 ($P > 0.05$).

Over the first three component axes combined (Table 25), microhabitat use by Eagle coho and chinook and chinook from Slim Creek were significantly different from random microhabitats (all $P < 0.005$). Microhabitat use by sympatric coho and chinook was different ($D^2 = 0.79$, $P < 0.001$), but allopatric and sympatric chinook were more similar in microhabitat use to each other than either was to coho ($D^2 = 0.56$). There was, however, a smaller difference between coho and Slim (allopatric) chinook microhabitats than between sympatric coho and chinook ($D^2 = 0.66$ vs $D^2 = 0.79$).

In 1986, microhabitats of sympatric chinook in the Eagle

Table 25. Matrix of Mahalanobis distances among microhabitat centroids for juvenile chinook and coho salmon, 1985. Values are based on the first three component axes and all comparisons are significant at $P < 0.001$. Ec=Eagle coho, Eck=Eagle chinook, Er=Eagle random, Sr=Slim random, Sck=Slim chinook.

	N	Ec	Eck	Er	Sr	Sck
Ec	110	-				
Eck	122	0.79				
Er	119	0.82	0.23			
Sr	115	1.58	0.35	0.55		
Sck	126	0.66	0.56	0.60	0.42	-

and Salmon rivers were similar to random microhabitats (PC1, $P > 0.05$), but chinook from Slim and Walker creeks and coho from Eagle and Salmon rivers used microhabitats distinct from random microhabitats ($P < 0.001$, Fig. 27). As in 1985, sympatric coho and chinook utilized different microhabitats; chinook were found in faster, more open water areas than coho ($P < 0.001$).

Notable microhabitat differences along PC 2 were between Salmon River chinook and coho; Slim and Walker chinook and Salmon chinook and between both populations of sympatric chinook (all $P < 0.001$, Fig. 27). No significant differences in microhabitats were evident along PC 3.

Over the first three microhabitat axes combined, coho and chinook from all streams used areas that differed significantly from random microhabitats, and sympatric coho and chinook used different microhabitats (Table 26). In fact, microhabitat differences between coho and chinook were such that, microhabitat use by chinook in the Eagle River was more similar to microhabitat use by chinook in the Salmon River than to Eagle River coho (and vice versa, Table 26). By contrast, allopatric chinook in both Walker and Slim creeks were found in microhabitats more similar to those of coho than to those of chinook from the Eagle or Salmon rivers (Table 26).

While there are general differences in microhabitat use among various populations of chinook and coho, there was also

Figure 27. Plots of mean (\pm SE) principal component scores summarizing microhabitat use by juvenile coho and chinook salmon, 1986.

MICROHABITAT USE: 1986

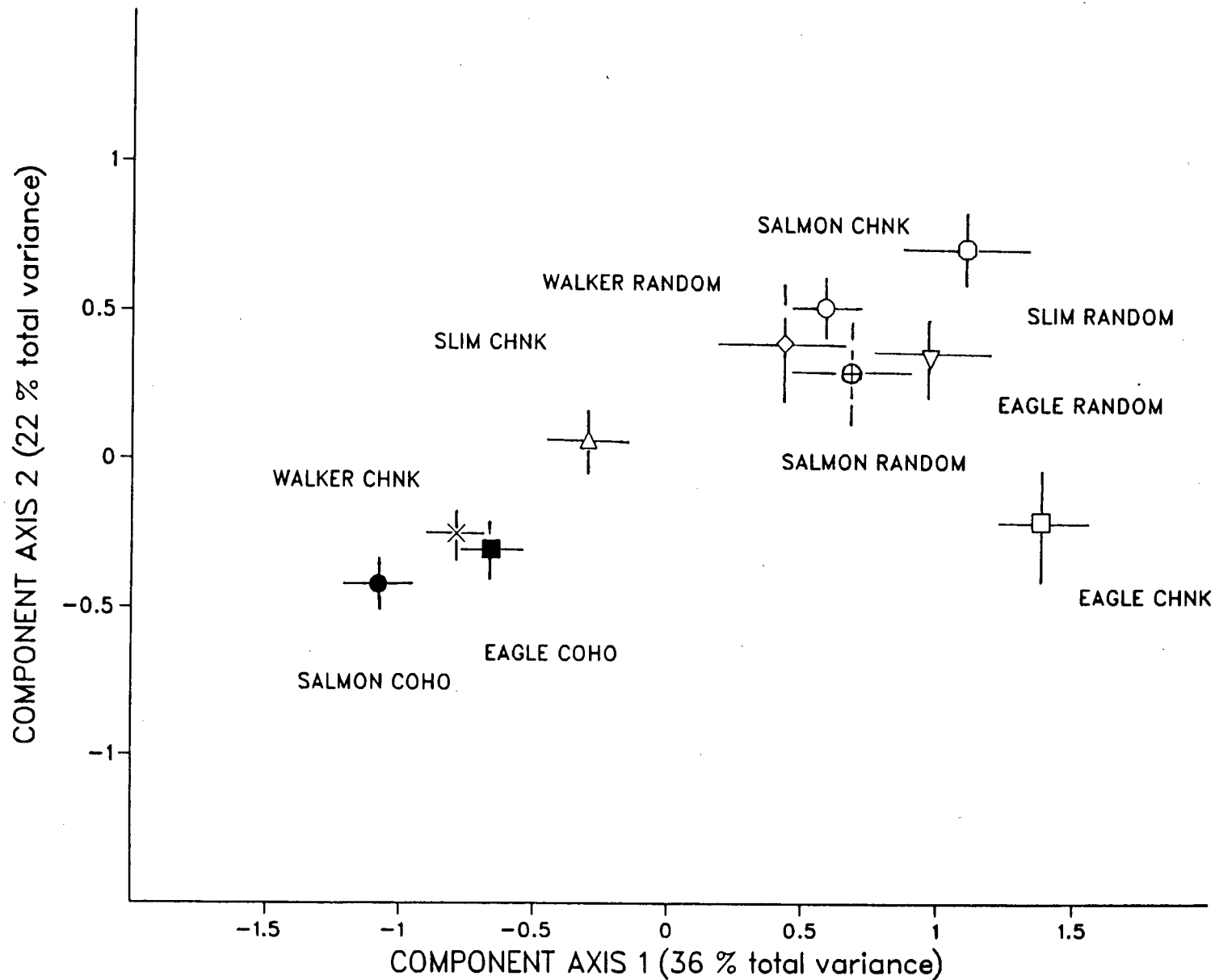


Table 26. Matrix of Mahalanobis distances among microhabitat centroids for juvenile chinook and coho salmon, 1986. Values are based on the first three component axes and all comparisons are significant at $P < 0.001$. Ec=Eagle coho, Eck=Eagle chinook, Samc=Salmon coho, Samck=Salmon chinook, Sck=Slim chinook, Wck=Walker chinook.

	N	Ec	Eck	Samc	Samck	Sck	Wck
Ec	150	-					
Eck	158	2.49	-				
Samc	156	0.15	3.68	-			
Samck	150	1.53	0.67	2.49	-		
Sck	180	0.19	1.61	0.62	0.65	-	
Wck	166	0.10	2.77	0.28	1.75	0.30	-

considerable variability within groups. For instance, consistent interspecific differences in microhabitat use were evident along transects with diverse characteristics (e.g. riffles running into pools), but considerable overlap in microhabitat use by sympatric species was observed in more homogeneous habitats (e.g. "run-like" habitats). In such habitats, water velocities and water depths occupied by coho and chinook were typically intermediate to those apparently preferred by each species.

3. EXPERIMENTAL INTRODUCTIONS OF JUVENILE COHO AND CHINOOK SALMON

Methods

Experimental animals

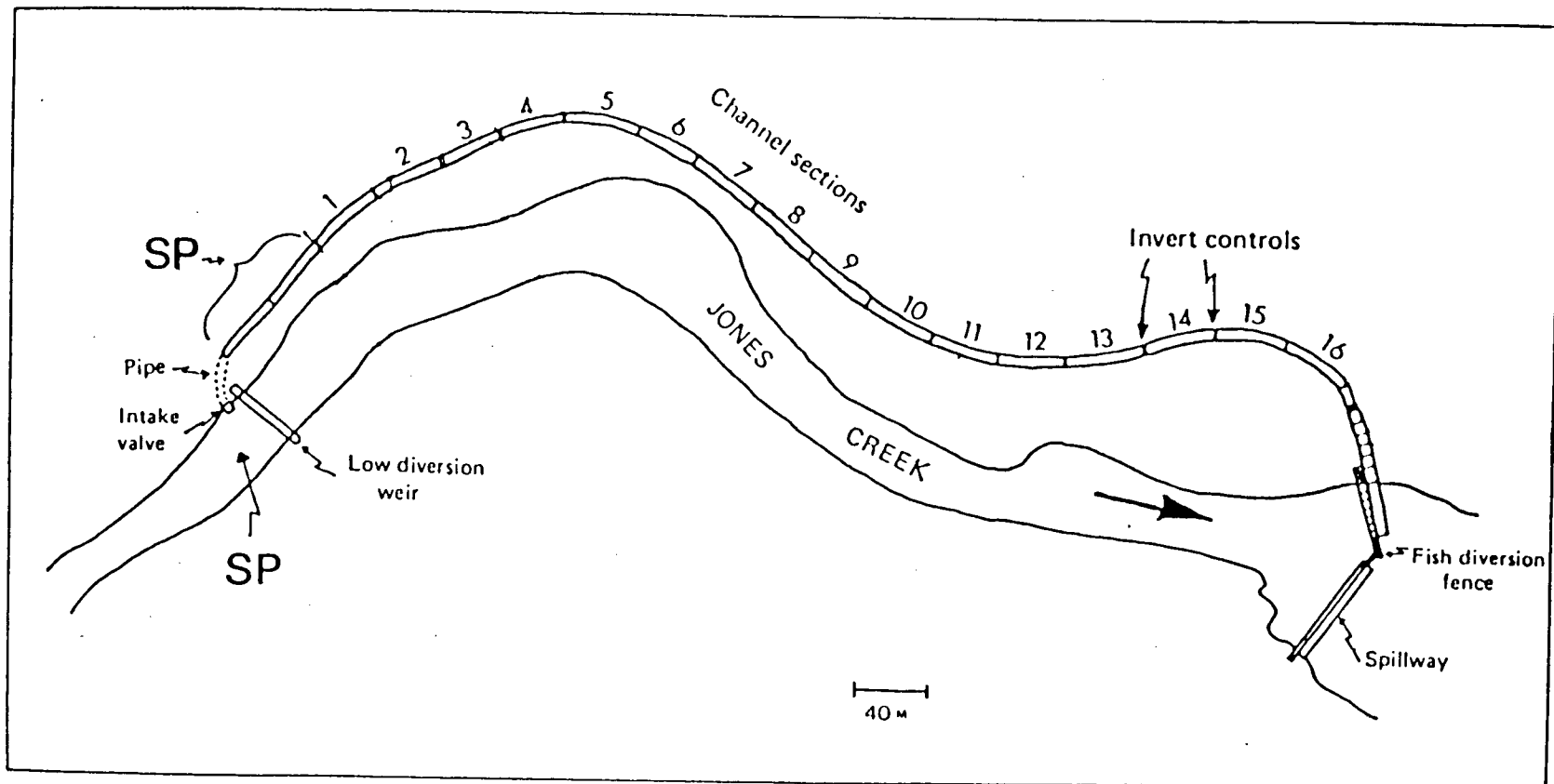
Juvenile coho and chinook salmon used in the experimental introductions were incubated and reared in the laboratory at the University. They were progeny from crosses of a number of males and females from Slim Creek, Eagle River, and Black Creek as described in Chapter 1.

Experimental facility

The experimental stream was a Fisheries and Oceans Canada pink salmon (O. gorbuscha) spawning channel located near Hope, B.C., about 150 km east of Vancouver (Fig. 28). The history, design, and operation of the controlled flow channel is detailed by Hourston and MacKinnon (1956) and Fraser and Fedorenko (1983).

Jones Creek channel is approximately 580 m long, 5 m wide and consists of sixteen sections, each 40 x 5 m (Fig. 28). Each section is demarked at its downstream end by "drop falls", constructed from railway ties, which provide a drop between adjacent sections of 10 to 30 cm. Thus, each section has a

Figure 28. The Jones Creek spawning channel facility..
SP=settling ponds. Experiments were conducted in channel
sections 3, 4, and 5 and the arrow indicates direction of
water flow. Redrawn from Fraser and Fedorenko (1983).



controlled water depth and velocity. The gravel within each section is graded and between 4 and 6 cm in diameter. A canopy of deciduous trees and salmonberry covers about 90% of the channel length. Intake to the channel from Jones Creek is controlled by a 1.0 m gate valve (Fig. 28) which delivers water into a 40 x 4 x 4 m settling pond at the head of the channel. The gate valve was opened 3.5 wk before experiments started to allow benthic invertebrates to colonize the substrate.

Experiments were restricted to three adjacent channel sections (Nos. 3, 4, and 5 according to Fig. 28) which were selected for their general similarity in water depth, water velocity, and amount of overhead cover. Each section was isolated from the section immediately up- and downstream by fences of 2.4 x 1.0 m panels as outlined in Colin and Tutty (1979). Panels were constructed of 5 x 8 cm wood frames onto which 0.6 cm wire screening was fastened. To further support the fence panels and to make them "fish-tight", a 1 m wide apron of polyethylene sheeting was fitted downstream along the bottom of each panel and anchored with sandbags.

Any fish moving downstream in the channel sections would be directed along the panels and into a trough which led to a live box (0.6 x 0.6 x 0.9 m). Fences were placed such that each section was 150 m in area (30 x 5 m).

A grid of bailer twine was suspended along the length of

each section at 20 cm intervals, 50 cm above the water surface. This grid prevented common mergansers, Mergus merganser, from entering the channel sections and preying on introduced salmon. At the downstream end of experimental section No. 5, a simple Wolf trap (Wolf 1950) was constructed to enumerate fish which may have escaped under the fence traps in each section. The experimental stream sections were considered to be "fish tight" because no fish were observed in the Wolf trap nor outside the fence traps during regular underwater surveys.

Experimental design and protocol

The potential for interaction with juvenile coho to influence habitat use and residence tendency of chinook was examined by experimentally testing three hypotheses in a 2 x 3 factorial design: (1) chinook emigration from the experimental sections when stocked with coho salmon is similar to that when chinook are stocked alone, (2) chinook habitat use when stocked with coho is similar to that when chinook are stocked alone, and (3) chinook from Slim Creek (allopatric) and the Eagle River (sympatric with coho) are similar with respect to (1) and (2) above. The experiment consisted of two levels of a "chinook population" factor (Slim and Eagle chinook) and three levels of a "species introduction" factor (chinook introduced alone at 1 fish/m², chinook plus coho each introduced at 1 fish/m², and chinook introduced alone at 2 fish/m²). Each treatment combination was replicated four times for a total of 24

introduction trials (2 populations x 3 species introduction treatments x 4 replications each). Mid-summer underwater censuses of the test populations in their natal streams and pilot introductions in the spawning channel suggested that initial fish densities of 1-2 fish/m² were appropriate.

Two days before an experiment, fish were isolated in holding tanks at the University, starved for 24 h, and placed in 75 l buckets lined with plastic bags three-fifths filled with water. The fish were transported to the Jones Creek experimental facility, held in the bags to allow the temperature to reach that of the channel water (about 0.5 h), and released into holding cages to be held overnight before being fed the next morning.

The morning after arrival at Jones Creek, 50 fish were dipnetted from the holding cages, measured (FL), returned to the holding cages and fed once. Twenty-four h later, they were introduced to quiet pools in each experimental section. Juvenile salmonids introduced into novel habitats often respond immediately, or within a few hours, by migrating downstream (Jenkins 1971; Bilby and Bisson 1987). To minimize the influence of the "novel habitat" factor on fish behaviour and habitat use, the traps at the end of each section were closed for the first 24 h after the fish were introduced to prevent them from emigrating. At 8:00 PM the following day and 8:00 AM, 12:00 Noon, and 8:00 PM for the next 6 d, fish entering the

downstream traps were enumerated and measured (FL).

Habitat use by juvenile coho and chinook was recorded over the trial periods by recording their occurrence in "pool" and "riffle" subsections in each channel section. Transects were established perpendicular to the water flow every 5 m along the length of each section. Water velocity and water depth were measured along these transects using an Ott current meter and a meter stick. Based on these measurements, subsections were selected in each section to represent "pool-" (velocities ≤ 15 cm/s) and "riffle-like" (velocities ≥ 25 cm/s) habitats. Pool subsections also tended to be deeper than riffles (Table 27). Water velocity and water depth were selected as factors to be varied because of their importance in contributing to microhabitat variability of wild salmon (Table 24). Eight subsections (four pools and four riffles, each 1.5 x 1.5 m) in each experimental section were marked by flagging their corners. Percent cover was estimated by eye and supplemented by the addition of rock and wood objects to a maximum of 30% of the surface area in pool habitats. In all riffle subsections, rock and wood instream cover was less than 30%.

Habitat use by coho and chinook was monitored by counting the number of fish in each subsection during snorkel censuses. Censuses were conducted on day 2 and day 4 of each trial at 10:00 and 14:00 for a total of four repeated counts per replicate. Repeated observations were used to account for

Table 27. Average water velocities and water depths in subsections of Jones Creek experimental stream sections. In each section, the values are the means (SE) of four pools and four riffles. Velocities measured in cm/s, depths measured in cm.

