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Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum)

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Throughout its native North Pacific, the chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), exists as two life-history types that are distinguished by the age at which juvenile salmon migrate to sea as smolts. 'Stream-type' chinook migrate seaward after 1 or more years of feeding in fresh water, whereas 'ocean-type' fish migrate to sea as newly emerged fry or after 2–3 months in fresh water. Stream-type chinook predominate in populations distant from the sea south of 56° N, and in both inland and coastal populations north of this point. By contrast, ocean-type chinook predominate in coastal populations south of 56° N, but are rare in populations in more northerly latitudes. Stream-type populations are associated with areas of low 'growth opportunity' (as measured by temperature and photoperiod regimes) and/or areas distant from the sea compared to ocean-type. Geographic variability in juvenile life history is suggested to result, in part, from environmental modulation of smolting timing via differences in growth opportunity among geographic areas. In addition, differences in migration distance and temperature regime may result in selection for different sizes at migration among populations which, through differences in growth opportunity, might promote geographic variability in age at seaward migration.

Key words: *Oncorhynchus tshawytscha*; juveniles; life history variation; environmental influence.

I. INTRODUCTION

Geographic variation among salmonid populations is extensive because of the diversity of environments in the geographic range of each species and because of the tendency of adults to return to their natal streams to spawn. Studies of intra-specific geographic variation have included allozyme frequencies (Ryman & Stahl, 1981; Wehrhahn & Powell, 1987), mitochondrial DNA (Birt *et al.*, 1986), developmental rate (Beacham & Murray, 1986), scale growth characters (Lear & Misra, 1978), morphology and meristics (Cavender, 1978; Riddell & Leggett, 1981; Claytor & MacCrimmon, 1988) and life-history traits (Schaffer & Elson, 1975; Healey & Heard, 1984; Myers *et al.*, 1986). Systematic studies of juvenile life history also have revealed considerable geographic variability (Withler, 1966; Power, 1981; Randall *et al.*, 1987; L'Abée-Lund *et al.*, 1989; Metcalfe & Thorpe, 1990).

The chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), is an anadromous species native to the North Pacific Ocean. Spawning populations in the eastern Pacific extend from as far south as the Ventura River (34° N) in south-central California, to Point Hope, Alaska, and perhaps east to the Mackenzie and Coppermine rivers (Hallock & Fry, 1967; McPhail & Lindsey, 1970; Lee *et al.*,

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1980; McLeod & O'Neil, 1983). In the western Pacific, populations appear to be less abundant and less widespread (Major *et al.*, 1978), but 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 commonly occur as one of two life-history types. 'Stream-type' chinook reside in fresh water for a year or more before migrating seaward as age 1 or older smolts (Gilbert, 1913; Healey, 1983). By contrast, 'ocean-type' chinook migrate seaward as recently-emerged fry or after feeding for 2-3 months in fresh water. The juvenile life-history types also appear to differ in ocean migration pattern, the timing of their adult spawning migration, and the tendency to mature precociously in fresh water (Healey, 1983; Taylor, 1989a). Evidence of genetic divergence between the life-history types in morphology, enzyme frequencies and behaviour (Carl & Healey, 1984; Taylor, 1988a, 1989b) is consistent with the idea that age at seaward migration is, at least in part, genetically controlled. Environmental factors, however, exert a strong influence on age at seaward migration in salmonids, especially those factors (primarily temperature and photoperiod) that influence 'growth opportunity' (Clarke & Shelbourne, 1986; Clarke *et al.*, 1989; Metcalfe & Thorpe, 1990; Thorpe *et al.*, 1989). In fact, for both Pacific and Atlantic salmonids, latitudinal gradients in temperature and photoperiod have long been thought to be, at least in part, causally related to parallel gradients in age at seaward migration (Allen, 1941; Withler, 1966; Ricker, 1972; Power, 1981; Healey, 1983; Randall *et al.*, 1987; L'Abée-Lund *et al.*, 1989; Metcalfe & Thorpe, 1990).