Physical variable	Stream section	Pool	Riffle
Velocity	3	8.7 (2.1)	22.0 (1.6)
Depth	3	30.6 (2.4)	24.4 (2.5)
Velocity	4	8.3 (2.2)	24.2 (3.6)
Depth	4	35.3 (2.5)	37.4 (1.4)
Velocity	5	10.7 (2.8)	26.4 (2.1)
Depth	5	32.1 (1.7)	26.2 (1.5)

volatility of habitat use by the salmon. During each census and for 1 h thereafter, the downstream traps were closed so that fish could not emigrate.

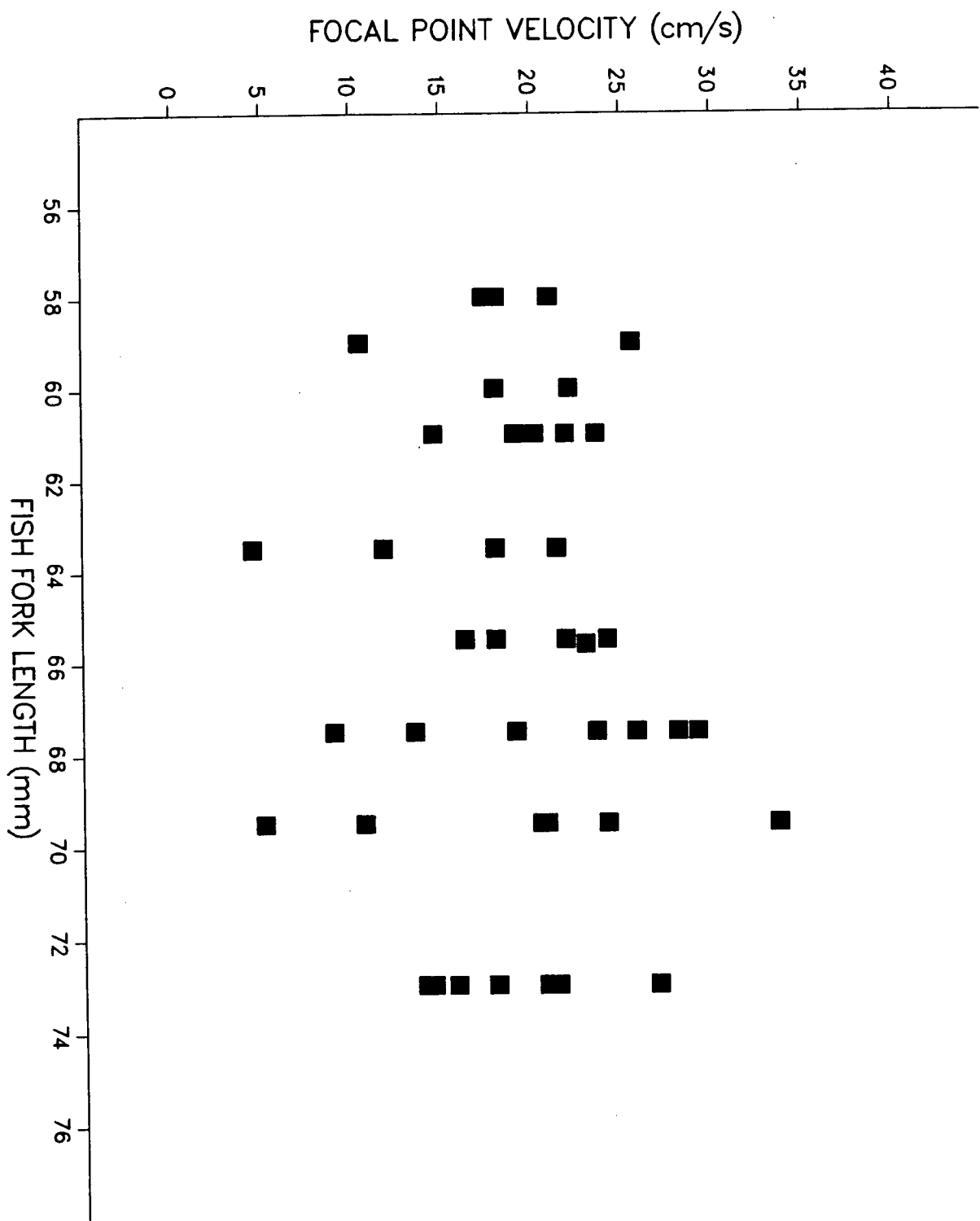
At the end of each trial a final census was conducted to determine the number of fish remaining in each section. The channel was then drained by closing the intake valve and all fish remaining in the channel were enumerated and preserved. Final census counts, or the number of fish collected when the sections were drained (whichever was greater), plus the number of fish enumerated in the traps were used to estimate "fish loss" from the sections. An average of 7.7 (± 0.94 SE) % of initial fish introduced were unaccounted for at the end of each trial (range 0-20%). Gravel size (4-6 cm diameter) was such that many fish were able to penetrate the gravel as the channel drained making their recovery difficult. "Unaccounted for" fish were most likely lost within the channel substrate rather than through escape or predation.

Water temperatures during the experiments ranged from a daily average of about 9°C in mid-May to 15°C in July. While in the channel, experimental populations of salmon fed on natural drift. Overnight drift samples indicated the presence of larval mayflies, Ephemerella spp., Epeorus, and Baetis, stoneflies, Chloroperla, and smaller numbers of caddisflies, Lepidostoma. Salmon were also observed to feed heavily at dusk on adult insects drifting on the water surface.

Chinook and coho salmon were sorted to be of similar size for the experiments. For the eight replicates when coho and chinook were introduced together, however, chinook were slightly larger; Slim chinook averaged (\pm SE, FL) 65.4 ± 0.51 mm, Eagle chinook 64.5 ± 0.74 mm, and coho 62.5 ± 1.1 mm.

To establish what influence these small differences in fish size may have had on habitat use, three pilot introductions of 150 fish each (two with chinook, one with coho) were performed. For each, fish were graded into 7 size classes (FL, mm): 58-59, 60-61, 62-63, 64-65, 66-67, 68-69, and 70-72 which covered the complete size range of fish used in the experiments. Fish in each size class were identified by cold brands applied at distinctive body positions using liquid nitrogen. After allowing the fish to adjust to the channel for 2 d, I recorded the positions of all fish within a 1 m path through the middle of the channel. Water velocity and water depth were recorded for each position and compared with the known length (size category mid-point) of fish occupying specific positions. In these introductions, body size was unrelated to either water velocity or water depth occupied (e.g. Fig. 29, r 's ranged between -0.12 and 0.16, for $40 < n < 50$, all $P > 0.05$). Small size variation between the experimental groups of salmon was, therefore, concluded not to be a factor confounding interpretation of any subsequent differences in habitat use.

Figure 29. Relationship between fish size and water velocity of microhabitats occupied. The data are from a trial using Slim Creek chinook.



Statistical analysis

Emigration tendency was expressed as the proportion of chinook entering the downstream traps over the 6 d trials. These data were arcsine square-root transformed and factorial analysis of variance was performed; species introduction treatment and chinook population were the main effects. When all fish initially introduced were denied emigration, isolated shoals of fish (10-40 in number) were often observed "roaming" about the experimental sections. Habitat characterization of such groups was problematic since they tended to drift in and out of subsections and to displace fish holding positions in subsections. Restrictions on the amount of time that the channel was available for experiments, and of fish number, prevented separate experiments being performed for emigration and habitat use. Therefore, habitat use was monitored when fish were free to emigrate, and thus initial fish densities changed over the course of the observations. Repeated measures analysis of covariance was used to test for differences in the number of chinook in pool and riffle habitats separately. The total number of fish counted during each census (as a measure of density) was the covariate, species introduction treatment and chinook population were the main effects, and observation day and period were the repeated measures. Homogeneity of covariate slopes was confirmed among treatment groups and a posteriori tests followed Tukey's procedure.

Results

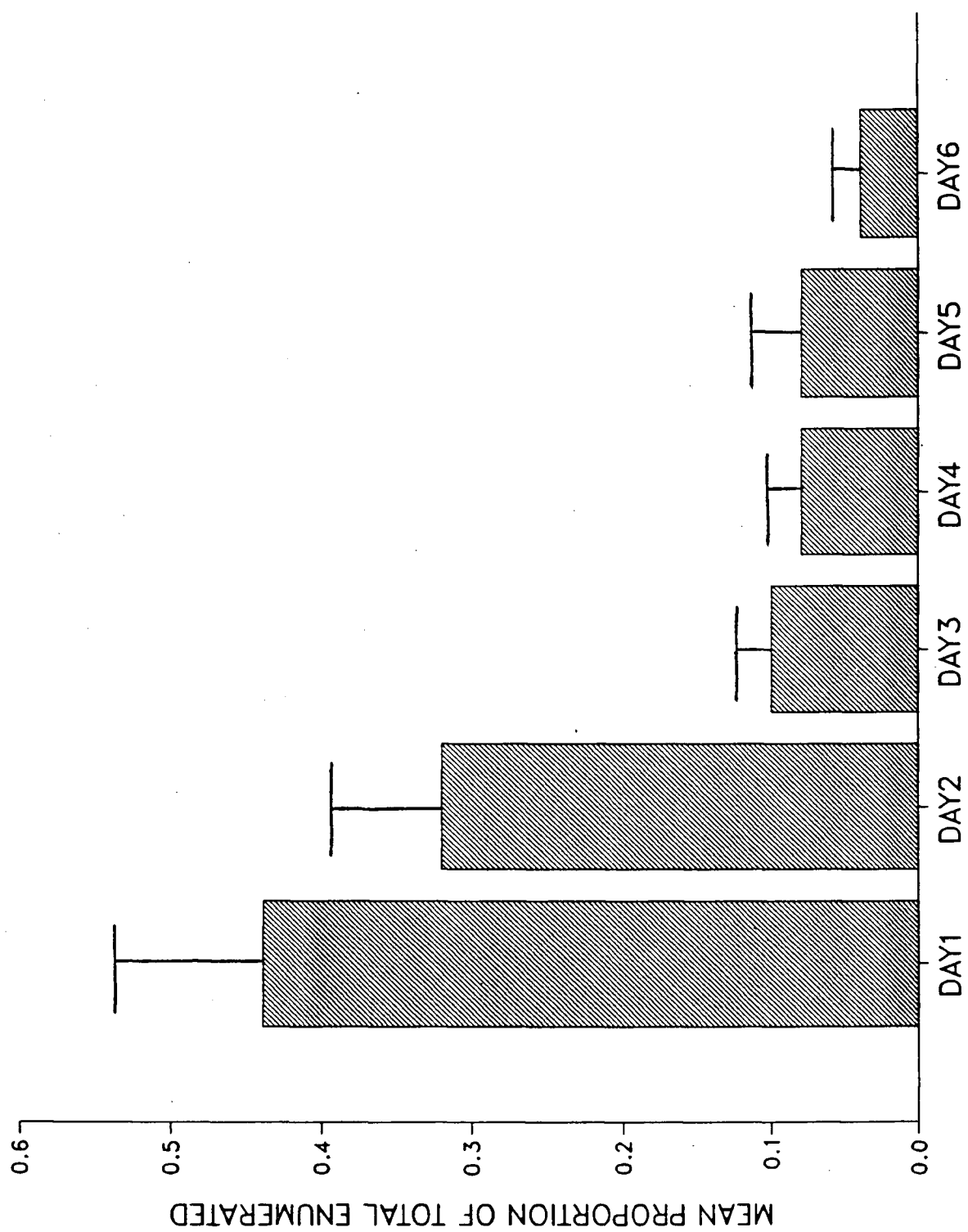
Initial behaviour

Upon introduction, juvenile coho and chinook reacted by seeking cover under large rocks or vegetation overhanging the channel margins. Others, in aggregations of 20-40, moved downstream to near the trap openings within 1-2 min. Large numbers of salmon could be seen holding positions upstream of the trap openings and fence panels. Within 1 h fish gradually moved upstream to take up positions in the middle and upper portions of the channel sections. After 2-3 h few fish were observed just upstream of the fence panels; rather individuals could be seen scattered throughout the sections often rising to the surface to strike at objects floating downstream and interacting with one another.

Emigration from the channel

An average 41% of chinook emigrated from the experimental sections over the course of the study when introduced alone at 1 fish/m². Most emigrating fish entered the traps during the first 3 d in any one trial (Fig. 30). Eagle and Slim chinook exhibited similar emigration tendency when introduced alone (Slim \bar{x} = 41.5%, Eagle \bar{x} = 40.5%). Sixty-one percent of chinook emigrated from the channel sections when introduced with an equal number of coho at 2 fish/m²; a higher percentage of Slim

Figure 30. Temporal changes in mean (\pm SE) proportion of total emigration by juvenile salmon in the experimental stream sections. Values were calculated from individual trials pooled across species and treatment (N=32).



Creek fish emigrated (\bar{x} =67%) compared to Eagle River chinook (\bar{x} =55%, Fig. 32). An intermediate percentage of initial chinook numbers emigrated from the channel sections (\bar{x} =49%) when they were introduced alone at 2 fish/m², Slim chinook again showed a slightly greater tendency to emigrate than Eagle chinook (\bar{x} =55 and 49% respectively).

Mean sizes for initial and emigrant fish were available for 12 of the 24 introduction trials; emigrants were often smaller than the mean size of fish initially introduced, but there were no significant differences (Bonferroni-adjusted t -tests, all $P>0.01$, Fig. 31).

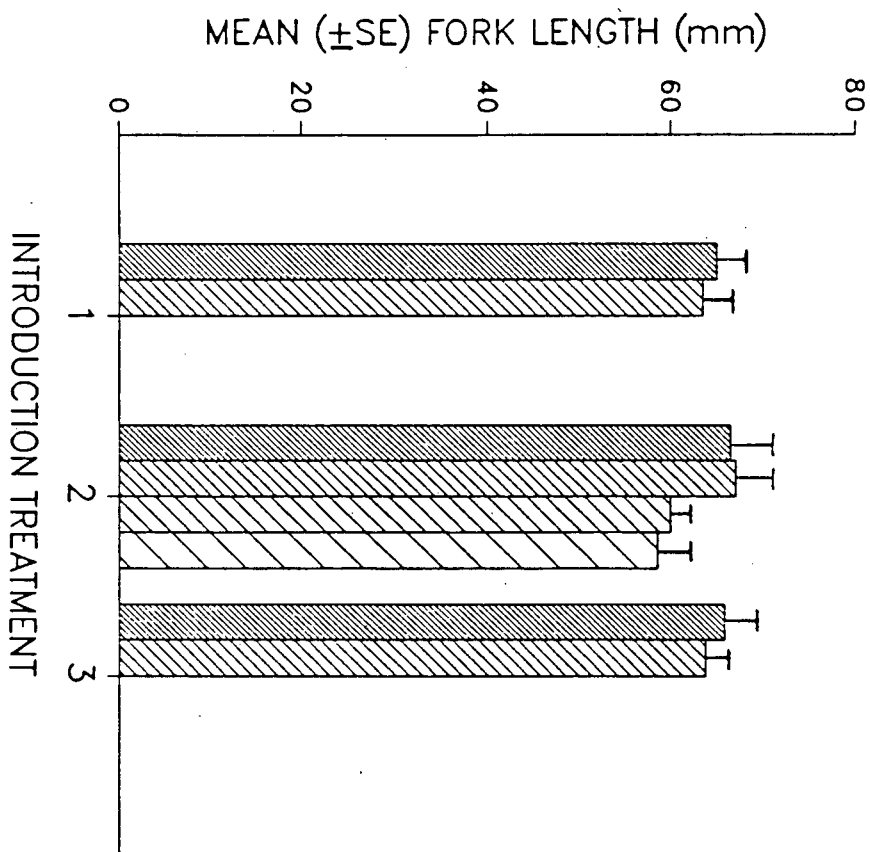
Overall, there was no influence of species introduction treatment on the percentage of initial chinook numbers which emigrated ($df=2,18$, $P=0.083$). There was also no difference in emigration tendency between Slim and Eagle chinook either overall ($df=1,18$, $P=0.24$), or in response to the species introduction treatments ($df=2,18$, species introduction \times population $P=0.76$). By contrast to the extensive movement by chinook salmon, an average of only 14 ± 3.9 (SE) % of initial coho numbers entered the traps.

Habitat use

In the experimental stream sections coho and chinook salmon used different habitats. Chinook were much more likely to be

Figure 31. Mean (+SE) sizes of initial and emigrant salmon juveniles. $\bar{3}1a$ =Slim Creek replicate 2, $31b$ =Eagle River replicate 4.

31a



31b

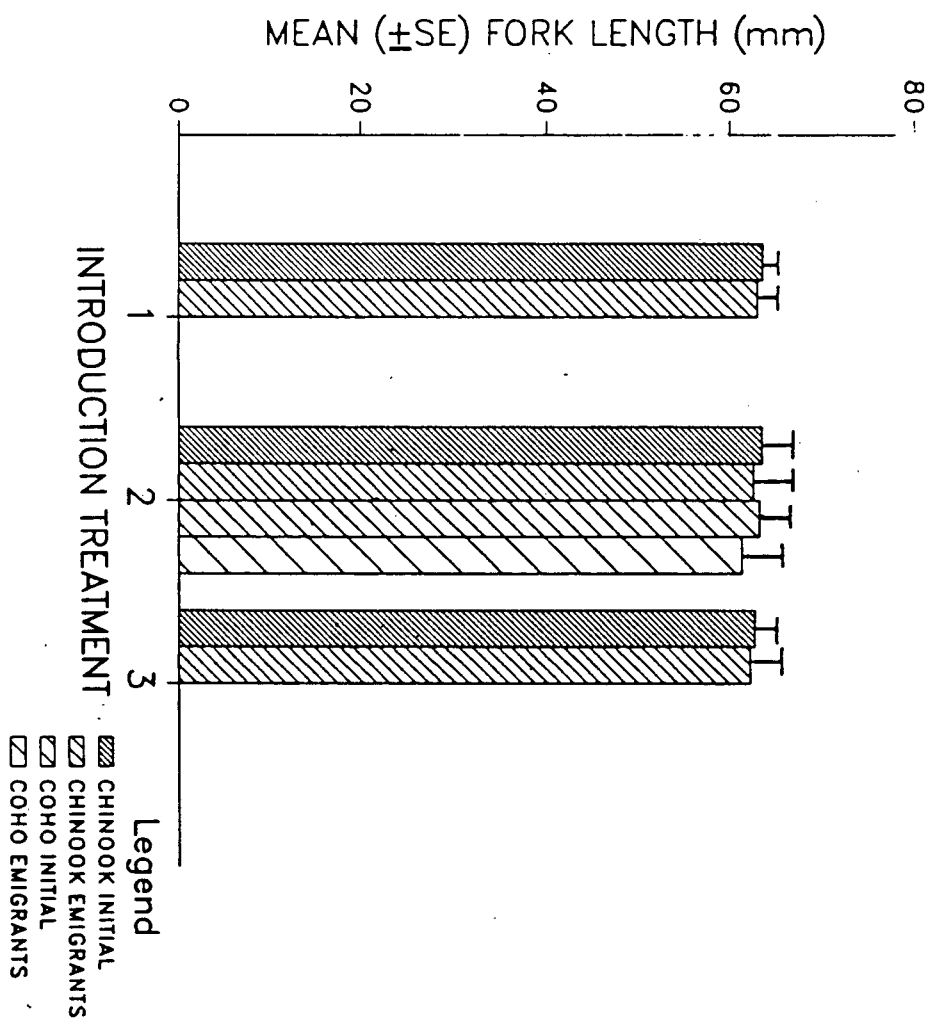
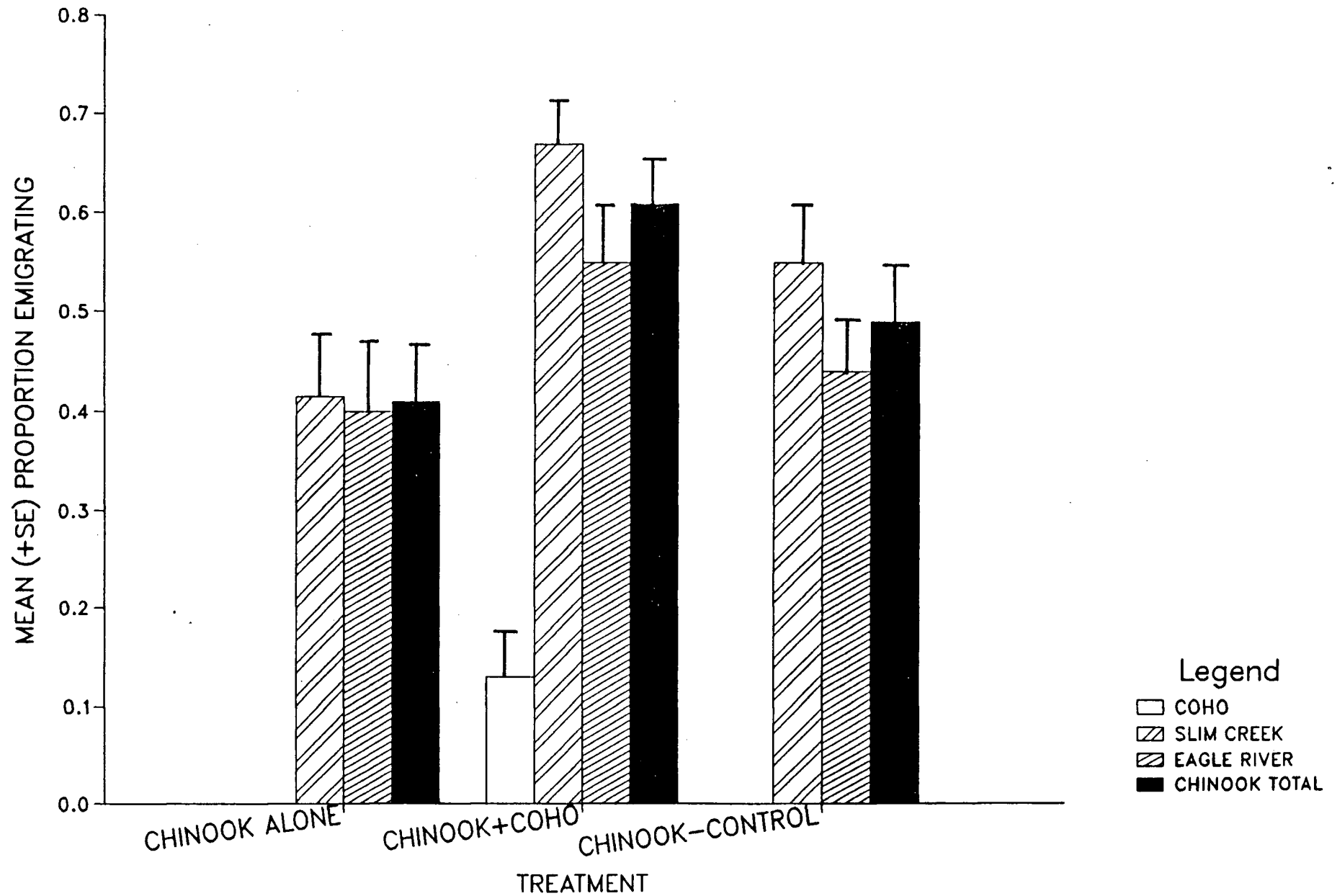


Figure 32. Mean (\pm SE) proportion emigration from experimental channel sections by chinook when introduced alone and with coho salmon.

JONES CREEK CHINOOK EMIGRATION EXPERIMENT



found in riffle habitats while coho were found almost exclusively in the pool habitats, a difference consistent with that observed in the wild (Fig. 33). Differential habitat use appeared to occur rapidly; observations from the stream banks indicated that coho were in pools and chinook in riffles within 1 d of introduction.

The number of chinook in pool habitats varied significantly among the treatments ($df=2,14$; $P=0.001$, Table 28). Fewer chinook were found in the pool habitats when introduced with coho than when introduced alone at 1 fish/m² ($P<0.05$, Table 28), but not at 2 fish/m² ($P>0.05$). More Slim fish were counted in pool habitats than Eagle chinook, but this difference was not significant (Table 28, $df=1,14$; $P=0.09$). Both populations responded by decreasing their numbers in pool habitats when introduced with coho although this effect was perhaps slightly stronger for Slim chinook (species introduction treatment \times population, $P=0.06$, $df=2,14$). The numbers of chinook in pools was stable both over observation periods and days (both repeated factors $P>0.1$).

Use of riffles by chinook was also influenced by species introduction treatment ($P<0.01$, Table 29); more fish used riffles when introduced with coho. Eagle and Slim chinook did not differ significantly in overall use of riffle habitats (Table 29, $df=1,14$; $P=0.23$). Although co-introduction with coho altered numbers of chinook in pool and riffle habitats, chinook

Figure 33. Relative use of pool and riffle habitats in Jones Creek experimental stream sections by coho and chinook salmon.

JONES CREEK HABITAT USE: CHINOOK AND COHO

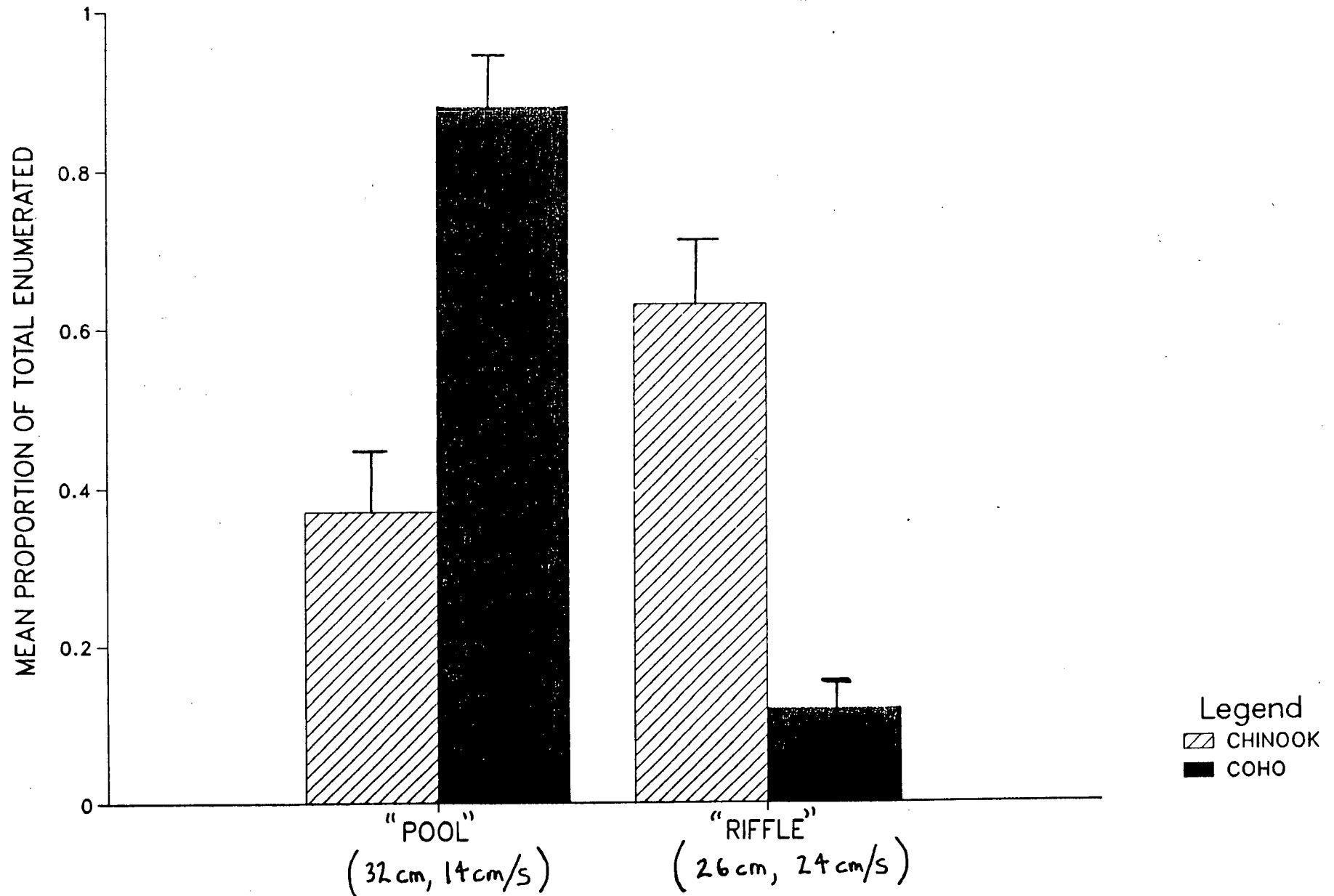


Table 28. Number (mean+SE) of chinook found in pool habitats in Jones Creek. Treatment 1=chinook initial density 1 fish/m², 2=chinook and coho at 2 fish/m², 3=chinook at 2 fish/m².

		Chinook population		
		Slim Creek	Eagle River	Mean
		4	4	8
Introduction Treatment	N			
1	4	26.7 (2.3)	21.6 (2.1)	24.0 (1.5)
2	4	13.2 (2.2)	16.6 (2.1)	14.3 (1.6)
3	4	21.8 (2.2)	16.2 (2.5)	22.4 (1.7)
Mean	12	21.6 (1.3)	18.1 (1.3)	19.8 (1.4)

Table 29. Number (+SE) of chinook found in riffle habitats in Jones Creek. Treatment 1=chinook initial density 1 fish/m², 2=chinook and coho at 2 fish/m², 3=chinook at 2 fish/m².

		Chinook population		
		Slim Creek	Eagle River	Mean
		4	4	8
Introduction Treatment	N			
1	4	32.3 (2.5)	37.6 (2.1)	35.2 (1.5)
2	4	43.4 (2.2)	42.5 (2.1)	42.8 (1.6)
3	4	37.4 (2.1)	43.0 (2.5)	40.1 (1.7)
Mean	12	37.6 (1.3)	41.2 (1.3)	39.4 (3.7)

were more numerous in riffles than in pools (same total surface area) regardless of whether they were introduced alone or with coho (Tables 28, 29). Therefore, chinook apparently preferred riffles over pools and introduction with coho only enhanced this preference.

Discussion

If behavioural interaction with coho salmon influences duration of freshwater residence by chinook several results were expected.

First, in numerous cases in which one species appears to influence the distribution or abundance of another the affected species is usually subordinate (Sheppard 1971; Morse 1974; Werner and Hall 1977; Schoener 1983; Nishikawa 1985; Ebersole 1986). In the present context, coho should socially dominate chinook if, through direct aggression, they influence freshwater residence by chinook. This expectation was realized in the laboratory stream tanks; newly-emerged coho were despotic over chinook although such domination did not appear to be uniform across chinook populations (Fig. 25).

Behavioural domination of chinook by coho is consistent with the results of Stein et al. (1972) who showed that in the Sixes River (Oregon) coho socially dominated chinook. In both the work of Stein et al. and the present study, coho tended not

only to direct more attacks at chinook than vice versa, but also to dominate upstream areas of experimental tanks where food was introduced. Stein et al. (1972) found that coho grew faster than chinook and suppressed their growth rates, a result that they concluded was a direct consequence of the behavioural subordination of chinook.

The behavioural domination of chinook by coho is consistent with studies that have reported that coho dominate several salmonids (Hartman 1965; Allee 1982; Fausch and White 1986; Glova 1986). At least in contrived situations, then, coho are able to dominate chinook and influence their distributions. The limited growth data reported by Stein et al. (1972) also suggest that some advantages in terms of growth may accrue to individual chinook that avoid, or disperse from, microhabitats occupied by coho.

The availability of suitable habitats is an important determinant of the size and distribution of fish populations (Chapman 1966; Allen 1969; Mundie 1974; Gorman and Karr 1978; Schlosser 1982; Newman and Waters 1989). Therefore, if behavioural interaction with coho influences duration of freshwater residence by chinook then the second expectation was that coho would influence some correlate of freshwater residence such as habitat use. Microhabitat use by allopatric and sympatric chinook provided support for this expectation. Coho and chinook used different microhabitats when together, but

chinook utilized "coho-like" pool habitats to a greater extent when coho were absent (Fig. 26, 27). Given the behavioural dominance of coho over chinook, a plausible explanation is that interspecific interaction in sympatry promotes differential microhabitat use. Differences in habitat use between chinook populations, particularly the use of pool, "coho-like" habitats by chinook in streams without coho, is consistent with this explanation.

Such an interpretation of the data is not without difficulties. First, some uncontrolled and unmeasured variable(s) that co-vary with the presence or absence of coho salmon and that influence habitat use might differ among the study populations (Connell 1983; Diamond 1986; Fausch 1988). The abundance and distribution of food and predators may influence habitat use in fishes (Chapman and Bjornn 1969; Everest and Chapman 1972; Werner et al. 1983; Power 1984; Harvey et al. 1988) and were uncontrolled in this study. However, because the habitat use results were consistent between years and across "treatment" populations, uncontrolled variation was probably not a confounding factor in my study.

A second limitation was that field populations were not manipulated. Therefore, a plausible alternative explanation for the results is that differences in microhabitat use result from genetic differences in habitat preference between coho and chinook and between Slim and Eagle chinook (Colwell and Fuentes

1975; Fausch 1988). The various species of Oncorhynchus differ in a variety of behavioural, physiological, and morphological traits (Brett 1952; Hikita 1962; Weisbart 1968; Hoar 1976) which suggests that they might differ in habitat preference as well. If the differences are indeed genetic, then they might be the result of past selection from interspecific interaction acting to favour individuals from both species which sought to reduce the costs of interspecific aggression by using alternative habitats. Present behavioural interaction may act only to reinforce differences in habitat preference. Alternatively, evolution of differences in habitat preference during allopatric divergence of coho and chinook from a common ancestor could also account for differences observed during secondary contact. Unfortunately, the historical nature of these alternative explanations makes their resolution difficult (Endler 1982; Connell 1983).

Numerous investigations involving both field and laboratory studies of behavioural interactions and habitat use have been conducted on sympatric fish species (e.g. Ebersole 1986; Hearn and Kynard 1986; Ross 1987). Studies of fish in experimental systems have implicated behavioural interaction (Fausch and White 1986; Glova 1986; Hearn and Kynard 1986), differences in habitat preference (Bustard and Narver 1975; Allee 1982), or a combination of both (Hartman 1965) as mechanisms promoting differential habitat use. Field populations have rarely been manipulated, but behavioural exclusion (Hixon 1980; Fausch and

White 1981), species differences in habitat preference (Everest and Chapman 1972; Hume and Northcote 1985), or both these factors (Ebersole 1986) apparently influence species habitat use in sympatry.