In this paper, I examine geographic distribution of stream- and ocean-type chinook populations with two goals in mind. First, to compile and summarize information on the distribution of the life-history types, and second, to determine if variability in life-history of juvenile chinook is associated with variability in abiotic environmental factors related to growth opportunity or with differences in a proposed selective factor, freshwater migration distance.

II. MATERIALS AND METHODS

Data concerning geographic variation in juvenile chinook freshwater life-history were 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 Laboratory of the Canadian Department of Fisheries and Oceans (555 West Hastings St., Vancouver, B.C.). Populations surveyed, their geographic region, and authority for juvenile life history are listed in Appendix 1.

During the surveys of the scale data, an effort was made to note potential biases in the mode of collection of scales. Only those samples with approximately equal numbers of males and females, and encompassing approximately equal proportions of the known total age (freshwater plus marine annuli) distributions for each population, were sampled. 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 point represents the number of scale annuli formed in fresh water and the number to the right of the decimal point

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 fresh water from the literature.

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 emergence (first feeding), total daylight hours during the growing season, and freshwater migration distance.

The first three variables involve measurements of temperature and photoperiod that regulate 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). Photoperiod experienced during early feeding influences growth and smolting of stream-type chinook and juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), (Clarke & Shelbourne, 1986; Clarke *et al.*, 1989; Thorarensen & Clarke, 1989). Salmon held under 'low' daylight (< 12 h) at first feeding grow faster and display physiological correlates of smolting earlier than those held under 'long' daylight periods at first feeding. Thorpe *et al.* (1989) demonstrated that temperature and photoperiod were good indices of 'growth opportunity' in laboratory populations of juvenile Atlantic salmon, *Salmo salar* L. 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 & Thorpe, 1990).

The final variable, freshwater migration distance, was chosen as a potential selective factor promoting differentiation in life-history. 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 which, through growth opportunity, might promote variability in age at migration.

Limited data 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 chinook's 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 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.). Approximately 70% of the among-stream variation in mean annual water temperature could be accounted for by variation in mean annual air temperature (d.f. = 1,49; $P < 0.0001$). Furthermore, Power (1981) and Metcalf & Thorpe (1990) found air temperature, as a measure of growing season length, to be a good predictor of smolting ages for Atlantic salmon populations.

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 at first feeding and early growth of juvenile salmon. Growth of juvenile chinook is temperature-dependent and juveniles reduce activity and feeding behaviour, and show 'hiding' behaviour at temperatures below about 4–5° C (Allen, 1969; Chapman & Bjornn, 1969; Taylor, 1988b). Also, Brett *et al.* (1969) reported that growth of sockeye salmon, *Oncorhynchus nerka* (Walbaum),

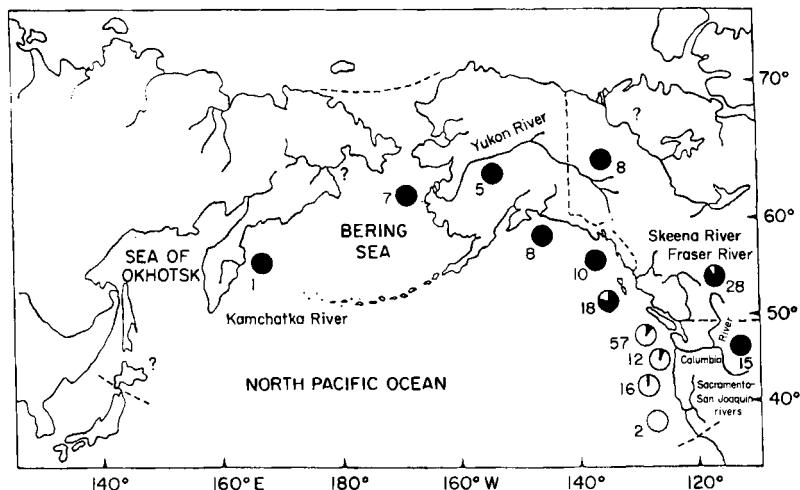


FIG. 1. Regional distribution of stream- and ocean-type juvenile chinook salmon life-histories in the North Pacific. Shading represents approximate percentage of each life-history type, i.e. solid symbols indicate 100% stream-type and open symbols 100% ocean-type. The numeral associated with each symbol represents the number of populations surveyed. Geographic regions surveyed correspond to (clockwise from left): Kamchatka R., south-western Alaska, lower Yukon R., upper Yukon R., south-central Alaska, south-eastern Alaska and northern British Columbia, central British Columbia, Fraser River, Vancouver Island and coastal Washington, lower Columbia R., upper Columbia R., coastal Oregon, and California.

during their first year of life, peaked between 5 and 17° C, and chinook are probably characterized by similar limits to growth efficiency.

Total hours of daylight during the growing season was calculated as the sum of all daylight hours over the period when air temperature was $\geq 4^\circ\text{C}$, and distances to the sea were measured 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 & Gulre, 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.

III. RESULTS

GEOGRAPHIC VARIATION IN JUVENILE LIFE HISTORY

The distribution of stream- and ocean-type chinook salmon in the North Pacific ranges from predominately ocean-type populations south of the Columbia River (coastal Oregon, Sacramento-San Joaquin Rivers), ocean-type in coastal and stream-type in inland regions of large systems between the Columbia River and the Skeena River (approximately 56°N), and predominately stream-type north of 56°N (Fig. 1). Where stream- and ocean-type populations are both common, e.g. in the Columbia River, ocean-type chinook predominate in tributaries of the lower reaches, whereas stream-type fish predominate in the headwater regions of the Columbia and of the Snake and Salmon River subdrainages (Fig. 2). Stream- and

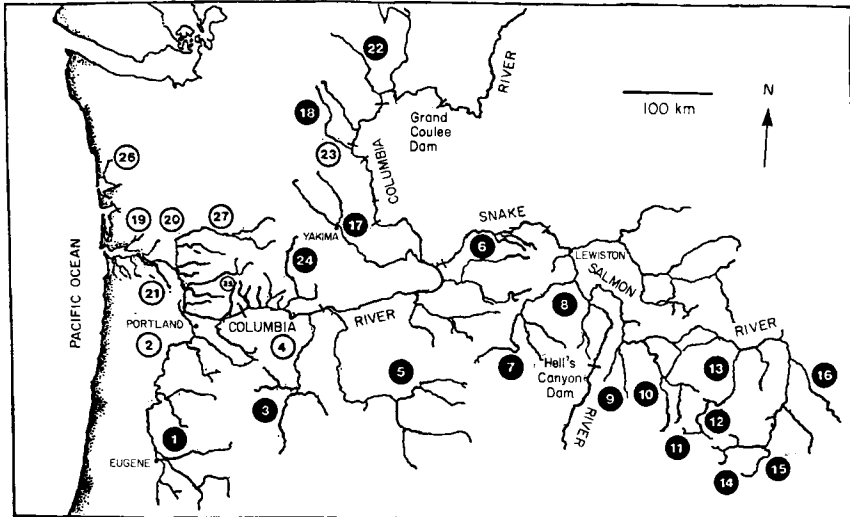


FIG. 2. Distribution of stream- (●) and ocean-type (○) chinook salmon life-histories in tributaries of the Columbia River. 1, upper Willamette R.; 2, lower Willamette R.; 3, upper Deschutes R.; 4, lower Deschutes R.; 5, John Day R.; 6, Tucannon R.; 7, Grande Ronde R.; 8, Imnaha R.; 9, Little Salmon R.; 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.

ocean-type salmon can be found in single tributaries of large systems such as the Columbia. Such subpopulations are usually spatially separated and associated with distinct seasonal adult spawning runs; stream-type are found in the headwaters and are associated with 'spring' or 'summer' run adults, whereas ocean-type chinook are found in the lower reaches and are associated with 'fall' run adult migration timing (e.g. Willamette and Deschutes rivers in the Columbia system; Fig. 2).

With increasing latitude, however, stream-type fish predominate both in coastal and interior streams (e.g. south-eastern Alaska, Yukon River; Figs 1, 3). In addition, smolt age 2 and 3 stream-type salmon become more common with increasing latitude and distance from the sea (e.g. Yukon River populations); stream-type salmon in more southern rivers are predominately age 1 smolts (e.g. Fraser River, Columbia River).