Differences in habitat use between coho and chinook were consistent between wild and experimental populations and these species show similar differences under simulated winter conditions (Taylor 1988). The results from Jones Creek suggest that differences in habitat use between coho and chinook are largely a function of differences in habitat preference with "reinforcing" behavioural interaction being of secondary importance. Fewer chinook used pools in the presence of coho than when alone, but chinook were most abundant in riffles under all conditions (Tables 28, 29). Thus, chinook preferred riffles, and the addition of coho appeared only to enhance this preference. Preference for pools by coho appeared to be even stronger (Fig. 30), but their habitat use in experimental allopatry was not tested. In sum, coho appeared to influence habitat use of chinook only in pools which are apparently the preferred habitat of coho (Dolloff 1987; Bisson et al. 1988).

A third expectation from the hypothesis that behavioural interaction with coho influences freshwater residence by chinook was that more chinook would emigrate from a system in the presence of coho than when alone. While chinook emigration was highest in the presence of coho in Jones Creek, it was not

significantly different from the increase in emigration caused by the increase in chinook density from $1-2/m^2$.

The differential influence of coho on habitat use by chinook between habitat types may explain, in part, the limited influence of coho on emigration tendency by chinook in Jones Creek. Marked differences in habitat use between the species probably lessen the extent of behavioural interaction and hence the chances of socially induced emigration. In addition, while statistically insignificant, Slim and Eagle chinook may have differed in their tendency to emigrate from the experimental sections (Fig. 32, cf. Jenkins 1971). This may have complicated detection of an effect of coho on chinook especially since behavioural domination by coho does not appear to be uniform among chinook populations (Fig. 25).

Differences in size between introduced salmon and emigrants were small and insignificant. Social status and relative dominance between individuals are often size-dependent (Chapman 1962; Abbott et al. 1988; Petrosky and Bjornn 1988), and if social interactions were important in influencing emigration by chinook then smaller individuals should have characterized the emigrants. Since this was not the case some other factor probably influenced emigration. Jenkins (1971) and Bilby and Bisson (1987) studied emigration in newly-introduced, hatchery raised rainbow trout and coho salmon respectively and also found that emigrant fish were not necessarily smaller than residents.

These authors suggested that initial emigration was due to fish responding to unfamiliar habitats as well as to social interactions.

Despite the possibility of emigration in response to unfamiliar habitats, this factor should have been consistent across treatments, yet more chinook emigrated in the presence of coho than when alone at comparable densities. The preference of coho for pool areas in this and other studies (Hartman 1965; Allee 1982; Bisson et al. 1988), the aggressive superiority of coho, and the preference for riffles by chinook probably acted together when coho were introduced to (i) increase the use of riffles by chinook and (ii) increase emigration by chinook. These results are consistent with the idea that the energetic demands of interspecific interactions can be reduced for a behavioural subordinate if it seeks refuge in alternate habitats. Such energetic advantages may result in selection favouring species specific habitat preferences (Morse 1974; Rosenzweig 1974).

There are few precedents for the study of interspecific interaction on freshwater residence tendency in salmonids. The data of Stein et al. (1972) suggest that a greater percentage of chinook emigrated from experimental troughs when stocked with coho than when stocked alone, although replications for their treatments which controlled for density differences were too few (1-3) to permit rigorous conclusions.

Spaulding et al. (1988) assessed the influence of releases of hatchery-reared coho on habitat use, emigration, and growth rate of wild chinook salmon in the Wenatchee River, Washington. These authors observed that coho were more aggressive towards chinook than vice versa and that habitat use, while similar immediately after the coho were released, was markedly different between the species soon thereafter. Consistent with the results from Jones Creek was the observation by Spaulding et al. (1988) that a much higher percentage of chinook used riffle habitats after coho, which used pools extensively, were introduced. By contrast to my results from Jones Creek, shifts in habitat by Wenatchee chinook were not associated with changes in emigration rates. In addition, Spaulding et al. (1988) found no effect of introduction of coho on growth rates of resident chinook.

Since experimental stream sections were much larger in the study by Spaulding et al. (1988), it is possible that suitable amounts of underutilized riffle habitats were present in the Wenatchee River treatment sections to "absorb" chinook displaced from pools after coho were introduced. This was probably not the case in Jones Creek, because even when chinook were introduced alone at 1 fish/m², roughly 40% emigrated.

Direct comparison to the study by Spaulding et al. (1988) is compromised somewhat since Wenatchee chinook were wild and

prior residents of the system while coho were hatchery-raised. These resident chinook were probably more familiar with their environment than the coho introduced into the Wenatchee River or the chinook in Jones Creek. In addition, prior residents are usually favoured in aggressive interactions (Chapman 1962; Mason and Chapman 1965). Consequently, the potential for coho to impact upon prior resident chinook may have been limited in the Wenatchee River study. Spaulding et al. (1988), however, concluded that segregation of coho in pools and chinook in riffle habitats reflected genetic differences in habitat preference and, to a lesser extent, behavioural domination by coho in pools.

Hearn and Kynard (1986) studied the relationship between rainbow trout (an exotic) and Atlantic salmon in streams of the northeast U.S. In laboratory stream channels, rainbow trout tended to be more aggressive than salmon and could displace them from pool habitats. In the field, the species were found in different habitats, and stocking stream sections with salmon did not increase emigration by prior resident trout (Hearn and Kynard 1986). Hatchery origin of the introduced salmon and the fact that the trout were resident in the stream before salmon were introduced, again, limit direct comparison to Jones Creek studies. Nevertheless, Hearn and Kynard (1986) concluded that habitat segregation between trout and Atlantic salmon was largely due to differences in habitat preference and probably only secondarily to interspecific aggression.

Comparison of these studies with those in Jones Creek suggests that habitat diversity is a major factor affecting the degree and outcome of interspecific behavioural interaction. The extent of species differences in habitat preferences and the relative availability of their respective preferred habitats are probably major determinants of the influence of behavioural interaction on a response such as emigration.

In summary, in contrived or very simple habitats (e.g. laboratory environments), particularly those with pool-like conditions, coho can behaviourally exclude chinook and, hence, probably promote emigration from such systems by chinook. By contrast, behavioural interaction with coho in natural environments is probably not a major factor influencing duration of freshwater residence (via interaction for habitat) since even in the relatively simple environment of Jones Creek coho and chinook specialized in different habitats. Perhaps in streams with very little opportunity for habitat specialization, or for chinook displaced from riffles by intraspecific interactions and attempting to reside in pool habitats, behavioural interaction with coho may promote alternative rearing patterns such as downstream migration to estuarine areas.

CHAPTER 4: GENERAL DISCUSSION

The foregoing study adds to those of Rich and Holmes (1928) and Carl and Healey (1984) by presenting evidence that life histories of juvenile chinook salmon are, at least in part, inherited. Additionally, the difference in the timing of the change from freshwater to estuarine and marine residence is associated with inherited differences in a suite of characters that are components of functionally important "strategies" for alternative life histories (Chapter 1). These observations provide evidence supporting the hypothesis that stream- and ocean-type salmon represent adaptive diversification, a feature that has undoubtedly been important to the chinook's widespread native distribution and successful colonization after introduction to non-native environments (Carl 1982; Flain 1983).

Environmental modulation of "growth opportunity", and abiotic factors selecting for size and time of downstream migration were suggested as instrumental to the evolution and present geographic distribution of alternative chinook life histories (Chapter 2). The investigation of competitive interactions between coho and chinook juveniles pointed away from behavioural domination of chinook by coho as a biotic environmental factor influencing chinook freshwater life history (Chapter 3). Habitat specialization by each species probably minimizes the potential for coho to influence directly the freshwater residence by chinook. This is consistent with the

conclusions reached in Chapters 1 and 2; variability in the duration of freshwater residence is at least partially genetically determined.

Genetic differences in habitat use and behaviour of coho and chinook could stem from past selection for habitat preference as a means of reducing the costs of aggressive interactions. Alternatively, species-specific habitat preferences could have evolved during allopatric divergence of coho and chinook from a common ancestor. While these alternatives cannot be resolved, the possibility of coevolution between these species is consistent with recent ideas concerning the development of the Pacific salmonid "species flock". Miller and Brannon (1982) postulated that the present diversity of salmonid life histories in the north Pacific evolved in a "crucible of competitive and exploitative interactions". Rosenzweig (1978) developed a theoretical model of "competitive speciation" and Gibbons (1979) applied a similar concept to sympatric speciation in three ichneumonid flies. In this model, intraspecific competition promotes the dispersal of individuals to vacant "island niches" that are discrete from those occupied by members of the source population (Rosenzweig 1978). Adjacent island niches are separated by "disruptive gaps" such that offspring of matings between occupants of distinct niches are selected against. Selection against hybrids then promotes the evolution of reproductive isolation between occupants of separate island niches. Might such a model apply to

differentiation within chinook and, in particular, to the evolution of alternative life histories?

The evolution of a complex, anadromous life history is thought to have been driven, in part, by food resource limitation in relatively unproductive freshwater stream environments (see Gross (1987) for a recent discussion). In this scenario, individuals adopting an anadromous life style were favoured by selection because the abundant food resources in estuarine and marine habitats provided the opportunity for enhanced growth. Ecologically, a consequence of incipient anadromy was that ancestral Oncorhynchus populations could reduce niche overlap by utilizing both freshwater and estuarine/marine rearing habitats. Further subdivision of habitat use could be accomplished through differences in the timing of the shift from freshwater to estuarine/marine habitats. Temporal niche differences were suggested by Carothers and Jaksic (1984) to be a consequence of interference (agonistic) interactions between species. As well, Wilbur (1980) offered the opinion that shifts in the timing of events in complex life cycles in amphibians are of major ecological significance because they contribute to species coexistence.

The foregoing discussion suggests that anadromy and heterochronic changes in the timing of the smolt transformation could represent alternative niche islands, as conceptualized by Rosenzweig (1978), as the basis of a competitive speciation

model of differentiation within Oncorhynchus. In fact, McCormick and Saunders (1987) proposed that heterochronic changes in hypo-osmoregulatory ability have driven an evolutionary trend from salinity tolerance at age 1 year or older in coho and masu salmon (O. masou) to rapid attainment of salinity tolerance and seaward migration as newly emerged fry in pink and chum salmon. Within this scheme, the diversity of juvenile life histories in chinook may have evolved as a "generalist" pattern, intermediate to the estuarine oriented early life histories of pink and chum salmon and the extended freshwater residence of coho, sockeye, and masu salmon. In sum, microevolutionary divergence in developmental rate, driven by competitive interactions, may have promoted differentiation within Oncorhynchus which, for chinook, has meant the evolution of both stream- and ocean-type life histories.

The variability in juvenile chinook life histories is associated with genetic differences in adult spawning migration timing (see Chapter 2). Stream- and ocean-type chinook also appear to have distinct behaviours and distributions during their oceanic phases (Healey 1983), differences that may be genetic in origin. Stream-type salmon migrate far afield northwesterly along the North America coast and may move offshore to at least 170°W longitude. Ocean-type chinook are more localized; they spend their marine life in nearshore waters, much closer to their stream of origin. There appears, therefore, to be a broad dimorphism within chinook salmon, but

it is unclear whether the distinction is ultimately rooted in the early life history, the timing of adult spawning migration, or the marine migrations. In consequence there are several ways in which it might be postulated that the alternative juvenile life histories could have evolved.

For instance, the sympatric occurrence of juvenile life history types in numerous rivers could have arisen from allopatric divergence followed by postglacial colonization. Alternatively, sympatric life history types could be the result of independent evolution in each of the systems in which they occur. While an "allopatric divergence-postglacial dispersal" argument could explain much of the macrogeographic variation in juvenile life histories (see Chapter 2), three observations suggest, or are at least consistent with the idea, that sympatric divergence may contribute to microgeographic variation.

First, there is evidence that within major regions, and sometimes single tributaries, stream- and ocean-type chinook are more similar to each other electrophoretically than either is to comparable life history types in other regions or rivers (Kristiansson and McIntyre 1976; Utter et al. 1989). If most of the loci examined are assumed to be selectively neutral (Utter et al. 1987), biochemical information argues that alternative life history types may have arisen independently in several faunal regions along the Pacific coast. Second, in sockeye

salmon, Oncorhynchus nerka, brown trout, Salmo trutta, and arctic charr, Salvelinus alpinus, anadromous and non-anadromous forms can give rise to one another, and probably have on numerous occasions (Foerster 1947; Behnke 1972; Ryman et al. 1979; Nordeng 1983; Scott 1984; Hindar et al. 1986; Foote et al. 1989). Therefore, over the ranges of these species, anadromous and freshwater resident forms probably do not represent distinct evolutionary lineages. A similar situation might exist for stream- and ocean-type chinook salmon; they have probably diverged on numerous occasions. Third, since both stream- and ocean-type individuals may be present in progeny from apparently single breeding populations (e.g. Reimers 1973), the polymorphism that would form the basis for sympatric divergence exists within populations.

If, in some areas, stream- and ocean-type chinook diverged in sympatry two questions arise: (i) what is the mechanism of divergence and how is it maintained? and (ii) have ocean-type salmon more commonly given rise to stream-type chinook or vice versa? Certain aspects of the environment and behaviour of Pacific salmon suggest that disruptive selection, i.e. selection in favour of two or more modal phenotypes (Futuyma 1986), may have promoted sympatric divergence.

For instance, Healey (1983) cited seasonal differences in accessibility to spawning areas and differences in migration distance between headwater and lower river tributaries as

examples of environmental heterogeneity that might provide opportunity for differential selection within river systems. In addition, the precise homing behaviour of salmonids for spawning provides a mechanism for reproductive isolation between source populations and descendants of individuals that strayed and colonized newly exposed habitats. Differential selection among habitats and habitat selection describe conditions where at least the maintenance of genetic polymorphism is most probable (Thoday and Boam 1959; Maynard Smith 1962; Hendrick et al. 1976; Hendrick 1986) and habitat selection during reproduction is a central theme in many cases of proposed sympatric divergence (Kosswig 1963; Tauber and Tauber 1977; McKaye 1980; Echelle and Kornfield 1984; Rice 1985). A final point which suggests that chinook salmon might diverge repeatedly in separate river systems is the observation that Pacific salmon disperse widely upon exposure to new habitats (e.g. during glacial recession), especially if source populations are small (Quinn and Fresh 1984). Such rapid dispersal is exemplified by the spread of chinook salmon along the east and west coasts of New Zealand (Flain 1981) and the rapid spread of pink salmon (Oncorhynchus gorbuscha) throughout the Great Lakes (Kwain 1987) after each was introduced to these non-native environments.

Sympatric divergence could explain the origin and maintenance of alternative life history types within systems such as the Nanaimo River. In this river, three spatially and genetically distinct breeding populations of chinook are

characterized by temporal differences in adult spawning migration and juvenile seaward migration (Carl and Healey 1984). Selective regimes probably vary among the lake dominated upper river, the middle river, and the estuarine dominated lower river. As well, maturing adults probably home to these areas. These observations are consistent with diversifying selection as a credible hypothesis to account for the origin and maintenance of alternative life histories. Since similarly diverse environments and differences in adult and juvenile migration timing occur within many other coastal streams in Washington, Oregon, and in the lower Columbia River it seems probable that disruptive selection may have occurred independently in many areas.

If sympatric life history types of chinook have arisen through disruptive selection since the last glaciation (14,000 y bp or about 3,500 generations), then chinook must be capable of rapid divergence. Recent (within the last 100 yr) introductions of anadromous chinook and sockeye salmon to New Zealand have resulted in the natural founding of freshwater resident populations, some of which are sympatric with anadromous fish (Stokell 1962; Flain 1972, 1982b; Scott 1984). In addition, from introductions of fall-spawning chinook and "odd-year" pink salmon to the Great Lakes, at least one spring spawning population of chinook (Kwain and Thomas 1984) and several populations of "even-year" pink salmon have developed. There is, furthermore, evidence of genetic differences among

naturalized Great Lakes pink salmon populations (Gharret et al. 1987), divergence stemming from an introduction of 21,000 fry from a single donor population in 13-15 generations. While the differences among the pink populations are small and the genetic basis of the other life history differences described is unknown, the possibility that natural selection might be responsible for the differences suggests that rapid divergence within Oncorhynchus species is possible.

The existence of sympatric intraspecific forms in salmonids, and other fishes (Echelle and Kornfield 1984; McPhail 1984), has been linked to environmental gradients or heterogeneity. For instance, Foote (1987) summarized arguments that related the sympatric occurrence of intraspecific forms in lake whitefish (Coregonus clupeaformis), sockeye salmon and kokanee, and arctic charr to factors such as lake or stream productivity, lake morphometry, and presence or absence of competitors. This appears to be the case for chinook salmon as well, since it is in structurally diverse, coastal river systems, where the costs of seaward migration presumably are low relative to upstream areas, that sympatric stream- and ocean-type chinook are most common. Differences among geographic regions in environmental conditions favourable to divergence (e.g. river length, estuary size) probably contribute to the distribution of sympatric life history types over the chinook's range.

Do stream-type chinook more commonly give rise to ocean-type chinook, or might the reverse divergence be most common? If one accepts the hypothesis that salmonids had a freshwater origin and that taxa have evolved towards reduced dependence on territorial stream residence (i.e. pink, chum and sockeye) (Tchernavin 1939; Behnke 1972; Dorofeyeva et al. 1981; Miller and Brannon 1982; Kendall and Behnke 1984; Smith and Stearley 1989; but see Thorpe 1982) then this might be interpreted as evidence that stream-type chinook more commonly give rise to ocean-type salmon.