The Kamchatka River, in the western Pacific, is also dominated by stream-type chinook (primarily smolt age 2 and 3) consistent with the life-history characteristics of populations at a similar latitude in the eastern Pacific (Fig. 1; Table I). In New Zealand, where chinook were successfully introduced in the late 1800s (Stokell, 1962), there is also an increasing occurrence of stream-type life-histories with increasing latitude (Table I).

Within the broad life-history designations of stream- and ocean-type chinook, the seasonal timing of the seaward migrations can extend from early spring as newly emerged fry (e.g. Sacramento and lower Columbia Rivers) to early summer migrations as 2–3-month-old parr (coastal British Columbia, lower Columbia River, coastal Oregon) to stream-type migrations that may extend from early

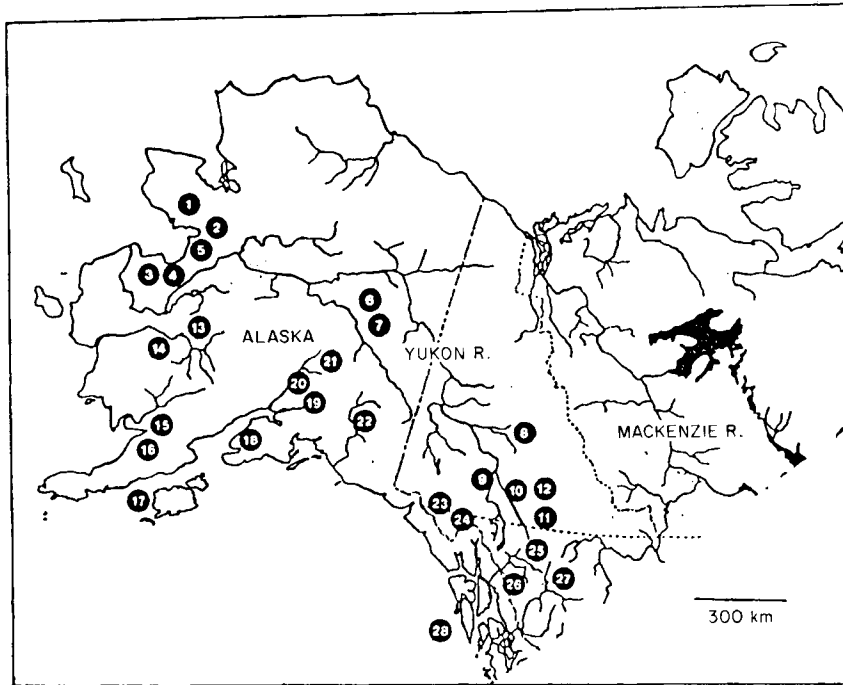


FIG. 3. Distribution of stream-type (●) chinook salmon in northern British Columbia, Alaska and Yukon. 1, Kwiniuk R.; 2, Unalakleet R.; 3, Andreafsky R.; 4, Anvik R.; 5, Nulato R.; 6, Chena R.; 7, Salcha R.; 8, Big Salmon R.; 9, Yukon R. (at Whitehorse); 10, Teslin R.; 11, Swift R.; 12, Nisultin R.; 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.; 26, Nahlin R. (Taku R.); 27, Tahltan and Little Tahltan Rivers (Stikine R.); 28, Harding R.

TABLE I. Juvenile chinook salmon life-history patterns in the Kamchatka River (Soviet Union) and several New Zealand rivers

River	Latitude	Years	Percent 'stream-type'	Reference
Kamchatka River	55°10'N	1965-70	100	Vronskiy (1972)
Glenariffe Stream	43°28'S	1967-76	8-34	Unwin (1986)
Rangitata River	43°35'S	1972-83	28	Davies <i>et al.</i> (1986)
Waitaki River	44°40'S	1976-83	26-66	James & Deverall (1987)
Moeraki Peninsula	45°20'S	1976	58	Flain (1981)

spring (Fraser River) to mid-summer (upper Yukon River). Taylor (1989b) gives a detailed account of geographic variability in migration timing and behaviour within the stream- and ocean-type life-history groupings.

ENVIRONMENTAL VARIABLES AND JUVENILE LIFE HISTORY

Information on juvenile life-history variation and environmental variation was collected from a total of 160 populations ranging from California to Alaska,

TABLE II. Variable coefficients from principal components analysis of environmental variables describing chinook salmon spawning and rearing streams. Emergel is the number of daylight hours at emergence (first feeding); total light is the total daylight hours over the growing season ($\geq 4^{\circ}\text{C}$)

Environmental variable	Coefficient	
	PC1	PC2
Air temperature	0.53	0.22
Distance to sea	-0.37	0.93
Emergel	-0.54	-0.26
Total light	0.55	0.15
Variance accounted for	79.2	95.9

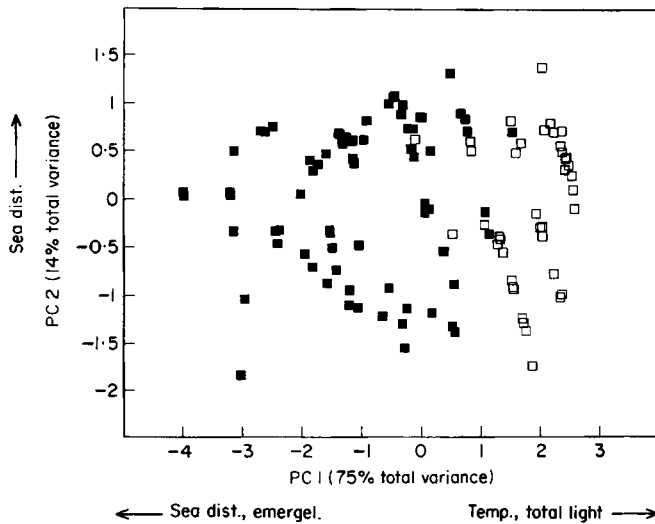


FIG. 4. Plot of principal component scores of stream- (■) and ocean-type (□) populations of chinook salmon along component axes 1 and 2. Distance to sea, mean annual air temperature, hours of daylight at emergence, and total annual hours of daylight are abbreviated as sea dist., temp., emergel, and total light, respectively.

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 two component axes (Table II). 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 air temperature and daylight hours over the growing season (positive coefficients). The second component axis (17% total variance)

was interpreted as primarily 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. 4). Mean PC scores between stream- and ocean-type chinook were, in fact, significantly different along PC1 (Mann-Whitney U -test, $P < 0.001$), but marginally 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 ($P > 0.05$). Therefore, populations with a stream-type life-history tended to be located distant from the sea and in regions with low growth opportunity relative to those with an ocean-type life-history.

IV. DISCUSSION

In the North Pacific, there are two dichotomies where variation in juvenile chinook life history appears to change abruptly (cf. Healey, 1983). First, both ocean- and stream-type chinook salmon are present south of about 56° N latitude, but only stream-type are found north of this. Second, south of 56° N, 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 predominate in coastal streams.

Fish species distributions and patterns of intraspecific variability along the North Pacific coast have been greatly influenced by glaciation and access routes from various refugia (Lindsey & McPhail, 1986; McPhail & Lindsey, 1986). Can historical factors account for the pattern of distribution of chinook life-history types? 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 & McPhail, 1986; McPhail & Lindsey, 1986). During deglaciation (beginning about 13 500 years ago), chinook dispersed from these northern and southern refugia along the Pacific coast (Lindsey & McPhail, 1986). South of the Taku River (about 58° N), rivers 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 south-eastern Alaska were probably colonized by chinook that persisted both in Cascadia and Beringia (Lindsey & McPhail, 1986); south-eastern 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 (as is presently the case), 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 56° 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 & McPhail, 1986). If, however, stream- and ocean-type chinook from Cascadia both colonized rivers in south-eastern Alaska and the Stikine River through to the Skeena River in northern B.C., areas which now have predominately stream-type chinook, this would suggest that some factors operating after postglacial dispersal contribute to geographic variation in juvenile life-history.