Both Zaugg et al. (1986) and Clarke (1987) reported that stream-type salmon may smolt during their first year of life if their growth opportunity is increased prior to the spring "migration window". Clarke (1987), however, was unable to modify the growth and smolting rates of ocean-type chinook which suggests that they are physiologically less flexible and their life history is under stronger genetic control. Perhaps such apparent canalization places limits on the potential for ocean-type chinook to give rise to stream-type salmon.

Alternatively, reversals of the apparent trend towards the evolution of more marine dependent taxa in salmonids are common and freshwater resident forms of various species are probably decedents of sympatric anadromous counterparts (Behnke 1972; Ryman 1983; Hindar et al. 1986; Foote et al. 1989). Indeed, ocean-type chinook have given rise to chinook with extended

freshwater residence in New Zealand waters (Flain 1979, 1980, 1982b). Therefore, some stream-type salmon might have evolved from ocean-type fish following the latter's upstream or northward colonization of newly deglaciated regions containing habitats that selected for increased size at smoltification (and hence extended stream residence).

Inherited phenotypic differentiation between stream- and ocean-type chinook (see Chapter 1) suggests that there would be selection for reproductive isolation in sympatry. While the life history types may be spatially separated during spawning, there are instances where stream- and ocean-type chinook spawn in close proximity or where both are present in single demes (Fulton 1968; Reimers 1973). In such cases it is intriguing to speculate about the degree to which such spawning populations or life history types within populations might also be reproductively isolated by behavioural differences.

Stream- and ocean-type life histories represent genetically based, functional diversification within chinook salmon. Such diversification has surely been important in the colonization and maintenance of populations in a species with perhaps the widest geographic range of Oncorhynchus. Finally, as for other examples of life history polymorphism in the Salmonidae, it is likely that chinook life history types are not

distinct evolutionary lineages; rather they probably result from repeated episodes of sympatric divergence over much of the north Pacific.

LITERATURE CITED

- Abbott, J.C., R.L. Dunbrack, and C.D. Orr. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (Salmo gairdneri). Behaviour 92(3/4):241-253.
- Allee, B.A. 1982. The role of interspecific competition in the distribution of salmonids in streams. pp. 111-122, In: E.L. Brannon and E.O. Salo [eds.] Proceedings of the salmon and trout migratory behavior symposium. University of Washington Press, Seattle.
- Allen, K.R. 1969. Limitations on production in salmonid populations in streams. pp. 3-20, In: T.G. Northcote [ed.] Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Allendorf, F.W., K.L. Knudsen and R.F. Leary. 1983. Adaptive significance of differences in the tissue-specific expression of a phosphoglucosmutase gene in rainbow trout. Proc. Natl. Acad. Sci. USA. 80:1397-1400.
- Altukhov, Yu., P. 1982. Biochemical population genetics and speciation. Evolution 36:1168-1182.
- Anon. 1977. Water temperatures. British Columbia and Yukon Territory. Volumes 1-4. Environment Canada, Inland Waters Directorate, Water Survey of Canada, Vancouver, B.C.
- Anon. 1982. Canadian climate normals, 1951-1980. Environment Canada, Atmospheric Environment Service, Ottawa.
- Anon. 1984. Symposium on Alternative Reproductive Tactics. Amer. Zool. 24:307-418.
- Arnold, S.J. 1983. Morphology, performance and fitness. Amer. Zool. 23:347-361.

- Aro, K.V. and M.P. Shepard. 1967. Spawning populations of North Pacific salmon: Pacific salmon in Canada. Intern. North Pacific Fish. Comm. Bull. No. 23:225-327.
- Arthur, W. 1982. Evolutionary consequences of interspecific competition. Adv. Ecol. Res. 12:126-187.
- Aspinwall, N.C. 1974. Genetic analysis of North American populations of the pink salmon, Oncorhynchus gorbuscha, possible evidence for the neutral mutation-random drift hypothesis. Evolution 28:295-305.
- Atkinson, C.E., J.H. Rose, and T.O. Duncan. 1967. Spawning populations of North Pacific salmon: Pacific salmon in the United States. INPFC Bull. No. 23:43-225.
- Bachman, R.A. 1982. A growth model for drift-feeding salmonids: a selective pressure for migration. Pages 128-135 in E.L. Brannon and E.O. Salo [eds.] Salmon and trout migratory behaviour symposium. University of Washington Press, Seattle
- Bakker, T., and E. Feuth-de Bruijn. 1988. Juvenile territoriality in sticklebacks (Gasterosteus aculeatus L.) Anim. Behav. 36:1556-1558.
- Balon, E.K. [ed.] 1980. Charrs. Fishes of the genus Salvelinus. W. Junk Publishers, The Hague.
- Beacham, T.D. and C.B. Murray. 1986. Comparative developmental biology of pink salmon, Oncorhynchus gorbuscha, in southern British Columbia. J. Fish Biol. 28:233-246.
- Beacham, T.D., F.C. Withler and R.B. Morley. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (Oncorhynchus keta) and coho salmon (O. kisutch). Can. J. Zool. 63:847-850.
- Beamish, F.W. 1978. Swimming capacity. pp. 101-187, In: W.S. Hoar and D.J. Randall [eds.] Fish Physiology Volume VII. Academic Press, Inc., New York.

- Behnke, R.J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Bd. Canada 29:639-671.
- Berg, L.S. 1948. Freshwater fishes of the U.S.S.R. and adjacent countries. Volume 1. Academy of Sciences, U.S.S.R. Translated from Russian by Israeli Program for Scientific Translation, Jerusalem.
- Berg, L.S. 1959. Vernal and hiemal races among anadromous fishes. J. Fish. Res. Bd. Canada 16:515-538.
- Bevern, K.A. and D.E. Gill. 1983. Interpreting geographic variation in life-history traits. Amer. Zool. 23:85-97.
- Bilby, R.E. and P.A. Bisson. 1987. Emigration and production of hatchery coho salmon (Oncorhynchus kisutch) stocked in streams draining an old-growth and a clear-cut watershed. Can. J. Fish. Aquat. Sci. 44:1397-1407.
- Bilton, H.T., D.F. Alderdice, and T.J. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (Oncorhynchus kisutch) on returns at maturity. Can. J. Fish. Aquat. Sci. 39:426-447.
- Birt, T.P., J.M. Green, and W.S. Davidson. 1986. Analysis of mitochondrial DNA in allopatric anadromous and nonanadromous Atlantic salmon, Salmo salar. Can. J. Zool. 64:118-120.
- Bisson, P.A., K. Sullivan and J.L. Neilson. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans. Am. Fish. Soc. 117:262-273.
- Blackburn, J. and W.C. Clarke. 1987. Revised procedure for the 24 hr seawater challenge test to measure seawater adaptability of juvenile salmonids. Can. Tech. Rpt. Fish. Aquat. Sci. 1515.
- Bock, W.J. 1980. The definition and recognition of biological adaptation. Amer. Zool. 20:217-227.

- Brannon, E.L. 1972. Mechanisms controlling the migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. 21.
- Brett, J.R. 1952. Temperature tolerances in young Pacific salmon, Oncorhynchus. J. Fish. Res. Bd. Canada 9:268-323.
- Brett, J.R. 1967. Swimming performance of sockeye salmon (Oncorhynchus nerka) in relation to fatigue time and temperature. J. Fish. Res. Bd. Canada 24:1731-1741.
- Brett, J.R. 1979. Environmental factors and growth. pp. 599-667, In: W.S. Hoar, D.J. Randall, and R. Brett [eds.] Fish Physiology Volume VIII. Bioenergetics and growth, Academic Press, New York.
- Brett, J.R. and J.E. Shelbourn. 1975. Growth rate of young sockeye salmon, Oncorhynchus nerka in relation to fish size and ration level. J. Fish. Res. Bd. Canada 32:2103-2110.
- Brett, J.R. and N.R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (Oncorhynchus nerka) in relation to size and temperature. J. Fish. Res. Bd. Canada 30:379-387.
- Brett, J.R., J.E. Shelbourn, and C.T. Shoop. 1969. Growth rate and body composition of fingerling sockeye, Oncorhynchus nerka, in relation to temperature and food ration. J. Fish. Res. Bd. Canada 26:2363-2394.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Canada 21:1183-1226.
- Brown, J.H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. Ecology 52:305-311.
- Brown, M.E. 1946. The growth of brown trout (Salmo trutta Linnaeus). I. Factors influencing the growth of trout fry. J. Exp. Biol. 22:118-129.

- Brown, R.F. and M.M. Musgrave. 1979. Preliminary catalogue of salmon streams and spawning escapements of Mission-Harrison subdistrict. Fish. Mar. Ser. Data Rep. No. 133.
- Bryant, F.G. and various coauthors. 1950. Survey of the Columbia River and its tributaries. Parts I-VII. U.S. Fish and Wildl. Ser. Spec. Sci. Rpt. Fish. Nos. 34-40.
- Bustard, D.R. and D.W. Narver. 1975. Preferences of juvenile coho salmon and cutthroat trout relative to simulated alteration of winter habitat. J. Fish. Res. Bd. Canada 32:681-687.
- Campbell, J.S. 1977. Spawning characteristics of brown trout and sea trout, Salmo trutta L., in Kirk Burn, River Tweed, Scotland. J. Fish Biol. 11:217-229.
- Carl, L.M. 1982. Natural reproduction of coho and chinook salmon in some Michigan streams. N. Am. J. Fish. Mgmt. 4:375-380.
- Carl, L.M. and M.C. Healey. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of chinook salmon (Oncorhynchus tshawytscha) in the Nanaimo River, British Columbia. Can J. Fish. Aquat
- Caro, T.M. and P. Bateson. 1986. Organization and ontogeny of alternative tactics. Animal Behaviour 34:1483-1489.
- Carothers, J.H. and F. Jaksic. 1984. Time as a niche difference: the role of interference competition. Oikos 42:403-406.
- Carscadden, J.E. and W.C. Leggett. 1975. Meristic differences in spawning populations of American shad, Alosa sapidissima: evidence for homing to tributaries of the St. John River, New Brunswick. J. Fish. Res. Bd. Canada 32:653-660.
- Cavender, T.M. 1978. Taxonomy and distribution of the bull trout, Salvelinus confluentus, (Suckley) from the American Northwest. Calif. Fish. Game. 64:139-174.
- Chambers, R.C. and W.C. Leggett. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (Psuedopleuronectes americanus) with a review of variation in other species. Can. J. Fis

- Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Bd Can. 19:1047-1080.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat. 100:345-357.
- Chapman, D.W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Trans. Am. Fish. Soc. 115:662-671.
- Chapman, D.W. and T.C. Bjornn. 1969. Distribution of salmonids in streams with particular reference to food and feeding. pp 153-176, In: T.G. Northcote [ed.] Symposium on salmon and trout in streams. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, B.C.
- Chiarello, N. and J. Roughgarden. 1984. Storage allocation in seasonal races of an annual plant: optimal versus actual allocation. Ecology 65:1290-1301.
- Clarke, G.H. 1929. Sacramento-San Joaquin salmon (Oncorhynchus tshawytscha) fishery of California. Calif. Fish Game Bull. No. 17.
- Clarke, W.C. 1982. Evaluation of the seawater challenge test as an index of marine survival. Aquaculture 28:177-183.
- Clarke, W.C. 1987. Growth and smolting of chum, coho and chinook salmon in response to photoperiod. DFO Info Memo Sept. 1987.
- Clarke, W.C. and J. Blackburn. 1977. A seawater challenge test to measure smolting of juvenile salmon. Can. Fish. Mar. Ser. Tech. Rep. No. 705.
- Clarke, W.C. and J.E. Shelbourn. 1985. Growth and development of seawater adaptability by juvenile fall chinook salmon (Oncorhynchus tshawytscha) in relation to temperature. Aquaculture 45:21-31.

- Clarke, W.C., and J.E. Shelbourn. 1986. Delayed photoperiod produces more uniform growth and greater seawater adaptability in underyearling coho salmon (Oncorhynchus kisutch). Aquaculture 56:287-299.
- Clarke, W.C. and R.E. Withler. 1987. Growth and smolting of Quesnel River chinook in response to photoperiod. DFO Info Memo Sept. 1987.
- Clarke, W.C., J.E. Shelbourn, T. Ogasawara, and T. Hirano. 1988. Effect of initial exposure to long and short daylength on growth, seawater adaptability and plasma hormone levels in underyearling coho (Oncorhynchus kisutch), chinook (O. tshawytscha), and chum (O. keta) salmon. Aquaculture. (In Press).
- Clayton, R.R. and H.R. MacCrimmon. 1988. Morphometric and meristic variability among North American Atlantic salmon (Salmo salar). Can. J. Zool. 66:310-317.
- Cole, K.S. and D.L.G. Noakes. 1980. Development of early social behaviour of rainbow trout, Salmo gairdneri, (Pisces: Salmonidae). Behavioural Processes 5:97-112.
- Colin, K. and B.D. Tutty. 1979. Juvenile salmonid field trapping manual. Can. Fish. Mar. Ser. MS. Rep. No. 1530.
- Colwell, R.K. and E.R. Fuentes. 1975. Experimental studies of the niche. Ann. Rev. Ecol. Syst. 6:281-310.
- Congleton, J.L., S.K. Davis, and S.R. Foley. 1982. Distribution, abundance, and outmigration timing of chum and chinook salmon fry in the Skagit salt marsh. pp. 153-163, In: E.L. Brannon and E.O. Salo. [eds.] Proc. Salmon and Trout Migratory Behavior Symposium. Univ. of Washington Press, Seattle.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122:661-696.
- Conte, F.P., H.H. Wagner, J. Fessler, and C. Gnose. 1966. Development of osmotic and ionic regulation in juvenile coho salmon (Oncorhynchus kisutch). Comp. Biochem. Physiol. 18:1-15.

- Conte, F.P., and H.H. Wagner. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout Salmo gairdneri. Comp. Biochem. Physiol. 14A:603-620.
- Cunjack, R.A. and J.M. Green. 1983. Habitat utilization by brook charr, Salvelinus fontinalis and rainbow trout, Salmo gairdneri, in Newfoundland waters. Can. J. Zool. 61:1214-1219.
- Cunjack, R.A. and J.M. Green. 1984. Species dominance by brook trout and rainbow trout in a simulated stream environment. Trans. Am. Fish. Soc. 113:737-743.
- Davies, S.F., J.R. Zeldis, and M.J. Unwin. 1986. Salmon and trout stocks of the Rangitata River. Fish. Environmental Rpt. No. 71.
- DeGraaf, D.A. and L.H. Bain. 1986. Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. Trans. Am. Fish. Soc. 115:671-681.
- Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. pp. 3-22, In: J. Diamond and T.J. Case [eds.] Community ecology. Harper and Row, New York, NY.
- Dickhoff, W.W. and C.V. Sullivan. 1987. Involvement of the thyroid gland in smoltification, with special reference to metabolic and developmental processes. Am. Fish. Soc. Symp. 1:197-210.
- Dixon, W.J. [ed.] 1983. BMDP statistical software. UCLA Press, Los Angeles.
- Dolloff, C.A. 1987. Seasonal population characteristics and habitat use by juvenile coho salmon in a small southeast Alaska stream. Trans. Am. Fish. Soc. 116:829-838.
- Dorofeyeva, Ye.A., Ye.A. Zinov'yev, V.A. Klyukanov, Yu.S. Reshetnikov, K.A. Savvaitova, and G.Kh. Shaposhnikova. 1981. The present state of research into the phylogeny and classification of the Salmonidae. J. Ichthyol. 20(5):1-20.

- Duffett-Smith, P. 1985. Practical astronomy with your calculator. 2nd Edition. Cambridge University Press, Cambridge.
- Ebersole, J.P. 1985. Niche separation of two damselfish species by aggression and differential microhabitat utilization. Ecology 66:14-20.
- Echelle, A.A., and I. Kornfield, [eds.] 1984. The evolution of fish species flocks. University of Maine Press, Orono, Maine.
- Elliot, J.M. 1986. Spatial distribution and behavioural movements of migratory trout, Salmo trutta in a Lake District stream. J. Anim. Ecol. 55:907-922.
- Endler, J.A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.
- Endler, J.A. 1980. Natural selection on colour patterns in Poecilia reticulata. Evolution 34:76-91.
- Endler, J.A. 1982. Problems in distinguishing historical from ecological factors in biogeography. Amer. Zool. 22:441-452.
- Endler, J.A. 1986. Natural selection in the wild. Monographs in population biology No. 21. Princeton University Press, Princeton, NJ.
- Etter, R.J. 1988. Physiological stress and color polymorphism in the intertidal snail Nucella lapillus. Evolution 42:660-681.
- Everest, F.H. 1967. Midget bentzel current speed tubes for ecological investigations. Limnol. Oceanogr. 12:179-180.
- Everest, F.H. and D.W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Bd. Canada 29:91-100.