Environmental and genetic factors differing among populations may both promote variability in life-history. For instance, the present results are consistent with the idea that variation among river systems in environmental factors influencing 'growth opportunity' can explain some of the variation among populations in the age at seaward migration (Holtby, 1988; L'Abée-Lund *et al.*, 1989; Thorpe *et al.*, 1989; Metcalfe & Thorpe, 1990). While the examined data were not appropriate for constructing a predictive model of age at seaward migration (e.g. Metcalfe & Thorpe, 1990), stream-type chinook were associated with river systems of lower growth opportunity than were ocean-type (Fig. 4).

Alternatively, selection for size at migration coupled with selection for migration during seasonal time 'windows' (Walters *et al.*, 1978; Lannan, 1980; Bilton *et al.*, 1982; Godin, 1982; Miller & Brannon, 1982; Holtby, 1988) might promote genetic differences in juvenile life-history. South of 56° N, stream-type salmon predominate in populations with long migrations, as they also do in both coastal and inland populations north of this latitude (Figs 1, 4). Increased migration distance probably selects for large size at migration, due to increased energetic demands (Gilhousen, 1980; Taylor & McPhail, 1985) and a greater exposure to freshwater predators (Larsson, 1985; Ruggertone, 1986) relative to short migrations. Furthermore, locomotor and osmoregulatory performance are both inhibited at low temperatures (i.e. cold climates north of 56°) (Brett, 1967; Knutsson & Grav, 1976; Beamish, 1978; Webb, 1978; Virtanen & Oikari, 1984). Therefore, selection might favour large smolt size in cold environments or those distant from the sea, because of the increased performance capabilities of larger fish (Brett & Glass, 1973; McCormick & Naiman, 1984; Hargreaves & LeBrasseur, 1986). Age at seaward migration is, at least in part, inherited in salmonids, which is a necessary condition for an hypothesized role of selection (Rich & Holmes, 1928; Ricker, 1972; Refstie *et al.*, 1977; Thorpe & Morgan, 1978; Carl & Healey, 1984; Taylor, 1988*a*, 1989*a,b*). Furthermore, if the selective mechanism outlined above is tenable, then size at migration should be positively related to length of migration but negatively related to sea temperature at ocean entry. These predictions, while untested for chinook salmon, describe relationships recently documented in anadromous brown trout, *Salmo trutta* L., populations in Norway (L'Abée-Lund *et al.*, 1989).

In conclusion, the present study provides support for the idea that variability in age at seaward migration in chinook salmon is, in part, promoted by variability in growth opportunity and environmental modulation (Smith-Gill, 1983) of smolting rate, but that such control might be limited by selection for size at migration.

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Appendix I

List of chinook salmon populations surveyed in the study, by region, with authority for juvenile life-history data. A.D.F.G. and C.D.F.G. are Alaska and California departments of Fish and Game, respectively; W.D.F. is Washington State Department of Fisheries; C.D.F.O. is Canadian Department of Fisheries and Oceans

Population	Region	Authority
Unalakleet R.	Norton Sound, Alaska	McBride & Wilcock (1983)
Kwiniuk R.	Norton Sound, Alaska	A.D.F.G. unpubl. data
Andreafsky R.	Yukon R., Alaska	McBride & Wilcock (1983)
Anvik R.	Yukon R., Alaska	McBride & Wilcock (1983)
Nulato R.	Yukon R., Alaska	McBride & Wilcock (1983)
Chena R.	Yukon R., Alaska	McBride & Wilcock (1983)
Salcha R.	Yukon R., Alaska	McBride & Wilcock (1983)
Kuskokwim R.	Southwestern Alaska	McBride & Wilcock (1983)
Holitna R.	Southwestern Alaska	McBride & Wilcock (1983)
Naknek R.	Southwestern Alaska	McBride & Wilcock (1983)
King Salmon R.	Bristol Bay, Alaska	McBride & Wilcock (1983)
Karluk R.	Southcentral Alaska	McBride & Wilcock (1983)
Anchor R.	Cook Inlet, Alaska	McBride & Wilcock (1983)
Little Susitna R.	Cook Inlet, Alaska	McBride & Wilcock (1983)
Montana Cr.	Cook Inlet, Alaska	McBride & Wilcock (1983)
Chulitna R.	Cook Inlet, Alaska	McBride & Wilcock (1983)
Copper R.	Southcentral Alaska	McBride & Wilcock (1983)
Alek R.	Southeastern Alaska	McBride & Wilcock (1983)
Tahini R.	Southeastern Alaska	A.D.F.G. unpubl. data
Harding R.	Southeastern Alaska	A.D.F.G. unpubl. data
Unuk R.	Southeastern Alaska	A.D.F.G. unpubl. data
Chickamin R.	Southeastern Alaska	A.D.F.G. unpubl. data
Bradfield Canal	Southeastern Alaska	A.D.F.G. unpubl. data
Big Salmon R.	Yukon R., Yukon	C.D.F.O. unpubl. data
Yukon R.	at Whitehorse, Yukon	C.D.F.O. unpubl. data
Teslin R.	Yukon R., Yukon	C.D.F.O. unpubl. data
Swift R.	Yukon R., Yukon	C.D.F.O. unpubl. data
Nisutlin R.	Yukon R., Yukon	C.D.F.O. unpubl. data
Nahlin R.	Northern British Columbia	C.D.F.O. unpubl. data
Nakina R.	Northern British Columbia	C.D.F.O. unpubl. data
Tahltan R.	Northern British Columbia	C.D.F.O. unpubl. data
Little Tahltan R.	Northern British Columbia	C.D.F.O. unpubl. data
Meziadin R.	Northern British Columbia	C.D.F.O. unpubl. data
Cranberry R.	Northern British Columbia	C.D.F.O. unpubl. data
Ishkheenickh R.	Northern British Columbia	C.D.F.O. unpubl. data
Kincolith R.	Northern British Columbia	C.D.F.O. unpubl. data
Bear R.	Northern British Columbia	C.D.F.O. unpubl. data
Babine R.	Northern British Columbia	C.D.F.O. unpubl. data
Kispiox R.	Northern British Columbia	C.D.F.O. unpubl. data
Yakoun R.	Northern British Columbia	C.D.F.O. unpubl. data
Eckstall R.	Northern British Columbia	C.D.F.O. unpubl. data
Kitsumkalum R.	Northern British Columbia	C.D.F.O. unpubl. data
Zymoetz R.	Northern British Columbia	C.D.F.O. unpubl. data
Morice R.	Northern British Columbia	Shepherd <i>et al.</i> (1986)
Kitimat R.	Central British Columbia	C.D.F.O. unpubl. data
Kildata R.	Central British Columbia	C.D.F.O. unpubl. data

Appendix I (Continued)

Population	Region	Authority
Hirsch Cr.	Central British Columbia	C.D.F.O. unpubl. data
Atnarko R.	Central British Columbia	C.D.F.O. unpubl. data
Bella Coola R.	Central British Columbia	C.D.F.O. unpubl. data
Kilbella R.	Central British Columbia	C.D.F.O. unpubl. data
Wannock R.	Central British Columbia	C.D.F.O. unpubl. data
Mussel Cr.	Central British Columbia	Shepherd <i>et al.</i> (1986)
Ahnuhati R.	Central British Columbia	Shepherd <i>et al.</i> (1986)
Nechako R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Stuart R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Salmon R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Willow R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
McGregor R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Walker Cr.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Holmes R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Tete Jean	Fraser River, British Columbia	C.D.F.O. unpubl. data
Swift Cr.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Slim Cr.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Bowron R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Quesnel R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Horsefly R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Chilcotin R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Chilko R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
North Thompson R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Blue R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Clearwater R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Deadman R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Eagle R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Salmon R.*	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
South Thompson R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Shuswap R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Adams R.	Fraser River, British Columbia	Shepherd <i>et al.</i> (1986)
Nicola R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Coldwater R.	Fraser River, British Columbia	C.D.F.O. unpubl. data
Birkenhead R.	Southwestern British Columbia	C.D.F.O. unpubl. data
Squamish R.	Southwestern British Columbia	C.D.F.O. unpubl. data
Ashlu R.	Southwestern British Columbia	C.D.F.O. unpubl. data
Marble R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Salmon R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Woss R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Conuma R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Campbell R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Quinsam R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Burman R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Gold R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Puntledge R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Little Qualicum R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Big Qualicum R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Alberni Canal	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Nanaimo R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Cowichan R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
San Juan R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data

*South Thompson R. subdrainage.