- Fausch, K.D. 1984. Profitable stream positions for juvenile salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* 62:441-451.
- Fausch, K.D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? *Can. J. Fish. Aquat. Sci.* 45:2238-2246.
- Fausch, K.D. and R. White. 1986. Competition among juveniles of coho salmon, brook trout and brown trout in a laboratory stream and implications for Great Lakes tributaries. *Trans. Am. Fish. Soc.* 115:363-381.
- Fausch, K.D. and R.J. White. 1981. Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. *Can. J. Fish. Aquat. Sci.* 38:1220-1227.
- Ferguson, M.M., and D.L.G. Noakes. 1982. Genetics of social behaviour in charrs (Salvelinus spp.). *Anim. Behav.* 30:128-134.
- Ferguson, M.M., and D.L.G. Noakes. 1983a. Behaviour-genetics of lake charr (Salvelinus namaycush) and brook charr (S. fontinalis): observation of backcross and F2 generations. *Zeitschrift fur Tierpsychol.* 62:72-86.
- Ferguson, M.M., and D.L.G. Noakes. 1983b. Movers and stayers: genetic analysis of mobility and positioning in hybrids of lake charr, Salvelinus namaycush and brook charr, S. fontinalis (Pisces:Salmonidae). *Behav. Genet.* 13:213-222.
- Fessler, J.L. and H.H. Wagner. 1969. Some morphological and biochemical changes in steelhead trout during the parr-smolt transformation. *J. Fish. Res. Bd. Canada* 26:2823-2841.
- Flain, M. 1980. Those dammed Clutha salmon. *Freshwater Catch Winter*, 1980:7.
- Flain, M. 1970. Precocious male quinnat salmon Oncorhynchus tshawytscha (Walbaum) in New Zealand. *New Zealand J. Mar. Freshw. Res.* 4:217-222.

- Flain, M. 1972. New Zealand salmon. Fisheries Division Reprint No. 49.
- Flain, M. 1979. Lake Paringa's unusual quinnat (chinook) stock. Freshw. Catch Spring 1979:7-8.
- Flain, M. 1981. Distribution of quinnat salmon, Oncorhynchus tshawytscha, off the east coast of the South Island, 1925-78. New Zealand J. Mar. Freshw. Res. 15:21-24.
- Flain, M. 1982a. Quinnat salmon runs, 1965-78, in the Glenariffe Stream, Rakai River, New Zealand. Fish. Res. Div. Occ. Publ. No. 28.
- Flain, M. 1982b. Quinnat salmon: a study. Freshwater Catch, Spring 1982:6-7.
- Flain, M. 1983. NZ only success with transplants. Freshwater Catch, Winter 1983:11-13.
- Foerster, R.E. 1947. Experiments to develop sea-run from land-locked sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada 7:88-93.
- Folmar, L.C., and W.W. Dickhoff. 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids: A review of selected literature. Aquaculture 21:1-37.
- Foote, C.J. 1987. An experimental examination of behavioural isolation between sockeye salmon and kokanee, the anadromous and nonanadromous forms of Oncorhynchus nerka. Ph.D. thesis, University of British Columbia, Vancouver.
- Foote, C.J., C.C. Wood, and R.E. Withler. 1989. Biochemical genetic comparison of sockeye salmon and kokanee, the anadromous and nonanadromous forms of Oncorhynchus nerka. Can. J. Fish. Aquat. Sci. 46:149-158.
- Fowler, L.G. 1972. Growth and mortality of fingerling chinook as affected by egg size. Prog. Fish. Cult. 34:66-69.

- Fox, D.L. and K.E. Gulre. 1976. Documentation for MIDAS. 3rd. Edition. Statistical research laboratory, University of Michigan, Ann Arbor, Michigan.
- Fraser, F.J. and A.Y. Fedorenko. 1983. Jones creek pink salmon spawning channel: A biological assessment, 1954-1982. Can. Tech. Rpt. Fish. Aquat. Sci. No. 1188.
- Fraser, F.J., P.J. Starr, and A.Y. Fedorenko. 1982. A review of the chinook and coho salmon of the Fraser River. Can. Tech. Rpt. Fish. Aquat. Sci. No. 1126.
- Fulton, L.A. 1968. Spawning areas and abundance of chinook salmon (Oncorhynchus tshawytscha) in the Columbia River basin - Past and present. U.S. Fish and Wildl. Ser. Spec. Sci. Rpt. Fish. No. 571.
- Futuyma, D.J. Sturm und Drang and the evolutionary synthesis. Evolution 42:217-226.
- Futuyma, D.J. 1986. Evolutionary biology. 2nd ed. Sinauer Press, Sunderland, Mass.
- Gaines, M.S., C.L. Baker and A.M. Vivas. 1979. Demographic attributes of dispersing southern bog lemmings (Synaptomys cooperi) in eastern Kansas. Oecologia 40:91-103.
- Gall, G. 1974. Influence of size of eggs and age of females on hatchability and growth in rainbow trout. Calif. Fish and Game 60:26-35.
- Gallup, G.G. 1968. Mirror-image stimulation. Psychol. Bull. 70:782-793.
- Gardner, A.S., Walker, A.F. and R.B. Greer. 1988. Morphometric analysis of two ecologically distinct forms of arctic charr, Salvelinus alpinus (L.), in Loch Rannoch, Scotland. J. Fish Biol. 32:901-910.
- Gharrett, A.J. and M.A. Thomason. 1987. Genetic changes in pink salmon (Oncorhynchus gorbuscha) following their introduction into the Great Lakes. Can. J. Fish. Aquat. Sci. 44:787-792.

- Gharrett, A.J., S.M. Shirley and G.R. Tromble. 1987. Genetic relationships among populations of Alaskan chinook salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat. Sci. 44:765-774.
- Gibbons, J.R.H. 1979. A model for sympatric speciation in Megarhyssa (Hymenoptera: Ichneumonidae): Competitive speciation. Am. Nat. 114:719-741.
- Gilbert, C.H. 1913. Age at maturity of Pacific coast salmon of the genus Oncorhynchus. Bull. U.S. Bureau Fish. 32:57-70.
- Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. Inter. Pac. Salmon Comm. Bull. No. 22.
- Glebe, B.D. and W.C. Leggett. 1976. Weight loss and energy expenditure of American shad during the freshwater migration. Final Rept. Prog. AFC-8, U.S. Nat. Mar. Fish. Ser.
- Glova, G. J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (Oncorhynchus kisutch) and coastal cutthroat trout (Salmo clarki) in a laboratory stream. Hydrobiologica 131:155-16
- Godin, J-G. 1982. Migrations of salmonid fishes during early life history phases: Daily and annual timing. In: E.L. Brannon and E.O. Salo [eds]. Salmon and Trout Migratory Behaviour Symposium. Univ. of Washington Press, Seattle.
- Godin, J-G., P.A. Dill, and D.E. Drury. 1974. Effects of thyroid hormones on behavior of yearling Atlantic salmon (Salmo salar). J. Fish. Aquat. Sci. 31:1787-1790.
- Gorman, O.T. and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59:507-515.
- Gould, S.J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Mass.

- Gould, S.J. and J.T Johnston. 1972. Geographic variation. Ann. Rev. Ecol. Syst. 3:489-456.
- Gould, S.J., and R.C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Royal Soc. Lond. B 205:281-298.
- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47-48.
- Gross, M.R. 1987. Evolution of diadromy in fishes. Am. Fish. Symp. No. 1:14-25.
- Grossman, G.D. and M.C. Freeman. 1987. Microhabitat use in a steam fish assemblage. J. Zool. (Lond.) 212:151-176.
- Hallock, R.J. and D.H. Fry, Jr. 1967. Five species of salmon, Oncorhynchus, in the Sacramento River, California. Calif. Fish and Game 53:5-23.
- Hargreaves, N.B., and R.J. LeBrasseur. 1986. Size selectivity of coho (Oncorhynchus kisutch) preying on chum salmon (O. keta). Can. J. Fish. Aquat. Sci. 43:581-586.
- Harrison, R.G. 1980. Dispersal polymorphisms in insects. Ann. Rev. Ecol. Syst. 11:95-118.
- Hartman, G.F. 1965. The role of behaviour in the ecology and interaction of underyearling coho salmon and steelhead trout. J. Fish. Res. Bd. Canada 22:1035-1081.
- Harvey, B.C., R.C. Cashner and W.J. Mathews. 1988. Differential effects of largemouth bass and smallmouth bass on habitat use by stoneroller minnows. J. Fish Biol. 33:481-487.
- Healey, M.C. 1980. Utilization of the Nanaimo River estuary by juvenile chinook salmon, Oncorhynchus tshawytscha. U.S. Fish and Wildl. Ser. Fish. Bull. 77:653-668.

- Healey, M.C. 1982. Timing and relative intensity of size selective mortality of juvenile chum salmon (Oncorhynchus keta) during early sea life. Can. J. Fish. Aquat. Sci. 39:952-957.
- Healey, M.C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook salmon (Oncorhynchus tshawytscha). Can. Field Nat. 97:427-433.
- Healey, M.C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. pp. 39-52, In: D.J. Meerburg [ed.] Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89.
- Healey, M.C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (Oncorhynchus nerka). pp. 110-117, In: H.D. Smith, L. Margolis and C.C. Wood [eds.] Sockeye salmon (Oncorhynchus nerka). Population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. No. 96.
- Healey, M.C. and W.R. Heard. 1984. Inter- and intrapopulation variation in the fecundity of chinook salmon (Oncorhynchus tshawytscha) and its relevance to life-history theory. Can. J. Fish. Aquat. Sci. 41:476-483.
- Healey, M.C., and F. P. Jordan. 1982. Observations on juvenile chum and chinook and spawning chinook in the Nanaimo River, British Columbia during 1975-81. Can. Man. Rpt. Fish. Aquat. Sci. No. 1659.
- Hearn, W. and B. Kynard. 1986. Habitat utilization and behavioral interaction of juvenile Atlantic salmon (Salmo salar) and rainbow trout (S. gairdneri) in tributaries of the White River of Vermont. Can. J. Fish. Aquat. Sci. 43:1988
- Heming, T.A., J.E. McInerney and D.F. Alderdice. 1982. Effect of temperature on initial feeding in alevins of chinook salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat. Sci. 39:1554-1562.
- Hendrick, P.W. 1986. Genetic polymorphism in heterogenous environments: a decade later. Ann. Rev. Ecol. Syst. 17:535-566.

- Hendrick, P.W., M.E. Ginevan, and E.P. Ewing. 1976. Genetic polymorphism in heterogenous environments. *Ann. Rev. Ecol. Syst.* 12:1-32.
- Hikita, H. 1956. Pacific salmon (Genus: Oncorhynchus) known to occur in the coasts and rivers within Hokkaido. *Sci. Rpt. Hokkaido Fish Hatchery* 11:25-44.
- Hikita, T. 1962. Ecological and morphological studies of the genus Oncorhynchus (Salmonidae) with particular reference on phylogeny. *Sci. Rpt. Hokkaido Salmon Hatchery No.* 17:1-97.
- Hillman, T.W., D.W. Chapman, and J.S. Griffith. 1988. Interaction between chinook salmon and redbside shiner in the lower Wenatchee River, Washington. Don Chapman Consultants Inc., Boise, Idaho.
- Hindar, K., B. Jonsson, J. Andrew and T.G. Northcote. 1988. Resource utilization of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. *Oecologia (Berlin)* 74:481-491.
- Hindar, K., N. Ryman and G. Stahl. 1986. Genetic differentiation among local populations charr, Salvelinus alpinus. *Biol. J. Linn. Soc.* 27:269-285.
- Hindar, K., and B. Johsson. 1982. Habitat and food segregation of dwarf and normal charr (Salvelinus alpinus) from Vangsvatnet Lake, Western Norway. *Can. J. Fish. Aquat. Sci.* 39:1030-1045.
- Hixon, M.A. 1980. Competitive interactions between California reef fishes of the genus Embiotoca. *Ecology* 61:918-931.
- Hoar, W.S. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. *J. Fish. Res. Board Can.* 8:241-263.
- Hoar, W.S. 1976. Smolt transformation: Evolution, behaviour and physiology. *J. Fish. Res. Board Can.* 33:1234-1252.

- Hoar, W.S. 1988. The physiology of smolting salmonids. *Fish Physiol.* 1969-1988, 11:275-234.
- Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (Oncorhynchus kisutch). *Can. J. Fish. Aquat. Sci.* 45:502-515.
- Hourston, W.R. and D. Mackinnon. 1956. Use of an artificial spawning channel by salmon. *Trans. Am. Fish. Soc.* 86:220-230.
- Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, Rana catesbiana. *Evolution* 32:850-871.
- Howell, P., K. Jones, D. Scarnecchia, L. Lavoy, W. Kendra, and D. Ortman. 1985. Stock assessment of Columbia River anadromous salmonids. Volume 1: Chinook, coho, chum and sockeye salmon stock summaries. Final Report to the Bonneville Power Administration, Portland, Oregon.
- Hubbs, C.L. and K.F. Lagler. 1967. Fishes of the Great Lakes Region. Cranbrook Inst. Sci. Bull. No. 26.
- Hume, J.M. and T.G. Northcote. 1985. Initial changes in use of space and food by experimentally segregated populations of Dolly Varden (Salvelinus malma) and cutthroat trout (Salmo clarkii). *Can. J. Fish. Aquat. Sci.* 42:101-1
- Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. *J. Fish. Res. Bd. Canada* 16:835-886.
- Huntingford, F.A. 1976. An investigation of the territorial behaviour of the threespine stickleback (Gasterosteus aculeatus) using principal components analysis. *Anim. Behav.* 24:822-834.
- Hutchings, J.A. and R.A. Myers. 1985. Mating between anadromous and nonanadromous Atlantic salmon, Salmo salar. *Can. J. Zool.* 63:2219-2221.

- Idler, D.R. and W.A. Clemens. 1959. The energy expenditure of Fraser River sockeye salmon during migration, spawning and death. Prog. Rept. Int. Pac. Salmon Fish. Comm. No. 6.
- Jaeger, R.G. 1971. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. Ecology 52:632-637.
- James, G.D. and K.R. Deverall. 1987. Quinnat salmon spawning in the lower Waitaki and Hakataramea Rivers, 1959-86. New Zealand Freshw. Fish. Rpt. No. 93.
- Jenkins, T.M. 1971. The role of social behavior in dispersal of introduced rainbow trout (Salmo gairdneri). J. Fish. Res. Bd. Canada 28:1019-1027.
- Johnson, J.H. 1981. Comparative food selection by coexisting subyearling coho, chinook salmon and rainbow trout in a tributary of Lake Ontario. New York Fish and Game J. 28:150-161.
- Johnson, J.H. and N.H. Ringler. 1981. Natural hybridization of Oncorhynchus kisutch and O. tshawytscha in a Lake Ontario tributary, with notes on meristic variation. Copeia 1981:712-722.
- Johnson, R.F. and R.K. Selander. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. Evolution 25:1-28.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar and S. trutta L.). Rpt. Freshw. Inst. Drott. 39:55-98.
- Keenleyside, M.A.H. 1979. Social organization. pp. 149-177, In: M.A.H. Keenleyside [ed.] Diversity and adaptation in fish behaviour. Zoophysiology Springer Verlag, Berlin.
- Kelso, B.W., T.G. Northcote and C.F. Wehrhahn. 1981. Genetic and environmental aspects of the response to water current by rainbow trout (Salmo gairdneri) originating from inlet and outlet streams of two lakes. Can. J. Zool. 59:2177-2185

- Kendall, A.W. Jr., and R.J. Behnke. 1984. Salmonidae: development and relationships. pp. 142-149, In: H.G. Moser -ed.] Ontogeny and systematics of fishes. Spec. Publ. Amer. Soc. Ichthyol. Herpetol. No. 1. Allen Press, Lawrence, Kansas.
- Kjelson, M.A., P.F. Raquel, and F. W. Fisher. 1982. Life history of fall-run juvenile chinook salmon, Oncorhynchus tshawytscha, in the Sacramento-San Joaquin Estuary, California. pp. 393-413, In: V.S. Kennedy -ed.] Estuarine Comparisons. Academic Press, New York, NY.
- Kornfield, I., D.C. Smith, D.S. Gagnon, and J. N. Taylor. 1982. The cichlid fishes of Cuatro Cienegas, Mexico: direct evidence of conspecificity among distinct trophic morphs. Evolution 36:658-664.
- Kosswig, C. 1963. Ways of speciation in fishes. Copeia 1963:238-244.
- Kratt, L.F. and R. Smith. 1979. Agonistic behaviour of age 0, age 1 and non-breeding adult arctic grayling Thymallus arcticus (Pallas). J. Fish Biol. 15:389-404.
- Kristiansson, A.C. and J.D. McIntyre. 1976. Genetic variation in chinook salmon (Oncorhynchus tshawytscha) from the Columbia River and three coastal Oregon rivers. Trans. Am. Fish. Soc. 105:620-623.
- Kwain, Wen-H. 1987. Biology of pink salmon in the North American Great Lakes. Am. Fish. Symp. No. 1:57-65.
- Kwain, Wen-H. and E. Thomas. 1984. First evidence of spring spawning chinook salmon in Lake Superior. N.A.J. Fish. Mgmt. 4:227-228.
- Lannan, J.E. 1980. Adaptive and behavioral responses to artificial propagation in a stock of chum salmon, Oncorhynchus keta. pp. 309-313, In: W.J. McNeil and D.C. Himsworth -ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.