Appendix I (Continued)

Population	Region	Authority
Gordan R.	Vancouver Is., British Columbia	C.D.F.O. unpubl. data
Nitinat R.	Vancouver Is., British Columbia	Shepherd <i>et al.</i> (1986)
Nooksack R.	Coastal Washington	W.D.F. unpubl. data
Skagit R.	Coastal Washington	W.D.F. unpubl. data
Stilligumish R.	Coastal Washington	W.D.F. unpubl. data
Skykomish R.	Coastal Washington	W.D.F. unpubl. data
Nisqually R.	Coastal Washington	W.D.F. unpubl. data
Hoh R.	Coastal Washington	W.D.F. unpubl. data
Queets R.	Coastal Washington	W.D.F. unpubl. data
Chehalis R.	Coastal Washington	W.D.F. unpubl. data
Quinault R.	Coastal Washington	W.D.F. unpubl. data
Upper Willamette R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Lower Willamette R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Upper Deschutes R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Lower Deschutes R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
John Day R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Tucannon R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Grande Ronde R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Imnaha R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Little Salmon R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
South Fork Salmon R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Bear Valley Cr.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Marsh Cr.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Middle Fork Salmon R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
East Fork Salmon R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Lemhi R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Yakima R.	Upper Columbia R.	W.D.F. unpubl. data
Wenatchee R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Lower Wenatchee R.	Upper Columbia R.	Howell <i>et al.</i> (1985)
Gray's R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Elochoman R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Klatskanie R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Methow R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Klickitat R.	Lower Columbia R.	W.D.F. unpubl. data
Washougal R.	Lower Columbia R.	W.D.F. unpubl. data
Cowlitz R.	Lower Columbia R.	Howell <i>et al.</i> (1985)
Nehalem R.	Coastal Oregon	Nicholas & Hankin (1988)
Wilson R.	Coastal Oregon	Nicholas & Hankin (1988)
Trask R.	Coastal Oregon	Nicholas & Hankin (1988)
Nestucca R.	Coastal Oregon	Nicholas & Hankin (1988)
Salmon R.	Coastal Oregon	Nicholas & Hankin (1988)
Siletz R.	Coastal Oregon	Nicholas & Hankin (1988)
Yaquina R.	Coastal Oregon	Nicholas & Hankin (1988)
Siuslaw R.	Coastal Oregon	Nicholas & Hankin (1988)
North Umpqua R.	Coastal Oregon	Nicholas & Hankin (1988)
Rogue R.	Coastal Oregon	Nicholas & Hankin (1988)
Coos R.	Coastal Oregon	Nicholas & Hankin (1988)
Coquile R.	Coastal Oregon	Nicholas & Hankin (1988)
Sixes R.	Coastal Oregon	Nicholas & Hankin (1988)
Chetco R.	Coastal Oregon	Nicholas & Hankin (1988)
Elk R.	Coastal Oregon	Nicholas & Hankin (1988)

Appendix I (Continued)

Population	Region	Authority
Hunter Cr.	Coastal Oregon	Nicholas & Hankin (1988)
Bogus Cr.	Klamath R., California	C.D.F.G. unpubl. data
Shasta R.	Klamath R., California	C.D.F.G. unpubl. data
Scott R.	Klamath R., California	C.D.F.G. unpubl. data
Salmon R.	Klamath R., California	C.D.F.G. unpubl. data
South Fork Trinity R.	Klamath R., California	C.D.F.G. unpubl. data
Sacramento R.	California	C.D.F.G. unpubl. data
Kamchatka R.	Soviet Union	Vronskiy (1972)
Glenariffe Stream	Rakaia R., New Zealand	Flain (1982); Unwin (1986)
Rangitata R.	New Zealand	Davies <i>et al.</i> (1986)
Waitaki R.	New Zealand	James & Deverall (1987)