- L'Abée-Lund, J.H., A.J. Jensen, B. Jonsson, L.M. Saettem, T.G. Heggberget, B.O. Johnsen, and T.F. Naesje. 1989. Latitudinal variation in life history characteristics of sea-run migrant brown trout Salmo trutta from 58 to 70 degrees North. J. Anima
- Larsson, P.-O. 1985. Predation on migratory smolt as a regulating factor in Baltic salmon, Salmo salar L., populations. J. Fish Biol. 26:391-397.
- Lavin, P.A., and J.D. McPhail. 1986. Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (Gasterosteus aculeatus). Can. J. Fish. Aquat. Sci. 43:2455-2463.
- Lavin, P.A., and J.D. McPhail. 1987. Morphological divergence and the organization of trophic characters among lacustrine populations of the threespine stickleback (Gasterosteus aculeatus). Can. J. Fish Aquat. Sci. 44:1820-1829.
- Lear, W.H. and R.K. Misra. 1978. Clinal variation in scale characters of Atlantic salmon (Salmo salar) based on discriminant function analysis. J. Fish. Res. Bd. Canada 35:43-47.
- Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McAllister and J.R. Stauffer Jr. 1980. Atlas of North American freshwater fishes. North Carolina Biological Survey Publ. No. 1980-12.
- Leggett, W.C., and J.E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (Alosa sapidissima): evidence for population specific life history strategies in fish. J. Fish. Res. Bd. Canada 35:1469-147
- Leider, S.A., D.W. Chilcote, and J.J. Loch. 1984. Spawning characteristics of sympatric populations of steelhead trout, Salmo gairdneri: evidence for partial reproductive isolation. Can. J. Fish. Aquat. Sci. 41:1454-1462.
- Levings, C.D., C.D. McAllister and B.D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia, by wild and hatchery-reared juvenile chinook salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat.

Sci. 43:1

- Levy, D.A. and C.D. Levings. 1978. A description of the fish community of the Squamish River estuary, B.C.: relative abundances, seasonal changes and feeding habits of salmonids. Fish. Mar. Ser. Manu. Rpt. No. 1475.
- Levy, D.A. and T.G. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Can. J. Fish. Aquat. Sci. 39:270-276.
- Lewontin, R.C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York.
- Liley, N.R. and B.H. Seghers. 1975. Factors affecting the morphology and behaviour of guppies in Trinidad. pp. 92-118, In: G.P. Baerends et al. [eds.] 1975 Function and evolution in behaviour. Clarendon Press, Oxford.
- Lindsey, C.C. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci. 38:1497-1506.
- Lindsey, C.C. and J.D. McPhail. 1986. Zoogeography of fishes of the Yukon and Mackenzie Basins. pp. 639-674, In: Hocutt, C.H. and E.O. Wiley [eds.] Zoogeography of North American Freshwater Fishes. Wiley and Sons.
- Lister, D.B. and C.E. Walker. 1966. The effect of flow control on freshwater survival of chum, coho and chinook salmon in the Big Qualicum River. Can. Fish. Cult. 37:3-26.
- Lister, D.B. and H.S. Genoe. 1970. Stream habitat utilization by cohabiting underyearlings of chinook and coho salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Bd. Canada 27:1215-1224.
- Loftus, W.F. and H. Lenon. 1977. Food habits of the salmon smolts, Oncorhynchus tshawytscha and O. keta, from Salcha River, Alaska. Trans. Am. Fish. Soc. 106:235-240.

- Lott, D.F. 1984. Intraspecific variability in the social systems of wild vertebrates. *Behaviour* 88:266-324.
- Lundqvist, H., and Eriksson, L-O. 1987. Annual rhythms of swimming behaviour and seawater adaptation in young Baltic salmon, Salmo salar, associated with smolting. *Environ. Biol. Fishes* 14:259-267.
- Maeda, N. and T. Hidaka. 1979. Ethological function of parr marks in a Japanese trout, Oncorhynchus masou f. ishikawai. *Zool. Mag.* 88:34-42.
- Major, R.L., and J.L. Mighell. 1969. Egg-to-migrant survival of spring chinook salmon (Oncorhynchus tshawytscha) in the Yakima River, Washington. *U.S. Fish and Wildl. Ser. Fish. Bull.* 67:347-359.
- Major, R.L., J. Ito, S. Ito, and H. Godfrey. 1978. Distribution and origin of chinook salmon (Oncorhynchus tshawytscha) in offshore waters of the north Pacific Ocean. *Int. North Pac. Fish. Comm. Bull. No.* 38.
- Marshall, D.E. and C.I. Manzon. 1980. Catalogue of salmon streams and spawning escapements of Prince George subdistrict. *Fish. Mar. Ser. Data Rep. No.* 79.
- Martin, D.J., C.J. Whitmus, L.E. Hachmeister, E.C. Volk and S.L. Schroder. 1987. Distribution and seasonal abundance of juvenile salmon and other fishes in the Yukon River delta. Report to NOAA, Ocean Assessment Division, Anchorage, Alaska.
- Martin, P. and H.C. Kramer. 1987. Individual differences in behaviour and their statistical consequences. *Anim. Behav.* 35:1366-1376.
- Martin, P. and P. Bateson. 1986. Measuring behaviour. An introductory guide. Cambridge University Press, Cambridge, Mass.
- Martin, R.M., W.R. Heard, and A.C. Wertheimer. 1981. Short-term rearing of pink salmon (Oncorhynchus gorbuscha) fry: effect on survival and biomass of returning adults. *Can. J. Fish. Aquat. Sci.* 38:554-558.

- Mason, J.C. and D.W. Chapman. 1965. Significance of early emergence, environmental rearing capacity and behavioural ecology of juvenile coho salmon in stream aquaria. J. Fish. Res. Bd. Canada 22:173-190.
- Mason, J.E. 1965. Salmon of the north Pacific Ocean-Part IX. Coho, chinook and masu salmon in offshore waters. 2. Chinook salmon in offshore waters. Bull. Int. North Pac. Fish. Comm. 16:41-73.
- Mather, K. 1955. Polymorphism as an outcome of disruptive selection. Evolution 9:52-61.
- Maynard Smith, J. 1962. Disruptive selection, polymorphism and sympatric speciation. Nature 195:60-62.
- Mayr, E. 1963. Animal species and evolution. The Belknap Press of Harvard University Press. Cambridge, Mass.
- Mayr, E. 1983. How to carry out the adaptationist program? Am. Nat. 121:324-334.
- McBride, D.N. and J.A. Wilcock. 1983. Alaska chinook salmon (Oncorhynchus tshawytscha Walbaum) catch and escapement, 1961-1980, with age, size, and sex composition estimates. Alaska Dept. Fish and Game Inform. Leaflet No. 212.
- McCabe, G.T. Jr., W.D. Muir, R.L. Emmett, and J.T. Durkin. 1983. Relationship between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. Fish. Bull. 81:815-826.
- McCormick, S.D. and R.J. Naiman. 1984a. Osmoregulation in the brook trout, Salvelinus fontinalis -I. Diel, photoperiod and growth related physiological changes in freshwater. Comp. Biochem. Physiol. 79A:7-16.
- McCormick, S.D. and R.J. Naiman. 1984b. Osmoregulation in the brook trout, Salvelinus fontinalis -II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comp. Biochem. Physiol. 79A:17-28.

- McCormick, S.D., and R.L. Saunders. 1987. Preparatory physiological adaptations for marine life of salmonids: Osmoregulation, growth, and metabolism. Am. Fish. Soc. Symp. 1:211-229.
- McInerney, J.E. 1964. Salinity preference: an orientation mechanism in salmon migration. J. Fish. Res. Bd. Can. 21:995-1018.
- McKaye, K.R. 1980. Seasonality in habitat selection by the gold color morph of Cichliso citrinellum and its relevance to sympatric speciation in the family Cichlidae. Environ. Biol. Fishes 5:75-79.
- McLeod, C.L. and J.P. O'Neill. 1983. Major range extensions of anadromous salmonids and first record of chinook salmon in the MacKenzie River drainage. Can. J. Zool. 61:2183-2184.
- McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (Gasterosteus): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. Can. J. Zool. 62:1402-1408.
- McPhail, J.D. and C.C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Bd. Canada Bull. No. 173.
- McPhail, J.D. and C.C. Lindsey. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia system and rivers north to the Stikine). pp. 615-637, In: Hocutt, C.H. and E.O. Wiley [eds.] Zoogeography of North American Freshwater Fishes. Wiley and Sons.
- Meehan, W.R. and D.R. Siniff. 1962. A study of the downstream migrations of anadromous fishes in the Taku River, Alaska. Trans. Am. Fish. Soc. 91:399-407
- Metcalfe, N.B. 1989. Differential response to a competitor by Atlantic salmon adopting alternative life-history strategies. Proc. R. Soc. London. B 236:21-27.
- Metcalfe, N.B. and J.E. Thorpe. 1989. Determinants of geographical variation in the age of seaward-migrating salmon, Salmo salar. J. Animal Ecol.: In Press.

- Metcalfe, N.B., F. Huntingford and J.E. Thorpe. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon Salmo salar. J. Animal Ecol. 57:463-474.
- Metcalfe, N.B., F.A. Huntingford, W.D. Graham, and J.E. Thorpe. 1989. Early social status and the development of life-history strategies in Atlantic salmon. Proc. Royal Soc. London B 236:7-19.
- Miller, R.J. and E.L. Brannon. 1982. The origin and development of life history patterns in Pacific salmonid. pp. 296-309, In E.L. Brannon and E.O. Salo [eds.] Proc. Salmon and Trout Migratory Behavior Symposium, Univ. Washington Press, Seattle.
- Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marshall. 1988. Larval size and recruitment mechanisms in fishes: towards a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657-1670.
- Milligan, P.A., W.O. Rublee, D.D. Cornett, and R.A.C. Johnston. 1983. The distribution and abundance of chinook salmon (Ocorhynchus tshawytscha) in the upper Yukon River basin as determined by a radio-tagging and spaghetti tagging
- Moffett, J.W. 1949. The first four years of king salmon maintenance below Shasta Dam, Sacramento River, California. Calif. Fish and Game 35:77-102.
- Morse, D.H. 1974. Niche breadth as a function of social dominance. Am. Nat. 108:818-830.
- Moyle, P.B. and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Trans. Am. Fish. Soc. 114:695-704.
- Mundie, H. 1974. Optimization of the salmonid nursery stream. J. Fish. Res. Bd. Canada 31:1827-1837.

- Murray, C.B., and J.D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (Oncorhynchus) embryos and alevins. Can. J. Zool. 66:266-273.
- Myers, R.A., J.A. Hutchings, and R.J. Gibson. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, Salmo salar. Can. J. Fish. Aquat. Sci. 43:1242-1248.
- Naesje, T.F., B. Jonsson and O.T. Sandlund. 1986. Drift of cisco and whitefish larvae in a Norwegian river. Trans. Am. Fish. Soc. 115:89-93.
- Needham, P.R., O.R. Smith and H.A. Hanson. 1940. Salmon salvage problems in relation to Shasta Dam, California, and notes on the biology of the Sacramento River salmon. Trans. Am. Fish. Soc. 70:55-69.
- Nei, M. and R.K. Koehn. 1983. The evolution of genes and proteins. Sinauer Press, Sunderland, Mass.
- Neilson, J.D. and G.H. Geen. 1986. First year growth of Sixes River chinook salmon as inferred from otoliths: effects on mortality and age-at-maturity. Trans. Am. Fish. Soc. 115:28-33.
- Neilson, J.D., G.H. Geen, and D. Bottom. 1985. Estuarine growth of juvenile chinook salmon, Oncorhynchus tshawytscha, as inferred from otolith microstructure. Can. J. Fish. Aquat. Sci. 42:899-908.
- Newman, R.M., and T.F. Waters. 1989. Differences in brown trout (Salmo trutta) production among contiguous sections of an entire stream. Can. J. Fish. Aquat. Sci. 46:203-213.
- Nicholas, J.W. and D.G. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Oregon Dept. Fish and Wildl. Information Report No. 88-1.

- Nishikawa, K.C. 1985. Competition and the evolution of aggressive behavior in two species of terrestrial salamanders. *Evolution* 39:1282-1294.
- Noakes, D.L.G. 1986. The genetic basis of fish behaviour. pp. 3-22, In: T.J. Pitcher [ed.] *The behaviour of teleost fishes*. Crom-Helm, London.
- Nordeng, H. 1983. Solution to the "Char Problem" based on Arctic char (Salvelinus alpinus) in Norway. *Can. J. Fish. Aquat. Sci.* 40:1372-1387.
- North, E. 1979. Aggressive behaviour in juvenile brown trout, Salmo trutta L.: an analysis of the wigwag display. *J. Fish Biol.* 15:571-577.
- Northcote, T.G. and N.A. Nilsson. 1981. Rainbow trout (Salmo gairdneri) and cutthroat trout (S. clarki) interactions in coastal, British Columbia lakes. *Can. J. Fish. Aquat. Sci.* 38:1228-1246.
- Orians, G.H., and M.F. Willson. 1964. Interspecific territories of birds. *Ecology* 45:736-745.
- Otto, R.G., and J.E. McInerney. 1969. Development of salinity preference in pre-smolt coho salmon. *J. Fish. Res. Bd. Canada* 27:793-800.
- Parker, R.R. 1971. Size-selective predation among juvenile salmon in a British Columbia inlet. *J. Fish. Res. Bd. Canada* 28:1503-1510.
- Parry, G. 1960. The development of salinity tolerance in the salmon, Salmo salar (L.), and some related species. *J. Exp. Biol.* 37:425-434.
- Parzefall, J. 1986. Behavioural ecology of cave-dwelling fishes. pp. 433-458, In: T.J. Pitcher [ed.] *The behaviour of teleost fishes*. Crom-Helm, London.
- Petrosky, C.E. and T.C. Bjornn. 1988. Response of wild rainbow trout (Salmo gairdneri) and cutthroat trout (S. clarki) to stocked rainbow trout in fertile and infertile streams. *Can. J. Fish. Aquat. Sci.* 45:2087-2105.

- Pimentel, R. 1979. Morphometrics. The multivariate analysis of biological data. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. Amer. Zool. 23:57-63.
- Power, G. 1981. Stock characteristics and catches of Atlantic salmon (Salmo salar) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38:1601-1611.
- Power, M.E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? Ecology 65:523-528.
- Quinn, T. and K. Fresh. 1984. Homing and straying in chinook salmon (Oncorhynchus tshawytscha) from Cowlitz River Hatchery, Washington. Can. J. Fish. Aquat. Sci. 41:1078-1082.
- Raleigh, R.F. 1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. Ecology 52:291-297.
- Randall, R.G. 1982. Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. Can. J. Zool. 60:2239-2244.
- Randall, R.G., M.C. Healey, and J.B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout and char. Am. Fish. Soc. Symp. 1:27-41.
- Raymond, J.A. 1981. Emigration of salmon smolts from Clear Creek, Alaska. Alaska Dept. Fish and Game Regional Report, Juneau, Alaska.
- Refstie, T., T.A. Steine, and T. Gjerdem. 1977. Selection experiments with salmon. II. Proportion of Atlantic salmon smoltifying at 1 year of age. Aquaculture 10:239-242.

- Reimers, P.E. 1968. Social behaviour among young chinook salmon. J. Fish. Res. Bd. Can. 25:2005-2008.
- Reimers, P.E. 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Ore. Fish Comm. Res. Rep. No. 4.
- Reimers, P.E. 1979. Success in a hatchery program with fall chinook salmon by simulating the natural history of the stock. Prog. Fish Cult. 41:192-195.
- Reimers, P.E. and R.E. Loeffel. 1967. The length of residence of juvenile fall chinook salmon in selected Columbia River tributaries. Ore. Fish Comm. Res. Briefs 13:5-19.
- Reisenbichler, R., J.D. McIntyre and R.J. Hallock. 1982. Relation between size of chinook salmon, Oncorhynchus tshawytscha, released at hatcheries and returns to hatcheries and ocean fisheries. Calif. Fish and Game 68:57-59.
- Rice, W.R. 1985. Disruptive selection on habitat preference and the evolution of reproductive isolation: an exploratory experiment. Evolution 39:645-656.
- Rich, W.H. 1920. Early history and seaward migration of chinook salmon in the Columbia and Sacramento Rivers. Bull. U.S. Bur. Fish. 37:1-73.
- Rich, W.H., and H.B. Holmes. 1928. Experiments in marking young chinook salmon on the Columbia River, 1916 to 1927. Bull. United States Bur. Fish. 44:215-264.
- Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. p. 19-160. In: R.C. Simon and P.A. Larkin [eds.] The stock concept in Pacific salmon. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, B.C.
- Ricker, W.E. 1979. Growth rates and models. pp. 678-736, In: W.S. Hoar, D.J. Randall, and J.R. Brett. [eds.] Fish Physiology Volume 8. Bioenergetics and growth, Academic Press, New York.

- Ricker, W.E. 1981. Changes in the average size and age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38:1636-1656.
- Riddell, B.E., and W.C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 38:308-320.
- Robertson, O.H. 1957. Survival of precociously mature king salmon male parr (Oncorhynchus tshawytscha (Juv.) after spawning. Calif. Dept. Fish and Game Bull. 43:119-130.
- Rosenau, M.L. and J.D. McPhail. 1987. Inherited difference in agonistic behavior between two populations of coho salmon. Trans. Am. Fish. Soc. 116:646-655.
- Rosenzweig, M.L. 1978. Competitive speciation. Biol. J. Linn. Soc. 10:275-289.
- Rousenfell, G.A. 1958. Anadromy in North American Salmonidae. U.S. Fish Wildl. Ser. Fish. Bull. 58:171-185.
- Rousenfell, G.A. 1962. Relationships among North American Salmonidae. U.S. Fish and Wildl. Ser. Fish. Bull. 62:235-270.
- Ruffner, J.A. 1985. Climates of the States. 3rd Edition. Gale Research Co., Detroit, MI.
- Ruggertone, G.T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Trans. Am. Fish. Soc. 115:736-743.
- Rutter, C. 1904. Natural history of the quinnat salmon. Bull. U.S. Fish. Comm. 22:65-141.
- Ryman, N. 1983. Patterns of distribution of biochemical genetic variation in salmonids: differences between species. Aquaculture 33:1-21.

- Ryman, N., F.W. Allendorf, and G. Stahl. 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout (Salmo trutta). Genetics 92:247-262.
- Schaffer, W.M. and P.F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56:577-590.
- Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecol. Mono. 52:395-414.
- Schluchter, M.D. and J.A. Lichatowich. 1977. Juvenile life histories of Rouge River spring chinook salmon (Oncorhynchus tshawytscha) (Walbaum), as determined by scale analysis. Oreg. Dept. Fish Wildl. Inf. Rept. Ser. Fish. 77-5.
- Shmidt, P. Yu. 1950. Fishes of the Sea of Okhotsk. Smithsonian Inst. Natl. Sci. Found. Translated from Russian by Israeli Program for Scientific Translation, Jerusalem.
- Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. 122:240-285.
- Scofield, N.B. 1900. Notes on an investigation of the movement and rate of growth of the quinnat salmon fry in the Sacramento River. Fifteenth Biennial Report, California State Board of Fish Commissioners, Sacramento.
- Scott, D. 1984. Origin of the New Zealand sockeye salmon, Oncorhynchus nerka (Walbaum). J. Royal Soc. New Zealand 14:245-249.
- Scott, W.B. and E.J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Bd. Canada Bull. 173.
- Sexton, O.J. and J.R. Bizer. 1978. Life history patterns of Ambystoma tigrinum in montane Colorado. Am Midl. Nat. 99:101-118.

- Shepherd, B.G., J.E. Hillaby, and R.J. Hutton. 1986a. Studies on Pacific salmon (Oncorhynchus spp.) in Phase 1 of the Salmonid Enhancement Program. Volume 2: Data Appendices. Can. Tech. Rep. Fish. Aquat. Sci. No. 1482.
- Shepherd, B.G., J.E. Hillaby, and R.J. Hutton. 1986b. Studies on Pacific salmon (Oncorhynchus spp.) in Phase 1 of the Salmonid Enhancement Program. Volume 1: Summary. Can. Tech. Rep. Fish. Aquat. Sci. No. 1482.
- Sheppard, D.H. 1971. Competition between two chipmunk species (Eutamias). Ecology 52:320-329.
- Shoener, T.W. 1987. Axes of controvesy in community ecology. pp. 8-16, In: W.J. Mathews and D.C. Heins. "eds." Community and evolutionary ecology of North American stream fishes. Univ. Oklahoma Press, Norman, Ok.
- Simenstad, C.A., K.L. Fresh, and E.O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. pp. 343-364, In: V.S. Kennedy "ed." Estuarine Comparisons. Academic Press Inc., New York, NY.
- Smith, G.R. and R.F. Stearley. 1989. The classification and scientific names of rainbow trout and cutthroat trout. Fisheries (Bethesda) 14:4-10.
- Smith, G.R. and T.N. Todd. 1984. Evolution of fish species flocks in north temperate lakes. pp. 45-68, In: Echelle, A.A., and I. Kornfield "eds." 1984. Evolution of Fish Species Flocks. University of Maine Press, Orono, Maine.
- Smith, S.R. 1969. Reproductive isolation in summer and winter races of steelhead trout. pp. 21-38, In: T.G. Northcote "ed." Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C
- Smith, T.B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. Nature 329:717-719.

- Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. Amer. Zool. 23:47-55.
- Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. 6th edition., Iowa State University Press, Ames, Iowa.
- Spaulding, J.S., T.W. Hillman, D.W. Chapman, and J.S. Griffith. 1988. Habitat selection, growth, and movement of chinook salmon and steelhead trout in response to introduced coho salmon in the Wenatchee River, Washington. Don Chapman Consultants Inc., Boise, Idaho.
- Stearns, S.C. 1976. Life history tactics: a review of the ideas. Quart. Rev. Biol. 51:3-47.
- Stearns, S.C. 1983. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. Amer. Zool. 23:65-75.
- Steel, R.G. and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw Hill Book Co., New York.
- Stein, R.A., P.E. Reimers and J.D. Hall. 1972. Social interaction between juvenile coho (Oncorhynchus kisutch) and fall chinook (O. tshawytscha) salmon in Sixes River, Oregon. J. Fish. Res. Board Can. 29:1737-1748.
- Stokell, G. 1962. Pacific salmon in New Zealand. Trans. Roy. Soc. New Zealand 2:181-190.
- Svardson, G. 1979. Speciation of Scandinavian Coregonus . Inst. Fw. Res. Drott. Rpt. 57:1-92.
- Symons, P.K. 1974. Territorial behaviour of juvenile Atlantic salmon reduces predation by brook trout. Can. J. Zool. 52:677-679.
- Synder, J.O. 1931. Salmon of the Klamath River. Calif. Dept. Fish and Game Bull. 34:1-130.

- Taborsky, M., B. Hudde, and P. Wirtz. 1987. Reproductive behaviour and ecology of Symphodus (Crenilabrus) ocellatus a European wrasse with four types of male behaviour. Behaviour 102:82-118.
- Tauber, C.A. and M.J. Tauber. 1977. Sympatric speciation based on allelic changes at three loci: evidence from natural populations in two habitats. Science 197:1298-1299.
- Tauber, C.A. and M.J. Tauber. 1981. Insect seasonal cycles: genetics and evolution. Ann. Rev. Ecol. Syst. 12:281-308.
- Taylor, E.B. 1989. Precocial male maturation in laboratory reared populations of juvenile chinook salmon, Oncorhynchus tshawytscha. Can. J. Zool. 67: In Press.
- Taylor, E.B. 1988. Water temperature and water velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream. Trans. Am. Fish. Soc. 117:22-28.
- Taylor, E.B. and J.D. McPhail. 1985a. Variation in body morphology among British Columbia populations of coho salmon (Oncorhynchus kisutch). Can. J. Fish. Aquat. Sci. 42:2020-2028.
- Taylor, E.B. and J.D. McPhail. 1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, Ocorhyncohus kisutch. Can. J. Fish. Aquat. Sci. 42:2029-2033.
- Tchernavin, V.V. 1939. The origin of salmon. Is its ancestry marine or freshwater? Salmon and Trout Magazine 95:120-140.
- Thoday, J.M. 1959. Effects of disruptive selection. I. Genetic flexibility. Genetics 13:187-203.
- Thoday, J.M. and T.B. Boam. 1959. Effects of disruptive selection. II Polymorphism and divergence without isolation. Genetics 13:204-218.

- Thomas, W.K., R.E. Withler, and A.T. Beckenbach. 1986. Mitochondrial DNA analysis of Pacific salmonid evolution. Can. J. Zool. 64:1058-1064.
- Thorarensen, H., and W.C. Clarke. 1989. Smoltification induced by a 'skeletal' photoperiod in underyearling coho salmon (Oncorhynchus kisutch). Fish Physiol. Biochem. 6:11-18.
- Thorpe, J.E. 1982. Migration in salmonids, with special reference to juvenile movements in freshwater. pp. 86-97, In: E.L. Brannon and E.O. Salo [eds.] Proc. Salmon and Trout Migratory Behavior Symposium. Univ. Washington Press, Seattle.
- Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, Salmo salar: freshwater influences and conflicts with smolting. pp. 7-14, In: D.J. Meerburg [ed.] Salmonid age at maturity. Spec. Publ. Fish. Aquat. Sci. No. 89.
- Thorpe, J.E. 1987. Smolting vs residency: developmental conflicts in salmonids. Am. Fish. Soc. Symp. 1:244-252.
- Thorpe, J.E. and M.I.G. Morgan. 1978. Parental influence on growth rate, smolting rate and survival in hatchery reared juvenile Atlantic salmon, S. salar. J. Fish Biol. 13:549-556.
- Thorpe, J.E., R.I.G. Morgan, D. Prestwell, and P.J. Higgins. 1988. Movement rhythms in juvenile Atlantic salmon, Salmo salar L. J. Fish Biol. 33:931-940.
- Thorpe, J.E., C.E. Adams, M.S. Miles, D.S. Keay. 1989. Some photoperiod and temperature influences on growth opportunity in juvenile Atlantic salmon, Salmo salar L. Aquaculture: In Press
- Thorpe, J.E., R.I.G. Morgan, C. Talbot, and M.S. Miles. 1983. Inheritance of developmental rates in Atlantic salmon. Aquaculture 33:119-128.
- Thorpe, J.E., and K.A. Mitchell. 1981. Stocks of Atlantic salmon (Salmo salar) in Britain and Ireland: discreteness, and current management. Can. J. Fish. Aquat. Sci. 38:1576-1590.

- Tsuyuki, H. and E. Roberts. 1966. Inter-species relationships within the genus Oncorhynchus based on biochemical systematics. J. Fish. Res. Bd. Canada 23:101-107.
- Tsuyuki, H. and S.N. Willisroft. 1977. Swimming stamina differences between genotypically distinct forms of rainbow trout (Salmo gairdneri) and steelhead trout. J. Fish. Res. Bd. Canada 34:996-1003.
- Unwin, M.J. 1986. Stream residence time, size characteristics, and migration patterns of juvenile chinook salmon (Oncorhynchus tshawytscha) from a tributary of the Rakaia River, New Zealand. N.Z. J. Mar. Fresh. Res. 20:231-252.
- Utter, F.M., F.W. Allendorf and G.O. Hodgins. 1973. Genetic variability and relationships of Pacific salmon and related trout species based on protein variation. Syst. Zool. 22:257-270.
- Utter, F.M., G. Milner, G. Stahl, and D. Teel. 1989. Genetic population structure of chinook salmon, Oncorhynchus tshawytscha, in the Pacific Northwest. U.S. Fish and Wildl. Ser. Fish. Bull., In Press.
- Utter, F.M., P. Aebersold, and G. Winans. 1987. Interpreting genetic variation detected by electrophoresis. pp. 21-46, In: Ryman, N. and F.M. Utter -eds. Population genetics and fishery management. Univ. of Washington Press, Seattle.
- Van Hying, J.M. 1973. Factors affecting the abundance of fall chinook salmon in the Columbia River. Res. Rpts. Fish Comm. Oregon 4:3-87.
- Van Rhijn, J.G. 1973. Behavioural dimorphism in male ruffs Philomachus pugnax (L.). Behaviour 47:153-229.
- Virtanen, E. and A. Oikari. 1984. Effects of low acclimation temperature on salinity adaptation in the presmolt salmon, Salmo salar L. Comp. Biochem. Physiol. 78A:387-392.

- Vronskiy, B.B. 1972. Reproductive biology of the Kamchatka River chinook salmon Oncorhynchus tshawytscha (Walbaum) J. J. Ichthyology 12:259-273.
- Wagner, H., F. Conte and J. Fessler. 1969. Development of osmotic and ionic regulation in two races of chinook salmon, Oncorhynchus tshawytscha. Comp. Biochem. Physiol. 29:325-341.
- Walker, C.E. 1976. Studies of the freshwater and anadromous fishes of the Yukon River within Canada. Canadian Department of the Environment, Fisheries and Marine Service Regional Report No. PAC T/76-7. Vancouver, B.C.
- Walters, C.J., R. Hilborn, R.M. Peterman, and M.J. Staley. 1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Bd. Canada 35:1303-1315.
- Warner, R.R. and S.G. Hoffman. 1980. Local population size as a determinant of mating system and sex composition in two tropical marine fish (Thalassoma spp.). Evolution 34:508-518.
- Webb, P.W. 1975. Hydromechanics and energetics of fish propulsion. Can. Fish. Mar. Ser. Bull. No. 180.
- Webb, P.W. 1978. Temperature effects on acceleration performance in rainbow trout, Salmo gairdneri. J. Fish. Res. Bd. Canada 35:1417-1422.
- Wehrhahn, C.F. and R. Powell. 1987. Electrophoretic variation, regional differences, and gene flow in the coho salmon (Oncorhynchus kisutch) of southern B.C. Can. J. Fish. Aquat. Sci. 44:822-831.
- Weisbart, M. 1968. Osmotic and ionic regulation in embryos, alevins, and fry of the five species of Pacific salmon. Can. J. Zool. 46:385-397.
- Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. Am. Nat. 128:319-339.

- Werner, E.E. and D.J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology* 58:869-876.
- Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittlebach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548.
- Wernstedt, F.L. 1972. World climatic data. Climatic Data Press.
- White, H.C. and A.G. Huntsman. 1938. Is local behaviour in salmon heritable? *J. Fish. Res. Bd. Canada* 9:1-18.
- Wilbur, H.M. 1980. Complex life cycles. *Ann. Rev. Ecol. Syst.* 11:67-93.
- Wilkinson, L. 1988. SYSTAT: The system for statistics. Evanston, IL. Systat Inc.
- Winans, G.A. and R.S. Nishioka. 1984. A multivariate description of change in body shape of coho salmon (Oncorhynchus kisutch) during smoltification. *Aquaculture* 66:235-245.
- Wingfield, J.C., G.F. Ball, R.E. Hegner, and M. Ramenofsky. 1987. Testosterone and aggression in birds. *Am. Sci.* 75:602-608.
- Withler, I.L. 1966. Variability in life history characteristics of steelhead trout (Salmo gairdneri) along the Pacific coast of North America. *J. Fish. Res. Bd. Canada* 23:365-393.
- Withler, R.E. 1985. Ldh-4 allozyme variability in North American sockeye salmon (Oncorhynchus nerka) populations. *Can. J. Zool.* 63:2924-2932.
- Withler, R.E., W.C. Clarke, B.E. Riddell, and H. Kreiberg. 1987. Genetic variation in freshwater survival and growth of chinook salmon (Oncorhynchus tshawytscha). *Aquaculture* 64:85-96.

- Wolf, P. 1950. A trap for the capture of fish and other organisms moving downstream. Trans. Am. Fish. Soc. 88:41-45.
- Wood, C.C. 1985. Dispersion of common mergansers (Mergus merganser) breeding pairs in relation to the availability of juvenile Pacific salmon in Vancouver Island streams. Can. J. Zool. 64:756-784.
- Wood, C.C., B.E. Riddell and D.T. Rutherford. 1987. Alternative juvenile life histories of sockeye salmon (Oncorhynchus nerka) and their contribution to production in the Stikine River, Northern British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 96:12-24.
- Wright, S. 1978. Evolution and the genetics of populations. Volume 4. Variability within and among natural populations. The University of Chicago Press, Chicago.
- Yevsin, Y.N. 1977. Morphological characteristics and variability of the summer sea trout (Salmo trutta) from the Pulmg'a and Malaya Kumzhevaya Rivers. J. Ichthyol. 17:350-356.
- Zar, J.H. 1984. Biostatistical analysis. 2nd Edition. Prentice-Hall, Inc., Englewood Cliffs, N.J.
- Zaugg, W.S., J.E. Bodle, J.E. Manning and E. Wold. 1986. Smolt transformation and seaward migration in 0-age progeny of adult spring chinook salmon (Oncorhynchus tshawytscha) matured early with photoperiod control. Can. J. Fish. Aquat. Sci. 43:885-888.

Publications:

- Taylor, E.B. 1989. Phenotypic correlates of life history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. **Journal of Animal Ecology** In Press.
- Taylor, E.B. 1989. Precocial male maturation in laboratory-reared populations of chinook salmon, *Oncorhynchus tshawytscha*. **Canadian Journal of Zoology** 67:0000-0000. (Accepted 21/10/88).
- Taylor, E.B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile coho and chinook salmon in a laboratory stream channel. **Transactions of the American Fisheries Society** 117:22-28.
- Taylor, E.B. 1988. Adaptive variation in rheotactic and agonistic behavior in newly-emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. **Canadian Journal of Fisheries and Aquatic Sciences** 45:237-243.
- Taylor, E.B. 1986. Differences in body morphology between wild and hatchery populations of juvenile coho salmon. **Progressive Fish Culturist** 48:171-176.
- Taylor, E.B. & P.A. Larkin. 1986. Current response and agonistic behavior in newly-emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. **Canadian Journal of Fisheries and Aquatic Sciences** 43:565-573.
- Taylor, E.B. & J.D. McPhail. 1986. Prolonged and burst swimming performance in anadromous and freshwater threespine stickleback, *Gasterosteus aculeatus*. **Canadian Journal of Zoology** 64:416-420.
- Taylor, E.B. & J.D. McPhail. 1985. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. **Canadian Journal of Fisheries and Aquatic Sciences** 42:2020-2028.
- Taylor, E.B. & J.D. McPhail. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. **Canadian Journal of Fisheries and Aquatic Sciences** 42:2029-2033.
- Taylor, E.B. & J.D. McPhail. 1985. Burst swimming performance and size-related predation in newly-emerged coho salmon, *Oncorhynchus kisutch*. **Transactions of the American Fisheries Society** 114:546-551.
- Taylor, E.B. & J.D. McPhail. 1985. Ontogeny of the startle response in young coho salmon, *Oncorhynchus kisutch*. **Transactions of the American Fisheries Society** 114:552-556.
- Thomas, T.E., P.J. Harrison & E.B. Taylor. 1985. Nitrogen uptake and growth of the germlings and mature thalli of *Fucus distichus*. **Marine Biology** 84:267-274.